A visual audience effect in a cavefish

Martin Plath\textsuperscript{1,4), Dennis Blum\textsuperscript{2), Ralph Tiedemann\textsuperscript{2) & Ingo Schlupp\textsuperscript{3)\textsuperscript{}}}

\textsuperscript{1) Unit of Animal Ecology, Department of Biochemistry and Biology, University of Potsdam, Maulbeerallee 1, 14469 Potsdam, Germany; \textsuperscript{2) Unit of Evolutionary Biology and Systematic Zoology, Department of Biochemistry and Biology, University of Potsdam, Karl-Liebknecht-Str. 24–25, 14476 Potsdam, Germany; \textsuperscript{3) Department of Zoology, University of Oklahoma, 730 Van Vleet Oval, Norman, OK 73019, USA}

(Accepted: 17 January 2008)

Summary
Audience effects occur when an observing (by-standing) animal influences the behaviour of an observed individual. A recent study (Plath, M., Blum, D., Schlupp, I. & Tiedemann, R., Anim. Behav. 75, 21-29 (2008)) has demonstrated an effect of a visual audience male on male mating preferences in the surface form of a livebearing fish, the Atlantic molly (\textit{Poecilia mexicana}). Surface dwelling \textit{P. mexicana} are highly aggressive; hence, males dedicating simultaneous attention to mate choice and aggressive interactions may explain this audience effect. Here we examined the effect of an audience on male mate choice in the cave form of that species, which — unlike other cavefishes — have maintained eyes and still respond to visual cues under experimental conditions. Cave mollies were especially interesting to study, because they have reduced aggressive behaviour. We gave males an opportunity to choose between two females, and we repeated the tests with an audience male present. The focal males tended to divide their attentions more equally between the two females when an audience male was presented. The observed effect did not statistically differ between surface and cave dwelling \textit{P. mexicana}, suggesting that (1) the response to a visual audience is maintained in this cavefish and (2) the described audience effect is largely independent of aggressive interactions among males. Generally, its adaptive significance may be linked to the avoidance of sperm competition when males sharing the same (innate) preferences compete for mates. Moreover, males may conceal their preference to prevent other males from copying their mate choice.

Keywords: cavefish, communication networks, mate choice, aggressive behaviour, sperm competition.

\textsuperscript{4) Corresponding author’s email address: mplath@rz.uni-potsdam.de

© Koninklijke Brill NV, Leiden, 2008, Behaviour 145, 931-947
Also available online - www.brill.nl/beh
Introduction

In many species mate choice occurs in a social environment, such that choosing a mate can be viewed as part of a larger communication network that involves more individuals than just the choosing individual and its potential mating partners (Danchin et al., 2004; Earley & Dugatkin, 2005; Matos & Schlupp, 2005). Generally, two forms of information exchange in animal communication networks have been particularly thoroughly examined. (1) Eavesdropping occurs when a receiver extracts information from a signaling interaction in which it has not taken part (McGregor, 1993; Oliveira et al., 1998; Doutrelant & McGregor, 2000; Johnstone, 2001; McGregor et al., 2001; Peake et al., 2001; Mennill & Ratcliffe, 2004; Naguib & Kipper, 2006). (2) Audience effect: the presence of an observing (‘by-standing’) individual can influence the behaviour of a pair of communicating individuals (Zajonc, 1965; Evans & Marler, 1991; Baltz & Clark, 1997; Doutrelant et al., 2001; Oliveira et al., 2001). In the context of mate choice, several studies have examined socially influenced (non-independent) mate choice of an observing individual in a communication network (Pruett-Jones, 1992; Kirkpatrick & Dugatkin, 1994; Westneat et al., 2000; for a review see Earley & Dugatkin, 2005). For example, eavesdropping may influence mate choice decisions, if females evaluate the quality of a male after the observation of male–male interactions (e.g., Otter et al., 1999; Doutrelant & McGregor, 2000; Mennill et al., 2003). Numerous studies have shown that individuals may also alter their mate choice decisions after they had seen other members of their own sex sexually interact with a potential mating partner (mate choice copying: e.g., Dugatkin, 1992, 2007; Dugatkin & Godin, 1992; Schlupp et al., 1994; Briggs et al., 1996; Witte & Ryan, 1998, 2002; Munger et al., 2004; Godin et al., 2005; Hill & Ryan, 2005; Widemo, 2006).

It is largely unknown whether or not, and to what extent, the mere presence of an audience affects the expression of mating preferences. In a recent study, males of a livebearing fish, the Atlantic molly (Poecilia mexicana), were given a choice between two females, and another (audience) male was presented visually during the second part of the trials. In that study, males spent significantly less time near the initially preferred female and spent more time near the initially rejected female when another (conspecific) male was present. No change was observed when no audience male was presented (‘control’), and only a weak effect was found when a heterospecific male
A visual audience effect in a cavefish

(a swordtail, Xiphophorus hellerii) was the audience (Plath et al., 2008). Those results suggest that the presence of a conspecific male strongly affects the expression of male mating preferences in this species.

Why do poeciliid males divide their attentions more equally between the two females in the presence of an audience? First, the evolutionary significance of altering mate choice behaviour may be linked, for example, to the increased risk of sperm competition, because the male competitor is likely to show the same intrinsic mating preferences. Alternatively, males may not be able to dedicate simultaneous attention to mate choice and the male competitor (see Plath et al., 2008 for a discussion). *P. mexicana* males are highly aggressive, and males may need to dedicate attention to either avoid larger, physically stronger males or attack smaller, inferior males. Dedicating attention to a rival may render accurate mate choice an impossible task. Inferior males could also ‘deliberately’ try to avoid aggressive interactions by moving away from the preferred female. The latter two scenarios imply that aggressive interactions play an important role in determining the expression of male mating preferences in the study species.

In the present study, we examined the effects of a visually presented audience on male mate choice decisions in a system in which it seems less straightforward to predict visual audience effects — the cave dwelling form of *P. mexicana* (cave molly). Cavefishes evolve from surface dwelling ancestors and, thus, allow for the observation of evolutionary processes accompanying the colonization of dark habitats (e.g., Protas et al., 2007). For example, cavefishes often reduce features that are no longer beneficial in their dark habitat, such as eyes and pigmentation (e.g., Wilkens, 2007), or they show reduction processes on a behavioural level (e.g., reduction of species recognition mechanisms: Riesch et al., 2006). Unlike many other cave animals that have completely reduced eyes, the cave molly possesses functional, albeit smaller eyes (Peters et al., 1973), and the absorption characteristics of the visual pigments are almost unchanged (Körner et al., 2006). Indeed, cave mollies were found to exhibit mate choice based on visual cues under laboratory conditions (Plath, 2004; Plath et al., 2004, 2006).

Surface dwelling *P. mexicana* males typically form dominance hierarchies, where dominant males (typically the largest males) aggressively defend shoals of females. By contrast, aggressive behaviour is genetically reduced in cave mollies, which show almost no aggressive behaviour (Parze-
fall, 1974, 1979, for analyses of the behavioural genetics of aggressive behaviour in population hybrids; see also Parzefall, 2001 for a review). This offers the unique opportunity to examine whether audience effects also occur in a system in which aggressive male–male interactions play no role. If aggression among males is a major factor determining the decrease of the strength of male preferences in the presence of an audience male, then we would expect no, or only a very weak audience effect in the population of cave mollies examined here. To study this, we designed a simultaneous choice experiment in which we gave light reared cave molly males an opportunity to choose between two visually presented females. In a second step we tested whether the initial male mating preference would be altered in the presence of another (audience) male.

Methods

Study organism

The cave mollies used in this study were descendants of animals collected in cave chamber XIII of the Cueva del Azufre in Tabasco, Mexico. Cave mollies were first collected in 1970 and stocks were repeatedly refreshed in 1975, 1982, 1996 and 2004. The behaviour tests were conducted in 2005. Test fish came from large, randomly outbred stocks maintained at the Institute of Biochemistry and Biology in Potsdam, Germany. Stocks comprising both sexes were reared in aerated and filtered 150–200 l aquaria at 27–30°C under a 16 : 8 h light/dark regime. Aquaria were well equipped with live and artificial plants and stones. Fish were fed twice daily with commercially available flake food, fish food tablets, and live red and white chironomid larvae. Focal males were isolated in 25 l tanks for 24 h before the tests. *P. mexicana* males show increased sexual activity after one day of sexual deprivation (Schlupp & Plath, 2005). Focal males were tested only once; however, due to the limited number of males available from our stocks, approximately half of the males were also used as audience males 2–4 days after they were used as a focal male. If former focal males were re-used as an audience male, they were not paired with the same male during a subsequent trial. Throughout this study, focal and audience males were non-familiar, i.e., they came from different stock tanks.
The green swordtails (*Xiphophorus hellerii*) used as heterospecific audience males were obtained from a commercial aquarium supplier and were kept in conditions similar to the mollies. Visual contact between the different stock tanks was not possible.

**Choice tests**

A standard test tank (80 cm length \(\times\) 30 cm height \(\times\) 30 cm depth) was divided into five sections of equal size: two lateral compartments were divided by transparent Plexiglas partitions to hold the stimulus fish, the remainder was visually divided by marks drawn on the front into a central ‘neutral zone’ and two lateral ‘preference zones’ (Figure 1). All sides except the front wall were covered by black plastic foil. The tank was filled to 15 cm with aged tap water of 27–28°C and was illuminated by a 40 W incandescent lamp 35 cm above the tank in addition to the room illumination (two 100 Watt neon tubes on the ceiling of the experimental room). Prior to a test, two stimulus females (a large (45.1 ± 0.9 mm standard length) and a small one (31.0 ± 0.8 mm, mean ± SE)) were taken from a stock tank and were introduced into one of the two stimulus compartments each. Stimulus females were exchanged between trials. We used female size as a choice criterion, because Atlantic molly males are known to show a strong preference for large female body size (Plath et al., 2006). Then, a focal male was introduced into a transparent Plexiglas cylinder (10 cm diameter) in the center of the neutral zone and was left undisturbed for 5 min. After the habituation period, the cylinder was gently lifted and measurement of male preferences was initiated. We measured the amount of time the male spent in each of the two preference zones, i.e., near both types of females during a 5-min observation period. To account for potential side-biases, the male was placed into the cylinder again after the first observation period, the two stimulus females were interchanged, and after another habituation phase of 5 min measurement of male preferences was repeated. This episode consisting of two test units is henceforth called the first part of a trial. Times spent near each stimulus female during the two test units were summed.

Directly after the first part, measurement of male preference was repeated, but an audience male was presented (second part of a trial; Figure 1). To initiate the second part of a trial, the focal male was introduced in his cylinder again. An audience male was then placed in another transparent cylinder
Figure 1. Experimental set-up for the mate choice tests. During the first part of a trial, a cave molly male (focal male) could choose between two simultaneously presented females. During the second part an audience male was visually presented in a clear Plexiglas cylinder in the neutral zone. For display purpose, fish are depicted at a supernatural size.

in the rear center of the neutral zone, equidistant to the two females. The audience male was confined in its cylinder throughout the experiment. After another 5-min acclimatization period, measurement of male association preferences and switching of side-assignments of the stimulus females between the two measurements was carried out as described above. During the second part of a trial the focal males experienced one of the following three treatments:

In treatment 1 a conspecific audience male was presented.

In treatment 2 we conducted a control experiment to determine if any effect detected was due to motivational changes over the time of an experiment.
For this control we used only an empty cylinder and no audience male during the second part.

Finally, in treatment 3 we asked whether the observed audience effect occurs only when a conspecific male is present. Alternatively, the effect might also be caused by the presence of any other male fish in the tank. In this control we used green swordtails (*Xiphophorus hellerii*) as audience males. This distantly related poeciliid species occurs in the vicinity of the Cueva del Azufre, but not inside the cave.

All fish were measured for standard length to the nearest mm after the trials (focal males 33.8 ± 0.8 mm; conspecific audience males 31.6 ± 0.9 mm; swordtail males 39.3 ± 0.7 mm). Approximately one half of the water in the test tank was exchanged every evening, i.e., after 2–3 tests. In total, we conducted $N = 45$ trials ($N = 25$ in treatment 1 and $N = 10$ each in treatments 2 and 3), i.e., 45 individual males were used as a focal male in only one trial each.

**Statistical analysis**

We decided a priori to discard trials in which the males spent less than 50% of the total time during the first part of a trial in the two outer compartments due to low response. Trials in which the males spent more than 80% of their choice time during both parts of the experiment in the same compartment were additionally discarded due to side bias (Plath et al., 2004). This led to two trials being discarded due to side-bias (both in treatment 3), while no incidence of low response was detected.

We asked whether males would alter their individual choice decisions between the two parts of a trial, i.e., before and after presentation of an audience. We, therefore, compared the relative time males spent near the preferred female during the first part of a trial (time spent near preferred female/(time preferred female + time non-preferred)) with the relative time spent near the same (initially preferred) female during the second part of a trial using paired $t$-tests.

We predicted that the focal males would spend more time in the neutral zone during the second part of a trial. Consequently, the absolute time spent associating with both females should be lower during the second part. Therefore, we did not use absolute association times when comparing preferences between the two parts of a trial, and all subsequent analyses were
conducted using a score that expressed the strength of change in male association preferences between the two parts of a trial (% time near the initially preferred female with an audience (second part) − % time near the preferred female without an audience (first part)). Hence, no change in male preferences would lead to a score of zero, negative values would indicate that the focal males spent less time near the initially preferred female in the second part of a trial and positive values would indicate that males spent relatively more time near the initially preferred female. We asked whether the pattern found in cave mollies would differ from the pattern found in surface dwelling *P. mexicana* males. We, therefore, compared the score between populations (surface form: Plath et al., 2008; cave form: this study) and treatments (conspecific audience, no audience or heterospecific audience) using a two-way ANOVA. Data are generally given as mean ± SE and were tested with Kolmogorov–Smirnov tests for normality. All percentages were arcsine (square-root)-transformed prior to statistical analysis. StatView 5.01 was used for the statistical analyses.

**Results**

*Effect of an audience on the behaviour of cave molly males*

**Treatment 1: Influence of a conspecific audience**

When we presented a conspecific male as audience during the second part of the trials, a significant change in the choice decisions of cave molly males was found between the first and the second part of the trials (paired *t*-test: *t*<sub>24</sub> = 4.30, *p* = 0.0002; Figure 2). 18 out of the 25 cave molly males (72%) spent proportionately less time near the initially preferred female and spent more time near the initially non-preferred female in the presence of another male (second part). Of these, 11 males (44%) reversed their initial preference, i.e., preferred the initially non-preferred female during the second part (whereby ‘preference’ was defined as a male spending > 50% of its time near a particular female).

We tested whether the size of the audience male (range: 23 to 40 mm) or the difference in size between the test male and the audience males (focal–audience; range −10 to +22 mm) correlated with the change of male preferences across the two parts of the trials, expressed as a preference score. We
Figure 2. The mean (± SE) time cave molly (P. mexicana) males spent associating with one of the two females presented (large vs. small P. mexicana female). During the first part of a trial, the focal male could choose between the females without an audience, while during the second part an audience male was visually presented. Audience males were: 1, a conspecific male; 2, no male (‘control’); or 3, a heterospecific (swordtail, Xiphophorus hellerii) male. Black bars indicate time spent near the initially preferred female, white bars indicate time spent near the initially non-preferred female. Note that absolute association times (s) are presented here, whereas the statistical analyses are based on relative association times (see Figure 3).

detected no effect of the audience male’s size or the size difference between the two males (Pearson correlations, absolute size: \( r_P = -0.05, p = 0.81, N = 25 \); size difference: \( r_P = 0.11, p = 0.60, N = 25 \)).
Treatment 2: No audience

In the second treatment (‘control’), no audience male was presented during the second part of the trials. We found no statistically significant difference in the relative time spent near the initially preferred female between the two parts of the trials (paired t-test: \( t_9 = 0.26, p = 0.80 \); Figure 2). Five out of ten cave molly males showed a decrease in their preferences during the second part of the test, two of which showed a slight preference for the opposite female during the second part.

Treatment 3: Heterospecific audience

When a heterospecific (swordtail) male was presented as audience, no statistically significant difference in male preferences was detected between the two parts of a trial (paired t-test: \( t_9 = 1.60, p = 0.15 \); Figure 2). Six of the 10 focal males showed a weaker preference during the second part of the experiment. Two males preferred the opposite female during the second part of the test.

Again, we tested for a potential influence of the size of the audience male (range: 35 to 41 mm) and the size difference between the focal male and the swordtail male (−20 to +2 mm) on the difference in male association preferences; none was detected (Pearson correlations, absolute size: \( r_P = -0.06, p = 0.87, N = 10 \); size difference: \( r_P = 0.06, p = 0.87, N = 10 \)).

Comparison between cave- and surface dwelling males

Here we included data from Plath et al. (2008) to compare surface dwelling and cave mollies. The interaction term had no significant effect in the ANOVA (mean square = 0.02, \( F_{2,80} = 0.22, p = 0.80 \)). There was no significant difference between populations (surface or cave; mean square = 0.08, \( F_{1,80} = 1.15, p = 0.29 \)), whereas the factor ‘treatment’ had a statistically significant effect (mean square = 0.26, \( F_{2,80} = 3.83, p = 0.026 \)). A post-hoc pair-wise comparison (Scheffe’s test) revealed that treatments 1 and 2 differed significantly \((p < 0.001)\), whereas the other comparisons (treatments 1–3 and 2–3) yielded non-significant differences \((p = 0.48 \text{ and } 0.47, \text{ respectively}; \text{ Figure 3})\).
A visual audience effect in a cavefish

Figure 3. The mean (± SE) difference in male association preferences of cave mollies during the three treatments (see main text), expressed as a score (% near initially preferred (second part) − % time spent near preferred female (first part)). Values close to zero indicate consistency of male preferences between the two parts of a trial (without, or with an audience male); negative values indicate that males spent relatively more time near the initially non-preferred female during the second part.

Time spent in the neutral zone

During the second part of the trials, the focal males spent more time in the neutral zone interacting with the conspecific audience male (treatment 1), as compared to the part of the experiment without audience. Interactions often included synchronized swimming up and down by both males, whereas aggressive displays were not observed.

We compared the increase in times spent in the neutral zone (time in neutral zone during second part − time during first part) across treatments. Again, we included data from Plath et al. (2008) to compare surface dwelling and cave mollies. The interaction term had no significant effect (mean square = 28 334.40, $F_{2,80} = 1.10, p = 0.34$) and was omitted from the ANOVA. There was no significant difference between populations (mean square = 67 088.01, $F_{1,80} = 2.60, p = 0.11$), whereas the factor ‘treatment’ had a statistically significant effect (mean square = 126 929.27, $F_{2,80} = 4.91, p = 0.010$). A post-hoc pair-wise comparison (Scheffe’s test) revealed that treatment 1 (+104.28 ± 24.19 s) differed significantly from treatment 2 (−25.00 ± 36.30 s; $p = 0.014$), whereas the other comparisons (treatments 1–3 (+28.35 ± 35.38 s) and treatments 2–3) yielded non-significant differences ($p = 0.32$ and 0.46, respectively).
Discussion

We gave cave molly (*P. mexicana*) males an opportunity to associate with a large vs. small conspecific female, and we repeated the choice tests while an audience male was visually presented. Focal males spent relatively less time near the initially preferred, but more time near the initially rejected female in the presence of a (conspecific) audience. This audience effect did not significantly differ from that found in surface dwelling *P. mexicana* males. In previous studies, audience effects have been examined primarily in an intra-sexual context. For example, an audience may influence the intensity of aggressive male–male interactions (Zajonc, 1965; Doutrelant et al., 2001; Oliveira et al., 2001; Matos & McGregor, 2002; Matos et al., 2003; Dziewczynski et al., 2005, 2006). Some studies reported that individuals may base their mate choice on information extracted from the observation of interactions among others (eavesdropping; Doutrelant & McGregor, 2000; Herb et al., 2003), but the question of whether, and to what extent, the presence of an audience influences mate choice decisions remained little investigated. Here, we report that an audience affects the strength of expression of a male mating preference. Not only did the focal males spend less time near the two stimulus females combined and more time in the neutral zone (near the audience) during the second part of the trials, but also their preferences declined (i.e., the difference in times spent near either type of females).

Basically, two explanations seem possible for why poeciliid males show weaker mating preferences in the presence of an audience male. The first hypothesis assumes that altering mate choice behaviour may be linked to the risk of sperm competition in the presence of competing males, given that other males in a male’s social environment will likely share the same (innate) preferences (such as the male mating preference for large female body size) and, thus, are likely to attempt mating with the same female. For example, *P. mexicana* males invariably prefer large females as mates (at least in the absence of an audience: Plath et al., 2006). Likewise, concealing mate choice may be a tactic employed by males to prevent other males from copying their own mate choice decision (see Schlupp & Ryan, 1997, for male mate choice copying in the related sailfin molly, *P. latipinna*).

An alternative explanation would be that the observed audience effect is the result of males dedicating simultaneous attention to mate choice and the male competitor. Indeed, surface dwelling *P. mexicana* are highly aggressive and form dominance hierarchies, whereby large, dominant males patrol
groups of females and defend them from smaller males, which in turn rely on a sneak-like mating tactic in the absence of dominant males. Hence, dominant males dedicate attention to observe small, inferior males to prevent them from mating; likewise, small, inferior males need to monitor males to avoid being attacked (Parzefall, 1969).

In contrast, cave mollies have reduced aggression almost entirely (Parzefall, 1974, 1979). The genetic reduction of energetically demanding behaviours appears to be an adaptation to life in a dark and sulfidic, energy-poor habitat (Tobler et al., 2006), where more energy needs to be allocated to somatic maintenance (Franssen et al., 2008; Plath, 2008). The present study, therefore, suggests that the observed audience effect cannot be explained on the sole basis of aggressive interactions among males. Further support for this interpretation comes from the observation that the body size of the audience male, as well as the size difference between the focal male and the audience male had no significant influence on the change in the focal males’ preferences. Apparently, the observed audience effect is independent of the perceived relative physical strength of the audience male. It must be mentioned though, that excluding the hypothesis of aggressive interactions distracting males from mate choice does not automatically mean that the first hypothesis (avoidance of sperm competition) is true. Indeed, future experiments will need to address the question what exactly causes the observed audience effect.

Surface dwelling \textit{P. mexicana} males showed a weaker preference when a conspecific audience male was presented during the second part of a trial, but showed no, or only a very weak change in preferences when no audience male or a heterospecific (swordtail) male was presented (Plath et al., 2008). Based on the finding that visual species recognition mechanisms appear to be reduced in the cave form of \textit{P. mexicana}, and cave mollies do not discriminate between a conspecific and an equal sized heterospecific stimulus fish (a swordtail, \textit{X. hellerii}; Riesch et al., 2006), one would predict that cave molly males would show the same response when a con- and a heterospecific audience male was present. Indeed, the decline of male preferences was qualitatively similar between treatments 1 and 3 in the case of the cave molly (Figure 3). However, no statistically significant difference was detected in the response to different treatments between surface and cave males (as would have been indicated by the interaction term ‘population’ × ‘treatment’). Our results (see ANOVA post-hoc tests) rather indicate that the response towards
a heterospecific audience male in *P. mexicana* males is intermediate to treatments 1 and 2.

The Plexiglas cylinder used for the presentation of the audience male was not sealed at the base. Nevertheless, exchange of chemical cues (pheromones) is very unlikely, since no ink was observed emanating from the cylinders in previous tests, during which a dye was used to detect potential ‘leakage’ (I. Schlupp, unpublished data). This also makes communication using vibrational cues unlikely. Therefore, the observed audience effect is likely based on visual cues only. It must be mentioned that the results of this study do not reflect the natural conditions inside the inner parts of the cave, where visual communication is impossible, and mollies need to rely on non-visual communication (Plath et al., 2004, 2006). For example, cave molly females and males were found to have maintained the visual preference for large body size shown by river dwelling mollies but to use non-visual sensory systems to detect large males under naturally dark conditions (Plath et al., 2004, 2006). However, using the same experimental design that had been employed in the study on surface dwelling males allowed us to compare the results directly between studies. The data from the present study indicate that just like the persistence of the visual preference for large conspecifics per se (Plath et al., 2004, 2006), a visually mediated behaviour has been maintained in this cavefish despite the absence of visual communication in its natural habitat. Such an evolutionary persistence may be due to an evolutionary time lag, or because this behaviour is currently still under selection. Indeed, it will be interesting to observe whether (non-visual) audience effects play a role in this system under naturally dark conditions.

To sum, visual audience effects in *P. mexicana* have been maintained during evolution into a cavefish. Our results demonstrate that visual audience effects are common in the study species, and that the expression of mating preferences may depend on the social environment in which mate choice occurs. The observed effect cannot be explained on the sole basis of aggressive interactions among males.

Acknowledgements

We thank C. Manteuffel for help with fish care. We appreciate the work of three anonymous reviewers that helped to improve the manuscript with their extremely thoughtful comments. Financial support came from the DFG (PL 470/1-1, PL 470/1-2). The Mexican Government
kindly issued permits to collect fish (291002-613-1577 and DGOPA/5864/260704/-2408). The experiments reported in this paper comply with the current German laws on animal experimentation.

References


A visual audience effect in a cavefish


