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The Biology of *Nomia* (*Epinomia*) *triangulifera* with Comparative Notes on Other Species of *Nomia*

BY

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The Biology of Nomia (Epinomia) triangulifera
With Comparative Notes on Other Species of Nomia

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EARLE A. CROSS ² and GEORGE E. BOHART ³

ABSTRACT: Observations on the biology and early stages of Nomia (Epinomia) triangulifera Vachal, N. (E.) nevadensis arizonensis Ckll., N. (Dieunomia) heteropoda (Say), and N. (Acunomia) melanderi Ckll. show that the subgenera Epinomia and Dieunomia are more closely related to each other than either is to Acunomia. Although nevadensis closely resembles triangulifera in many particulars, its brood cells, eggs, and developing larvae are somewhat intermediate between those of triangulifera and melanderi. In the same characteristics heteropoda is more like triangulifera, indicating that the relation between Dieunomia and Epinomia is better expressed by triangulifera than by nevadensis.

In contrast with the one species of Acunomia, the two species of Epinomia and the one of Dieunomia hold in common the following characteristics:
1. Flight period in August and September instead of July and August.
2. Host plants nearly limited to Compositae.
3. Tumulus with a lateral plugged entrance and a horizontal vestibule.
4. Brood cells pendant in series from one or two nearly straight, horizontal laterals.
5. Narrowly oval cells with conical and not obviously spiraled ceilings.
6. Pollen balls less convex above than below and with an equatorial flange.
7. Early stage larvae with lobate ventrolateral projections of the body segments.

N. (Epinomia) nevadensis approaches melanderi in having moderately long, well-arched eggs, a relatively shallow nest, and slightly more oval cells than the other two species.

All four species nest in soil that is low in organic material, sparsely vegetated, and damp nearly to the surface.

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INTRODUCTION

In a recent paper Cross (1958) redefined the taxonomic status of the genus *Nomia* Latreille on morphological grounds. He grouped the North American members of the genus into four subgenera: *Paranomina* Michener, *Acunomia* Cockerell, *Epinomia* Ashmead, and *Dieunomia* Cockerell. These were placed in two distinct units, the first composed of *Acunomia* and *Paranomina*, and the second *Epinomia* and *Dieunomia*. The following observations on the biologies of a limited number of species involving three of the four subgenera appear to support these groupings. In Table 1 a comparison is made of similarities and differences among the three subgenera based on studies conducted in Kansas and Utah in 1954, 1955, and 1959.4

Published information on the biology of *Nomia* is scanty, the most extensive papers being those on *N. (Acunomia) melanderi* Ckll. by W. P. Stephen (1959), G. E. Bohart (1947, 1950, 1952, 1959), and Bohart and Cross (1955). Information on species of *Paranomina* is limited to several observations by Cockerell (1934). The same is true of *Dieunomia* (Blair, 1935). More extensive papers by Pierce (1904) and Rau (1929) have summarized our knowledge of *N. (Epinomia) triangulifera* Vachal. Hicks (1926) and Cockerell (1898, 1934) have published short notes on the habits of *N. (Epinomia) nevadensis bakeri* Cockerell.

This paper deals primarily with studies of *N. triangulifera*. However, several nests of *N. (Epinomia) nevadensis arizonensis* Cockerell and one nest of *N. (Dieunomia) heteropoda* (Say) were examined and are discussed herein. A detailed study of *N. melanderi* will be published elsewhere, but a few features of its biology are brought out in the following discussion for purposes of comparison.

*Nomia triangulifera* Vachal

This medium-sized, black bee (Fig. 1) is distributed throughout the central United States from central Illinois and Minnesota westward to Utah and southern New Mexico. It is a gregarious species, often establishing many thousands of nests in a single site (Fig. 2).

NESTING SITES.—The nesting habits of this species were studied at the eight sites described below:

1. Five miles northwest of Lawrence, Kansas. The bees were nesting in great numbers on an alluvial sand deposit which resulted from the 1951 flooding of the Kansas River. The deposit occupies what was formerly an ox-bow lake of the river. The

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4. In Kansas by Cross; in Utah by Cross and Bohart.
area is now a rolling sandy waste, populated by scattered clumps of cottonwoods and invader annuals such as *Euphorbia hexagona*, *Helianthus annuus*, and *Cenchrus pauciflorus*. The sand deposits on the silt bed of the old lake are from 3 to 11 feet deep and are broken by innumerable thin, irregularly spaced strata of silt (none over 30 cm. deep). Probably because of the underlying silt bed, the sand holds its moisture fairly well below a depth of a foot or so, and at the level of the cells it is moist enough to pack.

2. A pasture two miles north of Topaz, Utah. This site occupies the slope of a borrow pit and is sub-irrigated, apparently from an adjacent canal. The top layer of soil to a depth of 21 cm. is a sandy loam, beneath which is a silt loam interspersed with narrow zones of clay loam. Vegetation is sparse but uniform over the entire site and consists of a cover of salt grass (*Distichlis stricta*). *N. triangulifera* shares some of the more moist portions of this site with the alkali bee, *N. melanderi*.

3. A series of alkaline mounds in an area with high artesian pressure near the Logan-Cache Airport in Cache Valley, Utah. The soil is a loam with moisture seeping upward to the surface throughout the season. On some of these mounds *N. triangulifera* occupies space with *N. melanderi*.

4. A steep road bank near Myton, Utah, with an eastern exposure. The surface is nearly bare and the soil ranges from a loam to a sandy loam except for scattered large rocks. Moisture is evident during dry weather below a vertical depth of about three inches.

5. A race track at Hinckley, Utah. The sandy soil on the track surface is underlain with a silt loam at a depth of three to five inches.

6. An alkali flat five miles west of Smithfield, Utah. The fine silt loam soil is nearly saturated with moisture during the nesting season.

7. A large, bare, clay loam slope in Pleasant Valley, Uinta Basin, Utah. On this site even the lightest rainfall fails to soak in.

8. A series of low sand dunes, some stabilized and some still slowly shifting, near Cornish, Utah. The soil is composed of almost pure sand with a zone of moderate compaction in the stabilized areas from one to two feet deep. The soil is completely dry for several inches and scarcely moist enough even at three feet to hold together when compressed in the hand.

Pierce (1904) and Rau (1929) found nests in heavy clay soils, and C. D. Michener (unpublished) observed a site near Colby,
Kansas, in hard heavy soil cleared of vegetation by occasional vehicular traffic.

From the foregoing, it is apparent that *triangulifera* nests in soils with a wide range of moisture and texture. In physical type, the soils include sand, sandy loam, loam, silt loam, and clay loam. The mechanical composition of several sites in Utah is shown in Table 2. An absence of crumb structure in the natural state and a low organic content are common to all sites observed. Appreciable moisture can always be found at deeper levels from 30 to 60 cm. and some sites are nearly saturated up to the surface, even in dry weather. Nevertheless, preference is always for areas well drained at the surface. The bees usually occupy knolls or gentle slopes, but in sandy washes or hard-packed clays they may choose level ground. The sites may be entirely bare or have sparse herbaceous growth, but the ground is never densely shaded.

In general, *triangulifera* seems to use the same criteria as *melanderi* for choosing its sites. However, it is less particular about moisture conditions at the surface and, unlike the latter, will nest in areas with several inches of loose, dry surface soil. In sites like the one at Topaz, where only the top layers of soil are sandy, the cells are always placed in a layer containing more silt or clay. The location of finer layers of soil, as well as moisture and temperature factors, seems to play a part in determining the depth of the brood cells. The deepest nests (2½ feet) were found at Cornish, Utah, where moisture was low and the sand was easy to excavate. The shallowest nests (11-14 inches) were found at Myton, Utah, where rocks and shaly spots were numerous at greater depths.

**Life Cycle.—Diapause.** Like all species of *Nomia* studied, *triangulifera* overwinters as a prepupa in a rigid and motionless state of diapause in which it can resist strong mechanical shocks, pressures, and fluctuations in temperature and humidity.

The prepupa of *triangulifera* is readily distinguished from that of *melanderi* by the sharper dorsal prominences on the thorax (Fig. 3). The integument is somewhat more rigid, and laboratory studies show it to be more subject to desiccation. Its color is usually butter-yellow with intersegmental bands of orange, especially dorsally on the thorax. For reasons discussed later it is sometimes white. *N. melanderi* prepupae, which are always white, have a slightly greyish tinge in contrast to the more opaque color of *triangulifera*.

Studies in progress at Utah and California on factors initiating the breaking of diapause in several species of ground-nesting bees,
including *N. triangulifera, melanderi,* and *nevadensis*, indicate that if the prepupae are held for 10 days or more at 75° F. and then incubated at 80° to 85° F., at least a few individuals will break diapause. However, a cold period prior to incubation assists diapause breaking. Work now in progress indicates that the longer the cold period (up to at least 120 days), the more rapid and complete is the breaking of diapause after the temperature is raised. Under natural conditions, the winter provides a sufficiently cold period of several months. Following this, the temperatures at the cell level are still too cool for diapause to break until late in June or July. At Topaz, Utah, all *triangulifera* in the nesting site were still in the prepupal stage on July 6, 1956, but a few showed signs of breaking diapause.

Visible signs of the termination of diapause consist of a slight softening of the body wall and a less pronounced angle between the thorax and abdomen. This stage is known as the propupa and begins with the actual molting to the pupal stage within the prepupal skin. During this period the bee exhibits faint response to external stimuli and makes occasional, almost imperceptible, flexing movements. Because the signs of this stage appear gradually, its duration is not certain, but in most cases it appears to last from two to four days.

**Shedding of the prepupal skin.** For several hours before shedding its skin, the insect increases its flexing movements and also makes a few slight rotating movements with its posterior end. Shedding of the larval skin by normal individuals lying on a piece of cellu-cotton takes from one to six minutes and proceeds smoothly in the usual pattern for holometabolous insects. Injured, desiccated, or otherwise abnormal prepupae usually fail to shed their skins completely. These pupae often continue to develop within the larval skin and may become almost fully pigmented before dying. Pupae kept in the laboratory at 80° F. and 75 percent relative humidity remained in the pupal stage an average of 14 days for both sexes with a usual range of 11 to 19 days. On the average it took six days for the eyes to become dark. A few pupae remained for an unaccountably long time in an unpigmented condition (up to 20 days) and then developed at the normal rate.

The unpigmented pupa is soft and motionless, although it can rotate its posterior end slightly when disturbed. As it hardens and becomes pigmented, the rotational movements increase and flexing movements of the body take place. The white pupa, al-
though delicate, can withstand handling and desiccation far better than after it is pigmented.

**Ecdysis.** For several hours before shedding its skin, the pupa increases the tempo of its rotating and flexing movements and is responsive to stimuli. The process of skin-shedding normally takes from 5 to 10 minutes. The newly emerged adult, although responsive to external stimuli, has soft, white wings and remains nearly motionless in its cell for about two days while the wings are hardening. The bee then tunnels to the surface, but does not venture forth at once. Apparently, the male takes flight within an hour, but the female usually remains in her natal burrow for at least 24 hours, spending much of this time just below the surface.

**Time of emergence.** Because males are more precocious about flying than females, it is difficult to determine how much sooner they develop into adults. Usually a few males appear at least a week before the first females take flight, and they are found in large numbers over the burrows during the last few days of this period. The pre-courtship flight of the males usually takes place in the first or second week of August, but in some localities and seasons, the first males are not seen until the third week.

**Pre-courtship flight.** Before the females begin to fly the males conduct a low, weaving flight over the nesting site and pounce on any female that shows her head above the surface. They often drop to the ground and dig at open holes or ones that have been opened and later plugged (Fig. 1). These are probably burrows containing females still too immature to venture forth. This activity by the males suggests that they respond to an odor produced by the young females.

**Mating.** When the females leave their burrows, they are at once seized by males. In this species, the female often resists the attentions of the male and many mating attempts result in short struggles ending with the escape of the female. Apparently, copulation rarely or never takes place during such encounters. Four examples of a definite courtship pattern, unlike any we have seen in other solitary bees, were noticed at the Lawrence and Topaz sites. Observation of a mating pair, beginning with actual copulation, was made on the window ledge of a greenhouse at Logan, Utah.

At the start of the courtship the female rests quietly on the ground and does not attempt to avoid the attentions of the male. The latter crawls upon her back and locks his forelegs beneath her mesothorax and his midlegs between her fore and hind wings and
under her propodeum. His hind legs lock beneath the posterior portion of her abdomen. During courtship and copulation the female extends her forewings slightly upward and outward, thus forming a sort of “cradle” for the thorax of the male. A type of “mating dance,” best described in two phases, is then performed by the male as follows:

1. He pulsates his abdomen rapidly and rhythmically, accompanying this with alternate vertical and lateral jerking of the antennae.

2. He flutters his wings, at the same time drumming his abdomen rapidly against that of the female.

These two phases alternate and last a few seconds each. The dance lasts several minutes, during which time the female remains passive and the male makes one or more mating attempts. Copulation ultimately takes place when the male slides posteriorly, reaching forward and slightly upward with the tip of his abdomen to contact the female. Actual copulation was seen to last from eight seconds to slightly more than one minute. During copulation the male strokes the female with his antennae at a rate of about one stroke per second.

Full courtship and mating were infrequently observed, which may indicate that the complete pattern is not always followed or that it sometimes occurs away from the nesting site. Males are common on Helianthus flowers and were observed there several times trying to mate without preliminary courtship.

Nesting period. Collection records of females give a good indication of the duration of the nesting period. Examination of 148 female specimens in collections made between 1890 and 1959 from all parts of the range showed that nearly all were taken between August 10 and September 15, but one was taken as late as October 2 (Lincoln, Nebraska). The few specimens available from the southern portions of the range did not indicate earlier emergence in such areas. Likewise, Cockerell (1898) records males and females at Las Cruces, New Mexico, on September 11 and 14. Considering that emergence of females continues for at least two weeks, as based on the appearance of new nests, and that few adults are still alive more than six weeks after the earliest emergence, it appears that the nesting period of individual females is seldom greater than one month. No evidence of a second generation has been found at any of the nesting sites, probably because the soil temperatures are too cool after mid-September for further development to take place.
In 1954 on the Lawrence site, nesting began near the middle of August. Only an occasional new nest was begun after September 18, and activity had tapered off by that time. By September 26 activity by adults had ceased. In 1958 on the Pleasant Valley, Utah site the first signs of nesting were observed on August 16. At this time there were still a few *N. melanderi* provisioning nests in the same area, but their activity had nearly ceased. On September 5, *triangulifera* activity had reached its peak and *melanderi* had disappeared. On September 23, no new nests of *triangulifera* could be found, and only a few adults still provisioning nests were seen. Several thousand fresh mounds of *melanderi*, representing a small second generation were now in evidence. On October 6, a few *melanderi* nests were still active, but no *triangulifera* adults could be found.

The coincidence between the nesting season of *triangulifera* and blooming of *Helianthus annuus* is apparently assured by the depth of the brood cells. The cells of *triangulifera* are always at least 5 to 31 cm. deeper than those of *melanderi*, where the two species nest together. Apparently, as a result of cooler temperatures at the greater depths, *triangulifera* emerges from a month to six weeks later than *melanderi*. The question arises, does the depth of the cells condition the choice of host plant or vice versa?

*N. triangulifera* usually starts nesting some time after *H. annuus* begins to bloom. This is particularly noticeable at Topaz, Utah, where the host plant begins to bloom in late July. Here the earlier bloom is well attended by certain bees, such as *Dufourea marginata* (Cresson) and *Diadasia enavata* (Cresson). It is only when the above species decline in numbers that females of *triangulifera* become common. This apparent mistiming of *triangulifera* may be a mechanism serving to decrease competition at the pollen source.

Males are present throughout the nesting period, but they become scarce sooner than the females. They often cluster at night on sweetclover and other tall plants in the vicinity of the nesting site. At Topaz, they were sometimes found on the same stem with males of *melanderi* but always in discreet groups. Cockerell (1898) records them clustered on flowers of *Aster*. Since males cannot always be found on plants at night, it is probable that, like *N. melanderi*, a greater or lesser number of them, depending upon climatic conditions, spend the night underground. A group of about 20 males was observed in a small subterranean pocket at the edge of the Topaz site. Both sexes take part in a weaving flight pattern.
over the nesting site. The hum produced by this flight is noticeably lower than that of *melanderi*, although the insects average only slightly larger.

**Nest building.** Without exception, each female constructs and provisions her own nest. Nests vary in their proximity. In the more crowded areas, they may be only \( \frac{3}{4} \) inch apart and, at this density, they are often clustered in groups about the size of a man’s hand. In less crowded areas, they may be scattered from one to five or more feet apart.

At the Lawrence site, bare sand was preferred over grassy areas for nesting, but several heavy concentrations were located in areas having a sparse growth of *Tribulus terrestris*. At Topaz, the most concentrated areas of nesting were on bare ground (Fig. 2) or where there was a sparse cover of salt grass. At the latter site, in areas where moisture was higher and the salt grass more dense, *N. melanderi* nests usually replaced those of *N. triangulifera*. Since some of the largest concentrations of nests at Lawrence were in small areas where the sand was shallow, it appears that the density of nests may be affected to some degree by the character of the substrate. In Kansas, nests begun late in the season were often built in the lee of dead branches and other sheltering objects.

Digging at Lawrence started at various hours during the day. This contrasts with the initial nest digging of *melanderi* in Utah, which always takes place in the late afternoon. The female first grasps the substrate with her mandibles, at the same time scratching vigorously with her fore and mid legs. If unsuccessful in loosening the crust, she usually flies a short distance and repeats the procedure. If successful, she uses her legs to push away the material loosened by her mandibles. She turns round and round, constantly repeating the digging and scraping procedure. In the sandy area at Lawrence, the top quarter-inch of crust proved the most difficult challenge and, after this crust was penetrated, digging proceeded at a rapid rate. Several one-day-old nests excavated in this area consisted of straight vertical shafts 36-66 cm. deep and had variously shaped dilations along their walls.

A picture of the nest-building sequence was obtained at the Lawrence and Topaz sites from the excavation of about 35 nests. First, the main tunnel is excavated (probably within the first 24 hours). This tunnel may be vertical or else inclined at various angles for a few centimeters before descending vertically (Fig. 4). In the sandy site at Lawrence its depth ranged from 50 to 110 cm.,
with an average of about 70 cm. Similar nest depths were observed in the sand dunes at Cornish. Five nests dug in the silt loam of the Topaz site averaged about 37 cm. and a number of nests in the heavier, wetter soil at Amalga, Utah, averaged 48 cm. The latter figure corresponds well to those of both Pierce and Rau (1904, 1929) who found nests descending to about 50 cm. in soil they described as a heavy clay. The diameter of the main shaft is nine mm. At the surface where it joins the vestibule the burrow narrows to about 7.5 mm. This narrowing of the main burrow at the entrance is common to the halictid bees and distinguishes their nests from those of andrenids and melittids.

At the Topaz site, the main shafts were more or less smooth and even in diameter, although they often had several short lateral branches; at the sandier Lawrence site they usually had numerous irregular dilations and lateral cell- and tunnel-like excavations. These dilations and excavations appeared to be made to obtain the fine silt particles with which the cells, cell laterals, and at least portions of the main shaft were lined.

In contrast to this situation the nests constructed in the sand dunes at Cornish, where there were no silt strata, had neither burrow dilations nor silt-lined cells and tunnels. Since the burrow walls at Cornish appeared to be lined with slightly finer sand grains than average for the surrounding soil, it appears that the species always lines its burrows with the finest materials available in the soil contacted during nest excavation.

The early tumulus is large (commonly about nine cm. in diameter), circular, and somewhat flattened on top. In this stage the nest entrance is located centrally in the tumulus and is often exposed (Fig. 4A). As excavation of the nest progresses, the tumulus comes to resemble a cone of loose soil which covers the entrance hole (Fig. 4B). After the first two or three days, the female begins to force her way laterally through the loose tumulus rather than from above, eventually forming a horizontal vestibule. The vestibule may be 5-10 cm. in length and is dug into the substrate as well as being formed from the tumulus (Fig. 4C). As wind erosion proceeds, the original tumulus becomes a scarcely visible elongate hump, having the nest entrance at its perimeter; finally only the tubular chimney remains (Fig. 5). The persistence of the vestibule even in such pure sand areas as Cornish indicates that it is lined with some form of cement.

When the bee leaves the nest, she pauses to kick the vestibule
full of loose sand. Upon returning she tunnels her way without pause through this plug, with the result that the vestibule is often partially destroyed. On one occasion, a bee was seen to carry damp sand from within the burrow and plug the entrance with it, but this may not be the usual procedure. At the Lawrence site, damaged vestibules were not repaired after nest construction was well under way. No fresh sand was noted outside the nest entrance after the vestibule had been constructed and plugged, and it is assumed that the sand resulting from further excavation was distributed into the various dilations and excavations of the main shaft. At the Cornish site, where no dilations are formed, the sand from late digging is apparently deposited in a vertical extension of the main burrow.

At the Lawrence site, the cells are vertically arranged and evenly spaced along one and sometimes two cell laterals (Fig. 6A-B). They are usually from two to three cm. apart as measured from the center of one cell opening to the center of the next. The cell laterals have the same diameter as the main shaft and vary in length, depending upon the number of cells pendant from them. The longest primary lateral seen had 12 cells and was 33 cm. long; the shortest had seven cells and was 20 cm. long. The primary lateral is usually curved gently in the horizontal plane, so that all cells along it are at about the same depth (Fig. 6A-3). In one case, the primary lateral was forked 4 cm. from the main shaft. One branch was 4.5 cm. long and carried only one cell, which was the seventh to be constructed in a series of eight. The primary lateral is provided with from 6 to 13 cells before it is completed and a new lateral begun. This second lateral may be above, on the same level with, or below the first, but the last situation seems to be the most common. The second lateral is short (the longest, six cm.) and carries at most two cells (Fig. 6B). At the Topaz and Cache Valley sites there are often several cell laterals, each of which is short and carries only a few cells.

At Lawrence the basal cell along the primary lateral is usually from 3.5 to 10 cm. from the main shaft. There is evidence, however, that the first cell to be excavated and completed is constructed from 7 to 10 cm. from the main shaft, and that later cells may be added between this cell and the main shaft. In a general way, a sequence of cell building along the cell lateral is followed in which consecutive cells are placed next to each other, the oldest closest to and the youngest farthest from the main shaft. That these se-
quences are not exact is apparent from two examples. Using the smallest numbers for the oldest cells, one 10-cell series was described in our notes as follows: shaft-10-6-1-2-3-4-5-7-8-9, and another series with eight cells: shaft-7-8-1-2-6-3-4-5.

Cells are first excavated as rough cavities in the sand and then given their final shaping with a lining of clay or, at least, fine particles of soil. The finished cells are narrow and taper more gradually toward the neck than those of most other halictine bees. The cell of *N. melanderi* is considerably more oval. Cell length from floor to ceiling is 20-22 mm., with a maximum width of 8.5 mm. When sealed the two ends of the cell have about the same taper and the side walls are nearly parallel (Fig. 7). The ceiling tapers more than that of *N. melanderi* and the spiral structure is less obvious. Although the building sequence is not readily determined from the finished structure, the ceiling is constructed like a coiled rope and the plug is added later. Above the ceiling, the neck, which is packed with sand, is about 6 mm. wide and 8-10 mm. long. The cell linings are smoothed and polished, but not to the extreme brightness found in the cells of *melanderi* and many other solitary bees. The lower 13 mm. is provided with a thin, waxy coat that becomes gradually thicker toward the bottom of the cell (Fig. 8).

The rate of cell construction and cell provisioning is not known, but two nests known to be 16 days old contained 8 and 10 completed cells. The maximum number of cells found in a completed nest was 15, with an average of 10 or 11.

After receiving its full complement of cells, a lateral is completely plugged with sand excavated from the main shaft (Fig. 6).

**Provisioning.** It is apparent that *triangulifera* prefers *Helianthus annuus* as a pollen source. However, there is evidence that it is not monolectic. A few females, some with pollen loads, have been taken on *Bidens involucrata*, *Grindelia squarrosa*, *Helianthus lenticularis*, *Rudbeckia triloba*, and *Silphium perfoliatum*, as well as *H. annuus*. Males have been taken on a variety of plants, including *Cleome serrulata*, *Medicago sativa*, *Bidens involucrata*, *Gilia* sp., *Grindelia squarrosa*, *Helianthus lenticularis*, *H. petiolaris*, *H. maximiliani*, *Polygonum* sp., *Rudbeckia triloba*, *Silphium perfoliatum*, *Solidago* sp., *Vernonia* sp., and *Aster* sp.

The number of foraging trips required to provision a cell is not known. However, at the Lawrence site, females presumably actively collecting spent from 1.5 to 2.5 hours per trip and remained in the nest from 9 to 15 minutes between trips. At this site probably
little or no time was spent in travel to and from the pollen source since the immediate area abounded in Helianthus. *N. triangulifera* usually carries an enormous pollen load, and probably no more than four trips are needed to supply a cell. Pollen is carried on the hind legs and also on the sides of the propodeum and the venter and sides of the abdomen (Fig. 9) where bands of scopal hairs are present on segments 2-6 (Fig. 10).

The female behaves in a distinctive manner while collecting pollen. She crawls over the disc-flowers with a wading motion, waggling her abdomen vigorously from side to side. Her fore and midlegs clean pollen from the head and thorax and pass it to the scopal hairs of the hind legs. The pollen she collects on her abdominal venter is repeatedly packed down with her hind legs.

The pollen is deposited in the cell without the addition of any nectar. Presumably, the latter is added at the time the entire food mass is shaped.

The pollen mass is distinctively shaped (Bohart, 1952). It is gently rounded on its upper surface, its edge forming a narrow flange by which it is suspended from the tapering wall of the cell (Fig. 4G). On close examination it can be seen that the top of the mass is formed as a lid fitting into the flanged, bowl-shaped lower portion. Beneath this flange, the mass conforms to the shape of the cell bottom, but it is usually separated from the floor by a narrow space. Dimensions of the pollen mass are approximately 8.2 by 4.5 mm. The provisions are as moist as they can be without losing shape, and they remain so until consumed (Fig. 11).

After the nest is completely provisioned, the female fills the lower portion of it with sand obtained from the walls of the main shaft and its various enlargements. As a result, the upper open portion contains many horizontal and oblique cell-like burrowings (Fig. 6).

Like many other halictines, the female of *N. triangulifera* shows little hesitation in entering her nest after returning from a flight. Recognition is probably by landmarks. When the nest was caged by the observer, when it had been stepped on, or when unfamiliar objects were placed close by, the returning bee made brief erratic attempts to find it, after which she left the area for varying periods of time, sometimes for an hour or more. This procedure was repeated until the nest opening was uncovered or until she found it herself. When the nest was undisturbed, entry was swift, the
In some cases it remains as a transverse bar on the venter of the body and in other cases it is smeared onto the fecal strips.

Transformation to the rigid prepupa (Fig. 13) takes place immediately after defecation is completed. The variation in prepupal color previously referred to appears to be associated with cell temperature. In Utah the month of September, 1959, was cool and damp. Most of the prepupae formed in late August and early September were pale, and many were white. Examination of the fecal strips revealed nothing but sunflower pollen shells. Apparently, the yellow prepupal color is derived from an oil in the sunflower pollen which only colors the integument at warm temperatures.

_Nomia nevadensis arizonensis_ Ckll.

This small bee is found from central Utah to central Jalisco, Mexico, and from western Arizona to western Texas. Fragmentary observations were made at a nesting site about three miles north of Delta, Utah. The site is situated on a north-sloping bank about 15 feet above the Sevier River. The area is evenly vegetated with salt grass (_Distichlis stricta_) interspersed among scattered greasewood plants (_Sorocactus vermiculatus_). The soil is a silt loam underlain by alluvial gravel at a depth of about 42 cm.

Observations were made on August 17, 1955, at which time nesting had just begun. The nests were scattered throughout the site in rather loose aggregations. Four were excavated and, although none were complete, it could be seen that their plan was similar to that of _N. triangulifera_ (Fig. 4E). The entrance was at one side of the tumulus and the burrow was a straight vertical shaft or was slightly inclined for a few centimeters before it turned vertically. The diameter of the shaft was 7.7 mm. The total depths of the nests examined ranged from 23 to 42 cm. Seven cells were examined. Two were being provisioned, three were complete with pollen and egg, and two contained larvae. The cells were similar to those of _N. triangulifera_, but slightly more oval. They measured approximately 19 by 7 mm., tapering to 4 mm. at the neck. As in the case of _N. triangulifera_ cells, they were suspended vertically from a horizontal lateral burrow which was sometimes slightly curved (Fig. 4E-7). In one nest, the first cell along the cell lateral was about 20 mm. from the main shaft, a second was 15 mm. beyond this, and a third was 15 mm. farther on. The lateral was excavated for 10 mm. beyond the last cell.

The pollen mass resembled that of _N. triangulifera_ but was
deeper, more angular beneath the flange, and had several characteristic seams along the bottom (Figs. 4F and 16). The egg was similar in size to that of *triangulifera*, but was somewhat longer and more arched like that of *N. melanderi* (Fig. 16). The growing larvae were likewise somewhat intermediate, but were shaped more like those of *triangulifera*. The dorsolateral prominences of the prepupa were less pronounced than those of *triangulifera*, but they were equally sharp (Fig. 3). Nearly all of the prepupae were light yellow, but a few were nearly white. Pollen shells taken from fecal strips in a cell with a white larva were from saltcedar (*Tamarix gallica*). Those from several cells with yellow larvae were of gumweed (*Grindelia squarrosa*). The differences in larval color observed probably resulted directly from coloring materials in the pollens consumed.

Two young females were found in the main shaft of one nest. One carried some pollen on its hind legs. This suggests the possibility that more than one female may occupy a nest; however, it is believed that the presence of the second female was accidental, since we have repeatedly observed that females without a nest of their own may often “inspect” burrows being constructed by their neighbors.

No freshly dug earth was seen on the site during the early forenoon, but it was evident around many nests at 5:30 p. m., indicating that digging takes place in the late afternoon.

Females were collected frequently on gumweed flowers and occasionally on saltcedar, but none were taken on sunflower, even though it was common in the vicinity of the site. This species was reported as an effective pollinator of alfalfa in the Imperial Valley of California, (Linsley, 1946), but it has never been found on alfalfa in Utah, even when the nesting site is adjacent to an alfalfa field.

At 80° F. and 75 percent relative humidity *nevadensis* remained in the pupal period an average of 11 days as compared with 14 days for *triangulifera* and 12½ days for *melanderi*. In this group of species, length of the pupal period appears to be associated with size rather than phyletic proximity.

Nomia (Dieunomia) heteropoda Say

This species is found from Maryland to western Arizona and southwest Utah, and from Minnesota to Texas. It was found nesting with *N. triangulifera* in the alluvial sand deposits at Lawrence.
The nests were rather uncommon and usually widely scattered, although some loose aggregations of four or five were seen. Little is known of the nesting habits of this bee. Blair (1935) reports that Mickel and Dawson found them nesting in sand, and that the burrows “extended down into the sand vertically for a distance of three or four feet.”

On September 11, 1954, one nest of this species was excavated by Cross and Rettenmeyer (Fig. 6C). The tumulus and horizontal chimney were as described for Nomia triangulifera. The main shaft extended vertically to a depth of 94 cm. The top 80 cm. of this shaft were in sand, the remaining 14 being in the underlying silt bed of the original ox-bow lake. The walls of the tunnel in the sandy portion were completely straight except for one dilation at a depth of 30 cm. This portion of the shaft was lined with clay as described for N. triangulifera. The 14 cm. in the silt layer included an irregular mass of tunnels and cell-like excavations arising from the main shaft. Many of these were packed with sand, others were open. It seemed obvious that the clay from these excavations was used to line the main shaft, cell laterals, and the cells.

One cell lateral was present at a depth of 50 cm. This lateral was 16 cm. long, and it, as well as the main shaft, had a diameter of 13 mm. Two cells were present on the lateral, and were vertical with their entrances along the bottom of the cell lateral as described for N. triangulifera. The more basal cell was about 8 cm. from the main shaft, and the second was 6 cm. beyond the first (measured from the center of the plug of one to the center of the plug of the other). The clay-lined cells were very large, measuring 56 by 11.5 mm., and were long and narrow, with little taper. The more distal of the cells was the younger and had not yet been provisioned, although it was complete. The more basal cell contained a pollen mass and egg. The shape of the pollen mass and the position of the egg were as described for N. triangulifera. Dimensions of the pollen mass were 11.5 by 6.4 mm. (Fig. 6H).

The females visited the flowers of Helianthus annuus in company with N. triangulifera.
### Table 1.—Comparisons of three subgenera of *Nomia*.

<table>
<thead>
<tr>
<th></th>
<th><em>Epinomia</em></th>
<th><em>Dieunomia</em></th>
<th><em>Acunomia</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(<em>N. triangulifera</em> &amp; <em>N. n. neovadensis</em>)</td>
<td>(<em>N. heteropoda</em>)</td>
<td>(<em>N. melanderi</em>)</td>
</tr>
<tr>
<td>Nest entrance plugged</td>
<td>yes</td>
<td>yes</td>
<td>no</td>
</tr>
<tr>
<td>Horizontal “vestibule”</td>
<td>present</td>
<td>present</td>
<td>absent</td>
</tr>
<tr>
<td>Nest depth</td>
<td>21-110 cm.</td>
<td>about 100 cm.</td>
<td>usually about 22.5 cm., rarely to 35 cm.</td>
</tr>
<tr>
<td>Cell arrangement</td>
<td>evenly spaced along horizontal laterals</td>
<td>evenly spaced along horizontal laterals</td>
<td>in loose clusters</td>
</tr>
<tr>
<td>Cell shape</td>
<td>relatively long and thin. Taper slowly and evenly to neck.*</td>
<td>relatively long and thin. Taper slowly and evenly to neck.</td>
<td>relatively “jug-shaped.” Taper rather sharply to neck.</td>
</tr>
<tr>
<td>Cell lining</td>
<td>dull to moderately bright</td>
<td>dull to moderately bright</td>
<td>mirror-bright</td>
</tr>
<tr>
<td>Interior face of cell plug</td>
<td>not obviously spiralled</td>
<td>not obviously spiralled</td>
<td>obviously spiralled</td>
</tr>
<tr>
<td>Shape of pollen mass</td>
<td>see description and figures</td>
<td>see description and figures</td>
<td>a dorsoventrally compressed ball</td>
</tr>
<tr>
<td>Fecal deposit</td>
<td>nearly confined to cell floor</td>
<td></td>
<td>extending ¼ cell height</td>
</tr>
<tr>
<td>Pollen sources</td>
<td>usually Compositae</td>
<td>Compositae</td>
<td>Leguminosae and others, but rarely Compositae</td>
</tr>
<tr>
<td>Flight period</td>
<td>August and September</td>
<td>August and September</td>
<td>late June to late August</td>
</tr>
<tr>
<td>Optimum temperature for growing larvae</td>
<td>70° F. (for <em>triangulifera</em>)</td>
<td></td>
<td>85° F.</td>
</tr>
</tbody>
</table>

* Cells of *neovadensis* slightly more oval than those of *triangulifera*. 
Table 2.—Mechanical composition of Utah soils used for nesting by Nomia triangulifera Vach.

<table>
<thead>
<tr>
<th>Location</th>
<th>Depth in inches</th>
<th>Mechanical composition, percent</th>
<th>Texture description</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Sand*</td>
<td>Silt**</td>
</tr>
<tr>
<td>Pleasant Valley</td>
<td>0–4</td>
<td>18</td>
<td>54</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>9</td>
<td>60</td>
</tr>
<tr>
<td>Myton</td>
<td>0–4</td>
<td>46</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>45</td>
<td>38</td>
</tr>
<tr>
<td>Topaz</td>
<td>0–4</td>
<td>45</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>16</td>
<td>64</td>
</tr>
<tr>
<td>Hinkley</td>
<td>0–4</td>
<td>15</td>
<td>61</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>17</td>
<td>60</td>
</tr>
<tr>
<td>Trenton</td>
<td>0–4</td>
<td>16</td>
<td>67</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>12</td>
<td>69</td>
</tr>
<tr>
<td>Amalga</td>
<td>0–4</td>
<td>18</td>
<td>68</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>13</td>
<td>71</td>
</tr>
<tr>
<td>Benson Ward</td>
<td>0–4</td>
<td>42</td>
<td>46</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>36</td>
<td>47</td>
</tr>
<tr>
<td>Cornish</td>
<td>0–4</td>
<td>93</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>4–8</td>
<td>93</td>
<td>5</td>
</tr>
</tbody>
</table>

* Particle diameters between 2.0 and .05 mm.
** Particle diameters between .05 and .002 mm.
† Particle diameters less than .002 mm.
‡ Particle diameters less than .005 mm. This includes silt particles between .005 and .002 mm.
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STEPHEN, W. P.

Biology of Nomia (Epinomia) Triangulifera

Fig. 3. Prepupae of (left to right) Nomia melanderi, nevadensis, and triangulifera.

Fig. 5. Wind-blown tumulus of Nomia triangulifera seen from above. Note horizontal plugged chimney and castings marking original extent of tumulus. Topaz, Utah, August, 1955.
Fig. 4. A-D Vertical sections of *Nomia triangulifera* nests, Lawrence, Kansas, August, 1954. Numbers indicate depth in centimeters.

A. New nest showing truncate early tumulus and vertical entrance.
B. Nest 26 hours old showing transition to cone-shaped tumulus and loss of open, vertical entrance.
C. Slightly older nest showing lateral entrance and dilations and lateral branches of main tunnel.
D-1. Nearly completed nest. Lateral excavations in clay stratum. Apex of excavation packed with sand taken from cells.
D-2. Lateral at 36 cm. as seen from above.
E-2. Lateral at 16 cm. seen from above.
F. Pollen mass of *Nomia nevadensis arizonensis*.
G. Pollen mass of *Nomia triangulifera*.
H. Pollen mass of *Nomia heteropoda*.
Fig. 6. A-B Vertical sections of *N. triangulifera* nests, Lawrence, Kansas, August, 1954. See Figure 4 for explanation of numbers.

A-1 and A-2. Nearly completed nest with primary cell lateral completed and packed with sand. Secondary lateral with one cell.

A-3. Primary cell lateral as seen from above.

B. Completed nest. Dead bee in tunnel at 62 cm. (tumulus as in Figure 5).

C. Nest of *Nomia heteropoda*, Lawrence, Kansas, September, 1954.
Fig. 7. Vertical section of sealed *Nomia triangulifera* cell with prepupal bee above fecal deposit. (Cell lined with mold hyphae.)
Fig. 8. Vertical section of *Nomia triangulifera* cell ready for provisioning.
Fig. 9. Female *Nomia triangulifera* entering nest with load of pollen.

Fig. 10. Abdomen of *Nomia triangulifera* showing sternal scopa. (Photo by C. W. Rettenmeyer.)
Fig. 11. Pollen mass and egg of *Nomia triangulifera* (note moist condition of pollen).

Fig. 12. Pollen mass and fully fed first instar larva of *Nomia triangulifera*. 
Fig. 13. Final instar larva (left) and transition to prepupa (right) of Nomia triangulifera.

Fig. 15. Normal (left) and dwarfed (right) prepupae of Nomia triangulifera.
Fig. 14. Final instar larva of *Nomia triangulifera* feeding on an excessively dry food mass.
Fig. 16. Cell of Nomia nevadensis arizonensis with pollen mass and egg.