

Cave fish looking for mates: A visual mating preference in surface- and cave-dwelling Atlantic mollies (*Poecilia mexicana*, Poeciliidae)

Höhlenfische bei der Partnerwahl: Eine visuelle Paarungspräferenz bei oberirdischen und höhlenbewohnenden Atlantikkärpflingen (*Poecilia mexicana*, Poeciliidae)

Martin Plath¹, Michael Tobler^{2,3} & Ingo Schlupp^{1,2}

¹Universität Hamburg, Biozentrum Grindel, Martin-Luther-King Platz 3, D-20146 Hamburg, mplath@zimserver.zoologie.uni-hamburg.de

²Universität Zürich, Zoologisches Institut, Winterthurerstraße 190, CH-8057 Zürich

³ETH Zürich, Departement Biologie, SOK ETH-Zentrum, Sonneggstrasse 23, CH-8092 Zürich

Zusammenfassung: Der Atlantikkärpfling *Poecilia mexicana* bewohnt eine Reihe von oberirdischen Flusshabitaten, aber auch eine Kalksandsteinhöhle in Tabasco, Mexiko. Im Gegensatz zu vielen anderen Höhlenfischen haben die Höhlenmollies noch immer funktionelle Augen. Es wurde untersucht, ob Weibchen einer Oberflächen- und der Höhlenpopulation visuelle Reize zur Partnerwahl nutzen können. Wir haben erwartet, dass die oberirdischen Weibchen in simultanen Wahlversuchen größere Männchen klar bevorzugen. In der Höhlenform hingegen sollte die Präferenz schwächer sein oder fehlen, da diese Fische unter natürlichen Bedingungen nicht visuell kommunizieren. Mittels einer Regressionsanalyse wurde gezeigt, dass nur Höhlenmollyweibchen deutlich zwischen zwei Männchen unterschiedlicher Größe unterscheiden. Diese Daten zeigen, dass die visuelle Präferenz für große Männchen in der Höhlenform bestehen bleibt. Es ist unklar, warum die Oberflächenform von *P. mexicana* in unserem Experiment keine Präferenz für große Männchen zeigte, obwohl in anderen Untersuchungen eine solche Präferenz nachgewiesen werden konnte.

Schlüsselwörter: höhlenbewohnende Mollys, Partnerwahl, sexuelle Selektion, visuelle Reize

Summary: The Atlantic molly *Poecilia mexicana* inhabits a variety of surface (river) habitats, but also a sulphurous limestone cave in Tabasco, Mexico. Unlike many other cave fishes, the cave molly has retained functional eyes. We asked whether females from a river population and cave molly females can use solely visual cues from males to choose their mates. We predicted that the river-dwelling females would strongly prefer the larger of two males in simultaneous choice tests. In the cave form, the response might be weaker or even absent, because naturally these fish do not communicate visually. Using regression analysis, we found that only “cave molly females” strongly discriminated between two unequal sized males, but not the “surface females”. Our data demonstrate that a visually mediated mating preference has persisted in the cave form. It remains unclear why the surface form did not show a preference for large males in this experiment, since earlier studies have shown that such a preference exists in river-dwelling *P. mexicana*.

Key words: cave molly, female choice, sexual selection, visual cues

1. Introduction

Cave fishes have been used as model organisms to study morphological modifications related to life in darkness such as eye and pigment reduction or the evolution of non-visual sensory or-

gans (e.g. POULSON 1963, BANISTER 1984, WILKENS 1988, WEBER et al. 1998, WEBER 2000). Recently, cave fishes have received interest in evolutionary developmental biology (JEFFREY 2001 for a review). Ecological studies have mainly focused on food availability in caves and the correlated

low abundance of cave fishes (PARZEFALL 1993b, TRAJANO 2001 for reviews). Especially in caves in temperate climates, food tends to be scarce (POULSON & WHITE 1969, BARR & HOLSINGER 1985, POULSON & LAVOIE 2000). Cave fishes may evolve physiological and/or morphological adaptations to cope with food scarcity, like additional fat-storing tissues (HÜPPOP 2000).

Studies on the behavioural ecology of cave fishes (like sexual selection by mate choice) are comparably rare (PARZEFALL 1993a, 2001 for reviews). In this study, we used a comparative approach to examine female choice in surface- and cave-dwelling populations of the Mexican livebearer *Poecilia mexicana* STEINDACHNER, 1863 (Poeciliidae, Teleostei). How is mate choice behaviour affected when this diurnal, highly visual species moves to a completely lightless habitat?

Together with the Mexican tetra, *Astyanax fasciatus* (Characidae; WILKENS 1988, JEFFREY 2001), the cave form of the Atlantic molly, *P. mexicana* is the most thoroughly studied cave fish (PARZEFALL 2001). While surface-dwelling *P. mexicana* are widely distributed in Mexican freshwaters (ROSEN & BAILEY 1963, MILLER 1966, 1983, SCHLUPP et al. 2002), cave-adapted *P. mexicana* are only known from one south Mexican limestone cave, the Cueva del Azufre (GORDON & ROSEN 1962, also called Cueva de Villa Luz, e.g. HOSE & PISAROWICZ 1999, and Cueva de las Sardinas, Parzefall 2001). Despite ubiquitous dissolved hydrogen sulphide, cave mollies occur at high density (PARZEFALL 2001). The Cueva del Azufre has been considered to be relatively energy-rich due to chemoautotrophic primary production (LANGECKER et al. 1996). Cave mollies are small, easy to breed and have relatively short generation intervals. Hence, cave mollies represent very good laboratory organisms.

Mollies caught in the cave are whitish pale. Light-reared offspring become greyish, however they remain to some extent less intensely coloured than surface *P. mexicana* (PETERS et al. 1973). Eyes are only slightly reduced in diameter, apparently following a gradient from the cave-mouth to the innermost cave chambers (PETERS et al. 1973). Cave mollies have more taste buds on the dorsal part of their heads and females possess an en-

larged “genital pad” (PARZEFALL 1970). This probably enhances signal transfer during “nipping”, a behaviour during which a male touches a female’s genital region with his snout to obtain chemical cues (ZEISKE 1968, PARZEFALL 1970, 1970, 1973). The pores of the lateral line head canal system are widened, and some canals remain uncovered during ontogenesis (WALTERS & WALTERS 1965, PARZEFALL 1970).

Previous behavioural studies have shown that cave mollies differ markedly from surface-dwelling ones in many aspects of their social behaviour: For example, aggressive and shoaling behaviour are reduced and territoriality is absent (PARZEFALL 1974, 1979, 1993b, 2001, pers. obs. in nature). In the context of reproductive behaviour, previous studies have concentrated on sex recognition (ZEISKE 1968, 1971, PLATH et al. 2001, 2003b).

In the present study, we examined the evolution of pre-copulatory mating preferences in *P. mexicana* females during the colonisation of their lightless habitat. We asked: How do visually mediated mating preferences evolve when animals colonise a habitat in which visual communication is impossible? Are visually mediated preferences reduced because they are functionless? MARLER & RYAN (1997) have suggested that seemingly useless (visual) mating preferences can persist although they have no apparent adaptive significance. The unisexual gynogenetic Amazon molly, *Poecilia formosa*, a clonal all-female species of hybrid origin that requires insemination by closely related species only to trigger embryogenesis (HUBBS & HUBBS 1932, SCHARITL et al. 1995), has been shown to exhibit a mating preference for large male body size although males do not genetically contribute to their offspring. *P. formosa* has probably inherited this preference from its sexual ancestors (MARLER & RYAN 1997). However, *P. formosa* females are likely to have a direct benefit of associating with large males due to sexual harassment by small males of the genetically parental species *P. latipinna* (SCHLUPP unpublished data) and *P. mexicana* (HEUBEL & PLATH unpublished data). In cave-dwelling *P. mexicana*, however, sexual harassment by males is lacking (PLATH et al. 2003a).

Some previous work has focussed on the question whether sexual selection by female choice still occurs in the cave molly. One important choice criterion is male body size: In livebearing fishes, males often show a pronounced polymorphism in body size (*P. latipinna*: SNELSON 1984, TRAVIS & WOODWARD 1989, TRAVIS 1994, *P. mexicana*: MENZEL & DARNELL 1973). A field study has shown that cave molly males also show a typical body size polymorphism (PLATH et al. 2003a). Males almost cease growth at maturation (SNELSON 1982, 1985). In many species, the age at maturation has been shown to be genetically determined and to vary considerably between individual males (*Xiphoborus*: PETERS 1964, KALLMAN et al. 1973, KALLMAN & BORKOSKI 1978, KALLMAN 1983, 1989, ZIMMERER & KALLMAN 1989, RYAN et al. 1992, *Limia perugiae*: ERBELDING-DENK et al. 1994). Female choice for large male body size has been described for a variety of poeciliids, e.g. *Xiphoborus nigrensis* (RYAN & WAGNER 1987, RYAN et al. 1990), *X. helleri* (KLAMROTH 1997, ROSENTHAL & EVANS 1998), *Heterandria formosa* (ASPBURY & BASOLO 2002), *Poeciliopsis occidentalis* (CONSTANZ 1975), *Poecilia reticulata* (REYNOLDS & GROSS 1992, ENDLER & HOUDE 1995), *P. latipinna* (SCHLUPP et al. 1994, BISAZZA & PILASTRO 1997, PTACEK & TRAVIS 1997, WITTE & RYAN 1998, GABOR 1999, GABOR & PAGE 2004) and *P. formosa* (MARLER & RYAN 1997).

Do *P. mexicana* females also prefer large males and how does this preference evolve in darkness? PLATH et al. (2004) gave females from three *P. mexicana* populations (surface-dwelling females from the Rio Oxolatan and from the cave entrance, and cave molly females, light- and dark-reared) a choice between a large and a small male in simultaneous choice tests (PLATH et al. 2004). To estimate which kind of cues are important for decision-making, the focal fish were given different kinds and amounts of information from the stimulus fish. Firstly, females were presented multiple cues (see JOHNSTONE 1996). The stimulus males were swimming in wire-mesh cylinders in light. Secondly, only non-visual cues could be perceived, because the tests were conducted in darkness under infrared conditions. In the third experiment, males were confined to transparent

Plexiglas cylinders in light, so that the female perceived visual cues.

All light-reared females showed a preference to associate with large males in the two experiments in light. In darkness, only cave molly females showed a preference. This data suggests that this mating preference is mediated mainly by visual cues in the surface form. The response to visual cues appears to have persisted in the cave molly. Furthermore, a non-visual preference seems to have evolved. Most probably, a sensory shift has occurred in a way that the lateral line is involved in detecting relevant cues to substitute for the absence of vision (PLATH et al. 2004). Vibrational signals have been shown to be involved in intersexual communication in salmon (SATOU et al. 1994).

The previous study comprises one problem in the interpretation of the response to visual cues: since the focal males have not been presented in separate tanks, chemical cues (pheromones) might partly have reached the female (e.g. LILEY 1966, CROW & LILEY 1979, BRETT & GROSSE 1982, MEYER & LILEY 1982, CRAPON DE CAPRONA & RYAN 1990, McLENNAN & RYAN 1997, 1999, HANKINSON & MORRIS 2003, SHOHEIT & WATT 2003). This is also true for the experiment with Plexiglas cylinders, which were open at the bottom. Another previous study has suggested that *P. mexicana* appears not to respond to water soluble chemical cues from conspecifics (WENZEL, SCHLUPP & PLATH unpubl. data). However, in the present study, we modified the experimental design to avoid the potentially confounding effect of chemical communication. Surface and cave molly females were given a choice between two males differing by size, while all three fish were swimming in separate aquaria. We predicted that surface females would spend more time near the larger of the two males. Do cave molly females still show a response to solely visual cues?

2. Material and Methods

We used mature *P. mexicana* originating from two different populations: the first (surface form) came from a typical stream, the Rio Oxolatan, in South-Mexico (Tabasco). The second (cave form)

originated from the hindmost cave chamber of a nearby limestone cave, the Cueva del Azufre (PLATH et al. 2003a, 2004). Populations were maintained as randomly outbred large aquarium stocks in several 100-200 l aquaria at 25-30 °C. Both populations were reared at a 12:12 hour light:dark illumination cycle in addition to natural daylight, making sure that even the cave form was familiar with light. Fish were fed twice daily *ad libitum* with commercially available fish flake food and *Artemia* nauplii.

Preference tests were conducted in a standard test tank (60 x 29.5 x 33 cm length x width x height). Two lines drawn on the front visually divided three equal compartments: two lateral preference zones and a central neutral zone (each 20 cm). We placed two smaller tanks (18 x 25 x 22 cm) directly adjacent to each preference zone to hold one stimulus male each. We adjusted the water level in all three aquaria (app. 20 cm). Blue cardboard covered the outer walls of the aquaria, except for the walls between the three tanks and the front walls. Illumination was provided by two 30 Watt neon-tubes approximately 35 cm above the water level. UV radiation was absent.

Before a test, two males were randomly taken from the stock tanks and introduced into one of the lateral stimulus tanks each. Males matched the population of the respective female. To initiate a trial, a focal female was gently introduced into the middle compartment. We measured the time the female spent in both preference zones during five minutes. After this time, we interchanged the two stimulus males and the measurement was repeated. This enabled us to detect side-biases. We *a priori* decided that trials in which a female spent more than 80 % of her choice time in only one of the two compartments were discarded as side-biases (surface form: 5, cave: 13). Trials in which the females spent less than 50 % of their time in the preference zones would have been discarded due to low response. After a trial, the standard lengths (SL) of all fish was carefully measured to the nearest full millimetre. Then, the three fish were transferred to another tank, so that all test fish were used only once for the tests.

We randomly labelled the two stimulus males as male A and male B. We calculated the dif-

ference in male SL as $SL \text{ of male A} - SL \text{ of male B}$. A corresponding preference score was calculated as the time the focal female spent in the proximity of male A – time near male B. We employed ANCOVA to analyse our data, where ‘population’ was the between factor and ‘male size difference’ was the covariate. We predicted that ‘population’ alone should not have a significant influence, because the preference-score-data should be evenly scattered over a broad range, where negative values would be predicted if male A is smaller than male B and positive values would be predicted if male A is larger than male B. Hence, we predicted a significant influence of the covariate ‘male size difference’. Finally, the interaction term ‘population’ x ‘male size difference’ indicates whether the preference functions of the two populations differ in slope. For a *post hoc* analysis, we also calculated the linear regressions between male body size difference and female preference scores for both populations. We predicted a positive regression-slope in the surface form. In the cave form, the slope might be lower or even zero.

3. Results

‘Population’ had no significant influence on female preferences (ANCOVA: $df = 1, F = 1.62, P = 0.21$), but the covariate ‘male body size difference’ had a significant influence (ANCOVA: $df = 1, F = 5.68, P = 0.023$). Hence, female preferences for the larger of two males are stronger the larger the difference in male body size is. There was a weak but non-significant influence of the interaction term ‘population’ x ‘male size difference’ (ANCOVA: $df = 1, F = 3.96, P = 0.054$). Hence, the two populations tended to differ in the slopes of the curves describing the correlation between male size difference and female preference score. A *post hoc* analysis showed that the linear regression was not significant in the surface form ($R^2 = 0.0023$, regression ANOVA: $df = 1, n = 20, F = 0.041, P = 0.84$; Figure 1), but was highly significant in the cave form, where a strong positive relationship was detected ($R^2 = 0.59, df = 1, n = 20, F = 25.52, P < 0.001$; Figure 1).

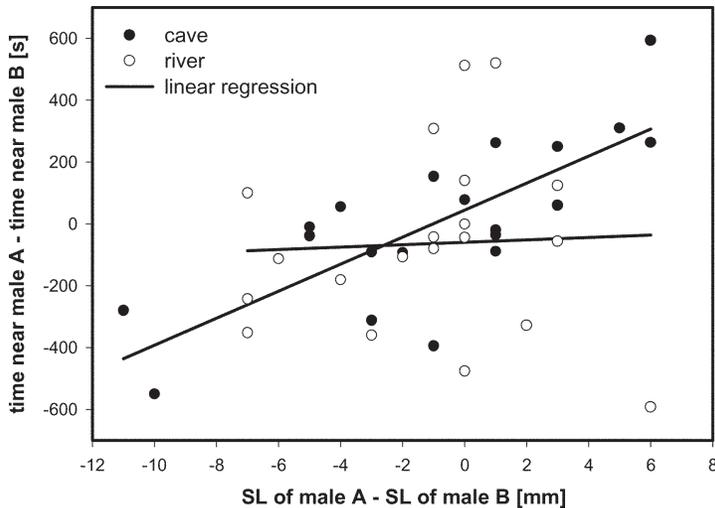


Fig. 1: Female preferences for large male body size in surface- ($R^2 = 0.0023$) and cave-dwelling *P. mexicana* ($R^2 = 0.59$). A female was given the opportunity to associate with two males (A and B) that differed by size. The fish were divided by transparent glass. Preferences are expressed as difference in the time spent in proximity of male A – time near male B. A positive slope indicates preference for large male size. $n = 20$ in each case. SL, male standard length.

Abb. 1: Weibliche Paarungspräferenzen für große Körpergröße der Männchen bei oberirdischen ($R^2 = 0.0023$) und höhlenbewohnenden *P. mexicana* ($R^2 = 0.59$). Einem Weibchen wurde die Möglichkeit gegeben, sich mit einem von zwei Männchen (A und B) zu vergesellschaften, die sich in der Größe unterschieden. Alle Fische waren durch Glas voneinander getrennt. Präferenzen sind als Differenzen der Aufenthalte nahe Männchen A und Männchen B angegeben. Eine positive Steigung der Regressionsgeraden deutet auf eine Bevorzugung großer Männchen hin. $n = 20$ in beiden Fällen. SL, männliche Standardlänge.

4. Discussion

We gave surface- and cave-dwelling *P. mexicana* females an opportunity to associate with one of two males which differed by size to varying degrees. The females perceived solely visual information, because the males were placed in separate aquaria adjacent to the female's tank. Contrary to our prediction, cave females strongly discriminated during the tests and preferred the larger male. In contrast, no preference was detected in the surface form.

Previous studies have demonstrated that surface females do show a visually mediated mating preference for large males (KÖRNER 1999; PLATH et al. 2004). It remains unclear why these females did not show a preference in the present study. Possibly, the surface females were more responsive to male traits other than body size *per se*, for example differences in the swimming speed of

the males. In the previous studies on mate choice in this population the males have been confined to relatively small cylinders (12 cm in diameter), in which the males could not move much (KÖRNER 1999, PLATH et al. 2004). Here, the males were swimming in comparably large aquaria, so that differences in their swimming performance may have been more evident to the females. Potentially, cave molly females are more responsive to the “more simple” trait body size, but the surface females also use additional, e.g. behavioural information for mate choice.

Why did the cave females exhibit a strong visually mediated preference for large males although in their natural habitat visual communication is impossible? Features that are not employed in darkness are often reduced in cave-dwellers. For example, cave fishes are often eyeless and unpigmented, and sometimes even scales are reduced (WEBER et al. 1998). Reduction pro-

cesses have also been reported for certain behaviours such as shoaling (cave tetras, *Astyanax fasciatus*, and cave mollies, *P. mexicana*: PARZEFALL 1993b, cave barb, *Garra barreimiae*: TIMMERMAN, SCHLUPP & PLATH in prep.), aggressive behaviour (*A. fasciatus*: BURCHARDS et al. 1985, *P. mexicana*: PARZEFALL 1974, 1979) and “alternative” size-dependent male mating behaviour (*P. mexicana*: PLATH et al. 2003a). On the one hand, the cave molly may be a phylogenetically young cave-dweller (PETERS et al. 1973), so that not enough time has elapsed for the regression of this visually mediated behaviour. Unlike many other cave fishes, which are sometimes considered phylogenetically old cave forms [like some of the cave populations of the Mexican tetras *Astyanax fasciatus* (WILKENS 1988)], eyes are only slightly smaller in the cave molly compared with that of epigeal *P. mexicana*. The visual pigments are almost unchanged (KÖRNER, SCHLUPP, PLATH & LOEW submitted). However, the retina is flattened and the outer part of the retinal cones are smaller (PETERS and PETERS 1968).

Both cave molly females (PLATH et al. 2001) and males (PLATH et al. 2003b) have lost the capability to discriminate between the sexes on the basis of visual cues. Hence, other visually mediated responses do show signs of regression, but the visually mediated mating preference for large male size does not. Hence, young phylogenetic age alone cannot explain the persistence of this mating preference in the cave molly. The pattern is also inconsistent with ongoing gene flow from surface populations into the cave population. Gene flow is unlikely because a 15 m high waterfall separates the creek flowing out of the cave from the river-dwelling population. Inside the cave, the population studied is separated from other cave pools by another waterfall, approximately 1.5 m high.

We hypothesise that the visual preference is maintained because a non-visual preference for the same trait enables mate choice in darkness in cave molly females (PLATH et al. 2004). If the neuronal “preference system” is being used even in darkness, there will be stabilising selection on it. As long as eyes are not reduced, visual cues may still be used as releaser for this preference

under laboratory conditions, but under natural conditions this preference uses exclusively non-visual cues. Our study demonstrates that seemingly “useless” visual mating preferences may persist even in the apparent absence of stabilising selection. Cave-dwelling Atlantic mollies are a unique model system to study evolutionary responses to environmental changes like the breakdown of visual communication in a lightless habitat.

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5. References

- ASPBURY, A.S., & A.L. BASOLO. 2002. Repeatable female preferences, mating order and mating success in the poeciliid fish, *Heterandria formosa*. *Behav. Ecol. Sociobiol.* 51, 238-244.
- BANISTER, K.E. 1984. A subterranean population of *Garra barreimiae* (Teleostei: Cyprinidae) from Oman, with comments on the concept of regressive evolution. *J. Nat. Hist.* 18, 927-938.
- BARR, T.C., & J.R. HOLSINGER. 1985. Speciation in cave faunas. *Ann. Rev. Ecol. Syst.* 16, 313-337.
- BISAZZA, A., & A. PILASTRO. 1997. Small male mating advantage and reversed size dimorphism in poeciliid fishes. *J. Fish Biol.* 50, 397-406.
- BRETT, A.T.D., & A. GROSSE. 1982. A reproductive pheromone in the Mexican poeciliid fish *Poecilia chica*. *Copeia* 1982, 219-223.
- BURCHARDS, H., A. DÖLLE, & J. PARZEFALL. 1985. Aggressive behaviour of an epigeal population of *Astyanax mexicanus* (Characidae, Pisces) and some observations of three subterranean populations. *Behav. Process.* 11, 225-235.
- CRAPON DE CAPRONA, M.D., & M. J. RYAN. 1990. Conspecific mate recognition in swordtails, *Xiphophorus nigrensis* and *X. pygmaeus* (Poeciliidae): olfactory and visual cues. *Anim. Behav.* 39, 290-296.
- CONSTANTZ, G.D. 1975. Behavioural ecology of mating in the gila topminnow, *Poeciliopsis occidentalis*

- (Cyprinodontiformes: Poeciliidae). *Ecology* 56, 966-973.
- R. T. CROW R. T. & N. R. LILEY. 1979. A sexual pheromone in the guppy, *Poecilia reticulata* (PETERS). *Can. J. Zool.* 57, 184-188.
- ENDLER, J. A. & A. E. HOUDE. 1995. Geographic variation in female preferences for male traits in *Poecilia reticulata*. *Evolution* 49, 456-468.
- ERBELDING-DENK, C., J. H. SCHRÖDER, M. SCHARITL, I. NANDA, M. SCHMID & J. T. EPPLEN. 1994. Male polymorphism in *Limia perugiae* (Pisces: Poeciliidae). *Behav. Genet.* 24, 95-101.
- GABOR, C. R. 1999. Association patterns of sailfin mollies (*Poecilia latipinna*): alternative hypotheses. *Behav. Ecol. Sociobiol.* 46, 333-340.
- GABOR, C. R. & R. PAGE. 2004. Female preference for large males in sailfin mollies, *Poecilia latipinna*: the importance of predation pressure and reproductive status. *Acta Ethol.* online first
- GORDON, M. S. & D. E. ROSEN. 1962. A cavernicolous form of the Poeciliid fish *Poecilia sphenops* from Tabasco, Mexico. *Copeia* 1962, 360-368.
- HANKINSON, S. J. & M. R. MORRIS. 2003. Avoiding a compromise between sexual selection and species recognition: female swordtail fish assess multiple species-specific cues. *Behav. Ecol.* 14, 282-287.
- HOSE, L. D. & J. A. PISAROWICZ. 1999. Cueva de Villa Luz, Tabasco, Mexico: Reconnaissance study of an active sulfur spring cave. *J. Cave Karst. Stud.* 61, 13-21.
- HUBBS, C. L. & L. C. HUBBS. 1932. Apparent parthenogenesis in nature in a form of fish of hybrid origin. *Science* 76, 628-630.
- HÜPPOP, K. 2000. How do cave animals cope with the food scarcity in caves?, pp. 159-188. In: *Ecosystems of the world 30: Subterranean ecosystems.* (H. WILKENS, D.C. CULVER, & W.F. HUMPHRIES, eds.). Elsevier, Amsterdam.
- JEFFERYJEFFREY, W. R. 2001. Cavefish as a model system in evolutionary developmental biology. *Dev. Biol.* 231, 1-12.
- JOHNSTONE, R. A. 1996. Multiple displays in animal communication: "backup signals" and "multiple messages." *Phil. Trans. R. Soc. Lond. B* 351, 329-338.
- KALLMAN, K. D. 1983. The sex determining mechanism of the poeciliid fish, *Xiphophorus montezumae*, and the genetic control of the sexual maturation process and adult size. *Copeia* 1983, 755-769.
- KALLMAN, K. D. 1989. Genetic control of size at maturity in *Xiphophorus*, pp. 163-184. In: *Ecology and Evolution of Livebearing Fishes (Poeciliidae)* (MEFFE, G.K., & F.F. SNELSON jr., eds.). Prentice Hall, New Jersey, 163-184.
- KALLMAN, K.D., & V. BORKOSKI. 1978. A sex-linked gene controlling the onset of sexual maturity in female and male platyfish (*Xiphophorus maculatus*), fecundity in females and adult size in males. *Genetics* 89, 79-119.
- KALLMAN, K.D., M.P. SCHREIBMAN, & V. BORKOSKI. 1973. Genetic control of gonadotrop differentiation in the platyfish, *Xiphophorus maculatus* (Poeciliidae). *Science* 181, 678-680
- KALLMAN, K.D., & V. BORKOSKI. 1978. A sex-linked gene controlling the onset of sexual maturity in female and male platyfish (*Xiphophorus maculatus*), fecundity in females and adult size in males. *Genetics* 89, 79-119.
- KLAMROTH, B. 1997. Intra- und intersexuelle Selektion beim Grünen Schwertträger (*Xiphophorus helleri*) PhD thesis, University of Hamburg.
- KÖRNER, K.E. 1999. Zur sexuellen Selektion höhlenlebender Atlantikkärpflinge, *Poecilia mexicana* STEINDACHNER 1863. PhD thesis, University of Hamburg.
- LANGECKER, T.G., H. WILKENS, & J. PARZEFALL. 1996. Studies on the trophic structure of an energy rich Mexican cave (Cueva de las Sardinias) containing sulfurous water. *Mem. Biospeol.* 23, 121-125.
- LILEY, N.R. 1966. Ethological isolating mechanisms in four sympatric species of poeciliid fishes. *Behaviour* 13, 1-197.
- MARLER, C.A., & M.J. RYAN. 1997. Origin and maintenance of a female mating preference. *Evolution* 51, 1244-1248.
- MCLENNAN, D.A., & M.J. RYAN. 1997. Response to conspecific and heterospecific olfactory cues in the swordtail *Xiphophorus cortezi*. *Anim. Behav.* 54, 1077-1088.
- MCLENNAN, D.A., & M.J. RYAN. 1999. Interspecific recognition and discrimination based upon olfactory cues in northern swordtails. *Evolution* 53, 880-888.
- MENZEL, B.M., & R.M. DARNELL. 1973. Systematics of *Poecilia mexicana* (Pisces: Poeciliidae) in Northern Mexico. *Copeia* 1973, 225-237.
- MEYER, J.H., & N.R. LILEY. 1982. The control of production of a sexual pheromone in the female guppy, *Poecilia reticulata*. *Can. J. Zool.* 60, 1505-1510.
- MILLER, R.R. 1966. Geographic distribution of Central American freshwater fishes. *Copeia* 1966, 773-802.
- MILLER, R.R. 1983. Checklist and key to the mollies of Mexico (Pisces: Poeciliidae: *Poecilia*, subgenus *Mollienesia*). *Copeia* 1983, 817-822.

- PARZEFALL, J. 1970. Morphologische Untersuchungen an einer Höhlenform von *Mollienestea sphenops* (Pisces, Poeciliidae). Z. Morph. Tiere 68, 323-342.
- PARZEFALL, J. 1973. Attraction and sexual cycle of Poeciliids, pp. 177-183. In: Genetics and mutagenesis of fish (SCHRÖDER, J.H., ed.). Springer Berlin, Heidelberg, New York.
- PARZEFALL, J. 1974. Rückbildung aggressiver Verhaltensweisen bei einer Höhlenform von *Poecilia sphenops* (Pisces, Poeciliidae). Z. Tierpsychol. 35, 66-84.
- PARZEFALL, J. 1979. Zur Genetik und biologischen Bedeutung des Aggressionsverhaltens von *Poecilia sphenops* (Pisces, Poeciliidae). Z. Tierpsychol. 50, 399-422.
- PARZEFALL, J. 1993a. Behavioural ecology of cave-dwelling fishes, pp. 573-608. In: Behaviour of teleost fishes, second edition (T.J. PITCHER (ed.). Chapman and Hall, London.
- PARZEFALL, J. 1993b. Schooling behaviour in population-hybrids of *Astyanax fasciatus* and *Poecilia mexicana* (Pisces, Characidae and Poeciliidae), pp. 297-303. In: Trends in Ichthyology: An International Perspective. (H. SCHRÖDER, H., J. BAUER, & M. SCHARTL, eds.). Blackwell Scientific, Oxford.
- PARZEFALL, J. 2001. A review on morphological and behavioural changes in the cave molly *Poecilia mexicana* from Tabasco, Mexico. Environ. Biol. Fish. 50, 263-275.
- PETERS, G. 1964. Vergleichende Untersuchungen an drei Subspecies von *Xiphophorus helleri* (Pisces). Z. Zool. Syst. Evolutionsforsch. 2, 185-271.
- PETERS, N., & G. PETERS. 1968. Zur genetischen Interpretation morphologischer Gesetzmäßigkeiten der degenerativen Evolution. Z. Morph. Tiere 62, 211-244.
- PETERS, N., G. PETERS, J. PARZEFALL, & H. WILKENS. 1973. Über degenerative und konstruktive Merkmale bei einer phylogenetisch jungen Höhlenform von *Poecilia sphenops* (Pisces, Poeciliidae). Int. Revue ges. Hydrobiol. 1973, 417-436.
- PLATH, M., K.E. KÖRNER, I. SCHLUPP, & J. PARZEFALL. 2001. Sex recognition and female preferences of cave mollies *Poecilia mexicana* (Poeciliidae, Teleostei) in light and darkness. Mem. Biospeol. 28, 163-167.
- PLATH, M., J. PARZEFALL, & I. SCHLUPP. 2003a. The role of sexual harassment in cave and surface dwelling populations of the Atlantic molly, *Poecilia mexicana* (Poeciliidae, Teleostei). Behav. Ecol. Sociobiol. 54, 303-309.
- PLATH, M., K. WIEDEMANN, J. PARZEFALL, & I. SCHLUPP. 2003b. Sex recognition in surface and dwelling male Atlantic mollies *Poecilia mexicana* (Poeciliidae, Teleostei). Behaviour 140, 765-782.
- PLATH, M., J. PARZEFALL, K.E. KÖRNER, & I. SCHLUPP. 2004. Sexual selection in darkness: Female mating preferences in surface- and cave-dwelling Atlantic mollies, *Poecilia mexicana* (Poeciliidae, Teleostei). Behav. Ecol. Sociobiol. 55, 596-601.
- POULSON, T.L. 1963. Cave adaptation in amblyopsid fishes. Am. Midl. Nat. 70, 257-290.
- POULSON, T.L., & W.B. WHITE. 1969. The cave environment. Science 165, 971-981.
- POULSON, T.L., & K.H. LAVOIE. 2000. The trophic basis of subterranean ecosystems, pp. 231-249. In: Ecosystems of the world 30: Subterranean ecosystems (H. WILKENS, D.C. CULVER, & W.F. HUMPHRIES, eds.). Elsevier, Amsterdam.
- PTACEK, M.B., & J. TRAVIS. 1997. Mate choice in the sailfin molly, *Poecilia latipinna*. Evolution 51, 1217-1231.
- REYNOLDS, J.D., & M.R. GROSS. 1992. Female mate preference enhances offspring growth and reproduction in a fish, *Poecilia reticulata*. Proc. Roy. Soc. Lond. B 250, 57-62.
- ROSEN, D.E., & R.M. BAILEY. 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography and systematics. Bull. Am. Mus. Nat. Hist. 126, 1-76.
- ROSENTHAL, G.G., & C.S. EVANS. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. Proc. Natl. Acad. Sci. USA 95, 4431-4436.
- RYAN, M.J., & W.E. WAGNER. 1987. Asymmetries in mating preferences between species: female swordtails prefer heterospecific mates. Science 236, 595-597.
- RYAN, M.J., D.K. HEWS, & W.E. WAGNER. 1990. Sexual selection on alleles that determine body size in the swordtail *Xiphophorus nigrensis*. Behav. Ecol. Sociobiol. 26, 231-237.
- RYAN, M.J., C.M. PEASE, & M.R. MORRIS. 1992. A genetic polymorphism in the swordtail *Xiphophorus nigrensis*: Testing the prediction of equal fitnesses. Am. Nat. 139, 21-31.
- SATOU, M., H.A. TAKEUCHI, J. NISHII, M. TANABE, S. KITAMURA, N. OKUMOTO, & M. IWATA. 1994. Behavioural and electrophysiological evidence that the lateral line is involved in the inter-sexual vibrational communication of the hime salmon (landlocked red salmon, *Oncorhynchus nerka*). J. Comp. Physiol. A 174, 539-549.
- SCHARTL, M., B. WILDE, & J. PARZEFALL. 1995. Evolutionary origin of a parthenoform, the amazon

- molly *Poecilia formosa*, on the basis of a molecular genealogy. *Evolution* 45, 827-835.
- SCHLUPP, I., C. MARLER, & M.J. RYAN. 1994. Benefit to male sailfin mollies of mating with heterospecific females. *Science* 236, 373-374.
- SCHLUPP, I., J. PARZEFALL, & M. SCHARTL. 2002. Biogeography of the uni-sexual amazon molly, *Poecilia formosa*. *J. Biogeogr.* 29, 1-6.
- SHOHET, A.J., & P.J. WATT. 2003. Female association preferences based on olfactory cues in the guppy, *Poecilia reticulata*. *Behav. Ecol. Sociobiol.* 55, 363-369.
- SNELSON, F.F. jr. 1982. Indeterminate growth in males of the sailfin molly, *Poecilia latipinna*. *Copeia* 1982, 296-304.
- SNELSON, F.F. jr. 1984. Seasonal maturation and growth of males in natural populations of *Poecilia latipinna*. *Copeia* 1984, 252-255.
- SNELSON, F.F. jr. 1985. Size and morphological variation in males of the sailfin molly, *Poecilia latipinna*. *Environ. Biol. Fish.* 13, 35-47.
- TRAJANO, E. 2001. Ecology of subterranean fishes: an overview. *Environ. Biol. Fish.* 62, 133-160.
- TRAVIS, J. 1994. Size-dependent behavioural variation and genetic control within and among populations, pp. 165-187. In: *Quantitative genetic approaches to animal behavior* (C.R.B. BOAKE, ed.). University of Chicago Press, Chicago.
- TRAVIS, J., & B.D. WOODWARD. 1989. Social context and courtship flexibility in male sailfin mollies, *Poecilia latipinna* (Pisces: Poeciliidae). *Anim. Behav.* 38, 1001-1011.
- WALTERS, L.H., & V.W. WALTERS. 1965. Laboratory observations on a cavernicolous Poeciliid from Tabasco, Mexico. *Copeia* 1965, 214-233.
- WEBER, A. 2000. Fish and amphibia, pp. 109-132. In: *Ecosystems of the world 30: Subterranean ecosystems* (H. WILKENS, D.C. CULVER, & W.F. HUMPHRIES, eds.). Elsevier, Amsterdam.
- WEBER, A., G.S. PROUDLOVE, J. PARZEFALL, H. WILKENS, & T.T. NALBANT. 1998. Pisces (Teleostei): Morphology, systematic diversity, distribution and ecology of stygobitic fishes, pp. 835-1373. In: *Encyclopaedia Biospeologica, Tome II.* (JUBERTHIE, C., & V. DECU, eds.) Société de Biospéologie, Moulis, Bucarest.
- WILKENS, H. 1988. Evolution and genetics of epigean and cave *Astyanax mexicanus* (Characidae, Pisces). *Evol. Biol.* 23, 271-367.
- WITTE, K., & M.J. RYAN. 1998. Male body length influences mate-choice copying in the sailfin molly *Poecilia latipinna*. *Behav. Ecol.* 9, 534-539.
- ZEISKE, E. 1968. Prädispositionen bei *Mollienesia sphenops* (Pisces, Poeciliidae) für einen Übergang zum Leben in subterranean Gewässern. *Z. vergl. Phys.* 58, 190-222.
- ZEISKE, E. 1971. Ethologische Mechanismen als Voraussetzung für einen Übergang zum Höhlenleben. Untersuchungen an Kaspar-Hauser-Männchen von *Poecilia sphenops* (Pisces, Poeciliidae). *Forma et functio* 1971, 270-282.
- ZIMMERER, E.J., & K.D. KALLMAN. 1989. Genetic basis for alternative reproductive tactics in the pygmy swordtail, *Xiphophorus nigrensis*. *Evolution* 43, 1298-1307.

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