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Survival of Broods under Parental Care and Parental Roles of the Cichlid Fish, *Lamprologus toae*, in Lake Tanganyika

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Abstract The survival of offspring guarded by both parents and by only the female parent who remained after experimental removal of the male parent was observed in the cichlid fish *Lamprologus toae* in its natural habitat. The number of offspring guarded by both parents abruptly decreased during the period from eggs through postlarvae. It became stable for low rate of mortality when the offspring were between 0.5 and 1.8 cm in body length. The number again decreased this time gradually after attaining 1.8 cm in body length. Mortality seemed to be caused by predation. Experimental removal of the male parent at any larval stage caused the decrease of offspring by predatory fishes. It seems that both parents are indispensable to protect the offspring against predators under natural conditions.

A great diversity in types of parental care is recognized in the cichlids of African lakes (Fryer, 1959; Fryer and Iles, 1972; Brichard, 1978). There are maternal and biparental species in Lake Tanganyika. The survival of offspring under parental care is especially of interest, but little has been studied about it in natural conditions. The author reported on the survival in the larval stage of the genus *Lamprologus* in Lake Tanganyika, but no consecutive observations have been performed on the survival of larvae under parental care in order to trace the fluctuation of the number of larvae in a brood (Nagoshi, 1985).

In the present study, successive observations under field conditions were carried out on the number of larvae guarded by the parents of *Lamprologus toae*, which is a typical monogamous substrate brooder, inhabiting shallow rocky area (Nagoshi, 1983). In biparental cichlid species there appears to be unequal division of parental duties between male and female which contributes to the survival of offspring. In order to evaluate the parental roles in the survival of offspring under parental care, experimental removals of the male were done at various developmental stages of the larvae guarded by the parents in the natural habitat.

Materials and methods

The field research was carried out at the rocky shore of Luhanga, located near the end of the north western coast of Lake Tanganyika from July to September 1985. Underwater observations were performed by SCUBA diving. By visual observation the number of *L. toae* larvae of some broods under parental care was followed at various stages at intervals of 2–4 days. These broods were distributed at depths between 1 and 5 m in the rocky area of about 300 m length along the shore. The number of larvae of each brood was estimated by eye.

Male parents guarding larvae were removed by spearing to evaluate the parental role of the male. Removals were also carried out for broods at various developmental stages of the larvae.

To know the stage of the larva, specimens were collected by hand net at the end of the observation-period and their body lengths were measured. The size at each estimation of number of larvae was estimated from the measured body length and the growth curve which had been obtained by Nagoshi (1985).

Results

Breeding. The breeding of *L. toae* is performed on rocky shores at depths between 1 and 5 m. Both parents guard their offspring in the breeding territory for about 12 weeks. Male and female parents rearing a brood ranged from 6.6 to 7.4 cm in body length and there is little difference in size between the sexes. As eggs are placed on flat rocks or boulders for 4–5 days, they are easily

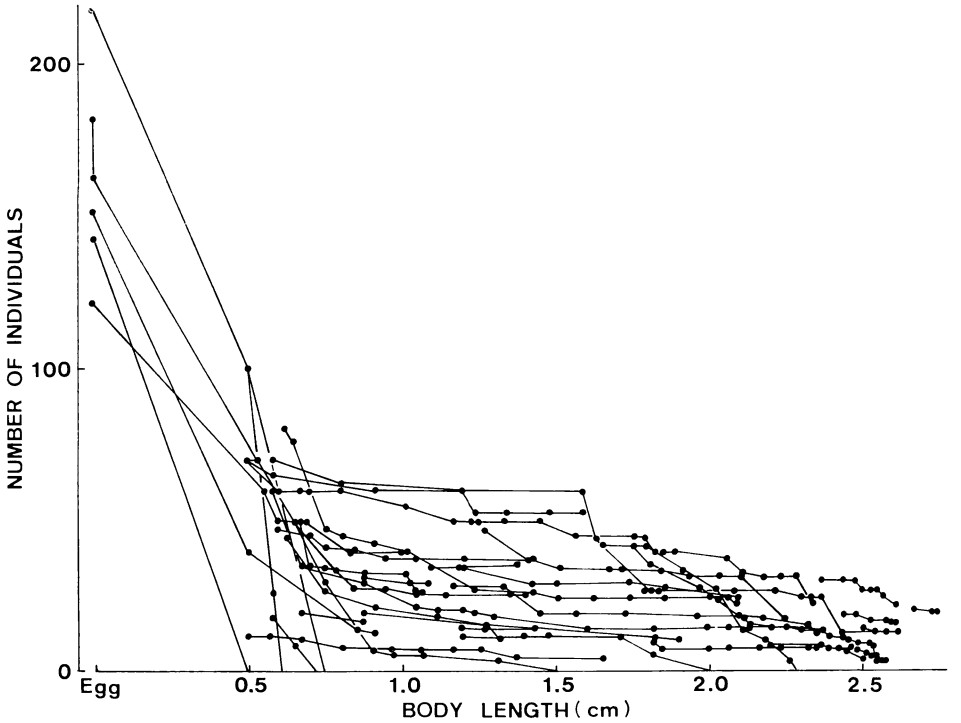

Fig. 1. Survival of offspring under parental care in the 42 broods.

observed. The hatching prolarva, 0.35 cm in body length, is transferred in the female's mouth to a neighboring narrow rock crevice. The larvae stay in the crevice until they become free swimming fry, 0.50 cm in body length. The female parent hovers near the spawning site to protect the eggs and larvae. The male parent also hovers around the spawning site, but further from its center than the female. Thus, there is some separation of parental roles between the sexes. The female parent is more involved in direct care of the young and the male parent more concerned with defense of the brood.

Originally in this species, a mature male and female establish a pair bond and guard their offspring. In the present study, however, it was observed that two males governed two females each with whom they guarded their offspring at different breeding sites. In one case, the younger brood disappeared from the breeding site at an early stage. In the other case, most of the younger brood were "farmed out" to another brood.

Survival of progeny. The number of larvae under parental care was estimated at various developmental stages for 42 broods at depths between 1 and 5 m from July to September 1985, until their independence (Fig. 1).

The estimation of 5 broods was begun just after spawning. Females laid 121–218 eggs (mean, 162) on the surface of rocks and boulders. Numbers were not estimated when the progeny were less than 0.5 cm in body length, because they formed clumps in narrow crevices between boulders.

The number of larvae surviving decreased with development, especially during the period from egg to the point at which the larvae became free swimming fry, 0.50 cm in body length. Two of the 5 broods disappeared by 3 weeks after spawning. The overall survival rate of offspring during this period was less than 40%. Based on the underwater observations the reduction in numbers during this period was caused by predation by the fishes, *Telmatochromis bifrenatus*, *T. temporalis* etc. The number of survivals scarcely changes between 0.8 and 1.8 cm in body length. The larvae of 2 mere broods disappeared from the breeding site during this period. In these cases, the male parents left the breeding site before the

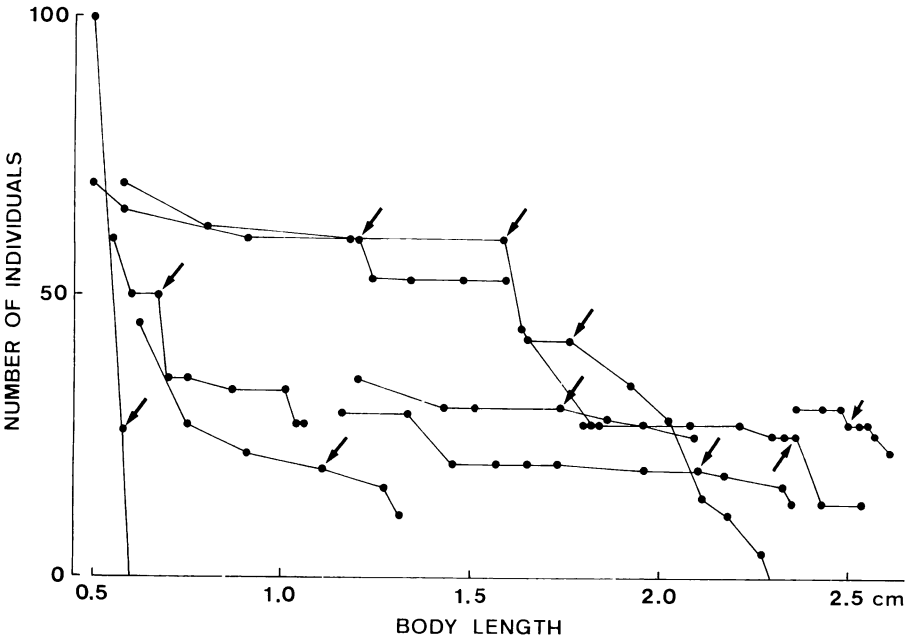

Fig. 2. Survival of offspring in the 11 broods under removal of the male parent. The arrows represent removal of the male parent.

disappearance of their larvae, suggesting that defense of offspring is weakened by the absence of the male parent. Offspring survival again decreased after reaching 1.8 cm in body length. This decrease seems to be related to predation caused by weak parental care. The male parent often disappears from the breeding site for long period of time. Moreover, the offspring sometimes left the breeding site and became independent of parental care. Consequently they were attacked by predatory fishes outside the breeding site. When offspring of about 2.5 cm in body length became independent of parental care, their survival rate was approximately 10% of spawned eggs.

Changes in numbers of offspring under parental care, can be roughly divided into three periods: 1) sharply decreasing (egg to 0.8 cm in body length), 2) stable (0.8 to 1.8 cm), and 3) gradually decreasing (more than 1.8 cm).

Male removal experiment. Of the 42 brooding pairs mentioned above, 11 were chosen for experimental removal of the male parent (Fig. 2). The removed males ranged from 6.62 to 7.38 cm in body length (mean, 6.89 cm). Removal of the male parent before the young reached the free swimming stage was followed by the disappearance of the offspring from the breeding site. The removal of the male when the offspring were 0.58 cm in body length also caused the disappearance of the offspring just after the removal. The disappearance was caused by the predation of fishes. Removal of the male when the offspring were 0.6 and 1.8 cm in body length caused the reduction and disappearance of the offspring. As the disappeared brood was guarded in shallow water less than 2.5 m depth in which subadult piscivorous fish were abundant, the offspring seemed to be preyed on by these fish. Removal of the male parent when the offspring were more than 1.8 cm in body length caused a slight reduction in survival of offspring. However, no disappearance of offspring occurred at this stage.

From these results it is considered that the effects of the absence of the male parent upon his offspring are decreased with the development of the offspring, but biparental care is indispensable for the offspring of *L. toae*, especially at the early stages of development.

Discussion

In general, the development of parental care corresponds with increasing survival rates in the animal kingdom (Ito, 1959; Wilson, 1975; Ito, 1978). The tendency is recognized also in fishes, particularly the Cichlidae. There is little information on the survival of fish larvae under parental care in the natural habitat. The author reported the survival curves of larvae under parental care in four species of the genus *Lamprologus* in Lake Tanganyika (Nagoshi, 1985). However, the curves were not obtained from successive observations of survival of offspring in a brood. In the present study, as the fluctuation of number of many broods was followed during parental care, the tendency of fluctuation in the number became clear. From these results larval development under parental care was divided into three periods: 1) sharply decreasing, 2) stable, and 3) gradually decreasing (parent-offspring conflict). It is thought that predation by fishes caused the decrease of larvae. As eggs are spawned in a clump and wrigglers congregate at the spawning site, they are an easy prey to predatory fishes, especially at night. Predators such as *Telmatochromis bifrenatus* and *T. temporalis* are abundant around the breeding site of *L. toae* (Hori et al., 1983). According to underwater observations, as they lie concealed under stones and in rock crevices and watch for a chance of predation of larvae under parental care, the guarding parents often fail to find them.

In the stable period, as the fry congregate around the parents, especially the female, the mortality due to predation is low. However, in the gradually decreasing period the numbers of a brood increase in age, size and mobility and approach independence from the parents. As the male parent goes away frequently from the breeding site, his defense of the brood becomes weak and female defense of breeding territory also becomes weak, offspring are captured by predatory fishes (Nakano and Nagoshi, unpublished).

A substrate brooding biparental species in which the eggs and fry are guarded by the both parents is the most primitive in the biparental care among cichlid fishes (Breder, 1934; Lowe (McConell), 1959; Oppenheimer, 1970; Dupuis and Keenleyside, 1982). The wrigglers and fry are defended by the parents, usually with some division of labour (Smith-Grayton and Keenleyside, 1978; Keenleyside, 1978; Keenleyside, 1979). In *L. toae*, there appears to be an unequal division of parental duties between male and female. The female performs more of the direct egg and fry-care behaviour in the central part of the breeding territory and the male is the more active defender of the offspring against predatory fishes in the peripheral region of the breeding territory. Therefore, if the male parent of *L. toae* is removed in the natural habitat, offspring survival will be reduced especially during the early stage. In the biparental cichlid species, *Herotilapia multispinosa*, if either of the parents is removed in the aquarium, the survival of offspring will be decreased by fish predation. However, loss of the male parent has somewhat less drastic effects on offspring survival than loss of the female parent (Keenleyside, 1978). Yanagisawa (1985) reported that one parent was experimentally removed from breeding pairs of *Perissodus microlepis* in Lake Tanganyika. He found "farming out" of the brood resulted from the loss of one of the brooding parents. In the present study, it was observed that 2 males had 2 females each whose offspring they guarded at different breeding sites. In these cases, the younger of the 2 broods disappeared from the breeding site by predation. This suggests the male parent is unable to protect more than one brood.

In many tropical waters, the young of non-mouthbrooding cichlid species need both parents to protect them from predators (Keenleyside and Bietz, 1981; Keenleyside, 1985). Barlow (1974) reported that a male cichlid, in a typically biparental species, who divides his parental defense effort between two or more females, run the risk of losing all his offspring to predators. In the biparental cichlids such as *L. toae*, both parents are indispensable to protect their offspring against predators. This seems to be related to the breeding places of the biparental cichlid fishes in which the predation pressure is high. As *L. elonatus*, *L. toae* and *L. tretocephalus* have their breeding sites in areas abundant with fish numbers and species, they appear to be biparental or monogamous. On the other hand, as *L. furcifer* and *L. modestus* prefer their breeding sites in the area which the predation pressures of other species is low (Nagoshi, 1983), they appear to be polygenous.

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タンガニイカ湖のカワスズメ科魚類 *Lamprologus toae* における親の保護下での子供の生残と雄親の役割

名越　誠

タンガニイカ湖西部湖岸域に生息し，両親が子供の保護をする *Lamprologus toae* において，保育中の子供の数の変動をスキューバ潜水により追跡した．卵から仔魚の発育初期の死亡率は高く，体長 0.8—1.8 cm の稚魚期には死亡率が低いが，その後 1.8 cm 以上になると再び死亡率が高くなった．子供の異なる発育段階で雄親を除去すると，卵から仔魚期では雌親だけでは保護できない．その後の発育段階でも雄親の除去は子供の死亡率を増大させた．これらの死亡率は他種魚類による捕食圧であり，子供を保護するためには両親の存在が不可欠であると考えられた．

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