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ORIGINAL ARTICLE

Do male fish prefer them big and colourful? Non-random male courtship effort in a viviparous fish with negligible paternal investment

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Abstract

In the majority of sexual species, there are asymmetries in reproductive effort, with males typically investing more in securing matings and females investing more in producing offspring. This causes males to mate less discriminately than females. Yet males may also become choosy if the following conditions are met: (a) that females vary in their reproductive value, (b) that males can perceive this variation, and (c) that mating with one female reduces the possibility of mating with another. These conditions may be met in the livebearing Goodeidae, a clade of Mexican fish whose females are often brightly coloured and whose males display costly ornaments and courtship as the only means to obtain matings. Males of the black-finned goodeid (*Girardinichthys viviparus*) have relatively simple, yet costly courtship behaviour, with mating probability depending on the duration of one-to-one courtship episodes, thus by courting one female they must ignore others. We evaluated whether the decision to court a female depends on her phenotype. Three variables of female phenotype were positively linked to the duration of male visits and to the frequency of displays performed by males: belly area, hue ("orangeness") and size. Since fecundity and offspring survival were also a positive function of female size, we conclude

that male *G. viviparus* evaluate the potential female reproductive value and allocate their courtship effort accordingly. Since male courtship effort is also influenced by female colouration, we suggest that our findings may help explaining the recurrent evolution of sexually dimorphic female colouration in this clade.

Significance statement

Amongst sexually reproducing species, females often invest heavily on offspring and mate only after selecting partners carefully, while males invest little on offspring but mate indiscriminately. In other cases, males carry the burden of raising offspring and are choosy. Thus, we see female mate choice in species with a bias towards maternal investment, and male mate choice in species with a bias towards paternal investment. Here we report male mate choice in a species with predominantly maternal investment; a viviparous fish whose females are choosy and whose males invest heavily on courtship. Males made longer visits to the wider bellied, and more orange-looking females, and larger (but not more orange) females produced more offspring which survived better, thus some attributes of females linked to their reproductive value influence how much time and effort males devote to court them.

Communicated by A. Pilastro

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s00265-017-2385-2) contains supplementary material, which is available to authorized users.

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Introduction

Asymmetries in parental investment normally determine which sex is the most discriminating (Trivers 1972; Lande 1980; Kokko et al. 2003). This is because the more one sex

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invest in offspring, the longer it takes for it to be free to re-mate (Sutherland and De Jong 1991), thus biasing the operational sex ratio (i.e. the proportion of available reproductive organisms) towards males (see Owens and Thompson 1994). Since female reproductive investment is typically larger than male investment, the most common scenario is that where operational sex ratios are male-biased. Here females, which are limited in the number of eggs that they can produce/nourish, can only increase their fitness by mating with high-quality partners, whereas males can potentially sire the offspring of many females if they can outcompete their rivals (their reproductive success increases with the number of fertilised eggs; Trivers 1972). Hence, typically, females are selective and males are under selection (see Bateman 1948).

There are factors beyond initial parental investment that may determine whether and to what extent members of one sex may mate selectively (Johnstone et al. 1996; Bonduriansky 2001; Kraaijeveld et al. 2007; Reading and Backwell 2007), giving rise to a variety of mating systems. A pre-requisite is that there is meaningful variation in reproductive value amongst members of one sex (Owens and Thompson 1994; Pélabon et al. 2003), and that such variation can be assessed by their potential partners. Additionally, it is necessary that mating with one partner reduces the likelihood of mating with another. This may happen (a) if post-mating investment in offspring is high (for instance in viviparous species), (b) if re-mating rate is otherwise impaired, for instance because sperm cannot be produced rapidly (Parker and Pizzari 2010), or if mate availability and probability of future encounters is low (Owens and Thompson 1994; Ramm and Stockley 2014), or (c) if securing matings is costly, either as it requires territorial defence (Reading and Backwell 2007) or investment in the production of nuptial gifts (Sakaluk 1984). Under some circumstances, male courtship effort can reduce its potential re-mating rate, as when females only mate after long expositions to male courtship (Halliday 1990; Goodeid fish; see below). Such rise in male reproductive effort could in turn lead to the evolution of male mate choice (Edward and Chapman 2011; see also Servedio and Lande 2006; South et al. 2009), provided, as indicated above, that there is detectable variation in female fecundity and/or in the viability of their offspring.

Male mate choice requires female characters that indicate potential benefits, either direct or indirect, for males (Servedio and Lande 2006). Thus on top of being attracted to females that are likely receptive or previously unmated (Guevara-Fiore et al. 2010; Gaskett et al. 2004; Ojanguren and Magurran 2004) males may show preferences for females bearing attributes that reflect fecundity, such as a large body size (Kraak and Bakker 1998; Dosen and Montgomerie 2004; Herdman et al. 2004; Arriaga and Schlupp 2013), abdominal distention (Rowland 1982; Nuttall and Keenleyside 1993; Reinhardt et al. 2008) or particular (e.g. carotenoid) colouration (Amundsen and Forsgren 2001). The link between female body size and fecundity has been demonstrated in many taxa (Bonduriansky 2001), including fish (Reznick 1983; Kraak and Bakker 1998). Other attributes such as female colouration can also signal aspects of female quality that males could use to choose a mate (e. g. Amudsen and Forsgren 2001; Massironi et al. 2005), and such attributes may thus be driven to fixation through male mate choice (South et al. 2009). Male mate choice can be expressed as a differential investment in alternative potential partners. For instance, if males can adjust their courtship performance in response to female perceived fecundity, this can be used as a measure of male selectivity (see Zoppoth et al. 2013; Stuart-Fox and Goode 2014).

The Black-finned goodeid, *Girardinichthys viviparus*, belongs to the Goodeinae. These are tooth-carps (Cyprinodontidae) related to the also viviparous, and more widely known, poeciliids, which include the Trinidadian guppy (*Poecilia reticulata*), the mosquito fish (*Gambusia* spp.), and the swordtails and platies (*Xiphophorus* spp.). An important difference between poeciliids and goodeines is that the males of the former have a gonopodium; a modified anal fin specialised to introduce sperm into the female gonopore and that allows males to mate coercively (Evans et al. 2003). This is absent in the males of the Goodeinae, which secure matings through the display of costly ornaments and courtship (Macías Garcia et al. 1998; Moyaho et al. 2004; Macías Garcia and Ramirez 2005; Ávila et al. 2011; Macías Garcia 2014), followed by a cooperative copulatory embrace (Bisazza 1997). Such reproductive method gives females almost complete control over matings, and is associated with an absence of alternative male mating tactics (Macías Garcia and Valero 2010; Macías Garcia 2014). *Girardinichthys viviparus* is a promiscuous species whose males constantly seek mating partners and whose females are only sexually receptive for a few days every 2 months, following parturition. Male courtship is particularly simple, consisting only of three elements. Fin display, a behaviour shared with other social contexts, where the dorsal and anal fins are erected as a first reaction to approaching males or females. Fin folding occurs after the fin display, with the male folding the dorsal and anal fins to the opposite side of the female; this element is only used in reproductive context and usually happens before the pre-copulatory embrace (Fig. 1c) which consist of the male swimming in synchrony with the female, virtually embracing her with his dorsal and anal fins, and occasionally attempting to tighten the grasp and to copulate (Saborío 2002; Méndez-Janovitz 2011; CMG personal observations). In response to these copulation attempts, the female can shake off or swim away from the male, thwarting the mating, or may actively participate in the copula by remaining attached to the male and moving in synchrony with it. Although this is one of the simplest courtship behaviours of all the ones described for the Goodeinae, it requires the males to concentrate their attention on only one female at a time, as they must approach, then maintain the ensuing embrace while following all the manoeuvres of the females (and repelling challenging males; Fig. 1d). Mating success is a function of the cumulative duration of the embrace (Saborío 2002), and hence constraints the male re-mating rate. Males and

Fig. 1 *Girardinichthys viviparus* female (**a**) and male (**b**). A pair in a precopulatory embrace is shown in (**c**), and two males challenging each other over which may court the female are shown in (**d**). Note the shiny markings on the flank of the female in (**a**), and the blackening of the whole body of a courting male (**c**). All photos by MM-J
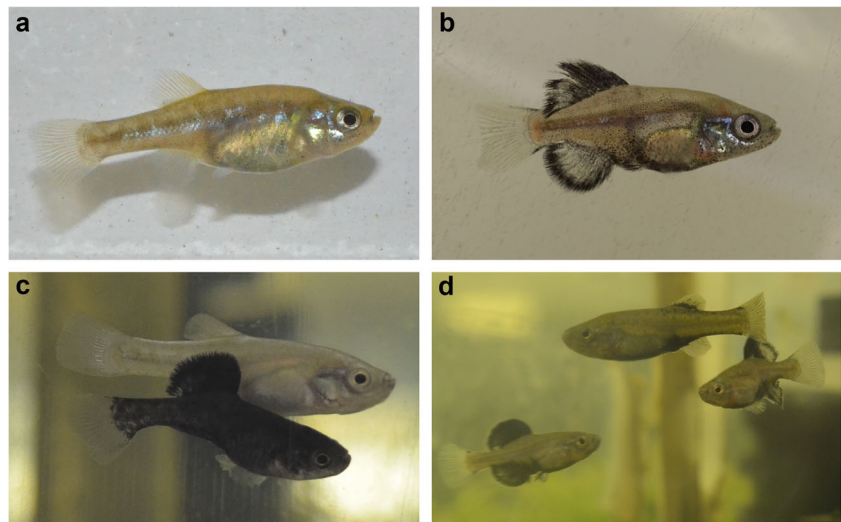
females are brown-orange with silver vertical lines on the flanks that are more conspicuous on females (Fig. 1a, b). During social encounters fish may become darker; some females develop a black zone on the belly and around the vent, while males may display blacked-rimmed fins or even completely black fins and body.

It is common amongst Goodeinae females to have some colour/colour patterns that are different from those of both conspecific males and heterospecific females (Macías Garcia 2014; MM-J and CMG unpubl. data), but neither the origin nor the function of those differences have been ascertained. In a few species studied, ornaments and/or courtship displays are costly to produce (Arellano-Aguilar and Macías Garcia 2008), and make males vulnerable to detection (Moyaho et al. 2004), or capture by predators (Macías Garcia et al. 1994, 1998), to fin damage (Macías Garcia and Ramírez 2005), and to parasite infection (Ávila et al. 2011). The elevated costs incurred by Goodeinae males to secure matings (see a review in Macías Garcia 2014) may be a consequence of adaptive female mate choice, but there is no information on whether the seemingly divergent colour patterns of females are the consequence of male mate choice, nor whether they are costly and thus make such hypothetical mate choice adaptive. We evaluated the first possibility—that female colouration is a target of male mate choice—using *G. viviparus* as a model. First, we asked whether male courtship behaviour depends on the female phenotype (body colour and body and fin size), and then whether the female phenotype is correlated with her reproductive performance. We measured courtship effort as the amount of time males spent within one body-length of the females (= visit to the females) and the frequency of displays that a male performed in front of each of two females of different phenotype, and used brood size and offspring survival as indexes of female reproductive performance.

Methods

Male mate choice

Adult *G. viviparus* of both sexes were collected from an outdoor pond at the Botanical Garden of the Instituto de Biología, Universidad Nacional Autónoma de México. This population was established by CMG with fish collected at Texcoco, in Mexico City, under the permit SGPA/DGVS/09253 provided by the Mexican Ministry for the Environment (SEMARNAT). Groups of three females and two or three males were kept in 40-L glass aquaria under a 12–12 h L-D photoperiod provided by overhanging fluorescent lamps (Magg™ T8 32w) and aeration-driven foam filters. Temperature in the room with the aquaria oscillated between 18 and 22 °C, and fish were fed commercial fish food flakes twice daily (Wardley™). One week before trials, 10 males were placed in isolation in a 40-L presentation aquarium (aquaria used exclusively for the trials) equipped as above.

Two groups of five males each were formed ($n = 10$ males). Males within each group were individually housed (see below) and exposed to 20 females presented in pairs ($n = 10$ pairs), thus we used a total of 20 female pairs ($n = 40$ females). Females were paired arbitrarily with the constraint that the two members of a pair were at a similar stage of pregnancy to avoid the confounding effect of the female breeding condition on male preferences. By using pregnant females, we hoped to provide males with some visual evidence of their fecundity. We did not attempt to maximise the size or colour differences within a pair, since the former might have overridden the influence of other fecundity-related female attributes, and because we did not have any prior information on which—if any—colour attribute(s) of females could be indicative of fecundity/condition and thus attractive to males. Thus male preferences were scored blindly by paring similar-looking females arbitrarily, and only measuring their size, colour and

reproductive performance after conducting the behavioural records. There were some differences in the moment of pregnancy at which females in each pair were presented to males (assessed retroactively as the number of days to parturition), hence we tested whether female colour was linked to the progress of gestation using linear models. Neither hue ($t = -1.058$, $p = 0.3$, $n = 28$), nor brightness ($t = -1.049$, $p = 0.304$, $n = 28$) or saturation ($t = -0.464$, $p = 0.647$, $n = 28$) co-varied with days to parturition.

To minimise handling stress, each female was scooped out of her home tank using a transparent plastic bag that was at the same time half filled with local water. We followed the preference trial method used by González-Zuarth and Macías Garcia (2006). The two bags containing the females of a pair were then hanged in opposite sides within the presentation aquarium. Then the behaviour of the local, free-swimming (and un-manipulated) male towards each female was recorded, and the female pair moved to the next presentation aquarium until the behaviour of all the five males towards the females of that pair had been quantified (see below). This procedure was repeated with both groups of 10 female pairs, each being presented to their corresponding five males in a randomised order, and the position of each female in the tank (left or right) was alternated between successive males (Table 1).

Each trial lasted 5 min of habituation followed by 15 min of behavioural records. During these, we registered (1) the duration of the visits (approaches to within one male body length of the bag, in seconds), by the male to each female, and (2) the frequency of displays performed during visits. Displays were not too frequent, thus we clustered together all three male courtship elements: fin display, fin folding and attempts of pre-copulatory embrace (described above). We choose these two variables (1) because time spent in front of a potential mate reflects preference, as it is correlated with the number of copulation attempts (González-Zuarth and Macías Garcia 2006), and (2) courtship has been used as a measure of male preference because, as it is costly, males must strategically decide how much to devote to each particular female (South et al. 2009, 2012; Stuart-Fox and Goode 2014). All females

Table 1 Samples used to evaluate male mating preferences and female morphology and reproductive performance

| Sample | Measurements | | | |
| | Male preference | | | |
	Males	Females	Brood size	Offspring survival
Group 1	5	20	16	
Group 2	5	20		
Additional broods			11	11
Total	10	40	27	11

were photographed at about the time of the trials. Logistical reasons determined that one quarter of them were measured immediately before, and three quarters of them immediately after the trials; a GLMM analysis showed that measuring females before or after the trials had no effect on the behaviour of the males towards them (time spent next to each female $z = -0.26$, $p = 0.8$, $n = 10$; frequency of courtship displays $z = -0.02$, $p = 0.99$, $n = 10$).

Female attributes

Morphology Females were photographed with a Nikon™ D5100 camera while being held within in a narrow (25.5 cm × 20.5 cm × 6 cm) glass tank with a metric (± 0.5 mm) and a grey scale attached to the front pane. The digital (16 megapixels) images were used to measure female colour (see below) and morphology. Using Adobe Photoshop™ (v. CS2 and CS5), we measured (1) the female standard length (SL, cm; from the tip of the mouth to the end of the caudal peduncle), (2) the area of the dorsal fin (cm^2), and (3) the major (cephalocaudal) and minor (dorsolateral) axes of the belly (cm), whose lateral projected area was approximated using the formula of an ellipse (cm^2). Belly area was taken to reflect fecundity of females at a similar moment during the gestation. In nature, fecundity can vary from less than 10 to 114 offspring (Díaz-Pardo and Ortíz-Jiménez 1986), and in laboratory, similar-sized females can have widely different numbers of offspring (see supplementary Online Resource 1), which would be evidenced by the distension of the belly before birth. In fish, including this species female size is linked to fecundity (see supplementary Online Resource 1), and has been shown to influence female attractiveness (see below; Rowland 1982; Nuttall and Keenleyside 1993; Kraak and Bakker 1998), thus in addition to belly area, we entered SL in the analyses. As goodeid females have a narrow window of receptivity after birth, belly width may reflect pregnancy progression that could determine male courting effort.

Colour Again using Adobe Photoshop™ (v. CS2), we standardised each photograph using the grey scale, and then quantified hue, saturation and brightness (HSB colour model) at 13 distinct points on the female body (Online Resource 2). Points were selected as those where either males or females of at least one species of the Goodeinae have a distinct colour patch (see Macías Garcia 2014). The 13 measures of each colour variable were averaged to yield a single measure of hue, of saturation and of brightness of each female. Analysing colour from photographs precludes the measurement of UV reflection in our fish. This is potentially complicated since in the sister species (*Girardinichthys multiradiatus*) UV-reflecting colour markings are present in both sexes and used by females during mate choice (Macías Garcia and Burt de Perera

2002). It must be noted, however, that UV colouration seems negatively linked to condition in that species (Arellano-Aguilar and Macías Garcia 2008). The potential role of UV in mate choice was not part of this study, but we are aware that at least some amount of it would have been present in our experiments since fluorescent tubes emit modest quantities of UV, and the females would be unlikely to be screened from it by the thin transparent layer of polyethylene.

Reproductive performance We used the first sample of 20 females to evaluate the possible links between female morphology and reproductive performance. Of these 20 females, which were kept in maternity enclosures within their home tanks, 16 gave birth to what we term "original" broods. Additionally, we isolated another group of 11 pregnant females which were kept in maternity enclosures within empty 40-L tanks, thus allowing their offspring to develop in a relatively large space free of other fish. We recorded (1) female

fecundity, as the number of offspring born (= brood size) to 27 females (16 original broods +11 additional ones), and (2) the number of offspring that survived to 6 weeks of age (= offspring survival) in the 11 additional broods (see Table 1). We assessed the associations between female phenotype (SL, fin size, belly area, colour) and reproductive performance (brood size and offspring survival).

Statistical analyses

We used two experimental groups, each composed of five males that were exposed to 20 females ($n = 10$ males and 40 females; Table 1). Consequently, we applied generalised linear mixed models (GLMM) to assess whether there was a link between female phenotype and male behaviour towards the females. We used as dependent variables (1) the duration of male visits, calculated as the sum of the seconds spend by the males in front, and within one body length of each female

Fig. 2 Mean duration of male visits to females as a function of **a** female hue and **b** female belly area. These graphics are visual representations of the raw data and do not depict the associations as established by the models
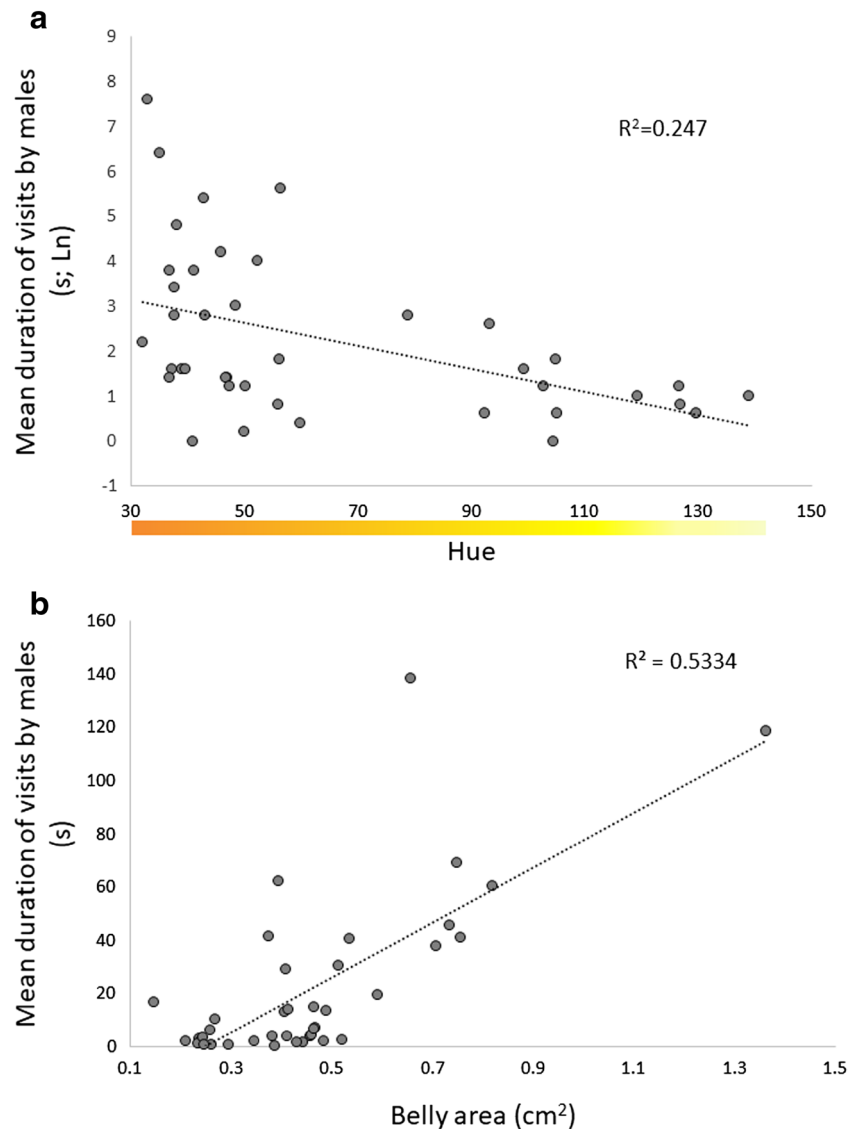
(multiplied by 10 to allow the use of a negative binomial function), and (2) the frequency of male courtship displays during those visits. Female hue, saturation, SL and belly area were entered as independent variables. Dorsal fin area and brightness were removed from the male preference models as they were strongly collinear with SL and hue, respectively. We used total duration, rather than frequency of visits, because previous work on Goodeids has shown that the former correlates with the probability of mating (González-Zuarth and Macías Garcia 2006). Additionally, in *G. viviparus* the probability that a female becomes pregnant is a function of the amount of time a male spends in close contact with her (Saborío 2002).

The initial exploration of the data using a GLMM model selection protocol revealed that the residuals did not follow a normal distribution. We thus ran the generalised models with a negative binomial and a Poisson zero-inflated distribution for the duration of the visits and frequency of courtship displays respectively. These error terms (negative binomial or Poisson)

were selected because they are appropriate when there is under- or over-dispersion of the data respectively. We ran 16 models, including the null model and all the possible additive variable combinations including in all of them male and female ID as random factors. We retained models whose difference in the Akaike criterion $\Delta AICc$ was < 2. As an additional criterion to aid the interpretation of the results was the relative AIC weight (w) of the models and the cumulative weight (cw) of the independent variables (related to the amount of variance explained by the models; Burnham and Anderson 2002).

Generalised linear models (GLM) were used to analyse the influence of female phenotype on reproductive performance, since these data contained neither nested, nor crossed factors. Dependent variables were brood size and offspring survival, and independent variables were hue, saturation, brightness, belly area and SL. Dorsal fin area was left out of the models because it was tightly correlated with SL. When testing the influence of mother phenotype on brood size, we used a Poisson distribution of the error term, whereas the error term

Fig. 3 Mean frequency of male courtship displays directed to females as a function of **a** female hue and **b** female belly area. These graphics are visual representations of the raw data and do not depict the associations as established by the models
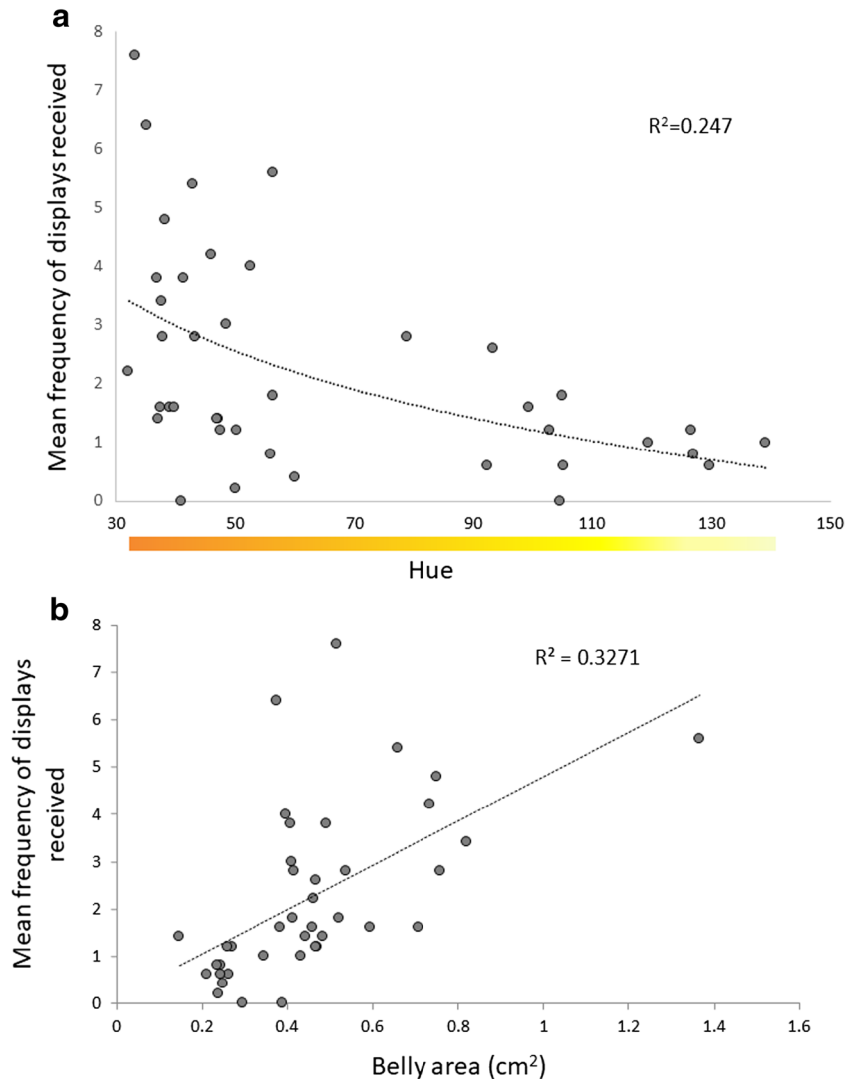
in models evaluating the influence on offspring survival was a grouped binomial distribution. Thirty-two additive models were run including all the possible variable combinations and the null model. Selection of models dealing with brood size followed the ΔAICc < 2 criterion, and selection of models on offspring survival followed the ΔQAICc < 2 criterion because we observed slight over-dispersion in the data. Relative AIC weight for each model and cumulative weights of independent variables were again used as additional criteria.

Results

The most supported models describe the impact of the female phenotype over the male response, or the association between female reproductive performance and its phenotype. These cannot be easily depicted. Instead, in Figs. 2, 3, 4, and 5, we present bivariate plots of the raw data to allow an approximate visualisation of the multivariate effects uncovered by the models.

Male mate choice

During the 15-min trials, females were visited by males for as much as 313.5 s (mean ± SD = 21.7 ± 48.7; $n = 40$). Duration of male visits was a function of female phenotype; males spent more time next to the females with wider bellies (Belly area cw = 0.95), and more orange in colour (lower values of) hue (cw = 0.88; Table 2; Fig. 2). The model with these two variables was both the one with higher support and higher explanatory power ($w = 0.67$; see five models with lower AICc in Online Resource 3).

Frequency of displays during visits to females (2.75 ± 5; range 0–43; $n = 40$) was also a function of female phenotype (Table 3; Fig. 3). Again, belly area had the largest (and

Fig. 4 Brood size was a function of both **a** female belly area and **b** female SL. These graphics are a visual representation of the raw data and do not depict the associations as established by the models
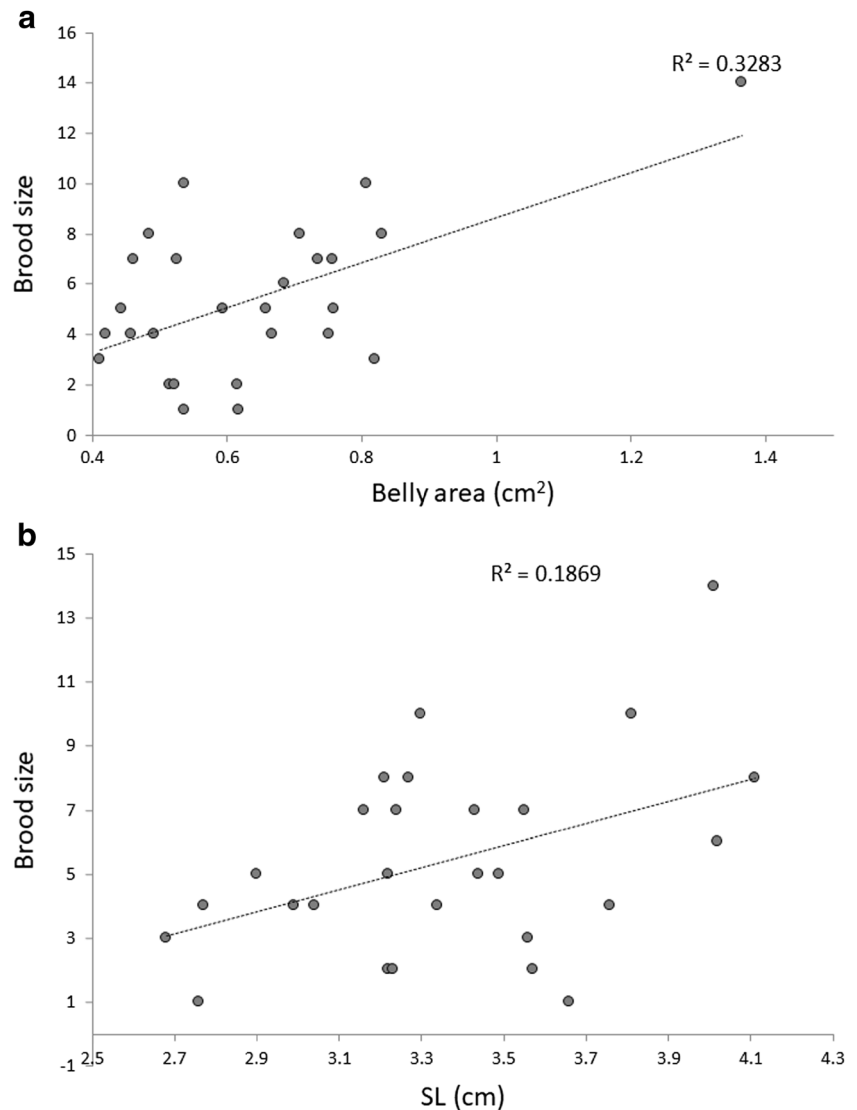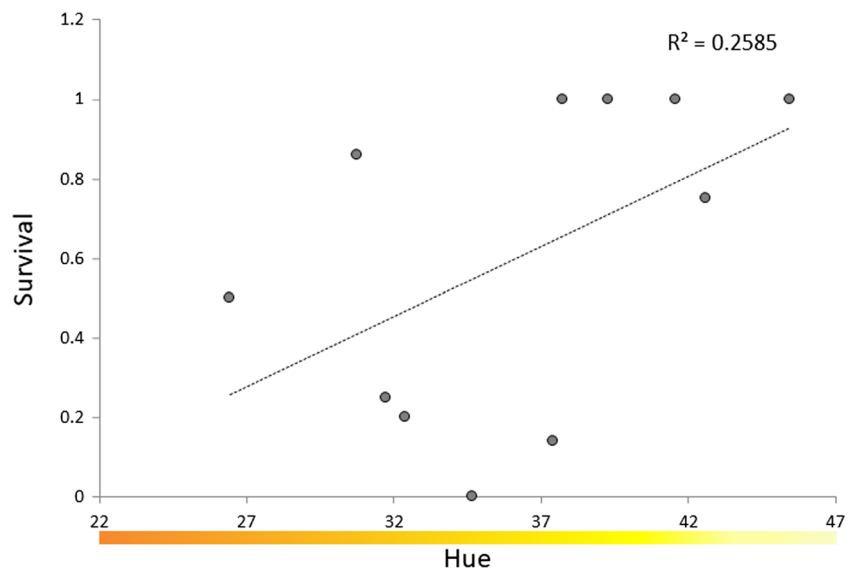
Fig. 5 Offspring survival (number of offspring alive at 6 weeks of age/brood size) as a function of female hue. This graphic is a visual representation of the raw data and do not depict the associations as established by the models

positive) influence on male behaviour (cw = 0.66), and as with the duration of visits, female "orangeness" hue (negative; cw = 0.56) also influenced male behaviour. The frequency of displays performed by males was also influenced positively by female size (SL; cw = 0.42) in male response (Table 3). Thus, males directed more displays to the wider bellied, largest, more orange coloured females. The three variables are included in the three best supported models (see five models with lower AICc in Online Resource 4).

Female attributes

Brood size in our sample ranged between 1 and 14 (5.4 ± 3; n = 27) and was a positive function of female belly area (cw = 0.86) and size (SL; cw = 0.36; Fig. 4), although female orangeness also made a modest contribution to the model

Table 2 Model with ΔAICc < 2, with total duration of male visits to females as dependent variable (see text). Tested models had negative binomial errors and a logit link function. Female and male identities were stated as random factors. Here and in Tables 3, 4 and 5 rows indicate the best supported additive models, with its corresponding AICc, ΔAICc and w (relative AIC weight) values. *P* values are in italics, and correspond to the variables included in the model in an additive way (in this case, time spent by males in front of females ~ Belly area + Hue). The lower part of the table shows the direction of the effect of each independent variable on the response (dependent) variable, and the cumulative AIC weight (cw) of each independent variable originally declared (i.e. including those removed during model selection)

			Explanatory variables in the model (additive)			
AICc	ΔAICc	W	Size	Belly area	Hue	Saturation
2078.23	0.00	0.67		*0.0003*	*0.002*	
Direction of the effect				+	−	
Cumulative weight			0.14	0.95	0.88	0.16

(cw = 0.30; Table 4) (see also Online Resource 5 which includes the best five models).

Offspring survival was a positive function of female size (SL, cw = 0.99) and a negative function of orangeness (i.e. positive cw = 1.0; Table 5; Fig. 5), belly area (cw = 0.37) and saturation (cw = 0.99) (see also Online Resource 6; which includes the best five models).

Discussion

We found that, when presented to pairs of females that differ in quality, male *G. viviparus* do not allocate their courtship time randomly. They make longer visits and perform more courtship displays to the females with wider bellies, while spend less time with thin-bellied females. They also devote greater effort to court females with bodies of a more orange hue.

Female size was not as important a target of male mate choice as has been found in other studies of male mate choice in fish (Rosenqvist 1990; Kraak and Bakker 1998; Werner and Lotem 2003; Naud et al. 2009; Arriaga and Schlupp 2013); instead, males were attracted to females with large bellies. This is puzzling since in many species, as well as in our sample, female size is a good predictor of fecundity (Coates 1988; Hislop 1988; Parker 1992; Kraak and Bakker 1998; Morita and Takashima 1998). One possibility is that belly area, which also indicates fecundity in *G. viviparus*, is of more value to males when deciding how to allocate courtship effort, since assortative mating, a norm in goodeid fish (Bisazza 1997), makes size-based male preferences ineffectual, as it would often lead males to court females they cannot mate with (see also Macías Garcia 1994). Additionally, a large, distended belly may be indicative of a female being near parturition, and hence approaching her receptive window, the only time

Table 3 Models with ΔAICc < 2, with number of displays performed by males in front of the females as dependent variable. We declared Poisson zero-inflated errors and log link function. Female and male identities were stated as random factors. Description of the Table layout as in Table 2

AICc	ΔAICc	W	Size	Belly area	Hue	Saturation
814.46	0.00	0.24		*0.002*	*0.055*	
814.82	0.35	0.20		*0.002*		
815.18	0.71	0.17	*0.002*		*0.014*	
Direction of the effect			+	+	−	
Cumulative weight			0.42	0.66	0.56	0.21

when they may be inseminated because goodeid females do not store sperm (Macías Garcia et al. 1998). Female size, on the other hand, was positively linked to offspring survival to 6 weeks of age, whereas belly area was not (it was weakly negatively linked to offspring survival). Since males had a weak preference for large females (Table 3), they do not seem to be making a maladaptive choice of females based on their morphology. Indeed, although mortality was higher amongst the offspring of females with wider bellies, their larger brood sizes over-compensated this effect, so that they produced more surviving descendants than females with smaller bellies (see Online Resource 7).

It should be noted that the slope, or even the shape of the functions linking female morphology with fecundity, offspring survival and male preferences may vary as a function of female size. We know that the sign of the correlation between female size and fecundity remains positive, but the slope is shallower amongst smaller than larger females (see Online Resource 1), and propose that this pattern is unrelated to the environment, as both samples were raised in aquaria under similar conditions. This suggests that male mating preferences should follow a similar trend, unless a negative, but similarly steep association linked female size with the survival of offspring from large females.

The story is more complex when we attend to colour. Female colour, specifically hue, influenced the amount of male courtship. Females with more orange hue received more

displays and longer visits. An orange hue may be the consequence of high concentration of carotenoids in the skin chromatophores (Goodwin 1951; Kodric-Brown 1989), and, since carotenoids play a role as antioxidant agents (Pike et al. 2007), an adaptive explanation would be that females in good condition appear orange and are hence preferred by males (Olson and Owens 1998; see Milinski and Bakker 1990). However, orangeness in our sample was not related to fecundity, and was negatively related to offspring survival.

It is puzzling why more orange females should have offspring of a reduced quality, as assessed by survival to the age of 6 weeks. Other works have reported that more colourful females lay more eggs but not more viable ones (e.g. Svensson et al. 2006), and this may be linked to a trade-off between attracting mates and investing in offspring (Chenoweth et al. 2006). A circumstance in which such compromise is likely to arise is when females face a shortage of potential partners. Male-biased predation has been demonstrated in the sister species (*G. multiradiatus*), where it leads to a female-biased sex ratio (Macías Garcia et al. 1998), probably because the large, sexually dimorphic median fins hamper the manoeuvers to escape predatory attacks (Macías Garcia et al. 1994). It is unknown whether male *G. viviparus* are disproportionately preyed on, yet they also have much larger median fins than females, and both species are sympatric with the aquatic specialist snake *Thamnophis melanogaster* (see Rossman 1996; Manjarrez et al. 2013). Thus, females may systematically advertise to attract (scarce) males, even at the expense of the quality of their offspring.

The negative link between orange colour and offspring survival may also arise as a compromise between current and future reproduction (Siefferman and Hill 2005). For instance, females may at some point decide to reduce investment in the current brood—which is possible as they are matrotrophic—and hence save resources, including carotenoids, for use in future broods. The accumulation of carotenoids would, additionally, increase their attractiveness and secure matings.

Still, the negative association between female orangeness and the quality of her current brood begs the question of why males should be more attracted to females with a relatively larger orange colouration. One possibility is that they have a perceptual bias towards orange, as has been shown in females

Table 4 Models with ΔAICc < 2, with brood size as the dependent variable. The models have Poisson errors and log link function. Description of the Table layout as in Table 2

AICc	ΔAICc	w	Size	Belly area	Hue	Saturation	Brightness
128.16	0	0.24		*0.0001*			
129.59	1.43	0.12		*0.0003*	*0.342*		
129.98	1.82	0.10	*0.471*	*0.027*			
Direction of the effect			+	+	−		
Cumulative weight			0.36	0.86	0.30	0.23	0.30

Table 5 Models with ΔQAICc < 2, with offspring survival (offspring alive at 6 weeks of age/total offspring born) as dependent variable. The models have grouped binomial errors and logit link function. Description of the table layout as in Table 2

QAICc	ΔQAICc	w	Size	Belly area	Hue	Saturation	Brightness
51.17	0	0.53	0.003		0.003	0.004	
52.03	0.86	0.34	0.009	0.093	0.008	0.008	
Direction of the effect			+	−	+	−	
Cumulative weight			0.99	0.37	1.0	0.99	0.11

of other fish (e.g. Rodd et al. 2002), and thus they fall into a sensory trap (Ryan 1990). This is plausible as sensory traps involving colour have played a role on the origin of Goodeid ornaments (Macías Garcia and Ramírez 2005; Macías Garcia and Saldivar Lemus 2012). Such bias may also be of environmental origin, since carotenoid intake affects colour perception (Sandkam et al. 2016), and males with a diet rich in carotenoids would in turn be more responsive to orange females.

Our results confirm male mate choice in a polygamous species with sex roles characterised by males which constantly try to obtain matings, and choosy females with a narrow window of receptivity. We also show that males preferentially court females with a larger reproductive potential, but the female attributes on which such choice is based seem to be also linked to a reduced offspring survival, presumably because of the conflicting demands faced by females of signalling to attract males vs. investing in current offspring.

Compliance with ethical standards

Data accessibility statement Data available at Dryad repository (https://doi.org/10.5061/dryad.9s380).

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