Animal Behaviour 235 (2026) 123560

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Sexual coercion dominates mating behaviour in the South American livebearing fish genus *Pseudopoecilia* (Cyprinodontiformes: Poeciliidae)

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ARTICLE INFO

Article history:
Received 30 September 2025
Initial acceptance 4 November 2025
Final acceptance 20 January 2026
Available online 13 April 2026
MS. number: A25-00597R

Keywords:
behaviour
coercion
poeciliid
sexual conflict
sexual selection

Studies aiming to advance our understanding of how sexual selection operates are often dominated by charismatic species with ornate visual signals. Research on the livebearing fish family Poeciliidae is no exception: heavily studied species often bear elaborate ornaments, such as sail-like dorsal fins and sword-like caudal fins. Yet the majority of poeciliid species have not evolved these traits. Because they lack morphology facilitating either display or direct male–male combat, unornamented poeciliid species are presumed to exclusively use coercive sneak copulations. Males in the poorly known genus *Pseudopoecilia* lack enlarged dorsal or caudal fins or striking colour patterns, have a long intromittent organ and show reduced male relative to female body size, providing an opportunity to test the hypothesis that these morphological traits are associated with coercive mating tactics. We predicted that courtship display would be infrequent (or absent) and that coercive mating attempts would dominate intersexual encounters in *Pseudopoecilia*. We also predicted that a potential indicator of male–male competition, intrasexual agonism, would be less frequent than intersexual coercion. Using video of free-swimming individuals across five geographically distant populations, we confirm that courtship display is absent and coercive interactions are dominant. Additionally, we found that mating behaviour was conserved across several populations. Male–male agonism was present in all populations but occurred at a lower rate than male–female coercion. This indicates that males are more likely to use coercive sneak copulations than direct competition with other males for mating opportunities. Male mating tactics in this genus fit our predictions, confirming that inferences about mating tactics in other unknown species may be possible with knowledge of male morphology. *Pseudopoecilia* joins a growing list of taxa in which coercion, rather than male–male competition or female choice, is the major mechanism of precopulatory sexual selection. We discuss potential behavioural and physiological counteradaptations to coercion that may mitigate potential costs to females.

Elaborate ornaments, armaments and other salient visual signals are important indicators used to predict the presence of strong sexual selection on phenotypic traits (Andersson, 1986; Berglund et al., 1996; Darwin, 1871; Fan et al., 2018; Jawor & Breitwisch, 2003; Ryan et al., 2019; Stuart–Fox & Ord, 2004; Tobias et al., 2012). Whether involved in courtship displays or in intrasexual competition, these traits have formed an important scaffolding for sexual selection research. For instance, exaggerated horns in *Onthophagus* beetles and antlers in red deer, *Cervus elaphus*, vary predictably with the strength of male–male competition (Clutton-Brock, 1982; Emlen et al., 2005; McCullough & Emlen, 2013). Similarly, the degree of male ornament elaboration scales with courtship display complexity in birds of paradise (Passeriformes:Paradisaeidae: Frith & Frith, 1988; Ligon et al., 2018; Miles & Fuxjager, 2018) and manakins (Passeriformes:Pipridae: Janisch et al., 2020; Porzio & Mota, 2025;

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https://doi.org/10.1016/j.anbehav.2026.123560
0003-3472/

Shogren et al., 2021). Likewise, courtship display in swordtail poeciliid fish (genus *Xiphophorus*) is linked to elaborate sword ornaments both intra- and interspecifically (Morris et al., 2005, 2008; Preising et al., 2024; Ryan & Causey, 1989).

Concentrating research efforts nearly exclusively on highly ornamented species may bias research efforts, precluding the opportunity to understand sexual selection in species with more subtle sex-specific features or cryptic coloration (Adamo et al., 2021; Fischer et al., 2025; Marcondes & Brumfield, 2019), in which sexual selection dynamics may differ compared to ornamented, sexually dimorphic species. Some authors consider the absence of male ornamentation and behavioural displays, and the presence of sneak copulations or sexual coercion, to indicate weakened precopulatory sexual selection (e.g. Furness et al., 2019; Pollux et al., 2014; but see West et al., 2024). Coercive mating, in which males circumvent female choice through forced matings (Clutton-Brock & Parker, 1995; Smit, 2025), is a ubiquitous source of sexual conflict (Arnqvist & Rowe, 2005), although conflict over mating can occur in species that also exhibit courtship displays (e.g. reducing female foraging rates in poeciliid fishes: Plath et al., 2007; Yang et al., 2023), in which females are afforded greater opportunity to choose. The evolution of male coercion has been shown to drive an array of behavioural and morphological counteradaptations in females (Arnqvist & Rowe, 2005; Brennan, 2016; Wallen et al., 2016) and is considered to be a third form of sexual selection alongside male—male competition and female choice (Smit, 2025; Smuts & Smuts, 1993; Watson-Capps, 2009).

Additionally, relationships between morphology and mating behaviour are not always straightforward. For example, courtship displays have sometimes been retained in lineages even after ornaments have been lost (Farr, 1989). For example, elaborate dorsal ‘sail’ fins are present in sister species *Poecilia velifera* and *Poecilia latipinna*, but have been lost in *Poecilia latipunctata*. Yet *P. latipunctata* males use courtship displays even in the absence of elaborate ‘sail’ fins (Ptacek, 1998; 2005). Similarly, species with ornamented males may not always present courtship displays, and species with reduced ornamentation may still have forms of courtship. For instance, *Poecilia gillii* and *P. latipinna* both have broad male size distributions, with higher ornamentation in larger males (Goldberg et al., 2019; Schlupp et al., 2006; Snelson, 1985). Large, ornamented *P. latipinna* use primarily courtship displays, yet large, ornamented *P. gillii* lack courtship entirely, instead utilizing display in male—male interactions (Baird, 1973; Furness et al., 2020; Travis, 1994). Additionally, some species in the genera *Poeciliopsis* and *Gambusia* have evolved display behaviours (Constanz, 1975; Martin et al., 2014), despite these lineages having either subtle ornamentation or none at all (Furness et al., 2019; Pollux et al., 2014). Although to date some genera have been studied intensively, the mating tactics used by the vast majority of poeciliid species remain undescribed (Garita-Alvarado, 2023; Rios-Cardenas & Morris, 2011).

The livebearing fish family Poeciliidae has emerged as a useful group to advance our understanding of sexual selection. Pronounced sexual dimorphism present in many species (Bisazza & Marin, 1995; Endler, 1983; Haskins & Haskins, 1949; Houde, 1997; Lindholm & Breden, 2002; Meyers et al., 2006; Ptacek & Travis, 1997; Ryan & Causey, 1989) reflects underlying asymmetries between the sexes in reproductive investment due to the presence of internal fertilization, gestation and sperm storage, causing sexual conflict and divergent reproductive strategies (Bisazza, 1993; Cummings, 2018; Reznick et al., 2021; Trivers, 1972). Although rife with diversity, a disproportionate amount of sexual selection research in poeciliids has focused on the taxa with elaborate ornamentation (e.g. modified caudal fins in species of *Xiphophorus* and dorsal fins in *Poecilia*) and courtship displays (Erbelding-Denk et al., 1994; Goldberg et al., 2019; Ryan & Causey, 1989; Schlupp et al., 1994; but see Bisazza & Pilastro, 1997; Bisazza et al., 2001; Constanz, 1975; Espinedo et al., 2010; Hughes, 1986). However, the majority of poeciliid species do not show sexual dimorphism in ornamentation. In fact, many species are sexually monochromatic or only have subtle morphological sex differences aside from the intromittent organ (Endler, 1983; Pollux et al., 2014). Unlike more ornamented species, these species tend to lack courtship displays, instead relying entirely on coercive mating, in which males circumvent female choice by performing sneak copulations regardless of their receptivity (Inman, Vuong, et al., 2025; Magurran, 2011; Pilastro et al., 1997; Seal, 1911). However, intensive study of mating strategies in some species has revealed courtship displays where they were not previously predicted to occur (Kolluru et al., 2014). Thus, we would benefit from examining behavioural interactions in a wider range of lineages lacking sex-specific ornamentation to assess the degree to which mating tactics track predictions based on morphological traits. We investigate the broad hypothesis that different male morphological characters facilitate different kinds of mating behaviours in a taxon with undescribed mating behaviour.

We examine male mating tactics in the poeciliid genus *Pseudopoecilia*, which is endemic to Ecuador, southern Colombia and northern Peru (Jiménez-Prado et al., 2015). Here, we study several Ecuadorian populations in the *Pseudopoecilia fria/festae* species complex. *Pseudopoecilia* males are characterized by a long gonopodium-to-body size ratio, small male relative to female size (Table 1) and minimal sexual dichromatism, features often associated with exclusively coercive mating behaviour (Bisazza, 1993). Across poeciliids, females exhibit mate preference for larger and more ornamented males, even when conspecifics lack such traits (Casner et al., 2016; Hankison & Morris, 2002; Rosenthal & Evans, 1998), especially when ornaments increase apparent size (MacLaren, 2006). However, more ornamented males are not always preferred by females (Kolluru et al., 2015; Wojan et al., 2018), making the link between a relative lack of ornamentation and the presence of mating tactics that circumvent female preference a testable hypothesis. Female-biased size dimorphism (female body size > male body size) and a lack of ornamentation in this system suggest that the opportunity for precopulatory female choice might be limited. Additionally, since the outcome of male—male contests is often determined by male size, smaller male sizes are expected to be favoured when intermale aggression is low relative to intersexual aggression associated with coercion (Bisazza, 1993). Note, however, that even if aggression directed towards females in the form of coercion is more frequent, several species in the family with relatively small male sizes still have frequent intermale aggression in addition to coercive tactics and harassment directed towards females (Bisazza, 1993; Bisazza et al., 1996; Bisazza & Marin, 1995; Smith, 2007).

Table 1
Welch two-sample *t* test results and effect sizes for body depth and standard length (SL) metrics

Comparison	Mean male size (cm)	Mean female size (cm)	Cohen’s *d*	*P*	SSD ratio
Male vs female: Standard length	2.082	2.231	-0.404	0.021	0.933
Male vs female; bodv depth	0.524	0.527	-0.034	0.431	0.993

SSD: sexual size dimorphism ratio. Females are significantly larger than males in standard length, but not body depth.

While no information on mating behaviour is available for any member of this genus (Furness et al., 2019), mating behaviour in the relatively closely related species *Heterandria formosa* is well described: males of this species perform coercive Gonopodial thrusts exclusively (Bisazza & Pilastro, 1997; Farr, 1989). In addition to being closely related, *H. formosa* and *Pseudopoecilia* sp. share morphological traits associated with coercive mating (long gonopodium and drab coloration; Bisazza, 1993). However, given the mating and social behaviour in this genus as well as the sister genus *Priapichthys* are unexplored, we are afforded the opportunity to test whether the suite of mating tactics used by an uncharacterized taxon can be predicted based on the diversity of male morphology and mating tactics across the whole family Poeciliidae (Furness et al., 2019; Pollux et al., 2014; Reznick et al., 2021). We use the gap in our understanding of *Pseudopoecilia* mating tactics to test the hypothesis that male morphological traits can be used to predict male mating behaviour. Specifically, we ask whether the male morphological traits associated with variation in mating tactics along a continuum from exclusive coercion to a mix of courtship and coercive tactics detailed in previous comparative studies can be used to predict mating behaviour in a novel taxon.

We predicted that, because smaller and less ornamented poeciliid males are generally less preferred by females but more successful at coercion than larger and more ornamented males, *Pseudopoecilia* males would rely on coercive tactics, with male courtship display and female preference playing less important roles in mating strategy. More specifically, we predicted that (1) *Pseudopoecilia* males would exhibit frequent Gonopodial thrusts and Fast chases, behaviours identified in other coercive poeciliid species (Fig. 1). Due to the higher coercion efficacy of smaller poeciliid males (Pilastro et al., 1997), we also predicted that (2) courtship displays would be either infrequent or absent in *Pseudopoecilia*. Finally, we (3) predicted that agonistic interactions (Aggressive nips and Fast chases) between males would be less frequent than agonistic interactions between the sexes.

METHODS

Study Species

The ancestor of the genus *Pseudopoecilia* dispersed from Central to South America, after the formation of the Andes (Reznick et al., 2017). The genus currently includes at most three species: *P. fria* (Eigenmann, Henn, & Wilson, 1914), *P. festae* (Boulenger, 1898) and *Pseudopoecilia austrocolumbiana* (Radda, 1987). However, we caution that the taxonomic status of species within *Pseudopoecilia*, particularly that of *P. fria* and *P. festae,* is not well resolved: some earlier sources describe *P. festae* and *P. fria* as synonyms based on a continuous distribution and little variation in male intromittent organ morphology (M. Meyer & Etzel, 1996; Radda, 1977, 1985), while others distinguish the two based on the number of lateral line scales (Glodek, 1978; Jiménez-Prado et al., 2015). Although we do not include the congener *P. austrocolumbiana* in this study, we include two out of the three known species (including both that are known to occur in Ecuador) but acknowledge taxonomic uncertainty as to their species status by referring to the species complex as '*Pseudopoecilia*'. In Ecuador, *Pseudopoecilia* populations inhabit a variety of freshwater streams and rivers from 0 to 800 m, with scattered populations of *P. fria* recently discovered above 1000 m on the western slopes of the Andes (GBIF, 2025). Throughout their range, *Pseudopoecilia* are common to abundant in shallow, moderately turbid streams or river margins with dense mats of aquatic vegetation, abundant invertebrate predators (e.g. belostomatid water bugs) and high overhead canopy cover (C. Inman, M. Ramsaroop, & L. Ávila, personal observation). Larger fish predators are common and highly diverse throughout the Choc ó-Andino region that this species complex inhabits (Jiménez-Prado et al., 2015).

The genus *Pseudopoecilia* is poorly studied, with information restricted to life history and systematics from a single population of putative *P. festae* (Reznick et al., 2017) as well as morphology, habitat use and behaviour and cognition of *P. fria* in the Rio Atacames watershed (Inman, Yeager, et al., 2025; Jiménez-Prado et al., 2020; Jiménez-Prado & Vásquez, 2021). Based on early samples from the '*P. festae*' type locality near Santa Elena, Ecuador, females were confirmed to carry multiple broods at different developmental stages simultaneously (i.e. have superfetation; Boulenger, 1898; Tortonese, 1949), which has also been confirmed for some other populations of the species complex (D. N. Reznick, personal communication, 2023). Populations collected during a sampling trip by D. N. Reznick in July 1988 appeared to be lecithotrophic, but populations need to be more broadly sampled for signs of matrotrophy due to the strong correlation between matrotrophy and superfetation across poeciliids (Furness et al., 2019; Reznick et al., 2021; D. N. Reznick, personal communication, 2023).

We collected seven geographically distinct populations of *P. fria* and *P. festae* between August 2024 (Los Angeles, Cañero and Manabi), November 2024 (Puca and Nueva Delicia) and May 2025 (Nanegal and Santo Domingo). Populations were temporarily housed in 35 cm^3 aquaria at the Universidad de las Américas - Quito for at least 2 weeks prior to behavioural assessments. Aquaria were maintained at (23 °C) under 12:12 h light:dark cycles typical of natural stream conditions.

Ethical Note

Our husbandry programme follows standard care protocols approximating the local conditions where fish were collected, including the same water source that feeds into many localities where we sampled fish. Fish were captured via hand-nets and transported by private vehicle in 5-gallon (18.9-litre) buckets with aeration. During transport, API Stress Zyme (https://www.apifishcare.com/) was added to the water to break down bacteria and stress hormones in the water to attenuate stress. Fish were temporarily housed in biologically established aquaria and acclimated prior to assays. Behavioural studies were designed to mitigate stress and filmed passively to limit any observer influence. Although fish were agonistic, the densities of fish in the present study (3 males and 3 females) were similar to or less than those observed in wild populations. All fish collection and care methods were approved by Institutional Animal Care and Use Committee of the University of Austin (IACUC Protocol Number AUP-2022-00224), and behavioural observations were approved by research permits granted from the Ministerio del Ambiente, Ecuador (permits MAATE-ARSFC-2024-0029 and MAATE-ARSFC-2025-0345). At the end of the study, fish were maintained in the laboratory for additional behavioural/cognition experiments until their natural death and subsequently deposited in the relevant aquatics museum.

Experimental Set-up

Behaviours were measured in group settings with even sex ratios, which are usually either at parity or female-biased in natural populations based on our sampling (C. Inman, M. Ramsaroop, & L. Ávila, personal observation). Regrettably, in populations from two locations (Los Angeles and Nueva Delicia), adult males experienced high mortality during transport and in the laboratory, so we were unable to achieve a 1:1 sex ratio in our observational

Behind approach: The actor positions itself under or behind the receiver within 2 cm (Constanz, 1975; Rosen & Tucker, 1961)

Frontal approach: The actor positions itself within 2 cm in front of the receiver. (Constanz, 1975)

Aggressive nipping: The actor bites at the side of the receiver (often coupled with chases or behind approaches) (Constanz, 1975; Deaton, 2008)

Side approach: The actor positions itself perpendicular to the receiver within 2 cm (Constanz, 1975)

Fast chase: The actor swiftly moves within 2 cm of the receiver from any direction. Chases are agonistic and contextually sexual, as in when males chase females (Constanz, 1975; Deaton, 2008; Hughes, 1985; Kolluru & Joyner, 1997; Ryan & Causey, 1989)

Gonoporal nibbling: The male positions itsell behind/underneath the female and touches the female's gonopore with the tip of its snout (Constanz, 1975; Kolluru & Joyner, 1997)

Gonopodial thrust: The male positions itself behind/underneath the female and extends the gonopodium quickly, pointing it towards the female gonopore. Thrusts are sexually coercive (Constanz, 1975; Deaton, 2008; Hughes, 1985; Kolluru & Joyner, 1997; Rosen & Tucker, 1961; Ryan & Causey, 1989)

Figure 1. Ethogram of commonly observed behaviours. Interactions are classified as agonistic if the receiver responds by fleeing or attacking, and nonagonistic for all others. Behaviours are further classified as sexual if they occur in a mating context. Behaviours are defined as coercive when they are both agonistic and sexual. Behavioural interpretations come from behavioural studies in other poeciliid fish (e.g. Constanz, 1975; Deaton, 2008; Hughes, 1985; Kolluru & Joyner, 1997; Rosen & Tucker, 1961; Ryan & Causey, 1989). These interactions were most commonly observed in an intersexual context, so we portray a male and a female in each one. However, interactions are not necessarily intersexual, and each sex is not confined to an actor or recipient role.

videos. Thus, to limit confounding effects of sex ratio on behaviour, we excluded observational videos of these populations from our study and only included even-sex ratio observational videos from Cañero, Manabí, Puca, Nanegal and Santo Domingo. For tank observations, we placed three males and three females into 7-litre, 25 × 23 × 13 cm empty glass tanks 24 h prior to the first video recording. All selected males had a fully developed gonopodium, while selected females lacked a modified anal fin but bore a gravid spot, a dark patch of pigmented scales that can be consistently used to identify mature and reproductively active females across poeciliid fishes (Benson, 2007; Norazmi-Lokman et al., 2016; Winemiller, 1993).

We observed a total of 84 fish (42 females and 42 males) across five populations in a total of 15 replicate tanks. Because the number of originally collected and surviving fish was uneven across populations, the number of tank replicates per population varied. For Cañero and Manabí, we filmed only a single group of six individuals from each population. We filmed two tank replicates (12 individuals) from Puca, and we filmed five tank replicates per population (30 individuals each) from Nanegal and Santo Domingo. After a 30 min acclimation period prior to filming, each tank of six fish was recorded for 30 min at two different times: once at 1000 hours local time and again at 1400 hours using a GoPro Hero 12 camera at a lateral viewing angle. We did not include cover or shelter in the tanks (besides in-tank heaters, behind which females sometimes hide), which could have changed behavioural dynamics in our tanks given that both sexes might use cover to their advantage (Darden & Croft, 2008; Malek & Long, 2019). Since each tank replicate was filmed for a total of 60 min (30 min at a time), Cañero and Manabí populations were filmed for a total of 60 min each, Puca was filmed for 120 min and Santo Domingo and Nanegal were filmed for a total of 300 min each.

Morphological Data

Our predictions on male mating behaviour were developed from morphological observations across all populations. Females had a significantly greater standard length (SL) than males (Welch two-sample t test: $df = 86.1$, $P = 0.021$). The sexual size dimorphism ratio (SSD ratio) was 0.933 (male:female), similar to that of other poeciliids with coercive strategies (Bisazza & Pilastro, 1997; Furness et al., 2019). Mean gonopodium length was 0.794 cm, or 38.1% of the mean male SL, which is consistent with the large gonopodium-to-standard length ratios expected from species that rely on coercive tactics (Bisazza & Pilastro, 1997; Furness et al., 2019). All morphological trait measures used standardized photographs of individual fish taken using a quartz converted ultraviolet (UV)-sensitive Canon EOS 7D camera combined with a metal body NIKKOR EL 80 mm lens (Yeager & Barnett, 2021). Since we did not perform colour analysis in this study, we did not include UV wavelengths in processing these images and only utilized images in the human visible range (400–700 nm). The camera was mounted on a tripod and the lens was fitted with a Baader UV-IR blocking filter that allowed transmission from 420 to 680 nm, quantified in ImageJ (Schneider et al., 2012).

Behavioural Quantification and Analysis

We focused on quantifying specific behavioural interactions between the sexes that function in a mating context (Fig. 2) and those that may represent intrasexual competition for mates (primarily in males). Behaviours were selected based upon their frequency and reliability to classify their role in other poeciliid species (Constanz, 1975; Farr et al., 1986; Kolluru & Joyner, 1997; Parzefall, 1969; Rosen & Tucker, 1961; Ryan & Causey, 1989), as well as their high frequency in our specific observation trials. For each specific behaviour, we documented the sex of the actor and of the recipient. This helped us distinguish among behaviours that were specific to the mating context (female-to-male or male-to-female) or intrasexual competition from more general social interactions. Behavioural observations were manually scored by one author (J. Koley), who was blinded to the a priori hypotheses, for the following behaviours: Fast chase, Aggressive nip, Parallel swim, Side approach, Frontal approach, Behind approach, Gonoporal nibbling, Frontal display and Gonopodium thrust (illustrated in detail in Fig. 1). Behaviours were coded using the behaviour logging software CowLog (version 3, Pastell, 2016).

Statistical Methods

The relative frequencies of each behavioural type (coercive: Gonopodial thrusts, Fast chases; potentially noncoercive: Frontal

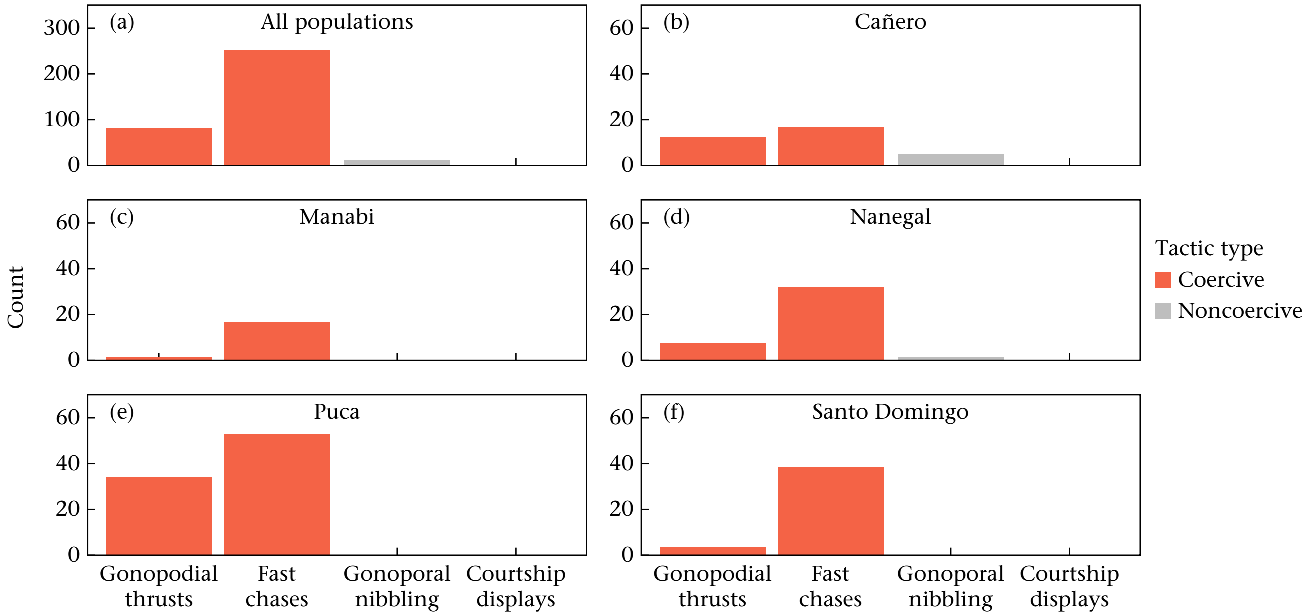

Figure 2. Frequency (counts) of coercive and noncoercive behaviours (a) across all populations and (b–f) in each population. In (a), rates of different mating behaviours are averaged across populations (individual graphs). Each bar is a behaviour categorized as coercive (agonistic + sexual; orange) or noncoercive (nonagonistic + sexual; grey).

display, Gonoporal nibbling) were pooled across all populations and compared with chi-square tests for given probabilities. All statistical analyses were performed using R software (R Core Team, 2025). *P* values were adjusted for multiple comparisons using Bonferroni correction (Armstrong, 2014). To assess the overall effect of population and mating behaviour category on frequency, we then constructed a negative binomial GLMM using the R package 'glmmTMB' (McGillycuddy et al., 2025) with count as the response variable, mating behaviour type, population and population*mating behaviour type as fixed effects. For assessing the effect of explanatory variables on behaviour frequency in this study, we used the negative binomial family of GLMMs due to the possibility of overdispersion in count data taken from a relatively small number of replicates (Dunn & Smyth, 2018; Stoklosa et al., 2022). Tank replicate served as a random effect, and we used the log(video duration in seconds) as a model offset to account for differences in video duration among populations and tank replicates. We then conducted a Wald type II ANOVA on the model to extract fixed effects using the 'car' package (Fox & Weisberg, 2019).

To determine whether approaches by males to females from different directions were followed by distinct types of mating behaviours, we computed the frequency of response behaviours, which we defined as the behaviour of a recipient that occurs within 2 s of an approach by an actor. The approach behaviours included in this analysis were 'Behind approach' by the male to the female, 'Side approach' by the male to the female and 'Frontal approach' by the male to the female. Possible response behaviours included every behaviour recorded other than the four approach behaviours. We then identified the top five response behaviours occurring after each approach type. To determine whether approach type, next behaviour or population affected frequency, we constructed a negative binomial GLMM with count as the response variable, and approach type, next behaviour, approach type*next behaviour and population as fixed effects, and tank replicate as a random effect. To account for differences in the number of replicates and thus duration of filming for each population, we also included log(total video duration) as a model offset. We conducted a Wald type III ANOVA on the model to extract fixed effects using the 'car' package.

Following comparison of responses across approach types, we conducted omnibus goodness-of-fit tests to assess variation in frequency of next behaviours. *P* values were adjusted for multiple comparisons using Bonferroni correction. Because expected values for some estimates were very low, we used Monte Carlo simulation with 10,000 replicates to estimate *P* values (North et al., 2002).

In our initial observations of *Pseudopoecilia*, we noticed high rates of agonistic interactions (C. Inman, M. Ramsaroop, & L. Ávila, D. Burbano, M. Pozo, & J. Yeager, personal observations), but it was unclear whether these were sex specific in terms of the aggressor and the recipient of aggression. Thus, we compared aggressive behaviour between the two potential intrasexual contexts and the two intersexual contexts (male-to-female, male-to-male, female-to-male, female-to-female). Because some aggressive behaviours (e.g. Gonopodial thrusts) could only be carried out by one sex and not the other, we excluded those behaviours from our analysis and instead compared two common aggressive behaviours in which both sexes had been previously observed as actor and recipient (Aggressive nips and Fast chases; Fig. 1) and aggregated them into a single metric. We first pooled agonism across populations using chi-square tests for given probabilities. To assess the overall effect of population and interaction type on frequency and to determine whether interaction type depended on population, we constructed a binomial GLMM using the 'glmmTMB' package. The GLMM included count as the response variable and population*interaction type, interaction type and population as fixed effects. Tank replicate served as a random effect, and we included log(video duration in seconds) as a model offset. To extract fixed effects, we conducted a Wald type II ANOVA on the GLMM using the 'car' package.

RESULTS

Consistent with our morphology-based predictions about the mating behaviour of *Pseudopoecilia*, we found Gonopodial thrusts and Fast chases across all populations assessed, but no concrete evidence of courtship display (Fig. 2). Pooling across populations, we found that the frequency of behavioural traits: Gonopodial thrusts, Fast chases and Gonoporal nibbling differed from one another (chi-square test for given probabilities: $\chi^2_2 = 266.11$, $P < 0.001$). Specifically, we found that the two hallmarks of coercive mating in other poeciliids, Fast chases and Gonopodial thrusts, were significantly more frequent than the one possibly noncoercive behaviour, Gonoporal nibbling (Fast chases versus Gonoporal nibbling: $\chi^2_1 = 221.54$, $P_{adj} < 0.001$, $k = 3$ comparisons; Gonopodial thrusts versus Gonoporal nibbling: $\chi^2_1 = 56.35$, $P_{adj} < 0.001$, $k = 3$ comparisons). Additionally, coercive Fast chases were significantly more frequent than coercive Gonopodial thrusts ($\chi^2_1 = 85.01$, $P < 0.001$, $k = 3$ comparisons), likely because females typically fled before males could approach them close enough to attempt a copulation. We also compared the relative frequency of the three different mating behaviours within each population and found that they differed significantly in each one (chi-square test of equal probabilities: $P < 0.05$, Bonferroni correction for three comparisons).

We constructed a negative binomial GLMM to examine the effect of population, mating behaviour type (Gonoporal nibbling, Fast chases, Gonopodial thrusts) and their interaction on the frequency of behaviours. We found that there was a significant effect of mating behaviour type ($\chi^2_2 = 28.31$, $P < 0.001$) and population ($\chi^2_4 = 16.91$, $P = 0.002$) but no effect of a behaviour type*population interaction ($\chi^2_7 = 11.62$, $P = 0.114$). Thus, we did not find evidence that the relative frequency of different male mating behaviours was dependent on population; mating tactics largely appeared to be conserved among populations.

We also considered variation in male approach angle, specifically whether males would be visible to females or not, and whether this angle resulted in downstream differences in the mating interactions that followed. In other poeciliids, it has been suggested that Frontal approaches should be immediately followed by courtship displays and/or indications of female receptivity (Bisazza, 1993; Godin, 1995; Luyten & Liley, 1985; Rosen & Tucker, 1961), while Behind approaches are followed by Fast chases and Gonopodial thrusts (Fig. 1). Consistent with these expectations, we found that the most common behaviour immediately following Behind approaches was Gonopodial thrusting, and male-initiated Fast chase was the second most common behaviour following Behind approaches (Fig. 3). However, contrary to expectations, Side approaches were followed by Fast chases and Gonopodial thrusts at similarly high frequencies to Behind approaches (Fig. 3). Frontal approaches, which were predicted to be followed by courtship or receptive female behaviour based on work in other poeciliids (Bisazza, 1993; Farr, 1989) occurred infrequently, but contrary to our expectations, they were more often followed by a male-to-female Fast chase than any other response type (although the difference in frequency across behaviours following Frontal approaches was not significant; $P > 0.05$; see below). In the type III ANOVA we ran on the binomial GLMM we constructed, we found that approach type had a significant effect on behaviour frequency ($\chi^2_3 = 9.80$, $P = 0.020$), as did next behaviour ($\chi^2_8 = 15.68$, $P = 0.016$), but, contrary to

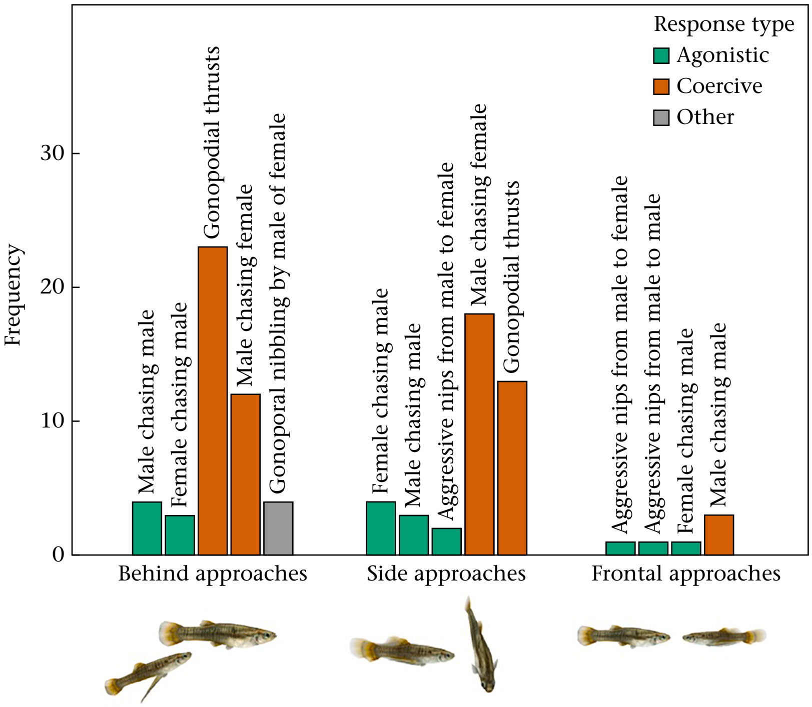

Figure 3. Top five most common response behaviours occurring in sequence (within 2 s) after each approach behaviour type. Behaviours are divided up into three categories: coercive behaviours (male-initiated Fast chases and Gonopodial thrusts), agonistic behaviours (other Fast chases and Aggressive nips) and other behaviours (Gonoporal nibbling and female-to-male Side approach).

expectations, there was no effect of approach type*next behaviour interaction ($\chi^2_3 = 1.68$, $P = 0.641$). Additionally, there was no effect of population ($\chi^2_4 = 7.38$, $P = 0.117$).

Next, we tested for an effect of response behaviour on count within each approach type, using omnibus goodness-of-fit tests with Monte Carlo simulation to estimate *P* values due to small expected values. Within Behind approaches, we did find that next behaviour had an effect on count ($\chi^2_2 = 744$, $P < 0.001$). Post hoc tests revealed that, within Behind approaches, the frequency of Gonopodial thrusts was significantly higher than the frequency of all other behaviours (Gonoporal nibbling, female-to-male Fast chases, male-to-male Fast chases; $P_{adj} < 0.001$, $k = 10$ comparisons) besides male-to-female Fast chases ($P > 0.05$). Male-to-female Fast chases were only significantly more frequent after Behind approaches than Gonoporal nibbling and did not differ in frequency from female-to-male Fast chases or male-to-male Fast chases. This indicates that Behind approaches primarily precede coercive Gonopodial thrusts and secondarily Fast chases. We also found that next behaviour affected count within Side approaches ($\chi^2_2 = 970$, $P < 0.001$). Since Side approaches usually occur within a female's field of view and do not offer the optimal angle for an attempted coercive copulation, we expected them to precede coercive Gonopodial thrusts and Fast chases infrequently. Instead, Gonopodial thrusts were the most frequent behaviour following Side approaches and did not significantly differ from male-to-female Fast chases in their frequency ($P_{adj} = 1.00$, $k = 10$ comparisons). Both Gonopodial thrusts and male-to-female Fast chases were significantly more frequent than every other behaviour (female-to-male Fast chase, Aggressive nips from female to male, male chasing male), while the other behaviours did not differ from one another in frequency ($P_{adj} > 0.05$, $k = 10$ comparisons). Thus, Side approaches tended to precede coercive behaviours as often as Behind approaches did and were not predictably associated with any other behaviours. This suggests that male-to-female intersexual aggression in a coercive context is more common than any other forms of aggression following Side approaches. In contrast, there was no effect of next behaviour on count within Frontal approaches ($\chi^2_2 = 322$, $P = 0.215$), which was an approach behaviour we expected to precede displays (if they occurred) and nonsexual aggressive interactions.

To determine whether agonistic interactions tended to be sex specific overall and whether they occurred primarily in a coercive or intrasexual competition context, we compared the frequency of male–male, male–female, female–male and female–female interactions. Because we were primarily interested in how aggression compared across different sex-specific actor and recipient combinations (and not in the type of aggressive behaviour), we combined two types of sex-neutral agonistic interaction in our comparison: Aggressive nips (bites) and Fast chases. The frequency of agonistic interactions differed across aggressor–recipient combinations independent of population (chi-square test for given probabilities: $\chi^2_3 = 136.1$, $P < 0.001$; Fig. 4a). Male agonistic behaviours directed towards females were more frequent than other interaction types (pairwise chi-square test for given probabilities; see Table 2). In general, females initiated agonistic interactions less often than males, and the recipient of female agonism did not differ by sex ($P = 1.00$; Table 2). In the negative binomial GLMM we constructed, there was no effect of population, interaction type or population*interaction type on count ($P > 0.05$). Overall, we found that agonistic interactions were more frequently initiated by males than by females and that male aggression more often occurred in a coercive context than in male–male combat. Female aggression, by contrast, was not sex specific and was directed towards males as often as it was towards other females.

DISCUSSION

We studied a poorly known species of poeciliid fish to test predicted relationships between sex-specific morphology and

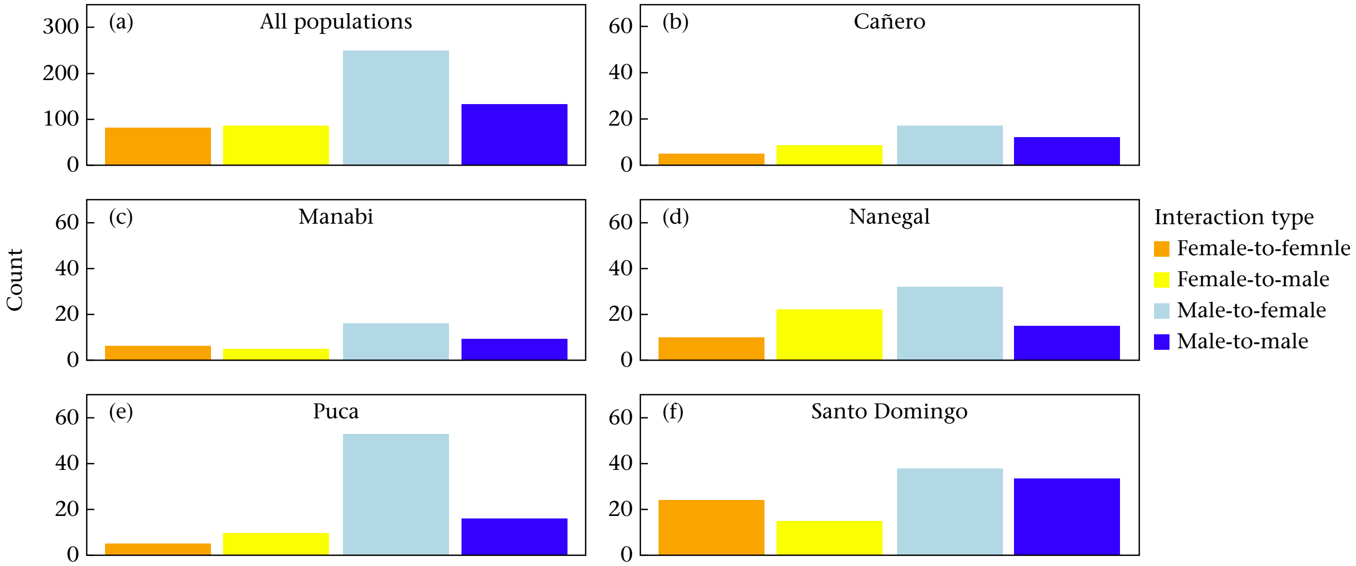

Figure 4. Frequency of agonistic behaviours (a) across all populations and (b–f) in each population. Agonistic interactions are colour-coded by the sex of the actor and receiver.

Table 2
Chi-square tests of agonistic interaction frequency between different actor–receiver pairs

Comparison	χ^2	P_{adj}
Male-to-female vs male-to-male	27.61	<0.001
Male-to-female vs female-to-male	80.40	<0.001
Male-to-female vs female-to-female	135.36	<0.001
Male-to-male vs female-to-male	15.11	<0.001
Female-to-male vs female-to-female	0.32	1.00
Female-to-female vs male-to-male	21.90	<0.001

Aggressive nips (bites) and Fast chases are the two behaviours included in the category of agonistic interaction. *P* values are adjusted according to the number of comparisons ($k = 6$) using Bonferroni corrections.

mating tactics. Specifically, we hypothesized that long gonopodia and limited male ornamentation coupled with small body size of males relative to females would be associated with exclusively coercive mating (Table 1). Indeed, we observed no evidence of courtship displays in any population, and we found that mating interactions were dominated by classic coercive behaviours (Fast chases and Gonopodial thrusts) (Fig. 3).

Our ethogram helped clarify the relevance of approach direction in relation to male mating attempts in poeciliids. Studies of other poeciliids suggest that if an approach is outside a female's field of view (e.g. behind or underneath), then coercive mating attempts in the form of a Gonopodial thrust may be more effective (Bisazza, 1993; Bisazza & Pilastro, 1997; Furness et al., 2020; Kolluru et al., 2014; Rosen & Tucker, 1961). Meanwhile, approaches from the side or the front may be more likely to precede courtship or aggression, rather than coercive mating. As predicted, approaches tended to be followed by Gonopodial thrusts or Fast chases when the approach was behind the female (Fig. 3). Behind approaches were commonly followed immediately by coercive Gonopodial thrusts, likely because the approach direction is outside the female's field of view, increasing the chances of an effective sneak copulation (Farr, 1980, 1989; Parzefall, 1969; Pilastro et al., 1997). In other contexts, such as courtship or territorial aggression, males may approach females from the side or front (Liley, 1966; Rosen & Tucker, 1961; Ryan & Causey, 1989). Side approaches were most commonly followed by Fast chases and Gonopodial thrusts, suggesting that even when males were relatively visible to females, they engaged in coercive mating tactics. Side approaches were nearly as common as Behind approaches, suggesting that they are frequently used in the context of coercion, and that males of this exclusively coercive taxon do not only approach females from behind (contrary to earlier literature about the approach direction of coercion, e.g. Luyten & Liley, 1985; Rosen & Tucker, 1961). This finding suggests that, contrary to our assumptions, there is likely no disadvantage to using Side approaches in a coercive context. Alternatively, the presence of Side approaches might indicate that males do exhibit some rudimentary form of courtship display that is less observable in a high-density group context, a possibility that might be investigated by carefully studying the interactions of male–female pairs. Additionally, it is imperative that we examine approach direction in the presence of greater visual occlusion and shelter, as these features could alter the ability of males to coerce or females to evade detection.

Consistent with the absence of courtship display, Frontal approaches were rare compared to all other approach types in our data set, and the five most common behaviours following Frontal approaches did not differ in frequency (Fig. 3). Thus, the approach behaviour most commonly associated with courtship in other poeciliid species (Frontal approaches) was rare, and even when males were salient to females upon approach (Side approaches), that approach tended to be immediately followed by coercive tactics (Fig. 3). Overall, both the frequency of different approach behaviour types as well as the mating behaviours that immediately followed them were consistent with a predominately coercive mating system.

Overall, agonistic interactions were more frequently initiated by males than females, and such aggression was more often directed towards females in the form of coercion than towards other males in a competitive context. Consistent with a smaller size and reduced ornamentation, direct male–male fighting was predicted to be reduced in *Pseudopoecilia* since energetic investments are instead invested in behaviours leading to sneak copulations. In theory, this is because sneak copulations allow males to circumvent direct male–male competition by directing their efforts towards pursuing females surreptitiously (Shuster &

Wade, 1991; Whitehouse, 1991). Yet in *Gambusia*, another poeciliid genus that is largely coercive and lacks elaborate ornamentation, male–male aggression is intense. The outcomes of these interactions dictate access to females and directly influence male reproductive success, yet once males have gained access to females, they still rely on coercive mating (Bisazza et al., 1996; Hughes, 1985). It is possible a similar process occurs in *Pseudopoecilia* populations with a higher frequency of agonistic interactions among males. In contrast, in other poeciliid species (often with more strongly female-biased sexual size dimorphism, favouring coercion), aggressive interactions occur between males but, as in *Pseudopoecilia,* at a lower rate than coercive interactions between males and females (Bisazza, 1993). In a close relative of *Pseudopoecilia*, *Heterandria formosa*, male–male agonism is common, but serves a different purpose, to help establish spacing between individuals rather than competition for access to females (Bisazza et al., 1996). This indicates that agonistic behaviours such as territoriality may facilitate female monopolization by individual males; however, territoriality may not be associated with larger male size or courtship displays as it is in some other poeciliids (Franck & Ribowski, 1993; Furness et al., 2020; Morris et al., 1992).

While courtship was absent and coercive interactions dominated intersexual interactions, coercive behaviours actually occurred at a lower rate than in other exclusively coercive poeciliid species. Gonopodial thrust rates in *Pseudopoecilia* (all population mean: 0.25 thrusts/min) are lower than those recorded in other exclusively coercive poeciliid species such as *Gambusia holbrooki* and *Girardinus falcatus*, which show Gonopodial thrust rates of 1.9 and 0.37 thrusts/min, respectively (Dadda, 2015). Wild observations of exclusively coercive species as well as mixed-tactic species indicate Gonopodial thrust rates approaching one/min (*Poecilia reticulata*: Farr, 1980; *Poecilia latipinna*: Travis & Woodward, 1989; *Gambusia holbrooki*: Bisazza & Marin, 1991). Future studies can confirm the frequency in wild *Pseudopoecilia.* Our findings suggest that even among taxa with exclusively coercive tactics, females may not experience identical coercion rates.

The only behaviour observed that may involve elements of cooperation, although falling short of courtship, was Gonoporal nibbling. Gonoporal nibbling allows males to chemically detect whether a female is carrying fertilizable ova. This could permit males to direct their efforts towards receptive females, rather than pursue females indiscriminately (Farr & Travis, 1989; Furness et al., 2020). *Poecilia gillii* males are comparatively large and territorial, with less coercion than we find in *Pseudopoecilia*, where males that exhibit higher rates of Gonoporal nibbling ostensibly focus their mating efforts on receptive females (Furness et al., 2020). However, in other poeciliid species, small (coercive) males have been found to be indiscriminate in their mating attempts, targeting both nonreceptive and receptive females equally (Sumner et al., 1994). In fact, smaller sailfin mollies strategically use Gonoporal nibbling to facilitate coercion, where it typically precedes Gonopodial thrusting (Farr et al., 1986). Therefore, although Gonoporal nibbling theoretically permits assessment of female receptivity prior to male mating attempts, we cannot rule out a function in coercive mating as well. Therefore, we are cautious in attributing Gonoporal nibbling to either cooperation or coercion until further studies can clarify its specific role in *Pseudopoecilia*.

We found that *Pseudopoecilia* males use Fast chases and Gonopodial thrusts, elements of a coercive mating strategy. Coercion is a classic source of sexual conflict, since it involves males attempting to optimize their own fitness at the expense of female fitness by forcing females above their optimal mating rate (Arnqvist & Rowe, 2005; Smit, 2025). Coercion has been found to drive sexual conflict across taxa including water striders (Arnqvist & Rowe, 2002; Han & Jablonski, 2010), bed bugs (Stutt & Siva-Jothy, 2001; Yan et al., 2024), primates (Smuts & Smuts, 1993; van Schaik et al., 2004) and waterfowl (Adler, 2010; McKinney et al., 1983; McKinney & Evarts, 1998). It is worth noting that sexual conflict can also occur in species that exhibit consensual courtship displays in addition to coercion (e.g. reduced female foraging rates in poeciliids: Plath et al., 2007; Yang et al., 2023).

Our sampling encompassed populations across the core of the *Pseudopoecilia fria/festae* distribution (a 26 000 sq. km area). We find surprisingly limited evidence that mating tactics differ geographically, with coercive tactics dominating mating behaviours at similar frequencies across populations (Fig. 2). *Pseudopoecilia* thus contrasts with other well-studied poeciliid taxa in having highly conserved behaviour over a large geographical range (e.g. *Poecilia reticulata*: Luyten & Liley, 1985; the Lake Miragoane *Limia* radiation: Rodríguez-Silva & Weaver, 2020). For instance, northern swordtails (*Xiphophorus* spp.) comprise nine species, some with courtship displays and elaborate ornaments and some without, that span a fraction of the area covered by the *Pseudopoecilia* species complex, approximately 11 500 sq. km (A. Meyer, 1997; Preising et al., 2024; Rauchenberger et al., 1990). Our findings raise important questions about why coercion remains the dominant mating tactic in some taxa, despite theoretical models suggesting a lack of evolutionary stability (Glover & Crowley, 2017) and the potential for display to evolve from coercion as a resolution to conflict (Kokko, 2005; Wang et al., 2015).

Our findings in *Pseudopoecilia* generally align with the coercive ‘sneaker male’ mating tactic found across poeciliids (Bisazza, 1993) and a wide range of other taxa. Such phenotypes appear to be produced by a trade-off, investing more heavily into intromittent organs than ornaments (Lank et al., 1995; Ota et al., 2011; Parker, 1990), while exhibiting behaviour that simultaneously circumvents potentially energetically costly interactions such as female preference and male–male combat (Ota & Kohda, 2015; Pilastro et al., 1997). However females are not defenceless against coercion and can respond with different counteradaptations. Sexual conflict has some parallels analogous to predator–prey interactions, proceeding from initial detection by a coercive male to pursuit and eventual capture (in this case a successful coercion attempt) (Endler, 1991; Langerhans, 2007; Lee et al., 2021). Females can attenuate detection and lower the frequency of harassment by coercive males with behavioural modifications such as foraging in habitats that males avoid (Darden & Croft, 2008), reducing overall activity (Galezo et al., 2018) and shoaling with other females (Agrillo et al., 2006; Dadda, 2015; Dadda et al., 2005). In many cases, encounters with coercive males may be inevitable, placing a premium on defensive responses to a coercion attempt, such as the ability to flee at high speed or dodge insemination.

Finally, as a last-resort defence against adverse fitness consequences of coercion, females can evolve postcopulatory mechanisms that can regulate female investment in offspring sired by different males (Simmons, 2005; Zeh & Zeh, 2001). Matrotrophy, the ability to provision developing offspring, may provide a mechanism for greater postcopulatory sexual selection (Furness et al., 2019; Pollux et al., 2014). However, despite the correlation between matrotrophy and superfetation across poeciliids, only lecithotrophy has been recorded in *Pseudopoecilia* (D. N. Reznick, personal communication, 19 July 2023), but whether some populations have evolved postfertilization maternal provisioning warrants further investigation.

Importantly, our study was confined to behavioural interactions involved in mating attempts, and we did not confirm whether successful mating occurred. Thus, we are making an assumption that a subset of the mating attempts we observed resulted in sperm transfer, and that the behaviours leading to successful mating were no different from those involved in unsuccessful mating. Future work would benefit from detailing the entire process, from the initiation of a mating attempt to successful mating and reproduction. Nonetheless, our study adds to the literature on mating tactics and male morphology in a model family for our understanding of sexual selection and lays the groundwork for future comparative studies. Clades exhibiting recurrent gains and losses of elaborate sexually selected traits are a major focus of sexual selection research (Wiens, 2001). Here, we reinforce that there is much to learn from taxa that exhibit a less dramatic range of sexually selected traits. In this study of a relatively drab poeciliid fish species complex native to Ecuador, we find that males rely exclusively on coercive tactics, but that frequent agonistic interactions occur in both sexes. Our findings suggest that the framework for linking morphological traits with behavioural traits can be applied to unstudied species. Our results reinforce the prediction that when male investment into body size and ornamentation is low and investment into the intromittent organ is high, mating tactics are dominated by coercive sneak copulations in poeciliid fish. Future work will seek to uncover how frequent aggression is initiated and resolved across both mating and nonmating contexts in this genus.

Author Contributions

Callen Inman: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Maxximus Ramsaroop:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Jyotishko Koley:** Writing – review & editing, Writing – original draft, Data curation. **Leonardo Ávila:** Writing – review & editing, Methodology, Investigation. **Dillan Burbano:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Micaela Pozo:** Writing – review & editing, Methodology, Investigation. **Jingping Graber:** Writing – review & editing, Visualization. **Justin Yeager:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Data Availability

Data are publicly available on GitHub: https://github.com/inmanc2/coercion_pseudopoecilia.

Declaration of Interest

None.

Acknowledgments

We thank Sunishka Thakur and Marina Hutchins for providing feedback on aspects of data visualization and conceptualization. We thank members of the Yeager lab at Universidad de Las Américas (UDLA), Quito, Ecuador, for their assistance in fish maintenance and thoughtful discussion on fish behaviour. J.Y. also acknowledges financial support from UDLA grant 483.A.XIV.24. C.I. and M.R. acknowledge Student Research Awards from the University of Texas at Austin's Department of Integrative Biology and Graduate Program in Ecology, Evolution, and Behavior, and C.I. acknowledges financial support from Braun & Gresham, LLC and Texas Ecological Laboratories. Research permits were granted from the Ministerio del Ambiente, Ecuador (MAATE-ARSFC-2024-0029 and MAATE-ARSFC-2025-0345). C.I. also thanks Michi Tobler for sharing elusive historical literature on *Pseudopoecilia* taxonomy and natural history that provided context for this and other studies. C.I. and J.Y. thank David Reznick for his correspondences and helpful discussions about *Pseudopoecilia* based on his time in the field in 1988.

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