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Brood Parasitism of a Bagrid Catfish (*Bagrus meridionalis*) by a Clariid Catfish (*Bathyclarias nyasensis*) in Lake Malawi, Africa

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Brood Parasitism of a Bagrid Catfish (*Bagrus meridionalis*) by a Clariid Catfish (*Bathyclarias nyasensis*) in Lake Malaŵi, Africa

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Bagrus meridionalis **(Bagridae; locally called Kampango) is a large substrate-spawning catfish endemic to Lake Malaŵi that exhibits bi-parental care and spawns primarily in the wet season from January to March. The female feeds her young trophic (unfertilized) eggs; the male orally collects offsite benthic organisms, which he brings back to feed the brood. While doing underwater videography in the lake, we observed evidence for brood parasitism of four Kampango nests by the most common clariid catfish in Lake Malaŵi, the endemic *Bathyclarias nyasensis* (locally called Bombe). Parasitized Kampango nests held Bombe young almost exclusively, and these were protected by Kampango adults until they exceeded 100 mm SL. We found that female and male Kampango fed the Bombe juveniles with trophic eggs and macroinvertebrates, respectively, as they do their own young. These observations represent a sophisticated example of cuckoo behavior in fishes.**

BROOD parasitism results when eggs and/or larvae of one individual are nurtured by another, may be interspecific or intraspecific, and has been reported in insects, fishes, amphibians, and birds (Lyon and Eadie, 2000; Ruxton and Broom, 2002). Often, offspring of the parasite receive protection against predators by the species parasitized. Several examples of one fish species being protected by another have been reported. Minnow species (Cyprinidae) that lay eggs in nests guarded by the male sunfishes (*Lepomis* spp.; Fletcher, 1993) benefit from increased aeration of the spawn (Johnston and Birkhead, 1988), reduced siltation (Hunter and Hasler, 1965), and protection from egg predators (Steele, 1978). Smallmouth Bass, *Micropterus dolomieu*, provided brood care for Longnose Gar, *Lepisosteus osseus*, which resulted in increased survival of both young (Goff, 1984). Ochi et al. (2001) reported eggs from a clariid catfish, *Dinotopterus cunningtoni*, deposited in the nest of the bagrid catfish, *Auchenoglanis occidentalis*, in Lake Tanganyika. Other examples of protection include the bagrid catfish (*Bagrus meridionalis*, locally known as Kampango), which defends young cichlids in Lake Malaŵi (McKaye and Oliver, 1980; McKaye, 1985; Konings, 2005), and an extreme form of brood parasitism practiced by the Cuckoo Catfish, *Synodontis multipunctatus*, which spawns above breeding cichlids in Lake Tanganyika, and whose eggs and young are mouth-brooded by the cichlids (Sato, 1986). This latter example is truly brood parasitism because the catfish fry feed upon the cichlid fry (Sato, 1986). The former examples may be commensal if, in fact, no energy is expended guarding additional young, if there is no predation on the host's young by the nest symbiont, and if the host's young receive no benefit, such as a reduction in the incidence of predation.

Parental-care patterns in most fishes differ from those of other vertebrates, particularly birds and mammals, in that 1) external fertilization makes male parent identity uncertain, so a male is less likely to invest in brood protection; 2) few fishes feed their young; 3) fishes, except for mouth-brooders and live bearers, do not incubate their young, so can protect very large clutches; and 4) fishes are usually able to defend their broods against predators (Perrone and Zaret, 1979). Kampango are large (ca. 0.7–1.0+m) substrate-spawning catfish endemic to Lake Malaŵi that exhibit bi-parental care. With fishes, bi-parental care is difficult to explain, unless it can be argued that parental investment by both parents promotes survival of the young to a greater extent than uniparental care (Perone and Zaret, 1979). LoVullo et al. (1992) reported that female Kampango feed their young trophic (unfertilized) eggs, while the male gathers macroinvertebrates from nearby sand habitats and carries them by mouth to young in the nest. The young leave the nest after approximately 60 days when they range in size between 40 and 70 mm SL (LoVullo et al., 1992). When the female is at the nest, the young Kampango gather around her vent to feed; when the male is on the nest, they gather around his opercular openings, where he discharges macroinvertebtates mixed with sand (LoVullo et al., 1992; McKaye et al., 1994) . Because both Kampango parents feed and protect mobile fry, the survival of the progeny is likely to be enhanced, more so than if nest protection was the sole function of the parents. Lake Malaŵi is home to other catfishes, many belonging to the endemic genus *Bathyclarias*, of which *B. nyasensis* (locally, Bombe, or Sapuwa [Jackson, 1959]) is the most abundant. Here we report observations of brood parasitism by *B. nyasensis*, and the complete acceptance of the parasite's young by *B. meridionalis*, including biparental protection and supplemental feeding.

MATERIALS AND METHODS

Observations were made while SCUBA diving in the southeastern arm of Lake Malaŵi at Zimbawe Rocks (13°57′54″S, 34°48′9″E) between early February to mid-March 2007 during 11 separate dives. Underwater videos were taken with a Sony digital camera contained in an Amphibico underwater housing to document the observations; videos are catalogued into the Penn State University Fish Museum (digital recordings catalogued into museum: PSU 4612—Bombe beneath the vent of Kampango female; PSU 4613—cichlid young in Kampango nest; PSU 4614—Bombe beneath the head of Kampango male). Most nests occurred on the rocks between 10–20 m deep. We used a small dip net to collect Bombe fry in two nests protected by Kampango. We anesthetized the fish in clove oil, euthanized them in 1% formalin, preserved them in 10% formalin, and

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transferred them to 70% ethanol for permanent storage in the Penn State University Fish Museum (PSU 4478; PSU 4479). We dissected the stomachs of the young and enumerated the contents.

RESULTS

Between 8 February and 11 March 2007, we observed 14 pairs of Kampango protecting broods in nests scattered around Zimbawe Rocks. One brood contained both Kampango (ca. 30) and cichlid (ca. 15) young, three had only Bombe (14–30 individuals), one contained approximately 20 Bombe (ca. 100 mm SL) and one Kampango (ca. 100 mm SL), while the remaining nine nests contained approximately 30–400 Kampango per nest. In nests with the highest numbers of Kampango, the juveniles were small (< 30 mm), while in those with fewer young, sizes were larger (> 50 mm), and the young assumed to be older.

At many of the nests we observed juvenile Kampango feeding from the parents, as described by LoVullo et al. (1992). We were surprised to observe the same feeding behavior by the Bombe juveniles. As the female Kampango hovered over nests with Bombe, young Bombe would congregate around their vents (Fig. 1A); when the male Kampango returned to the nest from foraging on surrounding sand substrates, young Bombe congregated around the opercular openings (Fig. 1B, Digital recording—PSU 4612; PSU 4614). At all times, young Bombe were in close association with an adult Kampango.

The first brood (PSU 4478) collected was comprised of 14 individual Bombe (102.1–119.2 mm SL), and the second (PSU 4479) of 26 individuals (52.3–73.1 mm SL). Eggs of Kampango were found in 100% of clariid stomachs. The mean number of eggs/stomach was 45.4 (9–101) for the first brood and 45.6 (23–89) for the second. Because of the feeding behavior observed, we assumed that these were trophic eggs produced by the female Kampango. In addition, we found midge larvae (Diptera), mayfly nymphs (Ephemeroptera), caddisfly nymphs (Trichoptera), water mites (Hydracarina), a potamonautid crab, leeches (Hirudinea), bivalve molluscs, and fish in the Bombe guts. Of the two fish found, one was too digested for identification, and the other, based on remnants of the caudal fin, appeared to be a bagrid juvenile.

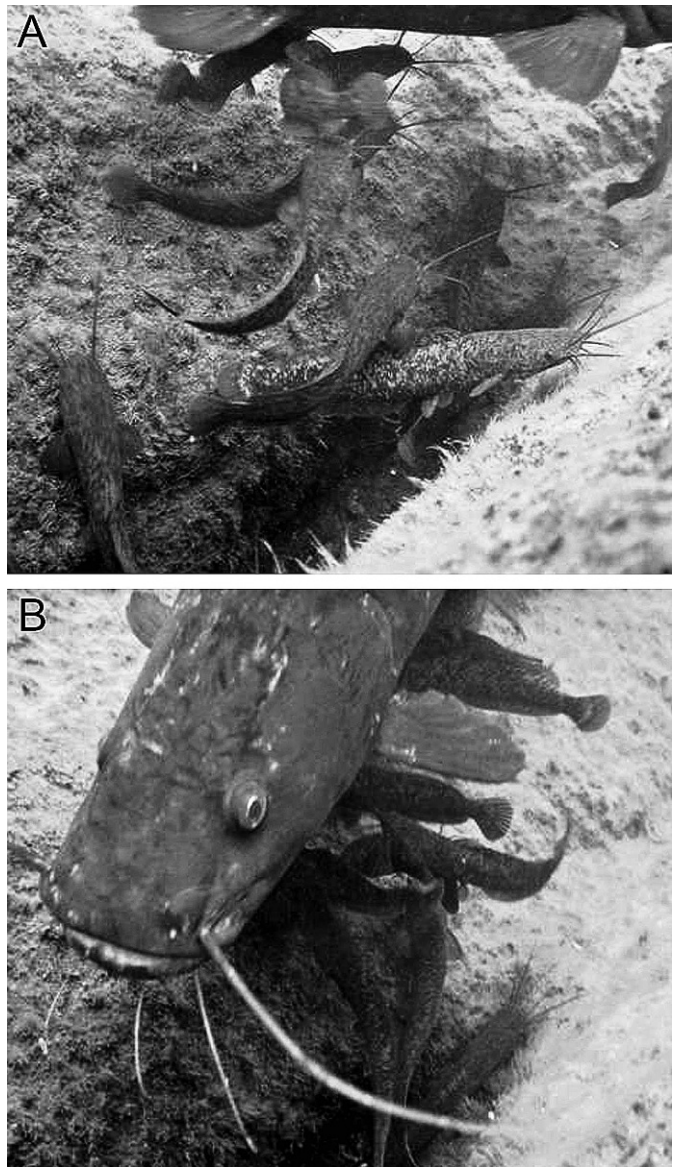

Fig. 1. *Bathyclarias nyasensis* young congregating around the vent of female *Bagrus meridionalis*, presumably feeding on trophic eggs (B); *Bathyclarias nyasensis* young congregating around gills of male *B. meridionalis*, presumably feeding on macroinvertebrates brought back to the nest.

DISCUSSION

This degree of brood parasitism is very rare in fishes. Our observations, from one rock reef during a month of diving, of four Kampango nests with clariid young, indicate that this form of parasitism is not uncommon, at least at that locality. The mechanism of nest invasion, however, is unclear. We may only speculate whether it is opportunistic or purposeful, because the breeding behavior and spawning sites of *B. nyasensis* are unknown (Thompson et al., 1996). Bombe might enter nests of Kampango as free-swimming fry that find their way into the bagrid nests at random after abandonment by their parents. If the young clariids restricted their movements within the rocky habitat, they would not be particularly vulnerable to predation by the mainly herbivorous fishes that inhabit those areas. Once they invade the bagrid nest, they could devour the bagrid eggs or young. Given the number of parasitized nests we observed at Zimbawe Rocks, however, accidental, random entry of bagrid nests seems an unlikely mechanism.

Conversely, adult Bombe may occasionally spawn over breeding Kampango, resulting in the eggs of both species in the nest. If Bombe guard their spawn, as do some clariids, the result is akin to that of ''farming out'' by some cichlids in being freed from having to protect young (Ochi and Yamagisawa, 2005). It also implies that Kampango adults are unable to detect the presence, or to remove, foreign eggs in their nest. Similar to bird cuckoos, Bombe young may hatch first, allowing young Bombe to feed on the bagrid eggs or larvae, leaving only Bombe to be raised by the Kampango. That hypothesis fits our observations of invaded nests containing Bombe young almost exclusively, and agrees with information about rapid growth rates and piscivorous feeding of young Bombe (Kaunda and Hecht, 2003). It will be difficult to test those alternatives in the field because Bombe often inhabit deep waters (Jackson, 1959) and may spawn at night. During our observations, one of us was

bitten on the hand by an adult Bombe as we approached the Kampango nest to video the young. We also observed an adult Bombe of the same size on two other occasions when we visited that nest, suggesting that the adult remained in the vicinity of the Bombe brood in the Kampango nest. Bombe are rarely observed while diving during daylight.

Whether young Bombe actively invade the Kampango nests or result from eggs deposited by spawning Bombe adults, as with *S. multipunctatus* in Lake Tanganika (Sato, 1986), the similarity in size of the Bombe in each Kampango nest indicates that each group represented a single brood. Bombe are the most numerous of the clariid catfishes in Lake Malaŵi (Jackson, 1959), while the cuckoo observations reported herein are relatively rare. One of us (JRS) has logged over 1600 hours of diving in Lake Malaŵi since 1983, yet had never observed this association between Kampango and Bombe. It seems unlikely that Bombe routinely are brooded by Kampango, given the absence of previous observations, but these behaviors of invasion and feeding represent opportunistic rather than obligatory events. If opportunistic, however, it is puzzling that we should observe this complex interaction four times within a month at this single location.

It should be noted that all Bombe in one of the broods we preserved exceeded 100 mm SL, and in the brood that also had one Kampango, we estimated the size of the Bombe and the Kampango to be approximately 100 cm. This differs with the observations of LoVullo et al. (1997), who reported that Kampango young left the nest when they were < 80 mm SL. The difference may have been the result of the regular disturbance of the brood by LoVullo et al. (1997).

With the exception of oophagy in sharks (*Lamna* spp.; Shann, 1923; Stribling et al., 1980), the consumption of embryonic siblings and unfertilized eggs in ovoviparous sharks (Moyle and Cech, 1988), and contacting behavior in some cichlids (Noakes, 1979), few fishes feed their young. True supplemental feeding as in birds, however, is practiced by Kampango, which not only provide trophic eggs but also leave the barren, rocky nest sites to collect and retrieve invertebrates from surrounding sandy areas for their young (LoVullo et al., 1992; McKaye et al., 1994). We were unable to directly observe female Kampango extruding eggs to the clariid young because of the frenetic activity of the Bombe near her vent. We did observe the young clariids congregating around the vent of the female Kampango and found Kampango eggs in the stomachs of the juvenile clariids collected from the nests; thus, we assumed these were trophic eggs because there was no evidence of male Kampango fertilizing the eggs prior to their consumption.

In addition to pieces of a small bagrid found in the stomach of one of the Bombe, we found macroinvertebrates in some Bombe stomachs, similar to those found in Kampango young (LoVullo et al., 1992). This demonstrates that not only did both Kampango parents protect the foreign broods, but both genders also were fooled into feeding them as they would their own young, with trophic eggs and macroinvertebrates. Irrespective of the mode of parasitism, *B. meridionalis* invests a great deal of energy in protecting and feeding parasitic, predatory clariid young in which they have no genetic contribution. As such, there is no indirect fitness benefit from rearing kin as discussed by Dierkes et al. (1999).

These observations strongly suggest brood parasitism instead of a mutualistic relationship between Kampango and cichlids as reported by McKaye (1985). McKaye (1985) did not report feeding of the cichlid young by the Kampango, and the adult Kampango were protecting both cichlid and Kampango young. In contrast, we found that, with the exception of one Kampango, the four broods observed were comprised entirely of Bombe young. McKaye (1985) suggested the selection pressure for the evolution of intra- and interspecific brood care (brood parasitism) might be a reduction in predation on the parent's offspring because of the presence of foreign young, but this does not appear to be the case here. Similar to brood parasitism of cichlids by *Synodontis multipunctatus*, alloparental care of Bombe by Kampango might represent another example of maladaptive, misdirected parental care (Wisenden, 1999).

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LITERATURE CITED

Dierkes, P., M. Taborsky, and U. Kohler. 1999. Reproductive parasitism of broodcare helpers in a cooperatively breeding fish. Behavioral Ecology 10:510–515.

Fletcher, D. E. 1993. Nest association of Dusky Shiners (*Notropis cummingsae*) and Redbreast Sunfish (*Lepomis auritus*), a potentially parasitic relationship. Copeia 1993: 159–167.

Goff, G. P. 1984. Brood care of Longnose Gar (*Lepisosteus osseus*) by Smallmouth Bass (*Micropterus dolomieui*). Copeia 1984:149–152.

Hunter, J. R., and A. D. Hasler. 1965. Spawning association of the redfin shiner, *Notropis umbratilis*, and the green sunfish, *Lepomis cyanellus*. Copeia 1965:265–281.

Jackson, P. B. N. 1959. Revision of the clariid catfishes of Nyasaland, with a description of a new genus and seven new species. Proceedings of the Zoological Society (London) 132:109–128.

Johnston, C. E., and W. S. Birkhead. 1988. Spawning in the Bandfin Shiner, *Notropis zonistius* (Pisces: Cyprinidae). Journal of the Alabama Academy of Science 59:30–33.

Kaunda, E., and T. Hecht. 2003. Life history traits of *Bathyclarias nyasensis* (Siluroidei) in Lake Malawi. African Zoology 38:45–55.

Konings, A. F. 2005. Celebrating Cichlids. Cichlid Press, El Paso, Texas.

LoVullo, T. J., J. R. Stauffer, Jr., and K. R. McKaye. 1992. Diet and growth of a brood of *Bagrus meridionalis* Günther (Siluriformes: Bagridae) in Lake Malawi, Africa. Copeia 1992:1084–1088.

Lyon, B. E., and J. M. Eadie. 2000. Family matters: kin selection and the evolution of conspecific brood parasitism. Proceedings of the National Academy of Sciences of the United States of America 97:12942–12944.

McKaye, K. R. 1985. Cichlid–catfish mutualistic defense of young in Lake Malawi, Africa. Oecologia 66:358–363.

McKaye, K. R., and M. K. Oliver. 1980. Geometry of a selfish school: defense of cichlid young by bagrid catfish in Lake Malawi, Africa. Animal Behaviour 28: 1287–1290.

McKaye, K. R., D. E. Mughogho, and J. R. Stauffer. 1994. Sex-role differentiation in feeding and defense of young by a biparental catfish, *Bagrus meridionalis*. Animal Behaviour 48:587–596.

Moyle, P. B., and J. J. Cech. 1988. Fishes: An Introduction to Ichthyology. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey.

Noakes, D. L. G. 1979. Parent-touching behavior by young fishes: incidence, function and causation. Environmental Biology of Fishes 4:389–400.

Ochi, H., T. Onchi, and Y. Yanagisawa. 2001. Alloparental care between catfishes in Lake Tanganyika. Journal of Fish Biology 59:1279–1286.

Ochi, H., and Y. Yanagisawa. 2005. Farming-out of offspring is a predominantly male tactic in a biparental mouthbrooding cichlid *Perrisodus mircolepis*. Environmental Biology of Fishes 73:335–340.

Perrone, M., Jr., and T. M. Zaret. 1979. Parental care patterns of fishes. American Naturalist 113:351–361.

Ruxton, G. D., and M. Broom. 2002. Intraspecific brood parasitism can increase the number of eggs that an individual lays in its own nest. Proceedings of the Royal Society of London: Biological Sciences 269:1989–1992.

Sato, T. 1986. A brood parasitic catfish of mouthbrooding cichlid fishes in Lake Tanganyika. Nature 323:58–59.

Shann, E. W. 1923. The embryonic development of the Porbeagle Shark, *Lamna cornubica*. Proceedings of the Zoological Society, London 11:61–171.

Steele, B. D. 1978. The reproductive strategy and energetics of Rosefin Shiner in Baregone Creek, Kentucky. Unpubl. Ph.D. diss., University of Louisville, Louisville, Kentucky.

Stribling, M. C., W. C. Hamlett, and J. P. Wourms. 1980. Developmental efficiency of oophagy, a method of viviparous embryonic nutrition displayed by the Sand Tiger Shark (*Engomphodus taurus*). Bulletin of the South Carolina Academy of Science 42:111.

Thompson, A. B., E. H. Allison, and B. P. Ngatunga. 1996. Distribution and breeding biology of offshore pelagic cyprinids and catfish in Lake Malawi/Niassa. Environmental Biology of Fishes 47:27–42.

Wisenden, B. D. 1999. Alloparental care in fishes. Reviews in Fish Biology and Fisheries 9:45–70.