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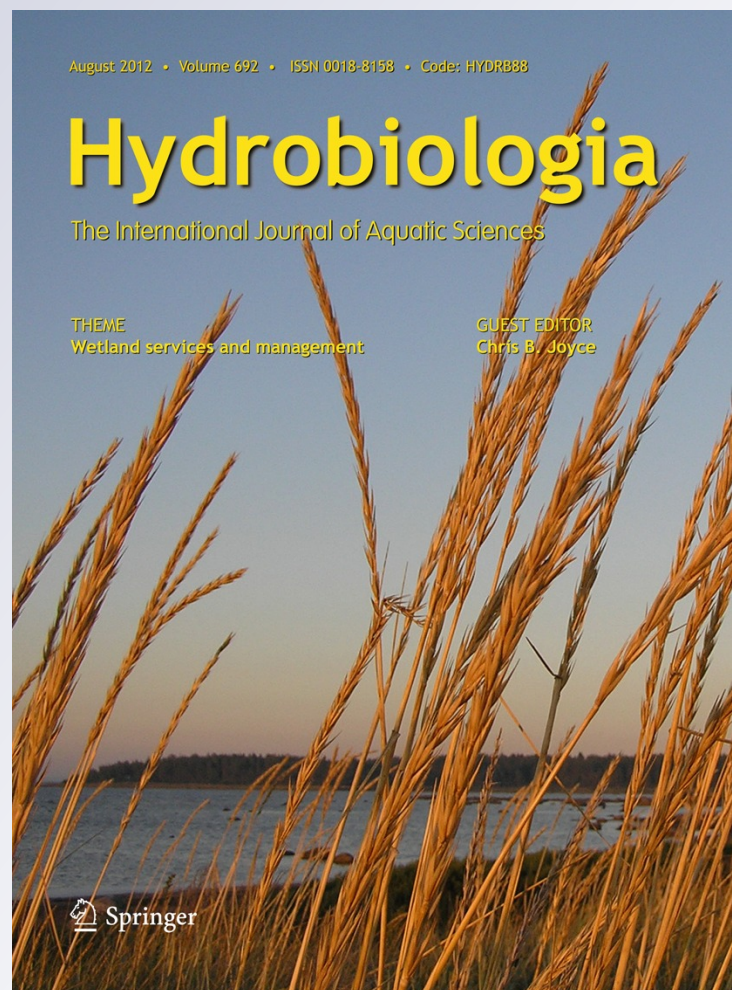
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Alternative egg-feeding tactics in *Telmatherina sarasinorum*, a trophic specialist of Lake Matano's evolving sailfin silversides fish radiation

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Abstract Feeding specialisation is a typical feature of adaptive animal radiations. Different kinds of feeding specialisations have evolved in the endemic sailfin silversides species flock in Lake Matano (Central Sulawesi, Indonesia), including egg-feeding. The present study focuses on *Telmatherina sarasinorum*, a sailfin silverside species feeding on the eggs of related *Telmatherina antoniae*. Stomach content analyses supported *T. antoniae* eggs to be the dominant food item, independent of daytime. We hypothesized that the egg-feeders use alternative tactics for maximising egg consumption under varying densities of both, spawning *T. antoniae* pairs and competing conspecific egg-feeders. Focal behavioural observations were applied to describe different feeding tactics

and to analyse feeding success and the related costs in terms of competitive interactions. Egg-feeders followed single courting pairs of *T. antoniae* or, alternatively, they switched between different spawning pairs. Following-behaviour, covering one or more spawning events of the host species, was positively related to enhanced egg consumption. Compared to feeding by switching frequently among different spawning pairs, the following tactic came at the cost of likewise increased competition. Behavioural observations suggest that some males monopolize courting pairs of *T. antoniae* and gain increased amounts of eggs compared to others avoiding competition by switching among pairs. The present results confirm that egg-feeding is a distinct trophic specialisation in *T. sarasinorum* and increase the scale of behavioural specialisation in Lake Matano's evolving *Telmatherina* radiation.

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Adaptive radiation

Introduction

Adaptive radiation predicts specialisation to trophic resources and the evolution of alternative strategies for exploiting them (Schluter, 2000). There are various animals that are oophagous (feed on eggs), a behaviour that is in most reported cases facultative (e.g. Randall,

1967; Shioyaki & Dotsu, 1983; Whoriskey & FitzGerald, 1985; Daan, 1987; FitzGerald, 1992; Bloxam et al., 1996; Shine et al., 2004; Hirayama et al., 2005; Järnegren et al., 2005; Light et al., 2005; Mehliş & Bakker, 2009). In East African cichlid fish radiations, spectacular trophic behaviours like head-ramming and snout-engulfing allow some species specialising on eggs or fry of heterospecific fishes (Wilhelm, 1980; Ribbink & Lewis, 1981; McKaye & Kocher, 1983; McKaye & van den Berghe, 1997; Ribbink & Ribbink, 1997; Ochi et al., 1999).

Egg-feeding, among other trophic specialisations, has also been reported in the adaptive radiation of sailfin silverside fishes (Teleostei: Atheriniformes: Telmatherinidae) endemic to the ancient graben Lake Matano in the central highlands of Sulawesi (Kottelat, 1991; Gray & McKinnon, 2006; Pfaender et al., 2010). This ultraoligotrophic (Haffner et al., 2001) and extraordinarily deep (>590 m) lake is the hydrological head of 'Wallace's dreamponds', i.e. the Malili Lakes system (Brooks, 1950; Cristescu et al., 2010). It is estimated to be roughly 1–2 Myr old (von Rintelen et al., 2004), and harbours endemic lineages of lacustrine radiations of diatoms, crustaceans, viviparous freshwater gastropods and freshwater fishes (Kottelat, 1990a, b, 1991; Kottelat et al., 1993; Bramburger et al., 2004, 2008; von Rintelen et al., 2004, 2007, 2010; Glaubrecht & von Rintelen, 2008; Schubart & Ng, 2008; Schubart et al., 2008; von Rintelen & Cai, 2009; Herder & Schlieven, 2010; summarised in von Rintelen et al., in press). The adaptive radiation of sailfin silversides (Herder et al., 2006a) has recently received substantial interest as a model system for studying the evolution of speciation processes (e.g. Gray & McKinnon, 2006; Gray et al., 2007, 2008a, b; Herder et al., 2006b, 2008; Schwarzer et al., 2008; Walter et al., 2009a, b; Pfaender et al., 2010, 2011; see Herder & Schlieven, 2010 for a summary). Lake Matano's sailfin silverside radiation consists of two major lineages, sharpfins and roundfins, identified among other characters by the shape of the second dorsal and anal fin of the males (Kottelat, 1991; Herder et al., 2006a, b). Reproductive isolation among the three roundfin 'morphospecies' is substantial but incomplete (Herder et al., 2008), which also appears to be the case in sharpfins (Herder et al., 2006a; Schwarzer et al., 2008). Although ingestion of eggs has also been shown in two other species of the radiation (Pfaender et al., 2010), records of egg-

feeding behaviour refer primarily to the sharpfin *Telmatherina sarasinorum* Kottelat (1991). This species has been reported to feed on eggs of con- and heterospecific sailfin silversides (Kottelat, 1991; Herder et al., 2006b; Gray et al., 2007, 2008a, b; Pfaender et al., 2010). The probability of conspecific oophagy (i.e. 'egg-cannibalism') by male *T. sarasinorum* increases with number of 'sneaking' males present at a spawning event (Gray & McKinnon, 2006; Gray et al., 2007).

In contrast to egg-cannibalism, heterospecific egg-feeding behaviour by *T. sarasinorum* targeting roundfin sailfin silversides has not been studied in detail. Oophagous behaviour of *T. sarasinorum* seems to be directed primarily towards the smaller of the two *Telmatherina antoniae* morphospecies (Kottelat, 1991; Gray & McKinnon, 2006; see Herder et al., 2008 for a description of size dimorphism in *T. antoniae*). The recent discovery of 'sneaky eating', whereby male *T. sarasinorum* eat the eggs of female roundfin *T. antoniae* Kottelat (1991) which they had previously induced to spawn (Gray et al., 2008a; F.H. & A.F.C., pers. obs.), has drawn attention to behavioural specialisations in *T. sarasinorum*.

In the present study, we focus on egg-feeding behaviour in *T. sarasinorum* directed to *T. antoniae* 'small'. Our hypotheses is that fish eggs are the most important food item in the stomach contents of individuals collected at spawning sites of *T. antoniae*. Egg-feeder behaviour is examined in situ, to determine if following a single spawning *T. antoniae* pair enhances the feeding success compared to switching host pairs. Finally, we explore the hypothesis that enhanced egg-feeding success comes at the cost of competition.

Materials and methods

Study system and focal follows

The present study focuses on egg-feeding tactics in *T. sarasinorum* at spawning sites (shallow beaches) of the 'small' morphospecies of *T. antoniae* (Herder et al., 2008). Lake Matano's sailfin silversides spawn throughout the year, several times a day and on different substrates (Gray & McKinnon, 2006). Spawning is promiscuous, with individuals changing partners several times within only a couple of minutes. Sailfin

silversides do not provide parental care and are not territorial (Gray & McKinnon, 2006). As determination of female sharpfin *Telmatherina* is challenging while snorkelling, the present study was restricted to the easily determinable brightly coloured males.

Field observations were made during the late dry season (6–26 November) 2006 at Lake Matano. Study sites were shallow, open waters dominated by gravel and sand, the major courting and spawning habitat of the ‘small’ morphospecies of *T. antoniae*. Focal observations were carried out on a total of 292 individual *T. sarasinorum* males (220 blue, 43 yellow, 29 blue-yellow males) at three sites in the lake [2 days with 58 focal follows near Salonsa (2°30.419'S, 121°19.960'E), 9 days with 136 focal follows near the inlet of River Lawa (2°25.879'S, 121°13.428'E) and 7 days with 98 focal follows near Sorowako at ‘Old Camp’ (2°31.402'S, 121°22.096'E)]. Focal follows were conducted by snorkelling between 0800 and 1700 h and documented with a pencil on a plastic tablet. Focal individuals were selected haphazardly by choosing the first male *T. sarasinorum* observed upon entering *T. antoniae* spawning sites. The repeated observation of the same individual was unlikely due to the high abundance of oophagous *T. sarasinorum* and courting *T. antoniae* ‘small’ at all sites (A.F.C. & F.H., pers. obs.; see also Herder et al., 2008). Additionally, the likelihood of recording multiple observations of the same individual was further reduced by switching snorkelling areas within sites between observations. To minimise any influence of the observer (A.F.C.) on fish behaviour, a distance of at least 1 m was maintained between the observer and the focal fish. *T. sarasinorum* and *T. antoniae* were identified following Kottelat (1991) and Herder et al. (2006b). Courting *T. antoniae* all belonged to the ‘small’ morph of *T. antoniae* and was identified as courting if two (male and female) individuals were swimming together close to the substrate, displaying courtship behaviour as described by Gray & McKinnon (2006). Focal follows of *T. sarasinorum* lasted between 1 and 10 min. Observation time was recorded to the nearest second, until the maximum observation time (10 min) had been reached or the observer lost sight of the fish.

An approach of the focal *T. sarasinorum* towards a courting *T. antoniae* pair was recorded as a ‘contact’ if the potential egg-feeder was within 50 cm of the target pair. Contacts exceeding 4 s were recorded as ‘follows’. This 5-s criterion was based on pilot

observations, which suggested that focal *T. sarasinorum* approached spawning pairs of *T. antoniae*, fed on the eggs and either left the pair or, alternatively, further followed the pair. Some of these ‘follows’ lasted for several minutes and affected several spawning events of a selected pair.

Two different modes of ‘picking’ (the movement of the focal fish to the substrate, followed by snapping towards it; see Hernandez et al., 2008) were distinguished: (i) substrate-poking, i.e. picking at the substrate in the absence of a recorded preceding *T. antoniae* spawning and (ii) egg-picking, defined as percussion-type picking immediately after a *T. antoniae* spawning event, exactly at the place of spawning (Fig. 1).

Potential ‘competitive interactions’ directed towards other sailfin silversides, independent of species and sex, were summarised as the number of behaviours exhibited per focal observation. Behaviours recorded as competitive interactions included ‘chase’ (aggressively following a single individual *Telmatherina*), ‘lateral display’ (the spreading of fins

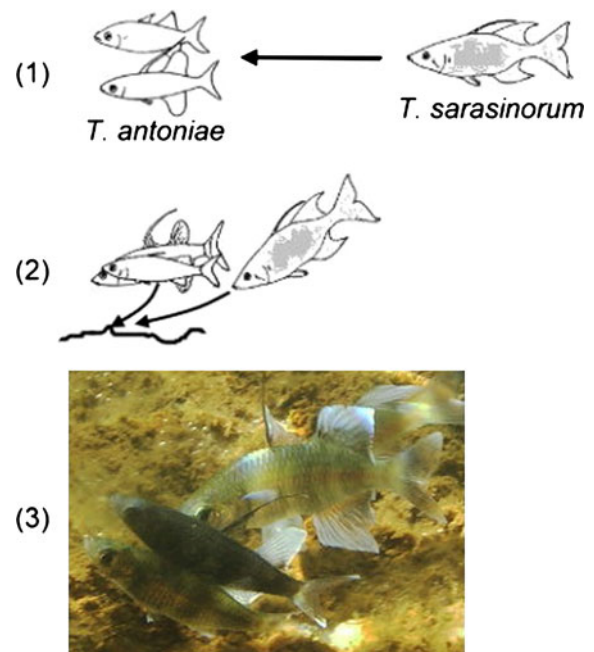


Fig. 1 Scheme of ‘egg-picking’ behaviour. (1) An individual *Telmatherina sarasinorum* is attracted by courtship behaviour of *Telmatherina antoniae*. (2) As the *T. antoniae* pair moves towards the substrate for spawning, the egg-feeder ‘darts’ towards the spawning site. (3) Immediately after spawning, the *T. sarasinorum* picks eggs at the spawning site

towards another *Telmatherina*), or 'fight' (aggressive interaction with spread fins in both individuals). The abundance of courting *T. antoniae* was classified into three categories for each focal follow ranging from one to three, one meaning few pairs of courting *T. antoniae*, two some pairs and three meaning many *T. antoniae* pairs. Focal observations when no host pairs were present (i.e. density of *T. antoniae* = 0) were excluded from the analysis.

Stomach content analyses

Adult male *T. sarasinorum* was collected close to the inlet of River Lawa (2°25.879'S, 121°13.428'E) from 0800 to 0959 ($n = 19$), 1000 to 1159 ($n = 22$), 1200 to 1359 ($n = 22$) and from 1400 to 1559 h ($n = 19$) in depths between 0.5 and 3 m on different days during the observation period. Fish were collected by two snorkellers (A.F.C. & F.H.) with a gillnet of 8 mm mesh size, 0.8 m depth and 6 m length. Given the fact that the species key available is widely based on male characters (Kottelat, 1991), the current investigations were restricted to males. Fish were killed by an overdose of clove oil, preserved in 4% formalin and later transferred to 70% ethanol for long-term storage at Zoologisches Forschungsmuseum Alexander Koenig, Bonn (ZFMK), Bavarian State Collection of Zoology, Munich (ZSM) and Museum Zoologicum Bogoriense, Bogor (MZB). In total, 82 individuals (yellow morphs: $n = 7$; blue morphs: $n = 75$) were dissected. Food items present in the gastrointestinal tract between oesophagus and pylorus were flattened and embedded in Gelvatol (polyvinylalcohol). Subsequently, the relative surface area of different food items was estimated for every individual fish using a reflected-light and a stereo-microscope (see Herder & Freyhof, 2006). Contents were classified as 'fish', 'fish eggs', 'algae', 'detritus', 'zooplankton', 'terrestrial insects', 'terrestrial plants', 'molluscs', 'sand' or 'unidentifiable rest' following Herder et al. (2008) and Pfaender et al. (2010). The term 'detritus' was used to describe organic material at different stages of decomposition; 'unidentifiable rest' was used to describe material that was not assigned to any of the other groups. Complete or fragmented fish eggs were recognised by comparing surface structure of ripe eggs from formalin-preserved ovaries of the 'small' *T. antoniae* (two individuals) with eggs from *T. sarasinorum* stomachs.

Statistical analyses

Statistical analyses were conducted using PAST 2.10 (Hammer et al., 2001) and SPSS 11.5.1 (Norusis, 1986). The non-parametric Kruskal–Wallis test was used to detect a significant difference in the median proportion of consumed eggs across the four diurnal sampling periods. Additionally, it was used to compare following-ratio of *T. sarasinorum* (the ratio of time that a focal male was following *T. antoniae* pairs relative to the total observation time for the individual male) among study sites. As the overall ANOVA was significant, post hoc LSD tests were used to compare the following-ratios. Spearman rank correlations were used to detect relationships between the following-ratio and three behaviours: substrate-poking, egg-picking and competitive interactions. These behaviours were estimated by dividing the frequency of each behaviour by the total observation time. A linear regressions analysis of the following-ratio and the three behaviours was carried out for the site Lawa.

Results

Stomach contents

Fish eggs corresponding in size and structure to eggs of *T. antoniae* were present in all of the *T. sarasinorum* stomachs dissected ($n = 82$). They represented the most frequent food item consumed [78.5% (median) of total stomach volume]. There was no evidence that egg consumption varied with time of day (Kruskal–Wallis test, $n = 82$, $df = 2$, $P > 0.05$; Fig. 2). Molluscs were the second most important item in the stomachs of *T. sarasinorum* (median = 20.0%), followed by detritus (median = 11.5%) and insects (median = 7.0%). None of the remaining food categories exceeded a median of 5.0% volume in total.

Behavioural observations

The observational data were restricted to focal follows in which 'host' pairs were present ($n = 204$). These observations include 1674 contacts between male *T. sarasinorum* and courting pairs of *T. antoniae*; 774 contacts without subsequent following-behaviour and 910 cases where the contact exceeded 5 s. In total,

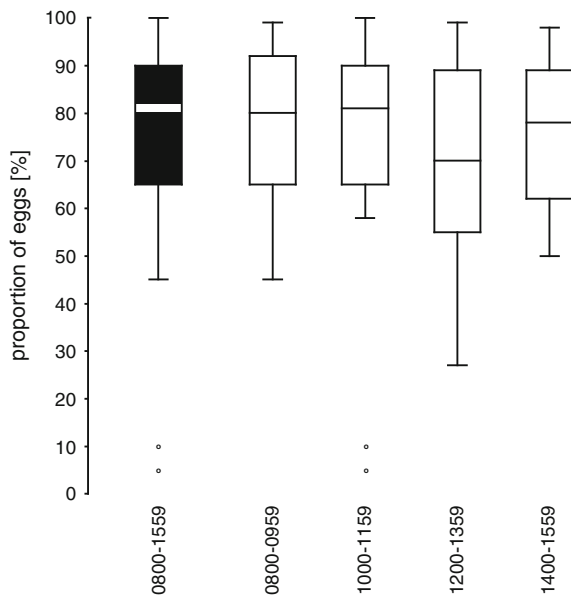


Fig. 2 Box and whisker plots indicate the proportion of eggs in stomach contents of male *T. sarasinorum* over the day. The centre line denotes the median value, the box encloses the inner two quartiles, the whiskers are drawn up to data points <1.5 times the box height and circles indicate outliers. Fish eggs were clearly the dominating content in stomachs of all *T. sarasinorum* examined, independent of daytime

males invested 33% of their time budget in the following courting pairs of *T. antoniae*.

The following-ratio differed among study sites (Kruskal–Wallis test: $n = 204$, $df = 2$, $P < 0.001$). Post hoc tests indicated a significantly higher following-ratio at River Lawa in comparison to Salonsa and Sorowako (both: $P < 0.001$).

Spearman rank correlation and linear regressions indicated a positive relationship between the following-ratio and both, egg-picking as well as competitive interactions, at all three sites. In contrast, the

following-ratio was negatively associated with substrate-poking behaviour (Table 1; Fig. 3).

Discussion

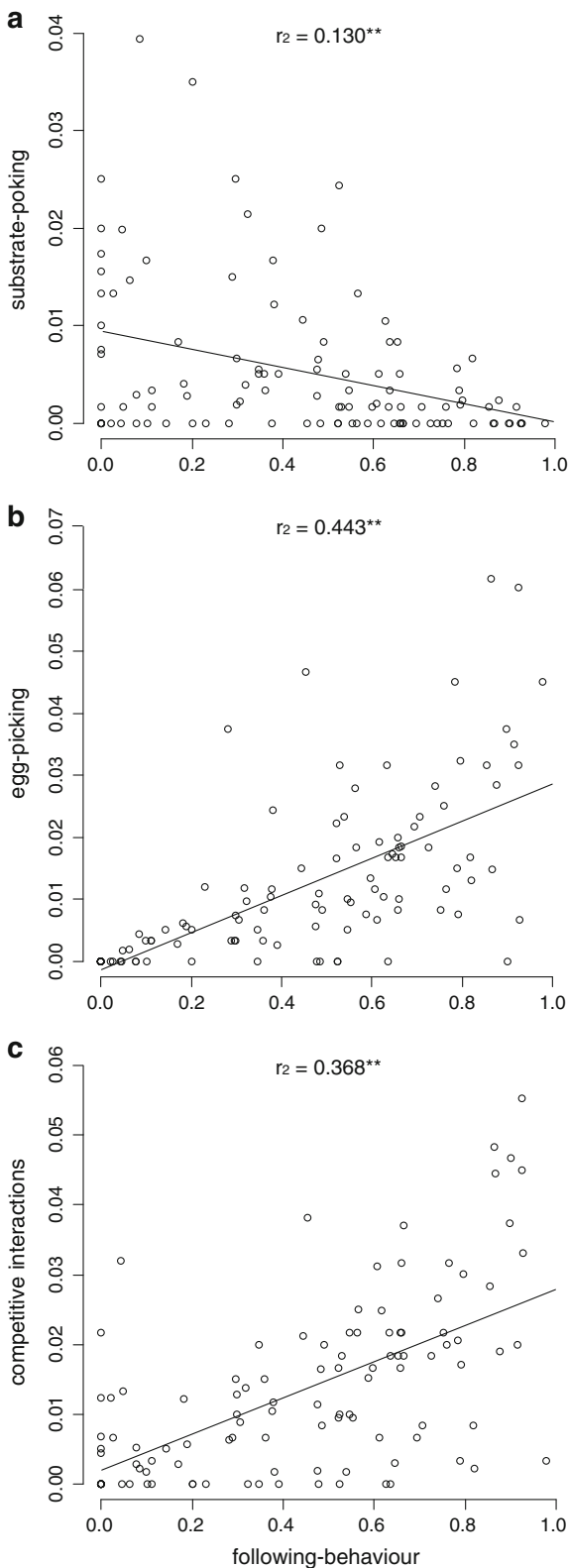
Analyses of both, stomach contents and behavioural observations, confirmed that egg-feeding was the dominant feeding mode of *T. sarasinorum* at *T. antoniae* spawning sites during the period of study. All *T. sarasinorum* examined or observed fed on eggs, suggesting that the species is oophagous, independent of time of day. Observational data demonstrated that the eggs originated from *T. antoniae*. No other sympatric fish species was affected by oophagous behaviour of the observed male *T. sarasinorum*.

The egg-feeders used different tactics to gain access to *T. antoniae* eggs. They either selected a pair, followed it and defended it against other potential egg-feeders, or, alternatively, they searched for different spawning pairs without following them. At all of the sites investigated, egg-picking and hence presumably also the egg consumption significantly increased with following effort, whereas picking behaviour without a preceding spawning of *T. antoniae* decreased with the following rate. The positive correlation between egg-picking behaviour and an increased following effort supports the hypothesis that monopolising single courting pairs of *T. antoniae* translated into enhanced egg-feeding success. However, this monopolisation comes obviously at the cost of increased levels of competition: the frequency of competitive interactions was positively related to a higher proportion of following-behaviour. Taken together, these results suggest that male *T. sarasinorum* invest in monopolising the high-energy food resource ‘fish egg’ when following spawning host pairs.

Table 1 Spearman correlation coefficients of the behaviours substrate-poking and egg-picking and the number of competitive interactions to the following-ratio

Behaviour [number per observation time (n/min)]	Sorowako ($n = 44$)	Lawa ($n = 110$)	Salonsa ($n = 50$)
Substrate-poking	-0.42*	-0.34**	-0.38*
Egg-picking	0.47*	0.75**	0.65**
Competitive interactions	0.74**	0.61**	0.30*

Correlations are indicated by study sites. With increasing following effort, competition and egg consumption increased, whereas feeding not associated with the monopolized pair of *T. antoniae* decreased. Details for the site Lawa are shown in Fig. 3. Stars indicate levels of significance (* $P < 0.05$; ** $P < 0.001$)



◀ **Fig. 3** Frequencies of behaviours related to egg-feeding, in accordance to the following-ratio of each focal follow observation at the site Lawa: **a** substrate-poking, **b** egg-picking and **c** the number of competitive interactions. Competition and egg consumption increased with time focal males followed pairs of *T. antoniae*, whereas picking without a preceding spawning of a host pair was negatively correlated with the following effort

Male *T. sarasinorum* were observed inducing heterospecific females to spawn in order to ate their eggs, i.e. sneaky-eating (Gray et al., 2008a, b). Conspicuously, all the four attempts of sneaky-eating recorded in the present study occurred at low densities of *T. antoniae*. This might indicate a further behavioural adaptation of the egg-feeder, used mainly during periods of low availability of eggs; alternatively or complementary, the success of male *T. sarasinorum* inducing female *T. antoniae* to spawn might be facilitated during periods of low *T. antoniae* abundances, i.e. low abundances of competing conspecific males, hypothesis that require further investigation.

The present case of egg predation raises questions regarding potential avoidance strategies in *T. antoniae*. Surprisingly, no behavioural response towards such a mechanism like aggression against egg-feeders has been recorded so far (Gray & McKinnon, 2006; personal observations F.H., A.F.C.). A possible explanation for this might be that fitness costs of occasional egg predation are comparatively low as *T. antoniae* spawns numerous times a day (Gray & McKinnon, 2006).

The present results are exclusively based on observations and stomach samples from major spawning sites of *T. antoniae* 'small'. A previous study based on sharpfin samples covering a wider array of habitats around Lake Matano (Pfaender et al., 2010) likewise reported substantial amounts of fish eggs in stomachs of *T. sarasinorum*. This suggests that egg-feeding is not restricted to areas of high host densities like those chosen for the present investigation. In addition, the occurrence of fish eggs in stomachs of two other sharpfin morphospecies (Pfaender et al., 2010) indicates that other species of the species flock also feed on fish eggs. There are, however, no indications thus far for behavioural specialisation in terms of following and monopolisation in order to obtain heterospecific eggs in these species.

Feeding specialisations like egg-feeding in the case of *T. sarasinorum* are discussed as a major force

driving adaptive speciation (Schluter, 2000; Coyne & Orr, 2004; Dieckmann et al., 2004). Fine-scaled morphological adaptations to resource use are evident in both sailfin silverside clades of Lake Matano (Herder et al., 2008; Pfaender et al., 2010, 2011), supporting the adaptive character of this lacustrine radiation (Herder et al., 2006b). The geologically young age of Lake Matano (approx. 1–2 Myr; see von Rintelen et al., 2004), on-going gene flow among some of sailfin silverside species endemic to Lake Matano (Herder et al., 2006b, 2008; Schwarzer et al., 2008) and the presence of individuals which are morphologically intermediate between different ‘sharpfin’ species (Herder et al., 2006a) suggest that these fishes are most likely in an early phase of species flock formation. Oophagy as a behavioural adaptation constitutes a unique trophic guild in the radiation of sailfin silversides and increases complexity of ecological interactions among members of the species flock.

Conclusions

Oophagy was the dominant feeding mode in male *T. sarasinorum* during the period of study. Eggs originated from spawning pairs of *T. antoniae*, a heterospecific member of the same species flock (Herder et al., 2006a), were obtained by different behavioural tactics. In contrast to frequently changing between different spawning host pairs (switching), monopolisation of single courting pairs was associated with higher egg-feeding success, but also with increased costs in terms of competing other egg-feeders. A trade-off between high energetic investment and likewise elevated feeding success when monopolising, versus lower efforts and success when switching, provides a plausible explanation.

Alternative modes of exploiting the high-nutrient resource ‘*T. antoniae* egg’ by *T. sarasinorum* might indicate a positive feedback loop (Crespi, 2004) of emerging sailfin silverside diversity, with one species providing the resource for specialisation of other species in an evolving flock. Such a loop appears plausible in case of the egg-feeding specialist and its alternative behavioural tactics and might add further dynamics to the evolution of complex radiations.

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