

Sneaky egg-eating in *Telmatherina sarasinorum*, an endemic fish from Sulawesi

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Observations of a novel behavioural tactic employed by egg-eating male *Telmatherina sarasinorum* are described. Four *T. sarasinorum* males were observed actively courting females of closely related *Telmatherina antoniae*, enticing the female to spawn, and then eating the eggs. The possible evolutionary implications of sneaky egg-eating behaviour are discussed.

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The Malili Lakes of south-central Sulawesi, Indonesia, recently hailed as ‘Wallace’s Dreamponds’ (Herder *et al.*, 2006a), are gaining recognition as a powerful model system for studying adaptive radiation in a variety of organisms, including crabs, snails (von Rintelen *et al.*, 2004; von Rintelen & Glaubrecht, 2005) and fishes (Roy *et al.*, 2004; Gray & McKinnon, 2006; Herder *et al.*, 2006a). Included in this group of endemic animals are the telmatherinid fishes (Atheriniformes: Telmatherinidae). The telmatherinids or sailfin silversides (Kottelat, 1991), are small, often brightly coloured fishes found throughout four of the lakes and numerous streams of the Malili Lakes drainage. All of the telmatherinids found in Lake Matano, the most isolated lake, are endemic, while Lakes Towuti and Mahalona share several species, and Lake Wawontoa only contains one confirmed telmatherinid. Several stream forms are found throughout the system, collectively called *Telmatherina bonti* (Weber & de Beaufort) [although this taxonomy may change as more thorough genetic analyses are conducted (Herder *et al.*, 2006b)].

Until recently almost nothing was known about the behavioural ecology of this group of fishes, other than brief behavioural notes included in Kottelat’s (1990, 1991) taxonomic descriptions. Given the recent interest in these fishes,

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especially with respect to the phylogenetic relationships among them (Roy *et al.*, 2004; Herder *et al.*, 2006a), it is desirable that some attention be given to the behaviour of the group. It was recently shown by Gray & McKinnon (2006) that mating behaviour is conserved across seven species and two of the lakes (Matano and Towuti), although some adaptations linked to ecological differences have also been noted between species. For example, parts of the male courtship ritual differ between species that live in the lake and those that are found in flowing water: the former swim in large circles adjacent to the female while enticing her to spawn, while in a flowing water species the male only performs a tight half circle display (Gray & McKinnon, 2006). This paper documents a unique behavioural tactic employed by one telmatherinid species, *Telmatherina sarasinorum* Kottelat, endemic to Lake Matano. This species is a documented egg cannibal that forages regularly (*i.e.* daily) on the freshly laid, unguarded eggs of both heterospecific and conspecific spawning pairs (Gray *et al.*, 2007). On average, 20% of observed *T. sarasinorum* spawning events involve conspecific cannibalism.

Over three field seasons (January to March 2003, January to May 2004, October to December 2004) systematic, quantitative observations of *T. sarasinorum* were made at eight sites around Lake Matano (Gray, 2007). It was found that in the morning (between 0630 and 1030 hours) male *T. sarasinorum* were mainly foraging rather than courting; the latter activity peaks later in the day (between 1030 and 1430 hours). Their foraging behaviour in shallow beach habitat often involves a male following a mating pair of *Telmatherina antoniae* Kottelat, a closely related congener also endemic to Lake Matano, and eating their eggs (Gray & McKinnon, 2006). Oophagy of heterospecific and conspecific eggs has been confirmed *via* stomach content analysis (Gray *et al.*, 2007). It is very difficult to see individual eggs during *in situ* behavioural observations, therefore the 'picking' behaviour employed by foraging fishes [which has been used to identify egg cannibalism in other studies (Neff, 2003; Gray *et al.*, 2007)] was used here to identify egg-eating. Male *T. sarasinorum* also sometimes guard a single *T. antoniae* pair by fighting off all other approaching fishes, including other *T. sarasinorum* males that may contend for the eggs and other *T. antoniae* males that might otherwise have challenged the paired *T. antoniae* male to a fight.

'Focal follows', which involved following individual male *T. sarasinorum*, were performed on 136 males between 0630 and 1030 hours from February to March 2003 ($n = 77$) and February to May 2004 ($n = 59$) at six shallow beach habitat sites. Only males that were actively guarding a *T. antoniae* mating pair, and were attempting to eat the eggs they were laying, were followed. Males were followed even if they switched to a different pair. A focal male was followed for 5 min by an observer using a snorkel and plastic paper and pencil to directly record observations on the males' foraging behaviour. Information on the number of spawning events and attempted egg-eating (*i.e.* 'picking' behaviour) were recorded.

During four independent focal observations on different males (11 and 12 February 2003 and 14 and 27 April 2004) at two different beach sites (2°19'39.0" S; 121°15'53.5" E and 2°17'46.7" S; 121°15'24.7" E) a behaviour, here termed 'sneaky' egg-eating, was observed. This behavioural tactic, described here for the first time as far as is known, is the deception of a female

of one species by a male of another, such that when the heterospecific male entices the female to spawn he eats the eggs that were just laid. In all four observations, a focal male *T. sarasinorum* that was guarding a pair of mating *T. antoniae* chased off the paired *T. antoniae* male and began courting the *T. antoniae* female. When the heterospecific pair went to the substratum to spawn, the female *T. antoniae* quivered [suggesting the release of eggs or sperm in female and male fishes, respectively (Gray & McKinnon, 2006)] but the *T. sarasinorum* male did not. Instead, he remained still alongside the female until she finished quivering, then immediately turned around and attempted to eat the eggs that the heterospecific female had just laid. The female left immediately after spawning, but the *T. sarasinorum* male did not follow as would generally happen when mating with females of his own species. This sneaky egg-eating behaviour has also been independently confirmed (four of 256 focal observations) in *T. sarasinorum* at two other locations (2°27'20.0" S; 121°21'37.0" E and 2°29'02.0"S; 121°25'02.0" E) around the lake (F. Herder, pers. comm.).

A particularly fascinating aspect of these observations is that it is not known if all the eggs are actually eaten, or if the lack of quivering on the part of the *T. sarasinorum* male means that no sperm are released and no eggs are fertilized. There is therefore a small possibility that hybridization could occur as a result of incomplete consumption of fertilized eggs. In a recent study, Herder *et al.* (2006a) report on the possibility of recent introgressive hybridization among sharpfin species of the telmatherinid group, which may be facilitating adaptive radiation. Although the interaction reported here is between a sharpfin (*T. sarasinorum*) and a roundfin (*T. antoniae*) species, this unique behavioural tactic could be one means for hybridization to occur between other sympatric telmatherinids.

The four independent observations of sneaky egg-eating behaviour suggest that it does occur at a low but appreciable frequency in *T. sarasinorum* (four of 136 focal observations). Lake Matano is considered to be of very low productivity with a narrow littoral zone and a low density of plankton (Haffner *et al.*, 2001). That many *T. sarasinorum* eat the eggs of other species on a daily basis (Kottelat, 1991; Gray *et al.*, 2007) suggests that the egg-eating specialization may have evolved in part as a result of the lack of alternative sources of nutrition. Sneaky egg-eating may be related to the conspecific egg cannibalism observed in mating *T. sarasinorum* males. In that case, egg cannibalism by spawning males is positively correlated with the number of cuckolding males (*i.e.* sneakers) present at a spawning event (Gray *et al.*, 2007), suggesting that a male is more likely to eat eggs the less likely he is to have fertilized them. This tactic fits well with current theory on the evolution of filial cannibalism (Manica, 2002): males appear to use egg cannibalism as a means of recouping energy spent on courting when the reproductive value of the spawning event is low. The observation that males will deceive females of a closely related species and eat eggs that would provide no reproductive value may be an extension of this behaviour in a low resource environment. Further observation of sneaky egg-eating will be required to better understand the evolutionary implications of this behaviour.

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