



# Do Maternal Food Deprivation and Offspring Predator Cues Interactively Affect Maternal Effort in Fish?

Francisca H. I. D. Segers\*, Barbara Gerber\* & Barbara Taborsky\*†

\* Behavioural Ecology, Institute of Ecology and Evolution, University of Bern, Hinterkappelen, Switzerland

† Evolution and Ecology Program, International Institute for Applied Systems Analysis (IIASA), Laxenburg, Austria

## Correspondence

Francisca Segers, Behavioural Ecology,  
Institute of Ecology and Evolution,  
University of Bern, Wohlenstrasse 50a,  
CH-3032 Hinterkappelen, Switzerland  
E-mail: francisca.segers@gmail.com

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## Abstract

The state of the environment parents are exposed to during reproduction can either facilitate or impair their ability to take care of their young. Thus, the environmental conditions experienced by parents can have a transgenerational impact on offspring phenotype and survival. Parental energetic needs and the variance in offspring predation risk have both been recognized as important factors influencing the quality and amount of parental care, but surprisingly, they are rarely manipulated simultaneously to investigate how parents adjust care to these potentially conflicting demands. In the maternally mouthbrooding cichlid *Simochromis pleurospilus*, we manipulated female body condition before spawning and exposure to offspring predator cues during brood care in a two-by-two factorial experiment. Subsequently, we measured the duration of brood care and the number and size of the released young. Furthermore, we stimulated females to take up their young by staged predator attacks and recorded the time before the young were released again. We found that food-deprived females produced smaller young and engaged less in brood care behaviour than well-nourished females. Final brood size and, related to this, female protective behaviour were interactively determined by nutritional state and predator exposure: well-nourished females without a predator encounter had smaller broods than all other females and at the same time were least likely to take up their young after a simulated predator attack. We discuss several mechanisms by which predator exposure and maternal nutrition might have influenced brood and offspring size. Our results highlight the importance to investigate the selective forces on parents and offspring in combination, if we aim to understand reproductive strategies.

## Introduction

Influences from the parental environment can be transmitted to offspring via parental effects and may profoundly affect the phenotype expressed in subsequent generations, for example, germination season in plants (e.g. Galloway 2001), offspring size (e.g. Naguib & Gil 2005; Taborsky 2006), natal dispersal (e.g. Tschirren et al. 2007) and egg quality (Blount

et al. 2002) in several bird and fish species. One highly influential mechanism by which parents can affect the phenotype of their offspring is by the quality of brood care. Thus, when the environmental conditions present during rearing affect brood care behaviour, they can have a transgenerational effect on offspring phenotype and fitness (e.g. Wapstra 2000; Kolbe & Janzen 2001; Jodice et al. 2006; Evans et al. 2007; Reardon & Chapman 2010).

Environmental conditions may govern how much parents are willing to invest in care. For example, in some species, parental effort is reduced when the body reserves drop below a critical level (e.g. Lavery & Kieffer 1994; Velando & Alonso-Alvarez 2003; Harding et al. 2009). In iteroparous species, resource scarcity often has negative fitness consequences for current offspring, as parents avoid jeopardizing their own chances for future reproduction (Stearns 1989). In several taxa, food-deprived parents were observed to shorten the duration of brood care (e.g. in insects, Scott & Traniello 1990; birds, Öst et al. 2003 and fish, Steinegger & Taborsky 2007), to invest less in guarding the brood and fanning the eggs (e.g. in cichlids, Smith & Wootton 1995; Townshend & Wootton 1985) or to produce less or smaller clutches (e.g. in cichlids, Townshend & Wootton 1985 or lizards, Du 2006). In several fish species, parents even cannibalize young if food becomes scarce (Okuda & Yanagisawa 1996; Kvarnemo et al. 1998; Manica 2004).

Parents need to forage in order to maintain elevated levels of body condition (Townshend & Wootton 1985), but predator avoidance and foraging are often conflicting demands (e.g. Lima & Dill 1990), resulting in a trade-off between time spent for feeding and for being vigilant (e.g. Fraser & Gilliam 1987; Martín et al. 2003, 2006). In species where parents do not feed their offspring, this trade-off forces parents to allocate their time between the defence of offspring against predators and their own food uptake. The predictions of optimal parental effort in the face of high offspring predation risk are contradictory. It may be beneficial to extend brood care when the predation risk for the young is high, for example by spending more time guarding the brood at the costs of own feeding time as observed in fish (e.g. Rangeley & Godin 1992; Taborsky & Foerster 2004; Steinhart et al. 2005; Cooke et al. 2008; Gravel & Cooke 2009) and lizards (Huang & Wang 2008). On the contrary, a greater risk of brood predation may also favour a reduced investment in brood care, thereby allowing parents to save energy for future reproduction that would otherwise be wasted (Roff 1992). In line with this hypothesis, several bird species reduce offspring provisioning (e.g. Fontaine & Martin 2006; Peluc et al. 2008), decrease their clutch size (Doligez & Clobert 2003; Eggers et al. 2006) or shorten the brood care period (e.g. Harfenist & Ydenberg 1995) in response to increased predation risk for offspring. Fish (Lachance & Fitzgerald 1992; Chin-Baarstad et al. 2009) and lizards (Huang 2008) have been observed to relax nest

defence or to cannibalize their entire broods. As protecting offspring from brood predators is costly (Chellappa & Huntingford 1989; Smith & Wootton 1995; Lindström 1998; Gravel & Cooke 2009), well-fed individuals may have the potential to increase parental effort in response to an enhanced offspring predation threat, whereas individuals with low reserves may be unable or unwilling to do so (Smith & Wootton 1995). Thus, as parental condition and offspring predation threat may interactively affect brood care strategies, it is surprising that, to the best of our knowledge, so far not a single experimental study manipulated both factors simultaneously to study how parents trade off their own energetic needs against their offspring's predation risk.

We investigated how the effort in offspring protection is traded off against parental energetic needs in a maternally mouthbrooding cichlid. Mouthbrooding cichlids are particularly suited to study these potentially conflicting demands as protection involves holding the young within the safety of the buccal cavity, but this partly or completely prevents females from feeding (Johnston 1974; Keenleyside 1991). We manipulated female body condition and perceived offspring predation risk in the Lake Tanganyika cichlid *Simochromis pleurospilus* in a two-by-two factorial experiment and measured their effect on female brood care and on offspring size. Generally, we expected a reduced reproductive investment when females were faced with food limitation, but an increase in brood care effort in the presence of perceived offspring predation risk.

## Methods

### Study species

*Simochromis pleurospilus* is a maternally mouthbrooding cichlid of the subfamily Tropheini, endemic to Lake Tanganyika in East Africa. It lives along the rocky littoral shores of the lake. Both adults and young feed on debris and epilithic algae. After mating, *S. pleurospilus* females mouthbrood the clutch and care for the young alone. Brood care of *S. pleurospilus* consists of two phases, after which the young are independent: (i) in the first phase, the female continuously keeps the eggs and larvae in her buccal cavity. During this time, the young use up yolk reserves, and both female and young do not feed. (ii) The second brooding phase starts after approximately 2 wk when the young are released for short periods from the mouth during which mothers and young can forage. When disturbed or attacked by

other fish, females take their young back into their mouth (Taborsky 2006).

While being outside the mouth of the mother, generally all fish in the lake would eat the young if given a chance to do so, regardless whether they are predatory species or algivorous species. In contrast, adult females are rather safe from predation at least during their activity period. Predators that would pose a threat to adult females have not been observed during day time in the field (Kotrschal, A., Massironi, M. & Taborsky, B., unpubl. data). Only at night, when females rest on the bottom of the lake, they could potentially be attacked by nocturnal predators. Although we cannot exclude that mouthbrooding increases a female's vulnerability to predators during night, adult predation risk is beyond the scope of our study.

#### Animal husbandry

The fish used for this experiment comprised first- and second-generation offspring of wild-caught individuals originating from the southern tip of Lake Tanganyika near Nkumbula Island, Zambia. To obtain the experimental clutches, we set up eight 200-l breeding tanks stocked with four to six randomly allocated females and one male. At the end of the experiment, we had obtained clutches from seven different males, each spawned 1–7 times. All females were individually marked by excising half of one dorsal fin ray. For the offspring predation risk manipulations, mouthbrooding females were moved to 100-l tanks. The conditions in all tanks mimicked the natural water and light conditions in Lake Tanganyika: water temperature was set to  $27 \pm 1^\circ\text{C}$  and a light/dark regime to 13 h : 11 h with 10-min dimmed light periods in the morning and evening. All breeding tanks were equipped with a layer of fine-grained sand, an internal biological filter, flow-erpot halves and opaque PVC plates and tubes to serve as shelters.

#### Body condition

To manipulate female body condition, four breeding tanks were assigned to a high-food (HF) treatment and the other four tanks received a low-food (LF) treatment. The HF females were fed *ad libitum* twice a day during 6 d/wk, whereas the LF females were fed *ad libitum* twice every fifth day during 30 d. Both treatment groups received Tetramin flakes. During the food treatment, the male was kept behind a transparent plastic partition to allow visual contact

between the fish but still to prevent mating. Water could flow through tiny gaps along the edges of the partition allowing also for olfactory contact, but food was unable to pass. The male was fed twice/d in both the HF and the LF tanks. To check for the effect of food treatment on female body condition, we measured the standard length (SL; to the nearest 0.5 mm) and weight (W; to the nearest 0.01 g) of each female before and after 30 d of food treatment. From these measures, we calculated female body condition as  $BC = 100 \cdot W / SL^3$  (Fulton's condition factor, Bolger & Connolly 1989). The mean condition values for the two food treatment groups before the food treatment were almost identical (high food:  $2.85 \pm 0.064$  SE and low food:  $2.83 \pm 0.065$  SE).

#### Experimental clutches

After the end of the food treatment, the transparent partition was removed and the male was released so that the fish were able to spawn. We checked for the occurrence of spawning early in the morning and late in the afternoon, thus obtaining an estimate of the spawning time with a precision of  $\pm 6$  h. All fish were now fed twice a day. As soon as all four experimental tanks contained a mouthbrooding female, the males were separated again by a partition and the food treatment was continued. It took HF and LF females approximately the same time to spawn (HF: mean  $18 \text{ d} \pm 2.9$  SE, LF: mean  $18 \text{ d} \pm 2.8$  SE).

#### Predation risk of young

The day after a female of the HF or the LF treatment had spawned, it was alternately assigned to the predator or to the control treatment and transferred individually to one of four experimental 100-l tanks. The experimental tanks were arranged as two blocks of three tanks. The two outer tanks of each block were stocked with brooding females. The central tanks were divided in two equal-sized compartments by an opaque partition. The female tanks and treatment compartments were equipped with two flower pot halves as shelter and biological filters. One compartment of each of the two central tanks was stocked with a *Ctenochromis horei* (mean 8 cm SL), a natural predator of the *S. pleurospilus* young, and the other compartment remained empty (control treatment). We took care to keep the temperature in these tanks constant at  $27.0^\circ\text{C}$  because egg development and brooding duration can be influenced by temperature (Taborsky & Foerster 2004). Removable

visual barriers could be placed between the experimental tanks and the central tanks allowing us to control the visual contact of the brooding females to the predator or control compartments.

During the first 4 d after the transfer to the experimental tanks (days 3–6 after spawning), the females could continuously see either the offspring predator or the empty compartment. At days 7–10 after spawning, females were exposed to the treatment compartments only twice/d for 30 min, once in the morning and once in the afternoon at randomized times. This intermittent exposure scheme was chosen to maintain the perceived offspring predation risk in the predator treatment at a certain level but at the same time to prevent habituation to the predator (Kavaliers & Choleris 2001; Taborsky & Foerster 2004).

Pilot trials had revealed that *S. pleurospilus* females respond to the visual presentation of a *C. horei* by showing open aggression towards it. Therefore, we observed the interactions between the female and the offspring predator once/d on days 7–10 during the first 15 min of the first predator exposure of a day. We noted the rates of overt aggression (fast approach, fin raising and mouth contact with glass towards the other fish) and restraint aggression (slow approach towards the other fish).

#### Data recording

The experimental set-up was surrounded by an opaque curtain to avoid disturbing or threatening the fish. During the behavioural observations and the threat stimulus tests, the observer stayed hidden behind the curtain. During daytime, females were filmed continuously from day 10 after spawning using remotely controlled video recording. This allowed us to determine the exact moment of the first release of young, which marks the end of the first brooding phase. (This never occurred before day 10 in our study species.) Additionally, we obtained the time when the females first released the young for  $\geq 10$  min. We counted the offspring once at the onset of the 2nd brooding phase (estimate from the video recordings) and once at the end of the experiment (direct count). Behavioural parameters obtained from the videos included the latencies until females took up the 1st young after a threat stimulus test, the time interval until they released the young again and the feeding rates of mothers. Feeding rates of young were obtained by direct observation from behind the curtain as the quality of the videos was not sufficient to see this.

#### Threat stimulus tests

During the 2nd brooding phase, i.e. the phase when the female temporarily releases her young, we exposed females repeatedly to simulated predator attacks to estimate their changing motivation to take up the young for protections with proceeding time. Each female was exposed to 12 successive threat stimuli. To simulate an attack by a predator, a stone attached to a string was pulled along the lid of the tank until it fell through an opening into the water. The first threat stimulus test was only performed once females released their young continuously for at least 10 min. We had to use this threshold criterion because threat stimulus tests could only be conducted when the young were outside of the mother's mouth and, right at the beginning of the 2nd brooding phase, *S. pleurospilus* females release their young for too short periods to enable us to perform these tests. If possible, the first threat stimulus test was conducted the day after the female had been observed to release the young for at least 10 min continuously; if females still released young for too short time intervals at that day, it was postponed to the following day. Afterwards, every second day, two stimulus tests per day were conducted. If only one test was possible on a day (i.e. when the females did not release the young a second time after the first test of the day), the second test was conducted the following day.

We recorded the time interval until the mother started to take up the young after the stimulus and the time when she released them again. If a female did not take up the young within 20 min after receiving the threat stimulus, we terminated the recording as obviously no uptake took place in response to the stimulus. In some cases, females were alerted by the approaching observer prematurely, and they took up the young already before the threat stimulus had been given. These tests were excluded from our analyses.

#### Feeding rates

From the following day after mothers had released their young for the first time, the fish were fed *Spirulina* pellets for tropical fish (Sera fish foods) in the evening. The young had not received any prior food. The food amount was calculated according to the biomass of fish per tank. We fed 12% of the body weight of the mother plus 0.0100 g/young at days 1–14 after first release and plus 0.0112 g/young at days 15–28 after first release.

After the onset of the threat stimulus tests, we started to record the feeding rates (number of bites at small food items on the substrate) of mothers and one randomly chosen young per brood. We did this twice every other day for 10 min, once in the morning and once in the afternoon. The observations were made on the days when no threat test took place. If a mother did not release her young for 10 min at these days, the observation took place the following day.

#### Termination of experimental trials

Females and young stayed in the experimental tanks until the end of the 2nd brooding phase, i.e. when the mother did not take up the young anymore on two consecutive days. At this time, the young were considered to be independent. Within 2 d after independence, we obtained the length of the juveniles by placing them on a 1-mm grid and estimated their SL to the nearest 0.5 mm under a binocular, and we measured their weight to the nearest 0.1 mg and lengths and weights of females for the last time. Then, the females and young were transferred to adult and juvenile stock tanks of our laboratory, respectively, and the experimental tanks were reused for other experimental females.

#### Data analysis

Statistical analyses were conducted using R 2.9.2 (R Development Core Team 2009). Our total sample comprised 25 females with six females for each treatment combination, except the LF group with predator ( $N = 7$ ). We used univariate ANCOVAs with female size (closest measurement before spawning) as covariate to investigate treatment effects on brood care durations and brood size. The interaction between food and predator treatment was always tested and removed from the model if not significant. We tested for treatment effects on mean offspring size while correcting for the length of the second brood care phase with an ANCOVA.

As we repeatedly tested the same individuals, the propensity of mothers to take up their young after a simulated predator attack was modelled using a generalized linear mixed effect model (GLMM) with a binomial distribution and female as random effect to correct for repeated measures. Only brood size was included in the model for uptake propensity and not female length as these two covariates were not independent (see Results section). The total aggression towards the predator and the feeding rates of both

mother and offspring were analysed using GLMMs with Poisson distributions and again female as random effect to correct for repeated measures. For the GLMMs, Wald tests were used to test the significance of the fixed effects and the models were fitted with the lmer function.

After a log transformation, the release latencies were analysed using a linear mixed effect model (LME). For this analysis, only the females that took up their young after being startled were taken into account. We tested for the interaction 'food treatment  $\times$  predator exposure' and interactions between our main effects and days after the start of the second brood care phase (days). To account for a non-linear decrease in latency time with progression of the second brood care phase, we added the square of days as an explanatory term to the model. Again, only brood size and not female length was included in the model; we did not test for interactions between brood size and the main effects, as we had no interest in possible interactions between these variables. We first explored the best structure of the random components (comparing random intercept models with random intercept and slope models) using restricted maximum likelihood (REML). Then, the non-significant interaction terms were backward-eliminated, using the  $t$ -statistic to check for significance (Zuur et al. 2008). In the result section, we show the  $t$ - and  $p$ -values of the non-significant interactions before they were removed from the model. Homogeneity of residuals of all our models was checked afterwards.

## Results

### Female body measurements

At the size measurement closest to spawning, females from the HF treatment had a higher body condition than LF females (LF:  $2.6 \pm 0.08$  SE and HF:  $2.9 \pm 0.08$  SE; ANOVA,  $F_{2, 22} = 5.14$ ,  $p = 0.03$ ), whereas there was no significant difference in body condition between the females of the different predator treatments ( $F_{2, 22} = 0.01$ ,  $p = 0.93$ ). Also, the interaction of the treatments did not significantly affect body condition ( $F_{3, 21} = 1.71$ ,  $p = 0.21$ ). Similarly, there were no significant differences in SL between the females of the different treatments at this time (ANOVA, food:  $F_{2, 22} = 0.87$ ,  $p = 0.36$ ; predator:  $F_{2, 22} = 1.40$ ,  $p = 0.25$ ; food  $\times$  predator:  $F_{3, 21} = 0.29$ ,  $p = 0.59$ ). Also, at the end of brood care, SL did not differ between the treatment groups (ANOVA, food:  $F_{2, 22} = 0.51$ ,  $p = 0.48$ ; predator:

$F_{2, 22} = 0.91$ ,  $p = 0.35$ ; food  $\times$  predator:  $F_{3, 21} = 0.14$ ,  $p = 0.71$ ). Females of the LF treatment still tended to have a lower body condition (ANOVA:  $F_{2, 22} = 3.71$ ,  $p = 0.07$ ), while neither the predator treatment ( $F_{2, 22} = 0.02$ ,  $p = 0.88$ ) nor the interaction between treatments ( $F_{3, 21} = 0.61$ ,  $p = 0.44$ ) affected body condition.

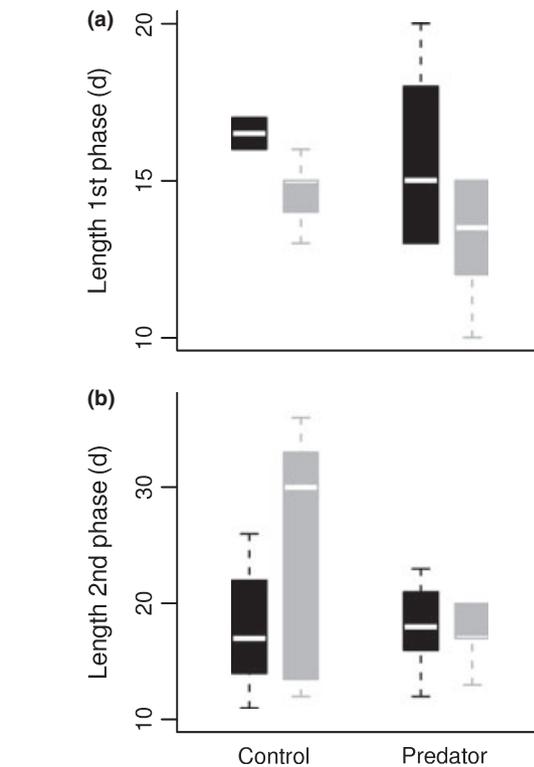
**Duration of brood care**

Neither the length of the first brood care phase (LM,  $F_{1, 23} = 0.74$ ,  $p = 0.40$ ) nor the total brood care duration was significantly related to brood size (LM,  $F_{1, 23} = 3.92$ ,  $p = 0.06$ ); however, brood size positively affected the length of the second brood care phase (LM,  $F_{1, 23} = 5.64$ ,  $p = 0.03$ ).

The first brooding phase was on average more than 2 d longer in HF females ( $16.25 \text{ d} \pm 2.09 \text{ SE}$ ) than in LF females ( $13.92 \text{ d} \pm 1.54 \text{ SE}$ ; Table 1, Fig. 1a). Instead, LF females tended to have a longer second brood care phase than HF females (Table 1, Fig. 1b). Consequently, the entire brood care duration until independence of the young was not affected by the food treatment (Table 1). Predator presence had no influence on the length of the first, the second or the total brood care period (Table 1). The second brood care phase and the total brood care period increased with female length (Table 1).

**Number and size of young**

Remarkably, LF females had more offspring at the end of the experiment than HF females (Table 1). Moreover, there was an interaction between the food and the predator treatment: HF females had more young when an offspring predator was present than when there was no predator (Table 1, Fig. 2). There was hardly any difference between the number of young females had at the beginning of the



**Fig. 1:** Effect of the food and predator treatment on the duration of the (a) 1st and the (b) 2nd brood care phase. The boxplots show medians, quartiles and 5th and 95th percentiles. Black represents the high-food females, grey the low-food females.

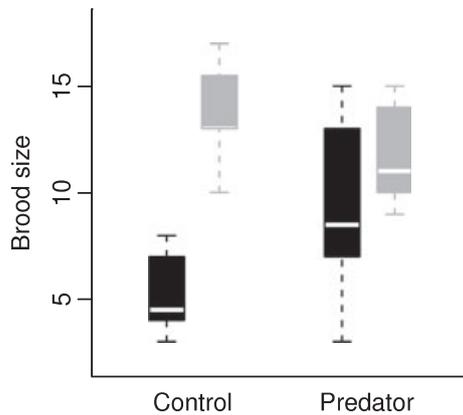
second brooding phase compared to the end (mean number of young at the start of brood care: 11.2; mean number of young at the end of the brood care period: 10.5), indicating that final brood sizes were not strongly affected by a differential mortality of young during the second phase.

Mean offspring size increased with the duration of the second brood care period (Table 2; Fig. 3). When controlling for this effect, independent young of HF

**Table 1:** ANCOVA of the effects of food treatment, predator exposure and female size on the durations of the first ( $F_{3, 21} = 4.92$ ,  $R^2 = 0.41$ ,  $p = 0.01$ ), the second ( $F_{3, 21} = 2.43$ ,  $R^2 = 0.26$ ,  $p = 0.09$ ), the total brood care period ( $F_{3, 21} = 2.47$ ,  $R^2 = 0.26$ ,  $p = 0.09$ ) and the number of young at the end of brood care ( $F_{4, 20} = 8.83$ ,  $R^2 = 0.64$ ,  $p < 0.001$ )

Variable	1st brood care phase		2nd brood care phase		Total brood care duration		Number of young	
	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>	<i>t</i>	<i>p</i>
Food treatment	2.99	<b>0.007</b>	-1.87	0.08	-1.10	0.30	-5.68	<b>&lt;0.001</b>
Predator exposure	-1.45	0.16	-0.36	0.72	-0.72	0.48	-1.58	0.13
Food $\times$ Predator	<i>0.29</i>	<i>0.77</i>	<i>1.18</i>	<i>0.25</i>	<i>1.23</i>	<i>0.23</i>	<i>3.00</i>	<b>0.007</b>
Female size	1.13	0.27	2.05	<b>0.05</b>	2.28	<b>0.03</b>	2.45	<b>0.02</b>

Significant *p*-values are marked in bold. Non-significant interactions that were removed from the models are in italics.

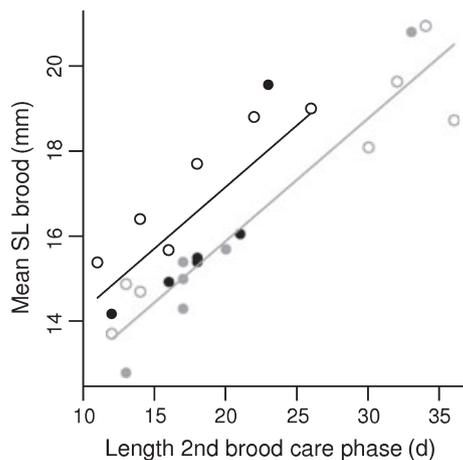


**Fig. 2:** Effect of the food and predator treatment on brood size. Box-plots as in Fig 1. Black represents the high-food females, grey the low-food females.

**Table 2:** ANCOVA of the effects of food treatment, predator exposure and duration of the 2nd brooding phase on the mean standard length of young at the end of brood care ( $F_{3, 21} = 40.19$ ,  $R^2 = 0.85$ ,  $p < 0.001$ )

Variable	Mean size of young	
	<i>t</i>	<i>p</i>
Food treatment	3.15	<b>0.005</b>
Predator exposure	-1.85	0.08
Food × Predator	-1.48	0.16
Duration 2nd phase	10.33	<b>&lt;0.001</b>

Significant p-values are marked in bold. The non-significant interaction (in italics) was removed from the model.



**Fig. 3:** The length of the 2nd brood care phase plotted against the mean standard length of a brood at the end of the 2nd brood care phase for both food treatments. Black and grey represent high-food and low-food females, respectively. Filled circles: clutches of which the mothers were exposed to a *Ctenochromis horei*; open circles: controls. The lines represent the best fit and show the effect of the maternal food treatment on the mean standard length of the brood.

females were on average larger than those of LF females (Table 2; Fig. 3), whereas predator presence tended to decrease average offspring size (Table 2). We did not include female standard length in this ANCOVA as this would over-parameterize the model and the duration of the second brood care phase increased with female size.

The treatment effect on offspring size described earlier could be related to differences in the duration of the first brooding phase between the four treatment groups as this duration was correlated with final offspring size when controlling for the duration of the second brooding phase (partial correlation,  $N = 25$ ,  $R = 0.50$ ,  $p = 0.007$ ).

**Female behaviour**

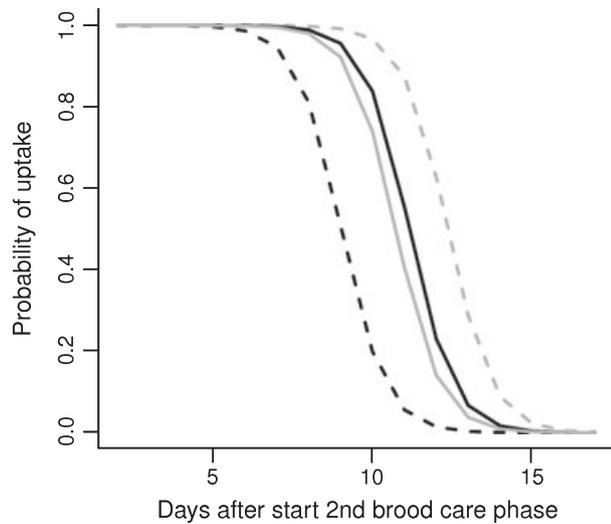
Food and predator treatments influenced the uptake propensity of females interactively. Among the LF females, exposed and non-exposed individuals had a similar propensity to take up their young (Table 3; Fig. 4). In contrast, the HF females did respond to the predator treatment: mothers with a predator experience were more willing to take up their young than those without (Table 3; Fig. 4). When including the brood size as covariate in the model, the effect of the food treatment and the interactive effect on uptake behaviour disappeared (Table 3).

The time until young were released after a startle test decreased as the second brood care phase progressed (Table 4). HF females initially had longer latencies to release their young after being startled than LF females (Table 4; Fig. 5); however, they showed a faster decrease in these latencies (Table 4: food × days). Predator exposure had no effect on the

**Table 3:** Generalized linear mixed effect model of the effects of food treatment and predator exposure on whether or not females took up their young after a simulated predator attack ( $N = 297$ )

Variable	Uptake of young (yes/no)			
	Brood size excluded		Brood size included	
	<i>z</i>	<i>p</i>	<i>z</i>	<i>p</i>
Food treatment	-2.58	<b>0.01</b>	-0.43	0.66
Predator exposure	-1.36	0.17	0.19	0.85
Food × Predator	2.10	<b>0.04</b>	1.70	0.09
Days	-7.97	<b>&lt;0.001</b>	-8.02	<b>&lt;0.001</b>
Brood size	-	-	1.35	0.18

'Days' refers to the number of days after the onset of the second brood care phase on which the test was conducted. Non-significant interactions that were removed from the models are in italics. Significant p-values are marked in bold.



**Fig. 4:** The propensity of a female to take up her young after a simulated predator attack in dependence of the time since the onset of the 2nd brood care phase for the four treatments. The black and grey lines represent high-food and low-food treatments, and the continuous and dotted lines represent predator and control treatment, respectively.

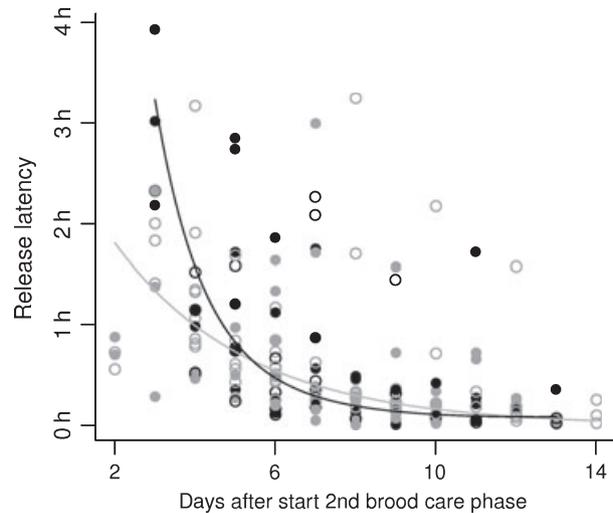
time mothers retained their young. Females with larger broods took longer time to release their young after a simulated predator attack (Table 4).

The feeding rates (bites/min) of both females and young were not significantly affected by either of

**Table 4:** LME of the effects of food treatment and predator exposure on the time a mother kept her brood in her mouth after a simulated predator attack (N = 187)

Variable	Latency time	
	t	p
Food treatment	2.53	<b>0.02</b>
Predator exposure	-0.66	0.52
Food × Predator	0.83	0.42
Days	-2.16	<b>0.03</b>
Days <sup>2</sup>	0.18	0.86
Brood size	2.03	<b>0.05</b>
Food × Days	-2.57	<b>0.01</b>
Food × Days <sup>2</sup>	2.31	<b>0.02</b>
Predator × Days	-0.97	0.33
Predator × Days <sup>2</sup>	0.77	0.45
Food × Predator × Days	1.26	0.21

'Days' refers to the number of days after the onset of the second brood care phase. The non-significant interactions were backward-eliminated, using ML to check for significance (see Methods). In the table, we show the t-values for non-significant interactions and those removed from the model are in italics. Significant p-values are marked in bold.



**Fig. 5:** Days after the start of the second brood care phase plotted against the time a mother kept her young in her mouth after a simulated predator attack after correcting for brood size (release latency). Black and grey colours represent high-food and low-food, respectively. Mothers that were exposed to a *Ctenochromis horei* are indicated by filled dots. The lines are the best fit lines and show the effect of the maternal food treatment on release latency.

the treatments; however, females that were exposed to predators tended to have lower feeding rates (Table 5). Offspring feeding rates increased with time, while female feeding rates decreased as the second brood care phase progressed (Table 5). Smaller females had higher feeding rates (Table 5).

The rate of total aggressive behaviour i.e. overt and restrained aggression towards the offspring pred-

**Table 5:** Generalized linear mixed effect models of the effects of food treatment and predator exposure on the number of bites during 10 min for females (N = 348) and young (N = 297)

Variable	Female feeding rate		Offspring feeding rate	
	z	p	z	p
Food treatment	0.61	0.54	1.31	0.19
Predator exposure	-1.71	0.08	0.02	0.98
Food × Predator	-0.23	0.82	0.16	0.87
Days	-2.15	<b>0.03</b>	38.69	<b>&lt;0.001</b>
Female size	-3.61	<b>&lt;0.001</b>	-	-
Brood size	1.73	0.08	0.89	0.38

'Days' refers to the number of days after the onset of the second brood care phase on which the feeding rates were recorded. Female size is the standard length of the female measured at the closest measurement before spawning. Non-significant interactions that were removed from the models are in italics. Significant p-values are marked in bold.

ator was higher in HF females (GLMM,  $N = 40$ ,  $z = 2.14$ ,  $p = 0.03$ ).

## Discussion

The food treatment before spawning influenced female investment in brood care. As expected, LF females terminated the first brooding phase earlier and thus starved for a shorter time than HF females. Instead, LF females tended to have a longer second brooding phase, so that the total brood care period was not affected by the food treatment. Low-food females had on average larger broods but produced smaller independent young than HF females. Moreover, they released their young faster after being startled and were less aggressive towards an offspring predator. As food treatment was strongly linked to offspring size and quantity, we cannot entirely exclude that differences in offspring quality between high- and LF females caused the observed effect of food treatment on brood care behaviour rather than the other way around. Noteworthy, in an unmanipulated laboratory population, body condition was not correlated with fecundity and egg size ( $n = 38$ , Segers & Taborsky, unpubl. data), although the body condition indices of this group varied across an even wider range than those of the females used for this experiment (laboratory population, min. 2.1 and max. 4.0; experimental females, min. 2.2 and max. 3.4). Therefore, we propose that the differences in brood characteristics we observed were caused by differences in brood care behaviour between the females of the two food treatments.

Offspring predation risk affected maternal effort only in interaction with the food treatment. In the control treatment, LF females produced considerably more young than HF females, whereas females of both food treatments had intermediate brood sizes when a predator had been presented. The propensity to take up the young after a threat stimulus followed the same interactive pattern, which suggests that uptake frequency depends on brood size. Indeed, the interactive effect of food deprivation and predator exposure on offspring retention time vanished when we controlled for brood size.

The observation that food-deprived females reduced the duration of the more demanding first brood care period and their effort in protecting young is consistent with parental investment and life history theory predicting that long-lived parents should avoid jeopardizing survival and future breeding attempts (Stearns 1989). Body condition-dependent brood care behaviour has been reported in

several taxa (e.g. birds, Drent & Daan 1980; Erikstad et al. 1993; Öst et al. 2003; insects, Scott & Traniello 1990). Many examples stem from biparental species, and here males were more likely than females to reduce parental effort in unfavourable conditions (e.g. Lavery & Kieffer 1994; Smith & Wootton 1995; Sanz et al. 2000; Steinegger & Taborsky 2007; Spencer et al. 2010). Our results provide one of the rare examples in which a female-only care species jeopardize offspring fitness in favour of future reproduction, and it is the first example in maternally mouthbrooding cichlids.

In hypoxic conditions, the maternally mouthbrooding cichlid *Pseudocrenilabrus multicolor* has a 27% shorter first brood care phase accompanied by a decrease in offspring size but not in egg size (Reardon & Chapman 2010). The authors hypothesized that under hypoxia, mothers may secrete hormones that speed up the development of their young allowing to release them earlier but at a smaller size. Such a scenario might also explain our observation that LF females had smaller offspring which were released earlier.

The longer first brooding phase of HF mothers may benefit the offspring. In a viviparous lizard, a prolonged pregnancy enhanced offspring locomotor performance, presumably because of a more complete development of the musculoskeletal system or neural pathways controlling movement (Shine & Olsson 2003). If such changes allow for higher escape speeds, then longer-retained offspring may have better chances of evading predators during early life. Accordingly, burst swim speed in young mouthbrooding cichlids increases with size and age of young (*Tropheus moorii*, Schürch & Taborsky 2005; *S. pleurospilus*, Segers & Taborsky 2011).

Surprisingly, the predator exposure did not affect the length of the first brooding phase, which is in contrast to the closely related mouthbrooding cichlid *C. horei* (Taborsky & Foerster 2004). This discrepancy may be explained by a substantial difference between the experimental set-ups. The predator exposure in the experiment by Taborsky & Foerster (2004) involved direct, continuous contact with the offspring predator. Despite the intermittent exposure regime, *S. pleurospilus* females may have had learned during the course of the experiment that the presented *C. horei* did not pose an acute risk for their young, thereby making a costly adjustment of brood care unnecessary. Future studies on the interactive effects of predation pressure and food deprivation on brood care effort should therefore consider providing

more 'realistic' signals of predation pressure incorporating different relevant stimuli.

Influences from the maternal environment became manifest not only in brood care effort but also in offspring phenotype and brood size. As overall HF females had smaller clutches but larger young at the end of the experiment compared with LF females, HF females seem to have prioritized the quality over the quantity of young. This result parallels findings in the pipefish *Syngnathus typhle*. In this species, males reduce the size of their brood, and the extent of this reduction is in favour of the size of their newborn (Ahnesjö 1992). Unexpectedly, the presence of an offspring predator levelled the food treatment-dependent brood size differences we observed.

Notably, broods of HF females without predator experience were much smaller than clutches of similar sized, unmanipulated but well-fed females bred in our laboratory (mean  $22 \pm 1.6$  SE,  $n = 38$ , Segers & Taborsky, unpubl. data). As the predator treatment could affect females only after spawning, females could not adjust their egg size and thereby the initial offspring size at hatching, to the perceived predation risk as known from other cichlids (cf. Taborsky et al. 2007; Segers & Taborsky, in revision). It seems, however, that HF females in the no-predator treatment reduced their brood size while the young were developing in the mouth, possibly by filial cannibalism. Partial filial cannibalism is a widespread phenomenon in fish (reviewed in Smith & Reay 1991; Manica 2002) including mouthbrooders (e.g. Mrowka 1987; Okuda & Yanagisawa 1996). The presence of a predator might have reduced the propensity of partial filial cannibalism in HF females (if we assume that cannibalism occurs) as the more offspring a female produces the more likely at least some young will survive the presence of offspring predators. As partial filial cannibalism is thought to buffer parents against a loss of body condition owing to the high energetic cost of care (Manica 2002), we had expected cannibalism to occur predominantly in LF females. Filial cannibalism has been mainly investigated in males, and several studies found a negative relationship between male condition and filial cannibalism (e.g. Marconato et al. 1993; Kraak 1996; Kvarnemo et al. 1998; Lindström 1998; Manica 2004).

But why should HF females cannibalize their eggs? The high food availability might have elevated the metabolic demands in these females, which could have led to egg cannibalism. However, this is unlikely because in such a situation, we would also

expect a short duration of the first brood care period in HF females. The opposite was the case. Furthermore, there appears to be no relationship between Fulton's condition factor and standard metabolic rate in *S. pleurospilus* (A. Kotrschal, S. Szidat & B. Taborsky, unpubl. data). Alternatively, siblicide followed by cannibalism ('adelphophagy', Blackburn et al. 1985) may have occurred in the mouth of HF females as their young were withheld from external food for a longer time than those of LF females owing to the longer first brood care phase. Nevertheless, as in our experiment, we could not determine initial clutch and egg sizes directly after spawning, the question must remain open why HF females without predator exposure had particularly small broods and larger young.

Mothers with larger clutches were more willing to take up their young after a simulated predator attack and subsequently kept the brood in their mouths for longer time. This is in line with previous studies that suggest that large broods are more valuable to parents, and therefore, parents should provide a higher level of care (e.g. Sargent 1988; Lavery & Keenleyside 1990; Tilgar & Kikas 2009; but see: Fitzgerald & Caza 1993; Pöysä et al. 1997). However, as we did not manipulate clutch sizes, we cannot exclude that high-quality mothers spawned more eggs and concurrently were able to provide better care (Clutton-Brock 1991).

The young of HF females may have attained larger sizes at independence because they grew faster during the second brooding phase. We did not observe a higher offspring feeding rate in young of HF females, however. Possibly, HF females released their young for feeding for longer time intervals, but as we did not record the total amount of time the young spent outside the mouth during the second brood care phase, this remains unknown. Alternatively, female *S. pleurospilus* may have responded by an increase in yolk quantity or quality to the HF treatment. In fish and a range of other taxa, however, larger and better-equipped eggs are usually produced in response to poor environmental conditions (e.g. arthropods: Brody & Lawlor 1984; Gliwicz & Guisande 1992; Vijendravarma et al. 2010; fish: Reznick & Yang 1993; Taborsky 2006), and, as mentioned before, body condition did not affect egg size in other females of our laboratory population ( $n = 38$ , Segers & Taborsky, unpubl. data).

As offspring size is thought to increase survival in fish (Sogard 1997), it is remarkable that the offspring sizes at which mothers terminate brood care differed greatly between females (Fig. 3). The length of the

second brood care period as well as the total brood care duration was positively related to female size. A shorter brood care period in smaller females suggests that providing brood care may be more costly for these individuals or that their buccal cavity provides less space for growing offspring. The latter explanation seems more likely as, unlike in most fish species (see: Heath & Blouw 1998), egg size decreases with female size in *S. pleurospilus* (Segers & Taborsky, unpubl. data). The quality of brood care is known to increase with parental size in a number of taxa (e.g. fish: Sabat 1994; Mackereth et al. 1999; insects: Hunt & Simmons 2000), and in salamanders, larger mothers raise larger offspring through improved post-natal brood care (Crespi & Lessig 2004). However, as far as we know, this is the first demonstration of a relationship between female body size, brood care duration and offspring size in mouthbrooding cichlids. Moreover, our study shows how variation in parental care affects offspring, information which is scarce for fishes (Amundsen 2003).

## Conclusion

Here, we examined how food deprivation and predation risk interactively affect female reproductive decisions. The presence of interactive effects on female reproductive traits highlights the importance of manipulating both nutritional state and offspring predation pressure when investigating trade-offs involved in brood care decisions. The food treatment influenced brood care patterns most strongly. Interestingly, in the presence of an offspring predator, females with high and low body reserves invested similarly in brood size and brood care, suggesting that predation risk can override some effects of resource availability. While our study shows that well-fed mothers produced fewer but larger young at the end of brood care and in the absence of predation risk they produce even fewer young, further work needs to be done to identify the specific mechanisms by which the maternal food environment and offspring predation pressure affect offspring size and brood size.

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