

Male-biased predation of a cave fish by a giant water bug

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Abstract Male-biased predation has been described from several epigeic species, and in many cases, intrinsic differences between the sexes (such as male ornaments) have been suggested as an explanation. Here we report on male-biased predation of a cave fish (*Poecilia mexicana*) by an aquatic insect (*Belostoma* sp.) in a Mexican sulfur cave. *P. mexicana* use aquatic surface respiration (ASR) to survive in their sulfidic, hypoxic habitat. We found that males typically exhibit more ASR activity than females, which leads to increased exposure to the sit-and-wait predator that catches fish near the water surface. Our finding is novel, because male vulnerability to predation is not directly related to male traits involved in courtship, but rather due to other sexual differences in behavior and ultimately, oxygen demands.

Keywords *Belostoma* · Male-biased mortality · Oxygen demands · *Poecilia mexicana* (Poeciliidae) · Predator–prey interaction

Introduction

Sex-biased predation is well-documented across many taxa (Jennings and Houseweart 1989; Acharya 1995; Rodd and Reznick 1997; Quinn and Kinnison 1999; Marshall and Ganders 2001; Lode et al. 2004). Differential susceptibility to predation is often associated with intrinsic differences between sexes (i.e., sexual dimorphism), where the presence of elaborate sexually selected traits (Endler 1980; Ryan et al. 1982; Houde 1997; Macías Garcia et al. 1998; Godin and McDonough 2003), differences in size (Trexler et al. 1994; Quinn and Kinnison 1999), or differences in behavior (Sommer 2000; Costantini et al. 2007) may affect the conspicuousness and/or encounter rates to predators. For example, in promiscuous, highly sexually dimorphic species, such as the Trinidadian guppy (*Poecilia reticulata*), males are not only more conspicuous but may dedicate less time to predator avoidance and antipredator behavior (Magurran and Nowak 1991; Magurran et al. 1992; Magurran and Seghers 1994).

Susceptibility to predation, however, also depends on extrinsic factors. For example, in a recent review, Domenici et al. (2007) highlighted the effects of adverse environmental conditions on the antipredator behavior of fishes. Hypoxia may impair individuals' escape behavior and alter the structure and dynamics of fish schools. For example, hypoxic conditions have been shown to reduce responsiveness to predator stimuli and to affect the directionality of escape reactions in several fish species (Lefrançois et al. 2005; Lefrançois and Domenici 2006). Furthermore, fish

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schools are less densely packed (Domenici et al. 2002; Israeli and Kimmel 1996), and school unity is more likely to be disrupted under low oxygen conditions (Domenici et al. 2000). Hypoxia may also increase predator encounter rates, thereby elevating the risk of predation especially by hypoxia-tolerant predators (Domenici et al. 2007). For example, the clam *Mya arenaria* reduces burial depth and increases siphon extension into the water column during severe hypoxia, thereby increasing the susceptibility to blue crab (*Callinectes sapidus*) predation (Taylor and Eggleston 2000). In fish that rely on air breathing or aquatic surface respiration (ASR) to cope with hypoxia, leaving shelter to surface increases exposure time to both aquatic (Wolf and Kramer 1987) and aerial predators (Kramer et al. 1983). If and how sex differences in the susceptibility to adverse abiotic conditions indirectly affect predation risk has thus far received little attention. In this study, we examined the effects of sex-specific responses to adverse environmental conditions on the predator–prey interaction of a predatory aquatic invertebrate (a belostomatid water bug) and a cave fish.

In the Cueva del Azufre system in southern Mexico, a small live-bearing fish (*Poecilia mexicana*, Poeciliidae) colonized a cave (Gordon and Rosen 1962) whose water is rich in hydrogen sulfide (H_2S) (Tobler et al. 2006). The spontaneous reaction of H_2S with oxygen not only creates hypoxic conditions (Cline and Richards 1969; Chen and Morris 1972), but H_2S is also a potent respiratory toxicant lethal to most metazoans even in micromolar concentrations (Torrans and Clemens 1982; Bagarinao 1992; Grieshaber and Völkel 1998). Sulfide detoxification in organisms capable of tolerating high and sustained concentrations of H_2S is primarily achieved through its oxidation to less toxic sulfur species and subsequent excretion through the kidneys (Curtis et al. 1972; Bagarinao 1992; Ip et al. 2004). Due to the hypoxic conditions in sulfidic habitats, oxygen available for respiration is generally limited, but at the same time oxygen is also required for coping with the toxic effects of H_2S .

Experiments in the natural habitat indicate that *P. mexicana* males have a higher susceptibility to the adverse conditions than females (Plath et al. 2007b). To survive in the hypoxic sulfidic environment, this species strongly relies on ASR (Plath et al. 2007b). During ASR, fish use the more oxygen-rich air–water interface (Lewis 1970; Kramer and Mehegan 1981). Here, *P. mexicana* may encounter the only known fish predator in the cave, a giant water bug of the genus *Belostoma* (Tobler et al. 2007). Belostomatids are sit-and-wait predators that gather on rocks along the water's edge posing with their front legs below and their abdominal spiracles above the water surface. Belostomatids catch bypassing prey items with their raptorial forelegs that are strongly incrassate, with the

femora often grooved to accept the tibiae (Menke 1979). *Belostoma* sp. in the Cueva del Azufre heavily prey on *P. mexicana* and preferentially prey on large-bodied individuals (Tobler et al. 2007). Here, we tested whether the higher susceptibility of males to the sulfidic and hypoxic conditions is reflected in a higher frequency of ASR, and whether sex differences in ASR frequency translate to differential susceptibility to predation by *Belostoma* sp.

Materials and methods

The study was conducted in the Cueva del Azufre, which is located near the village of Tapijulapa in the southern Mexican state of Tabasco. Details on the study site can be found in Tobler et al. (2006). To test for sex differences in the frequency of ASR, we reanalyzed data published in Plath et al. (2007b). *P. mexicana* males (28.4 ± 0.9 mm standard length, mean \pm SE) and females (36.0 ± 1.9 mm) were exposed to both water from a sulfidic cave spring (83.6 ± 28.1 μM H_2S , $21.2 \pm 1.3\%$ DO, $n=12$ measurements) and water from the same spring that was aerated for 1 h to remove H_2S (0.8 ± 1.2 μM H_2S , $88.2 \pm 1.7\%$ DO, $n=3$ measurements). H_2S measurements were conducted photometrically in the laboratory according to Cline (1969) and oxygen was determined using a Hydrolab Multiprobe 4A. Single fish were introduced into a clear plastic bottle with 300 ml of water. After a 5-min acclimatization period, we measured the time the fish spent at the surface performing ASR for 5 min. Longer acclimation times were not feasible under field conditions. Hence, increased metabolic rates due to handling stress may have affected the results; however, both males and females were handled equally. Subsequently, the fish was transferred to another bottle with water from the opposite treatment, and the measurement was repeated. The order of the water treatment was balanced. We calculated the proportion time an individual performed ASR. Data were arcsine-transformed and analyzed using a repeated measures ANOVA with 'water treatment' as within subjects factor and 'sex' as a between subjects factor. To account for differences in body size between males and females, we initially included standard length as a covariate. However, no significant effect of size was detected (mean square = 28,127.213, $F_{1,32} = 2.658$, $P = 0.113$); thus the covariate was excluded from the final model. All statistical analyses were performed with SPSS 11.

Fish and water bugs for the prey choice experiment were collected in cave chamber V of the Cueva del Azufre. The experiments were performed in 2-l PET bottles which were perforated by punching ca. 30 small (<5 mm) holes into the walls. This allowed for air and water exchange. We conducted 26 replicates. A male and a female *P. mexicana*, matched for size (standard length of males, mean \pm SD, $27.2 \pm$

2.5 mm; females, 28.4 ± 3.4 mm; paired t -test, $t_{24}=1.50$, $P=0.14$), were introduced to the bottle along with a water bug (length from the tip of the head to the end of the abdomen, mean \pm SD, 19.0 ± 4.3 mm). The bottles were then placed in a shallow area within the cave and fixed in place with rocks. Bottles were only partially submerged to allow the water bugs to breathe and the fish to perform ASR. After 24 h, we checked the replicates for signs of predation (either dead or living fish with puncture wounds). All surviving fish and water bugs were released at the original collection site following the experiment. To test for differential predation upon the sexes, data were analyzed using a paired sign test.

Results

Regardless of the water treatment, males were found to spend significantly more time at the water surface conducting ASR than females (Table 1; Fig. 1). Water treatment also had an effect, and fish performed less ASR in oxygenated water than in water that stemmed directly from a sulfidic source in the cave.

In the prey choice experiment, predation had occurred in 13 of the 26 replicates. In 11 cases (84.6%) only the male was captured, in one case only the female was captured, and in one case both fish were captured by the heteropterans (7.7% of cases each). This difference between the sexes was significant (paired sign test, $P=0.006$).

Discussion

Our results indicate that males generally exhibit higher frequencies of ASR, thus spending more time at the water surface where they are susceptible to *Belostoma* predation. The prey choice experiment confirmed that *Belostoma* sp. catch more *P. mexicana* males compared to equally sized females. These results suggest that sex-specific predation in

Table 1 Results from repeated measures GLM on the total time the fish spent at the surface exhibiting ASR

Source	df	Mean square	F	P
Water treatment	1	533,681.326	62.747	<0.0001
Water treatment x sex	1	85.898	0.010	0.921
Error (water treatment)	33	8,505.317		
Sex	1	75,843.528	6.803	0.014
Error	33	11,148.553		

The two water treatments (water directly from a sulfidic source and same water after 1 h of oxygenation) were used as within subjects factor (repeated measurement), and sex was included as a between subjects factor

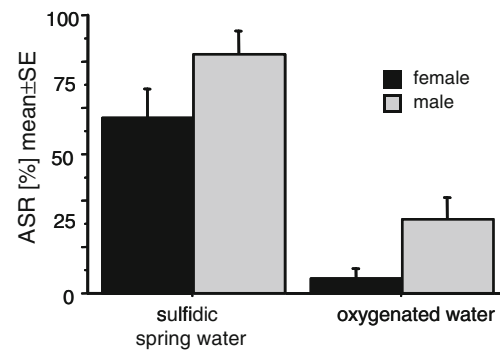


Fig. 1 The mean (\pm SE) time spent at the surface by female (black) and male (gray) cave fish (*P. mexicana*) while showing ASR. Note that the fish showed considerably less ASR in oxygenated water, but males always showed more ASR than females

the cave population of *P. mexicana* is at least partially mediated by sex-specific oxygen demands, which probably increased the encounter rate with water bugs. However, it cannot be fully ruled out that the result of the predation experiment was the consequence of male–female interactions, i.e., mating behavior exposing males to higher predation risk.

Males showed more ASR in both water treatments, i.e., under sulfidic/hypoxic and nonsulfidic/normoxic conditions. Hence, differences between males and females in oxygen demands seem to play a role. For example, male poeciliids are the mate-searching sex (Farr 1989) and show higher locomotive activity than females. Poeciliid males tend to switch frequently between shoals (Magurran 1998; Griffiths and Magurran 1998) and show more investigative behavior (Andreev 1994), which may come along with a generally higher activity metabolic rate. Even though sexual activity is reduced in the cave population of *P. mexicana*, probably as an adaptation to save energy (Plath et al. 2003, 2007a; Plath 2008), males still devote more time and energy to finding mates than females.

Sex-biased predation is usually associated with intrinsic differences in morphology or behavior between sexes; for example, many predators prefer males with flamboyant ornamentation or conspicuous courtship displays as prey (Burk 1982; Endler 1987; Magnhagen 1991; Macías Garcia et al. 1994, 1998; Godin and McDonough 2003; Moyaho et al. 2004). In this study, it seems that behavioral differences between the sexes could indirectly lead to higher vulnerability of males to predation. Our results support the claim that sexually dimorphic species can differ in various nonsexual behaviors (e.g., ASR) that affect survival (Magurran and Macías Garcia 2000).

It is generally assumed that caves lack specialized predator/y species due to limited resources and that trophic generalists are more common (Gibert and Deharveng 2002). The predator–prey interaction between a belostomatid and a cave fish in this system appears to be unique,

because the water bugs likely prey almost exclusively on cave *P. mexicana*. Not only do the water bugs occur in high densities (Tobler et al. 2007), but they exhibit specific predation patterns in terms of prey size (Plath et al. 2003; Tobler et al. 2007) and prey sex (this study). Due to size- and sex-specific predation patterns, predators can strongly influence the demography (e.g., Macías Garcia et al. 1998) and life history (e.g., Reznick and Endler 1982) of prey populations. Size-specific predation by the heteropterans for large-bodied fish is thought to counter sexual selection for large male body size due to female choice, leading to the maintenance of male size polymorphism (Plath et al. 2004a; see also Plath et al. 2003 and 2004b for a discussion). Future studies will examine how predation by *Belostoma* sp. affects life history traits in the cave population of *P. mexicana*.

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