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### Résumé

Nous avons mis en évidence les interactions qui s'établissent à longue distance, par des chants en duo, entre douze groupes familiaux de Gibbons (*Hylobates lar*), en Thaïlande. Les analyses statistiques montrent que les familles répondent plus volontiers par un duo à un chant en duo venant d'une famille voisine qu'à un chant en duo venant d'une famille non voisine. Les familles voisines se distinguent par un type particulier de réponse: une famille attend la fin du chant d'une famille voisine avant d'y répondre immédiatement par son propre chant en duo, de sorte que les deux duos ne se chevauchent pas. Les familles non voisines ne montrent par ce type de réponse. Nous démontrons que ce résultat est dû exclusivement au fait d'être ou de ne pas être voisins, et nullement au fait que l'autre famille est plus ou moins audible. Rien ne prouve, dans le cas où des chants se chevauchent, que la première famille qui chante modifie la longueur de son chant du fait de l'existence du second duo, que celui-ci provienne, ou non, d'une famille voisine. En règle générale, si on considère les familles qui se répondent les unes aux autres par leurs chants, il n'est pas possible d'identifier des familles qui tendraient à chanter en premier et d'autres qui attendraient d'en entendre une autre avant de chanter. Nous discutons les motifs pour lesquels les familles voisines se répondent plus par des chants que les familles qui ne sont pas voisines. Nous recherchons quelles peuvent être les fonctions de la tendance à éviter le chevauchement des chants en duo.

## BREEDER-HELPER CONFLICT IN A CICHLID FISH WITH BROODCARE HELPERS: AN EXPERIMENTAL ANALYSIS

by

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(With 10 Figures)  
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### Introduction

TRIVERS (1974) was first to explicitly emphasize that parents and offspring should not agree about the amount of parental investment an offspring receives and the amount of altruism between siblings (see also PARKER & MACNAIR, 1978; ROBINSON, 1980). Of course, conflicting interests should also be expected in cooperatively breeding species where parents are aided by offspring of former broods (ZAHAVI, 1974) or, more generally, within any social group with breeders and associates, whatever their relatedness. The evolution of helping is presumably often tied to the resolution of conflicts of interest (EMLEN, 1982). In cooperatively breeding birds the most obvious expressions of conflict include regular copulations by auxiliary males with the breeding female (see EMLLEN, 1982, p. 47, for references) and infanticide (VEHRENCAMP, 1977, 1978; TRAIL *et al.*, 1981; MUMME *et al.*, 1983). A cost/benefit analysis of brood-care helpers of the cooperatively breeding cichlid *Lamprologus brichardi* showed that they also occasionally parasitise the breeders' reproduction and cannibalise their eggs (TABORSKY, 1984). This paper is aiming at individuals' choices when they have several, experimentally varied alternatives. I ask whether the point at which helpers become independent is regulated by breeders or helpers, and I try to shift this point experimentally. This may show when costs of further family-membership and help-

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ing begin to exceed the benefits for either breeders or helpers. Although obvious, this approach has not as yet been pursued in any investigation on cooperative vertebrates.

The preconditions for the evolution of reciprocal altruism are similar to those for kin selection, as TRIVERS (1971) has remarked (see also ROTHSTEIN, 1980). Cooperative vertebrates fulfill many of these conditions (EMLEN, 1982; see LIGON, 1983, for a review of presumed reciprocity in cooperatively breeding birds). This prerequisite is, in *L. brichardi*, the existence of small and stable family groups, combined with individual recognition capabilities (HERT, 1985). It provides the opportunity for retaliating effectively against defection (AXELROD & HAMILTON, 1981). Besides, the donors' costs are presumably lower than the recipients' benefits:

#### Subjects and general methods

*L. brichardi* is a substrate breeding cichlid of up to 6.5 cm (max. field size) restricted to the rocky shore of Lake Tanganyika. (All sizes are given in standard length (SL) throughout this paper.) Field observations were made near Magara, Burundi. Pairs and their young from up to 4 successive broods defend family territories of ca. 25 cm radius around a hole or cleft used as a hiding place and for breeding. Young fish within families share in all parental duties, including defence, broodcare and territory maintenance. They are therefore called helpers. In laboratory experiments male and female helpers did not differ in the amount of egg and larvae care (32 broods with helpers of known sex, 5 male and 9 female helpers; size range 2.6-5 cm). Aggregations of variable sizes, consisting of non-reproductives without shelters and territories, are close to the family territories. Most aggregation members are  $\geq 3.5$  cm long and sexually mature. They remain in the same area and spend more than 80% of their time feeding (TABORSKY, 1982). Family members  $\geq 3.5$  cm long regularly visit the aggregations for plankton feeding. Further information on behaviour and social organisation is provided by TABORSKY & LIMBERGER (1981), LIMBERGER (1983) and TABORSKY (1984); a complete ethogram was made in the laboratory by KALAS (1975).

Fish were kept in 100-500 l tanks in the laboratory. The experimental tanks were 500 l (bottom: 128 + 73 cm, the bottom covered with gravel (1 mm grains); flowerpot halves, PVC-plates and differently shaped pieces of plexiglas served as shelters and spawning sites. Water temperature and quality, artificial light conditions and feeding schedules were held constant (for details see TABORSKY, 1982).

All fish used in experiments were weighed, measured and marked individually by injecting alcian blue into scale pouches or, in one experiment, by fin clipping. Pair-helper families consisted of parents and their young or of a pair with strange young; there is no detectable behavioural difference between these (TABORSKY, in press). Fish were allowed 3 min before all quantitative protocols to habituate to the observer. Video controls showed this amount of time was sufficient.

#### Preliminary information: The options of helpers

Most young of both sexes up to 3 cm in size stay in their natal family territory, where they usually remain when one or both parents are ex-

changed. Natural mortality of parents decreases the expected degree of relatedness ( $\bar{r}$ ) between helpers and both, present territory owners and their eggs, larvae and fry with the increasing age of helpers (TABORSKY & LIMBERGER, 1981). The proportion of helpers between 3 and 6 cm still found in families decreases with size compared to the number of family independent aggregation members. Helpers grow at a slower rate than aggregation members of equal size, and in the aquarium aggregation members were lighter than equal size helpers. So primarily the aggregation phase is a growth phase (TABORSKY, 1984; see also the activity distribution of fish within aggregations, TABORSKY, 1982). This difference in growth is particularly important as only the largest members of a population are able to get a territory of their own (TABORSKY & LIMBERGER, 1981). The helpers' costs of delayed growth are compensated for by an increase in the breeders (often parents) productivity and by a decreased mortality risk when staying in a protected territory. Thus at any time young (helpers) have the option of staying in a territory, with access to a defended shelter, under protection of bigger family members and with the chance of increasing the production of relatives, or of leaving for an aggregation and growing faster. Costs and benefits for both options change with age, as  $\bar{r}$  between helpers and newly produced eggs decreases and as the main daylight predator of *L. brichardi* young, *L. elongatus*, only catches young of up to 4-4.5 cm (SL) size in the field.

#### The preference of young

Experiment 1: Distribution of young with and without 'parents'.

*Rationale:* Young of the size range at which most helpers switch to aggregations in the field may move freely between two compartments, before a breeding pair is introduced into one compartment: Will the young stay in this experimentally induced "family territory", or leave for the other compartment either to join an aggregation of conspecifics or become territorial themselves? Is there any size-related difference in their choice?

*Method:* One third of a 500 l tank was partitioned by an opaque PVC-wall with holes and slots big enough for fish  $\leq 5$  cm in length to pass through. The compartments shared a filter and thus had water of equal quality and temperature; there were the same number (per unit area) and quality of shelters in both.

12 young of a mean size of 3.2 cm (range: 2.4-4.3) were distributed equally between both compartments (with respect to fish number and sizes). The distribution of young was

recorded throughout the experiment, for a mean of 2-3 times/day to obtain a mean 'distribution/day'. A pair (not the parents, see General Methods) was introduced into the larger compartment 1-2 weeks after the experiment began. Eight replicates with 8 different pairs and 96 different young were performed with a mean duration of 60 days. At the end of experiment the young were an average of 4 cm long (range: 2.7-5.3).

The 'mean distributions/day' were averaged for 3 periods: (i) before the pair was released, (ii) for the same interval after the pair was introduced (= short term effect of the pair), (iii) from one week after introduction of the pair until the end of experiment (= long term effect of the pair).

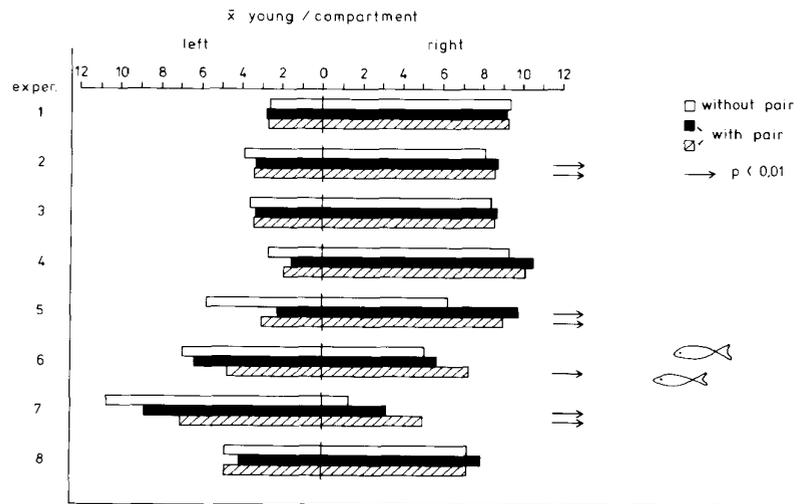


Fig. 1. Distributions of 12 potential helpers between two compartments before and after a pair was introduced into the larger (= right) compartment. Ordinate: 8 replicates; abscissa: mean number of young present on left and right hand sides of the divider (divider marked by a vertical line). Black bars: short term effect; hatched bars: long term effect (see text). The distributions before and after insertion of the pair (for short and long term effect) were compared within each replicate by the Lord test.

**Results and discussion:** When the pair was introduced, the distribution of young was already rather stable – only a few changes had occurred in the 5 days beforehand. The introduction of the pair did not induce the young to leave the thereby created 'family compartment' (Fig. 1). On the contrary, the distribution of young in 7 out of 8 experiments shifted slightly towards the pairs' compartments on a short and on a long time scale ( $p < 0.02$  and  $< 0.05$ ,  $N = 8$ ; Wilcoxon matched-pairs signed-ranks test). The young preferred to stay with, or even join, the breeding pair. This result was not due to a preference of the larger compartment: before the

pair was introduced, there was no significant trend from small to large compartments (first half of the period before the pair's introduction tested against the second,  $p > 0.05$ ; Wilcoxon test). The distribution of young was also influenced, but only in a minor way, by dominance relationships: in all experiments and in both compartments some young behaved territorial against each other. However larger young were not concentrated on the pair-less side and this suggests that a preference for this compartment combined with territoriality of the young was not responsible for the observed distribution.

The distribution of young was very stable in the last days or weeks of the experiment, with only one or two young changing compartments. When the pair bred, some of the young helped in direct broodcare. There was no consistent size difference between young sharing parental broodcare and those not doing so.

**Experiment 2: The preferences of helpers - parental or own territory?**

**Rationale:** Do potential helpers stay with a pair when they could have their own territory and perhaps even breed? The experimental alternative to the parental territory was superoptimal to that in the field, containing no inter- or intraspecific competition.

**Methods.** Tanks as in the previous experiment were used. 2 adults (5.0-6.9 cm; mean = 6.0; replicate 1 to 5 female and male, repl. 6 two females, repl. 7 two males) and 2 potential helpers (2.0-3.0 cm; mean = 2.4) were put into the large (4 replicates) or small (4 replicates) compartment. The holes and slots in the divider only allowed potential helpers through. The adults were transferred to the other compartment after 5-16 weeks (mean = 80 d). The experiment was stopped 3-8 weeks later (mean = 40 d), when the preferred residence of the potential helpers had been the same for at least two weeks. Potential helpers were 3.6-5.4 cm long (mean = 4.4) by the end of experiment. The mean residence of both young was determined everyday by recording which compartment they were in at 10 sec intervals over 10 min. These 'mean distributions' were averaged for 7 days (= mean/week). One of the 8 replicates had to be finished prematurely because of the great aggression between the two adults.

**Results and discussion.** The two young mainly stayed on the same side of the divider as the adults, regardless of whether this was the small or the large compartment ( $p < 0.02$ , binomial test; Fig. 2). The mean proportion of time the helpers spent in the adults' compartment before the latter were transferred to the other side was 80.0, 85.8, 88.8, 71.4, 57.1, 85.0 and 55.2%, respectively (Fig. 2, upper left to lower right). Then the young also changed to the other compartment. There was a significant

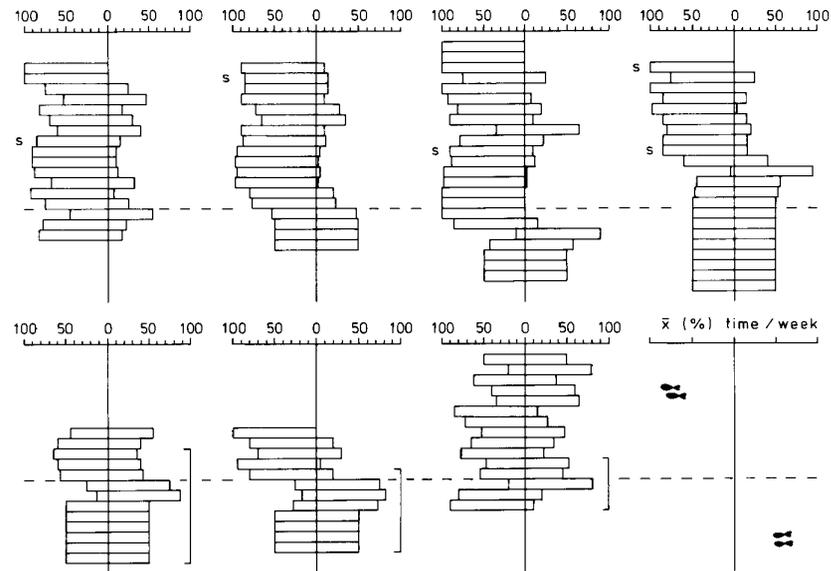


Fig. 2. Distributions of 2 potential helpers between two compartments, one of which contained two adults, 7 replicates; order of replicates: from top left to bottom right (see methods). Dividers are marked by vertical lines. The horizontal line separates the periods, in which the adults were on the left (= above the line) or right side of the divider (see down right for a sketch). Each bar marks the mean distribution per week for both potential helpers. S = spawning of the adults. Brackets mark periods, in which one of the adults was placed into a net (because of intolerance of the other adult).

difference in the helpers' distributions before and after the adults' transfer ( $p < 0.05$ ; Wilcoxon test). Towards the end of the experiment in 5 of 7 replicates one helper stayed with the adults, the second young was in the other compartment; in 2 others one young changed between compartments, the other stayed in the free compartment.

The young which left the adults' compartments were probably forced by others: certainly, by the other young in 2 observed cases and additionally by the female in a third. The fish in the free compartment was never initially territorial against the other. In 4 replicates the pair bred and presumably helpers had to increase their investment (substrate cleaning, digging, direct broodcare) but they still preferred to remain with the pair. There was no sex-specific trend for staying with the adults: 4 out of 9 male helpers remained as did 1 out of 4 female helpers; 2 other female helpers regularly switched between both compartments. In 5

replicates (no. 1-4 and 6) the two helpers were male and female and could, therefore, have reproduced themselves in the free compartment, as they were the same size as others which had already bred successfully in the aquarium. Nevertheless, they obviously preferred to stay in the territory of the adults, perhaps because the potential partner was a family member. Although some cooperatively breeding birds have mechanisms preventing the formation of breeding pairs composed of parents and their own young (WOOLFENDEN & FITZPATRICK, 1977; KOENIG & PITELKA, 1979; REYER, 1984), breeding does occur in groups of *L. brichardi* siblings raised together in a tank.

### Breeders expel helpers

The previous experiments suggest that usually young would prefer to remain in the family territory when they reach the size at which, in the field, most leave for aggregations. This is despite a considerably better alternative (in terms of obtaining a territory and reproducing) than the field equivalent. Helping is not a "last resort strategy", as proposed by KOENIG & PITELKA (1981). But how do helpers become independent? The following section will investigate whether breeders are responsible for the independence of the young, when and how they force helpers to leave and whether parents consider their demand for helpers.

### Preliminary information.

Larger helpers are more likely to be expelled. An experiment for the evaluation of helpers' growth and their contribution to parental breeding success (TABORSKY, 1984) was replicated 37 times. Eighty-one out of 131 helpers measuring a mean of 2.7 cm at the start of the experiment were expelled by the pair; the others stayed with the breeders until the end of experiment. The majority of expulsions happened to helpers between 3.5 and 4.5 cm long (Fig. 3). The declining rate of expulsions of helpers  $> 4.5$  cm is an effect of the experimental procedure (TABORSKY, 1982). Expelled helpers are not re-accepted, either when left in the tank or when removed and re-introduced.

The largest helpers in a family are usually expelled first. Expulsions by the pair may also be the usual way helpers in the field become independent as their sizes at the family to aggregation transfer (cf. TABORSKY & LIMBERGER, 1981, Fig. 3) correspond roughly to helper expulsion size in the aquarium.

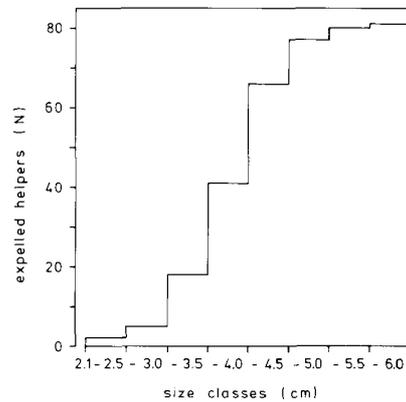


Fig. 3. Cumulative size distribution of helpers at expulsion.

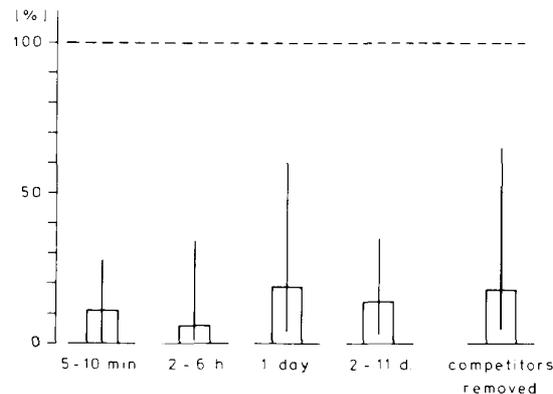


Fig. 4. Median attack rates of 15 pairs on their ostracised helper after competitors were introduced, as a proportion of the attack rate before the competitor release (= 100%). The abscissa marks time intervals between introduction of competitors and the protocol. Vertical lines mark interquartile ranges.

### Do breeders calculate their need for helpers?

*Rationale.* Pair members expel the fish who help them—a paradox at first glance, especially as helpers increase the pair's reproductive success (TABORSKY, 1984). If parents make the right decision in expelling their helpers, one might expect them to respond to a change in their cost/benefit ratio connected with the presence of helpers. This experi-

ment investigates whether territory owners calculate their need for helpers: the introduction of competitors, especially of those usually attacked by helpers, was expected to prolong the time for which a helper was tolerated.

*Methods.* The attack rate of pair members (parents and non-parents, see General methods) on their helper was recorded in 15 replicates, immediately after the helper was expelled from the territory (expelled helpers are usually near the water surface at the edge of the tank). Then the helper was briefly removed and re-introduced with 4-6 competitors which matched it approximately in size. These competitors were conspecifics in 10 replicates and *Julidochromis marlieri* or *J. regani* in 5, all space competitors in the field (TABORSKY, 1982). The attack rates of the pair members on helper and competitors were recorded for 12 min; simultaneously, in 7 replicates the helpers' attack rates on competitors before and after re-acceptance were recorded. Behaviour patterns recorded were: head down display, frontal approach, bumping against and the overt attacks of ramming, curved attack and biting (see TABORSKY, 1984).

*Results and discussion.* The pair's attack rate on the helper decreased considerably when the competitors were introduced ( $p < 0.005$ ; Wilcoxon test, one tailed; Fig. 4). In 13 out of 15 replicates both pair members reduced their rate, in 2 only one partner did. Even when the competitors were removed again the parental attacks were only 10-20% of the pre-competitor level. The rate of overt, as opposed to suppressed, attacks on the expelled helper also declined when the competitors were introduced: those of females fell in 8 out of 9 recorded replicates and those of males in 6 out of 10.

The decrease in parental attacks on expelled helpers could be due to (i) a random distribution of a more or less stable number of attacks on helper and competitors, or (ii) a deliberate re-acceptance of the helper by the pair. The low attack rates on the helper after the competitors' removal favours the second hypothesis. Parents make a clear difference between the expelled helper and strange fish of the same size (Fig. 5). The total number of attacks on the helper and competitors in each replicate was divided by the total number of attacked individuals. This mean attack rate per fish was compared to the number of attacks the helper received. In 14 out of 15 replicates the helper was attacked less often than would be expected if the pair did not differentiate between the former helper and other competitors ( $p < 0.005$ ; Wilcoxon test, one tailed). The same result applies when female and male rates are viewed separately.

This is especially interesting because the helper swam mostly in the midst of the group of strangers in the experiments with conspecific com-

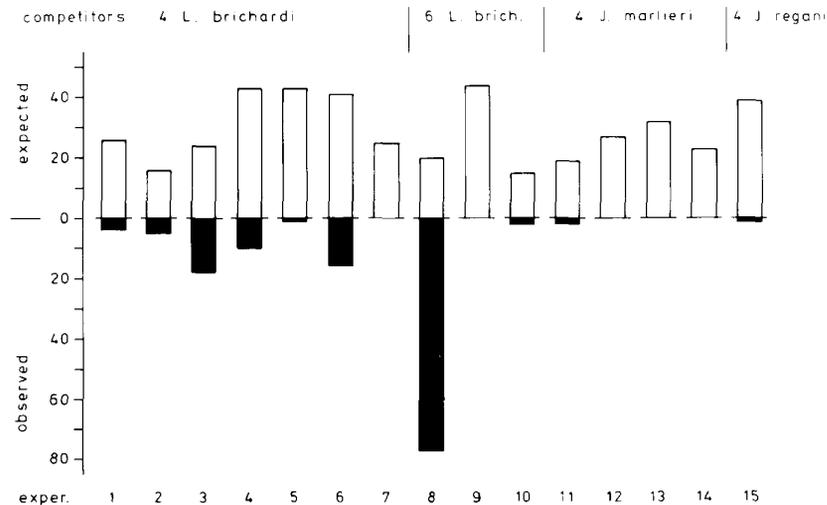


Fig. 5. Observed attack rates of breeders on their ostracised helper (black) compared to those expected (white); see text for how the expectation was derived. Abscissa: 15 replicates with different numbers and types of competitors (see above line). Ordinate: no. attacks/protocol.

petitors. This is a strong indication of the parents' ability to recognize their helpers individually, though probably not by using behavioural cues as there was no clear difference between helper and competitors when thus grouped. Subsequently HERT (1985) has proved experimentally that breeders know their helpers—the first proof of this often assumed ability in cooperative breeding vertebrates.

As a result of the reduced attack rate, helpers were re-accepted into the territory in 11 out of 13 replicates. Some even helped care for the next brood of the pair, long after the competitors had been removed. (Two further replicates had to be terminated prematurely as the helpers had been seriously injured by the parents before the competitors were introduced). The ultimate reason for this re-acceptance is very likely the helpers' strong contribution in territory defence. The breeders' preference for the expelled helper to strange young of the same size is presumably due to their information on their helper's reliability (its 'associate quality'; see WASSER, 1982). Usually the largest helper—the most frequently expelled—often defends the territory against space competitors, especially those of the same size range, whereas direct egg care is mainly performed by the smaller helpers (TABORSKY, 1982). In 5 out of 7

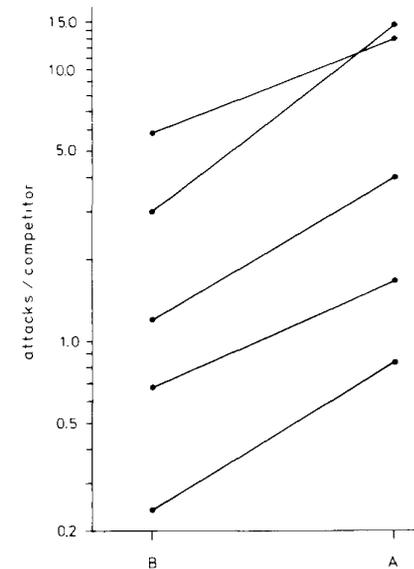


Fig. 6. Attack rates of helpers on competitors before (B) and after (A) the former were re-accepted in the breeders' territories, 5 replicates.

replicates the helpers' attack rates more than doubled after they were re-accepted (Fig. 6); two other helpers who were presumably strongly intimidated by their parents' aggression, did not attack at all and are therefore not in the graph.

Much larger helpers are usually found in storage tanks with strong intra- and interspecific competition than in those with little or no competition. This again suggests that parents tolerate helpers according to their needs. Additionally, young switching from family to aggregation in the field were on average slightly larger than those expelled in the laboratory experiments.

### The conflict of parents and helpers

Why, ultimately, do parents expel their largest helpers, although these are still willing to stay and share in various parental investments? The presence of large family members poses some risks to the owners of a territory, including parasitising the pair's reproduction, cannibalism on eggs, larvae and fry, the eventual loss of the territory to a helper and



competition for space (shelter) with fry and small young. All these risks increase with helpers' age, as (i)  $\bar{r}$  between territory owners and helpers decreases with time due to the natural replacement of breeders (TABORSKY & LIMBERGER, 1981), (ii) helpers become sexually mature and (iii) helpers' competitive ability increases as they approach the size of reproducing individuals. The important variables in helpers' cost/benefit relations may shift from 'kin-advantages', common to helpers and breeders, to 'individual advantages' that compete with the interests of the territory owners. The following section will examine separately the potential costs helpers pose to breeders.

#### Reproductive parasitism.

*Preliminary information.* Helpers 4-4.5 cm long may be sexually mature; dissection of such helpers caught in the field often revealed well developed ovaries and testes; in tanks fish in this size range often bred already: the smallest breeders were 3.4 (female) and 3.5 cm (male). Casual aquarium observations indicate that reproductive parasitism by helpers or reproductive competition of helpers and pair members may occur: in 1 out of 7 observed spawnings in families with large helpers a male helper turned into the spawning position next to the eggs only for a short time immediately after the pair had spawned. Another helper turned repeatedly into the spawning position when the pair was making intensive spawning movements without actual spawning. Both helpers were extremely submissive but tried hard to get close to the spawning site. In 5 out of the same 7 spawnings helpers were strongly attacked and held off the spawning site by one or both pair members shortly before the spawning (3 times mainly by the male, once by the female, once by both); the helper did not approach the spawning site in the two other cases. In other instances, one female spawned with her male helper and two males spawned with their female helper. In each case the faithless pair member attacked its former partner strongly, often joined by its "new partner", *i.e.* the former helper. One female even helped in caring for the eggs of its helper.

*Parental aggression throughout the spawning cycle.* A helper was 16 times more likely to be expelled on the day of spawning than between reproductive cycles (Table 1). This results from an analysis of 55 independent experiments in which in 66 instances one or several helpers were expelled by the pair members (N = 82 individuals; each expulsion event was

TABLE 1. Relative probabilities ( $p_{rel}/day$ ) of helpers' expulsions in the breeding cycle, standardized for the period between broods ( $p = 1$ ). The distribution is non-random ( $p < 0.001$ ,  $\chi^2$  one-sample test calculated with original data, broodcare period pooled). N days: durations of the different periods (which were chosen arbitrarily).

|                       | before spawning | day of spawning | eggs | larvae | freesw. fry | fry  | between broods |
|-----------------------|-----------------|-----------------|------|--------|-------------|------|----------------|
| N days                | 7               | 1               | 2.5  | 5      | 3.5         | 8    | 20             |
| $\frac{p_{rel}}{day}$ | 1.73            | 16              | 2.67 | 2.93   | 2.27        | 1.33 | 1              |

counted only once, no matter how many individuals were expelled in its course). This strongly suggests reproductive competition between territory holders and their helpers. However, expulsion probability remained high when eggs, larvae or freeswimming fry were present ( $p < 0.01$ ,  $\chi^2$  one-sample test; broodcare period compared with all other stages, day of spawning omitted). The increase before spawning was not significant.

*Predictions.* If the reproductive parasitism of helpers is an important variable in the evolution of this helper system, several predictions can be made for the behaviour of the territory owners. If pair members know the sexes of their helpers:

- each territory owner should mainly expel helpers of its own sex;
- male helpers should be expelled first—the size distributions of expelled male and female helpers should therefore be different and the sex ratio of expelled helpers should be male biased. This is because the costs for male breeders are probably higher (through fertilizations stolen by a helper) than those for female breeders (through eggs added by a helper).

If pair members do not know the sex of their helpers (there are some indications that adults have difficulty in recognising the sex of potential partners; presumably sex is identified by behavioural cues):

- pair males should be more likely than pair females to expel helpers. The reasons are (i) higher costs for male breeders (see (b)) and (ii) a higher expectation of male helper parasitism, as this is easier and less costly (sperm versus egg production) for males.

TABLE 2. Ratio of female to male attacks against expelled female and male helpers (n.s.; Fisher test). Numbers denote independent replicates

| attack r.                 |     | H = |    | N  |
|---------------------------|-----|-----|----|----|
|                           |     | ♀   | ♂  |    |
| $\frac{\sigma}{\rho} > 1$ | > 1 | 5   | 7  | 12 |
|                           | < 1 | 3   | 3  | 6  |
| $\frac{\sigma}{\rho} = 1$ | = 1 | 2   | 2  | 4  |
|                           | N   | 10  | 12 | 22 |

*Test of prediction (a).* Female and male attack rates on 22 expelled helpers of known sex were recorded in various experiments immediately after their eviction from the territory had been recognised. The ratio of female to male attacks (Table 2) reveals that pair members did not preferentially attack helpers of the same sex.

*Test of prediction (b).* The sex ratio of all helpers of known sex used in the experiments which were controlled for evictions of helpers was 1:1 (28 females:28 males). Nineteen female and 20 male helpers were expelled and the size distributions of the former and latter did not differ (= sizes measured at the time of expulsion; Kolmogorov-Smirnov two-sample test with  $\chi^2$  approximation, n.s.; Fig. 7), *i.e.* male helpers were not expelled earlier. In the graph I distinguished between helpers which had already participated in direct broodcare (= H cl. e.), and those which had not been observed in direct broodcare yet (often, because they were evicted from the territory before the pair's first brood). The sex ratio of expelled helpers which had shared in direct broodcare was 9 females:8 males (in all 16 female and 17 male helpers were observed participating in direct broodcare), and the sex-specific size distributions also did not differ from each other when these helpers were expelled (Kolmogorov-Smirnov test, as above; see Fig. 7).

*Test of prediction (c).* The ratio of female to male attack rates on 50 helpers (sex ratio as in (b)) was measured at the time of their expulsion.

The female mainly attacked in 24 cases, the male in 19 and both about equally in 7. The attack frequencies of parents on expelled helpers were recorded in detail for 15 replicates in 12 min protocols immediately after the expulsion (Fig. 8a). In 5 replicates there were more female attacks, in 8, more male attacks (in 2 further cases helpers were not attacked during the protocol time, they are not included in the graph). In 7 replicates the male showed relatively more overt versus suppressed attacks than the female, in 2 replicates it was the other way round (Fig. 8b; this difference was not significant;  $p > 0.1$ , Wilcoxon test). There is also a tendency for males to perform more overt than suppressed attacks against strange competitors of helper size than females do.

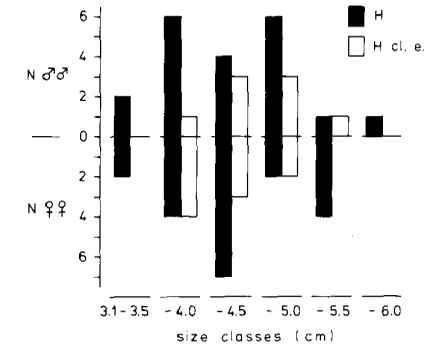


Fig. 7. Size distributions of female (down) and male helpers (up) when expelled from the territory. See text for distinction between helpers (H) and helpers which had cleaned eggs before (H cl. e.).

Only the field results produced evidence for the predictions: the female:male ratio of the largest (4-5.6 cm), presumably sexually mature helpers was exactly 2:1 (10 females, 5 males) whereas that of aggregation members was exactly 1:2 (15 females, 30 males). This is a significant difference ( $p < 0.05$ ,  $\chi^2$ -test). It was probably due to breeders' expulsions of helpers (neither expulsions nor voluntary emigrations of helpers were observed in the field). In conclusion, there is evidence of large helpers occasionally parasitizing on the reproduction of territory holders, but the importance of this factor is not completely clear. The experimental results suggest that reproductive parasitism is probably not the sole nor major ultimate reason for the conflict between pair members and their helpers.

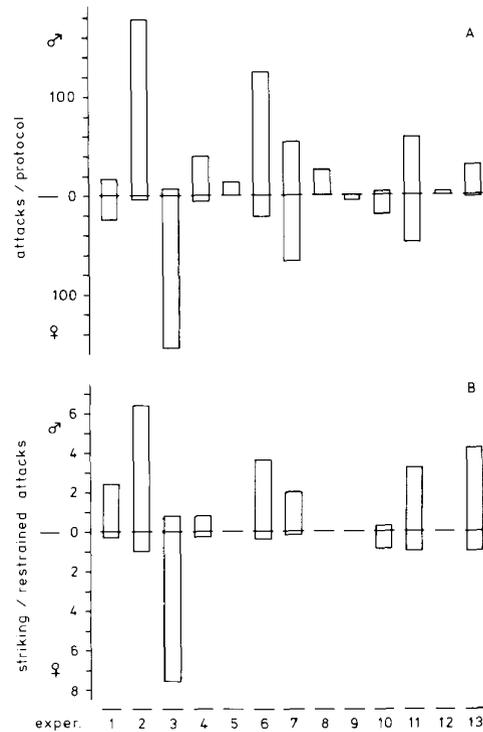


Fig. 8. A: Attack frequencies of females (down) and males (up) towards their helpers when these were expelled. Abscissa: 13 replicates. B: Ratios of striking/restrained attacks of females and males on helpers (see A).

### Cannibalism.

*Preliminary information.* Helpers could easily feed on eggs, larvae or small fry without any significant searching or handling costs. Cannibalism is widespread in fish (DOMINEY & BLUMER, 1984): conspecifics are nutritious. Conspecific eggs or larvae introduced into a strange tank are usually fed upon by *L. bichardi*, including fish of helper sizes, especially if these are not subordinate (see TABORSKY, 1982, Fig. 56, for a demonstration of cannibalism). SIEMENS (1984) showed in an experimental analysis that dominance is the principal factor determining whether young up to a certain size clean or eat strange eggs.

110 broods of more than 50 different pairs with helpers present were observed systematically during broodcare. Helpers cannibalized the eggs

of the breeding pair in 3 cases: this was done once by a family member with no caring experience (it was immediately chased away by the dominant helper) and twice by a dominant helper, hesitantly followed by a subdominant one (perhaps following its example). On two occasions a cannibal helper later cared for subsequent eggs of the same pair. Eggs were always eaten very quickly and secretively, and this was followed by very submissive behaviour in front of the female. She aggressively attacked helpers found feeding on eggs, showing clearly that the females distinguish cannibalism from egg care. However normal egg care includes feeding on eggs and larvae destroyed by bacteria and fungi, so perhaps on these occasions healthy eggs are sometimes also ingested. In addition, the increased probability of a helper's expulsion during the broodcare period (Table 1) could point to the importance of cannibalism.

*Predictions.* If cannibalism was important in the evolution of this helping system, three predictions can be made:

a) helpers should cannibalize eggs to which they are not closely related. They should therefore leave their natal territory and try to be accepted elsewhere. This is not the case (TABORSKY & LIMBERGER, 1981; TABORSKY, 1982);

b) the proportion of eggs surviving the broodcare phase (*i.e.* the relative breeding success of the territory owners) should be on average lower in broods with helpers than in those without. This is not the case (TABORSKY, 1984);

c) the  $\bar{r}$  between potential cannibals and victims within families declines with the age of helpers; large helpers should therefore reduce the pair's breeding success in comparison to small ones. Instead there is a positive—though not significant—relationship between helper's sizes (1.9–4.8 cm) and females' relative breeding success when their offspring reach the freeswimming stage ( $r_s = 0.245$ ,  $N = 18$ ; Spearman rank correlation coefficient;  $t = 1.01$ ).

Cannibalism does occur, but is obviously rare and is probably only a marginal influence on the cost/benefit ratios of breeders and helpers. Cannibalism is certainly restricted by the mother's aggression towards helpers: after spawning females attack their helpers heavily when they try to approach the eggs. Helpers usually respond with very intense and frequent submissive behaviour (tail quivering) and thus finally reach the eggs. Female aggression declines if they actually clean the eggs and surrounding substrate.

### Competition for the territory.

Large, sexually mature helpers might expel a parent or take over a part of the territory. If so one would expect (i) helpers to be sometimes about the same size as breeders, (ii) mutual aggression between helpers and breeders, and (iii) the largest helpers eventually taking over the territory, at least if the same-sex parent disappears.

Field observations revealed that helpers were smaller than territory owners. All pair members were  $\geq 5.6$  cm long (females: mean = 5.95,  $N = 26$ ; males: mean = 6.20,  $N = 25$ ) apart from one female (5.3 cm) of an unstable and dubious family. Only 11 out of 233 helpers (= 4.7%) from 35 families were  $\geq 5$  cm. The two largest helpers were 5.6 cm. The minimal size difference between helper and breeder in 58 families was 4 mm. This still allows unequivocal dominance relations (within families a size difference of 1 or 2 mm usually determines status). In 2 out of the 58 families an individual of the same size as the breeding female had regular contact with family members, but was hardly ever within their territory. These may have been former helpers.

Helpers show virtually no overt aggression towards their territory owners because of the size difference; indeed even the largest helpers are very submissive.

The third prediction also does not fit: helpers in the field do not take over vacant breeder-positions (TABORSKY, 1984), probably because of excessive competition: larger conspecifics are always present (*i.e.* aggregation members and breeders from other territories), as is interspecific pressure.

This all suggests that competition for the territory is of minor importance to the helper/breeder relationship. The reason is obviously helper's size: even the largest helpers are not able to compete for a territory, either with their territory owners or with non-family competitors. Perhaps this is ultimately caused by the early, "preventive" expulsion from the territory by the breeders? There still remains a small risk for breeders: helpers may eventually pair with their partner, as happened in 3 experimental situations in the laboratory (described above in the section on reproductive parasitism).

### Competition within the territory.

The major benefit for helpers is, presumably, to be able to stay in a protected territory, with free access to shelters (TABORSKY, 1984). Competition for these shelters may occur within expanding families as:

i) there is often only a limited number of shelters within the territory, sometimes only one or two;

ii) all family members occasionally hide in these shelters, individuals  $> 5$  cm mainly during the night;

iii) with increasing size, helpers simply require more space and this conflicts with the needs of territory owners as well as smaller young and fry;

iv) helpers' needs for shelter decrease as their size increases, especially after  $\sim 4$ -4.5 cm, when they are no longer endangered by their main predator, *L. elongatus*. These large helpers compete with less competitive young which have greater need of safe shelter.

I separated the territories found in the field into 3 classes: those with very few shelters (1 or 2 holes or clefts;  $N = 8$ ), with an intermediate number of shelters ( $N = 8$ ) and with many shelters (= in rubble areas;  $N = 9$ ). I predicted that the number of helpers and the size of the largest helper would increase with the amount of available shelter. This was confirmed by the data: the mean numbers of helpers  $> 2$  cm per family were 3.9, 5.9 and 7.8 respectively (H-test:  $p < 0.02$ , one tailed). The largest helper present in a family was a mean of 3.9, 4.5 and 4.7 cm (H-test:  $0.05 < p < 0.1$ ; there was a significant difference between the few-shelter class and the many-shelter class;  $p < 0.05$ ; U-test, one tailed). This indicates intra-family competition for shelters, but I have no experimental data to confirm it.

The analyses and arguments presented in this section suggest that not a single cost factor for breeders, but rather a combination of intra-territorial space competition and the risk of reproductive parasitism and cannibalism could be the ultimate reason for breeders' expulsion of helpers.

### Discussion

The ultimate causes for breeder-helper conflict in *L. brichardi*. The amount of aggression breeders impose on their helpers is determined by helper's size, breeder's stage in the reproductive cycle, and competition from outside the territory. There are four hypotheses which could account for this aggression and for the breeders' expelling helpers from the territory; these hypotheses are not mutually exclusive.

1) "Misdirected aggression". The mechanism of parental aggressiveness, well adapted for the natural situation, was perhaps en-

croached upon by the artificial experimental setup. The level of aggression may change within the reproductive cycle, reaching its peak around spawning and when there are eggs, larvae and freeswimming fry. There were usually no competitors present in the experiments except, in a few instances, ostracised conspecifics of helpers' sizes (TABORSKY, 1984). This lack of contestants might have been why the increased over-all aggressiveness of parents around spawning was directed against helpers. This hypothesis is not compatible with some of the results found: (i) the frequency of all aggressive interactions of breeders with all family members does not change in a comparable way to their probability of expelling helpers (TABORSKY, 1982, Fig. 16 and p. 49). (ii) only the largest helper was expelled, and neither small helpers (< 3 cm) nor the breeder's partner were attacked in this way. (iii) when strange young of the helper's size were introduced, the breeders demonstrated clearly that they can and do differentiate between their own helper—even when already expelled—and competitors from outside the territory. (iv) large helpers in storage and experimental tanks, where families were not isolated from other conspecifics or species, were also occasionally expelled (although usually when they were already a bit larger; see (2), below). I therefore feel that this hypothesis can be disregarded as an explanation for the breeders' expulsion of helpers.

2) "*Dispensable help*". As helpers grow their contribution shifts from direct broodcare to territory defence (TABORSKY, 1982). Perhaps therefore large helpers were not needed in an experimental situation lacking inter-territorial competition (resembling marginal territories in the field, e.g. territories 17 and 19 in LIMBERGER, 1983, Fig. 2). This hypothesis may explain (i) why larger helpers were tolerated in tanks with other conspecifics or other species (= competitive situations); (ii) why expelled helpers were reaccepted when competition was introduced; and (iii) why helpers in the field were, on average, slightly larger when shifting from family to aggregation than were laboratory helpers when expelled from the family. This hypothesis needs additional assumptions to explain (i) why helpers are expelled at all; (ii) the distribution of helpers' expulsions during the reproductive cycle (one would expect that help—if needed at all—would be most valuable to parents when they have eggs, larvae or small fry); and (iii) why females are so specifically aggressive towards helpers which approach a new clutch for the first time.

3) "*End of prolonged broodcare*". Helpers are well protected within breeders territories by larger family members (mainly the breeders) and

through having access to a shelter. There is a certain probability that helpers are former offspring of the breeders and therefore their toleration by the breeders is prolonged broodcare (ZAHAVI, 1974; LIGON, 1981; TABORSKY, 1982). This hypothesis may explain why only large (= old) helpers are expelled, as the probabilistic degree of relatedness ( $\bar{r}$ ) between breeders and helpers declines with helpers' age (TABORSKY & LIMBERGER, 1981). The hypothesis does not explain (i) why the parental aggression is dependent on the cycle; (ii) why parents (females) are so aggressive when helpers first approach their new eggs; and (iii) why helpers are expelled earlier when territorial competition is lacking (unless breeders take competition as an indication for increased predation pressure on their helpers).

4) "*Reproductive competition*". Helpers increase the reproductive success of their host breeders. As a helper's age increases,  $\bar{r}$  and, consequently, the advantage of helping to rear the breeders' offspring decreases. In terms of gene replication it may pay sexually mature helpers ( $\sim 4$  cm;  $\bar{r}$  to breeders' eggs  $\sim 0.35$ ; TABORSKY & LIMBERGER, 1981) to parasitize territory owners' breeding efforts by adding or fertilizing eggs ( $r$  to own young  $\geq 0.5$ , depending whether reproduction is with a parent) or to feed on breeders' eggs or larvae. The "common interests" of breeders and helpers may finally result in competition for the resources of a territory and from family investments. Breeders have a competitive advantage, as they are always larger than helpers. This hypothesis may account for (i) the increased expulsion rate of helpers when territory owners are breeding; (ii) the aggression towards helpers approaching a new brood for the first time; and (iii) the positive correlation between the probability of a helper's expulsion and its size (older helpers are more likely to behave selfishly). This hypothesis needs additional assumptions to explain why an increase in competition makes breeders more tolerant of helpers.

Obviously none of the remaining hypotheses (2, 3 and 4) can account exclusively for the phenomena described; this can only be accomplished by a combination of hypotheses 2 and 4 or 2, 3 and 4.

Cooperation of breeders and helpers versus "paying for staying".

I shall investigate how the hypotheses presented so far are related, using a graphical model of fitness costs and benefits, which changed with helper's age.



1) *Assumptions.* a) The ability of helpers to fulfill their duties increases with size: mouth size is definitely related to effective egg cleaning (*e.g.* small helpers cannot suck a whole egg at one time), removing sand and particles (the size of snails, *etc.*) and the increase in competitive ability is important for territory defence. My arbitrary assumption is that 4 cm helpers have almost acquired their maximum effectiveness ( $y = 0.97$ ; fish between 4 and 4.5 cm are capable of raising young of their own, without the help of others), while 2 cm helpers have two thirds ( $y = 0.67$ ) and 1 cm ones only about 20% ( $y = 0.18$ ) of their maximum effectiveness; the exact values are not critical for the model. I must stress that increase in ability is not due to learning: an experimental test showed that former helpers and naive controls breeding on their own did not differ in their ability to raise their first broods (TABORSKY, 1984).

b) Sexual maturity is achieved at a size of between 3.5 and 4.5 cm (for both sexes; TABORSKY, 1982).

c) The decisions of helpers and pair members depend on probabilistic degrees of relatedness ( $\bar{r}$ ) and not on the definite  $r$ . Helpers did not behave differently when one or both breeders were replaced, nor did the new breeders compared to their predecessors (TABORSKY, 1984).

d) The helpers' payoff for staying in their home territory will always be higher than that of living in an aggregation. This assumption is reasonable because (i) they gain protection in the territory (TABORSKY, 1984), (ii) they would have no chance of gaining their own reproductive territory anyway, due to competition with larger aggregation members and fish of other species and (iii) helpers try to stay whenever possible (see above, which possibly reflects this higher payoff).

e) For simplicity, I am assuming that helpers can only carry out one alternative at a time: they can either help or parasitize the breeders' reproductive effort.

2) *The payoff of helping versus parasitizing the breeders' reproduction.* The benefit of helping declines with a decrease in the degree of relatedness (Fig. 9, curve b). The assumed increase in the abilities of growing helpers (curve a) will, up to a certain size, reverse this tendency (see the product  $a \cdot b$ ). The helpers'  $\bar{r}$  to breeders' eggs drops to  $\sim 1/3$ , but they could obtain their own offspring through concealed reproduction in the home territory ( $r = 1/2$ ). Curve c shows the benefits of reproductive parasitism. Its shape is due to the attainment of maturity (see assumption (b)), the  $r$  to own offspring and the costs of producing germ cells. These costs, which may be rather low (see below), prevent the curve from reaching 0.5; their exact

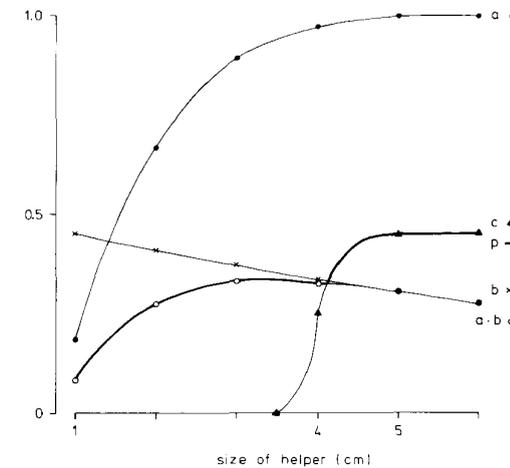


Fig. 9. The payoff helpers receive by helping compared to that for parasitizing the breeders reproduction. Abscissa: helper's size. Ordinate: relative benefit, besides for curve a. a = relative ability of helpers (1 = perfect ability). b = benefit derived from the effects of helping (= increased production by the breeders). Function assumed to be directly proportional to declining  $\bar{r}$  (derived from TABORSKY & LIMBERGER, 1981).  $a \cdot b$  = benefit from helping multiplied by actual ability to help at that size. c = benefit from reproductive parasitism, limited by attainment of maturity and by the costs derived from the production of germ cells (which may be rather low, see text). These costs prevent the curve from reaching 0.5). p = potential maximum payoff of helpers at the optimum (= helping or cheating, whichever is better).

value is not critical for the model as long as they do not reduce the helpers genetic payoff derived from own offspring to the level of  $\bar{r}$ , which is very unlikely. The effect of reproducing with a parent is disregarded as we do not know whether and to what extent the benefit of inbreeding—a further increase in  $r$ —is offset by deleterious effects. In any case, the higher  $r$  of helpers to their own young would strengthen the conclusions drawn. Curve p shows the maximum possible relative payoff of helpers. Helpers should switch from pure helping to reproductive parasitism when they reach the size indicated by curve c's intersection with the product curve ( $a \cdot b$ ).

3) *The payoff of staying as a function of risk and growth.* Young which remain in their natal territory are well protected, but grow more slowly. The relative benefits for staying (Fig. 10, curve a) are assumed to decline steadily because the helpers' costs (in terms of a reduced growth rate) in-

crease with size: the regression of helpers' growth rate (g/day) differed from that of aggregation members for the size range tested (2.5-4.5 cm;  $N_1 = 19$ ,  $N_2 = 18$ ;  $F = 7.769$ ;  $p < 0.01$ ). The benefits for staying will decline rapidly when the helpers pass the size at which they are no longer preyed upon by *L. elongatus* (~4-4.5 cm). Breeders' tolerance of helpers can be viewed as prolonged broodcare (see above); their benefit parallels that of the helper, devalued by  $\bar{r}$  (curve b in Fig. 10). A comparison of

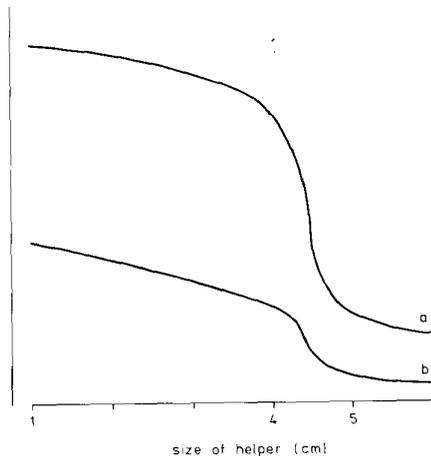


Fig. 10. The benefit from protection within a breeders' territory. Abscissa: helper's size. Ordinate: relative benefit. a = the payoff to helpers as a function of helpers' size. b = the payoff to breeders, which is proportional to that of helpers, multiplied by  $\bar{r}$ .

curves a and b indicates that it may pay to expel helpers even if the helpers' cost/benefit ratio makes them prefer to stay. The figure does not predict the point at which helpers should be expelled. This is completely dependent on the helpers' behaviour, which in turn should be influenced by their payoff-function (see Fig. 9).

4) *Reciprocity between breeders and large helpers.* Helpers longer than 4 cm can hardly be preyed upon by *L. elongatus*, the most prominent predator of young. At the same size helpers become sexually mature and may parasitize the breeders reproductive efforts; maturity may also enhance the helpers' payoff for feeding on breeders' eggs, as they can immediately convert this highly nutritious material into germ cells. The common interests of helpers and breeders may develop in opposite directions when

helpers reach maturity. Cooperation will eventually change to a relationship characterized by reciprocal altruism (TRIVERS, 1971): the breeders will still tolerate their helpers, even at some risk (reproductive competition), if these helpers pay by sharing in the breeders' duties (see Gaston, 1978a) and hence increase their reproductive output. The helpers will invest in the breeders' offspring, even at some cost (reduced growth), to be further protected by the breeders' territoriality and by access to a shelter site. The donor's costs (*i.e.* breeders' risk of reproductive competition and helpers' delayed growth) are presumably lower than the recipients benefits (*i.e.* pronounced increase of helpers' survival chances and increased production of offspring by breeders; see TABORSKY, 1984).

TRIVERS (1971) remarked that the preconditions for the evolution of reciprocal altruism are similar to those for kin selection (see also ROTHSTEIN, 1980). Cooperative vertebrates fulfill many of these conditions (EMLEN, 1982; see LIGON, 1983, for a review of presumed reciprocity in cooperatively breeding birds). This prerequisite is, in *L. brichardi*, the existence of small and stable family groups, combined with individual recognition capabilities (HERT, 1985). It provides the opportunity for retaliating effectively against defection (AXELROD & HAMILTON, 1981). Breeders do react in this manner when helpers try to feed on eggs instead of cleaning them or when they try to approach the spawning pair. Perhaps the increased aggression of females towards helpers which approach a new clutch is to test whether a helper responds with submissive behaviour and investment. TRIVERS (1971) also implied that there is a time lag between the mutual acts of the participants in reciprocal altruism. This is certainly true here: breeders' defensive actions and helpers' care of the young are usually temporally separated from each other.

The evidence of "paying for staying" is: (i) young stay and continue to help indiscriminately when one or both breeders are replaced (TABORSKY & LIMBERGER, 1981; TABORSKY, 1982), despite their presumed capacity to recognise individuals (HERT, 1985). (ii) helpers stay as long as possible, even when their options are superoptimal (*i.e.* they could reproduce for themselves). This points to the cardinal importance of a safe territory. (iii) helpers above a certain size are tolerated only when needed: the amount of competition directly influences breeders' tolerance of their (large) helpers.

The model might be tested by comparing families in the presence of small predators which can only prey upon small helpers (*e.g.* <3 cm)

with families in the presence of very large predators which can prey upon large helpers ( $\sim 4.5$  cm). Helpers should pay less to stay in the first situation, where staying is less valuable than in the second. They should also start to cheat earlier. Territorial competition (*i.e.* the need for helpers) could also be varied to test the relative importance for breeders of the helpers' payment and prolonged broodcare.

There is a very striking coincidence between the sizes at which helpers' predation risk drops and when they become sexually mature. If it is not for a physiological constraint then there are two possible reasons for helpers becoming sexually mature at about 4 cm, and not earlier. (i) The costs of producing germ cells may be too high compared to the size-limited output. However, comparison of the growth of independently breeding fish with that of equally large helpers did not show that egg and sperm production resulted in a decreased growth for the former (TABORSKY, 1984). Also, there is no evidence that male helpers attain maturity earlier than female helpers, although sperm is presumably less costly than eggs. (ii) Helpers may be selected to avoid the risk of being expelled by the breeders when they are endangered by *L. elongatus*. This would only be an appropriate interpretation if breeders could control their helpers' behaviour phenotypically (pure genotypic control would merely result in evolutionary dead ends). There is good evidence for phenotypic control of helpers by breeders (see above).

Current models of conflict between parent and offspring or breeders and helpers.

1) According to TRIVERS' (1974) model conflict can be expected between *L. brichardi* breeders and  $\sim 4$  cm long helpers whenever  $c < b < 3c$  (when  $c$  = donor's costs and  $b$  = receiver's benefits and if  $\bar{r}$  is assumed to be  $\sim 1/3$ ) and for 2 cm helpers only when  $c < b < 7/3c$  (if helpers' age is assumed to be 125 d and  $\bar{r} \sim 3/7$ ). A 4 cm helper's altruistic act towards breeders' eggs or larvae may be viewed as payment when its  $c/b$  ratio is between 1 and 3. Toleration and active protection of large helpers can be viewed as an additional investment by breeders aiming at gaining the aid provided in turn by helpers.

2) EMLEN (1982) discussed conflict in cooperative breeders: when the auxiliary gains and the breeder loses helping reduces the incremental cost to the breeder and thus minimizes the chances of the helper's expulsion (for a different presentation of a somewhat similar idea, see BROWN, in press). EMLEN expects this "less common" type of conflict in "species

with specialized ecological requirements, residing in a stable, predictable environment", species for which the option of independent breeding is consistently unavailable to the helpers. This is exactly the case with *L. brichardi*. Although many cooperatively breeding species fulfil similar criteria, there are, surprisingly, no other instances as yet reported in which this type of conflict had been explicitly established.

3) VEHCAMP (1979, 1983a & b) used an optimization model to show that high degrees of relatedness and low "dispersal chances" allow high levels of reproductive bias within social groups, culminating in the sole reproduction of dominants in species with helpers-at-the-nest. The model assumes that a subordinate's only strategy to avoid being manipulated is to leave the group, *i.e.* it does not allow for "cheating", expressed as a concealed parasitism on the dominants' reproductive effort. Therefore it is unsuitable, in its present form, for this case.

Breeder-helper conflict and reciprocity in other cooperatively breeding vertebrates.

Natural replacement of breeders causes the decline in  $\bar{r}$  for *L. brichardi*, and in Florida scrub jays (STALLCUP & WOOLFENDEN, 1978; WOOLFENDEN, 1978), jungle babblers (GASTON, 1978b), grey-crowned babblers (BROWN & BROWN, 1981a), Mexican jays (BROWN & BROWN, 1981b), splendid wrens (ROWLEY, 1981), green woodhoopoes (LIGON & LIGON, 1983) and for the 'primary helpers' in pied kingfishers (REYER, 1984). This may lead to conflict: in scrub jays, for example, the most intense aggression comes from step-fathers against step-sons. As in *L. brichardi*, aggression occurs mainly during copulation time (WOOLFENDEN & FITZPATRICK, 1977). But adult male helpers provide by far the most broodcare aid (STALLCUP & WOOLFENDEN, 1978), which may serve as payment for being allowed to stay. Similarly, ROOD (1978) found in dwarf mongooses that an immigrant female guarded "unrelated" young longer than did siblings and parents. Male pied kingfishers often try, by bringing food, to be accepted by several, "unrelated" breeders successively (= secondary helpers, REYER, 1980, 1984), perhaps the most elegant demonstration of a helper's 'payment'. Nevertheless, these male helpers are only tolerated by the step-fathers after the young have hatched and this may reflect the mated males' avoidance of reproductive competition.

I assumed that in *L. brichardi* reciprocal benefits predominantly shape the relationship of large, sexually mature helpers and breeders. This also

seems to be the case in green woodhoopoes, in which about 8% of helpers were not related to the nestlings they fed (LIGON & LIGON, 1983). Half of all breeders attained their status by inheriting the territory, or part of it, of the breeders they aided (LIGON, 1981). Additionally helpers may recruit their own future helpers when feeding other breeders' nestlings (LIGON & LIGON, 1978, 1983), a benefit also assumed for dwarf mongoose helpers (ROOD, 1978). The payoff of jungle babbler, Mexican jay, male Florida scrub jay and splendid wren helpers is mainly inheritance of breeding opportunities, as their habitat is saturated with conspecifics (GASTON, 1978b; WOOLFENDEN & FITZPATRICK, 1978; ROWLEY, 1981; BROWN & BROWN, 1984). Splendid wren male helpers additionally compete with male breeders: 2 out of 6 observed copulations were by helpers. Pied kingfisher secondary helpers took over the breeders site in 13 out of 16 cases and the female as their mate in 6 out of 16. Although these cases also show individual selection and "paying for staying" as presumably more important than kin selection, the helpers' main benefits clearly differ from those of *L. brichardi* helpers, for which protection is definitely more important than the inheritance of space or mate (TABORSKY, 1984).

Often the breeders' benefits are not as apparent as those of the subordinates they tolerate. In some species subordinates, usually the breeders' own offspring, do not help (*e.g.* mute swans, SCOTT, 1984, and references therein). In others, they do help the breeders, but without any measurable effect (*e.g.* in Arabian babblers, ZAHAVI, 1974; jungle babblers, GASTON, 1976; splendid wrens, ROWLEY, 1981; green woodhoopoes, LIGON, 1981). Breeders with helpers sometimes even have a lower reproductive success than those without (*e.g.* dunnocks, BIRKHEAD, 1981; the communal breeding pukekos, CRAIG, 1980; and prairie dogs, HOOGLAND, 1981, 1983). Why, then, do these subordinates help? Kin selection does not seem to be the reason. Nor can helping be viewed as "payment", unless the "helpers" are obligatorily cheating. Brown (in press) provides two possible explanations: an eventual, though never demonstrated increase of a helper's experience, and hypothetical benefits from the helper's "socialization", improved by the contact between helper and beneficiary (see also LIGON & LIGON, 1978, 1983). I want to propose a different hypothesis: Perhaps helping (*e.g.*, cleaning eggs) is simply a signal of submission, a kind of ritualized gesture. For example, there is a temporal and formal relationship (also with regard to releasing stimuli) in *L. brichardi* between some submissive behaviour and elements of broodcare (TABORSKY, 1982).

### Summary

This paper reports an experimental analysis of conflicting interests in the cooperatively breeding *Lamprologus brichardi* (Cichlidae). Helpers clearly prefer to stay in the family territory rather than leave for an aggregation of same-size young or for an unoccupied area—even when their chances of reproducing independently are superior to those in the field. Helpers usually attain independence when the breeders force them to leave the territory. Breeders' toleration of helpers depends on the stage in the reproductive cycle, the size of helpers and the need for helpers. Large, previously expelled helpers are reaccepted when competition is increased. In these circumstances breeders prefer their own former helpers to strange young. Experimental and field evidence suggests that 3 factors are ultimately important for the breeder/helper relationship: reproductive parasitism by mature helpers, eventual cannibalism on breeders' eggs and competition for shelter within the territory. A graphical model shows how the initially common interests of breeders and helpers develop divergently when helpers reach the size at which they become sexually mature and less susceptible to predation. Large helpers pay to stay. The relationship of breeders and large helpers meets the criterion of reciprocal altruism.

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### Zusammenfassung

Die Präferenzen brütender Tiere und ihrer Helfer wurden an dem sozialen Cichliden *Lamprologus brichardi* experimentell untersucht: Helfer ziehen das Familienterritorium einem unbesetzten Gebiet oder einer Ansammlung gleich großer Artgenossen vor. Dies gilt auch dann wenn sie die Möglichkeit haben, im unbesetzten Gebiet selbst zu brüten. Die Aggression der Territorienbesitzer sorgt für die Ablösung der Helfer von ihrem Heimgebiet. Der Zeitpunkt der Vertreibung hängt vom Fortpflanzungszyklus, der Größe der Helfer und dem Bedarf an Hilfe ab. Bei Erhöhung der Konkurrenz werden große, bereits vertriebene Helfer wieder aufgenommen; eigene Ex-Helfer werden dabei fremden Artgenossen der selben Größe immer vorgezogen. Der Konflikt zwischen Helfern und Brutpaar wird besonders beeinflusst durch die Gefahr von Fortpflanzungsparasitismus geschlechtsreifer Helfer, gelegentlichem Kannibalismus großer Helfer an Eiern des Brutpaars und vermutlich auch durch Konkurrenz um Versteckplätze im Territorium. Ein graphisches Modell veranschaulicht, wie sich anfänglich gemeinsame Interessen von Brutfischen und Helfern auseinanderentwickeln wenn letztere die Größe erreichen, mit der die Geschlechtsreife einsetzt und die Feindgefährdung drastisch abnimmt. Die Beziehung zwischen Brutfischen und ihren großen Helfern kann als reziprok altruistisch angesehen werden, wobei letztere mit ihrer Hilfe dafür bezahlen, im Territorium bleiben zu dürfen.