



## Female mouthbrooders adjust incubation duration to perceived risk of predation

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The protection of young from predators is an important and costly component of parental care, and this investment should be adjusted to the predation risk for the offspring. Parents are known to fine-tune defence intensity to the perceived need of protection, yet little attention has been paid to individual variation in the duration of brood defence. To optimize parental investment it may be beneficial to prolong brood care when the predation risk for the young is high. We tested whether cichlids of the species *Ctenochromis horei* adjust mouthbrooding duration to the perceived predation risk of their offspring. After spawning, females were transferred to an experimental tank, where they incubated the clutch either alone or in the presence of a natural predator of young. Females extended their incubation period by 4.3 days on average when the predator was present. During this prolonged incubation, young continued to grow in the female's buccal cavity. Interspawning interval was longer for females that incubated eggs than for those that did not, although incubation had no long-term negative effects on female condition or egg number or size. Incubating females may thus breed less frequently. Brood care duration should hence be considered as a flexible and potentially costly trait when investigating costs and benefits of parental care.

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Protection of young from predators is an essential component of brood care. In many care-giving species, defending or hiding offspring from predators is the only task performed by parents (Clutton-Brock 1991). The protection of young is likely to entail substantial costs for parents. While guarding a brood, parents often have substantially reduced feeding opportunities (e.g. Townsend 1986; Smith & Wootton 1995a), which may lower their condition and thereby their survival prospects or future reproductive performance (Hairston 1983). When growth is indeterminate, parental investment may retard growth, which may reduce future fecundity of females and mating success of males (Gross & Sargent 1985). Active defence against predators also entails energetic costs (Rangeley & Godin 1992; Lindström 1998; Koskela et al. 2000) and may put parents at risk of being injured or killed themselves (Curio &

Regelmann 1985; Montgomerie & Weatherhead 1988; Magnhagen & Vestergaard 1991).

To minimize these costs, parents should adjust the investment in protection to the perceived risk for the offspring. This can most directly be achieved by increasing attack rates against predators when the risk for young is enhanced. For example, male sticklebacks, *Gasterosteus aculeatus*, spent 60% of their time attacking a brood predator that was presented to them experimentally; as a consequence they engaged less in egg maintenance behaviours (Smith & Wootton 1995b). An alternative way to adjust care behaviour to perceived predation risk has not yet, to our knowledge, been considered in studies on costs of parental care. Shortly before young become independent, parents should be highly sensitive to the presence of potential predators of offspring. If the predation risk is high, parents should respond by prolonging their care period. Being protected for only a little longer may substantially enhance survival of the young. Such flexible adjustment of the brood care period should be favoured especially when the expected survival benefits for young increase steeply relative to the costs of extended care. In most fish and many other aquatic species,

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mortality decreases exponentially with body size, since the major predators are gape-size limited (e.g. Sogard 1997). Small size increments gained by the young during a prolonged care period may then exponentially increase their survival, at relatively low costs for the caring parent. It is likely that a fine-tuning of the brood care duration to perceived predation risk of young is optimal in many cases. However, small shifts in brood care duration will be difficult to detect under natural conditions, where other potential sources of variation, such as parental phenotype and environmental conditions other than predation risk, cannot be controlled. We therefore conducted a laboratory experiment to investigate whether females of the mouth-brooding African cichlid *Ctenochromis horei* adjust the duration of incubation to perceived offspring predation risk.

The buccal cavity of mouthbrooding fish provides an exceptionally safe breeding site. In most mouthbrooders, mothers incubate eggs and larvae in their buccal cavity until they are released as fully developed fry. Usually mothers do not feed during incubation. Incubation times vary between individuals in the wild (e.g. Ochi 1993). When predation risk is high for young, but not for adults, the benefits of prolonged incubation via further growth and better survival of the young may outweigh the costs of a longer starvation period for the parent. We tested whether female *C. horei* will extend incubation when in the presence of a predator of young, and whether prolonged incubation may result in immediate costs for females. First, we related body condition, growth rates and time to next spawning to incubation duration. Second, we investigated whether female traits and egg and clutch sizes of subsequent broods differ when incubation was allowed, or when it was experimentally prevented.

## METHODS

### Study Species

*Ctenochromis horei* is a carnivorous cichlid endemic to Lake Tanganyika, East Africa. It lives in stable mixed-sex groups with largely overlapping individual home ranges (Ochi 1993). Within groups, males establish a rank order and matings are almost exclusively obtained by the dominant male. The females incubate the eggs and hatched young in their buccal cavity for 15–23 days. Thereafter, the young are guarded outside the buccal cavity for on average 7 days, and taken up only when potential predators approach (Ochi 1993). Females do not feed during buccal incubation (Kuwamura 1986; personal observation in the laboratory).

### Maintenance and Spawning

The experiments were done at the KLIVV in Vienna, Austria. All fish were taken from stock tanks maintained at KLIVV. All *C. horei* females and three adult males shared a 2000-litre compartment of a 17 000-litre circular tank. In this compartment, the *C. horei* were kept under semi-natural conditions with respect to group composition and

habitat. The compartment was equipped with a 10-cm-layer of fine-grained river sand and with opaque PVC plates serving as shelters. All spawnings took place in this group compartment. Similar to the natural situation (Ochi 1993), males established a stable dominance hierarchy, and the dominant male apparently monopolized reproduction. Another endemic cichlid from Lake Tanganyika, *Lamprologus callipterus*, was used as a natural predator of young for the first experiment. These fish were taken from another 2000-litre compartment of the circular tank, where an all-male group of 11 individuals was kept. Fish that were removed from the breeding stock during the first experiment were transferred back to the group tank after the experiment.

The fish were fed 6 days a week with either a standard tropical fish flake food (4 days/week) or a mixture of frozen zooplankton (2 days/week). The water quality of the 17 000-litre circular tank was maintained by a central heating system (water temperature 27°C) and a biofilter system.

### Marking and Measuring

For the experiment, females needed to be identified individually on several occasions. As the females lacked natural markers for identification, we marked them by carefully cutting off two-thirds of a single fin ray of the dorsal fin with fine scissors. This marking method is very quick (about 10 s from catching to release) and there was no immediate behavioural reaction to the cutting. After release the fish swam and behaved as they did after any other manipulation. We had no indication that marking caused pain to the fish. Fins were regrown after 3–5 weeks depending on the size of the fish and location of the mark. Total length (TL) was measured ( $\pm 0.5$  mm in adults and  $\pm 0.1$  mm in young at independence, after the end of incubation). Adults were also weighed ( $\pm 0.01$  g) on an electronic balance. We calculated female condition as  $\text{weight}/\text{TL}^3 \times 100$ , which is the most commonly used condition index in fish (Bolger & Connolly 1989). Eggs were weighed individually ( $\pm 0.0001$  g).

### Experiment 1

In this experiment we tested whether female *C. horei* adjust their incubation period to the presence of a predator of young. The group compartment was checked daily for the presence of incubating females. If a female had spawned (which can be clearly seen from a protraction of her buccal cavity), she was caught with a hand net and placed in one of a set of fine-meshed 50-litre baskets hanging in a neighbouring 2000-litre compartment of the circular tank. The baskets were equipped with two flower-pot halves serving as shelters for the females and for young. Visual contact between the baskets was prevented by opaque plastic sheets. The fish in the baskets were fed an ad libitum ration of a standard dry flake food once per day. Each female was exposed to two treatments during successive broods. (1) In the predator treatment, the female reared a brood in the presence of a male *L. callipterus*, which naturally preys on various small

animals including eggs and small young of cichlids. (2) In the control treatment, the female reared a brood without any other fish present in her basket. The order of the two treatments was balanced among the nine experimental females (four times predator treatment first, three times control treatment first; two trials failed because one female produced only one brood, and one female died after completion of the first brood). One female completed two control treatment broods. Data of these two broods were averaged for this female.

A possible second control series might have had a same-sized nonpredatory fish to test whether any reaction by the female is a specific response to a predator of young. However, such a control is neither necessary nor possible. Virtually all fish of the littoral zone of Lake Tanganyika, including 'strictly' herbivorous species (personal observation), will prey on fish fry if they encounter them. Hence, the presence of any other fish that is large enough to catch and handle prey of the size of young after release (i.e. any fish larger than ca. 6 cm TL) will be regarded as a predator of young by a caring *C. horei* female.

During the predator treatments, the two fish had unrestricted contact with each other. The predators were of equal size or smaller (between 10 and 11 cm TL) than the *C. horei* females and posed no risk to them. During incubation, we never observed any aggressive interactions between the two fish. After finishing brood care, females were placed back into the group compartment, where they remained until they spawned again.

Water could diffuse freely through the mesh of the experimental baskets and between all compartments of the circular tank. This ensured identical water quality and temperature for all females incubating simultaneously. Furthermore, all females and young in both treatments received the same chemical cues about the presence of the experimental predators (and, via the central filter system, of other species of Lake Tanganyika cichlids kept in the nonexperimental compartments of the circular tank). The water temperature was measured every second day ( $\pm 0.1^\circ\text{C}$ ). Despite an automated temperature control system, the water temperature increased by  $1.8^\circ\text{C}$  during the experiment (21 January–24 July 1998), in parallel with that of the ambient temperature. We corrected incubation durations for this unavoidable variation in experimental conditions, because, in teleost fish, egg development strongly accelerates with increasing temperatures (see Altman & Dittmer 1966). We regressed incubation duration on the mean temperature during incubation of a given brood (regression analysis:  $R^2 = 0.33$ ,  $F_{1,13} = 6.37$ ,  $P = 0.026$ ) and used the residuals of this regression for further analyses.

Females differed in body length and weight, but we did not control for the effect of these variables on incubation duration since each female acted as her own control. Incubation duration did not depend on female size or weight (regression analyses: size:  $R^2 = 0.0078$ ,  $F_{1,6} = 0.047$ , NS; weight:  $R^2 = 0.025$ ,  $F_{1,6} = 0.15$ , NS;  $N = 8$  females incubating without a predator present).

Within a day of the end of incubation, we determined brood sizes and measured the body lengths of 10 randomly chosen young per brood (or all young for brood

sizes smaller than 10), except in five cases where no young were found.

## Experiment 2

In this experiment we investigated how incubation affects the interval to next spawning, the number and size of eggs in the next clutch and the size, weight and condition of females at next spawning. We compared the recorded traits for 14 female *C. horei* that (1) had lived under seminatural conditions in the group compartment for at least 6 months and had incubated several clutches there (control) or (2) had not incubated their last clutch (treatment). To prevent incubation, we coaxed females into releasing the eggs the day after spawning by gently dipping the fish's head in and out of a container of water. Since skipping a full incubation period may influence a female's reproductive performance for several successive broods, the control broods always preceded the treatment broods in this experiment. Eight females spawned twice within the experimental period of 3 months. One female carried already developed young when she was caught after her first brood, so female condition and egg size were available only for seven paired samples.

## Statistical Analyses

We used nonparametric statistics when (1) the conditions for parametric tests were violated or (2) sample sizes were  $<10$ , as data distributions cannot be reliably estimated for small sample sizes. All statistical tests are two tailed.

## Ethical Note

Experiment 1 involved a direct encounter of a natural predator of young, *L. callipterus*, with the incubating *C. horei* females and their young after release. This procedure was chosen for the following reasons. (1) A potential effect of predators of fry on female incubation duration can be tested conclusively only if a direct encounter between the predator and the female is allowed. Use of a model predator or a predator behind a barrier is not an alternative option because caring females habituate quickly to such stimuli. (2) It was impossible to solve our question by observations of natural encounters, because in the field situation there are no predator-free environments available as control sites and also incubation durations of individual mouthbrooding females cannot be determined exactly in the lake (B. Taborsky, personal observation).

We minimized the sample size (seven cases with a direct predator-prey encounter) to reduce encounters to the minimum required for analysis. To minimize stress during the experiments, we provided shelters for young and adults (see above). Usually, the *C. horei* female occupied one of the flowerpot halves, and the *L. callipterus* male either used the second shelter or stayed outside the shelters. Like other mouthbrooding cichlids, *C. horei* mothers usually release the young in a protected site or defend the young after release. Hence, the female shelters

presumably provided a safe site for young. In addition, young can always flee into the buccal mouth cavity of the mother during the first few days after incubation. Observations in large tanks with seminatural conditions (natural mix and densities of syntopic cichlid species of Lake Tanganyika; high variety and density of shelters) revealed, however, that even with numerous shelters about 95% of emerging young do not survive the first day of independence. Predation involves one fast strike by the predator during which a fry is killed immediately. Hence, the duration of potential suffering is extremely short (fractions of a second). In our experiments, we never found injured young or attacked young that were not immediately consumed by the predator or the mother herself (infanticide is occasionally observed in *C. horei*).

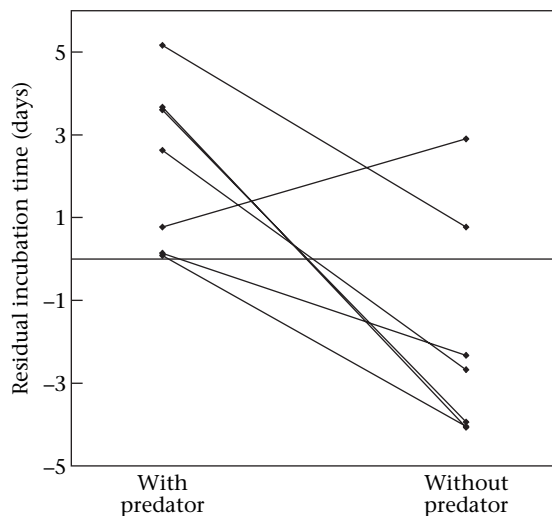
## RESULTS

### Duration of Incubation

In experiment 1, female *C. horei* incubated significantly longer when a predator of young was present during brooding (Wilcoxon signed-ranks test:  $T = 1$ ,  $N = 7$ ,  $P = 0.028$ ; Fig. 1). Without a predator present, females incubated for an average of 21.7 days. In the presence of a predator, they retained the young on average 4.3 days longer in their buccal cavity. This corresponds to a 20% extension of the incubation period. The guarding period following incubation could not be compared between treatments, because in five cases of the predator treatment no young were found in the experimental chamber at the daily check, most likely because they were preyed on.

### Size Advantage of Young

We predicted that prolonged care would give the young an opportunity to attain a larger size while they are still protected by the mother. Young tended to be larger at



**Figure 1.** Difference in incubation duration when a predator of young was present or absent ( $N = 7$ ). Residuals of the regression of incubation duration on the mean water temperature during a given brood are shown.

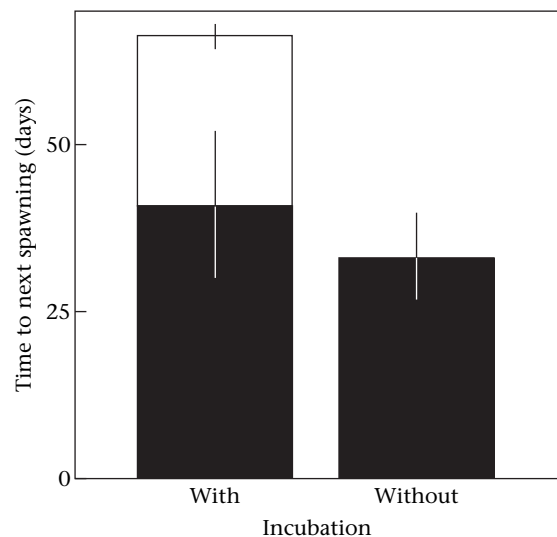
independence after longer brood care periods, although this was marginally significant (regression analysis:  $R^2 = 0.35$ ,  $F_{1,9} = 4.86$ ,  $N = 11$ ,  $P = 0.055$ ).

We estimated that the mean prolongation of incubation by 4.3 days found in the predator treatment translates to a length increment of 2.41 mm or 15.1% compared to the body size of independent young in the non-predator treatment (median 16.0 mm, interquartile range 15.8–16.6,  $N = 9$  broods). We arrived at this estimate by calculating mean growth rates of young from an assumed initial size of 5 mm (B. Taborsky, personal observation) at hatching, which takes place around day 4 of incubation, to the measured size at the end of brood care assuming linear length growth (see Discussion). Under this assumption, daily growth amounts to a mean  $\pm$  SD of  $0.56 \pm 0.078$  mm ( $N = 11$  broods).

### Potential Costs of Adjusting Brood Care

In experiment 2, we did not correct the time to next spawning and growth rates for female size as these traits did not correlate with total length (Spearman rank correlations: time to next spawning:  $r_s = 0.15$ , NS; growth rates:  $r_s = -0.32$ , NS; both  $N = 9$ ). None of the three response variables was significantly correlated with incubation duration (time to next spawning:  $r_s = 0.41$ ; body condition:  $r_s = 0.10$ ; growth rate:  $r_s = 0.024$ , all  $N = 8$ ). However, a potential response of female traits to the relatively small variation in incubation duration might have been masked in our data because of the small sample sizes.

As an alternative approach to test how incubation time affects female performance, we compared females that had incubated with those that had been prevented from incubating. The intervals between successive spawnings were almost twice as long in females that had engaged in incubation than in females that did not incubate (Mann-Whitney  $U$  test:  $U = 6$ ,  $N_1 = N_2 = 8$ ,  $P = 0.006$ ; Fig. 2).



**Figure 2.** Interval between two successive spawnings when females were allowed to incubate (experiment 1,  $N = 8$ ) or were prevented from incubating (experiment 2,  $N = 8$ ). Medians and quartiles are shown. □: Incubation period; ■: nonincubation period.

However, this prolongation of the interspawning interval appears to be entirely explained by the duration of incubation itself. The nonincubation periods between spawnings were similar in females with and without incubation ( $U = 28.5$ ,  $N_1 = N_2 = 8$ , NS; Fig. 2).

Female body condition (i.e. weight:length ratio) appeared to be a correlate of offspring fitness. Egg weight, which determines the amount of energy available for the early development of young, was correlated with female body condition (Pearson correlation:  $r_{11} = 0.71$ ,  $P = 0.007$ , for first clutches produced by females during experiment 2), but not with body length ( $r_{11} = 0.25$ , NS) or weight ( $r_{11} = 0.33$ , NS) alone. Clutch size did not correlate with body length, weight or body condition. Body condition was much lower in females directly after incubation than in females directly after spawning (Mann–Whitney  $U$  test:  $U = 2$ ,  $N_1 = 12$ ,  $N_2 = 8$ ,  $P < 0.001$ ; Fig. 3). However, females appeared to have recovered fully by the next spawning (Fig. 4a). When females had incubated before, they even tended to be in better condition than when they had not incubated, although not significantly so (Wilcoxon signed-ranks test:  $T = 3$ ,  $N = 7$ ,  $P = 0.063$ ). Correspondingly, eggs (Wilcoxon signed-ranks test:  $T = 1$ ,  $N = 7$ ,  $P = 0.028$ ; Fig. 4b) and total clutches ( $T = 1$ ,  $N = 7$ ,  $P < 0.03$ ) were heavier and the variance among eggs of a brood was lower (SD of egg weights:  $T = 1$ ,  $N = 7$ ,  $P = 0.028$ ) in females that had incubated. Females with or without incubation between two spawnings did not differ with regard to clutch size ( $T = 10$ ,  $N = 8$ , NS) and growth rates (Mann–Whitney  $U$  test:  $U = 32$ ,  $N_1 = 8$ ,  $N_2 = 8$ , NS).

DISCUSSION

We showed experimentally that females of a cichlid mouthbrooder adjust the time of incubation to the predation risk for their offspring. To our knowledge, a flexible adaptation of brood care duration to ambient ecological

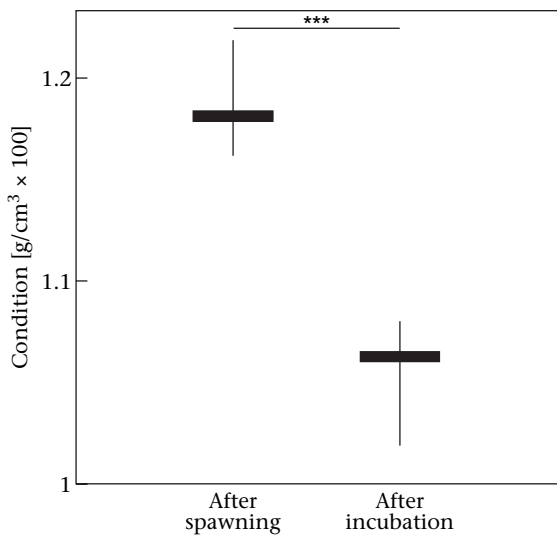


Figure 3. Body condition of females after spawning (experiment 2,  $N = 12$ ) and after incubation (experiment 1;  $N = 8$ ). Medians and quartiles are shown.  $***P < 0.001$ .

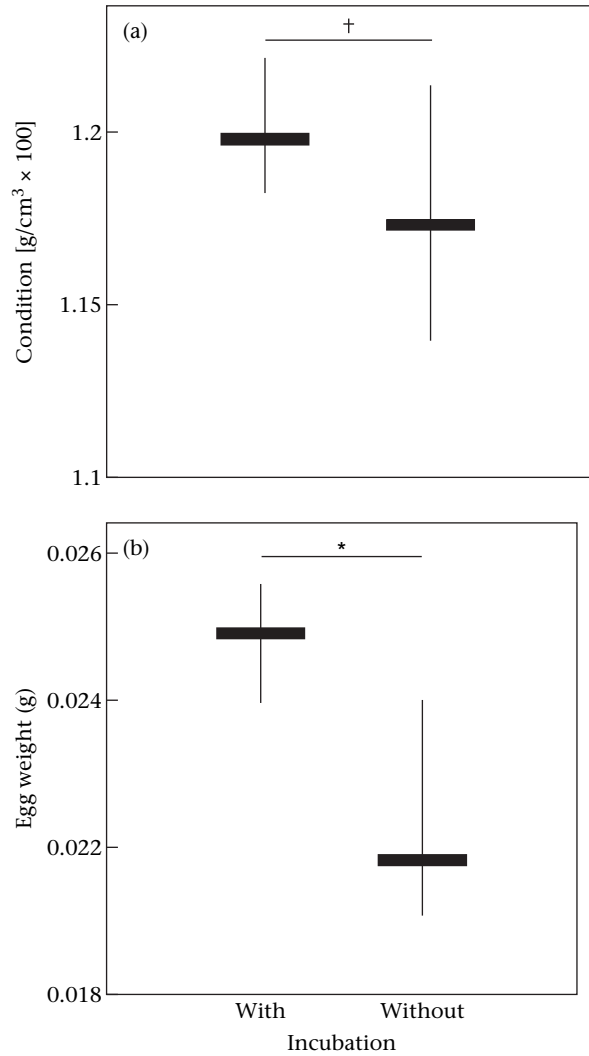


Figure 4. (a) Body condition and (b) egg weights after spawning, when females had incubated or had not incubated in the last reproductive period ( $N = 7$ ). Medians and quartiles are shown.  $†P < 0.1$ ;  $*P < 0.05$ .

conditions has not been demonstrated before, unless it has affected the performance or the value of the brood at the same time. For example, in the burying beetle, *Nicrophorus vespillo*, parents guarded their clutch longer when ambient temperatures were low (Meierhofer et al. 1999). In this case, however, larval development had slowed down, and it is likely that parents reacted to direct cues from their larvae rather than to temperature itself (Trumbo 1991; Meierhofer et al. 1999). It is highly unlikely that young of *C. horei* in our experiment assessed predation risk while being brooded within their mother's mouth, since the chemical information for young was identical in both treatments (see Methods). Therefore, the adjustment of parental care must have been triggered solely by environmental stimuli to the female.

The presence of a predator of the young frequently releases vehement attacks by guarding parents (see examples in Clutton-Brock 1991). The aggressiveness of a parent could be involved in the internal regulation of brood

care duration. Such a mechanism is unlikely to work for *C. horei*, however, as we never observed aggression by a mouthbrooding female towards other fish during the experiments, in the group compartment, in mixed-species stock tanks or in the field (personal observation). Alternatively, incubation duration may be adjusted via the female's reaction to take up her young when disturbed. This behaviour is usually shown for several days after the end of continuous incubation (Ochi 1993). If this 'take-up reaction' is stimulated continuously by the sight of a predator, it would induce the mother to hold back her young and thereby prolong the incubation period.

The flexible brood care behaviour observed in this study is likely to be adaptive, since young *C. horei* benefit from a size advantage when being brooded for longer. Our estimate of a 15% increase in body length in 4 days relies on the assumption that length growth is linear. Many ectotherms show linear growth rates as larvae and young (e.g. Roff 1983; Hanson et al. 1988; Jørgensen 1992). For example, larvae of the mouthbrooding cichlid *Tropheus moorii* show a linear weight increase from hatching to independence when no food is provided by the mother (Yanagisawa & Sato 1990), and we found a linear relation of body weight to body length in small young of the same species (R. Schürch & B. Taborsky, unpublished data). With increasing body size, the range of potential predators of young becomes smaller, as all major predators of small cichlids are fish which are gape-size limited. In addition, the escape abilities of young improve with size because of higher mobility and burst swimming speed (Garenc et al. 1999; Hale 1999). Usually, the mortality rate of fish drops with increasing body size either exponentially or following a hyperbolic function (Taborsky et al. 2003). During the early life stages, when mortality decreases steeply with size, even the smallest size increments during incubation may markedly increase survival after release, if predation risk is high.

Looking at our results from a different point of view, we found that females released young earlier when predation risk was low, even though (1) under low risk larger young should be privileged (e.g. in competitive interactions with other young) and (2) we did not find any negative effects of incubation on female condition and egg quality at the next spawning. On the contrary, after incubation females produced larger eggs and tended to be in better condition than when they did not incubate. It is therefore not obvious why females should incubate for less time than is possible under the space limits of the mouth cavity. However, the laboratory conditions may not have adequately reflected the ecological constraints present in nature, as food was never scarce during the experiments. In general, costs of reproduction are more likely to be demonstrated under limiting environmental conditions (reviewed in Reznick 1985; Neuhaus 2000). Furthermore, the observed decline in condition of incubating females may be dangerous under the natural predation risk for adults. Finally, long-term costs of prolonging incubation arise, as any additional day of incubation increases the interval between spawnings, and thereby reduces the maximum number of broods produced per lifetime.

To demonstrate an adjustment of brood care periods as a response to environmental cues, we compared two

qualitatively different levels of risk, the presence and the absence of a predator. This is certainly a simplification of the natural situation, where we would expect the adjustment to be a continuous response to density and proximity of predators. Varying these two factors experimentally should give insights into the fine-tuning of female decisions about brood care duration. Furthermore, our predator experiment should be repeated under restricted food rations to estimate potential negative effects of prolonged care on the female's future reproductive performance.

Numerous examples show that the intensity of certain brood care behaviours serving the maintenance and defence of offspring can be adjusted to both the need for care and the reproductive value of the offspring (Clutton-Brock 1991, chapter 9.4). However, the possibility of adjusting the duration of care has received surprisingly little attention. Here, we showed that brood care duration can be varied by parents in response to predation risk. In general, animals may often prolong those brood care stages during which they can protect their offspring effectively when predation risk is high, thereby delaying the time until offspring must leave this 'safe harbour'. Brood care duration, a flexible and potentially costly behaviour, should be included as a variable in future studies investigating costs and benefits of parental care.

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