

Sexually selected sexual selection: Can evolutionary retribution explain female ornamental colour?

Marcela Méndez-Janovitz^{1,2}  | Alejandro Gonzalez-Voyer¹ | Constantino Macías García¹ 

¹Instituto de Ecología, Universidad Nacional Autónoma de México, México City, México

²Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, México City, México

Correspondence

Constantino Macías García, Laboratorio de Conducta Animal, Instituto de Ecología, Universidad Nacional Autónoma de México, A. P. 70-275, C. P. 04510, Ciudad de México, México.

Email: maciasg@unam.mx

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Abstract

By preferring mates with increasingly costly ornaments or courtship displays, females cause an escalation of male reproductive costs. Such increased costs should promote male selectivity based on fecundity-linked female attributes, leading to female ornamentation in species with traditional sex roles. Consequently, female ornamentation should evolve more frequently in taxa where male reproduction is costly than in comparable taxa where it is cheaper. We assessed the prevalence of female ornamental colouration in two clades of viviparous cyprinodontid fish: the Goodeinae, where stringent female choice imposes male mating costs, and the Poeciliinae, whose males can circumvent female mate choice. We found that although in the Poeciliinae female ornamental colour is a correlated, but paler version of male coloration, females of the Goodeinae often display vivid ornamental colours that are distinct from those of males. Thus, male and female ornaments are not (phylo)genetically correlated in the Goodeinae. Furthermore, phylogenetic signal on male and female colour is clearly detectable in the Poeciliinae, but absent in the Goodeinae, suggesting that ornamental colour of males and females in the latter may be the consequence of selection. Given that enforceable female choice has promoted male ornaments, we propose that evolutionary retribution has promoted distinct female ornaments in the Goodeinae.

KEYWORDS

dichromatism, goodeinae, male mate choice, poeciliinae, viviparous fish

1 | INTRODUCTION

In species with chromatic vision, mate choice often results in the evolution of vivid colour patterns in one sex (Endler, 1983). Inasmuch as these can be costly to produce/maintain (Olson & Owens, 1998), they may reflect the condition of the bearer, thus making the choice of mating partner based on such colours adaptive (Zahavi, 1975). Asymmetries in the strength of mate choice between sexes may then lead to the evolution of dichromatism, i.e. the sexual difference in colour/colour pattern (Burns, 1998). Unlike sexual differences in ecology, which may also produce sexual dichromatism (see Johnson, Price, & Pruett-Jones, 2013), sexual

selection tends to produce a disproportionate frequency of cases in which dichromatism is the result of males being more brightly coloured than females (Hofmann, Cronin, & Omland, 2008). This is because anisogamy has led to higher re-mating rates for males than for females (Sutherland & De Jong, 1991; Trivers, 1972), with females becoming the choosy sex and selecting males based, often, on ornamental traits (Andersson, 1992). As a consequence, there has been a historical bias towards studying the causes of male ornamental colouration, with little, if any, focus on the origin of female ornaments (but see Wallace, 1891), except in cases of clear sex-role reversals (e.g. pipefish and sea dragons, Rosenqvist & Berglund, 2011; phalaropes, Kimball & Ligon, 1999).

Female mate choice may originally be based on one or a few attributes that either indicate that a particular male belongs to the right species, or that are adaptive in other contexts (see Fisher, 1930; male attributes may also be selected because they target female perceptual biases; see Endler & Basolo, 1998), and subsequent elaboration may lead to those traits becoming ornaments (see also Kirkpatrick, 1982; Kokko, 1997; Lande, 1980; O'Donald, 1962). Because of the linkage disequilibrium between the genes that control the expression of the ornament and of the preference, both traits are inherited by all the offspring. This leads to the probably maladaptive expression of male ornaments in females (although in some cases the correlation is adaptive; see, e.g., Torres & Velando, 2005) and of female mating preferences in males, and it takes subsequent selection to generate sex limitation of these traits (Rhen, 2000). In species with traditional sex roles, and in the absence of ecological differences between sexes, the default has been to adjudicate female bright colouration to a genetic correlation between sexes (Dale, Dey, Delhey, Kempnaers, & Valcu, 2015; Lande, 1980). This assumes that only male colour is subject to selection, yet recent work has shown that female colouration often experiences as many or more evolutionary changes than male colour (Dale et al., 2015; Heinsohn, Legge, & Endler, 2005; Hofmann et al., 2008; Price & Eaton, 2014). Such changes may be brought about as a consequence of adaptation to the visual background (i.e. selection for crypsis vis-à-vis predators or other selective agents) or of selection for conspicuousness. The latter can occur if males preferentially encounter, court and/or mate with the most colourful females, especially if those females are the ones with higher reproductive value (Remeš & Matysioková, 2013). For males to become selective, it is necessary for mating to be expensive, a circumstance that is met in species where breeding is costly (i.e. sperm is scarce, males provide parental care), or where males are themselves ornamented and thus pay nontrivial mating cost. The costs of male reproductive effort come not only from the physiological expenditure to produce conspicuous ornaments and courtship, but also from the predation risk that the bearers face (Macías García, Saborío, & Berea, 1998). The survival costs can modify the operational sex ratio (OSR; Forsgren, Amundsen, Borg, & Bjelvenmark, 2004), and the energy and sperm costs affect male mating rate (potential reproductive rate, PRR; Parker & Pizzari, 2010; Edward & Chapman, 2011). Both the OSR and the PRR are important factors that define which is the selective sex and how selective it is (Clutton-Brock & Parker, 1992).

Costly male ornamentation and courtship evolve in response to adaptive and enforceable female mate choice and can lead to female-biased operational sex ratios as males in good breeding condition become scarce. This can in turn promote male mating choosiness based on female attributes that reflect quality. We can evaluate this idea through a comparison between two clades that differ in the intensity of sexual selection acting on males and in the prevalence of female bright colour patterns. Sexually dichromatic species are common in two fish Subfamilies, Poeciliinae and Goodeinae, in which both the occurrence and the costs of male ornaments have been frequently studied (Arellano-Aguilar & Macías García, 2008; Bisazza,

Grapputo, & Nigro, 1997; Devigili, Kelley, Pilastro, & Evans, 2012; Endler, 1983; Karino & Haijima, 2001; Kodric-Brown, 1989; Macías García, 2014; Macías García & Burt de Perera, 2002; Macías García & Ramírez, 2005; Moyaho, García, & Manjarrez, 2004; Ritchie et al., 2007; Rosen & Tucker, 1961; Rosenthal, Flores Martínez, García de León, & Ryan, 2001; Schlupp et al., 2010), whereas studies of female colouration in species of either family are scarce.

Poeciliid males can circumvent female mate choice by directing gonopodial thrusts towards the female gonopore; a relatively inexpensive mating strategy that does not depend on costly courtship or ornamentation. Females have a generally lacklustre, uniform colouration, and in species where they are not drab, their colour patterns are duller versions of those of their colourful males (Endler, 1983). In a few species, it has been shown that males are attracted to larger females (Arriaga & Schlupp, 2013), presumably because their size may reflect fecundity (Herdman, Kelly, & Godin, 2004), but no instances of male mating preferences for colourful females have been documented among the poeciliids. Conversely, female mating preferences among the goodeids cannot be circumvented; thus, males rely on courtship and ornamentation to secure copulations (Macías García & Saborío, 2004; Ritchie, Webb, Graves, Magurran, & Macías García, 2005). This implies that sexual selection due to female choice is more stringent in goodeids than in poeciliids. Goodeid females often have bright colour patterns which differ both from those of conspecific males and from those of females of different species (Macías García, 2014). It is possible that male mate choice has been involved in promoting bright colour patterns in goodeid females. Recent evidence that this might be the case was demonstrated with males of *Girardinichthys viviparus* who prefer females that are both large and colourful (Méndez-Janovitz & Macías García, 2017).

The major aim of our study was to elucidate the possible origin (genetic correlation or male mate choice) of female colouration in poeciliids and goodeids. To achieve this, we used a comparative approach to 1) investigate the possible correlation between male and female colouration, and between these and the degree of dichromatism, 2) assess the degree to which the correlation between the colour of males and of females can be ascribed to shared ancestry, as opposed to alternative evolutionary forces (i.e. sexual selection), and 3) gauge the speed of the evolutionary change in male and female colour, so as to infer the likelihood that alternative evolutionary forces gave rise to the observed distribution of colourfulness along the phylogenies. By comparing the results of the above analyses when applied to poeciliids and to goodeids, we sought to reveal an effect of male mate choice, caused by stringent female choice (evolutionary retribution), on the evolution of female bright colouration. Our strategy involved 1) obtaining comparable scores of colourfulness and dichromatism of representative samples of goodeid and poeciliid species, 2) generating phylogenetic hypotheses of each family using only the species included in our sample and 3) evaluating within each family the likelihood that female colourfulness and male colourfulness are a) intercorrelated or b) evolved independently.

2 | MATERIALS AND METHODS

2.1 | Dichromatism and colourfulness indexes

Although there has been a long and sustained effort to understand the evolution of colour patterns in a variety of poeciliid species (Endler, 1983), there are no standardized measures (indexes) of dichromatism, nor quantitative data of the colouration of both sexes of any species. Because of the lack of information and of standardized photographs of most species, we first created qualitative indexes of dichromatism and of male and female colouration of poeciliid and goodeid species. These were derived from scores by independent judges based on carefully selected pictures from books, guides and reports (Axelrod, Burgess, Pronek, & Walls, 1992; Jacobs, 1971; Miller, Minckley, & Norris, 2005; de Ponce León & Rodríguez, 2010; Scott, 1987; Tobler, Greenway, & Culumber, 2015) and Internet websites (e.g. www.arkive.org, www.fishbase.org, (Froese & Pauly, 2018), <http://collections.mnh.si.edu/search/fishes/>, www.goodeidworkinggroup.com/) (see Supplementary online material for additional details). We searched for pictures of all the species included in the phylogenies of goodeids (Webb et al., 2004) and poeciliids (Pollux, Meredith, Springer, Garland, & Reznick, 2014) and incorporated in the study only those of which we had at least two pictures of different individuals of each sex. We used pictures of the most common and wild morphs, as our sampling was not designed to represent the full spectrum of variation in colour. We did not use images of ornamental varieties.

We recruited two groups of four graduate Biology students, each composed of two men and two women. Six of the eight observers were working on their graduate theses on behavioural ecology of insects (four) or birds (two), whereas the remaining two worked on the interphase between ecology and agriculture. All of them were naïve with respect to our hypothesis and had no experience working with fishes and especially with poeciliids or goodeids, ensuring that their evaluation was blind. One group assessed dichromatism, and the other scored colourfulness of fish of each sex. Every evaluator received a printed set of instructions and recording sheets. In total, we compiled pictures from 73 species (50 poeciliids and 23 goodeids) and used them to create two PowerPoint presentations, one to score dichromatism containing conspecific fish of both sexes in each slide and another to assess sex colourfulness, in which fish of a given species and sex were presented in each slide. Pictures were shown to the volunteers on a 23" computer screen (HP EliteOne 800; graphics card Intel(R) HD Graphics 4600, mode 1920 × 1080 pixels, true colour [32 bits], 60 Hz). All members of each group were shown the pictures at the same time to standardize ambient light conditions but were asked not to communicate before completing their scores.

Slides in the dichromatism presentation included the identity of the species in code and pictures of females and males (2–4 pictures of fish of each sex; females $x = 2.81 \pm 0.52$; males $x = 2.97 \pm 0.58$) identified by the appropriate symbol. The volunteers that evaluated dichromatism were asked to compare females and males on each slide at 13 specific zones of the body distributed across head,

flanks and fins, and to assign each species (= slide) a value of difference ranging from 1 to 3, where 1 means that sexes are of identical colour, 2 means that one sex has duller colouration than the other, and 3 means sexes have different colour at any given body zone. A fish silhouette displaying each of the 13 body zones and a definition of the scale were included in the set of instructions. Thus, each species was given 13 scores of dichromatism by each volunteer, and the sum of those 13 scores was taken to be that volunteer's assessment of colour dimorphism of any given species (dichromatism values thus ranged from 13 to 39). We then obtained the average dichromatism score of each species across the four volunteers, ending with a single species-specific score that was entered in the analyses (i.e. we used one dimorphism score per species).

The sex colourfulness presentation contained two slides per species, one with pictures of males and one with pictures of females (numbers were the same as above). Text on each slide included the species code and the sex of the fish displayed. Each slide contained also a 1–5 scale of colourfulness, with each value associated with a picture of a wild-type Cyprinodontiformes fish (neither Goodeidae nor Poeciliidae) as a visual example (1 = *Poropanchax normani* [female]; 2 = *Jordanella floridae* [female]; 3 = *Aplocheilichthys lineatus* [female]; 4 = *Jordanella floridae* [male]; 5 = *Simpsonichthys punctulatus* [male]). Thus, a score of 1 meant not colourful, that is that the fish is of a uniform dull colour, whereas 5 meant that the fish has a colour pattern with a predominance of distinct colour patches. We calculated for each species and sex the mean score from the four volunteers, and this value was entered in the analyses. We only used a single colourfulness score per species and sex.

Qualitative colour indices are subjective measures, but not therefore incorrect, as it has been demonstrated that, at wavelengths visible to the human eye, these are comparable with scores obtained from spectrophotometer measurements (Armenta, Dunn, & Whittingham, 2008). Recent studies have used subjective colour measures (Ciccotto & Mendelson, 2016), which are particularly useful when it is impossible or impractical to obtain spectrophotometric measures of all the species under study. There are computer programs designed to evaluate colouration and differences in colour patterns, but given the diverse origin and the unstandardized nature of the photographs in our sample, we could not use them to make comparisons (e.g. Van Belleghem et al., 2018). To assess the reliability of the scores generated by our observers, we compared the dichromatism scores (one per species, as above), with an alternative value of dichromatism obtained by subtracting the female from male colourfulness score (generated by a different group of observers). Both values were significantly correlated ($r = 0.57$, $F_{1,71} = 34.68$, $p < 0.00001$), demonstrating that at least for our sample, the use of humans to score colour yields consistent and reliable results, as both scores came from different groups of observers.

2.2 | Poeciliinae phylogeny

From GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>), we obtained the nucleotide sequences of (a) CYTB; (b) COI I; (c) ND2; and (d) 12S,

tRNA-Val and 16S, of the 50 poeciliid species from which we obtain dichromatism and colourfulness indices. We aligned all sequences for each gene with ClustalW (Thompson, Higgins, & Gibson, 1994) using MEGA7 (Kumar, Stecher, & Tamura, 2016). We then concatenated the sequences with Mesquite (Maddison & Maddison, 2015) to create a multi-gene matrix. We used Partition Finder (Lanfear, Calcott, Ho, & Guindon, 2012) to identify the most suitable gene partition and the best substitution model for each partition. The partitions obtained correspond to the four genes we used, and they all conformed to the same model (GTR+I+G). For the phylogenetic inference, we used maximum likelihood with the server RAXML BlackBox (Stamatakis, Hoover, & Rougemont, 2008), using the above model for each partition. To assess the confidence of the phylogenetic hypothesis, we performed 100 bootstrap iterations. Bootstrap support is presented for each node in the Supplementary online material (Figure S1).

2.3 | Comparative analyses

Comparative analyses require a good coverage of terminal taxa (species or genera) to allow meaningful inferences. Our analyses included 16 of the 20 genera (we place *Heterandria bimaculata* in the genus *Pseudoxiphophorus*; Morales-Cazan & Albert, 2012), and 50 of the 93 species included in the Poeciliinae phylogeny of Pollux et al. (2014). We also included 15 of the 17 Goodeinae genera and 23 of the 34 species included in the Webb et al. (2004) phylogeny (we count *Xenotoca* as different from "*Xenotoca*" (sic); Webb et al., 2004). Missing genera are *Scholichthys*, *Heterandria*, *Neoheterandria* and *Xenophallus* (Poeciliinae), and *Xenotaenia* and *Allophorus* (Goodeinae). These Poeciliinae genera include only monomorphic species, whereas one missing Goodeinae genus (*Xenotaenia*) is made up of one dichromatic species; hence, these absences are conservative.

We first explored the data by comparing the means of dichromatism and sex colouration of both families with a Student's *t* test using Statistica 10[®] (StatSoft Inc. 2011). Then, we conducted phylogenetically controlled analyses using a trimmed version of the goodeid phylogeny published by Webb et al. (2004) (Figure S2) and the poeciliid phylogeny that we generated. Because poeciliid phylogeny

was not ultrametric, we used non-parametric rate smoothing to transform the tree to an ultrametric phylogeny.

We performed two phylogenetic generalized least squares regressions (PGLS: Martins & Hansen, 1997) for each family separately, one to assess whether there is an association between dichromatism and colourfulness of either sex, and another to evaluate whether there is an association between male and female colourfulness. PGLS analyses were run including the maximum likelihood estimate of the lambda parameter (Freckleton, Harvey, & Pagel, 2002) which provides an estimate of the phylogenetic signal in the residuals. Values of lambda equal to 0 indicate that there is no phylogenetic signal, whereas at the other extreme, values of 1 indicate that evolution follows a Brownian motion model. We also estimated rates of phenotypic evolution, under a Brownian motion model, and tested the phylogenetic signal of male colouration, female colouration and dichromatism, to estimate the rate of change in the traits along the phylogeny and the degree to which closely related species tend to resemble each other in colourfulness and sexual dichromatism. For PGLS analysis, we used the packages *ape* (Paradis, Claude, & Strimmer, 2004) and *nlme* (Pinheiro, Bates, DebRoy, & Sarkar, 2016), whereas for estimates of rate of phenotypic evolution and phylogenetic signal, we used *geiger* (Harmon, Weir, Brock, Glor, & Wendell, 2008) and *phytools* (Revell, 2012), in the R Statistical Package v.3.3.2 (R Core Team, 2015).

3 | RESULTS

A description of colourfulness and sexual dimorphism between clades without controlling for phylogeny showed that, overall, goodeid females are significantly more colourful (mean = 3.41 ± 0.52 SD) than poeciliid females (mean = 2.78 ± 0.81 SD; $t = -3.42$, $df = 71$, $p = 0.001$), being in fact as colourful as poeciliid males (Figure 1). The comparison also showed that goodeid males are marginally significantly (mean = 3.78 ± 0.58 SD; $t = -1.99$, $df = 71$, $p = 0.05$) more colourful than poeciliid males (mean = 3.31 ± 1.05 SD). Mean dichromatism was not different between clades (Poeciliidae mean = 19.92 ± 4.3 SD; Goodeinae mean = 20.42 ± 5.13 SD; $t = -0.44$, $df = 71$, $p = 0.66$).

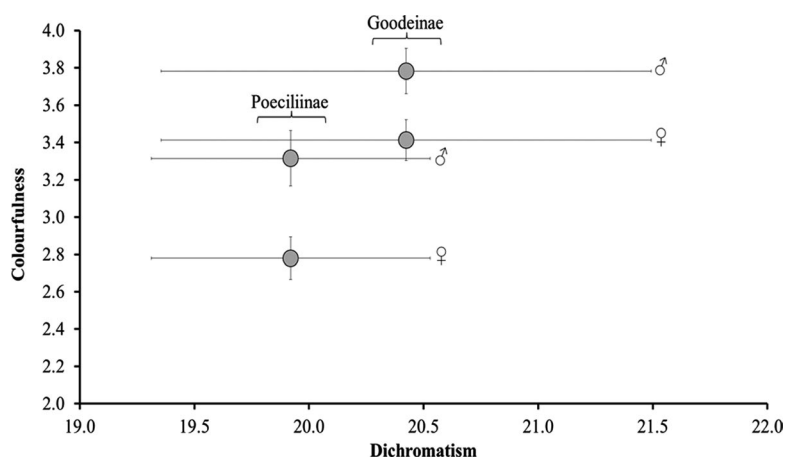


FIGURE 1 Dichromatism (mean \pm SE) and colourfulness (mean \pm SE) in Goodeinae ($n = 23$) and Poeciliinae ($n = 50$) species. Note that errors in dichromatism are necessarily the same for males and females [Correction added on 14 June 2019, after first online publication: data labels have been added to Figure 1 in this version.]

The PGLS analyses revealed that, in both clades, dichromatism is explained only by male colouration, with which it is closely related (Figure 2a); this association has a strong phylogenetic signal (inferred from a high λ value) in goodeids, but not in poeciliids (Table 1). Conversely, female colouration is not correlated with dichromatism in any clade (Figure 2b). In poeciliids, colouration is significantly associated between sexes (Figure 2c), and this association has some phylogenetic signal ($\lambda = 0.38$). Such correlation between female and male colouration is absent in goodeids (Figure 2c).

In goodeids, evolutionary rates of coloration were high (colourfulness; females, $\sigma^2 = 2.3$; males, $\sigma^2 = 2.9$) or very high (dichromatism; $\sigma^2 = 240$; Table 2). Interestingly, the phylogenetic signal of colourfulness in goodeids is eroded ($\lambda = 0$), suggesting that it changes frequently in response to other evolutionary forces. Goodeid dichromatism, on the other hand, has a strong phylogenetic signal ($\lambda = 0.78$), indicating that frequent changes of male and/or female colourfulness (which are themselves not constrained by phylogeny and are not intercorrelated) along certain clades are linked to changes in dichromatism. In contrast, poeciliid colourfulness (females, $\sigma^2 = 0.7$; males, $\sigma^2 = 1.1$) and dichromatism ($\sigma^2 = 18.8$) have low rates of change compared to Goodeids, and are moderately influenced by the phylogeny (colourfulness, females, $\lambda = 0.4$; males, $\lambda = 0.53$; dichromatism, $\lambda = 0.45$). Thus, goodeid females are not only more colourful than poeciliid females, but their colourfulness changes more, through their phylogeny, than that of female (or male) poeciliids.

4 | DISCUSSION

We set out to evaluate the prediction from our hypothesis of evolutionary retribution that in clades where female mate choice is linked to repeated evolution of costly male ornaments, female ornaments should evolve more frequently than in clades where female choice is less commonly responsible for the evolution of costly male ornaments. By comparing two nonsister clades of viviparous topminnows, we confirmed that males of the Goodeinae, who cannot circumvent female choice, are more colourful than females, but females are also brightly coloured (as much as males in the Poeciliinae where furtive mating occurs), and that Poeciliinae females are the least colourful of the four categories (Goodeinae males > Goodeinae females = Poeciliinae males > Poeciliinae females; Figure 1). Possible explanations for differences in colourfulness/brightness among fish clades caused by natural selection include (a) differences in diet, (b) differences in predation regimes and (c) differences in the visual background of their typical habitat (substrate colour, water colour/transparency, light intensity and vegetation) (Endler, 1978, 1980, 1983; Rodd, Hughes, Grether, & Baril, 2002).

Although no systematic comparisons of Poeciliinae and Goodeinae diet have been conducted, both clades include mostly dietary generalist species (e.g. Miller et al., 2005). This means, for instance, that the diet of a brightly coloured, dimorphic goodeid is likely similar to that of a monomorphic poeciliid (Trujillo Jiménez & Espinosa de los Monteros Viveros, 2006; Trujillo Jiménez & Toledo Beto, 2007; see Ramírez Carrillo & Macías García, 2015).

Along their respective geographic ranges, poeciliids are probably exposed to a larger variety of predatory fish than goodeids, who inhabit an area with relatively poor fish assemblages (Miller et al., 2005; Oberdorff et al., 2011). Still, families of known predators of poeciliids (e.g. Cummings, Rosenthal, & Ryan, 2003; Cichlidae, Endler, 1980; see Magurran, 2005) are sympatric with goodeids, who are also prey of visually guided semiaquatic snakes (Drummond, 1985; Drummond & Macías García, 1995; Macías García et al., 1998; Manjarrez, Rivas-González, Venegas-Barrera, & Moyaho, 2015); thus, it seems unlikely that predation pressures on colourful poeciliids are stronger than on colourful goodeids.

Finally, there are, again, no systematic comparisons of visual background of places inhabited by poeciliids and goodeids. The former are often found in transparent tropical streams (e.g. Endler, 1980), but are also found, perhaps in greater abundance, in murkier lowland rivers. Goodeids are also found in turbid environments in the shallow lakes of Central Mexico, but also in crystalline mountain lakes (see Figure S4 in Ramírez Carrillo & Macías García, 2015) and rivers of the Pacific Slope. It is hence unlikely that habitat differences explain the contrasting prevalence and intensity of bright colouration between the two clades.

Natural selection could be responsible for the enhanced colourfulness of goodeid females if there were sexual differences in ecology such as differential use of habitat or predation regime. In the species for which we have relevant data, it has been found that males and females occupy the same habitat (Macías García 1994) and are consumed by the same predators, although males can be at a higher risk on account of their ornaments (Macías García et al., 1998; Manjarrez et al., 2015; Moyaho et al., 2004). Still, it may be argued that the fact that males are particularly showy allows the females to develop somewhat bright colouration without being especially compromised by predation. This, however, would not explain why females should develop bright colour, only that those colours would be less punished by predation than the even brighter male ornamentation. Since both goodeids and poeciliids are shallow-water topminnows, an ecological explanation of the increased female colourfulness in goodeids should specify not only a putative ecological difference between sexes in the goodeids, but also between poeciliid and goodeid females. We are not aware of any such difference, but this possibility deserves further study.

In the absence of a compelling reason to support it, we feel justified to abandon the explanation that natural selection promoted the difference in female colourfulness between goodeids and poeciliids. This leaves us with our proposal that male mate choice for ornamented females is generating these differences. Goodeid females were, nevertheless, less colourful than conspecific males, yet we note that female ornamentation is not expected to be as conspicuous as that of males if the degree of exaggeration is proportional to the strength of the (male) preference (probably low in viviparous organisms) divided by the cost of its display, which must be added to the high female reproductive costs (Pomiankowski & Iwasa, 1998).

Dichromatism (which can be due to either sex being more colourful than the other, or both being equally colourful but with different

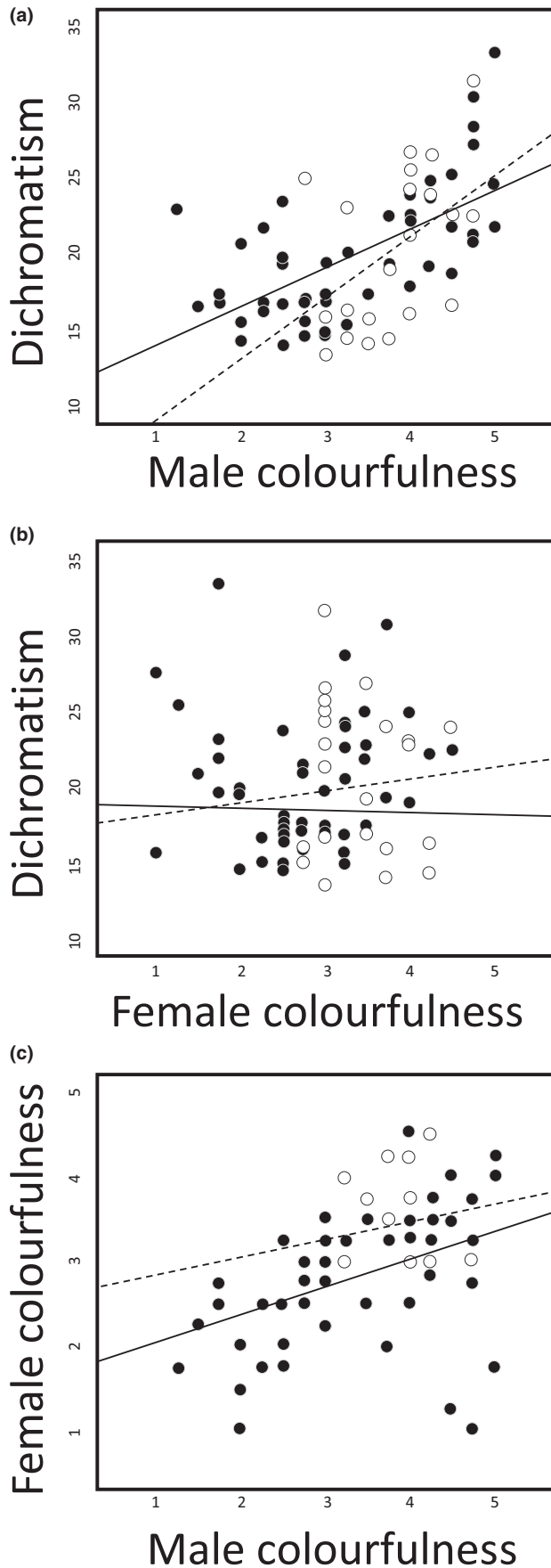


FIGURE 2 Plots that combine original data and PGLS results from both Subfamilies. Goodeid original data are represented as open circles and PGLS regression as a fragmented line. Poeciliid original data are represented as closed circles and PGLS regression as a continual line. (a) Correlation between male colourfulness and dichromatism, (b) correlation between female colourfulness and dichromatism and (c) correlation between male and female colourfulness

colour patterns) was, on average, as intense in the Goodeinae and in the Poeciliinae (Figure 1). Since Goodeinae females are brightly coloured, we initially expected that their colouration would influence the level of dichromatism (Hofmann et al., 2008). Although the slope of the regression of dichromatism on female colouration is steeper in goodeids than in poeciliids, neither is significant (Table 1, Figure 2b). This is consistent with males being more generally exposed to sexual selection via female mate choice. As we expected for the Poeciliinae, where males in some genera are colourful and females are largely dull-coloured, dichromatism was driven by male colouration (Figure 2a). In general, the role of male colourfulness in defining the degree of dichromatism is unsurprising whether female colouration is a criterion for male mate choice in both clades or not, given that even under evolutionary retribution, female mate choice would have driven male ornamentation in the first place. This means that the degree and prevalence of male colourfulness outweigh any possible phylogenetic effect of female colourfulness on the magnitude of sexual dichromatism.

Although goodeid sexual dichromatism is partly explained by phylogeny, male colouration and female colouration are not correlated to each other. In contrast, dichromatism among poeciliids is not explained by phylogeny, and female colouration is explained by male colouration, as they are strongly correlated (Table 1). These results suggest two possible pathways to female ornamentation: evolutionary retribution in goodeids and genetic correlation between sexes (Dale et al., 2015) in poeciliids. Poeciliid female colouration is likely the product of the latter.

When present, colourful marks of female poeciliids are paler versions of male ornamental colouration (see Endler, 1983). There is direct evidence that females carry the genetic predisposition to express many of the male colourful ornaments (e.g. Basolo, 2006) and that the actual expression is determined by the sex of the bearer (i.e. is sex-influenced), as in the guppy (*Poecilia reticulata*), whose normally drab females display characteristic male red spots if treated with testosterone (Haskins, Haskins, McLaughlin, & Hewitt, 1961; Jayasooriya et al., 2002). Thus, poeciliid females carry the alleles for and often express various elements of the male ornamental colouration, although usually in a subdued manner consistent with a degree of sex limitation. This is likely due to the male colouration being selected through female mating preferences for colourful males, whereas female colouration remains constrained by natural selection (Culumber & Tobler, 2017), which selects for the evolution of mechanisms of sex limitation. It is still possible that in goodeids, female bright colouration, although different from that of the males, is nevertheless determined by the same genes that produce

TABLE 1 Results from phylogenetic generalized least squares (PGLS) regressions of colourfulness among sexes, and in relation to dichromatism, for goodeids and poeciliids separately. λ = strength of the phylogenetic signal of residuals (unaccounted variation of the dependent variable), β = slope

Variable		Goodeinae				Poeciliinae			
Dependent	Explanatory	λ	$\beta \pm SE$	t	p	λ	$\beta \pm SE$	t	p
Dichromatism	♀ colour	0.83	0.79 ± 1.8	0.45	0.66	0.5	-0.15 ± 0.7	-0.2	0.84
Dichromatism	♂ colour	1.04	$4 \pm 4 \times 10^{-6}$	1.05×10^6	0	0.04	2.52 ± 0.5	5.37	0
♀ colour	♂ colour	-0.04	0.21 ± 0.2	1.09	0.29	0.39	0.32 ± 0.1	2.95	0.01

TABLE 2 Rate of colour and dichromatism phenotypic evolution of goodeids and of poeciliids. λ = strength of the phylogenetic signal, σ^2 = change rate, Loglik = log-likelihood of the model. A log-likelihood ratio test revealed that a lambda evolutionary model was more supported than a Brownian model in all cases (Goodeinae: females, $p = 0.011$, males, $p < 0.0001$, dichromatism, $p = 0.001$; Poeciliinae: females, $p < 0.0001$, males, $p < 0.0001$, dichromatism, $p < 0.0001$)

	Goodeinae					Poeciliinae				
	Brownian		Lambda			Brownian		Lambda		
	σ^2	Loglik	λ	σ^2	Loglik	σ^2	Loglik	λ	σ^2	Loglik
♀ colour	5.6	-20.5	0	2.3	-1.73	2.8	-73.2	0.4	0.7	-58.3
♂ colour	10.8	-28	0	2.9	-19.8	7.2	-96.7	0.53	1.1	-67.4
Dichromatism	537	-72.9	0.78	240.3	-67.4	67.7	-152.7	0.45	18.8	-140.3

the male-specific ornaments (i.e. is a pleiotropic effect of male ornamentation). To assess whether this is the case, or whether female ornamentation evolved de novo in goodeids, it would be useful to expose females to testosterone. This procedure leads to the expression of male-specific colouration in poeciliid females (e.g. Scharl et al., 1991); a similar result in goodeids would indicate that the female-specific bright colouration is not a pleiotropic manifestation of the genes involved in the expression of male ornaments.

There is some evidence of genetic correlation between male and female colour patterns in goodeids, but this is limited to one colour marking whose expression, in fact, has been suppressed in some species. The terminal yellow band (TYB), which in several goodeid species constitutes a sensory trap (Macías García & Ramírez, 2005; Macías García & Saldívar Lemus, 2012), is present in females of some species, but, interestingly, it is absent in the species where males exhibit the most conspicuous TYB (*Ameca splendens*; see Figure 1 in Macías García & Ramírez, 2005 and Figure 3 in Macías García & Valero, 2010). More commonly, female colourful marks are different from those of the males (Figure 3). This is not a case of reversed sexual dimorphism, since in all Goodeid species males have different body shape and larger and more colourful median fins than females (Macías García, 2014; Ritchie et al., 2007), a fact that, when studied, has been attributed to female mate choice for costly ornaments (reviewed by Macías García & Valero, 2010 and Macías García, 2014). Goodeinae female colourfulness is rather the consequence of females of several species evolving colourful body markings that are not found in males. It was recently demonstrated that female colour influences the amount of courtship received from males in one goodeid species whose females are not too colourful (Méndez-Janovitz &

Macías García, 2017), making it likely that male mate preferences based on colour would be even more evident in species where females are gaudily coloured. Thus, our findings accord with the idea that male costly ornamentation resulting from female mating preferences has led to the evolution of female ornamentation via male mate choice, that is evolutionary retribution.

Further evidence in favour of the hypothesis that female colouration in the Goodeinae has been driven by sexual selection comes from the fact that the colouration of both males and females is phylogenetically labile, which means that it changes at a rate that is fast and independent of ancestry, a pattern that is generally thought to indicate the action of selection (Bromham, 2016). Positive selection produces fast change rates (Bromham, 2016), but sexual selection can accelerate evolution even more through the runaway process (Iwasa & Pomiankowski, 1995; see also Gonzales-Voyer & Kolm, 2011). By contrast, poeciliid female colouration has had a slow rate of evolutionary change and a clear, albeit not very strong phylogenetic signal (Table 2). The fact that males are seemingly not selecting female colouration in poeciliids may be the reason behind its relatively slow change rate (even slower than that of males; Table 2), that is therefore likely due to stabilizing natural selection.

Recent establishment in a new habitat can accelerate the evolution of sexual traits (Yeh, 2004); hence, an alternative explanation for the differences in the velocity of colourfulness evolutionary change would be that the Goodeidae have diversified more recently (16.5 Myr; Webb et al., 2004) than the Poeciliidae (56.5–53.4 Myr; Reznick, Furness, Meredith, & Springer, 2017). This, however, cannot explain our result, since goodeid diversification (measured as speciation rate) has declined over time (Ritchie et al., 2005), but the rate at which their colourfulness changes is higher than in poeciliids.

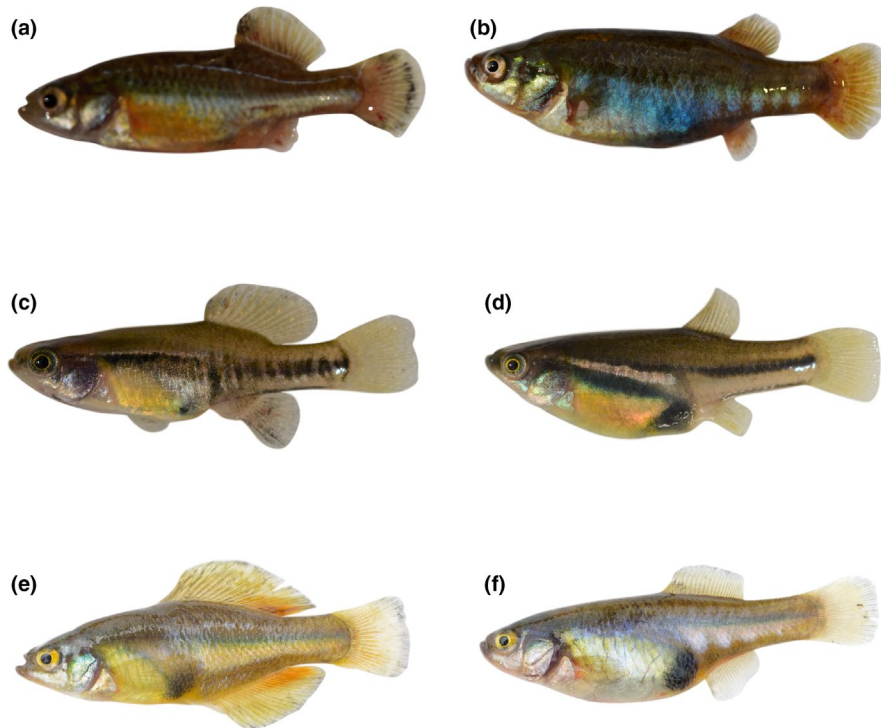


FIGURE 3 Goodeid males and females often differ in both colour and colour pattern. (a) *Allotoca dugesi*, (b) *Skiffia bilineata* and (c) *Girardinichthys multiradiatus*

In conclusion, goodeid females are as colourful as poeciliid males (whose colour explains dichromatism in their Subfamily), but their colouration is neither a product of male colouration, nor the result of phylogenetic inertia, suggesting that selective forces like male mate choice are promoting female bright colouration in goodeids. We identified different drivers of female colouration in the two clades studied, natural selection and genetic correlation in the Poeciliinae, sexual selection in the Goodeinae, as a possible example of one key difference in natural history (i.e. the relative stringency of female mate choice) altering the way evolutionary forces act on the female phenotype in separate clades. This inference requires a demonstration that there is phylogenetic concordance in goodeids between male mating preferences and female ornamentation (Badyaev & Hill, 2003). Our results do not exclude the possibility that natural rather than sexual selection is responsible for the evolution in the Goodeinae of female bright colouration. Under this scenario, the one Goodeinae case where males have been shown to prefer brightly coloured females (Méndez-Janovitz & Macías García, 2017) may be an example of subsequent evolution of male mating preferences based on female colour (see LeBas, 2006). We are not aware of any instance of a colour that is selected against in males (which can happen in the Goodeinae; see above), while at the same time being promoted in females by processes other than male mate choice, yet we cannot discard this possibility.

Our comparison between goodeids and poeciliids is a case evaluation of the hypothesis that evolutionary retribution can promote female ornamentation. Clearly, a contrast using only two clades does not allow for generalizations to be made, yet it can be used as a proof of principle. Indeed, poeciliid species have been used frequently to advance evolutionary hypotheses that subsequently gathered support from studies in other taxa (see Houde, 1997;

Magurran, 2005). Although our comparison was guided by the existence of a relevant attribute that influences the workings of mate choice and differs markedly between the two taxa (i.e. the extent to which females can thwart unwanted mating attempts), the hypothesis of evolutionary retribution can be tested in other animal groups. For instance, male mate choice based on female epigamic or fitness-linked attributes has been documented in two fish families, Blenniidae and Gobiidae, where shifts from “traditional” to “reversed” sex roles during courtship/mating (including the display of epigamic characters—courtship—by females) have been linked to costs incurred by males and/or to changes in sex ratio arising ultimately from the costs related to male advertisement to attract mating partners (Côte & Hunte, 1989; Forsgren et al., 2004). We suggest that interspecific comparison within each of those families (or even intraspecific comparisons across ecological gradients/dates in the case of *Gobiusculus flavescens*; Forsgren et al., 2004) should yield data relevant to test the hypothesis of evolutionary retribution. A similar case can be argued for fruit flies (*Drosophila melanogaster*), where evidence has linked courtship costs to male choosiness (Byrne & Rice, 2006). On the other hand, the damselflies (Zygoptera), among which female ornamental colouration is common (and resembles male morphology: e.g. Andrés, Sánchez-Guillén, & Cordero Riva, 2002), could be used as a stringent test of the hypothesis of evolutionary retribution.

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COMPLIANCE WITH ETHICAL STANDARDS

No live animals were used in this study. The authors declare that they have no conflict of interest.

ORCID

Marcela Méndez-Janovitz  <https://orcid.org/0000-0003-0448-5001>

Constantino Macías García  <https://orcid.org/0000-0003-3242-4214>

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