Journal of Fish Biology (2001) **58,** 1311–1319
doi:10.1006/jfbi.2000.1538, available online at http://www.idealibrary.com on IDEAL®

Bubble nest habitat characteristics of wild Siamese fighting fish

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(*Received 4 July 2000, Accepted 2 December 2000*)

Siamese fighting fish *Betta splendens* in Thailand inhabit shallow water amongst dense emergent vegetation near the margin of rice paddy fields. Nesting water was low in dissolved oxygen, pH, salinity but high in free carbon dioxide and temperature. This fish aggregated with a mean population density of 1·7 fish m^{-2} and an equal adult sex ratio. Males were heavier, longer and wider than females. The size of their bubble nest is in proportion to their weight and length.

Key words: habitat characteristics; bubble nest size; Siamese fighting fish; *Betta splendens*.

INTRODUCTION

Understanding of the basic ecology and natural history of wild Siamese fighting fish *Betta splendens* Regan in its natural habitat is limited. Most studies of fighting fish have concerned aggressive interactions and signalling (Thomson, 1963; Thomson & Strum, 1965; Clayton & Hinde, 1968; Halperin *et al.*, 1992, 1997, 1998; Oliveira *et al.*, 1998). In addition, all those studies have used heavily inbred pet-shop lines of fish selected artificially for hundreds of generations to stage fighting. These fish bear little resemblance to the wild fighting fish. More recently, use of fighting fish in evolutionary and life history research in the context of natural environments has begun (J. R. P. Halperin, pers. comm.).

The present study was conducted to further understanding of wild Siamese fighting fish in its environment and physiological ecology of habitat use. The study was made in rice paddy fields because during the breeding season wild Siamese fighting fish move from streams and ponds to more shallow, quiet, slow freshwater habitats to build their bubble nest and raise their offspring (pers. obs.). Population density, adult sex ratio and the bubble nest characteristics including length, width, depth and area were examined. Two hypotheses were tested: (1) the wild male Siamese fighting fish builds a bubble nest in proportion to its length and weight, and (2) the number of eggs per nest is correlated with the bubble nest area and male length.

MATERIALS AND METHODS

FISH BIOLOGY

The Siamese fighting fish is an anabantid native to Southeast Asia (Smith, 1945). Typical fighting fish habitats in Thailand are quiet, freshwater ponds with muddy

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0022–1112/01/051311+09 $35.00/0

bottoms or flooded rice paddy fields (Gordon & Axelrod, 1968). Unlike domesticated fighting fish, wild fighting fish are small, inconspicuous, and dull brown or green in colour. They hide beneath water plants, presumably to minimize predation from egrets, herons and kingfishers.

Males build bubble nests, court females, care for the developing eggs and newly hatched larval fish. Males defend territories in the water column near the surface that are centred on a bubble nest (Forselius, 1957). They have very aggressive social displays including gill cover erection, fin spread, biting and tail beating (Clayton & Hinde, 1968; Simpson, 1968). Usually fighting involves physical damage and can result in death. Females are duller in colour and usually smaller than males. After the females finish laying eggs, the males chase the mated females out of the bubble nest areas and provide sole parental care for eggs and larval fish.

STUDY SITE

All fieldwork was carried out during the middle of the breeding season (April and May 2000) in Nakhon Si Thammarat province, Thailand, between 0700 and 1100 hours before the bubble nest builders started to leave their nests for feeding (pers. obs.).

FISH SAMPLING

Seven individual 4 m^2 (2 × 2 m) plots were marked on the ground surface in the centre of the fighting fish population. The bubble nest length (b), width (a) and depth were measured to the nearest 0·01 mm by vernier callipers, and its area (A) estimated using the ellipsoid equation $A = \Pi ab$. The shortest distances between the bubble nests and the distances between the bubble nests and the nearest vegetation were measured to the nearest 0·1 cm by tape measure before capturing the male nest builders. The water temperature in the plots and the water depth at each nest were measured before capturing all the fish in the plot and calculating the maximum population density per m^2. The adult sex ratio was calculated as the number of sexually active males divided by the total number of sexually active adults in the plot (Kvarnemo & Ahnesjö, 1996; Jirotkul, 1999).

As most plots were <30 cm deep, they could not be used to estimate the amount of dissolved oxygen and free carbon dioxide because the water sample bottles needed to be filled without exposing them to the air to minimize the amount of oxygen from the air dissolving in the water samples. To overcome this problem, nine 1 l water samples were collected from the study and nearby areas $\geqslant$30 cm deep. The water samples were taken to the laboratory to measure pH using a pH meter, specific conductivity by using a Janway-4370, dissolved oxygen by using azide modification of iodometric method and free carbon dioxide by using titrimetric method (Greenberg *et al.*, 1985).

To get an estimate of male and female body weight, body length, body width and the bubble nest size, more fish outside the seven plots were collected and their bubble nests measured. The weights of these fish were measured to the nearest 0·01 g in the laboratory. The following procedure was followed in measuring the fish length and width: first, each fish was placed in an aquarium (25·0 × 12·5 × 16·0 cm) filled with water to depth of 3 cm. The fish was not anaesthetized because most types of anaesthetic alter fish appearance (Kodric-Brown, 1989); secondly, a plexiglas ruler was placed in the aquarium to provide a standard calibration; finally, after 1 min acclimatization, the fish was photographed with a digital camera (Sony Mavica, model-FD91). Then standard body length from the tip of the upper jaw to the caudal peduncle, and body width were estimated from the pictures.

All the eggs were collected from the nests and counted in the laboratory before the fish was captured. After counting, the diameters of 10 randomly selected eggs from each nest were measured to the nearest 0·01 mm using a vernier calliper.

DATA ANALYSIS

All variables for normality were tested using Lilliefors' test and transformed when necessary. Fish body weight, bubble nest area and the number of eggs per nest were log

TABLE I. The mean ± S.D. and range of habitat use by Siamese fighting fish (n=9)

Water characteristics	Mean ± S.D.	Range
pH	5·47 ± 0·15	5·28–5·80
Specific conductance (mS m^{-1})	27·75 ± 15·02	9·36–61·80
Dissolved oxygen (mg l^{-1})	3·79 ± 2·87	0·00–7·39
Free carbon dioxide (mg l^{-1})	0·81 ± 0·45	0·45–1·91
Depth (cm)	4·99 ± 2·34	2·00–9·40
Temperature (°C)	29·9 ± 1·4	27·00–31·50
Population density (individuals m^{-2})	1·7 ± 1·6	0·50–4·8
Adult sex ratio	0·65 ± 0·27	0·36–1·00

TABLE II. The mean ± S.D. of Siamese fighting fish weight, length and width

Body measurement	Males (n=70)	Females (n=76)	t-test	d.f.
Weight (g)	0·51 ± 0·13	0·32 ± 0·19	− 7·08*	94·2
Length (cm)	2·91 ± 0·24	2·43 ± 0·52	− 7·29*	108·4
Width (cm)	0·78 ± 0·07	0·64 ± 0·15	− 7·41*	109·5

n, Sample sizes; t-tests were two-sample tests with separated variance and Bonferroni adjustment, *P<0·001.

transformed to achieve normality. Non-parametric tests were used where normality or other assumptions of parametric tests were not met. All significance tests were two tailed.

RESULTS

HABITAT CHARACTERISTICS

Fighting fish inhabited shallow bodies of water (Table I) and marginal areas of the rice paddy field. These areas are typical slow water habitats with dense emergent vegetation on a clay-mud substratum. The water was characterized by high temperature, low oxygen, high free CO_2, low salinity and was acidic (Table I). Population density in the breeding aggregation was 1·7 fish m^{-2} with a sex ratio close to 1 : 1 M : F (Table I) (χ^2 test for 1 : 1 sex ratio: χ^2_6=5·20, NS).

SIZE RELATIONSHIP BETWEEN MALES AND FEMALES

All the fish collected in the field were estimated for male and female body weight, length and width. Wild fighting fish males are heavier and bigger than females (Table II). Male weight was highly correlated with its length and width (Pearson correlation coefficient: length: r_{68}=0·91, P<0·001; width: r_{68}=0·83, P<0·001). Female weight was also highly correlated with its length and width (length: r_{74}=0·92, P<0·001; width: r_{74}=0·90, P<0·001).

TABLE III. The mean ± S.D. and range of bubble nest width, length, depth, area, the distance between the nests to its nearest nest and egg diameter

Measurement	n	Mean ± S.D.	Range
Bubble nest width (mm)	64	28·72 ± 10·80	7·89–57·56
Bubble nest length (mm)	64	41·66 ± 14·12	11·78–82·89
Bubble nest depth (mm)	64	3·47 ± 2·62	0·32–15·10
Bubble nest area (mm)^2	64	4110·26 ± 2706·06	291·99–13 340·63
Distance to the nearest nest (cm)	18	111·1 ± 61·1	27·1–227·3
The number of eggs per nest	21	369·7 ± 227·2	165·0–964·0
Egg diameter (mm)	21	0·79 ± 0·11	0·54–1·24

n, Sample sizes.

MALE SIZE, BUBBLE NEST SIZE, AND THE NUMBER OF EGGS PER NEST

All 64 bubble nests (Table III) were in the emergent vegetation near the edges of the rice paddy field. Males were caught from only 44 nests. Bubble nest area was correlated with male length and weight (length: r_{42}=0·33, P<0·05; weight: r_{42}=0·35, P<0·05 [Fig. 1(a), (b)].

Twenty-one nests were found with fertilized eggs. The diameters of the eggs differed significantly amongst the nests (Table III) (one-way ANOVA: $F_{20,199}$=5·17, P<0·001). Males were caught from only 17 nests. The number of eggs in the nest was not correlated with male length, weight or bubble nest area (male length: r_{15}= − 0·40, NS; male weight: r_{15}= − 0·32, NS; bubble nest area: r_{18}=0·28, NS).

DISCUSSION

HABITAT CHARACTERISTICS

Several factors may account for the use of shallow and marginal habitats. First, predation by large fish may be restricted to deeper water (Winemiller & Leslie, 1992). Guppies *Poecilia reticulata* Peters were more likely to stay in shallow water in the presence of predaceous fish (Seghers, 1974*a*, *b*; Liley & Seghers, 1975). In threespine sticklebacks *Gasterosteus aculeatus* L., most vulnerable nests are those in deep water, far from the pool banks and without cover (FitzGerald *et al.*, 1992).

Secondly, fighting fish may benefit from reduced predator threat or interspecific competition by living in habitats with low oxygen availability. Dissolved oxygen concentrations of <3·5 mg l^{-1} were lethal to most fish within 24 h (Moore, 1942). In this study, fighting fish habitats had an average dissolved oxygen concentration of 3·79 mg l^{-1}. Fighting fish need to gulp air at the water surface as an adaptive response to hypoxic conditions.

Thirdly, water temperature rises more rapidly in a shallow area than in deep water. In this study, the average water temperature in the rice paddy field was 29·9° C. Many empirical studies have demonstrated that the water temperature of 30·0° C was the optimal temperature for breeding and egg development (Innes, 1950; Schneider, 1966; Gordon & Axelrod, 1968; Hoedeman, 1974). The warm

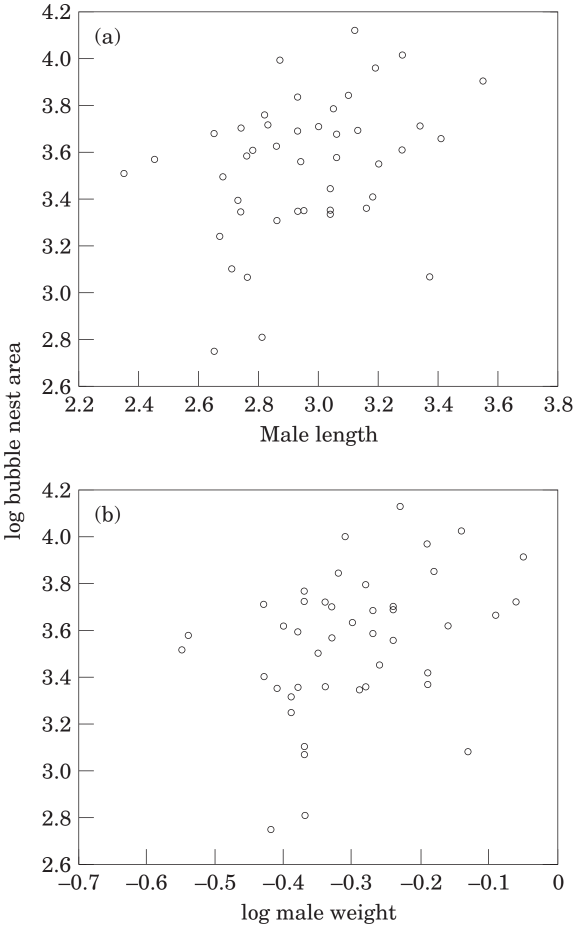

FIG. 1. Correlation between log bubble nest area (mm^2) and (a) male length (cm) and (b) log male weight (g), n=44.

water increases the frequency of bubble nest building, and the frequency of female spawning (Gordon & Axelrod, 1968). In addition, the warm water may decrease the egg hatching time and consequently reduce egg predation risks and the cost of male parental care.

Finally, fertilized eggs need to be aerated by being attached to bubble nests. Males retrieve eggs or larval fish that fall out of the nest or stray, and spew them back into the bubble nests (Gordon & Axelrod, 1968). Fertilized eggs and juveniles of fighting fish in shallow water habitats would have a higher survival rate than those in deeper water.

POPULATION DENSITY AND ADULT SEX RATIO

Population density varied considerably from plot to plot. Wild fighting fish tend to nest in aggregations. Dense male nesting aggregations are attractive to female threespine sticklebacks (Sargent, 1985). Male threespine sticklebacks in these environments showed higher motivation to court females, and less parental care.

In the plots that had a more male-biased sex ratio, there were eggs in the bubble nests. It was possible that these guarding males chased other nearby fighting fish including females out of their territories to minimize egg loss by predation. As a result, the adult sex ratio in the plots became more male-biased.

SIZE RELATIONSHIP BETWEEN MALES AND FEMALES

Wild Siamese fighting fish were sexually dimorphic in both weight and size. Males were heavier and bigger than females. This finding was similar to other studies. In species where males are bigger than females, the males are often the parental sex (Downhower *et al.*, 1983; Pyron, 1996). These males are likely to achieve higher reproductive success by being heavier and bigger for three reasons. First, males chase away mated females after they finish laying eggs because these females will eat their own fertilized eggs (Gordon & Axelrod, 1968). If males were smaller than females, they might not be able to prevent egg cannibalism by their mates.

Secondly, fertilized eggs need to be aerated in order to hatch successfully. This study showed that male length was correlated positively with bubble nest area. This suggests that bigger males can take care of a larger number of eggs than smaller males because they can build larger bubble nests to hang fertilized eggs and larval fish on. Therefore, larger males would achieve greater reproductive success.

Finally, bigger males tend to win fights over females as has been shown in many fish species such as angel blenny *Coralliozetus angelica* (Böhlke & Mead) (Hastings, 1988*a*), browncheek blenny *Acanthemblemaria crockeri* Beebe & Tee-Van (Hastings, 1988*b*), *Cichlasoma nigrofasciatum* (Günther) (Noonan, 1983), bullhead *Coltus gobio* L. (Bisazza & Marconato, 1988) and stickleback (Rowland, 1989*a*, *b*; Andersson, 1994). The males who win the fights are likely to be more successful in protecting their fertilized eggs and their juveniles from fish predators.

MALE SIZE, BUBBLE NEST SIZE, AND THE NUMBER OF EGGS PER NEST

The bigger males built larger bubble nests. The nests are an aerated place for fertilized eggs and larval fish. This suggests that the large nests would be able to handle more eggs and larval fish and can only be built by bigger males. However, the number of eggs per nest was not correlated with either male body size or bubble nest area. This finding is similar to that of Goulet & Green (1988) that the number of eggs laid by lumpfish *Cyclopterus lumpus* L. was independent of male size, nest locality or nest quality.

The results of this study may be explained by a small sample size in the field or a high turnover of broods of larger fish. The latter might be due to the fact that, although the larger males do not have larger broods at any one time, they can raise broods more frequently than smaller males because of their ability to fan their eggs faster. This fanning ability and larger bubble nest area mean more efficient oxygenation and faster embryo development.

WILD FIGHTING FISH *V.* DOMESTICATED FIGHTING FISH

There are several differences between wild and domesticated fishing fish. Domesticated males are 4·18 ± 0·39 cm long (Oliveira *et al.*, 1998) and females 3·0–5·0 cm (Chalokpunrat, 1982). The present wild fighting fish were much smaller than domesticated ones. The bigger size of both domesticated males and females affects the number of eggs per nest, the size of the eggs, and the bubble nest and bubble area.

First, domesticated females lay more eggs per nest (1161·5 eggs per nest, range 500–1500; Sirising, 1981; Saranrom, 1984; Donsakul, 1987; 500 eggs per nest, 200–700; Smith, 1950; Chalokpunrat, 1982) than do wild females, possibly due to size difference.

Second, the average diameter of the eggs laid by domesticated females is 0·89 mm (range 0·79–1·03) (Choola, 1930; Donsakul, 1987). This is greater than that of the eggs laid by wild females (but the range is narrower) and may be due to better food availability for domesticated females.

Finally, the average bubble nest size of the domesticated fish is 46·8 mm wide, 71·3 mm long, and 7·4 mm deep with an average area of 10 487·21 mm^2 (Donsakul, 1987), bigger than those built by wild males. They have to build bigger bubble nests to accommodate the greater number of eggs laid by domesticated females. While bigger wild males built bigger nests they did not receive more eggs per nest.

We thank J. Endler and J. Halperin for useful suggestions on experimental design, and J. Endler, T. na Nagara, I. Côte and an anonymous referee for comments on a previous version of the manuscript. Invaluable assistance in the field and laboratory was provided by P. Sugkong, S. Eadsi, N. Fangchonlajit, A. Dorgbua and U. Chavalit. This study was supported by the Institute of Research and Development, Walailak University.

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