Behavioral Ecology, 2025, Vol. 36, No. 1, arae099
https://doi.org/10.1093/beheco/arae099
Advance access publication 21 November 2024
Original Article

Male mating tactics are associated with distinct female cognitive-behavioral profiles in 4 poeciliids

Callen M. Inman[1,*], Alan Vuong[1], Ingo B. Schlupp[2,3], Molly E. Cummings[1]

[1]Department of Integrative Biology, The University of Texas, Austin, TX, United States
[2]School of Biological Sciences, University of Oklahoma, Norman, OK 73019, United States
[3]International Stock Center for Livebearing Fishes, University of Oklahoma, Norman, OK 73019, United States

*Corresponding author: Department of Integrative Biology, The University of Texas at Austin, J.T. Patterson Labs, 2415 Speedway, Austin, TX 78712, United States. Email: callen.inman@utexas.edu
Handling Editor: Emilie Snell-Rood

Male mating tactics, the morphological and behavioral traits that males employ to access potential mates, alter female space use, time budget, and ecology in ways that may have downstream consequences for female behavior and cognition. Courtship tactics, in which males display and females exercise preferences, are common in some taxa. In others, coercive tactics, in which males force matings with limited female choice, predominate. Because behavior and cognition often transcend a single context, we ask whether variation in male mating tactics predictably shapes female behavior and cognition outside of mating. Controlling for predation by using populations housed in ecologically identical mesocosms for multiple generations, we compared female behavioral and cognitive traits of 4 different species across the teleost fish family Poeciliidae. We compared all-coercive *Gambusia vittata* and *Heterandria formosa* to *Limia perugiae* and *Xiphophorus nigrensis*, species with both coercion and courtship. We assessed females on sociability, activity, boldness, stress movement, cognitive flexibility, and spatial learning. Mating system predicted variation in movement patterns, cognitive flexibility, and spatial learning. Mixed-tactic species showed higher activity, stress movement, and cognitive flexibility than coercion-only taxa. In spatial learning, the all-coercive *G. vittata* had the highest accuracy and was the only species to show evidence for learning across trials. Multivariate approaches identified movement traits as the largest factors differing between mating systems in cognitive-behavioral syndromes. This work provides the first suggestion that species-level variation in poeciliid male mating tactics is a potential factor contributing to differences in female behavior, cognition, and cognitive-behavioral syndromes.

Key words: behavioral syndrome; cognitive tradeoff; mating system; poeciliid fish; sexual conflict; social complexity.

Introduction

Male mating tactics, or the suite of morphological and behavioral traits by which males compete for access to females, have diverse consequences for females. Male mating tactics range from elaborate displays in which males invest significant amounts of time and resources (Mitoyen et al. 2019), to sneak copulations and coercive mating, in which a male neither guards a resource nor directly courts a female (Pilastro et al. 1997). Variation in male mating tactics among species has been shown to drive female morphological (Brennan and Prum 2015; Orbach et al. 2018; Carvalho et al. 2021), behavioral (Magurran and Seghers 1997; Jirotkul 1999; Takami and Sota 2007; Queller et al. 2022; Yang et al. 2023), and even cognitive (Queller et al. 2023) diversification. In cases where females exercise limited choice prior to mating and in which male harassment is frequent, they may exhibit distinct behavioral counter-adaptations to male mating behavior by forming social aggregations (Bon and Campan 1996; Dadda et al. 2005; Agrillo et al. 2006; Silk 2007; Brask et al. 2011; Dadda 2015) and reducing time spent foraging (Pilastro et al. 2003; Yang et al. 2023). In contrast, in mating systems with courtship, females may show distinct preferences for males with certain traits and actively seek out males that have certain ornaments and display behaviors (Kodric-Brown and Nicoletto 1996; Schlüter et al. 1998; Uy et al. 2001; Cummings et al. 2003; Rios-Cardenas et al. 2007; Schlupp et al. 2010; DuVal et al. 2013; Calabrese et al. 2014; Makowicz et al. 2016; Cummings and Endler 2018; Ryan et al. 2019).

There are several broad behavioral and cognitive axes that might be responsive to interspecific variation in male mating tactics. Boldness, or an animal's tendency to engage in risky behavior, is a broad behavioral axis that can be shaped by the social environment. For instance, a developmental study with a species of northern swordtail (*Xiphophorus nigrensis*) revealed that females raised in complex environments with both male courtship and coercion became bolder than females raised with only courtship or only coercion (Queller et al. 2022). Boldness also affects space use in the presence of high male harassment (Darden and Croft 2008) and covaries with an array of ecological variables, such as foraging ecology (Wilson et al. 1993), dispersal (Fraser et al. 2001; Rehage and Sih 2004), and predator inspection (Blaszcyk 2017). Female shoaling tendencies can also be influenced by male mating tactics (Pilastro et al. 2003). For instance, comparative work across several poeciliid fish species has shown that females from more highly coercive taxa shoal more closely with other females in the presence of males than females from taxa with

Received: 4 April 2024; **Revised:** 11 November 2024; **Editorial decision:** 18 November 2024; **Accepted:** 19 November 2024.

courtship (Dadda 2015). Along similar lines, female baseline activity might also be responsive to male mating tactics. If successfully evading coercion involves frequent movement responses, then activity levels may differ between females from all-coercive systems relative to females from taxa with a higher proportion of courtship tactics. So far only limited work has examined baseline activity rate in relation to male mating tactics. In stream water striders (*Aquarius remigis*), a species with high levels of coercive mating that females almost always attempt to resist (Rowe et al. 1996), females with lower baseline activity are more likely to engage in mating interactions with males (Wey et al. 2015). And in guppies (*Poecilia reticulata*), which have males that coerce and court, females reared in environments with higher rates of unsolicited male mating attempts were more active (Killen et al. 2016).

In addition to driving variation in female behavioral responses, divergence in male mating tactics is also expected to affect the evolutionary trajectory of female cognition (Cummings and Ramsey 2015; Cummings 2018), which can be broadly defined as the neuronal processes involved in the acquisition, retention, and use of information (Shettleworth 2010). Evidence suggesting that cognitive processes might be involved in coordinating responses to male mating tactics comes from studies in live-bearing fishes of the family Poeciliidae. Artificial selection for increased male gonopodium length (and presumably greater capacity for sexual coercion) in the all-coercive *Gambusia holbrooki* showed that female brain size increased in response (Booksmythe et al. 2016; Buechel et al. 2016, but see Culumber et al. 2020). In addition, selection for increased brain size in the guppy (*P. reticulata*) with mixed-tactic males that court and coerce revealed that larger brained females made more optimal mating decisions (Corral-López et al. 2017, 2020). Developmental studies in swordtails (*X. nigrensis*) with distinct male mating phenotypes (courters, coercers, and mixed-tactic males) have shown that different developmental exposures to these male types can directly influence cognitive abilities. For instance, female swordtails raised in simple social environments with single male mating tactics (either all coercion or all courtship) showed higher spatial accuracy and better spatial learning performance than females raised in more complex mating environments with both courtship and coercion present (Queller et al. 2023). This is somewhat surprising given that research with birds and mammals has suggested that more complex social environments place a higher demand on cognitive flexibility (Bond et al. 2007; Amici et al. 2008; Johnson-Ulrich and Holekamp 2020). Furthermore, short-term exposure (~30 min) to different swordtail male mating types revealed that females exposed to a mix of both courtship and coercive males engaged in neurogenomic learning pathways more than females exposed to only coercive types (Wong et al. 2011; Lynch et al. 2012; Wang et al. 2015; Wong and Cummings 2014).

Despite the fact that many of the behavioral and cognitive traits examined in relation to male mating behavior transcend a single context (Dochtermann and Dingemanse 2013), we lack an understanding of how variation in male mating behavior across species affects the evolution of female behavioral and cognitive traits outside of the mating context. Live-bearing fishes of the family Poeciliidae are an excellent taxonomic group to examine patterns generated by sexual selection because of the extensive variation in male mating tactics across species (Culumber and Tobler 2017). In most species of poeciliids, the sexes show large disparities in reproductive investment, as females have internal gestation over several weeks, whereas males contribute only sperm. As a result of this disparity in investment, male poeciliids have evolved divergent reproductive tactics to increase their likelihood of mating. The 2 primary mating tactics in poeciliids are courtship, in which males conspicuously display prominent dorsal or caudal fins, and sneak copulations, in which males approach females from behind and attempt to force them into mating. In some poeciliids, males flexibly switch between coercive and courtship tactics or fall into 2 or more fixed male types that exclusively employ either coercive or courtship tactics (Farr and Travis 1986; Ryan and Causey 1989; Erbelding-Denk et al. 1994). Such mixed-tactic mating systems involve higher social complexity, as females must learn and respond appropriately to a wider range of mating behaviors (Griebling et al. 2020). In other species, males do not display to females and instead rely exclusively on sneak copulations (Bisazza 1993; Plath et al. 2007). Although all male mating tactics can be costly to female poeciliids in terms of time away from foraging, coercive tactics are more disruptive than courtship to female foraging behavior (Yang et al. 2023), prevent females from exercising mate choice (Bisazza and Marin 1995), and may use gonopodial claws to overcome female resistance (Kwan et al 2013) increasing the likelihood of physical costs to females.

In this study, we utilize mating system variation present across 4 different poeciliid species from distinct clades (Fig. 1) to study its potential consequences for female behavior and cognition. We conduct behavioral and cognition experiments on 2 species with a mix of courtship and coercive mating tactics, *X. nigrensis* and *Limia perugiae* (Ryan and Causey 1989; Erbelding-Denk et al. 1994), and 2 species with only coercion, *Gambusia vittata* and *Heterandria formosa* (Bisazza 1993; Schrader et al. 2012). We carefully selected coercive taxa that were as phylogenetically distant as our mixed-tactic taxa. All 4 species come from distinct genera with similar levels of relatedness to one another (30 to 40 million years diverged; Reznick et al. 2017; Furness et al. 2019, Fig. 1). Although our limited, but phylogenetically broad, sampling approach prohibits us from conducting phylogenetic contrasts, it does allow us to detect potential mating system-associated patterns broadly found across clades. In our effort to identify cognitive and behavioral traits influenced by male mating tactics, we collected all females from multigenerational, single-species populations experiencing no fish predation (and limited avian predation) in similar ecological conditions (800-gallon outdoor mesocosms) at Brackenridge Field Laboratories in Austin, TX. Although behavioral and cognitive traits may differ from those found in wild-caught fish in their ancestral populations (D'Amore et al. 2019), our use of these source populations allows us to begin identifying variation by mating system while minimizing species-specific differences due to ecological variables such as predation (Brown et al. 2007; Burns and Rodd 2008; Magnhagen et al. 2012) and habitat (White and Brown 2014; He et al. 2019, but see Roth et al. 2011). Using females from these populations, we measure 4 behavioral traits (activity, movement under stress, sociability, and boldness) along with performance in 2 cognitive tasks (spatial learning and cognitive flexibility). We hypothesize that females with shared mating systems (either all-coercive or mixed-tactic) will show similar behavioral and cognitive traits. Based on prior research, we make the following predictions for behavioral and cognitive traits across the 4 species. Specifically, we predict that

(1) sociability will be higher in the all-coercive taxa based on comparative work across poeciliids (Dadda 2015),
(2) activity will be higher in all-coercive species based on previous work in guppies (Killen et al. 2016),

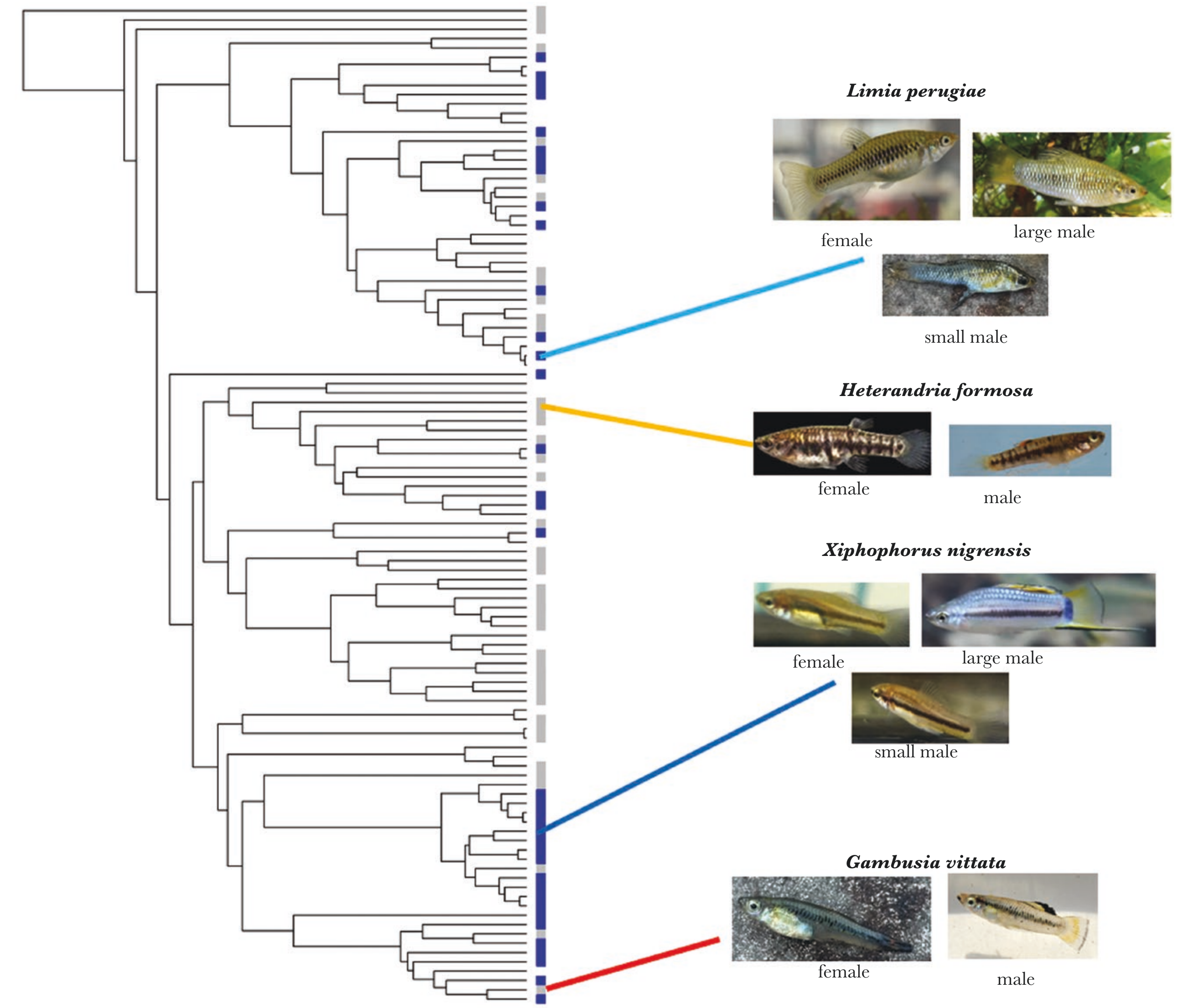


Fig. 1. Phylogeny of the family Poeciliidae. Modified with permission from Furness et al. (2019). This phylogeny shows the distribution of our 4 experimental species among the major clades of poeciliids. The phylogeny also shows the distribution of male mating tactics (blue for the presence of courtship, gray for the absence of the courtship). *Limia perugiae* large male and female images courtesy of Rodet Rodriguez-Silva. *Heterandria formosa* female image courtesy of NCFishes.com © Scott A. Smith, CC BY-SA- 4.0. Male image courtesy of Flickr © Brett Albanese, CC BY-NC-ND- 2.0. *Gambusia vittata* male image courtesy of Michi Tobler.

(3) boldness will be lower in all-coercive mating systems based on social manipulation rearing experiments in swordtails (Queller et al. 2022),
(4) spatial learning will be more advanced in the all-coercive species based on social manipulation rearing experiments in swordtails (Queller et al. 2023), and
(5) cognitive flexibility will be greater in mixed-tactic species based on correlations between social complexity and cognitive flexibility observed across bird and mammal species (Bond et al. 2007; Amici et al. 2008).

Methods

For testing in the battery of behavioral and cognitive assays, we first collected a total of 151 adult females of the 4 species (sample sizes of 29 *X. nigrensis*, 58 *L. perugiae*, 34 *H. formosa*, and 30 *G. vittata*) from single-species, mixed-sex, outdoor breeding tanks (> 800 gallons) at Brackenridge Field Laboratories (BFL) in Austin, Texas. These enclosures are seminatural environments that lack fish predators and are inaccessible to wading birds due to their depth (>1 m depth). The *X. nigrensis* and *G. vittata* populations were originally collected at the source of the Rio Choy in northern Mexico over 12 years prior to this study. The *L. perugiae* population was provided by the International Stock Center for Livebearing Fishes and was originally collected in 2016 from Lake Enriquillo, a hypersaline lake in the Dominican Republic. The *H. formosa* population was collected in northern Florida in 2016. To begin our comparative behavior and cognition assays, we collected the abovementioned *X. nigrensis*, *H. formosa*, and *G. vittata* populations from the BFL enclosures in May 2021. We collected 29 of the *L. perugiae* individuals in November 2020 for participation in the sociability and detour reaching tasks, and we collected the other 29 individuals in November 2021 for participation in scototaxis and route learning.

Behavioral and cognitive testing

We collected fish from each species-specific enclosure at BFL and acclimated them to laboratory conditions in Patterson Labs at UT Austin for at least 1 week prior to testing. Following this acclimation period, fish were socially isolated for 3 days prior to testing. Fish could interact with individuals in neighboring isolation tanks (via a shared transparent tank wall), but only 1 individual was present in each tank. Following the acclimation period, we tested individual fish on a battery of 4 different assays: sociability (shoaling), cognitive flexibility (detour reaching), boldness (scototaxis), and spatial learning (route learning). In total, we tested 151 females across the 4 species (see numbers above in collection info). We tested the first 30 *L. perugiae* females on sociability and detour reaching in November and December of 2020. We tested *X. nigrensis*, *G. vittata*, and *H. formosa* females on all 4 assays from June to August of 2021. We tested the second group of *L. perugiae* females ($n = 30$) on scototaxis and route learning from November to December of 2021. We isolated each individual for a period of 3 days prior to starting the battery of tests. Each individual underwent one assay per day over the course of 4 days. To reduce the potential carryover effects of a stressful assay on behavior in a subsequent assay (Bell 2013), we arranged assays in order of least stress-inducing to most stress-inducing: sociability assay (first), detour reaching (second), route learning (third), and scototaxis (fourth). We reasoned that the sociability assay was the least stressful due to the presence of a shoal of female conspecifics. And we reasoned that the scototaxis assay would be the most stressful assay due to the well-documented aversive properties of brightly lit environments for fish (Maximino et al. 2010) and the lack of female conspecifics.

Sociability

To evaluate general activity levels and social tendencies of all focal females, we conducted a sociability assay (Fig. 1a) using a shoal group of 5 conspecific females as in Queller et al. (2022) and with a similar design to Agrillo et al. (2006) and Plath and Schlupp (2008). We used an infrared camera (IR-Capable Monochrome GigE) to record videos of each trial and illuminated the tank with IR LED strips placed underneath the tank. Before the first assay of a given day, we placed 5 adult female reward fish on the “shoal” side of the transparent barrier for a 20-min habituation period. Next, the first focal fish was placed in an opaque PVC tube 10 cm in diameter on the opposite side of the plexiglass barrier from the shoal group for 5 min prior to the beginning of their trial. Once the habituation period was over, we removed the PVC tube, and the focal fish was recorded using the IR camera for a 10-min period.

We used EthovisionXT15 (Noldus) behavioral tracking software to quantify the behavior of each focal fish, including time spent in the 2 cm region adjacent to the reward shoal’s plexiglass barrier known as the interaction zone (Fig. 2a) and total distance moved. We evaluated focal female social behavior as the total time spent in the interaction zone and focal female activity levels by the total distance moved throughout the entire shoaling tank. We used this metric as a baseline measure of activity because it characterizes movement in a nonthreatening environment.

Detour reaching

We also measure cognitive flexibility, or the ability to shift attention and behavioral responses according to new contingencies (Badre and Wagner 2006), using a detour reaching task. This task assesses the facet of cognitive flexibility known as inhibitory control, or the ability to inhibit a preexisting response to a stimulus according to new information (van Horik et al. 2018).

We began the detour reaching assay (Fig. 2b) by placing a conspecific female reward fish in a transparent glass cylinder on the opposite end of the tank from the runway. We placed the focal fish behind a blue-felted habituation barrier 10 cm from the end of the runway and approximately 42 cm away from the reward fish on the opposite side of the glass barrier. 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 observers unaware of the study’s objectives for 2 measures (social motivation and problem-solving speed). We measured social motivation 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. 2b). We measured problem-solving speed as the time it took each fish to travel from the glass barrier to entering the reward zone (defined as more than half of its body passing through the reward zone entryway).

Route learning

To begin the assay, we placed 2 conspecific female reward fish in the transparent tube in Zone 3 (Fig. 2c). Following a 5-min habituation period for the reward fish, we placed the focal fish in a transparent habituation tube in Zone 1, from which the reward fish are visible. To evaluate spatial learning, we ran each focal fish through 5 consecutive route learning trials, with accuracy and solve time recorded for each trial. Before the first trial, we habituated each fish for 5 min in the transparent habituation tube in Zone 1. After the habituation period, we removed the tube and began filming for a period of 10 min. If the fish successfully solved the task (entered Zone 3) before the 10-min period ended, we contained the focal fish within the reward zone by placing a felted barrier to the reward entrance, and we gave it 5 min to spend interacting with the reward fish (to increase motivation to solve in subsequent rounds). If the focal fish did not solve the trial in 10 min, we gently nudged it with a hand net toward Zone 3 (to show the fish the correct route). For trials 2 to 5, we gave the focal fish a 2-min habituation period and a 5-min social interaction time with the reward at the end of each trial (except trial 5). If fish did not solve for 3 consecutive trials, they were considered “nonsolvers,” and we ended the assay after their third unsolved trial. Between trials, we completed a partial water change (one-fourth of tank water) to limit the possible effect of stress hormones from previously tested fish on route learning performance. We replaced each reward fish with a new reward fish after each focal fish completed their trials. Observers naïve to the hypotheses being tested in this study hand-scored route learning videos for the number of times each fish approached and passed through both wrong and correct doors in a given trial.

Scototaxis

To evaluate boldness tendencies and activity levels in a threatening environment (stress movement), we measured space use and total distance moved in a scototaxis tank (Fig. 2d). The scototaxis tank is divided into a brighter, more exposed white half and a darker, black half that can serve as a refuge. The majority of small fish species assessed on scototaxis, including zebrafish, swordtails, and guppies, show a consistent preference for the black compartment (Maximino et al. 2010; Queller et al. 2022), and anxiolytic compounds have been shown to alter the amount of time zebrafish spend in each half of the tank (Maximino et al. 2011; Ramsey et al. 2014). In our scototaxis assay, we considered individuals that spent more time in the exposed, white half of the

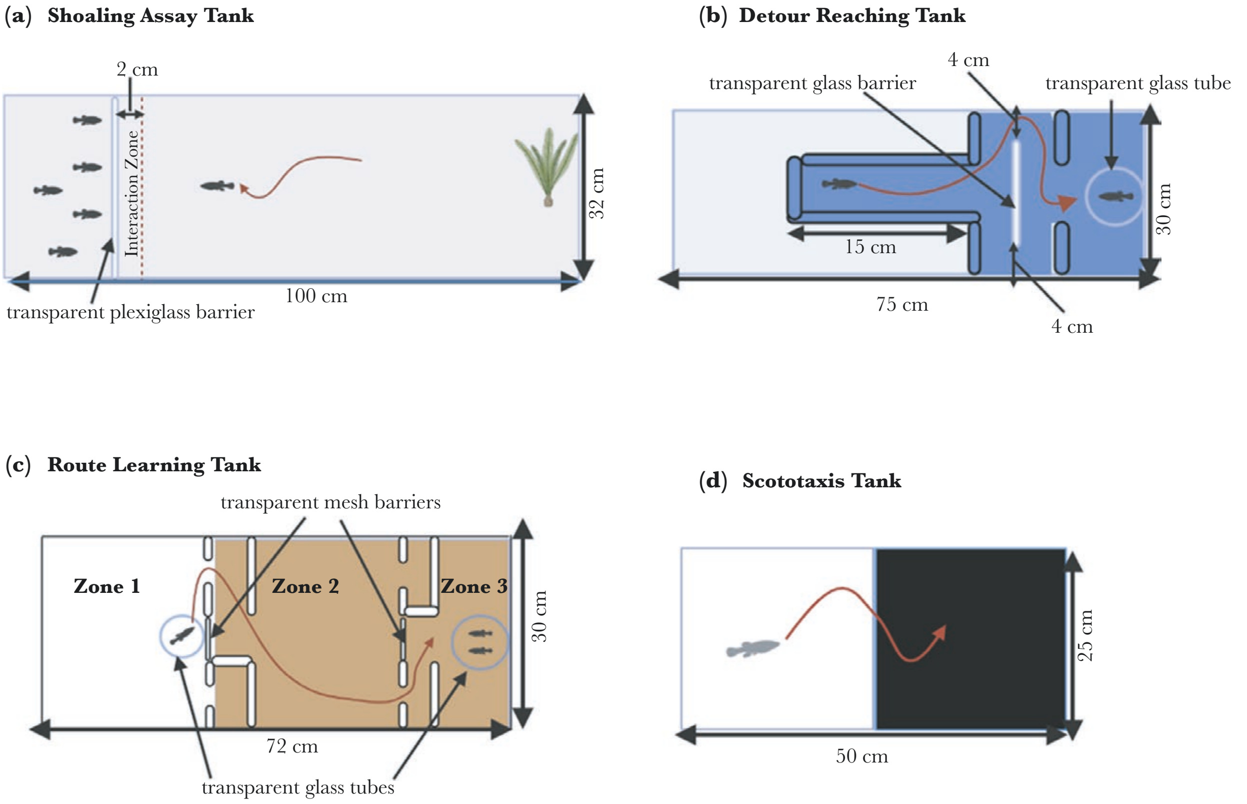


Fig. 2. Experimental tank schematics. (a) Shoaling assay tank. Five live conspecific females are placed to the left of the plexiglass barrier to serve as a shoal group. Subject females are released from a habituation tube placed in the center of the tank (not shown), video recordings are collected from above for 10 min, and movement (total distance moved in cm) and position (time spent in interaction zone) are tracked using Ethovision. (b) Detour reaching tank. One live conspecific female is placed in the glass tube on the right side of the tank to serve as the reward fish. Subject females are released from behind a barrier (not shown) placed 5 cm from the left end of the alley. After the fish finishes habituating in the left alley for 5 min, social motivation (time taken to reach the glass barrier in seconds) and solve time (time taken to reach the reward from the barrier) are recorded during a 10-min trial. (c) Route learning tank. Two conspecific female fish are placed in the transparent tube in Zone 3 of the experimental tank to serve as rewards. Subject females are released from the habituation tube in Zone 1, and time to Zone 3 and a number of wrong door entries are recorded across a 10-min trial. (d) Scototaxis tank. Subject females are initially habituated between 2 barriers straddling the boundary between the white and black zones (not shown). After a 5-min habituation period, female subjects are released and movement (total distance moved in cm) and position (time spent in the white and black zones) are tracked across a 10-min trial.

tank to be bolder. To begin each trial, we placed the focal fish in the middle of the tank (see Fig. 2d) between a black barrier and a white barrier for a 5-min habituation period (not shown in figure). Following habituation, we removed the barriers, and we began recording for a 10-min period. After each individual trial, we completed a full water change of the scototaxis tank to eliminate the effects of stress hormones in the water between different females undergoing scototaxis trials. We used Ethovision XT15 to quantify the total distance moved (stress movement) and total time spent in the white zone (boldness).

Statistical analysis

We analyzed behavioral and cognitive data using R (v4.2.0). According to results from the Shapiro–Wilk tests, none of the behavioral and cognitive variables measured across species were normally distributed. Thus, we used nonparametric Kruskal–Wallis tests to assess behavioral and cognitive traits across species and pairwise Dunn's tests for comparisons between species. For each Dunn's test result, we calculated a *P*-value that was adjusted for multiple comparisons using a Bonferroni correction. Additionally, to account for variation in body size within and among species, we constructed a set of general linear models (GLMs) for each behavioral and cognitive trait as the response variable, using standard length and mating system as fixed effects (for a list of models constructed, see Table S1). For each response variable, we assessed model fit using the Akaike information criterion (AIC) and ranked models from best fit to worst using Δ-AIC. We also computed Akaike weights to provide additional information about the strength of evidence in favor of one competitive model over another (Wagenmakers and Farrell 2004). For route learning performance across trials, we used a linear mixed-effects model to determine the effect of trial and species on the number of wrong door entries per trial. We also used a simple linear regression model to calculate the average slope of wrong door entries for each species between trials 1 and 3. To assess behavioral and cognitive-behavioral syndromes, we first conducted a linear discriminant analysis (LDA) to determine which behavioral and cognitive traits maximized differences among species in multivariate space. To assess behavioral and cognitive-behavioral syndrome structure within each species, we then employed structural equation modeling (henceforth SEM) facilitated by the R package lavaan (Rosseel 2012). For both LDA and SEM approaches, data from the species *L. perugiae* were excluded due to technical issues in the data collection process that prevented each individual from undergoing all 4 assays.

In our SEM approach to identify cognitive-behavioral syndromes, we determined the best-fit model of syndrome structure for each species independently. For each species, we constructed all possible models of syndrome structure (57 models total) formed by at least 2 of the behavioral and cognitive traits we measured. The behavioral syndrome was treated as the latent variable in each model, and each of the behavioral and cognitive traits included was an observed variable. We used 3 fit indices to determine model fit (Huang et al. 2020). The first fit index we used was a chi-squared test that measures the discrepancy between the sample and fitted covariance matrices of the model (Bentler and Bonett 1980). The second was a goodness-of-fit index (GFI) that checks the variances and covariances accounted for by the model to see how closely the model can replicate the observed covariance matrix (Hu and Bentler 1999). And the third was a root mean square error of approximation (RMSEA) that tests how well the model fits the population's covariance matrix (Sugawara and MacCallum 1993). Because these 3 fit indices incorporate slightly different aspects of model fit and have distinct biases, a model was deemed to be a good fit only if it met acceptable fit criteria for all 3 indices: a nonsignificant *P*-value from the chi-squared test, a GFI value > 0.9, and an RMSEA value < 0.5 (Schermelleh-Engel et al. 2003). For all models that met these 3 fit criteria, we used AIC to select the most parsimonious model of syndrome structure. The model with the lowest AIC score was deemed the best-fit model. Models with a<2 Δ-AIC were considered equally good fits.

Results

Shoaling: activity

We found that species differed in activity (total distance moved in a nonthreatening shoaling assay; Kruskal–Wallis test, $H = 24.453$, df = 3, $P < 0.001$; Fig. 3a). *Xiphophorus nigrensis* moved a significantly greater distance than both *G. vittata* and *H. formosa* but did not differ from *L. perugiae* (Fig. 3a, Table S1). Additionally, *L. perugiae* showed higher movement than *G. vittata* but not *H. formosa*. Consistent with these results, the best-fit GLM for activity included mating system as the sole fixed effect (Table 1). The other competitive (Δ-AIC < 2) model contained mating system and standard length as fixed effects, but only the effect of the mating system was significant when controlling for standard length ($\chi^2 = 23.69$, Table 1).

Shoaling: sociability

We found interspecific variation in time spent interacting with the conspecific shoal in the sociability assay (Kruskal–Wallis test, $H = 31.82$, df = 3, $P < 0.001$; Fig. 3c). *Limia perugiae* spent significantly less time in the interaction zone than each of the other species tested. *Xiphophorus nigrensis* and *H. formosa* spent the greatest amount of time interacting with conspecific females, but only *H. formosa* differed significantly from the intermediate *G. vittata* (Fig. 3c, Table S1). Consistent with the divergence of *L. perugiae* in sociability from the other 3 species, mating system and standard length were present in the best-fit GLM explaining sociability variation, but only mating system had a significant effect (Table 1).

Scototaxis: movement under stress

Species also differed significantly in their movement patterns under stress (total distance moved during scototaxis: Kruskal–Wallis test, $H = 54.003$, $P < 0.001$; Fig. 3b). *Xiphophorus nigrensis* moved a greater distance than all other species tested. *Limia perugiae* moved a greater distance than *H. formosa* but not *G. vittata* (Fig. 3b, Table S1). The best-fit GLM explaining stress movement variation included mating system and standard length as separate fixed effects, and the other competitive model included mating system, standard length, and an interaction term between the 2 variables. In both cases, only mating system showed a significant effect when accounting for other variables (Table 1).

Scototaxis: boldness

Species differed significantly in boldness during a scototaxis assay measured as time spent in the white half of the scototaxis tank (Kruskal–Wallis test, $H = 27.451$, $P < 0.001$; Fig. 2d). *Limia perugiae* spent less time in the white zone than each of the other species tested. The other 3 did not differ from one another in boldness (Fig. 3d, Table S1). The best-fit GLM for boldness included mating system as the sole fixed effect, whereas the other competitive model included mating system and standard length. In that model, only mating system showed a significant effect on boldness when controlling for standard length (Table 1).

Route learning

Examination of error rate (number of wrong door entries) across 5 trials revealed no statistically significant effect of trial on the number of wrong door entries (linear mixed-effects model, $F = 1.10$, $n = 122$, $P = 0.267$), but did show a significant effect of species ($F = 4.64$, $n = 122$, $P = 0.0046$; Fig. 3f). Because most reduction in errors occurred over the initial 3 trials, we examined slopes across trials 1 through 3. Both *G. vittata* and *L. perugiae* had a significant reduction in errors across trials 1 to 3 (i.e. error rate slope that significantly differed from 0 [*G. vittata*: $F = 13.84$, $\beta = -0.70$, df = 71, $P < 0.001$; *L. perugiae:* $F = 9.54$, $\beta = -0.67$, df = 85, $P = 0.003$]). Meanwhile, *H. formosa* did not have a slope that significantly differed from 0 ($F = 0.96$, $\beta = -0.20$, df = 75, $P = 0.33$); and *X. nigrensis* had a near-significant positive slope ($F = 3.846$, $\beta = 0.47$, df = 85, $P = 0.05$). In GLMs, the best-fit model explaining error rate slope included solely standard length; however, the effect of standard length was not significant. Fixed effects in the other competitive models were not significant, aside from an effect of standard length when accounting for both mating system and an interaction between mating system and standard length (Table 2).

Route learning: total errors across trials

Species also differed significantly in total number of errors across trials 2 to 5 (Kruskal–Wallis test: $H = 29.83$, df = 3, $P < 0.001$; Fig. 3h). *Gambusia vittata* made fewer errors than all other species (Fig. 3h, Table S2). Each of the other species did not differ from one another in total errors across trials. The best-fit GLM explaining variation in total errors included mating system alone, and the effect of mating system on total errors was significant. This effect held when accounting for variation in standard length (Table 2).

Detour reaching: social motivation

During the detour reaching task, species differed in social motivation (time to reach the barrier: Kruskal–Wallis test, $H = 36.47$, df = 3, $P < 0.001$, Fig. 3g). *Limia perugiae* took a significantly longer time to reach the barrier than all other species. All other species showed similar social motivation times (Fig. 3e, Table S2). The best-fit GLM explaining variation in social motivation included mating system, standard length, and an interaction term between the 2 variables. Only the interaction term was significant (Table 2).

Detour reaching: cognitive flexibility

Species differed significantly in their solve time in the detour reaching assay (time from barrier to social reward: Kruskal–Wallis

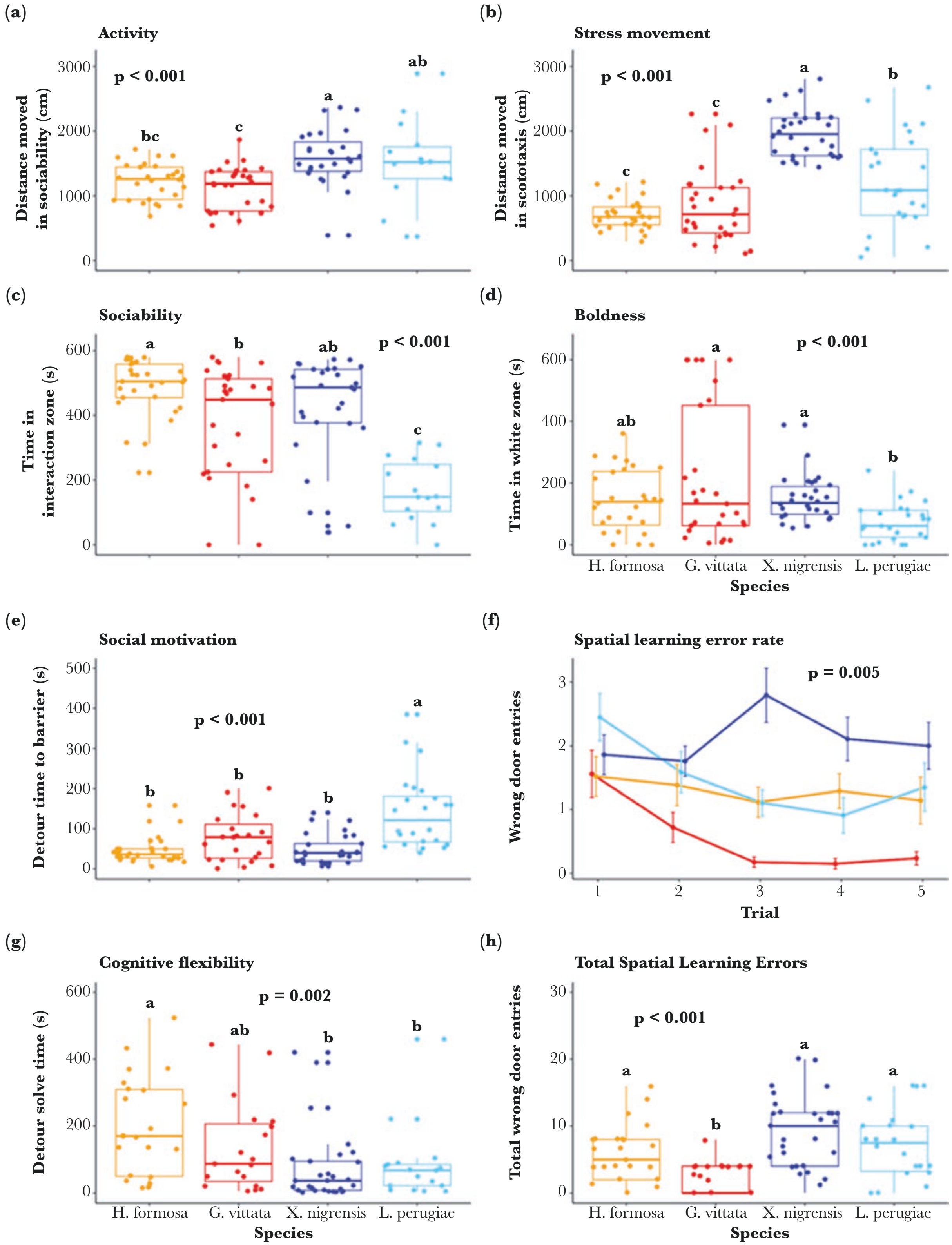


Fig. 3. Behavioral and cognitive traits across species. Species differed in (a) activity (total distance moved in cm) during the shoaling assay, (b) stress movement (total distance moved in cm) in the scototaxis assay, (c) sociability (time spent in the interaction zone (s)) in the shoaling assay, (d) boldness (time spent in the scototaxis white zone (s)), (e) social motivation (time taken to engage with the glass barrier (s) in detour), (f) spatial learning error rate (wrong door entries across trials), (g) inhibitory control (solve time (s) in detour), and (h) spatial learning accuracy (total number of wrong door entries in route learning trials 2 to 5). *P*-value associated with the Kruskal–Wallis test reported for each trait in the panels (a to e) and (g to h). The *P*-value in panel F corresponds to the effect of species in the Generalized Linear Mixed Model (GLMM) run on spatial learning. Lowercase letters in each boxplot correspond to post hoc Dunn's tests conducted between species. GLM results run with each trait as a response variable show consistent results and are reported in Tables 1 and 2.

Table 1. GLM results for behavioral assays. The 4 different GLMs constructed for each response variable measured in the behavioral assays (shoaling and scototaxis). For each trait, the models are ranked by AIC from best fit to worst fit. We also include AIC weight as a measure of the likelihood that a given model is the best fit for that response variable. For each trait's 2 best-fit models, the chi-squared value and *P*-value associated with each fixed effect generated by the ANOVA run on each GLM are reported.

Model	AIC	Δ-AIC	AIC weight	Fixed effect	χ^2 (P-value)
Activity ~ Mating System	1,256.32	0.00	0.54	Mating System	22.94 (1.67e–06)
Activity ~ Mating System + Standard Length	1,257.28	0.95	0.34	Mating System	23.69 (1.13e–06)
				Standard Length	1.02 (0.31)
Activity ~ Mating System * Standard Length	1,259.25	2.93	0.12		
Activity ~ Standard Length	1,276.83	20.50	0.00		
Sociability ~ Mating System + Standard Length	1,131.92	0.00	0.44	Mating System	8.03 (4.61e–03)
				Standard Length	3.1 (7.83e–02)
Sociability ~ Mating System*Standard Length	1,132.87	0.95	0.28	Mating System	0.32 (0.57)
				Standard Length	0.50 (0.48)
				Mating System * Standard Length	1.00 (0.32)
Sociability ~ Mating System	1,133.07	1.15	0.25		
Sociability ~ Standard Length	1,137.86	5.95	0.02		
Stress Movement ~ Mating System + Standard Length	1,454.66	0.00	0.41	Mating System	46.19 (1.08e–11)
				Standard Length	3.68 (0.06)
Stress Movement ~ Mating System * Standard Length	1,454.69	0.02	0.41	Mating System	6.48 (0.01)
				Standard Length	0.0083 (0.93)
				Mating System * Standard Length	1.91 (0.17)
Stress Movement ~ Mating System	1,456.39	1.73	0.18		
Stress Movement ~ Standard Length	1,491.18	36.52	0.00		
Boldness ~ Mating System	1,194.54	0.00	0.49	Mating System	4.29 (0.04)
Boldness ~ Mating System + Standard Length	1,195.70	1.16	0.28	Mating System	6.26 (0.01)
				Standard Length	0.82 (0.37)
Boldness ~ Mating System * Standard Length	1,196.83	2.29	0.16		
Boldness ~ Standard Length	1,199.95	5.41	0.03		

test, $H = 15.015$, df = 3, $P = 0.002$; Fig. 3h) with *H. formosa* taking a significantly longer time to solve than *X. nigrensis*. There were no differences between *G. vittata* and *H. formosa* or between *L. perugiae* and *X. nigrensis* (Fig. 3g, Table S2). The 2 best-fit GLMs explaining variation in cognitive flexibility were one that included mating system, standard length, and an interaction term and a second that included mating system alone. In the first model, when controlling for the other 2 variables, mating system had a significant effect on cognitive flexibility, as did the interaction term. In the second model, mating system alone had a near-significant effect on cognitive flexibility (Table 2).

Cognitive-behavioral syndromes

We evaluated cognitive-behavioral syndromes with 2 multivariate approaches: LDA and SEM. Both approaches converged on "stress movement" as being one of the largest factors separating species and mating systems in behavior and cognition.

Linear discriminant analysis

We found that behavioral and cognitive traits loaded onto 2 distinct axes of variation in an LDA that included 6 measures across our 4 assays: stress movement (total movement in scototaxis), activity (total movement in sociability), boldness (time in white in scototaxis), sociability (time interacting with shoal), cognitive flexibility (detour solve time), and spatial learning (error rate across trials 1 to 3; Fig. 3a). Note for the LDA, we were only able to include species for which we had a complete multivariate dataset at the level of the individual (*X. nigrensis, G. vittata, and H. formosa*). The primary axis (LD1) accounted for 84.6% of the trait variation across species and secondary axis (LD2) accounted for 15.4% (Fig. 4b). LD1 was largely determined by stress movement, whereas LD2 was primarily determined by boldness and, to a lesser extent, sociability (Fig. 4a). The 3 species differed significantly in LD1 scores (ANOVA, $F = 76.45$, df = 2, $P < 0.001$; Fig. 4c). *Xiphophorus nigrensis* had the highest LD1 score (1.89 ± 0.16), diverging from both *G. vittata* (–0.87 ± 0.31; Tukey test, $Z = 2.76$, $P < 0.001$) and *H. formosa* (–1.81 ± 0.21; $Z = 3.71$, $P < 0.001$), which had the lowest LD1 scores (and significantly lower than *G. vittata* ($Z = –0.94$, $P = 0.019$). Species also significantly differed in LD2 scores (ANOVA, $F = 12.1$, $P < 0.001$; Fig. 4d). *Gambusia vittata* females exhibited the highest LD2 scores (0.86 ± 0.26), differing from *X. nigrensis* (–0.17 ± 0.21; Tukey test, $Z = –1.04$, $P = 0.003$) and *H. formosa* (–0.76 ± 0.17; $Z = –1.63$, $P < 0.001$). *Xiphophorus nigrensis* and *H. formosa* did not differ in their LD2 scores ($Z = 0.59$, $P = 0.17$).

Structural equation modeling

To assess the overall syndrome structure, we first standardized the 6 behavioral and cognitive variables in *H. formosa* and *G. vittata*, due to large differences in variance between variables that would affect model convergence. We then constructed 57 models of syndrome structure for each of the 3 species (*X. nigrensis*, *G. vittata*, and *H. formosa*) that underwent all 4 assays. The models included some combination (between 3 and 6 variables) of stress movement, boldness, activity, sociability, cognitive flexibility, and spatial learning. Because we collected data on only 2 assays at a time with *L. perugiae* (sociability and detour for the 2020 group of 30 individuals and route learning and scototaxis for the 2021 group of 30 individuals), we did not construct models of syndrome

Table 2. GLM results for cognitive assays. The 4 different GLMs constructed for each response variable measured in the cognitive assays (detour reaching and route learning). For each trait, the models are ranked by AIC from best fit to worst fit and include AIC weight as a measure of the likelihood that a given model is the best fit for that response variable. For each trait's 2 best-fit models, the chi-squared value and *P*-value associated with each fixed effect generated by the ANOVA run on each GLM are reported.

Model	AIC	Δ-AIC	AIC weight	Fixed effect	χ^2 (*P*-value)
Social Motivation ~ Mating System * Standard Length	960.48	0.00	0.59	Mating System	3.47 (0.06)
				Standard Length	3.16 (0.08)
				Mating System * Standard Length	4.41 (0.04)
Social Motivation ~ Standard Length	962.23	1.75	0.24	Standard Length	41.60 (1.10e–10)
Social Motivation ~ Mating System + Standard Length	962.98	2.50	0.17		
Social Motivation ~ Mating System	990.18	29.70	0.00		
Cognitive Flexibility ~ Mating System * Standard Length	1,247.99	0.00	0.36	Mating System	5.27 (0.02)
				Standard Length	1.74 (0.19)
				Mating System * Standard Length	3.89 (0.05)
Cognitive Flexibility ~ Mating System	1,248.20	0.21	0.32	Mating System	3.70 (0.05)
Cognitive Flexibility ~ Mating System + Standard Length	1,249.97	1.98	0.13		
Cognitive Flexibility ~ Standard Length	1,251.89	3.90	0.05		
Spatial Learning (error rate slope trials 1 to 3) ~ Standard Length	279.59	0.00	0.24	Standard Length	1.99 (0.16)
Spatial Learning (error rate slope trials 1 to 3) ~ Mating System * Standard Length	279.88	0.29	0.21	Mating System	1.70 (0.19)
				Standard Length	4.38 (0.04)
				Mating System * Standard Length	2.28 (0.13)
Spatial Learning (error rate slope trials 1 to 3) ~ Mating System + Standard Length	280.24	0.65	0.17		
Spatial Learning (error rate slope trials 1 to 3) ~ Mating System	280.72	1.13	0.14		
Spatial Learning (total errors trials 1 to 3) ~ Mating System	479.21	0.00	0.60	Mating System	14.25 (1.60e–04)
Spatial Learning (total errors trials 1 to 3) ~ Mating System + Standard Length	480.75	1.54	0.28	Mating System	14.14 (1.70e–04)
				Standard Length	0.44 (0.51)
Spatial Learning (total errors trials 1 to 3) ~ Mating System * Standard Length	482.53	3.32	0.11		
Spatial Learning (total errors trials 1 to 3) ~ Standard Length	492.23	13.03	0.00		

structure for that species. After filtering out models that did not meet our 3 fit criteria, we compared AIC values across 11 models in *G. vittata*, 10 models in *H. formosa*, and 7 models in *X. nigrensis*. We found that each species had a single top-performing model as determined by Δ-AIC. The best-fit model for *X. nigrensis* consisted of detour speed, sociability, boldness, and spatial learning (Fig. 5a). The best-fit model for *G. vittata* consisted of stress movement, activity, detour speed, and sociability (Fig. 5b). The best-fit model for *H. formosa* consisted of stress movement, activity, detour speed, and boldness (Fig. 5c).

Discussion

Comparing these 4 poeciliid fish species, we found (i) no support for our behavioral predictions (sociability, activity, and boldness), (ii) compelling support for our cognitive predictions (cognitive flexibility and spatial learning), and (iii) novel emergent patterns identifying multivariate differences between species with different mating systems. Specifically, although not part of our original predictions, the strongest pattern we found was reduced movement in both a threatening (scototaxis) and nonthreatening (shoaling) context in the 2 all-coercive species relative to mixed-tactic species. Movement traits were also the primary features that differed between all-coercive and mixed-tactic species in cognitive-behavioral syndromes (Table 1; Figs 3, 4 and 5).

Behavioral variation across mating systems

Sociability results only partially conformed to our original predictions, that sociability would be stronger in the all-coercive species. The mixed-tactic species, *L. perugiae*, tended to have the lowest sociability. While this pattern was driven more strongly by mating system when controlling for standard length (Table 1), the mixed-tactic *X. nigrensis* showed a comparable level of sociability to that of the all-coercive species (Fig. 3c). It is possible that a pattern by mating system would have emerged had we used a male stimulus to induce shoaling behavior, such as in previous work (Dadda et al. 2005; Dadda 2015), or if we had tested individuals in free-swimming pairs, rather than focal and stimulus fish separated by a transparent barrier. Boldness patterns also failed to meet our prediction that females from mixed-tactic mating systems would be bolder based on a developmental rearing experiment

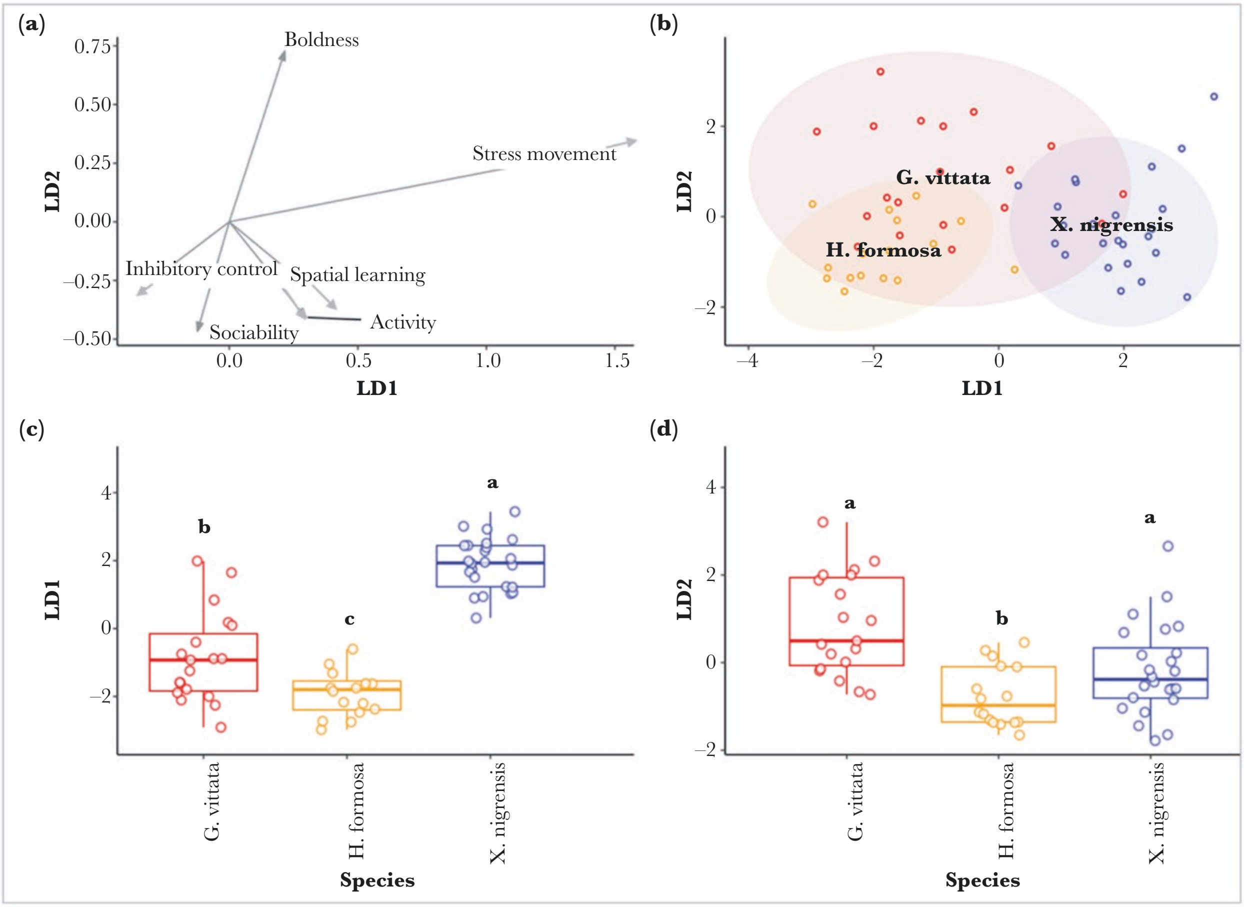


Fig. 4. Cognitive-behavioral profiles across species. LDA results show the axes in multivariate space that maximize differences in behavioral and cognitive traits across the 3 species included. (a) Linear discriminant loadings of each of the behavioral and cognitive traits onto the LD1 and LD2 axes. (b) Species-specific point clouds of the LDA results. The point clouds contain all values within the 95% confidence interval for the mean LD1 and LD2 scores of each species. The points represent individuals of each species. (c) LD1 scores across species. (d) LD2 scores across species. Letters indicate significant post hoc differences between species (Tukey test, $P < 0.05$).

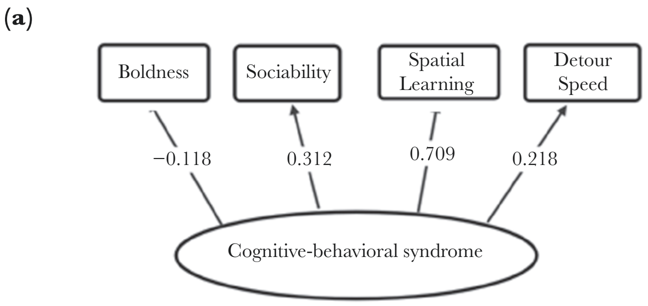
with *X. nigrensis* (Queller et al. 2022). Both coercive-only (*G. vittata*) and mixed-tactic (*X. nigrensis*) species showed high levels of boldness. The strongest behavioral pattern by mating system, however, was lower movement in all-coercive species in both a threatening context (stress movement during scototaxis, Fig. 3b; Table 1) and a neutral context (activity during shoaling; Fig. 3a, Table 1). Although species showed a similar pattern of variation in both contexts, the difference between the most active species (the mixed-tactic *X. nigrensis*) and the 2 all-coercive species (*G. vittata* and *H. formosa*) more than doubled in the threatening context (Fig. 3a and b). Importantly, mating system had a strong effect on stress movement and activity even when controlling for standard length (Table 1). This covariation of movement pattern with mating system across species runs counter to our prediction that baseline activity would be higher in all-coercive species. It differs from findings with water striders (Wey et al. 2015) and guppies (Killen et al. 2016), wherein lower activity females appear more vulnerable to unsolicited mating attempts by males.

We suggest a novel explanation for the unexpected pattern of reduced movement in females of all-coercive species. Specifically, females in exclusively coercive environments may have lower movement as a means of avoiding detection by coercive males.

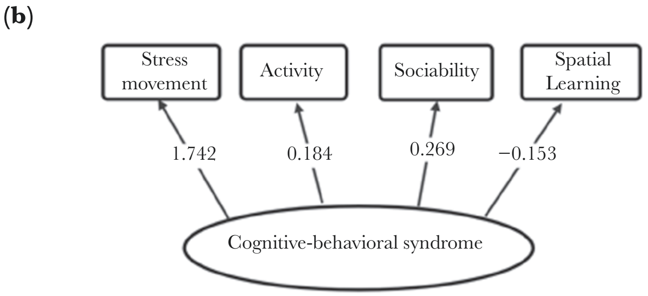
Because females in all-coercive mating systems have reduced opportunities to choose mates prior to mating (Ojanguren and Magurran 2007; Yang et al. 2023), they are under strong selective pressure to avoid male harassment and reduce the likelihood of unwanted mating attempts. One means of avoiding male harassment might involve “freezing,” or evading detection by a threat through background matching or other forms of crypsis (Eilam 2005; Staudinger et al. 2011; Yilmaz and Meister 2013; Brunyé et al. 2018). Because freezing involves preempting a threat rather than reacting to it, it often carries over to baseline activity measures (Edut and Eilam 2004; Eilam 2005). Comparative work on anuran tadpoles (Lawler 1989; Richardson 2001), dragonfly larvae (McPeek 1990), and damselfly larvae (Strobbe et al. 2011; Jiang and Mikolajewski 2018) has shown that high-predation environments favor reduced movement across contexts. Here, we suggest that, in the absence of predation, generalized freezing behavior may also play a role in a social context by facilitating female avoidance of costly interactions with males. To confirm the potential role of movement in mating interactions, future studies will have to assess whether females with lower baseline activity and stress movement are indeed more effective at preemptively avoiding male harassment in all-coercive poeciliid mating systems.

Cognitive variation by mating system

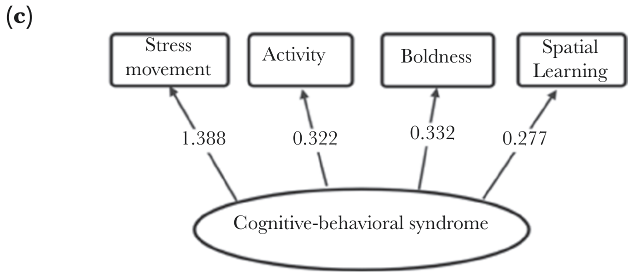
The females of mixed-tactic species tended to outperform all-coercive species in a measure of inhibitory control or cognitive



***X. nigrensis* top model**



***G. vittata* top model**



***H. formosa* top model**

Fig. 5. The best-fit SEM (as determined by AIC comparisons), along with standardized path coefficients, is shown for each species. These coefficients indicate the magnitude and direction of each variable's contribution to the overall syndrome structure. The best-fit model for (a) *X. nigrensis*, (b) *G. vittata*, and (c) *H. formosa*.

flexibility (latency to solve the detour task; Fig. 3g). These results align with the idea that female cognitive flexibility will be higher in mixed-tactic mating systems that place greater demands on female social cognition to make complex mating decisions (Houde 1997; Cummings and Ramsey 2015; Corral-López et al. 2017). A broad array of comparative studies has shown links between various measures of cognitive flexibility and social complexity, in corvids (Bond et al. 2007), primates (Amici et al. 2008), and hyenas (Johnson-Ulrich and Holekamp 2020).

Variation in cognitive flexibility can also be understood in relation to different levels of complexity in male–female communication. In the 2 species with courtship (*X. nigrensis* and *L. perugiae*), females receive and must appropriately respond to courtship displays by males; whereas males in coercive mating systems do not display and attempt to avoid detection to successfully copulate with females. Across a wide range of taxa, social complexity drives the evolution of both communicative complexity and enhanced learning of novel signals (Freeberg et al. 2012; Sewall 2015). For example, avian species that have more complex vocal learning abilities associated with greater male signal elaboration have been shown to have higher cognitive flexibility and problem-solving abilities (Audet et al. 2023). This is likely linked to increases in neuronal density and computational power that improve both communication and cognition (Audet et al. 2023). Thus, greater cognitive flexibility might also evolve in tandem with these traits as either a byproduct of selection for improved signal learning or because of advantages it confers in a more complex social realm.

While the 2 mixed-tactic species outperformed the 2 all-coercive species in a measure of cognitive flexibility, we found a very different pattern when examining spatial learning. Our findings suggest that spatial learning performance may trade off with cognitive flexibility in some of these species. The species with the best evidence of spatial learning in females (*G. vittata*, Fig. 3f and h) is an exclusively coercive species with high rates of male coercion (see supplemental material). *Gambusia vittata* females showed the strongest evidence for learning in the spatial task, coupled with lower cognitive flexibility performance in the detour task. Meanwhile, females from the mixed-tactic *X. nigrensis* were both the fastest of the 4 species to solve the cognitive flexibility task while showing no evidence for learning in the spatial learning task. Our results mirror a developmental study in *X. nigrensis* that found higher spatial learning accuracy in females raised in the presence of males employing a single mating tactic (coercion or courtship) than females raised in environments with both male tactics (Queller et al. 2023). These results conform to the broad pattern of memory-flexibility tradeoffs across bird species (Tello-Ramos et al. 2019). Bird species and populations with high rates of food caching have higher spatial memory (Tello-Ramos et al. 2018) but are worse than those with lower food caching at cognitive flexibility tasks (Hampton et al. 1998; Croston et al. 2017). Proactive interference, in which previously learned information interferes with learning new information, might explain why females of all-coercive species have low cognitive flexibility but stronger spatial learning as they may benefit from retaining information about safe refuges from harassment. Stable environments are expected to favor memory retention over cognitive flexibility due to the reliability of cues in the environment, and perhaps social environments with single mating tactics fit that mold. On the other hand, species that are met with constantly changing information about the environment, such as females in mixed-tactic mating systems, might benefit from having neural processes favoring flexibility over memory so that new associations can be more easily learned (Lewis and Kamil 2006; Tello-Ramos et al. 2019). While additional work will be required to confirm a link between cognitive performance and female mating decisions, our cognition results suggest that retention of information might be favored in highly coercive environments, whereas dynamic, mixed-tactic environments favor flexibility and responsiveness to novel inputs.

Cognitive-behavioral syndromes

Our characterization of female cognitive-behavioral syndromes across species (Fig. 4) and within species (Fig. 5) revealed that a specific combination of movement and cognition traits best defined the differences between all-coercive and mixed-tactic species in this study. Our multivariate analysis of cognitive-behavioral profiles revealed stress movement as the largest contributor to divergence among species, separating *X. nigrensis* from the 2 all-coercive species (LD1 scores in Fig. 4). Movement patterns (both activity and stress movement) along with spatial learning contributed to cognitive-behavioral syndrome structure only in the all-coercive species, *G. vittata* and *H. formosa* (Fig. 5). The presence of spatial learning and the 2 movement traits in the best-fit syndrome structure found using SEM suggests that all-coercive species might show a movement-cognition syndrome. This is consistent with a broader pattern of "slow" and "fast" behavioral types (Sih and Del Giudice 2012). "Slow" behavioral types tend to be less active and more accurate at solving tasks, whereas "fast" animals tend to be more active and faster at solving tasks. As a result, "Fast" animals tend to reap more short-term rewards while also incurring more risks. On the other hand, "slow" animals tend to be safer, but collect fewer rewards in the short term. Because females of all-coercive species inhabit environments where they are subject to high rates of male harassment, females might benefit from reduced movement to avoid detection by males and improved memory retention when movement (and increased exposure) is costly. Thus, the 2 all-coercive species seem to show a distinct "slow" cognitive-behavioral syndrome that is consistent with theory (Sih 1992) and empirical studies (Burns and Rodd 2008) about optimal decision-making in risky environments.

Conclusions and future directions

While our results derive from a limited number of poeciliid species, and thus cannot be generalized across the family, they provide some interesting possibilities as to the consequences of mating system variation for female behavior and cognition outside of mating. Specifically, our findings suggest that male mating tactics might play a role in shaping female movement and 2 domains of cognitive performance. Cognitive-behavioral syndrome structures mirror these findings: movement traits and spatial learning contribute to syndrome structure in both all-coercive species studied here. Meanwhile, cognitive flexibility contributes to syndrome structure uniquely in the mixed-tactic species, *X. nigrensis*. Notably, we observed these patterns in populations experiencing uniform, low-predation conditions for multiple generations in our outdoor mesocosms. By limiting the influence of confounding ecological variables that might affect behavioral development and evolution, our comparative study suggests that female behavior, cognition, and cognitive-behavioral syndromes can covary with male mating tactics and highlights the potential role of sexual selection in the emergence of these traits. While our findings across 4 species from disparate poeciliid clades are suggestive of important patterns by mating system, it will be crucial for future comparative studies to broaden sampling by examining these traits in other members of the family. Future studies should also consider finer-scale comparisons among members of the same genus with different mating systems, which allows for differences in phylogenetic relatedness to be more easily controlled. Additionally, while our study controlled for the influence of predation regime and habitat complexity on developmental and short evolutionary timescales by comparing species from predation-free and ecologically identical mesocosms, we cannot fully rule out the historical influence of ecological variables as contributors to species differences in behavior and cognition. Determining whether these findings in seminatural conditions hold among wild populations of poeciliids that experience predation and other variable ecological conditions will be critical in assessing the relative contributions of sexual selection and natural selection to behavioral and cognitive traits across species.

Supplementary material

Supplementary material is available at *Behavioral Ecology* online.

Acknowledgments

We thank Tuyet Tra, Hayes Koegeboehn, and Kayla Daly for playing integral roles in data collection for this manuscript. We thank the staff at the University of Texas Brackenridge Field Laboratories for the long-term maintenance of fish populations. We thank members of the Cummings Lab for their helpful feedback on earlier versions of the manuscript.

Funding

The authors thank NSF (IOS-1911826 award to MEC) and the UT Austin College of Natural Sciences for funding this research.

Author contributions

Callen Inman (Conceptualization [equal], Formal analysis [lead], Writing—original draft [lead], Writing—review & editing [lead]), Alan Vuong (Data curation [equal]), Ingo Schlupp (Resources [supporting], Writing—review & editing [supporting]), and Molly Cummings (Conceptualization [equal], Writing—original draft [supporting], Writing—review & editing [equal])

Data availability

Analyses reported in this article can be reproduced using the data provided by Inman et al. (2025).

References

Agrillo C, Dadda M, Bisazza A. 2006. Sexual harassment influences group choice in female mosquitofish. Ethology. 112:592–598. https://doi.org/10.1111/j.1439-0310.2006.01188.x.

Amici F, Aureli F, Call J. 2008. Fission-fusion dynamics, behavioral flexibility, and inhibitory control in primates. Curr Biol. 18:1415–1419. https://doi.org/10.1016/j.cub.2008.08.020.

Audet J-N, Couture M, Jarvis ED. 2023. Songbird species that display more-complex vocal learning are better problem-solvers and have larger brains. Science. 381:1170–1175. https://doi.org/10.1126/science.adh3428.

Badre D, Wagner AD. 2006. Computational and neurobiological mechanisms underlying cognitive flexibility. Proc Natl Acad Sci USA. 103:7186–7191. https://doi.org/10.1073/pnas.0509550103.

Bell A. 2013. Randomized or fixed order for studies of behavioral syndromes? Behav Ecol. 24:16–20. https://doi.org/10.1093/beheco/ars148.

Bentler P, Bonett D. 1980. Significance tests and goodness-of-fit in analysis of covariance structures. Psychol Bull. 88:588–606. https://doi.org/10.1037/0033-2909.88.3.588.

Bisazza A. 1993. Male competition, female mate choice and sexual size dimorphism in poeciliid fishes. Mar Behav Physiol. 23:257–286. https://doi.org/10.1080/10236249309378869.

Bisazza A, Marin G. 1995. Sexual selection and sexual size dimorphism in the eastern mosquitofish *Gambusia holbrooki* (Pisces Poeciliidae). Ethol Ecol Evol. 7:169–183. https://doi.org/10.1080/08927014.1995.9522963.

Blaszczyk MB. 2017. Boldness towards novel objects predicts predator inspection in wild vervet monkeys. Anim Behav. 123:91–100. https://doi.org/10.1016/j.anbehav.2016.10.017.

Bon R, Campan R. 1996. Unexplained sexual segregation in polygamous ungulates: a defense of an ontogenetic approach. Behav Process. 38:131–154. https://doi.org/10.1016/s0376-6357(96)00029-0.

Bond AB, Kamil AC, Balda RP. 2007. Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica*). J. Comp. Psychol. 121:372–379. https://doi.org/10.1037/0735-7036.121.4.372.

Booksmythe I, Head ML, Keogh JS, Jennions MD. 2016. Fitness consequences of artificial selection on relative male genital size. Nat Commun. 7:11597. https://doi.org/10.1038/ncomms11597.

Brask JB, Croft DP, Thompson K, Dabelsteen T, Darden SK. 2011. Social preferences based on sexual attractiveness: a female strategy to reduce male sexual attention. Proc R Soc B-Biol Sci. 279:1748–1753. https://doi.org/10.1098/rspb.2011.2212.

Brennan PLR, Prum RO. 2015. Mechanisms and evidence of genital coevolution: the roles of natural selection, mate choice, and sexual conflict. Cold Spring Harb Perspect Biol. 7:a017749. https://doi.org/10.1101/cshperspect.a017749.

Brown C, Burgess F, Braithwaite VA. 2007. Heritable and experiential effects on boldness in a tropical poeciliid. Behav Ecol Sociobiol. 62:237–243. https://doi.org/10.1007/s00265-007-0458-3.

Brunyé TT, Martis SB, Horner C, Kirejczyk JA, Rock K. 2018. Visual salience and biological motion interact to determine camouflaged target detectability. Appl Ergon. 73:1–6. https://doi.org/10.1016/j.apergo.2018.05.016.

Buechel SD, Booksmythe I, Kotrschal A, Jennions MD, Kolm N. 2016. Artificial selection on male genitalia length alters female brain size. Proc Biol Sci. 283:20161796. https://doi.org/10.1098/rspb.2016.1796.

Burns JG, Rodd FH. 2008. Hastiness, brain size and predation regime affect the performance of wild guppies in a spatial memory task. Anim Behav. 76:911–922. https://doi.org/10.1016/j.anbehav.2008.02.017.

Calabrese G, Brady P, Gruev V, Cummings ME. 2014. Polarization signaling in swordtails alters female mate preference. Proc Natl Acad Sci USA. 111:13397–13402. https://doi.org/10.1073/pnas.1321368111.

Carvalho APS, St Laurent RA, Toussaint EFA, Storer C, Dexter KM, Aduse-Poku K, Kawahara AY. 2021. Is sexual conflict a driver of speciation? A case study with a tribe of brush-footed butterflies. Syst Biol. 70:413–420. https://doi.org/10.1093/sysbio/syaa070.

Corral-López A, Bloch NI, Kotrschal A, van der Bijl W, Buechel SD, Mank JE, Kolm N. 2017. Female brain size affects the assessment of male attractiveness during mate choice. Sci Adv. 3:e1601990. https://doi.org/10.1126/sciadv.1601990.

Corral-López A, Romensky M, Kotrschal A, Buechel SD, Kolm N. 2020. Brain size affects responsiveness in mating behaviour to variation in predation pressure and sex ratio. J Evol Biol. 33:165–177. https://doi.org/10.1111/jeb.13556.

Croston R, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Parchman TL, Pravosudov VV. 2017. Predictably harsh environment is associated with reduced cognitive flexibility in wild food-caching mountain chickadees. Anim Behav. 123:139–149. https://doi.org/10.1016/j.anbehav.2016.10.004.

Culumber ZW, Engel N, Travis J, Hughes KA. 2020. Larger female brains do not reduce male sexual coercion. Anim Behav. 160:15–24. https://doi.org/10.1016/j.anbehav.2019.11.018.

Culumber ZW, Tobler M. 2017. Sex-specific evolution during the diversification of live-bearing fishes. Nat Ecol Evol. 1:1185–1191. https://doi.org/10.1038/s41559-017-0233-4.

Cummings ME. 2018. Sexual conflict and sexually dimorphic cognition—reviewing their relationship in poeciliid fishes. Behav Ecol Sociobiol. 72:1–13. doi: https://link.springer.com/article/10.1007/s00265-018-2483-9.

Cummings ME, Endler JA, Fuller RC. 2018. 25 years of sensory drive: the evidence and its watery bias. Curr Zool. 64:471–484. https://doi.org/10.1093/cz/zoy043.

Cummings ME, Ramsey ME. 2015. Mate choice as social cognition: predicting female behavioral and neural plasticity as a function of alternative male reproductive tactics. Curr Opin Behav Sci. 6:125–131. https://doi.org/10.1016/j.cobeha.2015.10.001.

Cummings ME, Rosenthal GG, Ryan MJ. 2003. A private ultraviolet channel in visual communication. Proc Biol Sci. 270:897–904. https://doi.org/10.1098/rspb.2003.2334.

D'Amore DM, Popescu VD, Morris MR. 2019. The influence of the invasive process on behaviours in an intentionally introduced hybrid, Xiphophorus helleri–maculatus. Animal Behaviour 156:79–85. doi:10.1016/j.anbehav.2019.08.009.

Dadda M. 2015. Female social response to male sexual harassment in poeciliid fish: a comparison of six species. Front Psychol. 6:1453. https://doi.org/10.3389/fpsyg.2015.01453.

Dadda M, Pilastro A, Bisazza A. 2005. Male sexual harassment and female schooling behaviour in the eastern mosquitofish. Anim Behav. 70:463–471. https://doi.org/10.1016/j.anbehav.2004.12.010.

Darden SK, Croft DP. 2008. Male harassment drives females to alter habitat use and leads to segregation of the sexes. Biol Lett. 4:449–451. https://doi.org/10.1098/rsbl.2008.0308.

Dochtermann NA, Dingemanse NJ. 2013. Behavioral syndromes as evolutionary constraints. Behav Ecol. 24:806–811. https://doi.org/10.1093/beheco/art002.

DuVal EH, Adkins-Regan AEE, Bronstein EJL. 2013. Female mate fidelity in a lek mating system and its implications for the evolution of cooperative lekking behavior. Am Nat. 181:213–222. https://doi.org/10.1086/668830.

Edut S, Eilam D. 2004. Protean behavior under barn-owl attack: voles alternate between freezing and fleeing and spiny mice flee in alternating patterns. Behav Brain Res. 155:207–216. https://doi.org/10.1016/j.bbr.2004.04.018.

Eilam D. 2005. Die hard: a blend of freezing and fleeing as a dynamic defense—implications for the control of defensive behavior. Neurosci Biobehav Rev. 29:1181–1191. https://doi.org/10.1016/j.neubiorev.2005.03.027.

Erbelding-Denk C, Schröder JH, Schartl M, Nanda I, Schmid M, Epplen JT. 1994. Male polymorphism in *Limia perugiae* (Pisces: Poeciliidae). Behav Genet. 24:95–101. https://doi.org/10.1007/BF01067933.

Farr JA, Travis J. 1986. Fertility Advertisement by female sailfin mollies, *Poecilia latipinna* (Pisces: Poeciliidae). Copeia. 1986:467–472. https://doi.org/10.2307/1445004.

Fraser DF, Gilliam JF, Daley MJ, Le AN, Skalski GT. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. Am Nat. 158:124–135. https://doi.org/10.1086/321307.

Freeberg TM, Dunbar RIM, Ord TJ. 2012. Social complexity as a proximate and ultimate factor in communicative complexity. Philos Trans R Soc Lond Ser B. 367:1785–1801. https://doi.org/10.1098/rstb.2011.0213.

Furness AI, Pollux BJA, Meredith RW, Springer MS, Reznick DN. 2019. How conflict shapes evolution in poeciliid fishes. Nat Commun. 10:3335. https://doi.org/10.1038/s41467-019-11307-5.

Griebling HJ, Rios-Cardenas O, Abbot J, Morris MR. 2020. A study of tactical and sexual dimorphism in cognition with insights for sexual conflict. Anim Behav. 170:43–50. https://doi.org/10.1016/j.anbehav.2020.10.006.

Hampton RR, Shettleworth SJ, Westwood RP. 1998. Proactive interference, recency, and associative strength: comparisons of black-capped chickadees and dark-eyed juncos. Anim Learn Behav. 26:475–485. https://doi.org/10.3758/bf03199241.

He P, Maldonado-Chaparro AA, Farine DR. 2019. The role of habitat configuration in shaping social structure: a gap in studies of animal social complexity. Behav Ecol Sociobiol. 73:9. https://doi.org/10.1007/s00265-018-2602-7.

Houde AE. 1997. Sex, color, and mate choice in guppies. Princeton, NJ: Princeton University Press [accessed 2023 Nov 24]. https://www.jstor.org/stable/j.ctvs32rtk.

Hu L, Bentler PM. 1999. Cutoff criteria for fit indexes in covariance structure analysis: Conventional criteria versus new alternatives. Struct Equ Modeling. 6:1–55. https://doi.org/10.1080/10705519909540118.

Huang P, St.Mary CM, Kimball RT. 2020. Habitat urbanization and stress response are primary predictors of personality variation in northern cardinals (*Cardinalis cardinalis*). J Urban Ecol. 6:juaa015. https://doi.org/10.1093/jue/juaa015.

Inman CM, Vuong A, Schlupp IB, Cummings ME. 2025. Data from: Male mating tactics are associated with distinct female cognitive-behavioral profiles in four poeciliids. Behav Ecol 34. https://doi.org/10.5061/dryad.d51c5b0bb.

Jiang B, Mikolajewski DJ. 2018. Shift in predation regime mediates diversification of foraging behaviour in a dragonfly genus. Ecol Entomol. 43:525–533. https://doi.org/10.1111/een.12530.

Jirotkul M. 1999. Operational sex ratio influences female preference and male–male competition in guppies. Anim Behav. 58:287–294. https://doi.org/10.1006/anbe.1999.1149.

Johnson-Ulrich L, Holekamp KE. 2020. Group size and social rank predict inhibitory control in spotted hyaenas. Anim Behav. 160:157–168. https://doi.org/10.1016/j.anbehav.2019.11.020.

Killen SS, Croft DP, Salin K, Darden SK. 2016. Male sexually coercive behaviour drives increased swimming efficiency in female guppies. Funct Ecol. 30:576–583. https://doi.org/10.1111/1365-2435.12527.

Kodric-Brown A, Nicoletto PF. 1996. Consensus among females in their choice of males in the guppy *Poecilia reticulata*. Behav Ecol Sociobiol. 39:395–400. https://doi.org/10.1007/s002650050306.

Kwan L, Cheng YY, Rodd FH, Rowe L. 2013. Sexual conflict and the function of genitalic claws in guppies (*Poecilia reticulata*). Biol Lett. 9:20130267. https://doi.org/10.1098/rsbl.2013.0267.

Lawler SP. 1989. Behavioural responses to predators and predation risk in four species of larval anurans. Anim Behav. 38:1039–1047. https://doi.org/10.1016/s0003-3472(89)80142-3.

Lewis J, Kamil A. 2006. Interference effects in the memory for serially presented locations in Clark's nutcrackers, *Nucifraga columbiana*. J Exp Psychol Anim Behav Process. 32:407–418. https://doi.org/10.1037/0097-7403.32.4.407.

Lynch KS, Ramsey ME, Cummings ME. 2012. The mate choice brain: comparing gene profiles between female choice and male coercive poeciliids. Genes Brain Behav. 11:222–229. https://doi.org/10.1111/j.1601-183X.2011.00742.x.

Magnhagen C, Hellström G, Borcherding J, Heynen M. 2012. Boldness in two perch populations—long-term differences and the effect of predation pressure. J Anim Ecol. 81:1311–1318. https://doi.org/10.1111/j.1365-2656.2012.02007.x.

Magurran AE, Seghers BH. 1997. Sexual conflict as a consequence of ecology: evidence from guppy, *Poecilia reticulata*, populations in Trinidad. Proc R Soc Lond B Biol Sci. 255:31–36. https://doi.org/10.1098/rspb.1994.0005.

Makowicz AM, Tanner JC, Dumas E, Siler CD, Schlupp I. 2016. Pre-existing biases for swords in mollies (Poecilia). Behav Ecol. 27:175–184. https://doi.org/10.1093/beheco/arv130.

Maximino C, da Silva AWB, Gouveia A, Herculano AM. 2011. Pharmacological analysis of zebrafish (*Danio rerio*) scototaxis. Prog Neuropsychopharmacol Biol Psychiatry. 35:624–631. https://doi.org/10.1016/j.pnpbp.2011.01.006.

Maximino C, Marques de Brito T, Dias CAG de M, Gouveia A, Morato S. 2010. Scototaxis as anxiety-like behavior in fish. Nat Protoc. 5:209–216. https://doi.org/10.1038/nprot.2009.225.

McPeek MA. 1990. Behavioral differences between Enallagma species (odonata) influencing differential vulnerability to predators. Ecology. 71:1714–1726. https://doi.org/10.2307/1937580.

Mitoyen C, Quigley C, Fusani L. 2019. Evolution and function of multimodal courtship displays. Ethology. 125:503–515. https://doi.org/10.1111/eth.12882.

Ojanguren AF, Magurran AE. 2007. Male harassment reduces short-term female fitness in guppies. Behaviour. 144:503–514. https://doi.org/10.1163/156853907780713055.

Orbach DN, Hedrick B, Würsig B, Mesnick SL, Brennan PLR. 2018. The evolution of genital shape variation in female cetaceans. Evolution. 72:261–273. https://doi.org/10.1111/evo.13395.

Pilastro A, Benetton S, Bisazza A. 2003. Female aggregation and male competition reduce costs of sexual harassment in the mosquitofish *Gambusia holbrooki*. Anim Behav. 65:1161–1167. https://doi.org/10.1006/anbe.2003.2118.

Pilastro A, Giacomello E, Bisazza A. 1997. Sexual selection for small size in male mosquitofish (*Gambusia holbrooki*). Proc R Soc Lond B Biol Sci. 264:1125–1129. https://doi.org/10.1098/rspb.1997.0155.

Plath M, Makowicz AM, Schlupp I, Tobler M. 2007. Sexual harassment in live-bearing fishes (Poeciliidae): comparing courting and noncourting species. Behav Ecol. 18:680–688. https://doi.org/10.1093/beheco/arm030.

Plath M, Schlupp I. 2008. Parallel evolution leads to reduced shoaling behavior in two cave dwelling populations of Atlantic mollies (*Poecilia mexicana*, Poeciliidae, Teleostei). Environ Biol Fish. 82:289–297. https://doi.org/10.1007/s10641-007-9291-9.

Queller PS, Adams ERM, Cummings ME. 2023. Life-long experience with male mating tactics shapes spatial cognition and coercion evasion in female swordtails. Fishes. 8:562. https://doi.org/10.3390/fishes8110562.

Queller PS, Shirali Y, Wallace KJ, DeAngelis RS, Yurt V, Reding LP, Cummings ME. 2022. Complex sexual-social environments produce high boldness and low aggression behavioral syndromes. Front Ecol Evol. 10. https://doi.org/10.3389/fevo.2022.1050569.

Ramsey ME, Vu W, Cummings ME. 2014. Testing synaptic plasticity in dynamic mate choice decisions: N-methyl d-aspartate receptor blockade disrupts female preference. Proc Biol Sci. 281:20140047. https://doi.org/10.1098/rspb.2014.0047.

Rehage JS, Sih A. 2004. Dispersal behavior, boldness, and the link to invasiveness: a comparison of four gambusia species. Biol Invasions. 6:379–391. https://doi.org/10.1023/b:binv.0000034618.93140.a5.

Reznick DN, Furness AI, Meredith RW, Springer MS. 2017. The origin and biogeographic diversification of fishes in the family Poeciliidae. PLoS One. 12:e0172546. https://doi.org/10.1371/journal.pone.0172546.

Richardson JML. 2001. A comparative study of activity levels in larval anurans and response to the presence of different predators. Behav Ecol. 12:51–58. https://doi.org/10.1093/oxfordjournals.beheco.a000378.

Rios-Cardenas O, Tudor MS, Morris MR. 2007. Female preference variation has implications for the maintenance of an alternative mating strategy in a swordtail fish. Anim Behav. 74:633–640. https://doi.org/10.1016/j.anbehav.2007.01.002.

Rosseel Y. 2012. lavaan: an R package for structural equation modeling. J Stat Softw. 48:1–36. https://doi.org/10.18637/jss.v048.i02.

Roth TC, LaDage LD, Freas CA, Pravosudov VV. 2011. Variation in memory and the hippocampus across populations from different climates: a common garden approach. Proc R Soc B-Biol Sci. 279:402–410. https://doi.org/10.1098/rspb.2011.1020.

Rowe L, Krupa JJ, Sih A. 1996. An experimental test of condition-dependent mating behavior and habitat choice by water striders in the wild. Behav Ecol. 7:474–479. https://doi.org/10.1093/beheco/7.4.474.

Ryan MJ, Akre KL, Baugh AT, Bernal XE, Lea AM, Leslie C, Still MB, Wylie DC, Rand AS. 2019. Nineteen years of consistently positive and strong female mate preferences despite individual variation. Am Nat. 194:125–134. https://doi.org/10.1086/704103.

Ryan MJ, Causey BA. 1989. "Alternative" mating behavior in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus* (Pisces: Poeciliidae). Behav Ecol Sociobiol. 24:341–348. https://doi.org/10.1007/bf00293262.

Schermelleh-Engel K, Moosbrugger H, Müller H. 2003. Evaluating the fit of structural equation models: tests of significance and descriptive goodness-of-fit measures. Methods Psychol Res. 8:23–74.

Schlupp I, Riesch R, Tobler M, Plath M, Parzefall J, Schartl M. 2010. A novel, sexually selected trait in poeciliid fishes: female preference for mustache-like, rostral filaments in male *Poecilia sphenops*. Behav Ecol Sociobiol. 64:1849–1855. https://doi.org/10.1007/s00265-010-0996-y.

Schlüter A, Parzefall J, Schlupp I. 1998. Female preference for symmetrical vertical bars in male sailfin mollies. Anim Behav. 56:147–153. https://doi.org/10.1006/anbe.1998.0762.

Schrader M, Apodaca JJ, Macrae PSD, Travis J. 2012. Population density does not influence male gonadal investment in the Least Killifish, *Heterandria formosa*. Ecol Evol. 2:2935–2942. https://doi.org/10.1002/ece3.402.

Sewall KB. 2015. Social complexity as a driver of communication and cognition. Integr Comp Biol. 55:384–395. https://doi.org/10.1093/icb/icv064.

Shettleworth SJ. 2010. Cognition, evolution, and behavior. 2nd ed. New York (NY): Oxford University Press.

Sih A. 1992. Prey uncertainty and the balancing of antipredator and feeding needs. Am Nat. 139:1052–1069. https://doi.org/10.1086/285372.

Sih A, Del Giudice M. 2012. Linking behavioural syndromes and cognition: a behavioural ecology perspective. Philos Trans R Soc Lond Ser B. 367:2762–2772. https://doi.org/10.1098/rstb.2012.0216.

Silk JB. 2007. Social components of fitness in primate groups. Science. 317:1347–1351. https://doi.org/10.1126/science.1140734.

Staudinger MD, Hanlon RT, Juanes F. 2011. Primary and secondary defences of squid to cruising and ambush fish predators: variable tactics and their survival value. Anim Behav. 81:585–594. https://doi.org/10.1016/j.anbehav.2010.12.002.

Strobbe F, McPeek MA, De Block M, Stoks R. 2011. Fish predation selects for reduced foraging activity. Behav Ecol Sociobiol. 65:241–247. https://doi.org/10.1007/s00265-010-1032-y.

Sugawara HM, MacCallum RC. 1993. Effect of estimation method on incremental fit indexes for covariance structure models. Appl Psychol Meas. 17:365–377. https://doi.org/10.1177/014662169301700405.

Takami Y, Sota T. 2007. Rapid diversification of male genitalia and mating strategies in Ohomopterus ground beetles. J Evol Biol. 20:1385–1395. https://doi.org/10.1111/j.1420-9101.2007.01338.x.

Tello-Ramos MC, Branch CL, Kozlovsky DY, Pitera AM, Pravosudov VV. 2019. Spatial memory and cognitive flexibility trade-offs: to be or not to be flexible, that is the question. Anim Behav. 147:129–136. https://doi.org/10.1016/j.anbehav.2018.02.019.

Tello-Ramos MC, Branch CL, Pitera AM, Kozlovsky DY, Bridge ES, Pravosudov VV. 2018. Memory in wild mountain chickadees from different elevations: comparing first-year birds with older survivors. Anim Behav. 137:149–160. https://doi.org/10.1016/j.anbehav.2017.12.019.

Uy JAC, Patricelli GL, Borgia G. 2001. Complex mate searching in the satin bowerbird *Ptilonorhynchus violaceus*. Am Naturalist. 158:530–542. https://doi.org/10.1086/323118.

van Horik JO, Langley EJG, Whiteside MA, Laker PR, Beardsworth CE, Madden JR. 2018. Do detour tasks provide accurate assays of inhibitory control? Proc Biol Sci. 285:20180150. https://doi.org/10.1098/rspb.2018.0150.

Wagenmakers E-J, Farrell S. 2004. AIC model selection using Akaike weights. Psychon Bull Rev. 11:192–196. https://doi.org/10.3758/bf03206482.

Wang S, Cummings M, Kirkpatrick M. 2015. Coevolution of male courtship and sexual conflict characters in mosquitofish. Behav Ecol. 26:1013–1020. https://doi.org/10.1093/beheco/arv049.

Wey TW, Chang AT, Montiglio P-O, Fogarty S, Sih A. 2015. Linking short-term behavior and personalities to feeding and mating rates in female water striders. Behav Ecol. 26:1196–1202. https://doi.org/10.1093/beheco/arv065.

White GE, Brown C. 2014. A comparison of spatial learning and memory capabilities in intertidal gobies. Behav Ecol Sociobiol. 68:1393–1401. https://doi.org/10.1007/s00265-014-1747-2.

Wilson DS, Coleman K, Clark AB, Biederman L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. J Comp Psychol. 107:250–260. https://doi.org/10.1037/0735-7036.107.3.250.

Wong RY, Cummings ME. 2014. Expression patterns of neuroligin-3 and tyrosine hydroxylase across the brain in mate choice contexts in female swordtails. Brain Behav Evol. 83:231–243. https://doi.org/10.1159/000360071.

Wong RY, So P, Cummings ME. 2011. How female size and male displays influence mate preference in a swordtail. Anim Behav. 82:691–697. https://doi.org/10.1016/j.anbehav.2011.06.024.

Yang Y, Grant E, López-Sepulcre A, Gordon SP. 2023. Female foraging strategy co-evolves with sexual harassment intensity in the Trinidadian guppy. Behav Ecol. 34:593–601. https://doi.org/10.1093/beheco/arad027.

Yilmaz M, Meister M. 2013. Rapid innate defensive responses of mice to looming visual stimuli. Curr Biol. 23:2011–2015. https://doi.org/10.1016/j.cub.2013.08.015.