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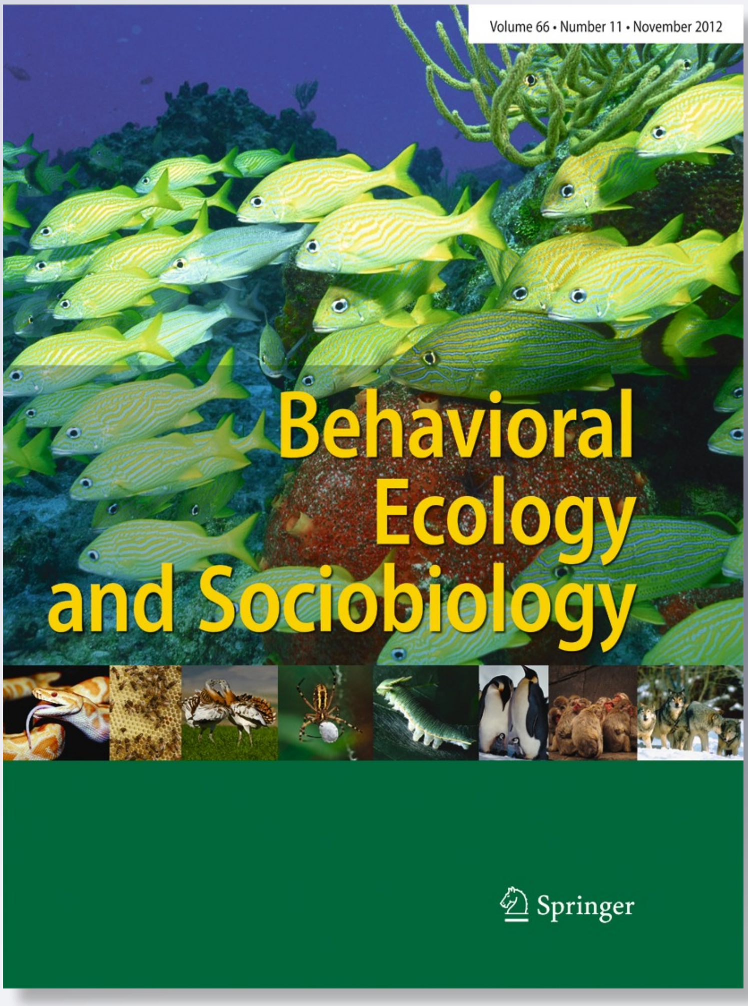

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ORIGINAL PAPER

Sex-specific plasticity in brain morphology depends on social environment of the guppy, *Poecilia reticulata*

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Abstract The vertebrate brain is a remarkably plastic organ, which responds quickly to environmental changes. However, to date, studies investigating plasticity in brain morphology have focused mostly on the physical properties of the surrounding environment, and little is known about brain plasticity in response to the social environment. Moreover, sex differences in brain plasticity remain virtually unexplored. Here, we tested how the social environment influenced brain morphology in adult males and females using experimental manipulation of the sex composition of social pairs (same sex vs. mixed sex) in the guppy (*Poecilia reticulata*). We detected substantial sex-specific plasticity in both the overall brain size (controlling for body size) and separate brain structures. The brain size was larger in males that interacted with females, and female optic tectum was larger in female-only groups. Overall, females had larger olfactory bulbs and cerebellum in comparison to males. While net sexual dimorphism in the brain structure can be explained in light of the known differences in boldness and foraging behaviour between the sexes, our results also support that cognitive demands associated with courtship behaviour can lead to plastic changes in the brain size. Our findings demonstrate that not only social environment can generate rapid, plastic responses in the vertebrate brain but also that such responses can depend strongly on sex.

Keywords Neural development · Plasticity · Social interactions · Sexual selection · Sexual dimorphism · Guppy · *Poecilia reticulata*

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Introduction

Variation in vertebrate brain morphology is striking at all taxonomic levels (Striedter 2005). However, the factors driving this variation are still not fully understood, although several studies undertaken at both the inter- and intraspecific levels have identified associations between the brain morphology and parental care (Gittleman 1994; Gonzalez-Voyer et al. 2009), tool use (Reader and Laland 2002) and food caching (Pravosudov and Clayton 2002), as well as the important links between the brain morphology and ecological factors such as diet (Hutcheon et al. 2002; Gonzalez-Voyer and Kolm 2010) and habitat complexities (Huber et al. 1997).

Sex differences in brain morphology form another source of variation that has received substantial attention. For instance, there are several reports of adaptive sexual dimorphism in separate brain structures, such as the larger forebrain areas in male songbirds (Nottebohm and Arnold 1976; De Groof et al. 2009). However, for sexual dimorphism in the actual brain size (controlling for body size), true demonstrations that are not merely the product of erroneous statistical procedures are rare (Forstmeier 2011; Kotrschal et al. 2012a). Despite the multitude of morphological and behavioural differences among the sexes (Andersson 1994; Arnqvist and Rowe 2005), theoretical predictions in terms of how sexual dimorphism should affect brain morphology are surprisingly scarce. One of the rare attempts to predict how sexual dimorphism in brain morphology may evolve was made by Lucia Jacobs (1996). Jacobs argued that cognitive demands of intra-sexual competition for mates and courtship behaviour should select for increased cognitive ability leading to the increased brain size or enhancement of particular brain structures. She therefore argued that cognitive ability and brain morphology should be more advanced in the sex that invests more into competition and/or courtship behaviours. Additionally, sexual brain dimorphism can occur in response to sex-specific differences in other aspects of ecology. For example, sex differences in feeding ecology can affect foraging behaviour differently in males and females and lead to sexual dimorphism in cognitive behaviours linked to foraging and, thereby, also brain morphology (Jacobs et al. 1990; Jacobs 1996). We note that, although the courting sex (most often the male) has been argued to have greater cognitive ability (Jacobs 1996), experimental evidence for greater cognitive ability in males is scarce. This may be because the choosy sex (most often the female) is under similarly strong cognitive selection since it should be able to interpret courtship signals and remember such signals to accurately compare the phenotypes of multiple individuals prior to choosing a partner. Hence, it is by no means trivial to accurately predict the outcome of how behaviours related to competition over mates should affect neural development and maintenance (see also Healy and Rowe 2007; Kotrschal et al. 2012a).

The vertebrate brain is not only highly variable at the intrinsic organismal level, but it is also a remarkably plastic organ that can respond rapidly to variation in the surrounding environment during development (e.g. Nottebohm 1981; Hofman and Swaab 2002; Gonda et al. 2009; Kotrschal et al. 2012b). To date, most studies investigating adaptive brain plasticity have focused on how environmental enrichment can influence brain morphology (e.g. Rosenzweig and Bennett 1996; Kihslinger and Nevitt 2006). For example, adding a single rock to the holding tanks of juvenile salmon leads to a larger cerebellum (Kihslinger and Nevitt 2006), the structure involved in motor control and coordination of movements and balance (Butler and Hodos 2005). However, how social environment affects plasticity in brain size and structure remains virtually unexplored. The rare exceptions are the analysis of brain plasticity in relation to early development in individuals kept in groups or solitarily in sticklebacks (Gonda et al. 2009) and the demonstration of plastic responses in brain morphology to variation in predation pressure in tadpoles (Gonda et al. 2010). Plasticity in brain morphology in relation to sexual interactions, however, has yet to be addressed. We find this surprising since, as described above, behaviours associated with intra-sexual competition over mates, courtship and actual mating are highly variable both within and between the sexes (Andersson 1994; Arnqvist and Rowe 2005) and have been proposed to have strong effects on cognition and brain morphology (Jacobs 1996; Kotrschal et al. 2012a).

One way to investigate sex-specific plasticity in brain morphology in response to changes in the social environment, with emphasis on sexual interactions, is to form experimental groups of individuals that differ in sex composition. Here, we use the guppy (*Poecilia reticulata*) as a model to investigate how the brain size and structure are affected by the social environment in both sexes. There are established differences in behaviour between the sexes, as females are generally more risk-sensitive (Piyapong et al. 2010) and males are among the most sexually ardent in the animal kingdom (Magurran 2005). Sexual harassment by males is common and has been shown to impose significant costs on females (Magurran and Seghers 1994) and even their offspring (Gasparini et al. 2012). Because of the combination of these sex differences, the documented effect of the social environment on life-history and sexually selected traits (Reznick and Yang 1993; Evans and Magurran 1999), and the known brain size plasticity in the guppy (Burns et al. 2009), it is an appropriate model organism for such investigations. Here, we compared the outcome of brain development in sexually mature individuals maintained either in same-sex or mixed-sex social pairs. Our analyses focus both on intrinsic sex differences in brain morphology and on sex-specific plasticity in brain morphology in response to the social environment.

Methods

We used 168 laboratory descendants of wild guppies (*P. reticulata*), whose founders were caught in the Quare River, Trinidad in 1998. Experiments were conducted on two different laboratory lines with known differences in the total brain size (Kotrschal et al., unpublished data), which allowed us to test for the robustness of our experimental manipulations in different genetic backgrounds. The fish were maintained in 4-litre tanks with a 2-cm layer of gravel and constant aeration on a 12:12 l/d lighting schedule. Temperature was held at 26–27 °C, and the fish were fed with flake food and live brine shrimp 6 days/week.

Experimental procedure

At the onset of maturity (when males showed fully developed colour pattern, age: ♂ 110±1.3 days, ♀ 108±1.7 days), we paired individuals with either a non-related partner of the opposite sex (60 pairs) or a same-sex sibling (24 pairs). Because guppies are cannibalistic, we divided the breeding tanks with a 3×3-mm net to allow newborn fish to escape from their parents. Since the smaller males could sometimes enter the juvenile zone, we checked for offspring daily and removed the males 1 week after the first clutch was produced (mean age 148.7±0.5 days). We euthanized the males with an overdose of benzocaine, measured their standard length to the nearest 0.01 mm using digital callipers and placed them in 5 % buffered paraformaldehyde. To ensure substantial investment into the reproduction in females, we allowed females to produce a second clutch before we sacrificed them (mean age 181.2±0.4 days) following the same procedure. The brains were removed under a stereomicroscope and weighed to the nearest 0.001 mg. We obtained the brain weight measures for 164 individuals (line 1: ♀ 30 opposite sex and 11 same sex, ♂ 30 opposite sex and 12 same sex; line 2: ♀ 29 opposite sex and 12 same sex, ♂ 30 opposite sex and 10 same sex; four fish died during the experiment) and volumetric measures of the brain structures for 161 fish, as three brains were damaged during dissection and excluded from the analyses.

Quantification of brain structure volumes

All dissections, digital image analyses and measurements were performed by one person (AK) and done blindly to treatment. To quantify the brain structure volumes, digital images of the dorsal, ventral, left and right sides of the brain were taken through a dissection microscope (Leica MZFLIII) using a digital camera (Leica DFC 490). For each image, the brain was placed to ensure that the brain was symmetrically positioned such that one hemisphere did not appear larger than the other based on perspective. For paired structures, both sides were measured, and the volumes were added to give a total structure volume. Following Pollen et al. (2007), the widths W of the six key structures (olfactory bulb, telencephalon, optic tectum, cerebellum, hypothalamus and dorsal medulla) were determined from the dorsal and ventral views, whereas lengths L and heights H were taken from the lateral views (Fig. 1). The width was defined as the maximal extension of a given structure perpendicular to the anatomical midline. The length L of a structure was defined as the maximal extension of a structure parallel to the estimated projection of the brain; the height H, as the maximal extension of the structure perpendicular to the estimated projection of the brain. The volume of the brain structures V was determined according to an ellipsoid model (van Staaden et al. 1995):

$$V = (L \times W \times H)\frac{\pi}{6}.$$

To determine the repeatability (Lessells and Boag 1987), the volume of all structures in ten randomly chosen specimens was measured twice. Repeatability for the structures was high (r=0.83–0.91, all p<0.001).

It is noteworthy that the brain weight and calculated structure volumes are relatively coarse measures of the brain anatomy and should be considered the first step in the investigation of how the social environment impacts brain plasticity. Future studies should resort to more fine-scale methods of three-dimensional imaging, such as MRI scans or sectioning on a microtome (Ullmann et al. 2010).

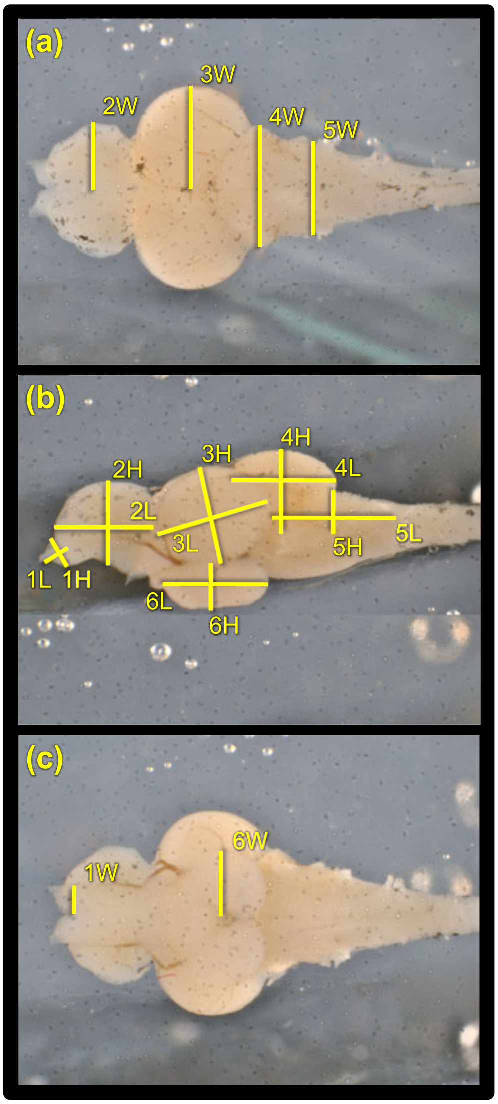

Fig. 1 Illustration of the measurements taken from the dorsal (**a**), lateral (**b**) and ventral (**c**) images to determine the size of various brain structures in *P. reticulata*. *W*, *H* and *L* refer to width, height and length, respectively. *1* Olfactory bulb, *2* telencephalon, *3* optic tectum, *4* cerebellum, *5* dorsal medulla, *6* hypothalamus

Statistical analysis

To analyse how sex and social environment influenced body size, we used a general linear mixed model (GLMM) with standard length as the dependent variable; sex, line, social environment and the interaction between sex and social environment as fixed factors; and home tank as a random factor. For analyses of how sex and social environment influenced the total brain size, we used a GLMM with the total brain weight (log-transformed) as the dependent variable; sex, line, social environment and the interaction between sex and social environment as fixed factors; home tank as the random factor; and log-transformed body size (standard length) as the covariate. To ensure that the slight age difference between the sexes did not influence the results, we included age as the covariate in an earlier model. Because it was not significant (p>0.3), it was excluded from the final model. To determine the potential line differences in plasticity, we included line × social environment as a factor in an earlier model. Because this was not significant, we excluded the term, together with all non-significant interactions (all $p>0.4$). To investigate the differential effects of social environment in males and females separately, we ran two additional separate GLMMs for the two sexes.

To analyse how sex and social environment influenced the volumes of different brain structures, we had to include tank as a random effect. Therefore, instead of the common MANCOVA design with all the brain structures as dependent variables and the brain and/or the body size as covariate, we analysed the brain structures in six separate GLMMs using the same model as for the total brain size. Following Benjamini and Hochberg (1995), we corrected for multiple testing by ordering all p values from the smallest to the largest and individually testing whether their rank and value met the significance criteria (note that MANCOVA produced qualitatively identical results, not shown here). As in the analyses of the total brain size, we included age as a covariate in earlier models. Since age was not significant (all $p>0.3$), it was excluded from the final model. To determine the potential line differences in plasticity, we included line × social environment as a factor in an earlier model. Because this was not significant, we excluded the term together with all non-significant interactions (all $p>0.3$). All analyses were done with a restricted maximum likelihood analysis implemented in SPSS 19.0. It should be noted that sampling or measurement errors in the covariate may lead to erroneous conclusions regarding the relationships between regressions across groupings, in which case reduced major axis regression should be used (Forstmeier 2011). However, to our knowledge, there are no implementations for reduced major axis regression for more complex designs including random effects and multiple interactions. Since the use of RMA would, in this case, lead to pseudo-replication and exclude the possibility to test for complex interactions, it could thus not be used for these analyses. The data was normally distributed, the variances were homogenous and none of the interactions between any of the factors and the covariates were significant (all $p>0.3$).

Results

Females were larger than males (GLMM: sex $F=125.1$, $p<0.001$; Table 1, Fig. 2a), but we did not detect any overall difference in the brain size between males and females after controlling for the body size (GLMM: sex $F=1.0$, $p=0.321$; Table 1, Fig. 2b). However, for the separate brain structures, females had a relatively larger cerebellum and olfactory bulbs than males (Table 1, Fig. 2a, b). We detected no other differences across the sexes in brain structure (Table 1). In

Table 1 Results of the GLMM of the total brain size and the six separate GLMMs for the brain structures with holding tank as the random effect

	Body size		Total brain		Olfactory bulbs		Telencephalon		Optic tectum		Cerebellum		Hypothalamus		Dorsal medulla	
Effect	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p	$F_{1,161}$	p
Body size	–	–	360.4	*	28.0	*	24.8	*	157.2	*	176.9	*	75.5	*	104.8	*
Line	2.5	0.119	51.9	*	0.9	0.35	10.5	0.002	28.5	*	10.0	0.002	5.0	0.028	5.5	0.021
Sex	125.1	*	1.0	0.32	8.2	**0.005**	0.7	0.39	0.2	0.68	6.0	**0.015**	1.8	0.18	0.2	0.68
Social environment	40.3	*	1.0	0.31	0.8	0.36	0.3	0.58	1.4	0.24	0.7	0.40	0.0	0.98	0.1	0.80
Sex × social environment	125.2	*	9.1	**0.003**	0.4	0.55	0.4	0.55	8.4	**0.004**	0.0	0.92	0.0	0.86	0.1	0.81

Note that the factor line was only included into the models to control for known variation in brain morphology between lines and that this factor will not be discussed further. All other statistically significant effects (after controlling for multiple testing; Benjamini and Hochberg 1995) are highlighted in bold. *$p<0.001$

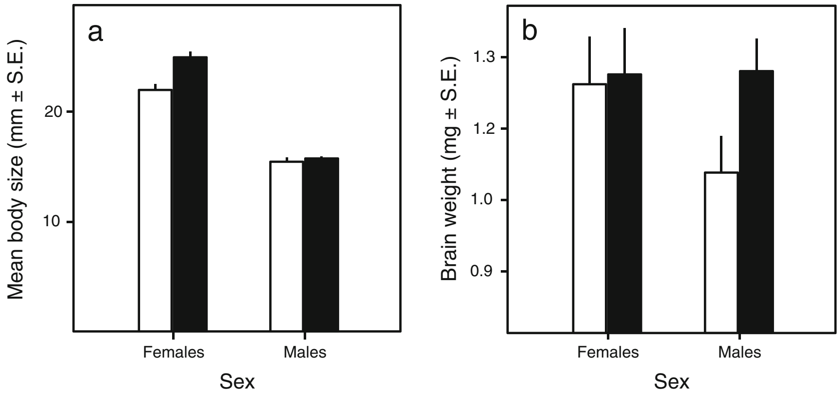

Fig. 2 Effects of sex and social environment on the body and brain size of guppies. Estimated marginal means of the body (**a**) and brain weight (**b**) across sex and social environment in fish kept in same-sex (*white bars*) and mixed-sex (*black bars*) groups

response to our manipulation of the social environment, there was a strong significant interaction between sex and social environment for the total brain size (Table 1). Males in the same-sex groups had relatively smaller brains than males paired with females, while female brains did not show differences in response to social environment manipulations (GLMM ♂: social environment F=4.9, p=0.032; GLMM ♀: social environment F=1.8, p=0.191; Fig. 2b). We detected an effect of treatment on body size that was independent from the effect on brain size: females paired with males were larger than females from the same-sex groups (GLMM: sex F=125.1, p<0.001; Table 1), while there was no body size difference in males from different social environments (GLMM: sex F=0.7, p=0.399; Fig. 2a). We also detected a significant interaction between sex and social environment for optic tectum. Females had a larger optic tectum in the same-sex groups than when paired with males, while optic tectum size did not differ between the males of both treatments (GLMM: sex×social environment F=8.4, p=0.004; Fig. 3c). We detected no other effects on the separate brain structures from our manipulation of the social environment (Table 1).

Discussion

We detected an intrinsic sexual dimorphism in brain structures but not in the overall brain size. Most importantly, we detected a sex-specific plastic response in the brain size to the social environment since males had larger brains when kept with females as compared to when kept in male-only pairs.

Intrinsic sex differences in brain morphology

The differences in mating behaviour between males and females in the guppy do not seem to be enough to cause a detectable sexual dimorphism in brain size. As mentioned above, methodologically correct demonstrations of sexual dimorphism in brain size are generally rare. Whether this is due to a genuine lack of such cases or them having been so far overlooked remains unclear (see Kotrschal et al. 2012a for the discussion on this). One striking example was recently found in two Icelandic populations of three-spined stickleback (*Gasterosteus aculeatus*), where males had >20 % larger brains than females (Kotrschal et al. 2012a). In the stickleback, males construct elaborate nests, display complex

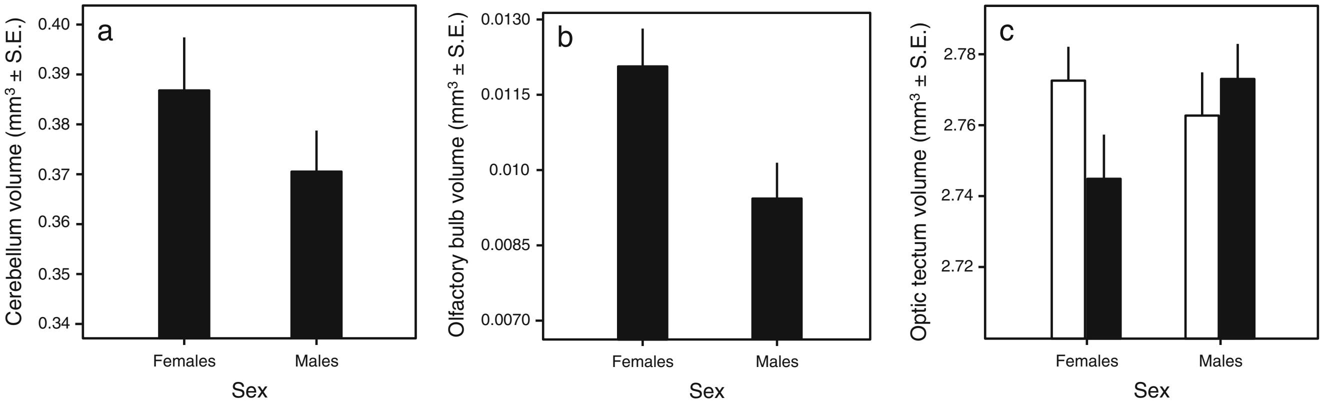

Fig. 3 Effects of sex and social environment on the brain structure volumes of guppies. Estimated marginal means of the cerebellum (**a**) and olfactory bulb (**b**) volumes across sexes and of the optic tectum (**c**) across sex and social environment in fish kept in same-sex (*white bars*) and mixed-sex (*black bars*) groups

courtship towards females prior to mating and provide parental care single-handedly (Bell and Foster 1994). Hence, the combination of all these different aspects of cognitive demands may be necessary to result in noticeable intrinsic sexual dimorphism in brain size. Alternatively, the sex-specific cognitive demands of competition over mates and courtship in males and the interpretation of male courtship signals and avoidance of sneak copulations in females (Houde 1997) may balance out and lead to similarly sized brains across the sexes in the guppy.

For the separate brain structures, we detected sexual dimorphism in both the olfactory bulbs and the cerebellum, which were larger in females (controlled for body size 2 and 14 %, respectively). Female guppies are generally much more active than males in terms of foraging activity, partially to compensate for costs associated with male harassment through increased foraging (Magurran and Seghers 1994; Croft et al. 2006; Piyapong et al. 2010). Females are also more innovative in a feeding situation, better at locating food and respond quicker to novel food sources (Laland and Reader 1999b; Laland and Reader 1999a). In the vertebrate brain, the cerebellum coordinates movements and certain aspects of learning (Butler and Hodos 2005; Rodriguez et al. 2005; Striedter 2005), while the olfactory bulbs are responsible for the reception and transmission of olfactory cues (Rosenzweig and Bennett 1996; Striedter 2005; Braithwaite 2006). We therefore suggest that the increased cognitive demands of higher overall activity and foraging efficiency in females contribute to sexual dimorphism in these structures in the guppy. As mentioned above, the increase in these separate structures was not enough to cause sexual dimorphism in the overall brain size. We attribute this to the relative smallness of the olfactory bulbs and the cerebellum in the guppy brain that make up less than 14 % of the overall brain volume.

Plastic responses in brain morphology to the social environment

Males developed larger brains when maintained with females compared to when kept in the same-sex environment, which demonstrates sex-specific plasticity in brain size in response to the social environment. Our results thus partly support the hypothesis by Jacobs (1996) in that cognitive demands of inter-sexual interactions may have led to the increased brain size in males kept with females. Male guppies court females intensely and perform a multitude of advanced courtship behaviours (Liley 1966; Houde 1997) including a high frequency of sneak copulations that require careful positioning in relation to the female (Pilastro et al. 2007). It is therefore possible that the combination of these complex behaviours lead to rapid development of the relative brain size to accommodate the cognitive requirements of male courtship. It is interesting that we find a sex-specific plasticity in support of Jacob's hypothesis, but there are no intrinsic differences in brain size in support of this hypothesis. The vertebrate brain is an energetically costly organ to develop and maintain (Aiello and Wheeler 1995). Perhaps, the increased energetic demands of a larger brain only allows for temporally limited plastic increases in brain size, as is the case for several brain structures in male starlings (*Sturnus vulgaris*), that increases in size only for a limited period during the mating season (De Groof et al. 2008). Alternatively, brain size may have decreased in the male-only environment due to a trade-off between energetic investment into neural development and male–male competition. Previous studies have demonstrated that male guppies tend to be bolder and more active in the company of other males than they are in the company of females (Griffiths 1996; Piyapong et al. 2010). Moreover, sperm production is generally highest in male-only groups (Evans and Magurran 1999). Since investment into sperm production is costly (Pitnick and Miller 2000), it is possible that similar to bats (Pitnick et al. 2006), a trade-off exists between investment into the neural tissue and investment into the testis size.

We also found an interaction between sex and social environment for the optic tectum as a result of relatively larger optic tectum in females in the same-sex pairs. The optic tectum mainly receives and processes visual stimuli (Rosenzweig and Bennett 1996; Striedter 2005; Braithwaite 2006), but below the outer shell of the tectum are also non-visual structures such as the tectal ventricle and the valvula of the cerebelli (Nieuwenhuys et al. 1998). A change in structural volume can therefore be due to changes in multiple substructures, and it is at the moment difficult to surmise what causes the optic tectum to be larger when females cohabit with other females. On the other hand, the use of body size as covariate in the model may have driven this difference because we found the (relatively larger) females from the mixed-sex groups to have a relatively smaller optic tectum. In that case, however, we would expect other structures to differ in a similar manner, which was not the case. Nevertheless, these results provide fruitful ground for future investigations into sex-specific plasticity of the different brain structures.

We found an interaction between sex and social environment for the body size. This was due to the relatively smaller females in the same-sex groups, whereas males did not differ in size according to the social environment. We attribute the smaller body size in females from same-sex groups to increased feeding competition among females. Opposite to males, female guppies are known to compete for and monopolise food (Griffiths 1996; Piyapong et al. 2010). Hence, more intense competition over food in the female-only pairs may have resulted in hampered growth. However, we did not find any increase in the total brain size or the volumes of different structures for females in the mixed-sex pairs compared to same-sex pairs. This suggests that the behaviours commonly observed in such interactions in females in the guppy, for instance interpreting and remembering male courtship signals and avoiding male mating attempts (Houde 1997), are not associated with (compared to male behaviours) increased cognitive demands translating into plasticity in brain size or brain structure volumes in females.

Conclusions

Previous studies have demonstrated plasticity in brain morphology in response to environmental cues such as habitat complexity and predation. Here, we demonstrate plasticity in vertebrate brain morphology in response to the social environment, and we also show that such plasticity can be sex-specific. Because of this, we suggest that future studies should consider the following: (a) the plastic responses in the brain to changes in the physical and social environments in both sexes and (b) both the cognitive demands and costly features of the behavioural repertoire to fully understand the patterns and underlying mechanisms of variation in vertebrate brain morphology.

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Ethical standards All performed experiments comply with the Swedish law and were approved by the Uppsala ethics committee.

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