

SOCIAL BEHAVIOUR OF LAMPROLOGUS SPECIES : FUNCTIONS AND MECHANISMS

by

M. TABORSKY, E. HERT, M. V. SIEMENS, P. STOERIG

Max-Planck-Institut für Verhaltensphysiologie
D-8131 Seewiesen, West Germany

Introduction

This paper summarizes major aims and results of our recent studies on the behaviour of 5 Lamprologus species. L. brichardi is a small substrate breeder with an extraordinary degree of sociality (Taborsky & Limberger 1981, Taborsky 1984). Here we report experiments on the coordination and task sharing of family members with regard to size and status, the regulation of intra-family interactions by individual recognition and the mechanism controlling broodcare behaviour of helpers. Observations of 4 snail breeding species aimed at a comparison of habitat preferences and mating structure. Experiments tested the influence of experience on decisions in intraspecific encounters of juvenile L. meeli.

Methods

L. brichardi were kept in tanks as described by Taborsky (1984). Task sharing was measured in 500 l tanks, each with a pair and 2 - 4 helpers of different sizes. One corner, which was separated from the major part of the tank by an opaque partition, contained the 5 most prominent competitors and predators as known from the field: (from left to right in fig. A, B and C; mean sizes are given on top of these figures) small and large Julidochromis marlieri or Telmatochromis temporalis, large L. elongatus, and small and large conspecifics. These "intruders" were successively introduced into the main compartment within a transparent glass tube for experimental periods of 30 min. Broodcare, territory maintenance, displays and overt attacks of pair and helpers were recorded. 9 replicates of this experiment were performed, each with a different set of individuals. Additional control replicates tested pairs without helpers.

A similar setup was used to test the breeders' reactions towards own and strange helpers and control "non-helpers" of equal sizes. In another setup a one-way-foil allowed breeders to see the helpers and controls in an adjacent tank, but not vice versa (33 l tanks; see Hert, 1985 for details).

To find the crucial factors controlling egg care, i.e. cleaning instead of cannibalizing eggs, clutches were exposed within the home shelters of breeders or young and their reactions were recorded (33 l tanks; see Siemens, 1984 for details).

11 - 12 specimens of the 4 snail breeding species were kept together for 22 months in a circular 7000 l tank (9 m²) equipped with 4 types of ground cover (equally distributed): fine-grained sand interspersed with plain PVC-ground, sand with empty snail shells, half flowerpots and rocks. For an experiment on the effect of social experience we kept 2 young L. meeli (fish A & B) of equal sizes in a 33 l tank, separated from each other by an opaque partition. For 100 min, A was introduced into a tank with 4 larger conspecifics, B was

correspondingly put to 4 smaller ones. A behaved always submissively, B was mostly dominant over his smaller tank mates. A and B were returned to their home tank, the partition between them was removed after 15 min and a shelter was introduced. Behaviour and success in getting the shelter were recorded.

All presented experimental results are statistically significant ($p < 0.05$).

Results

Males showed more attacks on large heterospecific competitors and predators than their mates. Both spent more time than their helpers with aggression on large intruders (fig. A). Depending on the stage of the brood cycle, helpers showed more aggressive displays than male breeders on small conspecifics and more than female breeders on small heterospecific competitors (fig. A). Territory maintenance was mainly done by helpers when large intruders were present, as was larvae cleaning in the presence of large conspecifics. With small competitors present, female breeders spent more time with egg care than helpers. Males did almost no direct broodcare at all in the presence of intruders.

When helpers of different sizes are compared, large ones spent more time with aggression on intruders (fig. B), while small helpers performed more territory maintenance (fig. C) and, in the presence of large, heterospecific intruders more cleaning of larvae. Medium sized helpers (1 or 2 at maximum per replicate) showed as little aggression at exposed strangers as small helpers, and medium amounts of territory care (see fig. C). To summarize, large intruders are mainly attacked by the pair while small helpers care for brood and territory. Small intruders are rather tackled by large helpers, while the female breeder cares for the territory and brood. As compared to control pairs without helpers, pair members with helpers save effort and still gain in the amount of brood and territory care by the helpers' participation: it is advantageous to have helpers (see also Taborsky, 1984).

But it is also important, which auxiliaries are present: fish of helpers' sizes sometimes feed on eggs instead of cleaning them, especially if they are not family members. How do breeders distinguish between young conspecifics? When experimentally introduced into their territory, own helpers were hardly attacked by breeders, while the latter were moderately aggressive against strange helpers and very aggressive towards strange non-helpers. Experiments which only gave breeders view of the young but not vice versa revealed that the differential treatment of strange helpers and non-helpers had been due to their reactions to breeders' attacks: Now, the breeders only distinguished between own helpers and strange young. Recognition of their own helpers relied on visual cues, as the exposed young were not in the same tank as the tested breeders (see Hert, 1985).

What ensures that helpers are caring for instead of feeding on eggs? Factors tested for their influence on controlling these options were size, sex, dominance status, territoriality, continuity of egg presence, experience, and the behaviour of social partners. For young tested in pairs dominance proved to be most important: 20 of 21 submissive young cleaned the presented eggs, 23 of 24 dominant young fed on them. In a second step 6 of the subordinates were made dominant by exchanging their larger social partners for smaller ones. Six

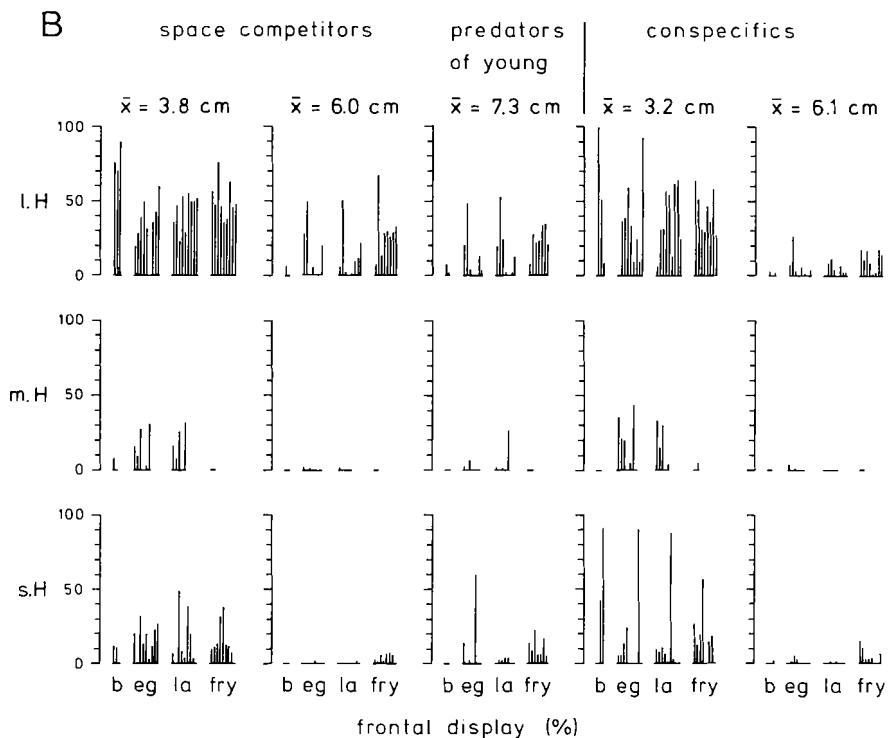
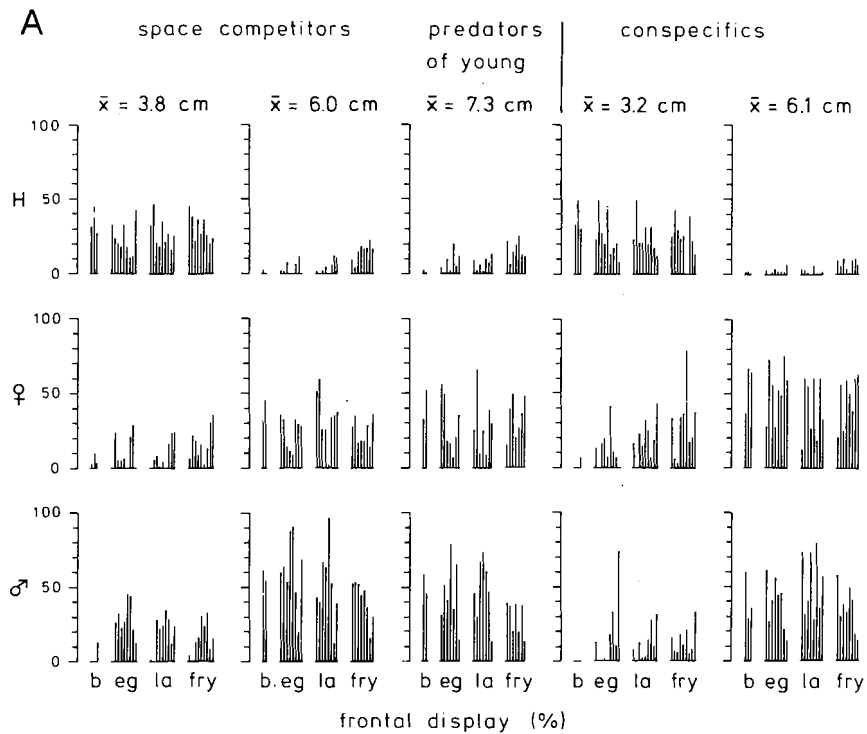


Figure A : Aggr. displays of helpers and pair members towards 5 types of intruders. Abszissa : before spawning, phases with eggs, larvae and fry. Ordinate : % of the total amounts of frontal display shown by male, female and the average helper, respectively. Each vertical bar dates from one recording, bars beneath one another come from the same exp. exposure.

Figure B : Similar to A, but for large, medium and small helpers.

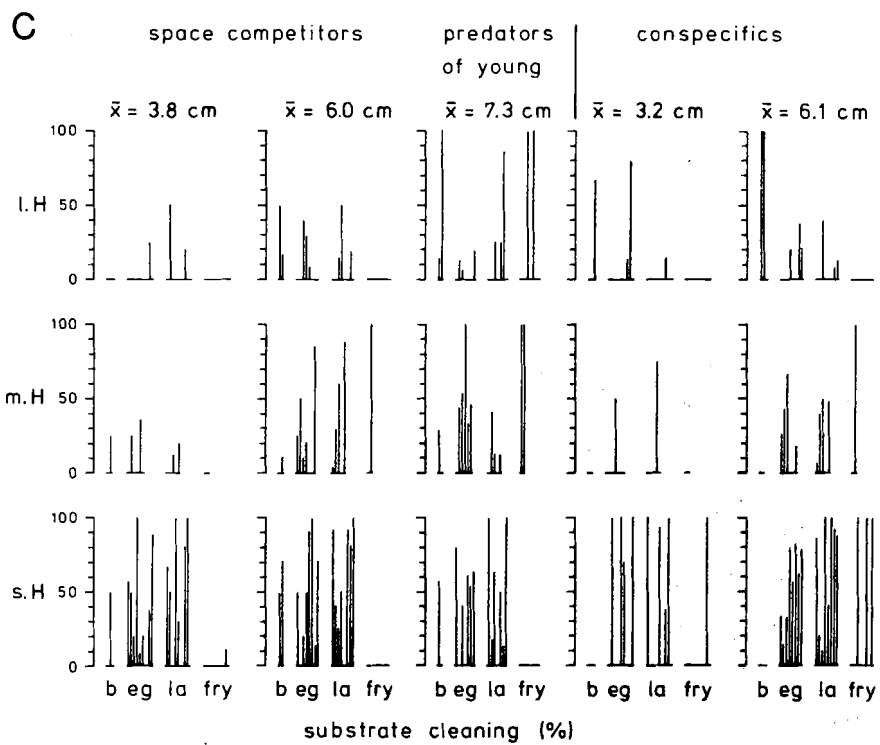


Figure C : Substrate cleaning in presence of intruders, plotted like B.

control subordinates of matched sizes were kept in submissive status by the continued presence of a larger social partner. Each day a test clutch was introduced. All formerly submissive egg cleaners turned into egg feeders as they became dominant, while all submissive controls continued to clean the eggs (fig. D). In a third step dominant egg feeders were reversed to become submissive again. 5 of 6 fish exclusively cleaned the eggs after becoming submissive. The existence of a territory, the continuity of egg presence and, for large and experienced potential helpers, the "model" behaviour of dominant social partners proved to have additional influence on the probability of cleaning presented eggs. Other factors control the breeders' broodcare (see Siemens, 1984).

The 4 snail breeding Lamprologus species differed in social behaviour and habitat choice. L. meeli was the most solitary species, with a preference for rocky substrate. Pairs bred in snail shells. L. ornatipinnis' males occasionally monopolized two females (harems). They mostly stayed on sandy areas with snail shells. L. "magarae" (undescribed species) was the most social species. Adults often joined roving aggregations of conspecifics. Breeders tolerated their young for a prolonged time, resulting in an overlap of successive broods in the territory similar to L. richardi. L. ocellatus did not breed. Although they mostly stayed around flower pots they were most territorial when owning snail shells.

An experiment tested the influence of recent social experience on agonistic behaviour of juvenile L. meeli in subsequent contests. An effect was demonstrated that is often recognized by animal keepers but broadly ignored by theoreticians modelling contest decisions: in 10 of 16 experimental pairs type B fish were more aggressive than their opponents (type A fish) which had been suppressed by larger conspecifics, and hence conquered the shelter site. In two cases it was the other way round. Four replicates did not result in a clear difference between fish A and B.

References

- HERT E., 1985. Individual recognition of helpers by the breeders in the cichlid fish Lamprologus richardi (Poll, 1974). Z. Tierpsychol., 68:313-325
- SIEMENS M. v., 1984. Die Regulation der Eipflege bei Helfern und Brutpaaren des Cichliden Lamprologus richardi (Poll 1974). Diplomarbeit, Univ. of Munich, 97pp.
- TABORSKY M. 1984. Broodcare helpers in the cichlid fish Lamprologus richardi: their costs and benefits. Anim. Behav., 32:1236-1252
- TABORSKY M. & D. LIMBERGER, 1981. Helpers in fish. Behav. Ecol. Sociobiol., 8:143-145