

Helpers in Fish

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Summary. Field data show that in the cichlid fish *Lamprologus brichardi* conspecifics other than the reproducing pair help in brood care and territory maintenance. The expected degree of relatedness between helpers and the eggs or larvae they tend lies between 0.25 and 0.5, decreasing with the helper's age. This decrease might influence the point of time at which helpers depart. Five other endemic Lake Tanganyika cichlids showing rather similar helping behaviour are described.

Introduction

Since Hamilton's influential work in 1964 much attention has been paid to seemingly altruistic behaviour in animals. Cases of 'helpers at the nest' in many bird species and of helpers or 'aunts' in carnivorous mammals and primates are being described more often in the literature (Reyer 1980; Macdonald 1979; Hrdy 1976). As for cold-blooded vertebrates, Wilson (1975) wrote: "But for some reason... they have not evolved cooperative nursery groups..." However, in a few parental cichlid species joint defence of neighbouring schools of young or adoption of strange fry have been observed (McKaye and McKaye 1977; Ribbink et al. 1980; Ward and Wyman 1975). Similarly, based on qualitative field observations Brichard (1978) suggested 'communal nurseries' in *Lamprologus brichardi*, a Lake Tanganyika cichlid. In contrast to his suggestion our detailed field analysis on the same species documents brood-care helpers and preferential investment in close kin; this provides the first known example within the vertebrates below the organisational level of birds. Some other endemic Tanganyika cichlids of the genera *Lamprologus* and *Juli-dochromis* resemble *L. brichardi* in their breeding system.

Methods, Results and Discussion

Our observations were made in Burundi (summer 1978) mainly by scuba diving in 3–10 m depth. Some 200 fish were marked individually by injecting alcian blue into scale pouches. In three instances, noted in the text, additional information was used from the laboratory, where an estimate of costs and benefits for helpers and parents is still running, measuring reproductive success in various experimental situations. Helpers in this species were previously observed in the aquarium by Kalas (1975, 1976).

L. brichardi is a monomorphic substrate brooder growing up to 6.5 cm standard length (maximum size in the field). A reproductive group (family), usually male, female and young of up to four different size classes, shares a common shelter site, where eggs and larvae are tended. 'Young' here means any individual smaller than the reproducing pair members, i.e. from free-swimming fry up to sexually mature fish ≤ 5.5 cm. An area of about 30 cm in diameter around the shelter site is defended. Occasionally one male monopolizes two female territories (harem). Pairs stay together for several broods.

Of 60 families analysed, 3 had no young, 5 had young of one age (i.e. size) class; in 13 families two age classes were present, in 25 families three and in 14 four classes. The mean number of young per family was 7.5 ± 1.42 ($\bar{x} \pm 2$ SE, i.e. 95% confidence interval; $n=60$). With increasing size of the young, their number per size class declined, e.g. ≥ 5 cm there were only one or two (if any) young per family.

Young participate in territory defence against conspecifics and other species. They also remove snails and particles from the shelter area, dig, and clean eggs and larvae. The behaviour of each individual in 15 families was recorded (3×4 or 3×8 min/1 day). Mean defence frequencies/10 min of females, males and young of two size classes are listed in Table 1

Table 1. Medians (*M*) and quartile deviations (*QD*) of 10-min defence frequencies of pair members, medium-sized (3.5–4.4 cm) and large (4.5–5.4 cm) helpers (*hh*)

| | <i>M</i> | <i>QD</i> | <i>n</i> |
|-----------|----------|-----------|----------|
| Females | 1.87 | 1.35 | 15 |
| Males | 1.04 | 0.86 | 14 |
| Medium hh | 0.83 | 1.46 | 13 |
| Large hh | 3.33 | 1.35 | 9 |

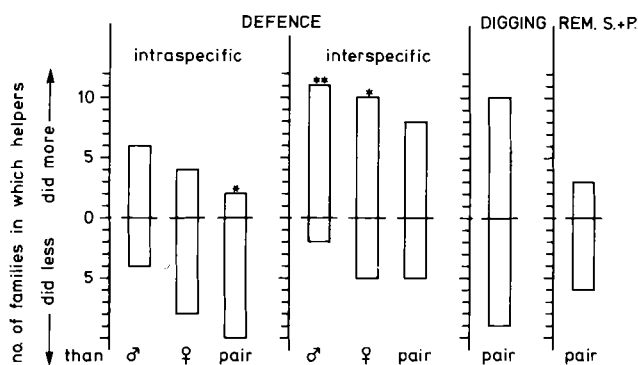


Fig. 1. Relative amounts of territorial defence, digging, and removing snails and particles (REM. S.+P.) done by helpers and pair members within families. Defence frequencies derived from behavioural protocols on 15 families (see text), data on digging and REM. s.+p. were collected during all field observations on more than 60 families. *, ** Difference from 50:50 significant with $P < 0.05$ and ≤ 0.01 respectively (Walsh test)

(all defence behaviours pooled). The larger the young, the more they defend ($P < 0.001$; three size classes; Kruskal-Wallis one-way ANOVA). The largest helpers (4.5–5.4 cm) contribute significantly more than pair-males ($P < 0.05$; Mann-Whitney *U*-test). Irrespective of size, helpers defend more often against interspecific intruders than against conspecifics ($P < 0.01$; Wilcoxon matched-pairs signed-ranks test). Comparatively, the pair-members showed more attacks on conspecifics (Fig. 1). Females performed more defence than males, but this difference was not significant with the data on hand ($P = 0.06$; *U*-test). Interspecifically, within families females defend more often than their mates ($P = 0.05$; Wilcoxon test), intraspecifically more often than small and medium-sized helpers (≤ 4.4 cm; $P = 0.01$; Walsh test).

As far as species could be identified, 83% of the helpers' defence was against space (hole) competitors (*Telmatochromis temporalis*, *T. bifrenatus*), 17% against the main predators of young < 4 cm (*L. elongatus*) and eggs (*Mastacembelus flavidus*).

Where family shelters are threatened by sand drift, digging is vital. An analysis of families differently exposed to sand showed a higher mortality of young < 3 cm in the more exposed families during a stormy period ($P < 0.02$; Kruskal-Wallis ANOVA). Digging bouts are usually performed by one or two family

members at a time. Family young dug and removed snails (probably egg predators) and particles, roughly as often as pair members (Fig. 1).

The cleaning of eggs and larvae could not be observed in the field because they are completely hidden in holes and crevices. But in the aquarium cleaning is performed about equally often by females and helpers while males hardly participate.

Helpers and beneficiaries (eggs, larvae or free-swimming fry) are assumed to be closely related. Although fry of up to 1 cm sometimes change between territories in the aquarium, this will hardly ever occur in the field, where neighbouring territories are too far apart. This is derived from the following data: The average distance between the nearest family shelters (territory centres) is 79 ± 9.8 cm ($\bar{x} \pm 2$ SE, i.e. 95% confidence interval; range: 30–220; $n = 63$ families). In four families the distances of 22 young (< 1.5 cm) from their home shelters were noted (16 samples at 15-s intervals, three times/1 day). The median distance that the farthest-ranging individuals strayed was 4.6 cm (range: 0–20 cm).

Family young ≥ 1.5 cm are extremely aggressive towards strange conspecifics, especially those of corresponding size. Strangers ≥ 3.5 cm are also chased away by pair members. To investigate any interfamily exchange of young, 27 families were observed for an average period of 4 weeks. They had a total of 267 young, most of them individually recognizable by size and many also by natural or artificial markings (fin clipping, colour marking). There was no evidence that young switched families, nor that strange individuals were adopted. Of 22 young (1.8–5.2 cm) released in or near strange family territories, none was accepted.

Young remained in the territory when one or both parents were naturally or experimentally replaced. Therefore, the mean degree of relatedness between helpers and beneficiaries (\bar{r}) also depends on the replacement rate of pair members. Of 60 paired adults watched without observer manipulation for a mean period of 26 days/adult (1,566 fish-days in total), only one female and one male disappeared (except that one whole family disappeared with its young). This replacement rate reduces the expected \bar{r} below that of full siblings, dependent on a helper's age (Fig. 2). Seasonal differences in the replacement rate seem unlikely because lake temperature and light – dark cycle are constant; *L. brichardi* breeds throughout the year. But we do not know if there are reproductive peaks and/or annual oscillations in food abundance.

A few field data indicated that growth rates in the field were slightly slower than in the laboratory. Aquarium data corrected for this difference suggest that at 4 cm fish (already sexually mature) will be about 280 days old, $\bar{r} \approx 0.35$. At about this size the number of helpers staying in families declines rapidly.

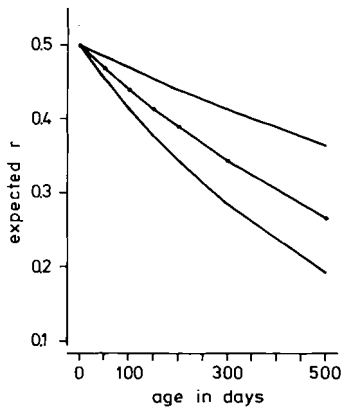


Fig. 2. Probabilistic degrees of relatedness between helpers and beneficiaries (eggs) as a function of a helper's age. Calculation of expected $r = 2 \left((1-p)^n \frac{1}{4} \right)$.

p = daily probability of disappearance per parent (central curve: $\frac{2}{1566}$ = measured replacement rate; upper curve: $\frac{1}{1566}$; lower curve: $\frac{3}{1566}$); n = helper's age in days; $\frac{1}{4}$ = coefficient of relatedness between helpers and beneficiaries through a single parent

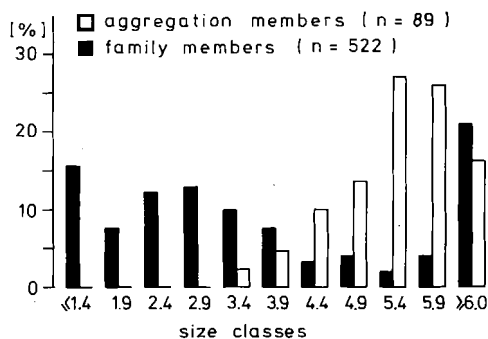


Fig. 3. Size distributions (abscissa: size classes in cm) of family and aggregation members, illustrating a shift of helpers to independent status centred around 3–5 cm standard (body) length. For family members in the 5.5–5.9 cm class, there is an overlap of the largest helpers with small pair members; above 6 cm only pair members were found within families

Few helpers stay up to 5.5 cm, being then approximately 500 days old ($\bar{r} \approx 0.25$).

Young leaving the family join non-reproductive aggregations (Fig. 3) of a few to several hundred fish. These remain localized, and individuals rarely switch between them. The aggregations are frequently visited by family members swimming up from their territories to feed on plankton. In contrast to families, members of aggregations do not usually have individual shelter sites. As the size distributions illustrate (Fig. 3), some of the largest individuals still live in aggregations, but many of them manage to obtain a territory and mate.

It is still unknown which evolutionary force leads to the prolonged stay of young in their natal territories and investing in brood care and territory maintenance in favour of progeny other than their own. It could either be the advantage of providing care to close kin, or any individual advantage, for example

the protection enjoyed in the parents' territories, an increased chance to replace a parent and breed by oneself, or a gain in brood-care experience. Results of experiments dealing with this aspect will be provided at a later date.

Similar forms of helping occur in other closely related cichlid species, although social systems of some vary greatly (unpublished observations). As yet, non-reproductives helping in direct brood care could be observed in *L. pulcher*, *Julidochromis ornatus*, *J. regani* and *J. marlieri* in the laboratory. Helpers joining in territory defence were observed in *L. pulcher*, *J. regani* and *J. marlieri* in the laboratory, and in *L. savoyi* and *J. marlieri* in the field. As to the *Julidochromis* species, data confirm laboratory observations by Kalas (1975; partly cited by him from G. Ritter, personal communication).

Subdominant male anemonefish, *Amphiprion akallopisos*, were referred to as helpers by Fricke (1979), as they defend a host anemone jointly with a breeding pair. But so far they have not been seen to participate in brood care nor in defence against egg predators.

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