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Late embryogenesis and immature development of *Osmia rufa cornigera* (Rossi) (Hymenoptera : Megachilidae)

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Summary — The first instar larva of *Osmia rufa cornigera* (Rossi) remains within the egg chorion except for spiracular line splits that allow the exchange of atmospheric gas as this stadium consumes embryonic fluids. The second instar larva is the first stadium to consume pollen and nectar. The second through fifth instar larvae are aggressive when disturbed. Immature development and larval behavior are compared to other *Osmia* species.

***Osmia rufa cornigera* — embryogenesis — postembryonic development**

Introduction

Osmia rufa L. is a common, widespread, vernal species found throughout most of Europe and north Africa (Raw, 1972; Peters, 1978). Three subspecies are recognized (Peters, 1978). Raw (1972) has provided most of the information on the basic biology of *O. rufa rufa* from England. Free and Williams (1970) and Holm (1973) have investigated the potential of this species as a pollinator of commercial crops.

This paper concerns late embryogenesis and immature development of *O. rufa* and compares these features to other *Osmia* species (Torchio, 1989).

Materials and Methods

Adult *Osmia rufa cornigera* (Rossi) were obtained near Belgrade, Yugoslavia. Five females and six males were released in a UDSA greenhouse at Logan, Utah, USA, in August, 1988. The greenhouse contained blooming white sweet clover, *Melilotus alba* Desc.; *Phacelia tanacetifolia* Bentham; cornflower, *Centaurea cyanus* L.; Mexican torch flower, *Coreopsis atkinsonia* Douglas; *Tithonia rotundifolia* (Mill.)

Blake; and evening primrose, *Oenothera hookeri* T. and G., as food and a source of nest-provisioning material. Wood drilled with holes of various diameters (3 through 7 mm) and lengths (10 to 15 cm), and mud, resin, etc. were supplied for nest construction.

Completed nests were dissected and cell provisions with attached immatures were transferred into clay blocks (Torchio, 1984) for observation. These clay blocks were placed in (25 x 145 mm) Petri dishes, moisture was added daily, and they were maintained in the laboratory at 23 ± 1 °C. Eggs near eclosion and larvae near ecdysis were monitored continuously for developmental changes. One egg was also placed in paraffin oil (DuPraw, 1967; Torchio, 1984) and observed continuously during eclosion. The terminology and illustrations of DuPraw (1967) are used to describe embryogenesis.

Results

The five nesting females constructed nests during a five-week period. Twelve nests and 24 cells were recovered; one female produced five nests, three females produced two nests, and one female produced one nest. Eight progeny died during the egg stage. Thirteen progeny were preserved as prepupae and three were preserved as pupae.

Egg

A freshly deposited egg of *Osmia r. cornigera* is white with a smooth highly reflective surface. It is an elongate ovoid with a slightly narrowed anterior tip. Eight eggs averaged 3.3 ± 0.2 mm (SD) long and had an anterior lateral third that was narrower (0.94 ± 0.06 mm) than the middle (1.17 ± 0.06 mm) or posterior third (1.14 ± 0.06 mm). Mesal and posterior measurements are slightly larger (1.2 ± 0.05 mm) dorsoventrally than laterally. An egg is embedded on the upper, outer surface of the provision; approximately one-sixth of the posteroventral surface is in contact with the provision and the unattached anterior tip is slightly elevated above the provision surface.

Embryogenesis

The Stage 8 embryo, with an embryonic membrane (amnion = serosa of DuPraw, 1967) and unpaired labral protuberance appears 36-48 h after the egg is laid. At Stage 8, the embryo is 2.7 ± 0.3 mm long and occupies a slightly anterior position within the rigid egg chorion; it is surrounded by embryonic fluid that also fills both ends of the egg. The embryonic membrane is appressed to the chorion anteriorly, but it is visible between the developing embryo and the posterior of the chorion. Small crater-like depressions cover the entire surface of the embryonic membrane. Each of these depressions is approximately 25 µm in diameter and they are approximately 50 to 100 µm apart posteriorly but closer anteriorly. The labrum migrates to its ventral position during the next 24 h, followed by the development of mandibular, maxillary, labial lobes, body segmentation and the anus (Stage 9). During the next 24 hr (86—96 h since the egg was laid), the mandibles and maxillae are defined and the embryo initiates its first movement, weak clypeal contractions and lateral movements of the head capsule. The terminal abdominal segments also contract inwardly and are periodically extended dorsally. These movements increase in intensity and are maintained as the embryo slowly rotates 180° on its long axis during approximately 25 to 30 min (4

observations *in situ,* and 1 in paraffin oil). Contractions during rotation begin with abdominal movements that progress forward until the head capsule is pulled ventrally and to the left or right (both left and right rotations were observed). The head capsule is then moved dorsoventrally and laterally several times before another abdominal contraction is initiated.

After rotation, the embryo's dorsal surface faces the dorsal surface of the egg chorion as the head capsule and abdominal movements increase in both intensity and duration; head capsule and anterior body segments are raised dorsally and then pulled rapidly down while the terminal body is first contracted inwardly and then extended posteriorly to almost reach the embryonic membrane. Distinct clypeal contractions are also visible as embryonic fluid moves through the buccal cavity and the digestive tract slowly fills with embryonic fluid. The tracheal system becomes visible before filling with metabolic gas.

Initially, the embryonic membrane is not contacted or deformed by embryo movements. After approximately 15—25 min of head capsule and abdominal movements, the expanding embryo's terminal body segments contact the transverse posterior surface of the embryonic membrane. This contact distorts the membrane and produces wave-like wrinkles over its surface. As the embryo elongates, the head capsule contacts the embryonic membrane and the membrane is pulled from the chorion. Within the next 10—15 min the embryonic membrane ruptures anteriorly and pieces float free in embryonic fluid. Almost immediately upon rupture, the tracheal system fills with metabolic gas beginning with thoracic spiracles and proceeding posteriorly; the system appears silvery-white. The embryo continues strong concentrations until the embryonic membrane disintegrates; the embryo continues to consume embryonic fluid for the next 1.30 ± 0.30 h (n = 4, range 0.45—2.00 h) and expands posteriorly almost filling the posterior tip of the egg.

Eclosion—ecdysis

The egg chorion begins to split along the spiracular line in the area of the second or third thoracic spiracles 96—100 h after being laid. The chorion splits open to the fifth and then to the eight abdominal spiracles as the expanding ventrolateral tubercles of the embryo are forced through the developing split (in paraffin oil, the split chorion moves dorsally between the second thoracic and first abdominal spiracles, and the first instar head capsule is lifted dorsally by thoracic expansion until freed from the chorion 3.30 h after the initial split in the egg chorion). After the egg chorion splits open along both spiracular lines, the now first instar larva (mostly covered with the egg chorion) breathes air and consumes embryonic fluid. This feeding causes the chorion to collapse about the head capsule until deep wrinkles develop between the head capsule and first thoracic segment. The feeding first instar larva slowly raises and lowers its head capsule until its anteroventral surface contacts the surface of the provision. As the first instar continues to feed on embryonic fluid, the contents of the digestive tract become increasingly visible through the chorion and first instar integument as additional creamy-white material moves posteriorly into the system and the ventrolateral tubercles expand further out of the chorion splits.

Ecdysis from first to second instar occurs 21.45 ± 5.05 h (n = 10, range

8—29 h) after the egg chorion splits open. Approximately 30 min before ecdysis, the larva initiates a strong pumping motion of its body and its thoracic terga begin to swell. The first instar integument and egg chorion covering the thoracic terga stretch until the thoracic intersegmental lines are obscured. The strength of these body contractions increases steadily until the chorion—integument ruptures along the mid-dorsal line of the second or third thoracic segment (five observations) or directly at the base of the head capsule (one observation) during one forceful body contraction. As the thoracic segments of the larva continue to swell, the head capsule is forced downward until the mouthparts touch or nearly touch the second thoracic sternite. The expansion also causes the split chorion-first instar integument to expand anteriorly and posteriorly until the ballooned thorax of the second instar larva is free of any residue covering. During the sloughing of the exuvia, the spiracles and major tracheal trunks slide out of the second instar spiracles and are carried off with the exuvia. Two minutes after the initial split occurs, the head capsule of the second instar larva is pulled up and is freed from the chorion and exuvia of first instar head capsule. Examination of head capsule exuviae showed that the lining of the buccal cavity, salivary opening and anterior portion of the salivary duct are also sloughed off during molting.

The second instar head capsule is then extented forward and the chorion attached to the exuvia of the first instar integument slides posteroventrally under the second instar. The second instar larva then begins a series of forward extensions and posterior contractions of the body segments at 15 sec intervals over the next 10—15 min period during which time the ventrolateral tuberacles expand and the egg chorion-first instar exuvia is moved posteriorly and compressed against the provision ventrally.

The second instar larva contacts the provision and initiates feeding 15—20 min after the integument of the first instar larva splits open. The whitish contents of the digestive tract are clearly visible through the clear, smooth, highly reflective second instar integument at this time, and the ventrolateral tuberacles rapidly disappear. It is, therefore, the second instar larva that initiates feeding on cell provisions five days after the egg has been laid.

Examination of exuviae showed that the first instar head capsule was split down the mid-line to the base of the labrum ($n = 6$).

Larval development and ecdysis

Second instar larvae feed for 19.15 ± 6.30 h ($n = 8$, range 10—28 h) before molting to the third instar. Third instar larvae molt after 25.35 ± 3.50 h ($n = 9$, range 18—30 h), and fourth instar larvae molt after 45.35 ± 4.55 h ($n = 9$, range 36—49 h). Second through fourth instar larvae remain attached posteroventrally to the provisions, and they feed in an ever-expanding arc. Fifth instar larvae feed for 19.50 ± 7.35 h ($n = 8$, range 9—30 h) prior to first defecation. Feeding and defecation continue for another 5.5 ± 2.3 days ($n = 4$, range 2—7 days) until cocoon formation is initiated.

The first fecal pellets are amorphous brownish black globs but subsequent particles are elongate, orange-red to red-brown cylinders ranging from 0.25—0.30 mm in diameter and 0.75—1.30 mm in length. Both ends of each fecal pellet are tapered and there are no surface grooves or ridges. The first pellets are deposited anteriorly in the cell, where

most of the fecal material accumulates. As the larva finishes consuming the provision it rotates in the cell and the remaining fecal pellets are deposited in the posterior section of the cell.

Second through fifth instar larvae are very aggressive when touched and they turn toward and bite repeatedly at objects touching them. When a fifth instar *Megachile rotundata* F. larva was placed in the cell of a recently molted fifth instar *O. r. cornigera* it was bitten repeatedly for almost 2 min. Twenty-four h later the *M. rotundata* larva (twice the size of the *O. r. cornigera* individual) had been killed.

Third to fifth larval ecdysis

Larval movements during third to fifth instar molts are similar to those observed in the first to second instar molt. However, strong dorsoventral movements of the head and dorsal body are lacking. These larval stadia feed almost continuously between molts. Feeding is, however, interrupted 1—2 h before ecdysis when the thoracic segments are periodically arched upward for 3—5 sec. This arching is followed by several upper body contractions before the larva resumes feeding. At ecdysis, the integument splits along the mid-dorsal line from the back of the head capsule to the second or third thoracic segment as the thorax is arched upward and carried forward. The split continues forward across the head capsule to the labrum and posteriorly to the fourth or fifth abdominal segment. The head capsule moves to a slightly ventral position as the thorax is expanded and this allows the exuvia to slide posteroventrally from the head capsule and first thoracic segment. At this juncture, monthparts are still encased in the old integument. They are slowly freed as the lining of the foregut and salivarium are pulled forward and then posteroventrally in 30—45 sec as the head capsule exuvia continues to slide posteroventrally. The remaining exuvia now slides rapidly off as the larva initiates dorsoventral undulations over a 5—10-min period.

Cocoon

The larva secretes salivary material from between the salivary lips forming a loose narrow network of single, whitish threads about the anterior end of the cell securing the accumulating fecal material. The larva lays down additional silk strands securing the fecal material as it accumulates in other parts of the cell. When feeding is completed, the larva spins an outer meshwork of silk threads over the entire surface of the cell. This meshwork is attached to and supported from the initial threads anchoring the fecal material. Most of the meshwork is loosely constructed. However, the anterior end consists of a narrower domed collar with a central, more steeply domed nipple area. The domed collar and central nipple area are composed of strands of silk laid down in a circular direction, thus giving the anterior tip of the cocoon greater definition. At this point the larva coats the inside of the meshwork with a translucent sheet of salivary material. This is accomplished by long sweeping movements with the salivary lips pressed against the meshwork. The initial sheeting material is soft and flexible and the larva continues to deposit this layer for approximately 24 h. The nipple area and anterior collar area are coated with a dense layer while the side wall layer is thinner. The larva now voids the remaining contents of the digestive tract in the form of 6—8 longitudinal smears

that begin at the base of the nipple and run two-thirds the length of the inner cocoon lining. This material plus additional sheeting allows the cocoon to harden somewhat as it turns dark red-brown. Cocoon formation requires an average of 5.0 ± 1.0 days (n = 4, range 4—6 days). The time from egg to post-cocoon spinning larva is approximately 20 days.

Discussion and Conclusion

Late embryogenesis and larval development described here for *Osmia rufa cornigera* are almost identical to those of *Osmia lignaria propinqua* Cresson (Torchio, 1989). Developmental times, under the same rearing conditions, are also similar. Thus, two species in the same subgenus (*Osmia*) show obligate second instar eclosion before pollen—nectar provisions are consumed. Malyshev (1935) and Maeta (1978) reported four larval instars in *Osmia* species. Malyshev (1935) found four larval instars by powdering *Osmia rufa* larvae with pollen between molts and Maeta (1978) confirmed the final four by continuous measurements of the width of head capsules in *Osmia* (*Osmia*) *cornifrons* (Radoszkowski). Their techniques did not demonstrate the first instar molt inside the split egg chorion.

There are two notable differences in larval development of *Osmia rufa cornigera* and *O. lignaria propinqua*. First, the second through fifth instar of *O. r. cornigera* are aggressive and respond to disturbances but *O. l. propinqua* larvae are passive to physical stimuli (Torchio, 1989). Aggressive larval behavior is characteristic of cleptoparasitic Apocrita larvae during periods when they destroy host immatures (Torchio, 1972; Rust and Thorp, 1972; Torchio, 1986; Torchio and Trostle, 1986) but it is an uncharacteristic feature of host species. Why then is *O. rufa* aggressive ? Perhaps this behavior serves as a defense against parasites and nest predators. This possibility should be considered when nest associates of *O. r. cornigera* are compared to those in nests of *O. r. rufa* reported by Raw (1972) (larvae of *O. r. rufa* are not aggressive) (Torchio, unpublished data).

The second difference involves cocoon construction. In *Osmia rufa*, the anterior collar and nipple area are spun during the formation of the outer meshwork of the cocoon; *Osmia lignaria propinqua* forms the nipple after the outer cocoon layer is spun by stretching the meshwork by elongation of its body aided by peristalsis (Torchio, 1989). As a result, the head capsule of the *O. l. propinqua* larva acts as a hydraulic press until sufficient pressure is exerted on the meshwork to stretch it outward into its nipple form. Torchio (1989) found that *Osmia cornuta* Latr. larvae form cocoon nipples by spinning this structure as an integral section of the outer meshwork. Thus, two species in the subgenus *Osmia* (*O. cornuta* and *O. rufa*) spin their cocoon nipples while a third species (*O. l. propinqua*) in the same subgenus (*Osmia*) shapes its cocoon nipple by expansion of the outer layer.

Torchio (1989) lists 28 larval behavioral and nesting characteristics observed in three species of *Osmia*. To these, we can add the aggressive larval behavior and cocoon-nipple structural differences observed in *O. rufa cornigera*. Biosystematically, these two taxa *(O. rufa and O. lignaria*) are similar in most respects but they differ in two specific characteristics.

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Résumé — Embryogenèse tardive et développement postembryonnaire chez *Osmia rufa cornigera* (Hym., Megachilidae). Les œufs récemment pondus d'*Osmia rufa cornigera* sont blanchâtres, avec une surface fortement réfléchissante. Leur taille moyenne est de 3,3 mm de long sur 1,1 mm de large et ils sont posés sur la partie supérieure externe des provisions.

Le stade 8 de l'embryon (DuPraw, 1967), avec sa protubérance labrale unique, apparaît 36 à 48 h après la ponte de l'œuf (To). Le stade 9 se développe durant les 24 h suivantes et l'embryon commence à bouger (stade 10) 48 h plus tard, soit 86 à 96 h après To. A ce moment-là, l'embryon tourne lentement de 180° autour de son axe longitudinal. Au bout d'une heure de rotation, la membrane embryonnaire se déchire et le système trachéal se remplit de gaz métabolique. L'embryon consomme le liquide embryonnaire.

Le chorion de l'œuf commence à se fendre, le long de la ligne stigmatique, dans la région des stigmates thoraciques, 96 à 100 h après To. Les tubercules ventrolatéraux de l'embryon se dilatent et sont poussés dans les fentes du chorion, et la larve de premier stade respire l'air atmosphérique. La capsule céphalique de la larve de 1er stade est encore enveloppée dans le chorion de l'œuf et la larve continue à consommer le liquide embryonnaire. Environ 24 h après la déchirure du chorion, a lieu la mue du 1er au 2e stade, le tégument du 1er stade se déchirant le long de la ligne médiane dorsale près de la capsule céphalique. La larve de second stade est la première à s'alimenter sur les provisions.

Les mues des 3e au 5e stade sont semblables à celle observée entre le 1er et le 2e stade, sauf pour une déchirure antérieure du tégument, depuis le derrière de la capsule céphalique, jusqu'au sommet du labre. Les larves du 2e au 5e stade sont agressives, se tournent vers l'objet qui les touche et le mordent. Elles sont capables de tuer des larves plus grosses.

Le cocon est formé de salive. Un premier réseau lâche de fils simples et blanchâtres est tissé près de l'extrêmité antérieure de la cellule. Ces fils maintiennent le matériel fécal contre les parois du mur. Lorsque l'alimentation est terminée, la larve tisse un filet externe de fils de soie sur toute la surface de la cellule avec un mamelon central sur la partie antérieure. La larve enduit l'intérieur du filet d'une garniture transparente faite de salive. Le développement de l'œuf à la larve qui tisse le cocon demande environ 20 jours.

Le développement larvaire d'*Osmia rufa cornigera* diffère de celui d'*O. lignaria* propinqua en 2 points : 1) l'agressivité des larves du 2e au 5e stade et 2) le mamelon antérieur tissé du cocon.

***Osmia rufa cornigera* — embryogenèse — développement postembryonnaire**

Zusammenfassung — Späte Embryogenese und Larvenentwicklung von *Osmia rufa cornigera* (Rossi) (Hymenoptera, Megachilidae). Frisch gelegte Eier von *Osmia rufa cornigera* sind weißlich und mit einer glänzenden Oberfläche versehen. Im Durchschnitt messen sie 3,3 mm in der Länge und 1,1 mm in der Breite; sie sind in der oberen und äußeren Oberfläche der Nahrungsvorräte eingebettet.

Der Embryo von Stadium 8 (DuPraw, 1967) mit unpaaren Labralvorwölbungen erscheint 36—48 h nach Ablage des Eies. Der Embryo des Statiums 9 entwickelt sich während der nächsten 24 h und weitere 48 h später, d. h. 86—98 h nach Ablage des Eies, zeigen sich die ersten Bewegungen (Stadium 10). Zu diesem Zeitpunkt dreht sich der Embryo langsam 180° um seine Längsachse. Innerhalb von einer Stunde der embryonalen Rotation zerreißt die Embryonal-Membran und das Trachealsystem füllt sich mit Gas aus dem Stoffwechsel. Der Embryo beginnt, Embryonalflüssigkeit aufzunehmen.

Das Eichorion beginnt sich 96—100 h nach Ablage des Eies entlang der Spirakularlinie in der Höhe der thorakalen Spirakeln zu spalten. Sich ventrolateral ausdehnende Vorwölbungen des Embryos zwängen sich durch die wachsende Spalte im Chorion, und die so entstandene Larve des 1. Stadiums beginnt atmosphärisches Gas zu atmen. Die Kopfkapsel der Larve des 1. Stadiums steckt aber noch immer im Eichorion und die Larve nimmt weiter Embryoflüssigkeit auf. Ungefähr 24 h nach der Spaltung des Eichorions häutet sich die Larve des 1. Statiums zum 2. Stadium indem die Haut von Eichorion + 1. Larvenstadium entlang der mittleren Dorsallinie in Nähe der Kopfkapsel aufplatzt. Diese Larve des 2. Stadiums beginnt jetzt erstmals mit der Aufnahme von Nahrung aus den Vorräten.

Die Häutungen des 3.—5. Stadiums laufen ähnlich ab wie die eben beschriebenen des 1. und 2. Stadiums, abgesehen davon, daß eine vordere Spalte im Integument auftritt, die von der Rückseite der Kopfkapsel bis zum Labrum reicht.

Larven des 2.—5. Stadiums verhalten sich aggressiv : Sie wenden sich zu Objekten und beissen sie wiederholt, wenn sie berührt werden. Sie sind imstande, größere Larven zu töten.

Der Kokon wird aus abgesondertem Speichel gebildet. Zuerst entsteht um das vordere Ende der Zelle ein loses Netz aus weißlichen Einzelfäden. Diese Fäden befestigen die Exkremente an der Zellwand. Sobald die Nahrungsaufnahme abgeschlossen ist, spinnt die Larve ein Außennetz von Seidenfäden über die gesamte Zelloberfläche, mit einem zentral gelegenen Nippel vorne. Dann kleidet die Larve die Innenseite des Kokons mit einer durchscheinenden Lage von Speichel aus.

Die Entwicklungsdauer vom Ei bis zur Larve nach Fertigstellung des Kokons beträgt etwa 20 Tage.

Die Larvenentwicklung von *Osmia rufa cornicera* unterscheidet sich in zweifacher Hinsicht von der Entwicklung von *Osmia lignaria propinqua* : 1) Die Aggressivität der Larve im 2.—5. Stadium, und 2) Dem gesponnenen Nippel am Vorderende des Kokons.

***Osmia rufa cornigera* — Embryogenese — Larvenentwicklung**

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