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THE BIOLOGY OF HETEROSTYLUM ROBUSTUM (DIPTERA: BOMBYLIIDAE),
A PARASITE OF THE ALKALI BEE

G. E. BOHART, W. P. STEPHEN, AND R. K. EPPLEY

ABSTRACT

Heterostylum robustum (Osten Sacken) is the principal parasite of the alkali bee (Nomia melanderi Ckll.) in the Northwestern States. It also parasitizes other species of Nomia and at least one species of both Nomadopsis and Halictus. It ejects eggs into and near the nest mounds of its host, but does not readily discriminate between nest burrows and other depressions in the ground. The first-instar larva finds its way to a host larval cell, where it waits until the host larva is full grown before feeding on it. The parasite larva passes through four instars, progressing from a slender, active first instar through a very brief second instar, and a soft, helpless third instar, to a tough, more active fourth instar. Some larvae apparently mature on a single host, but others partially drain the fluids from a second as well. In the late summer or fall the mature larva makes an overwintering cell in the upper few inches of soil. It pupates in the late spring, and shortly before ecdisis bores to the ground surface. The adult emerges as soon as the pupa thrusts its head and thorax clear of the surface. Mating usually takes place on vegetation surrounding the host nesting site.

As the principal parasite of the alkali bee (Nomia melanderi Ckll.) over much of its range, Heterostylum robustum (Osten Sacken) is an important economic insect. The alkali bee is an excellent alfalfa pollinator, chiefly responsible for the high yields in the major seed-growing areas of Washington, Oregon, Idaho, and Wyoming. In some areas where alkali bees were formerly abundant, robustum now holds their population to an insignificant level. The percentages of host prepupae destroyed vary from over 90 in nesting sites of Cache Valley, Utah, to 5 or less in some sites near Wapato, Washington. In many areas 20 to 40 percent of the host larvae are destroyed. In Oregon a nesting aggregation of over half a million bees in 1955 had an incidence of 91 percent parasitism in 1956. In 1957 the aggregation was only half as large, but parasitism
fell to 50 percent. In 1958 parasitism was 30 percent and the bee population appeared to be nearly stabilized.

Before 1946 there were several alkali bee nesting sites west of Logan, Utah, each containing over 100,000 nests. Bees from these sites were responsible for some excellent seed yields in neighboring fields. Todd (1946) described the ground on these sites as covered by thousands of empty bombyliid pupal skins. For the next 10 years parasitism in the Logan area was extremely high and alkali bee populations were too small to benefit the farmers appreciably. Since 1956 a slight reversal of this downward trend has been observed. It may have been the result of parasite control measures attempted on an experimental basis. However, another important dipterous parasite in this area, *Euphytomima nomivora* James, was controlled by the same measures, so that the benefit cannot be ascribed solely to bee fly control.

Apparently two factors have been responsible for the failure of the bombyliid parasite to wipe out its host completely in the Logan area. Each year a few of the bees nest in a solitary fashion and thus avoid the heavy attack suffered by the more gregarious individuals. Furthermore, some of the late-emerging bees continue to lay eggs after most of the parasites have disappeared and a partial second generation appears in late August after all the flies have disappeared. The first alkali bees to emerge each summer concentrate their nests in the most nearly ideal portions of the nesting sites. Consequently, several hundred to a thousand or more nests appear in these favored areas in spite of an annual parasitism of well over 90 percent.

**DISTRIBUTION AND HOST RANGE**

The recorded geographic range of *Heterostylum robustum* includes the Pacific and Rocky Mountain States as well as the southern Great Plains, the lower Mississippi Valley, and Florida (Painter 1930, 1958). In the Western States it is found primarily in the larger valleys. Since its range greatly exceeds that of *Nomia melanderi*, it must successfully parasite other species of bees. Frick (1958) stated that he has seen a specimen of *robustum* from Colorado labeled as a parasite of *Nomia bakeri* Ckll. In the vicinity of Logan it has been seen to deposit eggs in the nests of several species of solitary ground-nesting bees in and near the nesting sites of alkali bees. The larvae have been observed developing normally in the cells of *Nomia triangularis* Vachal and *Nomadopsis anthidius* Fowler. Early stages of the larvae have also been found feeding on pre-pupae of *Nomadopsis scutellaris* Fowler, a small species that nests in alkali bee sites, but fullgrown larvae and pupae have not been found in strict association with this species. The senior author once saw adults laying eggs in a small nesting site of *Halicuts rubicundus* Christ. Subsequently first- and third-instar larvae, which appeared normal, were seen on the host prepupe.

Although *robustum* seems to be an ever-present parasite in alkali bee nesting sites in Washington, Oregon, Idaho, northern Nevada, and northern Utah, it has not been found in Wyoming or central and southern Utah, although a single specimen of *Heterostylum englehardti* Painter was seen laying eggs in an alkali bee nesting site in central Utah (near Delta). In the Uintah Basin of eastern Utah a small number of larvae were taken which closely resembled *robustum*, but certain details observed in their life history were different from those observed for *robustum* in other areas.

In northern Utah and in Oregon the adults of *robustum* were observed taking nectar from flowers of alfalfa and sweetclover. However, its host-plant range probably includes many other flowers with moderately long corolla tubes. In 1947 it was conspicuously abundant in many alfalfa fields in northern Utah, but was never observed to trip the flowers. It rarely alighted on the flowers, preferring to sip nectar while
hovering directly in front of them. The habit of hovering while taking nectar has also been seen in *Bombylia* but not in *Anthrax, Exoprosopa*, and other short-tongued genera of *Bombylliidae* (Clausen 1940).

**ADULTS**

The adult (fig. 1) is conspicuous and fascinating as it persistently hovers and dips over alkali bee nests with its wings producing a continuous high-pitched whine. It is a large, robust species (fig. 2).
with unclouded wings, tan thorax, a gray, buff, and black pattern on the abdomen, and a long proboscis. With age it loses much of its abdominal hair and becomes nearly uniformly dark gray. The sexes are similar in appearance except that the males are holoptic and the females dichoptic (fig. 2).

On warm days emergence begins about 8 a.m. and continues until about 1 p.m., with the peak occurring between 9 and 10. After hardening, the still feeble adults fly to a nectar source and do not begin ovipositing over the nest for at least 2 days.

Emergence.—The first adult bee flies appear a week to 10 days earlier than the alkali bees, but their emergence period overlaps that of their host by several weeks. Emergence usually begins in late June, reaches its peak early in July, and is nearly complete by the middle of July. In any given year the start and peak of bombylid activity at different alkali bee sites in the same area may vary as much as 2 weeks. In 1956 and 1957 flies began emerging late in June in eastern Oregon and western Idaho, but in 1958 there was an early emergence and the flies appeared a month earlier (fig. 3). Although emergence tapers off rapidly, a few flies continue to emerge for several weeks. There is evidence that these late-emerging flies come from larvae that matured too late in the fall to move up to the normal zone for overwintering. The peak population of adults generally coincides with that of the host, but the host population remains high for several weeks longer.

Oviposition.—The parasites are active over the host nests after the temperature reaches 80° F., which is usually about 9 a.m. They are most abundant shortly before noon, and by about 2 p.m. most of them have taken shelter in surrounding vegetation where they exhibit a marked negative phototropism. In the greenhouse they seek the heaviest shade available.

Even though several hundred flies may emerge from 2 or 3 square yards of soil, rarely are more than one or two adults seen hovering over an area of the same size. Although the rate and distance of their dispersal from the point of emergence have not been determined, they must be considerable. On a small, rather isolated alkali bee site in Utah, attempts were made to trace the activities of marked flies. Of 162 individuals marked at the time they emerged in the summer of 1958, only two were seen during numerous subsequent observations. Of 45 marked while ovipositing, only one was seen in subsequent daily observations. Neither mortality nor disturbance caused by marking them appeared to be responsible for their disappearance. Marked individuals continued to oviposit as soon as they were released and in the laboratory they could be kept alive for more than a week.

In Oregon control of the fly was attempted on a small nesting site by scraping off the top layer of soil, killing each fly as it emerged, and swatting all ovipositing flies. In spite of this, nearly equal numbers of flies appeared on the site each day of the active season. Even when blocks of soil...
containing alkali bee larvae were moved to an area at least a mile from known sites and all flies emerging from them were killed, flies were numerous once bee activity began. Apparently the parasites not only disperse widely soon after emerging, but continue to shift their operations from one territory to another throughout their life.

The females (fig. 1) spend most of their flying time over the nests, hovering about 3/4 inch above the ground with their posterior legs held above their backs. When they perceive a hole or crack in the ground, they dip downward about 1/2 inch, give their abdomen a brisk downward "flick," and touch their hind tarsi to the ground. Apparently the egg is released at this moment. After discharging an egg, the female sometimes hovers again for a second or two and then releases another egg. She may repeat the process five or six times, after which she rises several inches and seeks other holes or cracks a few inches or feet away. *H. robustum* differs from certain other bombyllids in that it never lands during its ovipositing activities. *Bombylius* hovers over the nest mounds of its host, but it frequently lands and appears to lay some of its eggs while on the ground (observed in Utah by the senior author). According to Fabre (1913), *Anthrax* clings to the burrow entrance of *Chalicodoma* bees and lays its eggs by pressing the tip of its abdomen against the soil.

The egg-laying capacity of *robustum* is enormous. One female was observed to make 210 dips in 20 minutes. If she laid an egg each time she dipped, she must have laid at least 1,000 eggs during the day, even allowing for periods of relative inactivity. In Oregon 25 ovipositing females had an average of 169 (range 44 to 424) mature or nearly mature eggs in the lower ovaries and oviducts, and equal or greater numbers of undeveloped ova in the upper portion of the ovaries. Zakhvatkin (1931) states that *Calistoma deserorum*, a species parasitic on grasshopper egg masses, can produce from 1600 to 2000 eggs.

In spite of the rather thin scattering of parasites over the nesting sites, few holes or cracks escape oviposition. In 1955 a series of vials were dipped in black ink and buried flush with the ground surface. Each vial accumulated 50 or more eggs in a single day, indicating that the flies are accurate in their oviposition. However, accurate aim does not seem to be essential. When portions of a nesting site were boxed in with wire screen having a mesh just open enough to permit entry of the bees, the parasites released their eggs over the wire. When soil in the area was examined in the fall, the parasitism under the screens was nearly as great as in surrounding area.

Although the flies seem to be indiscriminate in their choice of depressions for oviposition, they are rarely found over areas where bees are not nesting in abundance. Artificial holes made several yards away from a nesting site are seldom visited. Perhaps the flies are guided to the nesting sites by their sense of smell.

**EGGS**

The eggs are 1.2 mm. long and 0.7 mm. wide. They are oval and equally tapered at each end. The chorion is smooth and white with pearly, iridescent reflections. The eggs have a mucilaginous coating to which soil particles adhere (fig. 4). When 42 eggs were brought to the laboratory and held at room temperature shortly after being laid, they hatched in 8 to 11 days, the average being 9. Since the incubation period is rather long, the eggs probably have to land in holes or cracks in the ground or in the crowns of plants to avoid lethal exposure to the sun.

**LARVAE**

The immature stages of the Bombyliidae undergo striking hypermetamorphosis. The various forms of the larvae and the peculiar modifications of the pupae represent obvious adaptations to changes in their mode of life from one stage to the next. The developmental stages of *robustum* are similar to those of other bombyllids, but they differ in several particulars.

**First instar.**—The first-instar larvae (fig. 5) are slender, planidiform, about 1.6 mm. long, nearly white, very active, and have a pair of long caudal bristles. The mouth parts, which are large in relation to the body, have a median pair of tonguelike hooks flanked by long, slender, maxillae which bear club-shaped palpi tipped with long bristles. The head and neck have eight pairs of bristles, and each thoracic segment has a single...
pair. Abdominal segments 2-6 have small, paired pseudopods, and segment 8 has a pair of double pseudopods near the posterior margin. The respiratory system appears to be peripneustic, although the abdominal spiracles anterior to the penultimate ones are poorly developed and may be vestigial.

The first-instar larvae inch their way along the ground by grasping it with their mouth hooks, flexing their body, making contact with their posterior pseudopods, and then pushing forward. Little is known regarding the activities of the first-instar larvae prior to feeding. They are never found on the host larva until it is in its final instar. Inspection of many cells in earlier stages of host development showed only a few first instars, and they were either inside the pollen ball or on the wall of the cell against the side of the ball. Although the tiny larvae may have been overlooked in the other cells examined, we are inclined to think that they are able to enter the cells through the entrance plug after the cells are sealed. This ability probably explains the occasional appearance in the early summer of robustum larvae in various stages feeding on overwintered prepupae and pupae (fig. 6). Early in the season the parasites probably eject many of their eggs into reopened burrows of the preceding season, and some of the first instars invade the cells of hosts that are late in breaking winter diapause.

If the parasite survives for long periods in the soil before invading a cell in which the host is a full-grown larva or prepupa, intensive egg laying early in the season probably results in a high rate of cell invasion throughout the season. The moderate parasitism of Nomia triangulifera, which provisions its nests after robustum adults have virtually disappeared, strongly suggests that parasitic larvae continue to invade cells for several weeks.

Although the first-instar larvae are not attracted to the host larva until it is full grown, they may require some prior nourishment.

According to Nininger (1916), first instars of Spogosyllum delia Loew may feed on a carpenter bee pollen mass for a month before implanting on the mature larva. Recently hatched larvae of robustum are not attracted to host larvae of any age and, when confined with prepupae, wander about and die within 24 hours at room temperature (75° F.). At lower temperatures (65° F.) they remain active for several days. While its host is defecating and transforming to a prepupa, the primary larva remains on it, but grows only slightly and does not appear to become attached. At this time it may merely feed on exudates and condensed moisture. Nevertheless, some feeding on the host before formation of the prepupa may be required, although the previously mentioned cases of implantation on overwintered hosts indicate otherwise. First-instar larvae of another bombyliid, Anthrax fur O. S., frequently wait until the overwintered prepupae of its host be

Fig. 7.—Unfed and fully fed first-instar Heterostylum robustum on last-instar Nomia melanderi.

Fig. 8.—Second-instar Heterostylum robustum.
pupate in May or June before attaching themselves (Linsley and MacSwain 1942).

In the Uinta Basin of eastern Utah several third-instar *Heterostylum* larvae were found on alkali bee prepupae on June 12 before nesting had started. Since no pupal exuviae or ovipositing parasites were found at this date or earlier, it appeared that these larvae had overwintered in the first instar. However, since adults were not collected for identification, it is not certain that the species involved was *robustum*.

In Utah two or three first-instar larvae are commonly found on a single host larva (fig. 7), but only one makes significant growth and molts to the next stage. The fate of the unsuccessful larvae has not been determined, but there has been no evidence of combat such as takes place with meloid or clerid larvae.

The larvae usually take their first position lying ventrally or laterally between two thoracic segments (fig. 7). When several parasites are on the same host, some may also be found between the anterior abdominal segments. The first instars do not attach themselves firmly and often change position after starting to feed.

The feeding larva remains in the first instar for about 36 hours, during which time it increases in length from 1.8 to 2.3 mm. and more than doubles in diameter. It is smoothly cylindrical at first, but moniliform when fully distended (fig. 7).

**Second instar.**—Larvae in the second-instar have only been seen a few times, and they appear to remain in this stage for 12 hours or less. This instar is flattened dorsoventrally with well-marked segments and no caudal filaments (fig. 8). The posterior spiracles are prominent and project over the base of the terminal segment. The little growth in this instar seems to have but slight importance in the larval development. A second instar has not been observed by other authors describing the larval stages of bombyliids. Even Berg (1940), who described in detail the larval stage of *Systoechus vulgaris*, did not observe it. Unfortunately, larvae of this instar were not preserved and now we have only a photograph, some sketches, and notes to verify its existence. It is possible that the instar here described as the second merely represents certain individuals of the instar described below as the third which, for some reason, failed to grow normally for the first 12 hours.

**Third Instar.**—This instar feeds for 2 or 3 days and grows rapidly, increasing in length from 2.3 to 8.3 mm. and in diameter at least three-fold. This instar has a creamy white, translucent ap-
pearance with many oval, opaque, white fat bodies clearly discernible in the abdomen. It curls around the body of its host and remains attached in one place to the ventral or lateral aspect of the thorax or abdomen (fig. 9). However, it has no difficulty in implanting itself again if its head is moved away from the host.

**Fourth instar.**—In this instar the larva is ventrally flattened, posteriorly tapered, and has a leathery, wrinkled integument, six pairs of bristles on the head and one pair ventrolaterally on each of the thoracic segments (fig. 11). The thoracic bristles articulate freely at the base and probably assist the larva in locomotion. There are no bristles on the caudal segment. This instar also has flat, wartlike knobs on each body segment and 13 slightly more prominent protuberances on the caudal segment. The numerous transverse wrinkles on all body segments serve to strengthen the body wall and allow for expansion. As the larva becomes distended, the wrinkles smooth out, but they remain sufficiently prominent to assist in locomotion.

The mouth parts at this stage are conspicuous and well sclerotized with a pair of median sword-like mouth hooks flanked by broad, heavy, shieldlike maxillae bearing small, peglike palpi on broad basal plates (fig. 12). The head has a peculiar hornlike labrum extending forward over the base of the mandibles. The respiratory system is similar to that of the third instar, with spiracles on the prothoracic and penultimate abdominal segments.

The larva readily releases its hold on the host when disturbed, but immediately fastens to it.
again with its maxillae and penetrates the integument with its mouth hooks. It readily attacks a new host and takes wasp or honey bee larvae without hesitating (fig. 13). If several parasites are placed in a container, they become cannibalistic.

The fourth instar feeds for 3 or 4 days and increases in length from 8.5 to 16 mm. In the laboratory in 1 day it consumes the fluids from the first host larva and then starts searching for another host. It readily feeds on another host larva but does not completely drain it unless it is considerably smaller than an alkali bee larva. Field observations in Utah indicate that the fourth instar commonly drains the first host and about half of the second. As it leaves the first cell, it plugs it tightly with dirt, sandwiching the empty host skin between the plug and the cell wall. It then burrows through the soil, filling the tunnel behind it until it finds another cell containing a prepupal bee. Within 2 days it drains this bee of about half its contents and leaves its cell. The half-eaten host larva is jammed against the cell wall with a loose plug of dirt (fig. 14). After draining the fluid from the first host, the parasite weighs 0.13 to 0.16 mg., and when full-grown it weighs 0.19 to 0.22 mg. It seems to be a remarkable feat for the parasite to complete its development on a single alkali bee prepupa (which weighs 0.126 to 0.198 mg.), but observations in Oregon indicate that this is normal in that area. Evidence for a consistent 1:1 ratio in Oregon consisted of an absence of partially consumed larvae or of last-instar parasites feeding on plump host larvae. The larvae increase their weight during the growth period approximately 458 times (from 0.0005 to 0.228 mg.).

Overwintering.—The full-grown larva burrows laterally and upwards from the brood chamber at the 5- to 10-inch level until it reaches a point 2 to 3½ inches below the soil surface. Here it excavates a large, roughly oval overwintering cell. Many genera of hymenoptera-parasitizing bombyliids do not leave the host cell (e.g., Anthrax, Toxophora, Poecilantrax), and have soft, relatively helpless last-instar larvae (Fabre 1913). Bombylus, like Heterostylum, leaves its host cell and has a tough, active last instar. However, the last instar of Bombylus is whiter than that of Heterostylum and not as rough in texture.

The robustum larva overwinters in a C-shaped position, either horizontally on its side or with
the anterior end directed downward (fig. 11). It is quiescent during this period, but when disturbed can straighten out and curl again without difficulty. Although some overwintering larvae can be found at a depth of 10 inches, these appear to be individuals that matured late in the season after soil temperatures dropped. It was observed in Oregon that a larva deep in the soil makes its way to the upper few inches before pupating in the spring. No evidence has been observed of a mature Heterostylum larva remaining in the soil more than one year, but the senior author has seen many 2-year-old larvae of Bombbylius as a parasite of Halictus farinosus Cress.

PUPAE

It is presumed that pupation takes place within the overwintering cell if it is sufficiently shallow. In the laboratory mature larvae have been seen to hollow out overwintering cells in plaster of Paris and pupate within them. The pupa (fig. 15) is white at first, but within 2 days it becomes yellowish brown, and a week later it turns darker as the adult forms within the pupal skin. As the pupa darkens it becomes very active, rotating whichever end is free and alternately extending and telescoping its abdominal segments. Structurally it is well equipped to drill and push its way through the soil. Its head is provided with three pairs of long backward-curved spines, and it has a double-bladed shovel-like structure at the base of the mouth parts. There is a pair of stout hooklets near the base of its wings, and each abdominal segment has a prominent circle of alternating hooks and long, strong bristles. Finally, its posterior segment is provided with a pair of long, sharp spines and several shorter ones.

Fabre (1913) described the manner in which Anthrax pupae break through their confining walls. Kunckel d’Herculais (1905), in discussing the emergence of Systropus from eucalpid cocoons, described the ability of the pupa to fill its digestive tract with air, thus inflating its body and bringing greater pressure to bear with the cutting structures on its head.

The pupa of robustum embeds the hooks of its head capsule into the upper part of its pupal cell and, by gyrating the abdomen, packs loose soil beneath it. Its anterior end is then gyrated, resulting in an excavation of the soil above it. This process is repeated until the pupa reaches the soil surface. The soil crust is broken and pushed back, and a few moments later the pupal head is visible, rotating back and forth about a
quarter of a turn. With each rotation the abdominal segments expand and contract in rhythmic waves. This activity soon forces the head and thorax clear of the ground. The upward motion of the pupa then ceases, and in less than a minute its thoracic skin splits down the back. As the split extends to the base of the head, the adult fly forces its way upward and out of the pupal case (fig. 16). It remains for a few minutes with the rear portion of its abdomen still in the case while the mouth parts, and finally the legs, are extended away from the body. It then drops forward onto its fore and mid legs, kicks itself free of its case with its hind legs, and crawls along the ground with its straplike wings slowly expanding. It mounts the first clod or stem it encounters and hangs with its head up to dry. As the wings expand and harden, droplets of fluid are released from the anus.

Within 10 minutes the adult is ready to fly, but it remains for several minutes more if undisturbed.

During the period of emergence and hardening, the flies are very vulnerable to predators. In northern Utah and in Oregon blackbirds, magpies, meadow larks, and English sparrows have been seen to feed on them, and there are probably many other bird predators. Although these birds feed on bees and flies alike, it is suspected that the flies, because of their initial sluggishness, are fed upon to a greater extent than the bees.

The pupal exuvium is usually anchored in the soil by its posterior half, and in compact, fine-grained soil it often remains intact and conspicuous for the remainder of the season. In such areas the presence of robustum in the nesting sites of bees can be determined most easily by looking for pupal exuviae. However, if the soil is sandy or loose at the surface, the wind soon loosens the pupal cases and blows them into windrows.

**MATING**

Mating usually takes place on the vegetation surrounding the site. However, in Oregon males were observed on several occasions to mate with newly emergent females on the nesting site. In one copulation observed in Utah the female was holding onto an upright stem with all three pairs of legs, and her body was inclined away from the stem at an angle of about 45 degrees. The male was facing away from the female with his body nearly horizontal and the tip of his abdomen bent upward to make contact at the proper angle. The female was motionless with her wings extending posteriorly in a resting position, but the male held his wings outstretched and intermittently fluttered them slightly. This mating was observed to last for 15 minutes, but the beginning of contact was not seen. The males do not pursue females over the Nomia burrows, although they can be seen hovering over the nesting area. Search for females apparently takes place in the morning before they are active over the nests and also in the afternoon when they take shelter in the surrounding vegetation.

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