THE BIOLOGY OF OXYBELUS QUADRINOTATUS SAY (HYMENOPTERA: SPHECIDAE)

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ABSTRACT

OXYBELUS QUADRINOTATUS SAY (HYMENOPTERA: SPHECIDAE)

By

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The life history of this small wasp is presented, based on observations in 1968, 1969, 1970, and 1971 on a sandy lot of the Michigan State University campus.

Observations include adult behavior preceding, during and after burrow construction, egg and larval development, provisioning, pupal case construction, and pupal development.

There are two generations per year, overwintering in the pupal stage. In 1971 there appeared to be a possible third generation due to the early spring. Oxybelus overwintering in the pupal stage usually emerge around the first week of June. Nesting activities reach a peak during the middle of July and terminate about the first week of August.

The burrow design consists of a tunnel with two to eight cells extending off the main burrow. The main tunnel is 4.5 cm. long and slants at a 45° angle with the ground surface.

Larval development takes 108 hours at which time all the provisioned flies are consumed. The pupal case in then laid up with sand grains spun together, which takes about 24 hours to complete.

Parasites include tiphiidae, bombyliids, and miltogrammine sarcophagid flies.

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Marvin Lee Goad

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INTRODUCTION

The tribe Oxybelini (spring digger wasps) has not attracted a great deal of attention in past years. Consequently, the knowledge of the bionomics and behavior of this tribe is very limited. Bohart and Schlinger (1956) mentioned that no complete history had been written on any species of the tribe.

In reviewing the literature several short papers were found depicting burrow construction and behavior of several species other than *Oxybelus quadrinotatus*.

The limited information written on *Oxybelus quadrinotatus* was done some time ago by Peckham (1898), Parker (1915), Williams (1936), and Strandtmann (1945). Besides these notes only casual mention is given *Oxybelus quadrinotatus* in other papers describing the method by which they carry their prey impaled on the ovipositor. This unique method of carrying prey has prompted at least casual mention by most authors who have worked on *Oxybelus sp*.

Knowledge of the biology and behavior of *Oxybelus quadrinotatus* could prove especially valuable because of their predatory habits on groups of economically important flies.

In 1956, Bohart and Schlinger revised a synonymic list of *Oxybelus* in which they differentiated 42 species and subspecies in the United States and Mexico.

BIOLOGY

The Nesting Area

The nesting area is located in an abandoned field located on the Michigan State University campus in East Lansing, Michigan, bordered by a paved parking lot, a closely mowed grassy field, a row of chicken coops, and a paved highway. Since the summer of 1968, much of the open sandy area which once existed has progressed through several seral stages. The vegetation consisted largely of grasses and cottonwood seedlings with the following herbaceous plants intermixed: yellow sweet clover, *Melilotus officinalis*; white sweet clover, *Melilotus alba*; queen ann's lace, *Daucus carota*; common ragweed, *Ambrosia artemisiifolia*; red clover, *Trifolium pratense*; rough-fruited cinquefoil, *Potentilla recta*; common milk weed, *Asclepias syriaca*; bull thistle, *Circium vulgare*.

The nesting site proper consisted of approximately 300 square feet of barren sandy soil devoid of vegetation (Fig. 1). The soil is composed of irregularly sized pink and white quartz sand. A thin crust of 6-10 mm. of firm damp sand exists on the surface and about 2.5 cm. below the surface.

Emergence and Pre-nesting Activity

Adults emerge between the last week of May and the first week of June. Adult activity was first noted on June 6, 1969, and on June 1, 1970. In 1968 a late spring appeared to affect the emergence of *Oxybelus*, as activity was not noted until June 14. In 1971, they emerged May 30 and were provisioning on June 1.

Both sexes appeared almost simultaneously. Males and females emerged randomly under laboratory conditions. On the day of emergence the wasps spent their time flying about the nesting area, and occasionally alighting on the sand and resting in the sun. Mating also occurred at this time.

Mating Activity

Krombein (1964) stated that O. emarginatus mated laying on their sides with copulation lasting for not more than 30 seconds. In O. sericeus copulation occurred on the sand with the male in the superimposed position for 15-30 seconds according to Bohart and Marsh (1960). The male taps the face of his mate with his antennae during copulation.

In O. quadrinotatus no courtship preliminaries were observed. The male while in flight pounced on the back of a resting female, clasped her tightly with his legs wrapped about her thorax, and on occasion clasped her head with his mandibles. The coupled pair immediately lay on their sides facing each other. A struggle ensued as the female attempts to free herself as they tumble over several times. When the female frees herself, both wasps scramble and fly off. Actual intromission is difficult to observe as the entire ritual lasts but 10-20 seconds.

The female apparently does not mate again. Males have been noted to attempt copulation on numerous occasions when the female was engaged in a variety of activities including burrow construction, provisioning, or upon her return to the nest. No actual coupling was observed on the abortive attempts.

Bohart and Marsh (1960) marked O. sericeus females and found them to be monagamous while provisioning a particular cell, pairing off with a new mate with each additional cell. They further noted that the female may re-mate with the original male when starting a new burrow. On one occasion, they recorded a female mating 50 or more times in a single day. It would appear that many of these "matings" would be what is described above as "abortive attempts."

They also reported an excess of males over females in O. sericeus, which is definitely not the case in O. quadrinotatus. At no time were more than three males ever observed on the sand plot at one time. From limited adult emergence in the laboratory it appears that females outnumber males by about 3.5 to one.

Burrow Construction

A distinctive behavior pattern is evident when O. quadrinotatus is seeking a suitable burrow site. She crawls over the surface of the sand in small semicircles, her wings slightly elevated, and her head tilted toward the sand. Moving back and forth, she intermittently chews particles of sand with her mandibles. This ritual may continue for twenty minutes before a site is selected for possible excavation.

Digging by O. quadrinotatus is done largely by the mandibles. The loose sand grains are swept beneath her abdomen with such force by the fore legs that the sand is kicked out behind her. The meso- and meta-legs are used entirely for support. She seldom completes the first burrow she starts. As many as six or seven may be started and abandoned. Abandoned sites were found to have an exceptionally thick crust of sand or a pebble directly in the path of the excavation.

Excavation proceeds much faster once the hard surface crust has been penetrated. Moist sand kicked up toward the entrance often plugs the burrow behind her as she penetrates deeper into the sand. At irregular intervals she emerges either backing out, kicking the sand out behind her, or pushing the plug of sand out with her head, "bulldozer" fashion. The head of O. sparideus is similarly used as described by Bohart, Lin, and Holland (1966). However, Bohart and Marsh (1960) described O. sericeus as pushing the sand out of the hole with her hind legs.

Once the plug was pushed out, O. quadrinotatus leveled the sand around the nest entrance. This was accomplished by moving backwards in a manner similar to excavation, then moving to one side and repeating the process until the excavated sand was completely leveled off in a large circumference around the entrance.

Bohart, Lin, and Holland (1966) described O. sparideus as tamping the plug of sand down in a circular back and forth motion, thus forming a crater with a diameter of 7 mm. and a depth of 2 mm. around the entrance. The sand crater is later used as material for final closure of the burrow.

Burrow Structure

The typical Oxybelus quadrinotatus burrow consists of a main tunnel with two to eight cells extending off at different angles and depth levels but not more than 5-6 cm. from the main burrow (Figs. 2-5). Tunnels extended 4.5 to 7.5 cm. in length, although they may be only 5-6 cm. at their deepest point below the surface for the tunnels slant about 45^{o} angle to the ground contour. Cells are slightly oval measuring approximately 5 mm. by 7 mm., but vary slightly in size according to the number and size of flies used as provisions.

Bohart, Lin, and Holland (1966) found that _O. sparideus_ constructed a similar type burrow. The main gallery is about 3 mm. wide and 11 cm. deep, with 2-3 cells radiating near the bottom. Bohart and Marsh (1960) found _O. sericeus_ burrows to be about 9 cm. deep, 3 mm. in diameter, straight down and terminating in 1-4 cells in a cluster.

Burrows of _O. emarginatus_ as described by Krombein and Kurczewski (1963) are quite similar to _quadrinotatus_ but differ by terminating with a cell.

With the initial excavation of the burrow the first cell, the deepest cell below the ground surface, is also constructed. Closure of the first cell is accomplished with sand which is excavated from the second cell; and in each cell subsequently, this process is repeated until all the cells are dug and closed successively to the last cell. The last cell, the nearest to the surface, is probably closed off by sand filled into the tunnel during final closure.

Bohart and Marsh (1960) commented that after _O. sericeus_ had provisioned the first cell the female goes head first into the burrow closing the main entrance behind her with sand which is apparently excavated from the second cell. Bohart, Lin, and Holland (1966), in timing the provisioning pattern of _O. sparideus_, stated that after six flies had been provisioned in the first cell the wasp remained in the nest for 22 minutes presumably closing the first cell and fashioning the second.

Once provisioning of the nest has begun O. quadrinotatus closes the entrance before leaving. Sand is kicked beneath the abdomen with the forelegs into the burrow entrance and smoothed over (Fig. 6). When the burrow is plugged it is impossible to tell where the entrance is located. Upon leaving the nest for the first time the wasp may make a couple of orientation flights around the area before seeking her provision.

Orientation

In 1898 the Peckhams wrote that Ammophila urnaria became familiar with the area by making short flights around its burrow before going afield for prey.

Tinbergen (1932) probed into the true wonder of a wasp's choice of landmarks. He arranged fir cones around the nest entrance of Philanthus triangulatum before she flew off for provisions. After she was gone, he moved the ring a few feet so the entrance was no longer within the circlet of cones. Upon returning to the site, she flew towards the ring, ignoring the real position of the nest. He further experimented and found that the wasp used as landmarks objects standing on the ground rather than those sunk into it.

Evans (1965) wrote that all solitary wasps which prepare the nest prior to hunting commonly make one or more orientation flights during or following preparation of the burrow. During these flights the wasp learns visual cues which guides it upon its homing flight. Van Iersel (1952) found that Bembix rostrata used markers without respect to their height but only to their total surface area; furthermore, this species appeared to employ concentric girdles of landmarks, parts of which effectively guided it to the nest even when other parts were severly disturbed. He also inferred that objects on the horizon, as seen from a position facing the nest, may be utilized when the area was disturbed.

It would appear that O. quadrinotatus has similar orientation cues. When small pebbles and herbs about the nest entrance were either removed, or altered in relation to one another, the returning female was unable to immediately ascertain the entrance to her burrow. She moved in semicircles nervously biting and scratching the sand in an attempt to locate the entrance. After several minutes of trial and error she usually found the entrance and deposited her prey. Before departing for additional provisions, however, she made several new orientation flights alternately landing and re-checking the burrow entrance. This behavior was manifested each additional time the immediate surroundings were changed while O. quadrinotatus was away seeking provisions. If the sand covering the burrow or in the immediate vicinity of the burrow were altered, but nearby emergent vegetation remained intact, no noticeable change was noted in the ability of the wasp to immediately discern the entrance to her burrow. It is thus apparent that quadrinotatus uses visual cues adjacent to her burrow to discern her nest entrance.

Whether or not O. quadrinotatus orient themselves to the general area by using horizon landmarks has not been determined. Chumurzynski (1964) released nesting females of Bembix rostrata at various distances to determine the outer limits of distance orientation. He found it to be between 0.5 and 0.7 km. In Ammophila pubescens, Baerends (1958) found this distance to be much less, about 40 m.; but, on the other hand, Philanthus triangulatum was exceedingly wide ranging and returned to the nest from distances of over 1 km.

O. quadrinotatus usually returned with prey in 3-10 minutes, averaging about 6 minutes. Considering the time involved in search for prey, actual subjugation of her prey, and her return heavily laden she could not possibly range more than several hundred yards for her provisions. Also, her prey were readily available less than 300 yards away from the nesting area. Distance orientation would thus seem to be of less importance to O. quadrinotatus than it is to more far ranging wasps.

Provisioning

Krombein and Kurczewski (1963) observed that O. emarginatus does not close its burrow temporarily when it departs to hunt flies. Bohart and Marsh (1960) similarly noted that O. sericeus also leaves the entrance open during her absence. In this connection, Ferton (1902) postulated that all Oxybelus which carry their prey impaled on their stinger temporarily close the nest entrance before departing, whereas those which clasp the prey by means of their hind legs leave the entrance open. This would appear to be true in O. emarginatus and O. sericeus as both carry their prey beneath them. Discrepancies in this postulation, however, do occur for Bohart, Lin, and Holland (1966) found O. sparideus carrying her prey, a large tachinid, clasped beneath her body with her hind legs and making a temporary closure of the entrance before leaving for more provisions.

Oxybelus quadrinotatus always carries her prey impaled on the tip of the sting or ovipositor. The sting is impaled into the ventral side of the thorax, usually between the first and second pair of legs. Whether the fly is paralyzed initially by the sting was never determined because O. quadrinotatus always had the fly impaled when it was sighted on the plot. Ashmead (1894) cites Verhoeff as authority for the statement that Oxybelus quadrinotatus does not paralyze its prey by stinging it because of the fact that the abdomen is too rigid to permit this action. He maintained that O. quadrinotatus instead kills her flies by crushing the thorax with her mandibles. However, O. quadrinotatus has been observed many times approaching the plot with a large fly and landing in such a manner as to dislodge the fly from the ovipositor. The wasp quickly pounces upon the fly, grabbing it with her mandibles and legs; then curling her abdomen beneath her, she "re-impales" the fly before attempting to uncover the burrow. Also, after observing many captured flies under the microscope, there was no evidence found to support the theory of the thorax being crushed or damaged during the capture. Although prey capture was never witnessed in O. quadrinotatus it would presumably be a very direct, rapid process of the wasp pouncing on a resting fly similar to that described in "re-impaling." Snoddy (1967) witnessed prey capture of O. emarginatus capturing Sumulium sp. on cows. He noted that the wasp depended upon sight to detect flies in the animals coat whereas the antenna was used to confirm the prey. He described the wasp grabbing the fly with her mandibles and legs and quickly driving the sting into the fly.

There has been some controversy in the past over the fact that O. quadrinotatus is thought to carry the fly with her third pair of legs when in flight. Whether the legs are used to help stabilize the fly in flight is hard to say for certain, as Oxybelus quadrinotatus are too small and fast to see such detail. The Peckhams take Fabre to task on this point and insist that this wasp does not impale the fly at all, but rather carries the fly with the hind legs, holding it tightly clasped by the head. In this way they account for the manner in which the fly projects behind the wasp in flight. When O. quadrinotatus is seen approaching the sand, it does look as if two wasps are flying in tandem, because the fly often is about the same size as the wasp.

Depending on where the female goes for her prey, the weather conditions, hunting success, etc., she is usually gone between 4 to 23 minutes, averaging about 6 minutes before returning. When returning with prey, she usually lands about 4 inches from the burrow entrance. She then walks to the burrow entrance and quickly scratches the sand back as she enters. If the fly should come off as she squeezes through the opening, she continues in, turns around, comes out head first, then pulls the fly inside with her mandibles as she backs down the tunnel. She usually remains in the burrow about 20-30 seconds. Sometimes she stays in the burrow several minutes which is presumably taken up by sealing off a cell and/or excavating a new one. On several occasions females were timed remaining below fifteen to twenty-two minutes before coming out. Exactly why one cell would require more time to fashion than another was never determined.

O. quadrinotatus Prey

A variety of flies are utilized by O. quadrinotatus as recorded from a random sample taken during the summer of 1971.

Rhagionidae		
Furcifera rufiventris (Loew)	1 ♀	
Syrphidae		
Toxomerus geminatus (Say)		1 ♂
Anthomyiidae		
Hylemyia platura (Meigen)	4 ♀♀	23 ♂♂
Muscidae		
Hebecnema umbratica (Meigen)		7 ♂♂
Hydrotaea armipes (Fallen)		13 ♂♂
Ophyra leucostoma (Wiedemann)		2 ♂♂
Musca domestica (Linnaeus)		1 ♂
Fannia canalicularis (Linnaeus)		11 ♂♂
Calliphoridae		
Protophormia terraenovae (Robineau-Desvoidy)		23 ♂♂
Bufolucilia silvarum (Meigen)		40 ♂♂
Sarcophagidae		
Metopia argyrocephala (Meigen)	2 ♀♀	
Helicobia repax (Walker)		3 ♂♂
Boettcheria cimbicis (Townsend)		2 ♂♂
Ravinia sp.		5 ♂♂
TOTALS	7 ♀♀	131 ♂♂

This list largely agrees with the combined prey records of Krombein (1948) and Bohart and Marsh (1960) who recorded O. quadrinotatus provisioning with Anthyomiidae, Calliphoridae, Sarcophagidae, Muscidae, and Therevidae. From the above totals, it would appear that males are used by a ratio of 19:1; however, this phenomena was not mentioned in any previous prey records.

The Egg

The egg is laid on the first fly provisioned in each cell. The egg may be positioned on either the left or right side of the propleuron of the fly with the anterior end attaching directly to the cervical region. The smooth semi-glossy egg measures 1.8 mm. long by .6 mm. It is semi-curved, banana-shaped, being slightly tapered at the ends and has an opaque, creamy-yellow appearance. O. sparideus also lays its egg on the first fly and is described by Bohart, Lin, and Holland (1966) as being enlarged at the anterior end. Krombein and Kurczewski (1963) described O. emarginatus as laying her sausage-shaped egg to one of the flies on the left side between the head and left front foreleg in an upright position.

The incubation period in Oxybelus quadrinotatus was approximately 2 1/2 days. This includes the time lapse between the initial laying of the egg and the time at which visible movements of feeding can be observed. Within twenty-four hours, the egg turns red on the mid-dorsal line which extends the length of the animal. Along the margins of this red midline the material becomes translucent and by 48 hours the heartbeat can be seen clearly. At this time the midline turns very dark, almost purple in color. Between 48-56 hours, the egg contents begin to constrict about 1 mm. from the anterior end. The constricted area is the beginning of cephalization, and segmentation appears within the next four hours. At this time, the pulsating blood can be clearly seen the full length of the larval body. The head area has a distinct localized pulse which can be seen under 200X magnification.

The Larva

Exactly when the egg hatches is difficult to determine positively, as the shedding of the chorion is not discernable. Bohart and Schlinger (1957) and the Peckhams (1398) site the egg of *O. quadrinotatus* as hatching in about one day, devouring its food and pupating in ten to fifteen days, emerging some two to three weeks later. Bohart, Lin, and Holland (1966) found *O. sparideus* eggs and record them hatching in 24-36 hours and the young larva feeding at the neck of the first fly.

Upon eclosion the young larva maneuvers immediately into position for feeding by moving its body in alternate wave contractions. When the head comes into contact with the fly, the larva moves its mandibles back and forth in a lateral motion. A small hole is chewed into the anterior region of the episternum and as the hole is enlarged by stripping away portions of the body wall, the soft muscle is exposed. The feeding tempo quickens as the larva takes in large amounts of juices and small particles of muscle tissue. This can be seen passing through the semi-transparent head capsule and down the esophagus. When the larva has finished the soft parts, the thoracic body wall

in turn is masticated into a pulp with only a few small fragments of the wall and apodemes remaining.

The head and abdomen of the fly are hollowed in a similar fashion. Entry into the head is usually made through the foramen magnum, or the compound eyes. The abdomen is consumed with exception of a few small bristles and tiny body wall fragments. The legs and wings are usually the last parts to be eaten. The larva will masticate most of these parts into a pulp extracting some juices, leaving small sections of the tibias and tarsal segments.

This feeding process is repeated on all subsequent provisioned flies. There is, however, no distinct sequence as to which parts of the subsequent prey are consumed for larval contact with the next prey determines the initial feeding site.

The number of larval stages was not determined exactly; however, visible changes in color and size appear to designate four. The first instar larva is believed to begin at 60 hours when the larva begins to feed (Fig. 8). The second instar appears at 96 hours when noticeable folds begin to form on the lateral margins of the body (Fig. 9). The third stage occurs at 120 hours (Fig. 10) when the larva turns to a bright pink and attains a length of 3 1/2 mm.-4 mm. The fourth, and possibly last, occurs at 168 hours when white specks appeared just prior to pupal case construction (Figs. 11-16). The mature larva, a whitish legless grub, attained full size after feeding for approximately 100-108 hours.

Pupal Case Construction

The Oxybelus quadrinotatus larva matures and immediately prepares the cell for pupal case construction. The cell and larva itself is cleared of all remnant parts of the prey including head capsules, wings, and legs. This may take from one to two hours. The larva gathers these extraneous fly parts together and masticates them into an indistinguishable pulp. Some fluids are extracted from this mass as it may be seen passing through the esophagus of the semi-transparent head capsule. This mass is masticated into a very slimy condition and then stretching the body out as far as it can reach, the larva placed them on the periphery of the cell-wall external to the position of the future pupal case. The gooey mass adheres to the sand and is secured further by the larva attaching silk strands in three or four different places.

Once the larval body and area are completely cleaned, the larva begins to form its pupal case by agglutinizing sand grains together and laying them one on top of the other.

The larva works laying on its dorsum and begins spinning its case by laying down several silk strands back and forth across the bottom of the cell. The larva reaches out from side to side picking off sand grains, wallowing them about in the mouth until each grain is coated with silk. The larva stretches out again and agglutinizes the sand grain to the silk strands (Fig. 11). As the larva returns to its original position, two silk strands are laid down, anchoring the grain in several places to the surrounding cell wall.

Usually the starting point of the pupal case is somewhere near the mid-section of the finished case. The larva rests itself across the silk strands initially laid down and begins to encircle itself with a girdle of sand grains (Figs. 12-13). Once the girdle reaches an approximate size of 1 1/2 mm. wide, extending completely around the larva, it switches ends and begins work on what will become the posterior end of the finished case (Figs. 14-16). When this was all enclosed, the larva continued to extrude more silk over the inside wall of sand grains.

As the pupal case nears completion, it becomes increasingly difficult for the larva to reach out for sand grains. The final void is closed by spinning silk strands back and forth on all sides of the tiny opening, lacing and drawing it closed with shorter and shorter strands, thus entombing itself.

Due to the excessive amount of silk used in final closure, the anterior end of the case is easily recognized. It not only appears to be darker in color, but is slightly larger in diameter. The average pupal case measures 3-5 mm. long by 1-2 mm. wide, but may vary in size slightly depending on the size of the individual larva. The entire process of spinning the pupal case takes about 24 hours plus two to three after closure to further agglutinize the inside with more silk.

The pupal case dries in approximately eight hours becoming very rigid and impervious to water. Its overall appearance is one of having been glued together because of the clear, silk-like saliva.

Pupal Development

The adult emerges some 24-26 days after it has spun the case. By opening a case, prior to emergence, some observations were made on the pupal development. Exactly when pupation occurs was never determined for once the case is opened during early development, the larva either desiccated or mold destroyed it.

The pupa was, however, observed during the latter portion of its development starting with the 16th day. Between 16-19 days, the eye pigments turn from a light brown color to black. Brown pigments appear in the mandibles on the 20th day. The entire head including eyes are black, while the thorax turns black dorsally and extending laterally on the 21st day. The femara are also grey to black and black streaks appear across the abdominal segments. From one hour to the next, the pupa may change position by rolling over inside the case.

Very little visible change occurs between 21 and 23 days, but on the 24th day, the tibial spurs shrink, harden, and become very dark. The tarsal claws which up to this point appear as round white tabs now become pointed, hard, and black in color. On the 25th day, the pupa begins to kick its legs and twists its head back and forth. The mandibles are exercised back and forth, apparently getting ready to begin chewing the pupal case open. More rotating is noted as the pupae is seldom in the same position from one hour to the next. Sometime between 26-29 days, the young wasp digs its way to freedom, after chewing the entire anterior end of the case out with its sickle-shaped mandibles.

Once the wasp digs its way to freedom, it remains motionless until the wings are dry and exercised properly. Depending upon the individual wasp, she will mate and begin provisioning within one to three days. Until then, it is believed that she orients herself to the general area, as she intermittently lands and takes off, making circles around the sand plot.

Pupal Data

During the months of June and July, the first generation larve pupates and remains inside the pupal case for a total of 24-26 days, the adult wasp chewing the anterior end out of the case and emerging.

The late July brood remains in the case over winter and emerges the next year. There are two generations per year, and a strong possibility of three in a few cases. The second generation emerges randomly during the first and second week of July while the third generation possibly emerges the first week of August.

In 1971 nine pupae were buried immediately after each larva had finished spinning its case. Each one was placed into a small plastic box and covered with 6 cm. of moist sand taken from the plot.

The boxes were then placed in an open sunny area to provide similar conditions to the original area, and water was added daily to prevent desiccation. Seven of the nine cases emerged on the 25th day, while the remaining two emerged on the 24th day and the 26th day. Seven females and two males emerged. After digging their way to the top the adult wasps dried off, at which time they began to exercise their wings and buzz around inside the boxes.

Parasites

Small miltogrammine sarcophagid flies are commonly observed buzzing around the entrances of Oxybelus quadrinotatus burrows. They often dart in and out of the burrow entrance when the wasp is busy placing a provision below. They seldom stay in for more than 5-10 seconds, but continue hovering over the entrance until the wasp comes out to make her temporary closure. When the wasp departs, the fly may attempt to scratch the temporary plug out; however, no success was ever observed.

The fly remains in the general vicinity; and every time the wasp returns, the fly dives in on her in what appears to be an attempt to larviposit on the prey transported by the wasp. Bohart and Marsh (1960) also record these flies as parasitizing O. sericeus. They mentioned the flies buzzing and striking at the wasp in what appeared to be larviposition. Several cells were found in O. sericeus burrows to be parasitized with maggots or puparia which were reared to adults and identified by H. J. Reinhard as Senotaina litoralis Allen. They made no mention of where the parasite larva was deposited or its relationship or competition with the Oxybelus larva for the fly provisions. Strandtmann (1945) mentioned Senotaina rubriventris (Macquart) as a possible parasite on O. quadrinotatus. The tiny flies were described as hovering around the nests and frequently following the wasp down into the burrow.

It was never determined in O. quadrinotatus exactly when the parasite larva was deposited. Only on one occasion was a very young larva found; it was deposited in the exact spot (between the head and thorax of the first fly) that O. quadrinotatus deposits her egg. The wasp egg or larva was absent in every case where the cell had been parasitized by the fly. It is believed that if the fly deposits her larva, the Oxybelus may never lay an egg in that particular cell. Another possibility is that the fly larva begins to feed immediately and may possibly consume the wasp egg if it is laid before the wasp egg hatches.

The parasite larva is a voracious feeder; it chews a hole through the abdomen and crawls inside the first provisioned fly. Then it devours the insides as it migrates toward the head. Once all of the flies are gutted in this fashion, the larva migrates 1-4 cm. away from the remnant fly parts and spins its red, semi-transparent pupal case. The adult emerges approximately 19-23 days after it pupates.

Thus it appears to follow a cycle similar to Oxybelus quadrinotatus, emerging one to two days prior to the wasp.

Bombyllids, tiphiids, and mutillids were also common around the nest sites; however, no attempts of parasitism were ever observed. However, two wasp pupae were opened, one of which contained a Tiphiidae pupae, Myrmosa sp. and a Bombyliidae, Anthrax albofasciatus albofasciatus Macquart.

Bohart, Lin, and Holland (1966) reported that O. sparideus was never found to be parasitized by either Miltogrammine Sarcophagids, Bombyliids, or Mutillids although all three parasites were common to the area. They accredited this to the fact that the burrow entrance was closed when the wasp was in the burrow for any extended period and due to its entrance-closing behavior prior to each departure in search in search of prey. Even though _O. quadrinotatus_ closes her burrow in similar fashion, Miltogrammine Sarcophagids, one Tiphiidae, and one Bombyliidae were found to be parasites. Two species of miltogrammine flies were found to be heavily parasitizing _O. quadrinotatus_. _Phrosinella fulvicornis_ (Coquillett) sits and watches from a rock or weed and then darts into the burrow at the opportune time to deposit her larvae while _Metopia argyrocephala_ (Meigen) continually buzzes around the burrow about 1/2 inch off the ground and often pursues the female wasp while returning with her provisions. It was observed several times that a wasp approaching her burrow with her prey was being chased by a _Metopia argyrocephala_ (Meigen). Instead of landing in the usual manner, the wasp would make wide circles around the plot in an apparent attempt to elude the fly. In most cases the fly would then hover, waiting for the wasp to uncover the entrance to go inside, at which time the fly would dart down the entrance behind her presumably larvipositing on the provisioned fly.

In the summer of 1971, 23 burrows of _Oxybelus quadrinotatus_ were dug up containing a total of 63 cells. Out of 63 cells, twenty showed signs of parasitism. In these cells empty head capsules and hollowed abdomens were found, which obviously had been cleaned out by a miltogrammine larva. However, no miltogrammine pupal cases were found in 15 of these cells, which means the larva had moved out of the range of my excavation or were lost in the sand. Miltogrammine pupae are very small ranging between 1 1/2-2 mm. in length.

Three miltogrammine pupal cases and two of their larvae, however, were found, all of which were reared to the adult stage.

If indeed the fifteen empty cells had been parasitized plus the five reared, this would account for about a 30% loss of _O. quadrinotatus_ to miltogrammine parasitization alone, not taking into account additional parasitism from tiphiids and bombyliids. Also, since two female _Metopia argyrocephala_ (Meigen) were found as provisions in a _O. quadrinotatus_ cell, this may suggest even more parasitism since Sarcophagids larviposit. Bohart, Lin, and Holland (1966) described this type of parasitism in _O. sparideus_. They found the unborn maggots within the provisioned flies abdomens to emerge within 24-36 hours, rapidly devouring all the provisions leaving the young wasp larva to starve.

Behavior

As stated by Kurczewski and Acciavatti (1968) in their discussion of _Crabro_ nesting behavior, it is very difficult to draw conclusions about _O. quadrinotatus_ behavior patterns as there simply has not been any detailed studies done with the genus.

It would be safe to say the two species _O. bipunctatus_ and _O. quadrinotatus_ do not exhibit numerous, clear-cut differences in their nesting behaviors. The following facets are very similar or indistinguishable; burrow construction, burrow niche, orientation flight, stinging and paralysis of prey, prey carrying and transport of fly into the burrow, prey storage, placement of prey in the cell, positioning of the egg, temporary closure of nest, and final closure.

Differences observed include preference of _O. quadrinotatus_ for digging on a knoll or into the side of a sloping bank; also the size of prey provisioned and the size of the wasp egg. Both species were constantly harrassed by the same miltogrammine flies and possibly parasitized about the same number of times. There was also noted a difference in the number of flies per cell due to the size difference in the provisioned flies of each specie.

GENERAL DISCUSSION

For the large number of known Oxybelus species, Bohart and Schlinger recorded that no complete biological information had been published as of 1957 on any species. This appears to be the case now; however, there are numerous notes and short papers on other species of *Oxybelus*.

Most of the notes on *Oxybelus quadrinotatus* appear to have been done some time ago. Among the North American writers, Peckham (1898), Parker (1915), and Williams (1936) have recorded most of the data on the subspecies, *Oxybelus uniglumis quadrinotatus*.

Oxybelus distribution records are also very incomplete and Bohart and Schlinger (1957) noted that the collections from 25 major entomological museums totaled only about 5,000 specimens. At least 1/2 of the total involved the three relatively common species, *emarginatus*, *uniglumis quadrinotatus*, and *californicus*. In 1957 an extensively revised synonymic list was given by Bohart and Schlinger; the list differentiated 42 species and subspecies in the United States and Mexico.

As in many other areas of entomology, there exists an open opportunity for research on this interesting group of wasps. *Oxybelus* life histories have no doubt been bypassed for others due to their inconspicuous habits and small size. This author would go one step further than Bohart and Schlinger (1959) by saying that not only is there a great need for more collecting in North America, but there is a great need for more indepth studies of their bionomics.

Economic Importance

At least two of the flies recorded as prey of Oxybelus quadrinotatus are of economic concern, such as Musca domestica and Hylemyia platura. Bequaert, as noted by Pate (1937: 375), explained that adults of Oxybelus pyrura (Rohwer) are called "policias" by natives of Guatemala because of their beneficial attack on adults of Simulium species, some of which are vectors of onchocerciasis. Also, several authors have recorded Oxybelus rufipes Taschenberg as a predator on tsetse flies in Africa. It would appear that some economic benefit may result from Oxybelus sp. near almost any place of habitation or agriculture since they all prey on certain groups of flies. Whether Oxybelus quadrinotatus should be considered as a possible biological control of seed and vegetable maggots is beyond the scope of this paper; however, it would certainly merit some consideration in wake of all the concern about pesticides.

It would appear that even though no economic gain ever develops from this study, quite possibly it will fill an existing lacuna and expose the fascinating biology of Oxybelus quadrinotatus. Further, it is hoped that this life history is as interesting to the reader to read as it was for the author to research.

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Figure 1. Site of nesting.

Figure 2. Typical nest of O. quadrinotatus with 5 cells.

Figure 3. Ibid. above illustrating orientation of the cells in relation to the burrow.

Figure 4. Typical nest of O. quadrinotatus with 4 cells.

Figure 5. Ibid. above illustrating orientation of the cells in relation to the burrow.


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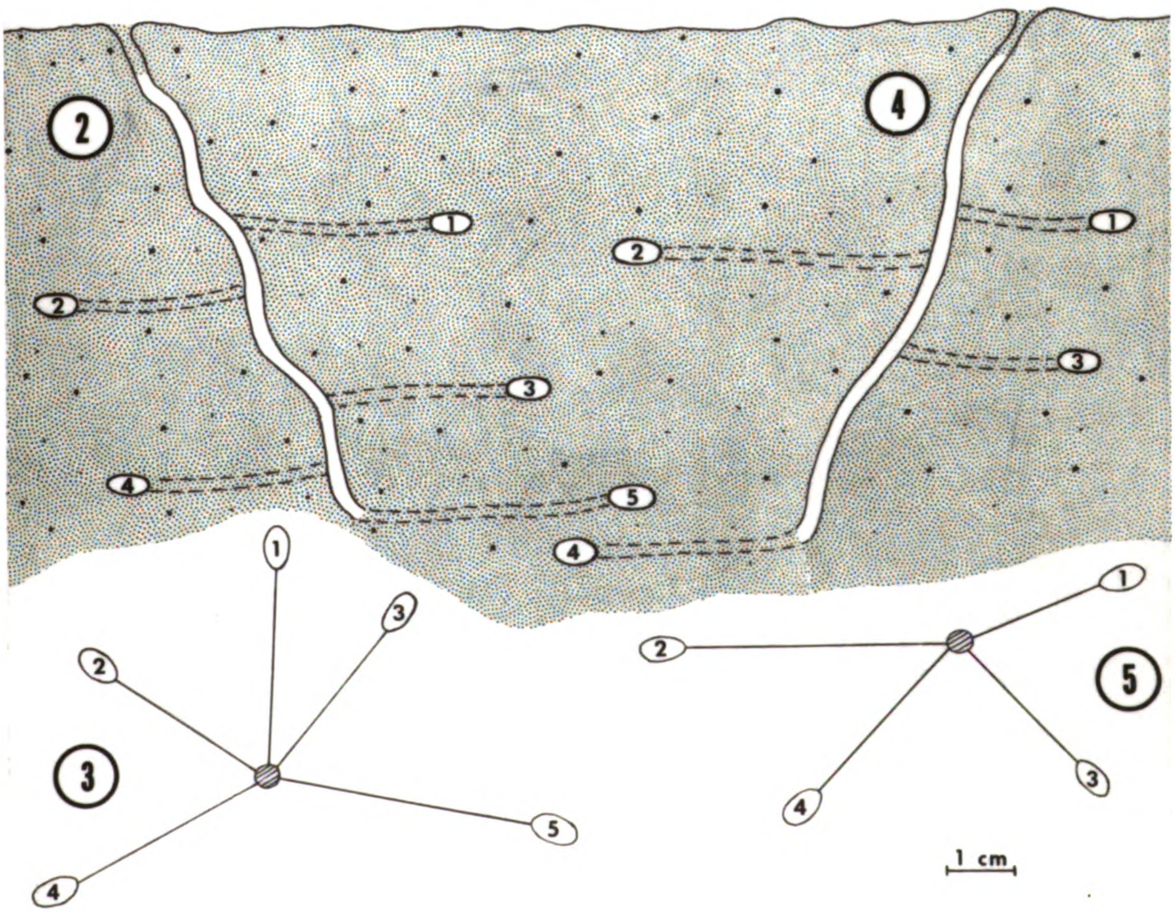
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Figure 6. _Oxybelus_ female uncovering burrow entrance after her return to the nest.

Figure 7. _Oxybelus_ female taking a fly into the burrow.

Figure 8. Sixty-hour-old larva of _Oxybelus_ feeding on a fly.

Figure 9. Ninety-six-hour-old larva of _Oxybelus_ after folds are visible feeding on a fly.

Figure 10. One hundred-twenty-hour-old larva of _Oxybelus_ feeding on a fly.


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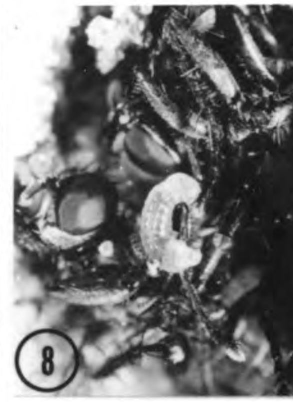
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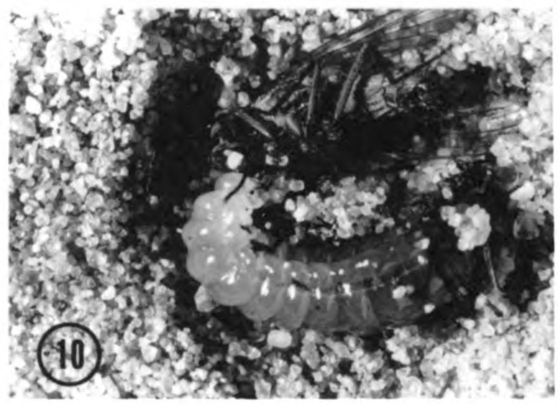
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Figure 11. Mature Larva cementing strands of silk to side of cell.

Figure 12. Beginning formation of the girdle.

Figure 13. Ibid. above.

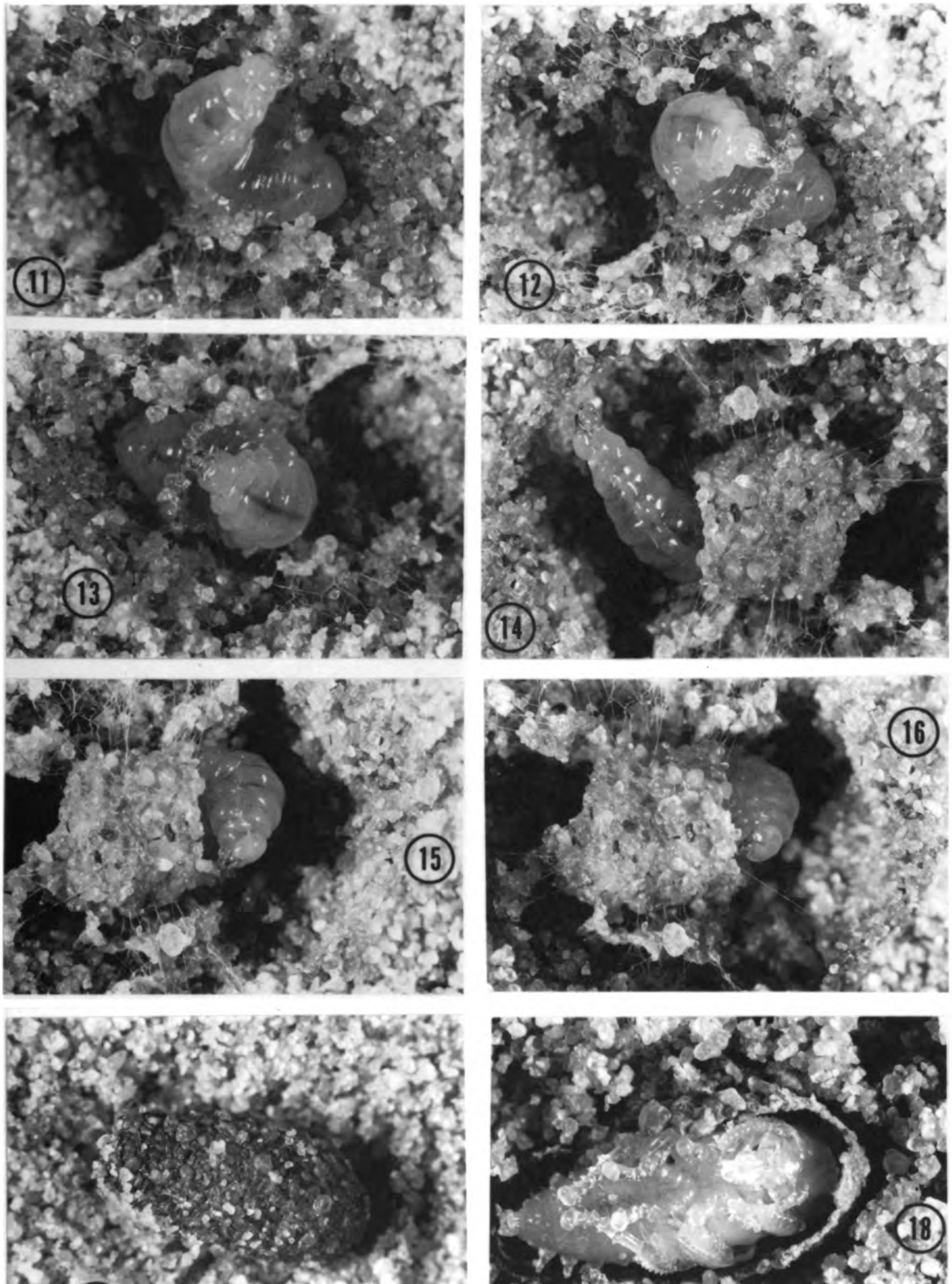
Figure 14. Girdle completed and mature larva stretching to attach another strand of silk to the sides of the cell.

Figure 15. Larva completing cocoon.

Figure 16. Ibid. above.

Figure 17. Completed cocoon.

Figure 18. Pupal cell cut open to show pupa.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