
Unusual allometry for sexual size dimorphism in a cichlid where males are extremely larger than females

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When males are the larger sex, a positive allometric relationship between male and female sizes is often found across populations of a single species (i.e. Rensch's rule). This pattern is typically explained by a sexual selection pressure on males. Here, we report that the allometric relationship was negative across populations of a shell-brooding cichlid fish *Lamprologus callipterus*, although males are extremely larger than females. Male *L. callipterus* collect and defend empty snail shells in each of which a female breeds. We found that, across six populations, male and female sizes are positively correlated with not only sexual and fecundity selection indices, but also with shell sizes. Given their different reproductive behaviours, these correlations mean that males are required to be more powerful, and thus larger, to transport larger shells, while female bodies are reduced to the shell size to enable them to enter the shells. Among the three size selections (sexual selection, fecundity selection and shell size), shell size explained the allometry, suggesting that females are more strongly subject to size selection associated with shell size availability than males. However, the allometry was violated when considering an additional population where size-selection regimes of males differed from that of other populations. Therefore, sexual size allometry will be violated by body size divergence induced by multiple selection regimes.

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1. Introduction

In most organisms, males and females have different body sizes as a result of adaptations to their disparate reproductive behaviours (i.e. sexual size dimorphism or SSD, Arak 1988; Andersson 1994; Fairbairn 1997; Blanckenhorn 2000, 2005; Fairbairn *et al.* 2007). Arguably, primary selection pressures driving SSD are sexual selection in males and fecundity selection in females. Therefore, in the simplest case, male-biased SSD (i.e. males larger than females) is predicted when sexual selection is stronger than fecundity selection, and *vice versa* (Andersson 1994; Blanckenhorn 2000, 2005).

Sexual selection, as well as natural selection, is sensitive to environmental conditions (e.g. nest density and predation risk, Reznick and Endler 1982) and, consequently, male size could be more diverse than female size among populations of species with male-biased SSD (Forsgren *et al.* 1996). Recently, several studies have detected that this interpopulation variation in the intensity of sexual selection shapes a pattern of interpopulation size variation, i.e. male size increases allometrically with female size across populations (i.e. $\Delta size_{male} > \Delta size_{female}$; Fairbairn and Preziosi 1994; Fairbairn 2005; Young 2005; Blanckenhorn *et al.* 2006; Pyron *et al.* 2007; Lengkeek *et al.* 2008; *see also* Walker and McCormick 2009). This pattern is known

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Abbreviations used: H, height; RMA, reduced major axis; SL, standard length; SSD, sexual size dimorphism; W, width

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as Rensch's rule, which was originally formulated across related species (Rensch 1950; Fairbairn 1997). The original Rensch's rule occurs in a wide range of taxa and is usually explained by intrasexual selection, as well as among-population allometry (Fairbairn 1997; Székely *et al.* 2004; Raihani *et al.* 2006; Dale *et al.* 2007). On the other hand, size allometry opposite to Rensch's rule (i.e. male size decreases allometrically with female size, $\Delta\text{size}_{\text{female}} > \Delta\text{size}_{\text{male}}$) is also found, though less frequently, in taxa in which female body size is strongly exposed to size selection (typically fecundity selection) and, consequently, females are larger than males (Head 1995; Prenter *et al.* 1999; Dale *et al.* 2007). However, selection pressures other than sexual and fecundity selection are seldom considered while explaining sexual size allometry (see Young 2005). Therefore, it is still unclear whether these size selections are really the most important forces causing the allometry and which selection pressures really shape sexual size allometry. Here, we report unusual among-population allometry for SSD in a Lake Tanganyika cichlid *Lamprologus callipterus*, which is neither explained by sexual selection nor fecundity selection.

This species is characterized as an obligate shell brooder, which always uses empty gastropod shells as a breeding substrate (Sato 1994; Sato and Gashagaza 1997). Reproductive behaviours of this species regarding the use of the shells are drastically different between the sexes, resulting in an extreme male-biased SSD (Sato 1994; Schütz and Taborsky 2000, 2005; see figure 1a). A nest male of *L. callipterus* iteratively transports the shells in his mouth and

makes a clump of the shells (hereafter 'nest', figure 1b) or otherwise takes over a nest held by another male fatigued with nest defence, resulting in extremely polygynous mating systems (Sato 1994). On the other hand, a female chooses a shell in a nest, puts her body in the shell, and deposits eggs on its inner wall (Sato 1994; figure 1c). Although females prefer larger shells, they spawn in the shells size-matched to their own bodies in the field because of female–female competition (Schütz and Taborsky 2005). Therefore, larger shells in which larger, more fecund females will spawn are also valuable for nest males, and thus preferentially accumulated by them (Sato 1994). However, unoccupied larger shells are limited in availability and thus nest males also compete for them (Sato 1994; Maan and Taborsky 2008). Schütz and her coworkers (Schütz and Taborsky 2000, 2005; Schütz *et al.* 2006) showed that body size of *L. callipterus* is closely related to fitness of both sexes; larger nest males can effectively collect larger shells, and have greater body reserves, and thus a higher resource-holding potential (see also Sato 1994); larger females produce a greater number of independent offspring, but their growth is limited because of size-dependent restriction in entering and spawning in the shells. These indicate that nest males are under size selection for large body size owing to the functional relationship between body size and shell size and intrasexual selection. In contrast, females are subjected to fecundity selection owing to the functional relationship between body size and shell size. In this study, we quantified these selection variables in seven populations and tested which variable explains sexual size allometry in *L. callipterus*.

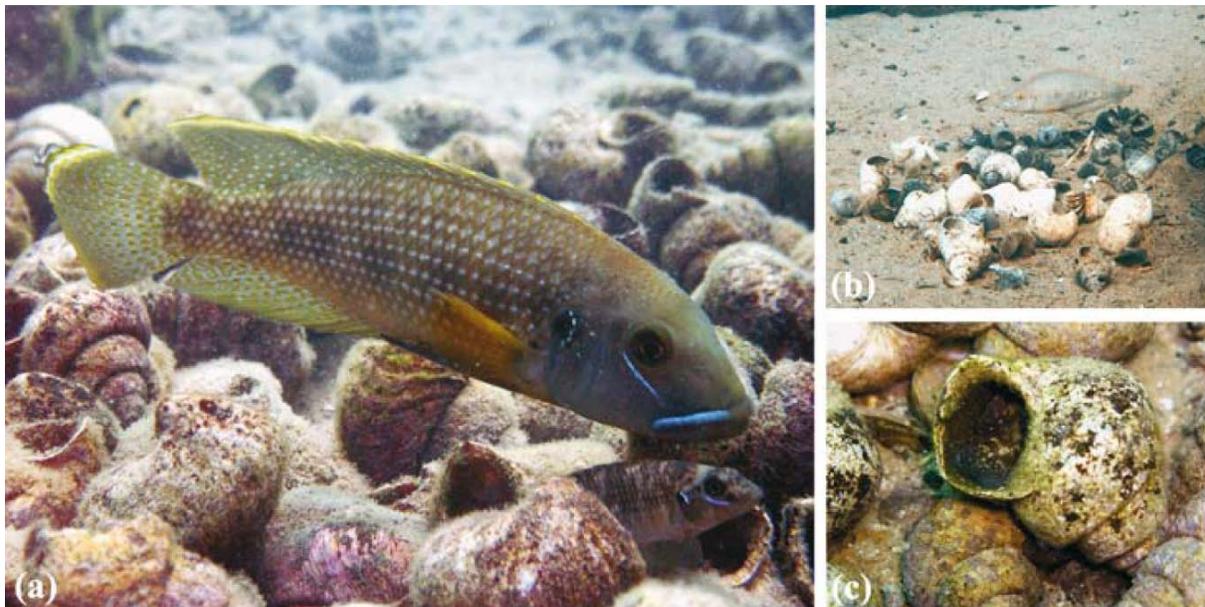


Figure 1. Pictures of *Lamprologus callipterus* in the wild. (a) A pair in Wonzye Point. The larger individual is a nest male. (b) He defends a clump of the shells (i.e. nest). (c) A female provides care for her brood in a shell.

2. Materials and methods

2.1 Field surveys

Samplings and field studies were conducted from August 1987 to January 1988 in two populations of the northern part of Lake Tanganyika (Kalundu and Muzumo); in January 1993 in another northern population (Rumonge) by TS; and from October to November 2005, 2006 and 2007 in a population of the southern part of the lake (Wonzye); from October to December 2007 at three southern populations (Isanga, Kasakalawe and Nkumbula Is.) by KO (figure 2). These samplings were carried out using SCUBA. Although this species is abundant all over the lake, we found nests of *L. callipterus* in only these seven populations out of more than 20 localities investigated. In Kalundu, Kasakalawe and Wonzye, shell-transporting behaviour has been reported (Sato 1994; Schütz and Taborsky 2000, 2005; Maan and Taborsky 2008). In addition, we found spontaneous shell-transporting males in Nkumbula Is. ($N=4$). We also found experimentally induced shell-transporting males in Isanga ($N=3$), Wonzye ($N=2$) and Muzumo ($N=2$, see p. 392 of Alcock 2005); males transported the shells that we put near each nest (approximately 2 m from the centre of the nest). Shell-transporting males were not observed in Rumonge, although such an experiment was not performed. In this population, clumps of shells are available to nest males without having to transport them, since the clumps are created as byproducts of digging activities for nesting by a cichlid, *Lamprologus cunningtoni* (Sato and Gashagaza 1997). On the other hand, spawning or brood-caring females were found in the shells in all the populations examined.

In this study, we examined three possible selection pressures acting on body size of each sex; shell size availability on both sexes, sexual selection on males, and fecundity selection on females. We did not consider selection in terms of food in this study, although food is a well-known ultimate factor that acts differently on the body size of both sexes, and consequently causes among-population variation in SSD (Hedrick and Temeles 1989; Shine 1989; Pearson *et al.* 2002). In *L. callipterus*, both sexes mainly forage a small shrimp species, *Limnocaridina latipes* (maximum body length=9 mm), which is plentiful on rock surfaces, or offspring of other fish species in the populations that we examined (Sato 1994; Yuma *et al.* 1998; Sato [unpublished data]; Takeuchi, Narita and Hori [unpublished data]). Therefore, size and availability of food and the intensity of competition for food would be minor factors for among-population variations in SSD.

In total, we captured 151 nest males defending their nests by a fence net and 487 females in the gastropod shells within the nests by hand. The nests were easily identified as clumps of shells (figure 1b). The presence of a female in the shell

was also readily identifiable by looking inside the shell from the entrance (figure 1c). Captured females were individually packed with their respective shells in small polyethylene bags (120×85 mm) with many water vents and transported to the laboratory. We measured their standard length (SL, nearest to 0.1 mm) in the laboratory. Of the captured fish, 126 nest males and 242 females were dissected after chilling on crushed ice or anesthetizing them with eugenol

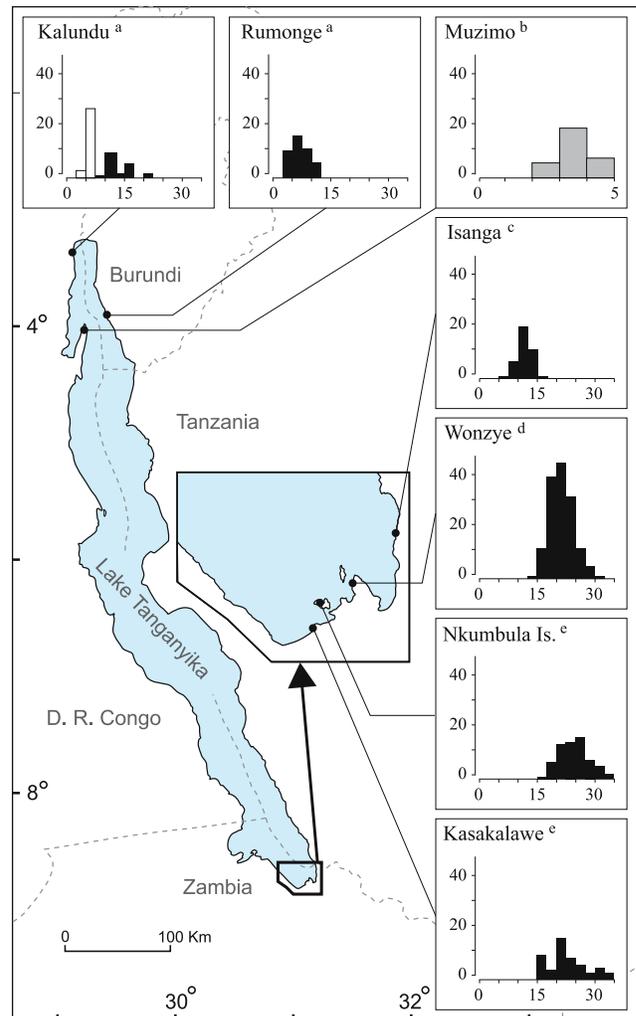


Figure 2. Study populations and variation in the size of shells that females used in each population. In the histograms, X and Y axes indicate shell size (cm³) and the number of shells, respectively. Only shells of a gastropod species, *Neothauma tanganyicense* (Viviparidae, ■), were found within the nests of *L. callipterus*, in all four southern populations ($N_{\text{Isanga}}=9$ nests, $N_{\text{Kasakalawe}}=16$, $N_{\text{Nkumbula Is.}}=16$ and $N_{\text{Wonzye}}=28$), and in Rumonge ($N=10$). However, the nests consisted of *Lavigeria grandis* (Thiaridae, ■) in Muzumo ($N=8$), and of both *N. tanganyicense* and *Paramelania damoni* (Pleuroceridae, □) in Kalundu ($N=8$, see Sato 1994). Different letters beside population names indicate significant differences corrected by the Bonferroni method.

to quantify fecundity selection (*see below*) or for studies with other purposes. The remaining 270 individuals were released at capture points after they were measured. We also measured height (H, to 0.1 mm) and width (W, to 0.1 mm) of 487 shells along the axis from the apex to the outer part of the lip, and along the vertical axis. Shell size was calculated as the volume of a corn ($=W \times H \times \pi / 12$).

To quantify the intensity of male–male competition, we set a quadrat in each population (1500 m² in Isanga, 3400 m² in Kalundu, 150 m² in Kasakalawe, 600 m² in Muzimo, 400 m² in Nkumbula Is. and 600 m² in Wonzye), and calculated nest density. This is because the lack of nest availability generally makes male–male competition intense in fish species where males compete for nest sites (Emlen and Oring 1977; Forsgren *et al.* 1996; Borg *et al.* 2002; Lehtonen and Lindström 2008). In this study, we did not consider intersexual selection, since there is no evidence that female mate choice is based on male body size (Schütz and Taborsky 2005).

In fish, there is generally a morphometric relationship between female body size and fecundity (i.e. larger bodies have larger abdomens that can hold a larger number of eggs). Therefore, we counted the number of eggs in the ovaries of gravid females ($N=98$) out of the 242 females dissected and examined whether fecundity selection acts on female body size. Further, to examine the effect of fecundity selection on sexual size allometry among populations, we quantified the intensity of fecundity selection by reduced major axis (RMA; model II regression) regression slope of the number of eggs on female body size in each population.

2.2 Statistical analyses

To examine sexual size allometry among populations, we performed a standard allometric analysis, i.e. RMA regression of \log_{10} (mean male SL) regressed on \log_{10} (mean female SL) (Fairbairn 1997, 2005). Rensch's rule means where the slope is greater than 1.0 (i.e. positive allometry), while converse Rensch's rule means where the slope is less than 1.0 (i.e. negative allometry) (Fairbairn 1997, 2005). We calculated 99% confidence intervals (CI) to statistically examine the slope of the regression. To clarify factors affecting allometry for SSD, we constructed a full model incorporating SSD as a dependent variable, and shell size, intensity of fecundity selection and intensity of male–male competition as independent variables. The model was refined using backward variable elimination. We lacked data for sexual selection and fecundity selection in Rumonge, since the studies in Rumonge were not originally designed to examine selection pressures acting on body size. Therefore, we did not include data of this population in the analyses, although body size, SSD and shell size are described. RMA regression was performed by using an (S)MATR program

(Falster *et al.* 2003) and other analyses were conducted with R (version 2.8.1).

3. Results

Males were larger than females in all the seven populations, but the magnitude of SSD varied greatly (table 1). In general, the extent of SSD is seldom extreme in species with male-biased SSD, but this species exhibited exceptional extreme male-biased SSD. In particular, males were 60 times heavier than females in the Muzimo population (this is the record for male-biased SSD). Males were considerably smaller in Rumonge compared with the other six populations (48.0 mm vs 95.8–116.0 mm SL), while females varied continuously among populations (table 1), resulting in moderate SSD (2.5 times difference in body weight) in Rumonge. Details of body size and SSD are summarized in table 1.

The size of the shells that females used varied widely among populations (Kruskal–Wallis test, $\chi^2 = 463.2$, $df=6$, $P < 0.0001$, $N=488$, figure 2). Mean body size of both the sexes increased with shell size across populations (males: Spearman correlation, $r_s = 0.928$, $P < 0.01$, figure 3a; females: linear regression, $r = 0.993$, $P < 0.001$, figure 3c). Shell size was normally distributed in all populations except Kalundu where two species of gastropods were used (Kolmogorov–Smirnov test, $P > 0.05$, for the six populations, $P < 0.05$ for Kalundu). However, each shell species was normally distributed ($P > 0.05$ for each shell species). This means that larger shells were scarce in all the populations examined (figure 2). Male body size increased with the intensity of intrasexual selection (i.e. nest density) across populations ($r_s = 0.928$, $P < 0.01$, figure 3b). In each population, larger females had a larger number of eggs in their ovaries (figure 4). Mean female size increased with the intensity of fecundity selection across populations (linear regression, $r = 0.967$, $P < 0.01$, figure 3d).

Allometric analysis showed that the lower and upper 99% CIs of the slope of \log (mean male size) regressed on \log (mean female size) were 0.10 and 0.98, respectively (RMA, slope = 0.31, $r^2 = 0.60$, $P = 0.069$, figure 5a), indicating that allometry for SSD was negative across populations. Multivariate analysis revealed that shell size was the predictor of SSD (table 2, figure 5b).

4. Discussion

In *L. callipterus*, body size and SSD varied substantially among populations, but males were always the larger sex. In this situation, Rensch's rule is expected to apply because of sexual selection acting strongly on males (Fairbairn and Preziosi 1994; Fairbairn 2005; Lengkeek *et al.* 2008; Walker and McCormick 2009,

Table 1. Summary of body size measurements of both sexes in seven populations of *L. callipterus*

Populations	Body weight (g)												SSD [†]						
	Standard length (mm)						ANOVA												
	Females			Nest males			Females			Nest males				ANOVA					
N	Mean	SD	Range	N	Mean	SD	Range	N	Mean	SD	Range	F	Range	F	Range	SL	BW		
Muzimo	46	27.9	1.5	25.3–31.0	22	104.0	5.1	95.4–114.3	46	0.48	0.10	0.30–0.75	22	28.86	4.28	21.5–38.4	2051.6**	3.73	59.76
Kalundu	59	36.0	5.5	25.7–49.2	14	95.8	6.9	86.3–110.1	59	1.22	0.59	0.38–2.81	14	20.83	5.51	14.4–32.0	744.3**	2.66	17.05
Isanga	42	43.4	4.2	33.4–50.2	25	113.9	6.3	103.3–124.3	42	2.07	0.61	0.86–3.43	25	31.95	6.93	20.0–44.8	779.1**	2.63	15.41
Kasakalawe	57	51.2	2.7	45.9–57.7	16	115.2	5.1	107.9–125.7	57	3.28	0.60	2.04–4.66	16	34.59	6.73	23.4–48.6	1243.1**	2.25	10.54
Wonzye	157	52.2	3.1	42.0–60.6	33	116.0	7.1	101.9–126.7	152	3.46	0.66	2.05–5.27	32	34.23	7.17	21.6–49.8	2743.0**	2.22	9.89
Nkumbula Is.	80	53.6	3.7	43.7–61.4	26	115.9	5.5	100.7–125.9	78	3.66	0.84	2.11–5.65	26	34.62	5.48	23.6–43.8	2370.8**	2.16	9.45
Rumonge	46	34.9	2.5	30.9–42.0	15	48.0	2.2	45.0–52.7	21	0.77	0.25	0.47–1.55	15	1.90	0.21	1.59–2.36	202.0**	1.38	2.45

** indicates $P < 0.0001$

† Sexual size dimorphism (SSD) indicates the ratio of males to females.

but see Kraushaar and Blanckenhorn 2002; Blanckenhorn *et al.* 2006). In *L. callipterus*, however, allometry for SSD was negative across populations, inconsistent with Rensch's rule.

Before asking why such unusual allometry for SSD occurs in this species, we first inquired why body size differs widely among populations. In this study, we found that nest male size increases with nest density. In this fish, nest males compete for the larger shells that females prefer. However, the larger shells are usually occupied by others, and nest males accordingly get them by stealing from the nests of neighbours, resulting in intense male–male combats between neighbours (Sato 1994; Maan and Taborsky 2008). Our pilot observations conducted in Wonzye revealed that nests with closer neighbours have more frequent intrusions of such thieves, i.e. competitors (Poisson regression, $r=0.46$, $P < 0.01$, $N=17$ nests [unpublished data]), suggesting that male–male competition is more intense when nest density is higher in this species (Sato 1994). Given these findings, the observed positive correlation between male size and nest density implies that intrasexual selection positively affects male body size. We found a positive correlation between female size and fecundity slope across populations. In each population, fecundity increased with female body size, perhaps due to a functional morphometric relationship between body and ovary size. Therefore, female body size should be subjected to fecundity selection in favour of large bodies.

In spite of these facts, neither of these two major selection pressures explained the negative allometry for SSD among populations of *L. callipterus*. Instead, the negative allometry was well explained by shell size. We found that shell size was positively correlated with the body sizes of both the sexes. In this fish, nest males are required to be more powerful, and thus larger in size, for transporting larger shells, while females enter the shells to spawn and thus their body size is strictly limited by the size of the shells available. Together with sexual and fecundity selection, larger is better for males, but female size is optimized between conflicting selection forces (i.e. fecundity selection and growth depression, *see also* Schütz *et al.* 2006). The correlations indicate independent adaptive responses of each sex to shell size, but not a correlated response of one sex to size selection on the other sex. The negative allometry for SSD is therefore explained by the female response to shell size availability.

However, the argument must be carefully considered, because males have a greater variation in size than females among populations, given the Rumonge population where males were unexpectedly small compared with other populations (*see* figures 3, 5). This exceptionally small male size cannot be solely explained by shell size, as Rumonge was an outlier in the relationship between body and shell

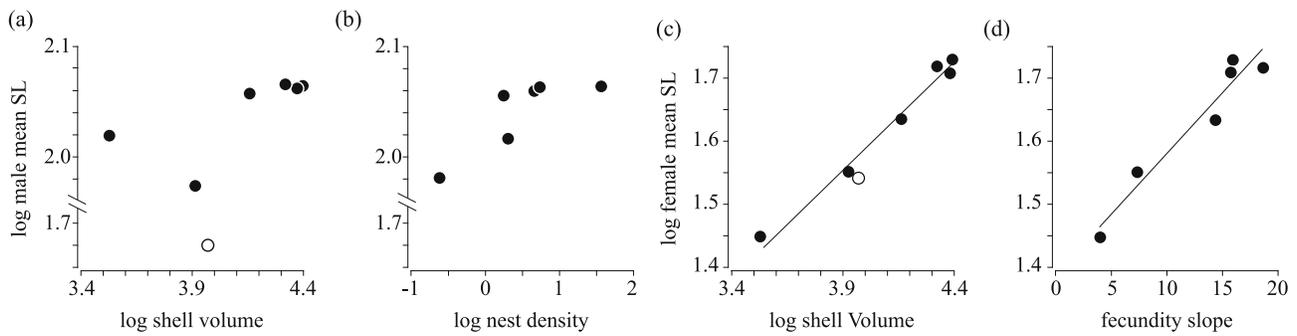


Figure 3. Across-population correlations between body size and possible selection pressures. Mean male body size was positively correlated with (a) shell size and (b) nest density across populations. Note that male size in Rumonge (a blank circle) is an outlier in the correlation with shell size. Mean female body size was positively correlated with (c) shell size and (d) fecundity slope across the populations. Note that female size in Rumonge is in a regression line (a solid line) with shell size across the other six populations.

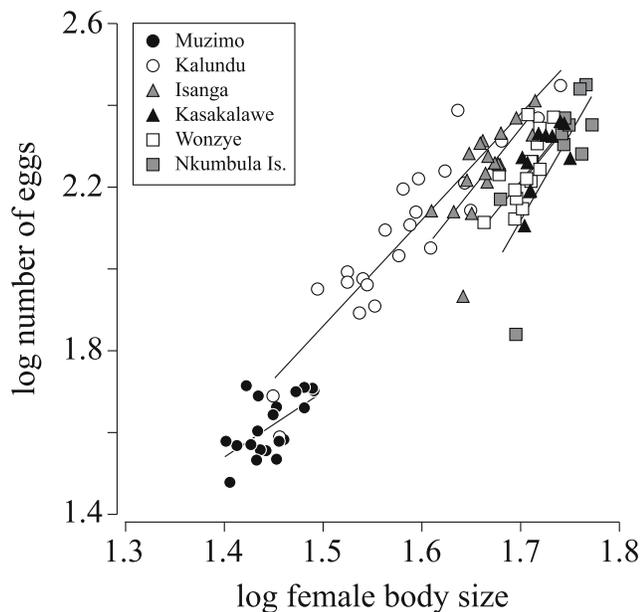


Figure 4. Females with a larger body size showed an increase in the number of eggs produced in all populations examined (Pearson correlation, Muzimo: $r=0.61$, $P<0.01$, $N=20$; Kalundu: $r=0.92$, $P<0.001$, $N=23$; Isanga: $r=0.79$, $P<0.001$, $N=18$; Kasakalawe: $r=0.62$, $P<0.05$, $N=11$; Wonzye: $r=0.43$, $P=0.01$, $N=14$; Nkumbula Is.: $r=0.80$, $P<0.01$, $N=11$).

size (figure 3a). Sexual selection is also unlikely, since the shell clumps created by the breeding activities of another species are the limited resource for reproduction in this population (rather than individual shells; *see* Methods). The clumps are widely scattered on the lake floor with a very low density (<0.01 nest/m², Sato [personal observation]), suggesting that nest males are exposed to intense intrasexual competition (Emlen and Oring 1977; Forsgren *et al.* 1996; Borg *et al.* 2002; Lehtonen and Lindström 2008).

Instead, two other selection pressures may explain the small male size in this population. First, nest males in Rumonge are likely to be freed from a strong size selection pressure induced by shell transporting (Sato and Gashagaza 1997). Indeed, they were much below the size required for transporting shells (i.e. <90 mm SL, Schütz and Taborsky 2005). Second, the small size of males in this population is considered to be an adaptation primarily to the habit of using the shells as a shelter. Rumonge nest males take refuge in the shells when they encounter any threats, as there is no other shelter available for nest males (Gashagaza *et al.* 1995). Therefore, male body size of the Rumonge and the other populations is under different size-selection pressures. On the other hand, the sizes of females are continuously variable among all populations in line with available shell sizes (figure 3c).

Importantly, the interpopulation allometry for SSD was violated when considering the Rumonge population. Sexual

Table 2. Multivariate analysis to detect factors predicting allometry for SSD.

Variable	Full model ($R^2 = 0.930$, $P = 0.041$)				Best-fit model ($R^2 = 0.953$, $P < 0.001$)			
	Coefficient	SE	t	P	Coefficient	SE	t	P
Shell size	-0.313	0.095	-3.283	0.082	-0.255	0.025	-10.14	0.0005
Nest density	0.009	0.018	0.518	0.656	NS	NS	NS	NS
Fecundity slope	0.003	0.006	0.504	0.664	NS	NS	NS	NS

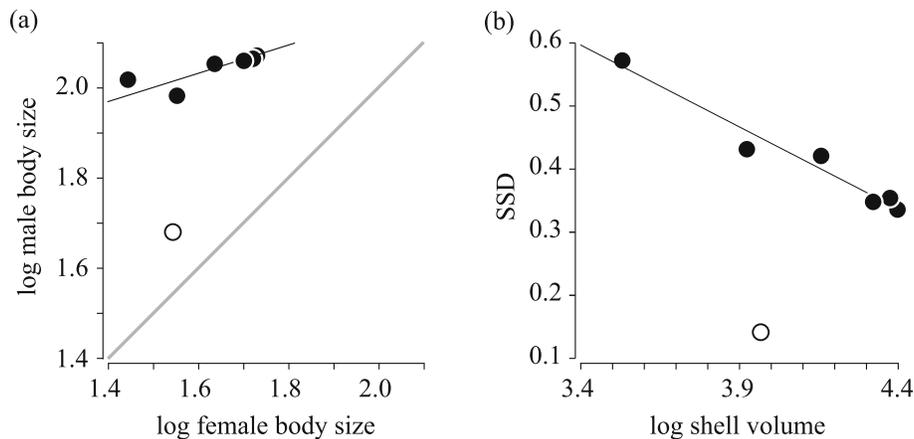


Figure 5. (a) Allometry for SSD inconsistent with Rensch's rule in *L. callipterus*. The light line illustrates an isometric line ($y=x$), and the solid line represents the slope of the RMA regression of \log_{10} (male size) on \log_{10} (female size) across all the populations except Rumonge. The linear relationship was broken when Rumonge (a blank circle) was included ($F_{1,5}=1.41$, $P>0.28$), suggesting that Rumonge was out of the allometric relationship. (b) Shell size well explained the interpopulation variation in SSD. A line represents a linear regression line across all the populations except Rumonge. The relationship was violated when Rumonge was included ($F_{1,5}=1.33$, $P>0.30$).

size allometry analyses consider only the situation that body size varies along the common size-selection regimes among populations or related species, typically sexual or fecundity selection. However, as in *L. callipterus*, actual animals might penetrate to alien environments and thus experience different size-selection regimes among populations, which are beyond theoretical expectations.

Originally, it was thought that interspecific allometry for SSD reflects the genetic response of individual species to selection through evolutionary time (Fairbairn 1997). On the other hand, it is possible that intraspecific variation in body size results from phenotypic plasticity, local genetic adaptations (Fairbairn 2005; Pyron *et al.* 2007; Lengkeek *et al.* 2008), or migration to the populations suited for their own phenotypes. In *L. callipterus*, body size plasticity might be a possible explanation for intraspecific allometry for SSD. First, females can change their growth rate according to shell size availability (Schütz and Taborsky 2005). Second, *L. callipterus* may travel among populations, since they take part in schools, roaming throughout offshore sandy bottom areas when young (Sato *et al.* 2004). It is suggested that gene flow among the southern populations occurs relatively frequently in such highly dispersed cichlids (e.g. *Lepidolamprologus attenuates* and *Neolamprologus tetracanthus*; Maeda Y and Nishida M [unpublished data]). Third, owing to this large dispersal potential and the population-specific patterns of size-selection pressures, *L. callipterus* will not necessarily face size selection pressures equivalent to those to which their parents were exposed. Ultimately, individuals that have the ability to plastically adjust their body size and life histories in response to the size availability of the reproductive resources will be favoured. On the other hand,

migration in the adult stages among populations suited for particular phenotypes does not seem to be adaptive. The roaming school moves randomly on the wide sandy bottom, rather than toward particular populations. Further, mortality and time costs involved in searching for suitable populations in schools seem to be extremely large, especially after the fish reach sexual maturation. Comprehensively, in *L. callipterus*, negative allometry means that females are more sensitive to local shell size, although nest males may have a wider range of size plasticity than females.

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Tanganyika from CRSN, the Burundi government, and the Zambian Ministry of Agriculture, Food and Fisheries, and complies with the laws of each country.

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