BROODCARE HELPERS IN THE CICHLID FISH *LAMPROLOGUS BRICHARDI*: THEIR COSTS AND BENEFITS

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Abstract. 'Helping' in birds and mammals involves seemingly altruistic behaviour. In the cichlid fish *Lamprologus birchardi* helpers are usually young of former broods staying in their parents' territories and participating in all kinds of parental duties (broodcare, territory maintenance and defence). The discovery of helpers in fish offered the chance of attempting an extensive analysis of potential costs and benefits influencing the evolution of helpers in a vertebrate. Three factors proved to be of major importance in the cost–benefit analysis of helping as opposed to leaving for family-independent non-reproductive aggregations. Due to investment and to their rank within a family's hierarchy, helpers grow at a slower rate than non-helpers. This cost is compensated for by (i) a lower mortality risk to helpers caused by their access to a defended shelter and by protection afforded by bigger family members, and (ii) a positive contribution by helpers to the future reproductive success of their parents: females with helpers produce bigger clutches and consequently more free-swimming fry (=siblings). Other variables, such as the helpers' influence on the relative breeding success of their parents, broodcare experience through helping, the chances of territory take-over, parasitism of parents' reproduction and cannibalism are of minor importance. Similar social organizations in other fish are discussed with respect to their ecology and are compared with cooperatively breeding birds and mammals.

In many vertebrates young stay with their parents for some time after broodcare has ceased (e.g. Kalas 1975; Wilson 1975; Ward & Wyman 1977; Taborsky & Limberger 1981; Brown, in press). The additional care of parental broods by young of former broods has been described for some 150 bird species and 25 different mammals (Emlen 1982a); of the cold-blooded vertebrates, it has been reported for six species of the cichlid genera *Julidochromis* and *Lamprologus* (Taborsky & Limberger 1981). In *L. brichardi*, a species with pairs and harems (Limberger 1983), young of both sexes stay for a prolonged time in their natal territory and share in all kinds of investment in territory and subsequent broods. Tasks are shared unequally among family members, depending on predation pressure, competition and the size of participants (Taborsky 1982).

Individuals sharing in parental duties are usually called 'helpers', an operational definition based merely on participation in investment and not necessarily presuming a benefit for parents and/or brood. The evolution of helping is of special interest, as it involves seemingly altruistic behaviour. A behaviour with a genetic basis should not decrease the fitness of the actor, otherwise, far from spreading, its gene coding would disappear from the gene pool of a population by natural selection. What benefits to

helpers could offset any implied costs of investment? ('Costs' and 'benefits' as used in this paper refer to a reduction or increase of inclusive fitness; see e.g. West-Eberhard 1975.) Many recent studies on birds and mammals have centred on this question (e.g. Woolfenden 1975; Reyer 1980; Emlen 1981), but in higher vertebrates it is hard to measure fitness-related costs and benefits, especially in the wild. Birds and mammals have long generation times, intervals between broods are usually long and home ranges are large and difficult to survey. Hence only certain parts of the cost–benefit ratio of helpers have been investigated so far (see Emlen 1978, 1982b; Brown, in press). Small cichlids, with fast brood succession, easy handling and small home ranges are much easier to observe than birds or mammals. The discovery of helpers in fish therefore offers the chance of studying all those theoretically predictable variables that possibly influence the fitness of helpers and parents. Relative effects on some of the fitness parameters can even be measured in the laboratory under easily controlled conditions.

This paper deals with the costs and benefits to *L. brichardi* helpers of staying in the parental territory and investing in brood care, territory maintenance and defence. Helpers share in cleaning of eggs, larvae and fry; removing sand

from the breeding hole; removing snails; defending the parental territory and breeding hole from conspecifics and from interspecific competitors and predators; and occasionally fanning the eggs and larvae. As a measure of helpers' costs, their growth rates were compared with those of family-independent individuals following an alternative mode of life. The helpers' potential benefits investigated were: rearing close kin, getting experience in broodcare, increasing the chance of territory take-over, better survival chances in a protected territory, parasitism of parents' reproduction and cannibalism of eggs, larvae or small fry. The range of possible benefits extends from those accruing to both helpers and breeders to those favouring helpers at the expense of the breeders they stay with (social parasitism).

Subjects

L. brichardi is a substrate breeder attaining a standard length (SL) of a maximum 6.5 cm in the field. The species is distributed along the rocky edges of Lake Tanganyika, from 3 to 45 m deep (Brichard 1978, personal observation). 'Islands' of rock occur between vast stretches of sand and gravel, so gene flow between populations is presumably low: there is no planktonic stage, and, even when in an aggregation, young and adults are confined to rocky areas and remain localized (unpublished data on marked individuals).

The sexes appear to be similar, but within pairs males are usually bigger than their partners ($P < 0.01$, $N = 24$; sign test). At 4–4.5 cm SL the fish are sexually mature. Pairs defend a territory of about 25-cm radius around a hole or cleft used as a hiding place and for breeding. Infrequently a male territory contains two female territories (Limberger 1983). Eggs and larvae are tended in the breeding hole. Most young stay in their natal territory for 2–3 subsequent breeding cycles, which presumably occur every 2–4 months (Taborsky 1982). Fry start to nip and clean around eggs when they are about 40 days old and approximately 1 cm in length. The majority of young leaves when about 4–5.5 cm, at an assumed age of 1 year or more. These former helpers join permanent aggregations consisting of a few up to several hundred fish, above and around the family territories. A fish of between 3 and 5.5 cm in length can still be a helper in a territory, or live family-independent within a localized aggregation that consists mainly of sexually mature but non-reproducing

individuals without shelter sites of their own. Sexing of 62 aggregation members in the field revealed a skewed sex ratio within aggregations (40 males : 22 females, $P < 0.05$; binomial test). Family members larger than about 3.5 cm visit these aggregations regularly for plankton feeding.

A short description of all recorded behaviour patterns is given by Taborsky (1982), and a complete ethogram by Kalas (1975). Of special interest for the present paper are all elements of defence, territory maintenance and brood care.

(1) Suppressed defence. This comprises a head down display (position lateral to opponent, maximum spread of fins), a frontal approach (fast movement against opponent stopped abruptly, opercula spread), tailbeat, S-bending (only intraspecific), bumping against (mouth impact on another fish, like a suppressed form of ramming; mainly shown between partners), and head jerking (accompanying the most intense social interactions).

(2) Overt attack. This includes ramming, curved attack (rapid curved approach, hit at apex and rapid retreat), biting and mouth fighting.

(3) Territory maintenance. This consists of digging (sand removal from the shelter area: vital for eggs, larvae and fry in sand-exposed shelter sites; see Taborsky & Limberger 1981), substrate cleaning (sucking at the substrate, mainly in holes or shelters, at potential spawning sites and around eggs and larvae) and removal of snails and particles (snails are mostly removed from the shelter area).

(4) Direct broodcare. This includes cleaning of eggs and larvae, mouthing of larvae and fry and fanning.

General Methods

Most fish observed quantitatively in laboratory and field were measured (SL), weighed (laboratory: to the nearest 0.01 g; field: to 0.1 g) and marked (mostly by injection of alcian blue). Eggs were counted shortly after being laid, fry on the first day of free-swimming and at regular intervals thereafter. (The mean error in counting fry was a 7% shortfall. This was assessed by catching fry immediately after counting.) Sex was determined by observing reproductive behaviour: males rarely share in direct broodcare. A number of control dissections showed this method to be reliable (details in Taborsky 1982). Analyses were done using non-parametric statistics (Siegel 1956); values of P given in this paper are two-tailed.

Field Observations

Observations were made near Magara, Burundi, mainly at a depth of 3–10 m; over 200 fish were weighed and sexed, and over 600 measured (including size estimates of small young). All families within the main observation area (about 1500 m²) and all aggregations in a part of it (about 450 m²) were checked for their composition (63 families, 4 aggregations; mean recording period = 1 month). Territories were mapped, and behaviour and average position of all members ($N = 131$) of 15 families and of 12 fish in aggregations were recorded (Limberger 1982; Taborsky 1982).

Laboratory Experiments

L. brichardi were kept in groups in 100–500-litre tanks, with isolated individuals in 11–33-litre tanks. Experimental tanks were 500 litre, unless otherwise stated. Bottoms were covered with 1 mm grained gravel. In storage tanks, lava stones served as shelters, in experimental tanks only flowerpot halves, PVC-plates and differently-shaped pieces of Plexiglas were used to allow broodcare observation. Behaviour was recorded on paper tape, three times per day for each individual for 12 min each (evenly distributed with regard to time of day). This was done daily while eggs were present, twice during the larval stage, once when fry entered the free-swimming stage and occasionally between broods. All quantitative observations of behaviour were preceded by 3 min to allow fish to habituate to the observer. Video recordings showed this time to be sufficient. For details of water temperature and quality, artificial light conditions (all held constant) and filtering see Taborsky (1982).

1. The Cost of Investment and Effects of Rank

Helpers share considerably in brood and territory care, defence against competitors for holes and against predators of eggs and fry. They also participate in interactions within the family, showing submissive behaviour (tail quivering), in particular, towards the breeding pair and other dominant family members, and aggressive behaviour to subordinates. None of these behaviours are performed by non-helpers (aggregation members) of the same size, except social interactions of low intensity. We thus predicted negative effects on the energy budgets of helpers. A reduced growth rate of helpers compared with non-family controls would prove higher energy costs, unless helpers could store reserves (fat, muscle proteins, etc.) to compensate

for their growth deficit when leaving their home territory. The growth rates of helpers were compared with those of two types of controls: (i) territorial controls, which had exclusive access to the substrate (= shelters and breeding holes), and (ii) aggregation members, which roamed freely in a tank without any shelter or breeding sites. (The mortality risk of helpers versus family-independents is treated in a later section; see Protection, p 1246.)

Methods

Helpers versus territorial controls. One third of a 500-litre tank was cut off by an opaque PVC-plate. A pair and 1–3 helpers (size range 2.5–5 cm) were placed in the larger compartment, and 2–6 controls of exactly the same size as the helpers were placed in the smaller compartment (= territorial controls); the fish biomass per volume was initially rather similar in both compartments. Fish from storage tanks were randomly chosen as helpers or controls. This is an appropriate procedure, because usually a young fish behaves as a helper whenever it is in the territory of a breeding pair. There was no indication that young of natural or experimentally combined families behaved differently, provided they were fully accepted (this was achieved by introducing young before adults and by a reasonable size difference). Water quality, substrate, light conditions, etc., were identical for helpers and controls. Food was offered in super-abundance (*Tubifex* or dry food at noon daily); this did not impair water quality, as tanks were large and fish density very low. Dominance status of the fish was checked regularly. The data on growth from the longest interval without change in dominance rank, on average 93 days, were used for analyses. Twenty-seven replicates produced data suitable for statistical analysis. Comparisons between helpers and controls ($N = 121$ individuals) were made for each of these independent replicates and differences were tested by the Wilcoxon matched-pairs signed-ranks test.

Helpers versus aggregation members. Twelve fish of helper size (2.4–4.2 cm) were put into each of two 500-litre tanks together with two adult males. All conditions were identical to the set-up with helpers, except that no structured substrate was provided for shelter. In these tanks the fish behaved like aggregation members in the field. Data from 18 fish could be used for statistical analysis; time between first and second measurement of size was 96 days. Comparisons

with helpers' growth rates were made using the Mann–Whitney U-test.

Results and Discussion

Helpers grow more slowly than family-independent fish of equal size: the mean growth rates of young (independent of type and status) are listed in Table I for four different size ranges. The relative growth rates of helpers and territorial controls are shown in Fig. 1. Helpers grew more slowly than controls of equal size ($P < 0.001$, $N = 54$, 16 tanks; the difference is also significant on a per-tank basis). The reduced growth of helpers is especially remarkable as (i) territorial controls were housed in the smaller compartments and usually growth correlates positively with tank size, and (ii) many controls produced and reared young of their own, while helpers only helped to rear parental broods. Figure 2 shows the growth rates of helpers and aggregation members. Here, too, helpers grew more slowly ($P < 0.05$, $N = 35$, 18); at the start of the experiment the sizes of helpers ($\bar{x} = 3.47$ cm) and aggregation members ($\bar{x} = 3.27$ cm) were well matched. Aggregation members also grew faster than territorial controls ($P < 0.05$, $N = 18$, 30; only territorials whose size at the start of the experiment was within the range of aggregation members were used; $\bar{x} = 3.46$). Reduced growth of helpers and territorial controls as opposed to aggregation members is presumably due to differential investment.

Hypotheses. Why do helpers grow more slowly than territorial controls? Within groups of territorial controls the most dominant fish grew faster than its companions ($P < 0.005$, $N = 26$; Wilcoxon test), although, being the largest initially, it was predicted that its growth rate should be slower (Table I). The dominant helper, however, grew more slowly than submissive ones ($P < 0.05$, $N = 12$; Wilcoxon test), while helpers of beta rank tended to grow fastest (see Taborsky 1982). Territorial controls also grew faster than

helpers, despite the fact that many of them even bred on their own, i.e. produced gametes and had to do all the broodcare by themselves. Two hypotheses may be postulated to explain these results.

(1) The determining factor for growth, besides investment, is an individual's rank within a hierarchy. This hypothesis assumes that growth is more affected by rank in dominant than in other helpers, as dominants are more often attacked by the breeding pair and show most submissive behaviour.

(2) Helpers actually delay growth so as to be tolerated for as long as possible in their home territory. Their chance of being expelled rises with size (Taborsky, in preparation); if they accumulated reserves (e.g. fat) to speed up

growth later when they leave the territory, helpers might be able to reduce their time as aggregation members.

A test. The above hypotheses result in different predictions: in the first hypothesis, helpers should weigh as much as or less than territorial controls (in relation to size); in the second they should be heavier. Figure 3 shows the weight/size ratios of helpers versus the different types of control. Helpers and controls were matched to eliminate different size effects (see Table I). Each individual occurs only once in each graph. Helpers weighed less than territorial controls ($P < 0.05$, $N = 24$; Wilcoxon test). There was no difference from ostracized controls ($N = 28$); these were fish in helper or control compartments that had been expelled from a territory, cornered somewhere below surface and confined in their movements. They had less access to food than helpers and territorial controls, e.g. observations shortly after *Tubifex* was given showed that expelled controls fed less ($P < 0.001$, $N = 10$, 9 and 10, 7; U-test). So the second hypothesis cannot account for the differences in growth of helpers and territorial controls: delayed growth is not part of a helper's strategy. Apart from investment, the growth of helpers is limited to various degrees by dominance relations, and depends on their rank positions.

Growth in aggregations. Helpers and territorial controls were heavier than aggregation members ($P < 0.01$, $N = 16$ both cases; Wilcoxon test). Aggregation members grew the fastest, but were the lightest relative to their size. So the aggregation phase is a growth phase: in the field each former helper goes through this phase until it is big enough to defend a territory of its own (Taborsky 1982).

2. The Benefits of Rearing Close Kin
Helpers and their beneficiaries, i.e. eggs, larvae, and small fry, are closely related (Taborsky & Limberger 1981). The tendency to help the parents in broodcare and defence could therefore spread by kin selection in the population if it resulted in a raised survival rate of close kin or if parents could increase their egg production on a short- or long-term basis (e.g. by growing faster).

Methods
The influence of helping on parents and their progeny, without interference of competitors or predators, was measured in the same experimental situation as described in section 1. As

Table I. Growth Rates of Young, Irrespective of their Status

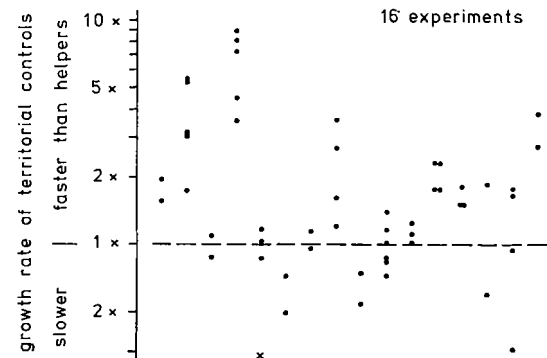| Size class | Daily increment (mean±SD) in: | | N |
	SL (mm)	Weight (g)	
2–2.9 cm	0.155 ± 0.041	0.0117 ± 0.0042	18
3–3.9 cm	0.132 ± 0.039	0.0162 ± 0.0051	40
4–4.9 cm	0.084 ± 0.044	0.0177 ± 0.0128	46
5–5.9 cm	0.049 ± 0.031	0.0166 ± 0.0109	23

SL: Standard length.

Fig. 1. Growth (increase in SL) of controls relative to helpers, compared within each of 16 experiments (abscissa). The cross in experiment 5 refers to one control that did not grow in the test interval. The growth rate of helpers was 0.111 ± 0.048 mm/day (mean±SD).
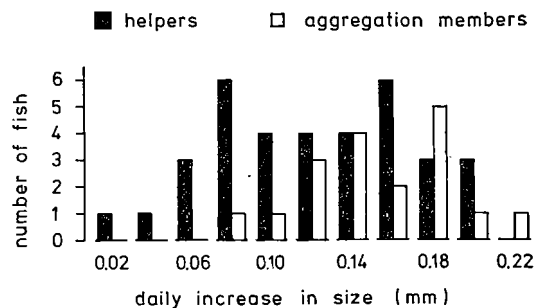

Fig. 2. Frequency distributions of growth rates (increase in SL) of helpers and aggregation members of initially equal size. Daily increase in size is divided into size classes of 0.02 mm; the upper limits of alternate size classes are given.
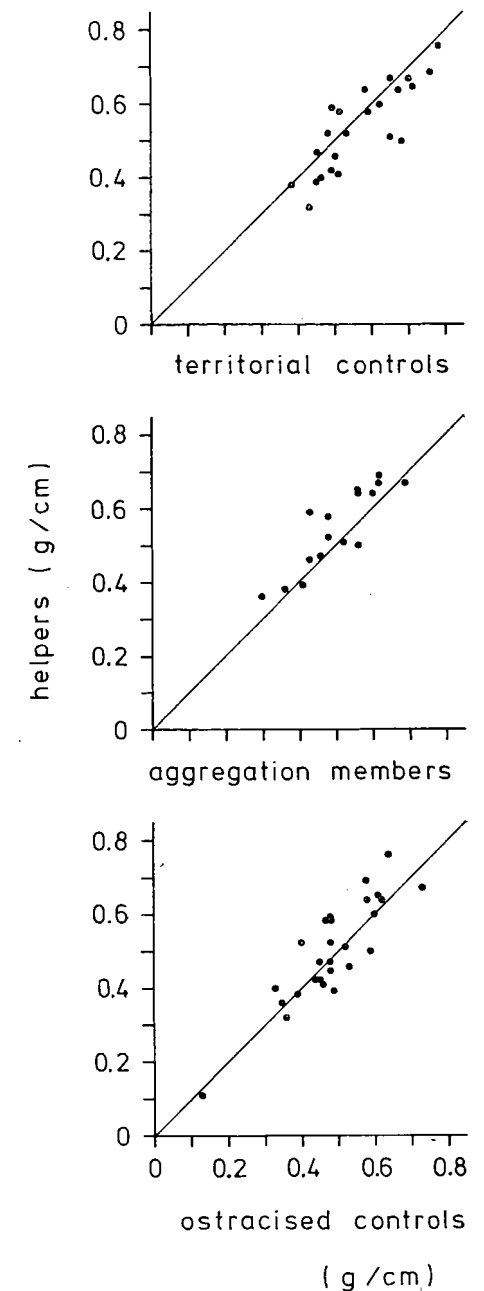

Fig. 3. Weight/size ratios of helpers compared with three types of controls. Each dot represents one helper and the control best matching in size at the start of the registration (size difference <3 mm; if several controls matched equally well, their growth rates were averaged). The diagonal separates controls lighter than helpers (above) from those heavier.

controls, pairs without helpers were put into compartments identical to those for pairs with helpers. Pairs were randomly assigned as experimentals or controls. In some experiments small helper fry were present, nipping at and around eggs. They were 40–100 days old and 1–2 cm in size. These helper fry were treated as an extra class, as it was questionable whether they would have any effect on breeders' reproductive success comparable with that of true helpers (defined in this study as fish above 2.5 cm SL).

Various parameters were recorded from 170 broods of 60 different females. Comparisons were made using the U-test. Four types of families were compared: (a) pairs without any helpers; (b) pairs with 1–3 helpers (>2.5 cm); (c) pairs with helper fry (various numbers); and (d) pairs with helpers and helper fry.

In a second experiment the effect of helpers on parental reproductive success was tested in a 9-m² circular tank (~8000 litres) in the presence of predators and competitors. Eighteen females, 18 males and 35 potential helpers were kept with 43 individuals of three different species, which had been observed to be the main daylight predators and competitors for holes and crevices at our observation site in the field (for details see Taborsky 1982).

Results and Discussion

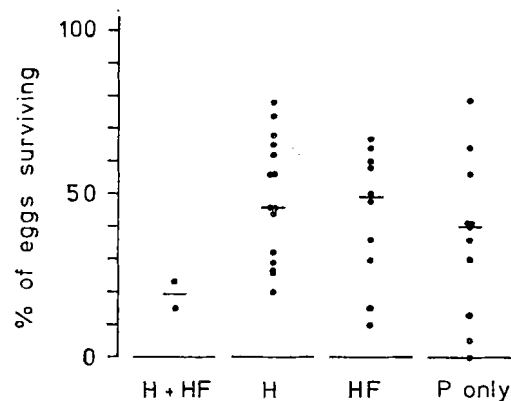Helpers have no effect on egg/larvae survival. Figure 4 shows the mean percentage of spawned

Fig. 4. Relative breeding success of pairs (P) with or without helpers (H) and helper fry (HF), expressed in survival rates to the day of free swimming. Each dot represents the mean of all broods an individual female had in the corresponding category. Dashes represent medians.

eggs surviving to the free-swimming stage (about day 10). The broods originate from 38 females in experiments without predators. There was no difference between females with or without helpers or helper fry. Sixteen females each raised two or three broods with and without helpers alternately. In 11 cases the broods with helpers were more successful, in five cases those without helpers were more successful. Broods with helpers seemed to be slightly more successful, as shown in Fig. 4, but this trend is not significant and even decreased with the increasing age of fry: survival to day 20 was more equal between the test groups than was survival to the first day of free-swimming.

Do females with helpers save investment? Females spent less time in territory maintenance when they had helpers (Taborsky 1982). By saving time and energy expenditure females with helpers might (a) reduce their intervals between broods, (b) produce more eggs and/or (c) grow faster.

(a) Helpers have no effect on brood intervals. Brood intervals were divided into those following successful broods and those following broods that failed to produce free-swimming fry. Again, means for females were compared for all four test groups. No differences were detected. The same is true for a comparison of brood intervals for individual females belonging to different test groups (with or without helpers) in alternate broods.

(b) Females with helpers produce more eggs. Egg numbers of 65 broods with or without helpers and helper fry are shown in Fig. 5. In experiments with helpers clutches were bigger (P<0.05, N = 31, 12). Females also produced more eggs in experiments with helper fry (P<0.05, N = 29, 12), and with helpers plus helper fry (P<0.01, N = 7, 12). This last result may have been influenced however by the size of the females: the test group with helpers and helper fry contained bigger females (x̄ = 6.2 cm) than the control group without helpers (x̄ = 5.7 cm). But females with helper fry only (x̄ = 5.7 cm) and females with helpers only (x̄ = 5.8 cm) were only as big as the control females without helpers. No difference was found in clutch sizes of females with either helper-type.

There was also a slight tendency for more eggs to survive when helpers were present. Absolute breeding success is a score which combines both measures. Females with helpers and/or helper fry had on average more free-swimming fry than females without any helpers. This difference was

significant when all females with helpers of any kind were combined (Fig. 6; P≤0.05, N = 27, 8). Unsuccessful broods, i.e. in which no free-swimming young were produced, were excluded from analysis. Many of the early unsuccessful broods were not fertilized, so failure often had nothing to do with broodcare. I want to stress that the difference in breeding success between pairs with and without helpers appeared even in a situation with superabundant food and excellent, constant water quality. Field condi-
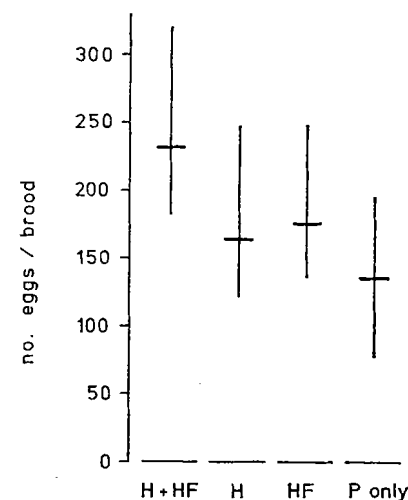

Fig. 5. Median clutch sizes of females with or without helpers (H) and helper fry (HF). Vertical lines represent interquartile ranges.
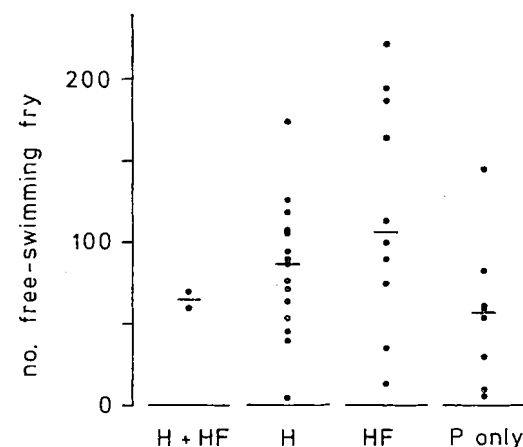

Fig. 6. Absolute breeding success of pairs (P) with or without helpers (H) and helper fry (HF) on day of free swimming. Symbols as in Fig. 4.

tions deviating from this experimental situation should only enhance the difference further.

(c) Helpers do not influence the growth of parents. By growing faster parents might ultimately produce bigger or better clutches and/or afford better protection for their eggs and young. Growth rates of 56 individuals (28 females and 28 males) were analysed. Data were divided into five categories depending on the situation of the parents in the interval between two consecutive size measurements: (1) without broods; (2) with broods plus helpers; (3) with broods plus helper fry; (4) with broods plus helpers and helper fry; (5) with broods without helpers. As in the young (see Table I), growth rates of breeding females and males were dependent on their size (females: r = −0.517, N = 45, P<0.001; males: r = −0.508, N = 41, P<0.001). For a statistical analysis, therefore, fish from the different categories were paired according to size and tested using the Wilcoxon test. In all, 45 female growth intervals and 43 male intervals were compared. An individual was included only once per category. There was no difference between the compared groups in either size or weight (Fig. 7). Also when the above categories were paired for the most similar egg number/day there was no difference in growth between parents with or without helpers (size and weight). The weight/size ratio at the end of the experiment was also analysed for the above categories; there was no difference here either. Female weight increment correlated negatively with the number of eggs produced in the respective interval (standardized for eggs/day; r = −0.348, N = 32; P = 0.05).

The experiment with predators and competitors. Eighty-five broods from 17 females were recorded in this experiment, but 70% of these failed to produce free-swimming young. Survival rates of eggs, larvae and fry did not differ for parents with or without helpers, nor did brood intervals, clutch sizes or parental growth. Because of excessive predation and a peculiar behaviour shown by some females at the onset of artificial dusk (see Taborsky 1982) most eggs disappeared on the day of spawning; I assume that this was the reason why females did not save energy by having a broodcare helper.

As in the previous experiment, there was a significant negative correlation between growth of females and number of eggs produced (size: P<0.05, N = 18; weight: P<0.01, N = 17; Spearman rank correlation coefficient). This suggests that females were limited by egg

production, even in the aquarium and with superabundant food.

Variables influencing breeding success. Eggs and larvae were cleaned more extensively when helpers were present. Nevertheless the percentage of eggs surviving to the free-swimming stage did not differ between families with and without helpers (relative breeding success). The effect of the quantity of direct broodcare on

egg/larvae survival was tested with two multivariate analyses as were their inter-relations with 12 other variables, all of which were potentially connected with broodcare and/or breeding success (see Taborsky 1982). Here I only want to point out three important results.

(a) No relationship was found between the amount of broodcare and the relative breeding success of a clutch.

(b) The amount of broodcare by females and helpers increased with clutch size.

(c) While brood succession within the experiments was positively correlated with clutch size (presumably through female growth), it was negatively correlated with relative breeding success (presumably through a changing number of additional subordinates in the tank; see Taborsky 1982).

Two conclusions may be drawn from these results.

(i) The fact that relative breeding success did not differ whether females had helpers or not might be due to the excellent conditions in the aquarium. In the natural situation the amount of broodcare would be expected to increase the number of surviving eggs and larvae, especially as females and helpers respond to bigger clutches with an increase in broodcare.

(ii) The fact that brood succession is positively related to the number of eggs produced, but negatively related to the proportion of eggs and larvae surviving, is presumably one reason why the influence of helpers on absolute breeding success was not as strongly pronounced as their influence on female clutch size.

Field data. As mentioned already, pair members and large helpers regularly visit the aggregation next to their territory. In the field, females spent a mean of 38.5% of their time outside their territory (25-cm radius around the shelter), males 60.1% and helpers larger than 4.5 cm SL 61.5%. Pair members and large helpers did not alternate their periods in the territory: for a mean of 82.5% of the time (SD = 11.2, $N = 19$) at least one of them was in the territory. This percentage of time the territory was guarded by an adult (= pair member or adult helper) was approximately the same whether families had a large helper or not. But in families without large helpers pair members spent more time in the territory ($P < 0.05$, $N = 8$, 11; U-test). As most feeding is done in aggregations, pair members without large helpers presumably have less time for feeding.
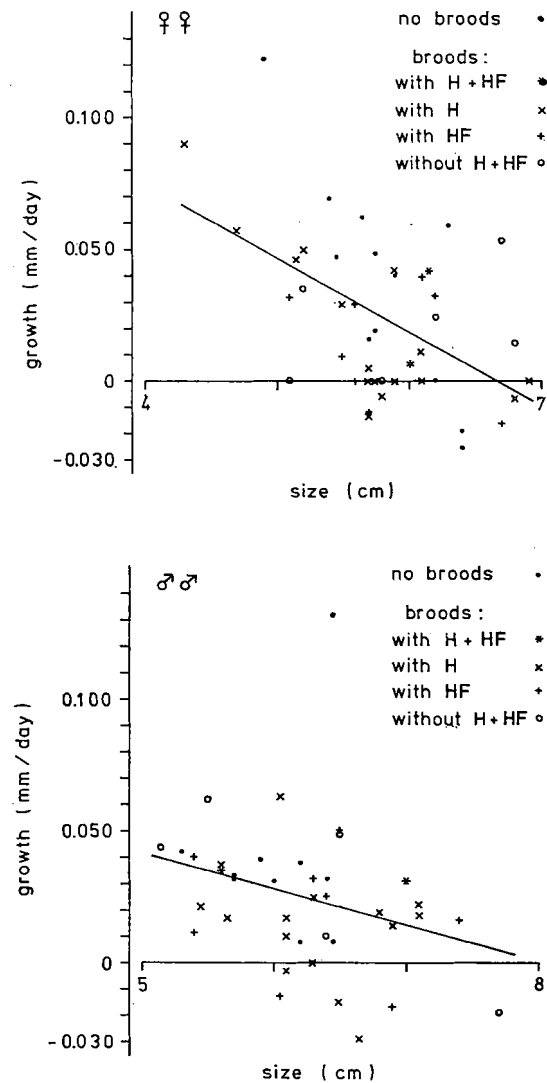
Fig. 7. Growth of females (above) and males (below) belonging to five different categories depending on their size. Values below the abscissa presumably result from measurement errors. H = helpers, HF = helper fry.
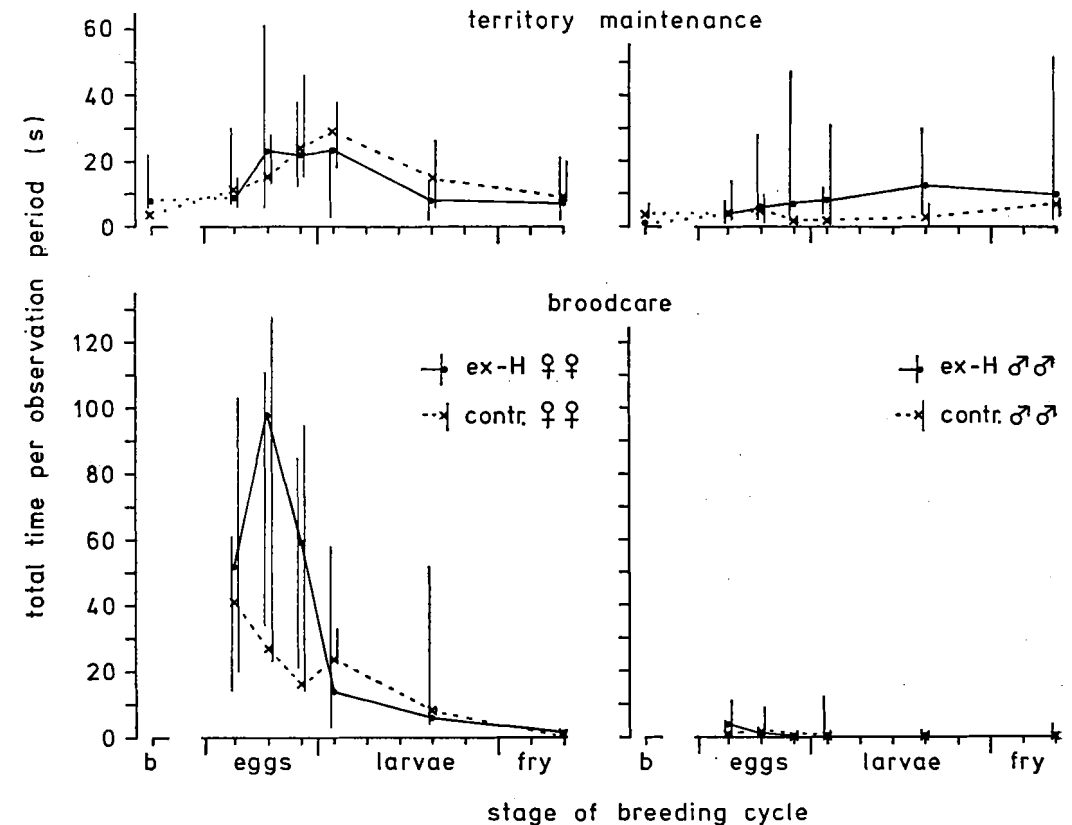
3. Broodcare Experience

By learning from parents and by increasing their own skill, helpers could profit from their experience when rearing their first own broods. Several types of experience may be important: (a) economical investment in broodcare and territory maintenance (to do as little as necessary); (b) effective allocation of time to different behaviours (e.g. direct broodcare, digging) within the breeding cycle; and (c) improved quality of direct and indirect broodcare (e.g. cleaning of eggs, fanning, removing snails). Some combination of these improvements might also affect former helpers' growth rates.

Methods

The first broods of former helpers and of same-size naive controls were compared. Former helpers (female or male) and controls were kept with inexperienced partners in compartments consisting of one third of a 500-litre tank. Conditions were held constant, as in the experiments described above. Behaviour was recorded during the first one to three brood cycles, statistical analyses were done using the U-test.

Results and Discussion

The quantity of broodcare. Former helpers and naive controls hardly differ in the quantity of care given to their own first broods. Time spent on the different duties of broodcare and territory maintenance for the first brood was compared between ex-helpers ($N = 5$ or 6) and controls ($N = 6$ or 7: N varied between the different brood cycle stages). There was no difference in direct broodcare behaviours. In territory main-

Fig. 8. Territory maintenance and direct broodcare behaviour of ex-helpers and controls, averaged for the first 1–3 of their own broods. Left: females, right: males; median values for 5–7 individuals (N varies with stage of breeding cycle) are shown for time spent in each type of behaviour per observation period (see subjects for behaviour patterns included and General methods for details of recording). Abscissa: stages within the breeding cycle in days; b = before spawning. Vertical lines represent interquartile ranges.

tenance, controls spent more time removing snails at the start of the egg and larval phases ($P < 0.05$), but as snail density was the only factor that could not be rigidly controlled, this cannot be unequivocally attributed to the difference in experience of test and control groups. At the start of the egg phase, former helpers tended to show more substrate cleaning than controls ($P = 0.053$); in the middle of the egg stage and when larvae hatched, controls spent more time feeding than helpers ($P < 0.05$ and $P < 0.02$ respectively).

A distinct development of the investment patterns of a female, which could possibly be revealed by comparing its first with its second and third broods, might also point to a 'head start' for former helpers. Suitable data for such a comparison existed for only six fish (four ex-helpers, two controls), but no trend was apparent in any of the investigated behaviour patterns of broodcare and territory maintenance.

There were not enough independent experiments to allow statistical analysis of quantity of broodcare by males (former helpers versus controls). But an effect of experience is less probable in male than in female ex-helpers, as male breeders (experienced or not), rarely participate in direct broodcare and invest in territory maintenance much less than females (differences are significant, Taborsky 1982; see also Fig. 8).

The distribution of broodcare. During the breeding cycle former helpers and controls do not differ in the distribution of their behaviour patterns. Behavioural data from the first to third breeding cycles of male and female ex-helpers and naive controls are shown in Fig. 8. Distributions of investment throughout the breeding cycle are very similar. Nor were differences detectable when behaviours were considered separately (not shown in the figure). Figure 8 indicates a difference between the females, former helpers showing more direct broodcare on the second and third days with eggs, but this difference is not significant, especially as at this stage the quantity of investment varied considerably between different females (see the interquartile ranges).

Reproductive success. The first progeny of former helpers and of naive fish survive equally well. The success of the first two broods of former helper females and of naive females of equal size is shown in Fig. 9. There was no difference in egg survival to day 10 nor day 20,

even when first and second broods were considered separately (these results were not altered when, to increase the number of controls, data were added from the first broods of four naive females that were kept in compartments twice as large as those in the other experiments). Also, when male ex-helpers were compared with naive males, no difference was indicated.

Former helpers and naive controls have similar clutch sizes, breeding intervals and growth rates. Analyses of clutch sizes of first broods and of the intervals between the first two or three own broods revealed no differences between former helpers and naive controls, either for females or males. Therefore the two groups did not differ in their absolute breeding success. Growth rates of 13 former helpers and 13 controls were measured during their first own broods. Ex-helpers and controls were size-matched for statistical comparison. No weight nor size gain differences were found between male or female ex-helpers and their respective controls.

These results suggest that helpers do not benefit from experience when they start to breed on their own. Apparently not only the quantity and distribution of behaviour in time, but also the quality of broodcare did not differ markedly whether a fish had former experience or not. This is remarkable, as the experience of helpers
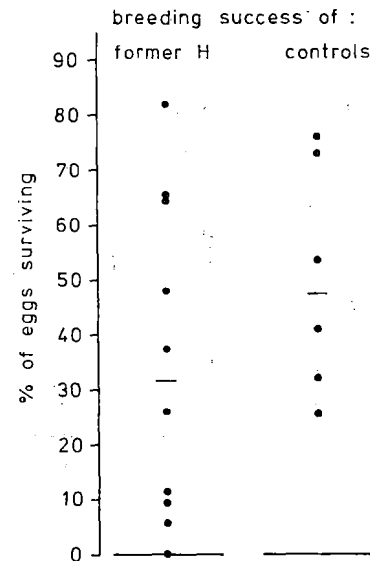

Fig. 9. Percentage of eggs surviving for female former helpers (H) and naive controls, measured at day of free swimming. Symbols as in Fig. 4.

and controls in the experiments differed much more than it usually does in the field. Aggregation members will normally have at least some experience with parental broods before breeding on their own, as they will usually overlap with at least one or two broods before leaving the territory. The fact that helpers did not learn about the quantity and distribution of direct broodcare from the breeding female was also indicated by the lack of a correlation between the amount of direct broodcare given by females and that given by their helpers (Taborsky 1982).

4. Inheritance of Territory

Large, sexually mature helpers could replace a parent or take over a part of their home territory. Compared with aggregation members they might also profit from their safe residence or greater familiarity with the area when trying to obtain their own territory.

Observations on the field population have shown that, with rare exceptions, helpers leave their home territory before they reach 5 cm in size. Only 11 of 233 helpers from 35 families were > 5 cm; the two largest were 5.6 cm. All pair members (of stable pairs) were $\geqslant 5.6$ cm. Most aggregations had members > 6 cm in size, competing for vacant breeding positions. As fighting ability is directly related to size, helpers will probably be unable to defend a newly vacated place, or expel a territory owner. This is supported by an experiment: we caught one or both parents of those 10 families having the largest helpers (all > 4.5 cm) in our field population. A helper never took over; instead it was always a bigger aggregation member that did. In most cases the helpers stayed with the new breeders.

5. Protection

All suitable shelter sites in the rocky *L. brichardi* habitat are occupied by fish of various species. Therefore staying in a territory as a tolerated beneficiary of stronger and more able hosts may be the only way to have permanent access to a shelter site. Parents and larger helpers may also afford protection against intruding predators. Helping could simply be the price for being allowed to stay.

Field Observations

The main diurnal predator of the young of *L. brichardi* is a large congeneric species, *L. elongatus* (up to 17 cm SL in the field). We often observed these predators lurking in the

vicinity of young $\leqslant 4$ cm long, sometimes lunging at one of them. Young that were experimentally separated from their home territory were sometimes beset by several predators while trying to find a shelter site.

Size distributions of non-reproductive members of families and aggregations show that the majority of young leave the family to join aggregations when they reach a size of 4–5 cm SL (Taborsky & Limberger 1981). This is the size at which they are no longer in danger from *L. elongatus*. When this predator appears, young $\leqslant 4$ cm usually dash for the substrate, whereas young $\geqslant 4.5$ cm appear unconcerned. But small family members (helpers) may even make lightning attacks on *L. elongatus* (curved attack swimming) from their shelters, darting back before the predator can react. In this way they often expel fish up to 10 times their own size. I suggest that permanent access to a shelter site is vital, especially for fish < 4 cm SL. In addition, the smaller, most endangered family members are protected by the defence of the breeding pair and bigger helpers.

During observations at night we saw various predatory catfish (see Brichard 1978 for species names), although unfortunately not when they were hunting. *L. brichardi* family members were found in their shelters, and some fish, most of them presumably aggregation members, sat exposed on sand or stones. It seems that at night *L. brichardi* of all sizes benefit from hiding in a shelter site, which means having access to a territory (as most suitable substrate is defended by fish of various species, see above).

Methods

The effect of parental defence on the mortality risk of helpers in the presence of predators was tested in the laboratory. A 500-litre tank was divided into two by an opaque wall. In each compartment, which were similar in all respects (water quality, light, etc.), five flowerpot halves were arranged in a circle. Four ($N = 4$ experimental set-ups) or five ($N = 5$ experimental set-ups) helpers were put into one compartment, together with an adult pair; the other compartment contained the same number of controls (four or five respectively), but no pair. The size range of helpers was small (< 0.5 cm within one experimental set-up; total range: 2–3.1 cm; $\bar{x} = 2.6$) and the sizes of controls were exactly matched. After 3 days of habituation and only when all fish had access to the flowerpot shelters, an individual *L. elongatus* was introduced into

each compartment (six individuals were used 7.1–8.4 cm SL). Left and right compartments and individual predators were balanced between tests and controls. Attack rates of adults on the predator and of the predator on young were recorded for 15 min at regular intervals, as well as the order of young preyed upon (helpers and controls were individually recognizable). Experiments stopped when all young had disappeared on one or the other side.

Results and Discussion

Median rates of attack by pairs on the predator are shown in Fig. 10. Immediately after introduction of the predator the adults attacked at a rate of about 8 attacks/min; some hours later and until the experiment ended attack rates remained at almost 1 attack/min. Thus adults continuously attack predators that are threatening helpers. Figure 11 shows the effect of parental attacks on the predator. In all experiments helpers were attacked less frequently than controls. The effect could still be seen at longer intervals after the introduction of a predator, but these data are not included in the figure.
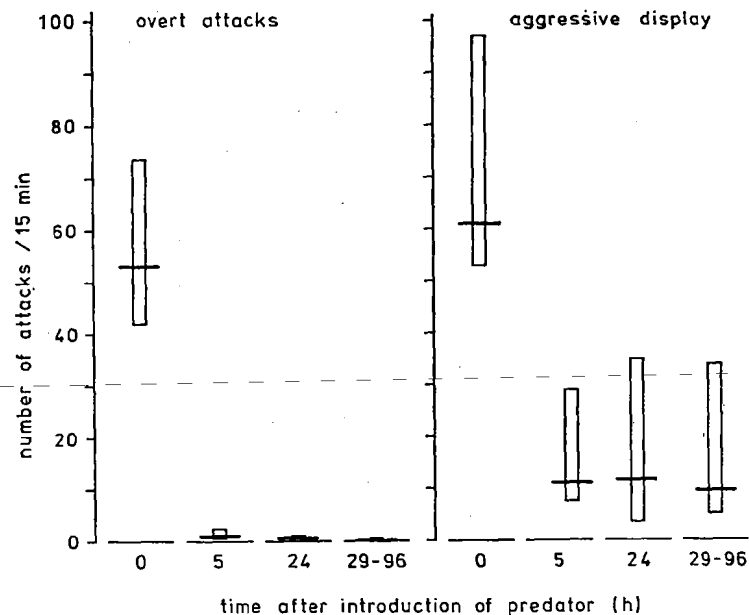
Helpers also survive better than unprotected fish of the same size. The importance of the protection afforded to helpers is best demonstrated by the order in which helpers and controls were caught by the predator (Fig. 12). Usually controls were caught first. At the end of an experiment, when all controls had disappeared, most helpers were still there.

Even minor differences in size influence the risk of mortality. The size range of young within the experiments was minimized (see above). Nevertheless the order of being caught by a predator was size-dependent: young caught first in an experiment were smaller than those caught last ($P < 0.05$; Wilcoxon test). As this effect appeared with sizes differing by less than 0.5 cm, one can imagine how important it might be for a helper not to leave its family too early in order to become an unprotected aggregation member.

I want to emphasize that the controls used in these experiments had access to shelters, yet the protection of the breeding pair resulted in a much higher survival rate of helpers. Aggregation members in the field often cannot hide, as all suitable crevices are occupied by territorial fish of various species. This might result in an

even greater difference between helpers and aggregation members in the risks they face from predators.

6. Cleptogamy and Cannibalism

Mature male helpers could fertilize their mother's or foster mother's eggs. Mature female helpers could add their own eggs and take advantage of other family members' broodcare. As the mean degree of relatedness between helpers and new eggs decreases with the helpers' age, larger helpers might perhaps benefit from feeding on highly nutritious eggs or fry.

Very occasionally, in the aquarium, I have observed a male helper trying to fertilize eggs when the parents or foster parents spawned. Young also ate eggs or fry sometimes, though this is very rare in undisturbed families. More detailed data on sneak-fertilization and cannibalism by helpers will be published in a later paper dealing with helper–parent conflict (see also Taborsky 1982). Here it can be stated briefly that both potential benefits were probably of minor influence in the evolution of helping, although an important effect was indicated on the departure of helpers from the home territory.

General Discussion

Experimental Design and an Inconvenient Question

As many data were obtained in the laboratory, under controlled conditions, one is tempted to question the reliability of investigating adaptations in an artificial environment. Three arguments support the approach pursued in this work. (1) The aquarium approximated to field conditions with respect to light schedule, water temperature and quality (see Taborsky 1982), the amount of space available to family members (at least to helpers up to 4 cm SL), and, in certain experiments, the types of competitors and predators used. (2) Population variables important for calculating r, the mean degree of relatedness between helpers and beneficiaries, were measured in the field (Taborsky & Limberger 1981). These and other data were obtained by repeated observations on tagged individuals, quantitative recordings of behaviour and by simple experiments. The field data yielded a relatively broad basis of information, from which specific questions could be addressed and worked upon under carefully controlled laboratory conditions. (3) Wherever comparisons of field and laboratory data were possible (e.g. in growth rates), results did not differ greatly (Taborsky 1982). Any differences (e.g. in feeding), were usually of a conservative nature, i.e. had a rather adverse effect with regard to the suggested hypotheses. Therefore it can be assumed that most of the significant results obtained in the laboratory would be even more pronounced in the field.

Fig. 10. Median attack rates of pairs ($N = 9$) against potential predators of their helpers directly after introduction of the predator and at intervals thereafter. Observations made after 29 h were pooled (most experiments had finished within 30 h). Vertical bars represent interquartile ranges.
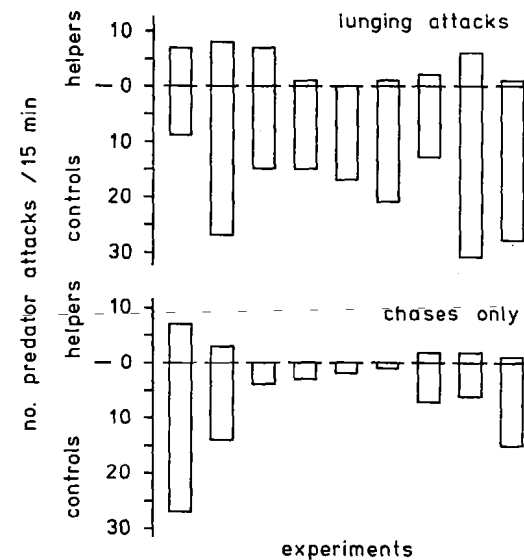

Fig. 11. Attack rates of introduced predators in the first 15 min performed on all helpers of a compartment and their corresponding controls. Experiments in chronological order.
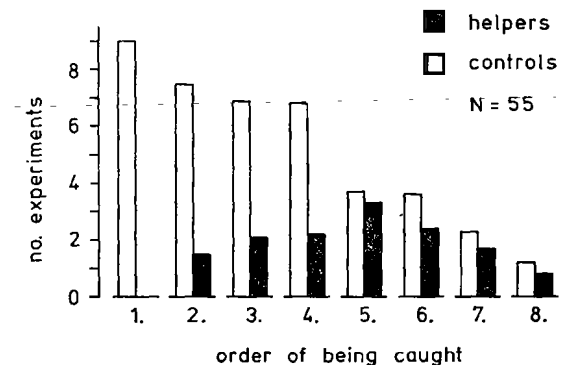

Fig. 12. Order in which helpers and their corresponding controls were caught by the predator in each of nine experiments. If helpers and controls disappeared within the same time interval, their rank was halved. N = total number of caught fish in all experiments.

The Costs for Helpers of Delayed Growth versus the Benefits of Increased Protection and Production of Close Kin

The aim of this study was to elucidate the costs and benefits most probably influencing the evolution of helping in *L. brichardi*. I attempted to consider all parameters with a possible bearing on the evolution of this elaborate social system. Three of the factors measured proved important, although a marginal influence of some others cannot of course be wholly excluded.

Firstly, helpers grow at a slower rate than non-helpers. This is due to investment in the territory and the brood, and to the status of helpers within a family rank order. The high amount of submissive behaviour is one possible cause for the detrimental effect on growth for certain ranks (Taborsky 1982). In natural populations, only the largest individuals succeed in breeding on their own. Delayed growth therefore means at least delayed reproduction. This and Reyer's data (1984) are the first proof of costs to helpers in a cooperative vertebrate (see Koenig & Pitelka 1981; Reyer 1984; Brown, in press).

Secondly, depending on size, the mortality risk of helpers is considerably lower than that of family independents. This is due to the access helpers have to a defended shelter site, and to the protection afforded by the defence of the breeding pair and any bigger helpers. The size distributions of helpers and aggregation members mirror the differing risks: above 4 cm, when the risk drops rapidly as the fish pass the *L. elongatus* prey-size threshold, the proportion of aggregation members increases considerably (Taborsky & Limberger 1981).

Thirdly, though helpers did not increase their parents' immediate breeding success, in terms of the percentage of eggs and larvae surviving, they had a positive effect on the pair's future success. Obviously female investment is limited. This became apparent even with superabundant food in the laboratory experiments: growth of females and the number of eggs produced were negatively correlated. Females of pairs with helpers produced bigger clutches than those without, and so had more free-swimming fry, i.e. young independent of further direct broodcare. This effect was admittedly not very pronounced, but as the laboratory conditions can probably be considered superior, in natural populations the effect of helpers may be more important. A clear pointer in this direction is the fact that, in the field, pair members with larger helpers spent less time in their territories than pairs without or with only small helpers. The time in aggregation is mainly spent in feeding, so parents with larger helpers not only save energy, but have more time to feed, though their territories are protected for about the same amounts of time as those of families without helpers. Additionally, aquarium data revealed that pair members spent less time in territory maintenance and in attacks against small competitors and egg predators when they had helpers (Taborsky 1982).

Fish Helpers and their Ecology

Selective factors favouring young remaining in their home territory. Many authors have assumed that, in a number of different bird species, habitat saturation or resource localization are the main causes of young remaining in their natal territories, resulting in extended families (e.g. Brown 1969, 1974; Koenig & Pitelka 1981; Emlen 1982a). This is probably true for *L. brichardi* also, for the habitat is densely inhabited by conspecifics and competitors with similar space requirements. Naturally or experimentally removed breeders were immediately replaced, mostly within 1 h (Taborsky 1982). But unlike most bird species, not only are potential nesting places limited in *L. brichardi*, but these same breeding holes also act as shelters for individuals of all sizes. A comparable situation is possible in the woodhoopoe, where Ligon & Ligon (1978) assumed access to roosting holes to be limiting, and in East African ground barbets, which also have helpers, and whose roosting holes are excavated in earth walls (Short & Horne 1979).) Presumably, helpers in *L. brichardi* do not stay at home only because they do not have the alternative of breeding themselves, but because they rely heavily on the protection they enjoy in their natal territories. This has important consequences for the decision a helper should make: 'The strategy of "helping" should, in all cases where resource localization is the primary selective force behind it, be adopted by an independent offspring only as a last resort strategy' (Koenig & Pitelka 1981). This is not true for *L. brichardi*. Choice experiments showed in fact that helpers stay even when given the chance to breed on their own (Taborsky, in preparation).

Helpers in other fish species. A look at other species of the same habitat, the rocky sublittoral of Lake Tanganyka, shows that many cichlids of the rather closely related genera *Lamprologus*, *Julidochromis* and *Telmatochromis* also have limited shelter sites and show quite similar behaviour. Young of *L. savoryi*, *L. pulcher*, *J. marlieri*, *J. ornatus* and *J. regani* remain for several successive broods and participate in broodcare and territory maintenance (Taborsky & Limberger 1981, unpublished data). Large young are tolerated in territories of adult *T. temporalis*, but we do not know whether they are usually offspring of the resident territory owners. According to our observations they do not engage in broodcare, but defend small shelters within the adults' territories. Even *L. elongatus*, although not territorial outside breeding cycles, protects its young for an exceptionally long time. We found territorial parents with schools of young about 3.5 cm SL.

There are very few other cases reported in fish of large young tolerated in breeders' territories: in *Etroplus maculatus*, another cichlid, tolerated young have been reported nearly up to territory-owner size (Ward & Wyman 1975). This species also lives in dense populations, so one might expect strong competition for suitable shelter sites. Adult anemonefish, *Amphiprion akallopisos*, accept young of different sizes in their defended anemone (Fricke 1979). As these are recruited from the plankton they are not close kin. Here too shelter sites (anemones) are very limited.

Fish Helpers Compared with Mammals and Birds

In birds and mammals, helpers feed the beneficiaries; in *L. brichardi* direct broodcare consists of cleaning the eggs, removing dead ones and sometimes also fanning. This difference has important consequences for the cost/benefit ratios of helpers, and therefore on the evolution of helping behaviour in fish compared with higher vertebrates. Presumably in fish, direct broodcare does not raise the mortality risk, whereas food gathering in higher vertebrates does (as recently shown in the pied kingfisher by Reyer 1984; it is perhaps also true for Florida scrub jays: pairs with helpers live longer; Stallcup & Woolfenden 1978).

The population structure of *L. brichardi* differs greatly from that of most bird species with helpers, when non-reproductives are considered. In bird species with helpers, floaters are rare (Koenig & Pitelka 1981; one exceptional case resembling the situation found in *L. brichardi* was described by Carrick 1972, for the Australian magpie). In *L. brichardi* nearly half of the mature fish (≥ 4 cm) in the population studied in the field were aggregation members (these correspond to floaters, though they do not truly 'float'): 92 ($= 44\%$) compared with 117 (56%) family members, measured within a strictly defined observation area (see also Taborsky & Limberger 1981, for size relations). But these non-reproductives compete not only for an opportunity to breed, but also for individual shelter sites. In *L. brichardi* the decision to be made is not therefore 'to breed or not to breed' (as generally suggested for birds and mammals), but rather to help (involving delayed growth but increased security) or to join an aggregation (with accelerated growth but a higher mortality risk).

Obtaining experience. This factor, although subject to speculation for many years (e.g. Skutch 1961; Brown, in press) has to my knowledge never yet been tested in an experimental analysis (see also Brown, in press; in Florida scrub jays (Woolfenden 1973), brown jays (Lawton & Guindon 1981) and splendid wrens (Rowley 1981) there are some hints on the subject). In the present study various parameters of broodcare and breeding success were compared between the first broods of former helpers and those of totally naive fish. No learning effect whatsoever appeared; this factor probably had only a minor influence, if any, on the evolution of helping in *L. brichardi*.

Rearing close kin. Increasingly, authors conclude that the influence of kin selection on the evolution of helping was over-emphasized in the first enthusiasm in the 1970s, when Hamilton's (1964) model spread through the scientific community (Koenig & Pitelka 1981; Brown, in press). But in some 15 species of birds and mammals, that is the majority of examples thoroughly investigated in this context, a positive, though small, effect (Brown, in press) of closely-related helpers has been found on the immediate reproductive success of assisted breeders (Emlen 1978, 1982b). In addition, for a few bird species, the time or energy burdens of breeders has been found to be lessened by the presence of helpers (Rowley 1965; Stallcup & Woolfenden 1978; Brown et al. 1978); predictably, in these cases, the reproductive value of breeders is increased.

L. brichardi belongs to the latter group: although helpers did not raise the survival rate of eggs or larvae in my experiments, parents saved investment (e.g. territory maintenance, defence against competitors; Taborsky 1982). Helpers influenced future breeding success in that aided females produced more eggs and consequently

more independent young (free-swimming stage = end of broodcare). I agree with Koenig & Pitelka's (1981) view that kin selection may not, in general, be an ultimate cause for the decision of young to remain in a territory (though in this context, relatedness may figure largely in the breeders' decision to tolerate the young, at least if this also involves protecting them or some other implied costs; see Taborsky 1982), but to my mind, kin selection must still be regarded as a most important factor in deciding whether or not young that stay also help (e.g. in the pied kingfisher, helpers with different degrees of relatedness to the breeders they assist do invest different amounts according to their expected degree of relatedness; Reyer 1984). Kin selection will also strongly influence where to stay (e.g. in the parental territory). From the breeders' viewpoint, toleration of helpers and their active protection is merely extended broodcare, as they are most probably their own young.

Paying for staying. As mutual interests are involved in helper–breeder relationships, a system based on reciprocity is possible (Gaston 1978; Emlen 1982b; Ligon 1983; Brown, in press). One could argue that this will work even better in close-kin groups, where the cheating payoff is reduced. But with increasing r (= degree of relatedness) conflicting interests decrease, and kin selection will dominate the evolution of behavioural traits and decisions. Unlike other species (but data as scarce), r in *L. brichardi* decreases with time: as helpers stay on when breeders are replaced, r decreases with helper age in proportion to the breeder mortality rate (Taborsky & Limberger 1981). There is strong evidence that kin and individual selection influence decisions according to their 'proportional representation'. The interests of small helpers and breeders (most likely offspring/ parents) overlap widely, while conflicting interests characterize the relationship between breeders and largest helpers (probably foster relationships). This will be discussed in more detail in a subsequent paper.

Acknowledgments

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