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It's in the eye of the beholder: visual lateralisation in response to the social environment in poeciliids

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The social environment offers fish complex information about the quality, performance, personality and other cues of potential mates and competitors simultaneously. It is likely, therefore, that the environmental information regarding the context of mate choice is perceived and processed differently in species and sexes in respect to lateralisation. The present study comparatively assessed visual lateralisation behaviour in response to different social or sexual stimuli in three closely related poeciliid species (*P. latipinna*, *P. mexicana*, *P. formosa*) in comparison to a more distantly related species (*P. reticulata*). Individuals were presented with four different social or sexual stimuli that were tested against a control stimulus; (a) a conspecific male, (b) a conspecific female, (c) a heterosexual conspecific pair, (d) three conspecific females (shoal). In order to approach a target stimulus, focal fish had to perform detours to the right or left of a vertically straight-shaped barrier. The three closely related poeciliid species, *P. latipinna*, *P. mexicana*, *P. formosa*, appeared to have a general tendency to turn right (*i.e.*, left-eye preference), whereas the more distantly related *P. reticulata* males and females showed an overall bias to the left (*i.e.*, right-eye preference) in response to various social–sexual incitements. Moreover, body size seemed to significantly influence especially the males' detour behaviour, with smaller males acting in opposition to their larger conspecifics in response to certain social stimuli. In this case, smaller and larger *Poecilia* spp. males responded in the same way as smaller and larger males of the other three poeciliid species. Therefore, results possibly point to differences in the degree of general social behaviour between closely and more distantly related species and mating motivation amongst larger and smaller individuals when placed in a novel social environment. Hence, present results possibly suggest a sex-specific functional lateralisation for the analysis of visual information and seem to support the closer ancestral relationships between the *Poecilia* spp. tested in this study and the more distantly related guppies in terms of their left–right lateralisation. Generally, present results suggest that functional asymmetries in behaviour could be widespread among vertebrates, thus supporting the hypothesis of an early evolution of lateralisation in brain and behaviour.

KEYWORDS
asymmetric eye use, cerebral lateralisation, detour behaviour, sexual interaction, social environment

1 | INTRODUCTION

Asymmetric processing of different cognitive functions is based on cerebral lateralisation (Bisazza & Brown, 2011; Corballis, 2009; Rogers, Vallortigara, & Andrew, 2013; Vallortigara & Rogers, 2005; Vallortigara & Versace, 2017; Versace & Vallortigara, 2015). Many of these cognitive functions such as language, face recognition, emotional response, or spatial and mathematical abilities were initially found to be clearly lateralised in humans (Chochon *et al.*, 1999; Floel *et al.*, 2001; Phelps *et al.*, 2001). Thus, hemispheric asymmetry was thought to be uniquely human, following the evolution of language, handedness, or tool use (Bisazza & Brown, 2011; Ocklenburg &

Güntürkün, 2012; Rogers & Vallortigara, 2015; Rogers et al., 2013). Subsequently, numerous studies have revealed functional hemispheric specialisation including left–right asymmetries of brain and behaviour in nearly all vertebrates including mammals (Quaranta et al., 2007; Quaresmini et al., 2014; Siniscalchi et al., 2013; Versace et al., 2007), birds (Chiandetti et al., 2013, 2017; George, 2010; Güntürkün & Manns, 2010; Rogers, 2008), reptiles (Bisazza, et al., 1998a; Bonati et al., 2008, 2010; Csermely et al., 2010, 2011; Bonati et al., 2013a, 2013b,c, 2017; Sovrano et al., 2018), amphibians (Bisazza et al., 1998a; Bisazza et al., 2002; Vallortigara, 2006; Sovrano, 2007), bony fishes (Dadda et al., 2010; Lippolis et al., 2009; Vallortigara & Rogers, 2005), cartilaginous and jawless fishes (Byrnes et al., 2016; Vila Pouca et al., 2018). Evidence for an asymmetrical organisation was found in several invertebrate species as well, such as Octopus vulgaris (Byrne et al., 2002; Schnell et al., 2018), Apis mellifera (Rogers & Vallortigara, 2008; Frasnelli et al., 2010; Rigosi et al., 2015), and Caenorhabditis elegans (Taylor et al., 2010). Accordingly, lateralisation appears to be an important principle of nervous system organisation and, consequently, it is considered as highly relevant for animal behaviour and survival (Ghirlanda et al., 2008; Ghirlanda & Vallortigara, 2004; Ocklenburg & Güntürkün, 2012; Vallortigara, 2000). A meaningful benefit for the animal's fitness via functional lateralisation may arise by means of a possible increase of neural capacity. That is, one hemisphere specialising on certain types of cognitive functions may help to avoid costly duplication of hemispheric involvement as well as processing capacity necessitated by matching of information between hemispheres (Ocklenburg & Güntürkün, 2017; Vallortigara, 2006). It appears to facilitate processing of complementary information that demand the simultaneous but different use of both hemispheres (Ocklenburg & Güntürkün, 2017; Rogers et al., 2004). For example, in female goldbelly topminnows Girardinus falcatus (Eigenmann 1903), lateralised individuals were found to be twice as fast as their non-lateralised conspecifics (obtained through selective breeding) when attending a feeding task (prey catching) with one eye while simultaneously observing potential predators with the other one (Dadda & Bisazza, 2006). Similar results were found previously in domestic chicks Gallus gallus domesticus in which cerebral lateralisation appeared to be associated with a better ability to perform two tasks simultaneously (foraging and vigilance for predators; Rogers et al., 2004).

In most bird and fish species, the eyes are distinctly laterally placed. Consequently, each eye basically perceives different aspects of the individual's surroundings (monocular vision). To give an example, chicks that predominantly use the left eye can recognise and distinguish familiar birds far more easily than when the same information is presented exclusively to the right eye (Vallortigara, 1992; Vallortigara & Andrew, 1994). Chicks react considerably faster to predators approaching from the left side than from the right side (Vallortigara, 2006). Likewise, lateralisation and its behavioural effects have been studied in a large variety of contexts such as antipredator behaviour, foraging behaviour, exploration and response to novelty, homing and spatial abilities and social behaviour including shoaling, social recognition, aggression, communication, or mating. For example, many fish species show an individually consistent tendency to detour an obstacle to one side while escaping from a predator (Bisazza et al., 2000a,b). Another study investigating the effects of predation pressure on the cognitive ability of eight different populations of Panamanian bishop Brachyrhaphis episcopi (Steindachner 1878) revealed that populations facing high predation pressures predominantly viewed predators with their right eye and novel objects with their left eye (Brown & Braithwaite, 2005). Rainbowfish Melanotaenia duboulayi (Castelnau 1878), Melanotaenia nigrans (Richardson 1843) showed a substantial right-eye bias while schooling with conspecifics in a mirror test (Bisazza & Brown, 2011). However, no significant preference for eye use was observed in low-predation populations.

The social environment offers fish complex information about the environment, predators, quality of the habitat regarding food, mates, etc. simultaneously (Bonnie & Earley, 2007, Danchin et al., 2004). It is, therefore, likely that the environmental information regarding different contexts is perceived and processed differently in respect to lateralisation. Even within different poeciliids, distinct variation between species have been observed in their preference to turn right or left facing different social stimuli. Using equally sized females as target stimuli in a detour test, female mosquitofish Gambusia holbrooki (Girard 1859) (Bisazza et al., 1998b; De Santi et al., 2000) and wild-caught female B. episcopi (Brown et al., 2007) displayed strong bias to use their left eye by turning right to detour the barrier. Likewise, left-eye preference has been revealed in several teleosts from different orders (Osteoglossiformes, Cypriniformes, Cyprinodontiformes, Beloniformes), indicating that right hemisphere specialisation (due to crossover of optic nerve fibres to the contralateral hemisphere at the optic chiasm) could be a general pattern for recognising social stimuli (Besson et al., 2017; Sovrano et al., 1999, 2001, 2016; Sovrano & Andrew, 2006). A preference for using one eye or the other in certain social contexts (e.g., shoal forming, social companions, potential mating partners) appears to be widespread across different fish species. Also, both wild and laboratory populations are often characterised by a large variety of lateralisation phenotypes (on an individual or a population level; Lucon-Xiccato & Bisazza, 2016). For example, sarasins minnows Oryzias sarasinorum (Popta 1905) were found to observe familiar conspecifics with their left eye and use their right eye to view unfamiliar individuals or objects (Sovrano, 2004). Swarming M. duboulayi predominantly using their left eye to view their shoal mates were generally found on the right side of their shoal, while the reverse is true for those individuals who prefer to view their conspecifics predominantly using their right eye (Bibost & Brown, 2014). An enhanced schooling performance (i.e., significantly more cohesion and coordination) has been observed in shoals composed of lateralised Giradinus spp. compared to shoals composed of non-lateralised individuals (Bisazza & Dadda, 2005). In mixed shoals composed of both lateralised and non-lateralised individuals, the latter were more likely found at the periphery of the shoal. Lateralised fishes rather assumed safer and energetically less expensive positions in the middle of the shoal (Bisazza & Dadda, 2005). Thereby, various degrees of lateralisation within a shoal would be a favourable feature as it allows faster responses to predators or prey on the periphery of the shoal and rapid responses to the behaviour of mates within the shoal (Brown, 2005; Vallortigara & Rogers, 2005).

As well as much important information about the environment, the social environment offers fish complex information about the quality, performance, personality and other cues of potential mates

and competitors relevant in the context of mate choice simultaneously as well. It is, therefore, possible that the environmental information in the wide context of mate choice is perceived and processed differently in respect to lateralisation. For example, Bisazza *et al.* (1997a) investigated whether males of five poeciliid species (*G. holbrooki*, *Gambusia nicaraguensis* (Günther 1866), *Poecilia reticulata* (Peters 1859), *Brachyrhaphis roseni* (Bussing 1988), *G. falcatus*) made detours to the right or left to pass a transparent obstacle in order to approach a group of conspecific females (*i.e.*, a potentially sexual stimulus). While males of *G. holbrooki*, *G. nicaraguensis* and *P. reticulata* significantly preferred to turn leftwards, males of *B. roseni* and *G. falcatus* significantly preferred to turn rightwards. Subsequently, *G. holbrooki* and *G. falcatus* males were additionally presented with an opaque obstacle or a dummy predator and responded with comparable biases to the right (opaque obstacle) and left (dummy predator). The authors concluded that the observed differences could have resulted from species-specific differences in the degree of sexual motivation in a novel environment. The two species that showed bias to the right with the females were less likely to exhibit sexual behaviour when placed in a novel environment. In another study, researchers examined the preferred detour responses of male *G. holbrooki* facing an obstacle consisting of straight vertical bars or a U-shaped obstacle through which a group of conspecific females was presented (Bisazza *et al.*, 1997b). While males showed a consistent population bias to detour leftwards facing straight vertical bars, they did not show any preference facing a U-shaped obstacle. Males kept their preference to turn left facing a simulated predator but chose indifferently when being presented with an empty target or a group of conspecific males (Bisazza *et al.*, 1997b). Female *P. reticulata* were found to observe a familiar conspecific by predominantly using their right eye, which changed to a left-eye-preference when being presented with an unfamiliar conspecific (Kaarthigeyan & Dharmaretnam, 2005).

Fish either observe single potential mates during mate choice, gathering private information and exhibiting independent mate choice, or they observe other conspecifics during sexual interaction (using public information, non-independent mate choice, Witte *et al.*, 2015). We aimed to examine whether males or females of different poeciliid species (*P. reticulata*, sailfin molly *Poecilia latipinna* (LeSueur 1821), Amazon molly *Poecilia formosa* (Girard 1859), Atlantic molly *Poecilia mexicana* (Steindachner 1863)) would show a preference for using a particular eye when observing social or sexual stimuli which are relevant in the use of public information in mate choice; *i.e.*, during mate-choice copying. Mate-choice copying occurs when an individual is altering his or her mate choice decision due to an observed mate choice decision of conspecifics. In *P. reticulata*, it has been shown that females as well as males copy the mate choice of same sex conspecifics (Auld & Godin, 2015; Dugatkin, 1992, 1996, 1998). Likewise, *P. mexicana* and *P. latipinna* use public information during mate choice (Gierszewski *et al.*, 2018; Heubel *et al.*, 2008; Schlupp *et al.*, 1994; Schlupp & Ryan, 1997; Witte *et al.*, 2018; Witte & Ryan, 1998; Witte & Ryan, 2002) as well as *P. formosa*, which copies the mate choice of other females as well (Heubel *et al.*, 2008). In the present study we investigated visual lateralisation in response to different social and sexual stimuli in three closely related poeciliid species

(*P. latipinna*, *P. mexicana*, *P. formosa*) and *P. reticulata*, which all have been shown to use private and public information in mate choice.

Here, we examined whether males and females of the same species would show similar or different direction preferences to detour a barrier with respect to social or sexual stimuli such as (a) a conspecific of the same sex or (b) of the opposite sex, (c) a heterosexual pair or (d) a group of three conspecific females. Moreover, we investigated whether the pattern of lateralisation in *P. formosa*, an all-female clonal hybrid species that originate from hybridisation between *P. mexicana* (maternal ancestor) and *P. latipinna* (paternal ancestor) about 100,000 generations ago (Hubbs & Hubbs, 1932; Schlupp & Riesch, 2011), be similar or different to the parental species. Additionally, we sought to answer further questions: are there differences regarding lateralisation between species? Do closer related species differ from a less related species, the guppy? Do smaller and larger sized individuals of the same sex or species show the same direction preference or do they differ? Do sexes or species differ in latency to approach a social or a (potentially) sexual stimulus?

Since these species naturally live in a similar social environment, the three closely related species (*P. latipinna*, *P. mexicana*, *P. formosa*) were expected to show similar asymmetries-direction preferences while approaching a social-sexual target stimulus (conspecifics of the same or opposite sex or a group of three conspecific females). As *P. formosa* females descended from *P. mexicana* females and *P. latipinna* males, we expected them to behave similarly to their parental ancestors when facing (potentially) sexual target stimuli (*P. latipinna* males or a sexually interacting pair). We expected that fish that are phylogenetically closely related will show similar tendencies in lateralisation. In comparison, *P. reticulata* (as a more distantly related poeciliid species often displaying a more intrusive mating style) were expected to show a different pattern of lateralisation. Due to different motivation in and biological relevance of certain social or sexual contexts in males and females as well as in smaller and larger individuals, we expected to find detour preferences in accordance with clearly pronounced differences in *P. latipinna*, *P. mexicana* as well as in *P. reticulata*. Latency differences were expected in accordance with motivation and biological relevance of a particular stimulus context (*i.e.*, social or sexual context).

2 | MATERIALS AND METHODS

The care and use of experimental animals complied with all relevant local animal welfare laws, guidelines and policies, and the use of animals have undergone an ethical review process. The performed experiments and handling of the fish were in line with the German Animal Welfare Act (Deutsches Tierschutzgesetz) and approved by the internal animal protection commissioner U. Gießelmann, University of Siegen and the national Veterinary Authority (Kreisveterinäramt Siegen-Wittgenstein).

2.1 | Model species

All species used in this comparative study were livebearers without parental care and belongs to the family Poeciliidae (Meffe & Snelson

Jr., 1989). They all live in mixed-sex shoals year round and have the opportunity to observe conspecifics when interacting with each other. *Poecilia latipinna* used in the experiments were wild fish caught from two different natural populations: Coleto Creek (CC), Victoria, Texas, USA and Comal River (CR), New Braunfels, Texas, USA. All male and female sailfin mollies used in experiments were sexually mature. *Poecilia mexicana* used in our experiments were mature adult descendants from a population from Tampico, Mexico, caught in 1995. *Poecilia formosa* females used in our experiments were wild-caught mature individuals from a creek of the Comal River area that were living in close sympatry with *P. latipinna* of the Comal River (CR) population. The *P. reticulata* used in the experiments were wild type-like mature adult descendants from a population from Trinidad, caught by the University of Bielefeld.

2.2 | Housing facilities

All individuals were housed in groups of approximately 75 individuals per species. They were kept in large tanks (80 x 35 x 40 cm^3) filled with aerated, filtered water (conductance: *c.* 250 µs cm^{-1}) at 24 ± 2°C, providing constant environmental conditions (conductivity, temperature and pH). Additionally, tanks were equipped with gravel substrates, plants and several hiding places. There was a 14:10 h light: dark cycle; all experiments were conducted during the day. Food (frozen chironomid larvae, frozen *Artemia* or JBL flake food; www.jbl.de) was provided *ad libitum* 7 days per week. Upon commencement of the experiments, experimental fish were separated in single tanks (40 x 25 x 41 cm^3) providing the same conditions as described above.

2.3 | Experimental setup

All experiments were performed using a similar setup and a similar experimental design as Bisazza *et al.* (1997a,b). Two U-shaped opaque white plastic panels (each 21 x 40 x 20 cm^3) comprising a runway in the middle (7 x 40 x 20 cm^3) were situated in a rectangular tank (100 x 50 x 40 cm^3; Figure 1). Individuals inside the runway could face a transparent barrier at both ends of the runway behind which a target stimulus was located. This barrier (17.5 x 2 x 17 cm^3) consisted of several vertical bars made of translucent yellow plastic straws (0.4 cm in diameter) with 0.2 cm gaps between them and was located in front of the target stimulus. The target stimuli were confined inside a transparent Plexiglas cylinder (11 cm in diameter) and were placed 2 cm behind the barrier. Accordingly, individuals (hereafter referred to as focal fish) were able to observe the target stimulus but had to swim left or right to pass the obstacle in front of it to approach the presented stimulus. An empty Plexiglas cylinder was used for controls. The test tank was filled with water to a depth of about 11 cm. Ceiling mounted fluorescent tubes (18 W) provided an even illumination during all experiments. Between the experiments, the water was purified and re-aerated using an external filter unit. Water was exchanged weekly.

2.4 | General procedure

Prior to experiments, each focal fish was introduced into the test tank for 15 min to become accustomed to the new environment. To begin
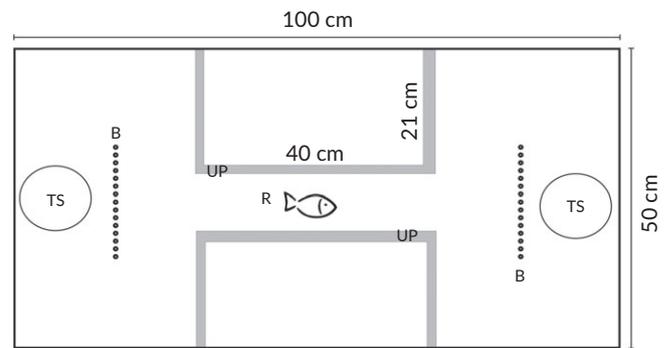

FIGURE 1 Top view of the experimental setup (modified from Bisazza *et al.*, 1997b). Within the rectangular experimental tank, two U-shaped opaque Perspex panels (UP) comprise a runway (R). The transparent barriers (B) at both ends of the runway allowed the focal fish to observe and proceed, alternately in opposite directions, to the 'target stimuli' (TS)

experimental testing and between each trial, the focal fish was gently nudged to enter the runway, which was then blocked at both ends using white opaque plastic boards. On one side, the Plexiglas cylinder confining the target stimulus was introduced by opening this end of the runway. To exclude a side bias in fish due to any possible irregularities of the setup, target stimuli were presented pseudo-randomly at both ends of the runway (Gellermann, 1933). Each focal fish was given 10 trials for each stimulus condition (Section 2.5). The time needed to detour the barrier (latency) and the direction of detour (right or left) were recorded for every individual. A decision was made as soon as the fish's body completely crossed an imaginary line near the barrier (Figure 1). There was a 3 min inter-trial interval to allow a stimulus switch. Moreover, both the position of the two barriers as well as of the target stimulus were alternated between focal fish. Following completion of the experiments, the standard body length (L_S) of each focal fish was recorded (Table 1).

2.5 | Stimulus presentations

There were four different social-sexual stimulus presentations comprising different target stimuli: (a) a single conspecific male, (b) a single conspecific female, (c) a conspecific heterosexual pair and (d) three conspecific females (shoal). An empty Plexiglas cylinder was used as a control (e). Regarding the hybrid species *P. formosa*, a single CR *P. latipinna* male (stimulus condition (a)) and a conspecific, heterosexual CR *P. latipinna* pair (stimulus condition (c)) were used. All individuals serving as target stimuli were randomly chosen from the respective stock tanks and used only once (*i.e.*, in 10 consecutive trials).

2.6 | Data analysis

Lateral asymmetries were analysed by calculating a lateralisation index for each focal fish after Bisazza *et al.* (1997a,b): ((detour to the right − detour to the left)−(detour to the right + detour to the left)) x 100. Positive values would indicate a preference to detour the barrier by turning right (*i.e.*, viewing the stimulus predominantly using the left eye), while negative values would indicate a preference to detour the

TABLE 1 Focal fish species and sex, mean standard body length (L$_S$) ± SD (mm) and their respective mean laterality preference[a] for all four species

Focal fish species	Sex	n	L$_S$ (mean ± SD, mm)	Target stimulus t-values				
				(a) Conspecific male	(b) Conspecific female	(c) Heterosexual conspecific pair	(d) Three conspecific females	(e) Controls (no target stimulus)
P. latipinna CR	Males	15	40.4 ± 6.4	1.472[NS]	0.604[NS]	0.590[NS]	1.293[NS]	0.587*
	Females	15	37.3 ± 3.4	2.697**	2.092[NS]	1.933[NS]	2.808*	0.959[NS]
P. latipinna CC	Males	15	44.7 ± 8.5	1.500[NS]	0.627[NS]	0.688[NS]	1.375[NS]	0.509[NS]
	Females	15	41.8 ± 5.8	2.500*	0.168[NS]	3.361**	2.467*	5.000***
P. mexicana	Males	15	36.3 ± 3.0	−0.269[NS]	0.000[NS]	1.000[NS]	−0.159[NS]	−0.807[NS]
	Females	15	41.5 ± 5.1	0.151[NS]	−1.388[NS]	−1.099[NS]	−1.382[NS]	1.128[NS]
P. formosa	Females	15	55.0 ± 7.3	1.825[NS]	1.047[NS]	1.682[NS]	3.416**	1.622[NS]
P. reticulata	Males	15	16.9 ± 3.3	2.110[NS]	1.468[NS]	0.376[NS]	0.199[NS]	0.000[NS]
	Females	15	25.7 ± 7.6	0.623[NS]	1.004*	0.951[NS]	0.626[NS]	1.974[NS]

CC, Coleto Creek; CR, Comal River.
NS, Not significant; *$P < 0.05$; **$P < 0.01$: ***$P < 0.001$.
Colour coding: Red = Significant preference to turn right, orange = non-significant trend to turn right, blue = significant preference to turn left, light blue = non-significant trend to turn left.
[a]Mean laterality preference = preference to detour the barrier by turning right or left when approaching the target stimulus (a) to (e).

barrier by turning left (*i.e.*, viewing the stimulus predominantly using the right eye). Departures from random choices (0%) were estimated by one-sample two-tailed *t*-tests performed on the mean values of the lateralisation indices. Differences between sexes and species were estimated by Mann–Whitney *U*-tests. Possible correlations between both factors were estimated using Pearson correlation coefficients. Side biases between individuals within a population appeared to mask lateralisation (*i.e.*, one individual consistently turned right and another one always turned left). As this would result in an overall lateralisation index of zero for this species or stimulus condition, potential side biases were additionally analysed using the absolute value (without ± sign) of the lateralisation index (*i.e.*, regardless of the chosen direction) to assess the strength of lateralisation. Furthermore, an ANOVA and a LSD *post hoc* test were performed to reveal using the lateralisation indices (dependent variable) against sex and species (between-subjects-factors). *F*-tests to assess the variance in lateralisation indices were also performed. For all tests, $P_{2-tailed} \leq 0.05$ was regarded significant.

3 | RESULTS

3.1 | Species-specific comparison of lateralisation: species-specific and sex-specific lateralisation indices

3.1.1 | *Poecilia latipinna* Comal River: males and females

At population level, *P. latipinna* CR males did not show a significant lateralisation in any of the stimulus conditions, but a significant left preference in the controls (empty cylinder; one-sample *t*-test: $n = 15$, (a) $P > 0.05$, (b) $P > 0.05$, (c) $P > 0.05$, (d) $P > 0.05$, (e) $P < 0.05$; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations (Figures 2 and 3). *Poecilia latipinna* CR females (population level analysis) significantly preferred to detour the barrier by turning right in stimulus conditions

(a) conspecific male (one-sample *t*-test: $n = 15$, $t = 2.7$, $P < 0.05$) and (d) 3 conspecific females (one-sample *t*-test: $n = 15$, $t = 2.8$, $P < 0.05$; Figure 2 and Table 1). These females also showed a strong tendency to detour the barrier by turning right in stimulus conditions (b) conspecific female (one-sample *t*-test: $n = 15$, $t = 2.1$, $P > 0.05$; Figure 2 and Table 1). They tended to detour the barrier on the right side when presenting a (c) heterosexual conspecific pair (one-sample *t*-test: $n = 15$, $t = 2.0$, $P > 0.05$) and chose indifferently in the control (e) using an empty Plexiglass cylinder (one-sample *t*-test: $n = 15$, $t = 1.0$, $P > 0.05$; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations between 24.7% and 38.3% (Figures 2 and 3).

3.1.2 | *Poecilia latipinna* Coleto Creek: males and females

At population level, *P. latipinna* CC males did not show a significant lateralisation in any of the stimulus conditions nor in controls (one-sample *t*-test: $n = 15$, (a) $P > 0.05$, (b) $P > 0.05$, (c) $P > 0.05$, (d) $P > 0.05$, (e) $P > 0.05$; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations between 30.9% and 41.2% (Figures 2 and 3). *Poecilia latipinna* CC females significantly preferred to detour the barrier by turning right in stimulus condition (a) conspecific male (one-sample *t*-test: $n = 15$, $t = 2.5$, $P < 0.05$; Figure 2 and Table 1) at population level. Moreover, they chose to detour by turning right when being presented with stimulus conditions (c) a heterosexual conspecific pair (one-sample *t*-test: $n = 15$, $t = 3.4$, $P < 0.01$), (d) 3 conspecific females (one-sample *t*-test: $n = 15$, $t = 2.5$, $P < 0.05$), as well as (e) the control using an empty Plexiglas cylinder (one-sample *t*-test: $n = 15$, $t = 5.0$, $P < 0.001$; Figure 2 and Table 1). Contrarily, no preference for turning right or left has been observed in stimulus condition (b) conspecific female (one-sample *t*-test: $n = 15$, $t = 0.2$, $P > 0.05$; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations between 20.9% and 37.2% (Figures 2 and 3).
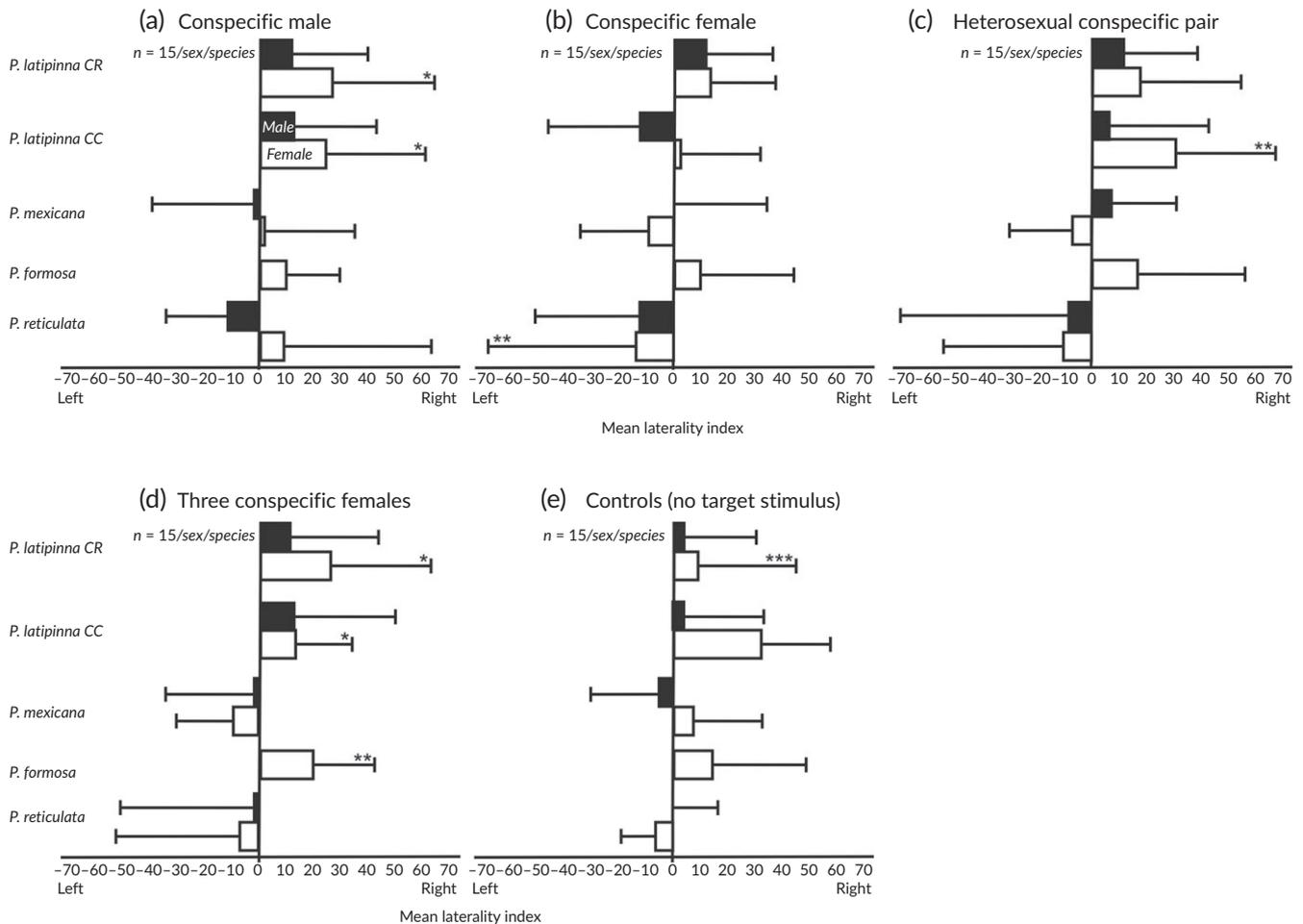
FIGURE 2 Mean lateralization indices (± SD) of *Poecilia* spp. for the different social target or sexual stimuli (a) to (e). Positive values indicate a preference for detour to the right, negative values indicate a preference for detour to the left. CC, Coleto Creek; CR, Comal River. □, Females; ■, males. * P < 0.05; ** P < 0.01; *** P < 0.001

3.1.3 | *Poecilia mexicana*: males and females

In *P. mexicana*, neither males nor females (population level analysis) showed a significant lateralisation in any of the stimulus conditions nor in controls (for each sex; one-sample *t*-test: n_{males} = 15, (a) P > 0.05, (b) P > 0.05, (c) P > 0.05, (d) P > 0.05, (e) P > 0.05; $n_{females}$ = 15, (a) P > 0.05, (b) P > 0.05, (c) P > 0.05, (d) P > 0.05, (e) P > 0.05; Figure 2 and Table 1). There was no difference between sexes observed in this species. However, considerable individual differences were observed, resulting in high standard deviations between 39% between 25.6% and 38.4% in males and 22.4% and 34.2% in females (Figures 2 and 3).

3.1.4 | *Poecilia formosa*: females

In *P. formosa*, individuals (population level analysis) showed no preference to detour the barrier when being presented with stimulus conditions (a) to (c) and in (e) controls (one-sample *t*-test: n = 15, (a) P > 0.05, (b) P > 0.05, (c) P > 0.05, (e) P > 0.05; Figure 2 and Table 1). However, they significantly preferred to detour the barrier by turning right when being presented with stimulus condition (d); *i.e.*, three conspecific females (one-sample *t*-test: n = 15, t = 3.4, P < 0.01; Figure 2 and Table 1). However,

considerable individual differences were observed, resulting in high standard deviations between 19.8% and 39.9% (Figures 2 and 3).

3.1.5 | *Poecilia reticulata*: males and females

At population level, *P. reticulata* males showed a slight trend to detour the barrier by turning left when being presented with stimulus conditions (a) to (c), but no preference in (d) and (e) controls (one-sample *t*-test: n = 15, (a) P > 0.05, (b) P > 0.05, (c) P > 0.05, (d) P > 0.05, (e) P > 0.05; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations between 8.4% and 25.55% (Figures 2 and 3). *P. reticulata* females preferred to detour a conspecific female on the left (b) and tended to detour the barrier by turning leftwards when being presented with stimulus conditions (c) and (e), ((b) P > 0.05, (c) P > 0.05, (e) P > 0.05). In stimulus condition (a) conspecific male and (d) three conspecific females, females showed no preference (one-sample *t*-test: n = 15, (a) P > 0.05, (d) P > 0.05; Figure 2 and Table 1). However, considerable individual differences were observed, resulting in high standard deviations (SD) between 18.3% and 59.5% (mean ± SD; cf. Supporting Information Figure S1).
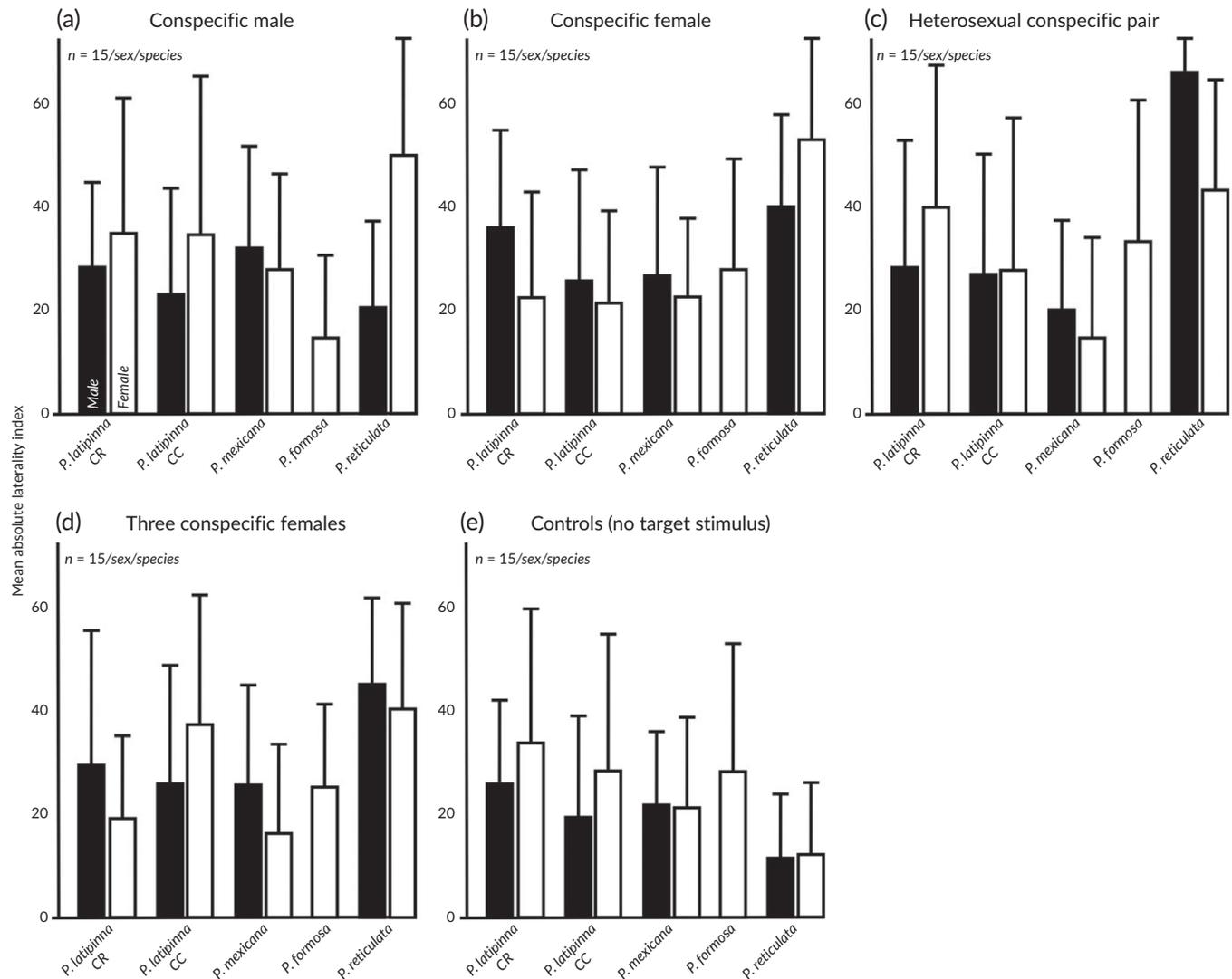
FIGURE 3   Strength of lateralization as mean values of absolute lateralization indices (+SD) independent of direction of *Poecilia* spp. for the different social target or sexual stimuli (a) to (e). CC, Coleto Creek; CR, Comal River. □, Females; ■, males. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

3.2 | Between species and sex comparison: lateralisation indices – power of lateralisation

We found a strong but non-significant preference with respect to sex but not to species in stimulus conditions (a) conspecific male (sex, $F_{3,104} = 2.554$, $P > 0.05$; species, $F_{3,104} = 1.052$, $P > 0.05$) and (b) conspecific female (sex, $F_{3,104} = 3.489$, $P > 0.05$; species, $F_{3,104} = 0.799$, $P > 0.05$; Figure 3).

Although there was no significant effect with respect to sex in stimulus condition (c) heterosexual conspecific pair (*i.e.*, males *v.* females; $F_{3,104} = 0.295$, $P > 0.05$), statistics revealed a significant effect with respect to the tested species (*i.e.*, regardless of sex; $F_{3,104} = 2.808$, $P < 0.05$). Furthermore, in response to stimulus condition (c) heterosexual conspecific pair, ANOVA testing revealed significant differences between females of different species ($F_{3,104} = 3.535$, $P < 0.05$).

There was no difference between sexes observed in any species regarding stimulus conditions (d) three conspecific females (*i.e.*, males *v.* females; sex, $F_{3,104} = 1.173$, $P > 0.05$; species, $F_{3,104} = 0.248$, $P > 0.05$)

and (e) control (species, $F_{3,104} = 1.927$, $P > 0.05$; sex, $F_{3,104} = 0.863$, $P > 0.05$; Figure 3). However, in response to stimulus condition (d) three conspecific females, ANOVA testing revealed significant differences between females of different species ($F_{3,104} = 3.675$, $P < 0.01$).

3.3 | Correlations between body length and lateralisation indices

Several associations between body length, lateralisation indices or latencies have been revealed in stimulus conditions (a) to (d) using Pearson correlation coefficients depending on sex and species. No associations were found in stimulus condition (e) control in any sex or species.

3.3.1 | Conspecific male stimulus

No associations were observed neither in males nor in females of *P. latipinna*, *P. mexicana* or *P. formosa* (Table 2). We found a significant association between L_S and the preferred detour direction (left or right) in *P. reticulata* males. Smaller males preferred to detour the

TABLE 2 Pearson Correlation (R) coefficients and 2–tailed P-value on laterality preference[a] and body length (L_S) for all four species

Focal fish	Sex	n	L_S (mean ± SD, mm)	Target stimulus R–value				
				(a) Conspecific male	(b) Conspecific female	(c) Heterosexual conspecific pair	(d) Three conspecific females	(e) Control (no target stimulus)
P. latipinna CR	Males	15	40.4 ± 6.4	0.150[NS]	0.422 [NS]	−0.196 [NS]	0.567*	−0.359 [NS]
	Females	15	37.3 ± 3.4	−0.190 [NS]	−0.096 [NS]	−0.042 [NS]	−0.266 [NS]	0.046 [NS]
P. latipinna CC	Males	15	44.7 ± 8.5	−0.169 [NS]	−0.322 [NS]	−0.199 [NS]	−0.618*	−0.138 [NS]
	Females	15	41.8 ± 5.8	0.214 [NS]	0.153 [NS]	0.244 [NS]	−0.444 [NS]	0.256 [NS]
P. mexicana	Males	15	36.3 ± 3.0	0.073 [NS]	−0.097 [NS]	−0.692*	0.194 [NS]	−0.236 [NS]
	Females	15	41.5 ± 5.1	−0.103 [NS]	0.409 [NS]	−0.006 [NS]	−0.176 [NS]	0.429 [NS]
P. formosa	Females	15	55.0 ± 7.3	−0.417 [NS]	0.017 [NS]	−0.684**	−0.286 [NS]	0.309 [NS]
P. reticulata	Males	15	16.9 ± 3.3	0.535*	0.524*	0.517*	0.058 [NS]	0.206 [NS]
	Females	15	25.7 ± 7.6	−0.013 [NS]	0.207 [NS]	0.145 [NS]	−0.198 [NS]	0.084 [NS]

CC, Coleto Creek; CR, Comal River.
NS, Not significant; *$P < 0.05$; **$P < 0.01$: ***$P < 0.001$.
Colour coding: red = smaller individuals prefer to turn right, while lager ones prefer to turn left, blue = smaller individuals prefer to turn left, while lager ones prefer to turn right.
[a]Mean laterality preference = preference to detour the barrier by turning right or left when approaching the target stimulus (a) to (e).

barrier by turning leftwards, while larger ones chose to turn rightwards (Pearson correlation: $P < 0.05$; Table 2). No associations were observed in female individuals (cf. Supporting Information Figure S1 and Table 2).

3.3.2 | Conspecific female stimulus

No associations were observed neither in males nor in females of *P. latipinna*, *P. mexicana* or *P. formosa* (Table 2). Smaller *P. reticulata* males preferred to detour the barrier by turning leftwards, while larger ones chose to turn rightwards (Pearson correlation: $R = 0.535$, $P < 0.05$; Supporting Information Figure S2 and Table 2). No associations were observed in female individuals (cf. Supporting Information Figure S1 and Table 2).

3.3.3 | Heterosexual conspecific pair stimulus

No associations were observed in *P. latipinna* (neither males nor females) nor in *P. mexicana* females (cf. Supporting Information Figure S1 and Table 2). In *P. mexicana* males, Pearson correlation coefficients revealed a significant association between L_S and the preferred detour direction (left or right). While smaller males preferred to turn to the left, larger ones preferred to pass the barrier by turning right (Pearson correlation: $R = -0.692$, $P < 0.05$; Supporting Information Figure S2 and Table 2). Similarly, a significant association L_S and the preferred detour direction (left or right) has been observed in *P. formosa* females. While smaller females preferred to turn to the right, larger ones preferred to pass the barrier by turning left (Pearson correlation: $R = -0.684$, $P < 0.01$; Supporting Information Figure S2 and Table 2). In *P. reticulata* males, a significant association between L_S and the preferred detour direction (left or right) was also observed. While smaller males preferred to turn left, larger ones preferred to pass the barrier by turning right (Pearson correlation: $R = 0.517$, $P < 0.05$; Supporting Information Figure S2 and Table 2). No associations were observed in female individuals (cf. Supporting Information Figure S1 and Table 2).

3.3.4 | Three conspecific females stimulus

In *P. latipinna* CC and CR males, we found a significant association between L_S and the preferred detour direction (left or right). Smaller *P. latipinna* CR males preferred to turn to the left, larger ones preferred to pass the barrier by turning right (Pearson correlation: $R = 0.567$, $P < 0.05$; Table 2). Contrarily, smaller *P. latipinna* CC males preferred to turn to the right, while larger ones preferred to pass the barrier by turning left (Pearson correlation: $R = -0.618$, $P < 0.05$; Supporting Information Figure S2 and Table 2). No associations were observed neither in *P. latipinna* females, in *P. mexicana* nor in *P. formosa* females (*cf*. Supporting Information Figure S1 and Table 2).

3.3.5 | Latencies and correlations between latency and lateralisation indices

We found no significant differences in latency to detour the barrier by turning right or left between species or sexes neither in *P. latipinna* CC and CR, *P. formosa* (stimulus conditions (a) to (e)), nor in *P. mexicana* (stimulus conditions (b) to (e); Figure 4). There was only one exception; *P. mexicana* females, which performed significantly faster compared to conspecific males in stimulus condition (a) conspecific male (one-sample t-test: $n = 15$, $t = -2.5$, $P < 0.05$). Although *P. reticulata* individuals appeared to perform faster when approaching a target stimulus, no significant differences were observed neither between males and females nor in comparison with the other three species (stimulus conditions (a) to (e); Figure 4). Pearson correlation coefficients revealed a significant association between latency and the preferred detour direction (left or right) in *P. mexicana* females as larger females needed significantly longer to decide when being presented with stimulus condition (d) three conspecific females (Pearson correlation: $R = 0.670$, $P < 0.01$; Supporting Information Figure S2). No associations were observed neither in *P. mexicana* females, nor in *P. latipinna* or *P. reticulata* (neither males nor females each).
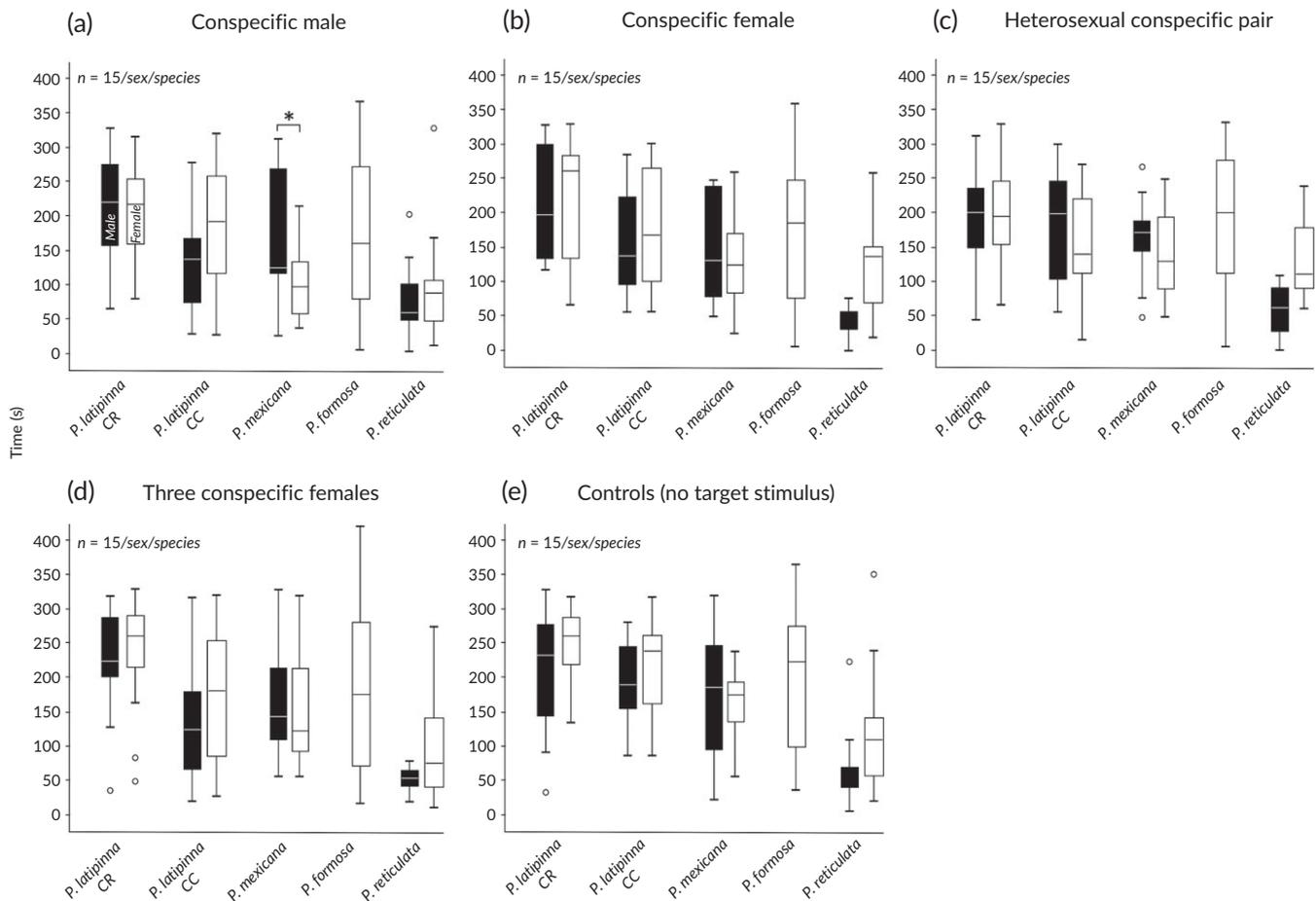
FIGURE 4 Box plots (——, median; □, 25–75th percentiles; ⊤, 95% range; ○, outliers) of mean latencies of *Poecilia* spp. when approaching the different social target stimuli (a) to (e). □, Females; ■, males. * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001

4 | DISCUSSION

We discovered a clear difference in detouring a barrier between females of different poeciliid species. We found a strong but not significant preference with respect to sex when presenting a conspecific male and a conspecific female as target stimuli. While *P. latipinna* CC and CR males generally chose indifferently in all stimulus conditions, *P. latipinna* females of both populations showed a distinct bias to the right (*i.e.*, left-eye preference) when being presented with potentially sexual or social target stimuli (population level analysis) with one exception. The hybrid *P. formosa* females showed no lateralisation, except in one situation: when three conspecific females were presented, they exhibited a significant preference to turn right. Males and females of *P. mexicana* showed no preference for one side in any of the presented social or sexual stimuli. However, the three closely related poeciliid species (*P. latipinna*, *P. mexicana*, *P. formosa*) appeared to have a general tendency to turn right (*i.e.*, left-eye preference) when approaching the target stimuli (cf. Supporting Information Figure S1 and Table 1). Conversely, the more distantly related *P. reticulata* males and females showed an overall bias to the left (*i.e.*, right-eye preference) in response to various social stimuli. Thus, present results (a) possibly suggest a sex-specific functional lateralisation for the analysis of visual information and (b) seem to support the closer ancestral relationships between the mollies tested in this study and

the more distantly related guppies in terms of their left–right lateralisation.

Earlier studies revealed that a predominant eye preference of fishes may vary between species, between populations of the same species, between individuals (Bisazza *et al.*, 2000; Brown *et al.*, 2004; Irving & Brown, 2013) and, also, depending on the social situation, on the fish's motivation (Poecilidae: Bisazza *et al.* 1997b, 1998b; Kaarthigeyan & Dharmaretnam, 2005; Adrianichthyidae: Sovrano, 2004; Melanotaeniidae: Bibost & Brown, 2013) and probably even on the emotive content of the stimuli (Ariyomo & Watt, 2013; Brown & Bibost, 2014; Reddon & Hurd, 2008). In various fish species and particularly in poeciliid species, the direction of a lateral bias was found to depend on the stimulus context when assessing biologically relevant stimuli, suggesting that it is likely to arise as a result of a preference in eye use. These observations coincide with findings of the present study, in which *P. latipinna* CC, CR females and *P. formosa* females exhibited a significant left-eye bias when being presented with three conspecific females. Likewise, *P. latipinna* CC and CR females significantly preferred their left eye by turning rightwards in response to a potentially sexual stimulus (*i.e.*, a conspecific male). *Poecilia latipinna* CC females maintained this preference when being presented with a heterosexual conspecific pair, putatively pointing to sexually motivated mate-choice copying and gathering of public information, respectively, which is known to be very pronounced in

poeciliid fishes. However, this alone does not conclusively explain the significant left-eye bias observed in *P. latipinna* CC, CR females and *P. formosa* females when being presented with three conspecific females (expected to be a non-sexual social stimulus for female focal fish). There was no bias in males in response to any social incitement (population level). Stimuli used in the present study may elicit a certain aggressiveness in the behaviour of males, such that these do not show a bias towards conspecifics of the same sex. Results for females support the idea that lateralisation appears to be influenced by the biological relevance of the presented stimuli, at least in poeciliid females tested in the present study. Furthermore, present results support the impression, that hybrid *P. formosa* females seemed to perform in the same way like *P. mexicana* females, their maternal ancestries.

Nevertheless, although the sexual motivation of the focal fish, its familiarity to the stimulus as well as the classification into sexual and non-sexual social contexts are important and could help to explain some parts of the present results, they do not seem to be the only rational explanations for the present observations. More specifically, being presented with a group of three conspecific females, *B. roseni* and *G. falcatus* showed a significant left-eye-preference, but were observed to predominantly use their right eye when assessing a sexually attractive stimulus (*i.e.*, opposite-sex conspecifics) in both males and females, but only if they were sexually motivated (Bisazza *et al.* 1997a, 1998b; Kaarthigeyan & Dharmaretnam, 2005). *G. holbrooki*, *G. falcatus* and *P. reticulata* males that were observed to resume mating behaviour soon after being introduced to a novel place, showed a right-eye bias when being presented with females as target stimuli. In these studies, considerable differences between males and females were attributed to differences in sexual or social motivation. Potentially sexual stimuli (conspecifics of the opposite sex) induced a strong right-eye bias in male-deprived females that was absent in non-deprived females and all tested males. Females exhibited a left-eye preference when being presented with non-sexual social stimuli (conspecifics of the same sex), which was again absent in males (Bisazza *et al.* 1998b). These results coincide with findings of male and female *P. reticulata* in the present study that appeared to predominantly use their right-eye when approaching a target stimulus.

When motivational factors were properly assessed, different fish species showed lateralisation in the same direction, suggesting that the direction of lateral asymmetries tends to be strikingly similar in closely related species (at least in Poeciliidae; Bisazza *et al.*, 1997b, 1998b, 2000b). In the present study, the most intriguing effects were observed between L_S and the preferred detour direction in *P. latipinna* and *P. mexicana* males as well as in *P. formosa* females in response to particular social stimuli. Smaller individuals decided significantly different from the larger representatives of their species (cf. Supporting Information Figure S1 and Table 1). Depending on the social context, smaller and larger sized individuals of the same species differed in their direction preference, resulting in a change in lateralisation (on the individual level) with its own size (cf. Supporting Information Figure S1 and Table 1). Remarkably, right or left-eye population biases associated with L_S were primarily found in male focal fish in the present study. In two social contexts (*i.e.*, conspecific pair, three conspecific females), smaller focal males (*P. mexicana*, *P. latipinna* CR) significantly preferred to approach the target stimuli by turning left

(right-eye preference), while larger ones detoured the barrier by turning right (left-eye preference). Surprisingly, this pattern was reversed in *P. latipinna* CC males: while smaller males preferred to turn to the right (left-eye preference), preference to pass the barrier by turning left (right-eye preference) was observed in larger ones in the same social context (*i.e.*, three conspecific females). These results could be indicative of a true difference between the *P. latipinna* CC and CR populations used in the present study (although this explanation remains speculative and requires further testing). As the only females in this study, *P. formosa* females also showed an association between body size and lateralisation, thereby again performing in the same way as their maternal relatives. While smaller females significantly preferred to turn right, larger ones preferred to bypass the barrier leftwards when approaching a heterosexual pair. Associative effects were also found in *P. reticulata* males when presenting a conspecific male or female as well as a conspecific pair. While larger males exhibited a significant left-eye preference when facing a conspecific male (*i.e.*, a potential rival), they switched to a significant right-eye preference when approaching a conspecific pair. The reverse (*i.e.*, significant left-eye preference) holds true for smaller males. However, larger *P. reticulata* males maintained their left-eye preference when approaching a single conspecific or a group of three females. The reverse effect was the same in smaller males when approaching a group of three females but appeared to be less pronounced facing a single conspecific female. A significant left-eye bias in response to females as target stimuli was also observed in rather shy poeciliid species (*B. roseni*, *G. falcatus*) when tested in an unknown environment (Bisazza *et al.* 1997b, 1998b). The authors concluded that they may have perceived the females as potential shoal mates rather than as potential mating partners. Furthermore, the described relationship between body size and eye preference in response to particular social incitements may be the result of a possibly different social status within a group.

Lateralisation may enhance (individual) cognitive abilities and more efficient responding in some species and contexts. These advantages of lateralisation at an individual level do not have to be shared implicitly in the same way by the entire population (*i.e.*, same lateralisation pattern in response to particular stimuli). Shoaling is an important anti-predator response in many poeciliid species, such as *P. reticulata* (Magurran & Seghers, 1994) and *P. formosa*, who live in the same habitat and in mixed shoals with *P. mexicana* or *P. latipinna* (McRobert & Bradner, 1998; Schlupp & Ryan, 1996). They typically form mixed-sex shoals comprising 10–20, or even more, individuals (Plath *et al.*, 2005; Seghers, 1974; Witte & Ryan, 2002). The present results (individual analysis) indicate various degrees of lateralisation to one site or the other in individuals of different populations, sex or species and complement observations on other shoaling fish species. Various degrees of lateralisation within a shoal would be a favourable feature as it allows faster responses to predators and prey on the periphery of the shoal and rapid responses to the behaviour of shoal mates (Brown, 2005; Vallortigara & Rogers, 2005). Thus, it appeared to be conclusive to find considerable individual differences in response to different social stimuli in all species. In the present study, distinct differences were observed on an individual level within the same sex of the same species and within the same sex between

different species (cf. Supporting Information Figure S1). These remarkable individual differences could possibly also help to explain the association between body size, detour behaviour and behaviour within the shoal (feeding, defensive, agonistic). Prior to experiments, all focal individuals of the present study were housed in groups of approximately 75 individuals per species and only separated into single tanks upon commencement of the experimental testing. In natural environments, it has been observed that dominant and bolder individuals become larger, directly or indirectly suppressing growth of smaller, subdominant individuals within their home shoal (Archard & Braithwaite, 2011; Brown & Braithwaite, 2004; Godin & Dugatkin, 1996). Similar social behaviour or dominance hierarchies could potentially have evolved in the tested individuals held under laboratory conditions. Social information (and the corresponding target stimuli abstracting different social contexts) could possibly be classified differently regarding their biological relevance and, consequently, the individual's appropriate response. Apparently, social stimuli providing potentially sexual information (*e.g.*, males tested with conspecific females or *vice versa* or a conspecific pair as target stimuli in a detour task) triggered a right-eye bias in females (*P. latipinna* CR, CC, *P. formosa*) as well as smaller males (*P. reticulata*, *P. mexicana*, *P. latipinna* CR) but virtually not in larger males. Thus, correlational results for males provide compelling evidence that lateralisation depends on the biological relevance of the stimulus.

In conclusion, the present study's population-level analysis showed distinct sex differences regarding visual lateralisation in four different poeciliids in response to target stimuli abstracting several different social or sexual contexts. These sex differences were observed particularly in both *P. latipinna* populations, while the other poeciliids showed less pronounced sex-specific preferences. Furthermore, considerable individual differences (*i.e.*, lateralisation pattern in response to particular stimuli) were observed across sexes and species, which are possibly related to the sexual motivation of the focal fish, its familiarity to the stimulus or shoaling. Moreover, intriguing associative effects have been discovered between L_S and the direction of lateralisation in males of all tested species, suggesting a correlation of L_S and the direction of lateralisation in males of all tested species. These effects may indicate differently pronounced motivation in and biological relevance of certain social contexts in smaller and larger individuals. Nevertheless, further analyses of ecological factors shaping lateralisation at both the individual and population level is needed. Lateralisation at the level of individuals should also be examined with regard to alternative life-history strategies (*e.g.*, sneaker males in *P. reticulata* and other poeciliids). Observation of strongly and weakly lateralised fishes occupying the same habitat in conjunction with the study of the neural substrate of lateralisation in the fish brain may explain above behaviour in more detail.

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