The Biology of Euphytomima nomiivora (Diptera: Sarcophagidae), a Parasite of the Alkali Bee, Nomia melanderi (Hymenoptera: Halictidae)

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THE BIOLOGY OF EUPHYTOMIMA NOMIVORA
(Diptera: Sarcophagidae), A PARASITE OF THE ALKALI BEE, NOMIA MELANDERI
(Hymenoptera: Halictidae)¹

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ABSTRACT

Euphytomima nomivora James, a miltogrammine sarcophagid found in the western United States, is a parasite in the cells of several halictid and andrenid bees. Although the alkali bee, Nomia melanderi Cockerell, is its principal host in Cache Valley, it also invades cells of Nomadopsis scutellaris (Fowler), Nomadopsis anthidius (Fowler), and Nomia triangulifera Vachal. The adult E. nomivora deposits eggs that hatch during oviposition. The young maggots that fall in or adjacent to the entrance to the nest of the alkali bee enter the nest, invade the host cell, usually destroy the host egg or young larva, and then feed on its provisions for 7 to 12 days. From one to five maggots may develop in a single cell when the temperature is 27.7°C. Then the maggot leaves the host cell and forms a puparium a few inches deeper in the soil. Only one generation per year develops in Cache Valley. Rain during the active season was the principal cause of mortality of the adult parasite. In 1964 and 1965 from 13 to 20 percent of the alkali bee cells in the nesting areas were parasitized, a rate that makes this parasite second in importance to the bombyllid fly, Heterostylum robustum (Osten Sacken).

INTRODUCTION

Euphytomima nomivora James, a miltogrammine sarcophagid fly, was first identified as a parasite of the alkali bee, Nomia melanderi Cockerell, in Logan, Utah in 1947 after it was found at a nesting site of the alkali bee near the Cache-Logan airport. Several specimens were sent to Dr. Maurice James of Washington State University who described it as a new genus and species (1955) but noted that it had previously been collected from other localities such as Imperial County, California and Globe, Arizona. Later, it was accidentally introduced into an artificial nesting site of alkali bees in North Logan where it became well established. The species has also been found as a parasite of the alkali bee in a small nesting site near North Ogden, Utah and in a somewhat larger one near Preston, Idaho. However, it has not been taken at the nesting sites of alkali bees in central and eastern Utah or in the important ones in the Snake River and Columbia River drainage basins of Idaho, Oregon, and Washington.

The life cycle of the alkali bee was treated in detail by Bohart and Cross (1955). The bee is distributed in scattered areas from the eastern slopes of the Rocky Mountains to the West Coast and from near the

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Canadian border to Sonora, Mexico and Baja California. Its largest populations occur in the intermountain valleys of the Northwest where the bee is important as a pollinator of alfalfa.

The present paper describes the life history and ecology of *Euphytomima nomiivora* and its significance as a parasite of the alkali bee.

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**TAXONOMY**

James (1955), in his description of *Euphytomima nomiivora* as a new genus and species, stated that it was closely related to *Euphyto Townsend*. Before publishing his description, he consulted with H. J. Reinhard for suggestions on the phylogenetic relationships of the genus and sent him some material. Apparently Reinhard did not see James' publication when it appeared, as he named *Euphyto rixosa* Reinhard (1956) on the basis of material of *Euphytomima nomiivora* sent to him by James (Moradeshaghi, 1966).

**MILTogrammine Biology**

*Review of literature:* Allen (1926) revised the Miltogrammini of North America and placed them for the first time in the Sarcophagidae rather than Tachinidae. His paper included brief notes on the life histories of the genera *Opsidiopsis, Taxigramma, Hilarella, Sphenometopa, Oestrohilarella, Pirosinella, Senotainia, Gymnoprosopa, Eumacronychia, Metopia, Opsidia*, and *Amobia*.

Evans (1957 to 1959) and Krombein (1950 to 1964) wrote a number of papers on the biology of aculeate wasps in which they listed the miltogrammine flies associated with each species of wasp and gave biological details for the genera *Metopia, Hilarella, Senotainia, Gymnoprosopa, Sarcomacronychia, Opsidiopsis, Eumacronychia*, and *Macronychia*.

Michener and Ordway (1963) described the life history of *Euphyto pollinaris* Reinhard as a natural enemy of the andrenid bee, *Perdita maculigera maculipennis* Graenicher; this is the only paper we could find dealing with a species at all closely related to *Euphytomima nomiivora*.

**Summary from the literature:**

1. Nearly all known species are parasitic on aculeate Hymenoptera. However, *Taxigramma* and *Hilarella* have been reared from Orthoptera (Allen 1926, Arnaud 1954).

2. Most genera are parasitic on wasps. Known exceptions are the genera *Euphyto* and *Euphytomima*, some species of *Metopia*, and *Senotainia tricuspis* Meigen which are parasites of bees.

3. Most genera parasitize hosts that burrow in the soil, but *Macronychia* and *Ptychoneura* parasitize stem-inhabiting wasps (Krom-
bein 1961), and *Amobia* is commonly reared from mud dauber wasps (Allen 1926).

4. Larvae of most species feed primarily on food stored by the host. However, *S. tricuspis* deposits its larvae on the neck region of adult honey bees, *Apis mellifera* L. The larvae feed mainly in the thorax, first on the hemolymph and later on the muscles (Sweetman 1963).

5. Miltostrongylus maggots affect the host larva indirectly by consuming the food stored for it (Allen 1926, Krombein 1964), and often they seek out and destroy the host egg (Allen 1926; Evans 1957, 1959; Krombein 1952) or first-stage larva (Krombein 1955).

6. All known genera normally deposit first-stage larvae (Allen 1926; Evans 1957, 1958; Krombein 1951, 1952, 1954; Krombein and Kurczewski 1963). D. G. Hall was quoted by Krombein (1952) as saying that presumably eggs are laid when the supply of living maggots is exhausted. In such cases, the eggs hatch within a few minutes of the time they are deposited.

7. The oviposition site seems to be associated with the structure of the compound eyes. Genera such as *Senotainia*, which have large eye facets anteriorly, a narrow frons, and larger compound eyes in the female than the male, follow the flight pattern of the host as it carries prey to the entrance of the burrow. When the host enters the nest, the parasite fly lays her young on the prey or on the body of the host (Allen 1926; Evans 1957, 1958, 1959). Other genera, including *Euphyto*, have more ordinary eyes and deposit their young just inside or close to the entrance to the host nest (Michener and Ordway 1963). Also, *Phrosinella julvicornis* (Coquillet) digs a small pit for its young near the entrance, a habit that appears to be correlated with the presence of a spiniferous ventral "foot" on the last segment of the first-stage maggot (Allen 1926).

8. The number of maggots per host cell varies for the individual cells of the same host. The most commonly reported number is one; the maximum is 24 (Evans 1957). In some cases, the contents of two cells are needed for one maggot to develop (Krombein 1955). In the laboratory, one maggot of *Euphyto pollinaris* consumed two and one-half pollen balls (Michener and Ordway 1963).

9. The length of the life cycle depends on environmental conditions. Some multivoltine species develop and metamorphose rapidly (Evans 1957). In the laboratory, the following species had periods of larval growth as indicated: *Senotainia vigilans* Allen, 4 days (Allen 1926); *Metopia lateralis* Macquart, 5 days (Krombein 1953); and *E. pollinaris*, 5 days (Michener and Ordway 1963).

The only reported pupal period was two weeks for *M. lateralis* (Krombein 1953). The whole life cycle for *M. lateralis* and *S. rubriventris* Macquart was recorded as 18 days (Krombein 1955).

10. Overwintering takes place in the pupal stage within puparia. Stem-inhabiting genera such as *Macronychia*, *Ptychoneura*, and *Amobia*
pupate in the stems (Allen 1926; Krombein 1964), and soil-inhabiting species such as *Senotanina* and *Metopia* pupate some distance from the host cell (Krombein 1955). Michener and Ordway (1963) imply that *E. pollinaris* also pupates away from the host cell.

**Biology of Adult *Euphytomima nomiivora***

**Diagnosis:** The adult parasite is easily recognized by its size (that of a house fly, *Musca domestica* L.) and its abdominal color pattern, which is characterized by three broad abdominal bands of black alternating with three of silvery grey, followed by a red-tipped fourth tergum and red terminal segments. The frons is as wide as the eye, and the tarsi are obscuously reddish (Fig. 1). The males are readily distinguished from the females by the more blunt apex of the abdomen and the red apical tergum occupying a ventral position (Figs. 14, 15).

**Emergence:** Depending on weather conditions, the flies emerged from mid to late June. In 1963, they were first observed on June 15, but in 1964, they were not seen until June 25, probably because of the rainy weather. Generally, the flies emerged two or three weeks earlier than the alkali bees, and during this period they laid eggs on nearby nest mounds of *Nomadopsis* and spent much of their time on whitish alkaline ground where bees do not necessarily nest. Probably most of these earlier flies developed in cells of *Nomadopsis* (which were nearly always several inches shallower than cells of alkali bees).

To learn how newly emerged flies make their way to the surface, we made a frame that would hold two pieces of glass about 2 cm apart. Moist sand was placed between the sheets of glass, and six fly puparia were inserted 16.4 cm deep. In a parallel experiment, a gallon jar was filled with the same kind of sand and provided with 10 puparia inserted at the same depth. The shape and direction of the galleries made by the flies in burrowing in the moist sand toward the surface could then be observed. Generally, they were straight, vertical, and about 2 mm in diameter, but along the way some dead ends and wide areas were observed that probably resulted from the presence of small rocks or tightly compacted sand. The emergence holes were elliptical and generally 3 mm long by 2 mm wide. While the flies were ascending through the sand, they assumed a vertical position with the head upward and the ptilinum protruding from the frontal lunule. They used the ptilinum as a drill to push the soil and make the emergence channels. During the process, they telescoped their abdominal segments into each other to provide a strong base for the drilling action.

In nature, after the flies emerged from the soil in the host nesting site, they ran around rapidly on the surface. At this time, they were from 6 to 8 mm long, and their ptilinum, which still protruded from the frontal lunule, looked like a yellowish sac. The thoracic bristles of the newly emerged flies appeared to be unusually long; those of the scutellum, which extended to the third abdominal segment, shook when
Euphytomima nomilvora. Fig. 1. Adult female. 2. Female ovipositing in burrow of Nomia melanderi. 3. Second stage maggot on pollen ball of N. melanderi. 4. Third stage maggots with remains of host pollen ball. 5. Puparia and mature maggots occupying overwintering chambers at same soil level. 6. Puparium showing enclosed pupa.

the flies stopped running. The yellowish abdominal bristles were conspicuously lighter on the ventral than the dorsal side, and the crumpled wings, which reached the third abdominal segment, were bowed toward each other. The wing membrane was dark grayish at first but soon became brownish basally. The legs of these teneral individuals were light yellowish and covered with relatively strong bristles.

About 30 minutes after the fly reached the surface, its body pigmentation intensified, beginning near the apex of the abdomen where the color changed gradually from whitish yellow to reddish yellow. Pigmentation of other parts of the abdomen soon occurred; on each seg-
ment it developed most rapidly dorsally and posteriorly. At the same time, the legs started darkening, the first pigmentation occurring between the segments and gradually spreading. The tarsal segments were the first to develop their full color.

Flies reared in the laboratory were able to extend their wings to the tip of the abdomen after 24 hours. However, none of them were able to completely expand their wings. The ptilinum was usually retracted into the frontal lunule about an hour after emergence, but it was sometimes protruded again when the flies were touched or otherwise disturbed. One fly remained alive for five days and was able to expand its ptilinum until its death. Most flies in captivity were fed on cantaloupe slices and sugar solution, but two that were kept unfed in a cage lived for three days.

Early activity on the nesting site: During about the first three weeks of adult activity, the flies were most abundant at the nesting sites of *Nomadopsis* which were adjacent to the nesting sites of *Nomia*. The first week they remained quietly on the bare, white alkaline mounds and sometimes touched or rubbed their heads with their front legs or preened their wings with their hind legs. Mating was infrequent and no oviposition occurred the first week, but the earliest oviposition took place at the nesting sites of *Nomadopsis* before the alkali bees were nesting. Also, early in the season, males were more abundant than females, but gradually the percentage of females increased until about the middle of July when the sexes were about equally numerous. Later in the season, females predominated.

The flies spent each night under sheltering objects such as stones, clods, or pieces of cow dung. Only one fly hid under each shelter, its head held toward the entrance and its legs stretched to allow the ventral side of the body to touch the ground. In such a position, it remained quiet until it was approached to within a few centimeters. Often when a fly was in its shelter, another fly would come to hide in the same place; however, the newcomer would leave as soon as it found the site already occupied. In rare instances, when the second fly arrived at the shelter, the first one became disturbed and left. Sometimes when a fly settled under a shelter before dark, it changed shelters before night.

Typical morning activities are indicated by the following account made on August 2, 1964: "From 7:30 to 8 AM with the soil temperature at 21°C the flies began to leave their shelters and preen themselves. Then they walked slowly, gradually accelerating their pace and taking short flights. From time to time, they stopped, usually orienting their bodies on a north-south axis and by the east side of light-reflecting objects. During such periods, which lasted from a few seconds to five minutes or more, they often preened their wings with their hind tarsi. Occasional mating, but no oviposition, occurred during the 'basking' period. After 10 AM mating, and especially oviposition, sharply increased."
Mating: When the temperature became warm enough (rarely much before 9 AM), the flies started mating. During the daytime, frequency of mating fluctuated according to the temperature and generally was highest from 9 to 11 AM and from 3 to 5 PM. From 11 AM to 3 PM, a few flies mated, but usually they rested quietly in the shade of various objects. Activity during this period seemed to be inhibited as much by the constant activity of the alkali bees as by the heat.

Sometimes the male (Fig. 15) pounced directly on the female (Fig. 14) from the air, but other times he landed near her and then jumped on her back. Then he rode on her dorsum with the end of his abdomen bent under hers and with his head reaching her scutellum. He pressed his front legs to her thorax, held the base of her wings with his midlegs, and extended his hind legs across the apex of her wings. During this period, the female stretched her legs, shook her body, and made intermittent buzzing noises. Usually, shortly after a male pounced on a female, he copulated with her for a few seconds and flew away. Sometimes he stayed on her for a longer time and copulated more than once. In the longest sexual encounter observed, the male was on the female from 9:58 until 10:33 AM. During the first minute, they copulated, but thereafter other males began to disturb them by diving down and hitting the male and even sitting on his back to try to mate with the female. When this happened, the first male bent the end of his abdomen and attached it to the female's genital area, thus preventing a successful approach by the other males. For 10 minutes, four successive males tried unsuccessfully to copulate with this female, after which she started to walk, carrying the male to the shadow of a clod where they stayed a few minutes. Then she flew with the male a short distance away and landed again. During this period, the female frequently buzzed and struggled, but the male held her tightly. At 10:33, the female flew, still carrying the male, for about two yards after which they separated.

Individuals of both sexes were seen to mate many times, but success of insemination was not determined.

Oviposition: In literature about miltogrammines, the egg is usually reported to hatch within the uterus, and the first-stage larva is deposited (Allen 1926; Evans 1957, 1958; Krombein 1951, 1952, 1954; Krombein and Kurczewski 1963). Only rarely is it mentioned that some flies lay eggs that are ready to hatch (Krombein 1952; Michener and Ordway 1963).

According to our observations, Euphytomima nomiivora is oviparous and deposits mature eggs. The larvae were ready to emerge during the process of oviposition, and the mouth hooks could be observed under the chorion. When the posterior end of the egg was extruded, it started moving from side to side. As soon as the front part of the egg was exposed, the head of the larva emerged from the chorion and attached itself to its mother's ovipositor. She then shook her ovipositor to release the egg, and the larva struggled to shed the chorion completely. Finally, the female shook her ovipositor rapidly and dropped the larva into the
host burrow or at its lip. Sometimes the larva did not have time to shed its chorion completely and was dropped unhatched. Deposition of each egg took from three to five seconds. In one observation, a maggot unable to shed its chorion during oviposition struggled and moved its head from side to side until the chorion was pushed halfway down its body. Then it stood on its posterior end and revolved the anterior part of its body for about 30 seconds until the chorion was shed completely.

Apparently the female could determine the presence of provisioned cells in the host burrow. To inspect a burrow, she placed her head in the entrance and sidled around it once or twice. If the burrow contained provisioned cells, she oviposited there. Often, after inspecting the burrow entrance, the fly left without ovipositing. When we excavated such nests, no pollen balls were present in the cells. Flies were also seen to inspect nests of the previous year and leave them without ovipositing. When we excavated burrows in which flies did oviposit, provisioned cells were always present.

The position of the female during oviposition depends on the host species. When she laid eggs in burrows of Nomia melanderi, she turned around after an inspection and inserted the end of her abdomen in the entrance to oviposit (Fig. 2). Sometimes the maggots fell deep into the burrow and other times they lodged at or near the rim. When the female chose a nest of Nomia triangulifera Vachal, she hung from the ceiling of the horizontal entrance and inserted the end of her abdomen into the burrow to release the egg. Such a chamber was examined after a visitation and found to contain a first-stage maggot on the floor. The entrances to burrows of Nomadopsis are filled with soil. Thus, the female (after making an inspection) turned around and used her hind legs to push the soil away and make a shallow pit in which to oviposit.

We determined how many eggs could be deposited by taking 20 females from the nesting site. The number of eggs in the ovarioles was as follows: 95, 83, 80, 36, 92, 34, 25, 4, 3, 13, 91, 9, 72, 67, 87, 52, 43, 98, 36, 14 (average of about 50). Some eggs were mature and as soon as these contacted the open air, the larvae started to tear the chorion and emerge. Immature eggs showed no activity even though the mouth hooks were visible in some; these eggs were placed on a piece of moist cellucotton inside a plastic box and kept in a cabinet at 27.7°C. The most mature eggs hatched during the first 24 hours; thereafter no hatching occurred, and the remaining eggs collapsed. Those that hatched were reared in the laboratory to the pupal stage.

Sensitivity to environmental conditions: Generally the parasitic flies were active in bright sunny weather and inhibited by cloudy conditions. Since the adult flies spent their time during the day on the bare nesting sites and during the night under cloths and cattle droppings, rain caused a high mortality, and after heavy rains, many dead flies were found in these hiding places. On August 12, 1964, a heavy night rain
so reduced the population that no flies could be found at the North Logan nesting site and only a few at the airport site for the rest of the season. Also, during high winds, the flies scattered and stopped flying. When the wind speed at the ground surface reached 25 miles per hour at the airport nesting site, the flies became completely inactive though several alkali bees and bombyliid flies were still flying.

The parasites were disturbed by the presence of many bees coming and going from the nest entrances and zig-zagging over them, but the bees seemed to pay no attention to the flies or maggots near the entrances.

LABORATORY STUDY OF LARVAL ACTIVITY AND DEVELOPMENT

For the study of normal activity of the maggot, artificial cells were prepared by drilling conical cavities in 1-inch cubes of plaster of Paris. The cavities, two-thirds of an inch deep by one-half of an inch wide at the top, were lined with paraffin wax and covered with a piece of cellophane held in place with a layer of beeswax. The cubes were placed in a covered plastic box and placed in a constant temperature cabinet.

Each cell was provided with the pollen ball of an alkali bee, some with a bee egg in the natural position on the top and some without. The pollen balls were kept moist by water droplets on the floor of the plastic box and by keeping the relative humidity of the holding cabinet above 65 percent (fiberglass wafers were placed in a tray of water). At first, the water droplets were placed on a piece of cotton in the boxes, but this provided a substrate for mold. Also, in the early trials, mold was a serious problem in the plaster of Paris cells and it was necessary to use 5-percent propionic acid to control it. When the cells were completely lined with paraffin, thus covering the substrate that was suitable for the growth of mold, the propionic acid was not needed.

The pollen balls were obtained by taking them from their cells in nests in the field, placing them in the plaster of Paris cells, and bringing them to the laboratory in an ice chest. First-stage maggots were placed in each cell by gently squeezing the abdomen of an adult female fly over the pollen ball. The maggots hatched from the eggs during oviposition just as they did in the field.

Eggs: As stated previously, eggs usually developed to maturity inside the body of the female flies. The mature egg was 0.8 mm long by 0.2 mm wide, brilliantly white, slightly arched, spindleform, and rounded at both ends. The region just behind the anterior end was slightly enlarged (Fig. 7). No reticulation or other irregularity was discerned on the external surface of the chorion. The mouth hooks and the dichotomous cephalopharyngeal skeleton were clearly visible through the chorion. Anteriorly the mouth hooks were shiny black, but posteriorly the skeleton became more brownish.

First stadium: In nature, first-stage maggots were vermiliform, had the same dimensions as the mature eggs, and possessed only posterior spiracles for respiration (Fig. 8). Short antennae were clearly visible
on the anterodorsal part of the head, and palpi (probably labial) could be seen just ventral to the mouth hooks (Fig. 8). The newly hatched maggots were active and usually shed the chorion while they were being extruded from the female. When the maggot was deposited on the rim of the entrance to the burrow of an alkali bee, it crawled in a tight circle and then traveled straight down the burrow. When the maggots were released in the pit of the burrow of Nomadopsis, they crawled into the soil to find the entrance. Sometimes they could not find it and wandered about until they became lost. Several maggots were seen crawling down burrows of alkali bees at a speed of about two inches per minute. Observed rates of descent in the burrows of Nomadopsis were a little slower. It is not known precisely how and when the maggot reaches the provisioned cells of the host though many burrows were excavated to obtain the answer.

In the laboratory, as soon as the first-stage maggot was squeezed onto a pollen ball, it started feeding and crawling over the ball. Sometimes it crawled directly under the ball and started feeding. The area in contact with the feeding maggot gradually became excessively watery. By the third day after attack, the entire pollen ball was liquid enough to spread across the bottom of the cell (Fig. 12), and the color of the pollen changed to grayish yellow. The same stages of decomposition in the pollen ball were often observed in the field.

The maggots began to crawl as soon as they contacted the ball. Even when they landed on a bee egg, they crawled for several minutes. If, while crawling, they encountered the egg, they implanted their mouth hooks in it and tore the chorion, always attacking either the ventral or lateral parts of the egg and taking from 5 to 15 minutes to destroy it. After the chorion was torn, they left the egg (which soon collapsed) and penetrated the pollen ball. The maggots penetrated indiscriminately into the top, sides, or underside of the ball but always left at least the caudal spiracles exposed and sometimes the posterior third of the body as well.

While the maggots fed on the honey-moistened pollen, they pumped their bodies and incessantly moved up and down in peristaltic activity. Many times, instead of digging deeply into the pollen ball, they only made a tunnel under the crust, thus making it possible for us to watch their activity. Even in this position, the last segment of the body was completely exposed. The first stadium usually lasted one day but occasionally two days. By this time, the fully developed first-stage maggot was 1.5 mm long and .25 mm in diameter. It shed its cuticle by leaving the pollen ball and positioning itself on the sides or bottom of the cell. At first, it made posterior to anterior wavelike movements. After about 10 minutes, the integument was torn at the head region. The movements continued, with the maggot moving its head from side to side, until the exuvium was removed from the anterior half of its body. Then it stood on its posterior end and moved its head until the skin was completely removed.
Apparently the maggot does not need to attack and kill the bee egg since the egg is not a necessary food. When, as usually happened, the maggot crawled first across the upper surface of the pollen ball, its chance of encountering the egg was high. However, it occasionally crawled down the side of the ball without contacting the egg and fed on the pollen ball. When several maggots were squeezed onto a pollen ball that did not have a bee egg, they developed normally. (In the field, we found pollen balls with intact bee eggs and second-stage maggots feeding beneath the balls.)

A pollen ball containing a newly hatched first-stage larva of the alkali bee was exposed to two first-instar maggots squeezed from a female. After they crawled onto the ball, both attacked the larva laterally by fastening their mouth hooks to the intersegmental area. A few moments later, they attacked the ventral side of the larva. About three minutes later, one left and penetrated the pollen ball but the other remained fastened to the intersegmental area while the bee larva struggled and revolved its head. During the next hour and a half, the maggot changed its position of attachment to the side of the host’s abdomen and finally to the thorax. Then, after a total of two hours, the maggot left the host larva and penetrated the pollen ball. The host larvae also fed on the ball while the parasite maggot was relatively inactive, but it turned dark and died on the following day. Both of these maggots developed to the pupal stage. Also, on four other occasions, we reared maggots that attacked an alkali bee larva and then the pollen ball. In each instance, they primarily attacked the thoracic region of the larva, but the larva’s posterior end was the first to darken.

Whenever more than one maggot was squeezed into a cell, some left and wandered to the rim of the cell or became lost. When three maggots were squeezed into each of 10 cells, all penetrated the food and behaved normally at first, but by the second day, only one maggot was found in each cell. Perhaps, when one maggot establishes itself, it produces a repellant. In our excavations, we often observed from two to five maggots feeding on one cell, but they were always of disparate sizes, an indication that they could not develop equally and harmoniously in close quarters.

Second stadium: The second-stage larva of the parasite observed in the laboratory was bright, yellowish-white, fusiform, and had both posterior and anterior spiracles. The yellow caudal spiracles, which had two vertical slits, were located in a deep cavity where they could be seen only from a caudal view. Each thoracic spiracle had five to six digits (called respiratory horns by some authors). Full grown second-stage maggots averaged about 2 mm long and 0.8 mm wide (Fig. 9).

The second-stage maggots behaved much like the first-stage but spent more of their time on the outer surface of the pollen ball (Fig. 3). Although they sometimes penetrated it, they never stayed more than
10 minutes before coming out. Perhaps development of the thoracic spiracles induces them to stay on the surface of the food mass. The second stadium lasted for two or three days, and during this period, the pollen ball became somewhat watery and dirty in appearance with splotches of cream-colored material on its surface. After two or three days of feeding, the maggot slowed its activities, fixed itself to the cell wall, and shed its cuticle in the manner described for the previous stage.

*Third stadium:* In the laboratory, the third-stage maggots were stout but fusiform and had both posterior and anterior spiracles (Fig. 10). The mouth hooks were prominent in this stage when the head region was thrust forward (Fig. 4). The cephalopharyngeal "skeleton" was nearly symmetrical but one of the spatula-shaped mouth hooks was slightly longer than the other (Figs. 11, 12). The anterior spiracles were located in the posterior part of the prothorax and had five or six digits. The posterior spiracles, which were located in a deep cavity, were brown and had three (sometimes only two) nearly vertical slits (Fig. 13).

This third (and final) stage was the most active and long lasting. The larva grew rapidly until it was full grown, that is, about 10 mm long and 3 to 4 mm wide. Its color varied according to the color of the pollen on which it fed. The third stadium usually lasted about four days, during which feeding was continuous. However, in some rearing containers in which moisture was kept at a low level, the stage was prolonged several days during which the larvae were restless and fed little.

When a single maggot was placed in a cell, it consumed about two-thirds of the pollen ball of the alkali bee. However, we were able to rear three maggots on one ball, and one cell found in the host nesting site contained five maggots of various sizes (Fig. 14) that eventually consumed all the available food and developed to undersized pupae.

Defecation took place during the second and third stadia. The maggots produced a dirty orange, watery material while feeding or crawling. This fecal material gradually darkened and became an amorphous solid, especially when defecation took place on the cell walls.

The entire larval period lasted about one week when the temperature was 27.7° C, but if humidity was low, it took 12 days. This time is similar to the five-day larval period that Michener and Ordway (1963) found for *Euphyto pollinaris* fed on pollen balls of *Perdita*.

*Puparium:* The puparium was brownish red and about 8 mm long and 3.5 mm wide. Its surface was somewhat smooth, but short transverse ridges were plainly visible on its dorsal surface. The posterior and anterior spiracles were present as in the active larva and the cephalopharyngeal skeleton could be seen through the integument, pressed against the inner wall of the anterior region (Fig. 6).

The puparia of *Euphytomima nomiivora* were a little larger and darker than those of *Euphyto pollinaris* (borrowed from Dr. C. D. Michener). Also, the digits of the thoracic spiracles of *Euphyto* were smaller and always six instead of varying between five and six, the
posterior spiracles were more elliptical than triangular, and the slits were less vertical.

In the laboratory, transformation from the third instar to the pupal stage was dependent on humidity. When water was dropped into rearing boxes in which the development of full grown maggots had been delayed by unfavorable dryness, they pupated without further delay. With normal humidity, they became sluggish before pupating, left their cells, wandered about in the plastic nest box for several hours, and then formed puparia. In later experiments, when the maggots wandered about, a little moistened sand was placed in the bottom of the box, and the maggots dug into it and formed puparia at once.

In nature, the maggots always left the bee cell before pupating, and the puparia were usually found at a deeper level than the host cells. At nesting sites of alkali bees, they were found seven to nine inches deep, but at nesting sites of Nomadopsis, they were only three to four inches deep. Often most of the maggots from one host nest formed puparia at the same level. No pupal chamber was formed, and the puparia were always closely invested by the compacted soil (Fig. 5). Generally, the larvae changed to puparia about the beginning of August. The first puparia, observed near nests of Nomadopsis, were smaller than those found near nests of alkali bees.

Soon after assuming its definitive shape, the puparium became creamy white. The spiracles darkened first, and then the other parts pigmented until after 24 hours the entire puparium was light brown (Fig. 5). Within three to four days, it had become a dark mahogany brown.

The exact duration of the pupal stage is not known, but generally, when puparia were overwintered in the field, flies emerged sooner than from puparia kept in the laboratory during the winter. Even when we brought puparia to the laboratory in the spring, adults emerged sooner than from the laboratory puparia. Differences in the time of emergence in the field are probably related to the depth at which the puparia are found in the nest areas of different species of host.

The number of generations per year was investigated by noting the wing condition of flies collected from late July until late August. Since the distal margins become frayed with age, the appearance of flies with perfect wings was taken to indicate the emergence of a new generation. Almost all flies examined had frayed wings except one found in mid-August. Furthermore, when a number of puparia formed early in the season were brought to the laboratory, no flies emerged before the end of the summer. These observations provide indicative but not conclusive evidence of a univoltine condition.

**Significance as a Parasite**

The importance of Euphytomima nomilvora in reducing populations of alkali bees was determined by sampling the nesting areas for host and parasite populations. Two procedures were followed: The first was a
Table 1. Number and species of insects taken from four 1.6 cu. ft. cores of soil taken from a nesting site of the alkali bee at Benson Ward, Utah, June 1964.

<table>
<thead>
<tr>
<th>Nomia melanderi</th>
<th>Heterostylum robustum</th>
<th>Euphytonima nomitivora</th>
<th>Total parasites</th>
</tr>
</thead>
<tbody>
<tr>
<td>6</td>
<td>8</td>
<td>7</td>
<td>15</td>
</tr>
<tr>
<td>4</td>
<td>4</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>34</td>
<td>11</td>
<td>9</td>
<td>20</td>
</tr>
<tr>
<td>7</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total</td>
<td>51</td>
<td>19</td>
<td>42</td>
</tr>
<tr>
<td>Average percentage parasitism</td>
<td>24.7*</td>
<td>20.4*</td>
<td>45.1*</td>
</tr>
</tbody>
</table>

* Assuming that each parasite destroys one host.

The numbers of immature stages of the alkali bee and of its two principal parasites obtained in 1964 from four core samples and in 1959 from three core samples are shown in Table 1 and Table 2 respectively. In both 1958 and 1963, parasitism by Euphytonima nomitivora was somewhat less than that by Heterostylum robustum (Osten Sacken). However, when we consider that occasionally two or more larvae of E. nomitivora develop in one host cell, but no more than one H. robustum ever does (and also that one larva of H. robustum frequently destroys two host larvae), the lesser importance of E. nomitivora is even more apparent. The percentage parasitism by the two species (assuming that each parasite destroyed one host) was remarkably similar for the two years: 27.1 and 24.7 by the bombyliid and 18.7 and 20.4 by the sarcophagid (Tables 1 and 2). These figures for parasitism are considerably lower than those reported for the same nesting site in previous years.

Table 2. Number and species of insects taken from three 9-cu. ft. cores of soil taken from a nesting site of the alkali bee at Benson Ward, Utah, May 1959.

<table>
<thead>
<tr>
<th>Nomia melanderi</th>
<th>Heterostylum robustum</th>
<th>Euphytonima nomitivora</th>
<th>Total parasites</th>
</tr>
</thead>
<tbody>
<tr>
<td>115</td>
<td>36</td>
<td>46</td>
<td>82</td>
</tr>
<tr>
<td>45</td>
<td>18</td>
<td>5</td>
<td>23</td>
</tr>
<tr>
<td>32</td>
<td>39</td>
<td>13</td>
<td>52</td>
</tr>
<tr>
<td>Total</td>
<td>186</td>
<td>93</td>
<td>157</td>
</tr>
<tr>
<td>Average percentage parasitism</td>
<td>27.1*</td>
<td>18.7*</td>
<td>45.8*</td>
</tr>
</tbody>
</table>

* Assuming that each parasite destroys one host.
Table 3. Numbers of cells of the alkali bee parasitized by *Heterostylum robustum* and *Euphytomyina nomilivora* at Benson Ward, Utah, August 1964.

<table>
<thead>
<tr>
<th>Date in August sampled</th>
<th><em>Heterostylum robustum</em></th>
<th></th>
<th><em>Euphytomyina nomilivora</em></th>
<th></th>
<th>Both species</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
<td>Percent</td>
<td>Number</td>
<td>Percent</td>
</tr>
<tr>
<td>3</td>
<td>2</td>
<td>6.5</td>
<td>10</td>
<td>33</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>10</td>
<td>6</td>
<td>20</td>
<td>9</td>
<td>30</td>
</tr>
<tr>
<td>7</td>
<td>9</td>
<td>30</td>
<td>4</td>
<td>13</td>
<td>13</td>
<td>43</td>
</tr>
<tr>
<td>9</td>
<td>9</td>
<td>26</td>
<td>3</td>
<td>10</td>
<td>11</td>
<td>36</td>
</tr>
<tr>
<td>11</td>
<td>7</td>
<td>23.5</td>
<td>5</td>
<td>16.5</td>
<td>12</td>
<td>40</td>
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<tr>
<td>13</td>
<td>5</td>
<td>16.5</td>
<td>5</td>
<td>16.5</td>
<td>10</td>
<td>33</td>
</tr>
<tr>
<td>15</td>
<td>12</td>
<td>40</td>
<td>3</td>
<td>10</td>
<td>15</td>
<td>50</td>
</tr>
<tr>
<td>17</td>
<td>3</td>
<td>10</td>
<td>3</td>
<td>10</td>
<td>6</td>
<td>20</td>
</tr>
<tr>
<td>19</td>
<td>3</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>10</td>
</tr>
<tr>
<td>21</td>
<td>8</td>
<td>26</td>
<td>4</td>
<td>13</td>
<td>12</td>
<td>40</td>
</tr>
<tr>
<td>23</td>
<td>1</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>Total 330 cells</td>
<td>62</td>
<td></td>
<td>44</td>
<td></td>
<td>105</td>
<td></td>
</tr>
<tr>
<td>Average percentage</td>
<td>18.3</td>
<td></td>
<td>13.2</td>
<td></td>
<td>31.63</td>
<td></td>
</tr>
<tr>
<td>parasitism</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* 30 cells sampled each date.

(Bohart 1950). The much lower host population in recent years may have accounted for the lower rates of parasitism.

The second procedure was used during August 1964 when late parasitism by *Euphytomyina nomilivora* overlapped early parasitism by *Heterostylum robustum*. This period was chosen to insure a valid comparison between the two parasites. From August 3 to August 23, counts were made every second day of the number of cells of alkali bees parasitized by both species (Table 3). The combined parasitism was 31.63 percent, 18.3 percent by *H. robustum* and 13.2 percent by *E. nomilivora*. This percentage is somewhat lower than the total parasitism by the same parasites during the entire preceding season. However, these data were obtained for only a restricted period during which the activity of the two flies overlapped.

**Discussion**

How the ovipositing female *Euphytomyina* determines the presence of provisioned cells before it oviposits in a burrow remains an unsolved problem. When the host bee carries pollen to the cells, it often leaves a scattering of grains on the burrow wall. Perhaps the fly detects the odor arising from these grains or from the pollen balls, or both, in the cells.

The apparent indifference of the host to the parasite is remarkable in view of the notice taken by other aculeate Hymenoptera of their
muscoid fly parasites. For example, the sweat bee, *Halictus rubicundus* (Christ), takes many evasive flights before entering its nest when anthomyiid flies of the genus *Leucophaea* are attempting to oviposit on the pollen load (personal observation). Sphexid wasps (*Ammophila* and others) often chase and sometimes seize the miltogrammine flies (*Scenotainia* spp.) that persistently try to larviposit on their prey as it is being dragged into the burrow (personal observation). Perhaps the alkali bee is indifferent to *Euphytomima* because this parasite never pursues its host even though it may be ovipositing when the bee is entering or leaving the nest.

A comparison between the biology of *Euphytomima nomiiivora* (as reported above) and *Euphyto pollinaris* [as reported by Michener and Ordway (1963)] indicates the following:

1. The adults of *Euphyto* emerge about two months earlier than those of *Euphytomima*. Both species alight on or near the entrance of the host nest, and both are similarly deterred in their activities by movement of air.

2. Both species lay eggs nearly ready to hatch, and in both, the segmentation and mouth hooks are visible. Larviposition (hatching as soon as the egg clears the ovipositor) is usual in *E. nomiiivora*, and the possibility of larviposition of *Euphyto pollinaris* was also mentioned by Michener and Ordway. However, *Euphytomima* places its maggot in the burrow or in a pit near the burrow, depending on the species of the host.

3. Maggots of both species crawl down toward the cells, but it is not known how they gain entrance to the host cells. Both species consume the provisions in the cells and attack any host eggs and larvae they encounter.

4. In the laboratory, the larval development of *Euphyto* took five days, and that of *Euphytomima* seven to 12 days. During larval growth, the *Euphyto* maggot consumed the provisions of two host cells, but in one instance three *Euphytomima* maggots developed to maturity on the provisions of one cell of an alkali bee. The small size of the *Perdita* pollen ball (the *Euphyto* host) compared with that of *Nomia* probably accounts for this difference.

5. When they were exposed to warmth in the laboratory, the *Euphyto* puparium broke diapause much earlier than in nature, but the same treatment delayed the breaking of diapause of *Euphytomima*.

**LITERATURE CITED**


