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Energy expenditure for mouthbrooding in a cichlid fish

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Summary. Energy costs of mouthbrooding were investigated in the East African maternal mouthbrooder *Pseudocrenilabrus multicolor* by measuring rates of oxygen consumption. Mothers with their brood in the mouth expended 15.7% more energy than mothers without their brood and 13.8% more than starving nonreproductive controls. After subtracting the energy expenditure of the brood, the excess is reduced to 4.7% and 3.2%, respectively, a difference that is not statistically significant. By contrast, feeding nonreproductive females expended more than twice as much energy as the other groups. We conclude that mouthbrooding is a low-cost strategy profiting from investments made during the preceding nonreproductive phase. The implications for the evolution of mouthbrooding are discussed within the context of ecological constraints.

Introduction

Mouthbrooding occurs in at least 8 families and 53 genera of teleost fish (Oppenheimer 1970) including several hundred species of cichlids (Fryer and Iles 1972; Keenleyside 1979). Since energy expenditure is presumed to be an important determinant of lifetime reproductive success, we investigated in the East African cichlid *Pseudocrenilabrus multicolor* how costly mouthbrooding is in terms of energy.

P. multicolor dominates the fish fauna of small and shallow waters around Lake Victoria. During spawning the female takes 20–100 eggs into her mouth and subsequently carries them there continuously for 10–11 days at 27° C. During this period no food is consumed. Hatching occurs 4 days after spawning. After 10–11 days the young, having re-

sorbed their yolk, are released from the mouth thereby enabling their mother to resume feeding. After a further 10–30 days, depending on the amount of food ingested, a new brooding cycle starts. In the laboratory females become reproductively mature at 3–4 months, reach an age of at least 18 months, and go through up to 15 brooding cycles in their life. For further details see Peters (1937), Reinboth (1956), Wickler (1962), and Mrowka (1982, 1987).

We determined rates of oxygen consumption (V_{O_2}) as an estimate of energy expenditure (Brett and Groves 1979). The procedure used is based on data relating to general aspects of energy metabolism in this species (Schierwater and Mrowka 1987).

Methods

The experimental fishes were kept at 27° C at a photoperiod of LD 12:12. Their ages varied from 5 to 8 months and their weights ranged from 0.7 to 1.6 g (mean \pm SD = 1.07 g \pm 0.236, $n=53$). Spawning dates were recorded for each fish. One day before testing each fish was individually isolated in a jar with a volume of 1.2 l. The measurements were taken over a period of 4–6 h. Oxygen concentration was determined with an oxygen electrode (WTW OXI 530). Details of culture conditions and measuring procedures are described elsewhere (Schierwater and Mrowka 1987).

To determine the energetic demand of mouthbrooding at various points in time (ranging from 1 to 10 days after spawning), mouthbrooding females were tested twice on two consecutive days, once with their brood in the mouth (BR+), once without it (BR-). The sequence was chosen randomly for each fish (Br+/BR-, $n=11$; BR-/BR+, $n=13$). For the procedures of brood removal and brood adoption see Mrowka (1985).

Two types of nonreproductive females (i.e. females between two brooding cycles) served as controls. These were CS fish ($n=19$) who were deprived of food for 2–10 days (reflecting the same variation as in BR+ and BR-), and CF fish ($n=10$) who were fed ad lib. up to the beginning of the experiment.

The weights of the females were always determined in the absence of a brood at the end of each measurement. In BR+

the number of young was determined at the end of each measurement, and in 10 cases also at the beginning of a measuring period.

To exclude the influence of locomotory activity, the fish were filmed during the measurement of oxygen consumption.

Each 30 min at 50 consecutive 5-s intervals we checked whether a fish was moving or not. If more than 20% of the checks

were positive the data were excluded from the statistical analysis (1 case in BR+ and BR-, 9 cases in CS).

To estimate oxygen consumption of the brood in the mouth, offspring from all stages (day 1 to day 10) were kept

in small Erlenmeyer flasks of about 100 ml volume for about 2-4 h. Since after hatching the larvae begin to move from day 5

onward, half of a brood was enclosed in a tiny gauze bag allowing gas exchange but preventing locomotory activity (nonmotile

larvae in a "simulated mouth"), the other half was kept in a freemoving state (motile larvae).

Because there are different allometric relationships between V_{O_2} and body weight for each type of activity (Brett and Groves

1979; Schiewater and Mrowka 1987) we determined for each test group the exponent in the equation $V_{O_2} = a BW^{exp}$ ($BW =$

body weight). To correct for the effect of body weight we calculated the V_{O_2} per metabolic body weight using the corresponding exponent (see Table 1). Estimations of metabolic rates (MR)

were derived from V_{O_2} values using an oxycaloric equivalent of 451 kJ/mol O_2 (Wisner 1986). Therefore we calculated 1 mg

$O_2 \cdot h^{-1}$ to equal 3.91 mW (milliwatt).

As all data fitted the normal distribution (after Pearson and Stephens 1964) parametric statistical tests were applied.

The means of BR+, BR(-), CS, and CF were compared using One-way ANOVA, followed by multiple Duncan tests

(Duncan 1955). Regression curves were calculated using the BMDP (BMDP4R) statistical software package (Dixon 1983).

Results

Offspring metabolism

Offspring metabolism increases rapidly with age, following an e-function regression curve (Fig. 1). The best fit was produced by dividing larval development into two parts. For days 1-5 the increase was most rapid ($exp = 0.662$). From days 6-10 the increase was still exponential, but smaller ($exp = 0.214$ for motile, 0.190 for nonmotile larvae). From day 8 on, larvae enclosed in the simulated "mouth" (non-motile) consumed less oxygen than their free-moving siblings. Therefore, the calculation of V_{O_2} of the brood in the mouth is based on the data from nonmotile larvae.

Maternal metabolism

Since in mouthbrooding fish the sequence of BR+ and BR- did not influence the results both types were pooled to form one group ($n = 24$). The test groups differed significantly (F ratio = 128.2, $P < 0.001$). The presence of a brood in the mouth significantly elevated metabolic rate, on average by 15.7% compared to BR-, and by 13.8% compared to CS (Table 1). After subtracting the MR

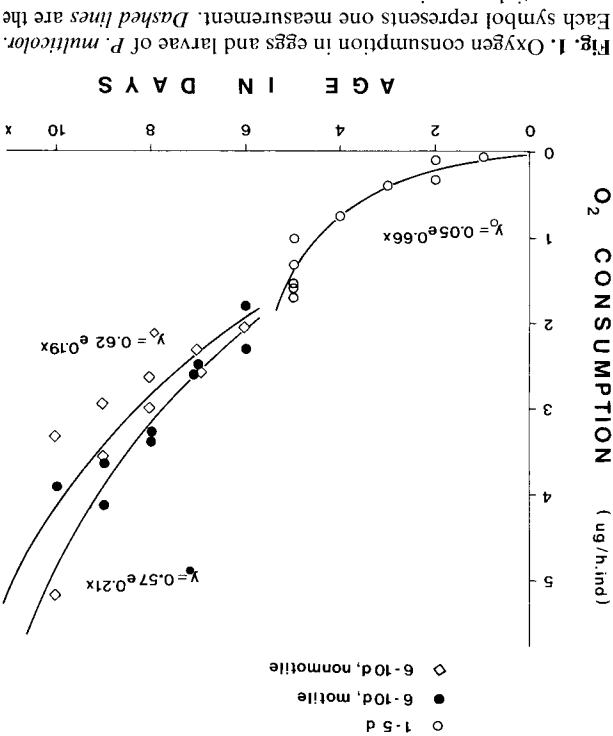


Fig. 1. Oxygen consumption in eggs and larvae of *P. multicolor*. Each symbol represents one measurement. Dashed lines are the exponential regressions

of the brood in the mouth (brood size = 25.1 ± 12) calculated on the basis of the regression curve from Fig. 1, the excess is reduced to about 4.7% and 3.2%, no longer significantly different from BR- or from CS. There were no differences between the reproductive females without a brood (BR-) and nonreproductive females that were starving (CS). By contrast, food intake increased the MR of nonreproductive females (CF) to more than twice that of all other groups. Thus, mouthbrooding females metabolized about 1590 J/10d less than feeding nonreproductive females.

The time after spawning did not influence the MR of BR+ (Table 2); the same is found in BR- ($r = 0.15$, $P > 0.3$). In contrast, the MR in BR+ ($BR(+) = BR + \text{minus } V_{O_2}$ or MR of the brood) decreased significantly with increasing time after spawning. The number of offspring present in the mouth had no effect on the MRs, either in BR+ or in BR+), despite the exponential increase of the individual MR with age, as noted above. This is due to the combined effect of a significant decrease in offspring number present in the mouth and a significant decrease of MR in BR+ with increased time after spawning (Table 2).

In only 3 out of 10 cases in which the number of young was counted before and after the measurement, were 1-3 offspring consumed by their mother. During the measuring period the average increase of

Table 1. Oxy

Test group

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BR(-)

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CF, well-fed

* $P < 0.05$;

Table 2. Pr

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Table 1. Oxygen consumption rates (V_{O_2}) and metabolic rates (MR) in mouthbrooding females

Test group	<i>n</i>	exponent	V_{O_2} mg/g ^{exp} ·h means ± SD	MR mW/g ^{exp} · means ± 95% CL	Results of Duncan tests
BR +	24	0.64	0.397 ± 0.066	1.56 ± 0.10] *] *] *
BR(+)	24	0.76	0.36 ± 0.069	1.41 ± 0.11	
BR -	24	0.59	0.343 ± 0.051	1.34 ± 0.08	
CS	19	0.67	0.349 ± 0.074	1.37 ± 0.13	
CF	10	0.74	0.83 ± 0.121	3.25 ± 0.29	**

BR +, with brood in the mouth; BR(+), BR + minus V_{O_2} or MR of the brood; BR -, without brood; CS, starved controls; CF, well-fed controls

* $P < 0.05$; ** $P < 0.001$ (compared with all other groups)

Table 2. Product-moment correlations between the metabolic rates (MR) of mothers with brood in the mouth (BR +), of the same mothers after subtracting the V_{O_2} of the brood (BR(+)), time after spawning (TI) and number of offspring present in the mouth (NO). In parentheses: level of significance $P < (two-tailed)$. $N = 24$

	BR +	BR (+)	TI
BR(+)	0.90 (0.001)		
TI	-0.25 (0.24)	-0.52 (0.01)	
NO	0.30 (0.16)	0.16 (0.44)	-0.41 (0.05)

brood size declined only from 26.5 ± 12.9 to 25.9 ± 12.8 ($N = 10$). Thus, no corrections were made for this.

Discussion

Oxygen uptake in fish eggs and larvae generally follows the exponential relationship $V_{O_2} = ae^{kt}$, where t is time and a and k are constants, depending largely on environmental conditions and age (Devillers 1965; Blaxter 1969). In *P. multicolor* the larvae feed exclusively on their yolk up to the time of release from the mouth (10 days at 27° C). Wet weight increases from approximately 2 mg (eggs at fertilization) to 4–5 mg after resorption of the yolk, presumably as a result of increased water content due to the conversion of yolk materials into body tissues. According to Winberg (1960) the allometric relationship between V_{O_2} and body weight holds also for larval metabolism. Therefore the shift after 4–5 days to a lower exponential increase of V_{O_2} might relate to an obvious increase

in body weight during this period. However, this explanation remains to be tested.

After eliminating the energy expenditure of the brood in the mouth, the remaining additional costs of mouthbrooding, if any, are minimal. They could relate to enhanced ventilation and to an intermittent behavioural action called "churning" or "chewing" leading to a turnover of the brood in the mouth (Shaw and Aronson 1954; Oppenheimer and Barlow 1968; Timms and Keenleyside 1975). The increase of the offspring's oxygen consumption with age is compensated by a decrease in brood size and a decrease in the mother's own consumption in the course of time after spawning. The latter may be explained by the observation that in the mouthbrooding cichlids *Tilapia melano-theron* (Oppenheimer and Barlow 1968) and *Aequidens paraguayensis* (Timms and Keenleyside 1975; Keenleyside 1979), after hatching churning decreases drastically, presumably because the offspring are increasingly less dependent on parental churning for respiration. Preliminary observations in *P. multicolor* point in the same direction.

Whereas the direct energetic costs of the particular behavioural pattern of mouthbrooding seem to be negligible, considerable indirect costs are incurred during the nonreproductive phase between two brooding cycles. This period is characterized by intense food intake by the females, combined with a high energy turnover as indicated by the oxygen consumption of feeding controls. Part of the food ingested contributes to maintenance, part to growth (Mrowka 1987), a further part to the production of a new egg batch in the ovary and, finally, a non-negligible part serves as energy storage for use during subsequent mouthbrooding, presumably in the form of lipids (Reinboth 1956). Only a quantitative assessment of the relative im-

portance of all four demands would allow calculation of the total costs of mouthbrooding. Such calculation is further complicated by the fact that part of the brood is consumed during mouthbrooding itself (Liebman 1933; Welcomme 1967; Mrowka 1987) and thus may serve as a further energy source. However, this effect played no substantial role during the short measuring period.

In terms of energy metabolism mouthbrooding in *P. multicolor*, as in most mouthbrooding cichlids, is characterized by two extremely different periods in the life-history: (1) an *investment phase* between two subsequent brooding cycles, characterized by high energy turnover and energy stored by high energy turnover and energy stored itself) characterized by low energy turnover capitalizing on investments made previously. It would be interesting to compare this broodcaring mode with alternative broodcaring modes found in substrate-brooding cichlids. Substrate-brooding seems to be associated with more direct costs because of enhanced locomotory activity due to brood defence, fanning, and feeding (Fryer and Iles 1972; Keenleyside 1979).

There is evidence that in cichlids mouthbrooding has evolved from substrate-brooding (Keenleyside 1979; Peters and Berns 1982). Changes in the allocation of energy expenditure to the different stages of the reproductive cycle might have played a significant selective role during the evolution of this behaviour. It should also be noted that oxygen might be a limiting factor with respect to survival chances during the dry season, as measured by the first author in April 1983 near Kisumu, Kenya. The author found mouthbrooding females even in waters with a temperature of 32°C, and an oxygen content of 2 mg/l. Mouthbrooding seems to be particularly suited to such extreme conditions.

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