SNEAKING BEHAVIOR OF THE NILE TILAPIA

GONÇALVES-de-FREITAS, E.[1] & NISHIDA, S.M.[2]

[1] Laboratory of Fish Behavior, Departamento de Zoologia, IBILCE, UNESP, R. Cristóvão Colombo, 2265, 15054-000, São José do Rio Preto, SP, Brazil. Aquaculture Center of UNESP (CAUNESP).
E-mail: elianeg@zoo.ibilce.unesp.br
[2] Laboratory of Ethology, Departamento de Fisiologia, IB, UNESP, 18618-000, Botucatu, SP, Brazil.
E-mail: nishida@ibb.unesp.br

ABSTRACT

This study describes the occurrence of sneaking behavior in adult Nile tilapia, *Oreochromis niloticus* (L.), a mouthbrooding cichilid fish. Nine groups composed of 2 males and 3 females were daily observed from 12:00 to 19:00 h up to the occurrence of reproduction (from 3 to 10 days). The dominant male (DM) established a territory, constructed nests, attracted the female and mated in all groups. In three of these groups, however, sneaking behavior was observed, with the subordinate male (SM) slipping between the couple after egg delivery and releasing milt close to the female's mouth and to the eggs. Thus, the female sucked the SM's milt and picked up the eggs into its mouth. These two mating tactics (territorial and sneaking) may be considered part of an evolutionarily stable strategy. Since aquarium size was restrictive, allowing only one male to build a nest, the expression of such sneaking behavior was considered to be dependent on environmental factors. The question of why only some SM displayed sneaking behavior is also discussed.

KeyWords: Reproduction, sneaking behavior, social rank, alternative mating tactics, evolutionarily stable strategy, Nile tilapia, *Oreochromis niloticus*.

RESUMO

Comportamento oportunista da tilápia do nilo

O presente estudo descreve a ocorrência de comportamento oportunista ("sneaking behavior") na tilápia-do-Nilo, *Oreochromis niloticus* (L.), um ciclídeo de cuidado parental intra-bucal ("mouthbrooding"). Nove grupos compostos de 2 machos e 3 fêmeas foram observados diariamente entre 12:00 e 19:00 h até a ocorrência da reprodução (de 3 a 10 dias). O macho dominante (DM) estabeleceu um território, construiu ninhos, atraiu fêmeas e acasalou em todos os grupos. Entretanto, em 3 desses grupos foi observado o comportamento oportunista, onde o macho submisso (SM) entrou rapidamente entre o casal durante a desova e espermiou próximo aos ovos e à boca da fêmea. Assim, a fêmea sorveu líquido espermático do SM e levou os ovos à boca. Essas duas táticas reprodutivas (territorial e oportunista) podem ser consideradas como parte de uma estratégia evolutivamente estável. Uma vez que o tamanho dos aquários foi restrito, permitindo a construção de ninho apenas por um dos machos, a expressão do comportamento oportunista foi considerada dependente de fatores ambientais. A questão do porque apenas alguns machos submissos exibem esse comportamento é também discutido.

Palavras-chave: Reprodução, sneaking behavior, hierarquia social, táticas alternativas de acasalamento, estratégia evolutivamente estável, tilápia do Nilo, *Oreochromis niloticus*.

INTRODUCTION

Dominance hierarchy and territorial defense are social components of indubitable biological value. Dominants and/or territory owners derive advantages from their social position, mainly concerning priority of access to feeding, mating, shelter and other environmental resources (Alcock, 1993). In spite of this, dominance does not assure exclusivity of advantages, and alternative mating (Gross, 1984; Ribbink, 1990) and feeding (Alcock, 1993) tactics allowing access of the subordinates to limited resources have been described.

Since the dominance-subordinance relationship is a widely spread biological phenomenon, alternative tactics for subordinance are as important as mechanisms for reaching a dominant position in a group. Although in some fish species the subordinates have their gonadal maturation inhibited by the dominant ones (Borowsky, 1987), in other fishes the subordinates are able to reproduce and some behavioral barriers still maintain priority of access to mating resources for the dominants. However, alternative behavioral tactics have evolved, enabling the subordinates to overcome such barriers (Alcock, 1993). Sneaking behavior is one of these tactics and may be performed only by species in which gonadal maturation is not socially inhibited.

The Nile tilapia, *Oreochromis niloticus*, is an African mouthbrooding cichlid fish in which a clear-cut territorial hierarchy does not inhibit gonadal maturation (Gonçalves & Nishida, 1994). This species was investigated here focusing on the occurrence of alternative mating tactics for the subordinate fish.

MATERIAL AND METHODS

The study was carried out at CEPTA, IBAMA, Pirassununga, SP, Brazil, where adult Nile tilapia, *Oreochromis niloticus* (L.), were held in 500-l tanks for 15 days prior the experiment. Disease prophylaxis was obtained with Methylene blue. Water temperature was kept at 27±1°C with a thermostat, and food was provided *ad libitum*. Natural photoperiod fluctuations were used. The technique of genital papilla inspection by methylene blue contrast as described by Afonso & Leboute (1993) was used for sexing.

The experimental design consisted of direct behavioral observations in 9 groups composed of 2 males and 3 females each. The hierarchical rank of the males and the reproductive behavior (including identification of the mating male) were observed. We also analyzed the frequency of dominant or subordinate mating males to determine the priority of access to reproductive resources.

The fish were individually recognized by partially cutting their caudal fin, as described by Alvarenga & Volpato (1995). The mean standard length of the fish was 13.00 ± 1.52 cm for dominant males, 11.55 ± 0.85 cm for subordinate males and 10.27 ± 1.25 cm for females. Since reproductive males are usually larger than females in the natural environment, each group was composed of at least one male larger than the females.

The fish were chosen according to reproductive features, such as male reddish caudal fin, developed genital papilla for both sexes, and female abdominal enlargement. These animals were kept in glass aquaria (60 cm x 60 cm x 30 cm) provided with biological filters and a 3 cm-high gravel substrate.

Hierarchical dominance was qualitatively recognized by the lighter body coloration (Falter, 1987; Volpato et al., 1989; Fernandes & Volpato, 1993) and by the performance of agonistic acts (Alvarenga & Volpato, 1995).

Since spawning never occurred by morning in pilot observations, the daily records of the groups were concentrated between 12:00 and 19:00 h. All the behavioral observations were dictated into an audio-recorder for further analysis.

After the female completed spawning and picked up the eggs into its mouth, the animals were sacrificed by bulb disruption and gonads were removed for identification of the maturation phase. The gonads were embedded in paraffin and the maturational stage was analyzed on permanent slides stained with hematoxylin/eosin. The gonadal maturation phase was determined according to Alves et al. (1983) in females and according to a method adapted from Romagosa (1991) in males.

RESULTS

Agonistic encounters started some minutes after grouping, with the largest fish (male) dominating the smallest ones, and only one dominant arose in each group. Hierarchy was settled on the first day and the dominant male (DM) defended its territory staying close to the bottom. It frequently chased and sometimes bit the other fish, moving them close to the surface or even to a corner of the aquarium.

One or two days after group formation, all the DM had started building a mouth-digging circular nest, which was defended against intruders (male or female). No nest was built by the other fish. In three groups we detected only one nest each, and in two groups we detected three nests each.

Mating occurred in the 9 groups, always involving the DM. The DM usually courted the largest female (but never the smallest one) displaying body undulations around it. Bites were used to lead the female to the nest. During the day when the female stayed in the nest spawning occurred (3 to 10 days after grouping).Inside the nest, the two mating fish stayed alongside each other and displayed body

undulations. At this time, the female also defended the nest against intruders, but only at the nest boundary, while the DM drove away the intruders all around the aquarium.

The courted female "cleaned" the nest moving stones outside of the nest with its mouth. Spawning occurred only after the couple showed a very clearly intumesced genital papilla which was inclined downwards. When the DM built more than one nest, spawning took place in the one built last.

The DM was positioned perpendicularly to the female, which waved vigorously its tail and laid an egg batch (Figure 1A). The DM then swam above the eggs and delivered milt on them. At this time, the female approached its mouth to the male's genital papilla, sucked milt (Figure 1B) and picked up the eggs into its mouth (Figure 1C). This pattern, including the delivery of new egg batches, was restarted up to 15 to 20 times during a total period of 20 to 50 min. After the spawning events ended, the DM left the nest before the female and again started to attack to the other fish. The female's mouthbrooding was carried outside the nest. After spawning the genital papillae of both fish were reddish.

Sneaking behavior was displayed by the subordinate male (SM) in 3 out of 9 groups. The SM slipped between a spawning couple and delivered milt. When the female turned to the DM, it approached its mouth to the SM's genital papilla and sucked milt from the SM (Figure 2). The DM almost immediately drove away the SM which would often return 3 or 4 times and repeat this sneaking behavior later on.

Although mating was performed by all DM and sneaking behavior was displayed by only 3 SM, gonadal inspection after grouping showed that all the males (DM and SM) had mature gonads.

DISCUSSION

This study showed that social rank may impose different ways to solve the same biological problem, i.e., reproduction. Male mating tactics are related to their social rank. Sexual behavior (territorial mating) consisted of nest building, courtship and mating (spawning and egg fertilization). While the dominant male (DM) followed all these steps, the subordinate one (SM) might use a sneaking tactic, exclusively consisting of releasing milt to fertilize the eggs of a female courted and induced to spawn by the DM. Such sneaking behavior is common in animals with external egg fertilization, such as fish, reptiles and amphibians (Alcock, 1993).

According to the game theory for reproduction competition (Maynard-Smith, 1974), these two tactics (territorial or sneaking mating) may be considered part of an evolutionarily stable strategy (ESS).

In some poecilid species, a socially mediated gonadal inhibition has been described (Borowsky, 1987), but the present data suggest that such maturational suppression may not occur in the Nile tilapia because the males (D and S) had mature gonads. This lack of suppression allows the Nile tilapia to engage in the sneaking tactic during reproductive competition.

Sneaking behavior may occur when the number of reproductive cichlid males exceeds the environmental availability for nest building (Ribbink, 1990). In fact, in the present study the aquarium area may have represented a space restriction allowing only one male to build a nest. In this case, the dominance status warranted territory holding and priority for the whole development of the territorial reproductive tactic. The sneak mating tactic is a second option that may be displayed when one male has no possibility to hold territory because of environmental conditions. This clearly shows a behavioral regulation of the reproductive tactic of Nile tilapia.

Why did some SM display no sneaking behavior despite their mature condition and the displaying of spawning by the couple? This is not an easy question to answer. According to Krebs & Davis (1995), large subordinate males fight with the DM and the smallest SM sneak. In this experiment, however, the size of the SM probably had no effect on the exhibition of such behavior, since the SM were slightly smaller than DM. However, two other not mutually exclusive logical possibilities may be proposed: a) balance between the SM maturation level (for instance, hormonal level) and the intensity of stimulation from the couple behavior (DM and female), or even other environmental factors; and b) genetic determination enabling some fish in the population to perform sneaking behavior. The genetic condition assumed to exist for ESS (Alcock, 1993) may be present in both possibilities. Moreover, in the balance supposed to exist in the first assumption, the previous reproductive history of the male may also be important since experience may modulate innate behavior (Alcock, 1993). This question, however, is an interesting subject for further investigation.

ACKNOWLEDGEMENTS

The authors thank P. S. Ceccarelli (Cepta, IBAMA) who permitted us to carry out this research in his laboratory; Dr. Heide S. L. dos Santos, Department of Animal Morphology and Physiology, CAUNESP, for helping with the identification of the maturation phase of the gonads; Dr. Denise C. Rossa-Feres (Department of Zoology, IBILCE, UNESP) and MSc. Elias F. L. de Freitas (UNIRP, S.J. Rio Preto) for suggestions about the early manuscript; and Dr. Gilson L. Volpato (Department of Physiology, IB, UNESP) for a critical review of the final manuscript.

REFERENCES

AFONSO, L.OB., LEBOUTE, E.L. Métodos para sexagem visual de alevinos de tilápia nilótica, *Oreochromis niloticus*. In: Encontro Rio-Grandense de Técnicos em Aquicultura, 4, 1993, Porto Alegre. Anais ... p. 100-103.

ALCOCK, J. *Animal behavior:* an evolutionary approach. Massachusetts: Sinauer Associates, 1993. 625p.

ALVARENGA, C.M.D., VOLPATO, G.L. Agonistic profile and metabolism in alevines of Nile tilapia. *Physiol. Behav.*, v. 57, p. 75-80, 1995.

ALVES, M. M., SANTOS, H.L. dos, LOPES, R.A., PETENUSCI, S.O., HAIASHI, C. Rhythm of development in oocyte of the Tilapia, *Oreochromis niloticus* L. (Pisces: Cichlidae): a morphometric and histochemical study. *Gegenbaurs Morphol. Jahrb.*, v.129, n. 5, p. 575-592, 1983.

BOROWSKY, R.L. Agonistic behavior and social inhibition of maturation in fishes of the genus *Xyphophorus* (Poecilidae). *Copeia*, v. 3, p. 792-796, 1987.

FALTER, U. Descriptions des padrons des colorations chez *Oreochromis niloticus* (L.) (Teleostei: Cichlidae). *Ann. Soc. R. Zool. Belg.*, v. 2, p. 201-219, 1987.

FERNANDES, M.O. , VOLPATO, G.L. Heterogeneous growth in the Nile tilapia: social stress and carbohydrate metabolysm. *Physiol. and Behav.*, v. 54, p. 319-323, 1993.

GONÇALVES, E., NISHIDA, S.M. Estratégias reprodutivas e hierarquia de dominância em peixes. *Anais de Etologia*, v.12, p. 31-52, 1994.

GROSS, M.R. Sunfish, salmon, and the evolution of alternative reproductive strategies and tactics in fishes. In: POTTS, G., WOOTON, R.J. eds.). *Fish reproduction:* Strategies and Tactics. London: Academic Press, 1984, p. 55-75.

KREBS, J.R. & DAVIES, N.B. (eds). Alternative breeding strategies. In: *An introduction to behavioural ecology*. Oxford: Blackwell Science Ltda, 1995, p. 244-264.

MAYNARD-SMITH, J. The theory of the games and the evolution of animal conflicts. *J. Theor. Biol.*, v. 47, p. 209-221, 1974.

RIBBINK, A.J. Alternative life-history styles of some African cichlid fishes. *Environ. Biol. of Fishes,* v. 28, p.87-100, 1990.

ROMAGOSA, E. *Mudanças morfológicas (microscopia de luz e eletrônica) das gônadas de Pacu (Piaractus mesopotamicus (HOMBERG, 1887)), durante o ciclo reprodutivo em condições de confinamento.* Rio Claro: Instituto de Biociências, 1991, 177 p. Dissertação (Mestrado) – Instituto de Biociências da UNESP.

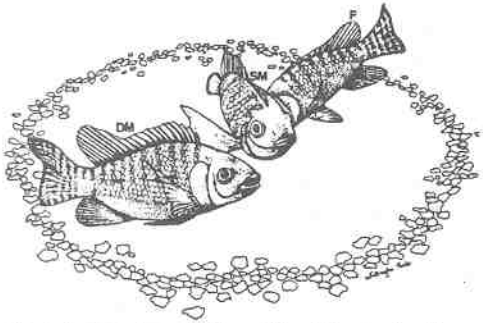

Fig. 1: Spawning behavior of the Nile tilapia in the nest. A: a couple with a batch of eggs, B: dominant fish delivering milt on the s and female approaching its mouth to the male's genital papilla, and C: female picking up the eggs into its mouth.

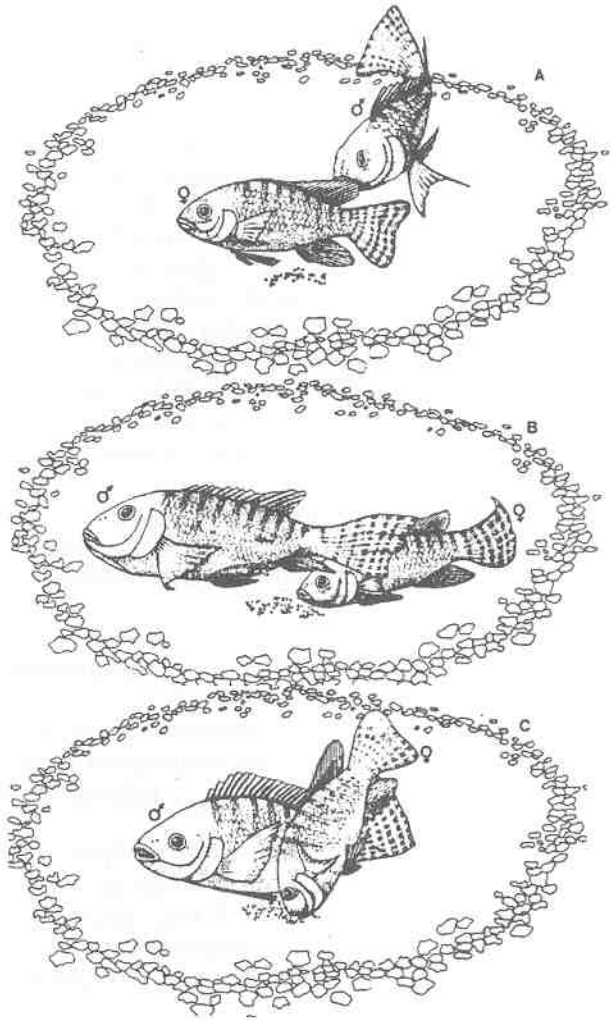

Fig. 2: Sneaking behavior in the Nile tilapia. The subordinate male (SM) slips between the couple and delivers milt. Thus, the female (F) might suck the subordinate's milt at this time. Soon the dominant male (DM) chases the subordinate away.