SHORT COMMUNICATION

The effect of bubble nest size on sexual selection in wild Siamese fighting fish

Mullica Jaroensutasinee[1] and Krisanadej Jaroensutasinee[2]

Abstract

Jaroensutasinee, M. and Jaroensutasinee, K.
The effect of bubble nest size on sexual selection in wild Siamese fighting fish
Songklanakarin J. Sci. Technol., 2003, 25(2) : 267-273

The effect of bubble nest size was tested on male contest and female preference in wild Siamese fighting fish, *Betta splendens* Regan, a sexually dimorphic fish that exhibits paternal care. Females presented with two potential mates of different bubble nest areas did not prefer larger bubble nest males. Larger bubble nest males were not more successful in male contests. There were no differences in fighting duration. Comparing agonistic behaviour between large and small bubble nest males, there were no differences between these two males concerning any agonistic behaviours during fighting.

Key words : bubble nest size, female preference, male contest, Siamese fighting fish, *Betta splendens*

[1]Ph.D. (Ecology, Evolution and Marine Biology), Asst. Prof., [2]Ph.D. (Computational Physics), Asst Prof., Institute of Science, Walailak University, Tha Sala, Nakhon Si Thammarat 80160 Thailand.
Corresponding e-mail: jmullica@wu.ac.th
Received, 12 June 2002 Accepted, 12 December 2002

บทคัดย่อ

มัลลิกา เจริญสุธาสินี และ กฤษณะเดช เจริญสุธาสินี

ผลของขนาดหวอดต่อการคัดเลือกพันธุ์ของปลากัดป่า

ว. สงขลานครินทร์ วทท. 2546 25(2) : 267-273

ได้ศึกษาอิทธิพลของขนาดหวอดต่อการแข่งขันระหว่างปลากัดป่าเพศผู้และความชอบของปลากัดป่าเพศเมียในปลากัดป่า *Betta splendens* Regan ปลากัดป่าเพศผู้มีขนาดต่างกันกับเพศเมีย และเป็นเพศที่ฟักไข่และเลี้ยงดูลูกอ่อน เมื่อนำปลากัดป่าเพศผู้ที่มีสร้างหวอดที่มีขนาดแตกต่างกันมาให้ปลากัดเพศเมียเลือก พบว่าปลากัดป่าเพศเมียไม่ได้มีความชอบปลากัดป่าเพศผู้ที่สร้างหวอดใหญ่กว่า เมื่อเปรียบเทียบพฤติกรรมการต่อสู้ระหว่างปลากัดป่าเพศผู้ที่สร้างหวอดขนาดต่างกันพบว่า พฤติกรรมการต่อสู้และระยะเวลาในการต่อสู้ไม่แตกต่างกัน ปลากัดป่าเพศผู้ที่สร้างหวอดขนาดใหญ่กว่าไม่ได้ประสบความสำเร็จในการต่อสู้กับปลากัดป่าที่สร้างหวอดขนาดเล็กกว่า

สำนักวิชาวิทยาศาสตร์ มหาวิทยาลัยวลัยลักษณ์ อำเภอท่าศาลา จังหวัดนครศรีธรรมราช 80160

Male territoriality is common in animals (Emlen & Oring, 1977). Many studies have demonstrated that females choose their mates based on their territory characteristics and nest site quality (e.g. Wells, 1977; Sargent, 1982; Alatalo *et al*., 1986; Thompson, 1986; Tsubaki & Ono, 1995). Male reproductive success correlates positively with nest size in many nest-holding fish species such as in plainfin midshipman, redlip blenny, and Japanese fluvial sculpin (DeMarini, 1988; Côte′ & Hunte, 1989; Natsumeda, 1998). Larger nest ensures a greater surface area for egg deposition; however, larger nests are more susceptible to take-over by other males, sneak by smaller males and/or be eaten by predators (Lindström, 1988; Magnhagen, 1992).

Male Siamese fighting fish *Betta splendens* Regan establish and defend territories in a water column near the surface (Forselius, 1957; Jaroensutasinee & Jaroensutasinee, 2001a, b). They construct their bubble nests in rice paddy fields, entice females to spawn in them and then care for the developing eggs and newly hatched larvae (Gordon & Axelrod, 1968; Jaroensutasinee & Jaroensutasinee, 2001a, b). The bubble nests are aerated places for fertilized eggs and larvae. Larger males tend to build larger bubble nests and are more likely to win fights (Jaroensutasinee & Jaroensutasinee, 2001b). Fertilised eggs need to be aerated in order to hatch successfully. Larger bubble nest areas can handle a greater number of fertilised eggs, provide more efficient oxygenation and support faster embryo development. Therefore, larger bubble nest males are able to achieve greater reproductive success.

The Siamese fighting fish (*Betta splendens*, Regan) is an anabantid native to Thailand, Malaysia, Cambodia and Myanmar (Smith, 1945). Typical fighting fish habitats in Thailand are quiet fresh water ponds with muddy 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 (Jaroensutasinee & Jaroensutasinee, 2001 a,b). They hide beneath water plants, presumably to minimise predation from turtles, snakes, fish-eating egrets, herons and kingfishers.

Male Siamese fighting fish have very aggressive social displays including gill cover erection, biting, tail beating, attacking and chasing (Simpson, 1968; Clayton & Hinde, 1968). Fighting usually involves physical damage and can result in death. Females are duller in colour and usually smaller than males (Jaroensutasinee & Jaroensutasinee, 2001a,b). After the females finish laying eggs, the males chase the mated females out of the bubble nest areas and solely provide parental care for developing eggs and larval fish.

We investigated the relationship between bubble nest area, female preference and male

contest in the wild Siamese fighting fish. The following predictions were made:

(1) If there is a female preference for a larger bubble nest area, then females should spend more time with larger bubble nest males than smaller ones while controlling for male body size.

(2) If larger bubble nest area is a good indicator of male condition, then (a) male body size should correlate with bubble nest area, (b) males who built larger bubble nests should win more fights against smaller bubble nest males, (c) larger bubble nest males should behave more aggressively when compared to smaller bubble nest males during male contests, and (d) the fighting duration between larger and smaller bubble nest males should decrease as the size difference of bubble nest areas between a fighting pair increases.

Materials and Methods

Data collection

The test subjects were wild fish captured in June 2001 - February 2002 from Nakhon Si Thammarat Province of Thailand. The fish were maintained in the laboratory with natural sunlight and fed daily with mosquito larvae. Males and gravid females were housed in separated 1-liter bottles.

The aquarium for the female preference tests was a 60-litre in capacity, measuring 0.60 x 0.36 x 0.30 m that was divided into three compartments with a removable clear plexiglas partition and an opaque plexiglas partition between the two males. The central compartment comprised 67% of the total test arena and contained the focal female. The two similar adjacent compartments were of equal size and each contained a male. The preference zone was demarcated in the centre compartment by drawing a line 10-cm away from the clear Plexiglas partition on the outside of the aquarium. The region next to the partition of each male was the preference zone for that male and the rest of the central compartment was considered to be a no-preference zone. Trials were conducted from 0900 to 1700 hours. All test animals were fed prior to testing.

We placed pairs of males matched in terms of in their standard body length into the aquarium and allowed them to build their bubble nests. Standard body length was measured as the distance from the anterior-most point of the upper jaw to the end of the caudal peduncle. Thirty-four trials were conducted. Each trial consisted of two 10-min observation periods. At the beginning of each trial, a focal female was placed in the centre of the no preference zone. The first observation period was initiated after a 5-min acclimation period. This acclimation period preceded each set of observations in the trial. During the observation period, the behaviour of the three test subjects was noted and the number of seconds the females spent in each of the three centre sections was recorded. At the completion of this first observation period, one of the bubble nests of the pair was chosen randomly and cut approximately in half. The same female was again placed in the centre section of the no preference zone for a 5-min acclimation period. This was followed by a second observation period. After this second observation period was completed, the focal female was removed to her bottle and a new female was placed in the centre section of the no preference zone for a 5-min acclimation period and then was observed. After this third observation period was done, the new focal female was placed in her home bottle.

For the female preference test, successful trials were those in which the test female approached each male at least once to ensure that both males were viewed by the female and all three participants actively courted. Each trial was conducted with new females and new pairs of matching males. Female preference for bubble nest area was expressed in two ways: (1) the difference in time spent near each male and (2) the ratio of the time difference plotted against the bubble nest area difference. The time spent difference was defined as the total time spent with males who built larger bubble nest minus the total time spent with males who built smaller bubble nests. The ratio of time spent difference was defined as the difference between the total nearness time with the larger bubble male and the total nearness time with the

smaller bubble male divided by the total nearness time with both males. Bubble nest area difference between the pair was defined as the area of the larger bubble nest males minus the area of the smaller bubble nest males.

For the male contest test, the pairs of males were placed in a one-litre bottle. The number of the five agonistic behaviours (i.e. gill cover erection, biting, tail beating, attacking and chasing) was observed for both males until one fish retreated. (1) Gill cover erection (G) was regarded as males erecting their gill covers while oriented towards or parallel to intruders. Lowering of the gill cover or swimming away from intruders ended gill cover erection. (2) Biting (B) was recorded when males used their mouthpart to bite or tear at intruders. (3) Tail beating (T) was defined as each separate beat of the tail towards intruders. (4) Attacking (A) was recorded when the focal male swam rapidly towards its intruder. (5) Chasing (C) was defined as rapid and continuous following. The contest duration was recorded as the period from the first agonistic behaviour until one fish retreated.

Data analysis

Parametric statistics were used when underlying assumptions were met, otherwise non-parametric tests were used. Linear regression was used to test for female preference. A Chi-squared test was used to test for the number of fights won by the larger bubble nest males. Paired *t*-tests were used to test for the number of agonistic behavioural differences between large and small males. One-way ANOVAs were used to test for fighting duration. All significant tests were two-tailed.

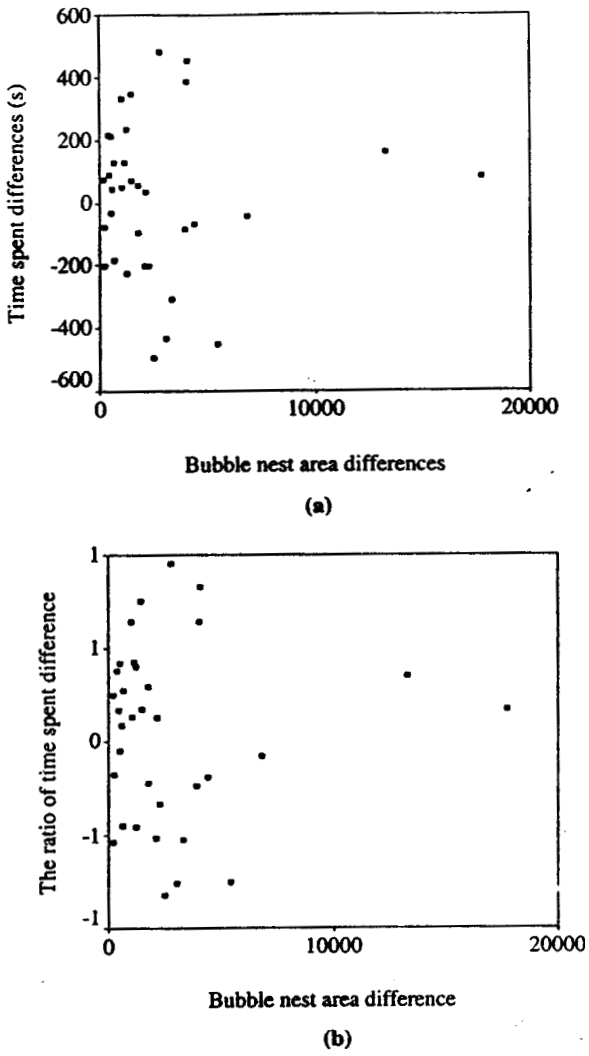

Figure 1. Female preference and bubble nest area difference. (a) time spent difference, and (b) the ratio of time spent difference.

Results

Female preference test

There was no female preference for larger bubble nest areas (linear regression: time difference: r^2 = 0.00, $F_{1,32}$ = 0.011, NS; time ratio difference: r^2 = 0.001, $F_{1,32}$ = 0.019, NS (Figure 1 a,b)). After reducing the size of the bubble nest area, there was also no female preference for larger bubble nest areas from the same females or the new set of females (linear regression: the same females: time spent difference: r^2 = 0.001, $F_{1,32}$ = 0.026, NS; the ratio of time spent difference: r^2 = 0.002, $F_{1,32}$ = 0.059, NS; the new set of females: time spent difference: r^2 = 0.011, $F_{1,32}$ = 0.369, NS; the ratio of time spent difference: r^2 = 0.023, $F_{1,32}$ = 0.765, NS).

Male contests

Male body size correlated positively with bubble nest area and bubble nest length and negatively with bubble nest height (Pearson correlation coefficient: bubble nest area: $r_{68} = 0.29$, $P<0.05$; length: $r_{68} = 0.27$, $P<0.05$; height: $r_{68} = -0.32$, $P<0.01$ (Figure 2a,b,c)).

There were no differences between larger and smaller bubble nest males concerning all agonistic behaviours during fighting (paired t-test for gill cover erection: $t_{33} = 0.31$, NS; tail beating: $t_{33} = 0.58$, NS; biting: $t_{33} = 0.17$, NS; attacking: $t_{33} = 0.57$, NS; chasing: $t_{33} = -1.20$, NS; total agonistic behaviour: $t_{33} = 0.57$, NS).

Larger bubble nest males were not more likely to win fights with smaller bubble nest males when these males were controlled for the same body size (Chi-square test: $\chi^2_1 = 0.47$, NS: larger bubble nest males won 19 of 34 pairs). There was no relationship between fighting duration and bubble nest area difference ($r^2 = 0.05$, $F_{1,32} = 1.49$, NS).

Discussion

Female preference has been reported for many teleost fish (Hay & McPhail, 1975; Kodric-Brown, 1977; Hughes, 1985). However, in this study, female fighting fish showed no preference for larger bubble nest males. This no preference result was not because females were not sexually receptive. We used gravid females that were sexually active and ready to mate within 3 hours after spending time with males who had their bubble nest present. Since larger bubble nest males are not more likely to win contests, it is very likely that females do not use bubble nest as an indicator of male quality. Jaroensutasinee & Jaroensutasinee (2001b) have shown that female mate choice in this species falls solely upon the males with the female passively accepting the winning male (i.e. usually larger males). Similar behaviour has been shown in many other species such as bees (Alcock, 1984), harvester ants (Davidson, 1982), scorpionflies (Thornhill, 1981), damselfish (Thresher & Moyer, 1983), bullfrogs (Howard, 1988), toads

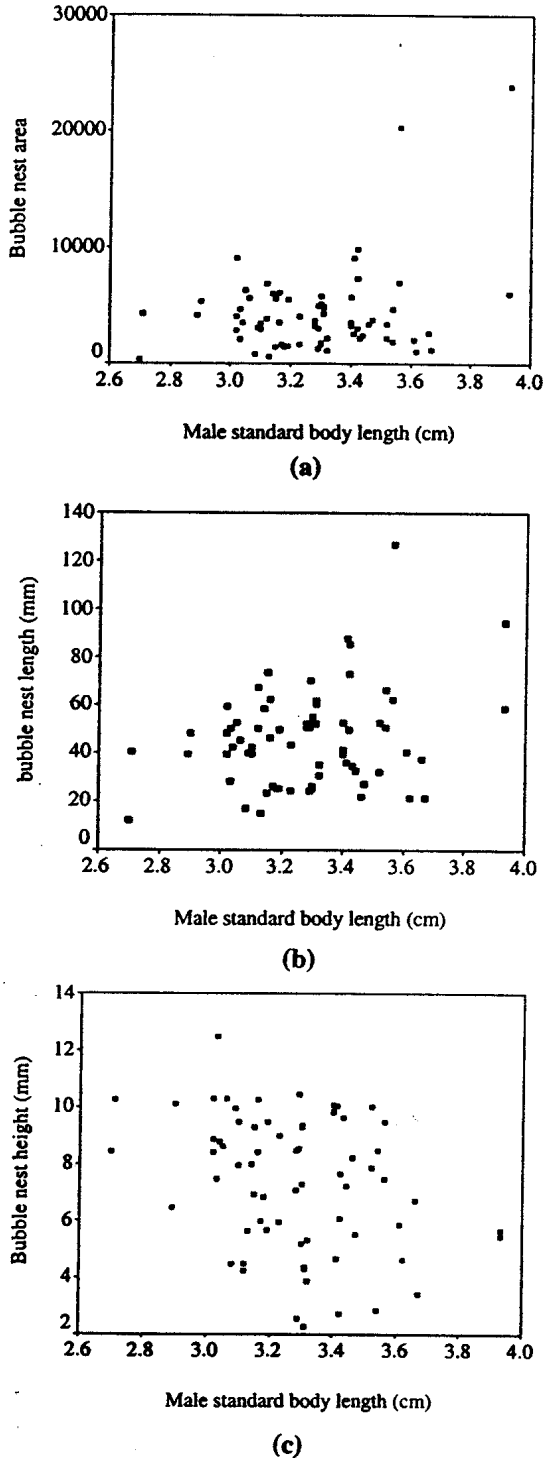

Figure 2. The correlation between male body size and (a) bubble nest area, (b) length and (c) height. Each point represents each individual male.

(Davies & Halliday, 1977, 1979), and iguanid lizards (Ruby, 1981).

The mating system of Siamese fighting fish involves competition among females for bubble nest sites and competition among males for access to females. Since males in this species defend territory, construct bubble nest and guard eggs and larvae, the operational sex ratio might become more female-biased. In addition, males that built large bubble nest are relatively scarce. Therefore, it appears to be not an adaptive response for females to develop a preference for large bubble nest males.

A number of studies have shown that winners and losers may differ in their behaviour during contests (Reichert, 1978; Enquist *et al*., 1985, 1990; Harvey & Corbet, 1986; Turner & Huntingford, 1986; Popp *et al*., 1990; Turner, 1994; Jaroensutasinee & Jaroensutasinee, 2001b) but none of them tested for bubble nest size asymmetries. Jaroensutasinee & Jaroensutasinee (2001b) have shown that large male fighting fish engaged in more chasing and attacking, and generally displayed more total agonistic behaviours than smaller males but no difference in the number of gill cover erections, tail beatings, attacking and biting has been noted. However, our results indicate that larger bubble nest males did not behave differently from smaller ones when we controlled for the body size.

In conclusion, larger bubble nest males did not win fights in male contests, and there was no female preference for larger bubble nest males. Sexual selection acting to increase male bubble nest size may be counteracted by natural selection acting on predation risk. Further investigation is still needed to fully understand how bubble nest area might affect male mating success.

Acknowledgments

We thank Professor Dr. John A. Endler for his useful suggestions concerning experimental design and data analysis and Amanda Roberts, Thana na Nagara and one anonymous referee for their comments on previous versions of the manuscript. Invaluable assistance in the laboratory was provided by Pathummas Sirisuk, Nitaya Klanniwat and Uthai Chavalit. This study was financially supported by the Institute of Research and Development, Walailak University.

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