Prey Type- and Size-related Handling Time of Larval Salamanders, *Onychodactylus japonicus*

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ABSTRACT : Time required for larval *Onychodactylus japonicus* to swallow prey was measured for various prey items differing in type and size under laboratory conditions. Handling time varied markedly from 10 to 1,640 seconds according to prey type and size. The relationship between handling time and prey size is described for three prey types.

INTRODUCTION

Recent foraging theories predict the optimal foraging behavior of predators confronted with different types of prey at different densities (see reviews in Schoener, 1971; Pyke et al., 1977; Krebs, 1978). The ratio of food value to handling time is generally considered to be an important variable in determining the profitability of each prey type. Therefore, measurement of handling time and elucidation of factors affecting it are essential to studying the problem of prey selection. The feeding ecology of larval salamanders has been studied by many authors (e.g., Martof, 1957; Dodson and Dodson, 1971; Rose and Armentrout, 1976; Burton, 1977; Brophy, 1980; Freda, 1983; Collins and Holomuzki, 1984; Petranka, 1984). Handling time has received little attention, although it is considered important as a cost of foraging. Here, we report on handling time of larval *Onychodactylus japonicus* for prey items differing in type and size, and discuss the factors affecting it.

MATERIALS AND METHODS

O. japonicus is a hynobiid salamander distributed in Honshu and Shikoku of Japan. The salamander breeds in mountain brooks, and the larval period lasts for 2-3 years (Sato, 1943; Hayase and Yamane, 1982). Eight larvae were collected from the Otaba River, Tokyo on 25 August 1983, and reared in the laboratory until the time of the experiment. Larvae were placed in plastic dishes (two to three per dish; 150 mm diameter, 92 mm high) filled with one liter of aerated water. A few pebbles

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(40–50 mm diameter) served as hiding places for larvae. They were kept at 13°C under a photoperiod of 14L : 10D. Chironomid larvae were supplied as food twice a week.

Feeding experiments were conducted from 27 November to 24 December 1983. Larvae were identified by body color patterns and clipped toes. Total length and snout-vent length were measured with a slide caliper. Since mouth width of living larvae was difficult to measure directly, it was estimated using the regression of mouth width (Y mm) on snout-vent length (X mm) obtained from preserved specimens: $Y = 0.189X + 0.061$ ($r = 0.96$, $n = 33$, $P < 0.001$).

Larval *O. japonicus* eat a variety of aquatic insect larvae including Ephemeroptera, Diptera, Trichoptera, and Plecoptera (unpublished data). In order to examine the effect of prey type on handling time, we used three prey types in the experiment: (1) chironomids, including two species of *Chironomus* (Chironomidae); (2) caddisflies, including several species of *Hydropsyche* (Hydropsychidae); (3) stoneflies, including several species of Perlidae and Perlodidae. Prey were collected from the field before each experiment and maintained in a large aerated tray for several days, except for chironomids which were purchased at aquarium stores.

We used body width of prey (width of prothorax in chironomids and head capsule in other taxa) as a measure of prey size. For these prey, dry body mass can be easily estimated from body width using the regressions described by Hayashi (1985). Body width was measured with an ocular micrometer, and then the prey was gently dropped near the head of a salamander hiding under pebbles. When the salamander attacked the prey, handling time was measured with a stop watch from when the prey was first captured until all swallowing movements stopped. Various prey items differing in type and size were given at random to the salamanders. However, only a small number of prey were given to an individual at a time, since satiation may affect handling time. This experiment was conducted in the daytime after fasting for at least 3 days. During the course of the experiment, water temperature was kept at 12–14°C.

RESULTS AND DISCUSSION

The mean and range of snout-vent length of these larvae were 30.8 mm (SD=2.1) and 28.0–33.0 mm at the beginning of the experiment, and 31.9 mm (SD=2.2) and 28.5–34.5 mm at the end. We measured handling time for 26 chironomids, 21 caddisflies, and 35 stoneflies. Mean prey size and handling time are listed in Table 1. Handling time varied markedly among trials, and the maximum one of 1,640 seconds indicates that it is an important cost of foraging when prey is large.

Regression and correlation analyses using log-transformed data on handling time showed that there was highly significant correlation between handling time and relative prey size (the ratio of prey width to salamander's mouth width): chironomids, $r=0.81$; caddisflies, $r=0.83$; stoneflies, $r=0.77$ (all P 's <0.001 ; Fig. 1). Analysis of covariance (Sokal and Rohlf, 1981) showed that there was significant difference among the slopes of the three regressions ($F_{2,76}=3.911$, $P<0.05$). Since the test between two regressions for chironomids and caddisflies showed no significant difference in slope ($F_{1,43}=0.611$, $P>0.25$) and elevation ($F_{1,44}=3.290$, $P>0.05$), a single regression was calculated from pooled data for these two types (Fig.1).

Relative prey size is an important factor determining handling time in many organisms (e.g., Werner, 1974; Kislalioglu and Gibson, 1976; Hayashi, 1985). This study demonstrates that relative prey size (prey width/salamander's mouth width) significantly affect handling time of larval *O. japonicus*, and is a good predictor of handling time for any prey type (Fig. 1). The type of prey is also an important factor. We have shown that handling time does not differ between chironomids and caddisflies having a similar elongated body shape, but is significantly lower for stoneflies with a quite different body shape. Because prey structure (shape and hardness) can affect feeding processes of predators, handling time differs among prey with different

Fig. 1. Handling time plotted against relative prey size (prey width/predator's mouth width). Black triangles indicate chironomids, white ones caddisflies, black circles stoneflies. The regression equation for each prey type is: $\log Y=8.89X+0.48$ ($r=0.84$, $n=47$) for chironomids and caddisflies; $\log Y=5.54X+0.39$ ($r=0.77$, $n=35$) for stoneflies.

Table 1. Body width(BW) of prey used in the experiment and handling time (HT).

Prey type	chironomids		caddisflies		stoneflies	
	BW(mm)	HT(sec)	BW(mm)	HT(sec)	BW(mm)	HT(sec)
Mean	0.75	66.5	0.92	135.6	1.85	215.8
SD	0.27	92.1	0.24	204.9	0.36	307.2
Range	0.40~1.30	10~368	0.50~1.50	25~990	1.20~2.50	18~1640
n	26		21		35	

morphologies (Sherry and McDade, 1982; Molles and Pietruszka, 1983; Hayashi, 1985). Difference in handling time between chironomid-caddisfly and stonefly types may reflect such morphological differences.

In addition, other factors are known to affect handling time of predators; for example, hunger level (Werner, 1974; Kislalioglu and Gibson, 1976; Zach and Falls, 1978), temperature (Griffiths, 1980; Hayashi, 1985), and degree of experience (Davies and Green, 1976). Among them, hunger level and temperature may be important for larval salamanders as a poikilothermic vertebrate animal.

This study clarifies the effect of prey type and size on handling time; a future problem will be to determine if these differences influence the diet selection of larval *O. japonicus* under field conditions.

ACKNOWLEDGMENTS

We wish to thank Prof. K. Miyashita of Tokyo Metropolitan University for critical reading of the manuscript. This study was supported in part by Grants-in-Aid (Nos. 58740308 and 59740327) from the Ministry of Education, Science and Culture, Japan.

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要 旨

ハコネサンショウウオ幼生の餌の処理時間について

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飼育条件下で、ハコネサンショウウオの幼生に種々のタイプ・大きさの餌を与え、その餌を捕えてから完全に飲み込むまでに要する処理時間を測定した。餌の処理時間は餌のタイプや大きさによって、10秒から1,640秒と著しく変化した。本研究では、餌のタイプや大きさから処理時間を推定するために、3種の餌タイプについて処理時間と餌の大きさの間の回帰式を求めた。