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Prey selection by molluscivorous cichlids foraging on a schistosomiasis vector snail, *Biomphalaria glabrata*

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Summary. This paper considers prey size selection by four molluscivorous cichlids feeding on the intermediate host snail of *Schistosoma* parasites, *Biomphalaria glabrata. Haplochromis ishmaeli* obtains its prey by crushing the snails between the pharyngeal jaws, whereas *H. xenognathus, H. sauvagei* and *Macropleurodus bicolor* apply both pharyngeal crushing and oral shelling. The fishes crushed significantly more snails with the highest reward in biomass per second of crushing. Oral shelling occurred far less often than pharyngeal crushing. Encounter rates with prey showed significant variations between different size classes of prey. The fish have no overall knowledge of snail availability in a tank. The probability that a snail will be eaten at encounter, calculated from the number encountered and the number eaten, reflects the prey size preference of the fish. Those snails with the highest biomass/crushing-time ratio had the highest probability of being crushed; observed and predicted prey size preferences corresponded well. Although for oral shelling the potential reward in biomass per second is of the same magnitude as for crushing, the probability of successful shelling is very low. Apparently the fish prefer prey with lowest risks.

Key words: Molluscivorous cichlids – Prey selection – *Biomphalaria glabrata*

Molluscivorous fishes have long been suggested as biocontrol organisms of snails that serve as intermediate hosts of trematode parasites such as *Schistosoma* spp. (Anderson & Gobert 1924). Although promising results were obtained in small scale field trials, no attempts have been made to formulate an effective method of using fish in biological control of snails (Slootweg 1985). The need for research in this field is well recognized (Hairston et al. 1975; McCullough 1981; Coates & Redding-Coates 1981).

Since 1977 the *Haplochromis* Ecology Survey Team of the Department of Ecological Morphology of the University of Leiden, The Netherlands, has been studying the species distribution and ecology of the haplochromine cichlid fish in the Mwanza Gulf (Tanzania) of Lake Victoria. Based on stomach contents and morphology these cichlids can be classified into eleven trophic groups which together utilize almost all food resources in the lake (Witte 1981 & 1984a). The four species used in the present study are molluscivores (snail-eaters). This trophic group has two subgroups: oral shellers and pharyngeal crushers (Greenwood 1974).

Oral shellers wrench their prey from the shell by taking hold of the exposed soft parts and shaking fiercely; the snail is extracted or torn apart.

Pharyngeal crushers have a strong pharyngeal jaw apparatus which enables the fish to crush snail shells. The shell fragments are usually separated and ejected after crushing, perhaps to avoid unfavourable effects on buoyancy (Hoogerhoud 1986b).

Some 20 species of snail-eating fishes have been caught in the Mwanza Gulf; half have not yet been described (Witte 1981; Hoogerhoud unpublished work). This diversity of snail-eating fishes provides an opportunity to study their comparative potential as biocontrol organisms against snails. Six fish species have been brought to the Zoologisch Laboratorium at Leiden, of which four were used for this study.

Optimal foraging theory can be an important tool in predicting the ability of snail-eating fish species to reduce snail populations. Of course much other information is required, e.g., population dynamics of snails and fish, but understanding of the foraging behaviour of the fishes is a first step. To gain maximal fitness it is plausible that a fish will optimize its foraging to be able to maximize its food intake. Major contributions to the understanding of fish foraging behaviour under laboratory and field conditions have been made by Werner and co-workers (review of optimal fish foraging: Townsend & Winfield 1985). Stein et al. (1984) examined how shell thickness influences selection by a snail-eating sunfish, *Lepomis microlophus*. The authors used an optimal foraging approach in which prey choice was related to energy and time cost/benefit (C/B) ratios. Selection among snail genera was consistent with differences in shell strength and a time C/B construct, operationally defined as handling time divided by prey dry mass. However, within any snail genus neither shell strength (smallest snails had weakest shells) nor time C/B (largest snails had minimal C/B) provided predictions consistent with results from experiments on selective predation. Stein et al. concluded therefore that no size selection occurred within a genus.

The approach here is based on the classical or first generation optimal foraging models (Krebs et al. 1983). The biomass intake per unit of handling time was calculated from prey dry mass and prey handling time. A fish maximising its food intake should select the prey items with highest reward in prey biomass per second handling time.

Experimental animals

Fish-species

For reasons given by Hoogerhoud (1984) the generic name *Haplochromis* is preferred to the new generic classification of Greenwood (1980).

The oral-shelling species used were *Macropleurodus bicolor* (Boulenger), *Haplochromis xenognathus* Greenwood and *Haplochromis sauvagei* (Pfeffer). Their diet consists mainly of prosobranch snails (mostly *Melanoides tuberculata* and *Bellamya unicolor*) and insects (Greenwood 1974; Katunzi 1983). Fryer & Iles (1972, page 75) described *M. bicolor* as being able to crush snails orally, but I never observed this type of prey handling in more than 100 experiments in tanks. Only the shell apertures were damaged by the oral shelling action. Although oral shelling is thought to be their feeding strategy surprisingly all 'oral shellers' used in the experiments were well able to crush smaller snails pharyngeally. It must be stressed, however, that the common prey species in Lake Victoria have a higher crushing resistance than these snails (Hoogerhoud unpublished work).

Haplochromis ishmaeli Boulenger is classified as a pharyngeal crusher; very occasionally this species also shells its prey. Its diet consists of prosobranch snails and occasionally bivalves (Hoogerhoud 1986b).

All fishes were caught in the Mwanza Gulf (Tanzania) of Lake Victoria in April and May 1984 and flown to the laboratory in Leiden within 24 h. They were fed a combination of minced heart, dry food, *Tubifex* and snails. All species bred successfully, but only wild-caught animals were used in the experiments: Greenwood (1964) and Witte (1984b) have demonstrated significant morphological differences between wild-caught and domestic specimens of the cichlids *Astatoreochromis alluaudi* and *Haplochromis squamipinnis*. These probably epigenetic changes in morphology may be related to the manner of feeding (Hoogerhoud 1986a).

Snails

Biomphalaria glabrata (Say), an intermediate host of *Schistosoma mansoni* in the New World, was reared on fresh lettuce in 200 l polypropylene transportation containers supplied with running tap water at a rate of 200 l a day, and with a 12 h light, 12 h dark regime.

Because of difficulty in extraction, the shells had to be dissolved before the dry shell and dry tissue mass could be calculated. The snails were first dried in 60° C oven for 3 days and weighed to the nearest 0.01 mg. The shells were then dissolved in 10% acetic acid for three days and the bodies were dried and weighed again.

Size selectivity experiments

The relationship between crushing time and snail size

Observations were made on isolated fish kept in 50 × 50 × 50 cm tanks at 26° C. The fish could see each other, which was most helpful in making them more cooperative. In preliminary experiments to determine the relationship between crushing time and snail size, snails were sorted into 0.5 mm size classes and offered in random order of size, five per class. Crushing time was defined as the time a fish needs to crush a snail completely, to swallow it, and to eject the remaining shell fragments. Snail length, defined as the maximum shell diameter (Fig. 1), was measured to the nearest 0.1 mm and crushing times to the nearest 0.1 s. Because satiation might influence the crushing time, observations were made on hungry fish, and stopped before the animal could be satiated; the number of snails necessary to satiate a fish was determined previously. If crushing times exceeded 4 min or snails were rejected, no larger snails were offered.

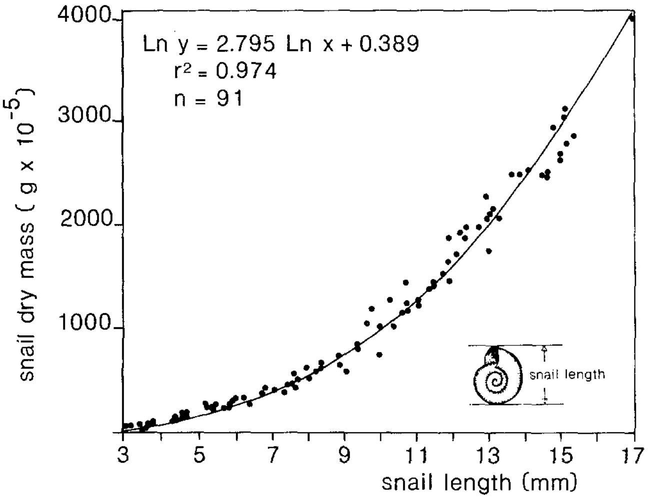

Fig. 1. Relationship between snail dry tissue mass and snail size. ('y' = snail dry mass (g × 10^{-5}); 'x' = snail length (mm)

Experimental set-up

Snails were divided into 13 1-mm size classes from 3 to 15 mm, the size range of snails which could successfully by reared in the laboratory; in natural habitats they can grow larger (±25 mm). Snails smaller than 3 mm were too small to handle. In order to study the effect of the quantity of offered food on diet composition, snails were offered in quantities of 2, 5 and 10 per class. The total number offered at once per experiment was therefore 26 (2 × 13), 65 (5 × 13), or 130 (10 × 13). Two snails per class is not enough to satiate a fish of the size used; 10 per class is more than enough. One experiment was carried out every day, hence starvation time before an experiment was about one day. The fish were allowed to eat for 1.5 h, the maximum time spent foraging in previous experiments, after which they showed no further interest. The remaining snails were recovered and measured. Snails not recovered were considered to be crushed. From previous observations, empty or half-empty shells were scored as shelled orally. Experiments were repeated four or five times with every fish for all three food levels. Five individual *H. ishmaeli* were tested, five *M. bicolor*, five *H. xenognathus* and four *H. sauvagei*. Some series of experiments could not be completed because of the sudden death or illness of some individuals; the incomplete data are given.

Table 1. Regression lines (least squares) of crushing times v. snail length for individual fishes

Fish	SL[a]	Regression line[b]	R^2	n
H. ishmaeli	100	Ln $Y=0.37\,X+0.15$	0.75	80
	114	Ln $Y=0.32\,X+0.16$	0.83	90
	115	Ln $Y=0.31\,X+0.40$	0.70	80
	120	Ln $Y=0.34\,X-0.05$	0.78	71
	123	Ln $Y=0.39\,X-0.38$	0.76	65
M. bicolor	88	Ln $Y=0.67\,X-0.89$	0.74	35
	98	Ln $Y=0.56\,X-0.99$	0.74	53
	114	Ln $Y=0.49\,X-0.66$	0.77	63
H. xenognathus	97	Ln $Y=0.86\,X-1.95$	0.84	40
	100	Ln $Y=0.60\,X-0.67$	0.70	36
	100	Ln $Y=0.53\,X-0.51$	0.72	53
	102	Ln $Y=0.63\,X-0.67$	0.66	35
	107	Ln $Y=0.54\,X-0.83$	0.80	52
H. sauvagei	92	Ln $Y=0.47\,X-0.52$	0.77	56
	95	Ln $Y=0.49\,X-0.05$	0.68	57
	101	Ln $Y=0.49\,X-0.19$	0.73	31
	102	Ln $Y=0.40\,X+0.39$	0.67	50

[a] SL = standard length fish (mm)

[b] All regression lines are significant; $P<0.001$ Y = crushing time (s); X = snail length (mm)

Results

The crushing time versus snail length curves follow a single-logarithmic best fit regression line (least squares, all highly significant, Table 1). Snail dry tissue mass is a double-logarithmic function of snail length (Fig. 1). This function is divided by the crushing-time function for every individual fish to calculate the biomass intake per unit of crushing time for all snail sizes (Figs. 2–5, curves). All curves have a maximum indicating the snail size with the highest reward per second crushing: a fish maximizing its intake rate per second should select those sizes.

H. ishmaeli (Fig. 2) were able to eat a wide size range of snails; only the largest were usually not eaten. Selectivity increased with increasing numbers of prey offered. (Read histograms from bottom to top for each individual fish.) For all five specimens the number of snails eaten per size class significantly corresponds to the snail dry mass obtained per second crushing for these size classes: the fishes eat most of the most profitable snail size class (Fig. 2).

The feeding behaviour of the so-called oral shelling species deviated strongly from that expected, many more snails were crushed than shelled (Figs. 3–5). Even at the lowest prey density, some fish did not shell a single snail (*Macropleurodus bicolor*, 117 mm standard length (further referred to as M.b.117); *Haplochromis xenognathus* 107 mm standard length (= H.x.107); *Haplochromis sauvagei* 101, 102 mm standard length (= H.s.101, H.s.102) (Figs. 3–5). These fishes could not have been satiated after the experiment because the number of snails eaten was insufficient.

With increasing number of snails offered, selectivity in crushing increased, as with *H. ishmaeli*.

Seven out of ten actually shelling fishes shelled relatively fewer snails at higher snail densities (Figs. 3–5; $P<0.05$).

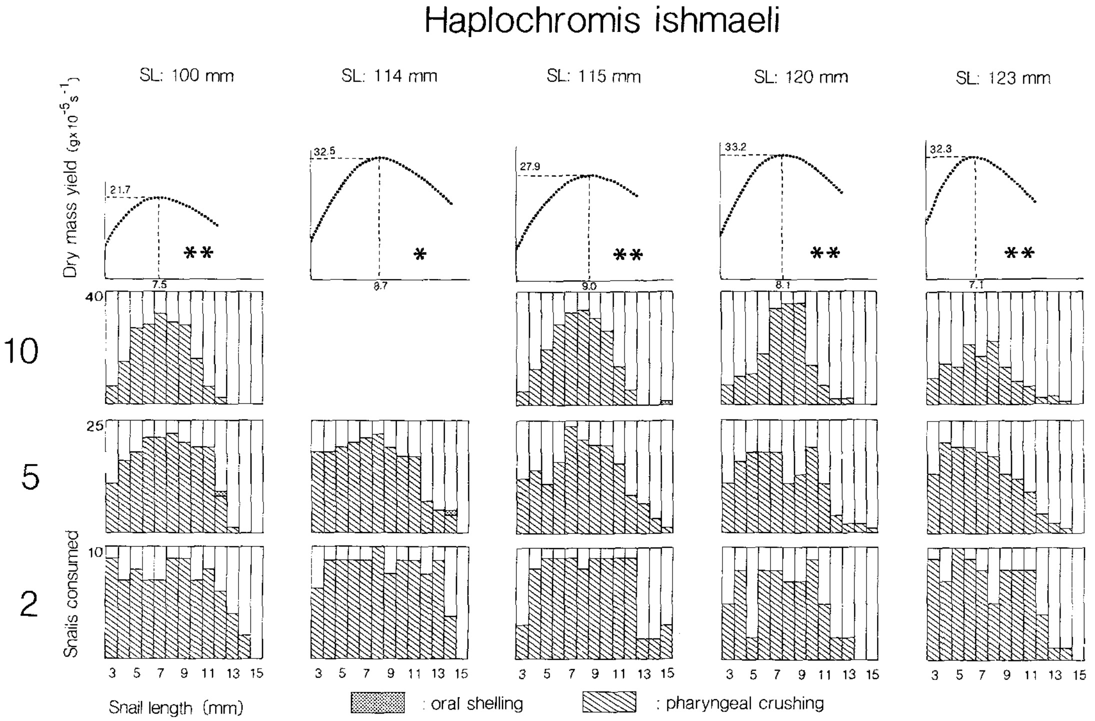

Fig. 2. *Haplochromis ishmaeli*. Individual standard lengths (SL) are shown at top. Top figures: snail dry mass obtained per s crushing indicating snail size with highest reward per s. Histograms depict number of snails eaten when offered 10 snails per size class per experiment (upper row; results are the sum of 4 experiments per fish), 5 snails per size class per experiment (middle row; sum of 5 experiments per fish), 2 snails per size class per experiment (lower row; sum of 5 experiments per fish). Asterisks indicate a significant correlation between snail dry mass obtained per second crushing (top figures), and the number of snails eaten when offered 10 snails per size class (except for SL 114, where results of 5 snails per size class were tested). Spearman rank correlation coefficient, * $P<0.05$; ** <0.01

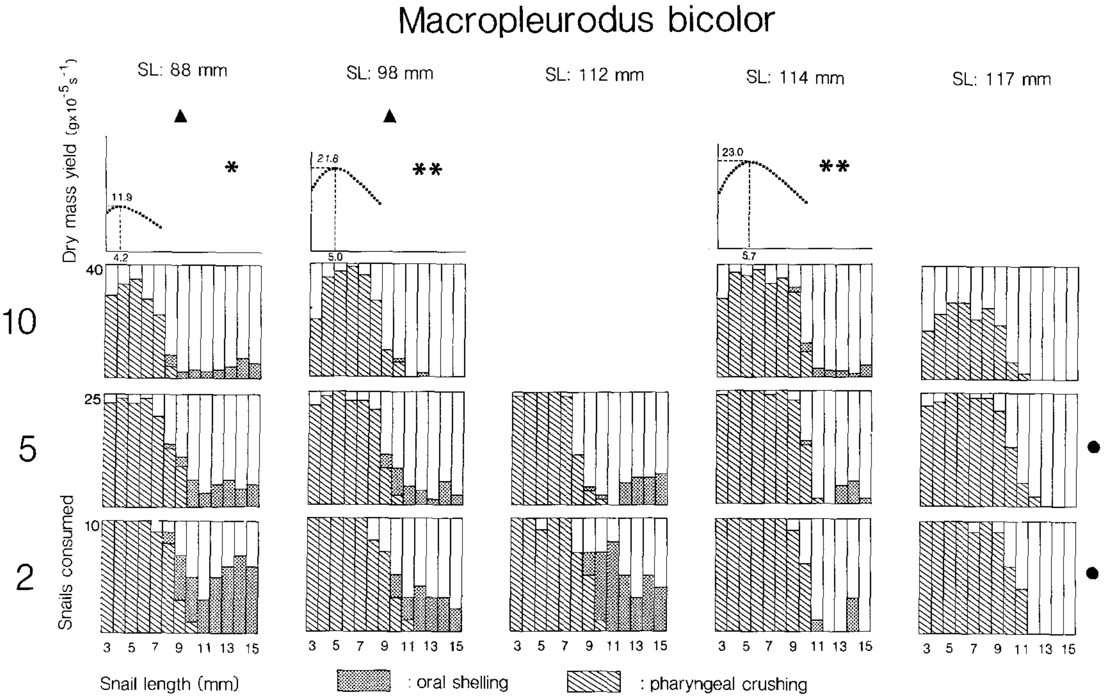

Fig. 3. *Macropleurodus bicolor.* As Fig. 2. A triangle indicates a fish that relatively shelled significantly fewer snails at higher snail densities (Spearman rank correlation, $P<0.05$). A dot indicates a series of experiments (horizontal row) in which smaller fish shelled significantly more snails than did larger ones (Spearman rank correlation, $P<0.05$)

In two out of three experiments, small *M. bicolor* shelled more snails than larger specimens did (Fig. 3). For *H. xenognathus* this only applies for one series of experiments with 5 snails per class (Fig. 4). (This corresponds with observa tions on *M. bicolor* in Lake Victoria: Hoogerhoud pers.-comm.) For *H. sauvagei* this trend was not found significant (Fig. 5) because, as for *H. xenognathus* (Fig. 4) the size range of fishes was too small.

The "oral-shelling" species select smaller snails and do not crush snails as large as *H. ishmaeli* does.

Discussion

At first sight, comparison of prey-size selection and snail dry mass obtained per second crushing shows that the oral shellers display a behaviour similar to that of the pharyngeal crusher *H. ishmaeli.* Ten out of twelve tested fishes significantly selected snails according to the reward in dry mass per second crushing. A more critical inspection of the data reveals slight inconsistencies. The prey size class eaten most by *M. bicolor* and *H. xenognathus* is somewhat larger than predicted, although the relationship between reward and number of snails eaten is still significant. *H. sauvagei* eats smaller snails; for two fish the relationship between number of snails eaten and reward in dry mass per second was not significant. This might imply that these fish do not select snails on a biomass/time ratio only. However, the results do not allow any further interpretation because no direct observations were done on encounter rates. Stein et al. (1984) assumed that a fish had an overall knowledge of the snails offered in a tank. This assumption implies that encounter rates can be neglected. But the necessity of including encounter rates can be defended; larger snails are more visible and therefore the encounter rates with these snails will be higher. This might also explain the inconsistencies in the results. If a fish eats as many snails from classes 'A' and 'B', but the encounter rate for 'B' is higher, automatically this will result in a higher probability of 'A' being eaten at encounter.

This uncertainty about the implications of encounter rates led to the formulation of the next set of experiments. Optimal foraging theories predict that a forager will always include the most profitable prey in its diet, no matter how abundant other prey items may be, i.e., the probability of the most profitable prey being eaten when encountered must be 100%, independent of encounter rates with other prey items (review in Hart 1986). So, in order to find the prey size preference of a fish, it is necessary to determine not only the number of prey eaten, but also the number of encounters with all prey sizes. With these data it is possible to see whether a fish is choosing the most profitable prey according to the biomass/time ratio.

Direct observations on pharyngeal crushing

Experimental set-up

A second series of experiments, to determine encounter rates, prey choice, and crushing times, was carried out with two specimens of *H. ishmaeli* (standard lengths 120 and 123 mm; coded H.i.120 and H.i.123) and two of *M. bicolor* (standard lengths 94 and 117 mm; coded M.b.94 and M.b.117). (The specimens are not the same as in the earlier experiments.) These two species were chosen because in the experiments *H. ishmaeli* is the most pronounced pharyngeal crusher and *M. bicolor* performed best as an oral sheller. Each fish was offered 20 and 7 snails per size class. To distinguish among the different size classes when observing, snails of the 3, 7, 11 and 15 mm classes were offered first, then in a second round of experiments the 5, 9, 13 and

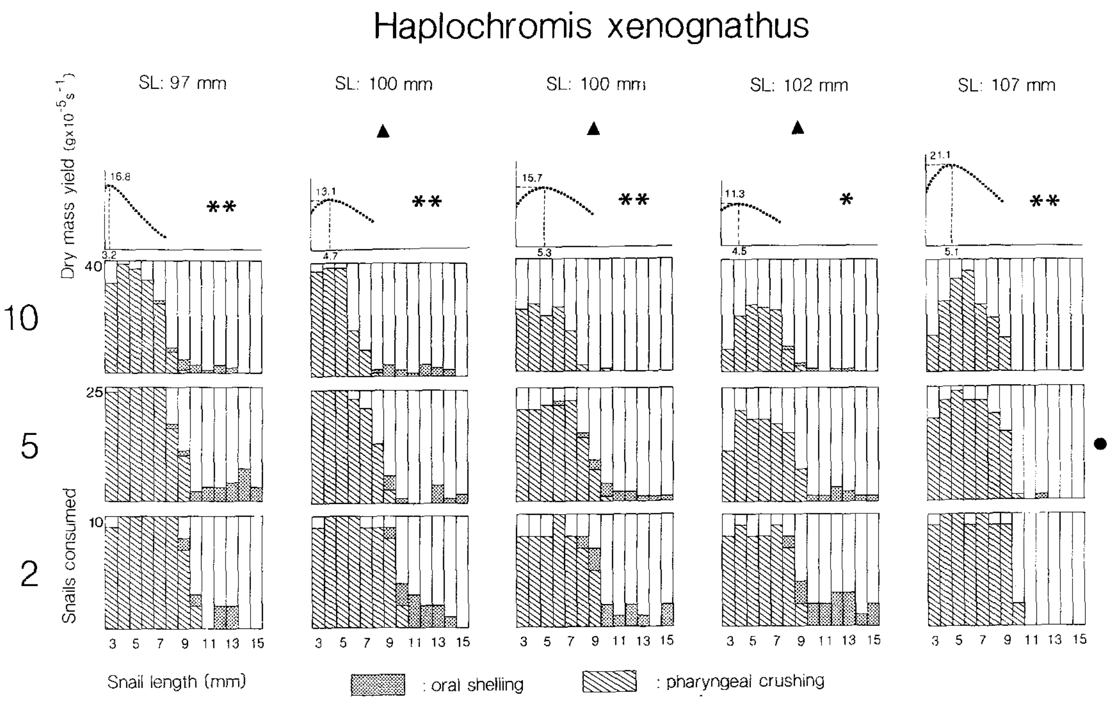

Fig. 4. *Haplochromis xenognathus*. As Figs. 2, 3

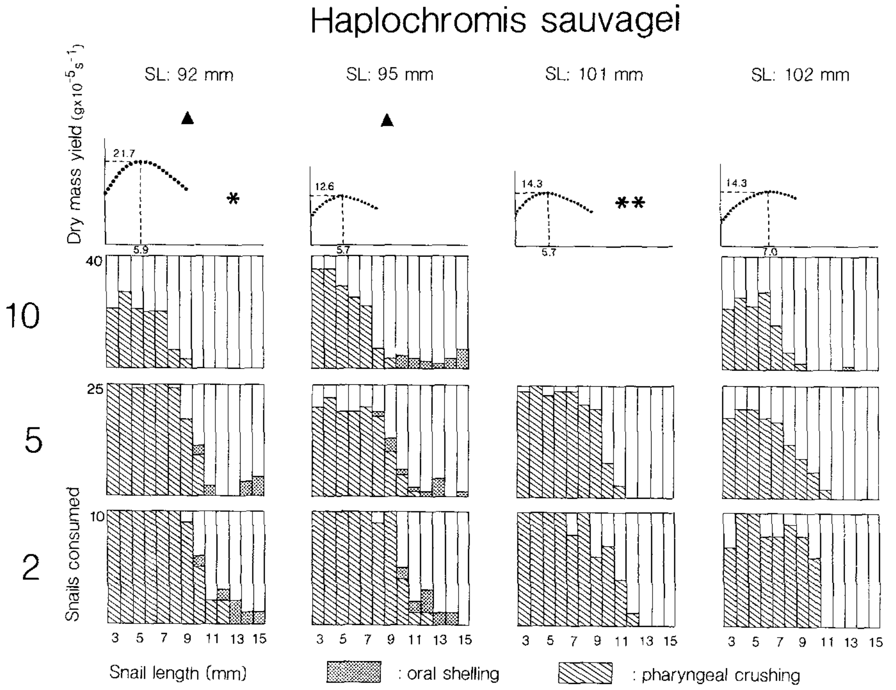

Fig. 5. *Haplochromis sauvagei*. As Fig. 2, 3. The asterisks for fish SL 101 apply to 5 snails per size class (see Fig. 2)

15 mm classes were offered. A behaviour recorder registered the number of encounters and time involved with each size class. Four types of encounters could be distinguished:

- *Attention:* the fish looks at a snail and may approach it.
- *Touching or biting:* the snail is pushed or partly taken into the mouth.
- *Crushing:* the fish attempts to crush a snail. The result can be recorded as successful or unsuccessful.
- *Oral shelling:* the fish attempts to shell the snail. This handling can also be recorded as successful or unsuccessful.

Often a sequence of behavioural acts was directed towards the same snail, e.g., attention, bite and crush. This kind of sequence was of course considered as one encounter, of which the duration was the sum of the three different actions. An experiment lasted until the fish paid no more attention to the snails, or until one size class was completely eaten. After the experiment a fish was allowed to eat snails until satiated. One experiment was carried out per day. Cichlids in general are sensitive to disturbances in the environment. Therefore the fish had to be at a high level of hunger to be cooperative (about 22 h starvation versus 1.5 h

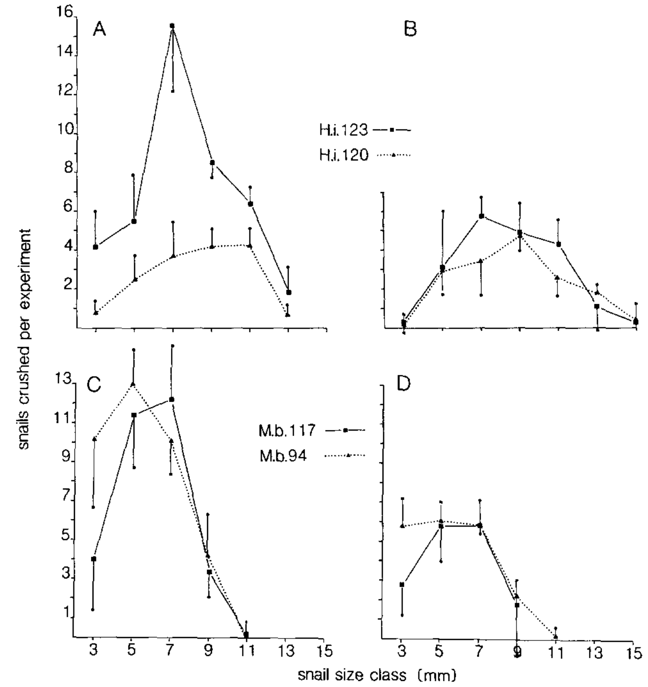

Fig. 6A–D. Mean number of snails in each size class crushed per experiment; bars indicate standard deviation. Lines connect points for display only, and do not indicate any relationship. N.B: the results are summed over two series of experiments; figures in parenthesis are number of experiments for each fish. **A** *H. ishmaeli*, offered 20 snails per size class; fish H.i.123 (5+6), H.i.120 (6+6). **B** *H. ishmaeli*, offered 7 snails per class; fish H.i.123 (7+8), H.i.120 (5+5). **C** *M. bicolor*, offered 20 snails per class; fish M.b.117 (9+5), M.b.94 (5+8). **D** *M. bicolor*, offered 7 snails per class; fish M.b.117 (5+5), M.b.94 (6+5)

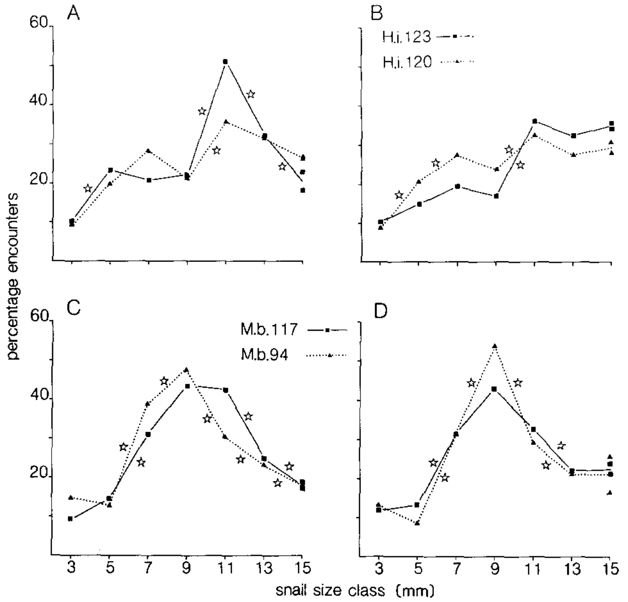

Fig. 7A–D. Encounters with each snail size class, expressed as percentage of total number of encounters. Stars indicate a significant difference in number of encounters between two size classes (ANOVA, $P<0.05$). Except where such significant differences exist, lines connecting points are for display only, and do not indicate any relationship. N.B: the figures are summed over two series of experiments; the total percentage of encounters is therefore 200%. Figures in parenthesis are total numbers of encounters in each series, for each fish. **A** *H. ishmaeli*, 20 snails per size class (H.i.123: 526+389; H.i.120: 282+320). **B** *H. ishmaeli*, 7 snails per size class (H.i.123: 251+352; H.i.120: 214+175). **C** *M. bicolor*, 20 snails per size class (M.b.117: 548+419; M.b.94: 217+222). **D** *M. bicolor*, 7 snails per size class (M.b.117: 516+681; M.b.94: 338+381)

in the experiments of Stein et al. 1984). Although hungry animals are generally considered to be less selective, the results of the experiments were considered satisfactory.

Results

The four fishes obtained their food mostly by crushing the snails. At 20 and 7 snails per class, *M. bicolor* only occasionally shelled a snail orally. In 48 experiments 679 snails were eaten, of which 15 were shelled. Accordingly the results presented below omit data on shelling. Because the data of the two series of experiments agreed closely, all results are presented in combined figures. The connecting lines between classes in Figs. 6–11 do not imply any relation except when levels of significance are given. Figure 6 displays the number of snails eaten per experiment. When offered 20 snails per class, three fishes (M.b.117, M.b.94 and H.i.123) ate more snails (*T*-test, $P<0.01$), compared to the experiments with 7 snails per class. H.i.120 ate the same number at both densities. M.b.94 ate more snails than M.b.117 at both densities. H.i.123 ate more snails than H.i.120 with 20 snails per class (*T*-test, $P<0.05$). Both *H. ishmaeli* ate snails from all size classes. The *M. bicolor* specimens crushed snails up to the 11 mm class.

The percentage distribution by snail size class of the total number of encounters (Fig. 7) does not show equal encounter rates for all classes. All results differed significantly from the hypothesis of equal encounter rates (ANOVA, $P<10^{-6}$). M.b.94 has a significant peak of encounters with class-9 snails at both densities. M.b.117 has a less pronounced but also significant peak of encounters with class-7, -9, -11 snails. *H. ishmaeli* displayed a significant increase in number of encounters with snail size class, except for H.i.123 at 20 snails per class, showing a significant peak in encounter rate with class-11 snails.

The probability that a snail will be eaten at encounter can be calculated for any size class by dividing the number of successful crushing attempts by the number of encounters (Fig. 8). This Figure gives an impression of the real prey size preference of a fish. The probability that a snail will be eaten by *M. bicolor* (Fig. 8C, D) shows a more pronounced prey size preference than the data on the number of snails eaten suggest (Fig. 6C, D). This can be explained by the differences in encounter rates. Because the number of encounters with class-7 snails is higher compared to class 5 snails (Fig. 7C, D), the probability class-7 snails being eaten at encounter is smaller when the same number of snails is eaten. Both *M. bicolor* showed a preference for class-5 snails, which had a more than 90% probability of being eaten at encounter. The results for *H. ishmaeli* are less clear, but H.i.120 appears to have a preference for class-9 snails; H.i.123 prefers class 7 snails at high density, but at low density class-9 snails had an equal chance of being eaten.

The mean crushing times for each size class can be derived (Table 2). No significant differences were found between the two *H. ishmaeli*, except for class-9 snails. M.b.117 had significantly shorter crushing times than M.b.94, which

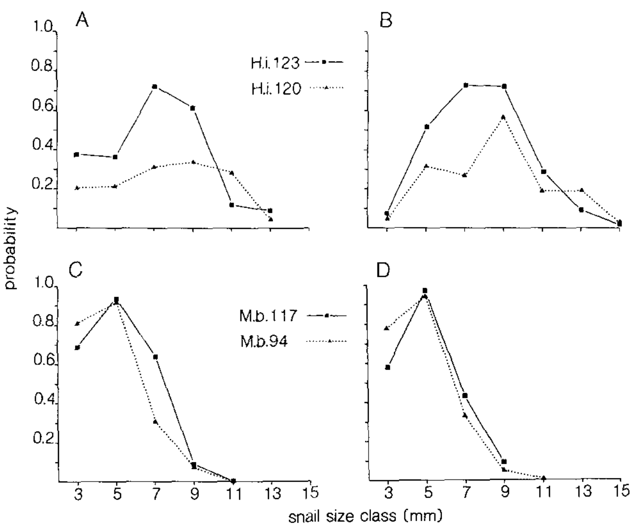

Fig. 8A–D. The relationship between the size of a snail and the probability that it will be crushed at encounter. Only successful crushing attempts are included: compare Fig. 10. *H. ishmaeli*, **A** 20 snails per class; **B** 7 snails per class. *M. bicolor*, **C** 20 snails per class; **D** 7 snails per class

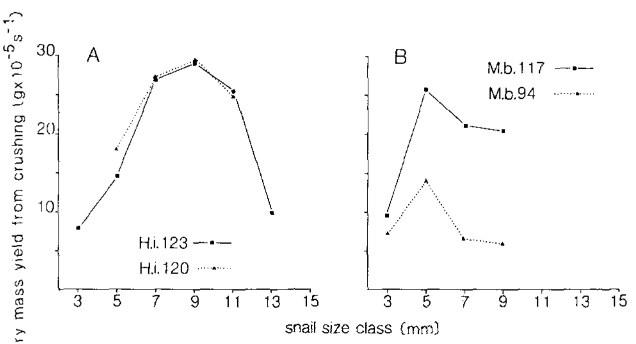

Fig. 9A, B. The relationship between snail size and snail dry mass obtained per second crushing. **A** *H. ishmaeli*. **B** *M. bicolor*

can be explained by the size difference of the fish. Both *H. ishmaeli* had shorter crushing times than *M. bicolor* when eating large snails (class 9). Differences in crushing times between snail size classes for the same individual fish are mostly significant, the larger size classes requiring longer crushing times.

Using the snail dry mass (Fig. 1) and the mean crushing time (Table 2), the biomass/time ratio can be calculated. The maximum amount of snail dry mass per second crushing is obtained if *H. ishmaeli* eats class-9 snails and *M. bicolor* eats class-5 snails (Fig. 9). The results may be biased by the greater number of larger snails rejected after a crushing attempt. Shell strength can vary considerably between similar-sized snails (Hoogerhoud 1986b). Provided that a fish is capable of testing the shell's strength in a few seconds, and thus able to select weaker shells, the actual crushing time for these larger snails should be higher, hence the reward per second crushing lower. This especially holds for M.b.117 and M.b.94 which often rejected class-9 and -11 snails (Fig. 10); H.i.120 and H.i.123 only rejected the largest class-13 and -15 snails.

Figure 11 shows the time spent per encounter (not counting the crushing attempts). Both *H. ishmaeli* showed a consistent pattern in all experiments, spending between 0.1–0.3 s per encounter, irrespective of prey size. There were no significant differences in time spent per class. Except for M.b.117 at 20 snails per class, *M. bicolor* showed significant differences in time spent per encounter between snail size classes (ANOVA, $P < 0.05$). M.b.94 spent significantly more time than *H. ishmaeli* on class-9 snails at 20 snails per class, and on class-9, -11 and -13 snails at 7 snails

Table 2. Mean crushing times (s) in each snail size-class, for individual fishes (standard length, mm, in parenthesis)

Fish	Snail size class (mm)										
	3		5		7		9		11		13
H. ishmaeli (123)											
Mean crushing time (s)	6.6		12.3		15.6	**	27.9	*	54.5	**	219.5
Standard deviation	3.7		7.5		7.9		19.1		32.0		87.6
Number of observations	16		12		60		9		30		11
H. ishmaeli (120)							*				
Mean crushing time (s)	–		10.0	*	15.5	*	27.3	**	55.6		–
Standard deviation	–		2.7		10.2		10.7		26.2		–
Number of observations	–		7		28		13		28		–
M. bicolor (117)			*				**				
Mean crushing time (s)	5.5		7.0		19.9		39.6		–		–
Standard deviation	2.3		3.4		10.5		15.4		–		–
Number of observations	30		74		83		23		–		–
M. bicolor (94)			**		**		**				
Mean crushing time (s)	7.3	**	12.7	**	63.7	**	134.1		–		–
Standard deviation	3.6		6.7		31.8		83.6		–		–
Number of observations	67		76		98		26		–		–

* Indicate a significant difference in mean crushing time between different snail size classes per fish (horizontal), and between different fishes per snail size class (vertical). (ANOVA, * $P < 0.05$; ** $P < 0.001$)

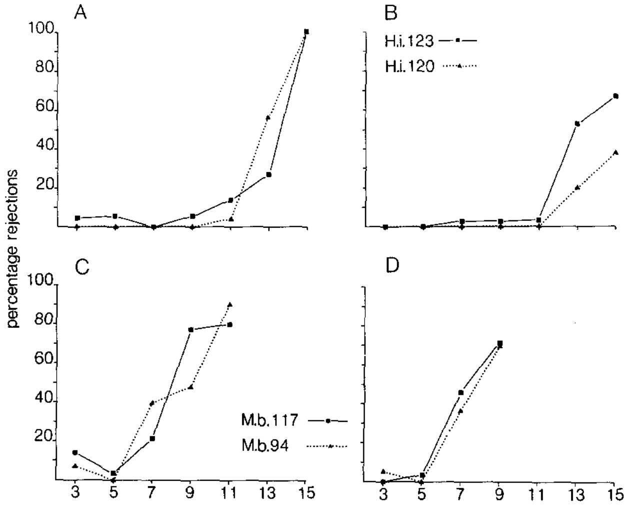

Fig. 10 A–D. The relationship between snail size and resistance to crushing, expressed as percentage rejections of the total number of crushing attempts. *H. ishmaeli*, **A** 20 snails per size class; **B** 7 snails per size class. *M. bicolor*, **C** 20 snails per size class; **D** 7 snails per size class

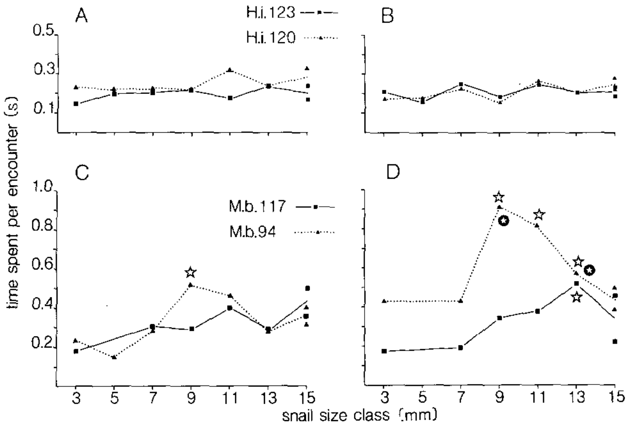

Fig. 11 A–D. The relationship between snail size and mean time spent per encounter, excluding crushing attempts. Stars indicate size classes on which *M. bicolor* spends significantly more time per encounter than *H. ishmaeli*. Stars in dots indicate significantly more time spent per encounter at 7 snails per size class than at 20 snails per class (ANOVA, $P<0.05$). *H. ishmaeli*, **A** 20 snails per size class; **B** 7 snails per size class; *M. bicolor*, **C** 20 snails per size class; **D** 7 snails per size class

per class. This fish also spent significantly more time on class-9 and -13 at low snail densities than at high density. M.b.117 only spent more time than *H. ishmaeli* on class-13 snails at 7 snails per class.

Discussion

Encounter rates differ considerably among size classes and therefore cannot be neglected in determining the prey size preference of a fish. The size preference is not necessarilly reflected in the number of snails eaten from any size class. This finding might explain the earlier small aberrations in predicted prey size preference and number of snails eaten (Figs. 3–5). The predicted and the observed prey size preferences match in this second series of experiments, however, except for H.i.123, 20 snails per class.

The increasing number of encounters (Fig. 7) with class-3 to class-9 snails for *M. bicolor* and class-3 to class-11 snails for *H. ishmaeli* can be explained by visibility; the larger snails are spotted earlier than the smaller ones. The decreasing encounter rates for larger snails in all experiments for *M. bicolor*, and once for *H. ishmaeli*, must be caused by another phenomenon. The fish probably do see the larger snails but do not recognize them as prey or the fish might have a search image of their prey, which increases the predator's efficiency at finding profitable items (Hart 1986). Even if they see the larger snails but ignore them, which results in a lower encounter rate because the observer does not see any change in behaviour, this does not interfere with earlier conclusions because these large snails are hardly ever eaten.

The probability that a snail will be eaten (Fig. 8) is similar at high and low snail densities for M.b.117, M.b.94, and H.i.123 (Spearman rank correlation, $P<0.05$). This appears to be in contrast with earlier results (Figs. 2–5), where size selectivity increased with prey density. The explanation lies in depletion of snail classes. In the first series of experiments, the fishes had a fixed foraging time of 1.5 h. If, at low densities, a size class became depleted, the fish were forced to eat other classes. With higher prey densities this depletion occurred later, and apparently selectivity was increased. In the second series of experiments, an experiment was terminated after depletion of any size class. The fish have a foraging pattern that is determined by snail encounter rates. In a tank the number of snails offered does not influence the probability a size class will be eaten.

The rise in time spent per encounter by *M. bicolor* at lower snail densities, in comparison to *H. ishmaeli* (Fig. 11 C, D), indicates an increasing attention to the other manner in which prey can be obtained, viz. oral shelling. Although no increasing number of oral shellings was observed, the fish did take more time to 'calculate their changes'. Shelling might not be favourable enough compared to crushing; the next section addresses this problem.

Shelling experiments

Experimental set-up

To obtain more results on oral shelling, the two *M. bicolor* specimens were offered 10 class-11 and 10 class-14 snails, which are too large to be crushed. The experiments were recorded as before. Before shelling, the fish observes its prey for some time and manoeuvres itself into a position to grab the snail's foot. Prey handling time is therefore defined as the total time a fish is involved with a snail; i.e., the sum of attention time (aiming), biting time (positioning the snail or unsuccessful shelling attempts), and shelling time (shelling and processing). Shelling time includes the grabbing of the snail, followed by fierce shaking of the head in order to extract the snail, and swallowing of the prey, which ends when the fish starts swimming and searching again. To calculate the amount of snail tissue the fish extracted, the remainder was dried, dissolved, and weighed as described above. From these results and the snail dry mass (Fig. 1), the mass of the removed part of the snail could be calculated.

Table 3. Snail dry mass that *M. bicolor* obtained by shelling

Fish code no.	M.b.117		M.b.94	
Snail length class (mm)	11	14	11	14
Number of snails	12	18	9	14
Mean mass extracted (g × 10^{-5})	336	711	416	646
Standard deviation of mean	134	337	210	374
Percentage extracted of total mass	26	28	33	27

Results

Both fish were able to extract almost a third of the snail tissue (Table 3). The large variation is reflected in the high standard deviations in Table 3; snail mass extracted ranged from 5% to 50%.

The shelling experiments are summarized in Table 4. The mean time spent on attention and biting is significantly higher than in any previous experiment (ANOVA, $P < 0.01$). No significant difference was found between M.b.117 and M.b.94. The dry mass obtained per second handling time (Table 4) is of the same magnitude as the crushing profitability (Fig. 9), but the probability of successful shelling is very low (Table 4).

Discussion

The preference of *M. bicolor* for crushing rather than shelling cannot be explained by profitability. For M.b.117 crushing class-5 snails gives a reward of 29 g × 10^{-5} s^{-1} (Fig. 9), and shelling class-14 snails gives 29.8 g × 10^{-5}/s^{-1}. For M.b.94 the rewards are 14 and 12.5 g × 10^{-5}/s^{-1} respectively. Yet the fish do not shell snails when crushable snail sizes are offered. The difference between crushing and shelling can be found in the likelihood of success. The probability of successful crushing can be over 90%. The reason for this is that, given an array of snail sizes, the fish apparently knows which snails it is able to crush. The fish may not be able to crush very large snails, but he may procure the prey by shelling. However, with shelling the chance of success is not only dependent on the fish's choice. If a fish decides to shell its prey, it may still fail because the technical problems with shelling are greater. For example the snail may withdraw itself into its shell before the fish can take hold of it. Another uncertainty lies in the reward of shelling. The amount of food obtained by shelling can vary from virtually nothing to half the snail. The amount of food obtained by crushing is constant and predictable from snail size.

One aspect of the foraging problem has not been taken into account, but might influence decision-making: energy costs of the different foraging methods were not calculated. Crushing requires strong action of the head muscles, especially those attached to the pharyngeal apparatus. Shelling requires a very short and rapid movement of the body, with fierce shaking of the head. These actions are mainly performed by the body musculature. Several fish predators were proven to prefer prey items with lowest attacking cost, although the net energy yield was equal to that of other prey items (summarized in Townsend and Winfield 1985).

Conclusion

Molluscivorous cichlids are capable of selecting the most profitable snail sizes, as shown by the high probability that the fish will eat snails with the highest biomass/handling time ratio. But it has also been shown that care must be taken in the interpretation of the predator's prey choice. Not only must the number of snails eaten from each size class be examined, but also the number of encounters with each size class. The number of encounters with different classes of snails was not constant. This is not in accordance with the assumption made by Stein et al. (1984) that a fish has an overall knowledge of the prey availability in the tank. Therefore, the probability that a prey will be eaten at encounter is a more reliable indication of the fish's food preference.

The biomass/time ratio does not explain the choice between oral shelling and pharyngeal crushing. Besides the prey profitability, other factors such as the likelihood of successful attack also influence the predator's behaviour. If other prey items become available, a predator has to make a choice among different prey and different forms of prey capture and prey handling, e.g., sucking (zooplankton), shelling or crushing (molluscs). All these possibilities have different energy yields, energy investments, probabilities of success, etc. The question whether fish optimize their food intake on a biomass/time ratio in these situations is currently being investigated.

The observed prey choice of the molluscivorous cichlid

Table 4. Results of shelling experiments

	Fish code no.	M.b.117		M.b.94	
	Snail length class (mm)	11	14	11	14
a.	Number of attention and/or bite	130	108	203	211
b.	Total time attention and/or bite (s)	153.2	126.6	321.0	369.0
c.	Mean time per attention and/or bite (s); b/a	1.18	1.17	1.58	1.75
d.	Standard deviation of mean	0.44	0.44	0.51	0.51
e.	Total shelling time (s)	114	112	142	558
f.	Total handling time (s); b+e	267.2	238.6	463.0	927.0
g.	Dry mass per shelling (g × 10^{-5}); Table 3	336	711	416	646
h.	Number of successful shellings	10	10	10	18
i.	Dry mass yield per shelling (g × 10^{-5} s^{-1}); $\frac{g \times h}{f}$	12.6	29.8	9.0	12.5
j.	Total number of encounters	158	118	214	229
k.	Probability of successful shelling; h/j	0.063	0.085	0.047	0.079

species is remarkable in several ways. In contrast with the results of Stein et al. (1984) who, for the sunfish *Lepomis microlophus*, did not find size selection among snails of the same species, the cichlids showed a size selection towards maximal gain in biomass per second handling-time. The fishes tested were wild-caught and had hardly ever been able to feed on *Biophalaria* snails before they were brought into the laboratory. Although *B. choanomphala* and *B. sudanica* are found in Lake Victoria, densities are very low compared to the common prosobranch snail species. Stomach contents of wild-caught fishes (Katunzi 1983; Witte and Hoogerhoud unpublished work.) suggest that the oral shelling species never crush a snail pharyngeally in Lake Victoria, because the common snail species there are too hard. The fish possibly have a genetically determined foraging behaviour, combined with rapid learning of profitability of unknown snail species. Preliminary results of experiments performed with cichlids feeding on *Bulinus truncatus* snails (another schistosomiasis vector, unknown from Lake Victoria) are similar to these presented in this paper (Van der Klaauw unpublished work).

Mittelbach (1981) demonstrated the feasability of developing a foraging model that predicts the diet composition of different sizes of bluegill sunfish (*Lepomis macrochirus;* Centrarchidae) foraging in three aquatic habitats. If the intake maximization premise also holds for other food items for the snail-eating cichlids, it may also be possible to predict the diet composition of these fishes in more natural habitats. This knowledge can be of great help in attempts to control schistosomiasis vector snails biologically.

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