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ORIGINAL ARTICLE

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Cave molly females (*Poecilia mexicana*, Poeciliidae, Teleostei) like well-fed males

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Abstract We examined the preference of Atlantic molly females (*Poecilia mexicana*) to associate with a well-fed or a starved male in simultaneous choice tests. Females from three different populations were tested in three treatments: (1) the females could choose on the basis of multiple cues from the males (visual plus non-visual); (2) only non-visual cues could be perceived in darkness, (3) only visual cues were presented. The three tested populations differ clearly in their ecology: one population occurs in a typical river habitat, the second one in a milky sulfur creek outside a cave, and the third population occurs in a cave habitat (cave molly). In the river-dwelling population, females never showed a preference. In the population from the sulfur creek, females preferred to associate with the well-nourished male when visual cues from the males were available. Only cave molly females exhibited a strong preference for well-nourished males in all treatments. A morphological comparison demonstrated that wild-caught males from river habitats are typically in a good nutritional state. In the sulfur creek, males showed signs of starvation. Cave molly males were in an even worse nutritional state. In the cave population, saturated males probably indicate high fitness, thereby driving the evolution of the preference for good male nutritional state.

Keywords Cave fish · Condition dependence · Female choice · Sexual selection · Sensory shift

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Introduction

A problem in sexual selection theory is the evolution of condition-dependent male signaling. Some theories on the evolution of female mate choice predict that male traits preferred by females reliably indicate male condition (e.g., Zahavi 1975; Hamilton and Zuk 1982; Kodric-Brown and Brown 1984; Andersson 1986, 1994; Pomiankowski 1988). However, such male signals do not necessarily indicate a male's present condition, but often reflect a male's performance in the recent past. For example, color ornaments are thought to reflect a male's access to certain food sources (e.g., Hill and Montgomerie 1994). The dietary carotenoid content during the molt will strongly influence the development of bright plumage coloration in male house finches (Hill 2000; Hill et al. 2002). Guppy females (*Poecilia reticulata*) prefer males that have had access to a carotenoid-rich diet (Kodric-Brown 1989; Grether 2000). Furthermore, parasitism limits the development of bright color patterns, and females may use brightness as an indicator of low parasite load (Hamilton and Zuk 1982; Milinski and Bakker 1990; Houde and Torio 1992). One condition-dependent trait that indicates a male's present condition is his nutritional state (i.e., energy reserves stored in tissues plus present amount of food in his stomach). Starvation is most probably a reliable indicator of a male's inability to cope with his (fluctuating) environment.

A number of studies have focused on how starved animals behave (e.g., Milinski and Heller 1978; Dill and Fraser 1984; Godin and Sproul 1988; Dugatkin and Godin 1998; Walker et al. 1999). Animals can also alter their behavior in response to whether other individuals experience starvation. For example, individual fish may respond differentially to hungry or satiated predators (*P. reticulata*: Licht 1989; *Gambusia affinis*: Smith and Belk 2001). Zebra-fish (*Danio rerio*) preferentially shoal with well-fed conspecifics (Krause et al. 1999), which may increase their future foraging success.

Female mating preferences and the indicator value of male saturation

Theory predicts that female preferences evolve relative to the "indicator value" of the male trait (Harvey and Bradbury 1991; Kirkpatrick and Ryan 1991; Andersson 1994; see also Grether 2000). Here we examined female mating preferences for good male nutritional state in a live-bearing fish, the Atlantic molly, *P. mexicana*. Do Atlantic molly females prefer well-nourished males? We studied the effects of food availability on the evolution of the female mating preference for well-nourished males, and we asked whether environmental conditions interact with the evolution of this mating preference. For this, we determined the nutritional state of males from river habitats, a sulfur creek flowing out of a cave, and from a sulfur cave, which is inhabited by a cavernicolous form of *P. mexicana*. We hypothesized that mating preferences relative to male nutrition are more pronounced in habitats with naturally low food supply.

Visibility conditions and female mating preferences

Unlike many other cave fishes (Wilkens 1988; Weber et al. 1998; Jeffrey 2001), the cave molly possesses functional eyes (Peters et al. 1973), and the visual pigments are almost unchanged (K.E. Körner et al., unpublished data). A previous study on female mating preferences has demonstrated that cave molly females have maintained the visual preference for large male body size shown by river-dwelling females (Plath et al. 2003c, 2004). Most interestingly, they preferred to associate with large males even in darkness, indicating that the detection of male size is taken over by a non-visual sensory system, probably the mechanosensory lateral line (Plath et al. 2003c, 2004). To examine the relative importance of both visual and non-visual cues, females were tested in three treatments, where: (1) visual plus non-visual information from the males could be perceived by the test female, or (2) only non-visual information, and (3) only visual information was available to the female.

In typical river habitats, *P. mexicana* forms shoals. Hence, association preferences for well-nourished conspecifics may be shoaling preferences rather than sexual preferences. In contrast, cave mollies have strikingly reduced shoaling (Parzefall 1993a). Shoaling is also to some extent reduced in the fish from the sulfur creek (Parzefall 1993a). Cave mollies also show no aggression (Parzefall 1974, 1979), and it seems that, in the wild, social interactions among cave mollies are almost exclusively sexual encounters. Consequently, female association preferences for well-nourished males in these populations would be mating preferences, not shoaling preferences.

Specifically, we asked whether *P. mexicana* females discriminate between starved and well-fed males and whether their preference for well-fed males relates to naturally low food availability of the habitat. In the river form, we predicted a visual preference, whereas females from the cave form might have a non-visual preference.

Methods

Study system

For a comparative approach, we used three populations of *P. mexicana* from adjacent, but vastly different habitats in Tabasco, south Mexico near Tapijulapa (Plath et al. 2003a). One population inhabits a river, the Río Oxolotan. The second inhabits an affluent sulfurous creek, the El Azufre, which is isolated from the Río Oxolotan by a waterfall approximately 15 m high (see Plath et al. 2003a, "PS0 population" therein). The water of this creek originates from inside a lightless limestone cave, the Cueva del Azufre. The third population used, the cave molly, stems from the innermost cave chamber (chamber XIII after Walters and Walters 1965). This population is isolated by a waterfall approximately 1.5 m high from other cave pools, which are also inhabited by mollies. The three habitats differ in visibility conditions. The Río Oxolotan is a mostly clear, seasonally turbid river, where females can use visual information for decision making. The water of the sulfur creek is milky due to a high amount of colloidal sulfur. Hence, vision is probably restricted to the upper few centimeters of the water column. Finally, inside the cave, visual communication is impossible and females would have to rely on non-visual cues for decision making (see Zeiske 1968; Plath et al. 2004).

The Río Oxolotan is a typical molly habitat, where algae and small invertebrates provide the primary food source for the inhabiting mollies. Food availability is considered to fluctuate spatially and temporarily, as it does for example in typical guppy (*P. reticulata*) river habitats (Endler 1995). By contrast, in the nearby cave habitat, hydrogen sulfide (H_2S) is used by sulfur bacteria for chemoautotrophic primary production. The environmental conditions in the cave are more stable, which is typical for subterranean ecosystems (Poulson and White 1969). Sulfur bacteria, chironomids (*Tendipes fulvipilus*) and their larvae, as well as bat guano, are the cave molly's food items (Langecker et al. 1996). Usually, the ecosystem of the Cueva del Azufre is thought to provide high amounts of food for the inhabiting mollies (Langecker et al. 1996; Parzefall 2001).

Nutritional state of *Poecilia mexicana* males

Wild-caught males

We determined the relative distension of the abdomen in wild net-caught *P. mexicana* males. To estimate male nutritional status, we did not use a traditional "condition factor" (weight per length). Instead we used a variable that can probably be directly perceived by females, the relative distension of the abdomen. The distension of the abdomen appears to be a good indicator of the nutritional state in males, whereas in females it may depend on their gestational state. To minimize stress for the fish, a digital image of each male was taken at the sampling site while the male was lying on a laminated engineering sheet (providing a millimeter grid), which allowed to calibrate the length of the fish. Measurements were done later with a computer using Adobe Photoshop 5.5. We determined the lengths of those lines representing the standard length and the maximum body height (i.e., the maximum distance between back and thoracic ventral region vertical to the body-length axis) directly on the screen at maximum size of the image. We calculated the ratio between maximum body height and standard length.

During repeated field trips to the Río Oxolotan, it was not possible to catch more than a few adult Atlantic mollies. To build laboratory stocks, we collected juveniles, which are ubiquitous in the river. Therefore, we decided to use digital photographs from two other river populations: one from Buena Vista (Río Tuxpan drainage system, Veracruz, Mexico, 21°05.9′N, 97°44.9′W), and one from Nuevo Padilla (Río Purification, Tamaulipas, 24°02.5′N, 98°54.1′W), which inhabit comparable habitats. Furthermore, we caught males in the sulfur creek (El Azufre) and inside cave chamber XIII. All fish were caught and photographed within 10 days in September 2002.

Laboratory-reared males

Is the measured variable, abdominal distension, a condition-dependent trait, and does it reliably indicate the nutritional state of males? To examine this, we also determined this variable in laboratory-reared males in September 2003 between 1500 hours and 1600 hours, i.e., 2–4 h after last being fed. Males were isolated in 25-l aquaria, not fed for 1 week and measured again. To minimize the number of food-deprived fish, this experiment was only conducted with the cave form. When the males were fed again, their abdomen gradually distended within some days, but not immediately after feeding, indicating that the abdominal distension does not just reflect recent intake of food in the stomach.

Choice tests

Study animals and housing conditions

For the choice tests, we used randomly outbred, large aquarium stocks of three *P. mexicana* populations. Stocks were founded in 1998. The river population was collected from the Río Oxolotan (17°27.6′N, 92°46.6′W). The sulfur creek population was collected from just outside of the mouth of the Cueva del Azufre (17°26.5′N, 92°46.5′W). The cave population was collected from the innermost cave chamber (chamber XIII). The fish were kept in the laboratory of the Biozentrum Grindel in Hamburg in 100–to 200-l tanks at 25–30°C under a 12:12 h light/dark cycle. Even the cave population was maintained at light, making sure that the fish were exposed to light during ontogeny. Previous studies have shown that light-reared cave molly females readily discriminate between males even in darkness (preference for large male size: Plath et al. 2003c, 2004). Fish were fed twice a day ad libitum with commercially available flake food, *Artemia* naupliae, water fleas, and *Tubifex* worms.

Treatment of the test fish

Groups of males (standard length, mean±SD, river: 35.4±3.4 mm; sulfur creek: 31.1±1.8 mm; cave: 34.0±2.8 mm) were isolated in 25-l aquaria (3 males per aquarium). To obtain males in starved condition, half of the males were fed normally, and the other half was deprived of food for 7–8 days. We kept both kinds of males isolated from females to guarantee that both food-deprived and well-fed males were sexually deprived for the same time span. No male died or acquired diseases due to this treatment. Females (standard length, mean±SD, river: 39.0±7.2 mm; sulfur creek: 36.7±4.3 mm; cave: 39.3±4.2 mm) were isolated from males in groups of 5–10 fish in 50-l aquaria for 4 days prior to the tests to standardize motivations. All test fish were mature and had had experience with the opposite sex.

Experimental set-up

Choice tests were conducted between March and April 2002 for the cave form, between October 2002 and January 2003 for the river population, and between October and December 2002 for the sulfur-creek population. We used association preferences to determine mating preferences. Association preferences have been shown to reflect mating preferences, e.g., in guppies (Kodric-Brown 1992), cichlids (Couldridge and Alexander 2001), and blennies (Gonçalves and Oliveira 2004).

We used a standard choice aquarium (100×35×35 cm), filled up to two-thirds with aged water of 25–27°C. The bottom was covered with a thin layer of black gravel. We marked three equal compartments by vertical lines drawn on the front (two preference zones and a central neutral zone). During the tests in light, the tank was illuminated by a 40-W neon tube installed 28 cm above the tank. UV radiation was absent. During the tests in darkness, a 500-W infrared bulb (wavelength >800 nm) was used instead. Atlantic mollies do not see in the infrared (Körner 1999). We placed a cylinder (12 cm diameter) in the center of each preference zone to hold one stimulus male each. Stimulus males matched the population of the test female. Test females could swim around the cylinders. Cylinder material differed according to the treatments: We used wire-mesh cylinders (mesh-width: 5 mm, wire diameter: 1 mm) for the treatments with availability of non-visual cues or transparent Plexiglas cylinders for the treatment with availability of only visual cues.

To estimate which cues (visual or non-visual) are being used by females to determine male nutritional state, we conducted three treatments, giving females different amounts of information from the stimulus males. In one treatment, both visual and non-visual cues from the males could be perceived ("all cues treatment"). Here, we asked whether females generally exhibit a preference for well-nourished males, at least when all sensory channels could be used to determine male nutritional state. In the second treatment, females could choose on the basis of solely non-visual cues in darkness ("non-visual cues treatment"). This treatment resembles the conditions inside the cave or in the deeper parts of the water column in the El Azufre. In the third treatment, females were allowed to choose on the basis of solely visual cues ("visual cues treatment"). This treatment was conducted to determine whether river and sulfur-creek females respond to solely visual cues, and whether the visually mediated preference has persisted in the cave form.

In the "all cues treatment", the males were presented in wire-mesh cylinders under illumination with visible light. In the "non-visual cues treatment", the same cylinders were used, but the trials were conducted under infrared illumination ("darkness"). In the "visual cues treatment", the males were confined to clear Plexiglas cylinders under illumination with visible light. Each female was tested in all three treatments. The order of the treatments was random. Females were placed in 50-l aquaria in groups of three to four females from the same population after a trial. Females could be individually identified by obvious size differences and sometimes by small fin damage. We decided not to test a female more than once per day, because their choosiness might be affected by a trial. Therefore, treatments were 2–7 days apart. Each pair of stimulus males was used only once per treatment. However, a stimulus pair may have been used in another treatment for another female on the same day. After the trials, males were returned to the stock tanks and fed immediately.

Measurement of female preferences

To initiate a trial, a starved and a non-starved male, matched for size (size difference <2 mm, mean difference 0.8±0.7 mm), were introduced into one of the cylinders each and given 5 min for acclimatization. A trial was terminated if the males did not swim freely in their cylinders after 5 min. After this time, we introduced a test female into the center of the neutral zone. Measurements were started when the female began to swim. We measured the time the female spent in either preference zone for 10 min. Then, we reversed the position of the cylinders from left to right and vice versa and measurement was repeated. This procedure was performed to detect side biases.

Statistical analysis

We tested for normal distribution and equal variance. Field data for the relative abdominal distension were compared among the populations using a one-way ANOVA. Laboratory data from cave molly males before and after food deprivation were analyzed using a paired *t*-test. We also compared these data with those from wild-caught cave molly males using two-sample *t*-tests. For the behavior tests, association times near either stimulus male during both parts of a trial were added. We decided a priori to exclude the following trials: trials in which the females spent more than 80% of their association time during both parts of a trial in only one preference zone, i.e. the female did not follow the stimulus, were considered side biases (river population: 2, sulfur creek: 3, cave: 7). Trials in which the females spent less than 50% of the observation time in either preference zone were discarded due to low response index (river population: 2). To test for association preferences, we compared the times a female spent near the saturated and the starved male during each treatment using paired *t*-tests. Furthermore, we tested for differences between populations and treatments. For this, we calculated the relative time spent near the saturated male [$\text{time}_{\text{saturated}}/(\text{time}_{\text{saturated}}+\text{time}_{\text{starved}})$]. Data were compared using "population" as between factor and "treatment" as the repeated measurement for a repeated measures ANOVA. Generally, all relative values were transformed as $y'=\arcsin$ [square-root (y)]. In case of multiple comparisons, α-levels were corrected according to the number of multiple comparisons using Bonferroni-adjustments ($\alpha'=\alpha$/number of multiple comparisons). If not noted otherwise, α-levels are 0.05. All *P*-values are two-tailed.

Results

Nutritional state

Nutritional state in wild-caught Poecilia mexicana males

The relative distension of the abdomen differed significantly between the populations (ANOVA: $F_{3,77}=25.78$, $P<0.0001$; Figs. 1 and 2). A post-hoc test showed that the two river populations did not differ [Fisher's protected least significant difference (PLSD): $P=0.78$]. Males from both river populations were in a better nutritional state than males from the sulfur creek (Fisher's PLSD: Buena Vista: $P=0.0002$, Nuevo Padilla: $P=0.0016$). Both males from the two river populations and males from the sulfur creek were in a better nutritional state than cave molly males (Fisher's PLSD: $P<0.0001$ in each case).

Nutritional state in laboratory-reared cave mollies

The relative distension of the abdomen significantly decreased when laboratory-reared cave molly males were deprived of food for 1 week (paired *t*-test: $t_{19}=10.86$, $\alpha'=0.025$, $P<0.001$; Fig. 2). Before starvation, the height/size ratio was significantly higher in laboratory-reared males than in wild-caught males (two-sample

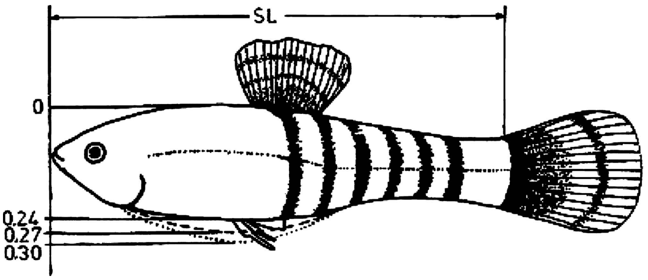

Fig. 1 The relative distension of the abdomen [ratio between maximum body height and standard length (SL)] as a measure of nutritional state in *Poecilia mexicana* males. The shapes of three males are shown at a height/size ratio of 0.24 (*solid*; indicating malnutrition found in cave molly males), 0.27 (*dashed*; a typical value in sulfur-creek males) and 0.30 (*dotted*; well-nourished river-dwelling males)

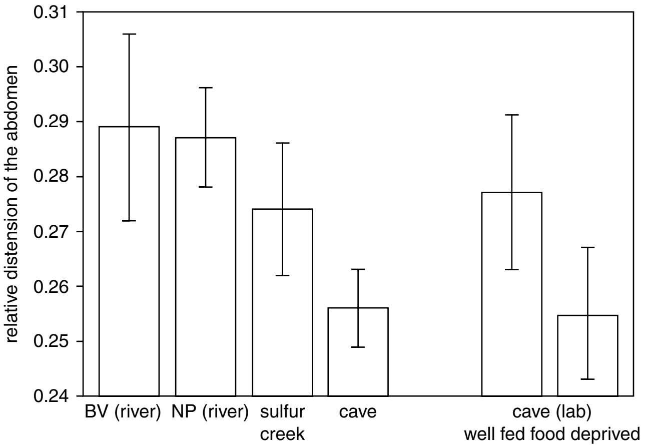

Fig. 2 Nutritional state of *P. mexicana* males from different populations. River populations: Buena Vista (*BV*, n=26), Nuevo Padilla (*NP*, n=18), sulfur-creek population (n=20), cave population (n=17) and laboratory-reared cave males (n=20), well fed and after 1 week of starvation. Relative distension of the abdomen (mean±SD), measured as the ratio between maximum body height and standard length. Low values indicate malnutrition (see also Fig. 1)

t-test: t_{35}=5.65, α'=0.025, P<0.001). When the laboratory-reared males were food-deprived, they did not differ from the males caught in the cave (two-sample t-test: t_{35}=−0.41, α'=0.025, P=0.69). When the males were fed again, the distension of the abdomen gradually increased in the course of some days, but this was not quantified.

Choice tests

River population

Females from the river population did not show a preference in any of the treatments (paired t-test: all cues treatment: t_{13}=0.25, P=0.81; non-visual cues treatment: t_{13}=0.89, P=0.39; visual cues treatment: t_{13}=1.76, P=0.10; Fig. 3a).

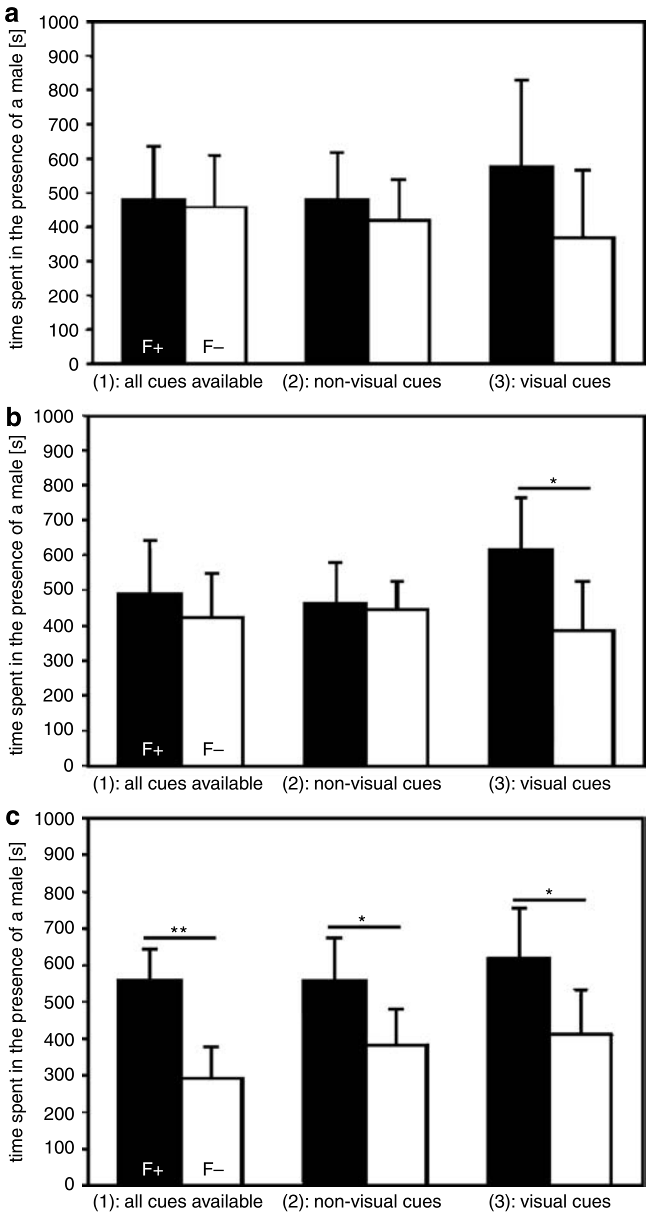

Fig. 3 The time (mean±SD) *P. mexicana* females spent near a well-fed male (F^+, *black bars*) and a male that had not been fed for 1 week (F^-, *white bars*). Females were given different amounts of information from the males: (*1*) multiple cues: males were confined in wire-mesh cylinders in light, (*2*) non-visual cues only: wire-mesh cylinders in darkness, (*3*) solely visual cues: transparent Plexiglas cylinders in light. **a** surface population (n=14), **b** sulfur-creek population (n=12), **c** cave molly (n=13). Paired t-tests, two-tailed (see details in text); *P<0.05, **P<0.01

Sulfur-creek population

Females from the sulfur-creek population spent significantly more time near the non-starved male when the males were presented in the visual cues treatment (paired t-test: t_{11}=2.85, P=0.016; Fig. 3b), but showed no preference in the other treatments (all cues treatment: t_{11}=0.89, P=0.39; non-visual cues treatment: t_{11}=0.35, P=0.74).

Cave population

In the cave form, females spent significantly more time near the fed male in all treatments, even in darkness (paired *t*-test: all cues treatment: $t_{12}=3.76$, $P=0.003$; non-visual cues treatment: $t_{12}=3.06$, $P=0.010$; visual cues treatment: $t_{12}=2.99$, $P=0.011$; Fig. 3c).

Comparison between populations and treatments

"Population" had a significant influence on the relative time spent near the fed male (repeated measures ANOVA: $F_{2,36}=15.45$, $P<0.0001$). A post-hoc test revealed that the cave population differed from the river and from the sulfur-creek population [Fisher's protected least significant difference (PLSD): both $P<0.0001$], whereas the river and sulfur-creek populations did not differ ($P=0.87$). "Treatment" had no significant effect (repeated measures ANOVA: $F_{2,72}=2.15$, $P=0.12$). The interaction term "population" × "treatment" also had no effect on the relative time spent near the well-fed male ($F_{4,72}=0.71$, $P=0.59$).

Discussion

We measured the time females from three different populations of the Atlantic molly spent associating with a food-deprived or a well-fed male in a simultaneous choice situation. Females from the different populations clearly differed in whether or not they preferred well-nourished males. River-dwelling females never showed any clear preference, but sulfur-creek females did so in the visual cues treatment. Cave molly females strongly preferred to associate with the well-fed male in all treatments. Why do cave molly females show a preference? Why do sulfur-creek females have a visual preference, but river females do not? Our study revealed that males from the sulfur creek and from the cave are showing signs of malnourishment, whereas river-dwelling mollies seem to have access to sufficient food. This may explain the weak response in the river population: if the trait has a low "indicator value", there will be no evolutionary response to it. In all populations studied, there was variance in male nutritional state (Fig. 2). Hence, under natural conditions, there is a potential for benefits to females by female choice both in river-dwelling, sulfur-creek and cave-dwelling *P. mexicana*.

The signs of starvation in the sulfur-creek and cave population were unexpected, because unlike many other cave ecosystems (Poulson and White 1969; Barr and Holsinger 1985; Poulson and Lavoie 2000), the Cueva del Azufre has so far been classified as energy rich (Langecker et al. 1996; Parzefall 2001). The cave supports a large population of cave mollies, with high population densities in many parts of the cave: 100–200 fish per square meter in some chambers (Parzefall 1993b, 2001), but lower densities of 10–12 animals per square meter in cave chamber XIII (after Körner 1999 and K.U. Heubel et al., unpublished data). Population densities in river habitats are 2–50 animals per square meter (Parzefall 1993b, 2001). The high density in some parts of the cave is also unusual for cave fishes (see Trajano 2001). Consequently, the cave ecosystem must be sufficiently energy-rich to support these populations, but densities may have reached a maximum. Alternatively, the cave may provide stable, but low-quality food, like sulfur bacteria.

The starved status of the cave and sulfur-creek fish may also be linked to the toxic properties of the water. There are several springs discharging water with hydrogen sulfide inside the cave. Therefore, the oxygen content of the water in- and outside the cave is low (I. Schlupp et al., unpublished data). The mollies show behavioral responses to the low oxygen content of the water: near sulfur sources, they spent most of their time near the more oxygenated water surface, which is a typical behavior of fishes in hypoxic environments (Lewis 1970; Kramer and Mehegan 1981; Kramer and McClure 1982; Chapman and Chapman 1993; Timmerman and Chapman 2003). Aerobic surface respiration may cause high energetic costs (Kramer 1983). Furthermore, under hypoxic conditions, fish often have to cease other behaviors like feeding (*P. reticulata*: Weber and Kramer 1983; *P. gilii*: Chapman and Chapman 1993). We assume that the extreme environmental conditions of the two sulfur habitats impose a cost on male nutritional status. Hence, the nutritional state may be a reliable indicator of a male's ability to cope with extreme abiotic conditions.

Why do sulfur-creek females discriminate only in the visual cues treatment? We predicted a preference in the all cues treatment, which allowed for a maximum of different cues (visual and non-visual) to pass through the wire mesh. In fact, in other treatments, this mode of presentation has led to stronger discrimination in *P. mexicana* (Plath et al. 2001, 2003b). Possibly, the wire-mesh material has limited the transfer of visual cues to some degree. Therefore, our data suggest that visual cues are important for female mate choice in the sulfur-creek population.

Cave females strongly preferred well-nourished males in all three treatments. The visual preference is unlikely to have evolved in darkness. Hence, cave molly females must have inherited the visual preference for well-nourished males from the nearest surface population. The cave and sulfur-creek populations are closely related (Möller 2001). However, cave mollies have evolved a novel non-visual preference. This parallels previous findings: cave molly females also show a preference for large male body size in darkness (Arndt et al. 2003; Plath et al. 2003c, 2004). Body shape changes after 1 week of starvation (Figs. 1 and 2). Different nutritional state may lead to a whole set of cues available for females: males may cause: (i) different water displacement signals, (ii) different amounts of water-soluble pheromones, or (iii) they may exhibit behavioral differences. Our data do not allow us to distinguish which of these alternative mechanisms are being used by cave molly females. Qualitatively, starved males were swimming more vigorously up and down in their stimulus cylinders. However, these differences were not quantified. Starved males might be less responsive to sexual signals and/or might not engage in sexual interactions easily, but qualitative observations showed that they were even more active that the fed males. The cave molly has a sensory basis for detecting mechanosensory information: some canals of the head canal system of the lateral line remain incompletely covered, leading to widened canal pores (Walters and Walters 1965; Parzefall 1970), and this is likely associated with modified mechanosensory properties. We assume that females use differences in body shape between the two males to determine their nutritional state.

In summary, Atlantic molly females of some populations do base their mate choice decisions on the present nutritional state of a male. The pattern of male nutritional state among the three populations is opposite to our predictions. Only females from habitats in which the fish are naturally in a bad nutritional state have a preference for good male nutritional state. This is in agreement with the idea that this preference has evolved relative to the indicator value of male malnutrition. In the cave and sulfur-creek habitats, good nutritional state of a male may be a more reliable indicator of male fitness than in river-dwelling mollies.

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