



## Giant males or dwarf females: what determines the extreme sexual size dimorphism in *Lamprologus callipterus*?

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In the Lake Tanganyika cichlid *Lamprologus callipterus*, males were >12 times heavier than females, the most extreme sexual size dimorphism in this direction among animals. *L. callipterus* males construct nests of empty snail shells in which the females breed. If the ancestors of *L. callipterus* were small cichlids, both sexes may have used shells for shelter. If the ancestors were larger, snail shells could not be used as shelters and would be important only for reproduction. In the field and the laboratory, females bred only in shells and the largest spawned in the largest shells. In the field, females chose larger shells than the average available in males' territories and did not copy the mate choice of other females. They never hid from predators in snail shells and they occurred commonly in areas without any potential shell shelters. In laboratory experiments females used shells only for reproduction and hardly for shelter. Therefore, it seems unlikely that *L. callipterus* descended from small shell-brooding cichlids which used shells for shelter, but more likely that the ancestors were of large or intermediate size, and that female size is constrained by the sizes of snail shells, which appear to be optimal breeding substrata.

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### INTRODUCTION

In the shell-brooding cichlid *Lamprologus callipterus* (Boulenger) from Lake Tanganyika, the average male is >12 times larger than the average female (mean weights at Wonzye Point, Zambia, males : females 33.21 : 2.74 g; Table I). This is the most extreme sexual size dimorphism (SSD) in this direction among animals. Darwin (1874) thought that natural selection could not cause marked sexual differences and proposed an alternative selective force, sexual selection. Since then, dimorphisms between males and females in colour, plumage or size have been attributed mainly to intersexual selection (female choice: Sæther *et al.*, 1986; Svensson & Petersson, 1987; Møller, 1990), or to intrasexual selection (competition between members of one sex: Shine, 1978; Basolo, 1990; Jormalainen *et al.*, 1994).

In general, the degree and direction of SSD is expected to depend on a balance of natural and sexual selection (Fisher, 1958; Lande, 1980). Strong causal links may exist between sexual size dimorphism and a skew in male mating success (Arak, 1988). Polygynous males in fish are usually bigger than monogamous

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TABLE I. Standard length ( $L_S$ ) and body weight ( $W$ ) of territorial male *Lamprologus callipterus* and breeding females at Wonzye Point and Kasakalawe Bay, Lake Tanganyika

	Sex	Wonzye Point November–December 1995			Kasakalawe Bay January–March 1997		
		Mean $\pm$ s.d.	Range	$n$	Mean $\pm$ s.d.	Range	$n$
$L_S$ (cm)	♂	11.6 $\pm$ 0.88	9.95–13.7	22	9.83 $\pm$ 0.71	8.25–11.625	43
	♀	4.58 $\pm$ 0.46	3.7–5.8	48	5.003 $\pm$ 0.285	4.6–5.6	28
$W$ (g)	♂	33.21 $\pm$ 4.75	21.36–40.56	22	22.6 $\pm$ 5.26	14.85–38.02	43
	♀	2.74 $\pm$ 0.958	1.47–5.5	48	3.042 $\pm$ 0.528	2.2–4.13	28

males (Barlow, 1991; Moyer *et al.*, 1983). In cichlids, males are generally slightly bigger than females, which probably is related functionally to the predominance of polygynous mating systems. The direction of SSD may be associated with different types of habitat, food and parental care (Erlandsson & Ribbink, 1997).

For *L. callipterus*, the particular breeding substratum may be of crucial functional importance in the evolution of large males and small females. The biggest males of this species defend territories and collect empty snail shells as spawning substrate by picking them up with the mouth and carrying them for some distance to their nests (Sato, 1994). Females enter these shells for spawning and care for the brood within the shell for 10–14 days, usually remaining inside their shell guarding and fanning the eggs and larvae. Hence, females must be small enough to fit into shells, at least partly (Sato, 1994). Males can fertilize eggs from outside the shell, so an upper size limit for males should not be exerted by the size of the breeding substratum. However, there may be a lower size limit for males to enable them to collect and carry empty shells into their nests efficiently.

Two alternative evolutionary scenarios may have led to the extreme SSD in *L. callipterus*. (1) If the ancestors of *L. callipterus* were small, shell-brooding cichlids (similar to today's female size), both sexes may have used shells for shelter as all other small shell-brooders do (Sato & Gashagaza, 1997). Males may have developed a larger size because of benefits in intrasexual competition. If shells are a superior breeding substratum, natural selection may have stabilized female size by setting an upper threshold for females to fit into shells. (2) If the ancestors were not small shell-brooding cichlids (about present male size or between male and female sizes), snail shells could not have been used as shelters. They may have been used increasingly for breeding when females were still small and growing, because they provided a superior breeding habitat due to their protection potential for eggs and larvae and due to their abundance. Natural selection may have imposed an upper size limit on females, but have shifted or stabilized males at large size because of size-related benefits for collecting and carrying shells (Schütz & Taborsky, *in press*).

This paper attempts to estimate the likelihood of these evolutionary scenarios by studying the functional significance of snail shells to *L. callipterus* of breeding female size. Six questions are asked, namely:

- (a) Which substrata do females choose for breeding?  
Do females prefer larger shells?  
Does shell size preference depend on their own body size?  
Do females copy the mate choice of other females?  
Are snail shells used regularly for shelter?  
What is the relative importance of shells as shelters or breeding sites?

## MATERIALS AND METHODS

At Wonzye Point, Lake Tanganyika (8°39'S; 31°12'E), nesting *L. callipterus* males were 12.12 times heavier on average than brooding females. At Kasakalawe Bay (8°46'S; 31°5'E), territorial *L. callipterus* males were 7.43 times heavier than brooding females (Table I). Snail shells large enough for *L. callipterus* females to fit into were found almost exclusively in territories of *L. callipterus* males (Sato, 1994; pers. obs.). In November–December 1995 and January–March 1997, 65 nesting males and 76 breeding females were caught and measured in the two study populations 10 km apart at 4.5–12 m depth in *L. callipterus* nests. The females were collected after breeding, i.e. when they left their brooding shell.

### BREEDING SUBSTRATA

*Neolamprologus birchardi* Poll, and other substratum-breeding cichlids use crevices for spawning, and in the lab they spawn readily under flower pot halves (Taborsky, 1984). In the field, we searched for breeding *L. callipterus* females in all substrata in a circle with 10 m diameter around 20 nests, for 10 min each. To test for the choice of breeding substratum in a controlled laboratory situation, three or four different sized *L. callipterus* females were kept together with one territorial male in each of 12 160-l tanks and offered as potential spawning substrata three flower-pot halves, crevices between the three filter systems in the aquarium, and 10 snail shells ( $n=37$  females in total).

### SHELL SIZE

To test if females spawn preferentially in shells of a certain size, the lengths of 148 occupied and 1383 unoccupied shells were measured with slide callipers (along the axis from the apex to the outer part of the lip; Stresemann, 1992) in 12 territories at Wonzye Point. This included all suitable shells contained in these territories. The numbers of available shells of different size classes were compared with the sizes of occupied shells. As mean shell size did not differ between territories (Kruskal–Wallis ANOVA  $t=10.76$ , d.f. 11,  $P=0.46$ ), all shell data were pooled.

### SHELL SIZE PREFERENCE DEPENDENT ON BODY SIZE

To test if the shell size preference depended on female body size, at Wonzye Point (January–March 1997) the lengths of 28 brood-caring females and their shells were recorded. In the laboratory, we kept three to four females together with a nesting male and 10 shells of different sizes (range 42–56 mm in length) in each of eight 160-l tanks. Twelve females spawned in this experiment, and their lengths and the lengths of the chosen shells were determined.

### COPYING

To test if females copy the mate choice of other females, all breeding females of 23 territories at Wonzye Point were counted every other day over 9 days around the full-moon peak spawning period (Nakai *et al.*, 1990) starting 7 days before full moon. In 11 of these territories, each breeding female was removed with its shell in each survey day during this period (maximum five females per nest in total). The other 12 territories

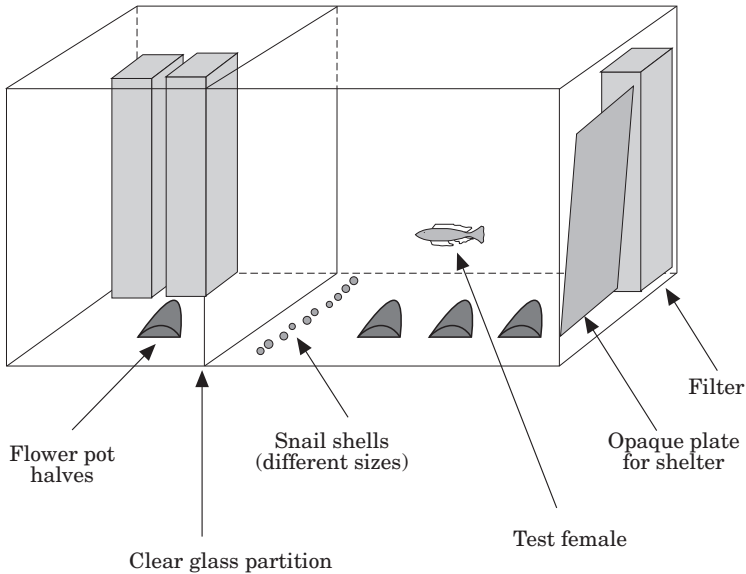


FIG. 1. Experimental setup to test the significance of snail shells for *L. callipterus* females. Left of partition: display-compartment, right: test-compartment.

served as controls. Then the mean daily increase of breeding females per nest was compared between experimental and control nests.

#### SHELTER

To test whether snail shells are used regularly for shelter, in March 1997 20 transects of  $150 \times 2$  m each and extending from 1–12 m in depth were checked at Kasakalawe Bay by dividing along them slowly at 1–2 m above the bottom. All *L. callipterus* were counted, and their lengths ( $L_s$ ) estimated by comparing the fish sizes with a measuring rod. The depth distribution of *L. callipterus* nests (in use and abandoned) was recorded. Empty snail shells were found only rarely outside *L. callipterus* nests, so this distribution corresponded very closely to the general distribution of shells.

#### SHELTER V. BREEDING SITES

To examine the relative importance of shells as shelters or breeding sites, one quarter of a 500-l tank was separated from the main compartment by a clear glass partition (Fig. 1). Ten snail shells were placed randomly with regard to size into the main compartment, in a line *c.* 10 cm from the partition. Shell volume was determined by the difference between their weight when empty and dry, and when full of water (1 g = 1 ml). Volume was correlated strongly with length of the shell ( $r = 0.888$ ,  $P < 0.001$ ,  $n = 30$ ). The order of the shells was changed between successive experimental females to avoid position effects. Three flower-pot halves, an opaque PVC board and a filter cube were added to the main compartment as potential shelters. For 3 weeks before the experiment the test females were kept in groups of three to four in 160-l tanks without males or shells, to be ready to spawn when the experiment started. At least 3 h before darkness prior to the first test day a measured female was introduced in the test tank and allowed to habituate to the main compartment. Each test female was confronted with a different situation on each of four consecutive days. In two experimental runs the test female was confronted with either a large male (potential nest-owner and mate) or another female (potential reproductive competitor) released into the small compartment. In the control experiment the small compartment was empty. In a fourth run, the female was confronted with a 15 cm long  $\times$  5 cm high plastic model predator [form resembling e.g. *Lepidiolamprologus elongatus* (Boulenger)] in the middle of her own compartment, to avoid frightening her

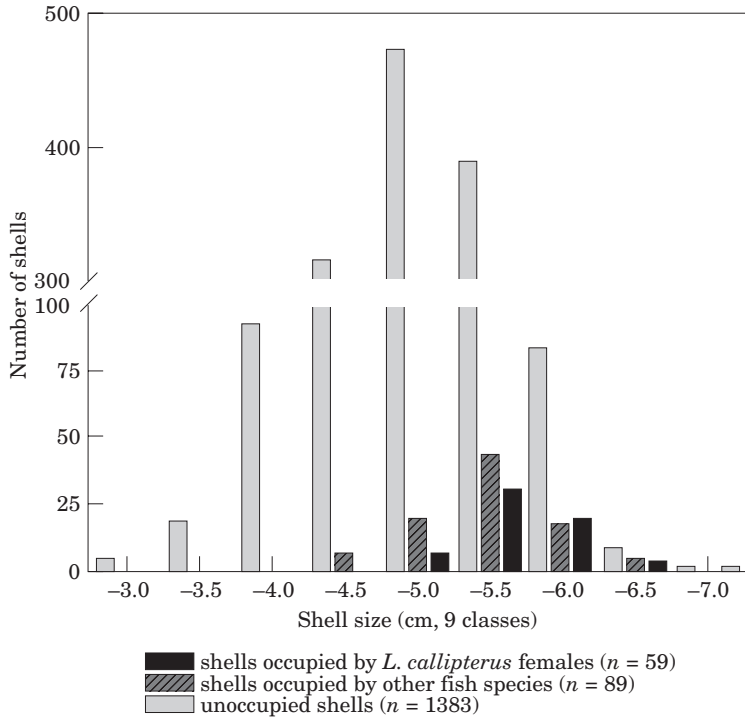


FIG. 2. Numbers of occupied and unoccupied *N. tanganicense* snail shells in male *L. callipterus* nests ( $n=153$  shells of 12 territories). Abscissa: upper limits of shell size classes.

away from the shells along the transparent partition (Fig. 1). (In preliminary experiments the females reacted to the model as a predator, hiding immediately.) The model was displayed in the main compartment once every 15 min and until the female took shelter. It was not displayed if the female was in a shelter already. The female's location before the model appeared was recorded and the shelter she chose in response. For the first two females the sequence of test situations was randomized. But as they appeared very nervous after seeing the predator and often hid for long intervals (even on the next day), the same standardized sequence was used for the other six females as follows: day 1 control; day 2 male; day 3 female; and day 4 predator. Each female was watched on each experimental day from 1030–1230, 1330–1530, and 1900–2100 hours, recording her location every 15 min. Four different locations were distinguished: lying on or in front of a shell; in a shell; at another potential shelter; or swimming at the partition. Throughout, the frequency of shell inspection (the female enters the shell partially or completely) was recorded.

## RESULTS

### BREEDING SUBSTRATA

In the field and laboratory females used only empty snail shells for breeding. In the field, we observed 76 spawning or brooding females in the two study populations, all of which used shells. The 37 females tested under controlled laboratory conditions with shells and alternative potential spawning substrata used only shells for spawning. In five years of other experiments and *c.* 120 recorded spawnings, no female spawned on any substratum other than shells,

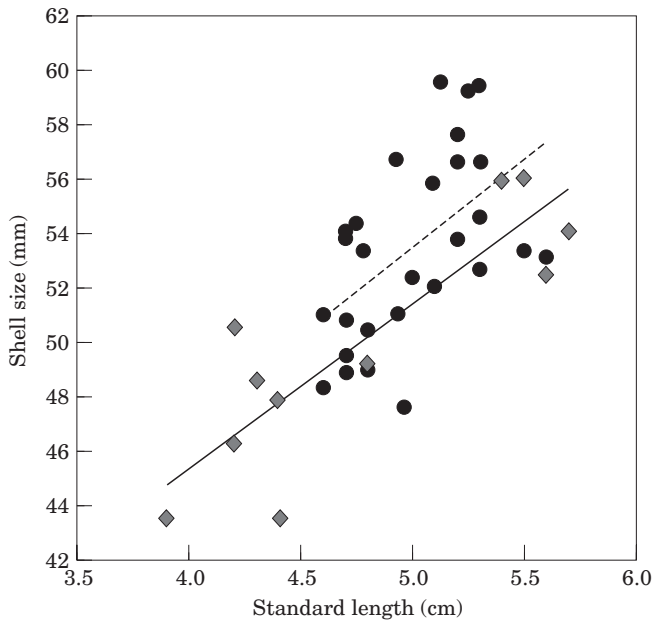


FIG. 3. Shell sizes used for breeding in relation to female standard length, in the field (●, ---) and in the laboratory (◇, —), including the regression lines.

except one which had no shells available and laid a few eggs on the sand bottom shortly after transfer from an aquarium containing a territorial male and snail shells.

#### SHELL SIZE

*L. callipterus* females chose shells that were larger than the average available ( $\chi^2=118.05$ ,  $P<0.001$ ,  $n=9$  shell size classes; Fig. 2), as did other fish species using shells in these territories ( $\chi^2=69.4$ ,  $P<0.001$ ,  $n=9$  shell size classes; Fig. 2).

#### SHELL SIZE PREFERENCE

Larger females used larger shells for breeding both in the field ( $r=0.5548$ ,  $P=0.002$ ,  $n=28$ ) and in the laboratory ( $r=0.8685$ ,  $P<0.001$ ,  $n=12$ ). Females did not spawn in the biggest available shells but in shells that corresponded to their own body size (Fig. 3; see size distribution of shells available in the field in Fig. 2). The slopes and intercepts of the shell-size regression on female length did not differ between field and laboratory (slope:  $t=0.097$ , d.f. 36,  $t_{36,0.995}=2.724$ ,  $P>0.2$ ; intercept:  $t=0.051$ ; d.f. 36,  $t_{36,0.995}=2.724$ ,  $P>0.2$ ; after Kleinbaum & Kupper, 1978).

#### COPYING

There was no significant difference in the numbers of new females per day, between territories from which breeding females had been removed and

TABLE II. Depth distributions (%) of *Lamprologus callipterus* territories with empty snail shells, and of specimens of different sizes. Repr. ♀-sized fish denotes fish within the size range of reproductive females (see text)

Depth (m)	1-3.0	3.1-6.0	6.1-9.0	9.1-12.0	<i>n</i>
Territories	0	0	81.8	18.2	24
Immature fish	1.01	12.12	51.52	35.35	99
Repr. ♀-sized fish	2.34	10.51	29.48	57.67	1323
Non-territorial males	2.82	11.26	24.65	61.27	426

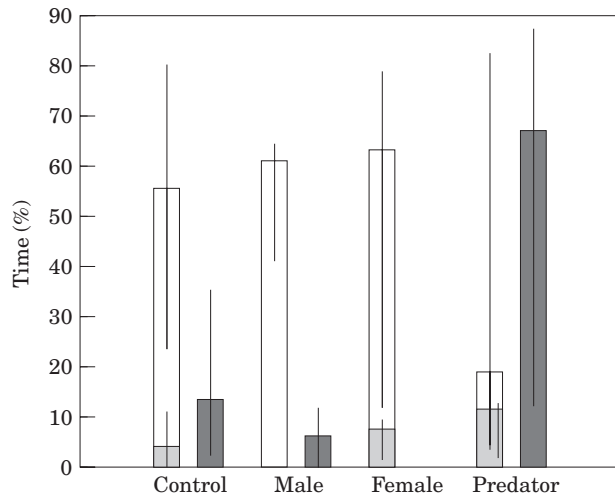


FIG. 4. Time (%) test females stayed at (□) or in (▨) shells, and at other places (■) in different experimental situations in the shell choice experiment (medians and quartiles).

unmanipulated control territories ( $z=0.806$ ,  $P=0.42$ ,  $n=11+12$ , Mann-Whitney  $U$ -test). Females did not spawn preferentially in nests which had been chosen already by other females.

#### SHELTER

Immature *L. callipterus* (<4.0 cm  $L_S$ ) and fish of female reproductive size (4.0-5.9 cm  $L_S$ ) occurred at all depths from 1 to 12 m, with larger numbers in deeper water (Table II), and at highest densities where nests were most abundant. The null hypothesis that the distributions of empty shells, and of *L. callipterus* that could hide in them, did not differ, could not be rejected (Fisher's exact two-by-two test,  $P=0.093$ ). Zero territories and 183 female-sized fish occurred between 1 and 6.5 m, and 22 territories and 1239 female-sized fish between 7 and 12 m depth. Non-territorial males (6.0-9.0 cm  $L_S$ ) were found at all depths, with numbers increasing with depth. Despite the high density of small *L. callipterus* at depths where snail shells were most abundant, these fish were not hiding in

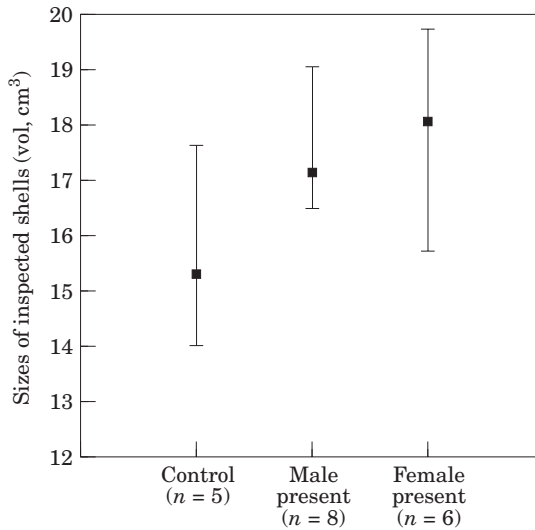


FIG. 5. Volumes of inspected snail shells (ml) in different experimental situations in the shell choice experiment (medians and quartiles).

empty shells, except for small mature parasitic males that hid occasionally from large territorial males within their nests.

#### SHELTER *V.* BREEDING SITES

In the experimental tests, the females' interest in the shells depended on the situation. With a dummy predator present, females stayed at places other than shells for two-thirds of the time (Fig. 4). In other situations they spent >50% of the time at or inside shells. The time spent at shells did not differ from the control when a conspecific was presented (Wilcoxon  $t=10.5$ ,  $P>0.05$ ,  $n=7$ ), or whether a male or another female was presented (Wilcoxon  $t=5.5$ ,  $P>0.05$ ,  $n=7$ ). But females spent longer at the shells when a conspecific rather than a predator was displayed (Wilcoxon  $t=0$ ,  $P<0.02$ ,  $n=7$ ; corrected  $P<0.05$ : sequential Bonferroni method to adjust significance levels when analyses involve the same data sets; Rice, 1989). Often the test females interact with the conspecific in the other compartment. At the partition, the test females showed only aggression: courtship behaviour occurred directly at the shells. The test females stayed next to the partition longer and were aggressive more often when another female was presented than when a male was (Wilcoxon  $t=0$ ,  $P<0.02$ ,  $n=7$ ). Two of eight test females spawned in a shell on the day a male was presented behind the partition.

With one exception, females hid from a dummy predator in shells only when they were <10 cm from a shell before the predator was presented. Three of seven females preferred alternative shelters even when those were further away than shells when the predator appeared. All six females that were nearer other shelters than shells, preferred them over shells.

When a potential mate or competitor appeared, four of eight females inspected bigger shells than in control situations (Friedman two-way ANOVA by ranks;  $P$ -values for all females:  $P_1<0.001$ ;  $P_2<0.001$ ;  $P_3=0.98$ ;  $P_4=0.73$ ;  $P_5<0.01$ ;



$P_6=0.33$ ;  $P_7=0.90$ ;  $P_8<0.01$ ). This relationship was significant for the whole sample (second order statistic (Sokal & Rohlf, 1981);  $\chi^2=47.73$ , d.f. 16,  $P<0.001$ ; Fig. 5). Female size and mean volume of inspected shells were not correlated (Pearson  $r=0.21$ ,  $P=0.618$ ,  $n=8$ ): so females preferred larger shells irrespective of their own size.

## DISCUSSION

### SHELLS AND REPRODUCTION

*L. callipterus* females bred only in empty snail shells and never in or on other substrata, as noted by many others in the wild (Sato, 1994; S. Balshine-Earn *et al.*, pers. comm.). At our study sites, shells were available primarily in nests of territorial *L. callipterus* males and only females that bred in these nests were protected from predators by the defence behaviour of the territorial male.

*L. callipterus* females spawned in shells larger than the average in males' nests. Shells in the nests were used for reproduction and hiding by several other shell brooders also (Sato & Gashagaza, 1997). These guest species also preferred bigger shells, limiting further the shells available for *L. callipterus* females. Female reproductive success increases with body size, so females have to trade off fecundity against availability of breeding substrata, which becomes scarcer with body size (Fig. 2). This trade-off is probably the major determinant of evolutionarily stable body size in these females (Sato, 1994; Schütz *et al.*, in press).

When intrasexual competition prevented females choosing freely between different sized shells in the wild (this study) or in a tank (Schütz & Taborsky, in press), they spawned in shells matching their own size and not in the largest available. When confronted by a potential partner or another female behind a glass partition, single females of whatever size chose the largest shells available. This choice difference between females with and without direct intrasexual competition indicates competition by females for large shells. Such shell competition was suggested also by the test female's aggression towards a displayed competitor, when that female tried to monopolize shells by staying much closer to them than in the control situation.

In the field, removal of brooding females from nests did not affect the recruitment of new females to either experimental or control nests: so female *L. callipterus* did not copy, which might have influenced preference for shell size.

### SHELLS AND HIDING

In the wild, *L. callipterus* of a size that could enter empty shells were abundant at all depths to 12 m, but most abundant where there were *L. callipterus* nests. However, c. 13% of such fish occurred at depths without empty shells, suggesting that shells may not be important for hiding. Also, in over 1000 h field observation, no *L. callipterus* hid from predators in empty shells, although small ones did hide under rocks or in the sand. Small mature parasitic males tried occasionally to enter shells with spawning females (Taborsky, 1998). These males stayed in or near nests often for hours, hiding in shells primarily to avoid expulsion by the territory owner. Other shell-brooding cichlids hid in shells often.

Field and laboratory data suggested that mature females use shells only for reproduction. Confronted with a conspecific behind a glass partition, test females spent >50% of their time close to shells, inspecting these frequently. They spent less time near shells when confronted with a predator, hiding in shells only if they were close to them already. If this occurred, they stayed in shelters sometimes for >1 h. So it is concluded that shells are not important as refuges for adult females, but may be used as such opportunistically.

#### EVOLUTIONARY SCENARIOS

The present data suggest that the first evolutionary scenario, where the ancestors of *L. callipterus* were small shell-brooders with both sexes using shells for shelter (as do most other shell-brooders; Sato & Gashagaza, 1997), is unlikely. The second scenario, where the ancestors were larger and did not breed in shells, is more likely. The sexes may have been of sizes intermediate between present female and territorial males, or as large as present males. If the latter, then only the limiting selection pressures acting on female body size would account for the present extreme size dimorphism: if the former, then selection pressures on body size would have acted in opposite directions on the sexes. Such a situation may have developed when empty shells became important as breeding substrata. Snail shells have different functional meanings for *L. callipterus* sexes. Females must be small enough to fit in them, while males must be large enough to transport them (Schütz & Taborsky, in press). Natural selection should have favoured females that matured early and stopped growing at a size when there were still enough shells suitable for breeding. Often in fish, size varies widely in both sexes at maturity (e.g. ayu *Plecoglossus altivelis* Temminck & Schlegel: males 9.1–21.9 cm; females 11.0–19.7 cm  $L_S$ ; Iguchi & Maekawa, 1993). Therefore, it is conceivable also that female ancestors of *L. callipterus* may have varied greatly in size at maturity. The smallest females may have chosen to spawn in empty shells instead of on other substrata, because these were abundant in Lake Tanganyika and provided protection for both them and their offspring. Thereby, females breeding in empty shells may have outcompeted females breeding elsewhere.

Territoriality in *L. callipterus* may have evolved as a consequence of males transporting shells. Baylis (1981) argued that when an optimal site for offspring development is scarce relative to a breeding population and is reusable, the male should monopolize it (male territoriality). Other shell-brooding cichlids of Lake Tanganyika, which also can reuse their breeding substrata, either defend single snail shells or occupy shells within *L. callipterus* territories. Only *L. callipterus* carries shells.

Present conclusions are consistent with the phylogenetic studies of Lake Tanganyika cichlids by Sturmbauer *et al.* (1994). Using gastropod shells for spawning appears to have evolved at least four times independently in the Lamprologini. Since the nearest analysed relatives of *L. callipterus* do not breed in shells, Sturmbauer *et al.* (1994) concluded that shell breeding in *L. callipterus* had evolved independently. In its closest relative, *Lepidiolamprologus elongatus*, both sexes are as big or bigger than *L. callipterus* nesting males (Sturmbauer *et al.*, 1994). In Nishida's (1997) maximum likelihood tree for 25 species of Tanganyika cichlids, the species most closely related to *L. callipterus* is

*Neolamprologus tetracanthus* (Boulenger), both of whose sexes can grow even larger than *L. callipterus* males. In his neighbour-joining tree derived from Roger's genetic distance on the basis of data from 21 loci in 70 Tanganyican cichlid species, *Lepidolamprologus profundicola* (Poll) was the nearest neighbour of *L. callipterus*. All three related species are not shell-brooders, and are bigger than *L. callipterus* nesting males. However, not all possibly related Lamprologini were included in these analyses, so these results should be regarded as tentative.

The present study indicates that the most extreme SSD among animals with males larger than females evolved, at least partly, through the requirements of the special breeding substratum. The sizes of available shells limit female body size, which is a natural selection mechanism. The sizes and weights of shells affect male size as well, but males must exceed a threshold size to carry shells efficiently (Schütz & Taborsky, *in press*). Natural selection should not be overlooked as a potential mechanism for the evolution of different body sizes of males and females in a species. Under particular circumstances, natural selection can play an even more important role than sexual selection for the evolution of sexual dimorphism.

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## References

- Arak, A. (1998). Sexual dimorphism in body size: a model and a test. *Evolution* **42**, 820–825.
- Barlow, G. W. (1991). Mating systems among cichlid fishes. In *Cichlid Fishes. Behaviour, Ecology and Evolution* (Keenleyside, M. H. A., ed.), pp. 173–190. London: Chapman & Hall.
- Basolo, A. L. (1990). Female preference predates the evolution of the sword in swordtail fish. *Science* **250**, 808–810.
- Baylis, J. R. (1981). The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. *Environmental Biology of Fishes* **6**, 223–251.
- Darwin, C. R. (1874). *The Descent of Man, and Selection in Relation to Sex*, 2nd edn. London: John Murray.
- Dugatkin, L. A. (1992). Sexual selection and imitation: females copy the mate choice of others. *American Naturalist* **139**, 1384–1389.
- Dugatkin, L. A. (1993). Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. *Behavioral Ecology* **4**, 289–292.
- Erlandsson, A. & Ribbink, A. J. (1997). Patterns of sexual size dimorphism in African cichlid fishes. *South African Journal of Science* **93**, 498–508.
- Fisher, R. A. (1958). *The Genetical Theory of Natural Selection*, 2nd edn. New York: Dover Publications.

- Iguchi, K. & Maekawa, K. (1993). Female mate preference and male mating success of Ayu fish, *Plecoglossus altivelis* (Osmeridae) under a promiscuous mating system. *Ethology* **95**, 193–201.
- Jormalainen, V., Merilaita, S. & Tuomi, J. (1994). Male choice and male–male competition in *Idotea baltica* (Crustacea, Isopoda). *Ethology* **96**, 46–57.
- Kleinbaum, D. G. & Kupper, L. L. (1978). *Applied Regression Analysis and Other Multivariable Methods*. Belmont, CA: Wadsworth.
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenetic characters. *Evolution* **34**, 292–305.
- Møller, A. P. (1990). Male tail length and female mate choice in the monogamous swallow *Hirundo rustica*. *Animal Behaviour* **39**, 458–465.
- Moyer, J. T., Thresher, R. E. & Colin, P. L. (1983). Courtship, spawning and inferred social organisation of American angelfishes (Genera *Pomacanthus*, *Holacanthus* and *Centropyge*, Pomacanthidae). *Environmental Biology of Fishes* **9**, 25–39.
- Nakai, K., Yanagisawa, Y., Sato, T., Niimura, Y. & Gashagaza, M. M. (1990). Lunar synchronization of spawning in cichlid fishes of the tribe Lamprologini in Lake Tanganyika. *Journal of Fish Biology* **37**, 589–598.
- Nishida, M. (1997). Phylogenetic relationships and evolution of Tanganyika cichlids: a molecular perspective. In *Fish Communities in Lake Tanganyika* (Hori, M., Nagoshi, M. & Yanagisawa, Y., eds), pp. 1–24. Kyoto: Kyoto University Press.
- Rice, W. R. (1989). Analysing tables of statistical tests. *Evolution* **43**, 223–225.
- Saether, B. E., Kaalaas, J. A., Loefaldli, L. & Andersen, R. (1986). Sexual size dimorphism and reproductive ecology in relation to mating system in waders. *Biological Journal of the Linnean Society* **28**, 273–284.
- 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. & Gashagaza, M. M. (1997). Shell-brooding cichlid fishes of Lake Tanganyika: their habitats and mating systems. In *Fish Communities in Lake Tanganyika* (Hori, M., Nagoshi, M. & Yanagisawa, Y., eds), pp. 219–240. Kyoto: Kyoto University Press.
- Schütz, D. & Taborsky, M. (in press). An extreme sexual size dimorphism in the shell brooding cichlid, *Lamprologus callipterus*: the influence of natural and sexual selection. *Evolution*.
- Schütz, D., Parker, G. A., Taborsky, M. & Sato, T. (in press). Giant males or dwarf females? A life history approach to optimal body sizes for males and females in an extremely size dimorphic cichlid. *American Naturalist*.
- Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia* **33**, 269–277.
- Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*, 2nd edn. New York: W. H. Freeman.
- Stresemann, E. (1992). *Wirbellose. Exkursionsfauna 1*. Berlin: Volk und Wissen.
- Sturmbauer, C., Verheyen, E. & Meyer, A. (1994). Mitochondrial phylogeny of the Lamprologini, the major substrate spawning lineage of cichlid fishes from Lake Tanganyika, Eastern Africa. *Molecular Biology and Evolution* **11**, 691–703.
- Svensson, B. G. & Petersson, E. (1987). Sex-role reversed courtship behaviour, sexual dimorphism and nuptial gifts in the dance fly *Epis borealis* (L.). *Annales Zoologica Fennica* **24**, 323–334.
- Taborsky, M. (1984). Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour* **32**, 1236–1252.
- Taborsky, M. (1998). Sperm competition in fish: ‘bourgeois’ males and parasitic spawning. *Trends in Ecology and Evolution* **13**, 222–227.