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ORIGINAL ARTICLE

Reduction of the association preference for conspecifics in cave-dwelling Atlantic mollies, *Poecilia mexicana*

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Abstract Cave animals are widely recognised as model organisms to study regressive evolutionary processes like the reduction of eyes. In this paper, we report on the regressive evolution of species discrimination in the cave molly, *Poecilia mexicana*, which, unlike other cave fishes, still has functional eyes. This allowed us to examine the response to both visual and non-visual cues involved in species discrimination. When surface-dwelling females were given a chance to associate with either a conspecific or a swordtail (*Xiphophorus hellerii*) female, they strongly preferred the conspecific female both when multiple cues and when solely visual cues were available to the female. No association preference was observed when only non-visual cues were provided. In contrast, cave-dwelling females showed no preference under all testing conditions, suggesting that species recognition mechanisms have been reduced. We discuss the role of species discrimination in relation to habitat differences.

Keywords Cave fish · Poeciliidae · *Xiphophorus* · Shoaling · Species recognition

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Introduction

The ability to recognise one's own species plays an important role in at least three aspects of many animals' lives: mate recognition, predator avoidance and gregariousness. Mate recognition comprises both species recognition and mate-quality recognition (Ryan and Rand 1993; Sherman et al. 1997), which means the identification of a genetically compatible mate and identification of a mate that can confer fitness benefits to the choosy individual or its offspring (e.g. Kyriacou and Hall 1982; Ratcliffe and Grant 1983; Petrie 1994). In fishes, the species component of mate recognition by females is often based upon visual cues such as size and colour (e.g. haplochromine cichlids: Seehausen et. al 1997; Couldridge and Alexander 2002; Jordan et al. 2003; pupfishes, *Cyprinodon beltrani* and *Cyprinodon labiosus*: Kodric-Brown and Strecker 2001) or olfactory signals (e.g. northern swordtails, *Xiphophorus montezumae*, *Xiphophorus nigrensis*, *Xiphophorus cortezi* and *Xiphophorus pygmaeus*: Crapon de Caprona and Ryan 1990; McLennan and Ryan 1997, 1999; Hankison and Morris 2003; and pupfish, *Cyprinodon maya*: Kodric-Brown and Strecker 2001).

Species recognition can also play an important role in the formation and maintenance of groups. For teleost fishes, simple social groups known as shoals can provide major antipredator benefits to individual members through increased vigilance, early predator detection (Magurran et al.

1995; Godin 1986; Magurran 1990) and a numerical dilution effect (Morgan and Godin 1985; Landeau and Terborgh 1986; Turner and Pitcher 1986). Many species prefer to associate with conspecifics (conspecific cueing: Kiester 1979; Wolf 1985; Allan and Pitcher 1986; Stamps 1988; Reed and Dobson 1993; Krause and Godin 1994; Persaud and Galef 2003 but see, e.g. Greig-Smith 1981; Barnard et al. 1982; Schlupp and Ryan 1996), possibly because phenotypically distinct individuals within a shoal are more likely to be attacked by predators than phenotypically similar individuals (the oddity effect: Landeau and Terborgh 1986; Theodorakis 1989; McRobert and Bradner 1998). The females in some species take shoal formation one step further, preferring to associate only with female conspecifics, possibly as a way to decrease male sexual harassment via numerical dilution of male coercion and increased female vigilance (e.g. mosquitofish, *Gambusia holbrooki*: Pilastro et al. 2003; Atlantic mollies, *Poecilia mexicana*: Parzefall 1969).

In this paper, we address the problem of species discrimination by examining the responses of female Atlantic mollies (*P. mexicana*) to a choice situation involving conspecific and heterospecific females. The Atlantic molly is an ideal system for studying the evolution of processes underlying species discrimination. Most populations are found in relatively shallow, clear waters; however, populations from Mexico have been discovered in a sulphurous creek with milky water due to a high concentration of colloidal sulphur (Tobler et al. 2006) and deep within a lightless cave (Gordon and Rosen 1962) which, to our knowledge, is the only cave-dwelling population of *P. mexicana*. The habitat characteristics are dramatically different between these three environments (Tobler et al. 2006), which in turn will affect the transmission of cues between senders and receivers. Such an effect has been documented in the cave population. Although the fish have functional eyes (Peters et al. 1973) with nearly the same visual pigments as their epigean relatives (Körner et al. 2006), visual communication is impossible in the complete darkness of the cave. However, cave mollies have been shown to readily respond to visual stimuli in a number of behavioural experiments (e.g. Plath et al. 2003b, 2006). Troglodytic females, however, are capable of discriminating between large and small males in the absence of light, something epigean females do not do (Plath et al. 2004a), possibly due to their hyper-developed lateral line system (Parzefall 1970). The effective use of the lateral line organ in navigation and object analysis has been shown in another cave fish, the blind cave tetra (*Astyanax fasciatus*: Burt de Perera 2004a,b). So while *P. mexicana* females retain the plesiomorphic poeciliid preference for large males (Plath et al. 2004a), one component of mate recognition, that ability is based upon a change of the sensory system used to detect information from the male.

How does the evolution of non-visual intersexual communication compare with species recognition mechanisms in this system? To answer this, we must consider another aspect of the Atlantic molly's natural history. In addition to the abiotic differences between the clear, milky and cave environments discussed above, piscine community structure also varies between habitats (Table 1; Tobler et al. 2006), ranging from multispecies assemblages to a (probably) single-species community in the cave. This eliminates selective pressures arising from interspecific competition for resources and from predators. It also eliminates the problem of identifying an appropriate mate in terms of species recognition, reducing mate choice to a question of identifying sex and quality. It is not surprising that the cave dwellers show a considerably weaker tendency to form shoals (Parzefall 1993) and display lower levels of aggression and sexual harassment than their surface-dwelling relatives (Parzefall 1974, 1979, 2001; Riesch et al. 2006). We were interested in asking whether these changes in social structure and interactions were correlated with a reduction in species discrimination. We argue that the selection arena involved with the maintenance of species discrimination in clear-water epigean populations no longer applies for the cave population, because many of

Table 1 Composition of fish communities in the three habitats in 2004: surface river (Río Oxolotan), milky sulphur creek (El Azufre) and cave (Cueva del Azufre)

Family	Species	Río Oxolotan	El Azufre	Cueva del Azufre
Characidae	*Astyanax fasciatus*	a	–	–
Cichlidae	*Cichlasoma salvini*	r	r	–
	Paraneetroplus gibbiceps	r	–	–
	Thorichthys helleri	c	–	–
	Vieja bifasciata	c	–	–
Batrachoididae	*Batrachoides goldmani*	r	–	–
Atherinopsidae	*Atherinella* sp.	c	–	–
Poeciliidae	*Heterophallus milleri*	c	–	–
	Heterandria bimaculata	r	r[a]	–
	Poecilia mexicana	c	a	a
	Xiphophorus hellerii	c	r[a]	–
Synbranchidae	*Ophisternon aenigmaticum*	?	?	r[b]

c Common, *a* abundant, *r* rare
[a] Occurs in a small clear water creek draining into the El Azufre
[b] Only occasional reports (Gordon and Rosen 1962; Parzefall, personal communication)

the benefits accruing to such an ability (e.g. predator avoidance, protection from harassment, etc.) do not exist in the cave habitat. This, in turn, will upset the evolutionary balance between costs and benefits, tipping the scale towards costs and creating a different selection arena, one that should favour the reduction in a cave individual's ability to recognise conspecifics. Based on this reasoning, we made two predictions about the way in which females from the three populations would react when given a choice between a female conspecific and heterospecific: (1) species discrimination will be stronger in the surface populations than the cave population and (2) within the surface populations, species discrimination will be weaker in the sulphur creek fish because their community is far less complex, and hence selection pressures are correspondingly reduced in the manner discussed above, when compared with fish from the clear-water habitat.

Materials and methods

Study organisms

Test fish were collected from the Río Oxolotan south of Tapijulapa in Tabasco, South Mexico (river population); the El Azufre, a milky sulphur creek flowing out of the Cueva del Azufre, isolated from the Río Oxolotan by a 15-m waterfall (sulphur creek population), and the rearmost and permanently dark chamber of the Cueva del Azufre (chamber XIII after Gordon and Rosen 1962; cave population). Green swordtails (*Xiphophorus hellerii*, Poeciliidae, Teleostei) were collected from a creek near Cordoba, Veracruz (Mexico). We chose *X. hellerii* as stimulus fish, because they share the habitat with *P. mexicana* from both surface populations (Table 1) and are non-predatory poeciliid fish. Only females were used in this study to eliminate any sexually motivated association preferences. *P. mexicana* and *X. hellerii* females are similar in body shape; however, *P. mexicana* females have a greyish colouration while *X. hellerii* females are brownish to olive-green with blue and red–brown lateral stripes.

Housing conditions

Fish were randomly bred and maintained in 100- to 200-l aquaria at 25–30°C in the laboratory of the Biozentrum Grindel, Hamburg. All species and populations were reared separately without visual contact with each other on a 16:8-h artificial light:dark cycle. The fish were fed ad libitum twice a day with commercially available flake food and *Artemia* nauplii, live water fleas and *Tubifex* worms. Four days before the experiment, the test females were removed from the stock tanks and kept in small groups in aquaria identical to the test tanks. We had only a limited number of green swordtail females (approximately 60), so they were used as stimulus fish twice, but neither under the same testing conditions nor together with the same *P. mexicana* females.

Choice experiments

The test aquarium (100×35×35 cm) was filled to two thirds with aged 26°C tap water and the bottom was covered with black gravel. Two vertical lines were drawn on the front of the tank dividing the aquarium into equally sized lateral preference zones and a central neutral zone. We placed a cylinder (12-cm in diameter) large enough to hold the stimulus fish in each preference zone. Focal fish were able to swim around these cylinders. The test tank was illuminated by a 40-W fluorescent light placed 39 cm above the aquarium when required. The observer was sitting quietly about 2 m from the test tank. When the experiment required darkness, two 500-W infrared bulbs (λ>800 nm) were used, installed above the preference zones. *P. mexicana* does not possess infrared-sensitive photoreceptors (Körner et al. 2006). The experiment procedure was recorded by an infrared-sensitive camera and the video signal was transferred to a monitor in a neighbouring room and scored directly.

The trials were carried out between 10:00 A.M. and 04:30 P.M. Before each trial, a *P. mexicana* female (standard length, mean±SD, 40.8±3.9 mm) and a *X. hellerii* female (40.6±3.4 mm) were introduced into one of the two cylinders, respectively. Conspecific stimulus females always came from the same population as the focal fish. All pairs of stimulus fish were matched for size (size difference 0.9±1.1 mm) and were given 5 min for habituation in their cylinders. A focal female (37.2±5.8 mm) was then gently introduced into the middle compartment. Measurements were initiated when the female began to swim freely. We measured the time the test female spent in each of the two preference zones during a 10-min observation period. To detect side biases, we gently switched the position of the two stimulus females and repeated the 10-min trial. We combined both trials for analysis.

As the three populations studied live in habitats with completely different spectral compositions, we controlled for the possibility that different sensory channels are being used in species discrimination performing experiments with three different illumination combinations. Each female was observed in only one experiment; however, due to the limited number of females in our stocks, some females were also used as a stimulus in a subsequent trial, but never on the same day.

Choice trials were run under three conditions: (1) all cues: stimulus fish were placed in wire-mesh cylinders (wire diameter 1 mm, mesh width 5 mm) and the trials were carried out under fluorescent light, providing the maximum number of cues from different sensory modalities for the choosing female; (2) visual cues only: as above except that the stimulus fish were confined in transparent Plexiglas cylinders, blocking the transmission of chemical and vibrational cues and (3) non-visual cues only: stimulus fish were placed in wire-mesh cylinders and trials were run in darkness.

Statistical treatment

The trials in which a test fish spent more than 80% of its choice time during both 10-min sessions in the same compartment were defined a priori as showing side biases and were eliminated (9 of 134 trials). We also eliminated trials in which the females spent less than 50% of their time in the preference zones (four trials).

We tested for population differences and for an influence of availability of visual and/or non-visual cues on the strength of preference (SOP). SOPs were calculated as: (time near conspecific − time near heterospecific female)/(time near conspecific + time near heterospecific). A two-way ANOVA on SOPs was carried out, in which ‘population’ was the between factor and ‘testing condition’ was the within factor. For post hoc contrasts, Fisher’s protected least significant difference (PLSD) was employed. We also tested for preferences of each population within each testing condition, i.e. differences in the time spent near either type of stimulus using paired *t* tests. All *P*-values are two-tailed.

Results

Pairwise comparison of association times

In the all cues experiment, *P. mexicana* of the river and sulphur creek populations showed a significant preference for the conspecific stimulus (river: t_{11}=3.37, P=0.006; sulphur creek: t_{12}=2.65, P=0.021; Fig. 1). Cave-dwelling *P. mexicana* did not show any preference (t_{14}=0.44, P=0.67; Fig. 1).

When only visual cues were available, females of the river and sulphur creek populations spent significantly more time near the conspecific female than near *X. hellerii* (river: t_{13}=7.08, P<0.001; sulphur creek: t_{11}=2.29, P=0.043; Fig. 2), whereas the cave form again did not show any preference (cave: t_{14}=0.16, P=0.88; Fig. 2).

In the absence of visible light, females of none of the *P. mexicana* populations showed a preference (river: t_{11}=−0.31, P=0.76; sulphur creek: t_{12}=0.61, P=0.55; cave: t_{14}=−0.84, *P*= 0.41; *Fig. 3).*

Comparison between populations and testing conditions

The river population showed the strongest response, the sulphur creek population responded weaker and the cave population showed the weakest preference (Figs. 1, 2 and 3). The factor ‘population’ had a significant influence on the strength of preference (Table 2). A post hoc test revealed that this was due to significant differences between the cave and river population (Fisher’s PLSD, P<0.0001)

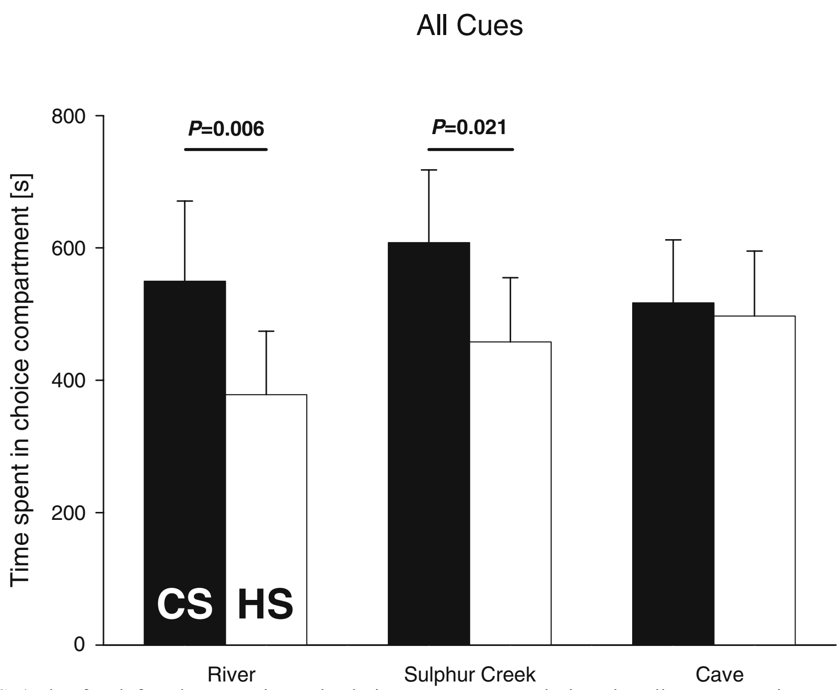

Fig. 1 The time (mean±SD) the focal female spent in each choice compartment during the all cues experiment. *CS*, conspecific fish; *HS*, heterospecific fish. Paired *t* tests; only significant results are shown

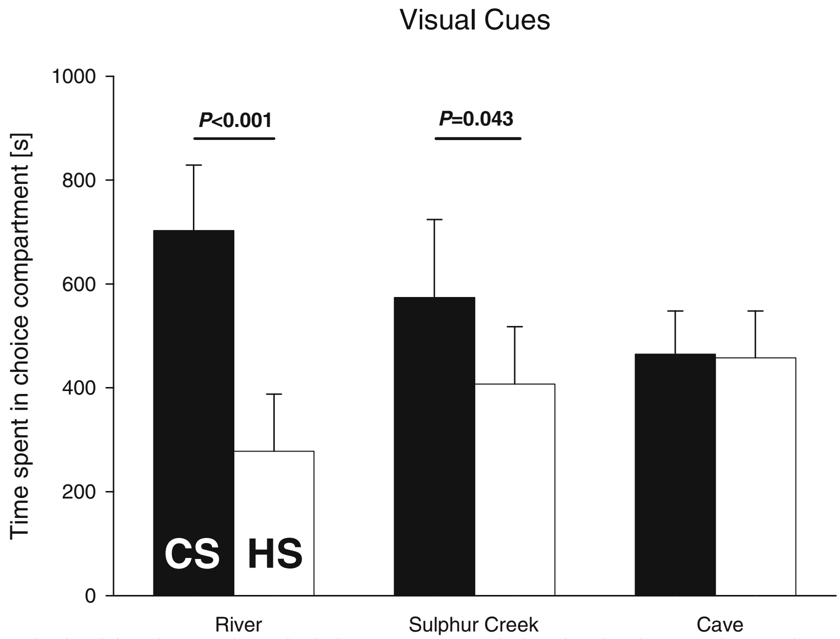

Fig. 2 The time (mean±SD) the focal female spent in each choice compartment during the visual cues only experiment. *CS*, conspecific fish; *HS*, heterospecific fish. Paired *t* tests; only significant results are shown

and between the cave and sulphur creek population (Fisher's PLSD, $P=0.013$), whereas there was no significant difference between the river and the sulphur creek population (Fisher's PLSD, $P=0.056$).

The factor 'testing condition' also had a significant influence on the strength of preference (Table 2), and this was due to significant differences between the all cues experiment and the non-visual cues experiment (Fisher's PLSD, $P=0.020$), and the visual cues only experiment and the non-visual cues experiment (Fisher's PLSD, $P<0.0001$), whereas the all cues experiment and the visual cues only experiment did not significantly differ (Fisher's PLSD, $P=0.063$). Hence, the strongest response was found when all cues were available, the second strongest when solely visual cues were provided and the strength of preference was lowest in darkness.

The interaction term 'population' × 'testing condition', too, had a significant influence (Table 2), indicating that the

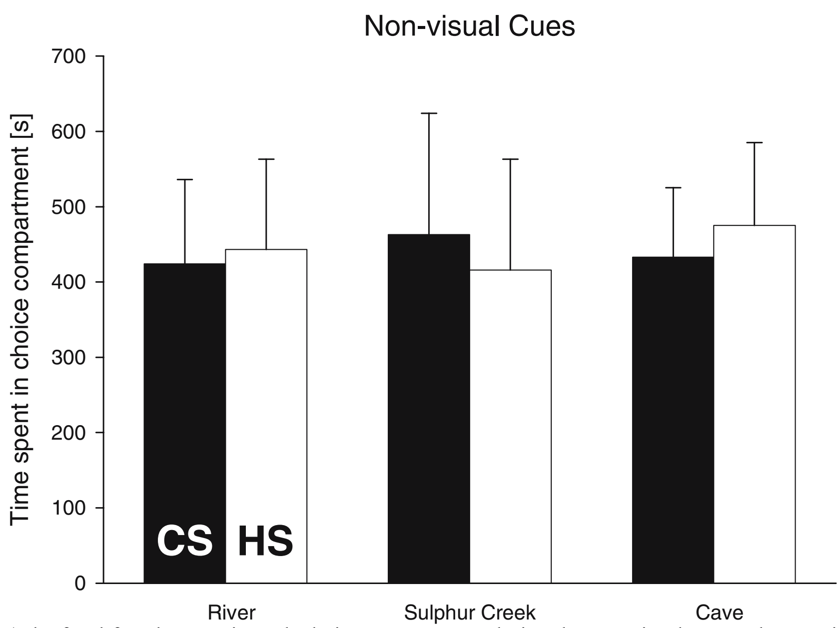

Fig. 3 The time (mean±SD) the focal female spent in each choice compartment during the non-visual cues only experiment. *CS*, conspecific fish; *HS*, heterospecific fish

Table 2 Results of the two-way ANOVA on the strength of preference

Factor	*df*	Sum of squares	Mean square	*F*	*P*
Population	2	0.87	0.44	9.34	0.0002
Treatment	2	0.85	0.43	9.16	0.0002
Population × treatment	4	0.65	0.16	3.51	0.0098
Residual	112	5.21	0.05		

Females from three populations of *P. mexicana* were given a choice between a conspecific and a heterospecific female under one of the following treatments: the stimulus fish were presented in a wire-mesh cylinder in light (all cues treatment), in a clear Plexiglas cylinder in light (visual cues treatment) or in a wire-mesh cylinder in darkness (non-visual cues treatment)

three populations differed in their response to the different experiments (Figs. 1, 2 and 3).

Shoaling

Cave mollies are known to show weaker shoaling tendencies than *P. mexicana* from surface populations. To exclude that this might have an influence on our results, we compared the total times spent in the preference zones between populations. No significant differences between the populations were detected (mean±SD, cave: 939±116 s; sulphur creek: 975±120 s; river: 928±106 s; ANOVA $F_{2,118}$=1.78, P=0.17).

Discussion

P. mexicana females from three different habitats (a clear river, a sulphur creek and a cave) did not react the same way when given a chance to associate with either a conspecific or heterospecific (swordtail) female. Epigean females showed a strong preference for the conspecific, while cave females showed no preference at all. It is interesting that epigean fish showed the strongest response when either all cues or just visual cues were available; they did not discriminate when only non-visual cues were provided. This suggests that surface-dwelling female Atlantic mollies need only visual cues to recognise the species of other females or at least to recognise and discriminate in favour of conspecifics. This, of course, begs the question of whether they, like some other poeciliid females (Crapon de Caprona and Ryan 1990; McLennan and Ryan 1997, 1999; Hankison and Morris 2003), use chemical cues in addition to visual cues when discriminating between conspecific and heterospecific males.

It is unlikely that the females' lack of response to non-visual cues was an artefact of testing under dark conditions. First, although all fish were raised in a lighted environment, previous studies under the same rearing and testing conditions demonstrated that light-reared cave molly females readily preferred large over small males (Plath et al. 2004a) and well-nourished over malnourished males (Plath et al. 2005), while both cave and river females preferred a male to no stimulus (Riesch et al. 2005). Second, as all females were used to a particular light:dark cycle and normally rested in the dark, we controlled for the effects of an activity biorhythm by conducting all trials during the females' main activity period. As mentioned above, previous experiments showed that both cave and river females were attracted to a male under dark conditions, indicating that they are capable of responding when transferred from light into darkness during the daytime (Riesch et al. 2005). Finally, all of the fish showed normal swimming behaviour under these testing conditions.

Our results confirm the hypothesis that species discrimination is important in surface-dwelling *P. mexicana* females. In river populations, the ability to recognise one's own species enables females to form conspecific all-female shoals. Such shoals are typically defended by one or a few dominant males (Parzefall 1969; personal observation in nature; see also Bisazza and Marin 1995 for *G. holbrooki*) and may be beneficial to females, because individuals in uniform shoals are less conspicuous to predators (Pitcher and Parrish 1993), are less subject to male sexual harassment (Pilastro et al. 2003) and thus may be able to spend more time feeding (Pilastro et al. 2003; Plath et al. 2003a). The benefits of shoaling would be larger in conspecific than in mixed species shoals, because female Atlantic mollies are more conspicuous to conspecific males who would not interact sexually with heterospecific females.

However, our results do not support the prediction that species discrimination by females would be weaker in the sulphur creek compared with the river population. There was a trend, albeit non-significant, for sulphur creek females to show a weaker preference for conspecifics when only visual cues were provided. Visual communication is restricted in this milky habitat. While the Río Oxolotan shows huge fluctuations in water levels and is turbid only during the rainy season, the sulphur creek shows consistent turbidity throughout the year. There may have been a subtle shift in this population towards incorporating information from non-visual cues into species discrimination. This trend needs to be examined further. In the milky water of the sulphur creek itself, only one other species of fish coexists with *P. mexicana* at very low density, the predatory cichlid, *Cichlasoma salvini* (Table 1). As in the river population, several predatory birds occur, like kingfishers, herons and egrets. Heterospecific poeciliids (swordtails and *Heterandria bimaculata*) occur only in a very small clear water affluent some meters from the cave exit. Toxic hydrogen sulphide apparently restricts their distribution (Tobler et al. 2006). In contrast, *P. mexicana* seems to tolerate H_2S and the mollies are found in the sulphur creek in high densities. Nevertheless, *P. mexicana* do also dwell in the clear water, so that they can experience heterospecific poeciliids at least temporarily. Sexual harassment is absent in this population (Plath et al. 2003a and unpublished data), so shoal formation would not provide benefits through male avoidance. Overall though, females would still benefit from forming uniform shoals to protect themselves from predation and, possibly, interspecific competition.

As predicted, cave molly females did not show any preference for associating with the conspecific female. A thorough analysis of the phylogenetic relationships of *P. mexicana* in the study area is as yet lacking, but a comparison of the mitochondrial control region suggests that the Río Oxolotan population and the cave population are closely related (Möller 2001). The most plausible scenario is that fish from the river entered the cave system and evolved into the cave molly. A recent study using microsatellite markers has shown that there is only limited gene flow between the surface and the cave populations (Plath et al., unpublished data). However, it is as yet unknown as to how long the three populations have been separated. Thus, if the river population does indeed represent the ancestral source of colonisers, then our data suggest that the female preference to spend time near same sexed conspecifics has been reduced in the course of cave colonisation. This reduction is associated with two derived changes in the cave fish. First, piscine predators are absent in the cave. Giant water bugs (*Belostoma* sp.) do prey on cave mollies (Plath et al. 2003a), but their hunting behaviour probably differs vastly from that of piscine predators in that they are thought to sit on stones closely above water level and catch fish passing by. Second, male sexual harassment is lacking in this population (Plath et al. 2003a, 2004b); indeed troglodytic males are in general less aggressive overall than their surface relatives (Parzefall 1979). Two benefits of species discrimination, avoidance of predators and males, are thus directly removed from the selection arena of the cave. An indirect result of the reduction in male harassment might be that females do not increase their feeding opportunities by associating with other females. Overall then, the reduction of benefits to cave females recognising and preferring to associate with other conspecific females will reduce the strength of selection maintaining that preference, which in turn is also expressed as a decrease in female shoaling tendencies, as noted by Parzefall (1993). One might argue that the reduction in shoaling is the sole reason for the lack of species discrimination of cave molly females. It should be noted, however, that females of the three populations did not exhibit differences in times spent associating with the stimulus fish in the experiments reported here. Hence, reduced shoaling alone does not explain the lack of species discrimination in the cave molly.

Cave fishes are currently widely used to study regressive processes like the reduction of eyes (Yamamoto and Jeffery 2000; Jeffery 2001, 2005; Wilkens and Strecker 2003; Yamamoto et al. 2004). The present study reports on a reduction process on the behavioural level in a cave fish. The study system of three proximate but geographically isolated *P. mexicana* populations inhabiting vastly different abiotic environments offers an unparalleled opportunity to study the evolution of several preferences and recognition mechanisms in both sexual and non-sexual contexts.

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