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## Reproductive parasitism: male and female responses to conspecific and heterospecific intrusions at spawning in a mouth-brooding cichlid *Ophthalmotilapia ventralis*

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A rare form of alternative reproductive behaviour without simultaneous parasitic spawning was observed in *Ophthalmotilapia ventralis*, a lekking mouth-brooding cichlid from Lake Tanganyika. Floater males attempted to sneak opportunistically into the territory to actively court the female, while the owner (bourgeois male) defended the territory against other potential intruders. Floater males had more body fat than territory owners and generally higher condition factors. In field experiments, the response of bourgeois males and courted females was tested towards floaters and egg predators (a catfish *Synodontis multipunctatus*) present in the territories. Territory owners responded aggressively particularly to floaters, and female responsiveness to bourgeois male courtship tended to decline when floaters were present. The potential influence of reproductive parasitism on sexual selection in mouth-brooding cichlids is discussed.

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Key words: alternative reproductive tactics; lekking; maternal mouthbrooders; multiple mating; sexual selection; sneaking.

### INTRODUCTION

Male alternative reproductive tactics (ART) are common in fishes (Taborsky, 1994, 2008). The most common parasitic reproductive tactic pursued by males is sneaking by which males attempt to fertilize eggs surreptitiously when a female spawns with a territorial (bourgeois) male (Taborsky, 1994, 1998). Reproductive parasites have been observed in both substratum-brooding cichlids (Sato, 1994; Sato *et al.*, 2004; Katoh *et al.*, 2005; Heg *et al.*, 2006; Ota & Kohda, 2006) and mouth-brooding cichlids (McKaye, 1983; Kuwamura, 1987; Chan & Ribbink, 1990; Ochi, 1993a, b, 1996; Rossiter, 1994; Rossiter & Yamagishi, 1997). Opportunistic sneaking attempts in

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mouthbrooders are performed either by neighbouring bourgeois males (Ochi, 1993a) or floaters, *i.e.* sexually mature individuals without a territory (Chan & Ribbink, 1990; Ochi, 1996; pers. obs.), which may be mimicking females (McKaye, 1983; Chan & Ribbink, 1990).

Multiple paternity has been observed in many mouth-brooding cichlids (Kellogg *et al.*, 1995; Parker & Kornfield, 1996; Maan *et al.*, 2004; Haesler, 2007). Sneakers may contribute to this either directly by fertilizing eggs or indirectly by driving females away from a male's territory to another male's territory (Ochi, 1993b; Hamilton *et al.*, 2006, Haesler, 2007). This is of general interest because sneaking may reduce the opportunity for sexual selection (Jones *et al.*, 2001; Singer *et al.*, 2006), and sexual selection has been invoked to explain the great species richness of the cichlid fauna in the East African Great Lakes (Kocher, 2004).

Besides sneakers, egg predators are another source of mating disturbance (Kellogg *et al.*, 1995). Egg predators comprised of conspecifics, generalist and specialized cichlids are numerous in Lake Malawi and are frequently attacked by bourgeois males (McKaye, 1983; Stauffer & McKaye, 1986; Kellogg *et al.*, 1995; M. P. Haesler pers. obs.). Both specialist and opportunistic egg predators of mouth-brooding cichlids have been reported also from Lake Victoria and Lake Tanganyika (Sato, 1986; Barel *et al.*, 1991; Nshombo, 1991; Ribbink & Ribbink, 1997).

A potential influence of egg predators and sneakers on sexual selection has been proposed by a theoretical model, showing that poor males can persist in a population if good males are more costly to females because they attract more enemies (such as egg predators or sneakers; Hamilton *et al.*, 2006). Sneakers may not necessarily be costly to females, but they are always costly to males. In general, however, females appear to counter-select against sneakers in most species, which suggests costs for females from mating with sneakers (Taborsky, 1994, 2008), although Candolin & Reynolds (2002), Svensson & Kvarnemo (2005) and Reichard *et al.* (2007) suggest that the presence of sneakers may be positive for females. The model by Hamilton *et al.* (2006) suggests that these parasitic males are more likely to persist if quality differences among bourgeois males are large, which should also influence female mate preferences. Thus, a third player in the mating game between bourgeois males and females can greatly affect sexual selection by influencing the multiple mating rate and the male quality distribution in a population (Hamilton *et al.*, 2006).

Here, the influence of the presence of floaters and egg predators is reported on mating behaviour in *Ophthalmotilapia ventralis* (Boulenger), a maternally mouth-brooding cichlid from Lake Tanganyika. Males aggregate in leks and build small bowers (a circular sandpatch) on top of a rock. Floaters are males that are potentially sexually mature (judged by body size and pelvic fin length) but not territorial. All sneaking behaviour that was observed in this population was performed by floater (*i.e.* non-territorial) males. Floater males entered territories during spawning to court the female and shed sperm on the bower of the territory owner. Gonad maturity, size and mass of floater males were compared to test whether these males were potentially capable of stealing fertilizations from territory owners. It was experimentally tested how bourgeois males responded to the presence of egg predators and floaters, and whether females adjust their mate choice to this situation. Females were expected to respond more strongly to the presence of egg predators than to the presence of floaters, as the former might pose greater fitness costs to them. Bourgeois males should respond strongly to both kinds of intruders.

## MATERIALS AND METHODS

The study was conducted at Kasakalawe Point (8° 47' S; 31° 05' E) at the southern end of Lake Tanganyika near Mpulungu, Zambia, during October and November 2005.

### BOURGEOIS MALES V. FLOATER MALES

Sixteen bourgeois (*i.e.* territorial) males and 16 floater (*i.e.* non-territorial) males were caught (1) to test whether floaters were sexually mature and thus capable of fertilizing eggs and (2) to compare sizes and masses between bourgeois and floater males. The fish were anaesthetized with clove oil and then decapitated. Standard length ( $L_S$ ), length of pelvic fins ( $L_P$ ) and mass ( $M$ ) were measured. The presence or absence of visceral fat was scored and gonad maturity (gonad score  $S_G$ ) was estimated using a scale of 1 to 5 (1, testes barely visible and completely transparent; 2, immature; 3, early ripening and mature; 4, late ripening; 5, ripe; Seehausen *et al.*, 1998). Body condition ( $K$ ) was calculated as  $K = 100 ML_S^{-3}$  (Bolger & Connolly, 1989).

### OBSERVATIONS OF PARASITIC SPAWNING BEHAVIOUR

During the course of a larger study (Haesler, 2007), spawning females were observed, followed and caught after they had completed spawning. During these observations, sneakings were observed several times. The fish were observed for a total period of 67 h focal female watching, plus an additional 42 h for the experiment explained below, *i.e.* a total of 109 h of observations. The number of eggs spawned was noted, as were any incidences of sneaking and whether the male lost his mate due to an interruption by floaters performing sneaking behaviour.

### BEHAVIOURAL EXPERIMENT

Either (1) an empty plastic bag (treatment E: transparent freezer bags; serving as a control and reference), (2) a plastic bag containing a *Synodontis multipunctatus* Boulenger catfish as an egg predator (treatment EP) or (3) a floater male (treatment F) were presented to a territory owner on the lek, placing it close to his bower (0.2–0.3 m away from bower). *Synodontis multipunctatus* is a brood parasite of mouth-brooding cichlids in Lake Tanganyika and an egg predator (Sato, 1986; H. Büscher, pers. comm.). Potential host species include *O. ventralis* (S. Immler, pers. comm.) and these fish have been bred in aquaria with *O. ventralis* as a host (T. Jermann, pers. comm.).

Experimental males were chosen haphazardly for a treatment. It was made sure, however, that factors potentially influencing female mate choice decisions (depth, location within the lek, bower and rock size) were equally distributed across treatments. The observations lasted for 10 min and all behaviours (courtship, aggression and feeding) were scored. A trial was considered successful if the focal male courted at least once during the observation period. Each male was used only once and for one treatment only, unless the trial was not successful; then the trial was repeated. After the observations, the bower and the rock on which the bower was located were measured. The bower consists of a circular, flat patch of very fine sand sifted through the gills by the territory owner. Height (minimum and maximum) and diameter (twice at right angle) of the rock and the diameter of the bower (twice at right angle) were measured and the means of these measurements were used for statistical analyses. The bowers of the males in the three different treatments did not differ from each other in diameter (Kruskal–Wallis ANOVA,  $n_E = 14$ ,  $n_F = 13$ ,  $n_{EP} = 21$ ,  $\text{mean}_E = 111$  mm,  $\text{mean}_F = 113$  mm,  $\text{mean}_{EP} = 122$  mm;  $P > 0.05$ ). The rocks were also not different between treatments (Kruskal–Wallis ANOVAs (1) for mean height:  $n_E = 10$ ,  $n_F = 13$ ,  $n_{EP} = 23$ ,  $\text{mean}_E = 124$  mm,  $\text{mean}_F = 154$  mm,  $\text{mean}_{EP} = 147$  mm,  $P > 0.05$  and (2) for mean area:  $n_E = 10$ ,  $n_F = 13$ ,  $n_{EP} = 23$ ,  $\text{mean}_E = 0.07$  m<sup>2</sup>,  $\text{mean}_F = 0.08$  m<sup>2</sup>,  $\text{mean}_{EP} = 0.08$  m<sup>2</sup>,  $P > 0.05$ ). There was no difference between treatments in success rates of replicates using as criterion that at least one courtship bout occurred per observation ( $\chi^2$  test,  $P > 0.05$ ;

treatment E: 21 of 36 trials were successful, treatment EP: 22 of 34 trials and treatment F: 20 of 41 trials).

For presentations, three different randomly chosen individuals of varying sizes and gonad maturity levels were used as floater males [73, 75 and 78 mm  $L_S$ , gonad scores ( $S_G$ ) 1, not known and 3] and two different catfish (both *S. multipunctatus*, size: 70 and 63 mm  $L_S$ ). The floater males used did not differ in their behaviour while being contained in the plastic bag; all of them tried to escape from the bag. The *S. multipunctatus* catfish simply sat there and hardly moved whilst in the bag. There was no chemical communication possible through the plastic bag during the experiment.

## RECORDED BEHAVIOUR

A typical courtship sequence proceeded as follows (Immler & Taborsky, 2009): a bourgeois male approached a female that appeared in the vicinity of his territory. After a quick lateral display, the male led the female to his bower with exaggerated undulation of the tail (scored as 'court'), which she may subsequently have entered if she followed him into his territory (scored as 'follow'). Then the male placed his genital papilla onto the bower and quivered, probably releasing sperm. He subsequently presented the egg dummies that are located at the end of his pelvic fins in front of the female on the bower where he had just quivered ('presenting'), which she may have taken into her mouth ('mouthing'). After she did so, the male left the bower and defended the territory, while the female may have laid an egg on her own. Females always lay only one egg at a time and the average clutch size is 13 eggs (Kuwamura, 1986). All of these behaviours were recorded. Other behaviours that were scored include aggressive interactions with conspecific and heterospecific fish (both, displays and overt attacks), feeding, bower building and attacks towards the plastic bag or the fish inside.

## STATISTICAL ANALYSIS

All non-parametric tests were performed using SPSS 11.5 for Windows (www.spss.com). Dixon test for outliers were performed in R (R Development Core Team; www.r-project.org; Komsta, 2006). One outlier in each treatment for number of attacks towards bag, and one in female responsiveness in treatment floater were found. For further statistical analysis, the outlier and the most extreme data point at the other end of the distribution were removed (Sokal & Rohlf, 1981). In addition to Kruskal–Wallis one-way ANOVA, the Dunnett's *t*-test, which specifies one group as a control or reference (treatment E: presentation of empty bag), was performed (Zar, 1999).

## RESULTS

### BODY SIZES AND GONAD SCORES OF BOURGEOIS AND FLOATER MALES

Floater males were significantly smaller, had significantly shorter pelvic fins relative to their  $L_S$ , were significantly lighter and their gonads were less mature than those of bourgeois (*i.e.*, territorial) males (Mann–Whitney *U*-tests,  $L_S$ :  $n_F = n_T = 16$ ,  $\text{mean}_F = 77.1$  mm,  $\text{mean}_T = 83.6$  mm,  $P < 0.01$ ;  $L_P L_S^{-1}$ :  $n_F = 13$ ,  $n_T = 15$ ,  $\text{mean}_F = 0.62$ ,  $\text{mean}_T = 0.69$ ,  $P < 0.01$ ;  $M$ :  $n_F = n_T = 14$ ,  $\text{mean}_F = 13.5$  g,  $\text{mean}_T = 15.4$  g,  $P < 0.01$ ; gonad score:  $n_F = n_T = 15$ ,  $\text{mean}_F = 2.57$ ,  $\text{mean}_T = 4.77$ ,  $P < 0.01$ ; Fig. 1). Three floaters had very mature testes ( $S_G \geq 4$ ) and seven out of 15 were most probably capable of producing sperm ( $S_G \geq 3$ ). Variation in  $S_G$  was 12 times larger in floaters than in bourgeois males (variances in  $S_G$  scores for floaters and bourgeois (territorial) males, respectively:  $\text{var}_F = 1.7$ ,  $\text{var}_T = 0.14$ ). All

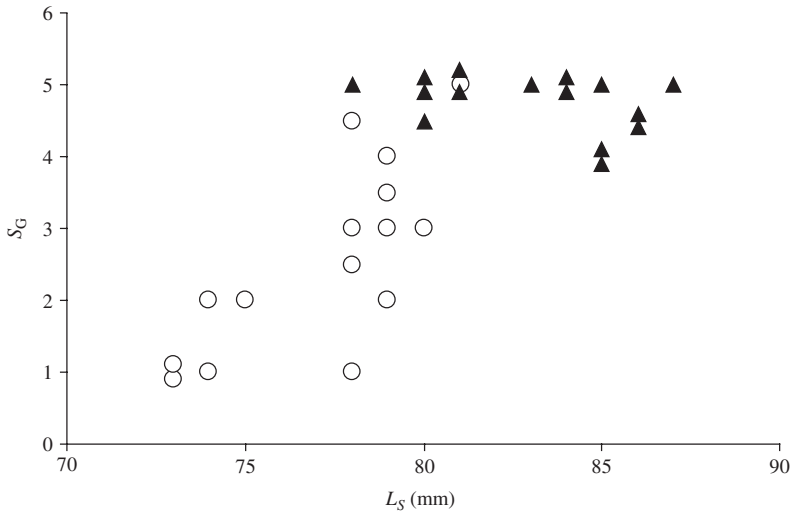


FIG. 1. Standard length ( $L_S$ ) plotted against gonad score ( $S_G$ ) in floater (○) and bourgeois male (▲) *Ophthalmotilapia ventralis*. Overlapping points were moved vertically (by  $\pm 0.1$  units) to make all data points visible.

floaters had large amounts of visceral fat, whereas bourgeois males usually had none (only three out of 15 bourgeois males had a little visceral fat). This was reflected in the difference between the  $K$  values of floaters and bourgeois males (Mann–Whitney  $U$ -test:  $n_F = n_T = 14$ ,  $P < 0.01$ ; Fig. 2).

#### OBSERVATIONS OF PARASITIC SPAWNINGS

Multiple sneaking attempts occurred in two out of five observed spawnings; two sneaking attempts in one spawning, and five in the other one. Only two of the five

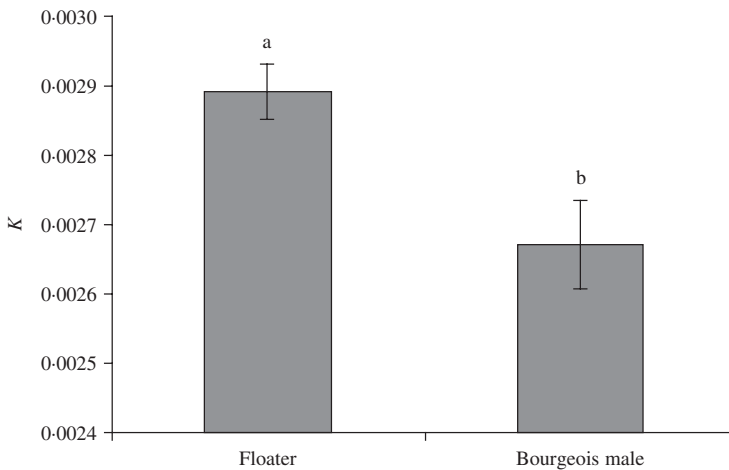


FIG. 2. Body condition factors ( $K$ ) of floater and bourgeois male *Ophthalmotilapia ventralis*. Different lower-case letters above columns indicate significant differences ( $P < 0.05$ ).

observed spawnings were observed until completion. In all five observed spawnings, a total of 33 laid eggs were recorded. The observed sneaking males were all non-territorial males (floaters), *i.e.* not bourgeois neighbours. Floaters invaded the territory and courted the female while the owner was absent chasing other fish and then sat on the bower briefly, apparently to release sperm. Bourgeois males chased away floaters immediately after detection. Both females always preferred the territory owners over floater males in the two observed spawnings with multiple sneaking, *i.e.* they did not respond to courtship behaviour of the parasitic male and even turned away from the courting floater males.

In the first observed spawning with intrusions by floaters the female left the bower, but the bourgeois male was able to court her back onto the bower. In the second observed spawning with intrusions by floaters, the territory owner lost his mate in three out of five intrusions; however, in these cases the female returned later to this male to continue spawning after having visited another male. No simultaneous parasitic spawnings were observed.

### BEHAVIOURAL EXPERIMENT

Male territory owners showed a lot more attacks on conspecific males than on the *S. multipunctatus* (Fig. 3). The empty bag was ignored with the exception of one fish out of 21 (Kruskal–Wallis ANOVA for overall treatment differences:  $n_E = 19$ ,  $n_F = 18$ ,  $n_{EP} = 20$ ,  $P < 0.01$ ; Table I). A *post hoc* test further revealed that the bag containing a floater male was significantly more often attacked than the bag containing an egg predator (Dunnett's *t*-test:  $n_F = 18$ ,  $n_{EP} = 20$ ,  $P < 0.01$ ). The number of attacks on the bag containing an egg predator was not significantly higher than that on the empty bag (Dunnett's *t*-test:  $n_E = 19$ ,  $n_{EP} = 20$ ,  $P > 0.05$ ). All other male

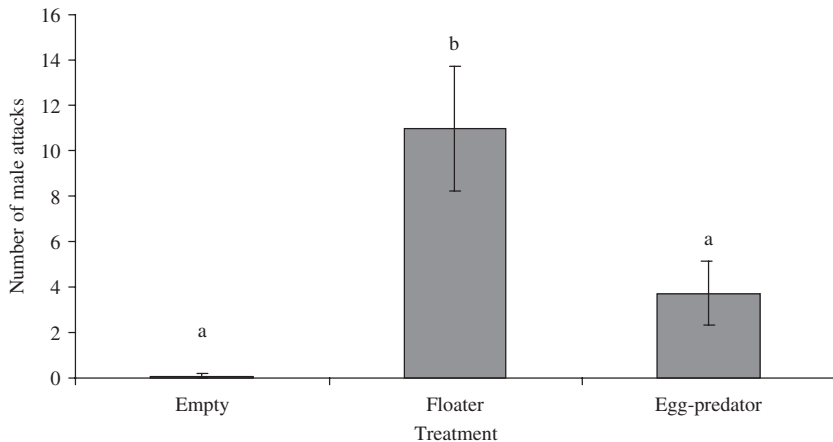


FIG. 3. Mean  $\pm$  S.E. number of attacks by the bourgeois male *Ophthalmotilapia ventralis* towards the plastic bag per 10 min observations. The bag either contained no fish (treatment 'empty',  $n = 21$ ), a conspecific male (treatment floater,  $n = 20$ ) or an egg predator (treatment 'egg predator',  $n = 22$ ). Different lower-case letters above columns indicate significant differences ( $P < 0.05$ ) between treatments. The figure represents the complete data distribution including outliers.

TABLE I. Test statistics of focal territorial male *Ophthalmotilapia ventralis* behaviour during the successful trials of the experiment (Kruskal–Wallis ANOVA of each scored behaviour). Only successful trials (*i.e.* when bourgeois males courted) are included

	CA male	CA fem	HA	Bag	BB	F	Court
$\chi^2$	2.51	0.09	1.36	37.33	0.53	0.70	1.14
<i>P</i>	>0.05	>0.05	>0.05	<0.01	>0.05	>0.05	>0.05

CA, aggression towards conspecific males (CA male) and females (CA fem); HA, aggression against heterospecific fish; Bag, attacks on plastic bag and its contents (including the empty bag); BB, bower building; F, feeding; Court, courtship behaviour. Sample sizes were  $n = 21$  for the empty bag,  $n = 20$  for the floater and  $n = 22$  for the egg predator treatments.

behaviours did not differ significantly between treatments (Table I). Female responsiveness did not vary significantly between treatments when all three conditions were jointly tested [female responsiveness (follows per courtship), Kruskal–Wallis ANOVA,  $n_E = 19$ ,  $n_F = 18$ ,  $n_{EP} = 20$ ,  $P > 0.05$ ; Fig. 4), but females tended although not significantly to respond less to bourgeois male courtship under the ‘floater’ treatment (Dunnett’s *t*-test with treatment E serving as the control:  $n_E = 21$ ,  $n_F = 18$ ,  $P > 0.05$ ).

## DISCUSSION

Several intrusions by floaters were observed in this study, and all observed sneaking behaviours were performed by non-territorial males (*i.e.* floaters) and not by

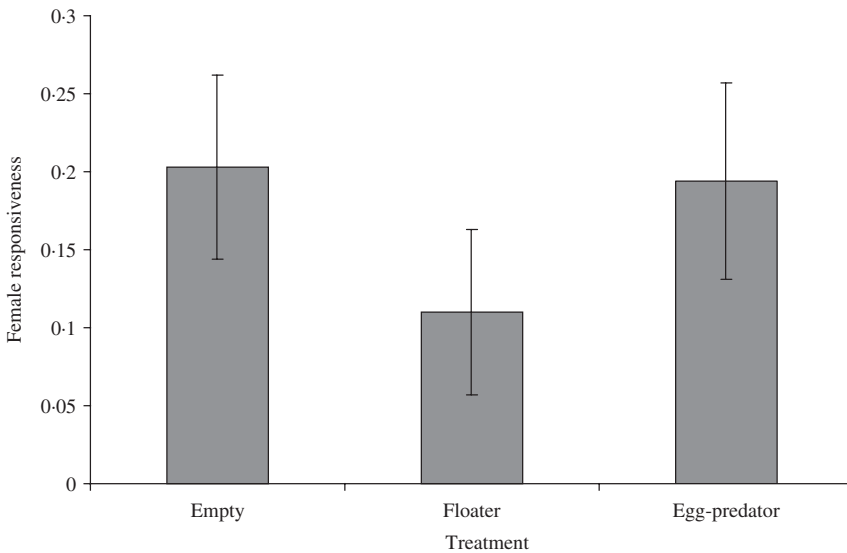


FIG. 4. Mean  $\pm$  s.e. female responsiveness (number of female follows per male courtship bout) to the courtship of the bourgeois male per 10 min observations in three treatments of *Ophthalmotilapia ventralis*. Sample sizes as in Fig. 3.

bourgeois neighbours. The sneaking behaviour reported here differs from typical sneaking behaviour because no simultaneous parasitic spawning is performed (Taborsky, 1994). Instead, floaters sneak into the territory while the bourgeois male is absent chasing away other potential intruders, and court the female as if they were the territory owner. This bears similarity to piracy behaviour (van den Berghe, 1988), but the ownership of the territory does not change and the floaters were always chased away by the bourgeois male. Territory owners may lose their mates in response to intrusions by floaters, albeit often only temporarily (Ochi, 1993b).

The differences in size and in the presence of fat between floaters and bourgeois males and the indication that larger fish generally have more mature gonads may suggest that *O. ventralis* males shift during ontogeny from being an opportunistic sneaker to becoming a territory owner, similar to what Chan & Ribbink (1990) described for a sunfish *Lepomis macrochira* Rafinesque and another cichlid *Pseudocrenilabrus philander* (Weber) species. Males might also switch back and forth between floater and territorial stages throughout their reproductive lifetime, accumulating reserves (*i.e.* raising their condition factor) before acquiring a territory. During this study, only floaters were observed to parasitize bourgeois male reproduction, but it cannot be ruled out that neighbouring bourgeois males might occasionally adopt this tactic too, as observed in other fishes (Sargent & Gebler, 1980; Ochi, 1993a; Lee & Bass, 2005). Such plastic, sequential ART are widespread in taxa with indeterminate growth such as most fishes (Taborsky, 1999, 2008).

Bourgeois males responded with strong aggression to conspecific males presented within their territory. They also responded aggressively to the *S. multipunctatus* but ignored the empty bag (Fig. 3; albeit the difference was not significant due to low statistical power of the pair-wise multiple comparison test), suggesting that they responded to the contents of the bag and not the bag *per se*. As males made such distinction between the three treatments, it can be assumed that the females were also able to distinguish between treatments. Although an overall effect of treatment on female behaviour was not confirmed, females tended to respond to bourgeois male courtship less often when a floater was presented than in the empty bag treatment, suggesting avoidance of parasitic males. It might be that females were mainly influenced by the bourgeois male's behaviour rather than the fish in the bag, but the behavioural frequencies (including courtship) of the former did not differ significantly between treatments, except for the attack frequencies towards the plastic bag. Females did not respond to the presence of *S. multipunctatus*, suggesting that they did not recognize the latter as a potential threat. Brood parasitism by *S. multipunctatus* may happen only rarely in *O. ventralis* and females might not be adapted to respond accordingly, whereas males may be selected to attack any intruder in their spawning territory. An additional experiment with another predator or another control (for instance an algae grazer) might help to clarify this issue.

There are a number of mouth-brooding cichlid species in which sneaking attempts by either floaters or territorial males have been reported (McKaye, 1983; Kuwamura, 1987; Chan & Ribbink, 1990; Ochi, 1993a, b, 1996; Rossiter, 1994; Rossiter & Yamagishi, 1997). The role of alternative reproductive tactics in sexual selection and their influence on mating patterns in mouth-brooding cichlids has not yet been investigated. It has been argued that extra-pair fertilizations (EPF) increase the opportunity for sexual selection (Kempnaers *et al.*, 1992). In species with external fertilization, however, sneakers may decrease rather than increase the opportunity for sexual



selection on male traits, as a greater proportion of males may get the chance to reproduce (Jones *et al.*, 2001; Singer *et al.*, 2006). EPF in birds differ from sneaking in fishes in two important ways. First, EPF in birds are usually obtained from territorial neighbours, *i.e.* bourgeois males sire offspring with their own mates and with females that are paired up with neighbours. In fishes, EPF are most often obtained by non-bourgeois males, *i.e.* by males that do not invest in the privileged access to females or fertilizable gametes (Taborsky, 1997). Second, there is a crucial difference in the way parasitic fertilizations are usually achieved. A female bird actively chooses another male for copulation (Kempnaers *et al.*, 1992), whereas in fishes, sneakers are usually not chosen by the female but try to steal fertilizations surreptitiously from a bourgeois male (Taborsky, 1994). In general, female fishes appear to counter-select against sneakers and to avoid bourgeois males with sneakers and satellite males in their vicinity (Sigurjonsdottir & Gunnarsson, 1989; van den Berghe *et al.*, 1989; Akagawa & Okiyama, 1993; Taborsky, 1994, 2008; Alonzo & Warner, 2000; for exceptions see Candolin & Reynolds, 2002; Svensson & Kvarnemo, 2005; Reichard *et al.*, 2007).

A similar mating pattern with non-bower holding males parasitizing bourgeois males has been described by Rossiter & Yamagishi (1997) for *Cyathopharynx furcifer* (Boulenger), a species closely related to *O. ventralis*. Here floaters also appear to release sperm onto the bower, while the bourgeois male is absent chasing away other potential intruders. The particular spawning pattern of these bower-building mouthbrooders with bourgeois males leaving their spawning mate to defend their territory provides an opportunity for floater males to sneak in and spawn with the female while the bourgeois male is absent. In contrast, in most substratum-brooders where the eggs and the sperm of the bourgeois male are released simultaneously, sneakers perform simultaneous parasitic spawning (Taborsky, 1994).

Disturbance of matings can lead to relaxation of sexual selection (Hamilton *et al.*, 2006). Intruding floater males and egg predators affect at least one component of sexual behaviour in *O. ventralis*, *i.e.* male defence. Bourgeois males responded strongly to the presence of both kinds of intruders, whereas females only tended to avoid parasitic males (*i.e.* floater males performing sneaking behaviour). To assess the effect of parasitic males on sexual selection in mouthbrooders, future studies will need to quantify fertilization success of such reproductive parasites, and especially how often successful (*i.e.* attractive) males lose their mating partner due to interruptions by reproductive parasites, and how this will affect the success of less attractive males on the lek.

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