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Prey selection of a shell-invading leech as predicted by optimal foraging theory with consumption success incorporated into estimation of prey profitability

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Summary

1. Optimal foraging theory assumes that a predator preys selectively to maximize fitness gain. The associated model assesses predator's fitness gain by estimating prey profitability in terms of appropriate foraging costs and benefits. While model developing, unsuccessful foraging was included in the model because it is inevitable and costly for a predator. However, it has rarely been taken into account in previous studies, nor has the consumption success been included in the estimation of prey profitability. Thus, although such model may successfully predict prey selection of many predators, it is inadequate in explaining prey selection of predators with highly variable consumption success.

2. In this study, we tested the prediction of optimal foraging model by accounting for consumption success in prey profitability for the prey selection of *Whitmania laevis* (Hirudinida: Hirudinidae), a shell-invading leech with highly variable consumption success in different prey. Five snail species, including three operculated species and two non-operculated species, were used as prey.

3. Our results showed that *W. laevis* exhibits prey-size selection. Leeches consumed more medium-sized snails among operculated species and more large-sized snails among non-operculated species, and the selection fitted the prediction of prey profitability by accounting for consumption success. Leeches also practiced prey-species selection, but such selectivity was confined to non-operculated species rather than snails with higher profitability.

4. Our study showed that when the consumption success was incorporated into the estimation of prey profitability, the optimal foraging model could, as predicting the prey-size selection of *W. laevis*, predict the prey selection of a predator with highly variable consumption success, which has been poorly predicted previously. This could also be the case for other predators with variable consumption success in future studies.

Key-words: consumption success, freshwater snail, optimal foraging theory, predatory leech, prey profitability, prey selection

Introduction

The optimal foraging theory, that attempts to explain and predict foraging behaviour of animals and which is based on the assumption that fitness associated with foraging is maximized by natural selection, was first proposed by Emlen (1966) and MacArthur & Pianka (1966) and later extended and examined by other workers (e.g. review by Pyke, Pullam & Charmov 1977; Elner & Hughes 1978; Hughes & Seed 1981; McQuaid 1994; Saito *et al.* 2004). Based on this theory, the foraging strategies and prey preference of an animal can be predicted by appropriate cost-benefit functions with properly chosen currencies that can assess fitness gain associated with foraging (Schoener 1971). In overviewing the components of the basic optimal foraging model provided by Schoener (1971), the fitness gain of a predator from a prey can be assessed by estimating the prey value, which is defined by net energy intake per unit

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handling time. Because unsuccessful predation is inevitable and is, to a greater or lesser extent, costly for a predator, this factor was also included in the estimation of prey value in Schoener's model. Thus, the estimation of the prey value for a predator would be influenced by the probability of unsuccessful predation.

By estimating prey value, the optimal foraging model has been found to be applicable to prey selection of many predators (e.g. mantid by Charnov 1976; crab by Elner & Hughes 1978 and Seed & Hughes 1995; Octopus by McQuaid 1994; polychaete by Saito *et al.* 2004). However, Sih & Cristensen (2001) found that the optimal foraging model was poorly predicting when used to explain prey selection by predators when the prey was relatively mobile to the predator although the model had great success in predicting prey selection by predators when the prey are relatively immobile. Sih & Cristensen (2001) suggested that this may be because most previous studies estimated prey profitability (prey value) without accounting for variations among prey in terms of capture or consumption success. By only accounting for assimilable energy or prey mass per unit time that a predator spent on a successful predation exercise, the cost and the influence of unsuccessful predation has been ignored in many studies. In cases where predators prey on relatively immobile prey or on prey with low defense ability, the capture and consumption success may not differ between prey items. Nevertheless, for predators consuming prey with high mobility or high defense ability, the capture success and consumption success resulting from prey vulnerability would differ among prey items. Therefore, capture and consumption success should be included in the estimation of prey profitability as proposed by Schoener (1971) and Sih & Christensen (2001). Estimation of prey profitability in relation to capture success or consumption success was, however, only considered in a few studies (Elner & Raffaelli 1980; Lawton & Hughes 1985).

Leeches are numerous and important predators in aquatic benthic systems, and their prey consumption and selection have been widely studied (Elliott 1973; Young & Ironmonger 1980; Davies *et al.* 1981; Davies, Wrona & Linton 1982; Anholt 1986; Brönmark & Malmqvist 1986; Sawyer 1986; Anholt & Davies 1987; Kelly & Cory 1987; Brown & Strouse 1988; Wrona & Calow 1988; Davies & Kasserra 1989; Brönmark 1992; Young, Martin & Seaby 1993; Martin, Seaby & Young 1994; Davies, Dratnal & Linton 1996; Govedich *et al.* 2004). In previous studies, most of the prey consumption of leeches was not tested or could not be predicted by the optimal foraging model. For example, the rhynchobdellid leech, *Glossiphonia complanata,* is a sit-and-wait predator, and its prey consumption depends on anti-predatory behaviour of prey rather than on active selection (Brönmark & Malmqvist 1986; Brönmark 1992). On the other hand, erpobdelliform predatory leeches are actively foraging predators that consume various species of prey. Their prey consumption is, however, more dependant on the mobility or vulnerability of prey than on active selection by the predator according to the prey profitability (Anholt 1986; Brown & Strouse 1988). On the other hand, only a few studies of the foraging ecology of hirudiniform predatory leeches have been conducted (Simon & Barnes 1996; Turbeville & Briggler 2003), and none of these examined strategies relating to prey consumption or prey-selective predation.

Whitmania laevis (Hirudinida: Hirudinidae, Phillips & Siddall 2009) is a hirudiniform leech that preys mainly on aquatic snails. According to Takahashi (1931) and our preliminary observations, the foraging process of *W. laevis* starts when the leech attaches its oral sucker to the snail. The leech then attaches its caudal sucker to the shell, finds the aperture of the snail, and then invades the shell using its attenuated head. After gradually contracting and curling its body on the snail during this invasion, *W. laevis* starts to feed on the snail and then stays still without any body contraction until it leaves the snail after the termination of feeding. Lai & Chen (2004) found that, when simultaneously offered the same number of three different-sized snails, *W. laevis* favoured middle-sized snails over small- or large-sized snails. This led to speculation that prey-size selection is correlated with prey profitability, which could probably be explained using the optimal foraging model. *Whitmania laevis* has also been observed to leave snails intact without physical injury after having gone through the entire foraging process. These unsuccessful predation efforts frequently occurred when preying on operculated snails, and consumption success apparently varied with snail species and snail size (Y.-T. Lai, personal observation). Although *W. laevis* normally consumes all the soft tissues of snails, leaving only the shell and operculum, there were cases in which leeches consumed only part of the soft tissue, and this also seemed to vary with snail species and size. These observations imply that consumption success and the consumption ratio of snail body should be considered in the estimation of prey profitability. This would enable testing of whether prey selection of *W. laevis* could be predicted by means of the optimal foraging model.

In this study, we first investigated whether *W. laevis* showed any preference for snail sizes, and then tested the correlation between prey profitability and prey size preference of leeches by using the optimal foraging model. In our estimation of prey profitability, we incorporated consumption success into our analyses as this may vary with snail sizes and species. This parameter has only been rarely considered when assessing prey profitability in the optimal foraging model previously. The ratio of prey body consumed by the predator was also included for a more accurate measure of prey profitability. After assessing the correlation between prey profitability and prey size preference, we investigated whether *W. laevis* prefers certain snail species over others, and examined the correlations between prey profitability and prey-species selection in leeches.

Materials and methods

We collected *W. laevis* from the Experimental Farm located at the main campus of National Taiwan University from August 2004 to August 2005. Leeches were kept individually in white, translucent, lidded plastic boxes (25 × 15 × 7·5 cm) that contained

1 L of dechlorinated tap water. They were acclimatized in incubators with a 12-h light : 12-h dark cycle at 20 ± 2 °C without feeding for at least 1 week before being used in experiments. On a biweekly basis, the wet weight of the leech was measured to an accuracy of 0·01 g after gently shaking the water off the body surface. The boxes were cleaned and tap water replaced at the same time.

As experimental prey, we chose five species of freshwater snails that live sympatrically with *W. laevis*, including three operculated species, i.e. apple snail *Pomacea canaliculata*, thiarid snail *Thiara tuberculata* and viviparid snail *Sinotaia quadrata*; and two non-operculated species, i.e. ear pond snail *Radix auricularia swinhoei* and tadpole snail *Physa acuta* (Fig. 1). These snails were collected from suburban areas of Taipei City and ponds on the main campus of NTU from March 2004 to December 2005. Different species of snails were raised separately in continuously aerated dechlorinated tap water and fed with lettuce. The tap water was replaced regularly, to maintain the breeding environment of the snails.

EXPERIMENT 1: PREY-SIZE SELECTION OF *W. LAEVIS*

In this experiment, we offered snails of different sizes to *W. laevis* to test if size selection affected predation of leeches on snails. We used two size classes of *W. laevis*, i.e. small (0·1–0·4 g) and large (1·0–1·6 g), and five snail species (mentioned above) as prey to examine the influence of leech size and prey species on prey-size selection of *W. laevis*. With the exception of the viviparid snail, each snail species had seven different size classes of the following aperture lengths: 1·1–2·0, 2·1–3·0, 3·1–4·0, 4·1–5·0, 5·1–6·0, 6·1–7·0 and 7·1–8·0 mm. Because the aperture lengths of the smallest viviparid snail are always > 2·0 mm, only six size classes of this species were used in the experiment.

The experiment was conducted in the same boxes where the leeches had been kept, and all boxes were placed in an incubator with a 12-h light : 12-h dark cycle at 20 °C. There were ten combination treatments among leech sizes (small and large) and snail species (apple snail, thiarid snail, viviparid snail, ear pond snail and tadpole snail), and we used 12 different leeches for each combination. Each leech was offered one snail species of each of the size classes, i.e. six of the viviparid snail or seven of the other species. The size classes of the consumed snails were recorded daily and replaced with other snails of the same size classes. Each trial was run for 5 days. To prevent the potential influence of different hunger levels between the beginning and the end of a trial (Anholt & Davies 1987), as well as to ensure that the snails were consumed by leeches of a normal appetite, statistical analysis was based exclusively on data from the last 3 days of the trial. If a leech did not consume any snail throughout the trial, it was excluded from the analysis.

The Kruskal–Wallis two-way analysis of variance (ANOVA) and Dunn two-sample comparison were used to test if the sizes of *W. laevis* and snail species affected the numbers of snails consumed by *W. laevis*. The Kolmogorov–Smirnov (K–S) with *P*-values of the

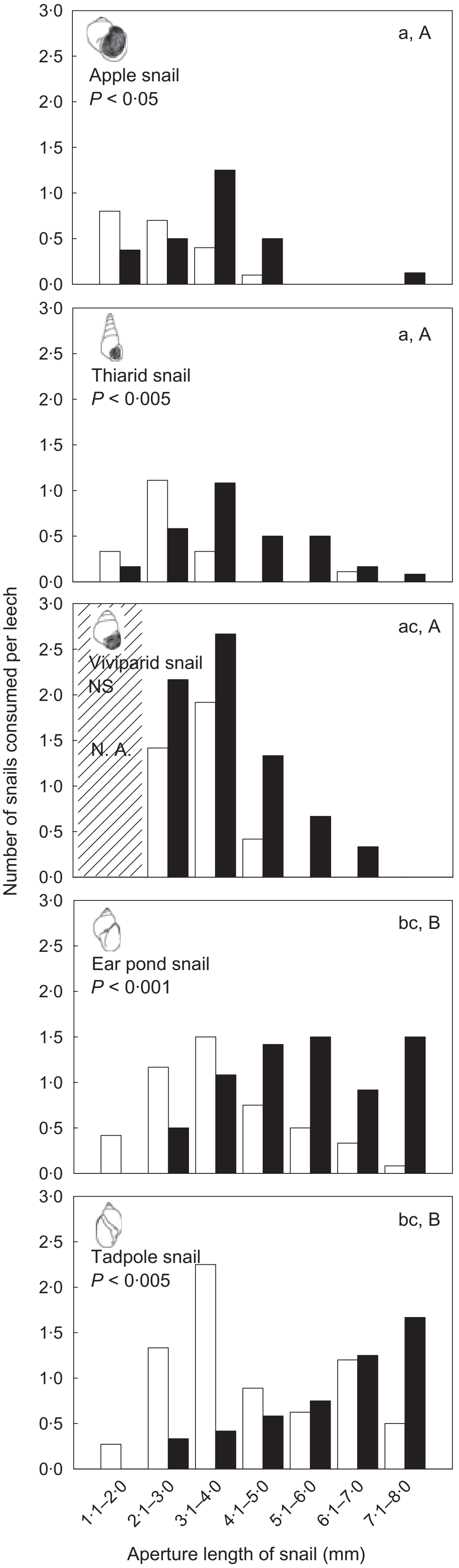

Fig. 1. Size distributions of apple snail, thiarid snail, viviparid snail, ear pond snail and tadpole snail consumed by small (0·1–0·4 g, white bar) or large (1·0–1·6 g, black bar) *Whitmania laevis* in 72 h. Values are the mean numbers of consumed snails. Hatched area indicates that snails of that size class are not naturally available (N.A.). *P*-values indicate the difference between the size distributions of snails consumed by leeches of two sizes. Lowercase and uppercase letters indicate the differences examined by Kolmogorov–Smirnov test among the size distributions of snails of the five species consumed by small and large leeches respectively.

sequential Bonferroni correction was used to analyse the effects of leech size and snail species on the distribution of snail sizes consumed by *W. laevis*.

EXPERIMENT 2: CORRELATION BETWEEN PREY PROFITABILITY AND PREY-SIZE SELECTION OF *W. LAEVIS*

In this experiment, we estimated the profitability of a snail to *W. laevis*, and determined whether profitability of predation on snails related to prey-size selection of *W. laevis* from results of Experiment 1.

We used 55 large *W. laevis* specimens in the experiment. In a trial, we chose a snail of a random size and placed it into a box with a leech. The snail was placed at a sufficient distance from the leech to ensure that the snail could naturally attach to the substrate with its foot. When the leech attached its oral sucker to the shell of the snail, the foraging process began. According to Takahashi (1931) and our preliminary observations, the foraging process of *W. laevis* can be separated into two phases. The first phase starts when the oral sucker of a leech attaches to the shell of the snail. The process ends when the leech curls its body and stays immobile without any signs of visible contraction. The second phase began immediately at the end of the first phase and ended when the leech left the prey snail. The time that a leech spends in the first phase was defined as the 'invasion time' and that in the second phase was the 'feeding time'. Invasion time, feeding time and the soft tissue weight provided by the prey snail as well as the proportion of snail consumed (consumption ratio) were recorded in each trial. Each leech was tested once in each snail species, and the order of feeding snail species to leeches was randomized. Since *W. laevis* preys at night, the trials were performed in dim red light to minimize photic stimuli as Simon & Barnes (1996).

Before each trail, tissue paper was used to wipe water off the shell surfaces of snails, prior to weighing the snails. After predation by *W. laevis*, we cleared away any unconsumed tissue, cleaned the shell and operculum of the snail, dried it in an oven at 60 °C for 24 h, and then weighed it to the nearest milligram. We determined the soft tissue weight (to the nearest milligram) of the snail by subtracting the weight of the shell and operculum from the weight of the snail before the trial.

If part of the soft tissue of the snails remained after a trial, we scored the consumption ratio of the snail into five classes according to the portion and amount of the remaining soft tissue before it was cleared away. The consumption ratio classes were defined as follows: a 25% ratio indicated that less than half of the visceral mass was consumed and the major portion of the visceral mass with the entire foot of the snail remained; a 50% ratio indicated that the whole visceral mass was consumed and only the foot remained; a ratio of 75% indicated that the entire visceral mass and upper half of the foot was eaten; a ratio of 100% indicated that the entire soft tissue of the snail was consumed. We later added a consumption ratio class of 87·5%, which indicated that only the muscle tissues on the inside of the operculum remained. Because leeches were starved prior to trials, they should have been able to consume all the soft tissue of their prey. The fact that some snails were only partially consumed therefore suggests that remaining tissue parts were considered inedible by *W. laevis*. Hence, we regarded the consumption ratio of the soft tissue as the ratio of edible soft tissue of a snail.

To investigate the consumption success of *W. laevis* when foraging on snails of different sizes and species, 20 of 55 large leeches were randomly chosen and tested individually in a trial, in which we offered the leech a snail of a particular size class and species and recorded the foraging result (not attack, success, failure and abandonment) in dim red light. The trials were tested with snails of each snail size class of each of the five species. Thus, a leech would not be tested twice in trials with a particular snail size class of a snail species, but might be tested repeatedly in different snail size classes and snail species. To prevent the influence of learning or experiential effects on foraging results, a leech was tested only once a day, and would not be tested again for at least 1–7 days. According to results from tests on the closely related leech *Haemopis marmorata* (Karrer & Sahley 1988), the learning effect of leeches can only last for 1 day after at least 16 days of daily training. Since each of our leeches was tested once a day in a trial with the interval of 1–7 days between two trials, we suggested that the learning effect in *W. laevis* was preventable in the experiment.

If a leech did not intend to prey on the snail throughout the consumption success trial, the result was considered as 'not attacking'. If there was any attacking attempt, we recorded the trial as 'attacking'. In attacking trials, if the leech successfully consumed the snail, we defined the result as 'success'. However, if the leech ended the foraging process but left the snail intact, or, in some rare cases, if the leech failed to attach to the snail shell while invading, we defined the result as 'failure'. In addition, we defined the attacking trial as 'abandonment' if the leech actively left the snail without going through the entire foraging process. We evaluated consumption success by calculating the rate of 'success trials/(success trials + failure trials)' for each size class of snails of all five species.

We used regression analysis to test relationships between snail size and the following measurements in each snail species: invasion time, feeding time, edible portion of the soft tissue of the snail and consumption success. The profitability of a snail to a leech was then estimated using the following equation: Profitability = $R_s \times R_e \times W/T_i$. W and T_i represent the soft tissue weight of a snail and the invasion time a *W. laevis* spent on a snail, respectively; and R_s and R_e are the consumption success and the ratio of edible soft tissue of the snail respectively. We chose invasion time (T_i) as the currency of the foraging cost because invasion into snails' shells appeared to have a high energy cost and was also a key determinant of successful consumption for leeches. Hence, this parameter should be a more appropriate currency of foraging cost than the conventional 'handling time', i.e. the sum of invasion time and feeding time in this study, for *W. laevis*. Prey profitability was compared to size distribution of snails (for each snail species) consumed by leeches in Experiment 1 in order to examine any possible correlation between them.

EXPERIMENT 3: CORRELATION BETWEEN PREY PROFITABILITY AND PREY-SPECIES SELECTION OF *W. LAEVIS*

In this experiment, we offered *W. laevis* snails of the same size from each of the five species to test prey-species selection among leeches. To determine whether this related to prey profitability, results then compared the profitability of each snail species (results obtained from Experiment 2).

To exclude the influence of size, we used snails of 3·1–4·0 mm in the experiment because the same consumption success for snails of five different species was determined when leeches preyed on snails of the 3·1–4·0 mm size category (for which the consumption success of each of the five snail species was 100%). By offering snails of the 3·1–4·0 mm category to leeches, we could also test if *W. laevis* actively selected preferred prey species. If *W. laevis* consumed five species of 3·1–4·0 mm category snails in equal numbers this would indicate that they do not actively select the species of prey. On the contrary, if consumption numbers varied among the five different species, the prey-species preference would be a result of active prey selection by leeches. In addition, we also used snails of the 6·1–7·0 mm size category from the five different snail species (on which leeches preyed with variable consumption success), and compared the results with those from different prey sizes, to determine the influence of consumption success on prey selection. In the experiment on snails of the 3·1–4·0 mm size class, we used 10 large specimens of *W. laevis*. Each of them was offered two snails of each of the five snail species, i.e. a total of 10 snails, as prey. In the experiment of snails of 6·1–7·0 mm, 10 other large *W. laevis* were used. Each of these was offered one snail of each the five snail species, i.e. a total of five snails, as prey. The experimental procedures were similar to those in the Experiment 1. In addition, we used the data on prey profitability obtained from Experiment 2 to test whether prey profitability could be used to predict prey-species selection of *W. laevis*.

We used a chi-squared homogeneity test to analyse if *W. laevis* preyed on snails of the five species without prey-species selection, i.e. if they consumed the same numbers of snails in each of the five species. We used the Kruskal–Wallis one-way ANOVA and Dunn two-sample comparison test to examine if the profitability of prey snails was different in the five snail species. We compared the numbers of snails consumed in the five snail species with the prey profitability of each snail species to determine if prey profitability could be used to predict prey-species selection by *W. laevis*.

Results

EXPERIMENT 1: PREY-SIZE SELECTION OF *W. LAEVIS*

The number of snails consumed by leeches in 72 h was significantly influenced by the size of *W. laevis* and the snail species type (Kruskal–Wallis two-way ANOVA: treatment, H_9 = 57·097, P < 0·001; leech size, H_1 = 11·357, P < 0·001; snail species, H_4 = 43·172, P < 0·001; Table 1). There was, however, no significant interaction between leech size and snail species (Kruskal–Wallis two-way ANOVA: H_3 = 2·694, NS). The average number of snails consumed by a small *W. laevis* was significantly less than that consumed by a large leech in 72 h, whereas the average numbers of apple snail and thiarid snail consumed by *W. laevis* in 72 h were significantly fewer than those of viviparid snail, ear pond snail and tadpole snail (Table 1).

The sizes of *W. laevis* leeches significantly affected the size distribution of snails consumed in 72 h, but trends differed between snail species (Fig. 1). The general trend was that the capability of consuming larger prey increased with leech size. However, when operculated snails were offered as prey, the sizes of favoured snails never exceeded a relatively low value of 4·0 mm, even though the distribution shifted towards larger snails when large leeches were used as predators. When non-operculated snails were offered as prey, the favoured size of snails consumed reached the upper extremes, indicating that the size distribution of snails could shift further to the right when large leeches were used as predators.

EXPERIMENT 2: CORRELATION BETWEEN PREY PROFITABILITY AND PREY-SIZE SELECTION OF *W. LAEVIS*

The invasion time spent by *W. laevis* on each of the five snail species was positively correlated to snail size (linear regression: apple snail, $F_{1,29}$ = 14·94, P < 0·001, R^2 = 0·348; thiarid snail, $F_{1,41}$ = 2·87, P < 0·1, R^2 = 0·067; viviparid snail, $F_{1,34}$ = 64·13, P < 0·0001, R^2 = 0·660; ear pond snail, $F_{1,48}$ = 69·56, P < 0·0001, R^2 = 0·597; tadpole snail, $F_{1,43}$ = 26·81, P < 0·0001, R^2 = 0·390; Fig. 2). The feeding time spent by *W. laevis* on a snail also increased with snail size, regardless of the snail species (nonlinear regression: apple snail, $F_{1,29}$ = 12·39, P < 0·005, R^2 = 0·307; thiarid snail, $F_{1,41}$ = 15·87, P < 0·0005, R^2 = 0·284; viviparid snail, $F_{1,34}$ = 113·70, P < 0·0001, R^2 = 0·775; ear pond snail: $F_{1,48}$ = 124·78, P < 0·0001, R^2 = 0·726; tadpole snail: $F_{1,43}$ = 89·60, P < 0·0001, R^2 = 0·681; Fig. 2). Generally, the invasion time and feeding time spent by *W. laevis* on a non-operculated snail was shorter than that spent on an operculated one.

The ratio of edible soft tissue of a snail was only influenced by the snail size in operculated species. In apple snail, thiarid snail and viviparid snail, the edible portion decreased as the snail size increased (linear regression: apple snail, $F_{1,29}$ = 33·18, P < 0·0001, R^2 = 0·542; thiarid snail, $F_{1,41}$ = 16·39, P < 0·0005, R^2 = 0·291; viviparid snail, $F_{1,34}$ = 45·75, P < 0·0001, R^2 = 0·581; Fig. 3), while in ear pond snail and tadpole snail, the edible portion was invariably 100%, irrespective of snail size (linear regression: ear pond snail, $F_{1,48}$ = 1·81, NS; Fig. 3).

Table 1. Numbers (mean ± SD) of five snail species consumed by two sizes of *Whitmania laevis* in 72 h

	Leech size		
Prey species	Small (0·1–0·4 g)	Large (1·0–1·6 g)	Average
Apple snail	1·82 ± 1·40 (11)	2·00 ± 1·84 (11)	1·91 ± 1·60 (22)^{a}
Thiarid snail	1·55 ± 0·93 (11)	3·08 ± 1·51 (12)	2·35 ± 1·47 (23)^{ac}
Viviparid snail	3·64 ± 1·54 (12)	7·09 ± 2·08 (12)	5·46 ± 1·47 (24)^{bd}
Ear pond snail	4·55 ± 1·91 (12)	6·73 ± 2·68 (12)	5·83 ± 2·53 (24)^{bd}
Tadpole snail	3·18 ± 2·08 (12)	5·18 ± 2·63 (12)	4·08 ± 2·50 (24)^{bc}
Average	3·05 ± 1·99 (58)^{a}	4·88 ± 2·96 (59)^{b}	

Numbers in parentheses are the replication of leeches. Superscripts indicate the differences examined by Dunn test comparisons among the averages.

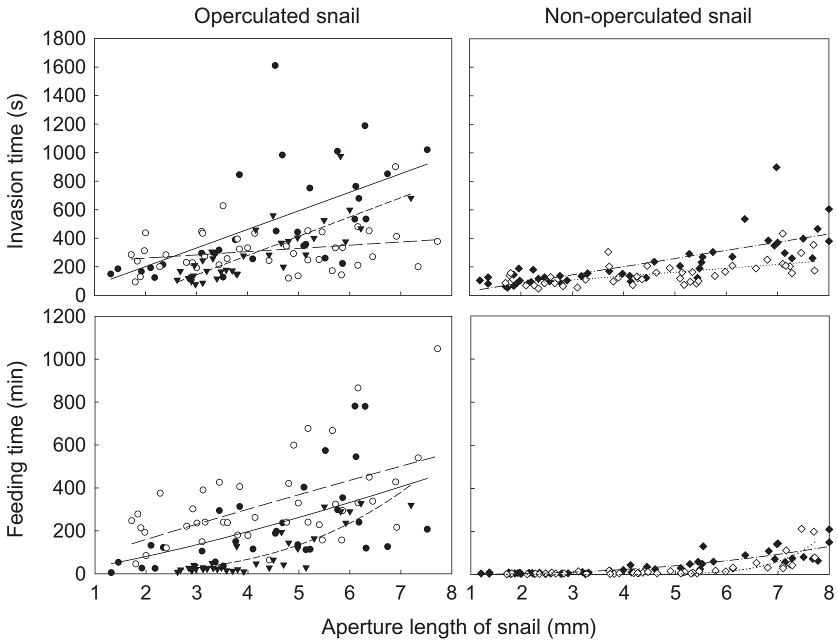

Fig. 2. Regression of the invasion time and feeding time *Whitmania laevis* (1·0–1·6 g) spent on snails to the aperture length of apple snail (●, solid line, invasion time: $y = 130{\cdot}061x - 58{\cdot}4173$; feeding time: $y = 32{\cdot}7007x^{1{\cdot}2936}$), thiarid snail (○, long dash line, invasion time: $y = 22{\cdot}6286x + 215{\cdot}3316$; feeding time: $y = 84{\cdot}7148x^{0{\cdot}9134}$), viviparid snail (▼, short dash line, invasion time: $y = 135{\cdot}0171x - 261{\cdot}159$; feeding time: $y = 0{\cdot}9356x^{3{\cdot}0866}$), ear pond snail (◆, dash-dot line, invasion time: $y = 57{\cdot}8247x - 27{\cdot}8251$; feeding time: $y = 2{\cdot}459x^{0{\cdot}7846}$) and tadpole snail (◇, dot line, invasion time: $y = 27{\cdot}3993x + 25{\cdot}6139$; feeding time: $y = 0{\cdot}00000075x^{9{\cdot}3526}$).

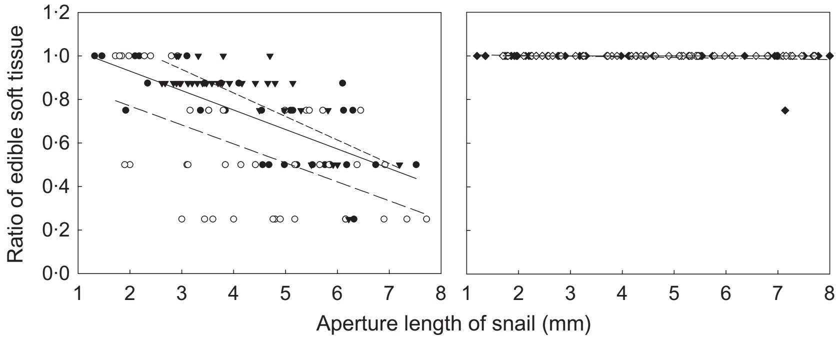

Fig. 3. Regression of the ratio of edible soft tissue of a snail to *Whitmania laevis* (1·0–1·6 g) to the aperture length of apple snail (●, solid line, $y = -0{\cdot}0895x + 1{\cdot}1093$), thiarid snail (○, long dash line, $y = -0{\cdot}0871x + 0{\cdot}9443$), viviparid snail (▼, short dash line, $y = -0{\cdot}108x + 1{\cdot}2619$), ear pond snail (◆, dash-dot line) and tadpole snail (◇).

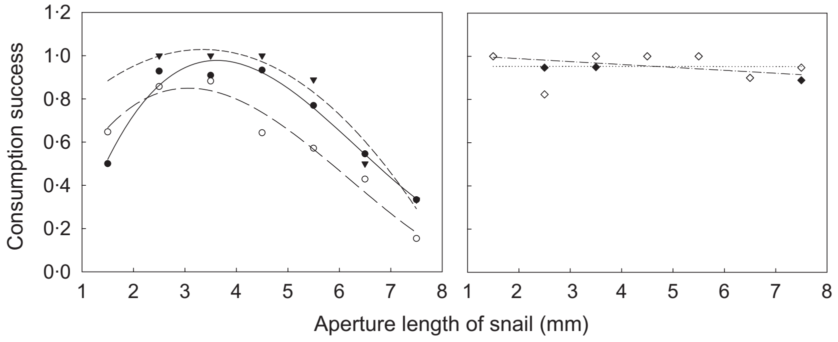

Fig. 4. Regression of the consumption success by *Whitmania laevis* (1·0–1·6 g) to the aperture length of apple snail (●, solid line, $y = 0{\cdot}0099x^3 - 0{\cdot}1884x^2 + 0{\cdot}9748x - 0{\cdot}5516$), thiarid snail (○, long dash line, $y = 0{\cdot}0068x^3 - 0{\cdot}1272x^2 + 0{\cdot}5869x + 0{\cdot}0487$), viviparid snail (▼, short dash line, $y = -0\ 0{\cdot}0427x^2 + 0{\cdot}2853x + 0{\cdot}5513$), ear pond snail (◆, dash-dot line) and tadpole snail (◇, dot line).

Two trends related to the consumption success of *W. laevis*. When leeches preyed on operculated species, i.e. apple snail, thiarid snail and viviparid snail, the consumption success first increased and then declined as prey size increased (nonlinear regression: apple snail, $F_{4,3} = 35{\cdot}72$, $P < 0{\cdot}01$, $R^2 = 0{\cdot}997$; thiarid snail, $F_{4,3} = 21{\cdot}90$, $P < 0{\cdot}05$, $R^2 = 0{\cdot}994$; viviparid snail, $F_{3,3} = 35{\cdot}80$, $P < 0{\cdot}01$, $R^2 = 0{\cdot}998$; Fig. 4). However, when leeches preyed on non-operculated snail species, i.e. ear pond snail and tadpole snail, the consumption success remained constant as snail size increased (linear regression: ear pond snail, $F_{1,5} = 3{\cdot}02$, NS, $R^2 = 0{\cdot}377$; tadpole snail, $F_{1,5} = 0{\cdot}00$, NS, $R^2 = 0$; Fig. 4).

Based on the above results, we first derived a regression equation of the ratio W/T_i against snail size for each snail species. We found that this ratio was positively correlated with the snail size (nonlinear regression: apple snail, $F_{1,29} = 29{\cdot}91$, $P < 0{\cdot}0001$, $R^2 = 0{\cdot}517$; thiarid snail, $F_{1,41} = 53{\cdot}85$, $P < 0{\cdot}0001$, $R^2 = 0{\cdot}574$; viviparid snail, $F_{1,34} = 24{\cdot}62$, $P < 0{\cdot}0001$, $R^2 = 0{\cdot}427$; ear pond snail, $F_{1,48} = 134{\cdot}29$, $P < 0{\cdot}0001$, $R^2 = 0{\cdot}741$; tadpole snail, $F_{1,43} = 100{\cdot}42$, $P < 0{\cdot}0001$, $R^2 = 0{\cdot}705$; Fig. 5) and this pattern was obviously different from the size distribution of consumed operculated snails (based on results from Experiment 1). We then calculated the profitability ($R_s \times R_e \times W/T_i$) of snails

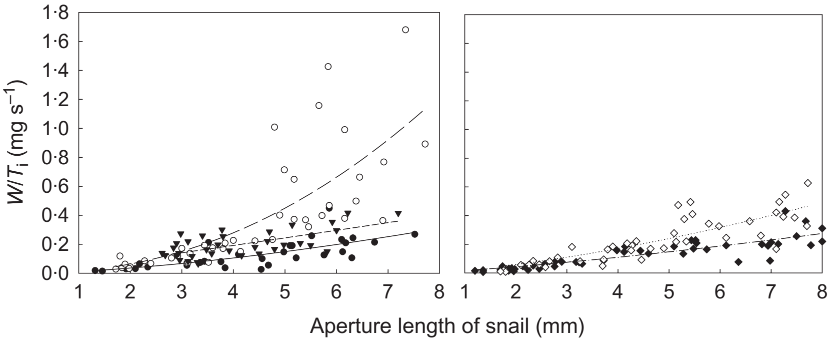

Fig. 5. Regression of the W/T_i [soft tissue weight of a snail/invasion time of *Whitmania laevis* (1·0–1·6 g)] to the aperture lengths of apple snail (●, solid line, $y = 0{\cdot}012x^{1{\cdot}5664}$), thiarid snail (○, long dash line, $y = 0{\cdot}0145x^{2{\cdot}1342}$), viviparid snail (▼, short dash line, $y = 0{\cdot}0435x^{1{\cdot}0704}$), ear pond snail (♦, dash-dot line, $y = 0{\cdot}0173x^{1{\cdot}3309}$) and tadpole snail (◇, dot line, $y = 0{\cdot}0205x^{1{\cdot}5287}$).

for each snail species and found that the prey profitability curves were similar to size distributions of both operculated and non-operculated snails consumed by leeches (based on results of experiment 1: Fig. 6). These results suggested that *W. laevis* may selectively prey on snails of a particular species according to prey profitability.

EXPERIMENT 3: CORRELATION BETWEEN PREY PROFITABILITY AND PREY-SPECIES SELECTION OF *W. LAEVIS*

In all trials, *W. laevis* significantly preferentially selected non-operculated snails over operculated snails (chi-squared homogeneity test: snails of 3·1–4·0 mm, $\chi^2_4 = 45 \cdot 128$, $P < 0{\cdot}0001$; snails of 6·1–7·0 mm, $\chi^2_4 = 26 \cdot 165$, $P < 0{\cdot}0001$; Fig. 7). In addition, profitability of snails significantly differed among the five snail species in both size classes (Kruskal–Wallis one-way ANOVA: snails of 3·1–4·0 mm, $H_4 = 14{\cdot}633$, $P < 0{\cdot}01$; snails of 6·1–7·0 mm, $H_4 = 13{\cdot}166$, $P < 0{\cdot}025$, Fig. 7). However, according to a Dunn test comparison, the rank of the prey profitability among the five snail species did not correlate with the prey-species preference of *W. laevis*. These results suggest that *W. laevis* do not prefer snails with higher prey profitability, but prefer non-operculated species, irrespective of the prey profitability.

Discussion

In many previous studies (e.g. Juanes 1992; Mascaró & Seed 2000, 2001; Saito *et al.* 2004; review by Sih & Cristensen 2001), the traditional prey profitability (*W/T*) matched with prey size preference of predators. In the case of *W. laevis*, however, the positive correlation between the ratio W/T_i and snail size only matched prey size preference in non-operculated snails, but not in operculated species. This implies that there are factors, besides energy gain and time cost, that influence prey-size selection by *W. laevis*. Our results indicated that consumption success played an important role in prey-size selection by leeches. This varied when leeches preyed on different-sized operculated snails, while it remained at 100% when leeches preyed on non-operculated snails. This result indicated that the consumption success in terms of prey vulnerability was significantly different, even in conspecific snails of different sizes, and should be considered in the estimation of prey profitability as Schoener (1971) did. In addition, the variable consumption success in our study agreed with the classification of predator-prey relative mobility and conclusions by Sih & Cristensen (2001). That is, as the mobile insect predator versus insect prey, *W. laevis* should be considered as a predator preying on mobile prey, and the prey vulnerability would be variable because of the variation of mobility among prey items. According to the analysis of Sih & Cristensen (2001), prey selection of predators consuming highly mobile prey did not fit the prediction of the optimal foraging model because of variable prey vulnerability resulting from high prey mobility. However, our result showed that the optimal foraging model can probably predict the prey selection of a predator on highly mobile prey if the consumption success relating to prey mobility is accounted for in the estimation of prey profitability. We even suggest that in addition to prey mobility there may be other factors, e.g. defense ability, which influence the capture or consumption success of a predator. The consumption success or capture success should therefore be included in the estimation of prey profitability, irrespective of the predator type and the prey mobility.

In previous studies on prey profitability (e.g. Elner & Raffaelli 1980; Lawton & Hughes 1985; Juanes 1992; Mascaró & Seed 2000, 2001; Roger, Coderre & Boivin 2000; Saito *et al.* 2004), predators were assumed to have consumed the entire soft tissues of their prey. However, part of the prey body, such as the shells and exoskeletons in invertebrates, may be difficult or even impossible to be consumed by a predator. In our result, the foot of operculated snails, especially the part attached to the inside of the operculum, was the main part of soft tissue that was not consumed by leeches. Furthermore, the unconsumed portions of tissue increased – from only the part attached on the inside of the operculum to the entire foot of a snail – as the size of operculated snails increased. We suggested that the compact muscular and connective tissue in the portion of tissue attached to the inside of the operculum and also to the foot of operculated snails (especially in larger snails) is firm and tough, and thus difficult for *W. laevis* to consume because leeches are not able to tear the tissue of prey into pieces and can only swallow soft tissue of prey using their attenuated head and small mouth. As the edible portion of snails represents the actual obtainable energy of the prey to the predator, and decreases proportionately with the snail size in operculated species, this should more or

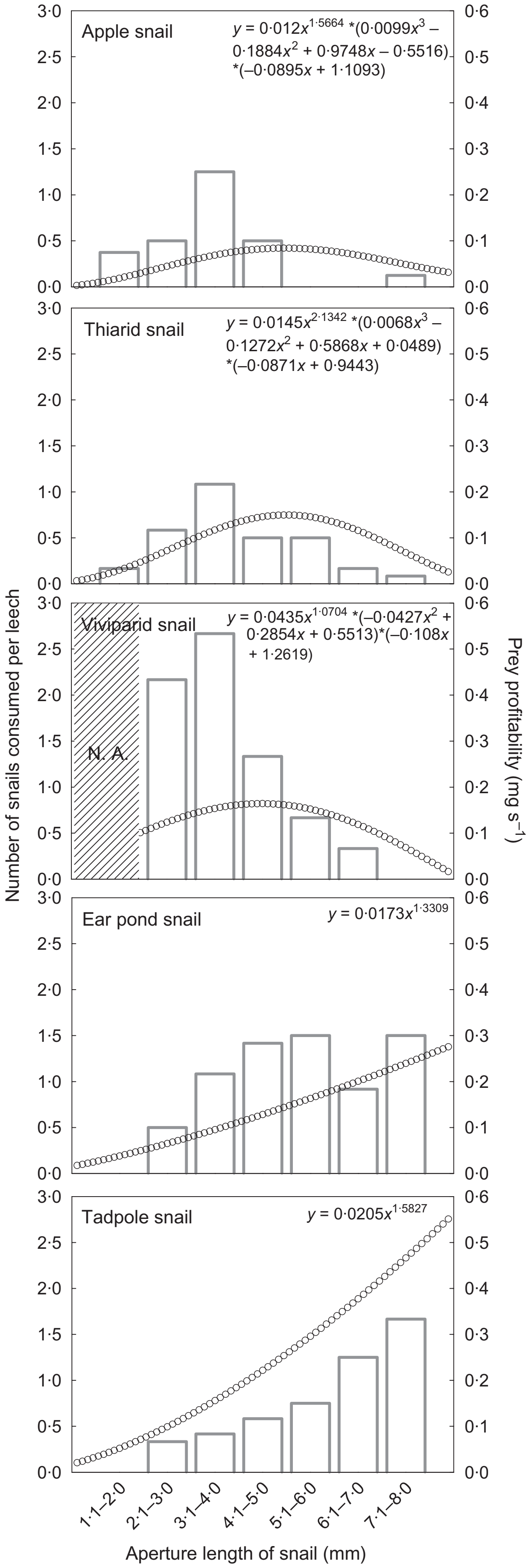

Fig. 6. Prey profitability (circle line, right score axis) of apple snail, thiarid snail, viviparid snail, ear pond snail and tadpole snail to *Whitmania laevis* (1·0–1·6 g). The bars are the distributions of mean numbers (left score axis) of different-sized snails consumed by *Whitmania laevis* in 72 h, which are the black bars shown in Fig. 2.

less influence the prey selection of leeches. As a consequence, we included the edible portion of prey snails in our estimation of prey profitability, and the prediction of prey profitability coincided with the prey size preference of *W. laevis,* for both operculated and non-operculated snail species.

In previous studies, the operculum was found to be an important defense against shell-invading predatory leeches (Brönmark & Malmqvist 1986; Kelly & Cory 1987). This is a primary reason for the different results, obtained in our experiments, when *W. laevis* preyed on operculated and non-operculated snails. Operculated snails were able to resist the invasion of *W. laevis* into their shells by steadily holding the operculum in place, and thus decreasing the consumption success of *W. laevis*. This was especially the case in large snails that had greater strength and in small snails that had less inner-shell space in which *W. laevis* was able to push the operculum. On the contrary, non-operculated snails only relied on anti-predator behaviours, e.g. rotating and shaking, as a protection against predation. A previous study by Brönmark & Malmqvist (1986) indicated that, although these anti-predator defenses of non-operculated snails were partially effective against the predatory rhynchobdellid leech *G. complanata*, maximum efficiency was mainly attained at the stage of encounter; thus the strategy could only delay the attachment of leeches onto shells and were, according to our observations, almost completely ineffectual at preventing consumption by *W. laevis*. Hence, in our study we found that non-operculated snails were always consumed successfully by leeches. The consumption success of *W. laevis* was therefore different in different-sized snails of operculated and non-operculated species.

In addition, with the effective defense of operculum, the numbers of snails consumed by leeches was generally less in operculated snails than in non-operculated snails. An unexpected result, however, is that the number of viviparid snail consumed by *W. laevis* was similar to that of non-operculated species. Because viviparid snails of < 4·0 mm were born lately and their opercula were thinner and softer than those of other operculated snails (e.g. the apple snail) of the same size (Y.-T. Lai, unpublished data), the resistance ability of viviparid snails of < 4·0 mm was lower than that of non-operculated snails. We hypothesized that this physical restriction led to a higher number of viviparid snails being consumed by *W. laevis*, resulting in a considerable amount of snails of < 4·0 mm being present in the size distribution of viviparid snails consumed by *W. laevis.* Results from our experiments lent support to this hypothesis. Furthermore, these results, relating to defense by the operculum, also confirmed that it would be better to take capture and consumption success in account in the estimation of prey profitability because there may be some factors other than prey mobility (for example,

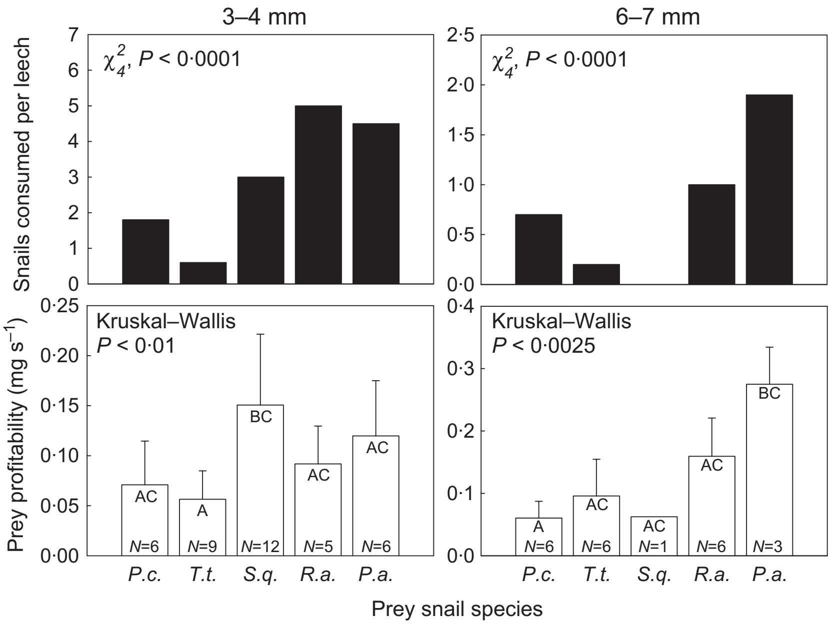

Fig. 7. The numbers of 3–4 and 6–7 mm snails of five snail species consumed by *Whitmania laevis* (1·0–1·6 g) in 72 h and the prey profitability of the five snail species to *W. laevis*. Values in the top figures are the mean numbers of snails consumed by a leech in 72 h, while values in the bottom figures are the mean ± SE of prey profitability. Capital letters on the top inside of the bars in the bottom figures indicate the differences of the means examined by Dunn test comparison.

defense ability of operculum) that can cause differences in prey vulnerability among different prey items.

The invasion time chosen as the currency of foraging cost in the estimation of prey profitability seemed appropriate in our study. In addition, in some trials we observed that leeches retracted their heads, and shortened and twisted their bodies when preying on operculated snails, which implied that they could possibly have received physical injuries from the closing opercula. This observation supported the suggestion that invasive behaviour might expose *W. laevis* to the risk of head injury, and that the invasion also represented a risk of physical harm in addition to being a major energy cost associated with foraging. This observation enhances the importance of invasion time when assessing foraging costs. Such a consideration is similar to that noted by Smallegange & Van Der Meer (2003), who chose 'breaking time' as the currency of foraging costs in crabs because claw damage to a crab, resulting from opening a mussel, was a significant cost. On the other hand, the size of operculated snails favoured by *W. laevis* was smaller than the optimal size for the highest prey profitability predicted in our study. We suggested that because *W. laevis* are exposed to risk of head injury during the invasion of operculated snails, selection of snails smaller than the most profitable size means that leeches confront snails with less strength as well as thinner and softer opercula, thus decreasing the risk of potential head injury. This phenomenon has also been found in studies of prey selection of crabs (Juanes 1992; Seed & Hughes 1995) in which crabs preferred smaller, more easily broken, and thus less profitable, mussels to avoid the risk of costly claw damage that could result from opening an optimal-sized mussel with a thicker shell.

Although our prey profitability with account for consumption success explained prey-size selection by *W. laevis*, it failed to predict the prey-species selection by *W. laevis*. According to our results, *W. laevis* always preferred to prey on non-operculated snails, but the prey profitability of non-operculated species was not always higher than that of operculated species. The consumption success, which might be a highly likely factor for predicting prey-species selection of predators (Sih & Cristensen 2001), was unlikely to profoundly influence prey-species selection in our case because the prey-species selection of *W. laevis* still existed even though consumption success on snails (3·1–4·0 mm) in five snail species was the same. We suggested that there may be two reasons for the disagreement between prey-species preference and our prediction on prey profitability. Firstly, when there are snails of the same profitability, *W. laevis* may prefer to prey on snails of a lower foraging cost. Since the foraging cost, i.e. the invasion time, was always less in non-operculated snails in our results, *W. laevis* would always choose non-operculated snails as prey in cases where both operculated and non-operculated snails of the same profitability were present at the same time. The other possible reason relates to risk of head injury, an important aspect of the foraging cost and probably is taken into account during predation of leeches, which was not included in our estimation of prey profitability. The profitability of operculated snails was therefore overestimated and should be much lower for *W. laevis*. Hence, *W. laevis* would always prefer to prey on non-operculated snails, which actually is more profitable because of the lower foraging cost due to a lower risk of head injury during invasion. Consequently, the absence of the operculum might be a character for *W. laevis* to recognize and associate with more favoured prey, with a possible higher consumption success and prey profitability, lower cost in invasion time, and an inevitably lower risk of head injury. This phenomenon – that a character is used by a predator to recognize the valuable prey – has also been found in studies of crabs, in which Mascaró & Seed (2000, 2001) found that the minimum dimension of the bivalve's shell was an important feature for crabs to recognize in order to make assessments of prey value.

Compared to other predatory leeches, *W. laevis* is the first leech species with prey selection that fits the prediction of prey profitability in an optimal foraging model. Although the foraging ecology and prey utilization of rhynchobdellid and arhynchobdellid predatory leeches have been tested previously (e.g. Davies, Wrona & Linton 1982; Brönmark & Malmqvist 1986; Wrona & Calow 1988; Blinn & Davies 1989; Davies & Kasserra 1989; Brönmark 1992; Martin, Seaby & Young 1994; Simon & Barnes 1996; Kreuter *et al.* 2008), prey selection of leeches was examined in only a few studies (Brönmark & Malmqvist 1986; Blinn & Davies 1989; Kreuter *et al.* 2008) and none of these investigated the reason that led to prey selection in leeches. Unlike the sit-and-wait rhynchobdellid leech *G. complanata* that consumes prey with lower anti-predator defenses (Brönmark & Malmqvist 1986; Brönmark 1992), or the erpobdelliform predatory leech *Nephelopsis obscura* that consumes prey with lower mobility or vulnerability (Anholt 1986; Brown & Strouse 1988), *W. laevis* should be able to actively select the prey with higher profitability by choosing optimal sizes of snails and non-operculated species according to our results. The manner in which *W. laevis* is able to distinguish prey sizes or the stage when this is first achieved is not clear. It is highly probable that this is only achieved after encounters with the prey. It is, however, also likely that *W. laevis* can detect and distinguish prey, at least the prey species, by chemosensory ability as is the case for some other predatory leeches (Sawyer 1986; Simon & Barnes 1996; Kreuter *et al.* 2008). If the absence of the operculum is a character used by *W. laevis* to recognize and associate with prey of higher value, it may have evolved to specifically detect, identify and follow non-operculated snails. Further studies are needed on the prey detection ability of this species.

Our study indicated the importance of consumption success. It has been suggested that this should be included in the estimation of prey value but has rarely been considered in previous studies when estimating prey profitability in the optimal foraging model. When we accounted for consumption success in the estimation of prey profitability, this led to a successful prediction of optimal foraging model to prey-size selection of *W. laevis* preying on freshwater snails. Since *W. laevis* is regarded as a predator that preys on mobile prey [according to the classification of Sih & Cristensen (2001)], it is highly probable that, with the inclusion of consumption success in the estimation of prey profitability, the optimal foraging model will be able to predict the prey selection of other predators that consume mobile prey with variable consumption success. In previous studies the model was unsuccessful in making this prediction. On the other hand, *W. laevis* exhibited prey-species selection, preferring non-operculated snail species, and this prey-species selection was poorly predicted by our estimation of prey profitability. However, the optimal foraging model may be successful in predicting prey-species selection of *W. laevis* when taking additional foraging costs into account when estimating prey profitability. Consequently, in our study we suggested that the estimation of prey profitability with account for consumption success should be considered in future optimal foraging studies to predict prey selection of predators. This would be particularly applicable to those predators that consume mobile prey with variable consumption success.

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