



Behavioural time–energy budgets of cooperatively breeding *Neolamprologus pulcher* (Pisces: Cichlidae)

MICHAEL TABORSKY & ASTRID GRANTNER

Konrad Lorenz-Institut für Vergleichende Verhaltensforschung (KLIVV)

(Received 30 January 1997; initial acceptance 10 March 1997;
final acceptance 4 May 1998; MS. number: 5467R)

ABSTRACT

We estimated the energy expenditures resulting from helping behaviour in the cooperatively breeding cichlid *N. pulcher* by measuring the metabolic rates directly associated with specific social and territory maintenance behaviours of individual pair males and females, and their helpers, in a respirometer. In pair males, pair females and helpers, routine metabolism was raised on average 4.4, 3.8 and 3.6 times, respectively, during agonistic behaviour. Helpers spent 3.3 and 6.1 times routine metabolism, respectively, on submissive behaviour (tail quivering) and digging. These estimates of energy expenditure were combined with laboratory time budgets, obtained previously, to calculate behavioural time–energy budgets for pair members and helpers. Both groups spent on average 98.5% of total metabolism on routine and standard metabolism. With regard to the energy expended on specific behaviours, pair males invested almost exclusively in intrafamily agonistic behaviour, while pair females and helpers shared the investment in territory maintenance and direct brood care. The behavioural energy budget of helpers was strongly determined by their submissive behaviour. This serves to maintain the social status of the helpers within the family hierarchy and may therefore be regarded as ‘paying for staying’, which may also be true for direct brood care and other helper duties. We conclude that the substantial energy expenditures associated with helping behaviours are probably partly responsible for the reduced growth rates of helpers. This is the first study in which energy expenditures associated with specific helping behaviours have been measured in brood care helpers, and it provides the first estimate of total behavioural energy expenditure in a cooperatively breeding fish.

© 1998 The Association for the Study of Animal Behaviour

Cooperatively breeding species allow us to test hypotheses that aim at explaining the adaptive value of apparently altruistic behaviour. The underlying assumption of these hypotheses is that brood care helpers gain benefits that compensate for the costs resulting from their help (Emlen 1991; Emlen et al. 1991).

Benefits for helpers have been investigated extensively, especially in birds (Stacey & Koenig 1990). Benefits that result from the performance of helping behaviours per se include the acquisition of experience in parental care or of essential foraging skills, and indirect fitness gains (Taborsky 1984; Woolfenden & Fitzpatrick 1984; Heinsohn & Cockburn 1994; Komdeur 1996).

Surprisingly, only a few studies have attempted to quantify the costs of helping behaviour (Taborsky 1982, 1984; Reyer 1984; Arnold 1990; Heinsohn & Cockburn 1994). These costs may include time and energy expendi-

ture, and mortality risk. The latter is presumably not important in most helper systems as philopatry raises the survival prospects of helpers compared with individuals that disperse (Brown 1987; Stacey & Koenig 1990). Time and energy spent on helping behaviour, however, may lead to physiological costs and long-term fitness consequences to helpers. This may be of particular importance if helpers are still growing, such as in species with flexible and indeterminate growth (e.g. fish).

Neolamprologus brichardi/pulcher (see Methods for taxonomy) is one of seven fish species known to have brood care helpers (Taborsky 1994). As part of a cost–benefit analysis of helping in *N. brichardi/pulcher*, Taborsky (1984) compared the growth rates of helpers and non-helping control fish under ad libitum food conditions. Helpers grew more slowly than similar sized nonhelping fish (whether or not they behaved territorially). Three different causes, not necessarily mutually exclusive, may explain the reduced growth of helpers: (1) their subordinate social status may have growth-depressing

Correspondence: M. Taborsky, KLIVV, Savoyenstr. 1a, A-1160 Vienna, Austria (email: m.taborsky@klivv.oew.ac.at).

behavioural or physiological consequences, for example via time constraints, or a reduced appetite or digestion efficiency; (2) increased energy expenditure resulting from helping behaviour may reduce growth; and (3) helpers may strategically decide to reduce growth in order to be accepted in their natal territory, as the probability of being expelled increases with body size (Taborsky 1985; von Siemens 1990); accumulated reserves (i.e. fat or protein stores) may be used to speed up somatic growth after helpers have left the territory.

Previous experiments provide evidence for causes 1 and 3. Cause 1 was tested by comparing the growth rates of helpers and territorial controls, that is, size-matched fish that defended their own territories and reproduced (Taborsky 1984). Territorial controls grew faster than helpers even though they put similar effort into brood care, territory maintenance and social interactions, and additionally, produced gametes. This result can be explained only by the difference in dominance ranks, that is, by the costs of submission. The third cause was tested by comparing the condition of helpers as opposed to aggregation fish. These live in groups of up to several hundred fish near the family territories and represent the natural alternative to helping (Taborsky & Limberger 1981). Helpers were heavier than same-sized aggregation fish (Taborsky 1984) and had higher fat contents (M. Taborsky & F. Neat, unpublished data).

The possibility that investment in helping behaviours may increase energy expenditure has not yet been tested. Helping behaviour in *N. brichardi/pulcher* includes territory defence and maintenance as well as direct brood care, but helpers also spend significant amounts of time displaying submissively to breeders. In this study, we estimated energy expenditure directly by measuring oxygen consumption rates of individual fish performing territory maintenance and submissive behaviours in a respirometer. Additionally, we compared the oxygen consumption rates of helpers and pair members (i.e. a male and female that constitute a breeding pair) when performing agonistic behaviour. We then combined the measured energy expenditures with time budgets previously obtained in the laboratory (Taborsky 1982) to quantify behavioural time–energy budgets of pair members and helpers.

METHODS

The Study Species

Neolamprologus brichardi and *N. pulcher* are presently considered to be two separate species (Poll 1974) but used to be considered subspecies (Trewavas & Poll 1952). The separation into species was based on the examination of only one specimen of *N. pulcher* (Poll 1974) and has not been undisputed (Konings 1988). Our laboratory and field observations on the social system and behaviour of both *N. brichardi* from Burundi (Taborsky & Limberger 1981; Taborsky 1982, 1984, 1985) and *N. pulcher* from Zambia (personal observation) indicate the invalidity of this division. A systematic study testing for statistical

differences of 13 morphological characters between the two species provides additional evidence (S. Balshine-Earn, E. Skubic, P. Dierkes, A. Grantner & M. Taborsky, unpublished data). This study was carried out with *N. pulcher* from the southernmost end of Lake Tanganyika (Mpulungu area, Zambia; reference specimens at the Natural History Museum, Vienna, numbers NMW 93644 for males and NMW 93645 for females, respectively); however, the description of the social system and the time budgets were obtained in previous studies on *N. brichardi* (see the respective references).

Neolamprologus pulcher is a substrate-brooding cichlid endemic to Lake Tanganyika. Families defend small territories along the rocky shores of the lake, from 3 to 45 m depth. Small caves and crevices within these territories serve as hiding and breeding places. The families usually consist of one breeding pair and on average seven to eight helpers of both sexes from previous broods. The helpers in a family belong to up to four size classes, and the largest helpers are already sexually mature (Taborsky & Limberger 1981). Helpers share in all duties of the breeding pair, including territory defence, territory maintenance (removing sand and particles), and direct brood care (cleaning and fanning eggs and mouthing larvae and free-swimming fry). There is no obvious behavioural difference between male and female helpers. Fish with no access to a territory form stable aggregations of up to several hundred fish that live and feed in the water column near the family territories. The family members temporarily join these aggregations to feed on plankton (Taborsky & Limberger 1981).

Housing Conditions

The fish were caught at the southern end of Lake Tanganyika in 1992, near Mbita Island at Mpulungu, Zambia. All experiments were carried out with these fish and their laboratory-reared offspring. The fish were kept in 50–500-litre tanks and families (see below) were provided with flowerpot halves as spawning sites. The bottom of all tanks was covered with sand of 1–1.5 mm grain size. Water quality was kept constant (see Taborsky 1982), the artificial light conditions were 13:11 h light:dark and the water temperature was a mean of 27°C (range 26–28°C). Food was provided once daily (newly hatched *Artemia salina* nauplia, frozen plankton, commercial flaked dry food). Test animals were food deprived for 24 h before the onset of an experiment to avoid increased metabolic rates after a meal (Beamish 1964; Jobling 1981).

Experimental Procedure and Oxygen Measurements

For oxygen measurements we used an intermittently closed respirometer, in which measuring and flow-through periods alternated with each other. During the measuring period we determined the decrease in oxygen tension in a defined water volume. During the

flow-through period deoxygenated water was replaced by aerated tank water, and excretory products were removed (see Forstner 1983 for a detailed description of the respirometer).

Two 160-litre tanks were placed side by side for the experiments. One tank contained the measuring unit of the respirometer, consisting of an aquarium pump, a valve system, and a stirring chamber with an oxygen electrode (YSI model 5750) which was connected to a strip-chart recorder (BBC model SE 111). The second tank contained the experimental chamber and the test fish. Silicone tubes connected the experimental chamber with the measuring unit. This set-up allowed us to measure the fish in their familiar territories and within their usual social environment. The chamber sizes used were 200 ml for fish weighing 1–3 g and 700 ml for heavier fish. The experimental water temperatures were between 26 and 28°C which corresponds to the natural thermal regime. Water temperatures were kept constant ($\pm 0.5^\circ\text{C}$) within an experimental session.

We set up families for the experiments in the laboratory by introducing three helper-sized fish (ca. 2.0–3.0 cm standard length; the sex of live fish of this size could not be determined reliably) into a 160-litre tank. After 5–60 min, when these fish had calmed down and were exploring their new environment, we added a breeding pair to this tank. After one or more helpers were accepted by the pair we waited for at least one entire breeding cycle before the family was transferred to the experimental tank. For the experiments we chose only families in which a helper had cleaned eggs at least once, so it was unequivocally classified as a helper. Additionally, we chose families in which individuals commonly showed one of the three target behaviours (see below). The experiments started 24 h after we had transferred the chosen family into the experimental tank. Individual fish were placed into the experimental chamber either by catching them with a hand net or by slowly moving a hand towards a fish and gently directing it into the chamber. Then they were tested after a habituation period of 2–3 h in the experimental chamber. An experimental session consisted of a variable number of single 4-min trials, depending on the behaviour of the experimental fish (average number of trials per fish=11.2; total number of fish tested=33). During each trial the behaviour (see below) and the oxygen consumption rate of the experimental fish were recorded simultaneously. At the end of each trial the oxygen saturation levels in the respiration chamber were $\geq 85\%$.

For comparison, resting oxygen consumption rates of the fish, measured at night and during the day when inactive (i.e. only spontaneous activities and no specific behaviours occurred), provided estimates of standard and routine metabolic rates, respectively (abbreviated as SMR and RMR; Fry 1957; Beamish 1964; see Grantner & Taborsky, 1998). We carried out the first and the final measurements with empty experimental chambers to correct for microbial respiration. We measured body mass and standard length of the fish after each experimental session. When all experiments were finished we returned the families to their original tanks.

Recorded Behaviours

The behaviours recorded were tail quivering (a submissive behaviour); digging (carrying or pushing sand: a territory maintenance behaviour); and agonistic behaviour (serves territory defence, but also occurs among family members). We stimulated agonistic behaviour by exposing individual helpers and pair males and females to their mirror images. We put a mirror in front of the chamber during the flow-through period. Usually, the fish attacked its mirror image immediately. The mirror was left in this position as long as the fish reacted to its mirror image. We provoked digging in helpers by providing them with a shelter (a piece of a flowerpot, which had been sterilized to prevent microbial respiration) covered with sterilized sand within the experimental chamber. The fish started to dig to get access to the potential hiding place. For calculations of oxygen consumption rates we corrected the volume of the experimental chamber for the volume of sand and shelter. Helpers showed tail quivering when dominant family members approached the experimental chamber. For a detailed description of the measured behaviours see Taborsky (1982) and Grantner & Taborsky (1998). We recorded the durations of specific behaviours during each trial with a keyboard-operated, electronic event recorder.

Analysis of Metabolic Rates

Trials were used in analyses when only one of the three behaviours specified above occurred, and when this behaviour lasted for at least 30% of total trial time (total number of trials=75, $N=29$ individual fish). Since we found a positive linear correlation between metabolic rate and behaviour duration during an experiment (Grantner & Taborsky, 1998), metabolic rates were standardized to a behaviour duration of 50% of total trial time. We standardized to an occurrence of 50% because this was close to the average proportion of time the target behaviours were shown during the trials, that is, it minimized the increase of measurement errors by multiplication. To calculate estimates of RMR we used trials where only spontaneous activities occurred (=79 trials, $N=33$ fish). SMR was calculated from measurements at night (10 trials per fish, $N=32$ fish). For comparisons of oxygen consumption between different types of individuals during specific behaviours, we expressed oxygen consumption as multiples of RMR to eliminate the effect of interindividual variation of routine metabolism.

Behavioural Time–Energy Budgets

Time budgets of the members of 11 pairs, and of their helpers, were obtained from first and second generation descendants of a northern population (*N. brichardi* from Burundi) in the laboratory, from 1978 to 1981. One breeding pair and one to several helpers of 2–5 cm standard length were each kept in a 500-litre glass tank. Water chemistry was adapted to values provided from Lake Tanganyika by Degens et al. (1971). Water temperature

was kept constant between 26 and 28.8°C and the tank water was continuously filtered and aerated by air filters. The light:dark cycle was 13:11 h starting at 0800 hours, with 10–20 min twilight in between. The tank bottom was covered with a layer of quartz sand (1.5–4 cm high; 1 mm grain size), and for shelter we provided flowerpot halves, as well as opaque PVC sheets and clear Plexiglas sheets and tubes. The use of these types of structures and their arrangement in the tank provided an unobstructed view of the fish, regardless of their location.

We recorded all detectable behaviours, except comfort behaviours and pure locomotion, of focal animals (one or two at a time) for observation periods of 12 min each, three times a day (starting at approximately 1000, 1430 and 1900 hours). Recording was continuous so that both behavioural frequencies and durations could be analysed. These recordings were repeated each day during the egg stage of the breeding cycle (usually lasting for 3 days), on 2 days of the larval stage, on the second or third day after the fry became free swimming, and for a varying number of days between two breeding cycles. Each of these observations was preceded by a period of 3 min 'pre-recording time', during which the observed animals could become accustomed to the presence of the observer. Remote video checks revealed that after this period no influence of the presence of an observer on the behaviour of the fish was detectable (Taborsky 1982). The data of all different times of day were subsequently combined, as there were no significant differences in behavioural time budgets with regard to time of day. To obtain time budgets representing an average breeding cycle of 47 days, the data obtained at the different stages of the cycle were standardized to the time periods these stages lasted on average (egg phase: 3.5 days; larval phase: 5 days; free-swimming fry phase: 3.5 days; phase between two cycles: 35 days). For further details see Taborsky (1982). The behaviours considered for this study were: agonistic interactions among family members; submissive behaviour; cleaning and fanning of eggs; mouthing of larvae and free-swimming fry; substrate cleaning; digging; and carrying of snail shells or other particles.

We calculated how much a specific behaviour increased metabolic rate by subtracting RMR from the metabolic rate of fish showing that behaviour. The average increase in metabolic rate was converted to J/g per h (conversion factor: 13.565 J/mg oxygen consumed; from Elliott & Davison 1975). For establishing comprehensive energy budgets, we estimated metabolic rates of behaviours that had not been measured in this study either by using very similar behaviours that had been measured, or by applying values measured during periods of moderate activity involving several different behaviours (see below). Egg fanning resembles tail quivering, and removing snail shells and debris resembles digging very closely, so the respective estimates were used. We estimated the energy expended when cleaning eggs, larvae or substrate by applying 'general activity values'. These values were derived from trials in which one or more behaviours occurred for less than 30% of the measuring time, that is, when the fish were moderately active but showed a mixture of behaviours.

The time budgets of pair members and helpers (median/h) were integrated with the energy expenditures for specific behaviours. These were added to the energy expended for SMR during night and RMR during daytime, respectively. We calculated the energy expended during specific behaviours by pair members and helpers for an entire breeding cycle of average length (47 days).

All statistical tests were two-tailed.

RESULTS

Resting Metabolism

SMR and RMR of pair males and females and of helpers, respectively, increased linearly with body mass when plotted on a doubly logarithmic scale (Fig. 1; all data given of 'pair members' refer to pairs with helpers, unless stated otherwise). We tested for differences between these three groups, irrespective of the effect of mass on metabolic rate. There were no significant differences in SMR and RMR between the three groups (ANCOVA: for RMR: $F_{2,30}=0.46$, $N=8, 7, 19$; $P=0.64$; for SMR: $F_{2,29}=1.02$, $N=8, 8, 17$; $P=0.37$).

Energy Expenditure During Specific Behaviours

Agonistic behaviour raised the metabolic rates of pair males, pair females and helpers 4.40 ± 1.92 ($Z=2.37$, $N=7$, $P<0.01$), 3.78 ± 0.85 ($Z=2.20$, $N=6$, $P<0.02$) and 3.55 ± 1.08 ($Z=3.82$, $N=8$, $P<0.001$) times above RMR, respectively ($\bar{X} \pm SD$; multiples are based on individual RMR values; Wilcoxon signed-ranks tests; absolute Z values are given throughout). Differences in metabolic rates between the three social groups were not significant (Kruskal–Wallis ANOVA: $H_2=1.12$, $P>0.5$).

In helpers, submissive behaviour and digging raised RMR by 3.28 ± 1.48 ($Z=2.02$, $N=6$, $P<0.02$) and 6.05 ± 3.14 ($Z=2.20$, $N=6$, $P<0.02$) times, respectively ($\bar{X} \pm SD$; Wilcoxon signed-ranks tests). A comparison of the multiples of RMR of the three different behaviours measured in helpers revealed no significant differences (Kruskal–Wallis ANOVA: $H_2=2.66$, $P>0.2$).

Behavioural Time–Energy Budgets

The time pair members and helpers spent on specific behaviours during one breeding cycle was recalculated from Taborsky (1982). Male breeders mainly spent time in agonistic interactions, while they showed very little direct brood care and territory maintenance behaviours (Fig. 2). Females did most of the digging and egg care; however, the difference from helpers was significant only during the early egg stages (Wilcoxon signed-ranks tests: $Z=1.96$ – 2.29 depending on stage, $N=8$ – 10 , $P_s \leq 0.05$). Helpers showed significantly more egg care than male breeders did (Wilcoxon signed-ranks test: $Z=2.09$, $N=10$, $P<0.05$), and they spent less time in aggressive but more in submissive (tail-quivering) behaviours than the pair members did, in all phases of the breeding cycle (Wilcoxon signed-ranks tests: $Z=2.20$ – 2.50 depending on stage, $N=6$ – 11 , $P_s < 0.05$).

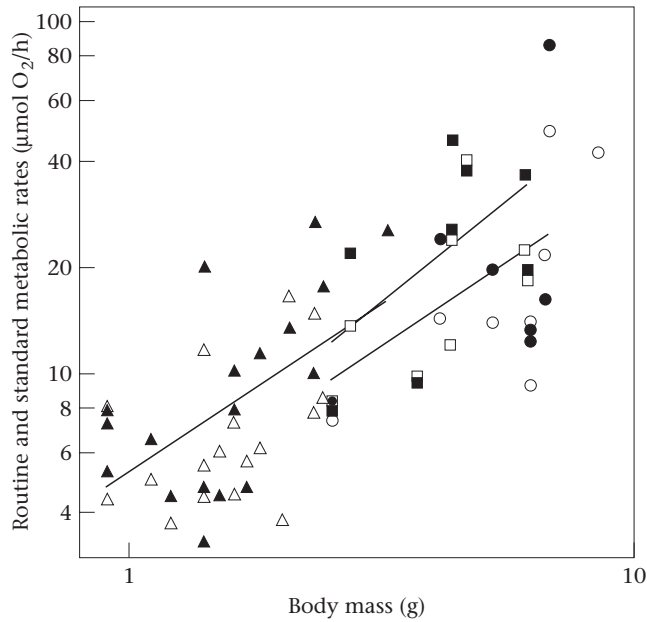


Figure 1. Routine (RMR; ●, ■, ▲) and standard (SMR; ○, □, △) metabolic rates of pair males (●, ○; $N=7,8$), pair females (■, □; $N=8,8$) and helpers (▲, △; $N=19,17$) in relation to body mass (M), plotted on logarithmic scales. Symbols represent average metabolic rates of individual fish. The regression lines indicate the linear relationship between body mass and RMR. Overall, the regressions were significant (both $P<0.001$; $\log \text{SMR}=0.65+0.86 \log M$, $r=0.79$; $\log \text{RMR}=0.75+0.86 \log M$, $r=0.70$). When separated for different types of individuals as shown in this figure, the regression was statistically significant only for males, and there were no significant differences between the three types of individuals (see text).

To compare the time and energy expenditure of pair males, pair females and helpers during the different stages of the breeding cycle, we combined the behaviours into three categories (Table 1). Social behaviours included agonistic and submissive behaviours; territory maintenance included substrate cleaning, digging and carrying; and direct brood care consisted of egg fanning and cleaning eggs, larvae and free-swimming fry. In addition to the differences mentioned above, it became evident that while eggs and larvae were present pair females spent significantly more time than their mates with both territory maintenance and direct brood care behaviours (Wilcoxon signed-ranks tests: $Z=2.11$ – 2.77 for egg and larval stages $N=17$ and 14 , $P_s<0.05$; seven pairs without helpers were included in this analysis). During the early egg stages, females also showed more aggression against helpers than pair males did (Wilcoxon signed-ranks test: $Z=1.99$, $N=10$, $P<0.05$).

In the next step, we integrated the energy expended on specific behaviours (Table 2) with the time budgets. In pair members and helpers, RMR and SMR accounted for $98.49 \pm 0.41\%$ ($\bar{X} \pm \text{SD}$) of the whole energy expenditure during a breeding cycle. Pair males, pair females and helpers devoted 1.5, 1.9 and 1.1% of total energy expenditure, respectively, to social, brood care and territory maintenance behaviours. Figure 3 illustrates how pair males and females and helpers partitioned their energy expenditure between specific behaviours. Males

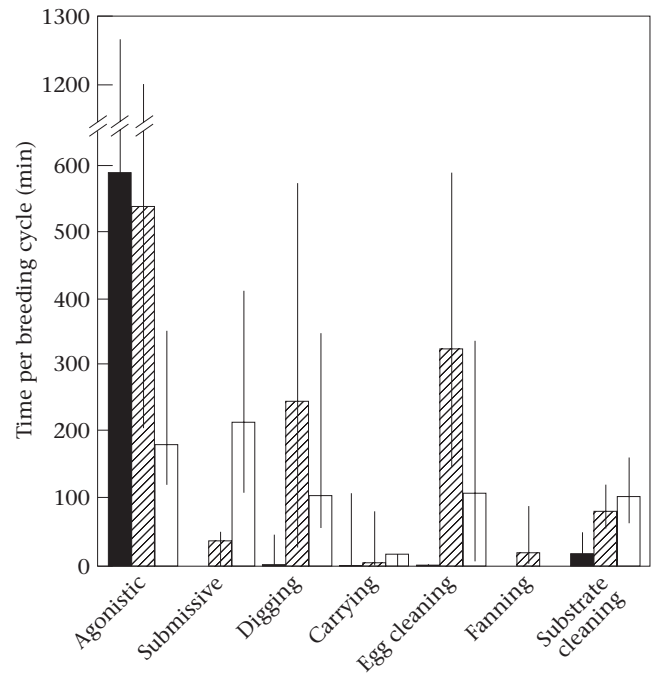


Figure 2. Time invested in specific behaviours during one breeding cycle by pair males (■), pair females (▨) and helpers (□). Bars are medians and interquartile ranges of agonistic behaviour, submissive behaviour, sand digging, carrying particles and snails, egg cleaning, egg fanning and substrate cleaning.

invested primarily in aggressive behaviour. The estimated energy expenditure of females contained a large proportion spent in aggression (64%), but also a large portion invested in territory maintenance and, compared with other family members, the greatest proportion of effort spent with direct brood care. The energy budget of helpers was dominated by the expenditure in submissive behaviour. Helpers spent much less energy in aggressive behaviour, which was mainly directed against other helpers, and their share of energy expenditure in territory maintenance behaviours was similar to that of females.

DISCUSSION

Energy Expenditure During Specific Behaviours

Agonistic, submissive and digging behaviours resulted in substantial metabolic increases in *N. pulcher*. Helpers and pair members expended between three and six times RMR on them. With regard to agonistic behaviour, the expenditures of pair members and helpers were similar. Here, agonistic behaviour included a variety of specific aggressive behaviours, ranging from moderate threat displays to overt attacks. Previous observations showed that pair members perform overt attacks such as ramming, curved attack, biting and mouth fighting more frequently than helpers do (Taborsky 1982). Because of their form and intensity, these behaviours appear to be energetically more costly than the more static displays such as head down display, opercula spreading or S-shaped bending and may therefore lead to higher energy expenditures for

Table 1. The relative shares of energy investment (%) of pair males, pair females and helpers of *N. pulcher* in social, territory maintenance and brood care behaviours during the different stages of the breeding cycle

	Stage			
	I	II	III	IV
Social behaviours				
Male	37.81	21.40	28.96	32.35
Female	41.82	31.58	33.15	52.52
Helper	20.37	47.02	37.9	15.13
Territory maintenance				
Male	—	10.25	1.39	3.48
Female	62.78	70.49	38.69	68.26
Helper	37.22	19.26	59.91	28.26
Direct brood care				
Male	—	0.54	0.42	—
Female	—	93.55	65.42	—
Helper	—	5.91	34.58	—

The breeding cycle was divided into four stages: (I) nonreproductive phase between two cycles; (II) egg phase; (III) larval phase; (IV) free-swimming fry phase (see Methods). Data represent average values divided into the following categories: male breeder; female breeder; and mean helper value within a family. Values within each behavioural category and each stage sum up to 100%.

pair members, when calculated on a more refined data base of behavioural energy budgets.

In helpers, the amount of energy expended when digging exceeded the expenditures resulting from agonistic and submissive behaviours nearly two-fold. However, this difference was not statistically significant.

Table 2. Estimates of energy expended (J/g per h) on specific social, territory maintenance and brood care behaviours by *N. pulcher*

Behavioural category	Pair males	Pair females	Helpers
Agonistic behaviour	3.056	3.497	2.755
Submissive behaviour	—	3.286	3.286
Digging	3.135	3.135	3.135
Carrying	3.135	3.135	3.135
Substrate cleaning	0.091	0.091	0.981
Egg cleaning	0.091	0.091	0.981
Egg fanning	—	3.286	—
Standard metabolism	1.470	1.926	1.985
Routine metabolism	2.027	2.48	2.724

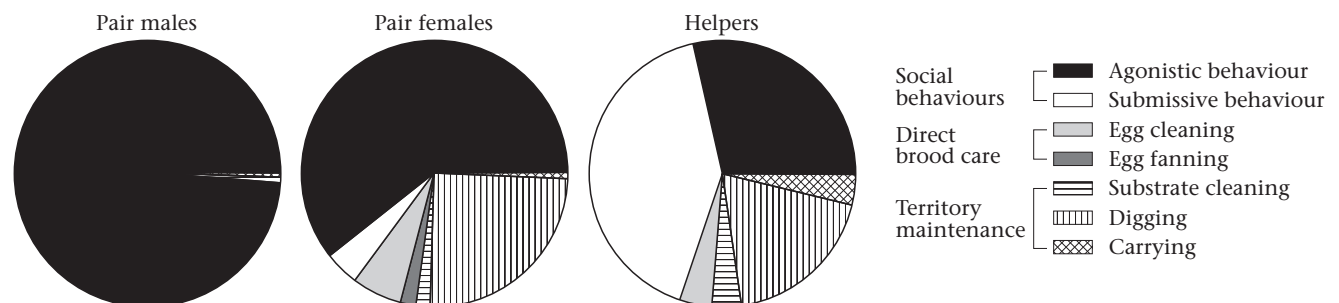
Data represent energy expenditures on top of routine metabolism (for calculations see Methods). Values given of standard and routine metabolism represent arithmetic means of all individuals measured of each category ($N=8,7$ males, $8,8$ females and $17,19$ helpers; SMR and RMR, respectively).

Exceptionally high metabolic costs were apparently associated with digging which involves the physical work of carrying a sand load for some distance, but our data suggest that agonistic and submissive behaviours had virtually similar metabolic costs.

Behavioural Time–Energy Budgets

In pair members and helpers, total behavioural energy expenditure appeared to be very little (1.5% on average) compared with resting metabolism which represented mainly the costs of body maintenance. The annual reproductive effort of fish has generally been estimated to be 10% of total energy input (Wootton 1985). This rough estimate includes the energy expenditures for gamete production, the development of secondary sexual characteristics, and reproductive behaviours. Only the latter was partly considered in this study. Unfortunately, there are no data available for a comparison of behavioural energy expenditures in other fish species.

The patterns of energy investment in specific behavioural categories by pair members and helpers showed

**Figure 3.** Energy expended on specific behaviours by pair males, pair females and helpers during a breeding cycle. Different patterns and/or shades of segments represent specific behaviours.

that, in the absence of predators and competitors for space, pair males invested almost exclusively in agonistic behaviour, which was targeted at females and helpers to maintain the dominance relationships within the family. The contribution of pair males to territory maintenance and direct brood care was extremely low, but peaked in the egg stage of the breeding cycle.

Pair females allocated nearly two-thirds of their energy spent on behaviour to intrafamily agonistic behaviour. Among all family members they contributed most to direct brood care, and they spent slightly more energetic effort than individual helpers on territory maintenance. On the behavioural level, the differential task sharing within families has been documented previously (Taborsky 1982, 1984; Limberger 1983; Taborsky et al. 1986). The investment of females in agonistic behaviour varied considerably with the different stages of the breeding cycle. Especially in the early egg stages, females showed high levels of agonistic behaviour towards their helpers. This may serve to reinforce the subordinate status of helpers to induce egg care behaviour and prevent egg cannibalism (von Siemens 1990).

At the same time, helpers must invest strongly in submissive behaviour. Submissive behaviour serves solely to maintain the subordinate social status of helpers within the family hierarchy, and is apparently important if helpers are to be tolerated in the territory (Taborsky 1985). Like brood care, territory defence and maintenance, submissive behaviour thereby serves as 'paying for staying' (Taborsky 1984, 1985). Our data suggest that submissive behaviour may lead to substantial energy costs for helpers. Generally, high costs are viewed as a prerequisite for the evolution of honest signals (Zahavi 1975; Grafen 1990). In *N. pulcher*, helpers accept these high costs of being tolerated for longer periods in a safe territory and in this way increase their chances of survival (see Taborsky 1984 for an extensive cost/benefit analysis of helpers of this species). Previous laboratory experiments have shown that helpers prefer to stay in their natal territory, even when given the opportunity to occupy a vacant territory and breed independently (Taborsky 1985).

We measured these time budgets under seminatural conditions in the laboratory. Only there was it possible to observe behaviour with that much detail and at all stages of the breeding cycle. Direct brood care behaviour in particular cannot be observed under natural conditions. Previous studies suggested that the behaviour and social system of these fish do not differ greatly between aquarium and field, at least for the aspects that can be directly compared. However, the energy investment in territory defence when potential competitors and predators are present needs to be considered in future studies, because here the fish were kept without competitors and predators. Additionally, the energy expended on swimming needs to be given some attention in future calculations of time-energy budgets.

Here we demonstrated that *N. pulcher* helpers incur increased energy expenditures as a result of their status and of their help. This expenditure probably constrains

the helpers' growth, in addition to the demonstrated effect of the submissive status of helpers on growth, and to the likely condition that helpers store reserves for future growth at the expense of present growth (Taborsky 1984). Future studies should try to unravel how much the growth patterns of *N. pulcher* helpers are shaped by each of these mechanisms.

Acknowledgments

We thank S. Balshine-Earn, A. Berglund, B. Kempnaers, T. Sato, B. Taborsky, H. Winkler and two anonymous referees for helpful comments on the manuscript, F. Bratter for technical support in the laboratory, H. Fuchs for help with the experiments, H. Forstner and M. Krotthammer from the University of Innsbruck and F. Schiemer, H. Keckeis and R. Paumann from the University of Vienna for providing a respirometer for parts of this study, and B. Kempnaers for help with statistics. This study was supported by the Fonds zur Förderung der Wissenschaftlichen Forschung, project No. P10916-BIO.

References

- Arnold, W. 1990. The evolution of marmot sociality: I. Why disperse late? *Behavioral Ecology and Sociobiology*, **27**, 229–237.
- Beamish, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. 2. Influence of weight and temperature on respiration of several species. *Canadian Journal of Zoology*, **42**, 177–188.
- Brown, J. L. 1987. *Helping and Communal Breeding in Birds: Ecology and Evolution*. Princeton, New Jersey: Princeton University Press.
- Degens, E. T., von Herzen, R. P. & Wong, H. K. 1971. Lake Tanganyika: water chemistry, sediments, geological structure. *Naturwissenschaften*, **58**, 229–241.
- Elliott, J. M. & Davison, W. 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia*, **19**, 195–201.
- Emlen, S. T. 1991. Evolution of cooperative breeding in birds and mammals. In: *Behavioural Ecology*. 3rd edn (Ed. by J. R. Krebs & N. B. Davies), pp. 301–337. Oxford: Blackwell Scientific Publications.
- Emlen, S. T., Reeve, H. K., Sherman, P. W., Wrege, P. H., Ratnieks, F. L. & Shellman-Reeve, J. 1991. Adaptive versus non-adaptive explanations of behavior: the case of alloparental helping. *American Naturalist*, **138**, 259–270.
- Forstner, H. 1983. An automated multiple-chamber intermittent-flow respirometer. In: *Polarographic Oxygen Sensors* (Ed. by E. Gnaiger & H. Forstner), pp. 111–126. Berlin: Springer Verlag.
- Fry, F. E. J. 1957. The aquatic respiration of fish. In: *The Physiology of Fishes* (Ed. by M. E. Brown), pp. 1–64. New York: Croom Helm.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology*, **144**, 517–546.
- Grantner, A. & Taborsky, M. 1998. The metabolic rates associated with resting, and with the performance of agonistic, submissive and digging behaviours in the cichlid fish *Neolamprologus pulcher* (Pisces: Cichlidae). *Journal of Comparative Physiology B*, **168**, 427–433.
- Heinsohn, R. G. & Cockburn, A. 1994. Helping is costly to young birds in cooperatively breeding white-winged crows. *Proceedings of the Royal Society of London, Series B*, **256**, 293–298.
- Jobling, M. 1981. The influence of feeding on the metabolic rate of fishes: a short review. *Journal of Fish Biology*, **18**, 385–400.

- Komdeur, J.** 1996. Influence of helping and breeding experience on reproductive performance in the Seychelle's warbler: a translocation experiment. *Behavioral Ecology*, **7**, 326–333.
- Konings, A.** 1988. *Tanganyika Cichlids*. Zevenhuizen, The Netherlands: Verduijn Cichlids & Lake Fish Movies.
- Limberger, D.** 1983. Pairs and harems in a cichlid fish, *Lamprologus brichardi*. *Zeitschrift für Tierpsychologie*, **62**, 115–144.
- Poll, M.** 1974. Contribution à la faune ichthyologique du lac Tanganyika, d'après les récoltes de P. Brichard. *Revue Zoologique africaine*, **88**, 99–110.
- Reyer, H. U.** 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher (*Ceryle rudis*). *Animal Behaviour*, **32**, 1163–1178.
- von Siemens, M.** 1990. Broodcare or egg cannibalism by parents and helpers in *Lamprologus brichardi* (Poll 1986) (Pisces: Cichlidae): a study on behavioural mechanisms. *Ethology*, **84**, 60–80.
- Stacey, P. B. & Koenig, W. D.** 1990. *Cooperative Breeding in Birds. Long-term Studies of Ecology and Behavior*. Cambridge: Cambridge University Press.
- Taborsky, M.** 1982. Brutpflegehelfer beim Cichliden *Lamprologus brichardi*, Poll (1974): eine Kosten/Nutzen-Analyse. PhD. thesis, Universität Wien.
- Taborsky, M.** 1984. Broodcare helpers in the cichlid fish *Lamprologus brichardi*: their costs and benefits. *Animal Behaviour*, **32**, 1236–1252.
- Taborsky, M.** 1985. Breeder–helper conflict in a cichlid fish with broodcare helpers: an experimental analysis. *Behaviour*, **95**, 45–75.
- Taborsky, M.** 1994. Sneakers, satellites, and helpers: parasitic and cooperative behavior in fish reproduction. *Advances in the Study of Behavior*, **23**, 1–100.
- Taborsky, M. & Limberger, D.** 1981. Helpers in fish. *Behavioral Ecology and Sociobiology*, **8**, 143–145.
- Taborsky, M., Hert, E., von Siemens, M. & Stoerig, P.** 1986. Social behaviour of *Lamprologus* species: functions and mechanisms. *Annales de Musée Royal de l'Afrique Centrale, Sciences Zoologiques*, **251**, 7–11.
- Trewavas, E. & Poll, M.** 1952. Three new species and two new subspecies of the genus *Lamprologus*, cichlid fishes of Lake Tanganyika. *Bulletin de l'Institut royal des sciences naturelles de Belgique XXVIII*, **50**, 1–16.
- Wolfenden, G. E. & Fitzpatrick, J. W.** 1984. *The Florida Scrub Jay: a Demography of a Cooperative-breeding Bird*. Princeton, New Jersey: Princeton University Press.
- Wootton, R. J.** 1985. Energetics of reproduction. In: *Fish Energetics: New Perspectives* (Ed. by P. Tytler & P. Calow), pp. 231–254. New York: Croom Helm.
- Zahavi, A.** 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology*, **53**, 205–214.