

Natural History Miscellany

Cuckoldry Incites Cannibalism: Male Fish Turn to Cannibalism When Perceived Certainty of Paternity Decreases

Suzanne M. Gray,^{1,*} Lawrence M. Dill,^{1,†} and Jeffrey S. McKinnon^{2,‡}

1. Behavioural Ecology Research Group, Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada;

2. Department of Biological Sciences, University of Wisconsin, Whitewater, Wisconsin 53190

Submitted April 14, 2006; Accepted September 5, 2006;

Electronically published December 20, 2006

Online enhancements: color version of figure 1, video.

ABSTRACT: Perceived certainty of paternity is expected to influence a male's behavior toward his offspring: if he is uncertain of his reproductive success with a current brood due to the presence of cuckolders, it may benefit him to invest instead in future reproduction. A decrease in perceived certainty of paternity incites filial cannibalism (the eating of one's own offspring) in some teleost fishes that provide parental care; however, no work has demonstrated that cannibalism increases proportionately with increased levels of cuckoldry. Here we show for the first time in a fish with no parental care that as the number of cuckolders at a spawning event increases, so does the probability that a male will cannibalize eggs. In field observations of *Telmatherina sarasinorum*, a small fish endemic to Sulawesi, Indonesia, males increased filial cannibalism behavior threefold in the presence of one cuckolder and nearly sixfold in the presence of two or more cuckolders. This suggests that males may use detection of cuckolders as an indication that the paternity of current offspring has been compromised.

Keywords: filial cannibalism, sneaking, *Telmatherina sarasinorum*.

The evolution of filial cannibalism (the consumption of one's own offspring) is thought to be driven by an energetic trade-off between caring for the current brood and

investing in future reproductive success by eating offspring (Rohwer 1978; Manica 2002*b*). In species with male parental care, a male's assessment of the value of the current brood can incorporate information on his own condition (i.e., energy reserves; Neff 2003*b*), the quality and availability of mates (Okuda et al. 2004), prey availability (Vinyoles et al. 1999), and his perceived certainty of paternity (Neff and Gross 2001; Neff 2003*a*; Manica 2004). If a male perceives that the value of his current brood is low, then eating the current brood, either wholly or partially, may improve his future reproductive success (Manica 2002*b*).

Most work, and all theory, on the evolution of filial cannibalism has focused on understanding the energetic trade-off in teleost fishes that provide parental care, mostly by males (Sargent 1992; Manica 2002*b*). Parental care requires an investment in both time and energy spent rearing or guarding offspring, whereas in the absence of parental care, there is no energetic cost beyond mating. In both cases, eating offspring is expected to add to future reproductive success through an energy gain (Manica 2002*b*); however, parental caregivers could also benefit by relieving themselves of low-value offspring. In species with parental care, it is hard to distinguish how the value of current offspring is evaluated because there can be multiple cues about paternity, availability of food and mates, and other factors, over an extended period of time (Neff and Sherman 2002), but by investigating cannibalism in the absence of parental care, we can examine the effect of perceived certainty of paternity in isolation.

Perceived certainty of paternity based on visual detection of cuckolders by a male could immediately indicate the value of potential offspring by providing information on expected relatedness (Neff and Sherman 2002). If this is true, then a male could use information on "sneakers" (i.e., their presence and number) to estimate his mating success and adjust his behavior toward current offspring accordingly. As a male's certainty of paternity decreases, such as when his spawning attempt is cuckolded by sneaker males, so does the value of the brood. Filial cannibalism could be a tactic to recoup energy lost to mating efforts

* E-mail: smgray@sfu.ca.

† E-mail: ldill@sfu.ca.

‡ E-mail: mckinnoj@uw.edu.

(e.g., through aggressive male-male interactions over mates) and hence increase energy for the next mating bout (Manica 2002b). The cost to a male of mistakenly consuming some of his own eggs may be high with respect to his reproductive fitness. However, this cost may be outweighed by the benefit of securing more energy to find another mating opportunity where his certainty of paternity is higher. We examined the relationship between filial cannibalism and sneaker presence and abundance using field observations of a small fish that does not provide parental care for young, and we predicted that both the presence of sneaker males and increased numbers of sneakers would result in increased cannibalism attempts by males.

Methods

Study Organism and Mating System

Telmatherina sarasinorum is a small, colorful fish endemic to Lake Matano, Sulawesi, Indonesia (Kottelat 1991), that spawns on the substrate and provides no parental care (Gray and McKinnon 2006; fig. 1, available in color in the online edition of the *American Naturalist*). Neither males nor females hold territories (S. M. Gray, personal observation). A detailed description of mating behavior in this species is given by Gray and McKinnon (2006); here we describe only the relevant details. Three behavioral tactics are employed by males: (1) courting males are identified as those males actively paired with and courting a female at the time of observation; (2) sneaker males are those males that, at the time of spawning between a female and a courting male, rush into a position parallel to the spawning pair and attempt to fertilize some of the eggs being spawned (indicated by quivering behavior typical of sperm release in many fishes, e.g., rainbow darters *Etheostoma caeruleum*; Fuller 1998); and, (3) nonmating cannibals are identified as males that dart in toward the spawning pair and attempt to eat the eggs but are not directly involved in the spawning event. An individual male may perform any of these behaviors depending on his current situation, and he may switch between tactics in a matter of seconds. For example, a courting male may lose a fight to another male and immediately switch to the sneaking tactic if the opportunity presents itself. Males fight intensely over females, and females can pair and spawn with many different males in a short period of time, although females do not spawn with all males they are paired with. Males do not invest any energy in care of their offspring postmating; however, they do spend a large amount of time (and thus energy) courting and retaining females pre spawning.

Lake Matano is relatively resource-poor (Haffner et al. 2001), and *T. sarasinorum* regularly consume congeneric

eggs (Kottelat 1991) as well as the eggs of other fish species (e.g., endemic gobies *Glossogobius* sp.; S. M. Gray and J. S. McKinnon, personal observation). Immediately after spawning, males turn to inspect the area where eggs were apparently laid, and they have often been observed “picking” at the substrate in that same spot in a similar manner to when they are consuming the eggs of other species. Picking behavior has been used to identify filial cannibalism in other systems (e.g., bluegill sunfish *Lepomis macrochirus*; Neff 2003b).

Observational Study and Analyses

This study took place in Lake Matano over three field seasons: January–March 2003, January–May 2004, and October–December 2004. *Telmatherina sarasinorum* spawn throughout the year in two distinct habitats: beach sites that are relatively shallow and flat and root sites that drop off steeply from shore and where spawning takes place on overhanging vegetation (Gray and McKinnon 2006). We do not distinguish spawning events based on habitat here, as there was no significant effect of habitat on sneaking and cannibalism (Wald $\chi^2 = 0.23$, $df = 1$, $P = .63$). Females are cryptically colored, whereas five male color morphs coexist (fig. 1). The role of male color will be explored elsewhere (S. M. Gray, unpublished data); here, data for all morphs are pooled. All male color morphs employ all three behavioral tactics and do not represent alternative reproductive strategies as seen in other systems (e.g., bluegill sunfish; Gross and Charnov 1980).

Focal follow observations ($n = 576$) of female *T. sarasinorum* were made by snorkeling along 13 transects (80 m long, 1–2 m deep) at nine sites around Lake Matano. Each site was visited between four and seven times over three field seasons, with each visit separated by at least 1 week. In our data set, the number of observations per site per date visited ranged from one to 28 (mean = eight observations per site per visit); observations were conducted by at least two (often three) observers, meaning that at one time, two or three separate females were being followed. Male density in mating habitats is high (approximately 47 per 80 × 2-m transect; Gray and McKinnon 2006). The operational sex ratio (females to males) was derived indirectly as the number of males paired with a female relative to the total number of males counted during a particular observation period and was found to be strongly male biased (range, 0.19–0.34; mean, 0.26 [± 0.06 SD]; S. M. Gray, unpublished data). The relatively high density of males in the mating habitat, coupled with the observation that these fish are mobile and often roam across or out of a particular site (S. M. Gray, personal observation), suggests that this is an open system and that the likelihood of resampling males is very small.



Figure 1: Courting *Telmatherina sarasinorum*. Five male color morphs with elaborate secondary sexual characteristics fight intensely over and mate with the same cryptically colored females. All color morphs can switch mating tactics between courting and sneaking very quickly, and all morphs appear to practice filial cannibalism. Color version available in the online edition of the *American Naturalist*.

Focal observations were conducted by haphazardly selecting a female paired with a male and observing her for 3–10 min. If the original courting male left the female (either by choice or because he lost a fight with another male), we continued to follow the female. We recorded all apparent spawning events, the number of males involved in the spawning event, whether each male was a courting male or a sneaker during that mating event, and any apparent incidence of cannibalism, (i.e., picking behavior at the site of spawning). We also recorded the presence of nonmating males that attempted to cannibalize eggs but were not directly involved in spawning. To confirm oophagy, we dissected the stomachs of 13 male fish caught on one of the transects during a time of peak mating (and conspecific cannibalism) and measured any eggs to determine whether they were likely *T. sarasinorum* eggs. It was logistically impossible to catch male fish directly after

observing picking behavior, and so our measure is an indirect one.

Spawning events were observed during only 385 of the 576 female follows included in this survey. Females often spawn with more than one male and several times with each male during an observation period. We considered the first spawning event for each different courting male (i.e., only males distinguishable by color and/or size; $n = 470$ courting males) to be independent of previous events, and only this subset of data was used for analyses (i.e., only 470 of 1,089 spawning events). We used a binomial logistic regression on courting male cannibalism (response variable) to determine the relative importance of the predictor variables sneaker presence ($n = 55$) and nonmating cannibal presence ($n = 60$). We used Pearson χ^2 tests to evaluate (1) whether the incidence of filial cannibalism by courting males (i.e., those paired with the

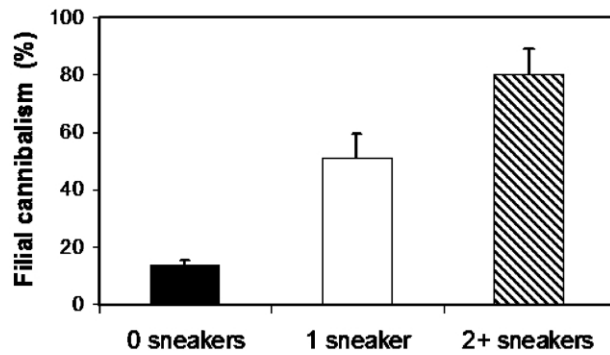


Figure 2: Filial cannibalism by courting male *Telmatherina sarasinorum* in the absence (0 sneakers, black bar, $n = 415$) or presence (1 sneaker, open bar, $n = 35$; 2 or more sneakers, hatched bar, $n = 20$) of sneakers (plus one binomial SE [Zar 1984]).

female at the time that spawning took place; Gray and McKinnon 2006) is associated with the presence of sneaker males and (2) whether filial cannibalism by courting males increases with the number of sneakers present at a given spawning event. Relatively few spawning events with multiple sneaker males present remained in the data set after removing nonindependent events, so we pooled those into one category representing events where two or more males were present.

Results

We found *Telmatherina sarasinorum* eggs in the stomachs of males, suggesting that picking behavior may result in the consumption of eggs. Of 13 male fish sampled, 11 had eggs of a size similar to *T. sarasinorum* eggs (average egg diameter = 1.34 mm, $n = 76$ eggs from three females; S. M. Gray, unpublished data) present in their stomachs, consistent with conspecific cannibalism. Females have never been observed practicing filial cannibalism, although both sexes appear to eat heterospecific eggs (Kottelat 1991; S. M. Gray and J. S. McKinnon, personal observation).

Twelve percent of all spawning events involved one or more sneaker males (range = 1–4 sneakers, mean = 1.6 [± 0.8 SD]). When sneakers were absent ($n = 415$), courting males attempted to cannibalize eggs after 13% of the spawnings (fig. 2). This behavior increased significantly in frequency to 62% when one or more sneakers were present ($n = 55$), suggesting that when a male's perceived certainty of paternity decreases, he is more likely to cannibalize ($\chi^2 = 70.6$, $df = 1$, $P < .0001$). Certainty of paternity should be a decreasing function of the number of sneakers present. Accordingly, when only one sneaker was present ($n = 35$), filial cannibalism by the courting male was three times more likely (51%), while there was a nearly

sixfold increase (80%) when two or more sneakers ($n = 20$) were present (fig. 2; $\chi^2 = 4.40$, $df = 1$, $P = .04$).

We observed conspecific cannibalism by males not involved in the spawning event (fig. 1; video 1, available in the online edition of the *American Naturalist*). These males are often involved in the fights that take place before spawning, and it is unclear whether they were not close enough or fast enough to attempt a sneak fertilization or chose to have a meal in lieu of mating. Such nonmating males attempted to cannibalize eggs at 13% of the spawning events (table 1). There was a 10% increase in the probability of filial cannibalism by courting males in the presence of these nonmating cannibalistic males (table 2). The binomial logistic regression used to determine the effects of sneakers and nonmating males on cannibalism by courting males (data presented in table 2) showed that both were significant. However, the effect of sneaker presence was stronger than the effect of the presence of nonmating cannibals (Wald χ^2 values, sneakers = 52.7 cf. nonmating males = 4.44; P sneakers $< .0001$ cf. P nonmating males = .04, $df = 1$), and there was no interaction between these factors (Wald χ^2 interaction = 0.004, $P = .94$, $df = 1$). Filial cannibalism by the courting male was three times more likely in the presence of sneakers compared with the presence of nonmating cannibal males, suggesting that certainty of paternity is a better predictor of filial cannibalism than the risk of egg loss to nonmating males (table 2).

Discussion

The probability of cannibalism by *Telmatherina sarasinorum* courting males increases with number of sneakers present (fig. 2). This positive relationship between male filial cannibalism and the number of sneaker males is consistent with the hypothesis that males use the presence of sneakers as an indicator of the value of the current brood and adjust their behavior based on perceived certainty of paternity.

Genetic tests of paternity, which at this time are not

Table 1: Proportion of spawning events where females and males of each behavioral category were present and proportion of spawning events where they were present and each attempted to cannibalize eggs

	Percent present at spawning event (n)	Percent cannibalism attempts (n)
Females	100 (470)	0 (0)
Courting male	100 (470)	20 (94)
Sneaker male	11.7 (55)	73 (40)
Nonmating cannibal (male)	12.8 (60)	100 (60)

Table 2: Proportion of filial cannibalism by focal courting males in the presence/absence of conspecific males, either sneakers or nonmating males (i.e., cannibals that did not participate in the spawning event)

Nonmating males	Sneakers	
	Present (<i>n</i>)	Absent (<i>n</i>)
Present	.75 (4)	.23 (56)
Absent	.62 (51)	.13 (359)

possible for *T. sarasinorum*, could help to determine whether males are consuming only nonrelated eggs, in which case eating eggs after cuckolded spawning events would be of no detriment to a male's fitness. Only one study has attempted to document filial cannibalism in nature in this manner. DeWoody et al. (2001) used microsatellite paternity analyses on embryos found in the stomachs of nest-tending male tessellated darters (*Etheostoma olmstedii*) and two sunfish species (*Lepomis auritus* and *Lepomis punctatus*). They determined that none of the males seemed able to discriminate between related and nonrelated embryos because both were consumed. Given that darter and sunfish males spend a significant amount of time caring for their offspring and still have not evolved the ability to differentiate between related and unrelated embryos when cannibalizing, it is unlikely that *T. sarasinorum* males, who spend no time caring for young, would evolve such an ability, especially since fertilization may not even be complete at the time of consumption. Male bluegill sunfish do change their parental behavior when cuckoldry is detected and paternity of the brood is mixed, and can even use olfactory cues to detect unrelated juvenile fish in the nest posthatching and adjust their effort accordingly (Neff 2003a; Neff and Sherman 2003); however, there is no evidence that they differentiate between kin and nonkin when cannibalizing.

A courting male's information on sneaker presence may not always be perfect (Neff 2003a), which may explain why there is some filial cannibalism even in the absence of sneakers (fig. 2, 0 sneakers). Males also may cannibalize if the chance of the eggs being eaten by others is high; if so, we would expect males to cannibalize to the same extent in the presence of other, nonmating cannibals as in the presence of sneakers, but there is no evidence for this. Females may also be expected to eat the eggs if the chance of them being eaten is high; however, the possibility that some eggs are fertilized and not eaten probably outweighs the energetic benefit she would gain by consuming the eggs. We have never observed females performing picking behavior after spawning (table 1), although we have observed them picking at the substrate after heterospecific spawning events.

Sometimes neither courting males nor sneakers attempt

to cannibalize (table 1), and it is possible that females do not always release eggs when appearing to spawn, as a tactic to avoid the loss of costly eggs to males. Although we have no information on the number of eggs released by females at each spawning event (there is no obvious egg mass laid), that number is likely to be low because they spawn continuously throughout the day. Also, a large proportion of the time that males and females make the effort to perform the typical quivering behavior on the substrate (see Gray and McKinnon 2006 for details), we expect that at least one egg is laid. Accordingly, we expect that eggs are present and being cannibalized at least some proportion of the time that males perform the picking behavior because otherwise the cost of the repeated behavior would be too high. "Testing" of a male's cannibalistic behavior by females has been shown in other fish, such as the Mediterranean blennioid *Aidablennius sphyinx*; Kraak and van den Berghe (1992) found that females laid only small clutches of eggs in empty males' nests. Those males that did not cannibalize the eggs received more eggs at a later date than did males that did consume the small clutches. Although it is not known whether the same female returns to inspect the same nest, the benefit to the male is obvious. Theory is being developed to incorporate female choice in studies of filial cannibalism (Lindström 2000; Manica 2002b), but little empirical work has been done. Further investigation of the female's role should enhance understanding of the evolution of filial cannibalism and mating strategies in *T. sarasinorum* and other systems.

Our results clearly show that the probability of filial cannibalism attempts in *T. sarasinorum* courting males increases in the presence of sneaker males, suggesting that they can use detection of sneakers as an indicator of lowered certainty of paternity. Since *T. sarasinorum* males do not invest in their offspring after egg laying, cannibalism cannot be a tactic used to optimize the trade-off between present and future reproduction (Rohwer 1978; Manica 2002a, 2002b, 2004), except with respect to recouping energy lost through mating efforts. Instead, it seems the male may benefit from the energy contained in the eggs, and the less likely he is to have fertilized the eggs, the more likely he is to eat them.

Acknowledgments

Assistance with fieldwork was provided by our Indonesian collaborator F. Y. Tantu, P. Hehanussa, LIPI (Indonesian Science Foundation), and our field assistants A. Crawford, D. Holm, A. Robertson, and S. van der Meer. Logistical support was provided by P. T. Inco. We are grateful to F. Breden, I. Côté, B. Crespi, the Dill Lab, and the FAB*Lab for their comments on the manuscript and E. Gray and S.

MacDonald for technical assistance. Financial support was provided by a National Science Foundation grant to J.S.M., Canadian International Development Agency–Eastern Indonesia Universities Development Project funding to L.M.D., and Natural Sciences and Engineering Research Council of Canada, PADI Project Aware Foundation, and Sigma-Xi Grants-in-Aid-of-Research funding to S.M.G.

Literature Cited

- DeWoody, J. A., D. E. Fletcher, S. D. Wilkins, and J. C. Avise. 2001. Genetic documentation of filial cannibalism in nature. *Proceedings of the National Academy of Sciences of the USA* 98:5090–5092.
- Fuller, R. C. 1998. Sperm competition affects male behaviour and sperm output in the rainbow darter. *Proceedings of the Royal Society B: Biological Sciences* 265:2365–2371.
- Gray, S. M., and J. S. McKinnon. 2006. A comparative description of mating behaviour in the endemic telmatherinid fishes of Sulawesi's Malili Lakes. *Environmental Biology of Fishes* 75:469–480.
- Gross, M. R., and E. L. Charnov. 1980. Alternative male life histories in bluegill sunfish. *Proceedings of the National Academy of Sciences of the USA* 77:6937–6940.
- Haffner, G. D., P. E. Hehanussa, and D. Hartoto. 2001. The biology and physical processes of large lakes of Indonesia: Lakes Matano and Towuti. Pages 183–192 in M. Munawar and R. E. Hecky, eds. *The great lakes of the world: food-web, health and integrity*. Backhuys, Leiden.
- Kottelat, M. 1991. Sailfin silversides (Pisces: Telmatherinidae) of Lake Matano, Sulawesi, Indonesia, with descriptions of six new species. *Ichthyological Exploration of Freshwaters* 1:321–344.
- Kraak, S. B. M., and E. P. van den Berghe. 1992. Do female fish assess paternal quality by means of test eggs? *Animal Behaviour* 43:865–867.
- Lindström, K. 2000. The evolution of filial cannibalism and female mate choice strategies as resolutions to sexual conflict in fishes. *Evolution* 54:617–627.
- Manica, A. 2002a. Alternative strategies for a father with a small brood: mate, cannibalise or care. *Behavioral Ecology and Sociobiology* 51:319–323.
- . 2002b. Filial cannibalism in teleost fish. *Biological Reviews* 77:261–277.
- . 2004. Parental fish change their cannibalistic behaviour in response to the cost-to-benefit ratio of parental care. *Animal Behaviour* 67:1015–1021.
- Neff, B. D. 2003a. Decisions about parental care in response to perceived paternity. *Nature* 422:716–719.
- . 2003b. Paternity and condition affect cannibalistic behavior in nest-tending bluegill sunfish. *Behavioral Ecology and Sociobiology* 54:377–384.
- Neff, B. D., and M. Gross. 2001. Dynamic adjustment of parental care in response to perceived paternity. *Proceedings of the Royal Society B: Biological Sciences* 268:1559–1565.
- Neff, B. D., and P. W. Sherman. 2002. Decision making and recognition mechanisms. *Proceedings of the Royal Society B: Biological Sciences* 269:1435–1441.
- . 2003. Nestling recognition via direct cues by parental male bluegill sunfish (*Lepomis macrochirus*). *Animal Cognition* 6:87–92.
- Okuda, N., S. Ito, and H. Iwao. 2004. Mate availability and somatic condition affect filial cannibalism in a paternal brooding goby. *Behaviour* 141:279–296.
- Rohwer, S. 1978. Parent cannibalism of offspring and egg raiding as a courtship strategy. *American Naturalist* 112:429–440.
- Sargent, R. C. 1992. Ecology of filial cannibalism in fish: theoretical perspectives. Pages 38–62 in M. A. Elgar and B. J. Crespi, eds. *Cannibalism: ecology and evolution among diverse taxa*. Oxford University Press, Oxford.
- Vinyoles, D., I. M. Côté, and A. de Sostoa. 1999. Egg cannibalism in river blennies: the role of natural prey availability. *Journal of Fish Biology* 55:1223–1232.
- Zar, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.

Natural History Editor: Henry M. Wilbur