

## Sex-role differentiation in feeding and defence of young by a biparental catfish, *Bagrus meridionalis*

KENNETH R. MCKAYE\*, DANIEL E. MUGHOGHO\* & JAY R. STAUFFER, JR†  
\*Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies, Frostburg,  
MD 21532, U.S.A.

†School of Forest Resources, Pennsylvania State University, University Park, PA 16802, U.S.A.

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**Abstract.** Parental feeding of young is well documented among endothermic vertebrates and social insects but is rare among fish. *Bagrus meridionalis* parents feed their young in a manner analogous to birds and social insects. Females feed trophic eggs to the young and the male burrows to expose benthic invertebrates for the young to eat. These behaviour patterns and parental defence of the young were directly observed with remote video-cameras. Division of labour between parents exists not only in the feeding of the young but also in their defence. Role differentiation in defence of the young was greatest when the young were subjected to the most attacks from predators. The female attacked and chased potential brood predators at the edge of the school while the male remained with the brood, executing more frontal displays. On the other hand, as the young grew older and predation decreased, both parents engaged in more sex-specific food provisioning behaviour such as egg release by the female and nest burrowing by the male. Parental role differentiation and monogamy in this species might have evolved both to enhance the growth rate of the young and to reduce their susceptibility to predation.

The evolution of parental care in fish and patterns of monogamy have attracted considerable attention (Keenleyside 1978; Shine 1978; Blumer 1979; Baylis 1981; Barlow 1984; Gross & Sargent 1985). Uniparental care is common in species that have polygynous or polyandrous mating systems. Among fish, such care is usually provided by the male (Blumer 1979). On the other hand, biparental care is common in fish species that have monogamous mating systems (Blumer 1979; Keenleyside 1979). The evidence suggests that, among species exhibiting biparental care, two parents are needed to protect free-swimming fry from predators (Keenleyside 1991). Although rarely examined in fish, however, both parents may also feed the young to promote growth.

Active parental feeding of young and role differentiation are fundamental aspects of parental care in endothermic vertebrates and social insects (Wilson 1975). Bird and mammalian parents often forage and bring food back to their young either by regurgitating it or directly feeding it to their young. Social insects may go even further in producing trophic eggs for their young to consume (Wilson 1971). Among terrestrial vertebrates, this production of 'nutritive' eggs for

larvae is known for the poison-arrow frog, *Dendrobates pumilio* (Weygoldt 1980). The external consumption of trophic eggs in fish has been reported once, by the bagrid catfish, *Bagrus meridionalis* (McKaye 1986a).

Despite the interest in comparing fish social systems to those of other vertebrates (Reese & Lighter 1978; Keenleyside 1985, 1991; Barlow 1986) the prolonged association of fish parents and offspring has not been extensively studied in situ. Field research has focused primarily upon cichlid fish (Keenleyside 1991) and secondarily upon catfish (Blumer 1986).

Among cichlids, females generally concentrate on activities associated closely with the brood, while males concentrate on defence and repulsion of predators (Keenleyside 1991). Separate roles for parents have been reported for several catfish species (Breder 1932; Fontaine 1944; Ruback 1975; Blumer 1982, 1985a; McKaye 1986a). However, no consistent pattern of role differentiation is apparent among catfish studied to date.

*Bagrus meridionalis*, which can reach over 1.5 m in length in Lake Malawi, has complex parental care. Typically both parents defend the young with the female normally on the outer perimeter



of the nest and the male in the interior with the young underneath. Females produce trophic eggs, and the young also forage upon benthic invertebrates which are obtained by the parents (McKaye 1986a). Both parents engage in mutualistic defence of young cichlid fish (McKaye & Oliver 1980; McKaye 1985; McKaye et al. 1992), and have sex-specific roles in the defence of young from predators (McKaye 1986a). We initiated this study to determine male and female time budgets for parental behaviour patterns and to determine how these change over time.

## METHODS

### Location and Procedure

We examined nine nests, all of which were 20–40 m beneath the surface on the southwest side of Thumbi Island West, Lake Malawi, Africa (35°50'E, 14°05'S; see McKaye 1981 for map). We examined one nest in April 1988, seven between October and December 1989, and one in January 1990. The longest any one nest was observed was 74 days. We recorded all observations using underwater video-cameras (RCA model no. CMR 300 with wide angle lens in Jaymar underwater housing). For nocturnal observations, we used an automatic timer to switch on the camera and underwater lights for 55 s every 17 min. We positioned the camera at the edge of each nest and videotaped all activity between 1 and 2 h; 69 h of recordings were made. We divided each 24-h circadian cycle into three time periods: morning (0501–1200 hours), afternoon (1201–1900 hours) and night (1901–0500 hours); during these periods, we made 24, 16 and eight observations, respectively. The total number of observations made on broods were as follows: 11 observations for young 1–15 days old, 12 for young 16–30 days old, nine for young 31–45 days old, five for young 46–60 days old, and 11 for young greater than 60 days old.

### Analysis of Videotapes

We made only a single observation of a nest in any cell for the 15-cell matrix of age versus time. We made repeat observations on the nine nests but always with a unique combination of time and/or age of young for a given nest. Therefore,

all observations in a cell were independent. We recorded the frequency and duration of each behavioural act performed by the parents in the nest; durations were determined to the nearest second, as was the total time that each parent spent within 50 cm of young. We made pair-wise comparisons of behaviour patterns exhibited by parents during each observation period using the Wilcoxon matched-pairs signed-ranks test ( $N=48$ ). We examined predation upon the brood by noting both the frequency of predatory attacks and the victims of those attacks. An attack was defined as an accelerated charge towards the brood by a predator. An edited tape of these recordings is available in the Pennsylvania State University (PSU) Fish Museum (catalogue no. 2330).

### Stomach Analysis of Young in Nest

We made 20 collections every other day from a brood of *B. meridionalis* (see Lovullo et al. 1992 for details of analysis). Of the 57 young whose stomachs were examined, 21 were between 15 and 30 days old and 36 were older than 30 days. For the purposes of this study we categorized the food items into three groups: zooplankton, benthic invertebrates and trophic eggs.

## RESULTS

### General Description of Catfish Behaviour

#### *Nest patrol (scene 11, PSU no. 2330)*

The fish circles the nest by using its caudal and pelvic fins. When the young are older than 15 days, the head moves from side to side (120–180°); each oscillation of the head lasts approximately 8 s. When the fry are younger than 15 days, the head moves through a shorter arc (5–120°), and more rapidly (2–5 s). The head points downwards at an angle of approximately 25° to the substratum. A slight forward motion aided by a rapid movement of pectoral fins often accompanies the head oscillations.

#### *Hover (scene 10, PSU no. 2330)*

The parent stays above the substratum with little detectable motion. Its ventral and dorsal fins



are fully spread, and the caudal fin shows a slow lateral movement.

*Attack (scenes 6 and 9, PSU no. 2330)*

Both predatory attacks by cichlid fish and defensive attacks by the catfish parents occur. Predatory cichlids make quick darts at the fry and immediately flee (McKaye et al. 1992). Parental catfish attacks are always directed towards predators. The parents often strike the predators with their mouth open, but they do not consume them. On one occasion, a male attacked a predator and then spat the apparently dead fish out of the nest (scene 9, PSU no. 2330).

*Chase (scene 6, PSU no. 2330)*

Predators are often chased away from the nest, usually when they have escaped early detection and have been able to strike at the young in the nest. Chasing consists of rapid swimming towards the predator with strong lateral caudal fin movements.

*Stationary (scene 16, PSU no. 2330)*

This behavioural act is similar to hovering, but instead of hovering in the water column, the parent descends to the substratum and remains stationary. During this phase the young are sheltered and protected beneath the parent.

*Frontal display (scene 7, PSU no. 2330)*

This act involves swift turning of the head in the direction of the predator, followed by raising of the dorsal fin, flexing the pectoral fins and rapid lateral movement of the caudal fin. All the other fins become fully spread and the operculum is flared. There is also a slight forward movement of the body.

*Burrowing (scenes 13, 14 and 15, PSU no. 2330)*

The parent points downwards with its mouth open and then plunges its head into the substratum at an angle of 30° plowing through the nest bottom. The parent propels itself from one side of the nest to the other with rapid quivering movements of its entire body. These movements stir and scatter debris throughout the nest. The

burrowing fish emerges from the other side of the nest with its head up and continues quivering. Sand and other benthic materials are expelled from the mouth and gills. After each digging bout, the young congregate around the male's mouth and gills, and feed on expelled debris.

*Egg fanning (scene 18, PSU no. 2330)*

During the egg-fanning stage, the male remains close to the nest bottom near the egg mass. The male often swims slowly around the nest with his head pointed downwards rhythmically moving its pectoral fins to ventilate and clean the eggs.

*Egg release (scene 17, PSU no. 2330)*

The female hovers 1 m above the bottom of the nest, with her fins fully spread and the anal and caudal fins tilted slightly downwards. Whenever the female catfish assumes this position, fry (as many as 20 at a time) swim towards the female, approaching her vent at a 50° angle. Young remain at the female's vent for about 75 s then return to the nest. Individual young alternate feeding at the female's vent without any overt aggression. As the first feeders return to the nest bottom, others move up to replace them. This behaviour occurs in bouts lasting approximately 3 min, during which time the young consume eggs released by females (McKaye 1986a).

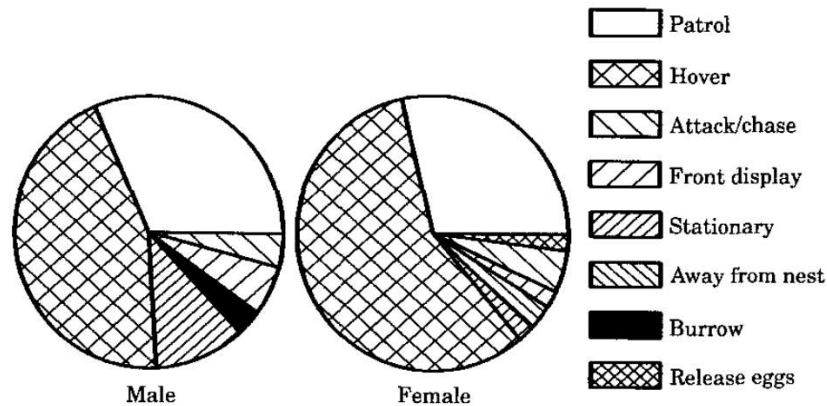
### Quantification of Parental Care Patterns

Females engaged in all behaviour patterns except egg fanning. Burrowing in the nest by females, however, was only observed once. Males engaged in all behaviour patterns except egg release, and they rarely left the nest (Fig. 1).

*Nest patrol*

When all observations were summed, parents spent approximately 30% of their time patrolling (Fig. 1). There was no variation in the diel pattern of patrols (Fig. 2a, Kruskal–Wallis test,  $P > 0.05$ ), nor was there any significant difference between the sexes in time spent patrolling (Wilcoxon matched-pairs signed-ranks test,  $P > 0.05$ ). The amount of time that both parents spent patrolling declined with increased age of young (Fig. 2a, Kruskal–Wallis test,  $P < 0.05$ ).





**Figure 1.** Average proportion of time males and females engaged in various types of behaviour with young ( $N=48$  observations/pair).

### Hover

Parents spent over 50% of their time hovering (Fig. 1). The amount of time spent hovering showed no diel variation (Fig. 2b, Kruskal–Wallis test,  $P>0.05$ ), but females spent more time hovering than males did (Wilcoxon test,  $P<0.05$ ).

The mean length of time females hovered increased with the age of the brood (Fig. 2b, Kruskal–Wallis test,  $P<0.05$ ). Males spent the most time hovering when the young were 46–60 days old, devoting as much as 80% of their time to the activity.

### Attacking and chasing predators

Both males and females spent approximately 4.5% of the time attacking and chasing potential predators off the nest (Fig. 1). Some diel variation in the pattern of chases and attacks existed (Fig. 2c, Kruskal–Wallis test,  $P<0.05$ ). Both males and females spent proportionally more time chasing and attacking in the afternoon than in the morning. No attacks on predators were observed at night. No predators were seen 'fleeing', nor did the parents exhibit any startled response when the lights came on.

When young were 16–60 days old, females spent more time attacking and chasing than males did (Fig. 2c, Wilcoxon test,  $P<0.05$ ). When young were less than 15 days old the amount of time spent by males and females attacking and chasing predators was almost identical (Fig. 2c, Wilcoxon test,  $P>0.05$ ). When the young were greater than 60 days old, the males spent more time attacking

and chasing predators than the females (Fig. 2c, Wilcoxon test,  $P<0.05$ ).

The amount of time parents spent attacking and chasing varied for both the male and the female (Kruskal–Wallis test,  $P<0.05$ ). When young were less than 15 days old, the amount of time devoted to attacking and chasing was approximately twice the rate as when fry were greater than 15 days old (Fig. 2c). After 15 days, cichlid mothers deposited their young into catfish broods and defended the outer perimeter of the nest (McKaye 1985).

### Frontal display

During the day, males spent significantly more time performing frontal displays than females did (Fig. 2d, Wilcoxon test,  $P<0.05$ ). There were variations in the amount of time males devoted to frontal displays as young grew older (Fig. 2d, Kruskal–Wallis,  $P<0.05$ ). Male frontal displays were most common when young were 15 days old or less. Thereafter, frontal displays decreased by 50% (Fig. 2d). The amount of time females devoted to frontal displays was, however, relatively constant throughout the entire brooding period.

### Stationary

Males spent significantly more time stationary than females (Fig. 2e, Wilcoxon test,  $P<0.05$ ). For both sexes, the amount of time spent stationary varied with the stage of brood development (Fig. 2d, Kruskal–Wallis test,  $P<0.05$ ). During the first



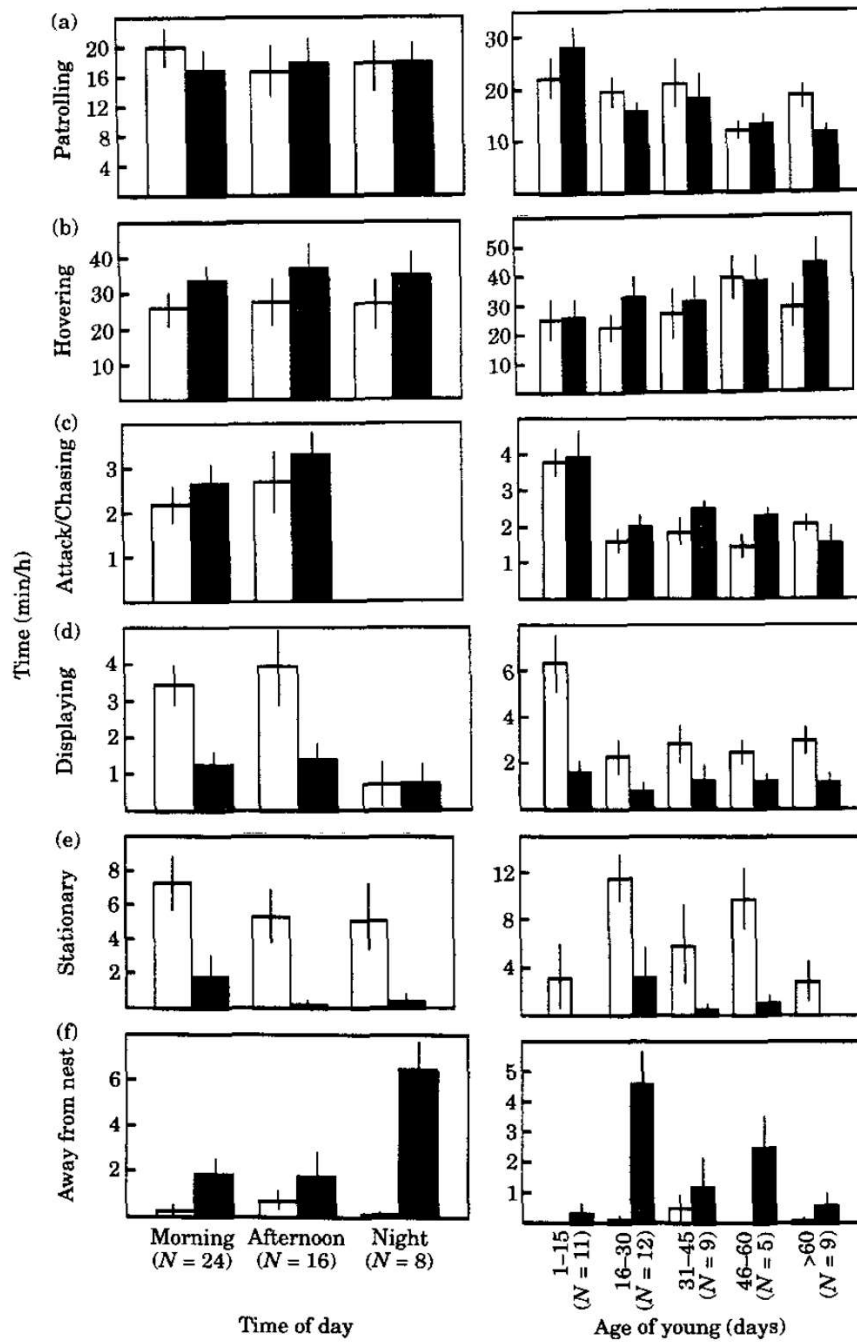
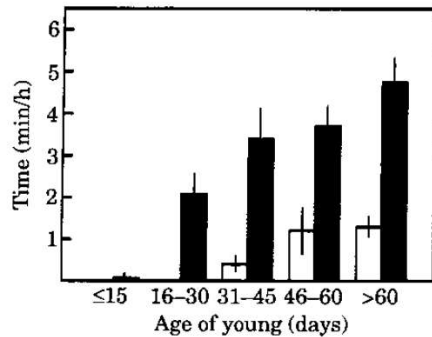
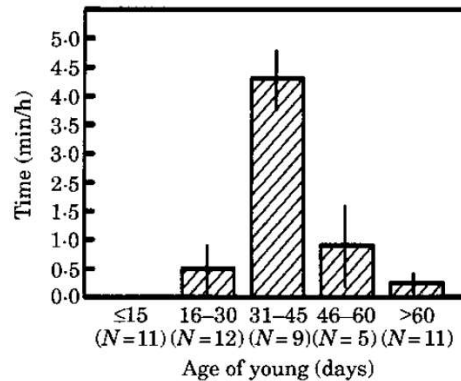


Figure 2. Mean ( $\pm$  SE) time that males ( $\square$ ) and females ( $\blacksquare$ ) spent (a) patrolling, (b) hovering, (c) attacking/chasing, (d) displaying, (e) stationary and (f) away from nest, throughout the day and with young of various ages ( $N$ =number of observations/pair).





**Figure 3.** Mean ( $\pm$  SE) time males spent burrowing at night ( $\blacksquare$ ;  $N=8$ ) and during the day ( $\square$ ;  $N=40$ ) at each interval of fry development.



**Figure 4.** Mean ( $\pm$  SE) time for egg release by females.

2 weeks of brood development, only the male devoted time to this behaviour. The greatest amount of stationary behaviour was observed when broods were between 15 and 30 days old.

#### Burrowing

Males spent significantly more time burrowing in the nest bottom than females did (Wilcoxon test,  $P<0.05$ ). This behaviour was observed only once in females at night, during the later stages of brood development. The amount of time males spent burrowing was three times higher at night than in daylight. Males burrowed and dug in the nest bottom with increasing frequency as fry grew older (Fig. 3). As the male catfish burrowed, the female swam towards the brood on the nest bottom possibly shielding them from predators.

#### Egg release

All observed egg-release bouts by the female and feeding by young occurred during the late morning (1000–1200 hours). Approximately 65% of the egg-releasing activities occurred when catfish broods were between 31 and 45 days old (Fig. 4). Egg releasing was not observed when the young were less than 15 days old.

#### Parents away from nest

The total time females spent away from the nest was four times greater (Fig. 2f, Wilcoxon test,  $P<0.05$ ) than the total time males spent away. Sex-specific diel patterns were evident in this activity. Females spent more time away from the

nest at night (Fig. 2f, Kruskal–Wallis test,  $P<0.05$ ). Males spent twice as much time away in the afternoon as they did during the morning or night (Fig. 2f, Kruskal–Wallis test,  $P<0.05$ ). Females spent the most time away from the nest when young were 16–30 days old (Fig. 2f, Kruskal–Wallis test,  $P<0.05$ ).

#### Parent–offspring interaction

Males were closer to their offspring significantly (Wilcoxon test,  $P<0.05$ ) more than females were; males were within 50 cm of the brood 90% of the time; whereas, females were this close only 50% of the time. Males were below females 98% of the time, and males provided the final defence against predators.

Brood size declined, due to predation, as young grew older (McKaye 1985). In the early stages of brood development, especially during the day, fry schooled cohesively and foraged on the substratum, remaining beneath the male. With increased age, the young catfish were more mobile and foraged throughout the nest, moving in a loosely packed school. At night, the young catfish were more active and widely dispersed within the nest (scene 15, PSU no. 2330).

When a predator approached, the male faced the predator and moved closer to the school. He twitched his head and caudal fin slightly, and raised his pectoral fins. Fry responded by forming a tightly packed school on the nest bottom directly under and around the male's head. The cichlid fry that were also in the nest occupied the outer perimeter. Both parents performed frontal displays that prompted cichlid young to retreat



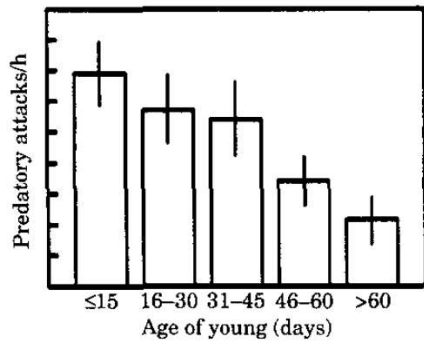


Figure 5. Mean ( $\pm$ SE) number of attacks by cichlid predators on catfish brood with young of various ages. (Sample sizes are given in Fig. 4.)

and prevented them from occupying the centre of the school.

The pattern of predation was bimodal with 90% of attacks occurring either before 1000 hours or between 1401 and 1900 hours (McKaye et al. 1992). The highest number of attacks occurred when young were less than 15 days old; the number of attacks declined as young grew older (Fig. 5, Kruskal-Wallis test,  $P < 0.05$ ).

#### Stomach analysis of young in nest

Of the 21 young examined between 15 and 30 days old, 17 had food in their stomachs, 11 had eggs, 10 had zooplankton and five had benthic invertebrates. Of the 36 young older than 30 days, 24 had food in their stomachs, 14 had eggs, four had zooplankton and 22 had benthic invertebrates. Older fry had higher occurrences of benthic invertebrates than did the young fry, whereas younger fry had a higher occurrence of zooplankton (Fig. 6).

## DISCUSSION

As in other monogamous care-giving pairs (Keenleyside 1979; Blumer 1986), division of labour between male and female *B. meridionalis* exists. Male bagrid catfish, unlike New World cichlids (Rogers 1987; Keenleyside 1991), were in close proximity to offspring. Males shielded young from predators by hovering close to the brood, and in times of danger performed more frontal displays than females, whereas females attacked and chased brood predators at the edge of the nest

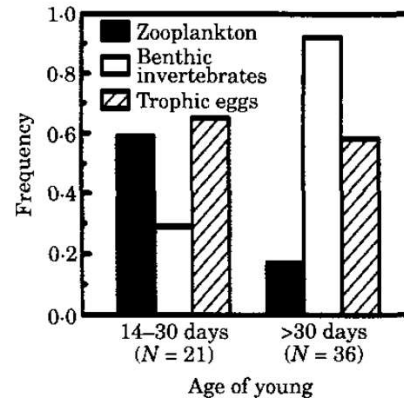


Figure 6. Frequency of food items in the stomachs of catfish young. More than one category of food can occur in a single stomach.

more than males. In general, more time was spent by both sexes on defensive parental activities (patrols, attacks, chases and frontal displays) during the first 2 weeks than during the rest of the brooding period (Fig. 2a, c, d). During the first 2 weeks the fry were subjected to the greatest number of attacks from predators (Fig. 5).

The two-tiered defence, with males close to the brood and females on the periphery, is a tactic that keeps predators away from catfish young (Rubeck 1975; Wootton & Potts 1984; Blumer 1985b). Because females are larger than males their size makes them more visible from a distance and might act to deter potential predators. This defensive strategy is similar to biparental cichlids, but the roles are reversed: among the cichlids, males are larger and are on the periphery (McKaye 1977, 1986b; McKaye & McKaye 1977; Perrone 1978; Keenleyside 1991).

In *B. meridionalis*, both members of the breeding pair actively defended their brood from potential predators. There was a complex relationship, however, between males and females in the manner in which they defended their brood. In the early stages of brood development, males spent more time closer to young and devoted more time to frontal displays (Fig. 2d) than females did. The brood was a tightly packed school and remained close to the male. During this time, females performed defensive and vigilant behaviour more frequently than males did. When a predator attacked, females moved further from their brood to chase predators, whereas males shielded young from predators.



The primary male defensive reaction was the frontal display.

During periods of low predatory activity, one parent can rest or forage while its mate looks out for predators (Perrone & Zaret 1979; Wittenberger & Tilson 1980; Itzkowitz 1986). Perrone & Zaret (1979) predicted that sex differences in parental behaviour should be more apparent during periods of low predation pressure. However, our data are equivocal in supporting this prediction and are open to other interpretations. For example, both parents concentrated on sex-specific activities such as nest burrowing by the male and egg release by the female as the broods grew older than 15 days (Figs 3 and 4). Although differentiation in these behaviour patterns was greater during periods of low predation, this might be due to the larger young being able to handle the foods produced by these behaviour patterns.

When fry were small and fed upon zooplankton, males rarely burrowed (Fig. 6; Perrone & Zaret 1979; McKaye et al. 1985), but they increased burrowing activity when young became older and could consume large food items, such as chironomids (Fig. 6; McKaye 1986a; Lovullo et al. 1992). Males also burrowed more frequently during the night (Fig. 3), when cichlid predators were inactive and young were not in danger. Burrowing reduced visibility by scattering debris throughout the nest and enabled small predators to approach undetected. However, as the young grew in size the daylight occurrence of this behaviour increased (Fig. 3) as the threat from predators decreased (Fig. 5).

Burrowing behaviour has been likened to the food gathering behaviour of bird parents (McKaye 1986a), and has also been observed among other fish such as *Cichlasoma nigrofasciatum* and *Cichlasoma panamense* (Meral 1973; Townshed & Wootton 1985; Keenleyside et al. 1990). Females of these cichlid species burrow in the nest bottom and stir food particles from the substratum with their quivering movements. The young forage on these particles (Krischik & Weber 1975). Immediately after each nest-burrowing bout by the male catfish, young congregated around the gills and mouth of the male, feeding on benthic materials. Females were observed burrowing only once. They fed the fry primarily by releasing unfertilized trophic eggs (McKaye 1986a). Unfortunately, with the station-

ary video, we were unable to observe burrowing outside the nest (Lovullo et al. 1992). Nevertheless, the videos demonstrated that the young never exited the nest and, therefore, did all of their feeding in the nest.

Because females are larger, have greater fat reserves (Blumer 1982), and perhaps forage at night while away from the nest (Fig. 2g), they may be in physiologically better condition to provide more active parental care than males. The amount of time males spent stationary or resting was higher than that spent by females (Fig. 2e). Stationary behaviour probably provides time for the smaller males to recuperate from more vigorous activity.

Parental care has two potential benefits: (1) it increases survival of young and (2) promotes growth of young (Wittenberger & Tilson 1980; Gross & Sargent 1985). Parents can ultimately leave more surviving progeny by producing smaller broods. Large females can produce more than 50 000 eggs, yet actually lay approximately 2000–4000 (McKaye 1986a). Enhancing the growth of young by providing food is an excellent strategy where predation pressure is intense (Gross & Sargent 1985). This argument is supported by the marked decline in predation pressure with increased age and size of the young (Fig. 5). The faster the young grow, the shorter the stage in which they are vulnerable to the full suite of small cichlid predators, because it is more difficult for these predators to capture and handle them.

During our 14 years of observing catfish broods, we have never seen a lone female guarding a brood. Approximately 10% of the broods encountered were tended by lone males. We conclude, therefore, that monogamy in this species is the female's prerogative and fits Barlow's (1986) model for large freshwater species. It appears that females benefit more from a monogamous relationship, which includes producing and feeding unfertilized eggs to young, than from polygamous relationships, in which all of their eggs would be fertilized by multiple males.

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