The functional significance of buccal feeding in the mouthbrooding cichlid *Tropheus moorii*

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Summary

The mouthbrooding cichlid *Tropheus moorii* exhibits an exceptional degree of maternal investment. Females produce very large eggs, which are incubated for a period of six weeks, and they feed their young in the mouth while starving themselves. Only very few fish species are known to feed their young. We hypothesized that feeding may either (1) benefit females directly if young develop faster, or (2) provide a size advantage to young. To distinguish between these mutually non-exclusive hypotheses, we measured costs and benefits arising for mouthbrooding females when feeding their young. Field observations revealed that mouthbrooding females reduced bite rates, locomotion and territorial defence compared to nonbrooding adults. Feeding rates correlated positively with locomotion, as fish moving around more also spent more time with territory defence and other social interactions. This suggests that buccal feeding is costly when compared to mere incubation without feeding the young. In an experiment, in which we controlled the access of females to food, we showed that these costs are apparently not counterbalanced by a benefit to females through a shorter incubation duration. Rather, fed young were larger, heavier and had higher burst-swimming speeds. The extreme maternal investment of *T. moorii* appears to yield fitness benefits to females by producing larger and stronger young, which consequently should have better survival chances in their natural environment.

Keywords: parental care, life history, mouth brooding, costs of reproduction, cichlices.

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Introduction

The strategies are diverse by which animals performing brood care provision offspring with energy. A well known example is the dichotomy between altricial and precocial birds, where either parents provide large quantities of food for young hatching from small eggs, or females produce large eggs with a high yolk content, but do not feed young after hatching (e.g., Rahn et al., 1975). This pattern reflects a trade-off between energy investment in eggs *vs.* young after hatching, or more generally, in earlier or later stages of offspring development. Even among closely related species considerable variation of energy investment patterns may occur. In alcids (Alcidae, Aves), for example, chicks of the Xantus' murrelet (*Synthliboramphus hypolecus*) fledge without being fed by their parents. On the other extreme, chicks of the Cassin's auklet (*Ptychoramphus alenticus*) remain in the nest for more than 40 days while being fed by their parents (Ydenberg, 1989).

A similar degree of variation in provisioning strategies occurs in the Tropheini, a tribe of African mouthbrooding cichlids endemic to Lake Tanganyika. While in the vast majority of mouthbrooders parents starve during incubation (Oppenheimer, 1970), some species of this tribe take up food while their clutch is held in the buccal cavity. In most of these species, the females themselves consume part of this food, but a certain proportion of it is taken up by the young (Yanagisawa & Nishida, 1991; Yanagisawa & Ochi, 1991). For example, *Pseudosimochromis curvifrons* produce small eggs and clutches relative to their body size. During the extended incubation period of eight weeks females almost double their bite rates, enabling them to feed their young and to feed for themselves about the same amount as during non-brooding phases (Kuwamura, 1986; B. Taborsky, unpubl. data). In contrast, *Simochromis* spp. produce larger eggs relative to body size, but provide no food for their young or feed themselves during incubation (Kuwamura, 1986; B. Taborsky, unpubl. data).

Tropheus moorii is exceptional among the Tropheini in that females produce very large, energy-rich eggs and also feed their young in the buccal cavity. *T. moorii* lays among the largest eggs relative to body size in cichlids, and probably even among fish in general (R. Coleman, pers. comm.). In contrast to other Tropheini exhibiting buccal feeding, *T. moorii* females are starving during the entire incubation period of six weeks (Yanagisawa & Sato, 1990). It is unclear why on top of producing such large eggs females also take up

food to feed their young, but do not consume food by themselves at the same time. Yanagisawa & Sato (1990) showed that unfed larvae of *T. moorii* survived well, but were lighter than normally developing young. Although this points towards a nutritional advantage of buccal feeding for young, these results could not be unequivocally interpreted. The weight differences may have resulted from a higher energy expenditure of larvae outside the mouth cavity, as in this study the unfed larvae moved around freely in a tank, while the fed larvae were incubated by their mothers.

Alternatively to potential growth benefits to young, we hypothesized that females may gain direct benefits from buccal feeding, for example through a shorter incubation time if young develop faster. In addition, it is as yet unclear whether browsing during incubation to feed the young requires a substantial energetic investment of females. If the activity budgets of browsing and non-browsing individuals were similar, one may assume that feeding young bears only small costs for females.

We examined the costs and benefits of buccal feeding in *T. moorii* in a combined field and laboratory study. In the field, we compared activity budgets of non-incubating and incubating females of *T. moorii* to get an estimate of potential activity costs arising from buccal feeding. In the lab, we investigated how food deprivation of incubating females affects incubation duration, number of independent young produced and the size, weight and burst-swimming speed of young at first release from the buccal cavity.

Methods

Study species

Tropheus moorii (Boulenger, 1898) is an epilithic algae-eating cichlid endemic to Lake Tanganyika. The sexes are monomorphic, and both females and males defend distinct feeding territories (Kawanabe, 1981; Yanagisawa & Nishida, 1991). Prior to spawning, females give up their territories and move to a male's territory, where they stay between 4 and 21 days. After spawning, females leave the male territory (Yanagisawa & Nishida, 1991). During the first 5 to 6 days females stay almost motionless in or close by a shelter site. After the larvae have hatched inside the buccal cavity, the females start to browse algae to provision their young. They increase their daily feeding rate in accordance with the progressing development of young (Yanagisawa & Sato, 1990; B. Taborsky, unpubl. data).

Study area

Field work was conducted at Kasakalawe Bay near Mpulungu, Zambia, at the southern tip of Lake Tanganyika. Fish were observed in an area of approx. 50×50 m between water depths of 0 to 3 m. In this area the sandy bottom was covered with several layers of boulders overgrown with turf algae, providing food for *T. moorii* and numerous crevices for hiding.

Data collection

To estimate the activity levels of free-ranging incubating and non-incubating *T. moorii*, time budgets were recorded from February to April 2002 by snorkelling and SCUBA diving. As in our study area it was in most cases not possible to capture a specific individual after the observations and the sexes look alike, the time budgets of non-incubating fish include males as well as females. Incubating females were recognised easily by their protruded bottom of the buccal cavity. The developmental stage of young within the buccal cavity was unknown. To minimize the likelihood of repeated observations of the same individual, the observation site within the study area was changed after each recording. As a focal animal for an observation, we chose the first fish of a given category (incubation or non-incubating) seen after arrival at a new site.

Time budgets were recorded between 7:00 h and 17:15 h, and each recording took 10 min. We recorded feeding rates and the time spent on locomotion and on social interactions (for definitions of behaviours see Table 1). Data were recorded underwater with pencil on a plastic board. If a fish moved out of sight during a 10-min observation period, the observation was not included in the analysis. During a 10-min observation period, the time a fish spent on different social interactions was pooled. Directly after a 10-min recording, the same individual was observed for another 5 min, during which we recorded the durations (in sec) of each social behaviour and its type (cf. Table 1). If an individual moved out of sight between the end of the first sampling period and the end of the second sampling period, the second sample was omitted from analysis.

Laboratory experiments

The experiments were conducted between June 2002 and April 2003 at the University of Bern, Switzerland. The experimental fish were taken from

Table 1. Definition of behaviours recorded in the field; numbers in brackets are the mean values for non-booding (*nb*) and brooding (*b*) fish.

Feeding rate	Number of bites per 10 min (*nb*: 142.4, *b*: 25.3)
Locomotory activity	Time spent swimming per 10 min (*nb*: 7′35″ min, *b*: 4′48″ min)
Social interactions	Time spent on the social behaviours defined below per 10 min (*nb*: 0′33″ min, *b*: 0′10″ min)
Fin spreading	Fish remains motionless and spreads dorsal and anal fins
Restrained aggression	Similar to fin spreading, but fish starts to move towards an opponent using the paired fins for swimming
Chase and flee	Fast swimming mode directed towards another fish or fleeing from it; thrust is generated with the caudal fin and axial body muscles
Body shaking	The fish is slightly bent and inclined, while the lateral side of the body is shown to the opponent and the fish is quivering

the breeding stock of *T. moorii* established in the lab of the University of Bern. This stock was built in 2001 from individuals of the first and second generation of wild caught fish. Before and after an experimental period fish were kept in mixed-sex groups of 10 to 15 adults in 450-l tanks. The tanks were equipped with a 5 cm layer of fine grained river sand, flowerpot-halves and PVC plates for shelter and two internal biological filters. Fish were kept at water temperatures of 26-27°C and on a light:dark regime of 13:11 h to simulate natural light conditions at Lake Tanganyika.

When a female had spawned and taken up the eggs, she was weighed on an electronic balance (with the clutch in her mouth) and moved to a 45-l tank. Females were assigned to either of two treatments, ad libitum food (cubes containing Tetramin® flake food, Tetra, Blacksburg, VA, USA, mixed with agarose gel) or no food. Fish of the two treatments were matched for size and weight. Twenty-six females spawned during the course of the experimental study, but only 13 finished incubation. The proportion of females finishing incubation was not affected by the treatment (χ^2-test, $p = 0.428$). Three of these 13 females raised two successive clutches during the sampling period, one brood in either of the two treatments. Two females of the food-treatment group had to be excluded from analysis because they did not take up any food until they released their juveniles, which means that no buccal feeding occurred in these cases.

At the end of the incubation period, i.e. after the female released the young for the first time, she was weighed for a second time (without brood), and her standard and total lengths were measured to the nearest mm. We then placed

the female back into the original 450-l group tank. On the same day, we measured standard and total lengths of all young of her brood to the nearest 0.1 mm, weighed them on an electronic balance to the nearest 10^{-4} g and determined their burst-swimming speed.

To measure burst-swimming speed, a young was placed in a glass channel of 40 cm length and 5 cm width, filled with 2 cm of water. The shallow water level prevented the fish from moving in the vertical dimension and thus simplified analysis. Under the channel we placed a grid with a mesh size of 1 mm to scale the swimming distances. After 5 min of acclimation in the glass channel, we startled the fish using a thin jet of tap water. The tap water was released from a medical catheter of 0.5 mm diameter, which was connected to a magnetic valve and then further to a tube that was attached to the tap. We could manually control the magnetic valve with a switch. We positioned the catheter 1 cm from the head of the fish (see Figure 1). The movements of the startled fish were recorded on digital video with a SONY DXC-107P camera (SONY Corporation, Japan) at 25 frames/s and an exposure time of 1/2000 s. De-interlaced still images of burst swimming sequences were obtained from video using Final Cut Pro 3.0 (Apple Computer, Inc.). We analysed the still image sequences with NIH ImageJ software (National Institutes of Health, USA). We analysed the position of the tip of the head in each image. For each juvenile, burst swimming was recorded four times. Recordings were separated by at least 1 min during which the fish was gently guided to the starting position.

After taking the measurements, the young fish were placed in a 200-l group tank to raise them to adulthood for future experiments. In the lab, we usually find a survival of 100% of *T. moorii* young when raised separately from larger conspecifics, which may prey on them. Accordingly, all young born during our experiments were healthy and survived from the day of release to an age of at least three months, irrespective of treatment.

Data analysis

Standard and total lengths were highly correlated in females (Spearman's correlation, $N = 13$, $r_S = 0.743$, $p = 0.003$) and young (Pearson's correlation, $N = 76$, $r = 0.993$, $p < 0.001$). We used only standard length (SL) as a measure of structural size for all further analyses. Morphological measurements of females and juveniles were used to compute the condition
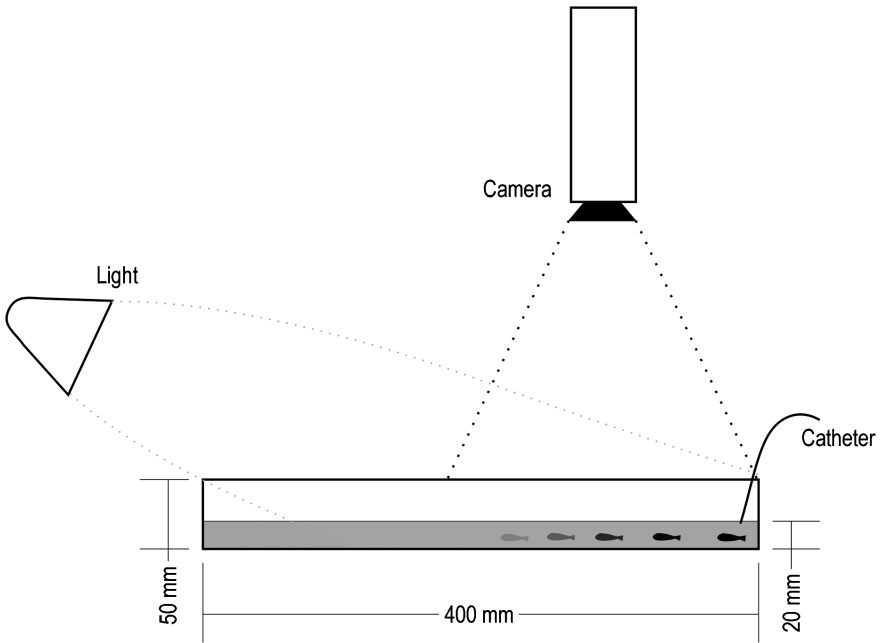
Figure 1. Set-up used to determine the burst swimming speed of young. The fish were startled with a jet of water from a catheter and recorded with a digital video camera. Each fish in the picture represents the changing position of the same fish in different frames (i.e., at different times).

factor K, where

$$K = weight[g]/length[\text{cm}]^3 \times 100$$

(see Bolger & Connoly, 1989). Burst-swimming speed was defined as the longest travel distance between two frames (1/25 s) in a trial. The 'maximum burst swimming speed' for each young was defined as the fastest trial among the four burst-swimming recordings.

We used ANOVA and Pearson correlation analyses when the data met the conditions for parametric testing. Among the activity data, bite rates deviated from a normal distribution and were square-root transformed to obtain normality. Size measurements of females, incubation duration and clutch size were compared between treatments using Mann-Whitney U tests, since sample sizes were too small to test data for normality. We used SPSS 10.0 (SPSS, Inc., USA) for our statistical analyses. All tests are two-tailed.

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Results

Activity of non-incubating and incubating fish in the field

Feeding rate increased during the course of the day in both non-incubating and incubating fish (Figure 2), while time spent for locomotion and social interactions did not vary significantly with time of day (Table 2). Throughout the day, incubating individuals fed at lower rates and spent less time on locomotion and social interactions than non-incubating fish (Table 2; Figure 2). The proportion of time spent for different categories of social behaviours (cf. Table 1) did not differ between incubating and non-incubating fish (MANOVA, Wilks' $\lambda = 0.838$, $p = 0.18$).

The time fish spent with locomotion correlated positively with their feeding rate, both for the total sample of adults observed (Figure 3, Pearson's correlation coefficient, $r = 0.768$, $p < 0.001$, $N = 39$) and for incubating females only ($r = 0.579$, $p = 0.012$, $N = 18$). The time spent on social interactions correlated positively with locomotory activity in all adults
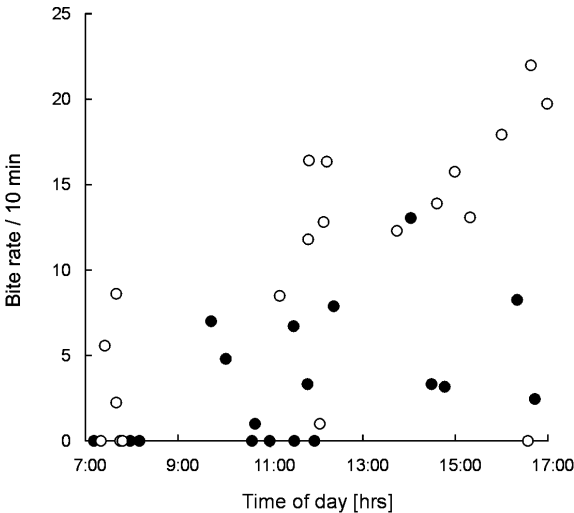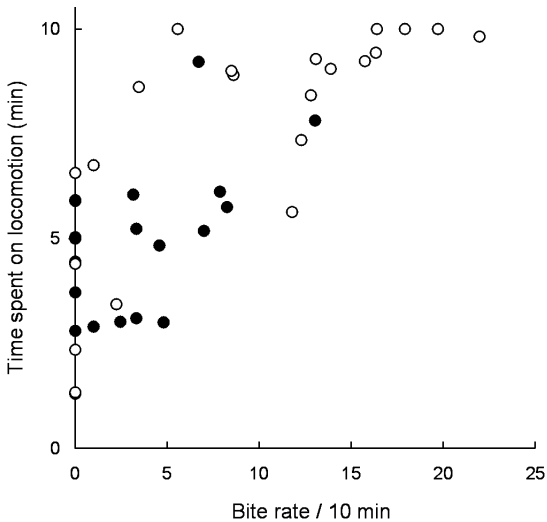

Figure 2. Diurnal variation of feeding activity (bite rates are square-root transformed); ○ non-incubating adults; ● incubating females.

Table 2. Influence of incubation status (non-incubating vs incubating fish) and time of day on feeding rates and time budgets.

Behaviour		$F_{2,36}$	p
Bite rates (square root transformed)	Incubation status	15.73	<0.001
	Time of day	22.13	<0.001
Locomotion	Incubation status	13.43	0.001
	Time of day	1.97	0.169
Social interactions	Incubation status	14.18	0.001
	Time of day	1.09	0.305

Figure 3. Correlation between locomotory and feeding activity (bite rates are square-root transformed); ○ non-incubating adults; ● incubating females.

(Pearson's correlation coefficient, $r = 0.485$, $p = 0.002$, $N = 39$), and the two variables tended to correlate when incubating females were analysed separately ($r = 0.401$, $p = 0.098$, $N = 18$).

As incubating *T. moorii* females take up food only to feed their young, a comparison between fish that did or did not feed during a recording provides an indication of potential activity costs of buccal feeding. Fish feeding during a 10-min recording showed more locomotion (Mann-Whitney *U* test: $U = 49$, $p = 0.001$, $N_1 = 28$, $N_2 = 11$), and they tended to engage more in

social behaviours (Mann-Whitney U test: $U = 99.5$, $p = 0.089$, $N_1 = 28$, $N_2 = 11$) than fish that did not feed.

Buccal feeding and female performance

Incubation duration tended to increase with female length (= SL; regression analysis, $R^2 = 0.28$, $p = 0.061$, $N = 13$). The residuals of incubation duration when regressed on SL tended to be larger when females received food during the laboratory experiments (Mann-Whitney U test, $U = 8.0$, $p = 0.08$, $N = 13$). Offspring number as determined at the end of incubation did not differ between treatments (Mann-Whitney U test, $U = 17.0$, NS, $N = 13$), but it increased with the weight of females measured after spawning, i.e. at the beginning of incubation (Spearman's correlation, $\rho = 0.68$, $p = 0.021$, $N = 11$).

Starvation resulted in a loss of female body condition during incubation of on average 13.9% (= median; quartiles: 9.3; 18.7, $N = 11$ females of the fed treatment). Neither the difference of female body condition between the beginning and the end of incubation nor the daily decrease of condition differed between treatments (Mann-Whitney U test; total decrease of K: $U = 14.0$, $p = 0.93$, $N = 11$; daily decrease of K: $U = 14.0$, $p = 0.93$, $N = 11$).

Buccal feeding and offspring performance

When young were fed by their mother during incubation, they were larger, heavier and had a higher body condition, as well as a higher maximum burst swimming speed at independence than young that had received no food (Table 3, Figure 4a-d). This effect might (partially) come about by differences in incubation duration. However, if incubation duration was fitted first in a regression model on the average values per brood, treatment remained significant or almost significant for all four parameters (fed: $N = 5$, unfed: $N = 6$; SL: $p = 0.021$, weight: $p = 0.01$, K: $p = 0.065$, speed: $p = 0.053$) whereas incubation duration was not significant (fed: $N = 5$, unfed $N = 6$, SL: $p = 0.301$, weight: $p = 0.312$, K: $p = 0.891$, speed: $p = 0.117$).

To test whether the different burst swimming speeds of young raised in the two treatments are solely explained by the body size differences between treatments, we tested for a relationship of standard length and swim speed of

Table 3. Influence of food treatment on length, weight, condition and swimming speed of young; young produced by the same female in a brood were nested within the treatment.

	df	MS	F	p
Standard Length				
Treatment hypothesis	1	0.818	13.51	<0.001
Treatment error	11	0.060		
Female(Treatment) hypothesis	11	0.066	104.41	<0.001
Female(Treatment) error	63	0.001		
Weight				
Treatment hypothesis	1	0.056	18.64	0.001
Treatment error	11	0.003		
Female(Treatment) hypothesis	11	0.0003	122.39	<0.001
Female(Treatment) error	64	0.00003		
Condition				
Treatment hypothesis	1	1.562	10.76	0.007
Treatment error	11	0.145		
Female(Treatment) hypothesis	11	0.157	6.85	<0.001
Female(Treatment) error	63	0.00229		
Speed				
Treatment hypothesis	1	0.215	11.56	0.008
Treatment error	9	0.019		
Female(Treatment) hypothesis	8	0.019	1.43	0.210
Female(Treatment) error	45	0.013		

individual young *within* treatments. In the fed treatment there was no significant effect of length on the burst swimming speed, while burst swimming speed tended to increase with size in the unfed treatment (Pearson's correlation; fed: $r = 0.09$, $p = 0.68$, $N = 24$; unfed: $r = 0.33$, $p = 0.072$, $N = 31$).

Discussion

Our results suggest that *T. moorii* females may pay activity costs for buccal feeding without gaining direct benefits through a faster reproductive rate. Rather they appear to benefit from producing bigger offspring with superior escape abilities. The additional energy expenditure for buccal feeding is stunning given that females pay high energetic costs for egg production and for starvation during incubation. A single *T. moorii* egg contains on average 1.29 KJ and weighs 0.045 g (B. Taborsky, unpubl. data), making up 0.3 %
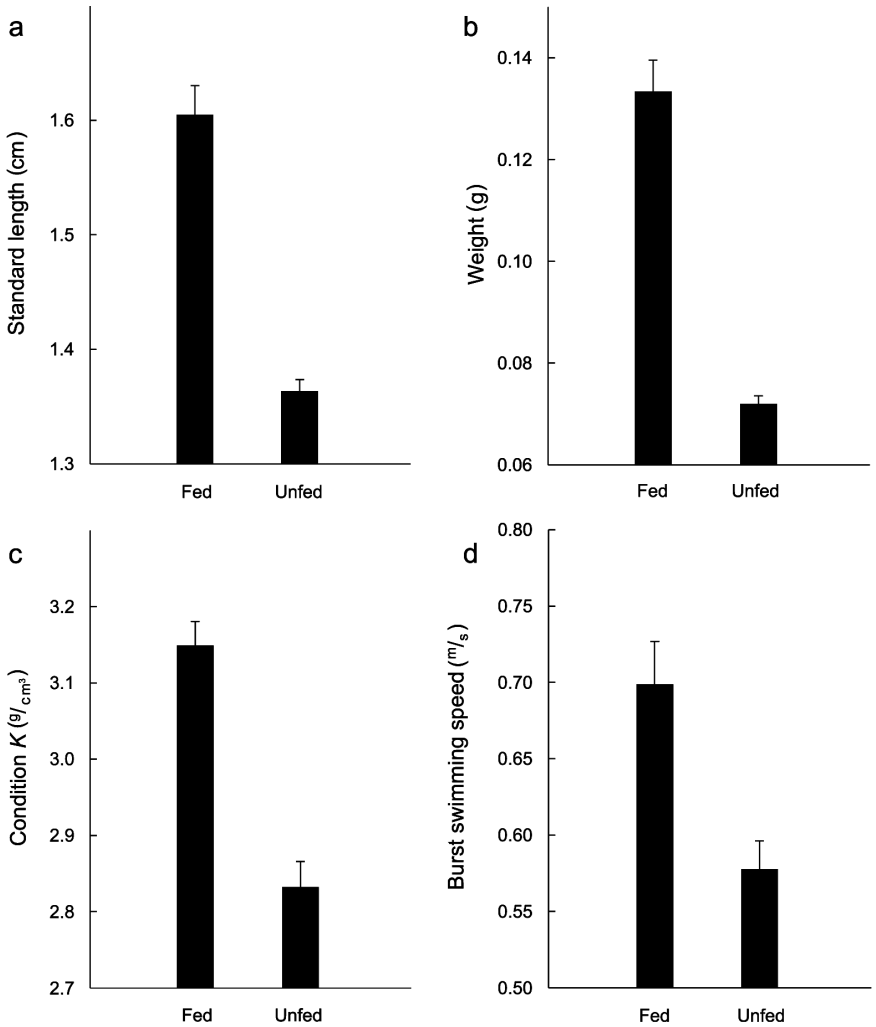
Figure 4. (a) Standard length, (b) weight, (c) condition factor and (d) burst swimming speed of fed and unfed young; means + SE.

of the body weight of an average sized adult female (i.e., 10 cm total length, Taborsky, 1999), which is among the largest relative egg sizes found in fish (R. Coleman, pers. comm.). During incubation, females do not take up food for themselves. While guts of non-incubating females in our study population in the field were filled on average to 60% with food (= median, range 5-100%, $N = 14$), guts of incubating females were usually empty (median =

0%, range 0-16%, $N = 8$; see also Yanagisawa & Sato, 1990). In contrast to females, guts of brooded young were found to be entirely filled with algae (Yanagisawa & Sato, 1990).

Feeding activity varied greatly, both in non-incubating and incubating *T. moorii*. A large part of this variation is due to an increase of feeding during the day (see also Sturmbauer & Dallinger, 1995), which is likely to be an adaptation of this algae feeder to the increasing energy content of algae with daytime (see Polunin & Klumpp, 1989; Zoufal & Taborsky, 1991). About 40% of the incubating females did not feed at all during a 10-min behavioural recording (as compared to 20% in non-incubating fish, see Figure 2), which can be partly explained by the fact that females do not feed during the time eggs are not yet hatched (Yanagisawa & Sato, 1990). In general, feeding activity was lower in incubating than in non-incubating individuals. As our data on feeding rates on non-incubating fish contain observations of females *and* males, potentially this difference could arise due to higher feeding rates of males compared to females rather than representing a difference of brooding *vs.* non-brooding. However, this is unlikely as Yanagisawa & Nishida (1991) found no difference of male and female feeding rates in solitary *T. moorii*, and they found even higher feeding rates in females when they consorted with a male.

Overall, feeding rates were positively related to locomotory activity. Fish that did not feed moved about significantly less than fish that fed during a recording. Feeding *T. moorii* swim around constantly, hovering over patches of algae and changing quickly between boulders. The energy expenditure for locomotion when feeding may be one important cost of buccal feeding. Each increase in relative swimming speed of fish by one body length $\times \sec^{-1}$ corresponds on average to a 2.3-fold elevation in metabolic rate (reviewed in Beamish, 1978). Moreover, incubating females of *T. moorii* are starving, which may lead to alterations in enzyme activities of muscle fibres. This may affect the swimming performance of the mother and in consequence her ability to escape a predator attack (as shown in starving cod, *Gadus morhua*; Martìnez et al., 2003).

Fish showing more locomotion were also engaged in more social interactions. Conversely, fish that did not feed during an observation not only moved less about but also tended to have less social interactions. These results may be explained by a lower encounter rate with conspecifics when

remaining stationary. Most social interactions involved aggressive and territorial behaviours, with the focal fish actively chasing or being chased by another fish. Hence, females provisioning their young by buccal feeding may incur substantial additional energetic costs from burst-swimming bouts during these interactions. In the cichlid *Neolamprologus pulcher* agonistic behaviours raised metabolic rates by four times compared to the resting metabolic rate (Grantner & Taborsky, 1998). As a consequence of higher activity, free-ranging females feeding their young should decrease more in weight or in body condition compared to females that only incubate them. In our lab experiments we did not detect such differences between feeding and non-feeding females, however. This is probably an experimental artefact as movements of females were strongly limited in the experimental tanks and females had no possibilities for social interactions. In addition, our sample sizes were low for these comparisons, because we could not measure weight after spawning in all females.

The second aim of our study was to identify the benefits of provisioning young in addition to incubating them in the mouth. Females may gain direct benefits, for example through a shorter incubation duration if young develop faster. Contrary to this hypothesis, incubation duration tended rather to be longer when females had access to food. Alternatively, females may gain from producing more or fitter young, with better competitive abilities and increased survival chances after release. Fed offspring were almost 20% longer and nearly twice as heavy as unfed individuals, while the number of young released to independence did not differ between treatments. Larger young should have clear fitness advantages over smaller ones, as in fish often size decides about the outcome of contests about resources (e.g. Koops & Grant, 1993) and predation risk usually drops exponentially with size (Sogard, 1997; Taborsky et al., 2003). Nutritional conditions during early development can also influence long-term life-history trajectories of organisms (Metcalfe & Monaghan, 2001). Faster growth may result in a larger adult body size and therefore in higher fecundity later in life (Billerbeck & Conover, 2001). Thus, apart from a short-term competitive and survival advantage, a larger size at release may positively influence the life histories of young also in the long run.

Fed young swam faster by almost 21% when escaping from a threat stimulus. This difference in burst swimming speed could be a consequence of size,

because thrust is a function of body length in fish (Webb & Blake, 1985; juvenile threespine stickleback *Gasterosteus aculeatus*, Garenc et al., 1999). In our experiments, speed tended to increase with length in young of the unfed treatment, but there was no relationship between these variables detectable in young of the fed treatment. A possible reason may be that young of the fed treatment increased their fat stores rather than muscle mass in proportion to body size (see Berg et al., 2001). This interpretation is supported by the finding that fed young had higher condition factors than unfed young. In addition, feeding may affect developmental parameters of muscle fibres, such as the number of muscle precursor cells or the timing and rate of fibre differentiation (Arendt, 2000). Hence, the higher swimming speed of fed young may have been due also to a better performance of their muscle tissue.

In summary, buccal feeding seems to enhance the survival prospects and competitive abilities of *T. moorii* young due to a size advantage and a better swimming performance. Incubating females apparently pay costs for buccal feeding, which may negatively affect female condition and thereby their prospects of future survival and reproduction (e.g. Williams, 1966; Stearns, 1992). Our experiments did not prove a trade-off between current and future reproduction, however costs of reproduction are generally more easily demonstrated under limiting environmental conditions (reviewed in Reznick, 1985; Neuhaus, 2000). The question remains, why *T. moorii* females invest in both, large eggs *and* feeding of young. We propose that limiting ecological conditions are the reason for this unusually high parental effort. *T. moorii* is one of the most abundant epilithic algae feeder of Lake Tanganyika occurring in very high densities (e.g., Karino, 1991). When habitats are saturated even a small competitive advantage through larger size may be valuable to obtain a greater share of limited resources. Hence mothers should be selected to provide each young with a maximum of resources before releasing them into independence.

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