

Brief communication

A comparative description of mating behaviour in the endemic telmatherinid fishes of Sulawesi's Malili Lakes

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Received 17 April 2005

Accepted 20 January 2006

Key words: Telmatherinidae, Sulawesi, endemic freshwater fish, mating system

Synopsis

The telmatherinid fishes of the Malili Lakes, Sulawesi, Indonesia provide a new and promising system for studying the processes maintaining diversity in nature, and especially for testing the generality of the influential findings emerging from studies of other fish systems. Here we develop the telmatherinid system by providing the first detailed descriptions of mating behaviour for seven species representing both of the major Malili lakes and all three genera. The mating behaviour of all seven species can be generalized, suggesting that particular behaviours are conserved within the group. For example, male–male competition in the form of lateral fin displays and physical fighting is evident in all seven species. Males also perform a circling behaviour alongside females that they are paired with, although the size of the circle varies across species. In some species egg cannibalism and/or sneaking behaviour are also prevalent. Interspecific comparisons of mating behaviour show that habitat may play an important role in driving behavioural differences between species. Parallel intraspecific variation in use of habitat and mating behaviours is also noted for two species. This study will facilitate future behavioural and evolutionary ecology research with this system.

Introduction

Fish radiations have been intensively studied by evolutionary ecologists seeking to understand the forces maintaining diversity in nature (Schluter 2000). To date, these studies have focused on a small number of taxa but it is important to test the generality of current findings with a wider range of lineages. The study of new groups may also lead to unanticipated insights and novel avenues of research. The Telmatherinidae are a relatively unknown family of fishes, the majority of which are restricted to the Malili Lakes of south-central Sulawesi, Indonesia (Figure 1).

Taxonomic descriptions of several of the species were first published by Boulenger (1897) and have most recently been revised by Kottelat (1990, 1991) and Aarn et al. (1998). However, these papers provide only very preliminary ecological and behavioural descriptions. Our goal is to provide a more detailed assessment of mating behaviour in this group of fishes as a step toward developing a promising new study system.

Two large lakes, Matano and Towuti, dominate the Malili Lakes system (Figure 1c). Each harbours at least seven distinct telmatherinid species according to Kottelat (1990, 1991) (but see Roy et al. 2004 for an argument on species descriptions

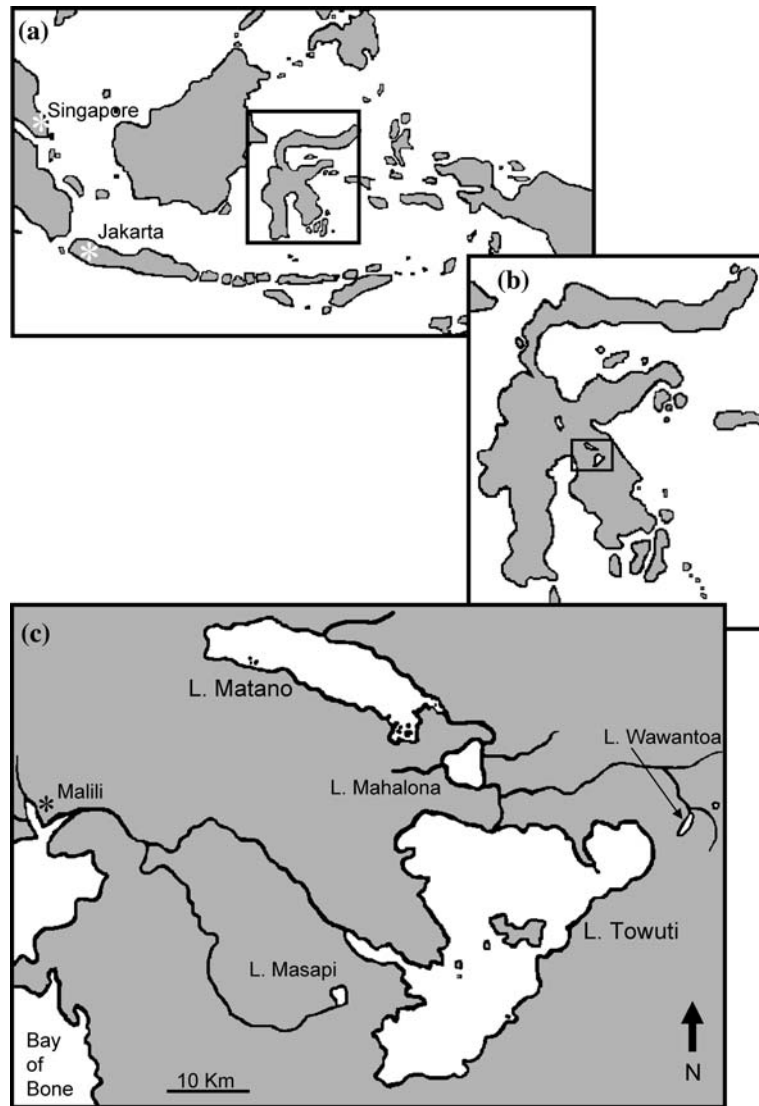


Figure 1. (a) A map of the Indonesian archipelago with the Island of Sulawesi boxed; (b) The Island of Sulawesi with the Malili Lakes system boxed; and, (c) The Malili Lakes system, which drains east into the ocean, Bay of Bone (maps were modified from Pt. INCO Ltd documents). Shaded areas represent land. All observations were recorded in Lakes Matano and Towuti, the two major lakes in the system.

in Matano). The system is currently the subject of intense study by several groups interested in the radiations of the telmatherinids and many other endemic organisms (Roy et al. 2004, von Rintelen et al. 2004, von Rintelen & Glaubrecht 2005, F. Herder & U. Schliewen, personal communication). Lake Matano is separated from the other lakes in the system by 90 m elevation and was formed approximately 1.7 million years ago (Haffner et al. 2001). Phylogenetic analysis sug-

gests an ancient (Martens 1997, McKinnon 2002) monophyletic origin of the Malili Lakes telmatherinids (Aarn et al. 1998, see also Roy et al. 2004), although more refined molecular techniques are now being used to test this (F. Herder & U. Schliewen and D. Roy, D. Heath, D. Haffner, P. Hehenussa, personal communications) and some species designations may change.

The telmatherinids are notable for the male colour polymorphism displayed by at least half of

the described species (Kottelat 1990, 1991). Males in these species tend to have blue, grey or yellow colouration, although some Lake Towuti species have additional red and purple elements. All species appear to be sexually dimorphic with the females tending to be dull grey or sandy coloured and the males having much larger and elongated dorsal and anal fins as well as being much more colourful. The male colour polymorphism (to be described in detail elsewhere) is similar to that seen in several African Rift Lake cichlids (Seehausen et al. 1999) but is generally less complex than in that system. In order to develop the telmatherinid system for evolutionary ecology investigations it is necessary to first learn more about the ecology and behaviour of these fish. Here we describe the mating behaviour of seven telmatherinid species as observed in nature.

Materials and methods

Mating behaviours (see Table 1 for terminology used to describe behaviours) of the family Telmatherinidae were observed in the natural habitat

over three time periods: January to March 2003, January to May 2004, and October to December 2004. The following seven species were observed mating: *Telmatherina antoniae*, *T. sarasinorum*, *T. wahjui*, and *T. "whitelips"* (undescribed species) from Lake Matano; and, *T. celebensis*, *Tominanga* sp., and *Paratherina* sp. from Lake Towuti.

Species recognition

Four of the seven observed species are found only in Lake Matano: *T. antoniae*, *T. sarasinorum*, *T. wahjui* (see Kottelat 1991 for morphological species descriptions) and *T. "whitelips"*. Reproductive adult *T. antoniae* (and possibly *T. sarasinorum*) varied greatly in size and shape and further molecular analyses may show species-level distinctions between them (F. Herder, personal communication). We categorized *T. antoniae* males into two major size classes, the smaller fish that have relatively shallow bodies and range from approximately 39–56 mm standard length and the larger individuals, which have deeper bodies and can reach over 80 mm in standard length (see also Kottelat 1991). Here we do not distinguish

Table 1. Terms used to describe general behaviours performed by males and/or females during mating, using existing terminology where applicable (Mortez & Rogers 2004). Males accompanying a female are called "paired males"; those without a female are called "single males".

Behaviour term	Description
<i>Performed by both sexes</i>	
Putative spawning	Male and female place abdomens together on the substrate and quiver. Egg and sperm are difficult to see by humans during these events; hence we use "putative"
Quiver	Performed by both sexes, usually simultaneously, while pressing abdomens to the substrate in a putative spawning
<i>Male behaviours</i>	
Approach	A single male swims toward a paired male
Circle	A paired male circles next to a female while the female searches
Display	Erection of the first and second dorsal fins and the anal fin by the paired male upon approach of a single male. If approach continues, the paired male moves his body laterally toward the other male, maintaining erect fin display
Eat	After a putative spawning a fish attempts to eat the freshly spawned egg(s)
Fight	Physical interaction between two males, usually between a paired male and an approaching single male. The two males circle each other head to tail, often biting each other on the flanks and tail
Nudge	Upon approach of a single male the paired male touches his head to the side of the female, pushing her away from the approaching male
Sneak	A single male rushes alongside the female when the paired male and female go to the substrate to spawn, and begins to quiver with the pair in an attempt to fertilize eggs
<i>Female behaviours</i>	
Search	Searching for a place to spawn; swimming is slow and erratic
Leave	The female swims quickly away from the male, usually into deeper water

between them since their mating behaviour is largely conserved and the great majority of our observations are of the smaller size class. *T. "whitelips"* is an undescribed species, or one that is misdiagnosed among another species from Lake Matano.

The remaining three observed species, *T. celebensis*, *Tominanga* sp. and *Paratherina* sp. are found in Lake Towuti (see Kottelat 1990 for morphological species descriptions). *T. celebensis* is also reportedly found in Lakes Mahalona and Wawontoa (Kottelat 1990). Species descriptions for the genus *Tominanga* are based on only 24 specimens from two lakes (Lakes Towuti and Mahalona) and possibly the adjoining Tominanga River (Kottelat 1990). We hesitate to name the species observed here because our observations in Lake Towuti do not entirely match those described by Kottelat (1990) although we are sure the fish observed belong to that genus. *Tominanga* are morphologically distinct from *Telmatherina* (Aarn et al. 1998); however, mating behaviour appears to be mostly conserved between the two genera. Only two observations of courting pairs of *Paratherina* were made on a single visit to Lake Towuti in February 2003. We were unable to assign the observed specimens to the species described by Kottelat (1990).

Sampling procedure

Transects, 80 m long and 1–2 m deep, were set at ten sites in Lake Matano and two sites in Lake Towuti. Fish density was determined by counting the number of male fish 2 m in front and 1 m to each side of the transect by an observer snorkelling along the transect. All observations of mating were recorded on or near the transect lines by snorkelling. Male and female focal follows were conducted for *T. antoniae*, *T. sarasinorum*, *T. celebensis* and *Tominanga* sp. but only male follows for the remaining species. Only two mating events were observed in *Paratherina* sp. and both males and females were followed simultaneously. The obvious sexual dimorphism in all species (males are colourful and have larger and elongated anal and dorsal fins) allows us to easily distinguish between males and females in the water (Figure 2a).

Male focal follows: A male focal follow was performed by haphazardly selecting a male paired with a female along or near a transect and following that male for 4–10 min with an underwater video camera (Sony miniDV camcorder, OceanImages underwater video housing). The male was followed regardless of whether or not he lost the original female. Mating behaviour was later determined from video analyses, noting position of the male relative to the female, activity of the male and interactions with other males, and putative spawning events.

Female focal follows: Information from all female follows was recorded directly by the observer on underwater paper because the cryptically coloured females are too difficult to follow in the LCD screen of the camera. A female paired with a male was again haphazardly chosen along or near a transect and observed for 4–10 min. The colour morph of the original male was recorded, as were male–male interactions and spawning events as above. Having both male and female follow data allow us to ask questions about the mating behaviour of each sex.

Mating events, such as spawning and male fighting, take place continuously throughout the day and an individual fish can experience several spawning bouts, exchange of partners, and fights within only a couple of minutes. We set a minimum and maximum time for observation in order to standardize results and to make sure we captured an individuals' behavioural pattern.

Results and discussion

Generalized mating behaviour

There are several generalities in the mating behaviours in all seven telmatherinid species we observed. First, there is no parental care; both males and females leave the spawning site immediately after apparent spawning, often together. All species are substrate spawners. Neither males nor females exhibit territoriality, although male fidelity to a particular spawning area may exist in some species (individually identifiable males were observed spawning along the same transect over a three-month period; personal observation). Both males and females appear to be promiscuous in all

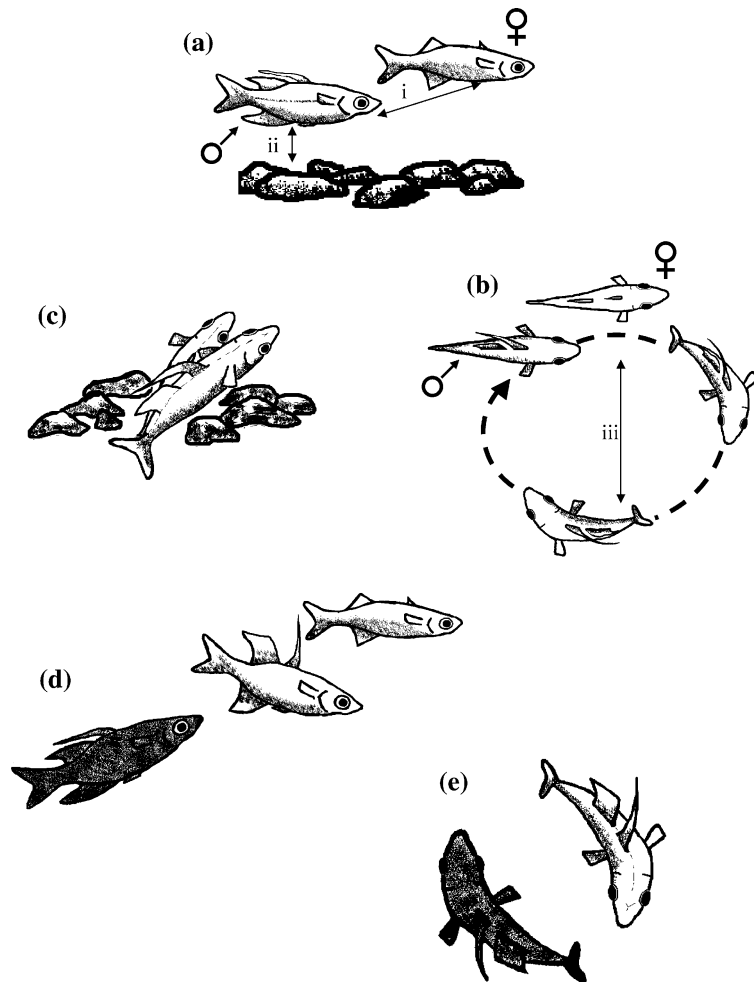


Figure 2. Graphical description of some aspects of generalized telmatherinid mating behaviour (see Table 1 for definitions of behavioural terminology). (a) Male and female pair up, where (i) is the distance the paired male swims behind and to the side from the female and (ii) is the distance the pair swims from the substrate; (b) the male circles alongside the female as she searches where (iii) is the diameter of the males' circle; (c) after searching a female chooses a place to spawn and the male and female press their abdomens to the substrate, and quiver in a putative spawning. Male–male interactions include: (d) the approach of a single male (black) causing the paired male to display; and, (e) if the approaching male persists, a fight between the two males ensues. The winner of the fight pairs with the female and spawns (c) or spawning can occur in the presence of a sneaker, often the loser of the fight (see Figure 3). Note that colour differences are for illustrative purposes only as all male morphs have been observed fighting each other. (Illustration by S.M. Gray).

species observed, switching partners frequently within a 10-min period and often spawning with different partners within that time frame.

The following is a generalized description of mating behaviour in the seven observed telmatherinids (Figure 2); species-specific differences are noted in Table 2 and further highlighted below. A male finds a female on the spawning habitat and either swims slightly behind or in front of the female, who appears to be searching

for a place to spawn (Figure 2a). If the female slows, the male circles forward and away from the female, ending parallel and very close to her (Figure 2b). Circling continues until the female presses her abdomen to the substrate, followed immediately by the male. The pair then quiver, apparently releasing sperm and egg (Figure 2c). The pair immediately leaves the spawning site and generally repeats the searching and circling behaviours unless interrupted by an approaching

Table 2. A comparison of mating behaviours between seven species of telmatherinid fishes from Lakes Matano (M) and Towuti (T), Malili Lakes District, South Sulawesi, Indonesia.

	<i>T. antoniae</i> (M)	<i>T. sarasinorum</i> (M)	<i>T. wahjui</i> (M)	<i>T. "whitelips"</i> (M)	<i>T. celebensis</i> (T)	<i>Tomnanga</i> sp. (T)	<i>Paratherina</i> sp. (T)
No. Observations	> 300	> 600	39	14	20	50	2
Mean density of males per 80 m transect (<i>n</i> = times counted)	16.2 (118) ^a	B: 22.2 (162) R: 71.8 (167)	25.4 (22)	4.7 (12)	24.7 (3)	B: 54.4 (8) R: > 1500 (2)	2.75 (4)
(a) Spawning substrate	Sand/mud, cobble, sometimes rocks and vegetation	B: Sand, small to medium cobble R: Overhanging roots and branches covered in algae	Small cobble, sand, mud, bivalve shells (flowing water ^b)	Small to medium cobble	Rocks and sand	B: Rocks, vertical surfaces R: Overhanging branches covered in algae	Rocks
(b) Spawning depth (m)	< 1–≥ 10	B: < 1–2 R: 1–3	1–2	1–3	1–3	B: 1–2 R: 1–4	3–4
(c) Distance pair swims above substrate (cm)	10	B: 5 R: 5–20	10–40	10	10	B: 5–10 R: 5–20	20
(d) Position of paired male relative to female (cm)	10 to the side and slightly ahead	15–30 to the side and ahead	5–10 to the side and slightly behind	10 to the side and behind	10 to side and 10–15 behind female	10 to the side and behind	20 to the side and behind
(e) Circling behaviour (relative size of circle, cm)	Small, 10–15 cm from female	B: Large, starts up to 30 cm from female	Very small, male turns on tip of tail in tight circle less than 5 cm from female	Large, starts up to 30 cm from female	Small, not more than 15 cm from female	B: Half circle, ends with males' head perpendicular to and facing females' abdomen R: Absent	Large, distance data unavailable
(f) Body position while spawning	Parallel	R: Absent B: Parallel	Parallel, facing upstream ^b	Head elevated 45 degrees	Parallel	B: Vertical against rocks R: Parallel	NA
(g) Fighting intensity ^c	Medium	R: Parallel B: Medium	Medium	Low	Medium	B: Medium R: High	Low
(h) Sneaking	No (rare)	Yes	Rare	No	Yes	Yes	NA
(i) Egg cannibalism	No	Yes	No	No	Yes	No	NA
(j) Male colour morphs ^d	Blue with white fins, yellow, blue with yellow fins	Blue with whitish/clear fins, yellow, grey with black fins, blue with yellow fins, grey with yellow head	Blue with whitish fins, yellow, grey	Blue (sometimes with white fins), yellow, grey (sometimes with white fins)	Blue, yellow, grey	14 morphs with various combinations of the following: <i>Body</i> : silver, red, yellow, orange; <i>Fin</i> : red, yellow, white, purple; <i>Head</i> : red, yellow; <i>Tail</i> : red, yellow	<i>Males</i> : Blue/black with white fins; <i>Females</i> : Grey with red and yellow fins

Table 2. (Continued).

T. sarasinorum and *Tominanga* sp. spawn in two distinct habitats: beach sites (B) and roots sites (R) and behaviours that differ between the two sites are distinguished. Data that are currently not available are designated NA. All depth and distance data are approximations measured *in situ* (Spawning depth could be greater than reported as only surface observations were made except for *T. antoniae* where SCUBA was also used on two occasions).

^a*T. antoniae* were counted along 120 m transects and so density was multiplied by 80/120 to standardize to 80 m, as reported for all other species. Additional transect analyses will be presented in future manuscripts.

^b*T. wahjui* spawn in the outlet of Lake Matano where water velocity is higher than elsewhere in the lake (i.e. at the interface between lake and river) therefore we refer to their spawning habitat as “flowing water” even though they are still in the lake basin. Use of the term “upstream” refers to the fact that fish orient head-first into the flow of water at the outlet of the lake.

^cFighting intensity was qualitatively categorized as low, medium or high based on time to escalation from display to fight, level of physical aggression, and speed of fights; low = very slow, little physical contact between males; medium = very aggressive, swift escalation to fight, much physical contact; high = almost immediate escalation to fight, continuous fights, biting and nudging very aggressive, very fast.

^dMale colour morphs are described as a solid colour meaning that the body and fins are qualitatively similar (e.g. yellow, refers to a male fish whose head and fins are both yellow), or as having variably coloured body parts (e.g. blue with yellow fins refers to a male fish with a blue body and yellow fins). *Tominanga* sp. has many combinations of colour patterns (e.g. silver body with red fins and yellow head) as indicated by the list provided.

male. Sometimes the female will instead leave the male and the spawning habitat for deeper water.

All seven species experience male–male competition over females. When a single male approaches a pair, the paired male displays laterally, forcing himself between the female and the approaching male (Figure 2d) while simultaneously nudging the female in the direction opposite to the approaching male. Males display vigorously to approaching males but rarely (and in a less vigorous manner) to females when other males are absent. The female may swim away or attempt to swim back toward the approaching male. If the approaching male does not retreat in response to the paired male’s display, the altercation may escalate into a fight (Figure 2e), although occasionally a paired male will give up a female without a fight. The winner of the fight takes on the role of paired male while the loser may attempt to sneak, depending upon the species (Figure 3a). A female may switch partners often depending on the outcome of fights, however she does not spawn with every male she is paired with and pairs spawning infrequently or not at all occasionally split up without a fight. This suggests that despite strong male–male competition, the female may be exercising some mate choice. In the species where male colour polymorphism exists, we have also observed all colour morphs fighting over and mating with the same females, suggesting that they are indeed morphs of the same species, not separate species.

Sneaking is a male mating tactic in this group, meaning that a male can either court a female or be a sneaker, and chooses which tactic to employ depending upon his current situation (e.g. a paired male that loses a fight may immediately choose to sneak on another pair). In telmatherinids that employ sneaking as a mating tactic, all colour morphs and adult males of various sizes have been observed sneaking indicating that sneaking is not an alternative reproductive strategy as seen in other fish such as the bluegill sunfish (Gross & Charnov 1980). We have often observed aborted spawning events if a female and paired male detect sneakers before commencement of quivering (i.e. apparent spawning). The pair usually then continues repeating the general courting and spawning behaviour as described above.

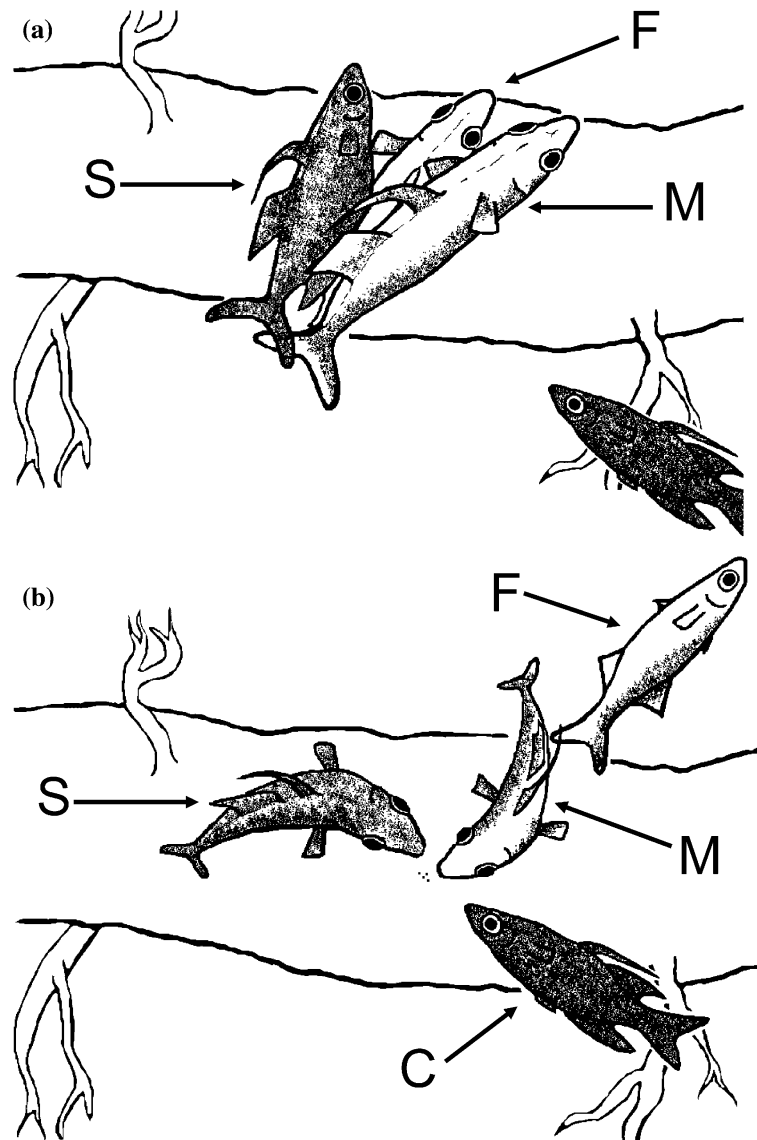


Figure 3. A graphical representation of *Telmatherina sarasinorum* sneaking and egg cannibalism behaviour at a root spawning site. (a) The female (F) and paired male (M) spawn as in Figure 2c but here are joined by a sneaker male (S) attempting to fertilize the eggs being spawned by the pair. (b) After spawning the female leaves the spawning site while the paired male and sneaker male turn around and attempt to eat the eggs and are joined by a non-sneaking cannibal (c). All colour morphs have been observed performing all behaviours and differences in shading here are for illustrative purposes. (Illustration by S.M. Gray).

Conspecific egg predation (i.e. cannibalism) is also prevalent in several species. This behaviour takes place immediately after spawning and often involves several males (Figure 3b): the paired male, sneakers, and single males in the vicinity but not close enough to sneak. Paired males (and sneakers if present) are therefore practising filial

cannibalism (defined as the eating of ones' own offspring, Rohwer 1978). The male turns around and attempts to eat the eggs immediately after he has (potentially) just fertilized them. Thus, both filial and conspecific egg cannibalism (by males not involved in the mating) can take place simultaneously (Figure 3b).

Interspecific comparison of mating behaviours
(See Table 2)

Mating habitat

One of the most striking differences in mating behaviour that we see among these seven species is the use of alternative mating habitats by *T. sarasinorum* and *Tominanga* sp. (Table 2a). The two habitats are: shallow beaches (1–2 m deep) composed of small cobble and sand typical of most other species, and deeper sites that drop-off quickly from the shoreline where overhanging, algae-covered branches, deadfall and roots compose the spawning habitat. Mating behaviour in beach sites follows the general telmatherinid model although there are several notable exceptions. *T. sarasinorum* males fight intensely, can switch mating tactics between courting a female and sneaking copulations, and frequently practise egg cannibalism, especially when sneakers are present (Gray et al., unpublished observations). *Tominanga* mating behaviour in beach sites also deviates slightly from the general pattern in that males often form small courting groups (average group size = 4 males to 1 female, range = 3–7 males to 1–2 females, $n = 16$ observed groups). One male appears to be paired with the female and male–male interactions take place within the group. If another male approaches, the paired male stays close to and parallel with the female while displaying to the approaching male. Instead of escalating to fighting, paired males vigorously nudge females while performing a zigzag manoeuvre that alternately displays each side of his body to the approaching male. This is performed while swimming quickly away from the approaching male in a flee rather than a fight. The female increases swimming speed away from the approaching males. Sneaking, but not cannibalism, has also been observed in this species.

In root sites males and females form swarms around the branches: groups of 5–400 fish for *T. sarasinorum* and 20 to approximately 1000 fish for *Tominanga* in an area approximately 1 m² ($n = 50$ and 4 swarms, respectively). Pairing between males and females in roots swarms is short-lived as males are constantly fighting and switching partners. Circling does not occur. Spawning in the swarms often involves sneaking (Figure 3a), sometimes involving up to 10 sneaker males. This is

frequently followed by egg cannibalism in *T. sarasinorum* (Figure 3b; Gray et al., unpublished observations) but not *Tominanga*. It is interesting to note that *T. sarasinorum*, with five distinct male colour morphs, and *Tominanga*, with at least 14 observed colour morphs (Table 2j), have the greatest morph diversity in Lake Matano and Lake Towuti, respectively, and are the only species known to use two spatially distinct mating habitats.

Another distinction in mating habitat that appears to influence mating behaviour is the flowing water in which *T. wahjui* lives and spawns (Table 2a). *T. wahjui* is found only at the outlet of Lake Matano where the water flows quickly into the Patea River. Courting pairs generally swim against the current. When another male approaches, the paired male displays laterally while nudging the female downstream, using the flow of the current to increase speed away from the approaching male. Fights also tend to go with the current rather than against it. The space between the paired male and female is reduced (less than 10 cm) and the circling diameter of the male is much tighter relative to the other species (Table 2d, e).

The availability of spawning habitat may have played a role in the evolution of mating behaviour diversity in this group. All species are substrate spawners and therefore require suitable substrate upon which to lay their eggs. Differences in spawning habitat may be lake-specific, although the within-lake variation in mating habitat (e.g. beach vs. roots; Table 2a) may be more important given that behaviour appears conserved across the two lakes. However, Lake Matano has steeper sides and is less productive than Lake Towuti (Haffner et al. 2001), which may make beach habitat more limiting in Matano. Shallow beach habitats in Lake Towuti are also more varied, providing level areas of sand or mud with small cobble, as is typically found in Lake Matano, and also beaches composed of large algae-covered rocks. We may then expect to see mating at greater depths in Matano (Table 2b) as shallow substrate is relatively limited.

Circling behaviour

Circling behaviour seems to be the most variable courting element of courtship, and alternatives may be contingent on the mating habitat (Table 2e). For instance, in *T. wahjui*, which mates in fast-flowing water, the paired male remains closer to the female

(5–10 cm) than in any other species, and has a circling diameter of approximately 5 cm, staying very close to the female at all times. In beach-spawning *Tominanga* only a half circle is performed: the male swims from behind the female, turns away from her and makes a half circle back toward the female such that his head aligns with her abdomen, and their bodies are perpendicular. The male then straightens out and resumes position slightly behind the female. Circling behaviour is completely absent in root spawning *T. sarasinorum* and *Tominanga* where male fish density is much higher relative to beach sites (Table 2).

Male–male competition

Male–male competition in the form of displays and fighting is obvious in this family (Table 2g; Figure 2d, e). Fighting intensity differs substantially between species with some notable behavioural differences and in some cases may be influenced by fish density (Table 2). Fights among *T. antoniae* males are often fierce, with the males forming a tight head to tail circle, both displaying and biting the other male (medium intensity). As the circling of the fight progresses the two move vertically in the water column toward the surface, sometimes even breaking the surface of the water. Males often lose the female while fighting, either to another male or because the female leaves the area. *T. celebensis* males appear to be the most aggressive as approaching males make darting movements toward the female, escalating a display to a full fight earlier than in most other species. *T. “whitelips”* fight least frequently and less aggressively relative to the other species (low intensity), which may be due to the low density of *T. “whitelips”* at the spawning habitat (Table 2: mean density = 4.7 fish per transect). Fighting behaviour among *Paratherina* males was the least intense in terms of the speed at which displaying and fighting took place; but it was continuous. In the two independently observed courting events in this species, courtship was similar to the other telmatherinids with the exception that in both cases, two males appeared to accompany the female as she searched. The males alternated in their role of paired or single male. The paired male would display toward the approaching male, escalating immediately to a fight. The two males swam in a circle, head to tail, slowly rising to the

surface while the female apparently continued to search. Both males returned to the female, the winner taking on the role of paired male with the loser trailing behind.

Among males of *T. sarasinorum* and *Tominanga* fighting intensity differs between spawning habitats and may reflect significant differences in density between habitats (Table 2: t -test = 11.87, $df = 1$, $p < 0.0001$; t -test = 12.57, $df = 1$, $p < 0.0001$, respectively). In root sites, where density is higher, pairing between males and females is short-lived as males are constantly fighting aggressively and switching partners (high intensity). In beach sites, where density is much lower, *T. sarasinorum* fight in the typical telmatherinid way, whereas *Tominanga* fighting behaviour differs in the small courting groups (see above).

Alternative male tactics

In several species males employ two mating tactics: courting and sneaking. Sneaking behaviour was observed in four of the seven species: *T. celebensis*, *T. sarasinorum*, *T. wahjui*, and *Tominanga* (Table 2h). We hypothesize that increased density may influence sneaking behaviour as sneaking appears more frequent in the high-density roots sites used by *T. sarasinorum* and *Tominanga*. In high-density sites it may be more difficult for paired females and males to detect sneakers. For example, Reichard et al. (2004) experimentally showed a significant increase in sneaking with male density in European bitterling (*Rhodeus sericeus*). However, further quantification of sneaking and observations of the remaining telmatherinid species are needed to confirm this. Sneaking in *T. sarasinorum* is also closely linked with egg cannibalism (Figure 3b, Table 2i): egg cannibalism in paired males increases substantially in the presence versus the absence of sneaker males (Gray, et al., unpublished observations). Corresponding data for *T. celebensis*, the only known egg predator in Lake Towuti, are lacking. This interaction between mating, sneaking and cannibalism in some species but not others is intriguing and further investigation of these phenomena will be enlightening with respect to the evolution of mating behaviour in telmatherinids (Gray et al., unpublished observations). Future studies will address such questions as, how often do males eat in the presence versus the absence of sneakers? It will also be important to map the

evolution of egg predation, sneaking and cannibalism when a robust phylogeny becomes available.

Cannibalism

Congeneric egg predation and cannibalism of conspecific eggs in *T. sarasinorum* and *T. celebensis* may also influence the evolution of mating behaviour with respect to predator avoidance (Table 2i). Telmatherinids as a whole appear to lay very few eggs at a time and spawn multiply in different locations throughout the day and year, likely decreasing the impact of egg predation. For example, *T. antoniae* defend the female they are paired with from all approaching conspecific males. They do, however, appear to tolerate the presence of one *T. sarasinorum* egg predator, which guards the pair from other would-be suitors and predators (Gray, personal observation). *T. antoniae* may then be trading off the loss of a few eggs to predation if the presence of a single *T. sarasinorum* lowers the intensity of male–male competition over the female. Further theoretical and observational work on this phenomenon is ongoing and will hopefully provide insight into the relationship between egg cannibalism and mating behaviour. Furthermore, many other vertebrates, as well as some larger invertebrates in Lake Matano (and possibly Lake Towuti) are equipped to avoid egg predation. For example, endemic *Glossogobius* sp. form pairs and guard nests of eggs; endemic halfbeaks (Hemiramphidae) are livebearers; endemic rice fish (*Oryzias*) carry egg sacks under their pelvic fins and, endemic snails (*Tylomelania*) internally brood young. This observation leads us to believe that egg predation may be a strong selective force shaping the species assemblage in the system and the mating behaviour of telmatherinids. Finally, we have found it very difficult to collect telmatherinid eggs after apparent spawnings, suggesting that eggs are highly cryptic and raising the possibility that some apparent spawnings are deceptive and eggs are not always deposited (for examples, see Peterson and Järvi 2001, Kume et al. 2002).

Conclusion

The mating behaviours of the telmatherinids observed here can be generalized, suggesting

conservation of mating behaviour in this radiation. Promiscuity and intense male–male interactions are common throughout the family, as is a lack of parental care. Putative adaptations to different habitats, such as the modifications to circling distance in the flowing water-dwelling *T. wahjui*, and increased intensity of fighting in *T. sarasinorum* and *Tominanga* in root site swarms, also exist. In addition, there is a potential correlation between high fish density in root sites and mating behaviours, especially with respect to sneaking and cannibalism.

The mating behaviour of the seven telmatherinid species described here gives only a tantalizing initial view of the diversity within this almost unstudied group of fishes. The fields of behavioural and evolutionary ecology will certainly benefit from further work that integrates the phylogenetic history, mating behaviour and colour patterns within in this radiation.

Acknowledgements

We thank L. Dill and the Dill-lab for their critical review and comments on the ms and F. Herder and U. Schliwen for insightful discussions. The following people helped with the fieldwork: A. Crawford, D. Holm, A. Robertson, S. van der Meer and F.Y. Tantu. We also thank Tantu for the important support he provided as our Indonesian collaborator. Pt.INCO provided logistical support, especially R.A. Lolo, S. Suardi, F. Iskandar, B. Wenzl, and J. Gowans. LIPI (Indonesian Science Foundation) provided permits to conduct research in Indonesia. This project was funded by an NSF Grant to J.S.M, CIDA – EIU-UDP funding to L.M.D., and NSERC, PADI Aware Foundation and Sigma-Xi Grants-In-Aid-Of-Research to S.M.G and equipment donations from Aqualung Canada.

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