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The influence of sexual selection and ecological constraints on an extreme sexual size dimorphism in a cichlid

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The degree of sexual size dimorphism (SSD) in the cichlid *Lamprologus callipterus* is the greatest recorded among species in which males exceed females in body size. Males collect and defend empty snail shells in which females breed. We report on the potential importance of different selection mechanisms and constraints on male and female body sizes. To test for the importance of sexual selection, we measured the reproductive behaviour of differently sized males and their reproductive success in the field. Larger males did not have larger nests than smaller males. In the laboratory, we performed male–male competition and female choice experiments and found an indirect effect of large body size on competitive ability and male reproductive success. Neither in the field nor in the laboratory did females choose particular males. To test for the importance of ecological constraints, we studied the significance of shell size for male and female body sizes. Shell-carrying experiments revealed a minimum male threshold size for the ability to carry *Neothauma* shells. Females chose larger shells than available on average in males' nests, and their reproductive success increased with shell size. However, their size is limited by the availability of large shells. We conclude that the divergent influence of an ecological constraint on male and female body sizes is primarily responsible for this extreme SSD, in combination with size-dependent mechanisms of intrasexual selection.

The evolution of a sexual size dimorphism (SSD) requires that selection acts differently on male and female body sizes (Parker 1992). Female fecundity and reproductive success increase with increasing body size (fecundity selection; Darwin 1874; Shine & Schwartzkopf 1992), which is probably why in fish the female is often the larger sex (Wootton 1990; for other animal taxa see Ghiselin 1974; Gilbert & Williamson 1983; Woolbright 1983). Size dimorphism in this direction can reach extreme levels, with females being larger than males by several orders of magnitude (body mass; e.g. dwarf males and giant females in deep-sea anglerfish, Bertelsen 1951; see Parker 1992; Vollrath 1998).

When males are the larger sex, SSD has been attributed mainly to sexual selection (e.g. Borgia 1981; Gwynne 1982; Harper 1985; Hedrick & Temeles 1989; Møller 1990; Andersson 1994), resulting either from mate choice (intersexual selection) or from direct competition between individuals of the same sex (intrasexual selection; Darwin 1874). If large males can monopolize more females than smaller males can, a male's reproductive success may rise with increasing body size even more strongly than a female's reproductive success does (Trillmich & Trillmich 1984; Saether et al. 1986; Shine 1994). Large male size may also evolve if females prefer to mate with large males, to choose either a good parent or a genetically superior father for their offspring (Borgia 1981; Gwynne 1982; Andersson 1994). However, the size dimorphism with males being bigger than females never rises to the extreme levels occurring in the other direction. Males are rarely twice as large as females, and, in general, male size does not exceed female size more than 10-fold (Parker 1992).

The greatest recorded SSD among species in which males exceed females in body size was found in the cichlid fish *Lamprologus callipterus*, which is endemic to Lake

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Tanganyika, East Africa (Schütz & Taborsky 2000). At Wonzye Point, Zambia, territorial males are on average more than 12 times heavier than the females with which they spawned (Schütz & Taborsky 2000). These males monopolize nests of clumps of empty gastropod shells, which they usually take over from predecessors. They add to nests by collecting nearby shells or by stealing from other nests (Konings 1988; Sato 1988, 1994). During the period of territory maintenance, males rarely feed and their body condition declines with increasing nest tenure, until they are ousted by heavier or fitter males (Sato 1994; personal observations). Females ready to spawn enter an empty shell in a nest, lay their eggs inside it and perform broodcare for 10–14 days (Takamura 1987; Sato 1994). During this period they stay permanently inside their shell. In the laboratory and in the field, females were never observed to breed on or in substrates other than snail shells (Schütz & Taborsky 2000). In our study population, snail shells were found only in nests of territorial males. Up to 30 breeding females have been found simultaneously in the nest of a male (M. Gashagaza & T. Sato, personal communication).

We studied the influence of ecology and different selection mechanisms on the evolution of large males and small females in *L. callipterus*. Intrasexual selection would be important for the evolution of this SSD if, because of their greater competitive ability, larger males are more likely to obtain a nest, defend better nests (i.e. with more or larger shells), or maintain their nests for longer than smaller males do. Intersexual selection would be important if females choose large males as mating partners, either directly (via male size or condition) or indirectly (via nest quality). Both mechanisms should result in greater reproductive success of large males.

Alternatively, empty snail shells as a special breeding substrate may constrain the body sizes of males and females in opposite directions. Only large males may be able to carry shells or carry them efficiently, which could lead to large male size via intrasexual selection (large males outcompete smaller conspecifics in their endeavour to obtain mates) or natural selection (reduced viability through energy depletion or increased risk of exposure to predators by inefficient shell carrying by small males). Snail shells may also limit female size, because females exclusively breed in gastropod shells (Schütz & Taborsky 2000) and must be small enough to fit into them. This may constrain female size despite fecundity benefits of larger size (D. Schütz, G. A. Parker, M. Taborsky & T. Sato, unpublished data).

In laboratory experiments and by direct observations in the field, we tested four nonexclusive hypotheses (for specific predictions see Table 1). Hypothesis 1: SSD depends on effects of male–male competition for access to females (intrasexual selection). Hypothesis 2: SSD depends on effects of female choice (intersexual selection). Hypothesis 3: SSD depends on effects of an ecological constraint on male body size, because of a size-dependent ability to transport shells. Hypothesis 4: SSD depends on effects of ecological constraints on female body size, because of a size-dependent limitation on entering and breeding in shells.

METHODS

General Field Methods

We studied a population of *L. callipterus* at Wonzye Point, east of Mpulungu, Zambia, at the southern end of Lake Tanganyika in November and December 1995. We used Scuba diving to observe the fish at depths of 4–10 m. We marked all examined territories ($N = 20$) with numbered stones, measured their water depths and counted suitable and unsuitable (i.e. damaged) shells. From 12 nests, we also measured, with slide callipers, all snail shells (along the axis from the apex to the outer part of the lip; Stresemann 1992; $N = 2448$ shells). The territorial males were caught with a fence net, measured (standard length, SL; i.e. front end of body to base of tail) and marked individually by injection of black ink into scale pouches at different places on the body. Nine randomly chosen males were brought to the surface and weighed.

In our study population, *L. callipterus* used shells of only one snail species for breeding: *Neothauma tanganicense*. We refer to the clumps of shells defended by a male as a nest and the total defended area including some margin (ca. 10 cm wide) around the nest as a territory. Nest size refers to the number of snail shells in a nest. The availability of snail shells as well as predation risk may differ between water depths (Sato & Gashagaza 1997). Therefore, we also tested for the influence of water depth on the distributions of nest owners' sizes and on shell numbers per nest.

General Laboratory Methods

All fish used for laboratory experiments, except those used for the female growth experiment (see below), were wild-caught fish from the southern population of Lake Tanganyika or their offspring. If not stated otherwise, the experiments were carried out in sections of a 16 700-litre circular aquarium with a diameter of 7.6 m and a depth of 0.8 m (Fig. 1). From the 16 equally sized trapezoid compartments we separated sections of two compartments each with permanent, opaque partitions (referred to as tanks). In front of these tanks we placed opaque screens with one-way mirrors to allow the observer to observe the fish without disturbance.

Before starting an experiment, all fish were measured (SL and weight, WT) and marked individually as in the field. We used *N. tanganicense* shells, modified by replacing a strip 2 × 2.5 cm wide of one side of the shell with a transparent Plexiglas window moulded by heat, to observe spawning and determine embryonic development. The size range of shells used in each experiment was 41.8–56.0 mm if not stated otherwise. We recorded each spawning event with date and place, the male and snail shell that had been chosen, and the identity of the female. When the fry had completely absorbed their yolk, 10–14 days after spawning, we carefully shook the female and fry out of the shells and counted the young. Male reproductive success was determined by the number of females breeding in their nests and the total number of fry emerging.

Table 1. Hypotheses, specific predictions, tests and results of field observations and laboratory experiments

Hypothesis	Prediction	Test	Result
(1) Intrasexual selection	(1) Owing to better competitive ability, large males have larger nests than small males	Field observation	No
	(2) Large males obtain nests more readily and hold them for longer than small males	Male–male competition experiment	±
(2) Intersexual selection	(3) Direct female choice: females prefer larger or heavier males	Field observation	No
		Female choice experiment	No
	(4) Indirect female choice: females choose males with larger nests	Field observation	Yes
		Female choice experiment	No
(3) Ecological constraints of male body size	(5) Males must reach a minimum size to carry shells	Shell-carrying experiment	Yes
	(6) Larger males carry shells more efficiently	Shell-carrying experiment	Yes
(4) Ecological constraints of female body size	(7) Females prefer large shells for spawning	Female choice experiment	Yes
	(8) Female reproductive success increases with relative shell size	Female choice experiment	Yes
	(9) Females adjust growth to available shell sizes	Female growth experiment	Yes

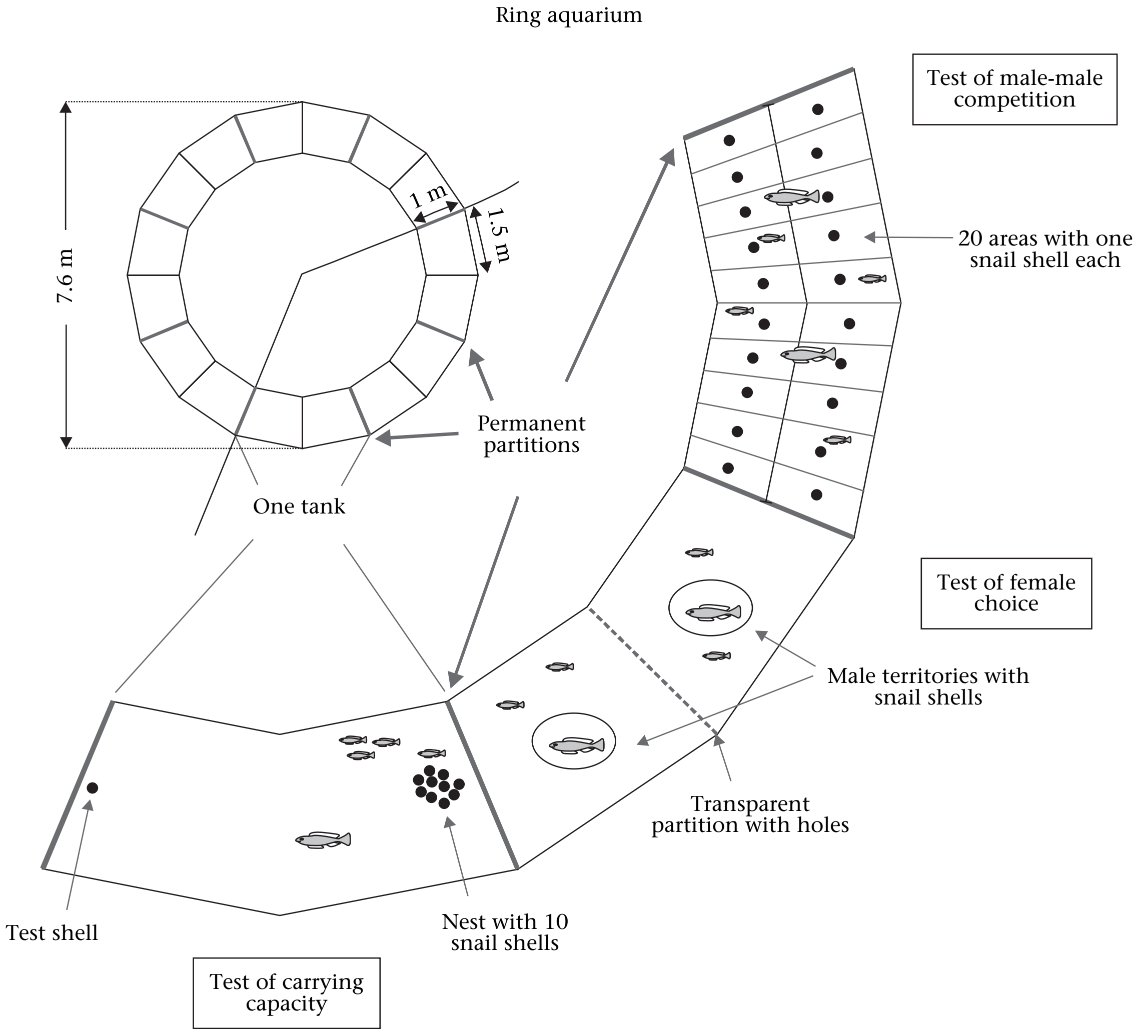

Figure 1. Set-up of three types of experiments performed in the ring aquarium. See text for details.

We quantified the behaviour of males in experiments using an event-recorder for 10 min each day. In pilot experiments (unpublished data), we found no effect of time of day on behaviour except immediately after feeding. Therefore, behavioural recordings omitted a 1-h period after feeding. We measured frequencies or durations of the following eight behaviour patterns performed in the context of courtship, aggression and communication. (1) Territory guarding (duration): the male stayed within or at most 10 cm away from his nest and defended it against conspecifics. (2) Chasing (frequency): the male swam quickly towards another fish and drove it away. Chasing is synonymous with 'direct attacks'. (3) Aggressive displays without direct body contact (frequencies): this includes (3a) frontal approach (fast movement against opponent, abrupt stop, spreading of opercula), (3b) spreading opercula and fins (without locomotion), and (3c) head-down display (position lateral to opponent). (4) Courtship behaviour (frequencies): this consisted of (4a) bump against (mouth impact on a female), (4b) head jerk (quick and intensive head shaking at the shell entrance when a female was present at the nest) and (4c) moving or turning a snail shell in front of a female. Means of these behavioural frequencies and durations were calculated per male and 10-min observation period from 14 daily recordings.

To test for effects of male–male competition, as well as direct and indirect female choice we ran three series of experiments (see below for details), in each of which nine different pairs of males were combined with different groups of four females. Each replicate lasted for 2 weeks. Females were kept in holding tanks before and between experiments for at least 3 weeks to ensure that they were sexually ripe at the beginning of each replicate. Between experimental series we changed the combinations of male and female groups, so that each male pair and female group was used in all three experiments, but in different combinations. We tested the same pairs of males in each of the three experiments for a better comparison of experimental effects. Since each pair of males was used in each of the three experiments, the body size differences between the two males were similar in all experiments.

Ethical Note

The marking technique did not have any adverse effects on the fish. In Vienna, the fish were kept in 200-litre aquaria between experiments with males and females kept separately in groups of four to five fish per tank. In general, water temperature was 26–27 °C, the light:dark regime was 14:10 h and the fish were fed once a day ad libitum, alternating frozen mosquito larvae and dry food. After the experiments, the fish, including the eggs, fry and young, were kept in the laboratory for further behaviour experiments. During the experiments we recorded aggression involving physical contact mainly by male fish. The only aggression involving physical contact was when one fish chased another one and bumped against it with his head. There was no biting or shoving nor any visible injuries, and we never had to treat any fish for injuries. Even when males were temporarily confined to a limited area in the tank by dominant conspecifics, they still fed normally, because no territorial behaviour was shown during the daily feeding period. Permission for the study was granted by the Fisheries Department of the Zambian Ministry of Agriculture and Fisheries.

Statistics

Data distributions were tested for normality when $N > 8$. Below this threshold or when distributions differed from normality at the 0.1 level, nonparametric statistics were used. Two-tailed tests were applied for all data.

Methods Used to Test Hypotheses 1–4

Hypothesis 1: intrasexual selection

To test whether large males defended better nests than small males in the field, we related the number and sizes of snail shells in the nest to male body size (SL) and condition ($C = WT/SL^3$; Bolger & Connolly 1989). There was no significant correlation between SL and condition in the laboratory and in the field (Pearson correlations: laboratory $r_{16} = -0.32$, $P = 0.19$; field 1995: $r_7 = -0.40$, $P = 0.28$; field 1997: $r_8 = -0.42$, $P = 0.22$). In a laboratory experiment testing for effects of direct male–male competition, two differently sized males were allowed to interact freely. At the onset of each of nine replicates, two males and four females were simultaneously released into the tank, with a transparent PVC tube. The bottom of the tank was partitioned with PVC-sticks into 20 areas of roughly equal dimensions, and an empty snail shell was placed in the middle of each of these areas (Fig. 1). Twice a day we noted the location of each individual fish, with at least 4 h between these observations, to check whether individual fish stayed consistently at particular places. We recorded whether a male established a territory and built a nest, and which of the two males did so first. We also recorded nest take-overs and nest-holding periods.

Hypothesis 2: intersexual selection

To check for direct female preference of males depending on size or condition in the field, we counted females breeding simultaneously in a nest and related this to male SL and condition. Since breeding varies with the lunar cycle in *L. callipterus*, with more females breeding at full moon than at new moon (Nakai et al. 1990), we counted all breeding females in male nests around full moon. In a laboratory experiment testing whether female choice depends on male size or condition, two males were prevented from escalating encounters and from stealing shells from each other by a transparent partition, with holes 15 mm in diameter, between the two compartments (Fig. 1). Females could move freely through the holes, whereas males could not. Before each of nine replicates, we trained four test females for 10–14 days to swim through the partition, by introducing them into the tank on one side of the partition and providing food on the other side. Every day the female compartment and the food compartment were exchanged. We recorded which females passed through the holes in the partition and we started the experiment only after we had seen each female doing this at least five times. Then we put 10 empty snail shells of matched sizes into each of the two compartments, before placing one male and two trained females on either side of the partition. For each experimental pair of males, we related the difference in male size (SL_1-SL_2) and condition factor (C_1-C_2) to the number of breeding females obtained by each male as a measure of female preference.

To test for indirect preference of females for males via their nest quality, in one full moon period we counted all females of 12 nests, from 7 days before to 2 days after full moon. The mean increase in breeding females per day over this 9-day period was calculated and related to the number of shells in the nest (separately for total number of shells and number of shells suitable for breeding). As females stay in the nest for up to 2 weeks after spawning if the brood develops successfully, but leave earlier if it does not, the number of new females per period (instead of total number of females in the nest) represents the mating success of nest males best. In a laboratory experiment investigating effects of nest quality on female choice, two males were tested with a clear Plexiglas partition in a similar experimental procedure as described above, but with males' nests differing in the number of shells. One male received five shells in his nest and the other one 15, with matched size distributions of shells between nests. In four replicates the smaller male got more shells and in four replicates the larger male got more shells. In one replicate the males were of equal size, because initial size differences had levelled out during the total experimental period of 9 months. We tested the influence of differences in shell numbers on the numbers of breeding females and offspring produced for each male pair with a pairwise comparison.

Hypothesis 3: ecological constraint for male size

To test for effects of male size on shell-carrying ability, we deposited 10 snail shells at one end of the tank and introduced four differently sized females into the tank to serve as potential partners. A test male was then introduced and a single snail shell of intermediate size (shell lengths: 48.7–49.8 mm) was put at the side of the tank opposite to the shell cluster (Fig. 1). We tested whether the experimental male would bring the single shell to the cluster, which would indicate that he regards it as his nest. Every day we checked the location of this experimental shell. When the male had transferred it to the shell cluster and spent most of his time there, we started the experiment. In 15 replicates of this experiment, we offered each of 15 individual males (size range: 7.2–12.0 cm SL) consecutively 10 differently sized, measured and marked test shells. Males had to carry these shells for a distance of 1.5 m to transport them into their nests. The experiment started when we gently introduced the first test shell. We noted the time when the test male first approached the shell to within 10 cm, if and when he started to carry it into his nest and at what height, and whether the shell was successfully transferred. For a measure of transport height, two observers estimated the maximum carrying height above ground simultaneously and independently, and the arithmetic mean of these estimates was taken. After a shell had been carried into the nest we introduced the next shell and again recorded the male's behaviour. We continued this procedure until the male had carried all 10 shells into his nest or no longer approached the presented shell. We randomized the sequence of the 10 presented shells for each male by pulling them out of a bucket blindly. When a male attempted to carry a shell but was apparently unable to do this, we subsequently offered one bigger and one smaller shell. When he did not move these shells in 1 h after first approaching them, we stopped the experiment. We related number of transported shells and mean transport height to male body size, and calculated the weight ratio between the heaviest carried shell and male weight in each replicate.

Hypothesis 4: ecological constraint for female size

Female fecundity is likely to increase with shell size because of a greater oxygen capacity of the larger water volume contained in the shell. To test for a potential influence of shell size on female reproductive success that is independent of female body size, we kept 30 females of different sizes in groups of three to four each in 200-litre aquaria in the laboratory. To each tank, we added one territorial male (≥ 9.0 cm SL) and 10 differently sized, individually marked snail shells (35–60 mm length). We noted the shell size chosen and the number of independent offspring produced. To test whether females select shells for spawning from the larger end of the size distribution, we compared the size ranks of chosen shells with the size ranks of available shells in the 18 replicates of the female choice experiment described above. To check whether the sizes of shells available during ontogeny might influence female growth, we compared the growth patterns of two groups of females from a Uvira population (Democratic Republic of Congo, wild stock), where *Neothauma* shells are limited and mainly the smaller *Paramelania* shells are used for breeding. In two 200-litre aquaria in the laboratory we kept two groups of six small, wild-caught females, each together with one territorial male from the same population, for 18 months. One group was held with 10 large *Neothauma* shells (shell lengths 48–59 mm), the other with 10 small *Paramelania* shells (shell lengths 25–38 mm). The females were immature at the beginning of the experiment (3.2–3.4 cm SL), when their sizes did not differ between the experimental groups (SL: Mann Whitney U test, two-tailed: $Z = -0.44$, $N_1 = N_2 = 6$, $P = 0.665$; WT: $Z = -0.58$, $N_1 = N_2 = 6$, $P = 0.564$). The fish were kept at the same water temperature (26 °C), which was checked continuously with an automatic temperature recorder ('hamster') in each tank. They were fed ad libitum with either frozen plankton or commercial flaked dry food. At the end of the experiment we measured the females again and compared body sizes and weights between groups. The fish were kept in the laboratory for further observation after the experiment.

RESULTS

Hypothesis 1: Intrasexual Selection

Contrary to prediction 1 (Table 1), in the field male size and the number of snail shells in their nests were not significantly related (Pearson correlation: $r_{18} = -0.15$, $P = 0.543$), and mean shell size did not differ between nests (Kruskal–Wallis ANOVA: $H_{11} = 10.76$, $P = 0.46$). However, the water depth at nest locations was positively correlated with the number of snail shells in the nests (Pearson correlation: $r_{18} = 0.48$, $P < 0.05$), whereas nest depth and male body size were negatively correlated with each other (SL: $r_{18} = -0.51$, $P < 0.05$). A partial correlation analysis of male size, water depth and the number of shells per nest confirmed the influence of water depth on shell numbers, independent of male body size (partial correlation: $P_{\text{total}} = 0.595$, $N = 17$; male size: $r_{\text{part}} = -0.145$, $P = 0.543$; depth: $r_{\text{part}} = 0.476$, $P = 0.034$).

In a test of the size-dependent nest-holding potential of males (prediction 2), in four experiments the larger male and in five experiments the smaller male had gathered all shells of both compartments after 2 days at the latest. In all cases, the other male was chased away and tolerated only at one bottom corner of the tank. In none of the nine experiments had both males established or held a nest at the same time. In three of the five experiments in which the smaller male established a territory first, it was taken over by the larger male after 2, 3, and 6 days, respectively. None of the smaller males took over the nest of a larger owner. The number of breeding females and the number of offspring produced did not differ between small and large males in this experiment (Wilcoxon tests, for both variables: $T = 14$, $N = 8$, $P = 0.6$). However, there was an indirect effect of male size on reproductive success. Larger males were more aggressive than their smaller test partners (Wilcoxon test: $T = 0$, $N = 8$, $P < 0.01$). More aggressive males held their nests significantly longer than did less aggressive males (Wilcoxon test: $T = 3$, $N = 8$, $P < 0.05$). The longer a male held a nest, the more females spawned with him (Pearson correlation: $r_8 = 0.8$, $P < 0.001$; $N = 10$ because in two replicates both males held nests subsequently), and the more females spawned with a male, the more offspring he sired ($r_8 = 0.97$, $P < 0.001$).

Hypothesis 2: Intersexual Selection

Contrary to prediction 3, in the field the number of breeding females present in a nest at full moon was not related to male nest owner size (Pearson correlation: $r_{11} = 0.12$, $P = 0.69$), or to male body condition ($r_7 = 0.32$, $P = 0.41$). In female choice experiments, the number of females that spawned in a nest and the number of offspring produced was not related to the difference in SL between the two males ($r_7 = 0.34$, $P = 0.36$). Three times the larger male sired more offspring (on average 150 young), and five times the smaller male did (on average 113 young). In one case, no male could spawn with any female. The reproductive success of the two males was also not related to their difference in body condition ($r_7 = 0.19$, $P = 0.61$). Four times the male with higher body condition sired more offspring (on average 125 young), and four times the male with lower body condition did (on average 129 young).

The test of indirect female choice (prediction 4) showed that, in the field, the number of new females acquired per day correlated positively with the number of snail shells in a nest (Pearson correlation: $r_{10} = 0.79$, $P = 0.002$; Fig. 2). Some nests contained several hundred damaged shells that were unsuitable for spawning, and were accumulated mainly at the nests' edges. In a partial correlation analysis, the number of suitable shells, and not the total number of shells, explained the variability in numbers of breeding females per nest (partial correlation: $P_{\text{total}} = 0.009$, $N = 12$; suitable shells: $r_{\text{part}} = 0.65$, $P = 0.03$; total shell number: $r_{\text{part}} = 0.27$, $P = 0.42$). However, in laboratory experiments, there was no difference in the number of breeding females (Wilcoxon test: $Z = 0$, $N = 9$, $P = 1$) or in the number of offspring produced (t test: $t_8 = 0.10$, $P = 0.92$) between males with five or 15 shells in their nests.

Hypothesis 3: Ecological Constraint on Male Size

As predicted (prediction 5), not all males were able to carry the experimental shells, and this ability was size dependent. From the 15 test males no male smaller than 9.0 cm ($N = 5$), but two of four males between 9.0 and 9.5 cm and all males larger than 9.5 cm ($N = 6$) were able to carry shells (Fig. 3). Three of the five males smaller than 9 cm tried to lift shells but did not succeed. The efficiency of carrying shells improved with increasing body size (prediction 6). With increasing size males carried more

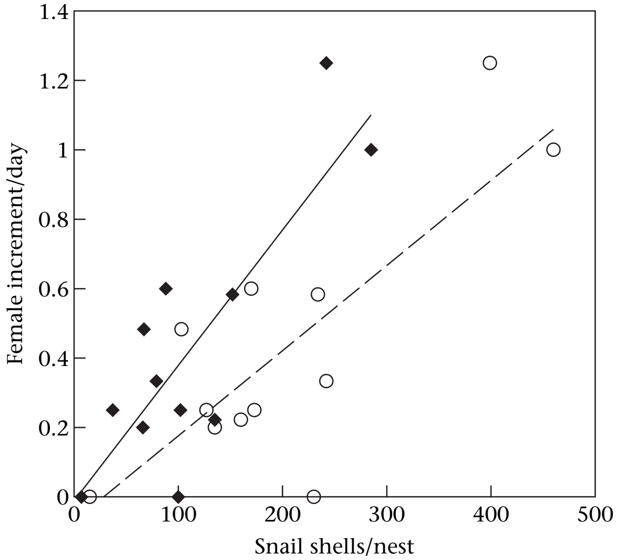

Figure 2. Mean daily increase in numbers of females per nest ($N = 12$ nests) in relation to the total number of shells (◆, —, $r = 0.79$, $P = 0.002$) and to the number of suitable shells (○, – – –, $r = 0.827$, $P = 0.001$).

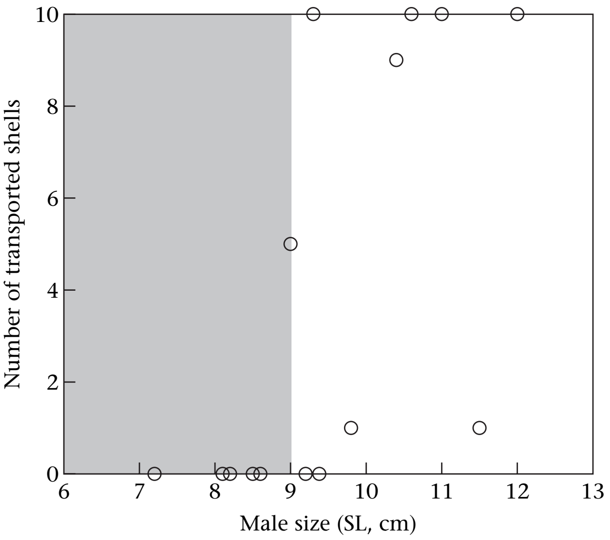

Figure 3. Number of shells (out of 10) carried into the nest in relation to male standard length. The shaded area marks the size range in which males were unable to transport shells.

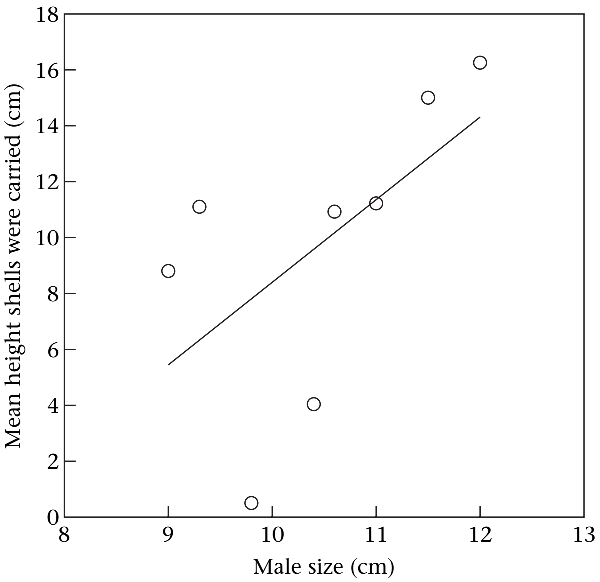

Figure 4. Average height from bottom at which shells were carried, in relation to male standard length. Regression line is shown: $r = 0.74$, $P = 0.037$.

shells into their nests (Spearman rank correlation: $r_S = 0.75$, $N = 15$, $P = 0.001$; Fig. 3) and they carried shells higher above ground ($r_S = 0.74$, $N = 8$, $P = 0.037$; Fig. 4). Larger males were able to carry heavier shells in relation to their own body weight than smaller males. With increasing body size the ratio of shell weight to body weight increased significantly for the heaviest shell a male could carry ($r_S = 0.523$, $N = 15$, $P = 0.045$), which means that males are able to carry disproportionately heavier shells as they get larger.

Hypothesis 4: Ecological Constraint on Female Size

In the two series of experiments, 36 of the 72 females spawned. As predicted (prediction 7), females preferred to spawn in larger than average shells in their mates' nests (binomial test: $Z = 5.5$, $N = 36$, $P < 0.001$; see Fig. 5 for size ranks of chosen shells). A multiple regression analysis showed that female size and shell size as independent variables explained a significant part of the variance in the number of offspring produced in these two series of experiments ($R^2 = 0.26$, $N = 30$, $P = 0.016$, prediction 8). Both female size ($r_{part} = 0.37$, $P = 0.045$) and shell size ($r_{part} = 0.39$, $P = 0.039$) had a significant effect on female reproductive success, independent of each other. Females breeding in larger shells relative to their body size had a higher reproductive success than females breeding in smaller shells relative to their own body size (relative shell size was measured as the residuals of the regression of female size and chosen shell size; Pearson correlation: $r_{28} = 0.36$, $P = 0.05$; Fig. 6).

As predicted (prediction 9), females adjusted growth to available shell sizes. After 18 months females held with the bigger *Neothauma* shells were significantly heavier (Mann–Whitney U test: $Z = 2.19$, $N_1 = 6$, $N_2 = 5$, $P = 0.028$) and tended to be longer ($Z = 1.92$, $N_1 = 6$, $N_2 = 5$, $P = 0.54$) than females held with the smaller *Paramelania* shells (Table 2).

DISCUSSION

Influence of Sexual Selection

Hypothesis 1: intrasexual selection

In our study population at Wonzye Point, larger males did not monopolize more or larger shells in their nests than did smaller males. An opposing influence of water

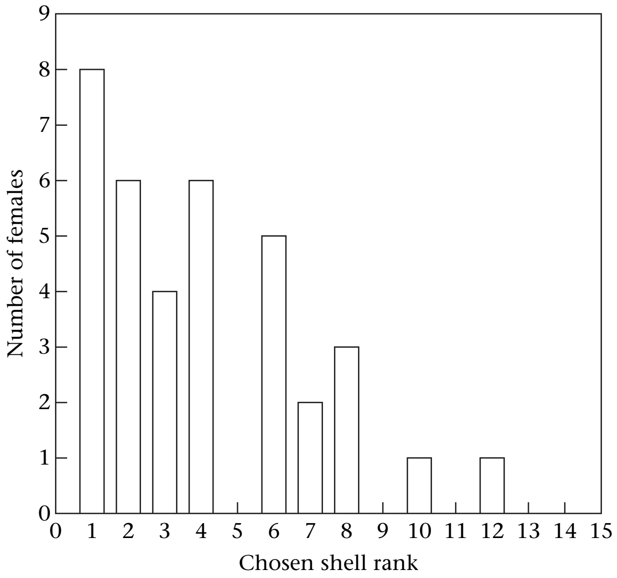

Figure 5. Size ranks of chosen shells of 36 spawning females in laboratory experiments. Rank 1 represents the largest shell and rank 15 the smallest.

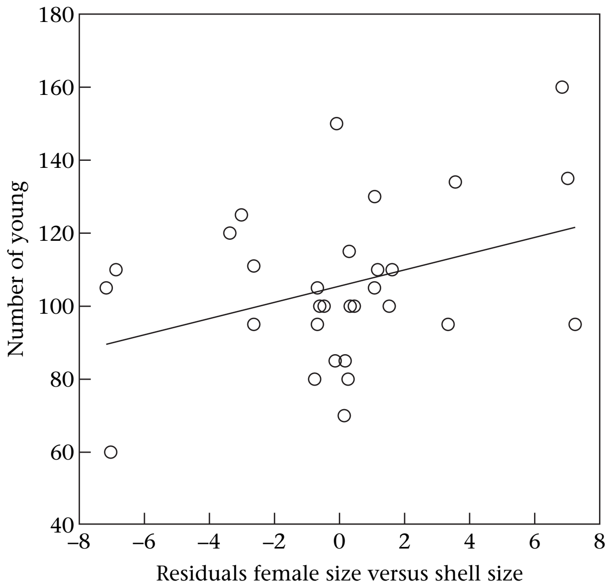

Figure 6. Number of offspring in relation to the residuals of the regression of female size and chosen shell size ($N = 30$). Regression line is shown: $r = 0.36$, $P = 0.05$.

depth on (1) the number of snail shells (positive correlation) and (2) the sizes of territorial males (negative correlation) may have caused this result. Larger males occupied nests in the shallower, rocky areas that had fewer shells, apparently because of the scarcity of *N. tanganicense* shells in this area. It may be that males preferred these nests because the deeper nests were located at the edge of the sand bottom where it is much more difficult to hide from predators. Predation on cichlid broods (Nakai et al. 1990) and adults (Abe 1997) is high in Lake Tanganyika, particularly at night. The transition zone between sand and rock may be especially risky, because clefts, overhanging rocks and holes for hiding are scarce there. In the field and in laboratory experiments, we observed *L. callipterus* hiding under rocks, in crevices between rocks or in flowerpot halves when threatened, but nest males never leave the nest area and do not hide in the sand like small conspecifics do (Schütz & Taborsky 2000). These observations suggest that the proximity of suitable hiding options may be important for nesting *L. callipterus* males.

M. Maan (unpublished data) studied another population of *L. callipterus* at Kasakalawe point west of Mpulungu (8°46.849′s, 31°4.882′E) where the habitat is much more homogenous and where larger males had more and larger shells in their nests. In the northern population near Uvira, Sato (1994) observed that male size tended to be positively related to shell size in their nests. Results of our laboratory experiments suggest that male body size may influence reproductive success, even though the effect was not direct. We found that larger males were more aggressive and defended their nests for longer than did smaller males. With increasing duration of nest tenure the numbers of breeding females increased, as did the numbers of fry produced by male nest owners. In seven of nine experiments, the larger male either was the only one holding a nest in the tank (four cases) or he took it over from his smaller experimental partner (three cases). This may indicate that larger males are competitively better in both defending and taking over a nest, which might be partly the result of size-dependent differences in energy reserves. These data confirm tentative results from the Uvira population where nest usurpation was also restricted to large and aggressive males (Sato 1994). However, in five of our nine experimental replicates the smaller male was the first to defend a nest, and in two cases he even kept it for the entire experimental period. This may indicate that despite an apparent size effect on male competitive ability, the effect on male reproductive success may be rather small in *L. callipterus*. In addition, our field results suggest that depth effects and local shell availability may strongly confound potential body size effects on male reproductive success. In summary, although there may be some influence of intrasexual selection on male body size, overall it appears to be rather weak and mostly indirect.

Hypothesis 2: intersexual selection

Neither in the field nor in the laboratory did females breed preferentially in nests of larger males or those in better body condition, and these males did not sire more offspring. It might be argued that sample sizes were insufficient to detect a significant effect ($N = 9$ pairs of males). However, despite weak positive correlations between the number of offspring produced and the size difference between males, the smaller males sired more offspring in five cases, whereas the larger males did so in only three cases. These results may suggest that direct female choice of male quality does not have an important role in the evolution of large male size. In our laboratory experiments we could not find any differences in courtship behaviour between the larger and smaller males (unpublished data), and therefore we think that differences

Table 2. Standard lengths (cm) and body mass (g) at the beginning and end of the female growth experiment, and relative size increase (%)

	Standard length			Body mass		
Females kept with	Start	End	Relative increase	Start	End	Relative increase
Large shells	3.275±0.3	4.02±0.26	22.75	0.903±0.17	1.70±0.29	88.36
Small shells	3.375±0.28	3.66±0.26	8.44	1.005±0.27	1.23±0.27	22.19

$N = 6$ for the large shell group and $N = 5$ for the small shell group, as one female died in the latter group during the experiment. Means are given ± SD.

in courtship intensity between the two males did not affect female choice behaviour.

However, more females did breed in large nests than in small ones. Indirect female choice of males via nest quality could select for large male size if there is a positive relation between these two parameters, although this has not been confirmed by our field data (see above). In addition, when we experimentally varied the number of snail shells within the males' nests in the laboratory, the number of breeding females and offspring did not vary between males as expected, despite a shell number ratio of 1:3. Again, this might have been caused by the limited sample size ($N = 9$ pairs of males) or differences between laboratory and field conditions (absolute numbers of shells or females involved), but there was not even a slight trend in the predicted direction. The shell numbers used in our experiment were relatively small but not unrealistic, because in the field the smallest natural nest had only seven suitable shells, and some small nests were very successful, both at Wonzye Point and Kasakalawe (personal observations; numbers of suitable shells per nest in our study area and season ranged from 7 to 285; $\overline{X}\pm SE=113.3\pm 80.7$). In summary, our results suggest that indirect female choice via nest quality also has only a minor effect on the evolution and maintenance of SSD in *L. callipterus*. However, even though we did not find evidence for direct or indirect female choice of male size, this might have been important for the evolution of SSD in *L. callipterus* in the past.

Influence of Ecological Constraints

Hypothesis 3: ecological constraint on male size

As revealed by our laboratory experiments, only larger males were able to transport empty *Neothauma* shells. All males tried to carry the shells, but males smaller than 9 cm SL often dropped them or were not able to lift larger shells at all. Larger males carried more shells into their nests, transported them higher above ground and were able to carry heavier shells in relation to body weight than did smaller males. The transport of shells is obligatory for *L. callipterus* males to maintain a nest successfully.

Differences in the body size of nest males between populations may be influenced by the nature of the breeding substrate (Taborsky 2001). At Rumonge, Burundi, *L. callipterus* males breed on the shell bed, which provides a virtually unlimited and rather homogeneous supply of *Neothauma* shells (Sato & Gashagaza 1997). There, territorial males are apparently not large enough to transport shells (Sato & Gashagaza 1997). In our study population at Wonzye Point, the abundance of *Neothauma* shells is limited which leads to extremely high competition for shells. Males must have a minimum body size to be able to carry shells, and large males have an advantage in carrying shells more efficiently and competing successfully for shells and territories. They can also collect larger shells, which are more attractive to larger, more fecund females. In our population, males that were too small to carry shells did not defend or maintain territories at all. Even though the population differences may point towards a phenotypically plastic trait, there is preliminary evidence for heritable growth in *L. callipterus* (Taborsky 2001). It is likely that selective pressures on male and female body sizes differ between populations depending on the sizes and distributions of shells, which will affect the evolution of the SSD.

Hypothesis 4: ecological constraint on female size

Females preferred to spawn in larger shells than were available on average in males' nests; only one of 36 experimental females bred in a shell that was smaller than the mean. Breeding in large shells relative to their own body size improved females' reproductive output, which may be caused by potential oxygen limitations in small shells that have a narrow tube constraining water exchange. When females were kept without female competitors and could choose freely between shells, they preferred the largest available shells, but in the field and when we kept more than one female in a tank, females usually spawned in the shell that matched their body size best (Schütz & Taborsky 2000). In the field, we followed individual females to estimate search times for suitable shells and found that search times for large shells were much higher than for small ones (D. Schütz, G. A. Parker, M. Taborsky & T. Sato, unpublished data). Because of the preference for large shells, the number of suitable shells available to females decreases with increasing body size, and therefore competition for large shells is high (D. Schütz, G. A. Parker, M. Taborsky & T. Sato, unpublished data). This high competition for large shells may ultimately limit average female size to a level below the maximum size potential provided by the largest available shells.

The results of our growth experiment suggest that the sizes of shells that are available during late ontogeny may influence female body size. In the south of Lake Tanganyika, large *N. tanganicense* shells are abundant and *L. callipterus* breeds exclusively in these shells. In contrast, at the northern end of the lake at Kalundu (Democratic Republic of Congo, 29°00′N, 8°30′E), *Neothauma* shells are rare and *L. callipterus* breeds primarily in empty shells of the smaller *Paramelania damoni* (Sato 1994). In this population, *L. callipterus* females do not grow as big as at the southern end of the Lake (Sato & Gashagaza 1997). We used females of the northern population in our growth experiment and found that when females were kept with the larger *Neothauma* shells they grew bigger than when kept with small *Paramelania* shells. In this experiment we did not separate females from each other because social isolation may strongly confound growth patterns of cichlids (Arendt & Wilson 1997; B. Taborsky & C. Küpper, unpublished data). Unfortunately, we could not repeat this experiment because, owing to the geopolitical situation, this population has not been accessible for several years. Therefore, the results of this experiment are preliminary. Potential confounding effects were probably small, however, because in the highly controlled experimental situation we were able to keep the conditions constant and similar between the experimental tanks.

General Conclusions

Our results suggest that sexual selection mechanisms are probably not as important as ecological constraints for the extent and evolution of the SSD in *L. callipterus*. As in many animals, male–male competition selects for large male body size in this species, but this influence does not appear to be particularly strong. Rather, this extreme SSD appears to be mainly affected by ecological constraints, with opposing selection pressures on the two sexes: males need to pass a threshold size to be able to carry shells, and carrying becomes more efficient (i.e. cheaper) the larger they get; females would gain from larger size because of increased fecundity, but their size is constrained by the limited size of their breeding substrate and by intrasexual competition for it (see also Shine 1989).

Often, constraints have been found to reduce SSD against the action of sexual selection by limiting the evolution of extreme body size in one of the two sexes. For example, a comparative study of North American passerines suggested that sexual selection for increased male size is balanced by energetic constraints of paternal care (Hughes & Hughes 1986; see also Cabana et al. 1982; Saether et al. 1986; Joensson & Alerstam 1990). However, in raptorial birds, the SSD with males being smaller than females has been attributed to natural selection mechanisms to overcome ecological constraints (e.g. Safina 1984; Temeles 1985). Raptorial birds preying on birds show a higher degree of dimorphism than others catching fish, reptiles or invertebrates, because the former experience more difficulties in prey capture. Gliwicz (1988) proposed that the SSD in small mustelids might also be explained by natural selection: the dimorphism (males > females) could be a result of a particular constraint acting on the body diameter of female weasels (*Mustela* spp.) only, which must be able to move through the burrows of their main prey. Female size may be limited in weasels because pregnancy increases their body diameter. Differences between males and females caused by divergence in food use was shown in hummingbirds, *Eulampis jugufaris* (Temeles et al. 2000) and in mosquitoes (Proctor et al. 1996). In the water spider, *Argyroneta aquatica*, males are bigger than females, which is exceptional for a spider (Schütz & Taborsky 2003). There is evidence in this species that ecological constraints under water are mainly responsible for this unusual SSD (Schütz & Taborsky 2003). In conclusion, ecological causation should not be overlooked in its importance for the origin and maintenance of sexual size dimorphisms.

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