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Socially cued anticipatory plasticity predicts male primary mating tactic but not mating behaviour rates

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Compared to many types of phenotypic plasticity, developmental plasticity of mating behaviour in response to the social environment has received less attention. Understanding this type of plasticity is a challenge because when individuals adjust their trait expression in response to the trait distributions of other individuals, they change the social cue that those trait distributions represent. This feedback may limit when behavioural plasticity in response to social cues will prove adaptive. We used a livebearing fish (sailfin molly, *Poecilia latipinna*) to test two models for social plasticity: (1) socially cued anticipatory plasticity, which hypothesizes that developing juveniles use social environment directly to predict their optimum phenotype, and (2) condition dependence, which hypothesizes that developing juveniles use social environment indirectly to assess their competitive standing relative to other members of the social environment. Using a full-sibling split-brood design, we reared juvenile fish from birth until maturity in one of four social treatments: (1) three unrelated juveniles, (2) three females, (3) one small male and two females or (4) one large male and two females. Assessing mating behaviours at maturity and 1 month postmaturity, we found that a male's primary reproductive tactic (odds of using a courtship display over sneaking behaviour) was directly affected by the social environment during development as predicted by socially cued anticipatory plasticity (males were more likely to court when reared only with females and more likely to sneak when reared only with juveniles). However, rates of each type of mating behaviour (courtship or sneaking) were affected by interactions between social environment and heritable factors (sire size class and male body size), contrary to predictions from either socially cued anticipatory plasticity or condition dependence. These results suggest that socially cued anticipatory plasticity may be an important driver in the evolution of alternative mating behaviours and more likely to affect behavioural repertoires than current models of developmental plasticity suggest.

Behavioural plasticity is widespread and plays a vital role in evolutionary and ecological processes, but there are important gaps in our knowledge of how and when animals use environmental cues to alter phenotypes (Ghalambor et al., 2010; Miner et al., 2005). The social environment is a particularly important component of the environment because it has the potential to affect both the development and fitness consequences of behavioural phenotypes (Bailey et al., 2010; Gross, 1991; Guevara-Fiore, 2012; McGlothlin et al., 2010). While behavioural plasticity in response to the adult social environment is well described (de Jong et al., 2009; Magellan & Magurran, 2007; Travis & Woodward, 1989; Weir et al., 2011), effects of the social environment experienced during juvenile development have focused more on their consequences for female mate choice or male–male social interactions (Arnold & Taborsky, 2010; Cory & Schneider, 2018; Kasumovic & Brooks, 2011; Kasumovic et al., 2012; Kraft et al., 2018; Macario et al., 2017, 2019; Taborsky et al., 2012). In particular, understanding the effects of early social experience on the development of mating behaviour repertoires in adulthood is critical to testing a growing body of theory predicting how organisms should use the social environment they experience in early life to alter their adult behavioural phenotypes once mature (Kasumovic & Brooks, 2011; Lange, Travis, et al., 2021).

An animal's social environment represents a qualitatively different cue from those envisioned in general theories for phenotypic plasticity in response to abiotic factors or biotic factors like temperature or predation (e.g. Palacio-López et al., 2015;

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Pfennig, 2021). For these types of cues, an individual's plastic response does not alter the cue itself. However, when an aspect of the social environment is the cue, each individual's response will alter the social cue for others. When cues are social, this feedback can limit the evolution of adaptive socially cued plasticity for irreversible traits that are fixed after development (Lange, Ptacek, et al., 2021; Lange, Travis, et al., 2021). However, behavioural phenotypes can be reversible, which creates further complications in theory (Lande, 2014) and in practice. In particular, the responsiveness of behaviour to the immediate social environment makes it more difficult to trace any effects of the social environment during juvenile development on subsequent behaviours performed in adulthood.

Understanding how variable social conditions affect the development of mating behaviours is especially salient when mating occurs in a competitive social context. One hypothesis for how the social environment affects the development of mating behaviours in adulthood is socially cued anticipatory plasticity (Kasumovic & Brooks, 2011), which proposes that the social environment during juvenile development has direct, lasting effects on adult phenotypes. Socially cued anticipatory plasticity predicts that individuals use the density of males and females present in the social environment during development to assess expected social competition when they reach reproductive age and that they irreversibly alter their phenotypes accordingly. Therefore, socially cued anticipatory plasticity predicts that the direction and intensity of sexual selection perceived by juveniles determines the mating behaviour phenotype expressed, regardless of the adult social environment encountered after maturation.

Different verbal models of how increased mate competition should affect mating behaviour via socially cued anticipatory plasticity have offered different predictions (Emlen & Oring, 1977; Kvarnemo & Ahnesjo, 1996; Shuster, 2010; Shuster & Wade, 2003). Some arguments predict that when competition over mates is low (e.g. in a female-biased sex ratio), male courtship display behaviour will be favoured because this is a situation in which females are more likely to exercise choice among males (Kvarnemo & Ahnesjo, 1996; Magellan & Magurran, 2007). The same argument suggests that in environments where competition over mates is high, such that one or several males can monopolize many matings (e.g. in male-biased environments or where many attractive males are present), males are expected to use more sneaking behaviour. By contrast, other verbal models make an opposite prediction (Shuster, 2010; Shuster & Wade, 2003). In these models, the argument is that when the sex ratio is female-skewed, satellite tactics will be more common because individual courting males will be unable to monopolize access to all females (Shuster, 2010; Shuster & Wade, 2003).

In contrast to socially cued anticipatory plasticity, an alternative set of models propose that social environment during development affects adult phenotypes indirectly via condition dependence (Gross & Repka, 1998a, 1998b; Lee, 2005; Repka & Gross, 1995). Models of condition-dependent tactics propose that individuals adopt alternative mating behaviours as a function of their status or condition relative to others in the population, rather than using social environment directly as a cue for behavioural expression (Gross & Repka, 1998a, 1998b; Lee, 2005; Repka & Gross, 1995). Condition dependence predicts that the social environment and a male's condition will interact to affect mating behaviour repertoire expressed as an adult. For example, absolute body size is often correlated with alternative mating behaviours; large males tend to use courtship or guarding behaviours, while smaller males tend to use sneaking or satellite behaviours (Oliveira et al., 2008; Shuster, 2010; Shuster & Wade, 2003). However, body size relative to other social competitors (a measure of condition or status in these models) can also affect mating behaviour decisions (Fagundes et al., 2012; Starks & Reeve, 1999; Wada et al., 2005). In this case, condition dependence predicts that the relationship between body size and mating behaviour will differ between social environments that vary in the size of other males, producing a body size $*$ social environment interaction. For example, males in social environments with smaller males may have a steeper slope between body size and courtship or sneaking behaviour because they perceive themselves to be in better body condition relative to other males in their social environment.

Empirical studies examining the effects of mate competition on mating behaviour have largely varied social contexts during adulthood, making it unclear whether socially cued anticipatory plasticity and/or condition dependence predict patterns of developmental plasticity in mating behaviour (de Jong et al., 2009; Magellan & Magurran, 2007; Starks & Reeve, 1999; Wada et al., 2005; Weir et al., 2011; Řežucha & Reichard, 2014). For example, in many species, males perform more courtship displays when they experience a more female-biased sex ratio during adulthood than when they experience more male-biased sex ratios (de Jong et al., 2009; Magellan & Magurran, 2007; Weir et al., 2011; Řežucha & Reichard, 2014). However, because these studies varied the immediate social context of adults, they did not test the predictions from socially cued anticipatory plasticity or condition dependence. Evidence for how variation in the strength of sexual selection perceived during ontogeny affects the development of alternative mating behaviours via socially cued anticipatory plasticity or condition dependence is more limited (Bailey et al., 2010; Cory & Schneider, 2018; Guevara-Fiore, 2012; Guevara-Fiore et al., 2012). In one study using field crickets, *Teleogryllus oceanicus*, males reared in auditory environments indicative of lower male densities were more likely to use satellite behaviour, a pattern opposite to how variation in sex ratio in adulthood affects alternative mating behaviour expression (Bailey et al., 2010).

We used the development of male mating behaviour repertoire in sailfin mollies, *Poecilia latipinna* (a livebearing fish), to test these two models of social plasticity (socially cued anticipatory plasticity and condition dependence). Male sailfin mollies show high levels of variation in the expression of mating behaviours and associated morphological and life history phenotypes (Luckner, 1979; Parzefall, 1969). Populations can vary spatially and temporally in demography and in the size distribution of adult males, making social cues a variable, and potentially important, environmental cue (Farr et al., 1986; Ptacek & Travis, 1996). In natural populations, the strength of the relationship between body size and mating behaviour expression varies (Ptacek & Travis, 1996), suggesting that cues experienced in the early social environment could be an important factor influencing the development of mating behaviour repertoire.

Empirical studies in sailfin mollies indicate that body size is usually strongly predictive of mating tactic; in many but not in all populations, there is a positive relationship between body size and the number of courtship displays and a negative relationship between body size and the number of sneaking attempts (Farr et al., 1986; Ptacek & Travis, 1996; Swanbrow Becker et al., 2012; Travis, 1994b; Travis & Woodward, 1989). In addition, male body size and male mating behaviours have a Y-linked genetic component (Loveless et al., 2009; Ptacek, 2005; Travis, 1994b). Small males mature quickly (50–60 days) and tend to use sneaking behaviour by swinging their relatively longer intromittent organ (a fused anal fin called the gonopodium) towards the opening of the female's genital tract (the gonopore) to transfer sperm without apparent cooperation from the female (Luckner, 1979; Ptacek & Travis, 1996; Swanbrow Becker et al., 2012; Travis, 1994a, 1994b). Large males, which take longer to mature (130–150 days), use courtship display behaviour where they raise their enlarged dorsal fin and perform a sigmoid display generally perpendicular to a female to elicit female cooperation in internal sperm transfer. Courtship displays increase apparent body size (lateral projection area), which is highly preferred by females (MacLaren, 2006; MacLaren et al., 2004). Intermediate-sized males are intermediate in time to maturation and morphology and are more plastic in their mating behaviour repertoire (Fraser et al., 2014; Travis & Woodward, 1989). Intermediate males tend to have intermediate values of sneaking and courtship displays compared with large and small males when alone, but they tend to use sneaking behaviour when in the presence of other males of either size. Therefore, although there are well-described patterns of size-specific mating tactic, behavioural rates and plasticity in response to adult social environment in sailfin mollies, it is not known how these relationships between body size and mating behaviour develop.

In this study, we tested two alternative hypotheses for how the early social environment affects the development of male mating behaviour repertoire in adulthood: socially cued anticipatory plasticity and condition dependence. We examined the mating behaviour of males at two stages of development (at maturity and 1 month after maturity) to assess whether any effects of the early social environment were reversible. To determine whether social environment affects the primary behaviour used (i.e. relative use of tactics) and the number of behaviours used (i.e. the rate of behaviours) differently, we evaluated two complementary measures of mating behaviour: (1) the odds of using a courtship display (versus a sneak), assessing which mating tactic a male primarily uses, and (2) the number of courtship displays and sneaking attempts, measuring the rate at which individuals use each of these tactics.

While socially cued anticipatory plasticity and condition dependence each predict that social environment will affect mating behaviour, socially cued anticipatory plasticity predicts direct effects of early social environment on behaviour while condition dependence predicts that the early social environment will interact with male body size to produce the mating phenotype. Specifically, socially cued anticipatory plasticity predicts that males reared in treatments with only females will differ in mating behaviours at maturity from those reared with fewer females and that mating behaviours will differ between males reared with adult males of different body sizes. Condition dependence models predict that body size will interact with early social environment to determine a male's mating behaviour rates and reliance on a particular tactic. Based on previous studies of sailfin molly behaviour (Ptacek & Travis, 1996; Swanbrow Becker et al., 2012; Travis, 1994b), we expected a positive relationship between male body size and courtship display rate. However, if males are responding to their own condition, we expected the positive relationship between body size and rates of courtship displays to also depend on the size of other males in the social environment they experienced during development. This would result in males reared with a small male to have a stronger relationship between body size and courtship displays than juvenile males reared with a large male.

METHODS

Experimental Design

Sailfin mollies were collected from the Steve's Ditch population in Wakulla County, Florida, U.S.A. (29°59′15.5″N, 84°23′21.6″W; Lange, Ptacek, et al., 2021; Ptacek & Travis, 1996; Seda et al., 2012) and housed in a laboratory at Florida State University, Tallahassee, Florida. Details of the mating design are described in Lange, Ptacek, et al. (2021), and methods for rearing conditions are identical with the exception of phenotypes measured. Briefly, wild-caught sires were divided into three size classes (mean ± SE: 7 small males: 27.143 ± 0.508 mm standard length (SL); 8 intermediate males: 41.625 ± 0.706 mm SL; 8 large males: 54.75 ± 0.726 SL) to control for Y-linked heritable effects (Loveless et al., 2009; Ptacek, 2005; Travis, 1994b). Each male was mated to a separate laboratory-reared unmated female that was the first-generation offspring of a unique wild-caught female to create 23 full-sibling families. Only one family per sire–dam combination was used. To limit differences in environments experienced among sires, all were collected in October (2014–2017; we worked to distribute sire sizes across years, dependent on laboratory space constraints; see Supplementary Table S1). To account for potential differences among sires due to year-to-year variation, we included the year in which the sire was collected in our analyses (see below).

At birth, each family was split among four different social treatments: (1) three unrelated juveniles, (2) three females, (3) one small male and two females or (4) one large male and two females ($N = 5$ full-sibling fry per social treatment). These social environments were chosen to mimic natural variation in adult male size and demography (Farr & Travis, 1986; Ptacek & Travis, 1996). In the wild, juveniles and adults tend to shoal separately; therefore, focal juveniles were separated from social treatments by clear, plastic, ultraviolet (UV)-permissive perforated dividers. These dividers allowed visual and chemical social cues while controlling for sources of resource competition that would otherwise differ between treatments but that would not be important in natural populations. Adults that made up the social environment treatments were wild caught, while juveniles were size-matched first-generation offspring of wild-caught adults (juvenile treatment individuals that matured were replaced with immature juveniles). Five siblings were reared in each family by social environment combination until they reared sexual maturation (mean age at maturity: 176.35 days, range 42–391 days). At maturation, individuals were removed from the tank and males were assessed for mating behaviour (see below). Because we raised focal juveniles from birth, the sex ratios for each family by social environment combination varied (mean 0.751 males per female, range all females to all males), which was accounted for by including sex-ratio differences in our statistical analyses (see below).

Mating Behaviour Assays

A male's mating behaviour towards a receptive wild-caught female was measured at two stages of maturity: at maturation and 1 month after maturation. To assess mating behaviour in the first reproductive bout, focal males were removed from the rearing environment at maturity and assessed for alternative mating behaviours alone towards a receptive female (see below). To allow for any treatment effects on timing of full development of secondary sexual characteristics and mating tactic (Rodd & Sokolowski, 1995), males were then exposed to a full-contact social environment for 1 month that was the same as the social treatment in which they were raised (see below for more details) and assessed for alternative mating behaviours 1 month postmaturity.

We used receptive females for this experiment because males increase rates of sexual behaviours towards receptive females (Farr & Travis, 1986). Females are receptive to mating 24–48 h after parturition and during this time they actively fertilize eggs with sperm (Snelson et al., 1986; Travis, 1994a). Receptive females were limiting, so each female was tested with up to two different males. Reuse of females was accounted for in the data analysis but never significantly influenced measures of males mating behaviour (see below). Due to space constraints, tester females were not individually identified. However, due to the long-running nature of the experiment, many different females were used. Because there is evidence of size-assortative associations between males and females in the wild (Travis, 1994a), we standardized relative size of males and females by using receptive females that were within ±10 mm SL of the focal male (Seda et al., 2012; Travis, 1994b). Males were measured for SL and isolated for 1 day prior to behaviour trials (Ptacek & Travis, 1996; Seda et al., 2012; Travis, 1994b). These assays replicate the general methods of previous behavioural studies of this species (Farr et al., 1986; Ptacek & Travis, 1996; Seda et al., 2012; Travis, 1994b).

All mating behaviour assays were performed in the morning (0715–1115 hours) in an 18.9-litre tank covered with black plastic on three sides. Focal males were given 15 min of acclimation alone in the testing tank, followed by 15 min of full-contact acclimation with the receptive female (Travis, 1994b). After the 30 min acclimation, a male's behaviour towards the receptive female was recorded for 10 min using the JWatcher version 1.0 event-recorder software (Blumstein et al., 2006) through a Windows 10 64-bit operating system. We recorded the number of four mating behaviours performed during the 10 min observation: courtship displays, gonopodial thrusts (sneaking behaviour), gonoporal nibbles and gonopodial swings (Farr et al., 1986; Luckner, 1979; Parzefall, 1969; Ptacek & Travis, 1996; Travis & Woodward, 1989). Here we report the results for rates of courtship displays and gonopodial thrusts because these are the alternative mating behaviour tactics used by male mollies. Mean and ranges of behaviours performed in the experiment are reported in Supplementary Table S2.

After the male's mating behaviour was assayed at maturity, he was placed in a 37.9-litre aquarium where he was able to fully interact with his social environment. This full-contact social environment replicated the transition fish experience in the wild, where, after maturation, they begin shoaling with other adults. It also replicated the social environment during development while avoiding introducing a new social interaction for the remaining siblings still developing. There were three differences between the developmental social environment and full-contact social environment. First, the individual fish that made up the full-contact social environment differed from the individuals in the focal male's rearing group. Second, the focal male was able to fully interact with the individuals in the full-contact social environment, whereas in his developmental social environment, the male only received visual and chemical cues. Third, the focal male's siblings were not present in the full-contact social environment. Focal males were identified by size in these treatments (males grow very little after maturation; Farr & Travis, 1989; Snelson, 1984; Travis, 1994a). The male was left in the full-contact social environment for 1 month, and at the end of this time, his behaviour towards a receptive female without competitors was retested in the same conditions as described above to assess his mating behaviours at the 1 month postmaturation stage.

The trials took place over 4 years (2015–2019) and, at most, a few individual males were observed on a given day. Therefore, to have a single observer for all behavioural trials, the observer (E.C.L.) was not blind to the hypotheses or the male treatment group. To account for potential unconscious bias, an observer naïve to both the hypotheses of this study and the identity of the male scored a subset of these trials on video ($N = 73$). We compared the naïve observer's tallies of number of displays and number of thrusts to E.C.L.'s live behaviour counts in two ways. First, we calculated Pearson correlations between observers for each behaviour; these correlations were significant and positive for all behaviours analysed (Supplementary Table S3). Second, we tested for effects of observer and interactions between observer and each of the fixed predictors in the design (social environment, sire size class, stage, focal male SL). We found no significant effects of observer or any interaction with observer (Supplementary Table S4). These analyses suggest that E.C.L. did not score behaviours in a way that would bias the results of this experiment. Therefore, we used the trials scored by E.C.L. for all subsequent analyses.

Statistical Analyses

A total of 164 males were included in this analysis; 164 were tested at maturity and 152 of these were tested 1 month postmaturation (12 males died before the 1 month postmaturity). All analyses were performed in SAS version 9.4 statistical software (SAS Institute, Cary, NC, U.S.A.) on a 64-bit Windows 10 operating system. To assess the effects of early social environment, sire size class and male body size on alternative mating tactics, we used generalized linear mixed models (GLMMs) with the ‘proc glimmix’ syntax in SAS. We included the effects of sire size class (a proxy for heritable effects) and social environment during development as fixed effects. We included a fixed effect of the SL of the focal male because previous studies of sailfin mollies have shown strong relationships between a male's size and his mating behaviour repertoire (Farr et al., 1986; Fraser et al., 2014; Ptacek & Travis, 1996; Seda, 2010; Travis, 1994a, 1994b; Travis & Woodward, 1989). We also included three covariates: the age at which an individual matured, the order in which the male matured in his tank and the year in which the sire was collected. We ran separate models on each stage of the trials (maturation or 1 month postmaturation) but see Supplementary material for a discussion of models where stages were combined (see Supplementary Methods and Results, Repeated Measures Analysis, Table S26).

We included all possible three-way interactions among fixed effects in initial models and used backward elimination to remove nonsignificant higher-order interactions and covariates ($P > 0.2$) in a stepwise manner in all analyses. We present the final models in the Results. To account for nonindependence among males from the same family and males reared in the same social environment aquaria, we included the identity of the family ($N = 23$, range 2–11 males per family), tank ($N = 80$) and sex ratio of developing juveniles ($N = 10$) as random effects. Variance and covariance estimates for random effects of all models are reported in Supplementary Table S5. To determine whether other potential predictors should be included in the model, we inspected residuals of this model against other possible linear and quadratic fixed effects of days since maturation, receptive female SL, whether this was the receptive female's first or second trial and time of day. These analyses showed that other predictors were not associated with mating behaviour and they were not included in final models. To assess whether slopes for the relationship between male SL and behaviour differed significantly between groups, we used post hoc slope comparisons using custom contrasts via the ‘estimate’ statement in SAS and corrected for multiple comparisons using the ‘adjust = simulate’ option or the sequential Bonferroni procedure as appropriate (Holm, 1979; Littell et al., 2006).

To assess the primary alternative tactic used, we analysed the odds of using a courtship display as the number of courtship displays divided by the number of thrusts using a lognormal distribution (see Supplementary material: ‘Events-trials analysis’ and Table S28 for a similar analysis controlling for activity rate). To determine if changes in the primary alternative tactic were driven by changes in courtship display and/or sneaking behaviour, we also assessed models for the number of courtship displays and the number of thrusts. Based on comparison of deviance values and visual inspection of residuals, we used a lognormal distribution to analyse the number of displays and a negative binomial distribution to analyse the number of sneaking attempts. To avoid taking a log of zero when using the lognormal distribution, we added one to counts of displays and sneaking attempts prior to analysis. All data fitted the assumptions of the statistical models (random effects normally distributed, appropriate link function giving approximately homogeneous variance across fixed effect groups, appropriate estimation of variance, no outliers) based on visual inspection of residual plots and the ratio of Pearson's chi-square statistic (a measure of residual dispersion) and degrees of freedom being approximately equal to one (Bolker et al., 2009). Male SL was centred and standardized to have a mean of zero and a standard deviation equal to one. We estimated denominator degrees of freedom in all models using the Kenward–Roger method (Bell et al., 2013, 2014; Littell et al., 2006), which adjusts for biases related to small sample size in parameter estimates and standard errors, is appropriate for models with correlated errors and accounts for random effects.

To compare the effect sizes of social environment, sire size class and male body size at maturation and 1 month postmaturation, we calculated Cohen's f^2 for each term (Cohen, 1988). Cohen's f^2 estimates the amount of variance uniquely attributed to each fixed effect in the model and is appropriate for mixed effects models (Selya et al., 2012). We used SAS to calculate Cohen's f^2 as described in Selya et al. (2012).

Ethical Note

Our protocols followed ASAB/ABS guidelines for ethical treatment of animals. Experimental designs were created to minimize negative impacts on all animals. For example, animals were exposed to natural social stimuli at natural densities, all aquaria had artificial plants for enrichment, no animals were marked and water quality was carefully monitored. The experiments were approved by the Florida State University Animal Care and Use Committee (protocols 1341, 1638).

RESULTS

Social Environment Strongly Influences Male Mating Tactic

To analyse a male's primary behaviour (i.e. the relative use of each of the two tactics), we assessed the log odds of using a courtship display. The social environment affected the odds of using a courtship display both at maturation ($F_{3,148} = 2.86$, $P = 0.039$) and 1 month postmaturation ($F_{3,50.72} = 3.13$, $P = 0.034$) in similar

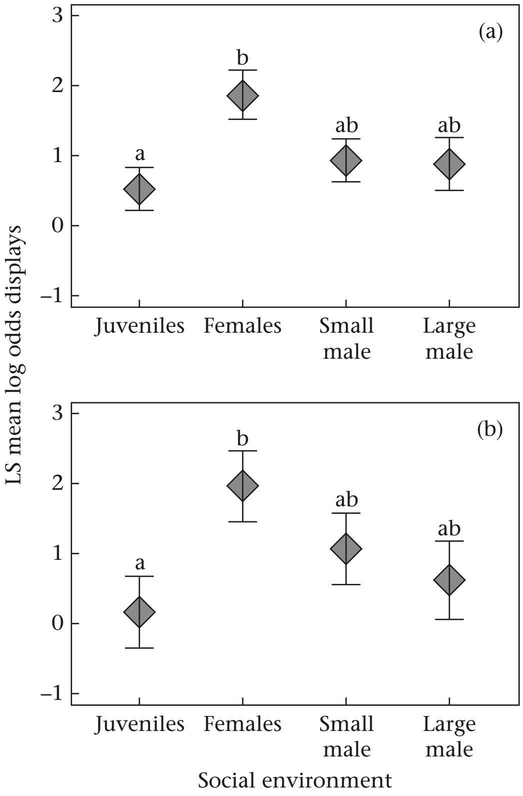

Figure 1. Log odds of performing a courtship display (a) at maturation and (b) 1 month postmaturation for males from different social rearing environments: three juveniles ($N = 48$ at maturation, $N = 46$ at 1 month postmaturation), three females ($N = 38$ at maturation, $N = 36$ at 1 month postmaturation), a small male and two females ($N = 45$ at maturation, $N = 40$ at 1 month postmaturation) or a large male and two females ($N = 33$ at maturation, $N = 30$ at 1 month postmaturation). Points display least square means ± SE on the log scale. Different letters denote significant post hoc differences between social environments (post hoc comparisons reported in Supplementary Tables S6 and S9).

Table 1
GLMM analysis of the proportion of courtship displays, the number of courtship displays and the number of sneaking attempts

Behaviour	Effect	At maturation				Postmaturation			
		ndf	*ddf*	*F*	*P*	*ndf*	*ddf*	*F*	*P*
Proportion of courtship displays (log odds)	Social environment	**3**	**148**	**2.86**	**0.039**	**3**	**50.72**	**3.13**	**0.034**
	Sire size	2	148	2.67	0.073	2	52.81	0.17	0.848
	Standard length	1	148	0	0.945	1	123.3	0.53	0.468
	Sire size∗social	6	148	2.03	0.065	6	52.69	1.54	0.185
	Sire size∗SL	**2**	**148**	**6.15**	**0.003**	–	–	–	–
	Sire year	–	–	–	–	3	59.03	2	0.124
	Maturation age	1	148	2.07	0.152	1	134	2.43	0.122
Number of courtship displays	Social environment	3	140	0.60	0.618	**3**	**125.6**	**4.92**	**0.003**
	Sire size	**2**	**140**	**5.13**	**0.007**	2	23.0	0.19	0.827
	Standard length	**1**	**140**	**6.57**	**0.012**	1	100.1	0.83	0.365
	Sire size∗social	6	140	1.75	0.114	6	121.4	0.67	0.673
	Sire size∗SL	**2**	**140**	**3.11**	**0.048**	2	91.8	0.10	0.907
	Social∗SL	3	140	0.77	0.512	3	124.8	0.42	0.741
	Sire size∗social∗SL	6	140	1.90	0.084	**6**	**122.9**	**2.18**	**0.0495**
Number of sneaking attempts	Social environment	**3**	**145**	**7.04**	**0.0002**	3	132	0.96	0.412
	Sire size	2	18.8	1.79	0.195	2	129.4	0.50	0.610
	Standard length	1	145	1.32	0.253	1	132	0.36	0.548
	Sire size∗social	**6**	**145**	**2.71**	**0.016**	**6**	**112.4**	**3.03**	**0.009**
	Sire size∗SL	**2**	**120.4**	**5.91**	**0.004**	–	–	–	–
	Social∗SL	**3**	**145**	**3.21**	**0.025**	3	131.3	2.65	0.052
	Sire year	–	–	–	–	**3**	**124.7**	**4.89**	**0.003**
	Maturation age	**1**	**145**	**6.25**	**0.014**	**1**	**132**	**7.59**	**0.007**

SL: standard length. Significant effects are bolded. Post hoc comparisons are reported in Supplementary Tables S6–S19. Solutions for fixed effects are reported in Supplementary Tables S20–S25.

ways (Table 1, Fig. 1). Males reared with females were twice as likely to use courtship displays over sneaking, while males reared with juveniles were equally likely to use courtship displays or sneaking. Primary mating strategy did not differ between males raised with a small or large male; these males reared with other males had odds of using a courtship display that were intermediate to those reared only with juveniles or females.

At maturation, the odds of using a courtship display was also affected by an interaction between a focal male's body size and the size of his sire ($F_{2,148} = 6.15$, $P = 0.003$; Table 1, Supplementary Fig. S1a). Males with small sires had the strongest positive relationship between body size and the odds of using a courtship display, and the slope was steeper than for males with intermediate or large sires (Supplementary Tables S7–S8). The smallest male from a small sire (SL = 24) was twice as likely to perform a sneaking attempt compared to a courtship display, while the largest male of this group (SL = 54) was 2.5 times more likely to perform a courtship display over a sneaking attempt (based on predicted values from the final model; Supplementary Fig. S1a; post hoc comparisons in Supplementary Tables S7–S8). There was no significant relationship between body size and the log odds of using courtship displays at maturation for males of intermediate and large sires.

Effects on Behavioural Rates Are Driven by Interactions between Social Environment and Heritable Factors

To determine what might be driving the differences in relative tactic use, we analysed the number of courtship displays and the number of sneaking attempts. These measures assessed the rate at which an individual used a particular mating tactic. Our results suggest that the effects of sire size, social environment and a male's body size at maturation on the odds of using a courtship display were driven by changes to both the number of courtship displays and sneaking attempts performed.

Social environment affected the number of courtship displays in a three-way interaction among social environment, sire size class and male body size that reached statistical significance only for males 1 month postmaturation (maturation: $F_{6,140} = 1.90$, $P = 0.084$; postmaturation: $F_{6,122.9} = 2.18$, $P = 0.0495$; Table 1, Fig. 2). For males with a small sire that were reared without adults (juvenile social group), courtship display rate tended to decrease with increases in male body size (Fig. 2a, post hoc comparisons in Supplementary Tables S12–S13). In this context, the largest focal male offspring (SL = 54) displayed 10 times less than the smallest (SL = 24) based on predicted values from the final model. There were no relationships between courtship display rate and body size

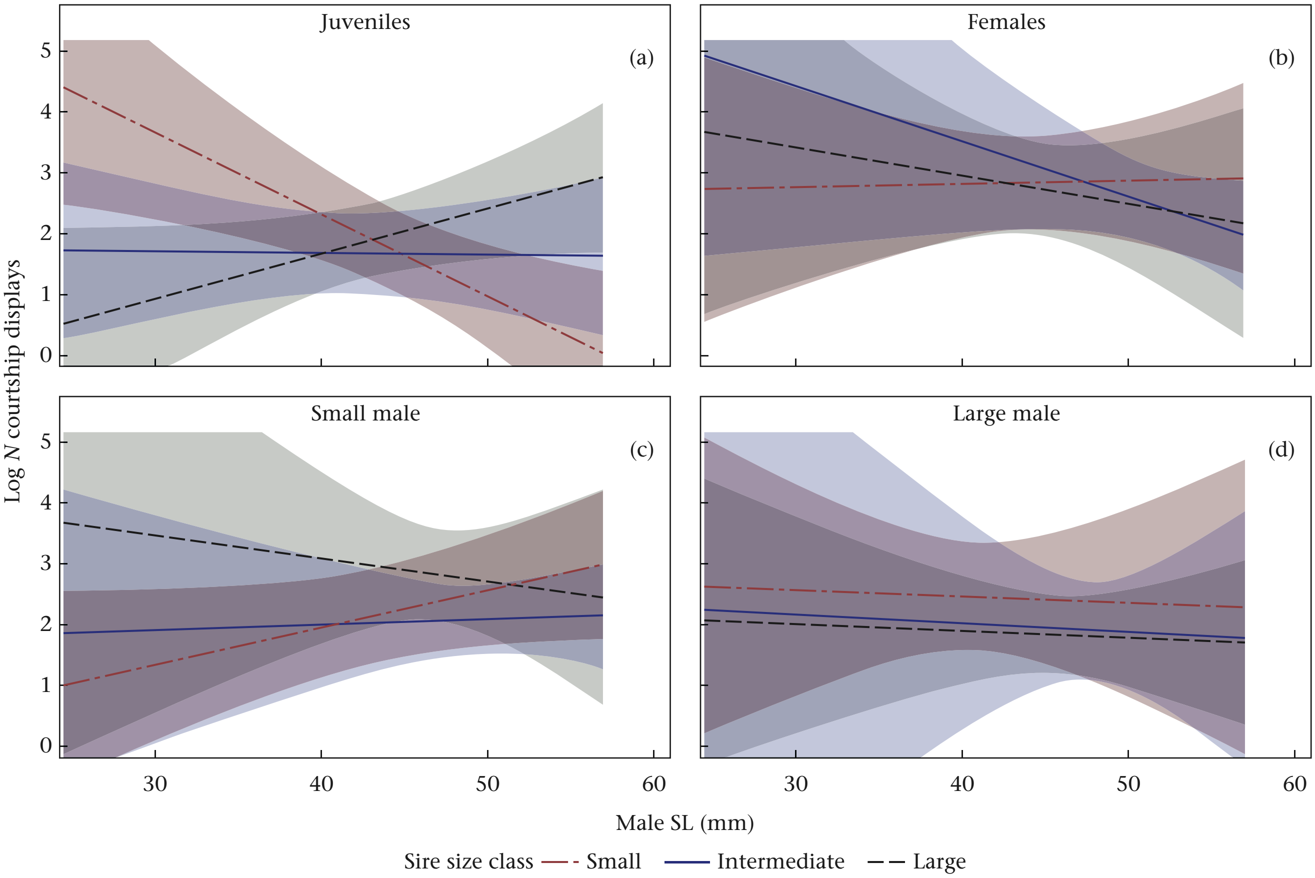

Figure 2. Relationship between the number of courtship displays performed towards a receptive female 1 month postmaturation and male body size (SL), sire size class and social environment during development. Lines and shading are the predicted relationship (±95% CI). Colours represent different sire sizes and panels represent social environment during development: (a) three juveniles ($N = 15$ from small sires, $N = 14$ from intermediate sires, $N = 17$ from large sires), (b) three females ($N = 11$ from small sires, $N = 15$ from intermediate sires, $N = 10$ from large sires), (c) small male + two females ($N = 11$ from small sires, $N = 19$ from intermediate sires, $N = 10$ from large sires), (d) large male + two females ($N = 7$ from small sires, $N = 9$ from intermediate sires, $N = 14$ from large sires). Courtship displays are on the log scale (post hoc comparisons reported in Supplementary Tables S12–S13; raw values are plotted in Supplementary Fig. S2).

for small-genotype males in other social contexts. For males whose sires were intermediate and large, there were also no significant relationships between number of displays and focal male SL (Fig. 2; post hoc comparisons in Supplementary Tables S12–S13). In addition, males who were reared in a small male social environment did not differ in the relationship between courtship display rate and body size from males reared in a large male social environment ($b = -0.170 \pm 0.411$, $t_{123.3} = -0.41$, $P = 0.680$, $P_{adj} = 0.998$).

Social environment also affected the rate of sneaking attempts both at maturation and 1 month postmaturation as did interactions between social environment, the focal male's body size and the size class of his sire. At maturity, the number of sneaking attempts was affected by two-way interactions between the social environment, the focal male's body size and the size class of his sire (social environment∗sire size class: $F_{6,145} = 2.71$, $P = 0.016$; Fig. 3a; social environment∗body size: $F_{3,145} = 3.21$, $P = 0.025$; Fig. 4; sire size class∗body size: $F_{2,120.4} = 5.91$, $P = 0.004$; Table 1, Supplementary Fig. S1c). One month postmaturity, only the sire size class∗social environment interaction was a significant predictor of sneaking behaviour (Fig. 3b, Table 1). Maturation age also had a negative relationship with the number of sneaking attempts both at maturation and 1 month postmaturation: older males used less sneaking behaviour (Table 1, Supplementary Tables S24–S25).

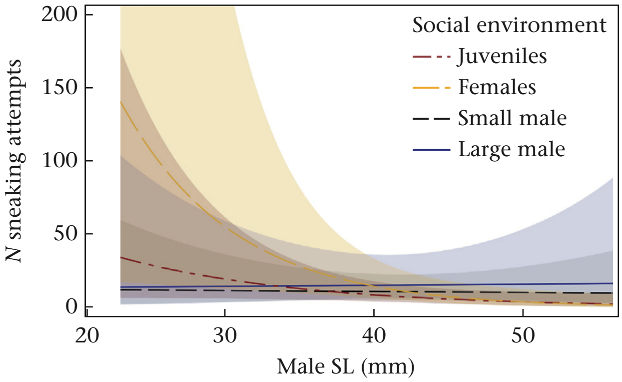

Figure 4. Predicted relationship (±95% CI) between male body size (SL) and the number of sneaking attempts performed at maturation for males from different social rearing environments: three juveniles ($N = 48$), three females ($N = 38$), a small male and two females ($N = 45$) or a large male and two females ($N = 33$). Colours represent different social environments (post hoc comparisons reported in Supplementary Tables S15–S16, raw values are plotted in Supplementary Fig. S3).

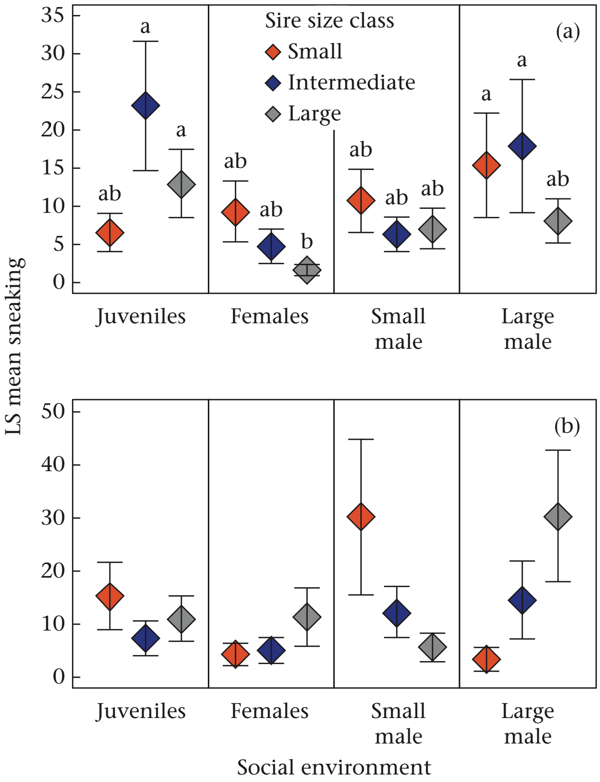

Figure 3. Relationship between the number of sneaking attempts directed towards a receptive female at (a) maturation ($N = 164$) and (b) 1 month postmaturation ($N = 152$) and male size class and social environment during development. Colours represent different sire sizes and the X axis depicts social environment during development: three juveniles (at maturation: $N = 15$ from small sires, $N = 16$ from intermediate sires, $N = 17$ from large sires; 1 month postmaturation: $N = 15$ from small sires, $N = 14$ from intermediate sires, $N = 17$ from large sires), three females (at maturation: $N = 11$ from small sires, $N = 15$ from intermediate sires, $N = 12$ from large sires; 1 month postmaturation: $N = 11$ from small sires, $N = 15$ from intermediate sires, $N = 10$ from large sires), small male + two females (at maturation: $N = 13$ from small sires, $N = 19$ from intermediate sires, $N = 13$ from large sires; 1 month postmaturation: $N = 11$ from small sires, $N = 19$ from intermediate sires, $N = 10$ from large sires), large male + two females (at maturation: $N = 9$ from small sires, $N = 9$ from intermediate sires, $N = 15$ from large sires; 1 month postmaturation: $N = 7$ from small sires, $N = 9$ from intermediate sires, $N = 14$ from large sires). Points display least square means ± SE. Different letters denote significant post hoc differences between sire size class by social environment groups (post hoc comparisons reported in Supplementary Tables S14 and S19).

The sire size class∗social environment interaction at maturity indicated that males whose sires were small were the least responsive to changing social environments during development in the number of sneaking attempts both at maturity and 1 month postmaturity (Table 1, Fig. 3; post hoc comparisons in Supplementary Table S14). In contrast, males from large and intermediate sires tended to change their sneaking behaviour rate in response to the social environment during development. For example, males with large sires used five-fold more sneaks at maturity when reared with juveniles compared to when they were reared with females (Fig. 3a). Males from intermediate sires tended to sneak more when reared with juveniles or a large male (Fig. 3a). While no effects were statistically significant after corrections for multiple comparisons, 1 month postmaturation, males from large and small sires tended to be the most responsive to changing social environments (Fig. 3b; post hoc comparisons in Supplementary Table S19).

At maturation, there was also a significant interaction between the social environment and focal male's body size on the number of sneaking attempts. There tended to be a negative relationship between male body size and number of sneaking attempts for individuals reared in the absence of males (e.g. with only juveniles or only females), while those reared with males of either size did not show a significant relationship between body size and number of sneaking attempts (Fig. 4, Supplementary Tables S15–S16). Males reared with females tended to have steeper negative slopes for the relationship between body size and sneaking rate at maturation than those reared with a male (Fig. 4, Supplementary Tables S15–S16). There were no differences in the relationship between body size and sneaking rate for individuals reared with different-sized males (Fig. 4, Supplementary Tables S15–S16).

An interaction between the focal male's body size and the size class of his sire also affected the direction and strength of the relationship between male body size and behavioural rates for both courtship and sneaking behaviour. At maturity, males with small sires had a significant negative relationship between their body size and the number of sneaking attempts and tended to have a significant positive relationship between body size and the number of courtship displays performed (Supplementary Figs. S2b, c;

Table 2
Cohen's f^2 estimates for social environment, sire size class and male body size (SL) at maturity and 1 month postmaturity for the proportion of courtship displays, the number of courtship displays and the number of sneaking attempts

Phenotype	Effect	At maturation	Postmaturation
Proportion of courtship displays (log odds)	Social environment	0.142	0.157
	Sire size	0.174	0.069
	SL	0.084	0.003
Number of courtship displays	Social environment	0.188	0.290
	Sire size	0.151	0.162
	SL	0.115	0.100
Number of sneaking attempts	Social environment	0.628	0.449
	Sire size	0.269	0.328
	SL	0.307	0.074

SL: standard length. Cohen's f^2 estimates how much variation is uniquely explained by each model term.

Tables S10, S17). Therefore, males with small sires used fewer sneaks and more courtship displays when they themselves were large and used more sneaks coupled with fewer courtship displays when they were small. The smallest male with a small sire (SL = 24) was expected to perform two displays and 24 sneaks, while the largest male with a small sire (SL = 54) was likely to perform 36 displays and six sneaks (based on predicted values from the final model; Supplementary Figs. S1b, c; post hoc comparisons in Supplementary Tables S10, S17). There was no relationship between body size and the number of courtship displays or sneaking attempts for males with intermediate or large sires (Fig. 2b, c, Supplementary Tables S10, S17).

Effects of Social Environment on Mating Behaviours Are Stronger 1 Month Postmaturation

For all measures of behaviour, the effect sizes of social environment, sire size class and body size were more similar in magnitude at maturity than at 1 month postmaturation (Table 2). By 1 month after maturity, social environment had the largest effect on all behaviours. The effect of social environment 1 month postmaturity on display behaviour (both the odds of using a courtship display and display rate) was especially strong compared to the effects of sire size class or male body size; for both measures of behaviour, social environment had about twice the effect on courtship displays than sire size class and more than 2.9 times the effect on courtship displays than male body size (Table 2). For sneaking rate, social environment had a large effect and sire size class had moderate effect 1 month postmaturity (Table 2).

DISCUSSION

We tested alternative hypotheses for the effects of the early social environment during development on plasticity in adult male mating behaviours in the sailfin molly. As predicted by socially cued anticipatory plasticity, we found that the primary mating tactic (e.g. whether males were more likely to use courtship displays or sneaking attempts) differed between social environments that varied in the number of females; males exposed only to females were more likely to use a courtship display compared to those exposed only to juveniles. This relationship held at both maturation and 1 month postmaturation. Therefore, plasticity of male mating repertoire might be an adaptive response to cues that juveniles receive about the adult sex ratio that allow them to predict which mating behaviour phenotypes best match adult social competition. In contrast, variance in the rates of each mating behaviour were predicted by interactions among the social environment during development, sire size class and body size that were not predicted by either socially cued anticipatory plasticity or condition dependence. Therefore, behavioural rates are unlikely to be shaped by cues of future competitive environment during the juvenile period as measured in this experiment.

Socially Cued Anticipatory Plasticity via Differences in Perceived Competition May Affect the Development of Primary Mating Behaviour

Our work demonstrates that experiencing different social environments as a juvenile can change how adults deploy alternative mating tactics, illustrating the importance of exploring interactions between juvenile and adult environments. Based on predictions from socially cued anticipatory plasticity, we expected that differences in perceived mating competition would drive the development of mating behaviours. For example, some verbal theories predict that when the operational sex ratio is female-biased, males should use less sneaking behaviour (Kvarnemo & Ahnesjo, 1996; Magellan & Magurran, 2007). Our results are consistent with this prediction: at maturity, males reared with three females used less sneaking and more courtship behaviour, males reared with another male and two females used an intermediate amount of sneaking and those reared in the absence of adult females used the most sneaking relative to courtship. Males showed a similar graded response in mating tactic 1 month postmaturation, indicating that these effects did not change after males gained sexual experience. Our results suggest that juveniles use the social environment during development to plastically adopt behavioural phenotypes to match perceived competitive environment in adulthood (Kasumovic & Brooks, 2011). These results are also consistent with empirical studies showing that males reduce sneaking behaviour in response to increased mate competition during adulthood in a variety of species including guppies, a related poecilid fish (de Jong et al., 2009; Magellan & Magurran, 2007; Weir et al., 2011; Řežucha & Reichard, 2014). Therefore, assessing how both the social environment during early development and the social environment during adulthood affect phenotypes and fitness is crucial to understanding how these alternative phenotypes evolve.

Studies in other species have reported different patterns of response to juvenile social environments (Bailey et al., 2010; Cory & Schneider, 2018; Guevara-Fiore, 2012; Guevara-Fiore et al., 2012). For example, guppies that experience more female-biased social environments as juveniles respond by reducing courtship rates and increasing sneaking attempts (Guevara-Fiore, 2012; Guevara-Fiore et al., 2012). In addition, in contrast to our results, after sexual experience with females, there were no effects of social environment during development on guppy mating tactics (Guevara-Fiore et al., 2012). Future studies should use comparative methods to elucidate general patterns of how social environment affects mating behaviour across closely related species.

Based on predictions from socially cued anticipatory plasticity, we also expected to find differences in mating behaviours between males that were reared with small or large males because large males are preferred by females (Gabor, 1999; Gabor & Page, 2003; MacLaren et al., 2004; MacLaren & Rowland, 2006; Ptacek & Travis, 1997; Schlupp et al., 1994). However, our results do not support this prediction. One hypothesis for why we did not find differences in mating tactics is that males were adjusting other phenotypes (e.g. body size) in response to differences in the sizes of the adult males. However, focal males in this experiment did not differ in average body size at maturity when reared with a large or small male during development (Lange, Ptacek, et al., 2021). Therefore, any direct effects of variation in the size of adult males during development on mating behaviour would not be due to socially cued differences in the body size of the focal males across these treatments. Instead, our results suggest that the number of females in the social environment may be the most important driver in the development of alternative mating behaviours. Females receptive to mating are a limited resource and the success of alternative strategies may depend on the operational sex ratio. Future studies should vary sex ratio in tandem with the size of males in the social environment to determine how these social cues interact to alter the development of mating behaviours and assess reproductive success in different social environments at adulthood to determine whether adult sex ratio and/or the size of adult males in the social environment best predicts fitness outcomes.

Limited Evidence for Condition-dependent Development of Mating Behaviour

The condition dependence hypothesis predicts that males will adjust their mating behaviour based on their size relative to other males in the social environment (Gross & Repka, 1998a, 1998b; Lee, 2005; Repka & Gross, 1995). Previous tests of this hypothesis in mollies have yielded inconsistent results. Farr et al. (1986) found that, in populations with smaller average male body size, males displayed more and sneaked less at a given body length than males from populations with larger average male body size. By contrast, Ptacek and Travis (1996) surveyed a larger number of populations and found inconsistent patterns (e.g. some populations followed the pattern described in Farr et al. (1986), but others did not).

Our results suggest that relative size is not as important in determining a male's courtship display rate as other factors in the social environment. If condition dependence played an important role, males reared with a small male would have had a stronger positive relationship between body size and courtship display rate than males reared in the presence of a large male. This was not the case. The greatest variation in the relationship between size and courtship displays was between sons of small males reared with juveniles, where there tended to be a negative relationship between size and courtship displays and all other social environments. A similar result occurred for sneaking behaviour: sneaking behaviour tended to be negatively associated with body size in males reared with juveniles or females and had no association with body size in individuals reared with other males. Future work should examine whether and how early social environments drive condition-dependent expression of alternative mating behaviours, or whether condition dependence may be more important in determining response to adult social environments.

Instead of relative size being important in determining behaviour rates, we found interactions between heritable and nonheritable factors. Previous work on mollies and other related taxa often report positive relationships between body size and the number of courtship displays and negative relationships between body size and the number of sneaking attempts (Erbelding-Denk et al., 1994; Farr et al., 1986; Ptacek & Travis, 1996; Ryan & Causey, 1989; Swanbrow Becker et al., 2012; Travis, 1994b; Travis & Woodward, 1989; Zimmerer & Kallman, 1989). In this study, when relationships between body size and courtship display rates were significantly different from zero, they were not always positive. Instead, the strength of this relationship depended on the presumed genotype of a male's sire, the social environment in which the male was reared and ontogenetic stage of maturation. Similarly, the strength of the negative relationship between body size and the number of sneaking attempts also varied with heritable and environmental factors. Therefore, the variation in the strength of the relationship between body size and behaviour that has been observed across populations in sailfin mollies (Farr et al., 1986; Ptacek & Travis, 1996) may be due to both heritable and environmental factors that affect the expression of these traits.

The results from this study suggest that more complicated interactions between factors that affect the rates of alternative mating behaviours in sailfin mollies likely underlie previously reported positive relationships between body size and the number of courtship displays and negative relationships between body size and the number of sneaking attempts. Indeed, if we model the number of alternative mating behaviours as a function of body size without other predictors, we find a significant positive relationship between body size and number of courtship displays ($b = 0.115$, $F_{1,137.8} = 5.17$, $P = 0.025$) and no relationship between body size and number of sneaking attempts ($b = -0.100$, $F_{1,159.6} = 1.11$, $P = 0.293$). However, this relationship ignores considerable complexity in how behaviour rates develop, as the fuller exploration of our results indicate. Therefore, our results show that when interactions between heritable and environmental factors are considered, new insights can be gained on well-described behavioural relationships.

Conclusions

Our results demonstrate that the early social environment can play a crucial role in the development of mating behaviours. Previous work on this topic focused on different types of adult behaviour (e.g. social interactions: Arnold & Taborsky, 2010; Taborsky et al., 2012; female mate preferences: Kasumovic et al., 2012; Macario et al., 2017, Macario et al., 2019) or different early social environments (Bailey et al., 2010; Cory & Schneider, 2018; Guevara-Fiore, 2012; Guevara-Fiore et al., 2012) that did not allow for a test of the relative importance of socially cued anticipatory plasticity and condition dependence on the development of mating behaviour. Results from the current study suggest that even within the context of mating behaviours, different behaviours can vary in how they respond to early social environments. Therefore, to understand how social environment affects the development and evolution of behaviour, future work is needed to assess what types of early social experiences most strongly drive adult behaviours across taxa.

In conclusion, we found support for the socially cued anticipatory plasticity hypothesis in the development of a male's primary mating tactic, but not in the rate at which he performs each mating behaviour in his repertoire. Our study suggests that socially cued anticipatory plasticity might be more likely to shape the evolution of alternative mating behaviours than condition dependence when early social experiences are considered. However, further studies that examine a range of ecologically relevant juvenile social environments in other species are needed to determine the relative importance of socially cued anticipatory plasticity and condition dependence for the development of alternative mating behaviours. In addition, our results indicate that socially cued anticipatory plasticity may be more likely to drive the evolution of reversible phenotypes than it is for irreversible phenotypes (Lange, Ptacek, et al., 2021; Lange, Travis, et al., 2021). Future work should also focus on determining whether, and when, we expect socially cued plasticity to evolve. For example, more work is needed to determine how feedbacks between social environment and socially cued plastic phenotypes affect the evolution of both reversible and irreversible mating behaviours.

Author Contributions

Elizabeth Lange: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – original draft, Writing – review & editing. **Stephen Erk**: Investigation, Writing – review & editing. **Margaret Ptacek**: Conceptualization, Methodology, Writing – review & editing. **Joseph Travis**: Conceptualization, Methodology, Supervision, Resources, Funding acquisition, Writing – review & editing. **Kimberly Hughes**: Conceptualization, Methodology, Supervision, Resources, Funding acquisition, Writing – review & editing.

Data Availability

All data used in this study are archived on the Mendeley Data Repository: https://doi.org/10.17632/35m3vs489g.1 (Lange et al., 2022).

Declaration of Interest

We declare that we have no conflict of interest.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2022.11.006.

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