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Article in *Hydrobiologia* · May 2004

DOI: 10.1023/B:HYDR.0000026504.39761.b3

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Costs of parental care on hunting behaviour of *Helobdella papillornata* (Euhirudinea: Glossiphoniidae)

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Received 28 April 2003; in revised form 2 December 2003; accepted 2 December 2003

Key words: annelid, foraging, leech, *Helobdella*, parental care

Abstract

Helobdella papillornata, an Australian freshwater leech, feeds primarily on snails and has a high level of parental care involving brooding eggs and young, with direct feeding of young. Parental costs and offspring benefits from these behaviours are poorly understood. A potential cost of parental care may be a change in the time taken to hunt prey. To test this hypothesis, the hunting behaviour of adults without progeny, parents with eggs, and parents with young were compared. We found that parents brooding eggs had a significantly ($P = 0.029$) longer lag time to begin hunting than parents brooding young, and spent significantly ($P = 0.018$) less time actively hunting than non-brooding adults. These costs, which may represent lost potential for the parent's future reproductive success, should be outweighed by the fitness benefits of improved growth and survival of offspring, if parental care is favoured by selection. The hunting costs of care in *Helobdella* and other benthic, dorsoventrally flattened leeches in the family Glossiphoniidae may be smaller than the costs of brood tending that would be imposed on other freshwater leeches, and this difference may help explain the restriction of care to a single clade of the Euhirudinea.

Introduction

Parental care has been extensively studied in many vertebrate groups and in some arthropods, and most current hypotheses on the evolution of parental care have been derived from these studies (Clutton-Brock, 1991). In contrast, parental care is much less understood in the majority of invertebrate taxa, even though it occurs in several different phyla. A broader taxonomic base of information on parental care is needed because comparisons across widely divergent taxa would allow us to determine which evolutionary hypotheses have general validity and which features are dependent on the idiosyncrasies of ecology or life-history in particular groups.

Within the annelid class Euhirudinea (leeches), members of a single monophyletic family, the Glossiphoniidae, brood eggs and feed their young after hatching, with variation in the duration and degree of care among individual species. The basis for understanding the distribution and variation of parental

care is the selective balance between the improvement in offspring fitness and the decrement to future parental fitness that result from the provision of care. A principal advantage of care in glossiphoniid leeches is thought to be protection of offspring from predation (Kutschera & Wirtz, 1986a,b; Govedich et al., 2001), but little is known of the costs.

Parental care is known to compromise foraging ability in many taxa (Clutton-Brock, 1991). For example, in the internal brooding Chilean oyster *Ostrea chilensis*, food uptake is reduced in brooding individuals resulting in reduced adult growth during the brooding period (Chaparro & Thompson, 1998). Crowl & Alexander (1989) found that male *Belostoma* water bugs with egg clutches on their backs captured mosquito fish at one-third the rate of unencumbered males and females. Even when offspring are not internally brooded or attached to the parent, time devoted to parental care may limit the quantity and quality of forage. For example, guarding clutches at fixed nest sites causes a decline in body weight or fat content in

the frog species *Eleutherodactylus coqui* (Townsend, 1986) and *Cophixalus perkeri* (Simon, 1983).

In contrast to the above cases, glossiphoniid leeches that brood eggs and young on their ventral surface seem to be able to hunt their invertebrate prey and feed normally when carrying a brood. However, it is possible that they may require more hunting time, expend greater effort, or suffer reduced success rates in pursuit of prey when egg masses or juveniles are attached. We examine these potential costs of care in the present study.

Helobdella papillornata is a common Australian freshwater glossiphoniid leech found in streams and lakes throughout mainland Australia (Govedich, 2001). This leech is a sit-and-wait predator which uses its anterior sucker to catch and subdue its prey. Once the prey is subdued, *H. papillornata* uses a protrusible proboscis to feed on the fluids and soft tissues of the prey (Govedich & Davies, 1998). *Helobdella papillornata* attacks a wide range of prey items including oligochaetes, insect larvae, and molluscs, with a preference for gastropods such as *Austropyrgus* spp., *Physa acuta* and *Potamopyrgus antipodarum* (Govedich & Davies, 1998; Govedich, unpubl. data).

Helobdella parents care for both eggs and young (Sawyer, 1986; Kutschera, 1989, 1992; Kutschera & Wirtz, 1986a,b; Davies, 1991; Davies & Govedich, 2001; Govedich, 2001; Govedich et al., 2001). Following fertilisation, *H. papillornata* lays 20 to 60 eggs that are attached directly to the ventral surface of the parent. After approximately 14 days, the eggs hatch and the newly emerged young remain attached to the parent's ventral surface for up to 60 days until they are capable of hunting on their own. Throughout the care period, the parent provides protection from predators, ventilates the eggs/young to ensure that they receive sufficient oxygen and provides prey to the juveniles after hatching (Govedich & Davies, 1998; Govedich, 2001; Govedich et al., 2001).

Methods

Helobdella papillornata used in this study came from a laboratory-bred population originally collected from Aura Vale Lake (37° 55' S, 145° 23' E), 25 km E of Melbourne, Australia. The laboratory population was fed a maintenance diet of one to two *Potamopyrgus antipodarum* snails per leech every seven days. Snails were collected weekly from Cardinia Creek (37° 59' S, 145° 29' E) near the source of the leech population.

For each feeding trial we selected five adult leeches without progeny, and five parents with eggs or five parents with young from the stock population. The entire experiment consisted of five trials: three with non-reproductives and egg-brooding parents, and two with non-reproductives and parents with juveniles. Prior to each feeding trial, the selected leeches were starved for five days. Each adult was photographed with an Olympus DP-10 digital camera mounted on an Olympus SZH-10 dissecting microscope, and its body size (length, width and area) determined using HLIImage⁺⁺ image analysis software (Western Vision Software, Salt Lake City, Utah, USA), measurements are given as means \pm SE. Each adult was then placed in a separate 7 \times 7 \times 5 cm plastic container filled with 200 ml of artificial pond water (pH 7.8, 80% O₂ saturation, salinity = 36.1 PPM, electrical conductivity 95.9 μ S) and left undisturbed for 24 hours before the start of the trial.

A feeding trial commenced with the addition of three adult *P. antipodarum* snails into each container. The subsequent behaviour of each leech was recorded on video tape for 12 hours. We replayed these tapes to determine the duration of three phases: (1) an inactive lag time between the introduction of snails and the initial hunting movements of the leech; (2) a searching phase from the initial movement to the point when the leech attached itself to the snail; and (3) a killing and feeding phase from attachment to the snail to abandonment of the empty shell. These phases might then be repeated for a second and third prey item.

We observed that *H. papillornata* occasionally interrupted a lag phase with short distance movements before resuming a resting state. In order to avoid exaggerating the length of the searching phase, any movement under five minutes in duration was considered part of the inactive phase. Similarly, a leech in the searching phase would occasionally come into contact with a snail, but would move on without attacking it. In order to prevent exaggeration of the feeding phase, leeches in this situation were considered to be still in the searching phase.

Body size may affect all three phases of predatory behaviour. We checked for differences in body size among leeches in the three reproductive states (non-reproductive, eggs, young) using a one-way ANOVA. We then tested for differences among reproductive states in the duration of each predation phase using an ANCOVA with body size as a covariate. A Tukey's *post-hoc* test was performed to determine differences between categories.

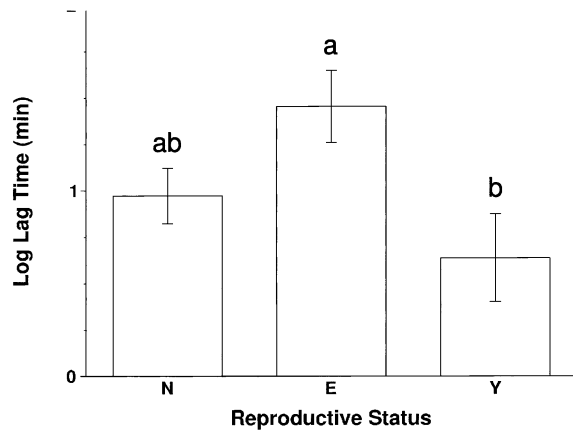


Figure 1. Lag time before *Helobdella papillornata* began hunting *Potamopyrgus antipodarum* snails: (N) non-parental adults, (E) parents brooding eggs and (Y) parents brooding young (a and b indicate a significant ($p < 0.05$) difference between groups).

Results

Body length, width and area (length \times width) were, respectively, 8.8 ± 0.2 mm, 3.5 ± 0.1 mm and 30.8 ± 1.6 mm² for non-reproductives ($N = 25$), 9.5 ± 0.3 mm, 3.5 ± 0.15 mm and 33.7 ± 1.8 mm² for egg-brooding parents ($N = 15$), and 9.3 ± 0.3 mm, 3.7 ± 0.2 mm and 34.8 ± 1.5 mm² for parents with juveniles ($N = 10$). These differences were not significant (ANOVA, $F_{2,47} = 1.37$, $P = 0.26$). The mean number of eggs that parents carried was 56.9 ± 2.0 with no significant difference in egg number between treatments (ANOVA, $F_{2,12} = 0.35$, $P = 0.71$).

We found that leech size had no effect ($P \geq 0.52$ for all cases) on the length of any of the three hunting phases. However, the reproductive state had a significant effect on the lag time taken to initiate feeding ($F_{2,47} = 3.82$, $P = 0.029$). Although there was no significant difference between the time taken for adults without progeny or parents with young to begin feeding ($P \geq 0.132$), parents with eggs took significantly longer ($P = 0.028$) to start searching than parents with young (Fig. 1).

Reproductive state had no effect on the time taken to conclude the feeding phase (Fig. 2). However, reproductive state did have a significant effect on the time taken to conclude the hunting phase ($F_{2,47} = 4.35$, $P = 0.0184$). Although there was no difference between the time taken for adults without progeny and parents with young to finish hunting ($P = 0.681$) and parents with eggs and with young ($P = 0.260$), parents

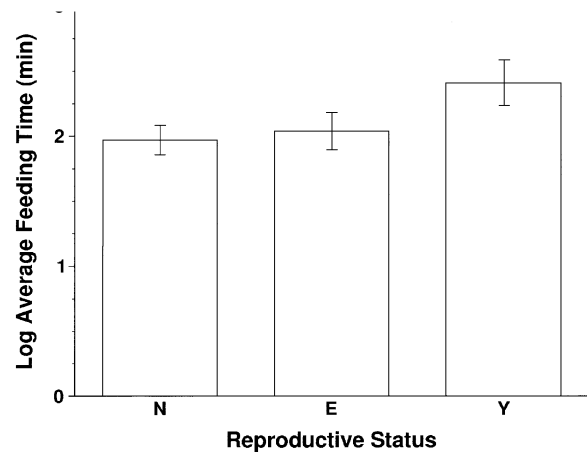


Figure 2. Time *Helobdella papillornata* spent feeding on *Potamopyrgus antipodarum* snails: (N) non-parental adults, (E) parents brooding eggs and (Y) parents brooding young.

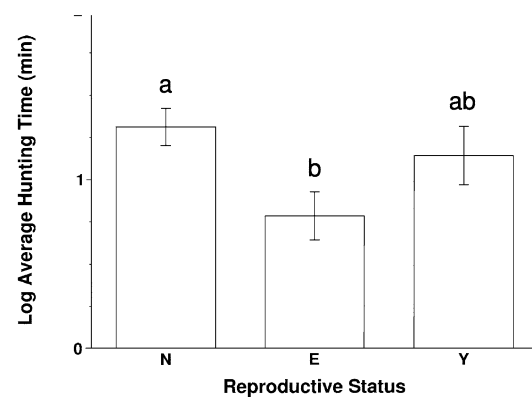


Figure 3. Time *Helobdella papillornata* spent hunting *Potamopyrgus antipodarum* snails: (N) non-parental adults, (E) parents brooding eggs and (Y) parents brooding young (a and b indicate a significant ($p < 0.05$) difference between groups).

with eggs spent significantly ($P = 0.014$) less time hunting than adults without progeny (Fig. 3).

Discussion

The results of this study suggest that reproductive state has two effects on feeding behaviour in *Helobdella papillornata*. First, a leech carrying eggs takes longer to start hunting than one that has no progeny or one with young. Second, a leech that is caring for eggs spends less time hunting snails than one that has no progeny or one that is carrying young. Both these examples can be seen as a trade-off between the fitness of the parent and the fitness of the progeny.

Parents with eggs seemed to remain in the inactive phase, with only a few making kills following a snail blundering into them. Since the eggs of *H. papillornata* are apparently quite fragile (if removed from the parent they do not develop), it could be hypothesized that the parent is remaining still to reduce the chances of damage to the ventrally placed eggs. Though this behaviour gives obvious benefits for the eggs, it may potentially result in a cost to the parent. As the eggs incubate over 14 days, the parent may starve with a subsequent reduction in survival. However, since *H. papillornata* feeds once every 7 to 14 days, it may be that any cost of this fast may be minimal or negligible.

It appears that the slight extension of the feeding phase (Fig. 3) seen in the parents with young, though not significant, can be attributed to the time taken for the young to feed. Moreover, on several occasions the parent was observed killing the snail, then leaving it for the brood alone to consume. By providing the snail to the young, in part or in total, the parent reduces the benefit of hunting and needs to hunt more often. In addition to the food lost to the young, energy is expended during the hunting process leading to a direct cost to the parent.

Though the young would benefit from parental provisioning, the costs are more difficult to attribute. The time spent feeding by the young may result in an increased exposure to predators and environmental hazards. If altruistic feeding is common, the increased hunting involved would only exacerbate this increased risk. However, since both parent and progeny are vulnerable to these hazards while feeding, the cost of this behaviour would affect both parent and young.

Acknowledgements

We would like to thank Phillip Diver for his assistance during this project and for helping in raising and caring for our *Helobdella papillornata*. This project was funded in part from a Monash University Research Fellowship awarded to Fredric Govedich and an Australian Research Council discovery projects

grant awarded to Martin Burd, Alan Lill and Fredric Govedich.

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