Maternal Aggression During the Mouthbrooding Cycle in the Cichlid Fish, *Oreochromis mossambicus*

Rui F. Oliveira* and Vitor C. Almada

Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Lisboa, Portugal

: :

Maternal aggression was studied in *Oreochromis mossambicus* during the mouthbrooding cycle. Brooding females were observed in heterosexual captive groups, and their agonistic interactions and behavioural activities were registered. Brooding females were classified into three classes according to the developmental stage of the brood they were incubating: phase 1, brooding eggs; phase 2, brooding fry with yolk-sac; phase 3, brooding fry with exogeneous feeding. The behaviour of the brooding females was compared with the behaviour of control non-incubating females. During the brooding cycle females become increasingly more aggressive toward other individuals, with their aggressiveness reaching a peak in phase 3. During the brooding cycle the females also suppress their feeding activities. The outcome of the agonistic interactions (victories–defeats) of the brooding females was positively correlated with the brooding phase but not with clutch size. The main function of maternal aggression in *O. mossambicus* seems to be the defence of the vulnerable brood against predators, including conspecifics, at a developmental stage when the fry start to forage outside the mother's mouth. Aggr. Behav. 24:187–196, 1998. © 1998 Wiley-Liss, Inc.

: :

Key words: maternal aggression; mouthbrooding; cichlids

INTRODUCTION

Despite the vast literature on maternal aggression in taxa that range from mammals to invertebrates [see Archer, 1988; Wilson, 1975], there has been a preponderance of studies on rodents [e.g., Parmigiani et al., 1988; Svare, 1981, 1990]. Although in bony fishes there are many forms of parental care that originated a substantial literature [Almada, 1990; Baylis, 1981; Blumer, 1979, 1982; Smith and Wootton, 1995], few studies have centered on parental aggression, even more so in the case of females.

*Correspondence to: Rui F. Oliveira, Unidade de Investigação em Eco-Etologia, Instituto Superior de Psicologia Aplicada, Rua Jardim do Tabaco 44, 1100 Lisboa, Portugal. E-mail: ruiol@ispa.pt

In *Oreochromis mossambicus* during the breeding season the males establish territories in dense aggregations (leks) visited by the females that spawn in the males' nests. Afterwards the females transport the eggs in their mouths and leave the lek, moving to shallow waters, where they mouthbrood the eggs and care for the fry [Bruton and Boltt, 1975; Fryer and Iles, 1972].

Although there are many studies on the sexual and agonistic behaviour of male cichlids of maternal brooding species, there are few data on the behaviour of females [see Keenleyside, 1991]. The behaviour of females has been studied mainly in relation to the interactions between mother and fry [Baerends and Baerends van Roon, 1950; Destexhe-Gomez and Ruwet, 1967; Fryer and Iles, 1972] Russock, 1986; Russock and Schein, 1974, 1977], leaving maternal aggression as a largely unexplored area. However, maternal aggression is a well developed phenomenon in this species, and as early as 1950 Baerends and Baerends van Roon, in their classic study of cichlid social behaviour, had clearly established that mouthbrooding females actively defend their fry and may even adopt a special mouthbrooding colouration pattern.

In this paper we compare the intraspecific aggression of females throughout the mouthbrooding cycle in captive *Oreochromis mossambicus.*

MATERIALS AND METHODS

Two community tanks (120 × 40 × 50 cm) were set up (Table I) and were regularly inspected for mouthbrooding females. When detected, these females, whose phase of incubation was not known *a priori,* were selected for behavioural observations. Four sessions of focal observations [see Martin and Bateson, 1993] of 5 min each were conducted for each female. During these observations, two recording methods were used: (a) instantaneous recoding [sensu Martin and Bateson, 1993] for behavioural activities (swimming, hovering, feeding, agonistic interaction, and nipping at the surface), in which the ongoing activity was noted every 30 sec; and (b) in addition, continuous recording [*sensu* Martin and Bateson, 1993] for social interactions, in which the identity of the opponent was also recorded.

For each observed mouthbrooding female, a control non-incubating female was observed using the same procedures. These females were selected within the same group and period to control for temporal variation in the social dynamics of the group and for between-group variation.

TABLE I. Composition of the Studied Groups

	Group 1	Group 2
N	14	14
Sex ratio (males:females)	9:5	9:5
Female SL[a] (min-max)	8–12 cm	8–10.5 cm
Male SL (min-max)	8–16 cm	7.5–14 cm
Number of territorial males (max)	3	4
Number of brooding females (max)	3	2

[a]SL, standard length

At the end of the observation period the observed females were captured with a hand net. The standard length of the female was measured and the number of eggs/fry brooded was recorded, after which the females were returned to their original aquaria. The females were classified in three classes according to the developmental stage of their broods: phase 1, incubating fertilized eggs; phase 2, incubating yolk-sac fry; phase 3, incubating fry without or with only vestigial yolk-sac and with the anus opened [i.e., with exogeneous feeding].

Each female was used only once for any of the above-mentioned classes to avoid pseudoreplication of data [pooling fallacy *sensu* Machlis et al., 1985]. Females were individually recognised by their relative sizes within the groups and by natural markings.

The data for each class of females were compared with their respective controls using non-parametric statistics [see Siegel and Castellan, 1988]. A goodness-of-fit simulation procedure [Almada and Oliveira, 1997] was also used to analyse in more detail the distribution of the agonistic interactions among the different classes of individuals present in the tanks (i.e., territorial males, non-territorial males, females, and brooding females).

RESULTS

Non-incubating females of *O. mossambicus* showed very low levels of aggression, both among themselves and toward males [as already described, see Oliveira, 1995; Oliveira and Almada, 1996], and presented a neutral colouration pattern [see Neil, 1964, for a description of the colouration patterns in *O. mossambicus*]. During the mouthbrooding cycle females became increasingly more aggressive toward other conspecifics, but unlike males they did not defend territories on the substrate but rather a mobile space around themselves. Their agonistic behaviour also seemed to differ from that of territorial males in that for mouthbrooding females the aggressive acts were restricted to charges, chases, and butting. The more stereotyped and elaborated displays of territorial males [i.e., frontal and lateral displays, pendelling, and mouthfighting; see Baerends and Baerends van Roon, 1950, for detailed descriptions of these behavioural acts] were never observed in mouthbrooding females. Their colouration pattern also changed gradually during the mouthbrooding cycle, and in its full form the fishes were light grey [dark 1 pattern *sensu* Neil, 1964] with a superimposed pattern of dark stripes; the eyes presented as horizontal bars in the irises, and there were dark lips and a mandibular spot.

When we compare the females in different phases with their respective controls for the outcome of agonistic interactions (i.e., victories–defeats), we found that for brooding phases 1 and 2 the differences were not significant [Mann-Whitney U test: phase 1, n = 6, z = –0.48, $P = 0.63$; phase 2, n = 8, z = –1.68, $P = 0.09$], and both classes of females and their controls showed negative values, as is typical of low rank fishes, including non-brooding females (see Fig. 1). In phase 3 this outcome became positive in brooding females and significantly different from the respective controls [Mann-Whitney U test: phase 3, n = 8, z = –3.36, $P < 0.001$], being typical of dominant fishes. If the aggressive acts delivered and received are compared separately, the following pattern emerges:
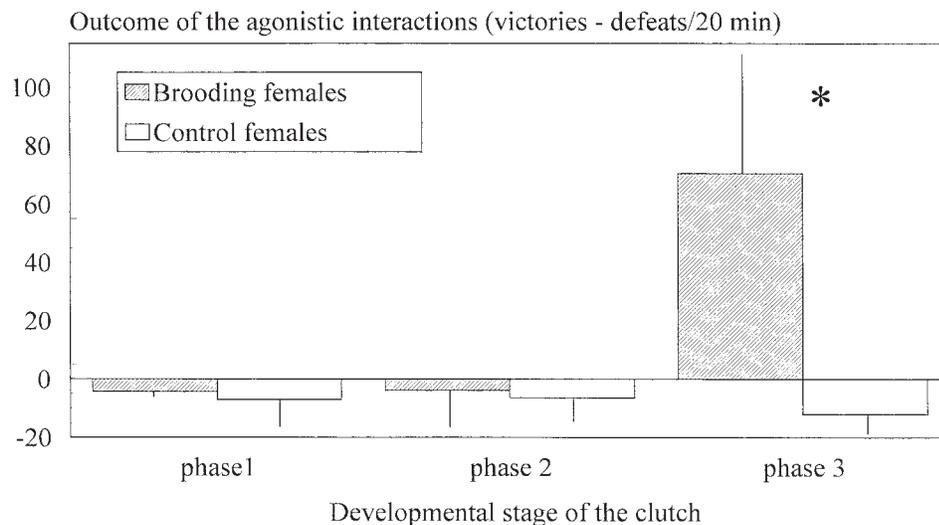
Outcome of the agonistic interactions (victories - defeats/20 min)

Fig. 1.   Variation (mean ± standard deviation) of the outcome of the agonistic interactions along the mouthbrooding cycle. Asterisk marks significant differences between incubating and control females.

(a) in brooding phase 1 the females did not attack other fishes, and the number of agonistic acts received did not differ from that of their controls (mean ± st.dev.: brooding group = 4.33 ± 1.63; control group = 7.00 ± 7.85; Mann-Whitney U test: n = 6, z = –0.48, $P = 0.63$);

(b) in brooding phase 2 the number of attacks by incubating females is significantly higher than that by controls (mean ± st.dev.: brooding group = 1.75 ± 1.91; control group = 0; Mann-Whitney U test: n = 8, z = –2.1, $P < 0.01$), but no difference was found in the number of acts received (mean ± st.dev.: brooding group = 5.63 ± 10.01; control group = 6.50 ± 5.53; Mann-Whitney U test: n = 8, z = –1.31, $P = 0.19$);

(c) in brooding phase 3 the incubating females performed a significantly higher number of attacks than controls (mean ± st.dev.: brooding group = 72.1 ± 41.6; control group = 0.13 ± 0.35; Mann-Whitney U test: n = 8, z = –3.36, $P < 0.001$) and were attacked less than controls (mean ± st.dev.: brooding group = 1.63 ± 3.85; control group = 12.25 ± 6.71; Mann-Whitney U test: n = 8, z = –3.04, $P < 0.01$).

In order to evaluate to what extent the level of aggression showed by mouthbrooding females was a function of the number of eggs/fry in their mouth, a partial correlation was computed between clutch size (number of eggs/fry), incubation phase (1, 2, or 3), and the outcome of agonistic interactions (victories–defeats). The correlation between agonistic outcome and incubation phase was significant (partial r = 0.66, n = 22, $P < 0.01$), but the effect of clutch size was not (partial r = 0.06, n = 22, $P = 0.81$). This result must be taken with caution since the size of the clutch decreases as incubation progresses (see Fig. 2; Kruskal-Wallis Anova: $H_{(2, n=22)} = 6.98$, $P < 0.05$). This trend remains even when we control for the size of the brooding females (clutch size vs. developmental stage controlling for female size: partial r = –0.61, n = 22, $P < 0.01$).

As mentioned in the Materials and Methods section, a simulation goodness-of-fit test

Clutch size (n)

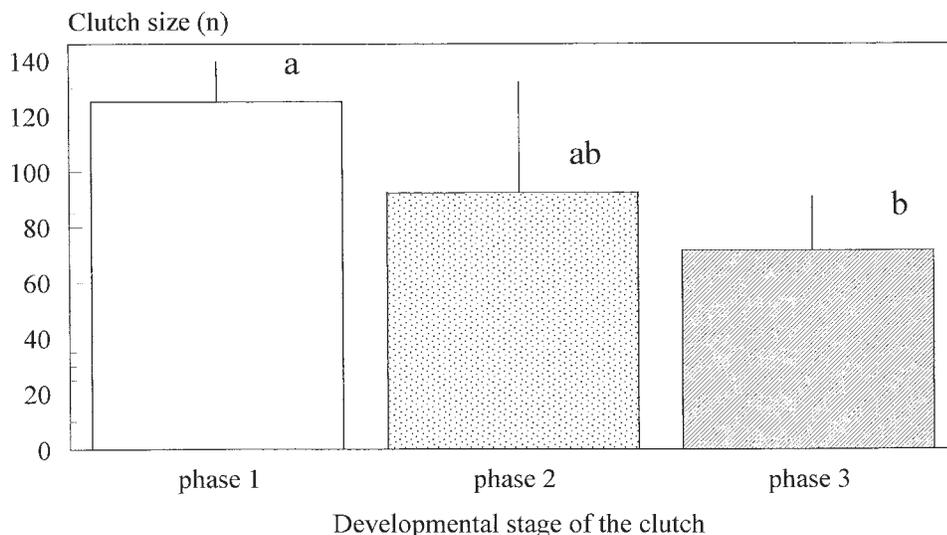Fig. 2. Variation (mean ± standard deviation) of the number of eggs/fry incubated by the females along the mouthbrooding cycle. Groups that differ significantly are marked with different letters.

was performed to evaluate the extent to which females of each phase differentially attacked fishes of different social categories and conversely to assess the differential importance of aggression directed toward them by fishes of the different classes. The expected frequencies were computed taking into account the expression of the different classes in the composition of the groups. The results of this analysis are summarized in Table II. Inspection of Table II shows that brooding females (a) preferentially attacked non-brooding females (in phases 2 and 3) and attacked other brooding females (in phase 3) and territorial males (in phases 2 and 3) less than expected and (b) were not attacked by non-brooding females and by non-territorial males (in all phases) and were attacked by other brooding females (in phases 1 and 2) and by territorial males (in phases 1 and 3) more than would be expected by chance.

In summary, we can say that for these captive groups, mouthbrooding females, especially in phase 3, experience a rise in their social status.

During the mouthbrooding cycle the females suppress their feeding activity except for the intake of a few food particles that seemed quite occasional (see Fig. 3).

DISCUSSION

Maternal aggression in *O. mossambicus* presents some interesting similarities with the maternal aggression in other quite diverse taxa. In animals as different as rodents and crustaceans, the social status of the brooding females rises during the parental phase [Figler et al., 1995; Maestripieri, 1992; Svare, 1981, 1990]. The main function of maternal aggression seems to be the defence of the vulnerable brood against predators, including conspecifics, and it is not to be confounded with aggression directed against the young themselves as a form of imposing control on their behaviour, enforcing winning, etc. [for a discussion of this topic see Archer, 1988; Wilson, 1975].

TABLE II. Distribution of the Agonistic Acts Given/Received by the Brooding Females for the Different Classes of Individuals Present in the Groups

Brooding phase/ agonistic acts	Frequencies	Opponent class				Goodness-of-fit simulation test
		Females	Brooding females	Males	Territorial males	
Phase 2,	Observed	7*	2	5	0*	$\chi^2 = 8.66$
acts given	Expected	3	2.1	5.6	3.3	$P = 0.091$
Phase 3,	Observed	180*	75*	248	78*	$\chi^2 = 70.1$
acts given	Expected	111.9	117.3	234.5	117.3	$P < 0.001$
Phase 1,	Observed	0*	13*	0*	13*	$\chi^2 = 44.4$
acts received	Expected	6.67	3.67	10	5.67	$P < 0.001$
Phase 2,	Observed	0*	36*	0*	8	$\chi^2 = 156.3$
acts received	Expected	9.4	6.7	17.7	10.2	$P < 0.001$
Phase 3,	Observed	0	0*	0*	13*	$\chi^2 = 43.3$
acts received	Expected	2.5	2.6	5.3	2.6	$P < 0.001$

*Significant differences between the observed and the expected values for specific classes of opponents, detected with the goodness-of-fit simulation test Adersim.
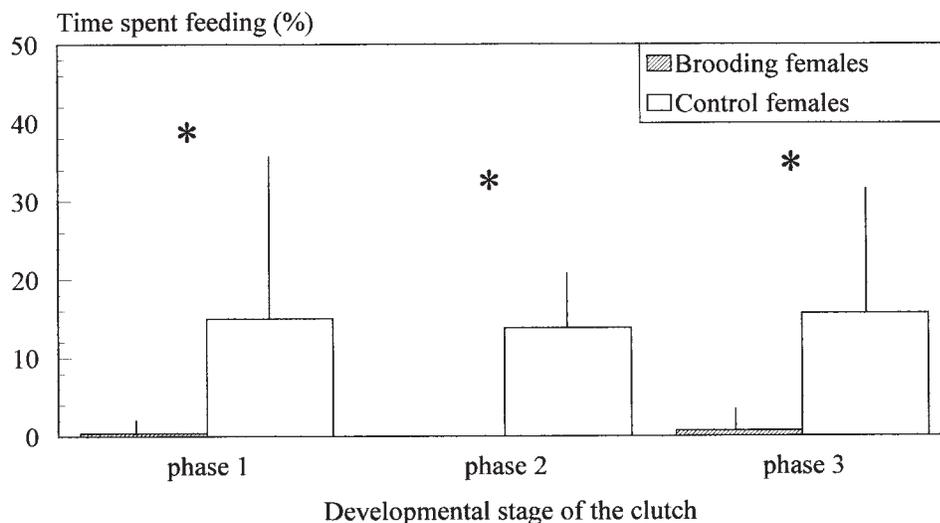
Time spent feeding (%)

Fig. 3.   Variation (mean ± standard deviation) of the time spent feeding by mouthbrooding and control females along the mouthbrooding cycle. Asterisks mark significant differences between incubating and control females.

Adjustments of the parental behaviour, including parental aggression and risks taken in the presence of a predator, as a function of clutch size and developmental stage of the clutch, have been reported [see Archer, 1988]. In the case of teleosts, the readiness and/ or the intensity of parental aggression is influenced both by the size and by the developmental stage of the clutches [e.g., *Pomatochistus microps*, Magnhagen and Vestergaard, 1993; *Micropterus dolomieui,* Ridgway, 1988, 1989; *Lepomis macrochirus,* Coleman et al., 1985; *Gasterosteus aculeatus,* Pressley, 1981; and *Cichlasoma nigrofasciatum,* Lavery and Keenleyside, 1990; Lavery and Colgan, 1991]. In *O. mossambicus,* although an influence of clutch size on the level of maternal aggression could not be demonstrated, an increase in maternal aggression was found with the advancement of development, peaking in phase 3.

In addition, when the brood was removed from the mouth of a female, her level of aggression quickly declined, and one day later her agonistic profile and colour pattern could not be distinguished from those of non-brooding females (Oliveira, personal observations). Similarly, when female rodents are separated from their pups a marked decrease in their level of aggression is described [e.g., Al-Malaki et al., 1980; Giordano et al., 1984; Svare, 1981].

The peak of maternal aggression in *O. mossambicus* when fry are mobile and capable of exogenous feeding (phase 3) strongly suggests that it may play an important role as a means of defending around the female a space where the fry may forage more safely.

There has been considerable debate on the evaluation of the extent to which forms of aggression that serve different functions represent distinct causal mechanisms [see Archer, 1988; Brain and Benton, 1981]. Although in our study the increase of aggression in brooding females generates social change in status, it is not obvious that this form of

aggression is causally identical to that displayed by *O. mossambicus* males in their territorial disputes. First, it must be remembered that an aquarium is a very limited space, and a process that in nature may simply keep a "free space" around a fish in a captive group may cause changes of social structure and even rudiments of territoriality as mere artifacts. Second, the agonistic repertoire of brooding females lacks the stereotyped displays and fighting behaviours exhibited by males in territorial disputes.

In this respect, maternal aggression in *O. mossambicus* is more reminiscent of the ontogenetically more precocious forms of aggression. In studies on the ontogeny of social behaviour in teleost fishes it was shown that the more direct components of the agonistic repertoire, like charging, chasing, and butting, preceded more elaborate and complex agonistic displays and fighting patterns [e.g., *Etroplus maculatus,* Wyman and Ward, 1973; *O. mossambicus,* Oliveira, unpublished data; see Huntingford, 1993, for a discussion]. This suggests that the more straightforward forms of aggression could be evolutionarily more archaic, leaving the problem of one vs. multiple aggression mechanisms as an open issue.

In teleost fishes the aggression involved in territorial disputes has been shown to be androgen dependent in various species [see Borg, 1994; Liley and Stacey, 1983]. In Pomacentrids and Centrarchids, whose males claim breeding territories where they subsequently care for their broods, it was found that during the parental phase there is a dissociation between the defence of the nest and the androgen levels, which decrease in this phase [*Lepomis macrochirus,* Kindler et al., 1989; *Chromis dispilus,* Pankhurst, 1990; and *Hypsypops rubicundus,* Sikkel, 1993]. A similar trend is also found for Syngnathids, where reproducing males present higher levels of circulating androgens than brooding ones [Mayer et al., 1993]. These findings suggest that territorial and parental defence may differ at least in some of their physiological determinants.

On the other hand, in other teleost fishes prolactin has been implicated in the control of parental behaviours, such as fanning the eggs and mucus production to feed the fry [Fiedler, 1962; Blüm, 1974; de Ruiter et al., 1986], in a similar vein to what has been documented in other vertebrates [see Nelson, 1995]. Nevertheless, in the case of *O. mossambicus* there is no increase in prolactin levels during the brooding phase [Wendelaar-Bonga et al., 1984], and interestingly testosterone shows a bimodal distribution during the brooding cycle, with one of its peaks occurring at the final phase of oral incubation, while the other precedes spawning [Smith and Haley, 1988]. Thus, even the generalizations among species on the endocrine aspects of parental aggression still need to be very cautious.

ACKNOWLEDGMENTS

REFERENCES

Al-Malaki S, Brain PF, Childs G, Benton D (1980): Factors influencing maternal attack on conspecific intruders by lactating female 'TO' strain mice. Aggressive Behavior 6:103–117.

Almada VC (1990): "Etologia da Reprodução e Cuidados Parentais nos Peixes Ósseos—Contributos para uma Abordagem Filogenética e Ecológica." University of Lisbon: Ph.D. Thesis.

Almada VC, Oliveira RF (1997): Sobre o uso de estatística de simulação em estudos de comportamento. Análise Psicológica 15:11–23.

Archer J (1988): "The Behavioural Biology of Aggression." Cambridge, England: Cambridge University Press.

Baerends GP, Baerends van Roon JM (1950): An introduction to the study of the ethology of cichlid fishes. Behaviour suppl. 1:1–242.

Baylis JR (1981): Paternal behaviour in fishes: A question of investment, timing or rate? Nature 276:738.

Blüm V (1974): Die rolle des prolaktins der Cichlidenbrutpflege. Fortschrift Zoologie 22:310–333.

Blumer LS (1979): Male parental care in the bony fishes. The Quarterly Reviews of Biology 54:149–161.

Blumer LS (1982): A bibliography and categorization of bony fishes exhibiting parental care. Zoological Journal of the Linnean Society 76:1–22.

Borg B (1994): Androgens in teleost fishes. Comparative Biochemistry and Physiology C 109:219–245.

Brain PF, Benton D (eds) (1981): "The Biology of Aggression." Alphen aan den Rijn: Sijthoff and Nordhoff.

Bruton MN, Boltt RE (1975): Aspects of the biology of *Tilapia mossambica* Peters (Pisces: Cichlidae) in a natural freshwater lake (Lake Sibaya, South Africa). Journal of Fish Biology 7:423–446.

Coleman RM, Gross MR, Sargent RC (1985): Parental investment decision rules: A test in bluegill sunfish. Behavioral Ecology & Sociobiology 18:59–66.

de Ruiter AJH, Wendelaar Bonga SE, Slijkhuis H, Baggerman B (1986): The effect of prolactin on fanning behavior in the male three-spined stickleback, *Gasterosteus aculeatus* L. General and Comparative Endocrinology 64:273–283.

Destexhe-Gomez F, Ruwet JC (1967): Impregnation et cohesion familiale chez les *Tilapia.* Annales de la Sociétè Royale de Zoologie de Belgique 97:161–173.

Fiedler K (1962): Die Wirkung von Prolactin auf das Verhalten des Lippfisches *Crenilabrus ocellatus* (Forskal). Zoologische Jahrbucher, Abt. Anatomie Zoologie und Physiologie der Tiere 69:609–620.

Figler MH, Twum M, Finkelstein JE, Peeke HVS (1995): Maternal aggression in red swamp crayfish (*Procambarus clarkii,* Girard): The relation between reproductive status and outcome of aggressive encounters with male and female conspecifics. Behaviour 132:107–125.

Fryer G, Iles TD (1972): "The Cichlid Fishes of The Great Lakes of Africa—Their Biology and Evolution." Edinburgh: Oliver & Boyd.

Giordano AL, Siegel HI, Rosenblatt JS (1984): Effects of mother-litter separation and reunion on maternal aggression and pup mortality. Physiology and Behavior 33:903–906.

Huntingford FA (1993): Development of behaviour in fish. In Pitcher TJ (ed): "Behaviour of Teleost Fishes." 2nd ed. London: Chapman & Hall, pp 57–83.

Keenleyside MHA (ed) (1991): "Cichlid Fishes—Behaviour, Ecology and Evolution." London: Chapman & Hall.

Kindler PM, Philipp DP, Gross MR, Bahr JM (1989): Serum 11-ketotestosterone and testosterone concentrations associated with reproduction in male bluegill (*Lepomis macrochirus:* Centrarchidae). General and Comparative Endocrinology 75:446–453.

Lavery RJ, Colgan PW (1991): Brood age and parental defence in the convict cichlid, *Cichlasoma nigrofasciatum* (Pisces: Cichlidae). Animal Behavior 41:945–951.

Lavery RJ, Keenleyside MHA (1990): Parental investment of a biparental cichlid fish, *Cichlasoma nigrofasciatum,* in relation to brood size and past investment. Animal Behavior 40:1128–1137.

Liley NR, Stacey NE (1983): Hormones, pheromones, and reproductive behavior in fish. In Hoar WS, Randall DJ, Donaldson EM (eds): "Fish Physiology—Vol. 9: Reproduction, Part B: Behavior and Fertility Control." New York: Academic Press, pp 1–63.

Machlis L, Dodd PWD, Fentress JC (1985): The pooling fallacy: Problems arising when individuals contribute more than one observation to the data set. Zeitschrift für Tierpsychologie 68:201–214.

Maestripieri D (1992): Functional aspects of maternal aggression in Mammals. Canadian Journal of Zoology 70:1069–1077.

Magnhagen C, Vestergaard K (1993): Brood size and offspring age affect risk-taking and aggression in nest-guarding common gobies. Behaviour 125:233–243.

Martin P, Bateson P (1993): "Measuring Behaviour: An Introductory Guide." 2nd ed. Cambridge, England: Cambridge University Press.

Mayer I, Rosenqvist G, Borg B, Ahnesjö I, Berglund A, Schulz RW (1993): Plasma levels of sex steroids in three species of pipefish (Syngnathidae). Canadian Journal of Zoology 71:1903–1907.

Neil EH (1964): An analysis of colour changes and social behaviour of *Tilapia mossambica.* University of California Publications in Zoology 75:1–58.

Nelson RJ (1995): "An Introduction to Behavioral Endocrinology." Sunderland, MA: Sinauer.

Oliveira RF (1995): "Etologia Social e Endocrinologia Comportamental da Tilápia *Oreochromis mossambicus* (Teleostei, Cichlidae)." University of Lisbon: Ph.D. Thesis.

Oliveira RF, Almada VC (1996): Dominance hierarchies and social structure in captive groups of the Mozambique tilapia *Oreochromis mossambicus.* (Teleostei, Cichlidae). Ethology Ecology & Evolution 8:39–55.

Pankhurst NW (1990): Changes in plasma levels of gonadal steroids during spawning behaviour in territorial male demoiselles *Chromis dispilus* (Pisces: Pomacentridae) sampled underwater. General and Comparative Endocrinology 79:215–225.

Parmigiani S, Brain PF, Mainardi D, Brunoni V (1988): Different patterns of biting attack employed by lactating female mice (*Mus domesticus*) in encounters with male and female conspecific intruders. Journal of Comparative Psychology 102:287–293.

Pressley PH (1981): Parental effort and the evolution of nest-guarding tactics in the three-spined stickleback, *Gasterosteus aculeatus.* L. Evolution 35:282–295.

Ridgway MS (1988): Developmental stage of offspring and brood defense in smallmouth bass (*Micropterus dolomieui*). Canadian Journal of Zoology 66:1722–1728.

Ridgway MS (1989): The parental response to brood size manipulation in smallmouth bass (*Micropterus dolomieui*). Ethology 80:47–54.

Russock HI (1986): Preferential behaviour of *Sarotherodon (Oreochromis) mossambicus* (Pisces: Cichlidae) fry to maternal models and its relevance to the concept of imprinting. Behaviour 96:304–321.

Russock HI, Schein MW (1974): Effect of early experience and age on the initial responsiveness of *Tilapia mossambica* fry to a maternal model. Animal Learning and Behaviour 2:111–114.

Russock HI, Schein MW (1977): Effect of age and experience on the filial behaviour of *Tilapia mossambica* fry (Pisces: Cichlidae). Behaviour 61:276–303.

Siegel S, Castellan NJ Jr (1988): "Nonparametric Statistics for the Behavioral Sciences." New York: McGraw Hill.

Sikkel PC (1993): Changes in plasma androgen levels associated with changes in male reproductive behavior in a brood cycling marine fish. General and Comparative Endocrinology 89:229–237.

Smith C, Wootton RJ (1995): The costs of parental care in teleost fishes. Reviews in Fish Biology and Fisheries 5:7–22.

Smith CJ, Haley SR (1988): Steroid profiles of the female tilapia, *Oreochromis mossambicus,* and correlation with oocyte growth and mouthbrooding behavior. General and Comparative Endocrinology 69:88–98.

Svare B (1981): Maternal aggression in mammals. In Gubernick DJ, Klopfer PH (eds): "Parental Care in Mammals." New York: Plenum Press, pp 179–210.

Svare B (1990): Maternal aggression: Hormonal, genetic, and developmental determinants. In Krasnegor NA, Bridges RS (eds): "Mammalian Parenting." Oxford: Oxford University Press, pp 118–132.

Wendelaar-Bonga SE, de Ruiter AJH, Slijkhuis H, Dirks L (1984): Is parental care in fish prolactin dependent? General and Comparative Endocrinology 53:460.

Wilson EO (1975): "Sociobiology: The New Synthesis." Cambridge, MA: Harvard University Press.

Wyman RL, Ward JA (1973): The development of behaviour in the cichlid fish *Etroplus maculatus.* Zeitschrift für Tierpsychologie 33:461–491.