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A. Grantner · M. Taborsky

The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae)

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Abstract We measured the metabolic rates as a direct estimate of energy expenditure of individual *Neolamprologus pulcher*, a cooperatively breeding cichlid fish, when resting and when performing agonistic, submissive or digging behaviours in a respirometer. Standard and routine metabolic rates increased linearly with body mass (range 0.9–8.4 g) when plotted on a doubly logarithmic scale (linear regression equations: standard metabolic rate: \log individual oxygen consumption rate = $0.65 + 0.86 \log$ body mass; routine metabolic rate: \log individual oxygen consumption rate = $0.75 + 0.86 \log$ body mass). Routine metabolic rates were, on average, 30% higher than standard metabolic rates. Submissive and agonistic behaviours raised routine metabolic rates by factors of 3.3 and 3.9, respectively. Digging resulted in a 6.1-fold increase of routine metabolic rates. Differences in metabolic rates between active and resting rates were statistically significant. However, those between the three behaviours were not. Mean opercular beat frequencies correlated significantly with routine metabolic rates and with metabolic rates when performing specific behaviours, which offers methodological prospects for field measurements. In *N. pulcher*, the high energy expenditure for submissive behaviour may indicate that this is a reliable signal. The considerable energy expenditure involved in territory defence suggests that these costs should be considered in addition to risk in cost-benefit analyses. This is the first study in which the energy expenditures of specific social and territory maintenance behaviours of individual fish were measured directly by respirometry and within the usual social setting of the fish.

Key words Behavioural energetics · Cooperative breeding · Respirometry · Cichlid fish · *Neolamprologus*

Abbreviations M body mass (g) · OBF opercular beat frequency (Hz) · OCR_M mass specific oxygen consumption rate ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) · OCR_{Ind} individual oxygen consumption rate ($\mu\text{mol O}_2 \text{ h}^{-1}$) · POS polarographic oxygen sensor · RMR routine metabolic rate, i.e. resting rate measured during the day ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$) · SDA specific dynamic action, i.e. the increase in metabolic rate following food consumption · SL standard length (cm) · SMR standard metabolic rate, i.e. resting rate measured during the night ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ h}^{-1}$)

Introduction

Both costs and benefits of specific behaviours must be considered when determining whether or not the behaviour is optimal in a particular context. Despite the fact that this is a key issue in behavioural ecology, many studies of costs and benefits rely on simplistic assumptions about costs and cost functions, especially when reproductive behaviour is concerned (Krebs and McCleery 1984; Clutton-Brock and Godfray 1991). Apart from risk, time and energy spent on the performance of specific behaviours may constrain the lifetime reproductive success of an individual and these are therefore important criteria in natural and sexual selection.

Several techniques have been used to estimate the energy expenditure of animals in the wild. For example, the application of doubly labelled water is suitable for measuring long term averages of energy expenditure of terrestrial animals (Tatner and Bryant 1989). Treadmill experiments have been used to estimate the energy expenditure of certain behaviours in reptiles and birds (e.g. locomotion and foraging behaviour of marine iguanas, *Amblyrhynchus cristatus*, Gleeson 1979; mound-tending behaviour in the malleefowl, *Leipoa ocellata*, Weathers et al. 1993). In fish, the energy

A. Grantner · M. Taborsky
Konrad Lorenz-Institut für Vergleichende Verhaltensforschung,
Savoyenstrasse 1a, A-1160 Vienna, Austria
e-mail: m.taborsky@klivv.oeaw.ac.at
Fax: 0043-1-4862121-28

expenditure of directed swimming locomotion has been measured in the lab (Beamish 1978) and physiological correlates like heart rates (Priede and Young 1977; Lucas and Armstrong 1991; Lucas et al. 1991) or gill ventilation rates (Oswald 1978; Weatherley et al. 1982; Rogers and Weatherley 1983) were measured to estimate field metabolic rates.

The suitability of all these techniques for a study of energy expenditures resulting from specific social and reproductive behaviours is limited. A comparison of the physiological consequences of specific behaviours is needed to understand how energy expenditures related to social status and behaviour will influence strategic decisions, for example during agonistic encounters (Huntingford and Turner 1987). In amphibians and crustaceans, respirometry was used to study the energetics of calling, agonistic and reproductive behaviour (Bucher et al. 1982; Ryan et al. 1983; Smith and Taylor 1993; Prestwich 1994; Huntingford et al. 1995). This has not been done in fish yet, though tropical fish in particular have attracted great attention from behavioural ecologists (e.g. Keenleyside 1991; Pitcher 1993; Taborsky 1994; Endler 1995). Only large and economically important species have been considered so far for respirometry, with emphasis on the influence of abiotic factors like temperature or oxygen supply on metabolic rate (Caulton 1977, 1978a, b; Saint-Paul 1983, 1988; Eccles 1985; Lezama and Günther 1992).

Indirect evidence for significant energy expenditures involved in the performance of specific social and reproductive behaviours in fish comes from experimental laboratory studies on egg fanning rates in three-spined sticklebacks (*Gasterosteus aculeatus*, Stanley 1983) and convict cichlids (*Cichlasoma nigrofasciatum*, Townshend and Wootton 1985). In both studies, starved fish showed reduced fanning rates, which indicates that the amount of fanning was adjusted to food limitations. Additionally, some studies applied relationships between tail-beat frequencies (Puckett and Dill 1985) or gill ventilation rates (Van Rooij and Videler 1996) and respiration rate obtained in the laboratory to estimate the energetic costs of territoriality in the field.

In the present study, our aim was to measure the oxygen consumption rates resulting from the performance of specific behaviours as a direct estimate of energy expenditure, and to compare them for different social and territory maintenance behaviours. Resting metabolic rates measured during night and day serve for comparison and their relationship to body mass will be discussed within the framework of existing data on fish respiration.

The Lake Tanganyika cichlid *Neolamprologus pulcher* has the most complex social structure so far described among fish (Taborsky 1994). It is a small species that readily breeds in the laboratory and that performs its natural range of behaviours even if confined to little space (Taborsky 1984). This renders it an ideal candidate for studies of behavioural energetics. We predicted exceptionally high metabolic rates to be associated with

digging behaviour, which includes the physical effort of carrying a sand load for a distance. We compared these rates to those arising from the performance of two different social behaviours, i.e. submissive and agonistic behaviour. We chose these behaviours as they are performed frequently by the fish and are essential for maintaining the dominance relationships within *N. pulcher* family groups.

Materials and methods

The study species

Current nomenclature considers *Neolamprologus brichardi* and *Neolamprologus pulcher* as two distinct species (Poll 1974), although they were considered subspecies previously (Trewavas and Poll 1952). We doubt the validity of this division, as it was based on a description of one individual *N. pulcher* only (Poll 1974). Additionally, our field and laboratory observations on the social system and behaviour of *N. brichardi* from Burundi (Taborsky and Limberger 1981; Taborsky 1982, 1984, 1985) and *N. pulcher* from Zambia (personal observation) strongly indicate the division is invalid. In a systematic study we tested for statistical differences in 13 morphometric measures and counts between individuals from the northernmost (*N. brichardi*, $n = 20$) and southernmost (*N. pulcher*, $n = 20$) populations. We did not find strong support for the separation into two species (S. Balshine-Earn et al., unpublished manuscript). Here, we refer to previous work on the northernmost morph, *N. brichardi*, for the description of the social system and the behaviours measured; however, all experiments were carried out with the southernmost morph, *N. pulcher*.

N. pulcher is a substrate brooding cichlid endemic to Lake Tanganyika (East Africa). Family groups of this species defend small territories around their breeding shelters in the rocky sublittoral zone of the lake. They consist of a breeding pair and offspring from three to four broods on average (Taborsky and Limberger 1981). These young share in all duties of broodcare, territory defence and maintenance and are hence referred to as "helpers". Helpers defend the territory against intruders, remove sand and snail shells from the breeding shelter and care for subsequent broods by mouthing eggs and larvae. In the north non-territorial fish live in stable feeding aggregations in the water column near the family territories (Taborsky and Limberger 1981).

Experimental animals and housing conditions

All experiments were performed with fish caught at the southern end of Lake Tanganyika near Mbita Island, Zambia, in 1992, and with the laboratory reared offspring of these individuals. The fish were kept separately or in family groups in 50–500 l tanks. The bottom of each tank was covered with gravel (particle size 1–1.5 mm). For shelter and as spawning substrate flowerpot-halves were provided. Water temperature was maintained at 27 °C (± 1 °C) by electric aquarium heaters; artificial light conditions were 13:11 L:D; water quality was held constant within certain limits, following Taborsky (1982); water filtering was provided with air-operated, foamed plastic filters. The fish were fed once daily, either with newly hatched nauplia of *Artemia salina*, frozen plankton or commercial flaked dry food. Test fish were deprived of food for the last 24 h before the start of an experimental session to avoid specific dynamic action (SDA) effects (Beamish 1964; Jobling 1981, 1983).

Families with one or several helpers were used for the experiments. The helpers had cleaned eggs before of one brood at least. They were observed before an experiment to find out if individuals showed specific behaviours frequently. The chosen family was then transferred to the experimental tank. The fish were allowed to habituate to the tank for 1 day before we started the experiment.

Respiratory measurements

Oxygen consumption rates were determined with help of an intermittently closed respirometer where measuring and flow-through periods alternate with each other. The respirometer consisted of an aquarium pump, a sequencing valve system, a stirring chamber with a polarographic oxygen sensor (POS; YSI model 5750) and an experimental chamber. The POS was connected to a strip-chart recorder (BBC model SE 111). For oxygen measurements the experimental chamber was connected to the POS and the decrease of oxygen concentration in a defined water volume was determined. During flow-through periods, aerated tank water replaced the deoxygenated water in the experimental chamber, and excretory products were also removed this way (see Forstner 1983 for a detailed description of the respirometer).

The test fish and the respirometer were put into two separate but adjacent 160 l tanks. This allowed fish to be tested in their familiar social setting within their territory, but without being disturbed by the water current that resulted from the action of the respirometer. The experimental chamber was placed into the tank that contained the test fish. Silicone tubes connected the experimental chamber to the respirometer.

The sizes of the experimental chambers needed to meet a compromise between two conflicting requirements: (1) a small size was needed to allow a quick exchange of oxygen concentrations and (2) a sufficiently large chamber size was needed to allow experimental animals to perform desired behaviours. We used two different chamber sizes, small chambers (volume 150 ml) for fish of 1–3 g, and large chambers (volume 600 ml) for fish heavier than 3 g.

Microbial oxygen consumption was measured before and after each experimental session with no fish in the experimental chamber (bacteria consumed $3.87 \pm 1.45\%$ of total oxygen available, mean \pm SD, $n = 10$ experimental sessions). Oxygen consumption rates of undisturbed fish that showed normal spontaneous activity were measured during the night and during the day to obtain estimates of standard and routine metabolic rates (SMR and RMR respectively; Fry 1957; Beamish 1964; Brett and Groves 1979). Measurements of RMR and all experiments were performed between 0900 and 2000 hours. Previous work revealed that there were no significant diurnal activity patterns in *N. pulcher* (Taborsky 1982).

Experimental water temperatures were between 26 °C and 28 °C, which corresponds to natural conditions (Taborsky 1982). Possible influences of variation in water temperature on metabolic rate were tested by comparing the residual SMR of the fish tested at the lowest (26.0–26.5 °C; $n = 7$) and highest (27.5–28.0 °C; $n = 6$) temperatures, respectively. Residuals were calculated from the regression of SMR and net body mass (M to adjust for the influence of mass on metabolic rate), see “Results,” Fig. 1. There were no significant differences between these two group differing in water temperature (Mann-Whitney U -test; $P > 0.1$, n.s.). Within an experimental session water temperatures were adjusted to similar levels in both tanks and were held constant (± 0.5 °C) throughout.

Experimental procedure

Individual fish were placed into the experimental chamber either by catching them with a hand net or by slowly moving the hand towards the fish and gently directing it into the chamber. This procedure caused increased respiration rates for some period. An experiment started after the test fish had recovered from handling, i.e. when its respiration rate was approximately constant for three subsequent measuring periods (equivalent to 45 min; see below). Recovery times were usually longer than 2 h. There was considerable individual variation in the reaction to the experimental situation. If test fish had not habituated after 4–5 h they were released from the experimental chamber and the experiment was terminated.

An experimental session consisted of several single trials, each lasting for 5 min, alternating with 10 min flow-through periods. In the following we refer to a total trial time of 4 min, as the se-

quencing valve system needed 30 s to switch from flow-through to measuring, and after 4 min of measuring again needed 30 s to switch back to flow-through. During each trial the oxygen consumption rate, the opercular beat frequency (OBF) and the behaviour of the fish were recorded. Behaviour and OBFs were recorded with a keyboard-operated electronic event recorder. The number of 4-min trials was variable and depended on the behaviour of the fish (see “Data analysis” for sample sizes). After the experiments were finished, M and standard length (SL) of each fish were measured.

Recorded behaviours

The behavioural categories are based on the description of Taborsky (1982); for a detailed ethogram see Kalas (1975).

Submissive behaviour

A subordinate fish with its tail fin turned towards a dominant, presses its body on the bottom and vibrates its tail and the caudal part of the dorsal fin. Tail quivering was shown by helpers when a member of the breeding pair approached the experimental chamber.

Digging

There are two kinds of digging behaviour; either sand is taken up with the mouth, carried away and then spat out, or a fish presses its body onto the bottom and pushes the sand forward with its extended lower jaw and aside with its tail with help of tail vibrations. We provoked digging behaviour of helpers in the experimental chamber by providing them with a shelter that was almost completely covered with sand (sand and shelter were sterilized before each experiment to prevent microbial oxygen consumption).

Agonistic behaviour

We recorded all aggressive behaviours of the test fish. This included opercula-spreading, tail-beat, S-shaped bending, bumping against, head-jerking, mouth-fighting, biting and ramming. Pair members and helpers showed agonistic behaviour when exposed to their mirror images. During the flow-through period a mirror was put in front of the experimental chamber. Usually the fish began to attack their mirror images after a few minutes. The mirror was left in this position as long as the test fish attacked its mirror image.

Data analysis

The total number of trials performed was 368 (average number of trials per fish = 11.2, range 2–36; total number of fish tested = 33). From this total, 79 trials were used to calculate estimates of RMR, as no behaviours were performed during these trials. All trials in which only one of the three selected behaviours was performed for more than 30% of the total trial time were considered for further analysis (= 75 trials; average number of trials per fish = 2.6, range 1–13, total number of fish included = 29). These data were standardized to an occurrence of 50% of the respective behaviour per total trial time by calculating the amount of oxygen consumed if the behaviour had been performed for the total trial time and then dividing the resulting number by two. This standardization was possible due to a positive correlation between performance period and oxygen consumption (see Fig. 2). For each individual (1) with more than five trials in which only one specific behaviour was performed, and (2) where the range of behaviour durations during these trials covered at least 60 s, a correlation between performance period (seconds spent on that specific behaviour) and mass specific oxygen consumption rate (OCR_M)

was calculated. A total of 14 individuals fulfilled criterion (1), but only 8 individuals satisfied both criteria. The overall significance was obtained by Fisher's procedure of combining tests (Sokal and Rohlf 1981, pp. 779–782).

Comparisons between SMR and RMR, and between resting rates (SMR, RMR) and active rates, i.e. when performing specific behaviours, were performed with help of Wilcoxon matched-pairs signed-ranks tests. The reduced sample size of $n = 5$ for the comparison between SMR and submissive behaviour resulted from a power failure during one night, in which one test fish died from oxygen starvation and hence had to be removed from the data set.

Regressions were fitted by the method of least squares to analyse the relationship between SMR and RMR and body mass. Comparisons of slopes of the linear regressions and of correlation coefficients followed Kleinbaum and Kupper (1978).

Results

Standard and routine metabolism

Standard and routine individual oxygen consumption rates (OCR_{Ind}) increased linearly with M when plotted on a doubly logarithmic scale (Fig. 1; general regression equation: $\log OCR_{Ind} = a + b \log M$; SMR: $a = 0.65 \pm 0.06$, $b = 0.86 \pm 0.12$; RMR: $a = 0.75 \pm 0.08$, $b = 0.86 \pm 0.16$; means \pm SE). The slopes of the regression lines were not significantly different from each other (large sample z -test for comparison of two slopes; $z = 0.033$, n.s.). When compared for individual fish, RMR was 1.3 ± 0.45 times SMR (mean \pm SD, $n = 31$; $z = 2.303$, $P < 0.02$; Wilcoxon matched-pairs test).

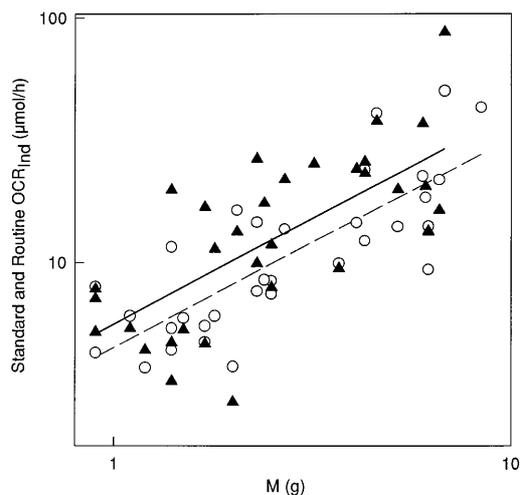


Fig. 1 Mass-specific increase of standard metabolic rate (SMR; $n = 32$) and routine metabolic rate (RMR; $n = 33$) plotted on logarithmic axes. Regression equations: SMR (open circles, hatched line): $\log OCR_{Ind} = 0.65 + 0.86 \log$ wet body mass (M) ($r = 0.791$); RMR (filled triangles, solid line): $\log OCR_{Ind} = 0.75 + 0.86 \log M$ ($r = 0.697$), (both $P < 0.001$). Each symbol represents the mean oxygen consumption rate of an individual during the night (SMR, $n = 10$ trials per individual) and during inactive periods at day (RMR, $n = 2.4 \pm 0.71$ trials per individual, mean \pm SD)

Metabolic rates when performing specific behaviours

Oxygen consumption during a trial correlated positively with the time the behaviour was performed during that trial (Fig. 2; $n = 8$, $P < 0.01$; test see “Data analysis”). The fish had significantly higher metabolic rates when performing specific behaviours as compared to RMR and SMR (Table 1). A comparison of the multiples of RMR and SMR between the three measured behaviours revealed no significant differences (Kruskal-Wallis ANOVA, RMR: $P < 0.16$, SMR: $P < 0.39$; both n.s.).

Opercular beat frequencies

Mean routine and active metabolism, respectively, correlated significantly with mean OBF (Fig. 3a, b). The correlation coefficients of routine and active rates with

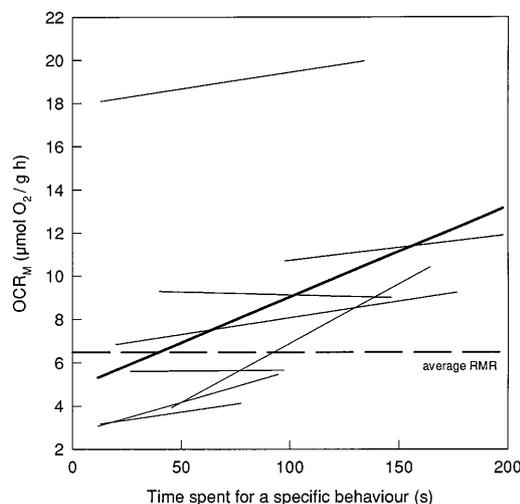


Fig. 2 The oxygen consumption rates during an experimental trial in dependence of the time spent with a specific behaviour ($n = 8$ individual fish that fulfilled the respective measurement criteria; see “Data analysis”). The regression lines of individual fish are given as well as the overall regression of the combined values of all fish (bold line; regression equation mass specific oxygen consumption rate (OCR_M) = $4.82 + 0.04$ time spent for a specific behaviour; $r = 0.446$, $P < 0.05$). The average RMR found is indicated by the horizontal, intermittent line

Table 1 Increase of metabolic rate due to the performance of specific behaviours in *Neolamprologus pulcher*, expressed as multiples of routine metabolic rate (RMR) and standard metabolic rate (SMR) (means \pm SD)

	Agonistic behaviour	Submissive behaviour	Digging
Multiples of RMR	$3.97 \pm 1.35^{**}$ ($n = 21$)	$3.28 \pm 1.48^*$ ($n = 6$)	$6.05 \pm 3.14^*$ ($n = 6$)
Multiples of SMR	$4.71 \pm 2.41^{**}$ ($n = 20$)	5.93 ± 3.54^a ($n = 5$)	$5.69 \pm 2.24^*$ ($n = 6$)

^a Difference could not be tested because of the small sample size (see “Data analysis”)

* $P < 0.03$, ** $P < 0.001$ indicate significant differences (see “Data analysis”)

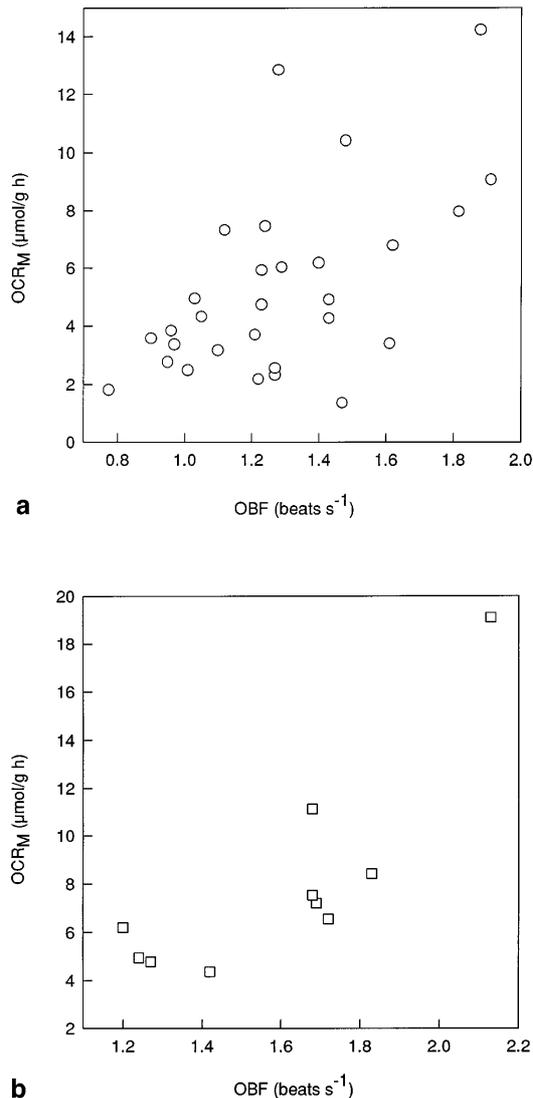


Fig. 3 Correlations between mean opercular beat frequency (*OBF*) and mean **a** routine ($r = 0.57$, $P < 0.001$, $n = 29$), and **b** active oxygen consumption rates, i.e. when performing specific behaviours ($r = 0.81$, $P < 0.005$, $n = 10$). See "Results" for a comparison of correlation coefficients

OBF did not differ significantly from each other ($z = 1.105$, n.s., z -test for comparison of two correlation coefficients).

Discussion

Standard and routine metabolism

Tropical stenothermal fish were assumed to have a higher SMR than temperate species as a result of the higher environmental temperatures they experience. Brett and Groves (1979) estimated a minimum rate of energy expenditure of $2.1 \text{ J g}^{-1} \text{ h}^{-1}$ for fish acclimated to 26°C . The mean SMR of *N. pulcher* acclimated to $26\text{--}28^\circ \text{C}$ was $2.199 \text{ J g}^{-1} \text{ h}^{-1}$ (conversion factor: 13.565 J mg^{-1}

oxygen consumed; Elliot and Davison 1975), which comes very close to the estimate of Brett and Groves (1979).

The relationship between resting metabolic rate and *M* that is known from other fish was confirmed in *N. pulcher*. In cold-water and temperate fish species a mean metabolic exponent of $b = 0.86 \pm 0.03$ of SMR was found (Brett and Groves 1979). This is exactly the same exponent that we found in *N. pulcher* for SMR and RMR. The metabolic exponents of other tropical fish species vary over a broad range, from 0.3 to 0.9 (Lezama and Günther 1992). This broad variation may result from intrinsic, physiological species characteristics, temperature, food ration, ontogenetic stage, reproductive state and adult *M*. The interaction of these factors and its effect on metabolism is still unclear (Wieser 1986).

RMR was on average 30% higher than SMR, while the mass specific increase of SMR and RMR, i.e. the slopes of the regression lines, were identical. During the day, the individuals operate on a higher metabolic level, apparently due to increased locomotory and sensory activity. Nocturnal observations revealed that the fish rest on the bottom. Merely holding position appears to be energetically less costly than performing spontaneous activities in the water column.

We should like to stress, however, that RMR and SMR are operationally defined conventions helping to standardize experimental conditions, but that, in general, the causal relationships underlying these metabolic rates are still poorly understood.

Metabolic rates when performing specific behaviours

The cost of active metabolism in nature (SMR + activity cost) was assumed to range from 1–3 times SMR in fish (Tytler and Calow 1985). This estimate was based on metabolic measurements of individuals swimming against an artificial water current. Metabolic costs associated with the performance of specific behaviours in *N. pulcher* by far exceeded this assumed value (mean 5.1 times SMR; range 2.2–11.5 times SMR). It has been suggested that a complex locomotory pattern would lead to higher metabolic rates than directed swimming locomotion (Forstner and Wieser 1990; Boisclair and Tang 1993).

Additionally, increased metabolic rates may result from digestion processes, i.e. the SDA effect. We excluded SDA-effects by testing the fish after a 24-h starvation period, i.e. when there was no digestion activity because the gut was empty. However, this could have led to a slight overestimation of the costs of behaviour as a certain level of SDA effect is always maintained in the natural situation where the fish feed more or less constantly during the day (Gashagaza 1988). In a future study, the effects of different nutritional states on RMR should be tested.

In *N. pulcher* we expected that digging would be exceptionally costly when compared to agonistic and

submissive behaviours, as the digging fish carry a considerable sand load for some distance. However, even though the metabolic rates of fish performing digging exceeded those measured during agonistic and submissive behaviour by 1.6 and 1.9-fold, respectively, these differences were not statistically significant.

Submissive behaviour is performed by subordinates when approached by dominant family members. The energy expenditure caused by the performance of submissive behaviour may be outweighed by the benefit of preventing attacks and consequential injury. Submissive behaviour that is energetically costly may be viewed as an honest and reliable signal for the dominant individual (Zahavi 1975; Grafen 1990).

Agonistic behaviour of the experimental fish was directed towards their own mirror images, which were meant to represent similar-sized conspecifics intruding into the territory. Field observations and aquarium experiments revealed that conspecific intruders are attacked specifically by family members of corresponding sizes (Taborsky and Limberger 1981; Taborsky 1982, 1984). Brett and Groves (1979) measured the change of SMR of a group of juvenile sockeye salmon, *Oncorhynchus nerka*, during aggressive interactions. Maximum metabolic rates during aggression were 4.1 times SMR, as calculated for 100 g of fish at 15 °C. The maximum rates measured in *N. pulcher* were about 2.5 times higher than the maximum values of *O. nerka*. However, in the groups of sockeye salmon the intensity of aggression may have differed between individuals, which would bias the maximum levels of metabolic rates of a group towards lower levels. Apart from this, aggression in *N. pulcher* was directed towards potential space competitors, while the juveniles in *O. nerka* may have competed only for certain positions in the group (Brett and Groves 1979). Agonistic behaviour may involve a broad range of aggressive display behaviours depending on the degree of escalation of the contest and on the resource value. Measuring energy expenditures related to different components of agonistic behaviour would further improve our understanding of fighting behaviour in general (Huntingford and Turner 1987).

Opercular beat frequencies

Both RMR and oxygen consumption rates when performing specific behaviours correlated positively with OBF. This relationship may help to estimate field metabolic rates of individual fish. Previous studies used radio telemetry to monitor activities of the opercular muscles or heart rates (Priede and Young 1977; Oswald 1978). The small body size of *N. pulcher* prohibits the application of such devices.

In conclusion, we regard the application of respirometry as a powerful tool for studying the energy expenditure associated with specific behaviours in fish. In *N. pulcher*, the results of this study allow the calculation

of behavioural time-energy budgets of helpers as opposed to pair members (Taborsky and Granther in press).

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