

Predation of a cave fish (*Poecilia mexicana*, Poeciliidae) by a giant water-bug (*Belostoma*, Belostomatidae) in a Mexican sulphur cave

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Abstract. 1. Caves are often assumed to be predator-free environments for cave fishes. This has been proposed to be a potential benefit of colonising these otherwise harsh environments. In order to test this hypothesis, the predator–prey interaction of a belostomatid (predator) and a cave fish (prey) occurring in the Cueva del Azufre (Tabasco, Mexico) was investigated with two separate experiments.

2. In one experiment, individual *Belostoma* were given a chance to prey on a cave fish, the cave form of the Atlantic molly (*Poecilia mexicana*), to estimate feeding rates and size-specific prey preferences of the predator. In the other experiment, population density of *Belostoma* was estimated using a mark–recapture analysis in one of the cave chambers.

3. Belostomatids were found to heavily prey on cave mollies and to exhibit a prey preference for large fish. The mark–recapture analysis revealed a high population density of the heteropterans in the cave.

4. The absence of predators in caves is not a general habitat feature for cave fishes. None the less predation regimes differ strikingly between epigeal and hypogean habitats. The prey preference of *Belostoma* indicates that cave-dwelling *P. mexicana* experience size-specific predation pressure comparable with surface populations, which may have implications for life-history evolution in this cave fish.

Key words. Cave ecology, cave fish, predator–prey interactions, prey preferences.

Introduction

Owing to the absence of photoautotrophic primary production, caves are usually considered energy-limited, and the food web of subterranean ecosystems relies on nutrient influx from epigeal habitats (Poulson & Lavoie, 2000). As a consequence, caves often harbour comparatively simple food webs consisting of few specialised cave-dwelling species. Specialisations of cave animals not only include traits that have evolved in response to permanent darkness itself (such as a reduction of pigmentation and the visual system and the elaboration of non-visual sensory organs) but also include adaptations ena-

bling cave-dwellers to cope with the food scarcity commonly found in cave ecosystems, such as an increased starvation resistance or reduced energy demands as a result of reduced metabolic rates (Hüppop, 2000; Langecker, 2000).

The absence of light and the associated scarcity of food render caves into rather extreme environments (Howarth, 1993). Consequently, cave colonisation is often viewed as an accidental process (Wilkens, 1979; Holsinger, 2000). Cave colonisation, however, may also be an active and adaptive process providing specific benefits to cave colonisers that range from environmental stability and the presence of unoccupied niches (Romero & Green, 2005) to protection from predators (Romero & Green, 2005) and parasites (Tobler *et al.*, 2007).

In the Cueva del Azufre in Tabasco, southern Mexico, the food web is based on chemoautotrophic bacterial primary production and the input of bat guano (Langecker *et al.*, 1996).

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This cave is thought to be different from many other cave systems in that its ecosystem is energy-rich even compared with photoautotrophic epigeal habitats (Langecker *et al.*, 1996; Tobler *et al.*, 2006). The most studied inhabitant of the Cueva del Azufre is a small live-bearing fish, the cave molly (Gordon & Rosen, 1962; Parzefall, 2001), a cave-dwelling population of the Atlantic molly (*Poecilia mexicana* Steindachner). Other populations of the Atlantic molly frequently inhabit freshwater surface habitats in Central America (Miller, 2005). Contrary to many other cave fishes, cave mollies occur at high densities. On average, 20 individuals per m² were recorded in the inner cave chamber X (Tobler *et al.*, 2006), but densities are even higher towards the cave exit (chambers III–VI, Tobler *et al.* pers. obs.). High population densities are not explained by abundant food, because cave mollies show strong signs of malnutrition (Plath *et al.*, 2005; Tobler *et al.*, 2006).

Compared with adjacent surface habitats, the Cueva del Azufre harbours a tremendously reduced fish community (Tobler *et al.*, 2006). Besides the cave molly, only the synbranchid eel *Ophisternon aenigmaticum* Rosen & Greenwood was occasionally reported from the cave (Gordon & Rosen, 1962; Parzefall, pers. comm.). The reduction of species diversity in this case seems not primarily to be driven by the absence of light or food scarcity but by the presence of high concentrations of toxic hydrogen sulphide (Tobler *et al.*, 2006). Consequently, inter-specific competition with other fishes is reduced and predatory fish are lacking in the cave. This is also true for avian predators that are known to heavily prey on fishes (Trexler *et al.*, 1994) and that are common in adjacent surface habitats (Tobler *et al.*, 2007). So far unstudied is the extent of filial cannibalism in the system; other poeciliid fishes are known to prey upon conspecific juveniles (Nesbit & Meffe, 1993).

In the present study, it is tested if cave mollies live in a predator-free environment. Generally, few other metazoans share their habitat with the cave molly (Gordon & Rosen, 1962). These include larvae of the dipteran *Tendipes fulvipilus* Rempel (Tendipedidae) that are one of the primary food sources for the mollies (Tobler, pers. obs.) and the crab *Avotrichodactylus bidens* Bott (Trichodactylidae; referred to as a potamonid species by Gordon & Rosen, 1962). While the cave molly's ecology and behaviour are intensely studied (Parzefall, 1993, 2001; Plath *et al.*, 2003, 2004; Tobler *et al.*, 2006), very limited information on the other inhabitants of the Cueva del Azufre is available so far.

This paper focuses on a further inhabitant of the cave, a giant water-bug of the genus *Belostoma*, and its role as a molly predator. *Belostoma* are large aquatic hemipterans that prey on aquatic insects, snails, amphibians, and fish (Menke, 1979). Belostomatids are sit-and-wait predators that catch bypassing prey items with their raptorial forelegs that are strongly incrassate, with the femora often grooved to accept the tibiae. Upon capture, *Belostoma* inject toxins causing prey paralysis and digestive enzymes causing tissue necrosis (Swart & Felgenhauer, 2003). In the Cueva del Azufre, *Belostoma* has been found to prey on cave mollies and, with a limited sample size of eight individuals, to prefer large prey items over small ones (Plath *et al.*, 2003).

Predation itself and size-specific predation in particular are known to affect life-history traits in surface-dwelling fish. For example, early maturity and small body size at maturity in the prey

species are positively selected under (size-specific) predation (Reznick & Ender, 1982; Johnson & Belk, 2001). Based on the finding that size distributions in cave molly populations appear not to differ from that of typical surface populations (Plath *et al.*, 2003) it was tested if a preference for large prey size could be detected in *Belostoma*. Furthermore, the population size of belostomatids in one cave chamber of the Cueva del Azufre was assessed.

In summary, we tested whether cave mollies live in a predator-free environment by examining if: (i) *Belostoma* prey on cave mollies; (ii) the water-bugs prefer large fish as prey; and (iii) the water-bugs occur at high density and thus are a potential selective factor in the evolution of cave mollies comparable with selection arising from avian and piscine predation in surface habitats.

Materials and methods

All experiments were performed in the Cueva del Azufre, Tabasco, Mexico in August 2004. Nomenclature of cave chambers followed Gordon and Rosen (1962). Details about the abiotic habitat properties can be found in Tobler *et al.* (2006).

Population size of *Belostoma*

To estimate population sizes, all visible *Belostoma* were collected by two people in cave chamber V during 30 min and were marked with a small dot of TippEx on the thorax. All marked individuals were then released at the collection site. Twenty-four hours later, cave chamber V was re-sampled with the same effort. Population size was estimated based on the recapture rate of marked individuals following Bailey (1951):

$$N_{\text{tot}} = \frac{N_1 * (N_2 + 1)}{N_3 + 1}$$

where N_{tot} is the estimated population size, N_1 is the number of individuals initially caught and marked, N_2 is the number of individuals caught after 24 h, and N_3 is the number of marked individuals in N_2 .

Prey choice in *Belostoma*

Fish and water-bugs for the prey choice experiments were collected in cave chamber V of the Cueva del Azufre. Prey choice experiments were performed in PET bottles (2 litres) that were perforated to allow exchange of water and air with the environment. Four large (standard length, mean \pm SD: 34.8 \pm 0.5 mm) and four small cave mollies (standard length, 23.4 \pm 0.6 mm) as well as a single individual of *Belostoma* (length from the tip of the head to the tip of the abdomen, mean \pm SD: 22.5 \pm 0.9 mm) were introduced into each bottle. Furthermore, a tablet of commercial fish food was added to each bottle. The bottles ($n = 20$) were then partially submerged in a shallow area of cave chamber V and fixed with rocks. Partial submersion was used to allow water-bugs to breathe. The bottles remained in the cave for 48 h and were then checked for fish preyed upon by *Belostoma*. The numbers of large

and small cave mollies consumed by *Belostoma* were compared with a Wilcoxon signed rank test using SPSS 11, SPSS Inc (Chicago, IL).

Results

Population size of *Belostoma*

Of 35 *Belostoma* marked, four could be recaptured 24 h later. The total number of individuals caught after 24 h was 47. Thus, the estimated population size of *Belostoma* in chamber V of the Cueva del Azufre was 336 ± 130 (mean \pm SE) individuals. Given a conservative estimate of the surface area of chamber V as 300 m², this results in a density of 1.12 ± 0.43 *Belostoma* per m².

Prey choice in *Belostoma*

All but three *Belostoma* (two of which were males carrying eggs) consumed at least one molly. In total, 70 of 160 mollies (44%) were consumed by the belostomatids, equalling a per capita capture rate of 1.75 mollies per water-bug per day. Mollies showed injuries at the tail, the body, as well as various parts of the head. An analysis of the captured fish revealed that the water-bugs consumed significantly more large mollies [median = 2 individuals per trial (IQR = 3.25)] than small mollies [median = 1 individual per trial (IQR = 1.25); $n = 20$, $Z = -2.355$, $P = 0.019$] during the period of 48 h.

Discussion

Belostoma are common in the Cueva del Azufre. Although a density of about one individual per m² may seem low, it has to be considered that these insects tend to accumulate on rocks along the water surface where they ambush prey with their front legs kept in the water and their abdomen in the air. Cave mollies can often be observed in the same microhabitat during foraging (midge larvae tend to accumulate along the rims of the water surface) and during aquatic surface respiration that allows survival in the sulphidic and hypoxic environment (Plath *et al.* in press). Thus, encounter rates between predators and prey may in fact be high.

Protection from predation has been considered a potential benefit of cave colonisation (Romero & Green, 2005); this, however, is not entirely the case for the Cueva del Azufre. The predation experiments indicated that *Belostoma* prey heavily on cave mollies. The high capture rate may be partly caused by the spatial limitations of the bottles in which the experiments were performed. The small container might have limited the prey's escape possibilities. The results, however, show that belostomatids are capable of preying on mollies multiple times over a period of 48 h. Previous studies showed that *Belostoma* are able to feed multiply over prolonged periods of time without a depletion of salivary enzymes (Swart & Felgenhauer, 2003). Our experiment, furthermore, indicates that *Belostoma* have a preference for larger prey items. This prey preference has previ-

ously been hypothesised to maintain the striking size polymorphism present in male cave mollies (Plath *et al.*, 2003), even though large males are preferred in sexual selection (Plath *et al.*, 2004). Size-specific predation has also been documented in surface habitats, e.g. herons preferentially prey on large mollies (Trexler *et al.*, 1994) and predatory cichlids preferably select large guppies as prey (Johansson *et al.*, 2004).

Because belostomatids occur at high densities and are generalist predators, they have been considered keystone species structuring the communities in which they are found and affect morphological, behavioural, and life-history modifications in their prey (Babbitt & Jordan, 1996; Chase, 1999; Kehr & Schnack, 1991). Certainly, *Belostoma* is the main, if not the only, predator of the cave molly. Other potential predators in the cave are either very rare (the synbranchid eel, *Ophisternon aenigmaticum*; Parzefall, pers. comm.) or did not prove to prey on cave mollies in comparable experiments (e.g. the crab, *Avotrichodactylus bidens*; Tobler *et al.* unpublished data).

It is yet unclear to what extent *Belostoma* in the Cueva del Azufre rely on other prey species (e.g. midge larvae). In our experiment, the water-bugs only had a chance to forage on cave mollies, but they may prefer other prey in a more natural situation. In that case, the predation pressure on cave mollies may be lower than implied by our experiment. Future work on the food web structure in the cave and prey preferences in *Belostoma* needs to clarify this.

Definitely, the kind of predation on *Poecilia mexicana* differs strikingly between different habitat types. In adjacent surface habitats, *Belostoma* were only recorded sporadically while piscivorous fish and birds are common (Tobler *et al.*, 2006, 2007). Beside darkness, hydrogen sulphide, and energy limitation, the differential predatory regime is one potential driving force in the evolution of the cave molly. Inhabiting a cave – albeit rich in toxic hydrogen sulphide – appears to provide benefits in terms of protection from predators for *Belostoma*, which is the top predator in this cave ecosystem, but not for the cave fish, *Poecilia mexicana*.

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