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Egg size and food abundance interactively affect juvenile growth and behaviour

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Summary

1. Comparative evidence from several animal taxa suggests that juveniles hatching from larger eggs have fitness benefits when growing up in a harsh environment, whereas under benign conditions egg size should be of less importance. However, the physiological and behavioural mechanisms responsible for these context-dependent fitness differences are as yet poorly understood.

2. We studied the interactions between the phenotype of developing offspring and their environment in the mouthbrooding cichlid *Simochromis pleurospilus*. We hand-raised young from large and small eggs, and measured their initial body size and burst swimming speed. Thereafter we raised half of each egg-size class on high and half on low food ration and followed their growth trajectories and behavioural development until the age of 12 weeks.

3. We found that larger eggs gave rise to larger young that had a higher burst swimming speed. Food ration greatly influenced long-term growth, while egg size predominantly affected fish size during the first 2 weeks of life. However, large egg size caused a size advantage of juveniles persisting throughout the experimental period.

4. Egg size and food ration interactively affected the hiding and foraging behaviour of young. In the low-food treatment, individuals from small eggs spent less time in shelter and showed a higher commitment to foraging than individuals from large eggs. In a natural setting, this should markedly increase predation risk of young originating from small eggs, particularly in poor environments. In contrast, when food was plentiful juveniles behaved similarly, irrespective of egg size.

5. Our results show that egg size affects juvenile growth trajectories and behaviour differently in different environments. While it is well-established that a large egg size raises offspring fitness particularly in harsh environments, our study suggests that this advantage arises through risk-averse behaviour being tightly linked to offspring size.

Key-words: maternal effects, offspring size evolution, early environment, size-selective mortality, predation risk, cichlids

Introduction

Many organisms experience the highest mortality rates during the early post-natal stages, making the juvenile period a critical phase in life (e.g. Janzen 1971; Gosselin & Qian 1997; Sogard 1997). Adaptations reducing early juvenile mortality are hence likely to evolve (Stearns & Koella 1986). If a mother is able to predict the quality of her offspring's environment, she may increase the survival chances of her offspring by adjusting their phenotype to the expected conditions. Such 'anticipatory maternal effects' can hence increase maternal fitness by increasing the fitness of offspring, if mothers have reliable cues to predict the post-natal environment of their offspring (Marshall & Uller 2007). In recent years numerous examples of such maternal effects have been reported in animals and plants, demonstrating a wide range of mechanisms by which mothers can alter offspring phenotype in response to environmental fluctuations (e.g. Rossiter 1996; De Fraipont *et al.* 2000; Eising *et al.* 2001; Galloway & Etterson 2007; Uller, Astheimer & Olsson 2007).

The maternal effect of egg size has received particular attention within this context (reviewed by Bernardo 1996), as it is usually found to be an important determinant of

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offspring size (e.g. Kaplan 1980; Hutchings 1991). Generally, offspring fitness is thought to increase with egg size, e.g. because of enhanced growth, starvation resistance and a larger reaction distance to potential predators (reviewed for fishes by Miller *et al.* 1988) of larger offspring. However, a fitness advantage of larger offspring size should never be taken for granted (Bagenal 1969; Bernardo 1996), as egg size does not always increase initial size, growth or survival of young (Lagomarsino, Francis & Barlow 1988; Kaplan 1992; Litvak & Leggett 1992; Ruohomäki, Hanhimäki & Haukioja 1993; Williams *et al.* 1993; Zhao, Chen & Brown 2001). Smaller offspring might equal or even surpass the survival benefits of initially larger conspecifics through compensatory mechanisms (Capinera 1979). Moreover, the benefits of maternal effects are often context-dependent (e.g. Fox, Thakar & Mousseau 1997; Mousseau & Fox 1998; Einum & Fleming 1999; Allen, Buckley & Marshall 2008), with egg size affecting the fitness of phenotypes differently in different environments. Theory predicts that in order for context-dependent provisioning in egg size to evolve, the survival of individual offspring in benign environments should depend little on egg size, while under adverse conditions, young from larger eggs should have a survival advantage (Goulden, Henry & Berrigan 1987). Indeed there is empirical evidence that under low food levels larger juveniles originating from larger eggs have survival advantages over conspecifics originating from smaller eggs (e.g. Hutchings 1991; Gliwicz & Guisande 1992; Einum & Fleming 1999; Bashey 2006; Camargo & Urbinati 2008; Donelson, Munday & McCormick 2009; Dziminski, Vercoe & Roberts 2009). Mothers predicting good rearing conditions for their young may thus afford to produce smaller eggs and rather take advantage of a higher fecundity (Smith & Fretwell 1974). Examples in arthropods (Brody & Lawlor 1984; Gliwicz & Guisande 1992; Fox, Thakar & Mousseau 1997; Vijendravarma, Narasimha & Kawecki 2010) and fish (Reznick & Yang 1993; Taborsky 2006a) suggest that females indeed invest less in individual offspring in anticipation of good rearing conditions for their young.

Often the mechanism behind an observed fitness effect of egg size is not identified, which is possibly due to the fact that individuals are usually not individually tracked from the egg stage (e.g. Camargo & Urbinati 2008; Donelson, Munday & McCormick 2009; Dziminski, Vercoe & Roberts 2009), so that the initial egg size is unknown. Therefore, more information on the consequences of egg size for the phenotype of individual offspring and on the persistence of the effects of egg size is required. Moreover, there is a need for studies which examine the behavioural mechanisms underlying the fitness benefits of different egg sizes in various environments. Furthermore, while most studies focus on starvation resistance (Hutchings 1991; Brown & Taylor 1992; Gliwicz & Guisande 1992; Zhao, Chen & Brown 2001) or competitive abilities (Einum & Fleming 1999; Bashey 2006), an increase in individual offspring size might also provide an advantage in the context of predator–prey interactions (Reznick 1982; Repka & Walls 1998; Hoverman, Auld & Relyea 2005; Taborsky, Skubic & Bruintjes 2007). A larger body size might make young less susceptible to negative size-selective mortality (e.g. Sogard 1997). Furthermore, it can influence predator avoidance in fish, as hiding time and starvation resistance were positively related to fish size (Krause *et al.* 1998), two behaviours that influence the susceptibility of individuals to predation (Lima & Dill 1990).

Fig. 1. Image of a 2-month-old *Simochromis pleurospilus* (picture by Karin Schneeberger).

Females of the African mouthbrooding cichlid *Simochromis pleurospilus* (Fig. 1) adjust their egg size in response to their own juvenile growth conditions (Taborsky 2006a). Mothers that were raised on a low food regime produced on average larger eggs than conspecifics raised on high food levels irrespective of prevailing food conditions. Here, we examine the potential survival benefits of hatching from a larger egg when facing food scarcity in *S. pleurospilus*. Egg size may determine initial hatchling size and it may directly affect growth trajectories. We hypothesize that in addition egg size may affect growth and survival prospects indirectly via altering risk-taking behaviour. We hand-raised individuals from a broad range of egg sizes, and followed their growth trajectories and their behavioural development individually. Our approach experimentally removed maternal care as potential determinant of offspring size, and it allowed us to disentangle the effects of egg size and resource availability on offspring growth trajectories and behaviour in the absence of additional variance generated by competitive interactions among siblings. First we established the relationship between egg size and offspring size and scored the burst swimming speed of the young. Secondly, we divided the eggs in two size classes, large and small. Half of each size class was individually raised with low-food and the other half with a high-food ration, and we monitored growth, foraging behaviour and hiding behaviour repeatedly. We expected that under high-food conditions, phenotypes will converge quickly, both with regard to size and behaviour, whereas under low-food conditions initial size differences are retained for longer with large-egg fish behaving more cautiously than small-egg ones.

Materials and methods

STUDY SPECIES

Simochromis pleurospilus lives along the rocky shores of Lake Tanganyika down to a depth of 12 m (Taborsky 2006a; Kotrschal & Taborsky (in press)). It reproduces year round. When a female is ready to spawn she visits males that defend small breeding territories and leaves directly after mating (Taborsky 2006b). Only females provide brood care, which consists of two phases. During a phase of about 2 weeks the mother has the clutch continuously in her mouth while the young feed only endogenously on their yolk supply. Gill movement by the female provides the young with aerated water. This phase is followed by a phase of another 2 weeks, in which the mother releases the young periodically for exogenous foraging (Taborsky 2006b). After independence the juveniles mainly live in shallow water, where they forage on filamentous turf algae. When they reach maturity they migrate to deeper waters (Taborsky 2006a).

ANIMAL HUSBANDRY AND EXPERIMENTAL DESIGN

We derived our experimental clutches from wild caught *S. pleurospilus* adults originating from the southern tip of Lake Tanganyika, near Nkumbula Island, Zambia, and from their first generation offspring. We created eight groups of 4–10 females together with a single male in tanks (dimensions: 122 × 33 × 51 and 122 × 61 × 61 cm) equipped with a biological filter and flower pot halves as shelters. In these breeding tanks females produced clutches of 6–48 eggs. After removing the clutches from a female's mouth mothers were weighed to the nearest 0·01 g on an electronic balance and standard lengths were measured to the nearest 0·5 mm

Within 1 day after spawning the eggs were removed from a female's buccal cavity by slightly pressing her cheeks. Each egg was placed individually on a moistened cotton pad to remove excess water from its surface and afterwards it was weighed to the nearest 0·1 mg on an electronic balance. Based on previous knowledge about egg size distributions in our laboratory population (Taborsky 2006a), eggs heavier than 17·5 mg were classified as large and eggs below 14·0 mg were classified as small. In relation to all clutches collected during the course of this study (overall range: 7·7–24·6 mg), the eggs used for the behaviour and growth measurements (small: 9·5–13·4 mg and large: 17·4–23·4 mg), were representative of the lower and upper third of the size range. Egg size variance is larger between females than within females in *S. pleurospilus* (F.H.I.D. Segers and B. Taborsky, unpublished data). Thus, all eggs from a clutch fell in the same size class in all cases. If a clutch was suited for the experiment we placed each of its eggs individually in a 250 mL Erlenmeyer flask. The flasks were diagonally fixed in a 45° angle in a tank (dimensions: 76 × 30 × 46 cm) while submerged in a water bath of 28 ± 1·0 °C. Plastic tubes (2 mm in diameter) connected to air pumps blew air into the flasks, resulting in continuous tumbling movements of the eggs. The set-up was kept in the dark to protect the eggs and larvae from light stress. We noted the time to hatching, which took on average 5 days.

On day 6 after hatching the surviving individuals from a clutch were transferred to a small net cage (dimensions: 16·5 × 12 × 13·5 cm) which was placed in the fish's future home tank. Each hatchling was individually assigned to a glass aquarium (dimensions: 40 × 25 × 25 cm) supplemented with 1·5 L of gravel, a biological filter and a flower pot half as shelter. The light–dark cycle was set to 13 : 11 h and the water temperature was kept constant at 26 ± 1 °C, mimicking the natural conditions at Lake Tanganyika. We created four treatment groups, small-egg/high-food, small-egg/low-food, large-egg/high-food and large-egg/low-food, by the following procedure: Each clutch, belonging to either the large or the small-egg size class, was split equally between a high or low food regime. We stopped collecting clutches when there were 15 individuals present in all four treatment groups. The 60 individuals stemmed from eight clutches (4–11 young per clutch), originating from seven males and seven females. One male was mated with two different females, and one female was mated with two different males. We are aware that including full siblings leads to some degree of genetic interdependence of data, but hand-raising 60 individuals from 60 different clutches with appropriate egg sizes was logistically impossible. To accommodate for this potential problem we used as many different males and females as possible within a reasonable time frame to spawn the experimental clutches and we assigned siblings in equal proportions to the two food treatments. Furthermore, we accounted statistically for potential family effects.

Fourteen days after hatching, that is, at the age the young had absorbed nearly all their yolk, the standard lengths of the fish were measured to the nearest 0·1 mm under a binocular. The young were weighed to the nearest 0·1 mg after the excess water had been removed by placing them briefly on a moistened cotton pad. After measuring, the 60 fish took part in the food experiment conducted between March 2007 and February 2008 involving burst swimming speed trials, growth measurements and behavioural observations (see below). To obtain a data set of the complete range of egg sizes, we continued to collect clutches including those containing medium sized eggs and tested for the effect of egg weight on hatchling size. We used the same methods for measuring egg and juvenile size as described above. In total we measured the egg sizes and standard length of 212 individuals of 25 clutches (4–12 individuals per clutch), spawned by 14 different males and 24 different females. All clutches were collected between March 2007 and October 2008.

FOOD TREATMENT AND GROWTH MEASUREMENTS

We count the age of the fish from the start of the food treatment onwards, that is, the day when the fish fed exogenously for the first time. Juveniles were fed Tetramin flake food 6 days a week with a ration corresponding to 12% (high food) and 4% (low food) of the mean, age-specific weight of *S. pleurospilus* (see Taborsky 2006a, b). The amount of food was adjusted every 14 days to the increasing size of the fish. Standard lengths and weights of fish were measured every 2 weeks until an age of 12 weeks (i.e. seven repeated measures per individual). To estimate body reserves of the fish, we also calculated Fulton's body condition index as weight (g)/standard length (cm)^3 × 100, which is the most commonly used condition index in fish (Bolger & Connoly 1989). One individual in the low food treatment died at an age of 69 days.

BURST SWIMMING SPEED

One reason why the fitness of fish hatched from large and small eggs might differ is their ability to avoid predators due to different swim speeds. Therefore, we determined the burst swimming speed of all experimental young at day 3 of the experiment. We constructed a test channel (dimensions 40 × 4×5 cm) with transparent walls and bottom that was filled to a height of 5 cm with water. The water temperature was kept at 26 ± 0·5 °C by a water bath surrounding the test channel. The set-up was placed on top of a grid with a mesh size of 1 cm to scale the swimming distances. Prior to testing the test fish was left to acclimatize in the channel for 10 min. To persuade a fish to swim at maximum speed we startled it by tapping once behind it with a probe and waited until it stopped swimming. Immediately afterwards we startled it two more times in the same way. All fish went through this procedure four times at 5 min intervals yielding 4 × 3 swimming spurts per fish. The movements of the fish were video recorded at 25 frames s^{-1}. The videos were analysed with NIH ImageJ software (National Institutes of Health, Bethesda, Maryland, USA). In each image we analysed the position of the tip of the head (cf. Schürch & Taborsky 2005). Burst-swimming speed was defined as the longest travel distance between two frames (1/25 s). We used maximum burst swim speeds for statistical analysis, that is, the highest swim speed obtained from all recordings of a fish. Due to technical problems we lost the recordings of 23 individuals, which left us with recordings of 15 individuals of the small-egg and 22 individuals of the large-egg group. Only egg size was considered in this experiment.

RISK TAKING PARADIGM

To measure the risk-taking propensity of fish during foraging, we aimed to develop an experimental test that is independent of the physical presence of a predator. In the laboratory, we observed that juvenile *S. pleurospilus* dig themselves in sand when they are frightened (F. Segers, personal observation). Therefore we did a control experiment with a separate set of juvenile fish. We confronted them with a substrate in which they cannot dig, namely dark grey plastic plates (2 mm thick), and tested if the fish considered this substrate as 'unsafe'. We placed a randomly chosen juvenile (1·0–2·0 cm SL) from our laboratory stock alone in a test tank with a bottom area of 25 × 40 cm consisting of two patches of fine grained sand (12·5 × 20) and two patches of dark grey plastic (12·5 × 20) and let it habituate to the set-up for 30 min. Then we removed an opaque partition thereby uncovering either an empty control tank or a tank which held a predator (*Ctenochromis horei*, a natural predator of *S. pleurospilus* juveniles in the wild, B. Taborsky personal observation). For 10 min we recorded whether the juvenile was over the sand or at the plate. We carried out the experiment with 30 individuals in total. The juveniles spent significantly less time on the plates during the predator exposure (Mann–Whitney *U*-test, $N_1 = 15, N_2 = 15, U = 22, P < 0{\cdot}001$).

BEHAVIOURAL OBSERVATIONS

To test for the differences in foraging and hiding behaviour between fish of the different treatments we observed the foraging activity on dark grey plastic plates, as we had established that fish consider these as 'unsafe' substrate (see above). The fish were transferred to a test tank with a bottom area of 50 × 40 cm covered with a 3 cm layer of fine grained sand and filled with water up to a height of 10 cm. In the centre of the tank bottom we placed a rectangular dark grey plastic plate (19 × 24 cm). On each side of the plate at a distance of 3 cm from the rim we placed two pebbles, partly stacked on top of each other as a shelter for the young. After 2 h habituation time we placed a standardized amount of food (0·1 g) right in the centre of the plate with the help of a plastic tube. The juveniles had not been fed for 24 h before the trials. We recorded the location of the fish for 10 min and noted if the fish had dug a shelter underneath the pebbles. Two fish of the small-egg/low-food group were excluded from the first trial because they had accidently received extra food prior to the experiment. We performed repeated measures on the foraging and hiding behaviour of the fish, on experimental day 10, 38 and 66.

DATA ANALYSIS

As maternal effects on offspring traits are known to decrease over time (Mousseau & Fox 1998) we expected them to be mainly present in the first weeks of the experimental period. Therefore we carried out two sets of statistical tests: (i) we analysed the first measurements separately to check for early ontogenetic effects; and (ii) we tested over all repeated measures to check for the consistency of effects. All analyses were done in R 2.9.2 (R Development Core Team 2009). We mostly used general and generalized linear mixed-effects models (LME and GLMM), depending on the distribution of the response variable. We always included clutch of origin as random effect, and for the analyses of repeated measures we included individuals nested within clutches as random effect. We did not test for significance of the random effect terms as they were not important for our question (Bolker *et al.* 2009). All tests are two-tailed with a significance level set to $\alpha = 0{\cdot}05$. All size, growth and swimming speed data were analysed with LME. For model selection we used the step-down protocols suggested by Zuur *et al.* (2008). We first explored the best structure of the random components (comparing random intercept models with random intercept and slope models) using REML (tests not shown). Then the non-significant terms (interactions and main effects) were backward eliminated, using ML to check for significance. The optimal model was in the end fitted with REML. In the result section we present the t- and *P*-values of all the fixed factors and interactions of the optimal model. Furthermore, we present the results of the likelihood ratio tests (L- and *P*-values) of the non-significant terms that were removed from the models. Exploratory data analysis revealed that the growth trajectories of length and weight were non-linear. To construct the non-linear curves of the growth trajectories we added the square of experimental day as an explanatory term to the models. A subsequent examination of the model fit confirmed that this approach sufficiently accounted for the observed non-linearity in growth. In addition the data of weight increase were linearized by cube root transformation. This transformation accounts for the relationship between size and weight which in fish generally has the form weight = $a \times \text{length}^3$ (with a being a scaling constant). The initial model used to analyse length and weight growth trajectories was 'food treatment × egg size class × experimental day × experimental day^2'. All behavioural data were analysed using GLMM. For the GLMMs we used the MASS package and the models were fitted with the glmmPQL function. The foraging propensity (yes/no) and the propensity to dig (yes/no) were analysed with a model based on a binomial distribution. The remaining behavioural data were analysed with models based on a poisson distribution. For the behavioural observations the initial models were 'food treatment × egg size class × experimental day (or standard length)' and 'food treatment × egg size class × body condition'. Experimental day was always entered as a covariate. Additionally all models were repeated with egg weight as a covariate instead of egg size class as a fixed factor in the model. When this procedure gave different qualitative results (i.e. different significance of factors and interactions of interest) we present these results as well. Homogeneity of residuals of all models was checked afterwards.

Results

BODY SIZE AND SWIMMING SPEED

Egg mass strongly determined standard length on day 19 after spawning (experimental day 0) (LME, $n = 212$, $t = 8{\cdot}09$,

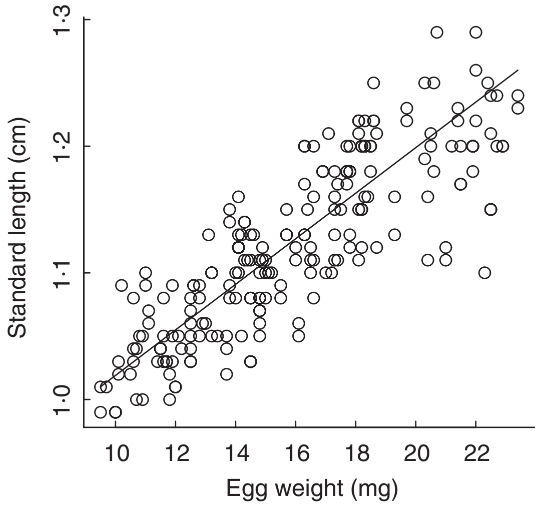

Fig. 2. Effect of egg weight on subsequent standard length of a juvenile *Simochromis pleurospilus* on day 19 after spawning. Each point represents a single individual. The line represents the best-fit line and was drawn based on the parameter estimates obtained from the linear mixed-effects models.

$P < 0{\cdot}001$, Fig. 2) and body mass (LME, $n = 212$, $t = 18{\cdot}39$, $P < 0{\cdot}001$). We had data on the standard length of the mother for 20 of the 25 clutches used in the analysis above. When controlling for female standard length there was no significant relationship between egg size and number (partial correlation, $r = -0{\cdot}18$, $n = 20$, $P = 0{\cdot}45$).

Young from the large-egg group had a significantly higher burst swimming speed than those from the small-egg group (LME, $n = 37$, $t = 8{\cdot}18$, $P < 0{\cdot}001$, Fig. 3). Qualitatively the results remained the same when adding egg weight as a covariate to the model instead of egg size class as a fixed factor.

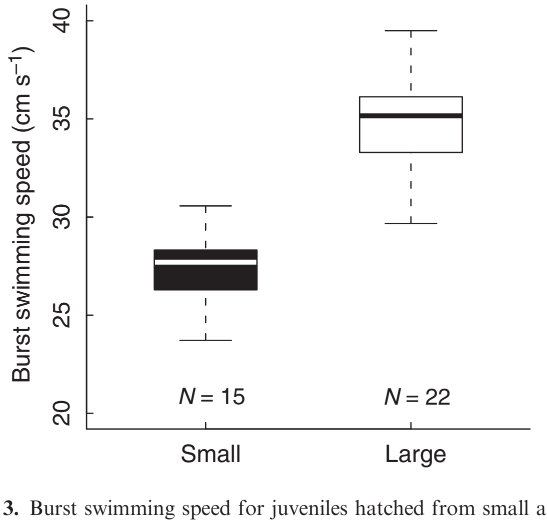

Fig. 3. Burst swimming speed for juveniles hatched from small and large eggs. The boxplots show medians, quartiles and 5th and 95th percentiles.

GROWTH

Naturally, standard length increased with age (i.e. 'Experimental day', see Table 1). Furthermore food level and experimental day interactively affected the standard length of the fish, as the high-food individuals grew faster than the low-food ones ('day × food', see Table 1; Fig. 4a). Yet, the growth rate of high-food fish decreased slightly after several weeks, as indicated by the significant interaction 'food × day^2' (Table 1). Corresponding with the results described earlier, fish hatched from large eggs were larger at the start of the experimental period (Egg size class; see Table 1). Growth of juveniles originating from large eggs was more non-linear ('egg × day^2', see Table 1): irrespective of food treatment, juveniles hatched from large eggs grew slower during the weeks 2–4 of the experiment, whereas afterwards the growth of both egg size classes was more similar (Fig. 4a). Body mass increase followed globally the same patterns as standard length (Table 1; Fig. 4b). On the last day of the experiment, fish hatched from large eggs still tended to be larger than conspecifics hatched from small eggs (LME, $n = 59$, $t = 2{\cdot}19$, $P = 0{\cdot}07$) independently of food treatment (egg size class × food treatment: $L = 0{\cdot}36$, $P = 0{\cdot}55$). There was no effect of egg size on body mass at the end of the experiment (egg size class: $L = 1{\cdot}00$, $P = 0{\cdot}32$; egg size class × food treatment: $L = 0{\cdot}42$, $P = 0{\cdot}52$). Using egg weight as a covariate instead of egg size as a fixed factor did not affect any of the qualitative results on length and mass growth.

FORAGING AND HIDING BEHAVIOUR

All fish had a decreasing propensity to forage at the plate with increasing age (i.e. experimental day; Table 2). This decrease proceeded more slowly in low-food than in high-food fish (experimental day × food treatment, Table 2), whereas egg size had no effect on this behaviour (Table 2). Also food treatment as a main effect did not influence the propensity to forage at the plate (Table 2). As age and standard length at a given age were highly correlated, we did not include them together in the same model. Analysing the above model with standard length instead of age again revealed that the propensity to forage at the plate strongly decreased with the size of the fish (Table 2). Neither food treatment, egg size class nor any interactions containing these factors influenced foraging behaviour when standard length was included in the model (Table 2). Repeating the model with egg weight as covariate did not give different results.

In general, the fish altered their behaviour with increasing size. By experimental day 66 only few fish left the shelter. Therefore, the data on feeding and shelter time could not be analysed with a model based on a normal distribution. To facilitate analysis we categorized the behaviour of the juveniles in four groups ranked by increasing risk-averseness: (i) individuals that foraged at the plate; (ii) individuals that entered the plate; (iii) individuals that left the shelter but stayed on the sand; and (iv) individuals that did not leave the shelter (Fig. 5a,c). Older fish and high-food fish were more

Table 1. Results from the linear mixed-effects models for standard length and weight ($n = 418$). The full-model was: experimental day × experimental day^2 × food treatment × egg size class. Non-significant terms were backward eliminated. The significant *P*-values are marked in bold. Next to the terms of the final model, the table contains the statistics of non-significant terms, that is, results of the likelihood ratio tests (*L*- and *P*-values). Non-significant and significant terms containing the interaction experimental day × experimental day^2 are not shown

	Standard length			Weight		
Model terms	*t*	d.f.	*P*	*t*	d.f.	*P*
Experimental day (day)	19·29	351	**< 0·001**	21·25	351	**< 0·001**
Food treatment (food)	0·01	51	0·99	0·18	51	0·86
Egg size class (egg)	5·28	6	**0·002**	7·00	6	**< 0·001**
Day^2	−0·96	351	0·34	−3·96	351	**< 0·001**
Food × day	14·88	351	**< 0·001**	15·85	351	**< 0·001**
Food × day^2	−5·07	351	**< 0·001**	−6·80	351	**< 0·001**
Egg × day^2	−4·38	351	**< 0·001**	−4·14	351	**< 0·001**
Removed non-significant terms		*L*	*P*		*L*	*P*
Food × egg		0·33	0·56		0·002	0·96
Egg × day		0·25	0·62		0·20	0·65
Food × egg × day^2		0·11	0·74		0·28	0·60
Food × egg × day		0·04	0·84		0·55	0·46

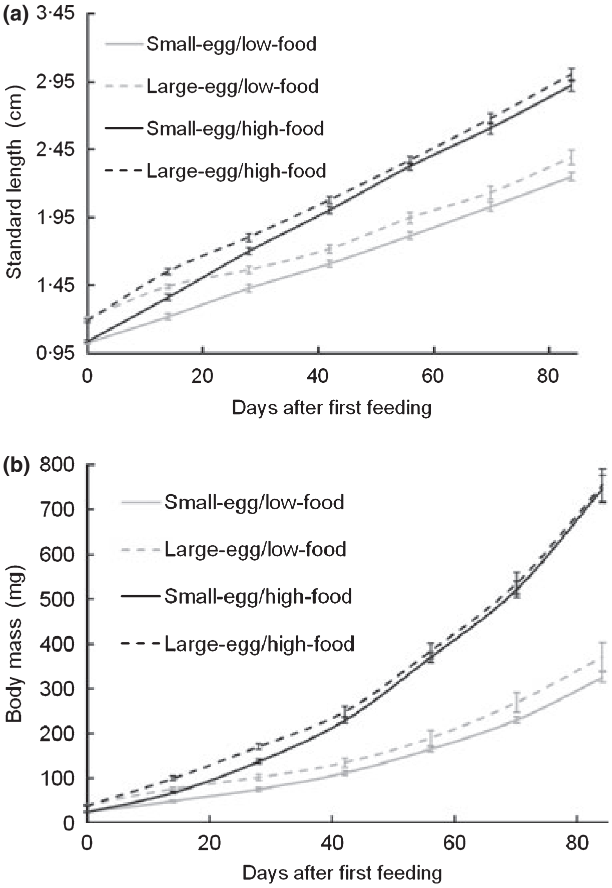

Fig. 4. Growth trajectories of the four treatment groups for (a) standard length and (b) body mass. Means and standard errors of the mean are shown for each measurement. The lines connect the means.

Table 2. Results from the generalized linear mixed-effects models for juvenile behaviour ($n = 178$) with either experimental day or body size as explanatory variable. Non-significant interactions were backwards eliminated. The significant *P*-values are marked in bold

	Fed from plate (yes/no)		Behavioural category	
	t	*P*	*t*	*P*
Model terms				
Experimental day (day)	−5·31	**< 0·001**	8·02	**< 0·001**
Food treatment (food)	0·64	0·53	−3·67	**< 0·001**
Egg size class (egg)	0·68	0·52	−0·37	0·72
Day × food	2·52	**0·01**		NS
Removed non-significant terms				
Day × egg	−0·36	0·72	−0·23	0·82
Day × food	–	–	−0·35	0·73
Food × egg	1·29	0·20	−1·93	0·06
Day × food × egg	−0·32	0·75	0·91	0·38
Model terms				
Body size (size)	−7·06	**< 0·001**	7·89	**< 0·001**
Food treatment (food)	1·54	0·13	−0·50	0·62
Egg size class (egg)	0·30	0·78	0·06	0·95
Removed non-significant terms				
Size × food	1·26	0·21	1·00	0·32
Size × egg	0·29	0·77	−0·67	0·50
Food × egg	1·46	0·15	−1·87	0·07
Size × food × egg	0·07	0·94	0·33	0·74

often found in the more risk-averse categories, whereas egg size-class had no effect (Table 2). Again we replaced age (experimental day) with standard length in the model. Larger fish were significantly more likely to be found in a more risk-averse category (Table 2). As food treatment influences fish size, food treatment was no longer significant (Table 2). Also the increasing propensity of larger fish to dig a shelter underneath the pebbles (GLMM, $t = 8{\cdot}38$, $P < 0{\cdot}001$) demonstrates that the behaviour of the fish is strongly size-dependent. Repeating the model with egg weight as a covariate instead of egg size class as a main effect revealed the same qualitative effects of food treatment (GLMM, $n = 178$,

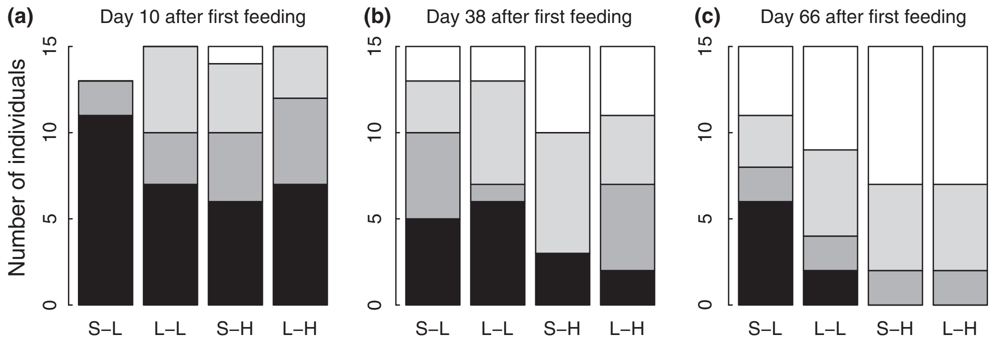

Fig. 5. The number of individuals from each treatment group that was allocated to a certain risk-averseness category for experimental day (a) 10, (b) 38 and (c) 66. The behaviour of the juveniles was categorized in four groups ranked by increasing risk-averseness: (i) individuals that foraged at the plate (black); (ii) individuals that entered the plate (dark grey); (iii) individuals that left the shelter but stayed on the sand (light grey); and (iv) individuals that did not leave the shelter (white). S-L: small-egg/low-food, L-L: large-egg/low-food, S-H: small-egg/high-food, L-H: large-egg/high-food, $n = 15$ except for the small-egg/low-food group on day 10 after first feeding, as two individuals were excluded from this trial (see Materials and methods section).

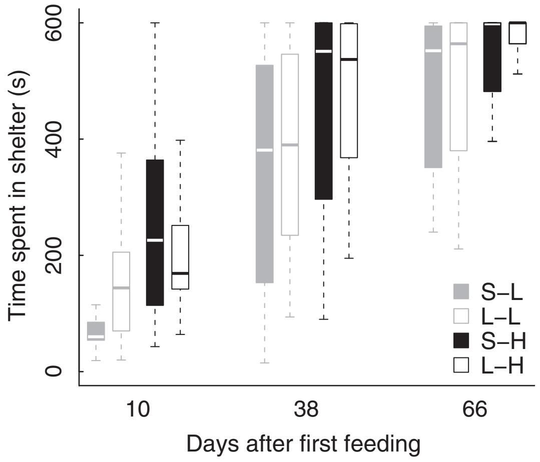

Fig. 6. The total time the fish spent hiding during 10 min observation time during the three trials for each treatment group. S-L: small-egg/low-food, L-L: large-egg/low-food, S-H: small-egg/high-food, L-H: large-egg/high-food. Boxplots as in Fig. 3.

Table 3. Results from the generalized linear mixed-effects models for juvenile behaviour ($n = 58$) on experimental day 10. Non-significant interactions were backwards eliminated. The significant *P*-values are marked in bold

	Fed from plate (yes/no)		Time in shelter	
	t	*P*	*t*	*P*
Model terms				
Food treatment (food)	−0·82	0·42	−0·82	0·42
Egg size class (egg)	−2·19	0·07	3·44	**0·01**
Body condition (BC)	−1·88	0·07	2·31	**0·03**
Food × egg	2·28	**0·03**	−3·71	**< 0·001**
Egg × BC	2·16	**0·04**	−3·36	**0·002**
Removed non-significant terms				
Food × BC	0·41	0·68	−0·81	0·42
Food × egg × BC	0·44	0·66	1·05	0·30

$t = -3{\cdot}44$, $P = 0{\cdot}001$) and experimental day ($t = 7{\cdot}99$, $P < 0{\cdot}001$). In addition, the interaction between food treatment and egg weight was significant ($t = 2{\cdot}42$, $P = 0{\cdot}02$), as among the low-food fish, juveniles from heavier eggs were more risk averse. Egg weight alone was not significant ($t = 1{\cdot}71$, $P = 0{\cdot}56$).

Additionally we examined whether a lack of body reserves drives juvenile behaviour, by testing for an effect of body condition that is, weight/standard length^3 × 100, on behaviour. We limited the analysis to experimental day 10 because at this early stage of ontogeny the variance in behaviour between the individuals was still largest (see Fig. 6). On experimental day 10 food treatment as main effect did not influence the propensity of the fish to forage at the plate and egg size class tended to have a negative effect (Table 3). Interestingly, there was a significant interaction between egg size and food treatment, namely the low-food fish originating from small eggs were significantly more likely to feed from the plate than the juveniles from the other treatments (Table 3). Body condition generally tended to decrease the propensity to forage at the plate, however, small-egg fish with a higher body condition were more likely to feed at the plate (egg size class × body condition: Table 3).

Similar results were found for the time spent in shelter by the fish on experimental day 10. Fish from small eggs hid longer, whereas food treatment as main effect did not affect the time spent in shelter by a fish (Table 3). The interaction between food treatment and egg size class was significant, however (Table 3). Among the low-food fish, the ones hatched from small eggs spent less time in shelter than those hatched from large eggs (Fig. 6). The time spent in shelter increased with body condition, but a significant interaction between egg size class and body condition (Table 3) indicated that among the small-egg juveniles hiding time decreased with body condition.

Repeating the analyses of juvenile behaviour on experimental day 10 with egg weight as a covariate did not alter the results.

Discussion

Our results show that egg size and food abundance interactively affect juvenile behaviour and physiology shortly after independence from maternal care, in a way that individuals originating from larger eggs can be expected to have survival benefits when facing food scarcity in nature. During the first 2 weeks after the onset of external feeding, young hatched from large eggs maintained a size advantage over small-egg young irrespective of food availability. In this period, they spent more time in shelter and were less committed to foraging, a behavioural strategy that may reduce predation risk (Lima & Dill 1990). Thus these traits would most likely confer survival advantages in food scarce environments where natural predators are present. In contrast, individuals hatched from different egg sizes behaved more similarly when food was abundant, suggesting that egg size is less important under these conditions. These results are in line with previous findings showing that juveniles from larger eggs have survival advantages particularly in low-food conditions (e.g. Hutchings 1991; Gliwicz & Guisande 1992; Einum & Fleming 1999; Bashey 2006; Camargo & Urbinati 2008; Donelson, Munday & McCormick 2009; Dziminski, Vercoe & Roberts 2009) (but see: Zhao, Chen & Brown 2001; Guinnee *et al.* 2007). Nevertheless, our results highlight behavioural traits related to survival that are under influence of egg size. Whether the observed variation of behavioural and physical phenotypes in *S. pleurospilus* due to differential maternal investment will actually result in fitness differences among offspring in nature can only be confirmed by a field study (e.g. Dziminski, Vercoe & Roberts 2009). However, it is highly likely that the marked phenotypic differences we found between juveniles from different egg sizes would have consequences under natural conditions.

Previous work showed that *S. pleurospilus* females lay smaller eggs when anticipating good post-natal conditions for their offspring (Taborsky 2006a). Investing less in individual offspring in anticipation of high food abundance may save females some reproductive investment, which can either be allocated to the production of more offspring (Smith & Fretwell 1974; Einum & Fleming 2000) or towards maintenance and future survival. Therefore, our results suggest that female *S. pleuropilus* might adaptively provision their young. On the other hand, we found no indication of a trade-off between egg size and egg number in our experiment, and this trade-off was so far only detected in *S. pleurospilus* mothers that had been raised in low-food conditions (Taborsky 2006a). Hence we assume that *S. pleurospilus* females laying smaller eggs will invest their saved resources in favour of future survival and reproduction.

In *S. pleurospilus* egg size apparently has the highest impact on the survival chances of young during the first few weeks of life, as during that time growth and behaviour were predominantly affected by egg size. Although there are exceptions (e.g. Gorman & Nager 2004), maternal effects are indeed generally thought to be most important in the earliest phase of an offspring's life (Bernardo 1996; Einum & Fleming 2000; Lindholm, Hunt & Brooks 2006). In our experiment, both the behaviour and the size of young hatched from different egg sizes converged with increasing age irrespective of the food conditions. Phenotypic convergence in offspring that differ in initial size due to maternal effects has been attributed to compensatory growth in various taxa (e.g. Wilson & Réale 2006; Reitzel & Heyland 2007; Camargo & Urbinati 2008). Although minor in comparison with food ratio, we found a strikingly long lasting effect of egg size on fish length and body mass (12 weeks). Persistent effects of egg size on juvenile body size have been reported in several fish species [e.g. 20 days in Siberian sturgeon, *Acipenser baeri* (Gisbert, Williot & Castelló-Orvay 2000); 140 days in Artic charr, *Salvelinus alpinus* (Wallace & Aasjord 1984)]. None of these studies tracked the growth trajectories in individual fish right from the egg stage and fish were always raised in groups. To our knowledge, our study is the first to document the persistence of egg size effects in individual fish hand-raised from the egg stage. Our approach allows us to determine what egg size contributes to the phenotype without the additional variance that competitive interactions between offspring would generate.

The initial lengths of juvenile *S. pleurospilus* hatched from large eggs were markedly larger (20%) than the lengths of small-egg juveniles. These size differences may profoundly affect survival, as juveniles hatched from large eggs had a higher burst swimming speed. An increased locomotory performance facilitates predator avoidance and is therefore associated with higher juvenile survival throughout the animal kingdom (e.g. Le Galliard, Clobert & Ferrière 2004; Husak 2006). Hence hatching from a larger egg can directly enhance the survival chances of young. To our knowledge our study is the first to investigate burst swimming speed of individuals of which the egg size is known. The reported differences could be a consequence of egg size resulting in a larger size of young, as generally in fishes, juvenile burst swimming speed increases with length (reviewed by Miller *et al.* 1988), and particularly it does so also in the very closely related *Tropheus moorii* (Schürch & Taborsky 2005). In contrast, Nadeau *et al.* (2009) found neither a maternal influence nor a body size effect on juvenile swimming performance, but they did not include egg size in their analysis.

Behavioural adaptations may also reduce the susceptibility to predation in young hatched from large eggs, particularly when conditions are harsh. The smallest group of fish in our experiment, that is, fish hatched from small eggs and kept at low-food conditions, spent least time in shelters and were most likely to feed in an unsafe surrounding. Both these behaviours are associated with a higher predation risk in nature (Lima & Dill 1990; Skelly 1994; Scharf *et al.* 2003). In general, feeding behaviour has well-known survival costs due to enhanced predation risk (Abrams 1991; Lima 1998). For example, *Rana catesbiana* tadpoles were more active when exposed to low food levels and consequently suffered a higher mortality (Anholt & Werner 1995). Foraging roach (*Rutilus rutilus*) showed a higher responsiveness to predator alarm substance with increasing size, supposedly as smaller fish have lower lipid reserves than larger ones forcing them to feed intensively in order to escape starvation (Jachner & Janecki 1999). Our results suggest that *S. pleurospilus* juveniles from small eggs facing low-food conditions show a stronger commitment to foraging, which might lead to an increased susceptibility to predation in these fish in their natural habitat. As we found a positive effect of body condition on risk-averse behaviour, our results support the hypothesis, that an increased foraging activity of young is driven by a lack of body reserves (cf. Jachner & Janecki 1999). Nevertheless, as body condition affected juvenile behaviour in addition to egg size and food conditions and, moreover, it influenced behaviour interactively with egg size, it seems that body condition cannot solely explain foraging activity in juvenile fish.

Behaviour and body size of juvenile *S. pleurospilus* were tightly linked, suggesting that size is the main driving force behind the observed behavioural differences. In turn, juvenile size depends strongly on the egg size and feeding conditions of young and therefore these two factors can be regarded as causative for the behaviour of juvenile *S. pleurospilus*. In addition to size-dependent behavioural differences in the first experimental trial, fish tended to spend less time foraging and were more likely to dig a shelter underneath the pebbles with increasing size and age during the course of the experiment. Theory predicts that prey should rather decrease foraging rates when predation risk is high (Lima & Bednekoff 1999). Bearing this in mind, the high commitment to foraging and the low propensity to seek shelter as observed in small fish seems counterintuitive. However, a recent study demonstrated that in the presence of intense gape-limited predation, risky foraging can evolve even in risky environments (Urban 2007). Juveniles may maximize their food intake and subsequently somatic growth rather than minimizing current predation risk (cf. Cresswell 1994; Biro, Post & Abrahams 2005) in order to grow into a size refuge, which may outweigh the immediate survival costs of high foraging rates. Even if a single predator species eats more larger than smaller prey items (e.g. Berger, Walters & Gotthard 2006; Segers, Dickey-Collas & Rijnsdorp 2007), all potential predators for a prey species must be taken into account when estimating the predation risk of a certain sized prey (Blanckenhorn 2000). In aquatic habitats, the number of potential predators generally decreases with prey size due to gape-size limitations (Sogard 1997). Hence juvenile prey can escape most of their predators by outgrowing the most vulnerable size range, the so-called 'mortality window' (e.g. see Post & Prankevicius 1987; Persson *et al.* 1996; Searcy & Sponaugle 2001). If juveniles hatched from small eggs grow up in an environment where food is scarce, they are either forced to stay longer within their mortality window or to take a higher risk to obtain food, and consequently will suffer heavy mortality. In poor environments a large egg size would hence help to reach the size refuge faster. It is highly likely that a size refuge exists for *S. pleurospilus* juveniles as all potential natural predators at Lake Tanganyika are gape-size limited fish or snakes (B. Taborsky, personal observation). A large egg size does not only shorten the time a juvenile is most vulnerable, but larger individuals may also have an advantage when competing over resources in the first weeks of their lives (Bashey 2008), helping large-egg juveniles to outgrow the mortality window even faster.

In our study maternal brood care was experimentally excluded, and so far it is not known if mouthbrooder mothers are able to compensate for small egg sizes by improved maternal care. Like most mouthbrooders, *S. pleurospilus* mothers do not feed their young, so it is difficult to imagine by what mechanism mothers could achieve compensatory growth in their young. Moreover, in our experiment egg size had such a persistent effect on body size that we consider it unlikely that these potential compensatory mechanisms would change our results greatly.

Conclusion

Egg size strongly affects body size in *S. pleurospilus*, and fish hatched from larger eggs swim faster. When food is scarce, juveniles originating from smaller eggs show more risk-prone behaviour that might make them more susceptible to predation. Thus, the more cautious behaviour of individuals originating from larger eggs may increase their survival chances when growing up under harsh conditions. The observed effects of egg size on juvenile growth and behaviour were most pronounced in the first weeks of life but weakened with time. While previous studies focused on the importance of competition as a selective force in offspring size evolution, our results suggest a link between offspring size and a behavioural mechanism that might contribute to the context-dependent benefits of egg size.

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