Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Contest versus scramble competition among males pursuing fixed or plastic alternative reproductive tactics

Corinna von Kuerthy[*], Michael Taborsky

Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

Reproductive and agonistic behaviours typically diverge between individuals pursuing alternative reproductive tactics (ARTs). When tactics are fixed for life, evolutionary theory predicts that the relative frequencies of alternative male genotypes are stabilized in a population by negative frequency dependence. This implies that competition is greatest between males pursuing the same tactic. The cichlid fish *Lamprologus callipterus* exhibits three male ARTs involving fixed and flexible tactics, and an extreme intrasexual size dimorphism determined by Mendelian inheritance. Large nest males defend territories and construct nests of empty snail shells in which females breed. In contrast, dwarf males pursuing a genetically fixed parasitic tactic enter shells surreptitiously during spawning in order to steal fertilizations. Sneaker males using another parasitic tactic, which is plastic and conditional, steal fertilizations opportunistically during spawning by quick intrusions into the nest. The variation in tactic origin and reproductive behaviour and the substantial asymmetry in body size render *L. callipterus* an ideal model system to study theoretical predictions regarding the types and intensity of contest behaviours among conspecific competitors pursuing ARTs. In an experiment exposing males to competitors using either the same or a different tactic, within-tactic competition was much more intense than between-tactic competition in bourgeois males, as predicted by evolutionary theory. In addition, the level of aggression displayed by bourgeois males against male intruders was apparently triggered by perceived differences in body size. In contrast to bourgeois males, parasitic males showed hardly any aggressive behaviour against other males, indicating that their contests follow the pattern of scramble competition. The conditions characterizing parasitic reproduction apparently select for rapid responsiveness when opportunities arise to fertilize eggs, whereas attacking other males in this situation seems inappropriate. Our results show that males pursuing ARTs diverge in the way they react to reproductive competition, mainly dependent on their overall resource defence strategy.

Male–male competition is common in the context of reproduction, and it is particularly intriguing if males pursue alternative reproductive tactics (ARTs; Gross, 1996; Oliveira, Taborsky, & Brockmann, 2008; Shuster & Wade, 2003; Taborsky & Brockmann, 2010). ARTs are characterized by bimodal or multimodal distributions of behavioural, physiological and sometimes morphological traits among same-sex conspecifics, typically in males, which result from disruptive sexual selection (Taborsky & Brockmann, 2010; Taborsky, Oliveira, & Brockmann, 2008). A crucial distinction between ARTs is their fundamentally different reproductive effort. At the behavioural level, large 'bourgeois' males generally defend and monopolize reproductive resources, which

creates opportunities for noncourting male competitors to exploit their effort (Neff, Fu, & Gross, 2003; Taborsky, 1994, 1997). Males of the bourgeois pathway compete by investing heavily in growth (Wirtz Ocaña, Schütz, Pachler, & Taborsky, 2013), conspicuous body ornaments (Candolin & Wong, 2008; Neat, Locatello, & Rasotto, 2003), territorial and courtship behaviour (Taborsky & Brockmann, 2010; Gross, 1982, 1996), extended phenotypes (Schaedelin & Taborsky, 2006, 2009), weaponry (Tschernavin, 1938) and acoustic or chemical signals (Barata et al. 2007; Laumen, Pern, & Blüm, 1974). In contrast, parasitic males typically benefit from an inconspicuous appearance when approaching a nest surreptitiously in order to steal fertilizations, thus exploiting the effort of bourgeois males (Taborsky, 1994; Warner, 1984). ARTs may be fixed for life (pygmy swordtail, *Xyphophorus nigrensis*: Zimmerer & Kallman, 1989; Ryan, Craig & Morris, 1993; marine isopod, *Paracerceis sculpta*: Shuster & Wade 1991; corkwing wrasse,

* Correspondence: C. von Kuerthy, Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Wohlenstr. 50a, 3032 Hinterkappelen, Switzerland.
E-mail address: corinna.vonkuerthy@iee.unibe.ch (C. von Kuerthy).

Symphodus melops: Uglem, Mayer & Rosenqvist, 2002), in which case individual males permanently pursue one of the tactics, or they may be plastic (Atlantic salmon, *Salmo salar*: Aubin-Horth & Dodson, 2004; dung beetle, *Onthophagus taurus*: Knell & Simmons, 2010; Columbian ground squirrel, *Urocitellus columbianus*: Raveh et al., 2010; African striped mouse, *Rhabdomys pumilio*: The correct citation is: Schradin. C. Schneider. C. & Lindholm. A.K. (2010) and is given in the reference list.), switching tactics reversibly or irreversibly during their lifetime (Taborsky et al., 2008). Althought there are numerous descriptive studies of plastic and fixed ARTs, information is scarce on how individuals of different tactics react and adjust to within versus between-tactic competition during reproduction. However, when individuals pursue different ARTs, reproductive competition may occur at either of two levels: for access to mates, or directly for fertilization of eggs or females. As a consequence, an individual may need to adjust the behaviour depending on its tactic and depending on the form of competition it is facing (e.g. within- versus between-tactic competition).

Evolutionary theory predicts that fixed ARTs are maintained by frequency-dependent selection (Gross, 1991; Maynard Smith, 1974). The logic is that if bourgeois male frequencies increase in a population, the average fitness of individuals performing a parasitic tactic would increase relative to the fitness of males pursuing the bourgeois tactic (Taborsky et al., 2008). This is because competition between males pursuing the same type of behaviour is predicted to be more intense than competition between males using different tactics when contesting resources and mates (Austad, 1984; Gross, 1991; Maynard Smith, 1974; Shuster & Wade, 2003; Taborsky & Brockmann, 2010).

In this study we aimed to compare tactic-specific rivalry in fixed and plastic ARTs. As a model we used the polygynous and biparental, snail shell-brooding cichlid *Lamprologus callipterus* from Lake Tanganyika, East Africa. This species is particularly interesting because males show both fixed alternative life history pathways and plastic tactic choice in one of the two alternative pathways (Wirtz Ocaña, Meidl, Bonfils, & Taborsky, 2014). In addition, alternative male tactics in this species exhibit an exceptional size dimorphism (Sato, Hirose, Taborsky, & Kimura, 2004; Taborsky, 2001). Large bourgeois nest males of *L. callipterus* collect empty snail shells (Mitchell, Wirtz Ocana, & Taborsky, 2014) and defend them against other males and predators (resource defence polygyny; Emlen & Oring, 1977), thereby providing protection to females breeding inside these shells (Emlen & Oring, 1977; Sato, 1994; Sato et al., 2004). The time a bourgeois male monopolizes and defends a nest can differ considerably between individual males (Schütz, Pachler, Ripmeester, Goffinet, & Taborsky, 2010). During the nest-holding period, bourgeois males are frequently challenged by other potential nest males trying to steal shells or to take over a nest (Maan & Taborsky, 2008), and by the interference of males pursuing one of two alternative mating tactics attempting to parasitize their reproductive effort (Sato et al., 2004; Taborsky, 1998, 2001). First, sneaker males of the bourgeois male pathway, typically younger and competitively inferior males, try to occasionally steal fertilizations from nest owners by opportunistically darting into a nest male's territory during spawning. When passing a certain threshold size (Schütz & Taborsky, 2005) and after accumulating sufficient energy stores (von Kuerthy, Tschirren, & Taborsky, 2015), these males may switch from sneaker to nest male status, attempting to hold a territory by themselves. The second parasitic tactic is employed by the much smaller and genetically divergent dwarf male, which halts growth long before reaching female size and weighs only 2.4% of the weight of nest males on average (Sato et al., 2004; Schütz & Taborsky, 2005; Taborsky, 2001). Dwarf males exist at low relative frequencies in

natural populations (Goffinet, 2007; Wirtz Ocaña et al., 2014) and pursue a different life history pathway with a highly specialized mating behaviour. Dwarf males try to steal fertilizations from territory holders by wriggling past a spawning female into the tip of the snail shell (Sato et al., 2004; Taborsky, 1998, 2008). From this position, they typically fertilize the majority of the eggs of a female (Wirtz Ocaña et al., 2014). The asymmetry in size and behaviour renders *L. callipterus* an ideal study system to study contests between conspecific competitors pursuing different ARTs.

Here we studied tactic-specific rivalry in *L. callipterus* during courtship. We tested bourgeois males, as well as plastic parasitic sneakers and fixed parasitic dwarf males in different standardized competitive test situations in order to quantify the responses of each type of male to (1) within- versus (2) between-tactic competition. We predicted that parasitic sneaker and dwarf males should rather stay inconspicuous, avoiding overt contests with bourgeois males, and as a consequence avoiding the costs of being attacked, chased or even injured. We expected between-tactic competition to generate a different response in nest males, because parasitic sneaker males usually pose a different and typically smaller threat (loss of some paternity) for the bourgeois males than competitors of the same tactic (potential nest take-overs; Maan & Taborsky, 2008). Dwarf males may pose a higher threat to the nest male (major loss of paternity for a particular brood; Wirtz Ocaña et al., 2014) than parasitic sneaker males, but much less threat than a bourgeois male intruder that may take over the nest and terminate the reproductive success of the nest owner altogether. We tested whether nest males respond appropriately to the different threats arising when parasitic sneakers or dwarf males intrude into their nest. We differentiated whether their response is based, for instance, on the body size or behaviour of an intruder, or whether it is based on the actual threat to be expected in terms of future stolen paternity.

Since each male tactic is predicted to incur the highest level of competition from rivals pursuing the same tactic, which results in negative frequency dependence, we also expected high levels of competition between males pursuing the same parasitic tactics. However, in parasitic males scramble competition (Toquenaga, 1990), selecting for a rapid response when opportunities for reproduction arise, might be a more appropriate way to compete, because such situations are hard to predict and responses should be swift. Ultimately, the intensity of contests between different tactics may strongly influence the amount of time nest males can invest in reproductive behaviours, and the amount of time needed to succeed in a contest may differ between different within- versus between-tactic contest situations.

Understanding how individuals pursuing different ARTs adjust to heterogeneous social environments and different forms of competition is important to our understanding of selective forces acting on males using ARTs.

METHODS

Experimental Design

Focal nest males of *L. callipterus* were placed in ca. 500-litre compartments (ca. 130 × 63 cm and 63 cm high) of 1000-litre tanks. We used wild-caught individuals from Lake Tanganyika and F1 descendants. Nest males were introduced into the compartment 1 week prior to the start of the experiment, and remained in the tank during the entire experimental period. Six empty snail shells of *Neothauma tanganyicense*, the standard breeding substrate of *L. callipterus,* were introduced into the tank on the day before the experiment started in order to induce territorial behaviour in focal nest males. Additionally, several hiding opportunities (empty cut-up plastic bottles and clay flowerpot

halves) were placed in each tank. The water temperature was kept constant at $27 \pm 2\,°C$ and the day:night cycle was 13:11 h. Salinity and hardness of the water matched the values of Lake Tanganyika closely (Taborsky, 1984) and all fish received food ad libitum twice a day (TetraMin: dry food/ fresh food: Artemia, Daphnia or mosquito larvae). On the experimental day, two ovulating females were introduced to the focal nest male's tank at ca. 0845 ($\pm$ 30 min).

Induction of Ovulation in Females

Ovulation in *L. callipterus* females was induced by intraperitoneal injection of LHRH (des-Gly10[D-Ala6]-Luteinizing Hormone-Releasing-Hormone-Ethylamide, Sigma–Aldrich L-4513) at 70 µg LHRH/10 g female body weight, following an established protocol (Hirschenhauser, Taborsky, Oliveira, Canàrio, & Oliveira, 2004) using a stock solution of LHRH mixed with freshwater teleost Ringer solution. This dosage results in an ovulation peak after approximately 48 h (Hirschenhauser et al., 2002). Ovulation in females was checked by inspecting the belly and genital papilla swelling (Trewavas, 1983). After the introduction of the female to the experimental tank (Fig. 1), courtship usually commenced without delay. The induction of ovulation in females allowed us to test a specific nest male's behavioural response to the presence of an ovulating female during a direct interaction with different conspecific male tactics in a standardized way.

The experiment comprised two major experimental phases. (1) Pre-exposure phase: initially, the nest males were kept in the experimental tank solely with two females for 1 h. This phase without the presence of male competitors served to initiate territorial and courtship behaviours. (2) Noncompetitive or competitive exposure phase: at the beginning of the second hour, a focal nest male was challenged with one of five possible test situations (Fig. 1a–e). In the noncompetitive test situation (Fig. 1a), the focal nest male was continuously kept together with only two females for both the pre-exposure phase and the exposure phase. In the competitive male exposure phase (Fig. 1b–e), the focal nest male was confronted with either a size-matched potential nest male

(Nm), two sneaker males (Sn), two dwarf males or one sneaker and one dwarf male (SnDw) for another 1 h (second hour of the experiment). The mixed test situations (Fig. 1e), in which all three male tactics were present at the same time, was used for a direct comparison of the response levels of the different males in a between-tactic test situation. In total, focal nest males remained in the tank until 5 h after the start of the experiment, when they were observed for the last time in order to test for potential time effects on their adjustment to a certain test situation. Our experimental design allowed us to investigate behavioural interactions between individuals of the same tactic, and interactions between territorial nest males with males of the two parasitic tactics. Also, the challenge that nest male intruders pose for a nest owner is inherently different from that posed by parasitic males, because territory ownership is at stake in the first case, and competition for fertilization of some eggs in the second. Furthermore and perhaps most importantly, competitors for territory ownership, i.e. intruding males of the nest male type, usually act singly in nature, whereas reproductive parasites often occur in groups. Therefore, our experimental design represents the best compromise possible for these experimental challenges between natural conditions and proper experimental control.

Focal nest males (total length of the fish (TL):10.0–12.6 cm) were sequentially tested in randomized order in each of the five test situations, with 1-week isolation intervals between the subsequent test situations. All fish were disturbed in a similar manner during the start of the experiment and at the start of the exposure phase, namely by opening the lid of the tank and slightly splashing the water at the surface (control) or by adding the intruder fish to the tank, respectively. Intruders from the nest male type (TL:10.0–12.1 cm) were chosen to be size matched whenever possible ($\pm$ 5 mm). Sneaker males were significantly smaller than nest males (TL: 6.6–9.9 cm) but were assumed to be sexually mature, because they had previously been observed to intensely interact with females in their original holding tanks. Within the sneaker (Sn) and the dwarf male (Dw; TL for both: 3.3–4.3 cm) test situations, the two male intruders from the same tactic were size
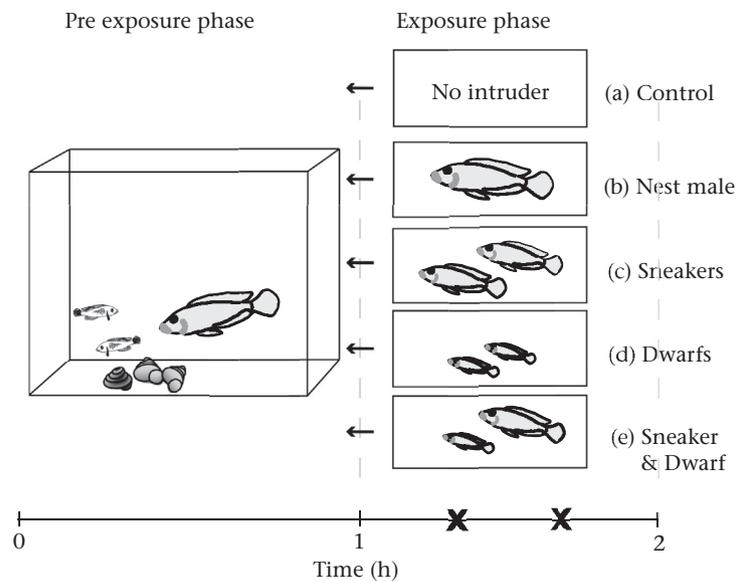

Figure 1. Experimental design. In the pre-exposure phase the nest male spent the first hour with two females in a 500-litre compartment. In the noncompetitive or competitive exposure phase during the second hour of the experiment the nest male was exposed to one of five possible test situations (a-e). (a) Control, without intruder male, (b) nest male intruder, (c) two sneaker males, (d) two dwarf males and (e) one sneaker and one dwarf male. Behavioural observations 20 min and 40 min after the start of the exposure phase are marked with an X.

matched. In the mixed tactic test situation (SnDw) the focal nest males always received new parasitic intruder males that they had not previously met in other test situations (Sn or Dw). During the entire experiment, focal individuals were allowed to freely interact with each other. We used fixed digital cameras placed in front of the aquaria to record all interactions of focal individuals.

Behavioural Observations

In all five test situations (Fig. 1a–e), we quantified the duration (s) of total aggression displayed by the nest owner towards intruder males and also the number of aggressive categories (overt aggression: chasing and biting; restrained aggression: fast approaches, head down postures, fin spreading, opercula spreading; see Schütz & Taborsky, 2005). Additionally, we quantified the duration (s) of total courtship behaviour (including zigzag swimming, bumping and shell mouthing; see Schütz, Heg-Bachar, Taborsky, & Heg, 2012), the duration (s) of aggressive behaviour (as described above) exhibited towards females only, the duration (s) of nest maintenance behaviours (shell manipulation, sand transport) and the duration (s) of passive behaviour (lying on ground or floating above ground). Behaviours were quantified with the aid of the software 'The Observer 5.0' (Noldus, Wageningen, The Netherlands). Each focal nest male was observed twice for 5 min (see Fig. 1) 20 and 40 min after the start of the exposure phase, when he was alone with the two females (Fig.1 a) or when in a competitive test situation with intruder males, respectively (Fig. 1b–e). We also recorded within- and between-tactic competition in parasitic males, as well as the time nest males displayed aggressive behaviours towards females, during the different test situations. After nest males had spent 1 h solely with the females (Fig. 1) and then 1 h in the exposure phase with other males (or alone in the control; Fig. 1a–e), individuals were sampled for hormones for another study. To allow repeated, noninvasive measurements after different test situations and to avoid invasive blood sampling, steroids were measured from fish-holding water, which was obtained by adding focal individuals to a glass beaker with clean sampling water (Hirschenhauser et al., 2002, 2004; Oliveira, Hirschenhauser, Carneiro, & Canário, 2002, Oliveira, Hirschenhauser, Canário, & Taborsky, 2003; Scott & Ellis, 2007; Scott et al., 2008). Afterwards, they were returned to the experimental tank and continued interacting with each other. We allowed individuals to interact with each other for the rest of the experimental day, and another recording of total nest male aggression (s) was taken 5 h after the start of the experiment. This observation was made in order to test whether nest males had resolved the different contests in all five different competitive test situations at this point in time.

Ethical Note

This experiment was approved by the Federal veterinary office of the canton Bern, Switzerland. For the induction of ovulation with LHRH, females ($N = 50$) were slightly anaesthetized using MS222. Following the injection with LHRH, four females at a time were kept in a 200-litre stimulation tank for 48 h, with a nest male for reproductive stimulation, snail shells unsuitable for breeding and several hiding places. This allowed us to survey the females' condition and behaviour in the period between the injection and the introduction to the experimental tank. No adverse effects of the treatment were observed at any time during the experiment. 13–15 focal nest males were challenged by the five different test situations. During the challenge we surveyed the tanks with digital cameras to check for the condition of all individuals and in order to prevent escalations of potential combats. None of the

experimental individuals were injured during these trials. We intended to end a test phase if there were any signs of physical damage caused by aggressive interactions. However, in only one case did we have to stop the experiment due to intense physical aggression between two nest males. At the end of the test phase, we removed all snail shells from each experimental tank, which led to an immediate decrease in territorial and aggressive behaviour. Shortly thereafter, all individuals were returned to their respective home tanks where they continued to be part of our breeding programme.

Statistical Analysis

The durations (s) of the two observations spent on nest male behaviours, taken 20 and 40 min after the start of the exposure phase (Fig. 1a–e), did not follow a trend that would suggest any time effects. We therefore calculated the mean of these two observations and used linear mixed-effects models (LMEs) to analyse the durations (s) of total aggressive behaviour and nest maintenance behaviours, and compared each behaviour between the different test situations. In the same manner, we calculated the mean numbers of chasing and biting events (overt aggression), and the numbers of fast approaches, fin spreading, head down and opercula spreading displays (restrained aggression) during the exposure phase (second hour). Since (1) we calculated the mean of two observations (of two counts) and (2) after transforming our data, the residuals of our LMEs were normally distributed, we compared behavioural events between treatments using LMEs. For the comparison of aggressive behaviours between treatments, the control treatment was not included in the model, since we only compared the aggressive behaviours of nest males towards intruder males in the competitive test situations (see Fig. 1). Aggressive behaviours of nest males towards females and, finally, total aggression of nest males in treatments at hour five were compared using LMEs.

Each LME included the behaviour as the response variable, the treatment as a fixed effect and fish ID as a random effect. We used square-root transformations of the response variables for most behaviours (means of total aggression, nest maintenance, fin spreading, chasing, fast approaches) to reduce heteroscedasticity. For the analysis of the means of head down, opercula spreading and biting displays in the different treatments we used Box-Cox transformations (Sakia, 1992). Model assumptions of homoscedasticity and residual normality were tested using graphics and Shapiro-Wilk and Lilliefors (Kolmogorov-Smirnov) normality tests. Since none of the standard transformations led to normally distributed residuals of one of our models, we used a permutation test (10 000 permutations) to compare the duration (s) of nest male courting behaviour between treatments. Spearman rank correlation analyses were used to test for a relationship between the amount of time nest males displayed aggressive behaviours and the amount they invested in either courtship or nest maintenance behaviours. All statistical analyses were performed using R 3.0.2 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). The R package 'nlme' (Pinheiro, Bates, DebRoy, & Sakar, 2012) was used to perform all LMEs. Multiple post hoc tests (Tukey) were performed using the 'multcomp' package (Hothorn, Bretz, & Westfall, 2008) and the 'Mass' package was used for the permutation tests (Sakia, 1992; Venables & Ripley, 2002). Adjusted *P* values are reported. One subject was removed from the analysis since it was apparently sick and behaved abnormally on one of the measurement days. This fish died shortly afterwards. Two behavioural observations were lost due to technical problems. In total, our sample sizes were between 13 and 15 in the different test situations.

RESULTS

Aggressive Behaviour

There was a significant difference in the amount of time nest males exhibited aggressive behaviours between the different test situations during the exposure phase (LME: square-root aggression versus treatment: $F_3 = 20.206$, $P < 0.0001$; Table 1), with the highest level exhibited towards intruders of the nest male tactic (within-tactic competition; Fig. 2, Table 1) and the lowest level exhibited when exposed to intruders of the parasitic dwarf male tactic (between-tactic competition; Fig. 2, Table 1). Nest male aggression levels, in both the nest male and the dwarf male test situations, differed significantly from the sneaker and mixed tactic test situations, while no difference was found between the latter two (Fig. 2, Table 1; for single restrained and overt behaviours see Fig. A1a, b and Tables A1–A6 in the Appendix).

When comparing nest male total aggression between treatments 5 h after the start of the experiment, we found no differences between the different competitive test situations (Table A7 in the Appendix).

We found neither between- nor within-tactic aggression in parasitic males. The rare interactions we observed, for example between sneaker males, did not seem to be aggressive. Nest males almost never bit females during the exposure phase, nor performed any other threat behaviours, such as fin spreads, head down or opercular spreading displays towards females. They did, however, perform fast approaches and chasing of females, but the frequencies of these behaviours did not differ between treatments (Tables A8 and A9 in the Appendix).

Reproductive Behaviour

The amount of time nest males displayed courtship differed between treatments (permutation test: $P < 0.01$; Table 2). Courting levels were highest in the control treatment without intruder males, but did not differ between the competitive test situations (Fig. 3a, Table 2). The time nest males displayed nest maintenance differed between treatments (LME: square-root maintenance versus treatment: $F_4 = 2.60$, $P < 0.05$), with nest males spending significantly more time showing nest maintenance in the control and the dwarf male treatment than in the nest male treatment (Fig. 3b, Table 3).

Relation Between Aggression and Reproductive Behaviour

We checked whether the time nest males displayed aggression was related to the time these males displayed reproductive
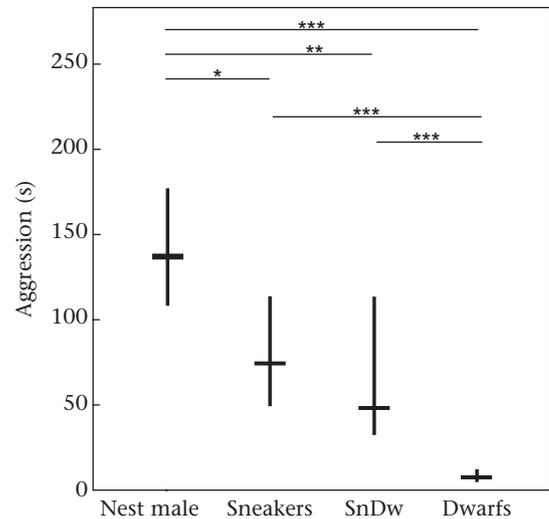

Figure 2. Amount of time (s) nest males spent displaying aggressive behaviour (including overt and restrained aggression) when exposed to the different test situations: nest male intruder, two sneaker males, one sneaker and one dwarf male (SnDw) and two dwarf males. The plot shows medians and interquartile ranges. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

behaviours (Fig. 4a, b). As the aggression shown against competitors is costly, not only regarding energy expenditure and injury risk but also the time expenditure (i.e. opportunity costs), we predicted a trade-off between the effort spent on contests and reproduction, including nest maintenance and courtship. There was a significant negative correlation between the mean time spent on aggressive behaviours and nest maintenance (Spearman rank correlation analysis: $r_S = -0.9$, $P < 0.05$). However, no such relationship was found between mean courtship and aggression levels in the different competitive treatments (Table A10 in the Appendix).

DISCUSSION

Within-tactic Competition

As suggested by evolutionary theory (Austad, 1984; Maynard Smith, 1974; Shuster & Wade, 2003; Taborsky & Brockmann, 2010), we found tactic-specific rivalry to be confirmed in nest males of *L. callipterus*, with 'within-tactic' competition higher than 'between-tactic' competition prior to spawning. The very high

Table 1
Aggressive behaviour displayed by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	−3.1384	1.0684	−2.938	**0.017**
Nm−SnDw=0	−3.8317	1.0476	−3.657	**0.001**
Nm−Dw=0	−8.5773	1.0684	−8.028	**<0.001**
Sn−SnDw=0	−0.6933	1.0476	−0.662	0.911
Sn−Dw=0	−5.4389	1.0684	−5.091	**<0.001**
Dw−SnDw=0	−4.7455	1.0476	−4.530	**<0.001**

Multiple post hoc tests of the time (s) focal nest males spent on aggressive behaviour when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals zero. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table 2
Comparison of courting behaviour (s) performed by nest males when exposed to the different test situations (see Fig. 1a–e)

Comparison of test situations	P
Nm−control	**0.034**
Sn−control	**0.003**
SnDw−control	**0.025**
Dw−control	**0.044**
Nm−Sn	0.966
Nm−SnDw	1
Nm−Dw	0.999
Sn−Dw	0.923
Sn−SnDw	0.971
Dw−SnDw	0.999

Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Results from permutation tests (10 000). Significant P values are marked in bold.
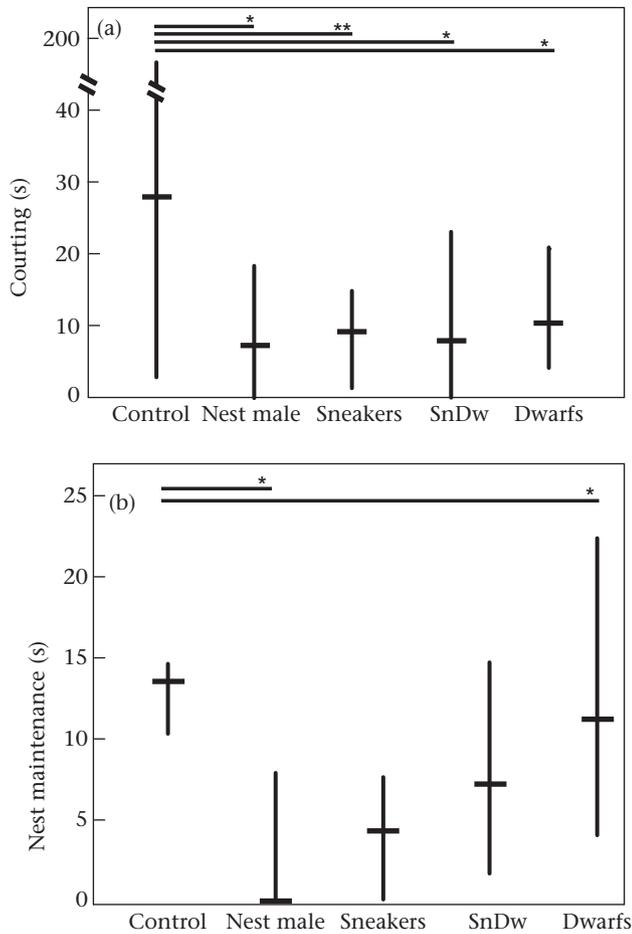
Figure 3. Amount of time (s) nest males spent displaying (a) courtship and (b) nest maintenance behaviours when exposed to the different test situations: control (without intruder male), nest male intruder, two sneaker males, one sneaker and one dwarf male (SnDw), and two dwarf males. The plot shows medians and interquartile ranges. *$P < 0.05$; **$P < 0.01$.

aggression levels of nest owners when challenged by sized-matched nest male intruders are expected (classical contest competition; Parker, 1982) in a system where breeding resources are often scarce (Parker, 1974). The pay-off for winning a contest in

Table 3
Nest maintenance behaviour displayed by nest males when exposed to the different test situations (see Fig. 1a–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−control=0	−2.14227	0.78292	−2.736	**0.049**
Sn−control=0	−1.34731	0.7671	−1.756	0.399
SnDw−control=0	−0.72110	0.76710	−0.940	0.881
Dw−control=0	0.04727	0.76710	0.062	1.000
Nm−Sn=0	0.794696	0.78292	1.015	0.848
Nm−Dw=0	2.18955	0.78292	2.797	**0.041**
Nm−SnDw=0	1.42117	0.78292	1.815	0.365
Sn−Dw=0	1.39459	0.76710	1.1818	0.363
Sn−SnDw=0	0.62621	0.76710	0.816	0.925
Dw−SnDw=0	0.76837	0.76710	1.002	0.854

Multiple post hoc tests of the time (s) focal nest males spent on nest maintenance behaviour when exposed to the different test situations or in the control. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals zero. P values were adjusted for multiple comparisons. Significant P values are marked in bold.
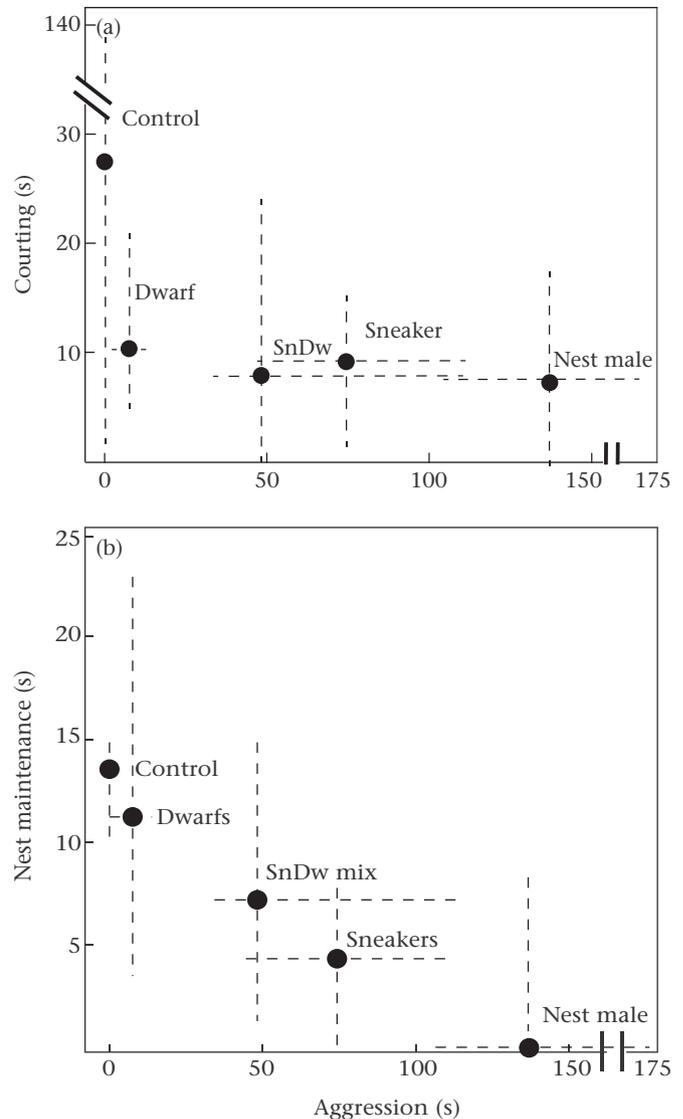

Figure 4. Relationship between (a) aggressive behaviours towards intruder males and courtship behaviours towards females and (b) aggressive behaviours towards intruder males and nest maintenance behaviour when exposed to the different test situations: control (without intruder male), nest male intruder, two sneaker males, one sneaker and one dwarf male (SnDw) and two dwarf males. In the control group with no intruder males, aggression levels (towards other males) are zero. The plots show the medians and interquartile ranges of both behavioural categories along both axes.

general might be larger for an owner of a territory than for the intruder male, because the owner may have spawned with females already, or he may at least have started to spawn in his nest and hence is protecting his own offspring. These young and the female are typically expelled from their shells by a new owner (Maan & Taborsky, 2008).

The high aggression levels during nest male within-tactic competition were accompanied by high frequencies of biting, opercula spreading and fin spreading displays, and by fast approaches, compared with all other test situations. Nest males clearly invest more in these presumably expensive behaviours when challenged for territory ownership than when encountering an intruder that might just fertilize some eggs (i.e. parasitic males). This higher defence effort of nest males against males of the same type may not only entail a higher injury risk, but also be one of the reasons for the decline of energy stores of nest males during their

long nest-holding period (von Kuerthy et al., 2015). One way to reduce costs from such escalated contests is the use of display behaviour revealing the size and strength of the nest owner. Opercula spreading probably serves to demonstrate the male's body size. This behaviour was often displayed in contests with male intruders of the same type, where size differences may be evaluated between opponents prior to escalation and potential injury. In this situation contestants can mutually assess their relative resource-holding potential, which allows the weaker individual to terminate the contest before escalation, thereby reducing energy expenditure and the risk of injury (Arnott & Elwood, 2010). However, to fully understand the meaning of these behaviours shown by *L. callipterus* during contests, their actual function should be further explored (Arnott & Elwood. 2010; Elwood & Arnott 2012). Five hours after the start of the experiment there were no differences in aggression between treatments, indicating that contests had been resolved by then.

Between-tactic Competition

Nest male aggression levels towards dwarf males were significantly lower than in all other test situations. While chasing, fast approaches and biting were observed in some rare cases, restrained behaviours such as fin spreads, opercula spreads and head down displays were never displayed by nest males towards a dwarf male intruder. This makes sense because dwarf males can be expelled immediately when detected, without risk of injury to the attacking nest male due to the enormous size difference (1:40 on average; Sato et al., 2004).

The second highest aggression level of nest males was found against sneaker males. While nest males chased and quickly approached sneaker males as much as they did when challenged by a potential nest male intruder, they performed significantly less overt biting and restrained fin spreads in the sneaker male treatment. The difference in the amount of time spent displaying aggressive behaviours between the sneaker male and nest male treatments suggests that sneaker males are perceived by the territory holder as less of a challenge than males potentially contesting territory ownership; only a minor loss of paternity is at stake when sneakers participate in spawning (Wirtz Ocaña et al., 2014). Selection should favour sneaker males avoiding direct contests (Taborsky, 2008). The lack of aggressive displays by sneaker males and the obvious asymmetry with nest males in their resource-holding potential may also be responsible for the rather low level of aggression nest males showed against sneakers. Asymmetries in resource-holding potential and body size typically explain the contest behaviour and outcome of male-male interactions (Hammerstein, 1981), especially if they are as pronounced as in the case of males pursuing ARTs.

Courting and Nest Maintenance

As the aggression shown against competitors involves time expenditure, we predicted a trade-off between the effort spent with contest and reproductive behaviours. The presence of intruder males, compared to the control treatment without competitors, significantly decreased the amount of time nest males spent on courtship, but this reduction did not differ between competitive treatments. Nest maintenance behaviours (collecting shells, rearranging shells and presenting them to females) did not differ between the nest male, the sneaker male and the mixed-tactic test situations. However, nest males spent significantly more time on nest maintenance behaviours in the control situation and the dwarf male treatment than in the nest male intruder situation. Besides attracting females to the nest, the increased investment in nest

maintenance behaviour might also indicate nest male surveillance of shells in which dwarf males could hide (Sato et al., 2004). It appears that if nest males are challenged by large intruder males they are distracted and limited in their investment in nest maintenance behaviours.

Hence there seems to be a trade-off between the duration and intensity of a combat (aggression) and other reproductive duties such as nest maintenance and courtship behaviours. Aggression in the competitive intruder treatments therefore seems to cause opportunity costs.

Within- and Between-tactic Competition in Parasitic Males

We did not find aggressive interactions between dwarf males. Since the natural frequencies of dwarf males are low (Wirtz Ocaña et al., 2014), this kind of competition maybe rare in nature. Sneaker males also rarely interacted with each other in an aggressive manner. In both dwarf and sneaker males, a rapid scramble competition response when opportunities for parasitic reproduction arise seems to provide better fitness returns than contests, and may be more likely to stabilize their tactic frequencies (Toquenaga, 1990). Although we did not witness clear scramble competition during our experiment, probably because of the lack of spawnings during the exposure phase of our experiment, we assume that parasitic males in *L. callipterus* would show scramble competition during a spawning, which has frequently been observed in the field and in other laboratory experiments (C. von Kuerthy & M. Taborsky, personal observation). Future work should focus on interactions of different tactics during actual spawning.

Aggression Against Females

Nest males performed fast approaches and chases against females, but this did not differ between test situations. Nest owners expel females from their nests in nature, if the females do not actively inspect shells or if they take too long to choose a shell for spawning. This may improve the chances that other, more motivated females will enter the nest, because females may also sometimes aggressively exclude each other from nests and shells (Schütz & Taborsky, 2005).

Conclusions

In conclusion, our results show that in the bourgeois male tactic of the snail shell-brooding cichlid *L. callipterus,* within-tactic competition is higher than between-tactic competition, as predicted by evolutionary theory. Additionally, our results suggest that the level of aggression displayed by bourgeois males towards intruders might be triggered by perceived differences in body size. We rarely found aggressive interactions between parasitic males in the different test situations, indicating that parasitic males in this species compete through scramble rather than contest competition. Our results suggest that in this species, males pursuing ARTs diverge in the way they respond to challenges in their social environment and to reproductive competition among representatives of the same or different tactics.

References

Arnott, G., & Elwood, R. W. (2010). Startle durations reveal visual assessment abilities during contests between convict cichlids. *Behavioural Processes, 84,* 750–756.

Aubin-Horth, N., & Dodson, J. J. (2004). Influence of individual body size and variable thresholds on the incidence of a sneaker male reproductive tactic in Atlantic Salmon. *Evolution, 58,* 136–144.

Austad, S. N. (1984). A classification of alternative reproductive behaviors and methods for field-testing ESS models. *American Zoologist, 24,* 309–319.

Barata, E., Hubbard, P., Almeida, O., Miranda, A., & Canario, A. (2007). Male urine signals social rank in the Mozambique tilapia (*Oreochromis mossambicus*). *BMC Biology, 5,* 54.

Candolin, U., & Wong, B. (2008). Mate choice. In C. Magnhagen, V. A. Braithwaite, E. Forsgren, & B. G. Kapoor (Eds.), *Fish behaviour* (pp. 337–376). Enfield. NH: Science Publishers.

Elwood, R. W., & Arnott, G. (2012). Understanding how animals fight with Lloyd Morgan's canon. *Animal Behaviour, 84,* 1095–1102.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science, 19,* 215–223.

Goffinet, O. (2007). *Sperm competition and sperm characteristics of* Lamprologus callipterus, *a shell-brooding cichlid fish with male alternative reproductive tactics (ARTs)* (Diploma thesis). Zürich, Switzerland: University of Zürich.

Gross, M. R. (1982). Sneakers, satellites and parentals: polymorphic mating strategies in North American sunfishes. *Zeitschrift für Tierpsychologie, 60,* 1–26.

Gross, M. R. (1991). Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 332,* 59–66.

Gross, M. R. (1996). Alternative reproductive strategies and tactics: diversity within sexes. *Trends in Ecology & Evolution, 11,* 92–98.

Hammerstein, P. (1981). The role of asymmetries in animal contests. *Animal Behaviour, 29,* 193–205.

Hirschenhauser, K., Ros, A., Carneiro, L., Oliveira, T., Silva, A., Canario, A., et al. (2002). Non-invasive hormone assessment from fish-holding water. *Advances in Ethology, 37,* 139.

Hirschenhauser, K., Taborsky, M., Oliveira, T., Canàrio, A. V. M., & Oliveira, R. F. (2004). A test of the 'challenge hypothesis' in cichlid fish: simulated partner and territory intruder experiments. *Animal Behaviour, 68,* 741–750.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal, 50,* 346–363.

Knell, R. J., & Simmons, L. W. (2010). Mating tactics determine patterns of condition in a dimorphic beetle. *Proceedings of the Royal Society B: Biological Sciences, 277,* 2347–2353.

Laumen, J., Pern, U., & Blüm, V. (1974). Investigations on the function and hormonal regulation of the anal appendices in *Blennius pavo* (Risso). *Journal of Experimental Zoology, 190,* 47–56.

Maan, M. E., & Taborsky, M. (2008). Sexual conflict over breeding substrate causes female expulsion and offspring loss in a cichlid fish. *Behavioral Ecology, 19,* 302–308.

Maynard Smith, J. (1974). The theory of games and the evolution of animal conflicts. *Journal of Theoretical Biology, 47,* 209–221.

Mitchell, J. S., Wirtz Ocana, S., & Taborsky, M. (2014). Male and female shell-brooding cichlids prefer different shell characteristics. *Animal Behaviour, 98,* 131–137.

Neat, F. C., Locatello, L., & Rasotto, M. B. (2003). Reproductive morphology in relation to alternative male reproductive tactics in *Scartella cristata*. *Journal of Fish Biology, 62,* 1381–1391.

Neff, B. D., Fu, P., & Gross, M. R. (2003). Sperm investment and alternative mating tactics in bluegill sunfish (*Lepomis macrochirus*). *Behavioral Ecology, 14,* 634–641.

Oliveira, R. F., Hirschenhauser, K., Canário, A. V. M., & Taborsky, M. (2003). Androgen levels of reproductive competitors in a co-operatively breeding cichlid. *Journal of Fish Biology, 63,* 1615–1620.

Oliveira, R. F., Hirschenhauser, K., Carneiro, L. A., & Canario, A. V. M. (2002). Social modulation of androgen levels in male teleost fish. *Comparative Biochemistry and Physiology Part B: Biochemistry and Molecular Biology, 132,* 203–215.

Oliveira, R. F., Taborsky, M., & Brockmann, H. J. (2008). *Alternative reproductive tactics: An integrative approach*. Cambridge, U.K.: Cambridge University Press.

Parker, G. A. (1974). Assessment strategy and the evolution of fighting behaviour. *Journal of theoretical Biology, 47,* 223–243.

Parker, G. A. (1982). Phenotype-limited evolutionary stable strategies. *Current Problems in Sociobiology,* 173–201.

Pinheiro, J., Bates, D., DebRoy, S., & Sakar, D. (2012). *nlme: Linear and nonlinear mixed effects models. R package version 3.1-103*. Vienna, Austria: R Foundation for Statistical Computing.

Raveh, S., Heg, D., Vincent, V., Coltman, D., Jamieson, G., Dobson, F., et al. (2010). Male reproductive tactics to increase paternity in the polygynandrous Canadian ground squirrel (*Urocitellus Columbianus*). *Behavioural Ecology and Sociobiology,* 1–2.

Ryan, M. J., Craig, M. P., & Morris, M. R. (1993). A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: testing the prediction of equal fitnesses.'. *American Naturalist,* 21–31.

Sakia, R. (1992). The Box-Cox transformation technique: a review. *Statistician,* 169–178.

Sato, T. (1994). Active accumulation of spawning substrate: a determinant of extreme polygyny in a shell-brooding cichlid fish. *Animal Behaviour, 48,* 669–678.

Sato, T., Hirose, M., Taborsky, M., & Kimura, S. (2004). Size-dependent male alternative reproductive tactics in the shell-brooding cichlid fish *Lamprologus callipterus* in Lake Tanganyika. *Ethology, 110,* 49–62.

Schaedelin, F. C., & Taborsky, M. (2006). Mating craters of *Cyathopharynx furcifer* (Cichlidae) are individually specific, extended phenotypes. *Animal Behaviour, 72,* 753–761.

Schaedelin, F. C., & Taborsky, M. (2009). Extended phenotypes as signals. *Biological Reviews, 84,* 293–313.

Schradin, C., Schneider, C., & Lindholm, A. K. (2010). The nasty neighbour in the striped mouse (*Rhabdomys pumilio*) steals paternity and elicits aggression. *Frontiers in Zoology, 7,* 19.

Schütz, D., Heg-Bachar, Z., Taborsky, M., & Heg, D. (2012). Spawning coordination of mates in a shell brooding cichlid. *International Journal of Evolutionary Biology, 2012,* 517849.

Schütz, D., Pachler, G., Ripmeester, E., Goffinet, O., & Taborsky, M. (2010). Reproductive investment of giants and dwarfs: specialized tactics in a cichlid fish with alternative male morphs. *Functional Ecology, 24,* 131–140.

Schütz, D., & Taborsky, M. (2005). The influence of sexual selection and ecological constraints on an extreme sexual size dimorphism in a cichlid. *Animal Behaviour, 70,* 539–549.

Scott, A. P., & Ellis, T. (2007). Measurement of fish steroids in water—a review. *General and comparative endocrinology, 153,* 392–400.

Scott, A. P., Hirschenhauser, K., Bender, N., Oliveira, R., Earley, R. L., Sebire, M., et al. (2008). Non-invasive measurement of steroids in fish-holding water: important considerations when applying the procedure to behaviour studies. *Behaviour, 145,* 1307–1328.

Shuster, S., & Wade, M. J. (1991). Equal mating success among male reproductive strategies in a marine isopod. *Nature, 350,* 608–610.

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton, NJ: Princeton University Press.

Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour, 32,* 1236–1252.

Taborsky, M. (1994). Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior, 23,* 1–100.

Taborsky, M. (1997). Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours? *Behavioural Ecology and Sociobiology, 41,* 361–362.

Taborsky, M. (1998). Sperm competition in fish: 'bourgeois' males and parasitic spawning. *Trends in Ecology & Evolution, 13,* 222–227.

Taborsky, M. (2001). The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *Journal of Heredity, 92,* 100–110.

Taborsky, M. (2008). Alternative reproductive tactics in fish. In R. F. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics* (pp. 251–299). Cambridge, U.K.: Cambridge University Press.

Taborsky, M., & Brockmann, H. J. (2010). Alternative Reproductive tactics and life history phenotypes. In P. Kappeler (Ed.), *Animal behaviour: Evolution and mechanisms* (pp. 537–586). Berlin, Germany: Springer.

Taborsky, M., Oliveira, R., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: concepts and questions. In R. F. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), *Alternative reproductive tactics* (pp. 1–22). Cambridge, U.K.: Cambridge University Press.

Toquenaga, Y. (1990). *The mechanisms of contest and scramble competition in Bruchid species. Bruchids and Legumes: economics, ecology and coevolution*. In K. Fujii, A. M. R. Gatehouse, C. D. Johnson, R. Mitchel, & T. Yoshida (Eds.) (pp. 341–349). Dordrecht, The Netherlands: Springer.

Trewavas, E. (1983). *Tilapiine fishes of the genera* Sarotherodon, Oreochromis *and* Danakilia. London, U.K.: Natural History Museum Publications.

Tschernavin, V. (1938). Changes in the salmon skull. *Transactions of the Zoological Society of London, 24,* 104–184.

Uglem, I., Mayer, I., & Rosenqvist, G. (2002). Variation in Plasma steroids and reproductive traits in dimorphic males of corkwing wrasse (*Symphodus melops* L.). *Hormones and Behavior, 41,* 396–404.

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S* (4th ed.). New York, NY: Springer.

von Kuerthy, C., Tschirren, L., & Taborsky, M. (2015). Alternative reproductive tactics in snail-shellbrooding cichlids diverge in energy reserve allocation. *Ecology and Evolution, 5*(10), 2060–2069.

Warner, R. R. (1984). Mating behavior and hermaphroditism in coral reef fishes. *American Scientist, 72,* 128–136.

Wirtz Ocaña, S., Meidl, P., Bonfils, D., & Taborsky, M. (2014). Y-linked Mendelian inheritance of giant and dwarf male morphs in shell-brooding cichlids. *Proceedings of the Royal Society B: Biological Sciences, 281.*

Wirtz Ocaña, S., Schütz, D., Pachler, G., & Taborsky, M. (2013). Paternal inheritance of growth in fish pursuing alternative reproductive tactics. *Ecology and Evolution,* 1614–1625.

Zimmerer, E. J., & Kallman, K. D. (1989). Genetic basis of alternative reproductive-tactics in the Pygmy Swordtail, *Xiphophorus nigrensis*. *Evolution, 43,* 1298–1307.
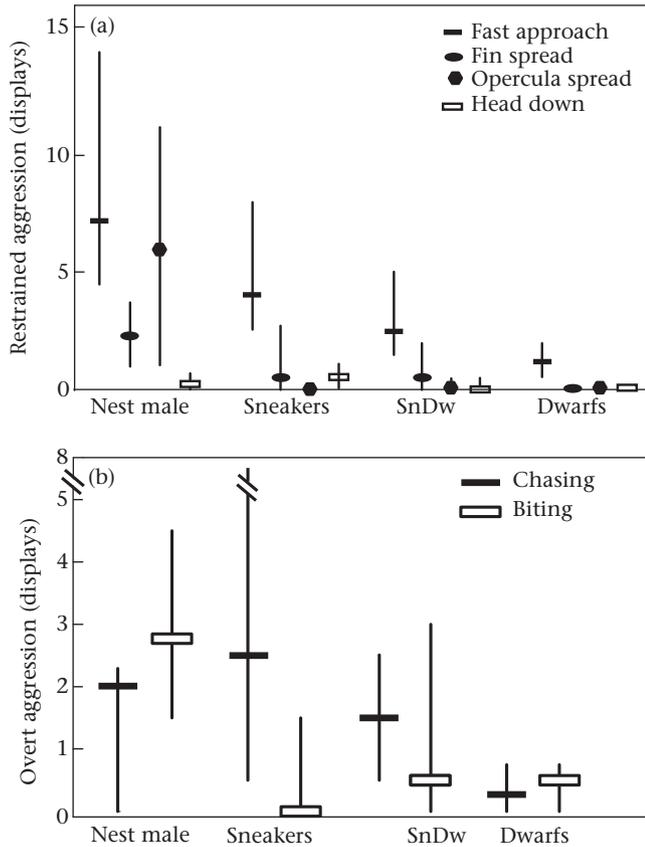
Appendix

Fig. A1. (a) Restrained and (b) overt aggression of nest males when exposed to competitors in the different test situations. Plots show medians and interquartile ranges. For an overview of the statistical results see Tables 6–10 in the Appendix.

Table A2
Biting displayed by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	0.24979	0.0605	4.129	**<0.001**
Nm−SnDw=0	0.19793	0.0601	3.292	**0.006**
Nm−Dw=0	0.27799	0.0614	4.522	**<0.001**
Sn−SnDw=0	−0.05186	0.0594	−0.872	0.819
Sn−Dw=0	0.02820	0.0604	0.466	0.966
Dw−SnDw=0	0.08005	0.0604	1.323	0.548

Multiple post hoc tests of biting events displayed by focal nest males (overt aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A3
Fast approaches displayed by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	−0.5818	0.3493	−1.665	0.342
Nm−SnDw=0	−0.9764	0.3470	−2.814	**0.026**
Nm−Dw=0	−1.7536	0.3548	−4.942	**<0.001**
Sn−SnDw=0	−0.3945	0.3436	−1.148	0.660
Sn−Dw=0	−1.1718	0.3491	−3.356	**0.005**
Dw−SnDw=0	−0.7772	0.3493	−2.225	0.116

Multiple post hoc tests of fast approaches displayed by focal nest males (restrained aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A1
Chasing behaviour displayed by nest males when challenged by different competitive test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	0.68293	0.41551	−1.644	0.354
Nm−SnDw=0	0.61186	0.41501	−1.474	0.453
Nm−Dw=0	−0.49237	0.42349	−1.163	0.650
Sn−SnDw=0	−0.07107	0.40734	−0.174	0.998
Sn−Dw=0	−1.17530	0.41550	−2.829	**0.024**
Dw−SnDw=0	−1.10423	0.41551	−2.658	**0.039**

Multiple post hoc tests of chasing events displayed by focal nest males (overt aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals zero. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A4
Fin spreading displayed by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	−0.69492	0.26907	−2.583	**0.048**
Nm−SnDw=0	−0.63490	0.26831	−2.366	0.083
Nm−Dw=0	−1.46030	0.27400	−5.330	**<0.001**
Sn−SnDw=0	0.06002	0.26399	0.227	0.996
Sn−Dw=0	−0.76538	0.26904	−2.845	**0.023**
Dw−SnDw=0	−0.82540	0.26907	−3.068	**0.012**

Multiple post hoc tests of fin spreading events displayed by focal nest males (restrained aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A5
Opercula spreading displays by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	0.6659	0.1050	6.342	**<0.001**
Nm−SnDw=0	0.5526	0.1045	5.285	**<0.001**
Nm−Dw=0	0.7685	0.1068	7.194	**<0.001**
Sn−SnDw=0	−0.1133	0.1031	−1.099	0.690
Sn−Dw=0	0.1026	0.1050	0.978	0.762
Dw−SnDw=0	0.2159	0.1050	0.168	0.168

Multiple post hoc tests of opercula spreading displayed by focal nest males (restrained aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A6
Head down displays by nest males when exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	−0.05494	0.09292	−0.591	0.935
Nm−SnDw=0	0.11142	0.09464	1.203	0.625
Nm−Dw=0	0.27237	0.09462	2.879	**0.021**
Sn−SnDw=0	0.16636	0.09118	1.825	0.262
Sn−Dw=0	0.32730	0.09291	3.523	**0.002**
Dw−SnDw=0	0.16094	0.09292	1.732	0.307

Multiple post hoc tests of head down displays by focal nest males (restrained aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons. Significant P values are marked in bold.

Table A7
Total aggression displayed by nest males 5 h after the start of the experiment when still exposed to the different test situations (see Fig. 1b–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−Sn=0	0.00002	0.19626	0.001	1.000
Nm−SnDw=0	0.26805	0.18679	1.435	0.477
Nm−Dw=0	0.36108	0.18302	1.427	0.482
Sn−SnDw=0	0.26784	0.19979	1.341	0.537
Sn−Dw=0	0.26087	0.19627	1.329	0.544
Dw−SnDw=0	−0.00697	0.18679	−0.037	1.000

Multiple post hoc tests of total aggression displayed by focal nest males (s) at hour 5 when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons.

Table A8
Fast approaches displayed by nest males towards females when exposed to the different test situations (see Fig. 1a–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−control=0	0.14103	0.58235	0.242	0.999
Sn−control=0	0.38462	0.57058	0.674	0.962
SnDw−control=0	−0.23077	0.57058	−0.404	0.994
Dw−control=0	0.34936	0.58235	0.600	0.975
Nm−Sn=0	0.24359	0.58235	−0.638	0.994
Nm−Dw=0	−0.37279	0.58235	−0.638	0.969
Nm−SnDw=0	0.20833	0.59388	−0.351	0.997
Sn−Dw=0	−0.61538	0.57058	−1.079	0.818
Sn−SnDw=0	−0.03526	0.58235	−0.062	1.000
Dw−SnDw=0	0.58013	0.58235	0.996	0.857

Multiple post hoc tests of fast approaches displayed by focal nest males towards females (restrained aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons.

Table A9
Chasing displays by nest males towards females when exposed to the different test situations (see Fig. 1a–e)

Comparison of test situations Linear hypothesis	Estimated difference	SE	Z	P
Nm−control=0	−0.19872	0.30387	−0.654	0.966
Sn−control=0	−0.30769	0.29773	−1.033	0.840
SnDw−control=0	−0.34625	0.29773	−1.163	0.773
Dw−control=0	−0.15705	0.30387	−0.517	0.986
Nm−Sn=0	−0.10897	0.30387	−0359	0.996
Nm−Dw=0	0.04167	0.30989	0.134	1.000
Nm−SnDw=0	−0.14744	0.30387	−0.485	0.989
Sn−Dw=0	0.15064	0.30387	0.496	0.988
Sn−SnDw=0	−0.03846	0.29773	−0.129	1.000
Dw−SnDw=0	0.18910	0.30387	0.622	0.972

Multiple post hoc tests of chasing displays by focal nest males towards females (overt aggression) when exposed to the different test situations. Nm = nest male intruder, Sn = sneaker intruders, Dw = dwarf male intruders, SnDw = mix of one sneaker and one dwarf male. Tests were performed against the null hypothesis that the difference between each compared pair equals 0. P values were adjusted for multiple comparisons.

Table A10
Relationship between nest male aggression and their reproductive behaviour

Relationship	S	r_S	P
Aggression versus courtship	34	−0.7	0.117
Aggression versus nest maintenance	38	−0.9	**0.042**

One-tailed Spearman rank correlation analysis of the relationship between total aggression (s) and courtship (s) and between total aggression (s) and nest maintenance (s). Significant P value is marked in bold.