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Active selection for large guppies, *Poecilia reticulata*, by the pike cichlid, *Crenicichla saxatilis*

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Size-selective predation has been proposed to be one important evolutionary force shaping life-history traits in guppies (*Poecilia reticulata*). Populations living in the presence of the ring-tailed pike cichlid (*Crenicichla saxatilis*) are smaller, mature earlier, allocate more energy to offspring and get more and smaller young than guppies in localities without *Crenicichla*. We investigated if *Crenicichla saxatilis* is a size-selective predator, if the selectivity is a result of active choice and if the optimal prey size can be explained according to an optimal foraging model. In single-prey experiments we quantified the predators' pre-capture costs (time), capture success, and post-capture costs (time) for four different prey sizes spanning from 10 to 40 mm total length. To see which of the components of the prey cycle the predator takes into account for its choice, we then predicted prey values and optimal prey size with 6 different models that included one or more of the prey cycle components.

In two multiple prey experiments, the cichlids were given the choice of the two and four different prey sizes simultaneously. *Crenicichla saxatilis* actively selected the largest guppies in both cases. The three prey-value functions that included handling time (post-capture cost) did not accurately predict the prey choice. Instead the prey-value functions that took into account pre-capture cost (approach and attack time) were able to correctly predict the choice of the largest guppy size, suggesting that pre-capture costs may be more important than post-capture costs for prey choice in *Crenicichla saxatilis*. The study confirms that *Crenicichla saxatilis* is a size-selective predator selecting large guppies, while earlier evidence for selectivity for large prey in *Crenicichla* cichlids has been weak and equivocal. Our result strengthen the possibility that size-selective predation is a mechanism in life-history evolution in guppies.

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Predation plays a key role for population dynamics, both through direct lethal effects (Wellborn 1994, Johnson and Belk 1999) and through indirect non-lethal effects on prey behaviour (Lima and Dill 1990, Sparrevik and Leonardsson 1999). Predation can be a strong selective force in the life-history evolution of prey traits; for example, size-selective predation affects the size-distribution of the prey and may thereby influence reproductive strategies (Johnson and Belk 1999). Through mechanisms such as this, predation work on

many levels, both on the predator's side and the prey's, and thus it is an important factor in attempts to explain how natural selection has affected the behaviours we observe in nature.

Prey selection, that is, a diet that is different from random assortment of available prey in the predator's environment (Ivlev 1961), and the mechanisms explaining prey selection have been studied for decades. Both active predator choice and passive mechanisms can explain prey selection. Passive mechanisms can be an

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effect of prey behaviour – such as size-dependent activity, affecting prey-predator encounter rates; or size-dependent escape capability, affecting capture success (Juanes 1994). Active mechanisms involve the predator's active choice to either attack or ignore an encountered prey. One explanation for the occurrence of size-selective predation is offered by optimal foraging theory (OFT), which predicts that a predator should choose the prey for which it gains the most energy per unit time, and thereby maximize its fitness (Stephen and Krebs 1986). Several studies have been performed to test this prediction. In general, studies using immobile prey have had more success in corroborating this hypothesis; whilst studies with mobile prey, such as fish consuming fish prey, have had lesser success (Sih and Christensen 2001). Sih and Christensen (2001) suggest that the discrepancy between immobile and mobile prey is due to missing information about the costs involved for the predator before catching a mobile prey, i.e. pre-capture costs, such as chasing, attacking, and following prey (Fig. 1).

A well-studied system, showing the possible effects of predation on life-history traits, (reviewed by Endler 1995, Magurran et al. 1995) is the pike-cichlid (*Crenicichla* sp.)–guppy (*Poecilia reticulata*) system in Trinidad. Reznick and Endler (1982) showed that in streams with different predator communities, guppy populations dif-

fered in size structure but also in the size and number of offspring that females would produce. They explained these differences by size-selective predation by the pike cichlid, *Crenicichla alta*, on large guppies. Selection for large individuals would then select for early maturation in guppy females and production of small and many offspring. In streams with *Rivulus harti*, a small and gape-limited predator (limited to small prey), the selection should favour large guppies, which reproduce later in life, thus allocating more energy to outgrow its predator. These females would therefore produce larger and fewer offspring (Reznick and Endler 1982). Even though this system has been thoroughly examined, the size selectivity of the main predator has been questioned. Seghers (1973) and Liley and Seghers (1975) showed in laboratory experiments that *C. alta* predation on guppies indicated selection for larger individuals; but Mattingly and Butler (1994) could not find the same selection for large prey. This uncertainty has led to alternative explanations of the life-history traits that are shown in guppies. Abrams and Rowe (1996) theoretically showed that these life-history traits could appear without size-selective predation, driven by an overall higher guppy mortality in *Crenicichla* sites. It has also been suggested that indirect non-lethal effects from predation on food abundance and habitat choice, also could explain these differences (Abrams 1991, Reznick et al. 2001).

The aim of this study was to examine prey choice in the ring-tailed pike cichlid (*Crenicichla saxatilis*). We tested if *C. saxatilis* is a size-selective predator and whether this selectivity is the result of active or passive prey choice, and if so, whether energetic gain (maximum energy per unit time, OFT) could explain active choice. We also wanted to assess if and how pre-capture behaviours, capture success, and post-capture behaviours affected OFT predictions, as suggested by Sih and Christensen (2001). Hence, we tested several prey-value models, including or excluding different prey behaviours. Also, we hoped to contribute to the unresolved issue of size selectivity in *Crenicichla* and thereby either strengthen or disprove the hypothesis of the effects of *Crenicichla* on guppy life-history traits.

To do this we performed two sets of behavioural experiments. In the first experiment we measured the pre-capture time, capture success, and post-capture time, for four different prey size-classes separately (Fig. 1). These data were used to generate several predictions of optimal prey size, which differed in complexity based on OFT. In the second experiment, *Crenicichla* were given the simultaneous choice between different prey size-classes, as in the first experiment. The actual choice made by *Crenicichla* was then compared with the predictions to assess which, if any, behaviours best explained the observed prey choice.

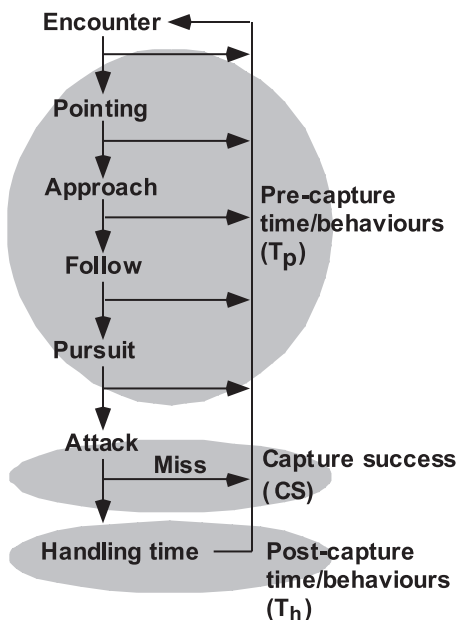


Fig. 1. The predation cycle. The predator encounters the prey, and several pre-capture behaviours can occur. The predator then decides to attack or not (active selection). An attack can result in either miss or capture, which will affect capture success (CS) i.e. how effective the predator is at catching its prey. If the predator succeeds in catching the prey, post-capture behaviours will follow, i.e. prey handling.

Methods

Experimental fish and maintenance

Crenicichla saxatilis is one of the pike cichlids in the *saxatilis* species complex, to which also *C. alta* and *C. frenata* belong (Coleman and Kutty 2001). *Crenicichla saxatilis* is found in coastal areas of Guiana and Surinam, i.e. within the natural range of native guppies. Most work in the pike cichlid–guppy system has been carried out on Trinidad. It is likely that the Trinidadian pike cichlid is *C. frenata* (Coleman and Kutty 2001), although Haskins et al. (1961) referred to the Trinidadian pike cichlid as *C. saxatilis* and most researchers after them have referred to it as *C. alta* (Seghers 1973, Reznick and Endler 1982, Houde 1997). *Crenicichla* is a diurnal predator that predominantly feeds on microcrustaceans and macro-invertebrates until it starts feeding on fish at a length of about 44 mm (Seghers 1973). Smaller individuals have occasionally been found with fish in the gut (Seghers 1973, Winemiller 1989, Mériçoux and Ponton 1998, Ponton and Mériçoux 2000). *Crenicichla* has been described as a pike-like carnivore (Haskins et al. 1961) with similar attack strategies – ambush and stalk – as the northern pike (*Esox lucius* L., Seghers 1973). *Crenicichla* is a territorial and mate-guarding predator and acts aggressively against conspecifics, but can also live in small groups of 2–5 individuals (Seghers 1973). *Crenicichla* species are often sympatric to guppy, and can impose a high predation pressure (Winemiller et al. 1990, Houde 1997). The *Crenicichla saxatilis* used in this study were in the size range of 110–140 mm total length (TL) or 129–151 mm TL for the different experiments. *Crenicichla* of these sizes are considered juveniles and piscivorous (Mériçoux and Ponton 1998). They were wild caught in Guyana within the native guppy range, and came to Sweden through the aquarium trade. The exact location of origin is not known, and therefore it was not possible to know if these *Crenicichla* individuals have actually lived in sympatry with guppies. We kept the *Crenicichla* individually separated in two 720-l holding tanks (2000 × 600 × 600 mm), each divided in 8 compartments (250 × 600 × 600 mm) separated by grey PVC sheets to prevent physical and visual interaction between individuals. Each compartment had its own air stone and one refuge of plastic pipe (200 mm long, 60 mm diameter). Every second day, *Crenicichla* were fed a diet of boiled shrimp, cut to pieces, and live guppies. One week prior to any experiments, *Crenicichla* were fed exclusively on guppies of different sizes.

For prey, we used 9–44 mm (TL) guppies from a Venezuelan wild-type stock, that have been kept in culture for several generations in large numbers and had not been exposed to selective breeding. The guppy is found in northeastern South America and in adjacent islands, for example Trinidad. It is a small, diurnal, live-bearing fish and is found in many different environ-

ments, from small head-streams and larger turbid rivers to brackish estuaries. Guppies are omnivores, feeding predominantly on algal films, small plankton and invertebrates (Dessault and Kramer 1981). The female and male are sexually dimorphic with regard to both size and colour. Females become much larger than males which cease growing when they reach maturity (Reznick and Endler 1982, Houde 1997). In this study, only females were used, except for the smallest size-class (10-mm), for which no sex separation could be done due to the absence of distinct sex-specific characteristics before maturity. We kept a population of 300–500 guppies of mixed sizes in an aerated 500-l holding tank (2000 × 500 × 500 mm) and fed them flake food and frozen *Chironomidae* twice daily.

All experiments were performed in four 310-l test tanks (1250 × 500 × 500 mm). The sides, back, and the bottom of each tank were covered with white plastic film to enhance contrast and to prevent fish from seeing into other experimental tanks. All holding tanks and experimental tanks were located in the same room under constant temperature (24 ± 0.4°C) and under a 12:12 light:dark cycle. One third of the water was exchanged in all tanks once per week, and water conditioner (10 ml/20 l water, Duplagaan, Dupla^R) was added to new water to reduce stress due to chlorine and metal ions. Fish maintenance and experiments comply with Swedish laws for scientific experiments, and were examined and approved by the Malmö/Lund committee for animal experiment ethics (permission No. M218-01).

Prey-value experiment

The experimental tanks were separated into one small (260 × 500 × 500 mm) and one large (990 × 500 × 500 mm) compartment with a sliding, grey, PVC partition, which was remote-controlled and could be removed without the experimenter being present in the room. The bare tanks were aerated until just before *Crenicichla* were transferred from the holding tank to the test tank with a hand net. *Crenicichla* were then allowed to acclimatize for a minimum of 60 minutes with the slide door open. Fifteen minutes before a test, the *Crenicichla* were gently pushed into the smaller compartment and the partition was lowered. Guppies were taken from the holding tank with a hand net and were mildly anaesthetized with tricaine methane sulfonate (MS-222) to allow length and weight measurements without damage to the fish. Prey weight was measured to the nearest 0.001 g and length to the closest 0.5 mm and the guppies were then put in a plastic container with water from the experimental tank, for a minimum of 60 minutes. The prey was then put into the larger compartment to allow acclimation for fifteen minutes, after which the video recording was started, and the partition was lifted. A

trial lasted until the guppy was consumed or for a maximum of fifteen minutes.

To be able to quantify prey value, eleven individual *Crenicichlas* were tested every third day, with one single guppy from each of four size-classes, in random order. The 11 *Crenicichla* used in this experiment were in the size range 110–140 mm TL (same sizes as for the four-prey experiment). Guppy size-classes (range) were 10 ± 1 , 20 ± 1 , 30 ± 1 , and 40 ± 3 mm respectively and weights (mean \pm SD) were 0.0074 ± 0.00089 , 0.065 ± 0.0083 , 0.256 ± 0.030 , and 0.84 ± 0.11 g wet weight. The trials were filmed and the following behaviours (Fig. 1) were manually quantified (times to the nearest 1/10 second).

Pre-capture behaviours

- 1) Pointing: the *Crenicichla* was motionless but directed towards a prey.
- 2) Approach: the *Crenicichla* was moving towards a non-moving prey.
- 3) Follow: the *Crenicichla* was following a moving prey at a slow pace.
- 4) Attack: a rapid burst towards a prey in order to capture it.

Capture success

Capture success (CS) was measured as number of captures divided by number of attacks for each individual replicate. Only replicates that actually ended in prey consumption were included in the analysis, resulting in capture success in each replicate being the inverse of number of attacks.

Post-capture behaviour

Handling time (T_h) was timed from the moment *Crenicichla* captured the prey until the prey was fully swallowed and the pharyngeal movement ceased and returned to normal.

Four-prey experiment

The experimental setup in the four-prey experiment was similar to the prey-value experiment, with the exception that four guppies, one individual from each size-class (10, 20, 30, and 40 mm), was put into the arena simultaneously. Each trial lasted until a *Crenicichla* had consumed at least one prey, or it was terminated after fifteen minutes if no prey was captured. Although *Crenicichla* frequently consumed multiple prey, only behaviours that preceded and included the first prey consumption were used in the analyses. From each trial

the consumed prey size was noted. Pre-capture time, capture success, and post-capture time for the different prey sizes could not be recorded from the four-prey experiment because it was often uncertain as to which prey the predators directed their action towards.

Two-prey experiment

To quantify capture success in prey-size selection experiments a complementary experiment was performed. Here, only two size-classes were used simultaneously. An observer, standing behind a tarpaulin and watching through a 35×110 mm opening, recorded the number of attacks towards the different sized prey and also the size of the first one consumed. The 14 predators used in this experiment were in the size range 129–151 mm TL and prey sizes were 13 ± 1 vs 29 ± 2 and 21 ± 2 vs 42 ± 2 mm TL. Experiments were conducted, over four to five consecutive days, at 8.30–10.00 am for size-classes 13- and 29-mm and 4.00–5.30 pm for size-classes 21- and 42-mm. Both prey were simultaneously cupped into the testing tank and the observations lasted for 20 min. As in the four-prey experiment, all measures used in the analyses were from the period until the first prey was consumed, although the *Crenicichla* often consumed both prey sizes.

Prey-value models and statistics

The data obtained in the single-prey experiments were used to calculate different prey values using six different theoretical models. The prey values were used to predict the optimal prey size and to evaluate how the different behaviours affected these values and the optimal prey choice (Table 1). We measured prey mass instead of energy content and assumed that the wet weight correlated linearly to energy content within the range of prey sizes used.

The times (($x+1$)-transformed to obtain normality) for the different prey sizes were compared with one-way ANOVA and Tukey's post-hoc test for each pre-capture behaviour. Times for these behaviours were then pooled to form total pre-capture time per attack (T_p). A Mann-Whitney U-test was used to test for differences in CS between prey sizes.

Since, in the four prey experiment, it was impossible to determine which prey size each attack was directed towards, the distribution of attacks was back-calculated by dividing the number of consumed prey in the four-prey experiments with the size-specific capture success that was derived from the single-prey experiments.

A χ^2 -test was used to test for selective consumption and number of attacks towards different prey sizes in the four-prey experiment. If active choice was not a factor,

Table 1. The six different prey-value functions. All functions include prey mass (m) and one or more of the different mechanisms: pre-capture costs (T_p), capture success (CS) and post-capture costs (T_h).

Abbreviation	Included mechanisms	Prey-value function
PV_{T_p}	Prey mass and pre-capture time	$\frac{m}{T_p}$
PV_{CS}	Prey mass and capture success	$CS \times m$
PV_{T_h}	Prey mass and handling time	$\frac{m}{T_h}$
PV_{CS, T_p}	Prey mass, capture success, and pre-capture time	$CS \frac{m}{T_h}$
PV_{T_h, T_p}	Prey mass, handling time, and pre-capture time	$\frac{m}{T_p + T_h}$
PV_{CS, T_h, T_p}	Prey mass, capture success, handling time, and pre-capture time	$\frac{m}{\frac{T_p}{CS} + T_h}$

the distribution of attacked prey would be expected to be random i.e. 25 % attacks towards each prey size-class.

In the two-prey experiment the two data-sets (13- vs 29-, and 21- vs 42-mm prey) were analysed separately. Chi-square-tests were used to test for differences in large vs small prey with respect to the number attacked and with respect to the number consumed. The four to five replicates per predator were pooled, and a log-linear model was used to test for differences in active choice and capture success between individual predators, and to test if capture success contributed to selectivity. In the hierarchical log-linear model, we used predator individual, attacked prey size, and attack result as main effects and included all interaction effects.

Results

Prey-value experiment

Not all eleven *Crenicichla* attacked and captured prey of all sizes (Table 2). Out of the eleven fish, 5, 9, 11 and 8 cichlids consumed the 10-, 20-, 30-, and 40-mm prey respectively, and only these replicates were used for further data analysis. Some other replicates resulted in attacks but not in prey consumption, especially in the smallest prey size (10-mm) where four *Crenicichla* attacked but did not consume prey (Table 2).

Regarding pre-capture behaviours, the *Crenicichla* cichlids spent most of the time on pointing and approaching and much less time following and attacking prey (Fig. 2). There were no significant differences

Table 2. Predators that attacked and consumed prey of the different prey sizes in the single-prey experiments. C = consumed prey, A = attacked but not consumed prey. Only replicates that ended in prey consumption were included in prey-value calculations.

Predator	Prey size			
	10 mm	20 mm	30 mm	40 mm
A	C	C	C	
B	A			A
C		C	C	C
D		C	C	C
E	C	C	C	C
F	A	C	C	C
G	C	C	C	C
H	C	C	C	C
I	A	C	C	C
J	C	C	C	C
K	A		C	

between prey sizes in pointing time or time spent following. However, the cichlids spent significantly more time approaching 10-mm prey than 40-mm prey, and they spent significantly more time attacking the largest prey than any of the other prey sizes. When the four different pre-capture behaviours were pooled into total pre-capture time (T_p) the predators appeared to spend more T_p on the smallest prey, but there were no significant differences between any of the prey sizes (ANOVA, $F = p = 0.107$, Fig. 3a).

Mean capture success was about 0.50 for the three smaller prey sizes and half as high for the largest prey size (Fig. 3b). However, when tested with a Kruskal-Wallis test there were no significant differences between prey sizes ($p = 0.18$).

Handling time (T_h) increased with prey size, especially the 40-mm prey took significantly longer time to handle (T_h) than all the other size-classes (ANOVA, $p < 0.001$, Fig. 3c). The only non-significant contrast in T_h was between the two smallest prey classes, 10-mm and 20-mm prey.

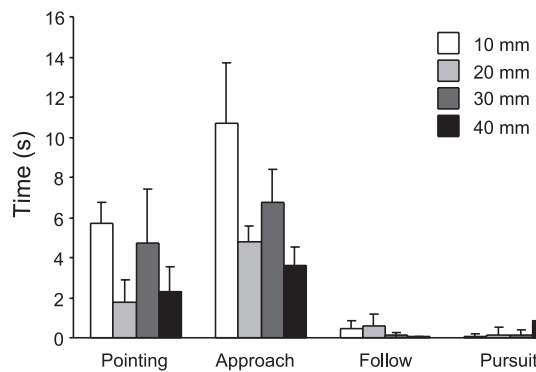


Fig. 2. Mean time (+SE) per prey cycle for the four different pre-capture behaviours. Times for these behaviours were pooled together and form pre-capture time (T_p) in Fig. 3a.

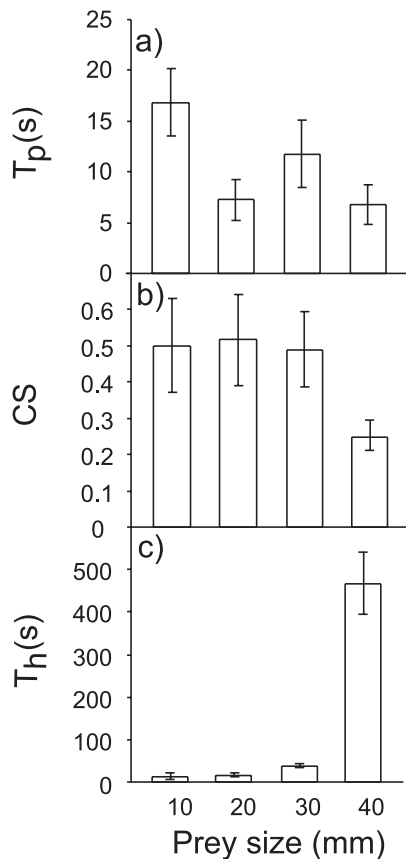


Fig. 3. (a) Pre-capture time per prey-cycle, (b) capture success, and (c) post-capture time (T_h) per consumed prey for the different prey sizes. These empirical values (mean \pm SE) are the basis for the different prey-value predictions in Fig. 4.

Predicted prey values

The prey-value models can be divided into two categories. In the first category, the largest prey were predicted to be the most profitable. Two prey-value models, PV_{T_p} and PV_{CS, T_p} (Fig. 4a, d), predicted that the 40-mm prey was more profitable than all others. A third model, PV_{CS} (Fig. 4c), predicted that the 2 larger size-classes were more profitable (30-mm and 40-mm were not significantly different; $p=0.14$, Tukey's post-hoc test).

The second category of prey-value predicted that intermediate sizes were more profitable. The PV_{CS, T_h, T_p} and PV_{T_p, T_h} models predict only 30-mm to be the best (Fig. 4e, f). The PV_{T_h} model predicted that both 20-mm and 30-mm were better (they were not significantly different, Fig. 4c). All three models in this category, intermediate is better, have handling time (T_h) in the prey-value function. All three models in the first category, largest is better, do not have T_h .

Four-prey experiment

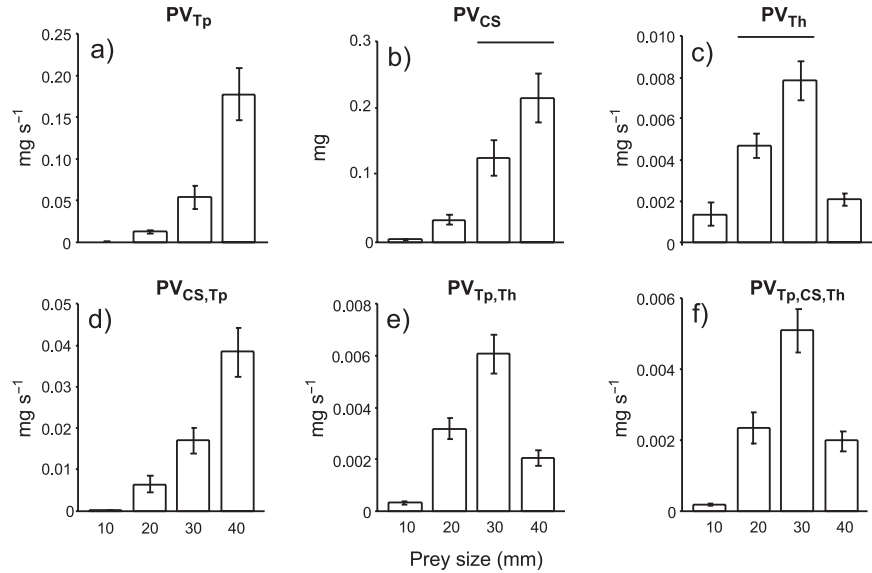
In the four-prey experiment, *Crenicichla* selectively consumed the largest available prey, 40-mm (Fig. 5a). In 14 out of 24 trials, the 40-mm prey was consumed, ($\chi^2=14.7$, 3 df, $n=24$, $p=0.002$). Expected prey number in each group (i.e. random selection) was low (six). Pooling the three smaller prey classes, while keeping 3 degrees of freedom, gave a more conservative test, resulting in $p < 0.005$. If we assume that capture success was the same as in the prey-value experiments, the required number of attacks for the resulting consumption was displaced even more towards the largest prey size (Fig. 5b).

Two-prey experiment

This selection experiment gave a result similar to the four-prey experiment. The 14 cichlids used in this experiment selectively attacked and consumed the larger prey, both when choosing between 13-mm and 29-mm prey and between 21-mm and 42-mm prey (Fig. 6). When comparing the 13-mm and 29-mm prey, both number of attacks and number of consumed prey differed significantly ($\chi^2=29.6$, $p < 0.001$, $df=1$, and $\chi^2=8.3$, $p < 0.004$, $df=1$, respectively). Likewise, for 21- and 42-mm prey, number of attacks and number of consumed prey differed significantly ($\chi^2=49.2$, $p < 0.001$, $df=1$, and $\chi^2=5.3$, $p=0.021$, $df=1$, respectively).

To test for differences in active choice and capture success between individual predators, and to test if capture success contributed to selectivity, we used a hierarchical log-linear model. In this model, predator individual, attacked prey size, and attack result were the main effects, and we included all interaction effects. For the 13- and 29-mm prey, all interaction effects were non-significant. This means that capture success (attacked prey size \times attack result) did not contribute to the selectivity and that the predator individuals did not differ in their active size choice (predator individual \times attacked prey size) or capture success (predator individual \times attack result). For the 21- and 42-mm prey, the result was different. The three-way interaction was non-significant, but the two-way interactions, predator individual \times attacked prey size and predator individual \times attack result, were both significant ($p < 0.001$, and $p=0.018$, respectively) and could not be excluded from the model. This means that the individual cichlids were different, both in their choice of prey sizes to attack and in their capture success. When taking predator differences into account, the two way interaction, attacked prey size \times attack result, was non-significant ($p=0.18$). Hence, different capture success for different prey sizes was not contributing to the selective consumption of prey.

Fig. 4. Prey-value predictions based on the prey-value experiments. Mean (\pm SE) prey value per size-class. Note that Fig. (b) is prey mass only, others are prey mass per time. Prey-value models (a), (b), and (d) predict that the largest prey (40-mm) is the most profitable prey, although in variant (b), 40-mm prey are not significantly more profitable than 30-mm prey. Prey-value models (c), (e), and (f) predict that the 30-mm prey are the most profitable size, but in model (c), profitability of 20-mm and 30-mm prey do not differ significantly. For calculation of the different prey values, see Table 1. The graphs show non-transformed data but for statistics $\log(x+1)$ -transformed values were used. One-way ANOVA with Tukey's post-hoc test was used to test



Discussion

The results show that *Crenicichla* selectively consumed the largest prey offered and that the selectivity was primarily the result of an active choice to attack large prey. Capture success was a potentially passive process that did not significantly contribute to selectivity. When using simple variants of optimal foraging models to predict the active prey choice, it turned out that, among commonly used models, those that included post-capture costs (handling time) did not adequately explain the prey choice. Instead, models that included pre-capture time were able to correctly predict that large prey would be chosen. Inclusion of capture success did not improve the predictive power of optimal-foraging models.

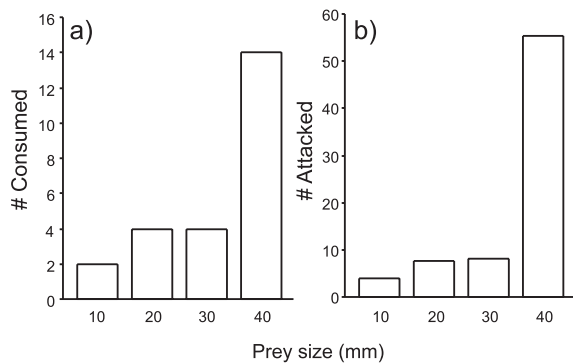


Fig. 5. Number of consumed prey in the four-prey experiment (a) and back calculated number of attacks per prey size-class (b).

Active or passive selection?

The two-prey experiment gives the clearest evidence for active prey selection in *Crenicichla*. Here, the actual number of attacks was observed, and we interpret the significantly higher number of attacks towards the larger prey size, both when choosing between 13- and 29-mm prey and between 21- and 42-mm prey, as active choice towards these prey sizes. The distribution of results from the attack part of this experiment is largely reflected in the consumption – large prey were consumed. Capture success for the different prey sizes did not statistically contribute to overall prey selection in this experiment. If

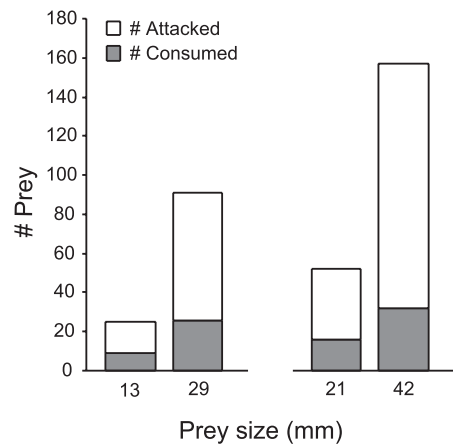


Fig. 6. Number of attacked and consumed prey in the two-prey experiment. The bars are number of attacks, and the shaded parts of the bars represent successful attacks ending in consumption. In these experiments the predators had a choice only between two prey sizes, 13-mm vs 29-mm prey and 21- vs 42-mm prey.

CS did have an impact on selectivity, that impact would affect selectivity in the opposite direction, i.e. towards small prey, weakening the strong selectivity towards large prey. In the four-prey experiment we had a similar result, but here we were not observing the actual attacks and had to assume that capture success was similar to the CS measured in the prey-value experiments. If this assumption holds true, the number of attacks was even more biased towards large prey than was the consumption; but the difference in CS between prey sizes was not significant, and we must conclude, therefore, that capture success did not contribute to selectivity in our study. This contrasts with many other studies where CS was negatively correlated to prey size (Juanes 1994, Christensen 1996). Higher vulnerability for smaller prey has been suggested to be an important mechanism contributing to the commonly found selective consumption of small prey in piscivore foraging studies. Also, fish larvae as they grow, generally reduce their vulnerability and capture success of predators (Miller et al. 1988).

Another passive process that potentially could contribute to selective consumption of large prey is predator-prey encounter rate (ER). The ER of different prey sizes is affected by the predator's ability to discover prey, which in turn is affected by prey activity and visibility. We assumed that ER in the limited scale of the experiment was approximately the same for all prey sizes since the prey was present in equal numbers, and the visibility in the tanks was good with clear water and relatively intense light. Moreover, we observed that *Crenicichla* could discover and act towards all prey sizes even in the far end of the tanks. Thus, even though size-specific ER may have contributed to the observed results, predator-prey encounter rate is not likely to have been the main mechanism generating the bias of the attack distribution towards large prey.

Stomach fullness, or satiation, is another passive mechanism that may affect selectivity and lead to consumption of small prey. In our experiments, the predators were allowed to consume just one prey per replicate. In the two-prey experiment, each predator was used in a maximum of 1 replicate per day. In the two-prey experiment, we used the same predator for the choice between 13- and 29-mm prey in the morning and the choice between 21- and 42-mm prey in the afternoon. Despite running two experiments the same day, our predators were able to consume the largest prey in both experiments. Hence, prey selection was not limited by stomach fullness.

Prey-value predictions

The six variants of prey-value models gave predictions that could roughly be divided into two groups. One group, consisting of three models (PV_{T_h} , PV_{T_p, T_h} ,

PV_{T_p, CS, T_h}), predicted that intermediate prey (mainly the 30-mm prey class) were the most profitable prey. The other group of models predicted that the largest prey (40-mm) should be the most profitable one. Models in the first group resemble the most commonly used prey-value models in optimal foraging theory (OFT) where handling time (T_h) is an important component. These models have given a similar prediction, of intermediate prey being the most profitable, in many other studies of piscivore foraging (Scharf et al. 1998, Hartman 2000, Juanes et al. 2001, 2002, Turesson et al. 2002). Smaller than optimal prey are less profitable because the mass is too small, and larger than optimal prey are less profitable because T_h is too long for these prey. In many studies, using the simplest prey-value models (prey mass/ T_h), the predators have consumed prey smaller than was predicted. Therefore, Sih and Christensen (2001) suggested that inclusion of CS and T_p would improve the predictive power of the model. In our study, the prey-value models based on handling time also predict intermediate prey sizes to be the most profitable; but the inclusion of other mechanisms, CS and T_p , does not increase the predictive power of the models as long as T_h is kept in the model. In fact, models including T_h fail to predict the actual outcome from the four-prey experiment. Our other three models, taking into account only pre-capture mechanisms (PV_{T_p} , PV_{CS} , $PV_{T_p, CS}$), predict the largest prey (40-mm) to be the most profitable size. These models also accurately predict the active selection of large prey in the four-prey experiment. In the two-prey experiment, the largest of the prey was consistently selected. However, it should be noted that the predators and prey were of a different size than in the prey-value experiment, so these experiments are not directly comparable.

Among the three models that predicted the largest prey size to be most profitable, the PV_{CS} -model failed to statistically show that the profitability of the largest prey (40-mm) was different from the second-largest prey (30-mm). Therefore, we have no support for the hypothesis that this model predicted the cichlids very strong active selection for large prey. Two of the remaining models (PV_{T_p} , $PV_{T_p, CS}$) correctly predicted the outcome of the four-prey experiment with statistical confidence. Since CS did not add to the predictive power in the $PV_{T_p, CS}$ -model, compared to the simpler PV_{T_p} -model, we think that this indicates that T_p is the most important mechanism for predicting *Crenicichla* size selection. We have not statistically compared the different prey-value predictions with the actual prey selection because we can not pinpoint a reasonable null hypothesis. Candidates include: cichlids should choose only prey from the most profitable prey class; or they should attack different prey sizes in proportion to their profitability.

If we assume that minimizing T_p per prey mass gained is an important mechanism in *Crenicichla* foraging, then

we must believe that pre-capture time is costly or limiting in some way. We think that, with respect to the behaviours pointing, approaching, following, or attacking prey, none is a substantial part of the total *Crenicichla* time budget. So why then should pre-capture time be limiting? One explanation would be that the opportunity for these behaviours is limited because prey encounters are limited. If the cichlids encounter prey on few occasions per day, they would then have to use the short times available for catching the prey in the most economical way. The guppy is a schooling species, and it is likely that the individual *Crenicichla* often simultaneously encounter differently sized guppies and they then have limited time for choosing and capturing prey. Attacking the one prey that gives the best profit in terms of prey mass per time before capture may then be a reasonable strategy. The *Crenicichla* swallow whole prey and probably consume just a few prey per day. Consequently, handling time may not be limiting at all.

Foraging theory has often been criticized for testing one but not alternative models of prey choice (Perry and Pianka 1997). Here, we have tested several different variants. However, other mechanisms may also be important for prey choice. Breck (1993) suggested that consumption in piscivores is likely to be limited by digestion rate or prey encounter rate. If prey availability is not limiting, the optimal choice may be to choose the prey that can be digested at the fastest rate. Digestion of prey has been suggested to be a surface-dependent process (Salvanes et al. 1995), with prey surface available for digestive enzymes limiting digestion. For single-fish meals, small fish may be digested at a higher rate than larger prey. However, this may be an effect of meal size rather than prey size, since several studies have shown that digestion rate is prey-size independent if meal size is held constant (*Lota lota* in Paakkonen et al. 1999, *Merlangius merlangius* in Andersen 1999, *Esox lucius* in Nilsson and Brönmark 2000).

Risk of predation or kleptoparasitism on the predator is another factor that may come into play in shaping the predator's food choice (Gilliam 1990). It is most probable that *Crenicichla* may be under risk of predation from other species in nature. Seghers (1973) found *Crenicichla* in the gut of *Hoplias malabaricus*, and it is also known that they are cannibalistic. Risk is probably elevated when handling prey. Size-dependent handling time has been suggested to be one reason why handling time should be considered a cost that favours consumption of small prey compared to large prey (Nilsson and Brönmark 1999). *Crenicichla* are indeed territorial and aggressive to each other, but the use of a refuge for handling prey may reduce the cost of handling substantially (Nilsson et al. 2000). If all time spent outside a refuge is risky, this may be a reason for *Crenicichla* to try to minimize pre-capture time (T_p), even in situations when prey availability is not limiting consumption.

In the prey-value experiments, we chose to analyse only data from the replicates that ended in prey capture (Table 2), because we wanted to be able to quantify all behaviours for all individuals analysed. Five replicates that included unsuccessful attacks were therefore omitted and a somewhat different picture would have emerged had these unsuccessful attacks been included in the capture-success results. One individual attacked but did not capture the 40-mm prey, which would have decreased mean CS slightly for the largest prey class. Four predators performed unsuccessful attacks on the 10-mm prey, which would have lowered the CS on this prey size to almost half, or 0.28 instead of 0.50. The result of this is an unusual relation between CS and prey size, with CS being highest for intermediate prey instead of the common relationship where CS decreases with prey size. A lower CS for the smallest prey class would not have changed the principal results of the prey-value predictions, because the smallest prey size was by far the least profitable prey according to all prey-value variants. A decreased CS would have made the smallest prey even less profitable in the prey-value variants where CS was included. The reason that almost half of the predators attacking 10-mm prey failed to capture these prey might depend on low motivation for capturing these low-value prey, or it might represent limited ability to capture these prey. It is strange that the pointing and approaching phases in the prey cycle were longer for the 10-mm prey than for the three larger prey classes. This might indicate that low motivation have been the reason both for long pre-capture times for small prey and the relatively low capture success. If low motivation was not the reason, it is possible that the smallest prey had size-related advantages regarding escape from the cichlids. The sizes of the prey that we used in our prey-value experiments were smaller than in most previous empirical studies of piscivory (Juanes 1994). Our guppies were in the size range of about 8–32 % of the predator length, while in most of the studies reviewed by Juanes (1994) prey sizes were in the range of 25–60 % of the predator length. The size range of prey is important because, while maximum speed increases with fish size (to the advantage of the predator over its prey), fast-start and acceleration are unrelated to fish size. Moreover, to the advantage of the prey, turning radius increases and turning rate decreases with increasing fish size (Domenici 2001). Hence, the result is a complex size-dependent relationship, giving small prey a possibly better chance (than larger prey) to escape an attack under certain circumstances where good manoeuvrability is more valuable than high maximum speed.

The earlier studies on *Crenicichla* size selectivity have given very inconsistent results: Seghers (1973), although often cited in order to give evidence for positive size-selective predation on large prey, found only a weak trend for selective consumption of large prey. Mattingly

and Butler (1994) found size-selective consumption of large prey in one out of six trials with *Crenicichla*, and the authors conclude that the results “do not support the assumptions made in other studies (Reznick and Endler 1982), that *Crenicichla* preys predominantly on large mature guppies”. Two studies that compared *Crenicichla* predation on guppy males vs females, without matching for size, also gave opposite results. Pocklington and Dill (1995) found a very strong selection for females and argued that the larger females were more profitable than males from an optimal-foraging perspective. However, Haskins et al. (1961) report very strong selective predation on males, when mixing groups of males and larger females. Finally, Seghers (1973) gave *Crenicichla* the choice of similarly sized males and females and did not find selective predation on either sex. Our experiments thus give the strongest experimental support for size selection for large guppies so far. This claim might possibly be grouped together with Pocklington and Dill (1995), if size differences explained selection for females in their study. A possible reason for the discrepancy in the results may be differences in experimental design between studies. Two practices, common in our experiments and Pocklington and Dill’s (1995), were that the cichlids were presented to only one prey of each size-class and only one consumed prey per replicate was noted. In the other studies, the predators were allowed to consume a number of prey from large groups (up to 50 individuals per group); thus, satiation may have reduced or reversed prey-size selectivity. The variety of results on *Crenicichla* prey-size selection raises a call for more studies – studies that look into the mechanisms controlling patterns of size selection, and studies that examine which situations in nature size-selective predation may be important.

Selective predation has attracted less interest lately, since a study on size-specific guppy mortality in a natural stream did not find any differences between *Crenicichla* and non-*Crenicichla* sites (Reznick et al. 1996), other than a higher mortality – independent of size – in *Crenicichla* sites. Moreover, theoretical work has shown that the differences in guppy life-history, between *Crenicichla* and non-*Crenicichla* sites, do not have to depend on size-selective predation, but can alternatively be explained by different predation pressures over all guppy sizes, together with density-dependent mechanisms (Bronikowski et al. 2002, Reznick et al. 2002). These suggested mechanisms are not mutually exclusive with size-selective predation, and our study clearly indicates that *Crenicichla*, in some situations, can be a size-selective predator, which is in line with early suggestions (Haskins 1961, Seghers 1973, Reznick and Endler 1982).

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