Ethology **110,** 49—62 (2004)

ISSN 0179–1613

Size-Dependent Male Alternative Reproductive Tactics in the Shell-Brooding Cichlid Fish *Lamprologus callipterus* in Lake Tanganyika

Tetsu Sato*, Mitsuru Hirose†, Michael Taborsky* & Seishi Kimura‡

**Department of Behavioural Ecology, Institute of Zoology, University of Bern, Hinterkappelen, Switzerland; †Inland Water Fisheries Experiment Station of Fukushima Prefectural Government, Inawashiro, Fukushima, Japan; ‡Fisheries Research Laboratory, Mie University, Shima, Mie, Japan*

Abstract

Reproductive parasitism among males is prevalent in fishes. Typically, small ripe males parasitize the reproductive effort of large bourgeois males by using various behavioural tactics. We examined the size-dependent advantages of parasitic behavioural tactics in a shell-brooding cichlid fish of Lake Tanganyika with three male types (large bourgeois males and medium–dwarf parasitic males). The extremely small 'dwarf males' weighing only 2.5% on average of large males, perform a specialized tactic in which they avoid attacks by the resident large males by entering the inner part of the whorl of the shell where a female is spawning. Field observations and a manipulation experiment revealed that the very small size of dwarf males is essential for utilizing this positional advantage. Larger dwarf males and medium males opportunistically adopt darting and sneaking which likely result in very low reproductive outcomes. The size associated advantage and disadvantage of parasitic tactics are the major factors shaping the size distribution of ripe males in this species. The success of parasitic spawning by dwarf males is determined not only by body size of the males, but also by the relative sizes of females and shells in which they spawn. These factors would affect the choice of different tactics among dwarf males. The analyses of body condition among ripe and unripe males across a wide range of body sizes suggested that onset of sexual activities at very small body sizes in dwarf males may be associated with higher condition factors that is a pre-requisite for maintaining investment in testes and intense reproductive activities.

Corresponding author: Tetsu Sato, WWF Japan, 3-1-14 Shiba, Minato-ku, Tokyo 105-0014, Japan. E-mail: tetsu@wwf.or.jp

U. S. Copyright Clearance Center Code Statement: 0179-1613/2004/11001–049/$15.00/0 www.blackwell-synergy.com

Introduction

Fishes exhibit a wide variety of male alternative reproductive tactics (Taborsky 1994, 1998, 2001; Gross 1996). Usually, large and dominant males monopolize access to reproductive resources and females (bourgeois tactic), while other, usually smaller males assume various behavioural tactics to steal fertilizations by shedding sperm simultaneously at spawning (parasitic tactic; Taborsky 1997). Parasitic spawning has been described in 140 species from 28 families (Taborsky 1998) and is thought to be due largely to the prevalence of external fertilization and to indeterminate growth that results in high size variation among mature males (Gross 1984; Taborsky 1999). Parasitic males are often much smaller than bourgeois males. In the extreme case of the Atlantic salmon, parasitic males weighed only 0.16% of the body weight of dominant males (Taborsky 1999).

Male alternative reproductive tactics may coexist in a population either as a consequence of frequency-dependent selection, with equal average fitness outcomes among different tactics (e.g. Maekawa & Onozato 1986; Gross 1991, 1996) or by opportunistic adoption of parasitic tactics among less competitive males that are unable to obtain primary access to females (e.g. Dominey 1984; Kodric-Brown 1986). Often, the small size of parasites has been assumed to be important for obtaining fertilization because of its combination with inconspicuousness, potential mimicry of females, or ability to hide (Warner & Robertson 1978; Gross 1984, 1985; Waltz & Wolf 1984; Hutchings & Myers 1988). These conditions may permit particular parasitic tactics to occur only within a limited range of body sizes and ages in any given species.

Here, we evaluate several factors likely to influence the success of four tactics of parasitic males of differing size in *Lamprologus callipterus*, a shell-brooding cichlid fish of Lake Tanganyika. In this species, large males control primary access to females by gathering empty gastropod shells into a nest as spawning and brooding substrate. They defend these nests against conspecific males, as females successively visit, spawn and guard the young in a shell for about 2 wk. The mating system is highly polygynous (Sato 1994; Taborsky 2001). Medium sized and extremely small males ('dwarf males', approx. 2.5% in weight of the large males) assume parasitic spawning either by darting or sneaking towards the shell where spawning takes place and releasing sperm into the entrance of the shell, or by passing the female and entering the shell completely to spawn at the inner part of the whorl of the shell (hereafter referred to as the inner whorl. Sato 1994; Taborsky 1998; Meidl 1999).

To better understand factors influencing the relationship between size and the success of alternative tactics employed differentially by males of different sizes, we examined the size distributions of ripe males and conducted field observations and manipulations. Male size, size of shells in which spawning takes place and female size were all evaluated as factors that could influence the decision and potential success of parasitic males. We compared relative sizes of dwarf males, females and shells between successful and failed cases of parasitic spawnings to determine the importance of these factors. We further compared body conditions of ripe and unripe males for a large size range to test the assumption that unripe males invest mainly in growth, while ripe males should aim to obtain a good body condition to be more competitive in intrasexual interactions. We close by discussing our findings in the context of current theory concerning the adaptive value of alternative male reproductive tactics.

Methods

Field observations were made in Lake Tanganyika at Wonzye Point near Mpulungu, Zambia, from Nov. 1995 to Feb. 1996, and from Aug. to Dec. 1996. Breeding behaviour of *L. callipterus* was recorded at depths of 5–11 m using SCUBA. We conducted 32 checks of all (37 to 42) nests found in the study area to determine the presence of medium and dwarf males and their spawning attempts (335 cases of spawning). Behavioural observations of undisturbed spawning activity were made at 45 haphazardly selected nests for periods of 10–30 min each. In 18 cases, the observer chased the large male from the nest at the end of observations to determine if parasitic males were present. If medium or dwarf males appeared, they were observed for 10–30 min, depending on constraints of diving time.

We evaluated factors affecting success of parasitic spawning among dwarf males that attempted to wriggle past the female into the inner whorl of the shell (wriggling: see results). When a dwarf male that aligned itself aside a spawning female was able to pass the female to enter the inner whorl, the tactic was deemed successful. In a pilot study, we found that if the dwarf males were unable to pass the female within 15 min, they were still unable to do so even after 1 h. After these observations, we collected the male, shell, and female inside the shell for size measurements ($n = 32$).

A total of 85 large, 22 medium, 113 dwarf males, 39 females and 47 shells were collected. These included the 32 dwarf males, females and shells collected after behavioural observations. Specimens were killed quickly by dipping them into formaldehyde solution. We collected medium and dwarf males with a similar sampling effort, but did not collect large males with the same intensity. The behavioural tactics of 59 large, 22 medium and 102 dwarf males were determined prior to collection. We also collected 159 males and 178 females ranging in size from 25 to 75 mm standard length (SL; distance from the tip of the snout to the end of the vertebral column) from roaming schools near the nesting area. We measured SL, body and gonad weights, and determined stomach contents of all collected specimens. For males, we calculated gonad-free condition factor ($CF = ((BW - GW/1000)) \times 10^5)/Sl^3$ and gonadosomatic index ($GSI = ((GW/1000)/BW) \times 100)$) where BW, GW and SL represented body weight in g, gonad weight in mg and standard length in mm, respectively).

In order to evaluate factors affecting success of wriggling tactic, we also measured the volume of shells in which females spawned, and the males attempted wriggling, by filling them with water and subtracting the weight of the empty shells from that of the water-filled shells. *Lamprologus callipterus* is one of the most common species in rocky and sandy areas of Lake Tanganyika occurring in large numbers wherever shells and suitable nesting sites are available (Sato & Gashagaza 1997). Therefore, sampling in the present study did not have a significant impact on the local population.

Results

Description of Reproductive Tactics of Medium and Dwarf Males

Mouthing and sperm release (Fig. 1a, b, c, d): This tactic was performed by medium and dwarf males, and the sequence of mouthing and sperm release was the same as that of large males (Sato 1994). The male stayed outside the nest, repeatedly darting towards the shell where spawning took place. When large males were chased from the nest, medium and dwarf males quickly touched the shell entrance with their mouth (mouthing), then moved forward to position the genital papilla over the shell entrance and stayed immobile for a while, probably shedding sperm (Sato 1994).

Wriggling (Fig 1e, f): This tactic was performed only by dwarf males. The dwarf male dived into the shell where a female was spawning, placed its body alongside the female in the shell, and tried to wriggle past the female to enter the inner whorl. In the successful attempts, most dwarf males wriggled past the female when she moved slightly. If they succeeded, these males stayed inside the shell until the end of spawning, which takes on average 6.1 h (Pachler 2001). The spawning of the large males continued even after the dwarf male entered the shell.

Variations of wriggling (nibbling; sit and wait): These were performed by dwarf males when trying to gain access to the inner whorl as was wriggling. Males that performed nibbling bit vigorously on the flanks of the female in the shell. When the female came out, the male tried to dive into the shell past the female. A group of dwarf males sometimes raided the nest and performed similar behaviour, which often resulted in cannibalism of eggs. Sit and wait refers to a tactic by which a dwarf male stayed inside an empty shell, perhaps waiting for a female to spawn there.

Size Distribution of Males

Ripe males with white and enlarged testes (Gonado-Somatic Indices (GSI) >0.4) appeared in three size clusters with $\bar{x} \pm$ SD SL at 34.2 ± 3.7 (range: 24.0–46.0, N = 172), 62.4 ± 6.9 (50.5–74.7, N = 23) and 114.0 ± 7.3 mm (96.0–130.0, N = 85; Fig. 2a and b). We refer to these size clusters as dwarf, medium and large males. The difference in abundance of dwarf and medium males in Fig. 2 probably accurately reflects the distribution in the population, while the abundance of large males may be underestimated. The mean SL of ripe females was 50.1 ± 3.7 mm, (range: 43.0–60.6 mm, N = 104). Among

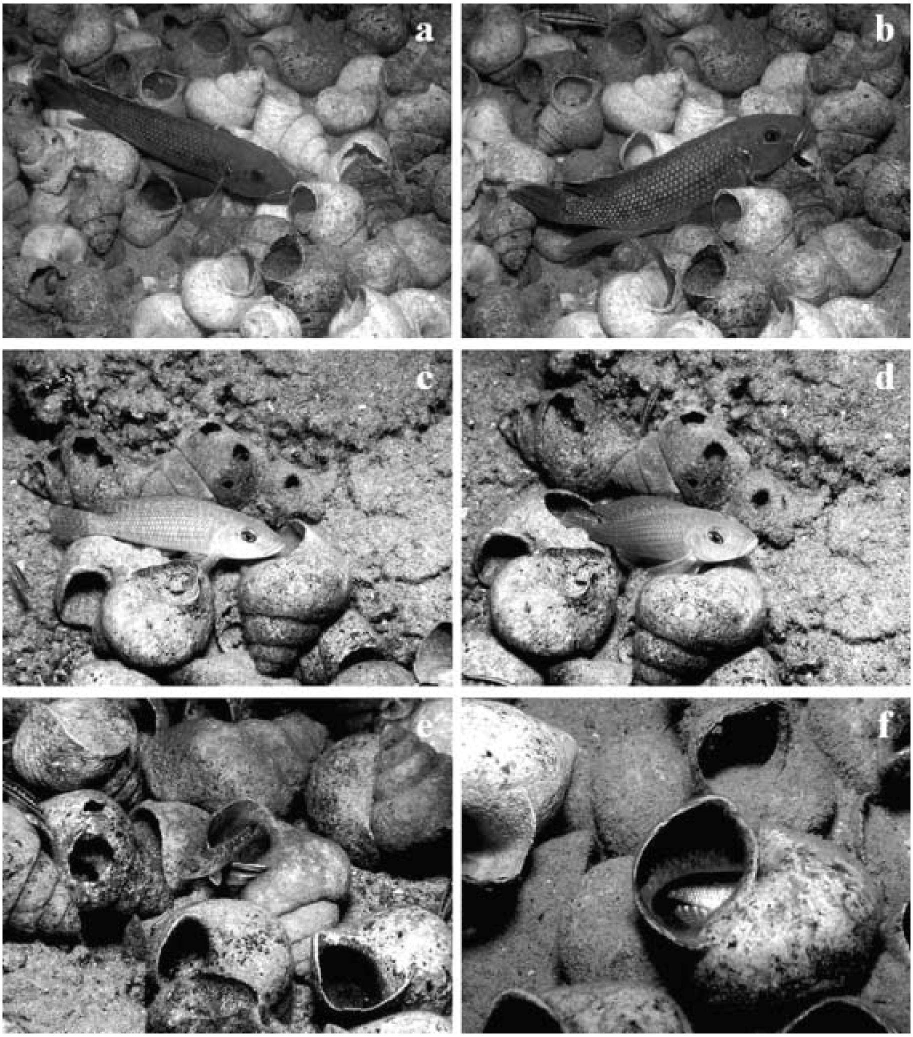

Fig. 1: Behavioural sequences of male reproductive tactics. Large males repeatedly perform mouthing and sperm release during spawning (a and b). Some dwarf and all medium males also adopt mouthing and sperm release to steal fertilization (c and d, by a medium male when the large male was temporarily chased away). Some dwarf males (e) also perform wriggling (f). See text for detailed description of behaviour

males collected in schools outside the breeding nests, 114 of 159 males were in the size range of dwarf males (28.0–47 mm) and 59 of them were ripe. One of 45 males was ripe in the size range of medium males (50–75 mm). Unripe males were found between 28.9 and 72.7 mm SL (Fig. 2c). Table 1 summarizes body weight, gonad weight and GSI of all ripe males belonging to the three types. The mean gonad weight were the highest in large males followed by medium and dwarf males. GSI were the highest in dwarf males followed by medium and large males.

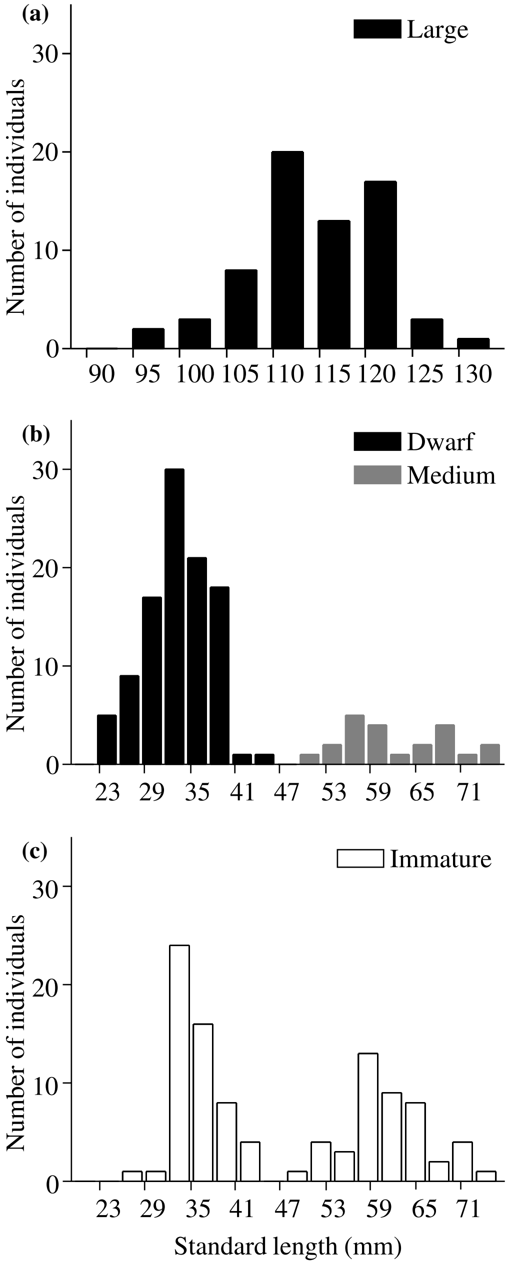

Fig. 2: Size distributions of large (a), dwarf and medium (b) and unripe males (c). See text for details

Table 1: Body weight (BW), gonad weight (GW), and gonadosomatic index (GSI) of three size clusters of ripe males ($\bar{x}$ ± SD and ranges in parentheses)

Male types	N	BW (g)	GW (mg)*	GSI (%)**
Large	59	37.5 ± 7.5 (24.9–59.0)	137.5 ± 40.9 (47.4–232.4)	0.37 ± 0.11 (0.11–0.68)
Medium	23	6.6 ± 2.2 (3.4–10.2)	99.4 ± 59.9 (8.1–246.8)	1.46 ± 0.72 (0.24–2.72)
Dwarf	102	0.9 ± 0.4 (0.3–2.2)	17.0 ± 7.8 (3.2–46.1)	1.99 ± 0.78 (0.33–4.89)

*ANOVA, $F_{(2,163)} = 271.7$, $p < 0.0001$ for all, Tukey's multiple comparison test, $q = 7.36$, $p < 0.001$ between large and medium, and $q = 14.70$, $p < 0.001$ between medium and dwarf.

**$F_{(2,163)} = 110.0$, $p < 0.0001$ for all, $q = 9.29$, $p < 0.001$ between large and medium, and $q = 4.82$, $p < 0.01$ between medium and dwarf.

Frequencies and Success of Male Reproductive Parasitism

In 335 spawnings in which the large male had been chased away by a human observer, dwarf males immediately appeared and performed parasitic spawning in 139 cases, medium males did it in six cases, and both dwarf and medium males in 12 cases. In total, dwarf and medium males attempted to spawn within a short period of the large male's absence in 47% of the cases. Among 102 spawning attempts by dwarf males in which the behavioural tactic was precisely identified, 28 adopted mouthing and sperm release, 56 wriggling, and 18 variations of wriggling. In 10 cases of 45 undisturbed observations of spawning, one or more parasitic males attempted to approach the shell where spawning took place. Dwarf males approached in seven cases, and medium males in three cases.

In two of three cases in which medium males attempted spawning during undisturbed observation, medium males successfully reached the shell entrance when the large male was attacked by a predator or engaged in a territorial contest, and remained immobile for a while (defined as a success of mouthing and sperm release). The successful sperm release by medium males accounted for 1.3% of all observed sperm release bouts that were mainly performed by large males (nine of 672). In the cases of attempted wriggling, two of seven dwarf males positioned themselves successfully alongside the spawning female in the shell. The large male expelled one of them, but the other one quickly entered the inner whorl. We never observed a successful application of mouthing and sperm release by dwarf males under undisturbed condition.

Sizes of Dwarf Males Performing Different Behavioural Tactics

Table 2 summarizes SLs and body weights of dwarf males adopting different behavioural tactics. The males adopting wriggling were significantly smaller than those performing mouthing and sperm release. Seven males switched between wriggling and mouthing and sperm release. These were between 33.2 and 40.9 mm SL in size ($\bar{x}$ ± SD of 37.6 ± 2.7 mm), corresponding to the larger half of

Table 2: Mean standard length (SL) and body weight (BW) of dwarf males employing different tactics ($\bar{x}$ ± SD and ranges in parentheses)

Tactics	N	SL (mm)*	BW (g)**
Mouthing and sperm release	28	37.1 ± 3.6 (30.9–46.0)	1.18 ± 0.37 (0.61–2.18)
Wriggling	56	32.2 ± 4.0 (24.0–40.9)	0.74 ± 0.29 (0.29–1.45)
Nibbling	9	36.5 ± 2.7 (32.0–40.6)	1.10 ± 0.24 (0.64–1.51)
Sit and Wait	9	33.4 ± 2.7 (28.0–37.3)	0.90 ± 0.23 (0.60–1.39)

*ANOVA, $F_{(3,98)} = 12.58$, $p < 0.001$ for all, Tukey's multiple comparison test, q = 8.15, $p < 0.001$ between mouthing and sperm release and wriggling, q = 4.58, $p < 0.01$ between wriggling and nibbling, and q = 3.76, $p < 0.05$ between mouthing and sperm release and sit and wait.

**$F_{(3,98)} = 13.78$, $p < 0.001$ for all, q = 8.65, $p < 0.001$ between mouthing and sperm release and wriggling, and q = 4.58, $p < 0.01$ between wriggling and nibbling.

wriggling males, and the smaller half of males that exhibited mouthing and sperm release. All 21 males smaller than 30.8 mm, except one which performed sit and wait, exhibited only wriggling. Six of eight males larger than 40 mm performed only mouthing and sperm release and two mixed the two tactics.

Factors Affecting Success of Wriggling

When we removed the large males, 12 of 32 dwarf males were successful in entering the inner whorl. The body mass of successful males tended to be smaller than that of unsuccessful males (Table 3). The body mass of females inside the shell was significantly smaller in successful cases than in failures. Shell volume correlated significantly with female body mass for both successful and failed cases, though the position of the regression line was significantly lower for successful cases than for failures (Fig 3a, Pearson's correlation coefficient, for successful cases: $FBW = 0.8314 + 0.1226 \times SHV$, r = 0.758, df = 1, $F = 13.51$, p = 0.004; for failures: $FBW = -0.3578 + 0.2204 \times SHV$, r = 0.820, df = 1, $F = 37.06$, $p < 0.001$, where FBW and SHV represent female body weights and shell volume, respectively; ANCOVA, slope: $F = 3.36$, df = 28, p = 0.077, and position: $F = 7.13$, df = 29, p = 0.012). The mass of males performing wriggling was not correlated with female mass and shell volume. However, the ratio of female mass and shell volume (FBW divided by SHV) correlated negatively with male

Table 3: Weight of dwarf males, female weight, and shell volume in successful and failed wriggling attempts ($\bar{x}$ ± SD)

		Body weight (g)		
	N	Male	Female	Shell volume
Success	12	0.64 ± 0.22	2.97 ± 0.63	17.43 ± 3.88
Failure	20	0.83 ± 0.27	3.69 ± 1.01	18.37 ± 3.74
t-test (df = 30)		t = 2.02, p = 0.053	t = 2.23, p = 0.03	t = 0,68, p = 0.50

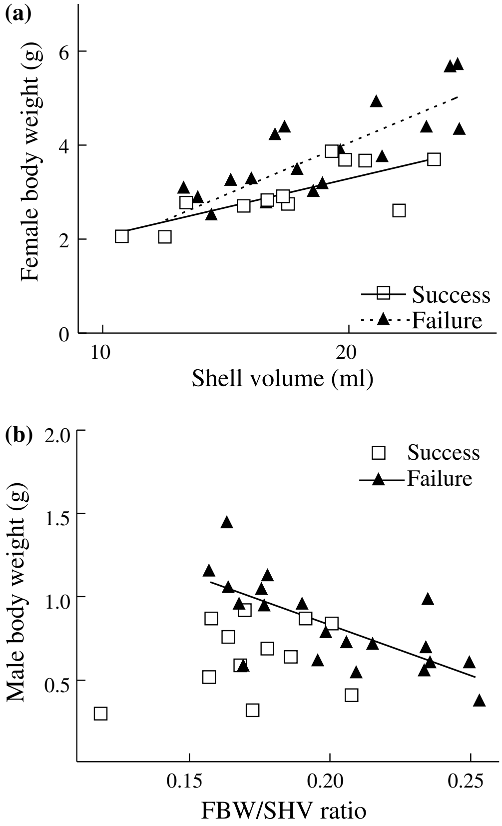

Fig. 3: A comparison of successful and unsuccessful attempts of dwarf males performing wriggling. (a) Correlation between female body weight and shell volume for successful and failed attempts of wriggling (b) Relation of the body weight of dwarf males and the ratio of female body weight to shell volume (FBW/SHV ratio) for success and failure cases

mass in failed attempts (Fig. 3b, $\text{MBW} = 2.039 - 6.043 \times (\text{FBW/SHV})$, $r = -0.709$, $df = 1$, $F = 18.24$, $p = 0.005$), but not in successful cases ($r = 0.31$, $df = 1$, $F = 1.04$, $p = 0.33$). No dwarf male was successful when the FBW/SHV ratio was larger than 0.208 ($n = 8$), or when the males were larger than 0.95 g in body mass ($n = 8$).

Body Condition of Males

The mean gonad-free condition factors of reproductively active males differed significantly among male types (Fig. 4a, ANOVA, $F_{(2,180)} = 120.6$, $p < 0.001$), with dwarf males being significantly lower than medium and large males (Tukey's multiple comparison test, $q = 11.90$, $p < 0.001$ between large and dwarf males, and $q = 11.29$, $p < 0.001$ between medium and dwarf males). In the size range of medium males, the mean condition factor of unripe males was

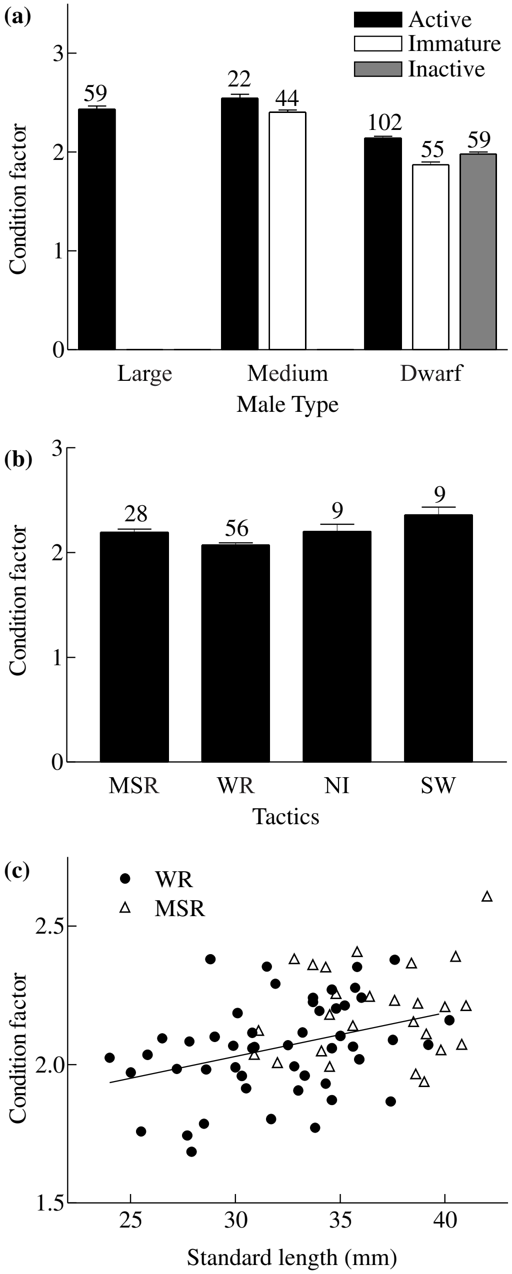

Fig. 4: Mean condition factors (± SD) among reproductively active males at the nests, unripe males in roaming schools, and males with ripe testes in schools (a), among dwarf males performing different tactics (b, MSR; mouthing and sperm release, WR; wriggling, NI; nibbling, SW; sit and wait), and the correlation between body sizes and condition factors among dwarf males performing wriggling and mouthing and sperm release (c, regression line applies to wriggling males)

significantly lower than ripe males (Fig. 4a, *t*-test, $t = 3.16$, $df = 64$, $p = 0.002$). In the size range of dwarf males, the mean condition factor was the highest in active dwarf males followed by ripe males in schools and unripe males (ANOVA, $F_{(2,213)} = 38.8$, $p < 0.001$ for all; $q = 7.35$, $p < 0.001$ between active dwarfs and ripe males in schools, and $q = 4.32$, $p < 0.01$ between ripe males in schools and unripe males).

Dwarf males adopting wriggling had lower condition factors than those performing mouthing and sperm release (Fig. 4b, ANOVA, $F_{(3,98)} = 8.86$, $p < 0.001$, Tukey's multiple comparison test, $q = 4.29$, $p < 0.05$). Condition factors correlated positively with body size in dwarf males performing wriggling (Fig. 4c, $r = 0.35$, $F_{(1,48)} = 6.7$, $p = 0.013$), but not for large, medium and dwarf males performing mouthing and sperm release.

Discussion

Reproductively active males of *L. callipterus* occur in three distinct classes which are defined by combinations of size, spawning behaviour, gonadal investment and body condition. The size range of dwarf and medium males are almost continuous, but medium males exclusively adopt mouthing and sperm release, while dwarf males also show a specialized wriggling tactic and invest more in gonads. Medium and large males are clearly distinguishable by a size gap (75–96 mm SL) and behavioural tactics. In the context of sperm competition, large males performing the bourgeois tactic, dwarf males adopting wriggling, and medium (and probably larger dwarf) males using the mouthing and sperm release tactic should be treated as different players. When the males adopt mouthing and sperm release, their opportunity to fertilize eggs is limited to a very narrow time window within the extended spawning period (> 6 h). The wriggling tactic allows dwarf males to release sperm without disturbance by the large male for the entire period after entering the inner whorl. Therefore, wriggling is probably a highly successful tactic if the male enters the inner whorl. This was confirmed by microsatellite DNA analyses (Meidl 1999). With nibbling and sit and wait, it is not entirely clear whether these tactics mainly aim at parasitic spawning.

Dwarf and medium males appeared in 47% of the cases in which large males were chased from their nests, and most attempted to spawn parasitically. Nesting males are often absent for similar short periods of time under natural conditions. During undisturbed observations, dwarf and medium males approached the shell in 22% of cases, but they only performed mouthing and sperm release in a few cases. These observations demonstrate the effectiveness of nest defence by large males. Despite an abundance of dwarf and medium males, large males face a low probability of sperm competition unless wriggling males enter a shell. This contrasts sharply with other fish species with specialized reproductive parasites (e.g. Taborsky et al. 1987; Gross 1991). The difference seems to be that dwarf and medium male *L. callipterus* must position themselves over the shell entrance, or they must dive into the small shell opening. Large male can effectively defend against potential parasites in both instances. Therefore, success of dwarf and medium males largely depends on the absence of large males.

Smaller dwarf males exclusively adopted wriggling, while the largest group of dwarf males performed only mouthing and sperm release. Dwarfs of intermediate sizes performed either of the tactics, sometimes switching between the two. These observations indicate that (1) the smallest males derive a large potential benefit from their size by the positional advantage inside the shell; and (2) larger dwarf males may switch to the less successful tactic depending on their size, which may be regarded as making the ‘best of a bad situation.’

The success of wriggling depends on sizes of males, females, and shells (Fig. 3a), as indicated by the importance of the ratio between female mass and shell volume (FBW/SHV ratio). Wriggling was most likely to be successful when small females were spawning in relatively large shells. There was a significant negative correlation between the FBW/SHV ratio and male body mass in the failed attempts, and there was no successful case when the ratio was large (Fig. 3b). These data suggest that males should attempt wriggling only when they are small relative to a given FBW/SHV ratio. Dwarf males should not select large females in relatively small shells although they may benefit from the higher fecundity of larger mates. Female choice may also affect the success of wriggling. A slight movement of the female appears to be necessary for a dwarf male to pass or at least to make it easier for them to enter the inner whorl of the shell.

Even though large dwarf males frequently attempt mouthing and sperm release, their success is apparently very limited. Therefore, males of intermediate sizes (45–50 mm SL) may have a low reproductive success, which may explain the scarcity of ripe males in this size range. Similarly, the absence of sexually active males in the size range between medium and large males (75–95 mm SL) is probably because of the reproductive disadvantage of males in this size class; they are too small to gather shells and maintain a nest (Sato 1994; Schütz & Taborsky 2000), yet are too large to approach a spawning site secretively. The similarity of the size distributions of ripe and unripe males in the dwarf and medium size classes suggests that these males regularly switch between ripe and unripe stages. Some dwarf males in schools of non-reproductive individuals had ripe testes but low condition factors. These individuals may have been in a phase of recovery from previous reproduction.

The low condition factors of dwarf males performing wriggling may result from their large investment in testes and sperm production at a very small body size. Body condition of these males improved with size, whereas this was not the case for males performing mouthing and sperm release. This suggests different patterns of investment in reproduction and growth among dwarf males adopting different tactics. Small dwarf males that wriggle appear to do so at the cost of body condition, possibly resulting in the tendency to remain small. In experiments under controlled laboratory conditions, all 19 wild-caught dwarf males stopped growing at around 40 mm SL (Taborsky 2001). These data suggest that at least a large proportion of reproductively active dwarf males, if not all of them, remains small for life.

In conclusion, our results indicate that a major factor shaping the size distribution of reproductively active males in *L. callipterus* is the positional advantage of small-sized dwarf males adopting wriggling in comparison with the rather opportunistic adoption of mouthing and sperm release by larger males. The major factors affecting the choice and success of wriggling are the body size of dwarf males and the relative sizes of females and shells in which they spawn. Early maturation in dwarf males seems to be associated with a good body condition that allows them to invest more in testes and reproductive activities. Although a small body size often has been assumed to enhance the ability of parasitic males to steal fertilizations, few studies have provided data demonstrating the size advantage (e.g. 'satellites' against 'parentals' in bluegill sunfish; Fu et al. 2001). Also, few studies have demonstrated that factors other than male body size affect the success of parasitic males. This study provides unequivocal evidence of an advantage of small size for parasitic males, and clarifies for the first time other factors affecting the success of parasitic tactics.

Acknowledgements

We thank the Lake Tanganyika Research Unit of the Department of Fisheries, Zambia, for their support in field research. This work was partly supported by a Grant-in-Aid for Overseas Scientific Research (No 07044194) from the Japan Ministry of Education, Science, Sports and Culture.

Literature Cited

Dominey, W. J. 1984: Alternative mating tactics and evolutionary stable strategies. Am. Zool. **24,** 385—396.

Fu, P., Neff, B. D. & Gross, M. R. 2001: Tactic-specific success in sperm competition. Proc. R. Soc. Lond. B Biol. Sci. **268,** 1105—1112.

Gross, M. R. 1984: Sunfish, salmon, and evolution of alternative reproductive strategies and tactics in fishes. In: Fish Reproduction: Strategies and Tactics (Potts, G. W. & Wooton, R. J. eds). Academic Press, London, pp. 55—75.

Gross, M. R. 1985: Disruptive selection for alternative life histories in salmon. Nature (London) **313,** 47—48.

Gross, M. R. 1991: Evolution of alternative reproductive strategies: Frequency-dependent sexual selection in male bluegill sunfish. Philos. Trans. R. Soc. Lond. B Biol. Sci. **332,** 59—66.

Gross, M. R. 1996: Alternative reproductive strategies and tactics: diversity within the sexes. Trends Ecol. Evol. **11,** 92—98.

Hutchings, J. A. & Myers, R. A. 1988: Mating success of alternative maturation phenotypes in male Atlantic salmon, *Salmo Salar*. Oecologia **75,** 169—174.

Kodric-Brown, A. 1986: Satellites and sneakers: Opportunistic male breeding tactics in pupfish (*Cyprinodon pecosensis*). Behav. Ecol. Sociobiol. **19,** 425—432.

Maekawa, K. & Onozato, H. 1986: Reproductive tactics and fertilization success of ripe male Muyabe charr, *Salvelinus malma miyabei.* Environ. Biol. Fishes **15,** 119—129.

Meidl, P. 1999: Microsatellite Analysis of Alternative Mating Tactics in *Lamprologus callipterus.* Diplomarbeit, Univ. of Vienna, Vienna, Austria.

Pachler, G. 2001: Sperm Competition and Alternative Mating Strategies in a Shell-Brooding Cichlid, *Lamprologus callipterus.* Diplomarbeit, Univ. of Vienna, Vienna, Austria.

Sato, T. 1994: Active accumulation of spawning substrate: a determinant of extreme polygyny in a shell-brooding cichlid fish. Anim. Behav. **48,** 669—678.

Sato, T. & Gashagaza, M. M. 1997: Shell-brooding cichlid fishes of Lake Tanganyika: their habitats and mating systems. In: Cichlid Fish Communities in Lake Tanganyika (Kawanabe, H., Hori, M. & Nagoshi, M. eds). Kyoto Univ. Academic Press, Kyoto, pp. 219–-240.

Schütz, D. & Taborsky, M. 2000: Giant males or dwarf females: what determines the extreme sexual dimorphosm in *Lamprologus callipterus*. J. Fish Biol. **57,** 1254—1265.

Taborsky, M. 1994: Sneakers, satellites and helpers: parasitic and cooperative behaviour in fish reproduction. Adv Study Behav **23,** 1—100.

Taborsky, M. 1997: Bourgeois and parasitic tactics: do we need collective, functional terms for alternative reproductive behaviours? Behav. Ecol. Sociobiol. **41,** 361—362.

Taborsky, M. 1998: Sperm competition in fish: 'bourgeois' males and parasitic spawning. Trends Ecol. Evol. **13,** 222—227.

Taborsky, M. 1999: Conflict or cooperation: what determines optimal solutions to competition in fish reproduction? In: Behaviour and Conservation of Littoral Fishes (Oliveira, R., Almada, V. & Goncalves, E. eds). ISPA, Lisbon, pp. 301–-349.

Taborsky, M. 2001: The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. J. Hered. **92,** 100—110.

Taborsky, M. Hudde, B. & Wirtz, P. 1987: Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. Behaviour **102,** 82—118.

Waltz, E. C. & Wolf, L. L. 1984: By Jove – Why do alternative mating tactics assume so many different forms? Am. Zool. **24,** 333—343.

Warner, R. R. & Robertson, D. R. 1978: Sexual patterns in the labroid fishes of the western Caribbean. I. The Wrasses (Labridae). Smithson. Contrib. Zool. **254,** 1—27.

Received: December 31, 2002

Initial acceptance: February 23, 2003

Final acceptance: September 15, 2003 (S. A. Foster)