

Reduction of a visually mediated association preference in the Cave molly (*Poecilia mexicana*, Poeciliidae, Teleostei)

Michael TOBLER^(1,2), Heike BURMEISTER⁽³⁾, Ingo SCHLUPP^(2,3), Martin PLATH^(2,3,4*)

¹⁾Zoologisches Institut, Universität Zürich, Winterthurerstr. 190, 8057 Zürich, Switzerland

²⁾Department of Zoology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, USA

³⁾Biozentrum Grindel, Universität Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

⁴⁾Abteilung für Evolutionsbiologie und Spezielle Zoologie, Institut für Biochemie und Biologie, Universität Potsdam, Karl-Liebknecht Str. 24-25, 14476 Potsdam, Germany

*corresponding author's e-mail: martin_plath@web.de

ABSTRACT

Several studies have reported on the persistence of visually mediated social preferences, such as preferences of females to associate with certain types of males, in an eyed cave fish, the Cave molly (*Poecilia mexicana*). However, so far most studies have examined preferences which are apparently currently under selection, i.e., the preferences are expressed also in darkness. In this paper we examined female preferences for (1) conspecific females and (2) males without a parasite-induced color change (black spot disease, BSD). In both cases, selection on the persistence of the preference is not apparent. As predicted, surface-dwelling females preferred conspecific over heterospecific females, but this preference was not found in the Cave molly. However, we found no evidence for female preferences relative to BSD-infection of males. We discuss that BSD-resistance probably has a low indicator value, so that this trait appears to be of minor importance for female mate choice even in surface-dwelling mollies.

Key words: sexual selection, indicator hypothesis, shoaling, association preferences, mate choice

INTRODUCTION

Near Tapijulapa (Tabasco, Mexico), a unique population of the widespread Atlantic molly, *Poecilia mexicana*, inhabits a sulfidic limestone cave, the Cueva del Azufre (syn. Cueva Villa Luz or Cueva de las Sardinas; Gordon and Rosen 1962). The cave population, also known as the Cave molly, differs in several characters from other populations of *P. mexicana*, which live in adjacent surface habitats like the sulfidic surface creek flowing out of the cave and other habitats without hydrogen sulfide (Tobler et al in press-b). Cave mollies have slightly reduced eyes and pigmentation. They possess widened pores of the head lateral line system and a pronounced genital pad in the female sex (Parzefall 2001). Despite reduced eye-diameter, Cave mollies are capable of vision. Beside these morphological adaptations to cave life, Cave mollies differ in an array of behavioral characteristics from surface-dwelling mollies. For example, Cave mollies have reduced energy-consuming behaviors like shoaling, aggression (Parzefall 1993) and "alternative" male sexual behavior (Plath et al 2003).

Since Cave mollies still have eyes, but naturally live in darkness, they offer a unique opportunity to study the evolution of social preferences, such as mating preferences, under changed environmental conditions. Previous studies have investigated the evolution of female mating preferences in the Cave molly. In these studies, mating preferences were determined as association preferences. For example, surface-dwelling Atlantic molly

females exhibited a mating preference for large males, which is mediated by visual cues (Plath et al 2004). A visually mediated preference is still found in the Cave molly and can be observed even when Cave molly females are presented video animations showing two males of different sizes (Plath et al 2003-b). However, under naturally dark conditions, Cave molly females have come to use a novel way of determining male body size by using non-visual (probably mechanosensory) cues: the female preference for large male body size can be observed even when two males of different sizes are presented in darkness (behind a plastic grid that is permeable for non-visual cues). Hence, the formerly visually mediated mating preference appears to have persisted, but under natural conditions – in darkness – females use another sensory system (probably the lateral line) to detect male quality (Plath et al 2003-b, 2004). This enables Cave molly females to express mating preferences even in darkness.

In another study we found females from the sulfur creek flowing out of the cave to show a visually mediated mating preference for well-nourished males (Plath et al 2005). This visual preference has even been enhanced in the Cave molly. Again, in the absence of light Cave molly females use non-visual cues to discriminate between two males differing in their nutritional state (Plath et al 2005).

The preferences reported above have likely evolved under strong selection, because mate choice may offer both direct and indirect benefits to the choosing indi-

vidual (Andersson 1994). In both cases, the response to visual cues has persisted, but the preference is also expressed in darkness. In this study, we examined the fate of two visual preferences which are unlikely to provide benefits in the cave population of *P. mexicana*: Firstly, we examined the preference of individual females to associate with a conspecific rather than a heterospecific female. Since Cave mollies do not share their habitat with other fish species (except for a burrowing synbranchid eel, *Ophisternon aenigmaticum*; Gordon and Rosen 1962), there should be no stabilizing selection on the preference to associate with conspecifics. Secondly, we examined the preference of females to avoid males infected with a parasite that causes a (visual) phenotypic change in infected males, namely black spots, whereby the parasite (a trematode) is encysted by the host's tissue. Melanophores in the host's tissue cause a black coloration of the cysts. This parasite type is absent in the cave, and – most importantly – infected males are most likely only visually distinguishable. Again, there should be no stabilizing selection on the preference to associate with healthy rather than parasitized males in the cave form of *P. mexicana*.

SPECIES RECOGNITION

In surface-dwelling fishes, species recognition can play an important role in the formation and maintenance of groups. Group-living offers a number of advantages, e.g., in terms of the avoidance of predation or foraging behavior (Krebs and Davies 1996). In fishes, simple social groups, known as shoals, provide benefits by protection from predators through increased vigilance, early predator detection and the “numerical dilution effect” (Godin 1986). Many species prefer to associate with conspecifics, a phenomenon known as conspecific cueing (Stamps 1988). This may be partly explained by the oddity effect: Phenotypically distinct individuals within a shoal are more likely attacked by predators than phenotypically similar individuals (McRobert and Bradner 1998). An additional reason for females to form conspecific all-female groups is the avoidance of male sexual harassment, as found in surface-dwelling *Poecilia mexicana* (Parzefall 1969).

In one part of our study, we investigated species recognition in two different populations of *P. mexicana*: a population from a clear water river near the Cueva del Azufre and the Cave molly. While fish from the surface population share their habitat with several other fish species, *P. mexicana* is the only fish species in the cave. Only a burrowing synbranchid eel *Ophisternon aenigmaticum* has only occasionally been found in the cave (Tobler et al in press-b). In contrast to the surface form, cave mollies show a considerably weaker tendency to form shoals (Parzefall 1993). Thus, it is very likely that species recognition is unimportant in the cave form, but is important in surface populations.

We compared the response (i.e., association preference) of *P. mexicana* females to a conspecific female or a female of a related species, *P. reticulata* (the Guppy). We predicted cave molly females not to discriminate between a conspecific and a heterospecific female, while *P. mexicana* females from the river population should do so.

PARASITE-MEDIATED SEXUAL SELECTION

Indicator hypotheses of sexual selection predict that females choose males as mates on the basis of traits that reveal differences in male conditions (Zahavi 1975; Hamilton and Zuk 1982; Andersson 1994 for a review). Females are expected to gain direct and/or indirect fitness benefits by mating with males exhibiting good body condition. Female preferences are thought to evolve to exploit the condition-dependence or “indicator value” of developmentally plastic male traits (Andersson 1994; Grether 2000; Plath et al 2005). Among other factors, parasites are thought to have a significant effect on the host's condition and the expression of several male traits. Thus, parasites are not only important direct selective factors, influencing the viability and fertility of their hosts (Bush et al 2001), but they can also serve as indicators to assess mate quality and are therefore assumed to play an essential role in sexual selection (Zahavi 1975; Hamilton and Zuk 1982; Andersson 1994). Although parasites often change the hosts' phenotype indirectly because ornamental traits are less expressed, they can also alter the male phenotype directly, e.g., in terms of changes in body proportions (Bush et al 2001) or behavior (Barber et al 2000; Moore 2002). If females can perceive such phenotypic changes, their mate choice decisions may be influenced (Endler and Lyles 1989).

In the second part of our study, we examined female choice relative to a parasite that directly affects the hosts' phenotype, black spot disease (BSD). BSD is caused by the metacercariae of a trematode (*Uvulifer* sp.), which induce the production of black spots on the body surface of the fish (Bush et al 2001). Indicator models of sexual selection predict that female preferences become more pronounced when male traits are better indicators of the benefits females potentially achieve by being choosy, for example as a consequence of habitat differences (Kirkpatrick and Ryan 1991; Andersson 1994; Grether 2000; Plath et al 2005). We examined female preferences relative to BSD infection in three populations of the Atlantic molly (*Poecilia mexicana*) from the Cueva del Azufre and two adjacent surface habitats. We asked whether female mating preferences are more pronounced in habitats in which the indicator value of BSD infection is high.

A parasitological study revealed that BSD prevalence is highest in normal freshwater habitats, but is significantly lower in the sulfidic creek outside the cave (El Azufre). Within the cave, BSD is absent (Tobler et al in press-a). Therefore, we predicted females from normal

surface habitats to use BSD-infection as an indicator to assess male quality, while females from the sulfur creek should show a weaker or even no preference regarding the infectious state of a male. Finally, in the cave, mollies evolve in the absence of BSD infection. Therefore, these females should not show a preference.

In summary, we examined the evolution of two visually mediated association preferences in females of the same species coming from widely different ecological backgrounds. Both preferences were predicted to be stronger in surface-dwelling females, because in their habitat species recognition and the recognition of non-parasitized males is adaptive, whereas the preferences should be reduced in the Cave molly.

METHODS

We used *P. mexicana* from laboratory stocks that were maintained in 50 – 200 l tanks at 24 – 30°C at the Biozentrum Grindel in Hamburg as randomly out-bred populations comprising both sexes. The three populations tested originated from the innermost chamber (XIII after Gordon and Rosen 1962) of the Cueva del Azufre, from the El Azufre and from an adjacent clear-water surface habitat (Río Oxolotan). For the species recognition experiments, only fish from the cave and clear-water river populations were used. All field sites are located near the village Tapijulapa (Tabasco, Mexico). Further details about the field sites can be found in Tobler et al (in press-b).

Species recognition

The tests on species recognition were carried out using life stimulus fish. Guppy (*P. reticulata*) females from a domestic aquarium strain were used as heterospecific stimuli. The females from this strain are much larger than females from natural guppy populations and often equal *P. mexicana* females in size. Guppies do not occur in the natural habitat of *P. mexicana*, however, they were chosen as one example of an equally sized, but distinctly differently colored fish. Females from the two species differed in shape and coloration, and they can easily be distinguished by the human eye. Prior to the tests, females from both species were isolated from males in 50 l aquaria. After the tests, all fish were returned into their stock tanks.

For the choice tests, a standard test aquarium (100 x 35 x 35 cm) was visually divided into three equal zones, one central neutral zone and two lateral preference zones. The tank was filled to two thirds with aged tap water of 28–30°C. Illumination was provided by two 30 W neon tubes from centrally above. A transparent Plexiglas cylinder for the stimulus fish was placed centrally in both preference zones. Before a trial, a conspecific female from the test female's population (39.46 ± 3.53 mm

standard length, mean \pm SD) and an equally sized guppy female (39.21 ± 1.64 mm; size difference 0.25 ± 2.83 mm) were randomly introduced in one of the two cylinders each. Stimuli were exchanged between the trials.

To initiate a trial, a *P. mexicana* female (40.10 ± 5.25 mm) was gently introduced into the neutral zone. Measurement was initiated when the female started to swim. We measured the time the female spent in the preference zones near either types of stimulus female during 10 minutes. To control for side-biases, the two cylinders were then gently interchanged and measurement was repeated. Association times from both parts of a trial were summed up.

Parasite-mediated mate choice

We tested female preferences relative to healthy and BSD infected males using video animations in a simultaneous choice test according to a previously published protocol (Tobler et al 2006). The video animations showed males in a straight movement from left to right and right to left in front of a uniform gray background. The same male was used to produce the two animations: one male had 12 artificially added black spots, whereas its otherwise identical copy had no spots. Black spots had been cut from digital photos of infected males taken from wild-caught males. Images were transformed into grayscale (Tobler et al 2006). By using video animation, we could exclude the possibility that female association preferences would be influenced by any other factor (such as behavioral differences) than the trait under consideration, i.e., black spots.

For the choice tests, two computer monitors were placed on either sides of our standard video test tank, which was visually divided into three sections by markings drawn on the front: A central neutral zone (25 cm) and two preference zones near the monitors (each 17.5 cm). Prior to a test, the video playbacks were started. A test female, randomly selected from a stock tank, was placed into a transparent Plexiglas cylinder in the middle of the neutral zone. The female was allowed to acclimate for five minutes. Then, the cylinder was carefully removed and an observation period of five minutes followed. We recorded the time spent in each preference zone. To detect side biases, the female was placed into the cylinder again, the video playbacks were switched and the measurement was repeated. After the test, the standard length of the female was measured to the closest millimeter. Females were then transferred into another tank, so that each female was only tested once.

Statistical analyses

We decided *a priori* to exclude side biases (more than 80% of time during both parts of a trial in only one preference zone) and trials with low response (less than 50%

of the time inside the preference zones). We assumed such females not to be motivated to choose (Landmann et al 1999).

To test for female association preferences within populations, the time spent near either type of stimulus was compared using paired *t*-tests. To test for population differences in female preferences, we calculated the strength of preference $[(\text{time}_{\text{healthy}} - \text{time}_{\text{BSD}}) / (\text{time}_{\text{healthy}} + \text{time}_{\text{BSD}})]$ and compared it among populations using two-sample *t*-test in case of the species recognition experiment, or ANCOVA in the BSD experiment. Alpha levels were corrected according to the number of multiple comparisons using Bonferroni adjustments ($\alpha' = 0.05/\text{number of multiple comparisons}$).

RESULTS

Species recognition

The surface fish from the Río Oxolotan spent significantly more time near the conspecific stimulus female than near the heterospecific female (paired *t*-test: $t_{11} = 6.57$, $P < 0.001$, $\alpha' = 0.025$; Figure 1). By contrast, association times near either type of stimulus did not differ in cave mollies (paired *t*-test: $t_{11} = 0.89$, $P = 0.39$, $\alpha' = 0.025$). The strength of preference differed significantly between the two populations (two-sample *t*-test: $t_{22} = 3.89$, $P < 0.001$, $\alpha' = 0.025$).

Parasite-mediated mate choice

20 females of each population were successfully tested. Females of all populations spent more time near the healthy male, but in all cases the difference was not significant (Río Oxolotan: $t_{19} = -1.44$; $P = 0.17$; $\alpha' = 0.025$;

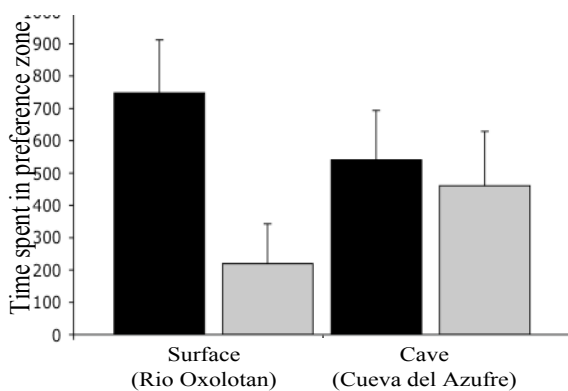


Fig. 1 – Time (mean ± SD) spent with conspecific (black bars) or heterospecific females (gray bars). *P. mexicana* females from the Río Oxolotan showed a significant preference for conspecifics, in the cave population, however, no significant preference was found ($N = 12$ for both populations).

El Azufre: $t_{19} = 0.015$, $P = 0.99$; Cueva del Azufre: $t_{19} = -1.23$, $P = 0.23$; Figure 2). An ANCOVA indicated that the populations did not significantly differ in their strength of preference (Table 1).

DISCUSSION

Previous studies have shown that several behavioral traits are reduced in Cave mollies: shoaling (Parzefall 1993), aggression (Parzefall 1974, 1979) and “alternative” male sexual behavior (Plath et al 2003-a). The present study revealed that the preference to associate with conspecifics is also reduced in Cave mollies. However, we found no evidence that surface and cave molly populations differ in their preferences relative to the infection of males with BSD.

Species recognition

Our result that surface-dwelling molly females discriminate between conspecifics and heterospecifics while Cave molly females showed no preference suggests that species recognition mechanisms are important in surface-dwelling *P. mexicana*, but less important in the cave population. Our results provide no explanation how this difference arises: An observed association preference indicates that the test fish did *perceive* differences between the stimuli, and was also *motivated to choose*. A negative result, such as in the case of the Cave molly, may be attributed to a reduction process on one of these levels or on both levels.

In the river form, the ability to recognize one's own species enables females to form conspecific all-female shoals. Such all-female shoals are typically defended by one or a few dominant males (Parzefall 1969) and

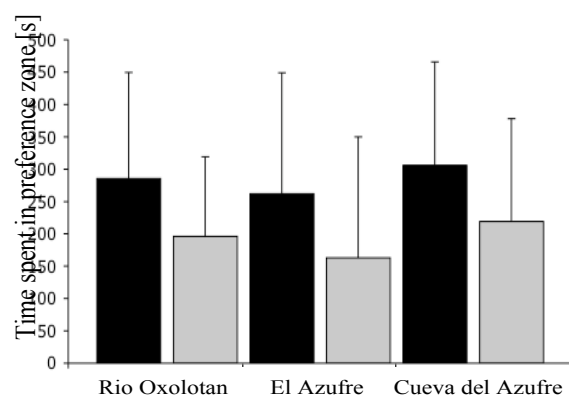


Fig. 2 – Female preferences relative to BSD-infection: The time (mean ± SD) spent near a monitor showing a healthy male (black bars) or a male infected with BSD (gray bars). None of the *P. mexicana* populations showed a significant preference for the healthy or infected male ($N = 20$ for all populations).

Table 1 - ANCOVA using the strength of preference in the experiment on parasite-mediated mate choice as dependent variable. SL standard length.

Source	Sum of Squares	df	Mean Square	<i>F</i>	<i>P</i>
Corrected Model	1.67	5	0.33	0.93	0.47
Intercept	0.36	1	0.36	1.00	0.32
Population	0.59	2	0.30	0.83	0.44
SL	0.27	1	0.27	0.75	0.39
Population * SL	0.67	2	0.34	0.94	0.40
Error	19.37	54	0.36		
Total	21.75	60			
Corrected Total	21.04	59			

may provide several benefits to the females: First, individuals in uniform shoals are less conspicuous to predators (McRobert and Bradner 1998). Second, shoaling with conspecifics may provide major benefits in terms of avoidance of male sexual harassment to females. *P. mexicana* females have significantly less time available for feeding in the presence of a male, compared with the time spent feeding in the presence of another female (Plath et al 2003a), suggesting strong male harassment. The benefits of shoaling would be larger in conspecific than in mixed species shoals, because *P. mexicana* males would not sexually interact with other (heterospecific) females.

Third, although only female-female interactions were observed in this study, the ability to discriminate species may have evolved in the context of mate-choice, where surface-dwelling females attempt to avoid heterospecific matings. The explanations suggested above, however, are not mutually exclusive, but may rather work in unison.

Cave molly females did not show any preference for the conspecific female. Our data suggest that the visual preference for conspecifics has been reduced in the course of cave colonization. The reduction of the preference from the river population to the cave population may be partly explained by the impossibility of visual communication in the cave due to the absence of light. Furthermore, Cave mollies have strongly reduced their shoaling tendency compared to river-dwelling mollies (Parzefall 1993). Firstly, predatory fishes are absent in the cave, and this may account for the reduction of shoaling. Very likely, shoaling provides little benefits in terms of predator avoidance in this system. Secondly, male sexual harassment was not detected in this population (Plath et al 2003). Thus, shoaling does not provide benefits in terms of avoidance of sexual harassment. We propose that the reduction of shoaling behavior and species recognition mechanisms coincide in the Cave molly: Once there is no benefit of (conspecific) shoaling, there is also no stabilizing selection on species recognition mechanisms.

Parasite-mediated mate choice

Due to the gradient of BSD prevalence in the three populations examined, with a reduced BSD prevalence in the sulfur creek and complete absence of BSD in the cave habitat, differences in the use of BSD-infection as an indicator to assess male quality were expected. While females from surface habitats were predicted to be choosy regarding the infection of males, females from the sulfur creek should have a weak or even no preference. Finally, cave mollies should not show any preference. However, in none of the populations tested did we find a significant preference.

A previous study using the same method as described here demonstrated that black spots can elicit female responses in the closely related Amazon molly (*P. formosa*), a unisexual hybrid species. Amazon mollies clearly discriminated between the two types of video animations and preferred the healthy (non-spotted) male (Tobler et al 2006). Females of the Sailfin molly (*P. latipinna*) as well as *P. mexicana* from North Mexican populations showed no association preferences regarding BSD just like the *P. mexicana* females from South Mexico tested here. The lack of a female preference raises the question if infection with BSD provides any information about male quality – at least for females of bisexual species. Møller et al (1999) discussed that randomly chosen parasite-host-systems are unlikely to reveal a negative association between the intensity of infection and mate quality. Most species harbor multiple parasites and often no unparasitized mates are available (Møller et al 1999; Tobler et al 2005, for parasites in Sailfin and Amazon mollies). Since BSD is not transmitted directly from fish to fish, females cannot gain *direct* fitness benefits by avoiding infections of themselves or their offspring as assumed by the contagion indicator hypothesis (Borgia 1986; Able 1996), but *indirect* benefits may still be possible.

A parasite's virulence has a large effect on its indicator value (Møller et al 1999). Parasites with a high virulence should have a higher indicator value than parasites with a lower virulence, even if females receive

indirect fitness benefits in a way that offspring quality is increased (e.g., by inheritance of resistance genes for the offspring; Hamilton and Zuk 1982). Resistance to highly virulent parasites should be more beneficial than resistance to benign parasites. After invading the skin of a fish, the metacercariae of *Uvulifer* sp. provoke the production of a fibrous capsule of host tissue around the parasite, which is followed by the migration of melanocytes into the cyst's wall (Spellman and Johnson 1987; Bush et al 2001). This is typically assumed to be costly: The penetration of the skin causes mechanical damage, which also facilitates secondary infections with other pathogens. Until the parasite becomes encapsulated, the host's metabolic demand increases significantly (Lemly and Esch 1984; Lane and Morris 2000; Bush et al 2001). In mollies, however, infected individuals do not show any reduction in body condition factors, oocyte numbers or gonosomatic indices (unpublished data), and in aquaria, BSD infected individuals are long-living and regularly produce offspring. In conclusion, *Uvulifer* sp. might be relatively benign parasite with only minor indicator value. This may account for the absence of a preference for uninfected males even in the river-dwelling form of *P. mexicana*.

General conclusions

While we found the predicted reduction of visually mediated preferences in the case of species recognition in Cave mollies, we found no parasite-mediated mate preferences even in river-dwelling *P. mexicana*. Our study suggests that female preferences relative to BSD-infection are lacking not only in northern Mexican *P. mexicana* (Tobler et al 2006), but also in several populations from southern Mexico (this study). It remains unclear, however why females of the sexual species *P. mexicana* and *P. latipinna* do not show a preference, but the gynogenetic, clonal hybrid species *P. formosa* does (Tobler et al 2006). This subject clearly warrants future research.

Several studies have reported on the persistence of visually mediated association preferences in Cave molly females (e.g., Plath et al 2003-b, 2004, 2005). In most cases where visually mediated preferences were detected in Cave mollies, the trait under consideration was perceivable also non-visually. For example, large male size can be assessed visually, but also by mechanosensory (water-pressure wave) cues (Plath et al 2004). Possibly, visual preferences persist in (eyed) cave fishes longer if the trait can also be perceived in darkness, i.e., if the preference is currently under selection. The preferences examined in this paper are most likely purely visually mediated, hence a reduction of species recognition in the Cave molly is not surprising.

In general, 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.

ACKNOWLEDGEMENTS

We thank A. Taebel – Hellwig, T.H. Dirks, I.D. Schmidt and the Aquarium-team for animal care and technical support. Financial support came from the DFG (PL 470/1-1) and from the University of Hamburg to M.P. I.S. was a Heisenberg fellow of the DFG. We thank the Mexican government for issuing permits: Permiso de pesca de fomento, numbers: 291002-613-1577 and DGOPA/5864/260704/-2408. We are indebted to the people of Tapijulapa for their hospitality during our field work preceding this study. The experiments reported in this paper comply with the current laws in Germany.

REFERENCES

- Able, D.J. 1996. The contagion indicator hypothesis for parasite-mediated sexual selection. *Proceedings of the National Academy of Science USA* 93: 2229-2233.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, New Jersey
- Barber, I., D. Hoare, J. Krause. 2000. Effects of parasites on fish behaviour: a review and evolutionary perspective. *Reviews in Fish Biology and Fisheries* 10: 131-165.
- Borgia, G. 1986. Satin bowerbird parasites: a test of the bright male hypothesis. *Behavioral Ecology and Sociobiology* 19: 355-358.
- Bush, A.O., J.C. Fernández, G.W. Esch, J.R. Seed. 2001. *Parasitism: The diversity and ecology of animal parasites*. Cambridge University Press, Cambridge.
- Endler, J.A., A.M. Lyles. 1989. Bright ideas about parasites. *Trends in Ecology and Evolution* 4: 246-248.
- Godin, J.G.J. 1986. Antipredator function of shoaling in teleost fishes: a selective review. *Naturaliste Canadien* 113: 241-250.
- Gordon, M.S., D.E. Rosen. 1962. A cavernicolous form of the Poeciliid fish *Poecilia sphenops* from Tabasco, México. *Copeia*: 360-368.
- Grether, G.F. 2000. Carotenoid limitation and mate preference evolution: a test of the indicator hypothesis in guppies (*Poecilia reticulata*). *Evolution* 54: 1712-1724.
- Hamilton, W.D., M. Zuk. 1982. Heritable true fitness and bright birds: A role of parasites? *Science* 218: 384-387.
- Kirkpatrick, M., M.J. Ryan. 1991. The paradox of the lek and the evolution of mating preferences. *Nature* 350: 33-38.
- Krebs, J.R., B.R. Davies. 1996. *Einführung in die Verhaltensökologie*, 3. Auflage. Blackwell Wissenschafts-Verlag, Berlin.

- Körner, K., I. Schlupp, M. Plath, E.R. Loew. 2006. Spectral sensitivity of mollies: comparing surface and cave-dwelling Atlantic mollies, *Poecilia mexicana*. *Journal of Fish Biology* 69: 54-65.
- Landmann, K., J. Parzefall, I. Schlupp. 1999. A sexual preference in the Amazon molly, *Poecilia formosa*. *Environmental Biology of Fishes* 56: 325-331.
- Lane, R.L., J.E. Morris. 2000. Biology, prevention, and effects of common grubs (digenetic trematodes) in freshwater fish. Technical Bulletin Series Iowa State University 115: 1-6.
- McRobert, S.P., J. Bradner. 1998. The influence of body coloration on shoaling preferences in fish. *Animal Behaviour* 56: 611-615.
- Moore, J. 2002. Parasites and the behaviour of animals. Oxford University Press, Oxford.
- Møller, A.P., P. Christe, E. Lux. 1999. Parasitism, host immune function, and sexual selection. *The Quarterly Review of Biology* 74: 3-20.
- Parzefall, J. 1969. Zur vergleichenden Ethologie verschiedener *Mollienesia*-Arten einschließlich einer Höhlenform von *M. sphenops*. *Behaviour* 33: 1-37.
- Parzefall, J. 1974. Rückbildung aggressiver Verhaltensweisen bei einer Höhlenform von *Mollienesia sphenops* (Pisces, Poeciliidae). *Zeitschrift für Tierpsychologie* 35: 66-84.
- Parzefall, J. 1979. Zur Genetik und biologischen Bedeutung des Aggressionsverhaltens von *Poecilia sphenops* (Pisces, Poeciliidae). *Zeitschrift für Tierpsychologie* 50: 399-422.
- Parzefall, J. 1993. Behavioural ecology of cave-dwelling fishes. In: Pitcher TJ (ed) *Behaviour of teleost fishes*, 2nd Edition. Chapman and Hall, London, pp 573-608.
- Parzefall, J. 2001. A review of morphological and behavioural changes in the cave molly, *Poecilia mexicana*, from Tabasco, Mexico. *Environmental Biology of Fishes* 62: 263-275.
- Plath, M., J. Parzefall, I. Schlupp. 2003-a. The role of sexual harassment in cave- and surface-dwelling populations of the Atlantic molly, *Poecilia mexicana* (Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology* 54: 303-309.
- Plath, M., K.E. Körner, J. Parzefall, I. Schlupp. 2003-b. Persistence of a visually mediated mating preference in the Cave molly, *Poecilia mexicana* (Poeciliidae, Teleostei). *Subterranean Biology* 1: 93-97.
- 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). *Behavioral Ecology and Sociobiology* 55: 596-601.
- Plath, M., K.U. Heubel, F.J. García de León, I. Schlupp. 2005. Cave molly females (*Poecilia mexicana*, Poeciliidae, Teleostei) like well-fed males. *Behavioral Ecology and Sociobiology* 58: 144-151.
- Riesch, R., M. Tobler, I. Schlupp, M. Plath. 2006. Regressive evolution of the preference to associate with conspecifics in surface- and cave-dwelling Atlantic mollies, *Poecilia mexicana* (Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology* 60: 794-802.
- Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131: 329-347.
- Tobler, M., T. Wahli, I. Schlupp. 2005. Comparison of parasite communities in native and introduced populations of sexual and asexual mollies of the genus *Poecilia* (Poeciliidae, Teleostei). *Journal of Fish Biology* 67: 1072-1082.
- Tobler, M., I. Schlupp, F.J. Garcia de Leon, M. Glaubrecht, M. Plath. in press-a. Extreme habitats as refuge from parasite infections: evidence from an extremophile fish. *Acta Oecologica*.
- Tobler, M., M. Plath, H. Burmeister, I. Schlupp. 2006. Black spots and female association preferences in a sexual/asexual mating complex (*Poecilia*, Poeciliidae, Teleostei). *Behavioral Ecology and Sociobiology* 60: 159-165.
- Tobler, M., I. Schlupp, K.U. Heubel, F.J. Garcia de Leon, O. Giere, M. Plath. in press-b. Life on the edge: Hydrogen sulfide and the fish communities of a Mexican cave and surrounding waters. *Extremophiles*.
- Zahavi, A. 1975. Mate selection - a selection for a handicap. *Journal of Theoretical Biology* 53: 205-214.