

Female reproductive mode shapes allometric scaling of male traits in live-bearing fishes (family Poeciliidae)

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Abstract

Reproductive mode is predicted to influence the form of sexual selection. The viviparity-driven conflict hypothesis posits that a shift from lecithotrophic (yolk-nourished) to matrotrophic (mother-nourished or placental) viviparity drives a shift from precopulatory towards post-copulatory sexual selection. In lecithotrophic species, we predict that precopulatory sexual selection will manifest as males exhibiting a broad distribution of sizes, and small and large males exhibiting contrasting phenotypes (morphology and coloration); conversely, in matrotrophic species, an emphasis on post-copulatory sexual selection will preclude these patterns. We test these predictions by gathering data on male size, morphology and coloration for five sympatric Costa Rican poeciliid species that differ in reproductive mode (i.e. lecithotrophy vs. matrotrophy). We find tentative support for these predictions of the viviparity-driven conflict hypothesis, with some interesting caveats and subtleties. In particular, we find that the three lecithotrophic species tend to show a broader distribution of male sizes than matrotrophic species. Furthermore, large males of such species tend to exhibit proportionately large dorsal and caudal fins and short gonopodia relative to small males, while these patterns are expressed to a lesser extent in the two matrotrophic species. Finally, large males in some of the lecithotrophic species exhibit darker fins relative to small males, a pattern not evident in either matrotrophic species. One unexpected finding was that even in the matrotrophic species *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata*, which lack courtship and dichromatic coloration, some morphological traits exhibit significant allometric relationships, suggesting that even in these species precopulatory sexual selection may be present and shaping size-specific male phenotypes in subtle ways.

KEYWORDS

allometry, lecithotrophy, matrotrophy, Poeciliidae, sexual selection, viviparity

1 | INTRODUCTION

In some species, males exhibit massive variation in size, morphology and mating behaviour, while in other, sometimes closely related,

species, all males appear and act quite similarly (Andersson, 1994; Taborsky et al., 2008). This belies the fact that sexual selection varies in intensity and form amongst different species. Although the root causes of such differences are likely multi-faceted, one key factor

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predicted to alter the form of sexual selection is reproductive mode (Zeh & Zeh, 2000). Reproductive mode refers to a suite of reproductive traits including whether fertilization is external or internal; if internal, whether the embryos are laid or birthed live; and if live-birth, whether embryos are provisioned by yolk or by the mother (Lombardi, 1998). When these three factors (i.e. location of fertilization, embryo retention time and mode of maternal provisioning) are considered together, most animal species can be placed into one of four categories: spawning, egg-laying, lecithotrophic (i.e. yolk-nourished) live-bearing, or matrotrophic (i.e. mother-nourished) live-bearing (Furness et al., 2015). The viviparity-driven conflict hypothesis posits that the evolution of viviparity or live-bearing, from an egg-laying ancestor, causes a shift from precopulatory towards post-copulatory sexual selection (Zeh & Zeh, 2000, 2008). In essence, if spawning or egg-laying females are to choose their mates they must do so, or are predicted to more fruitfully do so, prior to mating. This emphasis on choosing mates prior to the act of mating (i.e. precopulatory sexual selection) is predicted to favour such traits as male courtship, sexually dichromatic coloration or exaggerated display traits (Pollux et al., 2014). The evolution of viviparity opens up a new (post-copulatory) arena in which mates can be selected. Specifically, in live-bearing species, a prolonged internal gestation increases the importance of genomic compatibility between mother and offspring, especially in matrotrophic species in which the mother continues to provide nutrients after fertilization. Thus, viviparous females may more fruitfully mate with multiple males and use post-copulatory choice to select compatible mates and offspring (Zeh & Zeh, 2000, 2001). The mechanisms by which this could occur, often referred to as cryptic female choice, are varied and include sperm competition within the female reproductive tract, differential sperm usage or storage based on male genotype, selective embryo abortion or differential allocation to embryos based on genomic compatibility (Crespi & Semeniuk, 2004; Gasparini & Pilastro, 2011; Parker, 1984; Pryke et al., 2010; Wedekind, 1994; Zeh & Zeh, 1997, 2000).

The viviparity-driven conflict hypothesis was originally proposed to apply to the transition from egg-laying to live-bearing but the logic applies well to the transition from lecithotrophic to matrotrophic viviparity. In lecithotrophic live-bearers, eggs are provisioned with all resources required for development (i.e. yolk) prior to fertilization. The eggs thus are energetically costly and start out large in size. After such eggs are fertilized internally, the resulting embryos are gestated by the female without further maternal input—as evidenced by the fact that they lose weight over the course of gestation—until birth (Furness et al., 2021; Pires et al., 2011; Pollux et al., 2009). This reproductive mode has sometimes been referred to as ovoviviparity (Blackburn, 2000). In contrast, matrotrophic live-bearers begin with small unfertilized eggs. After internal fertilization, embryos substantially increase in weight as they are nutritionally provisioned by mothers over the course of gestation—for example by means of a placenta (Blackburn, 2015). It is in matrotrophic species where genomic compatibility between mother and offspring—for example at immune recognition loci or those involved in resource transfer—comes into play. This is predicted to be of much lesser concern in lecithotrophic species where embryos are internally gestated but with little maternal-offspring

connection or nutrient transfer. Furthermore, in lecithotrophic species eggs start out large so any post-fertilization embryo choice would result in a large initial investment being squandered. While in matrotrophic species, eggs start out small so post-fertilization embryo selection or differential allocation is predicted to be less costly. For both these reasons, we might expect precopulatory sexual selection to play a greater role in the mating systems of lecithotrophic live-bearing species and post-copulatory sexual selection to play a greater role in the mating systems of matrotrophic live-bearing species.

The live-bearing fish family Poeciliidae has provided fruitful testing grounds for this hypothesis because the family contains species that exhibit extensive variation in both female reproductive mode and the development of male sexually selected characters (Furness et al., 2019; Pollux et al., 2014). All species in the family, save one, give live-birth to offspring (Rosen & Bailey, 1963). Lecithotrophic viviparity is the more common and predicted ancestral state of the family, with at least nine independent origins of extensive matrotrophy (Furness et al., 2019). On the male side of the equation, different species exhibit variation in the development of male sexually selected traits including presence or absence of courtship, sexually dichromatic coloration, ornamental display traits and variation in two continuous characters important in mating strategy and success, gonopodium length and the magnitude of sexual size dimorphism (Pollux et al., 2014). In a family-wide phylogenetic comparative analysis, Pollux et al., (2014) showed that males of lecithotrophic species are more likely to exhibit courtship, sexually dichromatic coloration (i.e. males bright, females dull) and ornamentation (i.e. sail-like dorsal fin or sword-like caudal fin). Furthermore, males in lecithotrophic species exhibit shorter gonopodia and male and female size is closer to parity. The converse is that in matrotrophic species males and females tend to look alike, while males have long gonopodia and are much smaller than females. These latter two features facilitate sneak or coercive copulations by circumventing precopulatory female choice (Bisazza, 1993; Bisazza & Pilastro, 1997; Greven, 2005; Pilastro et al., 1997; Pollux et al., 2014). Thus, in sum, there is evidence for an emphasis on precopulatory sexual selection in lecithotrophic species (courtship, dichromatism and ornamentation) and post-copulatory sexual selection in matrotrophic species, as predicted by the viviparity-driven conflict hypothesis (Furness et al., 2019; Pollux et al., 2014). Here, we extend this work by making additional more detailed predictions, on how reproductive mode affects patterns of sexual selection and mating strategies. We then test these predictions by examining patterns of male size, morphological variation and coloration in five sympatric poeciliid species in a tropical stream community of Costa Rica.

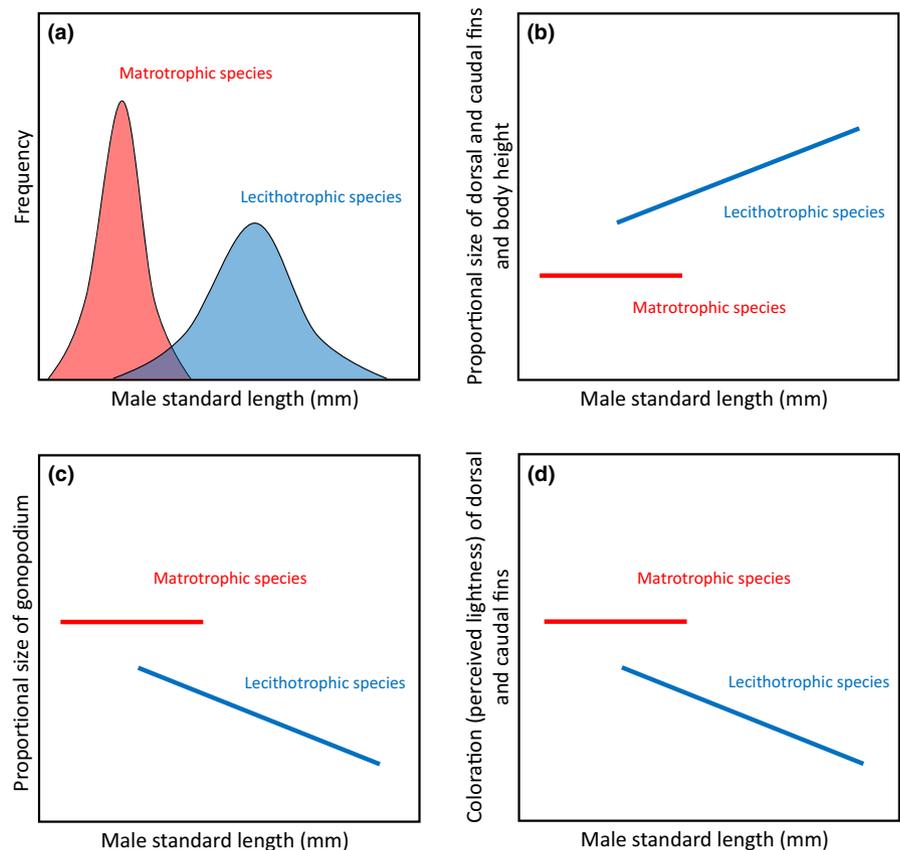
Specifically, we predict that the lecithotrophic species studied herein, *Poeciliopsis turrubarensis*, *Poecilia (Mollienesia) gillii* and *Brachyrhaphis roseni* (Cyprinodontiformes: Poeciliidae), will exhibit: i) a broad distribution of male sizes, that ii) large males will have proportionately deeper bodies, larger dorsal and caudal fins, and shorter gonopodia, and iii) large males will be more brightly coloured than small males (Figure 1). We predict the opposite for the two matrotrophic species, *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata* (Cyprinodontiformes: Poeciliidae). Specifically, males of such

species will exhibit: (a) a narrow distribution of male body sizes, (b) no relationship between male body size and fin (dorsal, caudal, and gonopodium) size, and (c) no difference in coloration as a function of male size (Figure 1). Each of these predictions is derived from an integration of the viviparity-driven conflict hypothesis and sexual selection theory with our knowledge of poeciliid biology. A number of studies in lecithotrophic poeciliid species have documented alternative male mating strategies and a broad distribution of male sizes (Rios-Cardenas & Morris, 2011). For example, in *Xiphophorus nigrensis* (Cyprinodontiformes: Poeciliidae), males exhibit contrasting phenotypes and mating strategies: large, brightly coloured and ornamented males primarily court females to engender cooperative mating, whereas small males exhibit subdued coloration and engage entirely in sneak or coercive copulation attempts, and intermediate males exhibit a mixed strategy (Ryan & Causey, 1989; Ryan et al., 1992). Similar phenomena have been found in other *Xiphophorus* species and the genus *Poecilia*, subgenera *Mollienesia* and *Limia* (Erbelding-Denk et al., 1994; Farr et al., 1986; Liotta et al., 2019; Rios-Cardenas & Morris, 2011). Comparable studies of male size variation, morphology, and mating behaviour are mostly lacking for highly matrotrophic species. We surmise this is likely the case because males of such species typically all look similar and do not exhibit the obvious size, coloration and morphological variation that frequently make lecithotrophic species obvious targets for the study of male alternative reproductive strategies.

Male traits associated with precopulatory sexual selection are often well developed in lecithotrophic species (Pollux et al., 2014). Moreover, prior studies have linked alternative reproductive tactics in lecithotrophic species with variation in male size and morphology

(Rios-Cardenas & Morris, 2011). Therefore, we predict such variation may be the norm in lecithotrophic species. Hence, we predict that lecithotrophic species will exhibit a broader distribution of male size (relative to matrotrophic species). In poeciliids, the dorsal and caudal fins are spread in aggressive male–male displays, and in a subset of species, this has been co-opted for courtship displays towards females (Goldberg et al., 2019). Display traits (i.e. fins) involved in attracting females are often overdeveloped in large males and underdeveloped in small males (Erbelding-Denk et al., 1994; Furness et al., 2020; Snelson, 1985). Applying this logic to our system, we predict that in lecithotrophic species, large males will exhibit proportionately large dorsal and caudal fins. In contrast, small males, if using a different mating strategy may employ coercive mating tactics that involve inconspicuousness to both larger aggressive males and to females which they attempt to forcibly mate. Thus, we predict that small males will exhibit proportionately smaller fin sizes and subdued coloration. The gonopodium or male intromittent organ has been found to be longer in matrotrophic species that typically lack courtship and rely on coercive mating, and shorter in lecithotrophic species which frequently have courtship (Pollux et al., 2014). Likewise, within some poeciliid species, a negative relationship has been found between male size and gonopodium length (Constanz, 1975; Erbelding-Denk et al., 1994; Furness et al., 2020; Snelson, 1985). Small males have proportionately long gonopodia and large males short gonopodia. This may suggest that large males are engendering cooperative mating or at the very least females are more receptive to mating with large males, while small males are not—with a longer gonopodium facilitating manoeuvrability during

FIGURE 1 Schematic representation of study predictions. (a) Males of lecithotrophic species are predicted to exhibit a broader size distribution than that of matrotrophic species (prediction i). (b) Males of lecithotrophic species are predicted to show significant positive allometry between male size and sexually selected traits (i.e. dorsal and caudal fins and body height), and (c) negative allometry between male size and gonopodium length, but we expect isometry in matrotrophic species (prediction ii). (d) Males of lecithotrophic species are predicted to show significant negative allometry between male size and perceived lightness of the dorsal and caudal fins (i.e. smaller males lighter fin coloration and larger males darker fin coloration), but we expect isometry in matrotrophic species (prediction iii)



these 'sneak' mating attempts (Bisazza, 1993; Greven, 2005). Thus, we predict this pattern will hold for lecithotrophic species but not matrotrophic species, which all lack courtship. We test each of these predictions by gathering field data on male body size, morphological traits and fin coloration for all five species.

2 | MATERIALS AND METHODS

Our field data collection protocol follows that of Furness et al., (2020) on *Poecilia gillii*. Here, we expanded this approach to include four additional sympatric poeciliid species (*Poeciliopsis retropinna*, *Poeciliopsis paucimaculata*, *Poeciliopsis turrubarensis* and *Brachyrhaphis roseni*) that differ in female reproductive mode and the expression of male sexually selected traits (Table 1). Specifically, here we include the most commonly found sympatric poeciliid species in our study region—rivers of the Térraba and Coto drainages of south-western Costa Rica. In brief, during the dry season of 2019 and 2020, we captured and took photographs of males of these five species in the field in Costa Rica (for site locations see Table S1). Data on male maturity, body and fin dimensions, and fin coloration were obtained from the digital photographs and these data were used to test the predictions of the viviparity-driven conflict hypothesis.

2.1 | Field data collection

At each site, fish were collected with a seine net. Males of the target species were placed into a bucket filled with water. At our field work station, these males were individually anaesthetized, using a

buffered MS-222 solution, before being photographed on a white cutting board containing a measurement scale. Males had their fins gently spread with the wetted bristles of a fine-tipped paint brush. Photographs of the left side of each male were taken with an Olympus Tough TG-6 camera attached to a tripod. Following recovery from the light anesthetization, males were released near the point of collection. Data on male maturity, body and fin dimensions, and fin coloration were obtained from the digital photographs. Maturity was judged based on gonopodial development. Specifically, in *Poecilia gillii* males were scored as mature when the gonopodial hood extended beyond the distal tip of the gonopodium (Furness et al., 2020). In each of the three *Poeciliopsis* species, males were scored as mature when the gonopodium was rod-like and opaque as opposed to flexible, short and clear. Finally, in *Brachyrhaphis roseni*, males were scored as mature when the gonopodium appeared like an unsheathed pointed sword with black pigmentation along its full length as opposed to being short, not-fully pigmented and covered in a clear sheath. The number of males of each species that were photographed and scored as mature can be found in Table S1. Only mature males were included in subsequent analyses.

2.2 | Body and fin dimensions

The following male phenotypic traits were measured from the photographs of each male using ImageJ software (Rasband, 2014; Schneider et al., 2012): (1) standard length (SL); (2) body height (BH); (3) gonopodium length (GL); (4) caudal fin height (CFH); (5) caudal fin width (CFW); (6) dorsal fin height (DFH); and (7) dorsal fin width (DFW). The standard length (SL) was measured from the tip of the

TABLE 1 Summary of female reproductive mode and male sexually selected traits, amongst the five study species (Hagmayr et al., 2018, 2020; Pollux et al., 2009, 2014; Reznick et al., 2002; Zúñiga-Vega et al., 2007)



Trait/Species		<i>Poeciliopsis retropinna</i>	<i>Poeciliopsis paucimaculata</i>	<i>Poeciliopsis turrubarensis</i>	<i>Brachyrhaphis roseni</i>	<i>Poecilia gillii</i>
Female reproductive mode	Placentation	Y	Y	N	N	N
	Matrotrophy Index	117	7.8	<1	<1	<1
	Superfetation Index	4	2	4	1	1
Male sexually selected traits	Courtship	N	N	N	Y	N
	Dichromatism	N	N	Y	N	Y
	Ornamentation	N	N	N	N	N

Note: The phylogenetic relationships of the study species are depicted at the top (Reznick et al., 2017). Our study included the five most commonly found sympatric poeciliid species in our study region (i.e. the Térraba and Coto drainages of south-western Costa Rica). This included two matrotrophic and three lecithotrophic species (please note that five species is too few to conduct reliable PGLS analyses; Mundry, 2014). The Matrotrophy Index, defined as the ratio of offspring dry weight at birth to an egg at fertilization, is a way to quantify the magnitude of post-fertilization maternal provisioning. Values less than 1 indicate lecithotrophy and greater than 1 matrotrophy (in this case nutrient transfer is via a follicular placenta). The Superfetation Index refers to the number of distinct broods a female can gestate simultaneously. For definitions of male sexually selected traits please refer to the introduction.

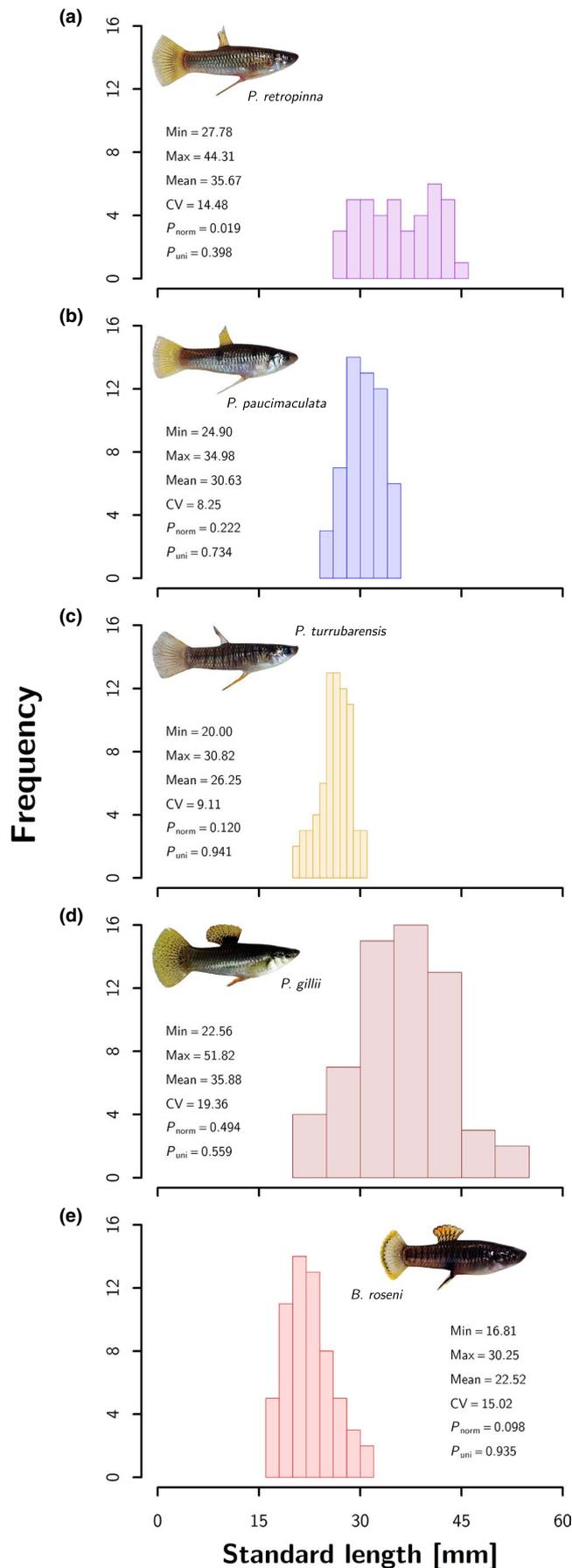


FIGURE 2 Frequency histograms of male standard length. (a) *Poeciliopsis retropinna*, (b) *Poeciliopsis paucimaculata*, (c) *Poeciliopsis turrubarensis*, (d) *Poecilia gillii* and (e) *Brachyrhaphis roseni*. Summary statistics of the distribution of male sizes, including minimum (Min), maximum (Max), and mean standard length, the coefficient of variation (CV) and statistics indicating whether the distribution differs from normality (Shapiro test p -value: P_{norm}), and unimodality (Hartigan's dip test p -value: P_{uni}) are indicated in each panel. Representative males of each species are also pictured

upper jaw to the outer margin of the hypural plate/base of the caudal peduncle. Body height (BH) was measured from the highest point on the dorsal surface to the lowest point on the abdomen. Gonopodium length (GL) was measured from the base to the distal tip of the male anal fin. Caudal fin height (CFH) was measured from the highest point to the lowest point on the caudal fin, and caudal fin width (CFW) was measured from the outer margin of the hypural plate to the outer margin of the caudal fin. Finally, dorsal fin height (DFH) was measured from the tip to the base of the longest fin ray, and dorsal fin width (DFW) from the anterior and posterior insertion points on the dorsal surface. We generated summary statistics and frequency histograms / density plots for each measured trait of each species and used a Shapiro–Wilk normality test to determine whether each distribution deviated from normality and Hartigan's dip test to determine whether the distribution differed from unimodality.

2.3 | Fin coloration

Using the photographs of each male and the image analysis software ImageJ (Rasband, 2014; Schneider et al., 2012), we performed a quantitative analysis of male fin coloration as a function of body size. For each male, we extracted (a) the perceived lightness of the dorsal and caudal fin, and (b) the proportion of black pixels in these fins. When calculating perceived lightness, the inclusion of black coloration can overshadow the nonblack coloration of the rest of the fins. Therefore, a small and representative subset of pixels was used to capture the nonblack component of fin coloration. For each species, we selected a small circular region from the dorsal and caudal fins (Figure S1). This patch of pixels was taken from the central upper region of the dorsal fin and central lower region of the caudal fin. The exact size and positioning varied slightly between different individuals because it was chosen to avoid the inclusion of black pigmentation and the darker fin rays (for pixel sampling location on the dorsal and caudal fins of representative males, see Figure S1). For this fin region, we extracted the average RGB colour (averaged over all pixels) using ImageJ. The perceived lightness (L^*) was subsequently calculated from the average RGB colour (Appendix S1, Calculating perceived lightness). The L^* is a measure of perceptual lightness that can take values between zero (black) and 100 (white) (Buckley & Giorgianni, 2015).

To calculate the proportion of black pixels in the dorsal and caudal fins, we first converted the image of each male into an eight-bit greyscale image. Each pixel can then take a value between zero (black) and 255 (white). We extracted the greyscale value of each pixel for each fin of each male and generated a histogram of all greyscale values of the dorsal and caudal fins (Figure S2). In the case of the dorsal fin of *Poecilia gillii* and *Brachyrhaphis roseni*, the two species that contained black fin pigmentation, there was a clear separation between the black structures of the fin and the rest. This allowed us to define a threshold value (40 in *Poecilia gillii* and 60 in *Brachyrhaphis roseni*; red vertical lines in Figure S2) at which a pixel is considered to be black or white, respectively. We used the same threshold values for the caudal fin. We checked this threshold value in a subset of the images, and it seems to accurately capture the black coloration of the fins (Figure S1). Finally, we calculated the proportion of black pixels in each fin.

2.4 | Statistical analyses

All models were fit in a Bayesian framework using the MCMCglmm package (Hadfield, 2010) in R v 3.5 (R Core Team 2020). Convergence was assessed by visual examination of the traces, and the autocorrelations of the parameter chain were checked to be less than 0.1. The priors, number of MCMC chains, iterations, burnin and thinning are given in Appendix S1.

We examined allometric relationships between the proportional size of body parts potentially involved in mating or sexual selection (i.e. BH, GL, CFH, CFW, DFH and DFW) and overall body size (i.e. standard length, SL). Specifically, the proportional size of each trait relative to overall body size (i.e. the trait divided by SL) was fitted as a function of SL, species, as well as SL \times species in a multivariate linear model allowing for the covariance between the residuals of all responses. A positive allometric relationship indicates that the given body part grows at a faster rate than does body size as a whole (i.e. large individuals have a proportionately larger body part than smaller individuals). In contrast, a negative allometric relationship indicates that the body part has a slower growth rate than does the body as a whole (i.e. small individuals have a proportionately larger body part than larger individuals).

To identify potential effects of male body size on fin coloration, we fitted (i) the perceived lightness in the dorsal and caudal fin, and (ii) the proportion of black pixels in the dorsal and caudal fin as a function of standard length (SL), species, as well as SL \times species, each in a bivariate linear model allowing for the covariance between the residuals of both responses. For (ii), we excluded males of *Poeciliopsis retropinna*, *Poeciliopsis paucimaculata* and *Poeciliopsis turrubarensis*, as males of these species do not appear to have black fin coloration (Figure S2). To optimize normality and homoscedasticity of the model residuals, the proportion of black pixels in the caudal fin was ln-transformed (Furness et al., 2020).

3 | RESULTS

3.1 | Distribution of male body size and other traits

Males of each species varied in their absolute size, the relative distribution of size classes, and the overall shape of the size distribution (Figure 2). *Brachyrhaphis roseni* males were the smallest (mean SL, 22.52 mm) and *Poecilia gillii* males the largest (mean SL, 35.88 mm). The coefficient of variation (CV) is a means to compare the breadth of species' size distributions, independent of the absolute sizes of males. *Poecilia gillii* exhibited the highest CV (19.36), then *Brachyrhaphis roseni* (15.02), followed by *Poeciliopsis retropinna* (14.48), *Poeciliopsis turrubarensis* (9.11), and finally *Poeciliopsis paucimaculata* (8.25). Only the male size distribution of *Poeciliopsis retropinna* differed from normality (Shapiro–Wilk normality test, $p = .019$). This species exhibited a uniform distribution of male size, with no clear peak in the data (Figure 2a). None of the five species had a male size distribution that differed from unimodality (Hartigan's dip test, $p > .05$). The distribution of each of the other measured morphological traits (i.e. BH, GL, CFH, CFW, DFH and DFW) did not differ from unimodality for any of the species (Hartigan's dip test, all $p > .05$), although in some cases they deviated from normality (Shapiro–Wilk normality test, $p < .05$) due to varying degrees of skewness or kurtosis (Table S2, Figure S3).

3.2 | Allometric relationships between morphological traits and standard length

Below we describe the allometric relationships between morphological traits (i.e. BH, GL, CFH, CFW, DFH and DFW) and standard length (SL) for each species. This information is displayed in Figure 3, and the full model details for each analysis can be found in Tables S3 and S4. Please also see Figure S4, and Tables S5 and S6 for similar analyses performed on \log_{10} transformed data, and the associated allometric scaling coefficients.

For *Poeciliopsis retropinna*, we found a significant positive allometric relationship between body size and proportional body height ($\beta_{\text{post.mean}} = 0.0014$, $P_{\text{MCMC}} = 0.004$; Figure 3a; Table S3a), caudal fin height ($\beta_{\text{post.mean}} = 0.0041$, $P_{\text{MCMC}} < 0.001$; Figure 3c; Table S3c) and dorsal fin height ($\beta_{\text{post.mean}} = 0.0016$, $P_{\text{MCMC}} < 0.001$; Figure 3e; Table S3e). The relationship between body size and proportional gonopodium length was significantly negative ($\beta_{\text{post.mean}} = -0.0018$, $P_{\text{MCMC}} < 0.001$; Figure 3b; Table S3b). Lastly, there was no significant relationship between body size and proportional caudal fin width ($\beta_{\text{post.mean}} = 0.0001$, $P_{\text{MCMC}} = 0.794$; Figure 3d; Table S3d) and dorsal fin width ($\beta_{\text{post.mean}} = 0.0003$, $P_{\text{MCMC}} = 0.328$; Figure 3f; Table S3f). Thus, large *Poeciliopsis retropinna* males had proportionately deeper bodies, higher caudal and dorsal fins and shorter gonopodia than smaller males (Figure 3).

For *Poeciliopsis paucimaculata*, we observed a significant positive allometric relationship between body size and proportional body height ($\beta_{\text{post.mean}} = 0.0023$, $P_{\text{MCMC}} < 0.001$; Figure 3a; Table S3a)

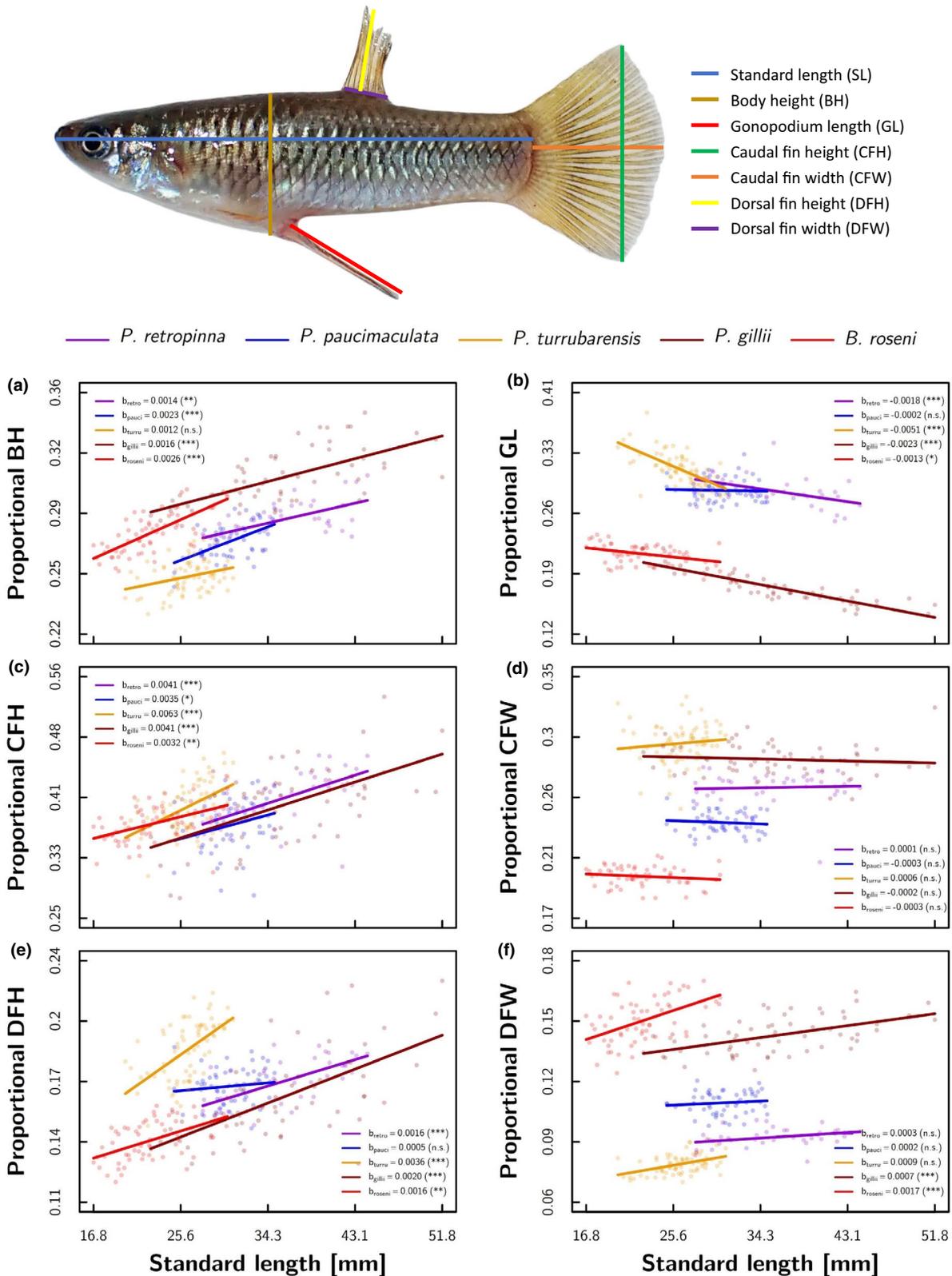


FIGURE 3 Allometric relationships between proportional (i.e. $y \cdot SL^{-1}$) morphological traits and standard length (SL) for all five poeciliid species. The traits that were measured are depicted on a male *Poeciliopsis retropinna* (top). Graphs depict the relationship between SL and proportional (a) body height (BH), (b) gonopodium length (GL), (c) caudal fin height (CFH), (d) caudal fin width (CFW), (e) dorsal fin height (DFH) and (f) dorsal fin width (DFW). The slope of the regression is given in each panel. A slope equal to 0 indicates isometry (proportional growth of the trait), greater than 0 hyperallometry (trait grows disproportionately faster than SL) and less than 0 hypoallometry (trait grows disproportionately slower than SL). The significance of a deviation of the allometric scaling from isometry (i.e. 0) is given in brackets. Significance codes: $P_{\text{MCMC}} < .001^{***}$, $<.01^{**}$, $\leq .05^*$, $>.05$ n.s.

and caudal fin height ($\beta_{\text{post.mean}} = 0.0035$, $P_{\text{MCMC}} = 0.038$; Figure 3c; Table S3c). There was no significant relationship between body size and proportional gonopodium length ($\beta_{\text{post.mean}} = -0.0002$, $P_{\text{MCMC}} = -0.812$; Figure 3b; Table S3b), caudal fin width ($\beta_{\text{post.mean}} = 0.0003$, $P_{\text{MCMC}} = 0.736$; Figure 3d; Table S3d), dorsal fin height ($\beta_{\text{post.mean}} = 0.0005$, $P_{\text{MCMC}} = 0.572$; Figure 3e; Table S3e) and dorsal fin width ($\beta_{\text{post.mean}} = 0.0002$, $P_{\text{MCMC}} = 0.670$; Figure 3f; Table S3f). Thus, large *Poeciliopsis paucimaculata* males had proportionately deeper bodies and higher caudal fins than smaller males (Figure 3).

For *Poeciliopsis turrubarensis*, there was a significant positive allometric relationship between body size and proportional caudal fin height ($\beta_{\text{post.mean}} = 0.0063$, $P_{\text{MCMC}} < 0.001$; Figure 3c; Table S3c) and dorsal fin height ($\beta_{\text{post.mean}} = 0.0036$, $P_{\text{MCMC}} < 0.001$; Figure 3e; Table S3e). The relationship between body size and proportional gonopodium length was significantly negative ($\beta_{\text{post.mean}} = -0.0051$, $P_{\text{MCMC}} < 0.001$; Figure 3b; Table S3b). Lastly, there was no significant relationship between body size and proportional body height ($\beta_{\text{post.mean}} = 0.0012$, $P_{\text{MCMC}} = 0.076$; Figure 3a; Table S3a), caudal fin width ($\beta_{\text{post.mean}} = 0.0006$, $P_{\text{MCMC}} = 0.370$; Figure 3d; Table S3d), and dorsal fin width ($\beta_{\text{post.mean}} = 0.0009$, $P_{\text{MCMC}} = 0.064$; Figure 3f; Table S3f). Thus, large *Poeciliopsis turrubarensis* males had proportionately higher caudal and dorsal fins and shorter gonopodia than smaller males (Figure 3).

For *Poecilia gillii*, a significant positive allometric relationship was found between body size and proportional body height ($\beta_{\text{post.mean}} = 0.0016$, $P_{\text{MCMC}} < 0.001$; Figure 3a; Table S3a), caudal fin height ($\beta_{\text{post.mean}} = 0.0041$, $P_{\text{MCMC}} < 0.001$; Figure 3c; Table S3c), dorsal fin height ($\beta_{\text{post.mean}} = 0.0020$, $P_{\text{MCMC}} < 0.001$; Figure 3e; Table S3e) and dorsal fin width ($\beta_{\text{post.mean}} = 0.0007$, $P_{\text{MCMC}} < 0.001$; Figure 3f; Table S3f). The relationship between body size and proportional gonopodium length was significantly negative ($\beta_{\text{post.mean}} = -0.0023$, $P_{\text{MCMC}} < 0.001$; Figure 3b; Table S3b). Lastly, there was no significant relationship between body size and proportional caudal fin width ($\beta_{\text{post.mean}} = -0.0002$, $P_{\text{MCMC}} = 0.532$; Figure 3d; Table S3d). Thus, large *Poecilia gillii* males had proportionately deeper bodies, larger dorsal and caudal fins and shorter gonopodia than smaller males (Figure 3).

For *Brachyrhaphis roseni*, we observed a significant positive allometric relationship between body size and proportional body height ($\beta_{\text{post.mean}} = 0.0026$, $P_{\text{MCMC}} < 0.001$; Figure 3a; Table S3a), caudal fin height ($\beta_{\text{post.mean}} = 0.0032$, $P_{\text{MCMC}} = 0.006$; Figure 3c; Table S3c), dorsal fin height ($\beta_{\text{post.mean}} = 0.0016$, $P_{\text{MCMC}} = 0.004$; Figure 3e; Table S3e) and dorsal fin width ($\beta_{\text{post.mean}} = 0.0017$, $P_{\text{MCMC}} < 0.001$; Figure 3f; Table S3f). The relationship between body size and proportional gonopodium length was significantly negative ($\beta_{\text{post.mean}} = -0.0013$, $P_{\text{MCMC}} = 0.028$; Figure 3b; Table S3b). Lastly, there was no significant relationship between body size and proportional caudal fin width ($\beta_{\text{post.mean}} = -0.0003$, $P_{\text{MCMC}} = 0.568$; Figure 3d; Table S3d). Thus, large *Brachyrhaphis roseni* males had proportionately deeper bodies, larger dorsal and caudal fins and shorter gonopodia than smaller males (Figure 3).

3.3 | Species-specific fin coloration as a function of male size

In *Poecilia gillii*, there was significant covariation between male standard length and dorsal fin lightness ($\beta_{\text{post.mean}} = -0.710$, $P_{\text{MCMC}} < 0.001$; Figure 4a; Table S7a, S8) and caudal fin lightness ($\beta_{\text{post.mean}} = -0.805$, $P_{\text{MCMC}} < 0.001$; Figure 4b; Table S7b, S8); larger males have darker dorsal and caudal fins compared to small males (Figure 4a,b). In *Poeciliopsis turrubarensis*, there was significant covariation between male standard length and dorsal fin lightness ($\beta_{\text{post.mean}} = -0.693$, $P_{\text{MCMC}} = 0.026$; Figure 4a; Table S7a, S8); larger males have darker dorsal fins compared to small males (Figure 4a). In each of the other species, there was no relationship between male standard length and dorsal or caudal fin lightness ($P_{\text{MCMC}} > 0.05$; Figure 4a,b; Table S7 and S8). In both *Poecilia gillii* and *Brachyrhaphis roseni*, the amount of black pigmentation on the dorsal fin linearly increased with male size (*Poecilia gillii*: $\beta_{\text{post.mean}} = 0.007$, $P_{\text{MCMC}} < 0.001$; Figure 4c; Table S9a, S10; *Brachyrhaphis roseni*: $\beta_{\text{post.mean}} = 0.013$, $P_{\text{MCMC}} < 0.001$; Figure 4c; Table S9a, S10). Furthermore, in both these species, the amount of black pigmentation on the caudal fin increased exponentially with male size (*Poecilia gillii*: $\beta_{\text{post.mean}} = 0.175$, $P_{\text{MCMC}} < 0.001$; Figure 4d; Table S9b, S10; *Brachyrhaphis roseni*: $\beta_{\text{post.mean}} = 0.120$, $P_{\text{MCMC}} = 0.004$; Figure 4d; Table S9b, S10). Thus, larger *Poecilia gillii* and *Brachyrhaphis roseni* males had a significantly greater proportion of their dorsal and caudal fins covered in black pigmentation (Figure 4). Males of *Poeciliopsis retropinna*, *Poeciliopsis paucimaculata* and *Poeciliopsis turrubarensis* did not exhibit any black fin coloration, irrespective of size (Figure S2).

4 | DISCUSSION

The viviparity-driven conflict hypothesis (Zeh & Zeh, 2000) predicts that precopulatory sexual selection predominates in lecithotrophic species and post-copulatory sexual selection in matrotrophic species. This proposition has found support in the live-bearing fish family Poeciliidae (Furness et al., 2019; Pollux et al., 2014). Here, we derived a series of further predictions regarding how patterns of sexual selection differ as a function of reproductive mode (i.e. lecithotrophic vs. matrotrophic viviparity). We then test these predictions within five sympatric poeciliid species in Costa Rica. Specifically, we predicted that (a) the three lecithotrophic species will exhibit a broader distribution of male sizes than matrotrophic species, potentially as a result of intense precopulatory sexual selection favouring alternative male mating strategies, (b) that within lecithotrophic species, large males will have proportionately deeper bodies, larger dorsal and caudal fins (positive allometry), and shorter gonopodia (negative allometry) compared to small males, while in matrotrophic species these relationships will be isometric, and (c) that within lecithotrophic species, larger males will have darker and more heavily black-pigmented dorsal and caudal fins compared to small males, while in matrotrophic species male fin coloration will

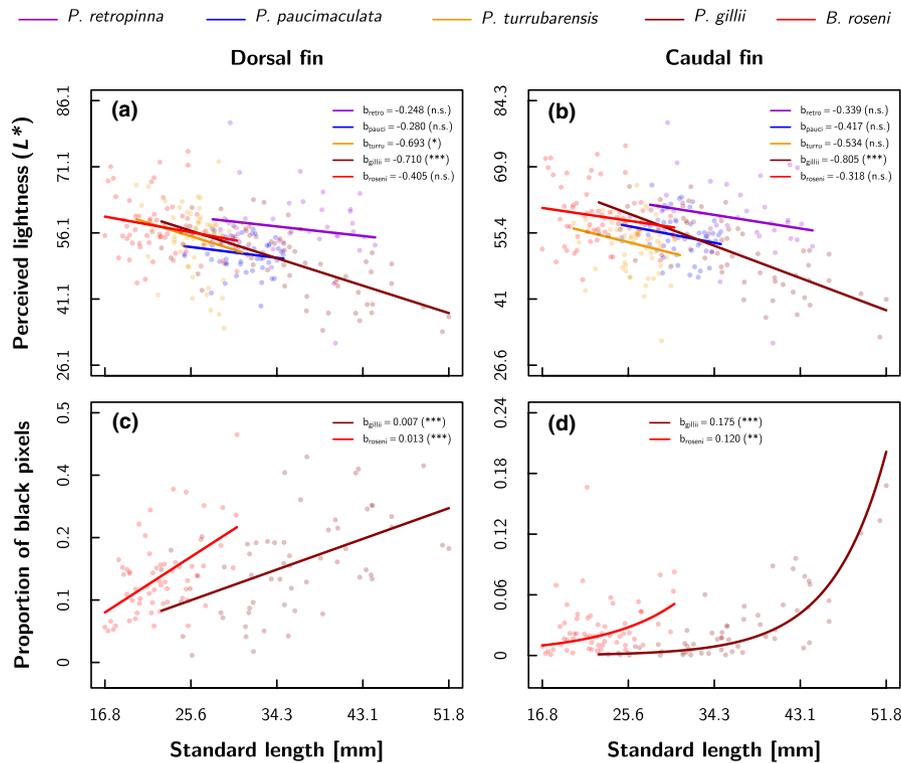


FIGURE 4 Species-specific fin coloration as a function of male standard length. Perceived lightness of the dorsal (a) and caudal (b) fins as a function of male standard length. Proportion of black pigmentation on the dorsal (c) and caudal (d) fins as a function of male standard length. The estimate and significance of the species-specific slopes are given in each panel. Significance codes: $P_{\text{MCMC}} < .001$ ***, $< .01$ ** , $\leq .05$ *, $> .05$ n.s

not differ as a function of size. Below we evaluate and discuss each of these predictions (Figure 1) in light of our results (Figures 2, 3, 4).

The lecithotrophic species, *Poecilia gillii* exhibited the highest coefficient of variation of male size—a means by which to compare the relative breadth of the size distribution amongst species. This was followed by the lecithotrophic *Brachyrhaphis roseni*, then by the matrotrophic *Poeciliopsis retropinna*, the lecithotrophic *Poeciliopsis turrubarensis*, and finally the matrotrophic *Poeciliopsis paucimaculata*. Thus, our prediction that lecithotrophic species would exhibit a broader distribution of male sizes (owing ultimately to divergence in mating tactics as a result of intense precopulatory sexual selection) was generally supported. However, we do note that the matrotrophic *Poeciliopsis retropinna* exhibited a higher coefficient of variation in male size than the lecithotrophic *Poeciliopsis turrubarensis*, suggesting that other factors besides reproductive mode influence male size distributions. Only the male size distribution of *Poeciliopsis retropinna* differed from normality, while none of the male size distributions deviated from a unimodal distribution. In some lecithotrophic, poeciliid species such as *Xiphophorus multilineatus*, *Phallichthys quadripunctatus*, *Brachyrhaphis rhabdophora* (2 out of 4 populations) and *Limia zonata* a bimodal or multimodal male size distribution has been reported (Cohen et al., 2015; Kolluru & Reznick, 1996; Reznick et al., 1993; Rios-Cardenas et al., 2018). The reason why the males of some lecithotrophic species exhibit bimodal size distributions, while others, including the five studied here, do not, is deserving of further study. It has been suggested that the evolution of alternative

reproductive tactics, and perhaps bimodal size distributions as a corollary, is related to the intensity of sexual selection (Gadgil, 1972; Taborsky et al., 2008).

We predicted that within lecithotrophic species, large males will have proportionately deeper bodies and larger dorsal and caudal fins (positive allometry), and shorter gonopodia (negative allometry) compared to small males, while in matrotrophic species these relationships will be isometric. We found some trends consistent with this prediction, but overall the data tell a somewhat more complicated, and interesting, story. Caudal fin width did not differ from isometry in any of the five species. This was the only measured trait in which this pattern was observed and makes for a striking contrast with caudal fin height, the only measured trait in which all five species exhibited positive allometry. This might suggest that caudal fin width is functionally constrained; perhaps this trait, more so than others, is tied to swimming performance such that sexually selected deviations from isometry are not favoured by selection. The lecithotrophic *Poecilia gillii* and *Brachyrhaphis roseni* exhibited significant allometry, in the predicted direction, for every measured trait except caudal fin width (see above). The lecithotrophic *Poeciliopsis turrubarensis*, exhibited significant allometry, in the predicted direction, for gonopodium length, caudal fin height and dorsal fin height, but isometry for body height, caudal fin width and dorsal fin width. Thus, for lecithotrophic species our findings are largely concordant with predictions; in these three species, large males tend to have proportionately deeper bodies, larger dorsal and caudal fins, and

shorter gonopodia relative to small males. The matrotrophic species, *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata*, did not exhibit isometry for all traits, as we had originally predicted. *Poeciliopsis retropinna* did exhibit isometry for caudal fin width and dorsal fin width, and *Poeciliopsis paucimaculata* exhibited isometry for gonopodium length, caudal fin width, dorsal fin height, and dorsal fin width. However, these species both exhibited significant positive allometry for body height and caudal fin height, and *Poeciliopsis retropinna* exhibited significant positive allometry for dorsal fin height and significant negative allometry for gonopodium length. Thus, large *Poeciliopsis paucimaculata* males had proportionately deeper bodies and higher caudal fins than smaller males, and large *Poeciliopsis retropinna* males had proportionately deeper bodies, higher caudal and dorsal fins and shorter gonopodia than smaller males. These significant allometric relationships are interesting and unexpected because neither of these species exhibit courtship, sexually dichromatic coloration or ornamental display traits (Pollux et al., 2014). In other words, males tend to look like females and they rely on sneak or coercive copulations. Presumably, there is an optimal ratio of body size to fin dimensions favoured by natural selection, and deviations from this isometric relationship have an underlying biological cause. In this case, we think the most plausible one is precopulatory sexual selection. We selected these specific traits for measurement because of their known function in female choice and male–male aggression in other poeciliid species (Benson & Basolo, 2006; Constanz, 1975; Goldberg et al., 2019; MacLaren et al., 2004; Prenter et al., 2008). In particular, in aggressive encounters between males of the genus *Poecilia* subgenus *Mollienesia* and *Limia*, the dorsal and caudal fins are fully spread (Furness et al., 2020; Goldberg et al., 2019). Likewise, in species in which it is present, courtship involves the male spreading his dorsal and caudal fins while displaying in front of the female and this is often accompanied by stereotypical swimming performances and a sigmoid body posture (Goldberg et al., 2019; Rios-Cardenas & Morris, 2011). That some of these traits exhibit significant allometric effects in matrotrophic species that lack courtship, dichromatism and ornamentation (when scored as binary presence-absence characters) suggests that even in these species, subtle precopulatory sexual selection is at play. We surmise that large males derive some benefit from having proportionately deeper bodies and larger caudal fins—and in *Poeciliopsis retropinna* larger dorsal fins and shorter gonopodia—relative to smaller males. It is yet to be determined whether the benefit is accrued because females prefer these traits in large males, they make large males more effective in encounters with other males, or some combination of the two.

Lastly, we tested how dorsal and caudal fin coloration varies as a function of male size. We predicted that in lecithotrophic species, larger males will have darker and more heavily black-pigmented dorsal and caudal fins compared to small males, while in matrotrophic species male fin coloration will not differ as a function of size. Our results generally support this prediction. Specifically, we found that two of three lecithotrophic species (*Poeciliopsis turrubarensis* and *Poecilia gillii*) showed the predicted relationship between male size and dorsal fin coloration, and one of three lecithotrophic species

(*Poecilia gillii*) showed the predicted relationship between male size and caudal fin coloration. In all cases, larger males exhibited darker fin coloration than small males. As predicted, neither of the two (sexually monochromatic) matrotrophic species showed a relationship between fin coloration and male size. Lastly, in both the lecithotrophic *Poecilia gillii* and *Brachyrhaphis roseni*, there was a strong positive relationship between male size and the proportion of black pigmentation on the dorsal and caudal fins. In these species, large males exhibited blacker fins. None of the three *Poeciliopsis* species exhibited any black pigmentation on their fins, irrespective of size. In other poeciliid species, male fin coloration (along with size) has been implicated in both female choice and the outcome of male–male encounters (Constanz, 1975; Endler, 1984; Franck et al., 2003; Horth et al., 2010; Hurtado-Gonzales & Uy, 2009; Jirotkul, 2000; Kingston et al., 2003; Kolluru et al., 2014; Ptacek et al., 2005). Thus, our interpretation of these significant patterns in the lecithotrophic species studied here is that they are likely functioning in a similar context. Large males apparently benefit in some way from having darker fins, while small males benefit from lighter and less black-pigmentation, perhaps to facilitate inconspicuousness and aid in sneak mating attempts.

A strength of our study was that several types of data (i.e. male size, morphological data and coloration) were collected from multiple co-occurring (i.e. sympatric) placental and nonplacental species. Taken together our results generally support the predictions of the viviparity-driven conflict hypothesis, although with some interesting caveats and subtleties. One unexpected finding was that even in the matrotrophic species *Poeciliopsis retropinna* and *Poeciliopsis paucimaculata*, which lack courtship, ornamentation and dichromatic coloration, some traits implicated in precopulatory sexual selection in other species exhibit significant allometric relationships. To take one concrete example, *Poeciliopsis retropinna* males exhibited significant negative allometry for gonopodium length, meaning small males have proportionately longer gonopodia than large males. This suggests that even in these species precopulatory sexual selection may be present and shaping size-specific male phenotypes in subtle ways. One limitation is that our study was conducted on only five species, precluding our ability to perform reliable phylogenetic comparative analyses. Nevertheless, the interesting trends uncovered in our study invite further testing of these patterns and their underlying causes in a larger comparative phylogenetic framework.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

AF, AH and BP conceived the project idea and collected the data. AH analysed the data. AF wrote the manuscript with comments from AH and BP.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data sets used in all analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.wh70rxwnh>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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