Turbidity affects association behaviour in male *Poecilia latipinna*

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(Received 28 October 2004, Accepted 10 August 2005)

Male association preferences in a bisexual-unisexual species complex were studied in clear and turbid environments. In south and central Texas, where the gynogenetic sexual-parasite *Poecilia formosa* lives syntopically with *Poecilia latipinna* as its sexual host species, association times of *P. latipinna* males with conspecific sexual and heterospecific asexual females in clear and turbid water were measured sequentially. Turbidity had an influence on male mate association behaviour. Males spent less time with any kind of female stimulus in turbid water. There was no preference for conspecific sexual females, either in turbid water or under clear conditions. Also, origin of males and acclimatization to turbid water had no effect. How turbidity as a source of visual noise might affect communication among individuals and how this environmental factor might contribute to the stability of this sexual-asexual mating complex in nature are discussed.

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Key words: communication; environmental noise; gynogenesis; male mate choice; *Poecilia formosa*; turbidity.

INTRODUCTION

Signalling interactions always take place in a specific ecological context and signals are adapted to constraints imposed by the environment (Endler, 1992; Bradbury & Vehrencamp, 1998). In nature, signalling behaviour may be affected by environmental background noise and thus lead to mistakes when communicating. Many naturally occurring fish habitats are considerably turbid throughout the year and others underlie high seasonal variation in turbidity. Especially in species with visual communication, turbidity can affect communicative behaviour by attenuating and masking signals and cues (Kirk, 1994; Bradbury & Vehrencamp, 1998). So far, studies on turbidity and its role

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in mating systems are rare. Effects of turbidity on mate choice were explicitly studied by Järvenpää & Lindström (2004) investigating the effect of experimentally increased algal turbidity on the mating system of the sand goby Pomatoschistus minutus (Pallas). Turbid water is also known to influence intraspecific interactions of poeciliids in a social context. Franck et al. (2001) studied female schooling preferences for spotted males in the green swordtail Xiphophorus helleri. They showed that schooling preferences of females changed in turbid water. Seehausen et al. (1997) discussed the impact of turbidity, caused by eutrophication, on sexual selection and reproductive isolation in Lake Victoria cichlids. Seehausen & van Alphen (1998) showed experimentally that females in the Pundamilia nyererei-complex (Witte-Maas & Witte) mate indiscriminately with both conspecific and heterospecific males under monochromatic light where colour differences do not show. Seehausen et al. (1997) have further shown that fewer sympatric cichlid species are found in turbid water areas and fishes from more turbid water are duller. Findings by Seehausen et al. (1997) suggest that recently increased turbidity levels impair colour vision in fishes thereby interfering with mate preferences.

Most other studies on fish behaviour and turbidity focused on predator-prey interactions (Gregory, 1993; Gregory & Northcote, 1993; van Eerden & Voslamber, 1995; Abrahams & Kattenfeld, 1997; Utne, 1997; Gregory & Levings, 1998; Mayama, 1998; Rowe & Dean, 1998; Beauchamp et al., 1999; Johnson & Hines, 1999; Reid et al., 1999; Utne-Palm, 1999; Vogel & Beauchamp, 1999; Hartman & Abrahams, 2000; Jepsen et al., 2001; Sweka & Hartman, 2001a, b).

Visual communication and mate preferences have been intensively studied in poeciliids. Several studies have addressed the issue of how visual properties of the environment, e.g. illumination (Long & Houde, 1989; Endler, 1991; Plath et al., 2004) or turbidity (Luyten & Liley, 1991; Franck et al., 2001; Magurran, 2001; Magurran & Phillip, 2001) interferes with visual communication in poeciliids.

Many studies addressed the question of male mate choice in poeciliids (Moore & McKay, 1971; Bisazza, 1989; Schlupp et al., 1991; Abrahams, 1993; Ryan et al., 1996; Ptacek & Travis, 1997; Schlupp & Ryan, 1997; Long & Rosenqvist, 1998; Gabor & Ryan, 2001; Smith et al., 2002). Male mate choice preferences are especially interesting to study in the context of the stability and maintenance of a bisexual-unisexual species complex. The Amazon molly Poecilia formosa (Girard) is such an all-female, sperm-dependent gynogenetic species (Ryan et al., 1996; Marler & Ryan, 1997; Marler et al., 1997; Körner et al., 1999; Landmann et al., 1999; Schlupp et al., 1999; Gabor & Ryan, 2001). Despite their clonal reproduction, females need to copulate with males of closely related species to obtain sperm they need to trigger embryogenesis (Hubbs & Hubbs, 1932; Schlupp et al., 1998). In Texas and north Mexico several populations of the sailfin molly Poecilia latipinna (Le Sueur) are sexually parasitized by the co-occurring Amazon molly, (Darnell & Abramoff, 1968; Ryan et al., 1996). In these populations males are confronted with a choice between conspecific and heterospecific females.

In such a mating complex, male mate choice should be crucial because matings with the sexual-parasite P. formosa do not lead to any direct fitness benefits. Several studies show male preferences for conspecific sexual females (Hubbs,
1964; Woodhead & Armstrong, 1985; Schlupp et al., 1991, 1998; Ryan et al., 1996; Schlupp & Ryan, 1997; Gabor & Ryan, 2001; Niemeitz et al., 2002) while others present and discuss controversial results on male preferences in this complex (Balsano et al., 1981, 1985; Woodhead & Armstrong, 1985; Schlupp et al., 1991). Such non-discriminating male mating behaviour in this sexual-asexual mating complex could be explained by heterospecific mate-copying. Males may gain an indirect benefit of increased attractiveness to conspecific females observing those heterospecific matings with Amazon mollies (Schlupp et al., 1994; Heubel 2004).

Previous behavioural studies were always conducted under clear water conditions. Two different experimental techniques were used: (1) visual preference tests or (2) mate choice experiments allowing full interaction. In visual preference tests, focal fish and stimuli were separated by dividers and association time with the stimulus was measured (Woodhead & Armstrong, 1985; Schlupp et al., 1991; Schlupp & Ryan, 1997). On the other hand, in experimental designs allowing free interactions of focal fish and stimuli, actual mating attempts were counted (Woodhead & Armstrong, 1985; Schlupp et al., 1991; Ryan et al., 1996; Gabor & Ryan, 2001). By allowing direct interaction between focal fish and stimulus, however, it is not possible to distinguish between the male and female contribution to the occurrence of the measured mate preference. Association preferences on the other hand relate to preferences for potential mates and thus are unaffected by any active interference by the stimulus. When studying preferences for potential mates with the aim to compare those preferences within and between individuals, measuring association preferences should be the preferred method (Wagner, 1998).

Association preferences have been shown to reflect mating preferences in various groups of fishes, e.g. in guppies Poecilia reticulata Peters (Kodric-Brown, 1992), cichlids (Coulridge & Alexander, 2001) and blennies (Gonçalves & Oliveira, 2005). Gabor (1999), however, showed that association preferences for body size in P. latipinna may also occur in other contexts that are not related to mating.

Both types of experiments can be conducted as simultaneous tests with a choice between different stimuli, or as sequential tests with a serial presentation of different stimuli. According to Wagner (1998), simultaneous stimulus presentations can confound preference and sampling behaviour. Choice tests in general can result in an artificial amplification of preferences (Wagner et al., 1995).

The availability of visual information changes substantially with visibility in the water e.g. by limiting the range or bandwidth of signals and cues (Endler, 1990; Kirk, 1994; Bradbury & Vehrencamp, 1998; Losey et al., 1999). Therefore, it is important to include turbidity as an environmental factor in experiments studying preferences in fishes.

As implicitly suggested by Bradbury & Vehrencamp (1998) and Endler (1990), in the specific case addressed in this study, turbidity might influence male association preferences or impair mate-choice. This may potentially increase the cost of mate assessment and consequently, lowering the threshold of mating with the ‘wrong’ females, the sexual-parasites. As far as is known, this is the first study on the effect of turbidity on male preferences. Specifically, whether turbidity affects male association preferences and what the potential impact of this might be on the stability and maintenance of this sexual and asexual species complex were investigated.
FISHES

Two sets of experiments were conducted. In the first set, individuals from a population in south Texas (‘Weslaco’) were tested, originating from the Rio Grande river system drainage (26° 7’ N; 97° 57’ W; Hidalgo county, TX, U.S.A.) (Gabor & Ryan, 2001). Regular surveys during the preceding year showed that in this population the frequency of P. formosa, the sexual-parasite, was high and measured turbidity levels had been high (Table I) (Heubel, 2004). In the second set, P. latipinna males originating from a population in central Texas (29° 43’ N; 98° 8’ W; Comal River, New Braunfels, TX, U.S.A.) (Witte & Ryan, 2002) were tested. This population has a very low frequency of P. formosa and clear water throughout the year (Table I) (Heubel, 2004). Poecilia latipinna females and P. formosa originating from the same population and, due to the lack of sufficient numbers of P. formosa in the Comal-population, a nearby population from the same drainage system (San Marcos River near Martindale, Texas, U.S.A.) (Schlupp et al., 1994), were used (Table I).

All fishes were collected in the field during September and October 2002, between 1 month and 1 week before testing. In the laboratory (Section of Integrative Biology, University of Texas in Austin, U.S.A.), males and females were kept visually separated in different 20–60 l tanks at 25°C on a 12 L : 12 D artificial illumination cycle. All fishes were fed daily with commercially available flake food. All individuals were caught in the wild as mature adults and thus considered to be sexually experienced. Females were reproductive during that time of the year as indicated by juveniles found at field sites during sampling (pers. obs.).

Only females with a minimum size of 28 mm standard length (Lₒ) were used to prevent inadvertent use of immature males instead of females as stimuli (Hubbs, 1964). After completing the experiments, all fishes were released into large outdoor breeding tanks at the Brackenridge Field Laboratory at the University of Texas in Austin, U.S.A.

TURBIDITY

Turbid water in the test tank was created by adding argillaceous earth powder (3.6 g Edasil® bentonite dissolved in 50 ml water and poured in 80 l). The same method had been used before (Abrahams & Kattenfeld, 1997; Hartman & Abrahams, 2000; Franck et al., 2001). In turbid tanks, turbidity was kept at 25 nephelometric turbidity units.

Table I. Field observations (mean ± s.e.) of turbidity and population in 2001 and 2002

<table>
<thead>
<tr>
<th>Population samples</th>
<th>South Texas Weslaco</th>
<th>Central Texas Comal</th>
</tr>
</thead>
<tbody>
<tr>
<td>Turbidity (NTU)¹</td>
<td>273±0 ± 28·0</td>
<td>3·0 ± 1·4</td>
</tr>
<tr>
<td>Proportion of Poecilia formosa²</td>
<td>0·49 ± 0·06</td>
<td>0·02 ± 0·01</td>
</tr>
<tr>
<td>Female asexual:sexual, ratio³</td>
<td>2·07 ± 0·39</td>
<td>0·03 ± 0·01</td>
</tr>
<tr>
<td>Number of adult Poecilia species sampled</td>
<td>1303</td>
<td>1628</td>
</tr>
</tbody>
</table>

1Turbidity was measured as nephelometric turbidity units (NTU) with a shuttered turbidity (ISO 7027) nephelometer with 880 nm LED in a Hydrolab® Data Sonde 4 water quality multiprobe.
2Proportion of P. formosa in mixed populations with Poecilia latipinna is the ratio of numbers of adult P. formosa to all adult P. formosa and P. latipinna combined.
3Female asexual:sexual ratio is the ratio of unisexual adult P. formosa to sexual adult P. latipinna females.

(NTU). In clear water tanks, turbidity was kept at <5 NTU. Turbidity was measured before every series of trials on a given day as well as before and after every water change using the same shuttered turbidity sensor (ISO 7027) nephelometer with 880 nm LED in a Hydrolab® Data Sonde 4 water quality multiprobe as used in the field. In situ turbidity levels in the tested populations are shown in Table I.

Water in the test tanks was changed weekly or, additionally, either when clogging of Edasil particles occurred in the turbid tank or turbidity levels in the clear tank increased. After every 40 l water change 1.8 g dissolved bentonite was added to the turbid tank.

In order to test the effect of turbidity on male preferences, an association preference test setup was used as the preferred method. This setup allows using comparably higher levels of turbidity maintained experimentally in the tank. It would have been impossible to observe direct interactions reliably, e.g. courtship behaviour or copulation attempts, as it would have been necessary in an experimental setup to allow full interactions between male and female using turbid water. In a pilot study, it turned out that 25 NTU was the maximum degree of turbidity that could be used experimentally in an association preference test when observing males’ and females’ movements in a tank.

EXPERIMENTAL SETUP

Trials were carried out in two identical test tanks (120 x 30 x 52 cm). One tank contained clear water, the other one turbid water. Both tanks had a layer of gravel on the bottom.

Illumination was provided by two fluorescent 40 W tubes per tank, which emitted visible light plus UV. The short ends and the rear long ends of the tanks were covered with grey Teflon sheet that reflects light of all wavelengths equally (K. Lunau pers. comm.). All dividers and the cylinder (10 x 10 cm) for acclimatization were made of UV translucent Plexiglas.

Turbidity, water level and temperature were kept stable at 25°C during the experiment. Before the start of a trial, the water in both tanks was stirred thoroughly. Particles settled very slowly. Measuring turbidity levels before and after testing confirmed that the turbidity level did not decrease during a series of four test units. Equal turbidity levels were confirmed by measuring NTU each day before experiments were carried out.

Each test tank was divided into five equal compartments: The two outer (stimuli: female or empty) compartments were separated by transparent dividers. The dividers were fitted tightly to reduce flow of water and thus limit potential exchange of mechanosensoric or chemical cues between the compartments in this visual association preference test. The three inner compartments were only virtually divided by pen markings on the front of the tank. Thus, the test male could swim freely within these three inner compartments. The middle compartment was a neutral zone. The time a male spent in this zone was not counted. The two zones close to the dividers were the preference zones. Having two preference zones, one adjacent to the female stimulus and one at the opposite end of the tank next to the empty compartment, allowed not only preferences for presented stimuli to be tested, but avoidance behaviour to be detected also. To control for potential side biases, side assignment of stimuli was determined randomly for each of the four units. Side assignment, however, did not differ from an equal distribution.

Every P. latipinna male (n = 69) was sequentially tested in four different test units which immediately followed each other in randomized order: (1) conspecific sexual female stimulus, clear water; (2) sexual-parasite P. formosa stimulus, clear water; (3) conspecific sexual female stimulus, turbid water; (4) sexual-parasite P. formosa stimulus, turbid water. The time males spent in association with the female stimulus as the response variable was recorded.

The procedure of sequential testing suited the natural situation. It is not known yet how males evaluate females under turbid conditions. Thus, it cannot be assumed that males can observe several females at the same time under turbid conditions. Furthermore, it is unlikely that chemical markers of previous fishes may potentially
influence the behaviour of the following fishes (Sumner et al., 1994; Wenzel, 1997). Given these circumstances, testing sequentially seemed to be the more natural approach.

Pairs of _P. latipinna_ and _P. formosa_ female stimuli were matched for size and originated from the same population. A new pair of female stimuli had been used for each replicate. Thus each female stimulus was presented twice to a single male: once under clear and once under turbid conditions in randomized order. For each of the four test units, the test male was placed in the clear cylinder in the centre of the neutral zone after the female had been placed into the assigned compartment. After a 5 min acclimatization phase, the cylinder was gently removed and the trial started. The time the male spent in either the right or the left preference zone was counted for 5 min. This procedure was repeated until the complete set of all four trial units was carried out. Thus, for each male a complete testing period lasted 40 min including acclimation times.

**CONTROL EXPERIMENT**

A difference in male association preference tests between the two tested populations might have been expected. It is not easy, however, to determine what factor may actually cause such a difference in male behaviour. Males that originated from the ‘Comal’ population may respond differently in association preference tests for two reasons: (1) no prior experience on how to cope with turbid conditions, and (2) generally lowered proportions of _P. formosa_, and thus lowered probabilities to encounter asexual females in nature.

To control for habituation to the different turbidity levels in the two habitats the males originated from, males from the ‘clear water’ population (Comal), which had not been exposed to turbid water in their natural habitat, were kept under two different treatments. Males were kept in clear \( n = 22 \) or turbid \( n = 25 \) water in 25–100 l tanks for at least 5 days prior to testing and then individuals from both housing treatments were tested sequentially in the four different test units. Males from the turbid population were kept in the laboratory under clear water conditions prior to testing.

In the housing tanks for the control experiment, turbid water was created in the same way as in the experimental tank and maintained by a circulating pump where the filter material was removed. In addition, the water in turbid tanks was stirred thoroughly every morning.

**DATA ANALYSIS**

For this repeated measures experimental design, a partly nested fixed factors repeated measurement ANOVA was performed using generalized linear models (GLM). The effect of female species (conspecific vs. heterospecific) and turbidity level (clear vs. turbid) was investigated as within subject factors and male population origin as a between subject factor on association time a male spent with the stimulus female as a response variable.

Cases where males spent most of the observed time in the neutral zone in the tank centre in all four sequential trial units, were _a priori_ excluded from further analysis. Hence, these males showed a generally insufficient low response index \( I_R \); time spent in preference zones divided by observation time \( I_R < 0.5 \).

To obtain normally distributed data, the time (s) spent with stimulus females were transformed using reflection and square root transformation (Tabachnick & Fidell, 2001). Thereby, \( x' = \sqrt{k - x} \) and \( k = 301 \); the constant from which each score (0–300 s association time) is subtracted so that the smallest score is one. Variances did not differ significantly (Bartlett-Box-\( F \)-test for homoscedasticity). All transformed variables did not significantly differ from a normal distribution (Kolmogorov–Smirnov one sample test for normality with Lilliefors corrected probabilities). Greenehouse-Geisser corrected degrees of freedom (d.f.) were used testing within-subject effects. All \( P \)-values are two-tailed. Unless stated otherwise, averages are presented as mean \( \pm s.e. \) The data were analysed using SPSS 11.5.
RESULTS

A total of 77 trials was conducted. Eight trials were excluded from further analysis due to insufficient response indices. An exploratory analysis including these data, however, did not change the results.

Males showed a strong response to female stimuli as compared to the empty compartment (paired \(t\)-test d.f. = 68, \(P < 0.001\)). No avoidance of female stimuli occurred.

Under clear water conditions \(P.\) latipinna males spent 208.2 ± 9.0 s in association time with conspecific females, and 212.2 ± 10.2 s with the sexual-parasite \(P.\) formosa (Fig. 1). Under turbid conditions, males in general spent less time in association with the female stimuli. Males spent 162.0 ± 12.0 s with \(P.\) latipinna and 183.2 ± 11.6 s with \(P.\) formosa (Fig. 1). The effect of stimulus females’ species and turbidity level as within subject factors and male population origin as between subject factor was tested on male association time with females in a repeated measure ANOVA (reflected square root transformed data). Under clear water conditions males spent significantly more time with the stimulus female than under turbid conditions (Fig. 1) (ANOVA, d.f. = 1 and 42, \(P = 0.007\)). They did not, however, spend more time with conspecific (\(P.\) latipinna) than sexually parasitizing females (\(P.\) formosa) (ANOVA, d.f. = 1 and 42, \(P = 0.149\)). Population origin (Comal v. Weslaco) did not affect association preferences (ANOVA, d.f. = 1 and 42, \(P = 0.413\)). There was no significant effect of any interaction involving turbidity level, female stimulus species or population (ANOVA, d.f. = 1 and 42, \(P > 0.28\)).

Thus it was found that turbidity level alone had an effect on time males spent with a stimulus female. This effect was independent of stimulus female species or population origin of the male.

Acclimatization to clear v. turbid housing conditions of males originating from the clear population did not significantly affect the time males spent with

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**Fig. 1.** Association time (mean ± s.e.) of \(Poecilia\) latipinna males (\(n = 69\)) spent in clear (<5 NTU) or turbid (>25 NTU) water with different female stimuli. Females were either conspecific sailfin mollies (\(P.\) latipinna) or unisexual Amazon mollies (\(Poecilia\) formosa). Trials were sequential visual preference tests. **, \(P < 0.01\).
stimulus females (ANOVA, d.f. = 1 and 45, $P = 0.218$), regardless of stimulus females’ species and test turbidity levels (ANOVA, d.f. = 2.5 and 113.2, $P = 0.886$).

**DISCUSSION**

Males spent less time with any kind of female stimulus in turbid water. Clearly, turbidity has an influence on male association behaviour. Interestingly, there was no preference for conspecific sexual females, either in turbid water or under clear conditions. Also, origin of males and acclimatization to turbid water had no effect.

**EFFECTS OF TURBIDITY**

Turbidity generally decreases the overall amount of ambient light in the water column. In addition, depending on the source that causes turbidity, it also affects other properties of light. Light in turbid water is more scattered and depending on the colour of the particles will change its colour (Endler, 1990; Heavens & Ditchburn, 1991; Bradbury & Vehrencamp, 1998).

In the specific case of turbidity in the natural habitats of the mollies of the Gulf coastal plains of south and central Texas, clay particles are the main source of turbidity. Clay consists of layered silicate minerals causing scattering of light. Clay particles have sizes similar to the wavelength of visual light and thus predominantly cause Mie scattering by which smaller wavelengths, especially UV, are relatively more scattered than longer wavelengths (Heavens & Ditchburn, 1991; Bradbury & Vehrencamp, 1998; Losey et al., 1999). This scattering of light can be viewed as ‘noise’ in visual communication.

The bentonite used to create turbidity in the experiments is a layered silicate mineral and thus very similar (physical and chemical properties) to the natural source of turbidity in the field (Spearing, 1991; Wermund, 1999). There are linear relationships between dissolved bentonite concentration, NTU measurements, and settable solids in natural streams (Duchrow & Everhart, 1971). Not only physical properties, e.g. changes in visual environment, but also the physiologic effects of a turbid environment upon mollies should be similar in the field and in the experiment.

Natural habitats of mollies differ widely in the turbidity measured (Table I), but the more typical and common habitats are turbid throughout the year (Heubel, 2004; pers. obs.). The single clear water population (Comal) forms an exception: the water is clear because it is only a few metres downstream from a springhead. Here both species were recently introduced, *P. latipinna* in the 1930s (Brown, 1953) and *P. formosa* in the 1950s (Hubbs, 1953). Turbid water may affect male mating behaviour by prolonging the sampling interval and males may need more time to detect females. Additional experiments using a longer test interval should be carried out in the future. To what extent variability in turbidity is correlated with signal design and communication also needs further examination.
CONSEQUENCES FOR SIGNAL DESIGN

It is well documented that environmental conditions influence signal design and signalling behaviour (Wiley & Richards, 1982; Halliday & Slater, 1983; Endler, 1992; 1993). For example, great tits shift to higher maximum frequencies of their songs in a noisy, urban environment (Slabekooorn & Peet, 2003) and anoline lizards adjust their visual signalling behaviour, e.g. head bobbing, to maximize the contrast with background movements of the vegetation as environmental visual noise (Fleishman, 1992). Background noise dependent adjustment of song amplitude has been reported in nightingales (Brumm & Todt, 2002), and male colour morphs vary according to different light environments in bluefin killifish Lucania goodei Jordan (Fuller, 2002). Acoustic communication may vary dependent upon changing weather conditions: under windy conditions in penguins (Lengagne et al., 1999) and in rainy weather in tawny owls (Lengagne & Slater, 2002). Comparable to background noise, hampered propagation and perception, and differing light conditions in the above mentioned studies, turbidity might have an effect on visual signals in mollies. The effect of turbidity on visual signalling and mate choice behaviour needs to be studied in the future. Behavioural adaptations to turbid conditions might be comparable to those adaptations to different light environments studied in guppies: adaptations to changing light conditions include increase of courtship frequency (Long & Houde, 1989; Long & Rosenqvist, 1998), redundancy and replication of signals or a shift towards a different sensory mode (Endler, 1992). As a sensory compensation for decreased visual detection of a predator, fathead minnows Pimephales promelas Rafinesque were more sensitive to chemical alarm cues in turbid water (Hartman & Abrahams, 2000).

Turbidity does not only affect the range of a signal (or cue) by attenuation but also its properties. Because shorter wavelengths are affected relatively stronger by the small clay particles, the colour spectrum of the signal changes over distance. Female mollies are not particularly colourful. Interestingly, unlike P. formosa, P. latipinna females may have a yellow or orange coloured body and lines of dark spots on scales (Hubbs, 1991). This colouration may make females more conspicuous to males under turbid conditions.

ABSENCE OF MALE PREFERENCE

It was not possible to find male preferences for conspecific females. Several other studies have reported such preferences using approximately the same sample sizes, but a few other studies could not find such a male preference for conspecific females opposing the co-occurring sexual-parasite P. formosa (Balsano et al., 1981, 1985; Woodhead & Armstrong, 1985; Schlupp et al., 1991; Heubel, 2004). In visual association preference tests, males preferred conspecific females, but in a set-up allowing full body interaction, Schlupp et al., (1991) provided an explanation for the lack of preference: females that were receptive to males were more attractive to males, independent of species. Generally, the preferences seem less strong when testing association time allowing only visual signals than in full-interaction set-ups.
There are several potential explanations for the lack of a preference for conspecific females. In this experiment, important information may not have been available, although it is not known what exactly this may have been. Under the given circumstances males may have perceived it to be less costly for them not to prefer conspecific females. A potential mechanism may be influenced by the females’ sexual cycle (Parzefall, 1973): females are receptive only for a few days during each monthly cycle. Therefore, only a small proportion of females are fertile at any given time. Testing sequentially rather than simultaneously (Wagner, 1998) may also have contributed to the absence of a male preference reported here. Males may spend more time with a female that is presented without an alternative, because there is no alternative and males may be selected not to forsake any potential matings (Schlupp & Ryan, 1997). Alternatively, mate choice under turbid conditions might become so costly, especially time consuming, that males will do better by indiscriminately mating with every female. Additionally, a benefit to males via mate-copying (Schlupp et al., 1994; Heubel, 2004) might further reduce the costs of ‘wrong’ matings, but this applies only to situations in which the interactions can actually be perceived. To what extend mate-copying occurs in turbid water and which communicative channels and cues females may use, needs further examination.

Although other studies provide evidence for male preferences for conspecific females, the present study may indicate that such preferences are not always as clear and pronounced as expected. The absence of a clear preference for conspecific sexual females in the mating complex of the gynogenetic P. formosa and its sperm donating sexual host species may contribute to the maintenance of coexistence of sexual and asexual females in this complex.

We thank B.M. Gartner for help with the experiments and fieldwork and D. Mollaghan for help with animal care. This paper is part of a doctoral thesis (K.U.H.). This study was supported by a grant from Deutsche Forschungsgemeinschaft (DFG SCHL 7–2). I. S. was supported by a Heisenberg fellowship of the DFG. We thank M.J. Ryan for providing facilities and his extensive support throughout all stages of this study. We thank the Brackenridge Field Laboratory at the University of Texas in Austin for use of their facilities. We additionally thank M. Cummings, J. Parzefall, P. Gienapp and K. Röper for discussions. K. Lindström and two anonymous referees kindly commented on earlier versions of the manuscript.

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