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Original Article

Body size, mating system, and ecology interact to shape behaviour and cognition in two syntopic pairs of poeciliid fish

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ABSTRACT

Female traits often covary with male mating tactics. In single-tactic mating systems, males show a restricted range of phenotypes. In contrast, in mixed-tactic species, males vary in behaviour, size, and coloration. The consequences of such differences in mating system for female behaviour and cognition are poorly understood. Poeciliid fish are an excellent clade for addressing this question: males of some species have exclusively forced mating (all-coercive), whereas others (mixed-tactic) also display or defend territories. We compared exploration, shyness, social motivation, and cognitive flexibility in two syntopic species pairs: all-coercive *Gambusia affinis* and mixed-tactic *Poecilia latipinna* (Texas), and all-coercive *Pseudopoecilia fria* and mixed-tactic *Poecilia gilli* (Ecuador). Species differed by mating system in social motivation, exploration, and inhibitory control at each location. However, directionality diverged from studies in predator-free conditions. All-coercive taxa were more exploratory and socially motivated in both pairs and more cognitively flexible in the Ecuadorian pair. Relationships between shyness, mating system, and body size contrasted between the locations, implicating ecology. General linear models revealed size and location to supersede mating system in explaining trait variation. We show that mating system alone cannot explain species-level variation in female behaviour and cognition, and we discuss factors, such as predation regime, that might also shape traits.

Keywords: male mating tactics; cognition; social complexity; alternative reproductive strategy; coercive mating; sexual conflict; sexual selection; Poeciliidae; Poecilia; Gambusia; multifarious selection

INTRODUCTION

Across diverse species, male mating tactics have been shown to influence the diversification of female morphological, physiological, and behavioural traits on both developmental (Queller *et al.* 2022, 2023, Thakur *et al.* 2025) and evolutionary (Gavrilets 2000, Bonduriansky 2011, Brennan and Prum 2015) time scales. Male mating tactics fall along a continuum from intersexual cooperation to conflict, ranging from displays, in which males use elaborate ornaments to elicit female receptivity (e.g. Carranza *et al.* 1990, Johnson *et al.* 2000, Mitoyen *et al.* 2019), to uncooperative coercive mating, in which males attempt to mate with females regardless of their receptivity (Arnqvist and Rowe 1997). Courtship requires female attraction and cooperation to result in successful mating. In contrast, coercive mating allows males to circumvent precopulatory female choice by performing sneak copulations or physically manipulating females into mating (Muller *et al.* 2011, Burke and Holwell 2021, Snow and Prum 2023). The types of male mating tactics that females experience have profound consequences for the expression of female choice (Snow *et al.* 2019, Smit 2025) and are important in shaping female behavioural responses.

From the female perspective, mating systems can also differ in their level of social complexity or in the range of interactions and number of distinct social phenotypes that individuals experience (Kappeler *et al.* 2019, Peckre *et al.* 2019). In a variety of vertebrate species, males show alternative reproductive tactics, which can manifest as discrete morphs or as a broad phenotypic continuum of mating behaviours (Taborsky *et al.* 1987, Neff *et al.* 2003, Brockmann and Taborsky 2008, Shuster 2010, Noble *et al.* 2013). Such systems are thought to place higher cognitive demands on females,

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because they must learn to distinguish and respond appropriately to a wide range of male mating tactics (Cummings and Ramsey 2015) that vary in their costliness to females (Thirgood 1991, Chapman *et al.* 2003, Plath *et al.* 2007, Yang *et al.* 2023). At the other end of the social complexity spectrum, males exhibit a narrow range of phenotypes, such as in lekking birds with exclusive male display (Kokko *et al.* 1999, Reynolds *et al.* 2009) or in mammals, insects, and fish with exclusive male coercion (e.g. Galimberti *et al.* 2000, Bisazza *et al.* 2001, Estrada *et al.* 2010). In such 'single-tactic' systems, females need only learn and respond to a single type of male interaction, potentially lowering demands on cognitive processes involved in female decision-making but also placing a premium on adaptive behavioural responses to whatever male mating tactic they repeatedly encounter (Cummings 2018).

Teleost fishes in the family Poeciliidae show extensive variation in the social complexity of mating systems from the female perspective. The majority of poeciliid species have single-tactic mating systems in which males exclusively coerce females into mating (Magurran 2011). Males of these species usually have long intromittent organs (gonopodia) relative to their body length, lack sex-specific ornamentation, and are smaller in size than females (Bisazza and Marin 1995, Langerhans 2011). In contrast, some poeciliid species have evolved mixed-tactic mating systems in which all males perform both courtship and coercion (e.g. guppies, *Poecilia reticulata*) or have alternative reproductive male phenotypes with discrete sets of mating tactics (e.g. courtship only, coercion only, or both coercion and courtship) (Ryan and Causey 1989, Bisazza 1993, Erbelding-Denk *et al.* 1994, Liotta *et al.* 2019). In mixed-tactic systems, females can exercise precopulatory mate choice and are not exclusively subject to coercion. Because females must learn and respond appropriately to a wider range of behavioural and morphological phenotypes, these mating systems represent higher social complexity for females (Cummings and Ramsey 2015).

Developmental and comparative studies have begun to identify female behavioural and cognitive traits that covary as a function of male mating tactic diversity. Much of this work has been conducted in teleost fishes of the family Poeciliidae. Socially controlled rearing experiments with alternative male reproductive phenotypes of the swordtail fish *Xiphophorus nigrensis* suggest that male mating tactics can play a role in the development of female boldness and aggression (Queller *et al.* 2022), spatial cognition (Queller *et al.* 2023), and stress coping styles (Thakur *et al.* 2025). *Xiphophorus nigrensis* females reared in coercion-only environments are less bold (Queller *et al.* 2022) and are better at spatial learning than females raised with a mix of tactics (Queller *et al.* 2023). However, other work has shown that females raised with coercive males do not have higher cognitive flexibility (as measured with reversal learning) or spatial learning ability relative to females raised in isolation (*Poeciliopsis gracilis*; Ernst *et al.* 2024).

Further study examining related female traits across four poeciliid fish species from predator-free populations revealed that female activity, exploration, and cognitive flexibility covaried with mating system (Inman *et al.* 2024). Specifically, females from the two all-coercive poeciliid species showed lower cognitive flexibility (in the form of inhibitory control) and reduced movement in both threatening and non-threatening contexts than females experiencing a combination of male tactics (Inman *et al.* 2024). The higher cognitive flexibility observed in mixed-tactic species was largely consistent with predictions about the consequences of social complexity for cognitive abilities and aligns with comparative work across taxa such as birds and primates (Amici *et al.* 2008, Audet *et al.* 2023). Given that reduced movement increases the efficacy of crypsis in threatening antipredator contexts (Ioannou and Krause 2009, Yilmaz and Meister 2013, van Bergen and Beldade 2019), movement reduction in females of all-coercive species might help females to evade detection in the face of harassment by coercive males. General cognitive processes might also be impacted by changes in the rate of coercive mating tactics relative to cooperative or courtship tactics. Artificial selection for longer gonopodia, which increase the efficacy of sexual coercion, in the all-coercive *Gambusia holbrooki* resulted in larger relative brain size in females (Booksmythe *et al.* 2016, Buechel *et al.* 2016, but see Culumber *et al.* 2020).

Mating system is not the only force that can shape behavioural and cognitive traits. For instance, predation is an important driver of diversification in behaviour and cognition (Huntingford 1976, Bell and Sih 2007, Mikolajewski *et al.* 2010, Heinen-Kay *et al.* 2016). In particular, natural selection from predators has been shown to affect movement patterns in a variety of systems. For instance, tadpoles experiencing higher predation risk move less (Richardson 2001), and less mobile anuran tadpoles show higher survival in the presence of predators (Lawler 1989, Azevedo-Ramos *et al.* 1992). Likewise, in damselfly larvae, higher predation risk consistently results in lower activity (Brodin and Johansson 2004, Strobbe *et al.* 2011, Swaegers *et al.* 2017). Predation risk also alters escape behaviour in rodents, leading to elevated or reduced movement, depending on species and habitat type (Edut and Eilam 2003, Eilam 2005). In addition to movement behaviours, predation risk can shape cognitive abilities, such as recognition (Ferrari *et al.* 2008, Ferrari 2014) and spatial memory (Brown and Braithwaite 2005, Heathcote *et al.* 2023). Theory suggests that cognitive flexibility might be favoured in the face of higher predation risk because animals must respond appropriately to predator cues and shift rapidly between vigilance and routine tasks, such as foraging or mating (Lima and Dill 1990, Sih and McCarthy 2002), and the few studies testing this prediction have shown that early-life experience of predation risk increased cognitive flexibility (Vila Pouca *et al.* 2021). Coarse proxies for cognitive ability, such as brain size, have also been shown to be correlated with adaptive antipredator behaviour. Selection from predators has been shown to favour larger brain size in female guppies (Kotrschal *et al.* 2015, 2017) but smaller brains in male Trinidadian killifish (Walsh *et al.* 2016). In guppies, females adjusted their copulation rate according to predation threat only if they were artificially selected for larger brains (Corral-López *et al.* 2017, 2020).

Although both predation and mating system have been implicated in shaping movement patterns and cognition independently, the weight of evidence for the role of mating system comes largely from captive fish populations that have lacked predators for multiple generations (Queller *et al.* 2022, 2023, Ernst *et al.* 2024, Thakur *et al.* 2025, Inman *et al.* 2024). Specifically, studies examining the impact of sexual selection on behavioural trait variation often examine it in isolation or they fail to acknowledge covariation between mating system dynamics and ecology in nature. Meanwhile, studies of natural selection on behaviour and cognition often generalize across populations or species without including mating system as a covariate. In the wild, trait variation often reflects a balance between divergent natural and sexual selection

(Maan and Seehausen 2011, Cummings and Crothers 2013) and can result in trade-offs across populations when the direction of one form of selection opposes the other (Gustafsson *et al.* 1995, Langerhans *et al.* 2005). Behavioural ecologists therefore would benefit from a clearer understanding of how multifarious sources of selection in the wild interact to shape behavioural evolution. A first step towards this broader goal requires us to understand whether the same sexual selection dynamics have similar effects on behaviour and cognition across different environments.

Here, we ask whether patterns attributed to mating system in movement and cognitive ability in predator-free populations (Queller *et al.* 2022, 2023, Inman *et al.* 2024, Thakur *et al.* 2025) persist in wild populations experiencing predation. We attempt to answer this question by also investigating whether variation in the mating system (coercion-only vs. multiple male tactics) affects behaviour and cognition in a similar manner in wild female poeciliids between two widely separated locations with different predator communities. As in a previous study (Inman *et al.* 2024), we compare female cognitive and behavioural traits from two all-coercive poeciliid species and two mixed-tactic poeciliid species. However, in the present study, we collect females from natural populations where they are subject to both natural and sexual selection pressures. At each location, we compare species that represent different mating systems yet inhabit the same microhabitat (syntopic pairs). We investigate whether mating system variation from all-coercive to mixed-tactic would also result in: (i) reduced movement in all-coercive species; and (ii) increased cognitive flexibility in mixed-tactic species across two very different geographical and ecological contexts (Texas, USA vs. Ecuador; Fig. 1).

The first pair we examine consists of *Poecilia latipinna* and *Gambusia affinis* from Brushy Creek, a tributary of the Brazos River in central Texas (Fig. 1). *Poecilia latipinna* has a mixed-tactic mating system, with different male size classes that engage in different rates of courtship and coercion (Farr *et al.* 1986). Large males are colourful, possess an especially large dorsal fin (sailfin), and perform elaborate courtship displays that allow for female choice (Snelson 1985, Travis and Woodward 1989). In contrast, small males have reduced ornamentation, show lower courtship rates (Farr *et al.* 1986), and mate indiscriminately (Woodhead and Armstrong 1985, Sumner *et al.* 1994). Female *Poecilia latipinna* prefer to mate with large males (Schlupp *et al.* 1994, Ptacek and Travis 1996) and preferentially associate with them in a social context (Gabor 1999). In contrast, *G. affinis* has an exclusively coercive mating system, in which males frequently harass females and perform sneak copulations (Farr 1989, Smith 2007, Deaton 2008). *Gambusia affinis* has limited male size variation, female-biased sexual size dimorphism, and the males have long gonopodia relative to standard length (Furness *et al.* 2019).

The second syntopic species pair consists of *Poecilia gilli* and *Pseudopoecilia fria* from the Rio Atacames watershed in the Esmeraldas province, Ecuador, where *Poecilia gilli* was introduced 5 years before this study (Fig. 1; Jimenez-Prado *et al.* 2015). Preliminary observations of *Pseudopoecilia fria* suggest that males and females engage primarily in agonistic interactions, including frequent male harassment of females, fast chases, and behind approaches typical of all-coercive mating systems (Bisazza 1993). In contrast, *Poecilia gilli* exhibits size-specific male mating tactics like its congener, *Poecilia latipinna* (Furness *et al.* 2020). Larger males do not actively chase females and instead are thought to mate primarily with receptive females on their home territories, whereas smaller males chase and harass females at a higher rate (Furness *et al.* 2020).

To quantify the effects of mating system on female behaviour and cognition, we assessed shyness–boldness attributes (including shyness, immobility, and exploration in a threatening environment), social motivation, and inhibitory control as a measure of cognitive flexibility. We hypothesize that taxa experiencing exclusive male coercion will have higher female social motivation (the tendency of an individual to approach a female conspecific) (Balshine *et al.* 2017). Social aggregation among poeciliid females has been shown to dilute the risk of male harassment (Pilastro *et al.* 2003, Dadda *et al.* 2005, Dadda 2015). We hypothesize that high rates of male harassment in all-coercive mating systems will favour lower female exploratory behaviour in threatening environments (stress movement) as a means of evading detection (as found in other poeciliid species inhabiting predator-free conditions; Inman *et al.* 2024). We also hypothesize that the mating system will have an influence on cognitive flexibility, or the ability to reconfigure responses to stimuli in order to adjust to shifting task demands (Badre and Wagner 2006). We assess a type of cognitive flexibility known as inhibitory control, which is the ability of an individual to inhibit a prepotent response in favour of a deliberate, goal-directed one (van Horik *et al.* 2018). In this task, individuals low in cognitive flexibility might persist in certain prepotent behaviours (such as remaining at the transparent barrier, rather than moving around the barrier to access the social reward), whereas more cognitively flexible individuals are able to adopt new strategies that lead to a solution (Thompson *et al.* 1989, Lucon-Xiccato and Bisazza 2017). We expect more complex mating systems, in which females must differentially recognize and respond to a wider range of male phenotypes and tactics, to require higher cognitive flexibility (including inhibitory control) (Cummings and Ramsey 2015). This prediction is consistent with comparative and developmental work on different facets of cognitive flexibility in fish, in addition to birds and mammals (Bond *et al.* 2007, Amici *et al.* 2008, Inman *et al.* 2024, Triki *et al.* 2024, but see MacLean *et al.* 2014). Lastly, if predation has a greater influence on trait development than mating system dynamics, we expect to see strong differences between locations, in addition to an effect of body size (because predation pressure can scale with prey body size).

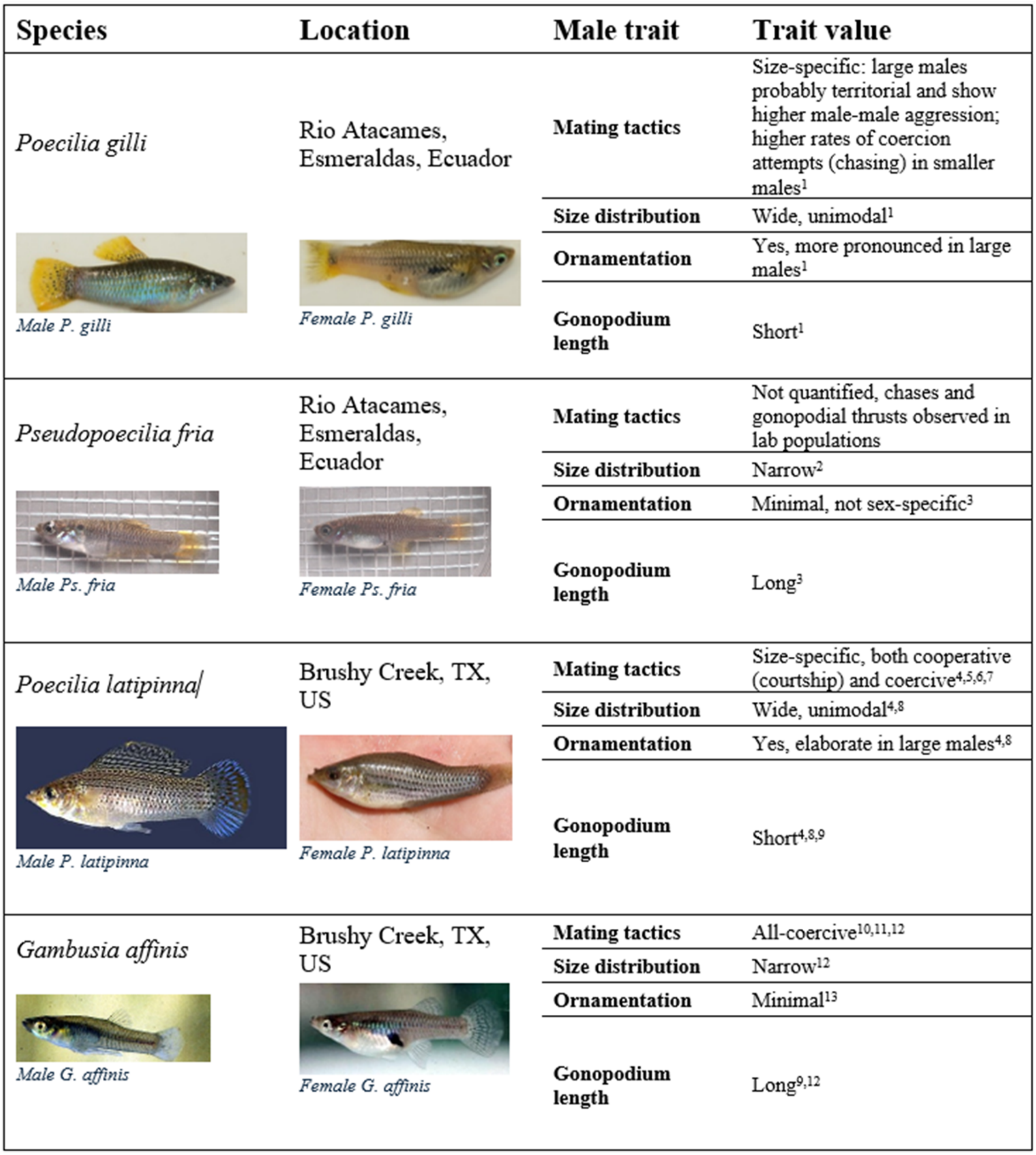
MATERIALS AND METHODS

Collection of Brushy Creek syntopic pair

To assay the first syntopic species pair, we collected 30 adult female *Poecilia latipinna* and 30 adult female *Gambusia affinis* in May 2022 using a seine and dip nets from shallows along the southern shore of Brushy Creek in Round Rock, Williamson County, TX, USA (30.512555, −97.694888). Fish were subsequently transported to J.T. Patterson Labs at The University of Texas at Austin, where they were housed in species-specific community tanks. Fish were fed a diet of Cargill and TetraMin flakes once daily. Each community tank included a bubbler attached to a sponge filter, generating flow. Water was kept at a constant temperature of 25.6°C.

Site characteristics

The Brushy Creek habitat exhibits high structural complexity in vegetation and depth on a small spatial scale, having multiple channels separated by shoals and islands. In addition to the two



Species	Location	Male trait	Trait value
Poecilia gilli *Male P. gilli*	Rio Atacames, Esmeraldas, Ecuador *Female P. gilli*	**Mating tactics**	Size-specific: large males probably territorial and show higher male-male aggression; higher rates of coercion attempts (chasing) in smaller males[1]
		Size distribution	Wide, unimodal[1]
		Ornamentation	Yes, more pronounced in large males[1]
		Gonopodium length	Short[1]
Pseudopoecilia fria *Male Ps. fria*	Rio Atacames, Esmeraldas, Ecuador *Female Ps. fria*	**Mating tactics**	Not quantified, chases and gonopodial thrusts observed in lab populations
		Size distribution	Narrow[2]
		Ornamentation	Minimal, not sex-specific[3]
		Gonopodium length	Long[3]
Poecilia latipinna *Male P. latipinna*	Brushy Creek, TX, US *Female P. latipinna*	**Mating tactics**	Size-specific, both cooperative (courtship) and coercive[4,5,6,7]
		Size distribution	Wide, unimodal[4,8]
		Ornamentation	Yes, elaborate in large males[4,8]
		Gonopodium length	Short[4,8,9]
Gambusia affinis *Male G. affinis*	Brushy Creek, TX, US *Female G. affinis*	**Mating tactics**	All-coercive[10,11,12]
		Size distribution	Narrow[12]
		Ornamentation	Minimal[13]
		Gonopodium length	Long[9,12]

Figure 1. [1]Furness *et al.* 2020, [2]Jiménez-Prado *et al.* 2020, [3]Jimenez-Prado *et al.* 2015, [4]Farr *et al.* 1986, [5]Travis and Woodward 1989, [6]Ptacek and Travis 1996, [7]Becker *et al.* 2012, [8]Snelson 1985, [9]Pollux *et al.* 2014, [10]Peden 1972, [11]Hughes 1985, [12]Deaton 2008, [13]Casner *et al.* 2016. *Poecilia gilli* male and female images courtesy of iNaturalist © Eric van den Berghe, CC BY-NC 4.0. *Pseudopoecilia fria* male and female images courtesy of Leo Ávila. *Poecilia latipinna* male image courtesy of Wikipedia user Anthony DiPierro, Public Domain. *Poecilia latipinna* female image courtesy of iNaturalist © geosesarma, CC BY 4.0. *Gambusia affinis* male image courtesy of Wikipedia user NOZO, CC BY-SA 3.0. *Gambusia affinis* female image courtesy of Wikipedia user Toniher, Public Domain.

focal species, the adjacent deeper waters are occupied by a variety of piscivorous fish species, including one species of catfish (*Ictalarus punctatus*), three species of bass (*Micropterus treculii, Micropterus salmoides*, and *Micropterus dolomieu*), and six species of sunfish (*Lepomis macrochirus, Lepomis microlophus, Lepomis auritus, Lepomis gulosus, Lepomis cyanellus*, and *Lepomis aquilensis*) (Hendrickson and Cohen 2022). The area is also visited frequently by wading birds (*Butorides viridescens, Nyctanassa violacea, Ardea alba, Ardea herodias*, and *Egretta thula*), all of which have been observed foraging in nearby shallows. Although we have not quantified mortality rates of poeciliids from predators, the diversity of piscivorous fish and bird species is high. Thus, we characterized this location as 'high predation'.

Collection of Rio Atacames syntopic pair

For testing the Rio Atacames species pair on the battery of assays, we collected 29 adult female *Pseudopoecilia fria* and 31 adult female *Poecilia gilli* from two locations in close proximity along Rio Atacames in Esmeraldas, Ecuador (0.6977537, −79.8376472 and 0.7419822, −79.8452314) in December 2022. After collection, fish were transported to an outdoor laboratory space in Tonsupa, Esmeraldas, Ecuador, where they were housed in species-specific community tanks. Fish were fed a diet of Cargill and TetraMin flakes once daily, and each community tank included a bubbler attached to a sponge filter to generate flow. Water was kept at a constant temperature of 25°C.

Site characteristics

The species were collected in a single-channel waterway that is low in overall structural complexity and underwater vegetation, but high in turbidity in low-flow stretches. Here, the two poeciliids coexist with a piscivorous characid (*Eretmobrycon ecuadorensis*) and two piscivorous cichlid species (*Andinoacara blombergi* and *Oreochromis niloticus*) in a fish community that is low in overall species diversity (Jiménez-Prado and Vásquez 2021). Avian predator data are not available for Rio Atacames, but various species of ardeids similar to those found at Brushy Creek have been recorded at the sites.

Behavioural and cognitive testing

Fish collected at Brushy Creek were acclimated to laboratory conditions in Patterson Labs at UT Austin for ≥1 week prior to social isolation. Fish collected at Rio Atacames were acclimated to outdoor laboratory conditions on a covered patio in Tonsupa, Esmeraldas, Ecuador. Following this acclimation period, fish were socially isolated for 3 days prior to testing. Fish could interact with individuals in neighbouring isolation tanks (via a shared transparent or mesh tank wall), but only one individual was present in each tank. Following the acclimation period, we tested individual fish on a cognitive flexibility (detour reaching) assay and a scototaxis assay (Fig. 2). To reduce the potential carryover effects of a stressful assay on behaviour in a subsequent assay (Bell 2013), we arranged assays in order of least stress-inducing to most stress-inducing: detour reaching assay (first) and scototaxis (second), with each fish spending 3 days in social isolation between the two assays. We reasoned that the detour reaching assay is the less stressful assay because of the presence of visible female conspecifics and that the scototaxis assay is the more stressful assay owing to the well-documented aversive properties of brightly lit environments for a broad range of fish species (Maximino *et al.* 2010) and the lack of female conspecifics. We assayed all 57 fish from Brushy Creek between June and August of 2022 and all 48 fish from Rio Atacames in December of 2022.

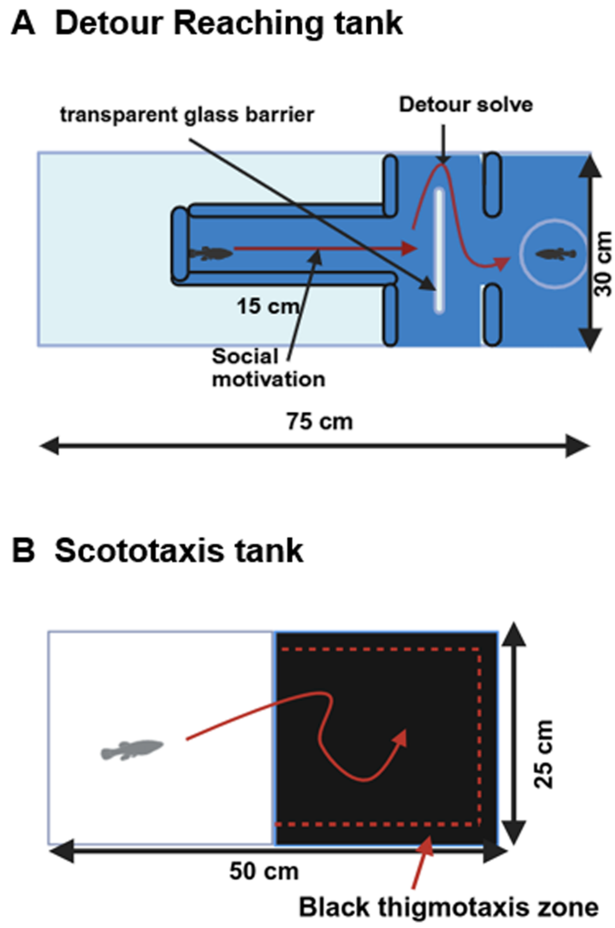


Figure 2. Diagrams of the detour reaching assay tank (A) and scototaxis assay tank (B). In A, we use the latency to approach the glass barrier (within 2 cm) as our measure of 'social motivation'. We calculated detour solve time as the latency to enter the reward zone after initial approach to the glass barrier. In B, we measured the following three behaviours: shyness (time spent in the black thigmotaxis zone), as time spent within 2 cm of the black zone edge; exploration in a threatening environment (i.e. stress movement), as the total distance moved (in centimetres) throughout the assay; and immobility, as the total time (in seconds) spent motionless during the assay.

Detour reaching

We used a detour reaching task to measure both social motivation and cognitive flexibility (Fig. 2A). We measured inhibitory control as a component of cognitive flexibility, or the ability to shift attention and behavioural responses according to new contingencies (Badre and Wagner 2006). Inhibitory control specifically refers to the ability to inhibit a pre-existing response to a stimulus according to new information (van Horik *et al.* 2018). To complete the detour reaching task, fish must inhibit their initial impulse to keep moving forwards through the barrier and circumnavigate it instead (Fig. 2A). We began the assay by placing a larger-than-average conspecific female reward fish in a transparent glass cylinder on the opposite end of the tank from the runway. A larger-than-average stimulus fish was chosen to ensure that it was always visible to the focal fish. We placed the focal fish behind a blue-felted habituation barrier 10 cm from the end of the runway and ~42 cm away from the reward fish on the opposite side of the glass barrier (Fig. 2A). The focal fish underwent a 5 min habituation period behind the felted barrier. To start each trial, the barrier was removed, and the focal fish was recorded for a 10 min observation period using a Nikon D3300 camera.

Detour video recordings were hand-scored by undergraduate students, unaware of the objectives of the study, for two measures: latency to engage with glass barrier and solve time. We measured latency to engage with the glass barrier as our measure of social motivation and calculated it as the time it took each focal fish to travel from the start position (release from habituation) to the glass barrier (within 2 cm; see Fig. 3) or to turn its body fully parallel to the glass barrier after exiting the habituation alley. We measured detour solve time as the time it took each fish to travel from the glass barrier to the reward zone (defined as more than half of its body passing through the reward zone entryway).

Scototaxis

The scototaxis assay simulates exposed and sheltered areas through a tank divided into bright (white) and dark (black halves), respectively. This assay has been used to assess shyness–boldness attributes across a number of small fish species. These species, including poeciliids, consistently show aversive responses to bright light and spend more time in the black zone (Maximino *et al.* 2010). To begin each trial, we placed the focal fish in the middle of the tank (Fig. 2B) between a black barrier and a white barrier for a 5 min habituation period (not shown in the figure).

Following habituation, we removed the barriers, and we began video recording for a 10 min period. After each individual trial, we completed a full water change of the scototaxis tank.

We used Ethovision XT15 to quantify time spent in different areas of the tank, distance moved throughout the tank, and time spent immobile over the course of the assay. We used the scototaxis assay to assess three traits: (i) shyness; (ii) freezing (immobility); and (iii) exploratory behaviour under threat ('stress movement'). To assess shyness, we measured the amount of time spent in the most sheltered part of the tank, the black thigmotaxis zone. To assess immobility (a proxy for freezing behaviour), we measured the total time spent immobile (defined as a <4% change in the orientation of an animal's body from one sample to the next). Lastly, we evaluated total distance moved divided by the standard length of the focal fish as a measure of exploration in a threatening environment. This metric is distinct from a more general activity measure that is customarily measured in a non-threatening context (Dingemanse *et al.* 2007, Réale *et al.* 2007, Etheredge *et al.* 2018, Inman *et al.* 2024).

Statistical analysis

We analysed behavioural and cognitive data using R v.4.2.0 (R Core Team 2025). According to results from Shapiro–Wilk tests, none of the behavioural and cognitive variables measured across species were normally distributed. We therefore used non-parametric Wilcoxon rank-sum tests for comparisons between species with divergent mating systems at each location. We then explored how mating system, location, and body size influenced behavioural and cognitive trait variation by constructing a set of general linear models (GLMs). We included absolute body size (standard length) as a variable because it has been shown to be sensitive to predation pressure in poeciliids (Rosenthal *et al.* 2001, Basolo and Wagner 2004, Brown and Braithwaite 2004), and species and individuals varied significantly in standard length (Fig. 3A). We also included a relative body size measure (relative standard length) as a proxy for age because female poeciliids have indeterminate growth (Hughes 1986, Vargas and de Sostoa 1996), and age might influence behaviour and learning ability independently of absolute size (Kodric-Brown and Nicoletto 2001, Leris and Reader 2016). We calculated 'relative standard length' by subtracting the mean standard length of each species from the standard length of each individual. Negative values represent shorter standard lengths (younger individuals) relative to the species mean, and positive values represent longer standard lengths (older individuals).

To evaluate how location, mating system, body size, and age influenced variation in behaviours across all four species, we constructed a full GLM consisting of the following: behaviour ~ absolute standard length × location + mating system × location + relative standard length. All terms within the interaction were also evaluated as separate fixed effects. Therefore, our model included five fixed effects and two interactions. Behaviours evaluated included those measured during scototaxis: exploration in a threatening environment (stress movement), immobility (freezing), and time in black thigmotaxis zone (shyness), in addition to a social motivation proxy measured in detour (latency to glass barrier).

To evaluate how location, mating system, body size, age, and behavioural tendencies (social motivation, stress movement, freezing) influenced variation in cognitive flexibility across all four species, we constructed a full GLM consisting of: detour solve time ~ detour latency to barrier + distance moved + time immobile + relative standard length + absolute standard length × location + mating system × location. After logarithmically transforming the variables to fit a Gaussian distribution, we used the 'dredge' function in the R package MuMIn to rank all possible models for each behavioural and cognitive response variable by AICc, or Akaike's Information Criterion corrected for small sample sizes (Bartoń 2025). The best-fitting model for each response variable had the lowest AICc (Table 1), and for each best-fitting model we assessed the significance of fixed effects using either ANOVA type 2 or type 3 tests depending on the presence or absence of interaction terms.

RESULTS

Pairwise comparisons of measured traits across syntopic species pairs revealed species-level differences at each location in social motivation (Fig. 3B), cognitive flexibility (Fig. 3C), exploration in a threatening environment (Fig. 4A), immobility (Fig. 4B), and shyness (Fig. 4C). Social motivation (latency to engage with barrier in detour task) was the only trait with species-level differences that fitted predictions based on previous studies. Females of the all-coercive species approached conspecific females faster than females from mixed-tactic species at Brushy Creek (Fig. 3B; Wilcoxon test, $W = 125.5$, $P = .003$). In contrast, species-level differences in cognitive flexibility at Rio Atacames (Fig. 3C) and exploration at both locations (Fig. 4A) were opposite to the pattern observed in predator-free populations from other poeciliids (Inman *et al.* 2024; Supporting Information, Fig. S1). Specifically, females from the all-coercive mating system (*Pseudopoecilia fria*) were significantly faster at solving the detour task than females from the mixed-tactic species (*Poecilia gilli*; Fig. 3C; $W = 450.5$, $P < .001$). Furthermore, females from all-coercive taxa at both Rio Atacames and Brushy Creek also showed greater exploration in threatening environments (stress movement) than their syntopic pairs with mixed-tactic mating systems (Fig. 4A; Brushy Creek: $W = 621$, $P < .001$; Rio Atacames: $W = 170$, $P = .011$). These patterns are directly opposed to those observed from previous research comparing poeciliid females from all-coercive and mixed-tactic species occupying predator-free populations (Inman *et al.* 2024; Supporting Information, Fig. S2).

We also observed that some traits showed opposing patterns by mating system between the two locations (Fig. 4C, D). At Brushy Creek, the location with greater predation pressure, we found that *G. affinis* females from an all-coercive mating system spent more time in the thigmotaxis zones of the black side of the scototaxis tank (shyness) than *Poecilia latipinna* females with a mixed-tactic system (Wilcoxon test, $W = 609$, $P = .003$; Fig. 4C). Meanwhile, at Rio Atacames, the location with fewer predators, we observed the opposite pattern: *Poecilia gilli* females from a mixed-tactic system showed higher shyness than *Pseudopoecilia fria* females with an all-coercive mating system ($W = 264$, $P = .015$). Additionally, we observed location-specific differences in the correlation between body size and shyness (Fig. 4D). Across all females at Rio Atacames, we found a significant positive correlation between standard length and time in the black thigmotaxis zone (Spearman rank correlation: $r = 0.4$, $P = .01$). Meanwhile,

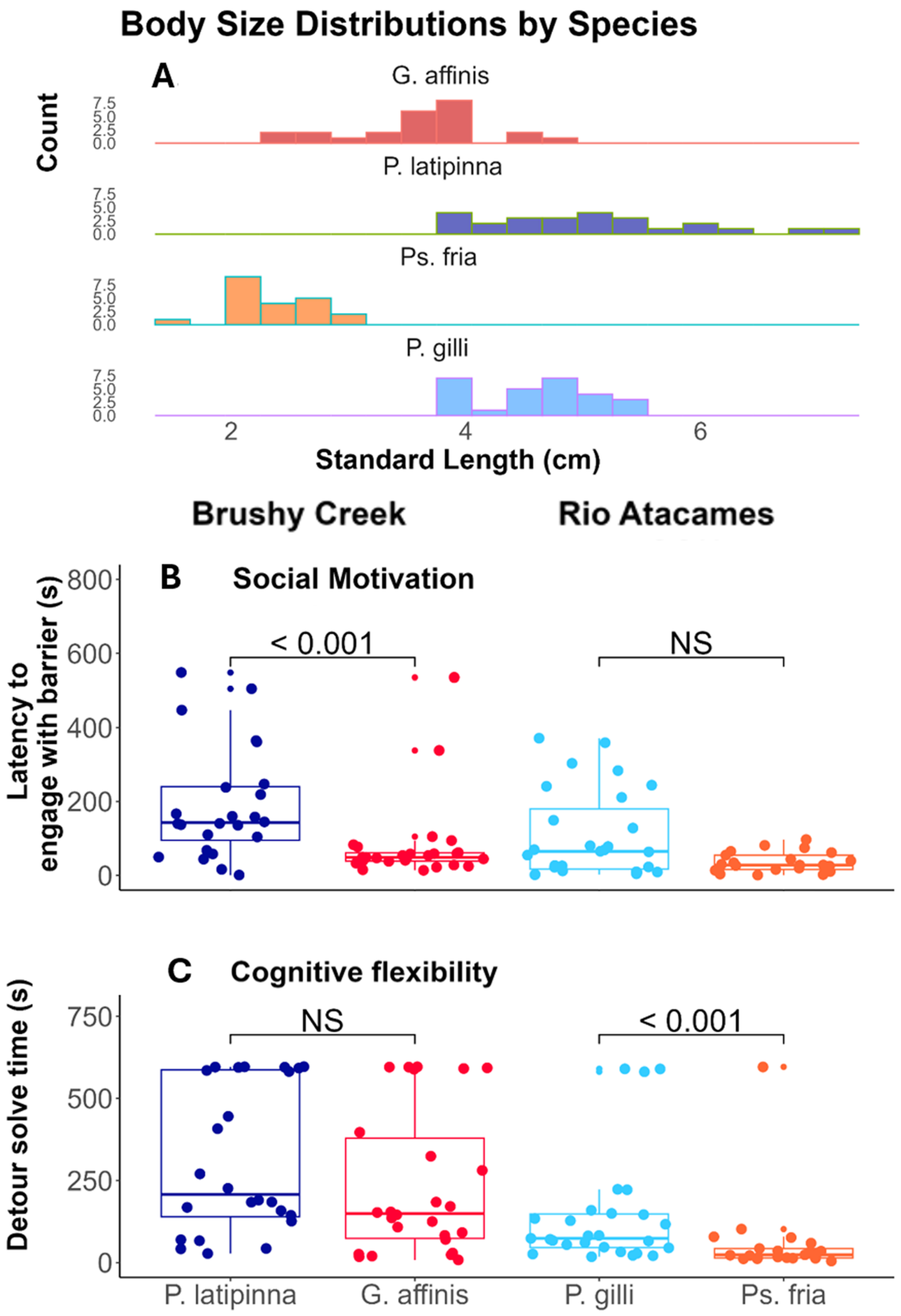


Figure 3. Body size distributions and detour reaching variation across species. Cool colours indicate mixed-tactic mating systems, whereas warm colours indicate all-coercive mating systems. A, standard length (our measure of body size) differed by species wild populations ($H = 68.7$, $P < .001$, d.f. = 3). B, social motivation (as measured by latency to approach the barrier in the detour task), with lower latency representing higher levels of social motivation. Significant (<.05) *P*-values from Wilcoxon rank sum tests conducted between syntopic species are shown above each pair (non-significant *P*-values are indicated by 'NS'). C, cognitive flexibility across species. Faster detour solve times represent higher cognitive flexibility (see Fig. 2 and the Materials and Methods for background on calculation of cognitive flexibility).

females from the location with higher predation pressure (Brushy Creek) showed a near-significant negative correlation between body size and time in the black thigmotaxis zone (Spearman rank correlation: $r = -0.25$, $P = .08$; Fig. 4D). This interaction between mating system and location was confirmed with our GLM analyses evaluating shyness variation across the four species (Table 1). The best-fitting model for shyness (time in black thigmotaxis ~ mating system + location + mating system × location) included a significant interaction term between mating system and location ($P = .002$; Table 1). Specifically, the all-coercive species had higher shyness than the mixed-tactic species at Brushy Creek, whereas the mixed-tactic species was shyer at Rio Atacames than the all-coercive species. Thus, the effect of mating system on shyness is directionally different depending on the location.

Examining relationships between traits within species, we noticed that three of the four species shared a positive correlation between exploratory tendencies and social motivation, and a fourth (*Poecilia gilli*) showed a non-significant trend in the same

Table 1. The best-fitting general linear model according to AICc (Akaike's Information Criterion corrected for small sample sizes) for each behavioural or cognitive response variable; here we include the model, AICc value, and statistics associated with each fixed effect. Bold text indicates a significant p-value associated with the ANOVA performed on the best-fitting GLM for each response variable.

Model	AICc	Fixed effect	χ^2 (*P*-value)
Black thigmotaxis (scototaxis) ~ Mating System × Location	1118.6	Mating system	2.68 (.11)
		Location	0.01 (.94)
		Mating system × Location	**9.87 (.002)**
Distance moved (scototaxis) ~ Mating system + Absolute standard length	1420.4	Mating system	2.35 (.13)
		Absolute standard length	**36.37 (<.001)**
Time spent immobile (scototaxis) ~ Absolute standard length × Location	1104.4	Absolute standard length	1.29 (.26)
		Location	**13.10 (<.001)**
		Absolute standard length × Location	2.49 (.11)
Latency to barrier (detour) ~ Absolute standard length + Location	1105.8	Absolute standard length	**21.6 (<.001)**
		Location	2.89 (.09)
Solve time (detour) ~ Latency to barrier (detour) + Location + Distance moved (scototaxis)	1192.7	Location	**7.17 (.007)**
		Latency to barrier	**8.75 (.003)**
		Distance moved (scototaxis)	2.41 (.12)

direction (Fig. 5; Spearman rank correlation between total distance moved in scototaxis and latency to barrier in detour assay for *Poecilia latipinna:* r = −0.47, *P* = .02; *G. affinis:* r = −0.82, *P* = .008; *Poecilia gilli:* r = −0.34, *P* = .08; and *Pseudopoecilia fria:* r = −0.53, *P* = .014). Thus, across species, individuals that were more exploratory in threatening conditions tended to be more socially active or motivated (shorter latency to interact with the reward fish).

We also observed a strong effect of location and body size that explained much of the variation in how these female fish respond to threatening environments (behaviours measured in scototaxis; Fig. 5; Table 1) and novel environments (behaviour measured in detour; Table 1). Females from both species collected at Brushy Creek showed a significant negative correlation between exploratory behaviour and immobility in scototaxis (Fig. 5A, B; *Poecilia latipinna:* r = −0.64, *P* < .001; *G. affinis:* r = −0.41, *P* = .033). Meanwhile, females from Rio Atacames had the opposite relationship (Fig. 5C; *Poecilia gilli:* r = 0.47, *P* = .039) or none at all (Fig. 5D; *Pseudopoecilia fria:* r = 0.19, *P* = .456). Furthermore, females from both taxa at the more predator-rich Brushy Creek location shared the same relationships between body size, exploratory behaviour, and immobility, with larger females exhibiting significantly greater immobility (Fig. 5A, B; *Poecilia latipinna:* r = 0.45, *P* = .028; *G. affinis:* r = 0.48, *P* = .019) and less exploration in threatening environments (*Poecilia latipinna:* r = −0.66, *P* < .001; *G. affinis:* r = −0.63, *P* = .001) than smaller females. In contrast, females from Rio Atacames showed no significant correlations between these traits and body size (Fig. 5C, D). The best-fitting GLM for immobility (time spent immobile ~ absolute standard length × location) identified location as the only significant explanatory factor (Table 1; location: *P* < .001). Although an interaction term between absolute standard length and location was present in the top model (probably owing to the stronger positive effect of absolute standard length on immobility at Brushy Creek than at Rio Atacames, where there was no effect), the interaction was not a significant fixed effect in the model (Table 1; *P* = .11).

The best-fitting GLM for exploration in threatening conditions [distance moved (scototaxis) ~ mating system + absolute standard length] identified body size as the only significant factor across species (Table 1; absolute standard length, *P* < .001), and body size was also the only significant factor in the best-fitting GLM for social motivation [latency to barrier (detour) ~ absolute standard length + location; Table 1; absolute standard length, *P* < .001]. The best-fitting GLM explaining variation in cognitive flexibility across all four species involved both location and behaviour traits [Table 1; solve time (detour) ~ latency to barrier (detour) + location + distance moved in scototaxis]. Of the three factors in the model, only location and social motivation were significant (*P* = .007 and *P* = .003, respectively).

DISCUSSION

Overall, we found signs that both natural and sexual selection influence female behavioural and cognitive traits in wild poeciliid species. We predicted that variation in mating system would consistently shape stress movement and cognitive flexibility across both pairs of syntopic species. However, we found that few traits were predicted solely by mating system, and they did not directly parallel patterns observed in other poeciliid species from predator-free mesocosms (as in the study by Inman *et al.* 2024). Instead, we found an interaction between mating system and location affecting shyness: the all-coercive species at the high-predation location was shyer than the mixed-tactic species, whereas the mixed-tactic species at the low-predation location was shyer than the all-coercive species. Location and body size were major explanatory factors across all other traits. Notably, there was not a strong effect of body size on movement traits or social motivation in a previous study on poeciliids from predator-free mesocosms (Inman *et al.* 2024; Supporting Information, Fig. S2). Thus, our findings from wild populations of poeciliids suggest a possible influence of predation regime on trait variation.

As predicted, social motivation was higher in all-coercive species within locations (Fig. 3B). Females of all-coercive species showed the highest social motivation (e.g. lowest latency to approach conspecifics in the detour; Fig. 3B). This pattern in wild poeciliid females overall matched the pattern observed in predator-free populations (Inman *et al.* 2024; Supporting Information, Fig. S1). And both findings are consistent with prior data showing that females experiencing higher rates of male coercion

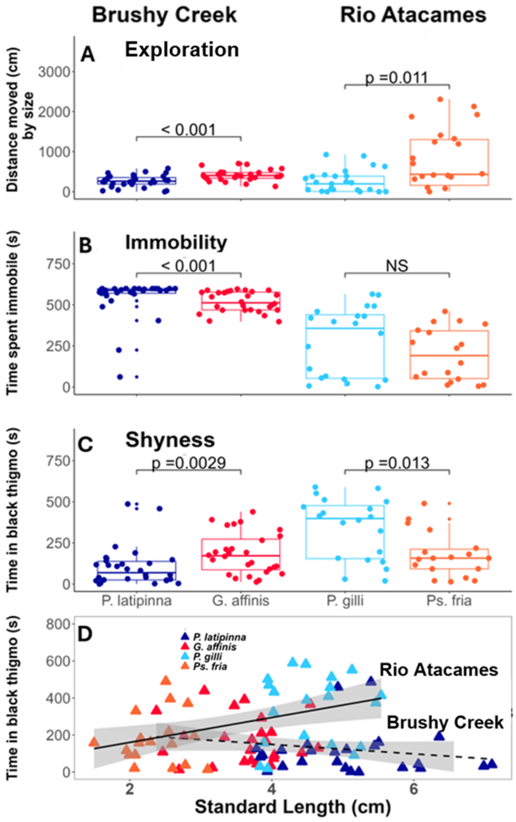


Figure 4. Variation across species in behavioural traits measured during the scototaxis assay. A, exploration in a threatening environment [total distance moved (in centimetres)/standard length (in centimetres)], B, Immobility (total time spent motionless). C, shyness (total time in black thigmotaxis zone; see Fig. 2). Significant (<.05) P-values from Wilcoxon rank sum tests conducted between syntopic species are shown above each pair (non-significant P-values are indicated by 'NS'). D, Spearman rank correlations between fish standard length (x-axis) and shyness (time in black thigmotaxis zone, y-axis) for each location. The dashed line for the Brushy Creek pair indicates a near-significant P-value ($r = -0.25$, $P = .08$), whereas the continuous line for Rio Atacames indicates a significant P-value ($r = 0.4$, $P = .013$).

aggregate more tightly (Dadda 2015), which functions to dilute the risk of male harassment to an individual female (Dadda *et al.* 2005). Interestingly, we also found that this behaviour covaried with body size, significantly within the all-coercive *G. affinis* females (Fig. 5) and across all four species (Table 1). Specifically, we found that larger individuals were less socially motivated (slower latency to approach barrier; Fig. 5). Importantly, relative body size (our proxy for age) was not a significant factor in explaining variation in social motivation across the four species (Table 1). Hence, it is body size rather than age that determines variation in this behaviour. This distinction rules out the possibility that this phenomenon is driven by older individuals learning to associate with other females to avoid male harassment. Studies of other freshwater organisms suggest that smaller individuals benefit more from aggregating with larger ones than vice versa (Rodgers *et al.* 2015). Given that we tended to use larger-than-average females as stimulus fish in the detour assay, our results might be explained by this phenomenon.

Although social motivation matched predictions based upon mating system, the species-level differences in cognitive flexibility did not. In contrast to previous work with predator-free populations, in which females of mixed-tactic species were more cognitively flexible than females of all-coercive species (Inman *et al.* 2024), our investigation with wild populations found the opposite pattern (Fig. 3C). All-coercive *Pseudopoecilia fria* females outperformed mixed-tactic *Poecilia gilli* females in solving an inhibitory control task at Rio Atacames, with a non-significant trend for a similar pattern at Brushy Creek. The location effect observed here implicates the influence of ecology on cognitive flexibility. However, the direction of this effect is contrary to predictions for how predation pressure is expected to shape cognitive flexibility. A previous laboratory study has shown that guppies reared with predatory cues have higher cognitive flexibility in a reversal learning task than guppies reared in the absence of predators (Vila Pouca *et al.* 2021). In contrast, in our study, syntopic species from the lower predation location (Rio Atacames; Jiménez-Prado and Vásquez 2021) were more cognitively flexible than those from the higher predation location (Brushy Creek; Hendrickson and Cohen 2022).

Female exploration in threatening conditions across the four wild species also showed opposite trends by mating system in comparison to predator-free populations (Fig. 4A; Supporting Information, Fig. S2). Specifically, we found females from all-coercive taxa at both Brushy Creek and Rio Atacames to exhibit greater exploration in threatening conditions than each mixed-tactic syntopic species (Fig. 4A). The strongest predictor for variation in exploration was body size across all four species (Table 1), and the relationship appears to be the strongest in the population with higher predation pressure (Brushy Creek; Fig. 4). Both coercive and mixed-tactic species from Brushy Creek showed significant negative correlations between exploration in threatening conditions and body size (distance moved in scototaxis and standard length; Fig. 5A, B). This suggests that larger individuals at this higher-predation location exhibited lower exploration tendencies than smaller individuals (Fig. 5A, B; Table 1). The species and location differences observed in female immobility mirror the pattern in exploration, with the mixed-tactic species showing greater immobility than the all-coercive species at both locations (and Brushy Creek in particular) (Fig. 4B; Table 1). Thus, greater predation pressure seems to favour a general reduction in movement, and the costs associated with greater movement (e.g. higher detectability by would-be predators) might be too great to offset any potential foraging benefits.

Additionally, size is an important mediator of predator–prey interactions. Predators are constrained by the maximum prey size they can capture or ingest (Nilsson and Brönmark 2000, Radloff and Du Toit 2004, Mihalitsis and Bellwood 2017), but larger prey are more detectable (Eriksson 1985) and should be preferred because of their greater nutritional payoff (Krebs *et al.* 1977). Predation on poeciliids fits this prediction: predators, from aquatic insects to wading birds and cichlids, have been shown preferentially to target larger poeciliids as prey (Britton and Moser 1982, Trexler *et al.* 1994, Rosenthal *et al.* 2001, Johansson *et al.* 2004, Tobler *et al.* 2007). Most studies of piscine meso-carnivores, such as bass and cichlids, predict an optimal prey size of ~4 cm, and experimental work has shown that cichlids measuring 10–15 cm,

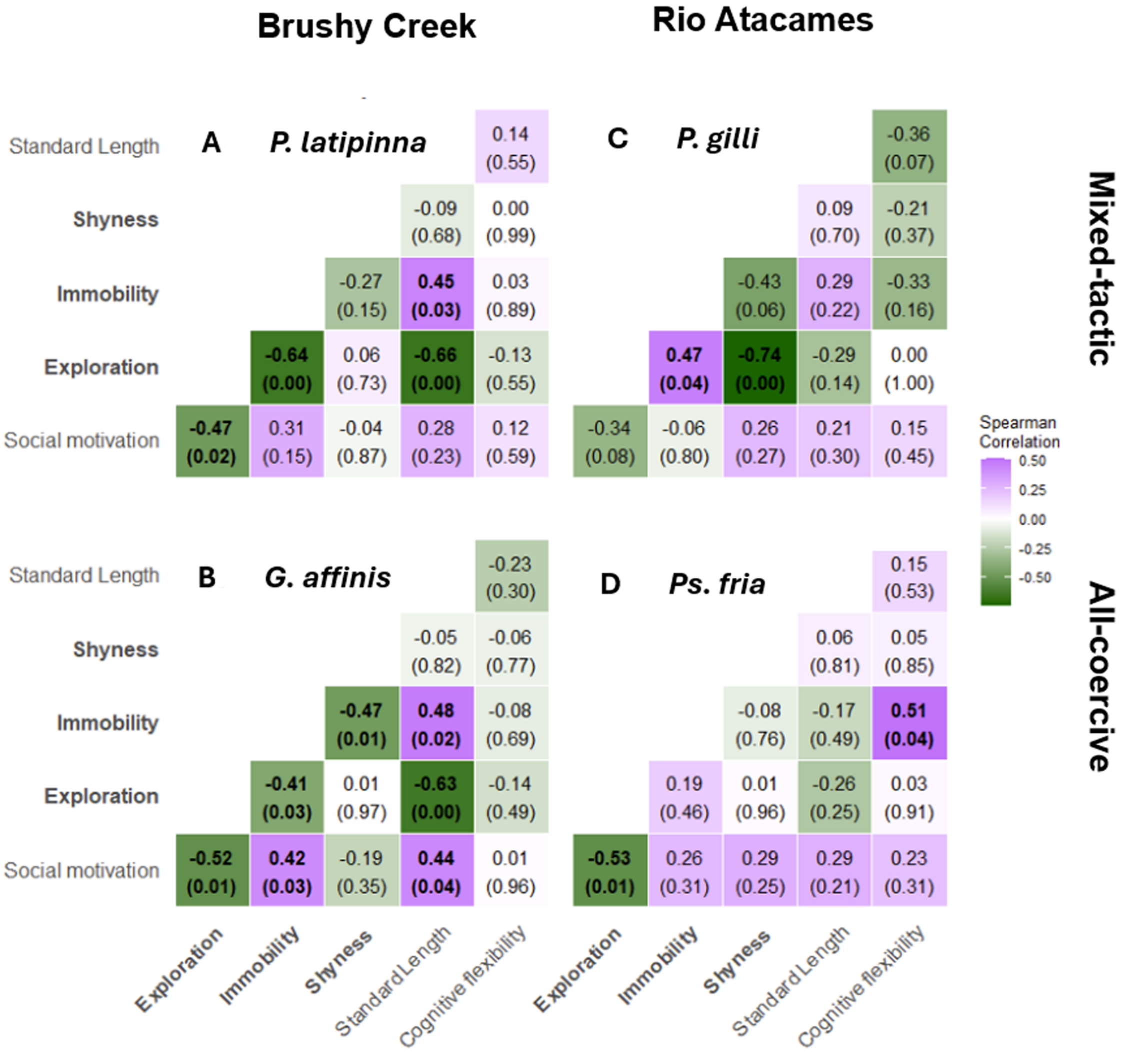


Figure 5. Spearman rank correlation heatmaps computed for each pair of traits in Brushy Creek species (A, B) and Rio Atacames species (C, D). A, *Poecilia latipinna*. B, *Gambusia affinis*. C, *Poecilia gilli*. D, *Pseudopoecilia fria*. Scototaxis variable labels are shown in bold to distinguish them from variables measured in detour reaching and standard length. Spearman rank correlations with significant (<.05) *P*-values are in bold.

a typical size for the sunfish and cichlid species present at Brushy Creek, preferentially attack 4 cm guppies over three smaller available size classes (Johansson *et al.* 2004). This 4 cm optimum falls in the middle of the size ranges of *Poecilia gilli* and *Poecilia latipinna* and in the upper half of the size range of *G. affinis*. Thus, we suggest that individuals with larger body sizes, particularly at the higher-predation location (Fig. 5A, B), exhibit greater freezing and less exploration because they are preferred as prey.

It is not surprising that exploration and immobility might be affected by factors other than mating system and instead are more strongly influenced by predation risk. Lower baseline movement reduces prey detection by limiting conspicuous movements or enhancing concealment. Accordingly, diverse aquatic prey species, such as dragonflies, damselflies, anuran tadpoles, and teleost fish, that are more vulnerable to predators move less (e.g. Lawler 1989, Savino and Stein 1989, Richardson 2001, Jiang and Mikolajewski 2018). However, despite the advantages of immobility to predator evasion, fish populations at high predation risk often show higher activity in response to predation as a means of increasing foraging efficiency under risk (Huntingford 1993, Dingemanse *et al.* 2007, Archard and Braithwaite 2011). Given that the range of optimal behavioural responses to predators is vast (Fraser and Huntingford 1986), understanding the relationship of immobility to predation risk in poeciliids requires investigation of behaviour across replicate high- and low-predation regimes (e.g. Brown and Braithwaite 2004, Brown *et al.* 2005, 2007).

Perhaps our most intriguing finding was the interaction effect between location and mating system on female shyness variation (Fig. 4C; Table 1). At the higher predation location (Brushy Creek), females of the all-coercive species (*G. affinis*) were shyer than mixed-tactic females (*Poecilia latipinna*). Meanwhile, at the lower predation location (Rio Atacames), we found the opposite pattern. Interestingly, the pattern observed in the lower predation pair (Rio Atacames) is contrary to patterns found in laboratory-reared northern swordtail females from predator-free mesocosms. Female swordtails reared with courting and coercive males were bolder than females reared with only coercive males (Queller *et al.* 2022). Conversely, increases in the rate of male harassment have been shown to drive female guppies into riskier habitats (Darden and Croft 2008). In our study, ecological variation between locations appears to influence shyness, based on the contrasting relationships between female size and shyness by location in the wild (Fig. 4D). Specifically, we found a positive relationship between shyness and size at Rio Atacames, the lower-predation location, and a near-significant negative relationship between shyness and size at Brushy Creek, the higher-predation location (Fig. 4D).

Given that body size–shyness correlations differ between locations and are not dependent on species within locations, this pattern might be driven by differential (and possibly size-specific) predation between locations. Larger individuals might be less shy at the higher-predation location (Brushy Creek) because they must still effectively engage in activities such as foraging and mating despite the constant risk of mortality imposed by predators (Brown *et al.* 2007). Individuals that have experienced a greater number of predation attempts are likely to be more effective at deploying antipredator responses immediately in response to an attack, making boldness less costly even if predation is size specific (Ferrari *et al.* 2005, Turner *et al.* 2006, West *et al.* 2018). Larger individuals at the high-predation location (Brushy Creek) might freeze more and move less, but they might simultaneously be more likely to spend time in less sheltered environments (i.e. less shy) (Fig. 4D). This indicates that different behavioural antipredator strategies (e.g. sheltering behaviour and freezing) can be decoupled in these poeciliids. Deploying both behaviours at an equally high frequency might result in lower rates of food intake and lower probability of mating, whereas relying on one might lower risk without coming at the cost of other routine activities (Lima and Bednekoff 1999, Sih and McCarthy 2002, Mirza *et al.* 2006).

At the lower-predation location (Rio Atacames), on the contrary, the link between greater shyness and larger body size aligns with a metabolic hypothesis suggesting that larger individuals tend to be shyer. Because metabolic rate per unit of body mass decreases with size, foraging motivation should also decline with size, leading to lower boldness in larger individuals (Clarke and Johnston 1999, Brown and Braithwaite 2004, Brown *et al.* 2005). At locations with higher predation pressure, such as Brushy Creek, predation pressure might be influential enough on the boldness–shyness continuum that this general metabolic pattern is reversed.

CONCLUSION

Despite a clear signature of mating system shaping movement patterns and cognitive flexibility in previous work on predator-free environments (Inman *et al.* 2024), in the presence of predation, we found that ecological variation and body size play equally important roles in shaping these traits. Body size explained much of the variation in most traits we measured (Table 1), a pattern that was largely not observed in predator-free conditions (Inman *et al.* 2024; Supporting Information, Figs S1, S2). We also found evidence that shyness might be affected by complex interactions between mating system, size, and ecology. Our findings suggest that, even when species vary greatly in mating system characteristics, ecological factors might interact with or swamp the effects of sexual selection to shape female behavioural and cognitive traits.

Notably, however, the use of only four species at two locations limits the conclusions that can be drawn. Although the two all-coercive species (*G. affinis* and *Pseudopoecilia fria*) are distantly related (from lineages that have independently retained the ancestral state of exclusive coercion), *Poecilia gilli* and *Poecilia latipinna* are in the same genus and represent a single origin of mixed-tactic mating systems. Thus, our conclusions cannot be generalized to other poeciliid lineages that have evolved cooperative/courtship mating tactics (such as *Xiphophorus*). Additionally, the role of ecological factors might be determined more precisely by comparing populations of the same pairs of species that experience different ecological conditions (Jourdan *et al.* 2016, Riesch *et al.* 2016). Given that the locations in our study are inhabited by different pairs of species in different regions of the world, there are more factors that differ between them than merely predator communities. Future work examining species pairs that differ in mating system along ecological gradients of predation and other important ecological parameters would more fully disentangle the roles of ecology, size, and mating system in shaping trait variation.

Our results suggest that the relationships among mating system, behaviour, and cognition differ by ecology and region. Our general finding that the relationship between body size and behavioural and cognitive traits is not consistent between locations suggests that variable natural selection pressures, rather than physiological constraints, shape this relationship. The lack of consistency with previous work on populations in semi-natural conditions suggests that females of different poeciliid species might vary in behaviour and cognition for reasons other than mating system variation, and that patterns found in populations living in artificial conditions without predators might not carry over to wild populations (D’Amore *et al.* 2019). Despite the small number of species and locations used, our study provides an exciting first suggestion that multifarious forms of sexual and natural selection interact to shape female behaviour and cognition in wild populations.

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SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY STATEMENT

Data are publicly available at the following GitHub repository: https://github.com/inmanc2/matingtacticsxecology.

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