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Reproductive Behaviour and Parental Care of the Leech *Helobdella triserialis* (Hirudinea: Glossiphoniidae)

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Abstract

The reproductive biology of the leech *Helobdella triserialis* E. Blanchard 1849 was investigated in animals kept in aquaria. After mutual exchange of pseudospermatophores the leeches produce cocoons. Five to 8 cocoons, each containing 2–20 eggs, are attached to the belly of the parent and carried around. On encountering a water snail (which would eat unprotected cocoons rapidly) the parent protects the cocoons by covering them with its body (forming a temporary brood chamber). Larvae and young are both carried around attached to the belly of the leech. The parent attacks water snails (*Physa gyrina, Tropicorbis navanensis*) by inserting its proboscis into the soft parts of the snail and sucking the body fluid of the prey. The attached juvenile leeches participate in the meal by sucking on those parts of the snail that were pierced by the proboscis of the parent. Because of this provision of food the young grow from 1 to about 6 mm in length (i.e. about 30-fold in volume) while being carried and fed by the parent They develop the typical pigmentation of the adult and leave the parent at an advanced stage of development to lead an independent life.

Introduction

Parental care among aquatic invertebrates evolved at least in part in response to egg predation (Diesel 1989). Within the Clitellata, parental care is known only in the family Glossiphoniidae, indicating that this behaviour probably arose *de novo* in that group of leeches (Sawyer 1971). Like all leeches, the glossiphoniids are protandrous hermaphrodites. Insemination is achieved by mutual exchange of pseudospermatophores, which are attached to the body surface of conspecifics. After deposition of the pseudospermatophore, the body surface of the recipient undergoes a conspicuous histolysis and the spermatozoa are released into the body of the partner (Brandes 1901, Myers 1935).

The leeches produce thin-walled cocoons containing large eggs that are rich in yolk. The parent places its body over the cocoons and protects the eggs, larvae and young from predatory attacks (Kutschera 1984, Sawyer 1986). Leeches of the genus *Helobdella* attach their cocoons to the ventral surface of their body and pro-

vide food for the developing young (KUTSCHERA and WIRTZ 1986a, b, KUTSCHERA 1989). As yet, this high degree of parental investment has only been observed in three *Helobdella* species. However, the genus *Helobdella*, which has its center of distribution in South America, comprises more than 25 species and many subspecies (KUTSCHERA 1988, SAWYER 1972, 1986).

Helobdella triserialis is widely distributed in North- and South America. The leeches feed almost exclusively on water snails (SAWYER 1972, 1986). Although the development of the embryo of *H. triserialis* has been analyzed in detail (e.g., WEISBLAT et al. 1980, SAWYER 1986), little is known about reproduction in this species. The reproductive biology of *H. triserialis* is described with special attention given to the parental care.

Materials and Techniques

Observations and experiments were carried out between October 1985 and September 1987. *Helobdella triserialis* E. Blanchard 1849 (syn. *H. lineata* Verrill 1874, see SAWYER 1986) (adult size 15–27 mm) were collected from the underside of rocks and leaves in a small, slow running creek which contained many pondweeds (*Potamogeton* sp.) in Stanford, California. The leeches were kept at room temperature (18–23 °C) in small aquaria (18×13×12 cm) or petri dishes (∅ 5,5 cm, depth of water 4–5 mm) which contained a few plants from their native habitat. They were fed on watersnails (*Physa gyrina*, *Tropicorbis havanensis*), which were very common in their habitat.

Results

Copulation, Cocoon production

The mutual transfer of pseudospermatophores occurred after a short embrace of the partners with the anterior parts of their bodies. The pseudospermatophores (about 1 mm long) were attached preferentially to the region around the gonopores and disappeared 1–2 days after implantation. Leeches carrying 2–3 spermatophores were frequently observed, indicating that copulation may be repeated several times with different partners. Attachment of pseudospermatophores also occurred during the period of carrying cocoons, larvae and young.

Three to 6 days after insemination the leeches produced cocoons. Leeches that are about to lay cocoons could easily be identified by their enlarged white ovaries containing the mature eggs. The cocoons are poduced inside the body by clitellar glands surrounding the female gonopore (NAGAO 1958). They are enclosed by a thin, transparent membrane containing the pink eggs (WEISBLAT et al. 1980). Five to 8 ball-shaped cocoons (diameter 1,5–2 mm) containing 2–20 eggs (Fig. 1a, b) were produced and attached to the posterior ventral surface of the parent as described for other *Helobdella* species (KUTSCHERA and WIRTZ 1986a, KUTSCHERA 1989). The cocoons are completely protected by the body of the parent while being produced and attached to the ventral side of the leech (Fig. 2a).

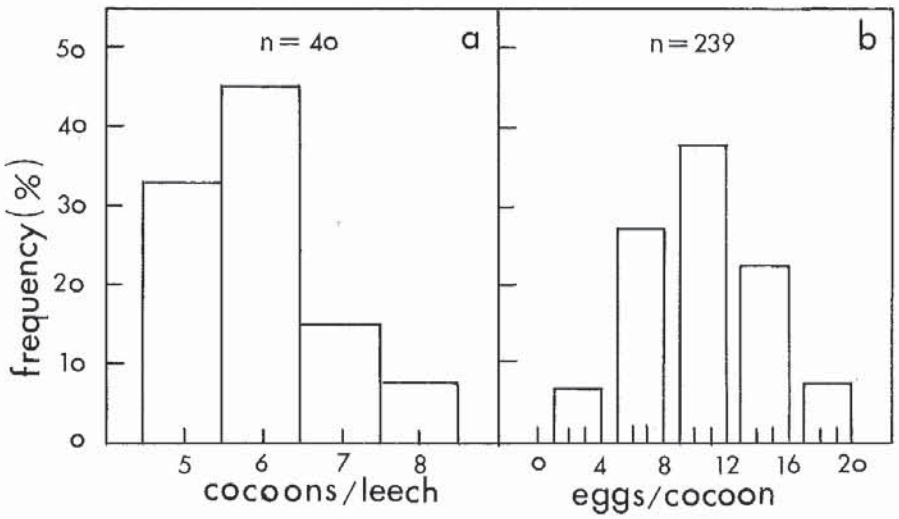

Fig. 1. Frequency distribution of cocoons per leech (a) and eggs per cocoon (b)

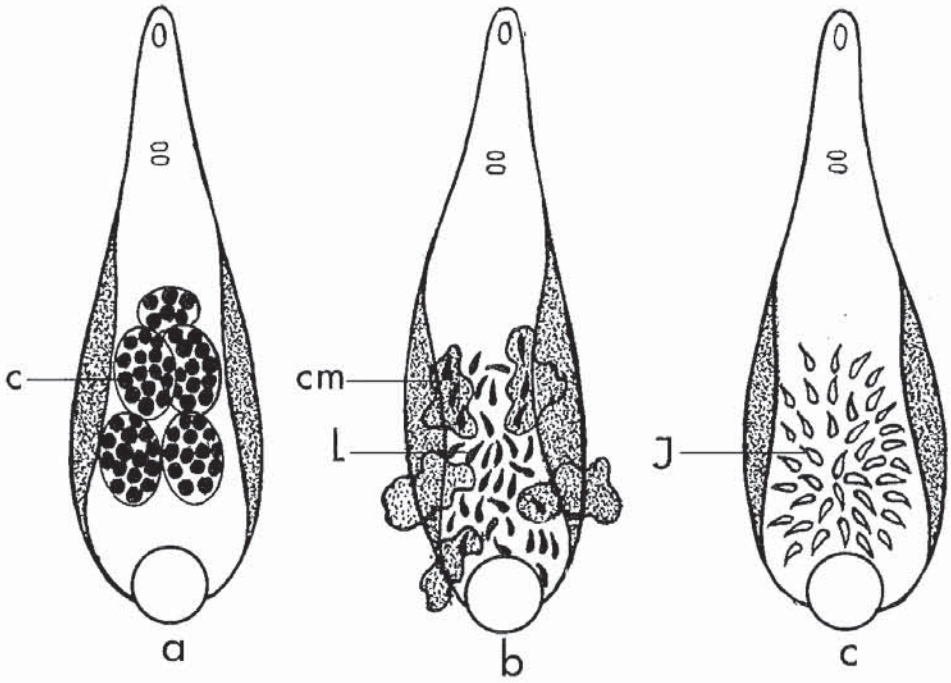

Fig. 2. Ventral views of *Helobdella triserialis* carrying 5 cocoons attached to the parent (a); after hatching of the larvae and degeneration of the cocoon membranes (b), and with juvenile leeches attached to the ventral surface of the parent with their posterior suckers (c). c = cocoons; cm = cocoon membrane; J = juvenile leeches; L = larvae

Parental care

After the last cocoon has been attached to the ventral surface of the parent the leech started to move around, fanning the cocoons with fresh water by ventilatory movements of its body. The cocoons can be completely surrounded by the body flanks forming a temporary brood pouch (SAWYER 1986). By this means the cocoons

were protected from predatory attacks (Fig. 3). Isolated cocoons were rapidly eaten by water snails (*Physa gyrina*, *Tropicorbis havanensis*), which are probably their main predator.

Five to 6 days after egg-laying the larvae hatched and attached themselves to the ventral side of the parent within the transparent, thin cocoon membrane. During the process of hatching the parent fanned fresh water over the enclosed larvae by rhytmic, contracting movements of its body flanks. The larvae are attached to the belly of the parent by an anterior embryonic attachment organ (NAGAO 1958). Two to 3 days later the transparent cocoon membrane degenerated and developed a dark-brown colour (Fig. 2b). Within the following 3 days the larvae used up their yolk supply and developed into juvenile leeches. The transparent young are attached to the belly of the parent with their posterior suckers (Fig. 2c). They were carried around by the parent for a further 4 to 5 weeks.

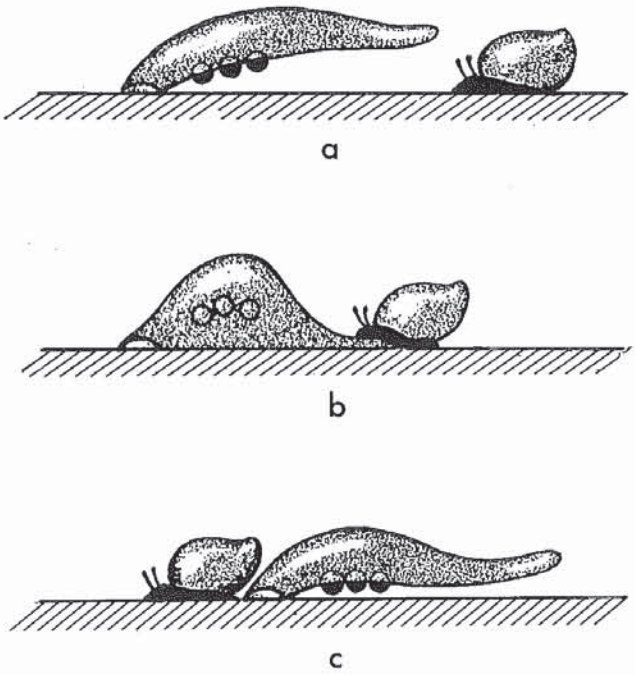

Fig. 3. The temporary brood chamber of *Helobdella triserialis*. A leech carrying cocoons on its belly encounters a water snail (a); at the moment of contact between leech and snail the parent encloses the cocoons by pressing its body flanks firmly on the substrate (temporary brood pouch) (b) until the snail leaves the brooding leech (c)

During the period of carrying cocoons, larvae, and young the parent continued to feed on water snails. No significant difference between the foraging and feeding behaviour of brooding versus non-brooding leeches was observed, i.e., the mobility of the leech does not seem to be impaired by the brood attached to its belly.

The young participated in the meal of the parent. The parental leech captured a snail by attaching its oral sucker to the shell of the prey (Fig. 4a, b). The snail tried to escape from the predator by vigorous movements of its body ("avoiding behaviour", see SAWYER 1986). In some cases the snail suceeded to escape from the

leech. The parent pushed the snail to the anterior part of its body by bending its anterior ventrally, and inserted its proboscis (Fig. 4b, c). It immediately began to suck off the blood from the snail, which stopped attempting to escape. The young creeped to the prey and sucked blood from those parts of the snail that were wounded by the proboscis of the parent (Fig. 4c, 5a). When the crop caeca of the parent were filled with blood the leech withdrew its proboscis and the young continued to suck blood from what is left of the snail (Fig. 4d) until the shell was empty. During this last phase the parent fans with undulatory movements of its body. The whole feeding process (Fig. 4a–d) lasts 1–2 hours.

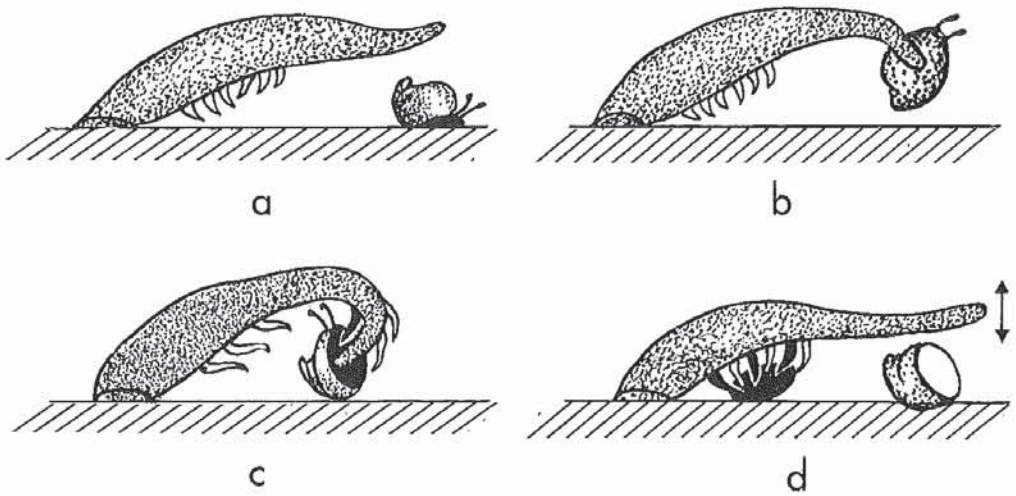

Fig. 4. Prey catching and feeding behaviour of *Helobdella triserialis*. A leech carrying young encounters a water snail (a) and attaches its oral sucker to the shell of the snail (b). The leech inserts its proboscis and starts to suck the soft parts of the snail; the juvenile leeches participate by feeding on the wounded regions of the prey (c). The young suck on the remaining soft parts of the snail, while the parent makes ventilatory movements with its body (arrow). The empty shell is left behind (d)

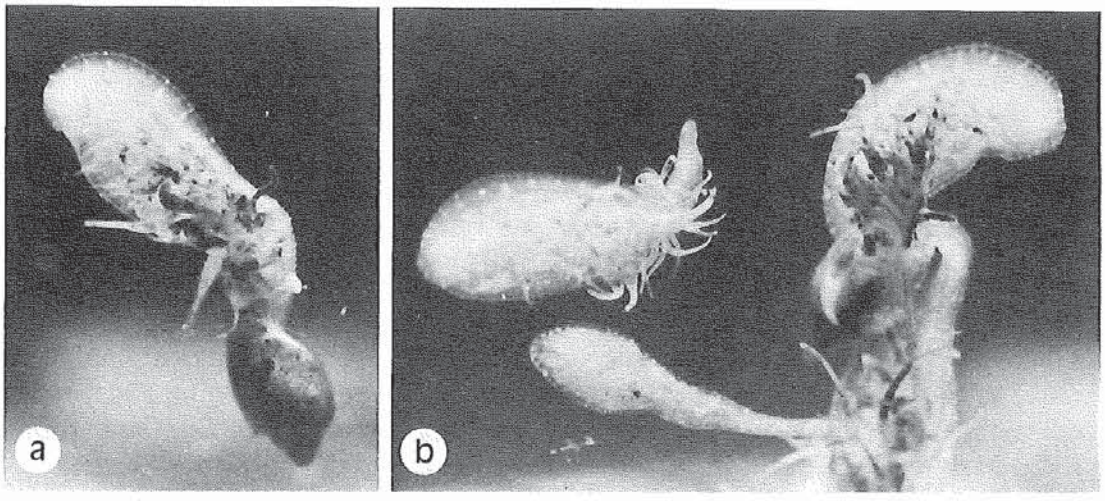

Fig. 5. Communal feeding of *Helobdella triserialis*. A leech carrying young in the process of feeding on a snail (*Physa gyrina*) (a). Three other leeches in the vicinity are attracted and a second leech carrying young feeds simultaneously on the same snail (b). Note the dark colour of the crop caeca of the young as a result of feeding.

During the period of feeding the leech is often joined by several other leeches (communal feeding, Fig. 5 a, b). Within the next 2 – 3 days the parent and the young digest the blood. I have observed about 10 times that a parent captured a snail and pushed it to its young, without sucking blood itself. However, in most cases observed, both the parent and the young took up blood simultaneously, as shown in Figs. 4 and 5. Due to this provision of food the young grow from 1 to 6 mm in length (i.e. about 30-fold in volume) within 4 – 5 weeks (Fig. 6 a – c). The young leave the parent when they have reached about 30% its size when they have developed their final pigmentation (Fig. 6 c). They feed on small water snails (*Physa gyrina*) as described for adult leeches (Figs. 4, 5).

Survival of young isolated from the parent

In order to determine whether the young are able to suck blood from snails when their parent is absent 20 young leeches (about 1 mm long, Fig. 6 a) were isolated from their parent and offered water snails (*Physa gyrina*). In spite of the fact that the young were able to live independently from their parent for up to 3 weeks, they never sucked blood and died in the presence of the water snails. This experiment was repeated three times with the same result.

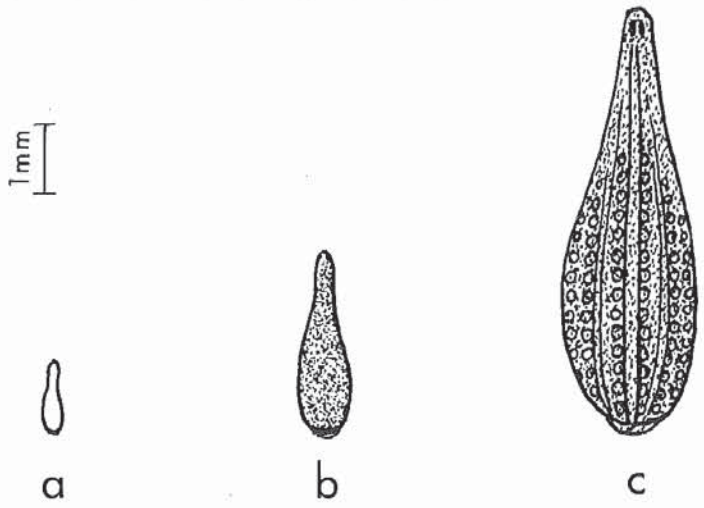

Fig. 6. Development of the young while being cared for by the parent. A transparent juvenile leech after hatching from the larva (a); after 2 (b) and 4 (c) weeks with the parent

Young leeches with their juvenile proboscis are apparently unable to pierce the intact skin of a water snail. When snails that had been crushed between forceps were given to the young the leeches were able to suck blood from the wounded regions. This is in agreement with the observation that the attached young only suck blood from those regions of the snail that were pierced by the sturdy proboscis of the parent (Fig. 4 c).

Discussion

WILSON (1971, 1975) postulated that parental care may evolve when (a) animals exploit unusually harsh environments; (b) competition for scarce, specialized food resources is high; or (c) early life-stages are endangered by predators or parasites. The question of why brooding evolved only in glossiphoniid leeches, but not in other Clitellata, has long been a matter of debate (MILNE and CALOW 1990). In accordance with hypothesis (c) SAWYER (1971) suggested that predation pressure from water snails was probably the most important factor in the evolution of parental care in leeches.

Recent investigations on several glossiphoniids support this hypothesis. The "snail leech" *Glossiphonia complanata* attaches its egg capsules to the substrate, covers them with its body and defends its cocoons actively against water snails (KUTSCHERA 1984). However, the egg protection provided by *G. complanata* is not perfect: sometimes one or even all cocoons are eaten by water snails (KUTSCHERA 1984). Leeches of the genus *Helobdella* attach their cocoons directly to their belly and carry them around (SAWYER 1986, KUTSCHERA and WIRTZ 1986a, b, KUTSCHERA 1989). If the brooding parent encounters a water snail (which eats unprotected cocoons rapidly) it inflects the body flanks ventrally as the body arches in such a way that the cocoons are completely covered by the parent. This temporary brood chamber (SAWYER 1971) is only maintained as long as a snail (or another potential egg predator) is present (Fig. 3). This mode of egg protection is very efficient: I have never observed that a water snail succeeded in feeding on cocoons. This does, however, frequently occur in breeding *G. complanata.*

SAWYER (1971) suggested that the permanent brood pouch, which evolved independently in two species, *Marsupiobdella africana* in South Africa and *Maiabdella batracophilia* in South America, may be regarded as a modification of the temporary brood pouch of *Helobdella.* However, a detailed investigation of the development and anatomy of the brood pouch of *M. africana* revealed that the marsupium has not only a protective function. It may enable the leech to locate a potential host (toads of the genus *Xenopus*) before the young have left the parent. At the moment of contact with the toad the young are discharged explosively (VAN DER LANDE and TINSLEY 1976). Thus, in *M. africana* the parent not only protects its offspring but in addition provides the first meal for the young.

In *H. triserialis* and other related species a similar advanced parental care behaviour has evolved (KUTSCHERA and WIRTZ 1986a). Moreover, the results presented here show that juvenile *H. triserialis* can only grow normally when their parent allows them to participate in its meal (Figs. 4, 5). Thus, provision of food by the parent is not only a secondary benefit of parental care (MILNE and CALOW 1990), but an imperative requirement for the survival of the juvenile leeches.

Zusammenfassung

Die Fortpflanzungsbiologie und Brutpflege des Egels *Helobdella triserialis* E. Blanchard 1849 wurde untersucht. Nach Kopulation durch Austausch von Pseudospermatophoren produzieren die Egel 5–8 Eikokons, welche am Bauch befestigt umher getragen und vom Muttertier aktiv vor

Wasserschnecken geschützt werden. Larven und Jungtiere werden ebenfalls am Muttertier befestigt getragen. Der Egel fängt Wasserschnecken (*Physa gyrina*, *Tropicorbis havanensis*) und saugt diese aus. Die Jungen saugen an den Beutetieren des Mutteregels mit und wachsen daher innerhalb von 4–5 Wochen um das 30fache des Körpervolumens, bevor sie das Muttertier verlassen.

Acknowledgement

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