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Temporal Costs of Feeding and Predation Rates in *Betta splendens* (Regan) in Relation to Body Weight, Feed Type and Sex

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Abstrak: Masa untuk menjadi kenyang dan kadar pemangsaan dikaji untuk spesies ikan hiasan, *Betta splendens*, dari aspek berat badan, jenis makanan dan jantina. Masa untuk kenyang meningkat apabila berat badan meningkat. Masa yang minimum untuk memberi makan iaitu 13 min, cukup untuk ikan dalam kumpulan berat badan yang terendah (0.025 g) dan yang maksimum ialah 41–45 min untuk ikan dalam kumpulan berat badan yang tertinggi (1.52 g). Jumlah dan berat organisma mangsa yang maksimum telah dimakan pada 10 min yang pertama semasa makanan diberi dan beransur-ansur turun pada setiap 10 min kemudian, dalam semua kelas berat *B. splendens*. Kadar pemangsaan adalah paling tinggi (84 mg g^{-1} ikan hidup) dalam kumpulan berat badan terendah dan paling rendah (18 mg g^{-1} ikan hidup) dalam kumpulan berat badan tertinggi. Kadar pemangsaan yang tinggi mungkin disebabkan ikan menjadi kenyang dengan cepat dalam kumpulan berat badan terendah. Ikan yang memakan larva *Chironomus* dan *Culex pipiens* dan *Artemia* sp. kenyang dalam jangkamasa 17, 27 dan 40–45 min masing-masing. Ikan jantan dan betina *B. splendens* yang dibela berasingan, memakan jumlah dan berat organisma mangsa yang lebih besar, dan kenyang lebih cepat daripada yang dibela bersama dalam satu akuarium. Ikan *B. splendens* jantan meregang sirip kaudal dan meggigit ikan betina yang telah mengurangkan jumlah mangsa yang telah dimakan bagi kedua-dua ikan jantan dan betina yang dibela bersama.

Kata kunci: Kos Temporal, Berat Badan, Jenis Makanan, Jantina, Pemangsaan, Kekenyangan, *Betta splendens*

Abstract: Satiation time and predation rate were studied in an ornamental fish, *Betta splendens,* as a function of body weight, feed type and sex. The satiation time increased with increases in body weight. A minimum feeding duration of 13 min was sufficient for the smallest size group tested (0.025 g) and a maximum duration of 41–45 min was required for the largest size group (1.52 g). The maximum number and weight of prey organisms were consumed during the first 10 min of feeding and gradually declined in every successive 10 min period in all weight classes of *B. splendens*. The predation rate was highest (84 mg g^{-1} live fish) in the smallest size group and lowest (18 mg g^{-1} live fish) in the largest size group tested. The high predation rate could have resulted in quick satiation in smaller size groups. Fish consuming the larvae of *Chironomus* and *Culex pipiens* and *Artemia* sp. were satiated within 17, 27 and 40–45 min, respectively. Male and female *B. splendens* that were reared individually consumed a larger number and weight of prey organisms and were satiated more quickly than those reared together in an aquarium. Male *B. splendens* stretched their caudal fin and bit the female more times, which increased the satiation time and reduced the feed consumption rate in both males and females when they were reared together.

Keywords: Temporal Cost, Body Weight, Feed Type, Sex, Predation, Satiation, *Betta splendens*

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INTRODUCTION

Food is the most significant factor affecting growth and metabolism in fish (Brown 1957). The success of an organism depends mainly on the choice of foods that provide all necessary nutrients. Natural prey organisms differ from each other not only in size and chemical composition, but also in initiating feeding responses on the part of the predator. Temporal cost, which is usually neglected, requires as much consideration as the energy cost of predation. The temporal cost of feeding is an important factor in fish (Ellis & Borden 1970; Chiszar & Windell 1973; Mathavan & Christopher 1980; Pandian & Vivekanandan 1984), and it varies according to the size, quality and behaviour of prey organisms (James *et al.* 1993).

The aquarium fish known as the Siamese fighting fish, *B. splendens*, are relatively new to aquaculture. They are marketed all over the world (Jameson & Santhanam 1996). The quality and quantity of feed and feeding duration are the most important factors to obtain maximum growth of aquarium fish and may substantially reduce the production cost. In the present study, an attempt has been made to study the temporal cost of predation of an aquarium fish, *B. splendens,* in relation to body weight, feed type and sex.

MATERIALS AND METHODS

Sexually mature *B. splendens* brood (1:1 ratio of male and female) were reared in a cement cistern tank (1.75 in x 1.50 in; 110 L capacity) containing 50 L of water and regularly fed with minced pieces of beef liver. The tank was filled with dechlorinated fresh water, and a few aquatic weeds were put into the tank to allow for construction of bubble nests by male individuals and to allow females to escape from aggressive males. Water was changed twice a week. Females laid eggs, and males collected the eggs and incubated them. Eggs were hatched within 36–42 hrs, and fry led a free swimming life after 72 hrs. The fry were fed *Infusoria* for the first 10 days, and thereafter with *Artemia nauplii*. Three series of experiments were conducted in the present study.

Different size groups of experimental *B. splendens* fish were obtained from the laboratory bred stock animals and acclimated separately for a week. Healthy individuals were sorted into five size groups and fed *ad libitum* with *Artemia* sp (0.38 mg). The prey organism, *Artemia* sp., was collected from a local saltpan, brought to the laboratory in plastic buckets and maintained in sea water. Before feeding, prey organisms were washed 3–4 times with fresh water to remove the salt content on their surface. The different size groups of *B. splendens* (Group A = 0.025 $\pm$ 0, B = 0.210 $\pm$ 0.02, C = 0.391 $\pm$ 0.04, D = 0.904 $\pm$ 0.08 and E = 1.520 $\pm$ 0.16 g) were weighed in an electrical monopan balance to 0.1 mg accuracy. To determine satiation time, test animals were starved for 24 hrs prior to the commencement of the feeding experiment. The chosen size groups were individually reared in circular glass aquaria each containing 5 L of water, and six triplicates were maintained for each size group. A weighed quantity (0.1 g) of uniformly sized prey organisms (wet weight = 0.38 mg per

individual *Artemia*) were introduced into each aquarium containing test animals. The number of prey organisms consumed was continuously observed with the help of a stopwatch at 1-min intervals up to 30 min and at 5-min intervals from 31 to 60 min. The experiment was repeated for six days from 0800 to 1500 hrs at 29ºC $\pm$ 0.5ºC. Care was taken to keep the density of prey organisms (263 individuals) constant by adding *Artemia* as they were predated. The prey organisms were completely removed from the aquaria after satiation of the chosen test animals. The rate of food consumption/predation was calculated by dividing the total weight of prey organisms consumed by the live weight of the fish. A correlation coefficient was calculated based on the method of least squares (Zar 1974).

In a second experiment, healthy *B. splendens* individuals (0.904 $\pm$ 0.03g) were selected from the laboratory bred stock animals and acclimated for a week. They were divided into three groups and correspondingly fed *ad libitum* with *Artemia* sp. or larvae of *Chironomus* or *C. pipiens*. The test fish were starved for a day prior to the commencement of the experiment. Each group consisted of six replicates and was maintained in 5 L of water. The prey organisms, *Artemia* sp. (0.38 mg wet weight per individual), *Chironomus* larva (2.62 mg wet weight per individual) and *C. pipiens* larva (1.92 mg wet weight per individual) were collected from their environments. The larvae of *Chironomus* and *C. pipiens* were allowed to remain in tap water for 12 hrs to evacuate their gut contents. Before feeding, *Artemia* sp. were washed 3–4 times with fresh water to remove the salt content on their surface. The time required for satiation for each prey organism was observed. For other details, please refer the first series of experiments.

In a third experiment, healthy male (0.904 $\pm$ 0.03 g) and female (0.880 $\pm$ 0.03 g) *B. splendens* individuals were separately collected from the laboratory bred stock and maintained in glass aquaria for a week. They were fed *ad libitum* with adult *Artemia* sp. The test animal was fasted for a day prior to commencement of the experiment. The experiments were conducted in glass aquaria containing 5 L of water, and each treatment was repeated for six days from 0800 to 1500 hrs at 29ºC $\pm$ 0.5ºC. In this series, the temporal cost of feeding was observed in male and female *B. splendens* individually and collectively. For individual exposure on satiation time, male and female *B. splendens* were reared separately in glass aquaria, and for combined exposure, male and female individuals were reared together. Satiation time was observed for 1 hr. During the measurement of the temporal cost of feeding in both treatments, sexual behaviours, such as the number of times the male bit the female and the number of times the male and female stretched their caudal fins, were also recorded. Student's t-test was used to detect the significance of differences between the mean values of the experimental groups. For other details, please refer to the first series of experiments.

RESULTS AND DISCUSSION

The mean number of prey organisms, *Artemia* sp., consumed by *B. splendens* gradually increased as time progressed in all weight classes (Table 1). The present study revealed that the satiation time of *B. splendens* increased as the body weight increased, and a 45 min feeding duration was enough for larger animals (1.52 g). A predator is considered to be satiated when it does not accept any more food after continuous feeding (Brett 1971). Size of predator, quality, size and density of prey, hunger level of predator and temperature have important effects on satiation time and feeding rate in aquatic predators (Mathavan 1976; James *et al.* 1993). Elliott (1975) reported that satiation time of *Salmo trutta* fed on *Gammarus* was greatly increased with increase in body weight. Pandian *et al.* (1979) found that satiation time was greatly influenced by body weight; the dragonfly nymph *Mesogomphus lineatus* weighing 50, 100 and 160 mg satiated at 12, 16.6 and 39.4 min, respectively. The quick satiation in smaller size groups of *B. splendens* compared to larger ones may be due to higher consumption or predation rates in the former (84 mg g^{-1} live fish) than in the latter (18 mg g^{-1} live fish). A significant negative correlation ($r = –0.963$; $P < 0.01$) was obtained for the rate of food consumption and a positive correlation ($r = 0.986$; $P < 0.01$) for satiation time when the body size of *B. splendens* was related to food consumption and satiation time.

Table 1: Prey consumption by different weight classes of *B. splendens* as a function of time after exposure to the prey. Each value is the mean of six observations for six days.

Time (min)	Size groups*									
	A		B		C		D		E	
	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed
1	–	–	3	1.14	10	3.8	11.5	4.37	16	6.08
2	0.5	0.19	4.5	1.71	7	2.66	3	1.14	6	2.28
3	0.5	0.19	3.5	1.33	2	0.76	2	0.76	6	2.28
4	0.5	0.19	0.5	0.19	5.5	2.09	2	0.76	4	1.52
5	–	–	1.5	0.57	1.5	0.57	2	0.76	2	0.76
6	0.5	0.19	2.5	0.95	1	0.38	–	–	2	0.76
7	1	0.38	2	0.76	1.5	0.57	1.5	0.57	3	1.14
8	0.5	0.19	1	0.38	0.5	0.19	1.5	0.57	3	1.14
9	0.5	0.19	–	–	0.5	0.19	1.5	0.57	1	0.38
10	–	–	0.5	0.19	0.5	0.19	0.5	0.19	2	0.76

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Table 1: *(continued)*

Time (min)	Size groups*									
	A		B		C		D		E	
	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed
11	–	–	–	–	0.5	0.19	1.5	0.57	2	0.76
12	0.5	0.19	1	0.38	–	–	1.5	0.57	1	0.38
13	1	0.38	–	–	0.5	0.19	1	0.38	2	0.76
14	–	–	1.5	0.57	0.5	0.19	3	1.14	2	0.76
15	–	–	2	0.76	0.5	0.19	–	–	2	0.76
16	–	–	1.5	0.57	–	–	1	0.38	1	0.38
17	–	–	0.5	0.19	0.5	0.19	1.5	0.57	1	0.38
18	–	–	0.5	0.19	0.5	0.19	2	0.76	1	0.38
19	–	–	1	0.38	–	–	1.5	0.57	1	0.38
20	–	–	1	0.38	0.5	0.19	–	–	2	0.76
21	–	–	0.5	0.19	–	–	–	–	–	–
22	–	–	–	–	0.5	0.19	1	0.38	1	0.38
23	–	–	–	–	0.5	0.19	0.5	0.19	1	0.38
24	–	–	–	–	–	–	0.5	0.19	1	0.38
25	–	–	–	–	1	0.38	2	0.76	2	0.76
26	–	–	–	–	0.5	0.19	1	0.38	–	–
27	–	–	–	–	–	–	1.5	0.57	1	0.38
28	–	–	–	–	–	–	0.5	0.19	–	–
29	–	–	–	–	–	–	1.5	0.57	2	0.76
30	–	–	–	–	–	–	1	0.38	1	0.38
31–35	–	–	–	–	–	–	3	1.14	1	0.38
36–40	–	–	–	–	–	–	1	0.38	1	0.38
41–45	–	–	–	–	–	–	–	–	1	0.38

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Table 1: *(continued)*

Time (min)	Size groups*									
	A		B		C		D		E	
	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed	Mean no. of *Artemia* sp. consumed	Weight of *Artemia* sp. consumed
Total	5.5	2.09	28.5	10.83	34.5	13.11	52	19.76	72	27.36
Feeding rate (mg g^{-1} fish)	83.60 ± 6.13		51.57 ± 4.21		33.53 ± 2.38		21.86 ± 1.15		18.00 ± 1.26	

Note *: A = 0.025 g; B = 0.210 g; C = 0.391 g; D = 0.904 g; E = 1.520 g

Correlation coefficient
Body size vs Feeding rate = –0.963; $P < 0.01$
Body size vs Satiation time = 0.986; $P < 0.01$

Small stomach capacity may be another reason for quick satiation in small animals. Generally, small animals have a higher metabolic rate, which perhaps resulted in a faster predation rate. Sampath and Lilly Premila (1995) suggested that small animals showed higher metabolic rate than larger ones mainly because of the differential growth rates (allometric growth) of many individual body parts in small animals. Mathavan and Christopher (1980) reported that *Macropodus cupanus* fed on mosquito larvae required a satiation time of 60 min/day. James *et al.* (1997) reported that a 17 min feeding duration was sufficient for the smallest size group (0.016 g) and a maximum duration of 1 hr was required for the largest size group (3.6 g) of *Xiphophorus helleri* fed on *Artemia* sp.

The maximum number of *Artemia* sp. was consumed during the first 10 min of feeding in all weight classes of *B. splendens,* and then predation gradually declined in successive 10 min feedings (Fig. 1). The precipitous decline in predation rate after 10 min of feeding in *B. splendens* is typical of many predators (Beukema 1968; Ellis & Borden 1970; Mathavan 1976; James *et al.* 1997). Holling (1966) suggested that as flies were killed by the mantis *Hiarodula crassa*, there was a resulting decrease in the mantis' hunger, which in turn caused a drastic decline in attack rate until hunger was stabilised. Obviously, when the stomach of the predator is full, it ceases to attack and feed on prey organisms.

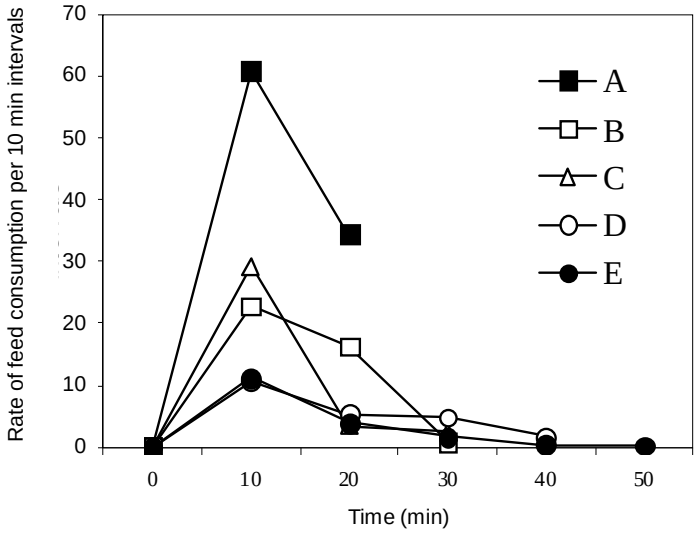

Figure 1: Rate of feed consumption (mg g^{-1} fish) of *B. splendens* fed on *Artemia* sp. at 10 min intervals as a function of body weight. A = 0.025; B = 0.210; C = 0.391; D = 0.904; E = 1.520 g.

The present study reveals that the total number of *Chironomus* larvae consumed by *B. splendens* was 27. This value increased to 31 and 52 in the cases of *C. pipiens* and *Artemia* sp. and satiation occurred at 17, 27 and 40–45 min. The rate of feed consumption of animals fed with *Chironomus* larva was 78 mg g^{-1} fish, and it significantly decreased to 66 ($t = 24.02$; $P < 0.01$) and 22 ($t = 4.00$; $P < 0.01$) mg g^{-1} fish in animals fed on *C. pipiens* and *Artemia* sp. (Table 2). The difference in the satiation time of the fish may be attributed to the size and quality of the prey organisms. The *Chironomus* and *C. pipiens* larvae were larger and heavier and were better able to catch the attention of *B. splendens* by virtue of their wriggling movements (James *et al.* 1993) than *Artemia* sp. Predation on larger prey even at low density enhances the feeding rate and satiates the fish more quickly than predation on smaller prey in higher density; consumption of one larva of *Chironomus* and *C. pipiens* was equivalent to consumption of 6.9 and 5 individuals of *Artemia* sp. *B. splendens* fed on small size prey organisms, *Artemia* sp., spent more than twice as much time feeding as those fed on larvae of *Chironomus*. Pandian and Vivekanandan (1984) reported that the temporal cost of filter feeding detritivorous and herbivorous fish was several times more than that of carnivorous fish.

Table 2: Effect of feed types on satiation time, number of prey organisms consumed and rate of feed consumption in *B. splendens.* Each value is the mean of six observations.

Parameters	Feed types		
	Artemia sp.	*Chironomus* larva	*C. pipiens*
Number of prey organisms consumed	52.00 ± 4.00	27.00 ± 1.50	31.00 ± 2.00
Weight of the prey organisms (mg)	19.76 ± 1.44	70.74 ± 6.35	59.52 ± 4.80
Time required for satiation (min)	42.50 ± 2.50	17.00 ± 1.00	27.00 ± 2.00
Feeding rate (mg g^{-1} fish)	21.86 ± 2.42	78.25 ± 4.67	65.84 ± 5.13

Note: Student's t-test : Feeding rate

Chironomus larva vs *Artemia* sp. : $t = 24.02$; $P < 0.01$
Chironomus larva vs *C. pipiens* : $t = 4.00$; $P < 0.01$

Table 3 shows the satiation time of male and female *B. splendens* reared individually and collectively. Male and female *B. splendens* reared individually consumed a larger number of prey organisms than those reared collectively in an aquarium. For instance, individually reared male and female *B. splendens* consumed 21 and 52 prey organisms of *Artemia* sp., and these values respectively decreased to 13 and 29 when they were reared together. Reductions in consumption of 38% and 44% occurred when male and female *B. splendens* were reared together. The satiation times of males and females reared individually were 20 and 35–40 min, and these values increased to 35–40 and 40–45 min when they were reared together. This occurred because male and female *B. splendens* displayed some sexual courtship behaviour when they were reared together in an aquarium. The most prominent sexual behaviours of male *B. splendens* were stretching its caudal fin and chasing and biting the female aggressively, while females displayed stretching of the caudal fin only. For instance, when male and female individuals were reared collectively, they stretched their caudal fins 61 and 3 times respectively, and the male bit the female 77 times during the feeding time, resulting in a reduction of its feed consumption rate. Based on the results of the present study, it is recommended that large, nutritionally rich prey organisms be preferred for ornamental fish culture to obtain maximum feeding and growth at minimum temporal cost.

Table 3: Individual and collective rearing of male and female *B. splendens* on prey consumption, satiation time and sexual behaviour. Each value is the mean of six observations for six days.

Parameters	Individual Rearing		Collective Rearing	
	Male	Female	Male	Female
Number of *Artemia* sp. consumed	21.00 ± 1.3	52.20 ± 0.40	13.00 ± 0.68	29.00 ± 1.65
Weight of *Artemia* sp. consumed (mg)	7.89 ± 0.23	19.76 ± 1.11	5.32 ± 0.41	11.02 ± 0.85
Time required for satiation (min)	20.00 ± 1.34	40.00 ± 2.40	40.00 ± 2.15	45 ± 3.80
Rate of feed consumption (mg g^{-1} fish)	9.06 ± 0.43	21.86 ± 1.35	5.89 ± 0.16	12.52 ± 0.78
Number of times male/female caudal fin stretched	5.00 ± 0.50	–	61.00 ± 4.00	3.00 ± 0
Number of times male bit the female	–	–	–	77.00 ± 6.00

Note: Student's t-test: Individual vs Collective rearing
No. of *Artemia* sp. consumed
Male vs Male : t = 13.67; P < 0.01
Female vs Female : t = 30.34; P < 0.01
Rate of feed consumption
Male vs Male : t = 14.95; P < 0.01
Female vs Female : t = 13.54; P < 0.01

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