The life-cycle and feeding of the African freshwater leech *Helobdella conifera* (Glossiphoniidae)

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The life-cycle, breeding and feeding of the freshwater leech *Helobdella conifera* were examined in the laboratory. The life-cycle is annual with the young brooded by the parent for the first two months after hatching. Sexual maturity is attained two months after leaving the parent when the first batch of eggs are produced and the young brooded. The number of broods ranges from one to four with the majority producing three. A few young leeches fed on the snail *Helisoma duryi* while still attached to the parent but the majority did not feed until 11 days after leaving the parent with 12–23 small (4.0–7.0 mm) snails consumed before producing their first batch of eggs. The life time consumption of small snails ranged from 26–60 with no correlation between the numbers of snails consumed and the numbers of broods or the numbers of progeny. Leeches only fed on small, live *H. duryi* and did not feed on large (10.0–13.0 mm) individuals although they fed as scavengers on dead large snails. A strong preference was exhibited by *H. conifera* for small *H. duryi* compared to small *P. acuta* with the most of the feeding occurring in the dark.

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First described from Uganda, *Helobdella conifera* (Moore, 1933) has been recorded throughout Africa (Sciacchitano 1963; Soos 1969; Oosthuizen & Curtis 1990; Wilken & Appleton 1991) including Egypt (El-Shimy 1987, 1990; El-Shimy & Hamada 1990; El-Shimy & Obuid-Allah 1992) and also Israel (Bromley 1994).

Like many members of the Glossiphoniidae, *H. conifera* has been reported feeding on gastropod snails (El-Shimy 1987; El-Shimy & Hamada 1990; Wilken & Appleton 1991) although Oosthuizen & Curtis (1990) also recorded aquatic insect larvae and other aquatic invertebrates as prey. Predation on gastropods by glossiphoniid leeches is well documented (reviewed in Klemm 1975); (Brönmark 1992; Moser & Willis 1994; Young, Martin & Seaby 1993; Young, Seaby & Martin 1995) but only a few species, for example, *Helobdella triserialis* (Ringuelet) and *H. robusta* (Shankland, Bissen & Weisblat 1991), feed exclusively on gastropods or molluscs (Goncalves & Pellegrino 1967, Shankland *et al.* 1991).

Little is known about the life cycle of *H. conifera* except that brooding of young was observed in August (Bromley 1994) in Israel and in February, March, May, June and October (El-Shimy 1987) in Egypt. In this study the life cycle and feeding biology of *H. conifera* are examined in the laboratory. Specifically the duration of the life cycle, the number of eggs and young produced, and the timing and duration of brooding were determined. Concurrently the number of prey (gastropods) consumed were determined and in a series of laboratory experiments prey species and size preferences examined.

Methods

Adult *Helobdella conifera* were collected from small ponds near Pretoria, Gauteng Province, Republic of South Africa and maintained in the laboratory in dechlorinated Pretoria tap water (pH 7.6–7.7) at 19–22°C with a 12:12 h light:dark regime and *ad libitum* prey (*Helisoma duryi*, shell height (diameter) 4.0–7.0 mm). Only eggs or young released by these leeches were used in the life history and feeding experiments. All experiments were conducted in glass pots (110 mm diameter, 60 mm deep) containing 375 ml dechlorinated Pretoria tap water replaced every five days.

Leeches hatched from eggs in the laboratory and the progeny which left the parent on the same day were provided with *ad libitum H. duryi* every five days and observed throughout their life cycle. The time from hatching of an egg to sexual maturity, to the production of the first batch of eggs and the intervals between successive batches of eggs until death were determined, together with the number of progeny per brood and life time total number of progeny produced. The numbers of snails consumed by individuals were also recorded.

Leeches ($n = 16$) with empty crops which left the parent on the same day were maintained for three days with 40 small *H. duryi* (shell height 4.0–7.0 mm) and allowed to feed. To determine if *H. conifera* could feed on both small and large *H. duryi*, one group ($n = 8$) was provided with *ad libitum* small snails and the second group ($n = 8$) with *ad libitum* large (shell height 10.0–13.0 mm) snails. The leeches were observed daily for 60 days (snails replaced daily) and the numbers feeding and producing eggs recorded. Six leeches which survived 60 days without feeding (although provided with large snails) were individually provided with one fresh, dead, large *H. duryi* to see if they could feed as scavengers.

Thirty individuals, all leaving the parent *H. conifera* on the same day, were maintained for 10 days with 50 small *H. duryi* before being divided into three equal groups. The first group was individually maintained with 10 small snails replaced daily for 30 days with a small stone as a shelter; the second group was individually provided with 10 small snails replaced daily for three days without a shelter; and the third group was individually provided with 10 small snails for 14 h every five days for 30 days. For each individual leech the number of snails consumed was recorded together with the time to the production of eggs and brood size. Response variables were analysed using one-way ANOVA followed by Tukey's pair-wise comparison of means.

To determine if predation occurred differentially in the dark, 18 individuals from the brood of one parent were individually maintained with 10 small *H. duryi* on a 12:12 h light:dark regime for 18 days (snails replaced daily) and the number of snails consumed in the light and in the dark determined. Response variables in the light and dark were compared using a repeated measures ANOVA.

To determine if there was prey preference between *H. duryi* and *P. acuta*, 70 *H. conifera* were individually maintained for 23 days without shelter with five small *H. duryi* and five small *P. acuta* (replaced daily). The number of each species of snail consumed or used as a shelter was recorded, with response variables analysed using Chi-Square goodness-of-fit.

Confirmity of response variables to model assumptions was tested using F_{max} Test for homoscedasticity and Lilliefor's Test for normality. All tests were conducted following Zar (1980) using SYSTAT (version 5.02) (Wilkinson 1990). The significance of all tests was determined at $p < 0.05$. Variation is reported as mean ± standard error.

Results

The time between egg and production of the first cocoon by *H. conifera* was 103.4 ± 6.72 days compared to a total life span from egg to death of 309.8 ± 13.39 days. After hatching the young were brooded on the parent with the time from departure from the parent to production of the first eggs being 56.4 ± 5.35 days and to completion of the life cycle and death of 264.4 ± 15.75 days.

The number of broods ranged from one to four (2.78 ± 0.32) with the time between successive broods increasing from 41.1 ± 2.92 days between broods 1 and 2 to 65.5 ± 8.50 between broods 3 and 4. The number of progeny was highest in the second brood (117.3 _ 15.59) and lowest in the fourth brood (14.5 ± 14.5) with a total lifetime number of progeny of 209.0 ± 26.42 (Table 1). The time from the departure of the last brood to the death of the parent was 81.2 ± 11.53 days which was not correlated with the number of brood produced ($t_{0.05(2),7} = 1.99$; $p = 0.201$) with an individual producing only one brood not surviving significantly longer after departure of the brood than individuals producing three or four broods (Table 1).

The time from leaving the parent to first feeding on live snails ranged from three to 15 days (10.89 ± 1.09). An average of 17.25 ± 1.45 snails were consumed before the first eggs were produced and all the individuals producing a second brood consumed less snails (9.86 ± 1.91) before producing the second brood. The total lifetime consumption of snails was 46.5 ± 3.68. There was a significant positive correlation between the number of progeny in brood 1 (Table 1) and the number of snails consumed ($t_{0.5(2),2} = 4.70$; $p = 0.042$). Consumption of snails could not be calculated between broods 2 and 4 because juveniles sometimes fed with the adult leeches before leaving the parent. Consequently snail consumption was not correlated with the number of batches of cocoons ($t_{0.5(2),6} = 2.02$; $p = 0.09$) and the duration of the life cycle ($t_{0.5(2),2} = 4.12$; $p > 0.05$) (Table 2).

Table 1 Life-history data time (days) from hatching to death, hatching to first egg production, from last brood to death and time from departure from parent to first egg production and to death (range with mean ± *SE* in days) for *Helobdella conifera* maintained in the laboratory at 19–22°C with *ad libitum* prey (*Helisoma duryi*) together with the time (days) between broods, the number of progeny in each brood of the total life time number of progeny. *n* = sample size

	Range	Mean ± *SE*	*n*
Time from			
hatching to death	280–360	309.8 ± 13.39	5
hatching to egg production	86–116	103.4 ± 6.72	5
last brood to death	45–148	81.2 ± 11.53	9
Time from departure from parent to			
egg production	35–76	56.4 ± 5.35	9
death	163–321	264.4 ± 15.75	9
Time between broods			
1–2	34–50	41.1 ± 2.92	8
2–3	26–86	47.8 ± 8.36	6
3–4	57–74	65.5 ± 8.50	2
Number of progeny in brood			
1	0–108	63.8 ± 12.25	9
2	51–192	117.3 ± 15.59	8
3	0–167	56.7 ± 23.99	6
4	0–29	14.5 ± 14.15	2
Total lifetime number of progeny	88–325	209.0 ± 26.42	9

For eight mature *H. conifera* examined in detail, the total number of young feeding while attached ranged from one to 21 with a trend for young to stay on the parent longer when more feedings occurred (Table 3). The average time between meals was 4.74 ± 0.33 days, however, upon production of a brood *H. conifera* significantly increased the time between meals ($t_{22,363} = 7.215$, $p < 0.001$) so that the average time to first feeding after production of cocoons was 14.95 ± 1.71 days.

Helobdella conifera ($n = 8$) provided with small (4.0–7.5 mm) live snails all fed avidly and all produced eggs but none of the leeches ($n = 8$) provided with large (10.0–13.0 mm) snails had material in the gut and two died. After 60 days the remaining six leeches which had not fed on large, live snails were each given a dead large snail. All of the leeches fed, indicating that they could feed as scavengers but not as active predators.

There was no significant difference in the time from leaving the parent to the formation of the first eggs in *Helobdella conifera* provided with *ad libitum* small snails and no effect of providing shelter on the number of prey consumed. However, when fed only every fifth day, the time to the formation of the

Table 2 The number (range with mean ± *SE*) of snails consumed by *Helobdella conifera* before the production of eggs and between successive broods of eggs and the time (days) from hatching to the first feeding on snails (*Helisoma duryi*), from last feeding to death, between meals and time after one brood production to the next feeding. *n* = sample size

	Range	Mean ± *SE*	*n*
Time to first feeding (*n* = 8)	3–15	10.89 ± 1.09	8
No. snails consumed:			
before first egg brood	12–23	17.3 ± 1.45	8
between 1st and 2nd broods	3–19	9.9 ± 1.91	7
between 2nd and 3rd broods	1–14	7.6 ± 2.69	5
between 3rd and 4th broods	6–17	11.5 ± 5.50	2
from last brood to death	3–23	12.5 ± 2.54	8
Lifetime consumption of snails	26–60	46.5 ± 3.68	8
Time from last feeding to death	12–76	34.4 ± 6.603	8
Average time between meals		4.74 ± 0.33	8
Average time after cocoon production to next meal		14.95 ± 1.70	8

first eggs significantly increased ($F_{(2)(24)}$ = 106.07; $p < 0.001$) and the number of prey consumed significantly decreased ($F_{(2)(24)}$ = 174.89; $p < 0.001$) (Table 4).

The average proportional consumption of prey by 18 *H. conifera* provided with small snails for 23 days on a 12:12 h light :dark regime in the dark was 0.885 ± 0.024 with a significant ($F_{1,17}$ = 257.1, $p < 0.001$) decrease in consumption in the light (0.115 ± 0.024).

When given the opportunity to feed on either small *P. corneus* or *P. acuta* of the same size, *H. conifera* showed a clear preference for *P. corneus* ($\chi^2_{(1)}$ = 75.4; $p < 0.001$). Of the 420 snails consumed, 299 were *H. duryi* and only 121 *P. acuta*. Of 203 snails used for shelter or attachment 200 were *H. duryi*, indicating a significant preference ($\chi^2_{(1)}$ = 191.20; $p < 0.001$) by *H. conifera*.

In experiments with adults provided with prey while brooding young, some young fed on prey while still attached to the parent. Of 372 snails consumed by nine adult *H. conifera* over their lifespan, at least 52 (14%) of the snails consumed were fed upon jointly by adult and brooding juveniles.

The low variance in the time between departing from the parent to the first independent meal on a snail suggests that the energetic state of the juveniles may be the trigger for leeches to depart the parent. This is supported by examination of recently detached young which had empty crops with no visible particulate matter visible.

Table 3 The number (mean ± *SE*) of meals taken by young *Helobdella conifera* (*n* = 8) while still attached to the parent together with the number of young brooded by each parent, the number of times both parent and attached young fed simultaneously, the time (days) after egg laying until the attached young fed, the number of days on the parent from egg to departure of last young and the number of days from the first to last departure of young

Brood size	106.8 ± 11.36
Total no. feedings by attached young	10.5 ± 3.09
Total no. of feedings by young alone	4.0 ± 1.55
Total no. days on parents	59.8 ± 8.50
Day after egg when first young left parent	36.0 ± 4.45
No. days for brood to leave parent	23.8 ± 5.60

Table 4 The time (days) from leaving the parent to the formation of the first eggs by *Helobdella conifera* provided with (i) *ad libitum* small snails (*Helisoma duryi*) with a stone shelter, (ii) with *ad libitum* small snails without a shelter and (iii) small snails every fifth day, together with the total number of prey consumed. *n* = number of replicates. Groups denoted by the same letter were not significantly different from each other ($p < 0.05$)

	Time to 1st cocoon	Total prey consumed
(i)	33.6 ± 1.35 x	16.2 ± 1.32 y
(ii)	33.1 ± 0.32 x	16.8 ± 1.75 y
(iii)	45.9 ± 2.54	7.0 ± 1.15

Discussion

With a total life span in the laboratory (at 19–22°) of just over 300 days, it is a reasonable assumption that *Helobdella conifera* in the field with water temperatures around 20°C has an annual life cycle. Without quantitative data, El-Shimy (1987) estimated the life span to be between seven and 12 months in water temperatures of 20–25°C. After hatching, the first two months are spent on the parent before the young leave the parent. In contrast El-Shimy (1987) reported that the young left after only one month. After approximately another two months sexual maturity is attained and the first batch of eggs is produced and brooded. The number of broods produced range from one to four with the majority producing three broods and only the odd individual producing more, similar to the non-quantitative estimate of three to five broods by El-Shimy (1987). The time interval between broods increased with successive broods, and the number of broods produced was not correlated with the total number of progeny produced or the total life span of the individuals.

There was evidence from this study and El-Shimy (1987) that some young leeches attached to the parent fed or partially fed when the parent was eating, similar to the observations by Kutschera (1989, 1992), Kutschera & Wirtz (1986a, b, c) for *H. stagnalis* (L.), *H. californica*, and *H. striata*. The majority of young did not feed while attached to the parent and survived on stored products from the egg. Most young started feeding on small live snails (*Helisoma duryi*) on the 11th day after departure from the parent with 12–23 snails consumed before their first batch of eggs were produced. With a lifetime consumption of 26–60 snails, there was no correlation between the number of snails consumed and the number of broods produced or the number of progeny produced. Inability to accurately quantify joint consumption of prey by parents and young probably played an important role in the absence of a relationship between prey consumption and the number of broods or number of progeny after the production of the first brood.

Helobdella conifera is primarily a predator on prey small enough for it to subdue and does not actively feed on large snails. When starved *H. conifera* will, however, feed on damaged fresh snails and thus can act as a scavenger. While the majority of glossiphoniids are predators, consuming the body fluids and killing the prey, several studies (e.g. Bennike 1943; Wilkialis 1964; Gruffydd 1965; Hatto 1968; Sarah 1971; Klemm 1973, 1975, 1976) have demonstrated a parasite–host association with molluscs. *Helobdella conifera* did not feed parasitically in this study but its capacity to feed as a scavenger was demonstrated and is perhaps typical of many glossiphoniids (Young *et al.* 1995). Feeding by *H. conifera* showed a significant preference for *H. duryi* compared to *P. acuta* of the same size and also showed a preference for *H. duryi* as a substrate, either as a hiding place or as a precursor to feeding. The majority of feeding by *H. conifera* occurred in the dark. Feeding of *H. conifera* was not affected by the provision of a stone as shelter possibly because the prey (snails) can serve as both prey and shelter. When provided with *ad libitum* prey on a daily basis more prey were consumed and eggs were produced earlier than by *H. conifera* provided with *ad libitum* prey only every fifth day. *Helobdella conifera* has also been reported feeding on *Biomphalaria alexandrina*, *Bulinus truncatus*, *Gyraulus mareoticus*, *Lanistes carinatus* by El-Shimy (1987), on *Physa acuta*, *Aplexa marmorata*, *Bulinus tropicus* and *Lymnaea natalensis* by Wilken & Appleton (1991) and on *Biomphalaris alexandrina* and *Bulinus truncatus* by El-Shimy & Hamada (1990).

There was no evidence of prey avoidance reaction by *H. duryi* attacked by *H. conifera*, but *P. acuta* did show such behaviour (Wilken & Appleton 1991) and probably contributed to the significantly lower feeding on *P. acuta*. This is not the only factor involved because *H. conifera* also significantly preferred *H. duryi* as a hiding place or shelter compared to *P. acuta*.

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