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Short note/Kurze Mitteilung

Do cave mollies (*Poecilia mexicana*) obtain information about the resource value of food patches from shoal mates?*

Erhalten Höhlenmollys (*Poecilia mexicana*) von Schwarmmitgliedern Informationen über den Wert von Futterressourcen?

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Zusammenfassung: Schwarmfische könnten Strategien entwickeln, um unterschiedlichen Nahrungs- bzw. Beutedichten effizient auszubeuten. Zunächst sollten alle Fische die beutereiche Zone bejagen, bis diese auf das Niveau der beuteärmeren Zone dezimiert ist, dann sollte sich der Schwarm gleichmäßig auf beide Zonen verteilen. Höhlenbewohnenden *Poecilia mexicana* wurden zwei Zonen mit unterschiedlicher Beutedichte (*Tubifex tubifex*) angeboten und die Fisch- sowie Beutetieranzahl im zeitlichen Verlauf protokolliert. Die Anzahl von *T. tubifex* nahm in der beutereichen Zone zunächst steil ab, jedoch wurden ebenfalls in der beutearmen Zone einige „Würmer“ von einigen wenigen Höhlenmollys gefressen. Eine gleichmäßige Verteilung der Höhlenmollys auf beide Zonen erfolgte mit einer deutlichen Verzögerung zur Gleichverteilung der Beutetiere, was auf einen fehlenden oder zumindest sehr geringen Informationsfluss innerhalb des Fischschwarms hinweist.

The distribution of prey items in aquatic habitats tends to be disjunctive (Milinski 1994), and shoaling fish may develop strategies to exploit food patches efficiently (MPG 2000). A recent theoretical model (fig. 1 A, MPG 2000) provides specific predictions for how fish shoals should exploit two zones with strongly different abundance of food items: Initially, all fish should exploit the high-food-abundance-zone until food abundance reaches that of the other (low-abundance) zone. Once food abundance is identical in both zones, the shoal should split and exploit both zones equally (fig. 1a). This process, however, requires that some individuals gather information about the current food availability in both zones, which obviously keeps those individuals from feeding at the same time – evidently, such a behavior requires some form of reciprocity or ‘Tit-for-Tat’ to evolve. In fact, an increasing body of literature shows that fish shoals are often not entirely open and anonymous (e.g., Frommen & Bakker 2004, Frommen et al. 2007, Croft et al. 2009), so reciprocity or Tit-for-Tat may be a driving force behind the evolution of cooperative behavior in shoaling fishes (e.g., Stephens et al. 1997, Croft et al. 2006).

In this study, we investigated the exploitation of food sources of different quality in the cave molly, a subterranean population of the livebearer *Poecilia mexicana* Steindachner, 1863 (Poeciliidae, Teleostei). *Poecilia mexicana* is widespread in Central America (Miller 2005). The cave mollies used here came from a sulfidic limestone cave in southern Mexico, the Cueva del Azufre (Gordon & Rosen 1962). Unlike in

*Dedicated to Prof. Dr. Frank Kirschbaum on the occasion of his 65th birthday and retirement.

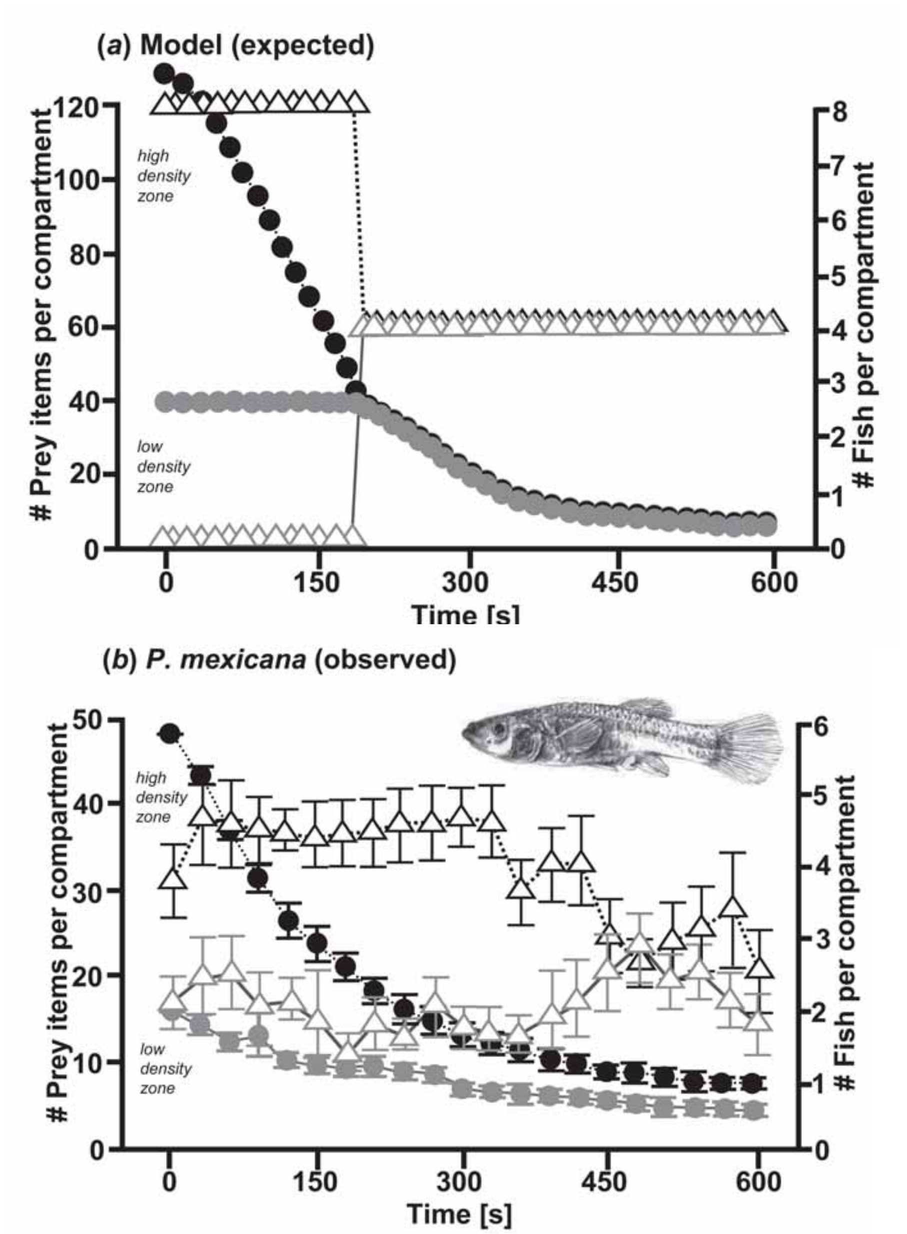
other cave fishes, eyes are only slightly reduced in diameter, apparently following a gradient from the cave-mouth to the innermost cave chambers (Peters et al. 1973, Plath et al. 2007), and cave mollies still respond to visual cues when reared in light (e.g. Plath et al. 2006). Furthermore, cave mollies are a valuable model system to study the evolution of cooperative behavior in shoaling fishes, because – given the lack of visual communication in the cave – reciprocity or Tit-for-Tat seem unlikely to evolve in the 'anonymity' of darkness. Hence, we predict that cave molly shoals should lack an efficient communication network and cave mollies should therefore show a less uniform utilization of food patches than described above.

We used 32 lab-reared cave mollies (27-34 mm standard length), which were housed in groups of eight individuals in four aerated and filtered test tanks (30 x 40 x 60 cm) at a constant temperature of 28°C under a natural light: dark cycle. All fish were given one week for acclimation before the tests started. During this time, they were fed twice daily with commercially available flake food (TetraMin®). Each tank contained four 24-well-microtiter plates, so the fish could habituate to the presence of the microtiter plates. At the beginning of a test (between 10:30 and 13:00 hrs) two plates were filled with one prey item (*Tubifex tubifex* Müller, 1774) per well (equaling 48 worms) and were placed on one side of the tank, close to the shorter side. The other two plates were filled to only one third (16 worms) and were placed on the other side. Side-assignment for the high- and low-abundance food source was altered for each trial. Once the first worm was consumed by one of the test fish, we started the 10 min observation phase. Every 30 s, we noted the number of worms ingested per zone as well as the number of fish foraging in each of the two zones. Observations were done by two persons simultaneously. The same procedure was repeated on six consecutive days, and mean values for that period were calculated for each test tank.

As predicted by theory (Fig. 1a, MPG 2000), the mean abundance of *T. tubifex* worms at the beginning of the tests decreased more steeply in the high-abundance-zone (Fig. 1 B). Contrary to this prediction, however, some worms were initially ingested also in the low-abundance-zone. Indeed, some fish resided in the low-abundance-zone even at the beginning of the tests (fig. 1b). While the magnitude of difference between the two zones in numbers of food items was lost after approximately 200-250 s, most fish remained in the high-abundance-zone until app. 400 s after the start of the tests (fig. 1b). Hence, there was a pronounced delay in the response of the test fish to decreased food availability in the high-abundance-zone.

The distribution pattern of cave mollies reported here –with a delayed response to decreased food availability– provides evidence for our prediction and suggests that information transfer in groups of cave mollies is absent or at least less efficient. As an evolutionary response to the absence of avian and fish predators, cave mollies have reduced their tendency to form shoals (Parzefall 1993, Plath & Schlupp 2008), which was corroborated here by the fact that not all fish resided in the same compartment at the beginning of the tests. Therefore, it appears highly unlikely that groups of mollies, as found in some places inside the cave, are more than just open, anonymous accumulations of fish, and reciprocity is unlikely to operate in their naturally dark habitat. Furthermore, since aggression, dominance hierarchies, and the associated alternative mating strategies of inferior males are clearly reduced in cave mollies (e.g., Parzefall 1974, Plath et al. 2003, Riesch et al. 2006), it is unlikely that this spatial pattern is simply the byproduct of any type of dominance hierarchies.

The natural food source of cave mollies includes invertebrate prey like the larvae of the midge *Tendipes fulvipilus* (Tobler 2008). The delayed response to varying levels of food availability may (partly) explain the small-scale distribution patterns in the cave, where locally observable accumulations of mollies may indicate that prey was recently available. The



Figs. 1a and b: Prediction from a theoretical model (**a**) for the distribution of shoaling fish (triangles) when exploiting two food patches (circles) with different food availability (after MPG 2000) and results from an experiment using cave mollies (*Poecilia mexicana*; **b**). Black symbols: high food abundance zone, gray symbols: low abundance zone. Depicted are means ± S.E.

Abb. 1a und b: Vorhersage eines theoretischen Modells (**a**) zur Verteilung schwarmbildender Fische (dreieckige Symbole), die zwei Zonen mit unterschiedlicher Nahrungsverfügbarkeit (runde Symbole) nutzen (nach MPG 2000), sowie Ergebnisse eines Experiments, in dem Höhlenmollys (*Poecilia mexicana*; **b**) verwendet wurden. Schwarze Symbole: Zone hoher Nahrungsverfügbarkeit, graue Symbole: Zone niedriger Nahrungsverfügbarkeit. Abgebildet sind Mittelwerte ± S.E.

importance of food availability and other (abiotic) factors (H_2S- and the correlated O_2-concentrations, TOBLER et al. 2006, 2008) for the very patchy small-scale distribution of cave mollies inside the Cueva del Azufre will be the subject of extensive future research.

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