

An optimality approach to male and female body sizes in an extremely size-dimorphic cichlid fish

Dolores Schütz,^{1,2} Geoffrey A. Parker,³ Michael Taborsky² and Tetsu Sato⁴

¹Konrad Lorenz Institut für Vergleichende Verhaltensforschung (KLIVV), Austrian Academy of Sciences, Vienna, Austria, ²Department of Behavioural Ecology, Institute of Zoology, University of Bern, Bern, Switzerland, ³Population and Evolutionary Biology Research Group, School of Biological Sciences, University of Liverpool, Liverpool, UK and ⁴Lake Victoria Project, Graduate School of Bioscience and Biotechnology, Tokyo Institute of Technology, Yokohama, Japan

ABSTRACT

Question: Can intrasexual selection on male size and natural selection on female size in the shell-brooding cichlid *Lamprologus callipterus* explain the greatest male/female sexual size dimorphism (SSD) reported to date among animals?

Mathematical methods: (1) Mortality model to predict male and female body sizes. (2) Gain rate maximization and (3) combined mortality/gain rate maximization model to predict female size. We compared observed body sizes in the field with predictions from these models.

Key assumptions: (1) Body size at sexual maturity is determined by a trade-off between survival to sexual maturity and (a) number of mates in males and (b) fecundity in females. (2) Female body size is constrained by increasing search costs, because (3) shells large enough for breeding become limited as females become larger.

Results: (1) Male body size predicted by the mortality model matches size as found in the field closely, but the model strongly overestimated female size. (2) The female body size predicted by the gain rate maximization model fitted well within the range of sizes observed in the field. (3) Including the effect of mortality into this model hardly changes the prediction.

Conclusions: (1) Intersexual selection can explain male body size, but fecundity selection alone cannot explain female size. (2) The breeding substrate strongly constrains female size. (3) The extreme male-biased SSD is due to strong selection on the body sizes of both sexes in opposite directions.

Keywords: ecological constraints, ESS model, natural selection, sexual size dimorphism, shell brooding.

INTRODUCTION

Sexual size dimorphism (SSD) arises from different selection pressures on male and female body sizes (e.g. Schulte-Hostedde *et al.*, 2002; Blanckenhorn, 2005). When females are the larger sex, it is

* Author to whom all correspondence should be addressed. e-mail: michael.taborsky@esh.unibe.ch
Consult the copyright statement on the inside front cover for non-commercial copying policies.

usually attributed to the effects of natural selection acting on female fecundity (Ghiselin, 1974; Woolbright, 1983; Carothers, 1984; Bisazza, 1993). Sexual size dimorphisms with females larger than males can take extreme forms, as in deep-sea anglerfish, where ‘dwarf’ males may be about half a million times lighter than females (e.g. Ghiselin, 1974; Pietsch, 2005).

The opposite SSD (males larger than females) never rises to such extremes: male size is rarely more than twice female size (Parker, 1992). When body size or some other character (e.g. tail length) is larger in males than in females, this is usually attributed to sexual selection (Darwin, 1874), acting through male–male competition [intrasexual selection (e.g. Shine, 1978; Wiklund and Forsberg, 1991)] or through female choice [intersexual selection (e.g. Basolo, 1990; Jormalainen *et al.*, 1994)]. Polygamy and increased male–male competition often correlate with the direction and extent of sexual dimorphism (Cheverud *et al.*, 1985; Björklund, 1991; Weckerly, 1998; Loison *et al.*, 1999; Székely *et al.*, 2000). In different species of angelfish, for example, Moyer *et al.* (1983) found that species with harems, leks, and promiscuous explosive breeding were most dimorphic.

Other primary selective forces for the evolution of different body sizes of males and females could be natural selection, for reduction in food competition between the sexes (Darwin, 1874; Carothers, 1984), for increasing the feeding efficiency in one sex (Bielefeldt *et al.*, 1992), or for different requirements of locomotion (Schütz and Taborsky, 2003). The degree of SSD may also relate to the male role in parental care (Hughes and Hughes, 1986).

Lamprologus callipterus, a shell-brooding cichlid of Lake Tanganyika, shows an extreme SSD with territorial males being on average more than 12 times bigger than females [body mass (Sato, 1994; Schütz and Taborsky, 2000)]. Although in cichlids males are usually larger than females or of similar size (Erlandsson and Ribbink, 1997), this is the most extreme SSD in this direction known among animals. Our experimental study suggested that male and female sizes in *L. callipterus* were limited in opposite directions by their breeding substrate, empty gastropod shells. Males need to be large enough to collect and carry the shells, and females must be small enough to fit into shells for breeding (Schütz and Taborsky, 2005). An influence of intrasexual selection on male size was also suggested, but intersexual selection appeared to be of minor importance (Schütz and Taborsky, 2005).

Our aim here is to determine whether intrasexual selection on male size and natural selection on female size can explain the extreme SSD of *L. callipterus*. We first examine whether a life-history strategy model of SSD in fish (Parker, 1992) can explain adult sizes, here called model 1. Applying the same male model, we then model optimal female size under the assumption that females are selected to maximize reproductive gain rate (number of offspring per unit time, model 2) and compare this with the first model’s prediction. We wish to compare two quite different effects on female body size – the effect of mortality (model 1) and the constraint on female reproductive rate generated by the availability of suitable shells (model 2). There is no relationship between the two models, model 1 being the normative model, while model 2 would explain that shell availability is likely to constrain female size very strongly. Finally, we combine the mortality and gain rate models for females to determine which exerts the stronger effect (model 3). Predictions are then compared with observed fish sizes in the field.

For males, model 1 predicts the optimal switch size to nest male status, even though males may have reproduced already as sneakers (see Fig. 1). From the low participation and success rates of sneakers, we argue that the sneaker phase is largely a growth phase on the pathway to nest male status (Parker, 1992; Taborsky, 2001). Males of sneaker size are found mainly in schools that roam about feeding (Parker, 1992). Their contribution to male lifetime

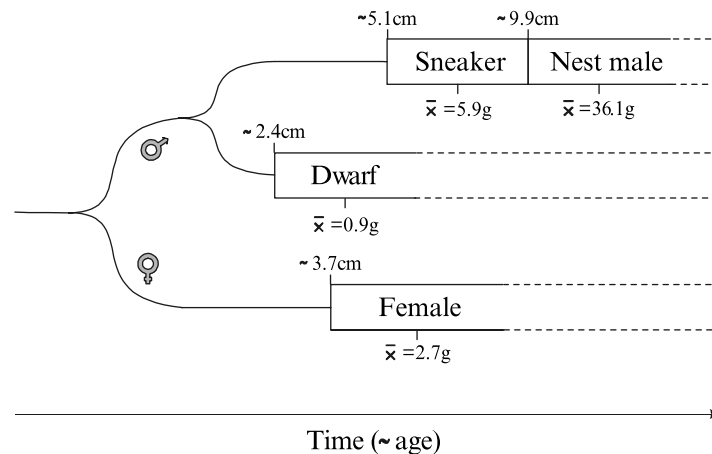


Fig. 1. Alternative life-history pathways in *L. callipterus*. Numbers indicate mean observed body weight (WT, g) and minimum observed standard body length (SL, cm) in the field. The abscissa represents time (i.e. the age of the fish).

reproductive success is apparently very small (Meidl, 1999; Sato *et al.*, 2004), suggesting that their influence on the switch age to nest male behaviour can be ignored. The presence of mature testes and sperm in only a small proportion of medium-sized males [i.e. sneakers (Rijneveld, 2002)] probably reflects an opportunistic tactic with low costs and benefits. Since growth continues after the switch ages, but more so in males than in females, the SSD ratio increases for adult averages [in the field, this is 13.18 (body mass ratio) or 14.90 (standard length³ ratio)].

NATURAL HISTORY OF *LAMPROLOGUS CALLIPTERUS*

Large, territorial males defend territories and collect empty snail shells as spawning substrate ['nest males' (Sato, 1994)]. Females reach sexual maturity after approximately 6 months; males become territorial after more than one year. In the laboratory, females and males survived several years, but from otolith data from field samples it appears that maximum longevity in nature is about 3 years (N. Rijneveld, E. Ripmeester and M. Taborsky, unpublished data). Both sexes continue to grow after maturity, although at a slower rate than before maturity. Reproduction varies with a lunar cycle, and a female can produce several clutches per year. Females always change shells/mates between clutches; they leave the shell after brood-care, feed in roaming schools for some time, and when ready to spawn again, search for a new breeding substrate. Males can hold their territories for several months, and many females may breed simultaneously in the same territory.

In our study areas near Mpulungu, Zambia, only empty shells of the gastropod *Neothauma tanganicense* are used for breeding. Male size and the number of shells in their nests were not significantly related to each other (Schütz and Taborsky, 2005). Females enter a shell for spawning and care for eggs and larvae for 10–14 days by fanning and guarding. Reproductive success increases with female body size, and the largest females spawn in the largest shells (Schütz and Taborsky, 2000).

In addition to nest males, two other types of male exist, both of which are reproductively parasitic on nest males (Sato *et al.*, 2004) (see Table 1 for body and gonad sizes of the three male

Table 1. Observed measures of standard length (SL, mm), body weight (BW, g), gonad weight (GW, mg), and gonadosomatic index ($GSI = GW/WT \times 100$) of the three male types at Wonzye Point (mean $\pm$ standard deviation (range))

Male type	<i>n</i>	Standard length	Body weight	Gonad weight	Gonadosomatic index
Nest male	30	112.7 $\pm$ 10.1 (95.0–128.9)	36.1 $\pm$ 7.3 (21.4–49.8)	124.9 $\pm$ 37.9 (64.6–225.9)	0.36 $\pm$ 0.12 (0.17–0.59)
Sneaker	10	59.8 $\pm$ 6.0 (50.5–69.4)	5.9 $\pm$ 2.0 (3.4–9.0)	59.2 $\pm$ 35.4 (8.1–106.4)	0.94 $\pm$ 0.43 (0.24–1.36)
Dwarf	551	33.4 $\pm$ 3.8 (24.0–40.9)	0.9 $\pm$ 0.3 (0.3–1.5)	13.8 $\pm$ 5.4 (3.2–26.8)	1.73 $\pm$ 0.72 (0.33–3.84)

types). Males have two alternative life-history pathways (Fig. 1). Males on the pathway of continuous growth towards nest male status may first behave as sneakers, by entering a territory during spawning to fertilize eggs while the territory owner is inattentive. Their tactic is opportunistic and transitional and occurs typically before the switch to nest male behaviour (Taborsky, 2001). In the other pathway, males remain very small and attempt to enter shells in which females are spawning ('dwarf males' (Taborsky, 1998, 2001; Sato *et al.*, 2004)). They halt growth before reaching female size and remain parasitic throughout life (Taborsky, 2001).

Parasitic spawnings are rare under natural conditions. In 45 completely observed spawning events, two sneakers and one dwarf male participated successfully (Sato *et al.*, 2004). In seven nests in which the nest owners spawned with 43 females in total, the ratio of nest male/sneaker ejaculations was 1853/30 [or 62:1; continuous video recordings in the field (Pachler, 2001)]. Using microsatellite markers, Meidl (1999) found that six sneakers observed to participate in two spawnings in the field sired only 3% of the offspring produced. From these data we estimate that only 0.13% of young produced under natural conditions are sired by sneakers (4.4% of undisturbed spawning events with sneaker participation, with 3% of offspring sired by sneakers in these cases). In contrast, dwarf males were more successful (Meidl, 1999).

In this paper, we focus on the extreme SSD found in this species, which is the size of nest males relative to adult females. Variables required for parameter estimates of the models and for the comparison between predicted and observed sizes were obtained in the field at the southern end of Lake Tanganyika (Schütz and Taborsky, 2000, 2005). The way in which selection acts on dwarf males' size is not considered here; these males follow a different life-history pathway (Taborsky, 2001) (see Fig. 1).

ANALYSIS

For males, we used an optimality model (1) to predict the optimal size for switching to nest male status (for simplicity called 'maturity'). The fitness optimum is determined by the trade-off between intrasexual competition and survival to maturity. For females, we used model 1 to predict the optimal size at sexual maturity, but the fitness optimum is determined by the trade-off between fecundity and survival to maturity. For simplification, we refer to model 1 as the 'mortality model'. To determine whether female size is more strongly constrained by the size distribution of available shells than survival to maturity, we used model 2, in which optimal female size at maturity is determined by the trade-off between fecundity

and the interval between successive broods. We refer to model 2 as the ‘gain rate maximization model’. In the combined mortality/gain rate maximization model (3), we combine the two effects on female body size.

A match between the body sizes predicted from these models and those observed in the field would suggest that these trade-offs may have moulded the body sizes of *L. callipterus*. As a measure of body mass we used cubed standard length (SL^3) of individual fish (Beverton, 1987).

Model 1: mortality model

The fitness, W , of a given individual is the product of its expected number of breeding episodes, P , and its reproductive success per breeding episode, R , where both are functions of the switch age from growth to maturity, t_f for females and t_m for males (see Parker, 1992, for details). Reproductive success gained per breeding episode (for males, the number of spawning females; for females, the number of gametes produced) relates to adult body size, given that maturity occurs at t_f in females and onset of nest male status occurs at t_m in males. Thus for females

$$W_f(t_f) = P_f(t_f) \cdot R_f(s_f(t_f)) \quad (1a)$$

where R depends on body size, s_f , which depends on switch age, t_f .

Male fitness is derived by an evolutionarily stable strategy (ESS) approach. In a population playing the ESS switch age, t_m^* , the fitness of a mutant male deviating by playing $t_m \neq t_m^*$ is

$$W_m(t_m, t_m^*) = P_m(t_m) \cdot R_m(s_m(t_m), t_m^*) \quad (1b)$$

Let P_i be the expected number of breeding episodes viewed from time of hatching ($t = 0$), and d_i the instantaneous death rate, where the subscript i refers to the sex (m or f). We assumed that d_i is constant with respect to age, because it did not vary in our field data (see below). The chance of survival to adulthood is $\exp(-d_i t_i)$. The expected number of breeding episodes, given that an individual has survived to maturity, is proportional to the adult lifespan, which is $1/d_i$ (see Charnov, 1993). Thus for sex i , we can write

$$P_i \propto \exp(-d_i t_i)/d_i \quad (2)$$

Optimal switch age, t_i^* , for sex i is found by setting $\partial W_i / \partial t_i = 0$, subject to $\partial^2 W_i / \partial t_i^2 < 0$ for a maximum. This is given by

$$\frac{\partial R_i^*}{\partial t_i} = d_i R_i^* \quad (3)$$

(see Parker, 1992).

Growth

Fish growth typically approximates to the growth function proposed by von Bertalanffy (1957), which is sigmoidal, rising to an asymptotic maximum size. However, Day and Taylor (1997) reasonably argued that direct use of this function is inappropriate for estimating optimal time of maturity, since it itself arises from the decreased expenditure on growth after maturity. Lester *et al.* (2004) have argued that von Bertalanffy is essentially the correct function for fish growth before maturity, if modified to include parameters for metabolic

Table 2. Parameters fitted to the linear growth function in males and females, and statistics (mean $\pm$ standard error)

	Growth rate, K	Age at which size is theoretically zero, t_0	n	χ^2
Males	1.056 ± 0.0858	109.6 ± 12.79	40	7105.252
Females	0.5509 ± 0.0769	78.94 ± 11.65	16	1270.37

intake and maintenance. The modifications generate linear growth before maturity, and so here we take body mass (i.e. SL^3 or simply s) at time t as

$$SL^3(t) = s(t) = K(t - t_0) \quad (4)$$

where K is the juvenile growth rate in SL^3 , and t_0 is a constant defining an age at which body size is (theoretically) zero. The best fits for the linear growth functions (here SL^3 , equation 2), obtained from field data (for detailed methods, see subsection ‘Parameter estimates’), and statistics are given in Table 2. Male growth rate in the field was almost twice as high as female (more strictly, juvenile) growth rate.

Reproductive success

In the field and in the laboratory, females did not choose males according to size (Schütz and Taborsky, 2005). Neither nest size (i.e. number of shells per nest) nor mean shell size per nest was related to male body size (Schütz and Taborsky, 2005). However, larger males had higher competitive ability and reproductive success, which was measured as number of shells with brood-caring females inside. A given male’s reproductive success therefore is assumed to be proportional to his body size relative to the ESS size, s_m^* , at maturity:

$$R_m(S_m(t_m), t_m^*) = c \cdot \left[\frac{s_m(t_m)}{s_m^*} \right]^a \quad (5)$$

where a and c are positive constants, and s_m is the body size (SL^3) of a rare strategy deviating by playing a maturity size of $s_m \neq s_m^*$. The ESS size, s_m^* (taken as the mean body size of nest males), and the number of spawning females obtained by males of different sizes, $R(s_m(t_m))$, were estimated from field data (see ‘Parameter estimates’). The mean body size (11.27 cm standard length) of nest males in the field, when cubed, serves as an approximation for s_m^* ; it will be somewhat greater than the mass at which males start to defend nests because of indeterminate growth. Since mean shell size did not differ between nests of different sized males (see Schuetz and Taborsky 2005), female size was not factored in the equation.

Female reproductive success per breeding episode, R_f , is assumed to equal the number of eggs produced, G_f , which relates to female size, s_f , as

$$R_f(s_f) = G_f(s_f) = g_f \cdot s_f^r \quad (6)$$

where g_f and r are constants.

Mortality rates

The probability of surviving to time t (days) is $S_t = \exp(-d_i t)$; hence $d_i = -\ln(S_i)/t$, where d_i

is the instantaneous mortality rate (units day^{-1}). Mortality rates were obtained from field data (see 'Parameter estimates').

Optimal switch sizes

Optimal switch times for females (t_f^*) and males (t_m^*) were calculated by substituting the explicit functions for growth, reproductive success, and juvenile mortality into (3):

$$t_f^* = 1/d_f + t_{0f} \text{ for females} \quad (7a)$$

$$t_m^* = a/d_m + t_{0m} \text{ for males} \quad (7b)$$

where t_{0i} is the time where body mass is theoretically zero (see equation 4). The optimal switch time for females is $t_f^* = 715.88$ days, and that for males $t_m^* = 624.17$ days. Optimal switch sizes were found by calculating the sizes at t_f^* and t_m^* from the linear growth curves (4), and gave $\text{SL}^3 = 543.39 \text{ cm}^3$ ($\text{SL} = 8.168 \text{ cm}$) for males and $\text{SL}^3 = 350.89 \text{ cm}^3$ ($\text{SL} = 7.053 \text{ cm}$) for females (see Fig. 2). Note that this method of calculating the optimal switch sizes is based on the modification of the von Bertalanffy growth curve proposed by Lester *et al.* (2004), and must be seen as an approximate estimate of the onset of maturity.

Parameter estimates

Growth. To estimate juvenile growth rates (in SL^3), we used unpublished data provided by C.J. Rijneveld (see also Rijneveld, 2002), who collected *L. callipterus* at Kasakalawe Bay and

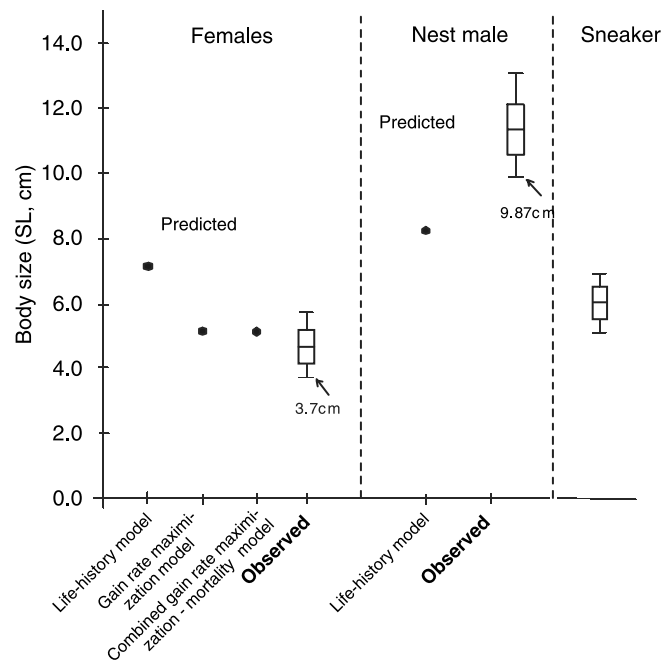


Fig. 2. Predicted and observed body sizes of *L. callipterus* males and females. Boxes indicate mean observed standard body length (SL) $\pm$ standard deviations in the field; lines indicate the total size range (at Wonzye Point). The observed minimum switch sizes are given in the graph (SL, cm) for comparison with the predictions.

counted all daily micro-scale sagittal otolith bands in 16 juvenile fish (< mature females) and 50 immature males (> mature females). We assumed that otoliths start to grow at the age of about 3 weeks (Rijneveld, 2002) and took fish age as the number of bands + 20.

Within the size range of immature females, we assumed that males and females show the same growth pattern; both sexes feed in large feeding schools without any dominance hierarchies and have the same lifestyles. Sixteen juveniles of unknown sex, smaller than mature females, were therefore used to estimate female growth rate. With increasing size and increasing number of otolith rings, age estimation became more difficult. In older individuals, rings in damaged areas could sometimes not be counted precisely, and had to be extrapolated. Potential error therefore increased with increasing age/size. For this reason, in estimating male growth rate we included only the 16 juveniles mentioned above, plus 24 immature males of nest male type younger than one year. Both K and t_0 were estimated by applying standard curve-fitting procedures to the data (Kleinbaum and Kupper, 1978).

Male reproductive success. We caught and measured 14 nest males at depths of 9–12 m at Kasakalawe Bay near Mpulungu, Zambia. To determine male reproductive success, we counted the number of brood-caring females within their nests, calculated the average male body mass, and determined the ratio of each male mass to the average mass. Parameters a and c were estimated by fitting a curve to these data (Fig. 3), which gave $a = 3.822 \pm 1.408$ and $c = 5.731 \pm 1.795$ (values $\pm$ standard errors, $\chi^2 = 26.09$).

Female reproductive success. In the laboratory, we measured and marked 35 females and placed them in 100-litre tanks together with nest males. Ten days after each female spawned, the female and young were carefully shaken out of their shells and the offspring counted. We regressed $\log_{10}$ (number of eggs) against $\log_{10}$ (female SL^3) and found a highly significant

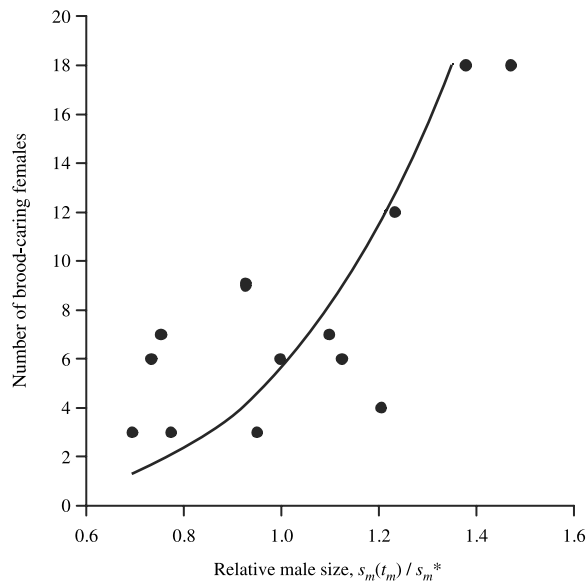


Fig. 3. Relative male size and reproductive success, measured as the number of brood-caring females simultaneously present in a male's nest.

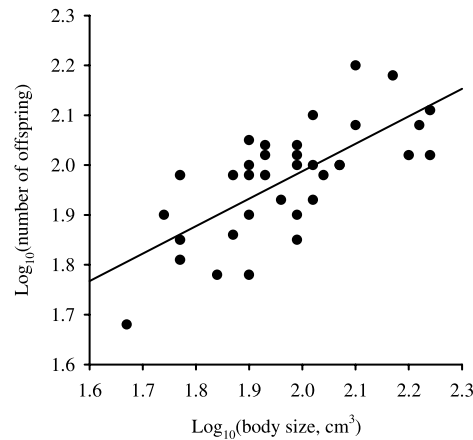


Fig. 4. Female size and reproductive success (with regression line). Data on body size (cm^3) and offspring number were log-transformed.

positive relationship ($t_{34} = 5.67$, $P < 0.001$; Fig. 4), with the slope $r = 0.998$ (Fig. 4), taken as 1.0 as expected for direct proportionality.

Male mortality. To estimate male mortality rate, d_m , we counted all males > 6.0 cm standard length along transects at Kasakalawe Bay (six size classes, sexing of fish < 6.0 cm was impossible). By scuba diving, we checked two transects along the bottom from 1 to 12 m depth (150 m long, 2 m wide) ten times each within 10 days, during which period the fish could not have moved from one size class to the next. Sizes were transformed into mass estimates, SL^3 . Assuming a stable age distribution, we calculated (i) the proportion of males surviving to each size class, and (ii) the time taken to grow from one size class to the next, t , from the best fitting von Bertalanffy growth function. Mortality rate did not appear to change with size ($r^2 = -0.2559$, $n = 5$ size classes, $P = 0.385$), so d_m was taken as the average across all size classes.

Female mortality. To estimate female survival, S_f , we collected 31 breeding females from 14 nests in the field and transferred them to aquaria (three size classes). After they finished brood care and left their shells, their body length was measured and the time to grow from one size class to the next and their average daily mortality were calculated as described for males. Thus for five size classes of males and two size classes of females, we were able to calculate the proportion of fish surviving from this class to the next and the time it takes to survive from one size class to the next (Table 3a, b).

The instantaneous mortality rate, d_i , was calculated from the average mortality across size classes, giving for males $d_m = 0.00748$ (Table 3a) and for females $d_f = 0.00157$ (Table 3b).

Model 2: gain rate maximization model

Selection is assumed to maximize female reproductive gain rate. Our aim is to examine whether female size can be explained entirely by the constraint of finding suitable shells for her eggs – that is, aside from all the other considerations covered in model 1. Fitness, W_f , is

Table 3. Mortality rates (see ‘Analysis’ for details)

Size class (cm ³)	Proportion surviving	Time (days)	Daily mortality rate, d_m
(a) Males			
210–400	113/313	101.1	0.0101
410–600	56/113	129.8	0.00541
610–800	14/56	134.5	0.0103
810–1000	6/14	150.9	0.0056
1000–1200	1/6	297.5	0.00602
(b) Females			
75–125	12/19	493	0.000932
125–175	2/12	811.2	0.00221

Note: The mortality rates did not differ significantly between size classes (see text).

the number of gametes, G_f , produced at a given spawning, divided by the total time it takes the female to complete investment in this egg batch:

$$W_f(s_f) = \frac{G_f(s_f)}{C + T_s(s_f)} \quad (8)$$

where $C = (T_d + T_l + T_b)$ is the time taken for the female to develop the eggs (T_d), lay (T_l), and care for the brood (T_b). $T_s(s_f)$ is the time it takes to find a suitable shell for laying. We accept that reproduction peaks around full moon and (8) assumes continuous breeding (i.e. many batches over a long expected adult lifetime). However, we believe it to be a valid approximation since there are always females searching for shells, laying eggs, and breeding (i.e. also around new moon). Fitness is maximized by maximizing the rate of production of progeny during this long time.

In the laboratory, we tested whether the time to develop a clutch, T_d , depends on female size. From 57 females between 3.6 and 5.9 cm standard length held with nest males (maximum of three females per male), we measured the time between leaving a shell after brood care and laying the next clutch. Nest males were present, and females had plenty of shells to minimize searching time for suitable shells. T_d averaged 47 days and was unrelated to female size (Kruskal-Wallis ANOVA, d.f. = 5, $\chi^2 = 7.73$, $P = 0.1719$). Brood care varied between 10 and 14 days and we took $T_b = 12$ days. Spawning in the field took about 6 h, which is half of the length of the daylight period. Since there is usually no reproductive activity at night (M. Taborsky, unpublished field video data), we took $T_l = 1/2$ day. Hence $C = 47 + 1/2 + 12 = 59.5$ days.

Time T_s to find a suitable shell for laying depends on body size, s_f : as females become larger the number of suitable shells decreases. Setting $\partial W_f / \partial s_f = 0$, the optimal switch size, s_f^* , has

$$\frac{G'_f(s_f^*)}{G_f(s_f^*)} = \frac{T'_s(s_f^*)}{C + T_s(s_f^*)} \quad (9)$$

where the primes are the first derivatives with respect to s_f . Using (6) gives

$$\frac{G'_f(s_f^*)}{G_f(s_f^*)} = \frac{r}{s_f^*} \quad (10)$$

We estimated the average searching time for average-sized females, T_{sav} , by assuming that the ratio of laying to searching females equals the ratio of laying to searching times. It was easy to determine whether a female was searching or laying: searching females may enter a shell to test its suitability, but do not remain longer than a few minutes before leaving or spawning, whereas laying females remain inside and repeatedly interact with the nest male. From simultaneously counting 39 spawning females and 156 searching females in territories at Wonye Point, we calculated $T_{sav} = 2$ days.

From the size distribution of shells in field nests and the relation between female size and shell size chosen (Schütz and Taborsky, 2000), we estimated the average number of shells available for an average sized female (4.6 cm SL), i.e. $A_{av} = 482$, which is the number of shells in the size class chosen plus all larger shells. We could similarly approximate the number of shells available to a female of size class i , A_i , and then estimate searching times for a female of size class i as ($T_{si} = T_{sav} A_{av}/A_i$) days, where $T_{sav} = 2$ days. The function for T_s that fitted the data best had the form

$$T_s(s_f) = \exp(v(s_f - b)) \quad (11)$$

where $v = 0.04112 \pm 0.000451$ and $b = 76.51 \pm 1.836$ (values $\pm$ standard errors, $\chi^2 = 42.38$).

Although we could not solve s_f^* explicitly, substituting (10) for G'/G , and (11) for $T_s(s_f)$ into (9) gives the following result for optimal female size, s_f^* :

$$s_f^* = \frac{r\{C \cdot \exp[-v(s_f^* - b)] + 1.0\}}{v} \quad (12)$$

where $r = 1.0$, $C = 59.5$. By iteration, s_f^* was found to be 138.308 cm^3 or 5.171 cm standard length.

Model 3: combined mortality/gain rate maximization model

Finally, we predict female size by combining the mortality and gain rate maximization models. Fitness is defined as in equation (1a) for model 1, but the expected number of breeding episodes for a female viewed from hatching, P_f , is defined in terms of model 2. P_f is the probability of survival to adulthood, multiplied by the female's expected lifetime divided by the time ($C + T_s(s_f)$) taken to complete each breeding episode, i.e.

$$P_f(t_f) = e^{-d_f t_f} \cdot \frac{1}{d_f} \cdot \frac{1}{C + T_s(s_f(t_f))} \quad (13)$$

(cf. equation 2). Knowing that exponent $r = 1.0$ in equation (6), we take the reproductive gain per episode as

$$R_f(s_f(t_f)) = G_f = g_f s_f(t_f) = g_f K(t_f - t_{0f}) \quad (14)$$

Applying equation (1a), we obtain

$$W_f = e^{-d_f t_f} \cdot \frac{1}{d_f} \cdot \frac{1}{C + T_s(s_f(t_f))} \cdot G_f(s_f(t_f)) \quad (15)$$

Maximizing fitness with respect to time t_f by setting $dW_f/dt_f = 0$, from (1) gives

$$\frac{dG_f/dt_f}{G_f} = d_f + \frac{C + dT_s/dt_f}{C + T_s} \quad (16)$$

which is the equivalent of equation (3) for this case.

Explicitly, taking T_s from (11)

$$W_f = e^{-d_f t_f} \cdot \frac{1}{d_f} \cdot \frac{g_f K(t_f - t_{0f})}{C + \exp[v(K(t_f - t_{0f}) - b)]} \quad (17)$$

so that fitness is maximized when

$$(t_f^* - t_{0f})^{-1} = d_f + vK / \{C \exp[-v(K(t_f^* - t_{0f}) - b)] + 1\} \quad (18)$$

where t_f^* is the optimal maturity time. We cannot solve this equation explicitly for t_f^* , but can solve it numerically.

COMPARISON OF PREDICTIONS AND OBSERVATIONS

We compared body size predictions from the three models with those observed in the field (Fig. 2). All statistical analyses tested for two-tailed probabilities.

Note that the mortality model (1) predicts *minimum* and not average size of nesting males and females in the field. It predicts the switch to nest male size quite well, but strongly overestimates the female switch size to maturity (about twice that observed). Figure 2 gives mean observed body sizes for nest males, sneakers, and females, and the ranges found in the field. To obtain estimates of the error on the predictions, we used Box and colleagues' (1978) method (the square of a fractional error in a product equals the sum of squares of fractional errors in the quantities multiplied) to find the combined standard error of K and t_0 . We then predicted s_m^* and s_f^* at the upper and lower combined standard error limits, but the errors were too small to appear in the graph (females: 350.67–351.09 cm³ or 7.052–7.055 cm; males: 543.25–544.04 cm³ or 8.159–8.164 cm).

For the gain rate maximization model (2), Box and colleagues' (1978) method could not be used because of the complexity of the calculation involving s_f^* (equation 12), with errors on three parameters, r , b , and v .

The female size predicted from (12) matches the field observation quite well (Fig. 2), despite the fact that model 2 does not account for mortality. Statistical comparisons between predicted and observed are not possible because (i) observed adult sizes will be greater than switch sizes because of indeterminate growth, and (ii) there is no obvious way to obtain an exact mean switch size in the field, though it will be close to the lower end of the size ranges shown (see values included in Fig. 2). The combined model (3) predicts t_f^* to be 311 days, which gives a size of 127.84 cm³ or 5.03 cm (i.e. almost the same as the gain rate model alone), which clearly exerts the major influence on the solution for s_f^* .

DISCUSSION

Model 1 suggests that the trade-off between survival and intrasexual competition can explain male body size, but that the analogous trade-off between survival and fecundity cannot explain female body size and hence the extreme SSD in *L. callipterus*. Predicted male size only marginally exceeds predicted female size, giving a switch size (SL³) ratio prediction

of 1.55 (nest male/adult female size). For adult averages in the field, SSD is much higher than this: 13.18 (body mass ratio) or 14.90 (SL^3 ratio).

We also estimated the effect of sperm competition on nest male size from competition with dwarf males, based on calculations involving fertilization gains by dwarf males assuming (for simplicity) that sperm competition always occurs. Sperm competition can increase optimal switch size to nest male status only marginally if the raffle is fair and fertilization success is related to body size (see Parker, 1992), since the territorial male is so much bigger than the dwarf. If the dwarf's sperm are favoured arbitrarily by a factor of 9:1 (Parker, 1990) – this is plausible because of its privileged position during spawning (see Taborsky, 1998, Figure 1; Meidl, 1999) – then switch age is increased by some 80.6 days compared with zero sperm competition. The optimal territorial male switch size is then $SL = 8.57$ cm, an increase of 0.42 cm (5%). Any effect of sperm competition on male size is therefore likely to be small relative to male–male competition.

Although model 1 strongly overestimates female body size (standard length about twice as high as observed; Fig. 2), the size predicted from model 2 matches the field observations quite well, despite the fact that this model does not account for mortality. Thus without the limitation imposed on female size by the special breeding substrate [availability of suitable shells (Schütz and Taborsky, 2000)], females would likely be much larger. Some comparative data also hint at support for model 2 (Schütz and Taborsky, 2005): in a northern population at Kalundu (Congo), *L. callipterus* breeds mainly in shells of a much smaller species, *Paramelania damoni* (Sato, 1994). There, females are also much smaller.

In males, large size is not constrained by shell size – indeed, males must exceed a minimum size to be able to carry shells efficiently (Schütz and Taborsky, 2005). In contrast to other shell-brooding cichlids, *L. callipterus* is the only species in which the male actively transports shells (Sato and Gashagaza, 1997). Males of other shell brooders are typically much smaller than *L. callipterus* males and lack the ability to carry shells (Sato and Gashagaza, 1997). In another *L. callipterus* population at Rumonge, Burundi, large *Neothauma* shells are superabundant, and there is no need for males to collect shells (Sato and Gashagaza, 1997). In this population, nest males are much smaller than in the southern population [on average 4.7 cm SL (Sato and Gashagaza, 1997)], probably because competition between males is reduced (Taborsky, 2001). It is possible that intrasexual selection initially drove male size in *L. callipterus* into a size range where shell-carrying is possible, which then selected for even larger sizes due to size-dependent carrying efficiency (Schütz and Taborsky, 2005). The extreme SSD may hence be a consequence of a combination of both mechanisms.

In mammals, male-biased SSD is predominant, and usually attributed to the prevalence of polygynous mating patterns. In stoats (*Mustela erminea*), females are smaller than males because burrows constrain the diameter of pregnant females: an energetic model predicted that males are close to the survival optimum for size, whereas females are below it because of the constraint of burrow diameter during pregnancy (Sandell, 1989). The SSD probably results from selection for smaller size acting on females (Sandell, 1989).

Although we have followed the conventional life-history strategy approach of regarding growth as a fixed constraint, we would ideally allow age-dependent growth rates to be shaped strategically by selection in our models, concurrently with switch ages to maturity. At present we see no obvious way of doing this.

We conclude that while standard mortality effects on life history (model 1) will operate to shape size in both sexes, it is the special constraint of shell size on female size that dominates the determination of female size (model 2). In the combined model (3), the inclusion of

mortality hardly changes the optimal female size. The most extreme male-biased SSD currently known among animals appears to result from strong selection on the body sizes of both sexes, acting in opposite directions. In *L. callipterus* males, strong intrasexual selection and a lower size limit imposed by the need to carry shells (Schütz and Taborsky, 2005) strongly favour large body size. In females, the need to fit into shells for breeding imposes selection to minimize searching time for a suitable breeding substrate, which strongly favours small body size, counteracting fecundity selection.

ACKNOWLEDGEMENTS

We thank the Fisheries Department of the Zambian Ministry of Agriculture and Cooperatives, especially G. Mudenda and L. Mwape, for study permission and valuable logistical help, and H. Ochi and M. Hori for practical help at the Lake. A. Dakka, R. Shapola, Mr. Green, Augustin, David, Bonfes, and Micki provided logistical and practical help, H. Weix and P. Meidl were magnificent field assistants. D.S. thanks W. Wickler for supporting this study and E. Skubic for discussions and help with mathematics. We thank C.J. Rinjeveld for kindly providing data, F. Bratter for fish care, and P. Dierkes, K. Förster, B. Kempenaers, J. Lamprecht, G. Pachler, M. Ritzmeier, E. Skubic, Y. Teuschl, and H. Winkler for useful comments on earlier versions of the manuscript. Trips of D.S. to Liverpool were supported by the ÖAW and the Royal Society of London. This work was funded by the Austrian FWF, project P 10916-Bio, the German DAAD, and the Swiss SNSF (grant 3100-064396 to M.T.).

REFERENCES

- Basolo, A.L. 1990. Female preference predates the evolution of the sword in swordtail fish. *Science*, **250**: 808–810.
- Beverton, R.J.H. 1987. Longevity in fish: some ecological and evolutionary considerations. In *Evolution of Longevity in Animals* (A.D. Woodhead and K.H. Thompson, eds.), pp. 161–186. New York: Plenum Press.
- Bielefeldt, J., Rosenfield, R.N. and Papp, J.M. 1992. Unfounded assumptions about diet of the Cooper's hawk. *Condor*, **94**: 427–436.
- Bisazza, A. 1993. Male competition, female mate choice and sexual size dimorphism in poeciliid fishes. *Mar. Behav. Physiol.*, **23**: 257–286.
- Björklund, M. 1991. Evolution, phylogeny, sexual dimorphism and mating systems in the grackles (*Quiscalus* ssp.: Icterinae). *Evolution*, **45**: 608–621.
- Blanckenhorn, W.U. 2005. Behavioral causes and consequences of sexual size dimorphism. *Ethology*, **111**: 977–1016.
- Box, G.E.P., Hunter, W.G. and Hunter, J.S. 1978. *Statistics for Experimenters*. New York: Wiley.
- Carothers, J.H. 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *Am. Nat.*, **124**: 224–254.
- Charnov, E.L. 1993. *Life History Invariants: Some Explorations of Symmetry in Evolutionary Ecology*. Oxford: Oxford University Press.
- Cheverud, J.M., Dow, M.M. and Leutenegger, W. 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: sexual dimorphism in body weight among primates. *Evolution*, **39**: 1335–1351.
- Darwin, C. 1874. *The Descent of Man, and Selection in Relation to Sex*, 2nd edn. London: John Murray.
- Day, T. and Taylor, P.D. 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.*, **149**: 381–393.

- Erlandsson, A. and Ribbink, A.J. 1997. Patterns of sexual size dimorphism in African cichlid fishes. *S. Afr. J. Sci.*, **93**: 498–508.
- Ghiselin, M.T. 1974. *The Economy of Nature and the Evolution of Sex*. Berkeley, CA: University of California Press.
- Hughes, A.L. and Hughes, M.K. 1986. Paternal investment and sexual size dimorphism in North American passerines. *Oikos*, **46**: 171–175.
- Jormalainen, V., Merilaita, S. and Tuomi, J. 1994. Male choice and male–male competition in *Idotea baltica* (Crustacea, Isopoda). *Ethology*, **96**: 46–57.
- Kleinbaum, D.G. and Kupper, L.L. 1978. *Applied Regression Analysis and Other Multivariable Methods*. Belmont, CA: Wadsworth Publishing.
- Lester, N.P., Shuter, B.J. and Abrams, P.A. 2004. Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proc. R. Soc. Lond. B*, **271**: 1625–1631.
- Loison, A., Gaillard, J.M., Pelabon, C. and Yoccoz, N.G. 1999. What factors shape sexual size dimorphism in ungulates? *Evol. Ecol. Res.*, **1**: 611–633.
- Meidl, P. 1999. Microsatellite analysis of alternative mating tactics in *Lamprologus callipterus*. Diploma thesis, University of Vienna, Vienna.
- Moyer, J.T., Thresher, R.E. and Colin, P.L. 1983. Courtship, spawning and inferred social-organization of american angelfishes (Genera Pomacanthus, Holacanthus and Centropyge, Pomacanthidae). *Environ. Biol. Fish.*, **9**: 25–39.
- Pachler, G. 2001. Sperm competition and alternative mating strategies in a shell-brooding cichlid, *Lamprologus callipterus*. Diploma thesis, University of Vienna, Vienna.
- Parker, G.A. 1990. Sperm competition games: raffles and roles. *Proc. R. Soc. Lond. B*, **242**: 120–126.
- Parker, G.A. 1992. The evolution of sexual dimorphism in fish. *J. Fish. Biol.*, **41**: 1–20.
- Pietsch, T.W. 2005. Dimorphism, parasitism, and sex revisited: modes of reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). *Ichthyol. Res.*, **52**: 207–236.
- Rijneveld, N. 2002. Local population structure of *Lamprologus callipterus*, a polygynous shell-brooding cichlid of Lake Tanganyika. Diploma thesis, Riksuniversiteit Groningen, Groningen.
- Sandell, M. 1989. Ecological energetics, optimal body size and sexual size dimorphism: a model applied to the stoat, *Mustela erminea* L. *Funct. Ecol.*, **3**: 315–324.
- Sato, T. 1994. Active accumulation of spawning substrate: a determinant of extreme polygyny in a shell-brooding cichlid. *Anim. Behav.*, **48**: 669–678.
- Sato, T. and Gashagaza, M.M. 1997. *Shell-brooding Cichlid Fishes of Lake Tanganyika: Their Habitats and Mating Systems*. Kyoto: Kyoto University Press.
- Sato, T., Hirose, M., Taborsky, M. and Kimura, S. 2004. Size dependent male alternative reproductive tactics in the shell-brooding cichlid *Lamprologus callipterus* in Lake Tanganyika. *Ethology*, **110**: 49–62.
- Schulte-Hostedde, A.I., Millar, J.S. and Gibbs, H.L. 2002. Female biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution*, **56**: 2519–2529.
- Schütz, D. and Taborsky, M. 2000. Giant males or dwarf females: what determines the extreme sexual size dimorphism in *Lamprologus callipterus*? *J. Fish. Biol.*, **57**: 1254–1265.
- Schütz, D. and Taborsky, M. 2003. Adaptations to an aquatic life may be responsible for the reversed sexual size dimorphism in the water spider, *Argyroneta aquatica*. *Evol. Ecol. Res.*, **5**: 105–117.
- Schütz, D. and Taborsky, M. 2005. The influence of sexual selection and ecological constraints on an extreme sexual size dimorphism in a cichlid. *Anim. Behav.*, **70**: 539–549.
- Shine, R. 1978. Sexual size dimorphism and male combat in snakes. *Oecologia*, **33**: 269–277.
- Szekely, T., Reynolds, J.D. and Figuerola, J. 2000. Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution*, **54**: 1404–1413.
- Taborsky, M. 1998. Sperm competition in fish: ‘bourgeois’ males and parasitic spawning. *Trends Ecol. Evol.*, **13**: 222–227.

- Taborsky, M. 2001. The evolution of bourgeois, parasitic, and cooperative reproductive behaviors in fishes. *J. Heredity*, **92**: 100–110.
- von Bertalanffy, L. 1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, **32**: 217–231.
- Weckerly, F.W. 1998. Sexual-size dimorphism: influence of mass and mating systems in the most dimorphic mammals. *J. Mammol.*, **79**: 33–52.
- Wiklund, C. and Forsberg, J. 1991. Sexual size dimorphism in relation to female polygamy and protandry in butterflies: a comparative study of Swedish Pieridae and Satyridae. *Oikos*, **60**: 373–381.
- Woolbright, L.L. 1983. Sexual selection and size dimorphism in anuran amphibia. *Am. Nat.*, **121**: 110–119.