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Sex differences in the plasticity of life history in response to social environment

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Predicting how social environment affects life history variation is critical to understanding if, and when, selection favors alternative life history development, especially in systems in which social interactions change over time or space. Although sexual selection theory predicts that males and females should respond differently to variation in the social environment, few studies have examined the responses of both male and female phenotypes to the same gradient of social environment. In this study, we used a livebearing fish to determine how males and females altered their life histories in response to variation in the social environment during development. We found that both males and females delayed maturity and attained larger sizes when their social environment included adults, in contrast to developing in juvenile-only environments. The magnitude of this effect differed substantially between the sexes. The common pattern of response in the sexes suggested that life history trade-offs, rather than sexual selection, is responsible for these changes in life history expression. These effects make the relationship between genotype and phenotype depend strongly on the environment experienced by each individual. These results indicate that social environment is an important driver of life history variation in sailfin mollies and can be at least as important as abiotic effects.

KEY WORDS: **Development, life history, sex-specific variation, sexual selection, social environment.**

Life history phenotypes are striking examples of traits that are subject to strong natural selection but are also highly variable (Charlesworth and Hughes 2000; Stearns 2000; Mitchell-Olds et al. 2007; Charlesworth 2015). Life history traits determine the timing and magnitude of major events such as birth, maturation, reproduction, and survival and are therefore under strong natural selection (Stearns 1992; Charlesworth 1994; Roff 2002). Consequently, one might predict that a single life history strategy that maximizes fitness in the local environment would evolve rapidly and resist invasion by alternative tactics. However, life history phenotypes can be highly variable within populations, and genetic variation in these traits generally exceeds that for other phenotypes (Price and Schluter 1991; Houle 1992; Hansen et al. 2011). Understanding why this is so is a long-standing, but as yet unresolved, problem in evolutionary biology (Charlesworth 2015).

The social environment is a particularly important factor for the expression of life histories. Social interactions can be crucial factors in both the developmental regulation (Rodd and Sokolowski 1995; Walling et al. 2007; Bailey et al. 2010) and the fitness consequences of alternative life history phenotypes (Gross 1985; Rotenberry and Zuk 2016). Nonetheless, the role of the social environment in generating and maintaining life history variation is understudied relative to the role of abiotic environmental factors (reviewed in Nylin and Gotthard 1998; West-Eberhard 2003; Murren et al. 2015).

The difference in emphasis between social and abiotic environmental factors is particularly striking for studies of the transition to sexual maturity. The timing of this transition and the body size at which it occurs can be major determinants of fitness (Roff 1992; Stearns 1992) but the precise effects on fitness can differ between the sexes. Sexual selection theory predicts that variation in social environment will affect males' and females' age and size at maturation differently because it can alter both the number and quality of potential mates (Emlen and Oring 1977; Kokko and Rankin 2006; Kasumovic and Brooks 2011; Procter

et al. 2012). In an environment with high-quality mates, selection could favor early maturation in females while favoring males that delay maturation when there is higher competition. For example, in green swordtails (*Xiphophorus hellerii*), females exposed to a high-quality male during development matured earlier than females exposed to a low-quality male, whereas males had the opposite response (Walling et al. 2007). This contrast between the expected effects of sexual selection on life history patterns in females and males is an underappreciated source of sexual conflict.

Additional theoretical considerations generate opposite predictions for how social environment affects development. For example, in the context of alternative mating tactics, it has been hypothesized that increased social competition that occurs in environments with many high-quality males favors the adoption of alternative strategies; consequently, males may mature earlier and at smaller sizes as the quality of males in the population increases (Shuster and Wade 2003; Taborsky and Brockmann 2010). Furthermore, if large males prefer larger females and/or if female size confers increased fecundity, females may delay maturation in an environment when mate quality is high, to reach a size where reproduction is maximized as predicted by life history theory (Stearns 1976, 1977). Therefore, it is unclear if variation in social environment should promote or erode sexual conflict.

Although many studies have shown that social environment can affect age and size at maturity (Fullerton and Cowley 1971; Vandenbergh et al. 1972; Sohn 1977a,b; Thompson et al. 1993; Kolluru and Reznick 1996; Holbrook and Schal 1998; Heino et al. 2002; Kasumovic and Brooks 2011; Kasumovic et al. 2013; Boulton et al. 2016; Kasumovic et al. 2016; Neumann and Schneider 2016; Culumber et al. 2018), the majority are focused on only one sex. This makes it impossible to test theory that predicts sexual conflict for these life history patterns. The few studies that have examined both sexes are consistent with sexual selection theory where increased male-male competition is expected to favor early maturation in females and delayed maturation in males (Walling et al. 2007; Kasumovic et al. 2011). However, to date, there are too few studies that assess the generality of this pattern.

Sailfin mollies, *Poecilia latipinna*, offer an excellent opportunity to investigate socially-mediated sex differences in the development of life history traits. Males vary greatly in developmental rate within populations, resulting in striking variation in male age and size at maturity within a single population (Hubbs 1942; Kilby 1955; Snelson 1985; Farr et al. 1986; Ptacek and Travis 1996; Seda et al. 2012). Because male growth is nearly determinate, size at maturity defines male size throughout adulthood (Snelson 1984; Travis et al. 1989; Travis 1994a). Small, sneaker males mature in as little as 50–70 days and use a forced copulation technique, whereas large males can take 130–150 days to mature and use courtship display behavior to entice female cooperation in mating (Travis 1994a,b; Ptacek and Travis 1997). Females prefer larger males as mates (Schlupp et al. 1994; Ptacek and Travis 1997; Gabor 1999; Witte and Noltemeier 2002; Witte and Ryan 2002; Gabor and Page 2003; MacLaren et al. 2004; MacLaren 2006) and larger females are preferred by males (Travis 1994a; Ptacek and Travis 1997). Female growth is indeterminate (Travis 1994a); therefore, unlike males, maturing at a small size does not mean a female will not grow to be large. In addition, although the adult sex ratio is female-biased in natural populations (Simanek 1978; Snelson and Wetherington 1980), the operational sex ratio is strongly male-biased as females are only receptive to mating 24–48 h post parturition. Therefore, male-male competition is strong.

Both genetic and environmental factors have been implicated in regulating life history variation in mollies. Common garden experiments indicated high heritability and Y-linkage of male age, size, and courtship display behavior at maturity (Trexler and Travis 1990; Travis 1994a,b). For example, male body size at maturity has a sire-son regression slope of 1.02 ± 0.09, suggesting strong Y-linkage (Travis 1994b). Female life history traits also have a heritable component (Trexler and Travis 1990). At the same time, age and size at maturity are plastic with respect to abiotic environmental factors, although these factors affect males less than females (Trexler and Travis 1990; Trexler et al. 1990).

In this study, we reared offspring of sires of different size classes in four different social environments to determine how male and female life history expression is influenced by social environment during development. First, we assessed the effects of social environment on life history. In doing so, we tested the predictions of sexual selection theory: (i) in environments with more competition among males (e.g., when there are more males present or when the males present are higher quality), males should mature later at a larger body size; (ii) in environments with more competition among males, females should mature earlier at a smaller size. We also explore support for two alternative hypotheses for plasticity in male and female life history traits: (i) in environments with more competition among males, males should express alternative mating phenotypes and therefore mature at smaller sizes; (ii) in environments with more competition among males, females should delay maturation to reach a size where reproduction is maximized, as life history theory predicts.

Second, we tested the prediction that males and females exhibit differences in the relative influence of social environment and nonsocial environment effects. Because previous studies reported higher heritability of size and age at maturation in males than females (Trexler and Travis 1990; Travis 1994a,b), and concluded that body length is strongly Y-linked (Travis 1994a,b), we predicted that sire size class would have a stronger effect on male life history than on female life history. This prediction is

supported by the greater plasticity of female mollies in response to variation in the abiotic environment (Trexler and Travis 1990; Trexler et al. 1990), and thus we predicted a similar contrast between the sexes in response to the social environment.

Finally, we hypothesized that the effects of the social environment on age and size at maturity would occur through effects on growth rate. We predicted that juveniles would show the highest growth rates in environments that consisted only of other juveniles and the lowest growth rates in social environments containing large males. Based on traditional life history theory (reviewed in Roff 1992; Stearns 1992; Charlesworth 1994) and theory for optimal reaction norms (Rowe and Ludwig 1991; Stearns 2015), we hypothesized that where the relationship between age and size at maturity was shallowest (i.e., representing slow growth), individuals would mature early at smaller sizes. In environments where the relationship between age and size at maturity was steepest (i.e., fast growth), individuals would mature later at larger sizes.

Methods

MATING DESIGN

All sailfin mollies used as sires and social groups were collected from the Steve's Ditch population in Wakulla County, FL (29°59′15.5″N, 84°23′21.6″W; Seda et al. 2012) and housed in a laboratory at Florida State University, Tallahassee, FL. All fish were kept in static aquaria with a 14:10 h light/dark cycle and a room temperature of 27°C. Males were divided into nonoverlapping size classes based on alternative life history phenotype (Travis and Woodward 1989; Seda et al. 2012; Fraser et al. 2014). Large males were >50 mm standard length (SL—measured from the tip of the snout to the base of the caudal peduncle), intermediate males were 38–45 mm, and small males were <30 mm.

A schematic of the breeding design is shown in Figure 1. Eight large males (mean SL: 54.75 ± 0.726 mm s.e.), eight intermediate males (mean SL: 41.625 ± 0.706 mm s.e.), and seven small males (mean SL: 27.143 ± 0.508 mm s.e.) from collections in October 2014, 2015, 2016, and 2017 were used as sires. Sires were collected in the early fall to limit variation in social and other environments experienced by males during development. Female mollies can store sperm, so dams were lab-reared virgin female offspring of wild females collected at the same time as the males used as sires. A total of 23 families were reared, each representing a different sire and dam; each dam was the offspring of a different wild-caught female.

Each sire was mated to a virgin female in a 37.9-l aquarium. Within 24 h of birth, resulting full-sibling broods were split between four social treatments in a full-sibling split-brood design. Fry from each family were divided among the four social treatments, using five fry per family per treatment. The social envi-

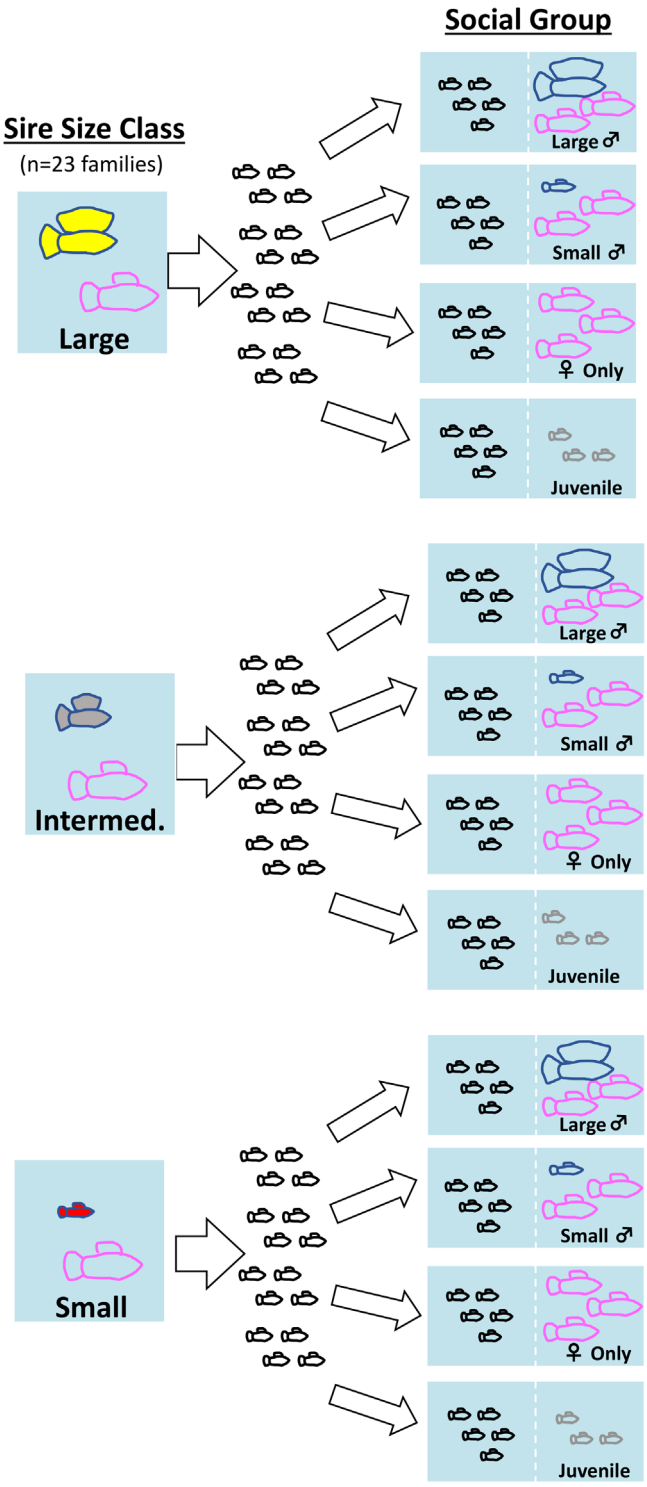

Figure 1. Schematic of the experimental design. Sires were divided into three size classes and each sire was mated to a virgin female. Resulting offspring were split among four social environments ($n = 5$ fry per social environment) and reared until maturity. In this figure, males are outlined in blue and females are outlined in pink. Focal juveniles are outlined in black and nonfocal juveniles are outlined in gray.

ronments were (a) one large adult male + two adult females; (b) one small adult male + two adult females; (c) three adult females; (d) three unrelated "nonfocal" juveniles. These social treatments were chosen to mimic a range of social environments an individual juvenile molly could experience over time and space in the wild where the population varies in the size of adult males and demography (Farr and Travis 1986; Ptacek and Travis 1996). Fish were housed in 76-l aquaria divided by a UV-permissive plastic sheet with small holes to allow transfer of visual and chemical cues. Groups of five siblings, which will be referred to as "focal fish," resided in one half of the tank. Social-context fish resided in the other half. Monthly surveys of the focal population (2015-2018) indicated that small juveniles (<15 mm) and adults do not shoal together, so our assay mimicked this partial physical segregation. In addition, adults are voracious eaters, so this design mitigated density and food competition effects between juveniles and adults.

Fish were fed ground Tetramin© flake food once daily. Social context fish were fed ad libitum. Food amounts for developing focal fish were measured per capita and increased as the focal fish aged (Travis et al. 1989). Developing fish were inspected daily for signs of maturation (completion of gonopodium development for males; presence of brood spot for females; Cummings 1943; Constantz 1989). At maturity, focal fish were removed from the rearing environment, and age at maturity, standard length, and wet mass were recorded. We measured the length of fish on a measuring board with a ruler as the length from the tip of the snout to the base of the caudal peduncle to the nearest millimeter. Wet mass to the nearest 0.001 g was assessed on a Mettler Toledo ML203T scale. Juveniles cannot be sexed until start of sexual maturation; thus, we also recorded sex ratio of matured juveniles in each tank and the maturation order as the order that each focal fish reached sexual maturation in a given tank from 1 to 5. The described experimental conditions were approved by the University Animal Care and Use Committee (protocols 1341; 1638).

STATISTICAL ANALYSES

A total of 178 focal males and 246 focal females were reared in this experiment; six juvenile males and 22 unsexed juveniles died before maturation. Males that took longer than 400 days to mature ($n = 3$) and females that matured in longer than 200 days ($n = 5$) were outliers and were removed from the analysis. In addition, females that were last to mature were removed because of the small sample size ($n = 5$). In total, three unique males and nine unique females were removed from the analysis. The final dataset included 175 focal males and 237 focal females.

To determine if male and female life history traits were affected by sire size class, social environment during development, and/or an interaction between these effects, we used general linear mixed models (GLMMs) implemented in the *Mixed* procedure in SAS v9.4 statistical software (SAS Institute, Cary, NC) on a 64-bit Windows 10 operating system. Based on previous experiments that assessed abiotic influences on male and female life history (Trexler and Travis 1990; Trexler et al. 1990), we a priori hypothesized that males and females would respond to social environment differently. Therefore, to assess effects of sire size class and social environment on life history traits, we analyzed each sex independently. Sire size class, social environment, maturation order, and all possible two-way interactions between these terms were included as fixed effects in each of the sex-specific statistical models. Family ($N = 23$), tank (to account for measurements of the five siblings raised in each aquarium; males: $N = 84$ tanks, females: $N = 91$ tanks), and sex ratio of the focal juveniles within each tank ($N = 10$, range all females to all males, with a mean of 0.751 males per female) were modeled as random effects. Estimates for random effects are reported in Tables S1 and S2.

To test for differences in growth rates among social environments, and because age and size at maturity are correlated (male length: Pearson's $r = 0.766$, d.f. $= 174$, $P < 0.0001$; male mass: Pearson's $r = 0.731$, d.f. $= 174$, $P < 0.0001$; female length: Pearson's $r = 0.876$, d.f. $= 236$, $P < 0.0001$; female mass: Pearson's $r = 0.867$, d.f. $= 236$, $P < 0.0001$), we assessed statistical models for length and mass where age at maturation was included as a covariate. When age was used as a covariate, it was centered to a mean of zero and standardized to a standard deviation of one. We only assessed linear effects of age as a continuous predictor.

In all analyses, we used backward elimination to remove nonsignificant interactions ($P > 0.2$) in a stepwise manner. The models presented in the results are the final models after removal of nonsignificant interactions. The data in all final models met the assumptions of the analysis without transformation. In all models, we estimated denominator degrees of freedom using the Kenward–Roger method (Littell et al. 2006; Bell et al. 2013; Bell et al. 2014). This method is appropriate for models with correlated errors, adjusts for biases in parameter estimates and standard errors due to small sample sizes, and accounts for random effects. To compare groups within significant factors with more than two levels, we used post hoc comparisons of least square means where we corrected for multiple comparisons using the adjust = simulate option in "proc mixed." This option computes *P*-values for differences between groups using a simulated distribution of *t*-values and keeps the error rate below $\alpha = 0.05$ experiment-wise.

To compare the effects of social environment, sire size, and other predictors between male and female life history traits, we calculated Cohen's f^2 for each fixed term in our models (Cohen 1988). Cohen's f^2 estimates the local effect size of each term in the model (the amount of variation uniquely accounted for by one

Table 1. GLMM analysis of factors predicting male ($N = 175$) age (A), length (B), mass (C), length given age (D), and mass given age (E) at maturity. Significant effects are bolded.

Phenotype	Effect	DF_{Num}	DF_{Den}	F-value	P-value
(A) Male age	**Social environment**	3	54.2	4.97	**0.004**
	Sire size	2	20.7	1.61	0.225
	Maturation order	4	96.3	36.65	**<0.0001**
(B) Male length	**Social environment**	3	54.5	3.16	**0.032**
	Sire size	2	19.8	3.77	**0.041**
	Maturation order	4	104	32.98	**<0.0001**
(C) Male mass	**Social environment**	3	45.6	4.02	**0.013**
	Sire size	2	19.6	4.03	**0.034**
	Sire size* Social environment	6	45.7	1.66	0.153
	Maturation order	4	108	15.59	**<0.0001**
(D) Male length	Social environment	3	43	1.11	0.356
Given age	Sire size	2	19.4	3.51	0.050
	Maturation order	4	134	4.41	**0.002**
	Maturation age	1	153	86.60	**<0.0001**
	Age* Order	4	130	5.51	**0.0004**
(E) Male mass	Social environment	3	42.9	2.15	0.107
Given age	**Sire size**	2	20.2	3.97	**0.035**
	Maturation order	4	141	4.95	**0.001**
	Maturation age	1	152	53.86	**<0.0001**
	Age* Order	4	139	2.79	**0.029**

predictor variable, over and above that of all other predictors) and is appropriate for hierarchical mixed-effects analyses with both categorical and continuous predictors (Selya et al. 2012). We calculated Cohen's f^2 in SAS using the approach outlined in Selya et al. (2012). Based on Cohen (1988), we considered an effect size between 0.02 and 0.15 as small, one between 0.16 and 0.35 as moderate, and an effect greater than 0.35 as large.

Results

MALE LIFE HISTORY TRAITS

The social environment and maturation order, but not sire size class, affected male age at maturity (Table 1A; Figs. 2–4). Juvenile males that were reared in the presence of other adults took 32–54% longer to mature than those reared with only juveniles (Fig. 2A). The pairwise comparisons indicated that the average age at maturity of males exposed to another male was significantly older than the average age of males exposed to juveniles, but that the average age of males exposed to females was not, despite the difference being comparable in magnitude (post hoc comparisons in Table S3A). Necessarily, males that matured later in order within a tank matured at an older age (Fig. 4A; post hoc comparisons in Table S4A). The magnitude of the effect was, however, substantial; the last males to mature in a tank were 47–51% older than the first males to mature. Neither sire size (Fig. 3A) nor any interactions between predictors had a significant effect on male maturation age (Table 1A).

To determine which factors affected male size at maturity, we first considered the effects of social environment, sire size, and maturation order, without including maturation age as a covariate (Table 1B,C). The results of these analyses were similar to those of age at maturity. In these analyses, males exposed to adults matured at a larger size than males exposed only to juveniles (Figs. 2C and S1A; post hoc comparisons in Table S3B,C). Males that matured later in order in a given tank matured considerably larger than their siblings that matured earlier (Figs. 4C and S3A; post hoc comparisons in Table S4B,C). However, in contrast to the convex relationship between maturation order and age at maturity, the relationship between maturation order and size at maturity was concave: males maturing first and second did not differ in age at maturation, but first maturing males were 19% smaller than those maturing second; males maturing last were 21% older, but the same size as those maturing immediately prior in order (i.e., fourth; Fig. 4C). Unlike the results for age at maturity, the size of a male's sire affected both length and wet mass at maturation (Table 1B,C; Figs. 3C and S2A). Males with intermediate-size sires were 11% longer and 31% heavier at maturity than those with small sires (Figs. 3C and S2A; post hoc comparisons in Table S5). Males with large sires did not differ in size from males

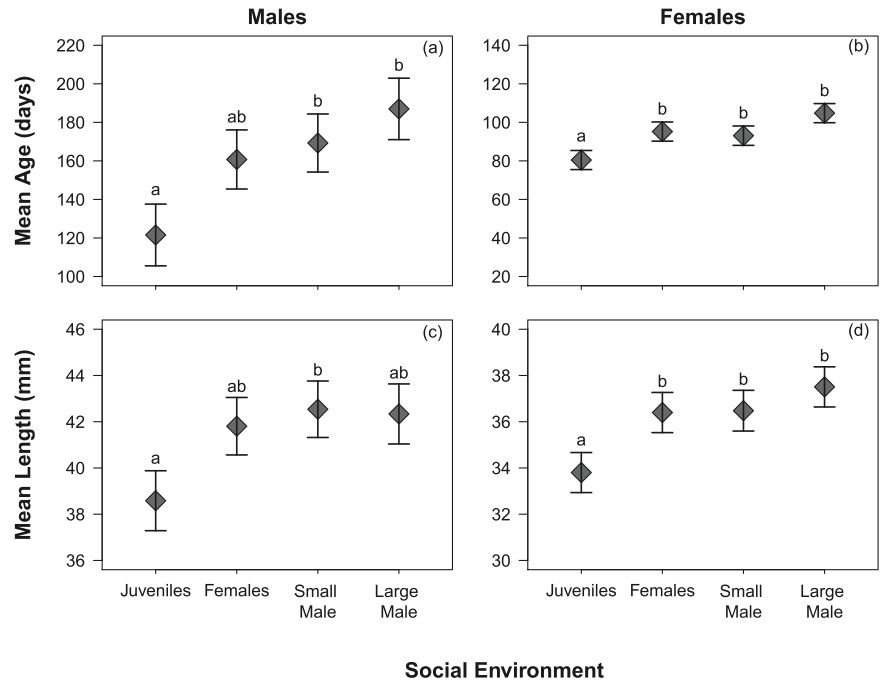

Figure 2. Age (A and B) and length (C and D) at maturity for males (A and C) or females (B and D) that experienced three juveniles (N_{males} = 50, $N_{females}$ = 61), three females (N_{males} = 42, $N_{females}$ = 62), a small male and two females (N_{males} = 48, $N_{females}$ = 55), or a large male and two females (N_{males} = 35, $N_{females}$ = 59) as their social environment during development. Points display least square means ± standard error. Length is uncorrected for age at maturity. Different letters denote significant post hoc differences between social environments (post hoc comparisons reported in Tables S3 and S9).

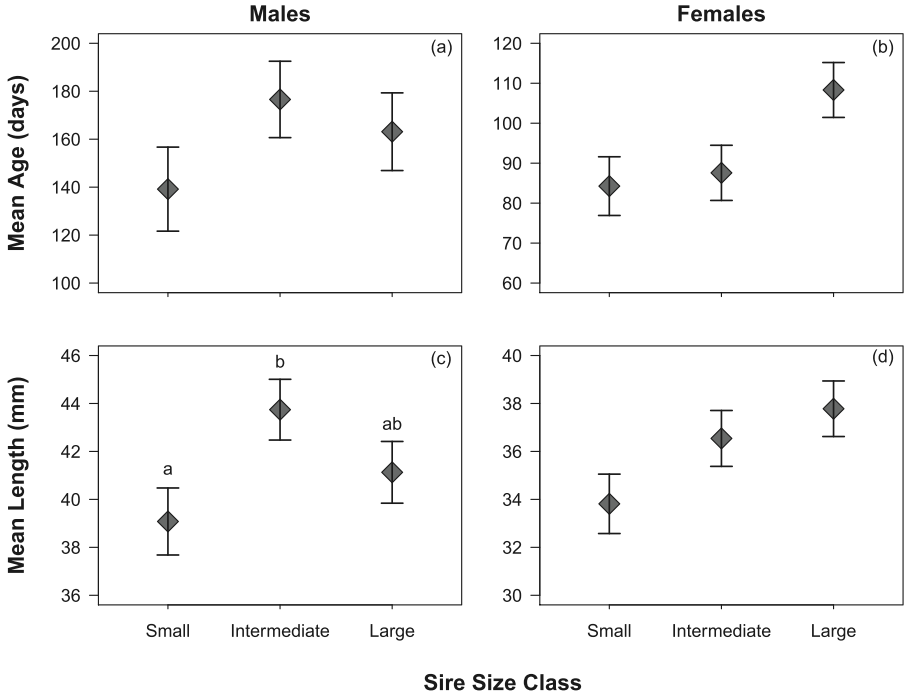

Figure 3. Age (A and B) and length (C and D) at maturity for males (A and C) or females (B and D) that had small (N_{males} = 53, $N_{females}$ = 73), intermediate (N_{males} = 64, $N_{females}$ = 77), or large (N_{males} = 58, $N_{females}$ = 87) fathers. Points display least square means ± standard error. Length is uncorrected for age at maturity. Different letters denote significant post hoc differences between sire size classes (post hoc comparisons reported in Tables S5 and S11).

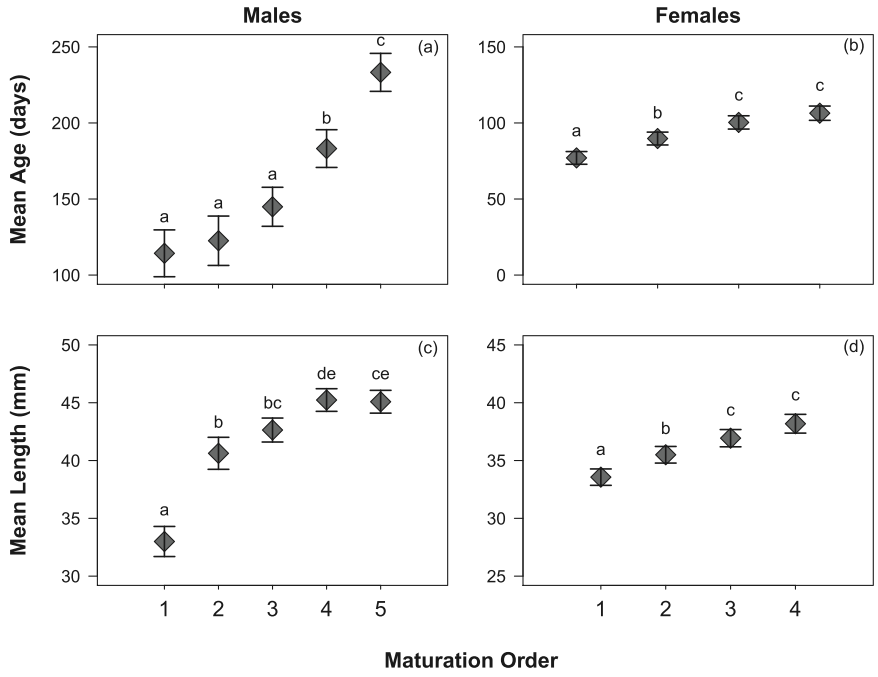

Figure 4. Age (A and B) and length (C and D) at maturity for males (A and C) or females (B and D) that were the first ($N_{males} = 16$, $N_{females} = 86$), second ($N_{males} = 14$, $N_{females} = 74$), third ($N_{males} = 40$, $N_{females} = 50$), fourth ($N_{males} = 50$, $N_{females} = 27$), or fifth ($N_{males} = 55$) individual to mature in their tank. Points display least square means ± standard error. Length is uncorrected for age at maturity. Different letters denote significant post hoc differences between maturation orders (post hoc comparisons reported in Tables S4 and S10).

with small or intermediate sires (Figs. 3C and S2A; post hoc comparisons in Table S5).

To test our hypotheses about growth, we also examined the effects of social environment, sire size, and maturation order on size at maturity using maturation age as a covariate. In these analyses, social environment had no effect on male size once its effect on age was taken into account (Table 1D,E). By contrast, sire size affected mass at maturity and tended to affect length at maturity, given age (Table 1D,E; Fig. S4A,C; post hoc comparisons in Table S6). The effect of sire size given age at maturation was similar to the effect of sire size without age as a covariate: males whose sires were intermediate in size matured larger, even given their age, than males with either small or large sires. However, males with fathers of different size classes did not differ significantly in length after adjustments for multiple comparisons (Fig. S4A,C; Table S6).

The relationship between maturation order and size at maturity, as demonstrated by analyses of size that included maturation age as a covariate, was especially revealing (Figs. 5A and S5A). In general, males that matured later in order in a given tank had a shallower relationship of size to age at maturity than those that matured earlier (Figs. 5A and S5A; post hoc comparisons in Tables S7 and S8) and there was a significant interaction between maturation order and age (Table 1D,E). This is consistent with a slower growth rate for males that matured later. For example, a 50-day delay in maturation in males that were the first to mature in their tanks increased their length by ∼14%; the same delay in males that were the last to mature in their tanks increased length by only ∼4% (Fig. 5A). Males that matured third in the tank also had a faster length growth rate than those that matured fourth or fifth (Fig. 5A; post hoc comparisons in Table S8A).

Maturation order had, by far, the strongest effect on all male life history traits (Table 2) except in models that included age as a covariate. The effect of social environment on age at maturity was slightly larger than that of sire size, whereas the reverse was true for size at maturity. The inclusion of age at maturity as a covariate for size at maturity showed that the effect of age on size overwhelmed all other effects in magnitude.

FEMALE LIFE HISTORY TRAITS

There were similarities and differences between the control of female life history traits and the control of male life history traits. As in males, female age at maturity was affected by social environment during development (Table 3A). Females that were reared in the presence of adults took 15–30% longer to reach sexual maturation than females that experienced only juveniles in their social environment (Fig. 2B; post hoc comparisons in Table S9A). However, the magnitude of delay was smaller in females compared to that of males (32–47%). Females that developed with a large male also tended to mature at 12% older ages than females reared with a small male, but this difference was not significant after correcting for multiple comparisons. Again,

Table 2. Cohen's f^2 local effect size estimates for male ($N = 175$) and female ($N = 237$) life history traits. Cohen's f^2 estimates reflect the amount of variation uniquely explained by each term in the model.

Phenotype	Effect	Male Cohen's f^2	Female Cohen's f^2
Age	Social environment	0.116	0.104
	Sire size	0.045	0.178
	Maturation order	0.310	0.126
Length	Social environment	0.086	0.069
	Sire size	0.115	0.164
	Maturation order	0.522	0.095
Mass	Social environment	0.151	0.052
	Sire size	0.188	0.125
	Maturation order	0.270	0.073
Length given age	Social environment	0.022	0.046
	Sire size	0.077	0.207
	Maturation order	0.616	0.016
	Maturation age	1.260	3.100
Mass given age	Social environment	0.039	0.097
	Sire size	0.088	0.224
	Maturation order	0.325	0.021
	Maturation age	0.992	3.256

Table 3. GLMM analysis of factors predicting female ($N = 237$) age (A), length (B), mass (C), length given age (D), and mass given age (E) at maturity. Significant effects are bolded.

Phenotype	Effect	DF_{Num}	DF_{Den}	F-value	P-value
(A) Female age	**Social environment**	3	63.9	9.41	**<0.0001**
	Sire size	2	19.8	3.50	0.050
	Maturation order	3	154	55.93	**<0.0001**
(B) Female length	**Social environment**	3	67.2	6.70	**0.001**
	Sire size	2	19.8	2.84	0.083
	Maturation order	3	157	37.59	**<0.0001**
(C) Female mass	**Social environment**	3	68	5.03	**0.003**
	Sire size	2	19.7	2.15	0.143
	Maturation order	3	158	27.39	**<0.0001**
(D) Female length	Social environment	3	63.6	0.37	0.774
Given age	**Sire size**	2	20	5.45	**0.013**
	Maturation order	3	182	1.82	0.144
	Maturation age	1	169	394.06	**<0.0001**
	Age* Order	3	176	9.61	**<0.0001**
	Age* Social environment	3	152	4.44	**0.005**
(E) Female mass	Social environment	3	62.3	0.64	0.594
Given age	**Sire size**	2	20.6	7.24	**0.004**
	Maturation order	3	186	0.53	0.660
	Maturation age	1	149	400.73	**<0.0001**
	Age* Order	3	182	2.24	0.085
	Age* Social environment	3	135	6.78	**0.0003**

by necessity, maturation order was associated with female age at maturity (Table 3A). The extent of the delay in females was smaller than that of males; the last females to mature in a tank were ∼28% older than those that matured first (compared to the 47–50% delay in males; Fig. 4B; post hoc comparisons in Table S10A).

In contrast to the results for males, the size of a female's sire tended to affect her age at maturity (Table 3A). Females with

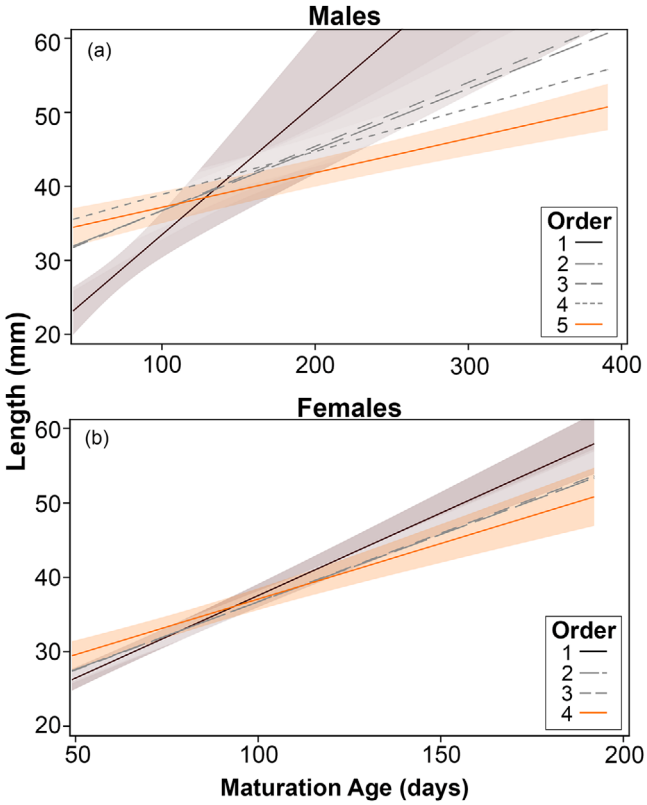

Figure 5. The predicted relationship (±95% CI) between age and length at maturity for males (A) or females (B) that matured in different orders. Colors and line types represent different maturation orders for males or females that were first (N_{males} = 16, $N_{females}$ = 86), second (N_{males} = 14, $N_{females}$ = 74), third (N_{males} = 40, $N_{females}$ = 50), fourth (N_{males} = 50, $N_{females}$ = 27), or fifth (N_{males} = 55) individual to mature (post hoc comparisons reported in Tables S7, S8, S15, and S16). The first and last maturing individual are highlighted in color for each sex.

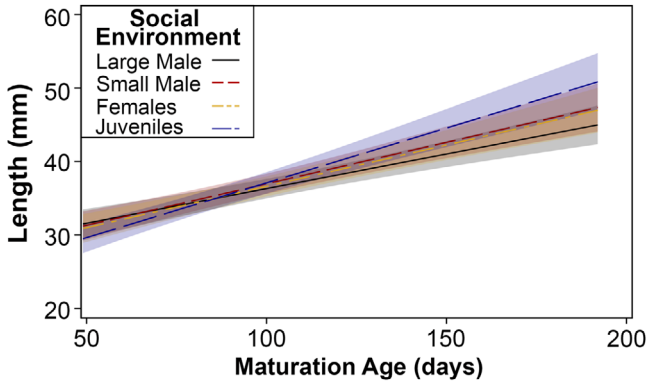

Figure 6. The predicted relationship (±95% CI) between age and length at maturity for females reared in different social environments. Colors represent different social environments (three juveniles: N = 61; three females: N = 62; a small male and two females: N = 55; or a large male and two females: N = 59) females experienced during development (post hoc comparisons reported in Tables S13 and S14).

large sires took 22% longer to mature than females with small sires, although this pairwise comparison was not significant after corrected for multiple comparisons (Fig. 3B; post hoc comparisons in Table S11). Females with large sires did not differ in age at maturity from females with intermediate sires, and those with intermediate sires did not differ in age at maturity from females with small sires.

The patterns of female size at maturity, without accounting for age, were different from those seen in male size at maturity with respect to effects of sire size, but similar with respect to effects of social environment. Females with large sires matured larger than those with small or intermediate sires, although, uncorrected for age, the effect was not statistically significant (Table 3B,C; Figs. 3D and S2B). Females reared with adults were 8–10% longer and 21–33% heavier than those reared with juveniles (Figs. 2D and S1B; post hoc comparisons in Table S9B,C); this change was similar in magnitude to the change in size among social environments in males. As expected, females that matured later in order were larger than females that matured earlier in order (Figs. 4D and S3B; post hoc comparisons in Table S10B,C); however, the magnitude of change in female size with order was much less than in males.

The effect of sire size class became statistically significant once age at maturity was taken into account (Table 3D,E). Females with intermediate sires were 6% longer and 16–22% heavier at maturity for a given maturation age than females with small or large sires (Fig. S4B,D; post hoc comparisons in Table S12). There was no difference in size at maturity given age between females with small and large sires. This suggests that females with sires of varying sizes differ in how age and size covary; daughters of large sires have delayed age at maturity (Fig. 3B), whereas females with intermediate sires have increased size given age at maturity (Fig. S4B,D).

Taking age into account revealed another difference between the sexes: unlike the case in males, the relationship between age at maturity and size at maturity in females was affected by social environment. This is evident in the significant interaction between age at maturity and social environment (Table 3D,E). Juveniles females reared with only juveniles grew more quickly (Figs. 6 and S6; post hoc comparisons in Tables S13 and S14), but reached a shorter total length (Fig. 2B) and tended to have lower mass (Fig. S1B) than those reared with adults. Females reared with a large male increased in mass more slowly when compared to females that were raised with adult females (Fig. S6; Table S14B). Female length, but not mass, was affected by an interaction between maturation age and order (Table 3D,E). Females that matured second and third did not differ from one another in

growth rates as measured by length, but females that matured in all other pairwise combinations differed in growth (Figs. 5B and S5B; post hoc comparisons in Tables S15 and S16).

The effect sizes of social environment, sire size, and maturation order in females showed that sire size had a larger effect than maturation order or social environment (Table 2). The differences in effect sizes were small for age at maturity but more pronounced in size at maturity. For size at maturity, effects of maturation order and social environment were comparable.

CONTRAST BETWEEN SEXES

The relative importance of social environment, sire size, and maturation order was substantially different between the sexes, as evidenced by the comparison of each effect size between the sexes (Table 2). Sire size class generally had larger effects on female than on male life history traits. By contrast, the order of maturation had much larger effects on male traits than female traits, and in males, largely overwhelming all other effects. The effect of the social environment on age at maturity was comparable in males and females but differed for size at maturity. For absolute size at maturity, whether measured as length or mass, the effect of the social environment was greater in males than females. Adjusting for age, the effect of the social environment on size at maturity was greater for females than for males. However, the effect of age of maturity on size at maturity, whether measured as length or mass, overwhelmed all other effects in both sexes. In that light, the effects on size, adjusted for age, will largely reflect those of age itself, for which maturation order was overwhelmingly important for males, whereas sire size was most important for size of females at maturity.

Discussion

We examined the effects of social environment on male and female life history traits, controlling for sire size class effects, to evaluate the contributions of these factors to individual variation in life history traits. We found that male and female life history traits were affected by social environment, specifically the distinction between exposure to adults during development and exposure only to other juveniles. Males and females responded similarly in direction to variation in social environment, but the effect was stronger in males for size at maturity than females. However, social environment affected growth rates of females, but not males. In contrast to the effects of social environment, the effects of sire size class were stronger in females than in males. Maturation order exerted a strong effect on males but a comparatively weaker one on females. Overall, our results indicate that social cues affect male and female life history phenotypes, but that males are far more sensitive to social cues than females.

SOCIAL ENVIRONMENT EFFECTS ON MALE AND FEMALE LIFE HISTORY ARE NOT CONSISTENT WITH PREDICTIONS FROM SEXUAL SELECTION THEORY

Social environment affected male and female age, length, and mass at maturity in similar directions. If mollies were responding to social environment to alter their life history phenotypes to match the competitive social environment they expected to experience in adulthood, we would expect males to delay maturation and females to mature earlier when there are cues of high-quality males or male-male competition for mates (Kasumovic and Brooks 2011). Alternative hypotheses suggest that males will express alternative mating phenotypes and mature at smaller sizes in the presence of male-male competition and/or that females might maximize reproduction by delaying maturation when males in the environment are of high-quality. Our data do not support these predictions. Both males and females tended to mature at later ages and larger sizes when reared in the presence of adults but did not differ in response to the size of adult males in the social environment. In contrast, males and females responded as expected under sexual selection theory in a related livebearing fish species (*Xiphophorus hellerii*); when reared in an environment with high-quality males, developing males increased their age at maturity and females decreased in both age and size at maturity (Walling et al. 2007). We varied mate quality between the large and small male social environments and expected that the large male social cue represented an environment with high-quality males, as females would perceive them, because larger males are highly preferred by females (Schlupp et al. 1994; Ptacek and Travis 1997; Gabor 1999; Witte and Noltemeier 2002; Witte and Ryan 2002; Gabor and Page 2003; MacLaren et al. 2004; MacLaren 2006). However, we found no significant differences in life history between individuals reared with large or small males. In fact, the trend for female life history patterns in response to differences in mate quality was opposite to that predicted by sexual selection theory: females delayed maturation when in the presence of preferred males. Delaying maturation in females may be beneficial as it results in increased size at maturation; fecundity increases rapidly with increases in female size (Travis et al. 1990) and large males preferentially court larger females (Ptacek and Travis 1997).

Future work should examine if there is a benefit to delaying maturation in females reared in different social environments. An alternative hypothesis is that females are responding to the presence of other females in their social environment and thus delaying maturation in response to perceived female-female competition. Future studies could examine sex ratio in tandem with mate quality to determine the effects of competition for mates versus mate quality on life history development. In addition, comparative studies of social effects on life history traits in poeciliid fishes would elucidate if the differences in responses to social

environment between the current study and Walling et al. (2007) are due to biological differences or experimental artifact.

Instead of responding to the juvenile social environment as a predictor of the competitive environment expected as adults, mollies may have adjusted their life history phenotypes based on perceived mortality rates (reviewed in Roff 1992; Stearns 1992; Charlesworth 1994). We found that when individuals were reared with juveniles, they matured early and at smaller sizes. Experiencing only juveniles in the social environment may be a cue of high adult mortality, and thus life history theory predicts that early maturation is favored. Conversely, when reared with adults, which could be a cue of low adult mortality, individuals delayed maturation and reached a larger size. This suggests that mollies are responding to differences in perceived mortality, rather than changes in mate competition environment. Therefore, life history theory may predict differences in age and size at maturity better than sexual selection theory.

The magnitude of the effects of social environment on size was greater in males than in females. One possible explanation is that male size at maturation is more plastic than female size at maturation due to sex-specific trade-offs between life history traits and sexually selected characters and therefore one might expect a greater response in males (Travis 1994a). In mollies, males have a demographic benefit to maturing early at small size, but because females prefer to mate with large males (Schlupp et al. 1994; Ptacek and Travis 1997; Gabor 1999; Witte and Noltemeier 2002; Witte and Ryan 2002; Gabor and Page 2003; MacLaren et al. 2004; MacLaren 2006), there is also a cost to this strategy. Male size is fixed at maturity, and thus, small males will never reap the sexual selection benefits of large size (Snelson 1984; Travis et al. 1989; Travis 1994a). In contrast, males that mature at larger sizes pay a cost of delayed reproduction, but likely have higher mating success once mature. Therefore, males may have been selected to have more social plasticity in age and size at maturation. Conversely, females continue to grow after they reach sexual maturation (Travis 1994a). Therefore, even though larger females are more fecund (Travis et al. 1990) and are preferred by large males (Ptacek and Travis 1997), given that they survive, all females will grow to a large size. Consequently, the benefits of social plasticity in age and size at maturation may be reduced in females. Alternately, our results could reflect nonadaptive processes. For example, plasticity in females might be a correlated response to selection for plasticity in males. Future work should measure the fitness benefits of the observed plastic responses in males and females to test these hypotheses.

We also saw changes in the relationships between age and size at maturity, resulting in reaction norms with different slopes. Social environment affected the relationship between age and size at maturity in females, but not in males. The effect of social environment in females suggests that female growth rates differed among the social treatments; however, this effect was small. In contrast to our predictions, females reared with males had slower growth rates and tended to mature at equal or larger sizes than those reared without males. These results again suggest that mollies are not responding to differences in the level of male-male competition and are instead responding to a cue that differentiates juvenile environments from adult ones.

Growth was also influenced by maturation order in both sexes. Males and females that matured first in their tanks were growing faster, but matured at smaller sizes, whereas individuals that matured later grew slower and matured at larger sizes. At first glance, these growth patterns may seem opposite to those predicted by life history theory, where individuals with faster growth are expected to mature at early ages and larger sizes and those with slower growth are expected to mature at later ages and smaller sizes (reviewed in Roff 1992; Stearns 1992). However, this same theory predicts that if the risk of mortality during the juvenile stage is low and the benefits to large size outweigh the costs, individuals with slow growth should delay maturation until they reach a larger size.

There is evidence that large size is favored in sailfin mollies. In both males and females, larger size may be favored via sexual selection; large males are preferred by females (Schlupp et al. 1994; Ptacek and Travis 1997; Gabor 1999; Witte and Noltemeier 2002; Witte and Ryan 2002; Gabor and Page 2003; MacLaren et al. 2004; MacLaren 2006), and large females are both more fecund (Travis et al. 1990) and preferred by large males (Ptacek and Travis 1997). Large individuals of both sexes are more likely to survive severe winters (Trexler et al. 1992), but they do pay a fitness cost as they are more likely to be preyed upon by birds in some environments (Trexler et al. 1994). Therefore, although increased size is linked to increased reproductive success and winter survival, it is not clear if the benefits of large size outweigh the cost of delayed maturation in environments where bird predation is high. Future studies should examine the fitness of individuals with different age-size relationships to determine if the delay in maturation for slow-growing individuals represents an adaptive shift.

One potential caveat is that we did not mark individual fish, so we were unable to track individual grow rates through time. An alternative explanation for the positive relationship between age and size at maturity is that the fish are all growing at the same rate, but some social cue causes differences in the threshold for initiating maturation. Such a threshold for maturation timing could create the positive relationships between age and size at maturation observed in mollies of both sexes and explain the strong effect of maturation order on male size at maturity. Marking interacting juveniles to measure each individual's growth trajectory would provide more precise data to understand if mollies

adhere to this classic life history prediction, or if they represent an interesting outlier.

Previous studies in poeciliid fishes have examined how juvenile-juvenile interactions affect male life history traits (Borowsky 1973; Sohn 1977a,b; Borowsky 1978, 1987). These so-called "leap fish" studies generally show that the first male to mature in the tank is the largest juvenile and subsequent maturing males delay maturation until they are larger than previous males that matured. Borowsky (1987) suggested that this pattern was the result of antagonistic interactions between juveniles as increased aggressive bites resulted in increased time to maturation for fish that did not mature first. However, a previous study on mollies did not find this same delay in maturation for fish reared in pairs and reported low levels of aggression (Farr and Travis 1989). In the current study, the order in which an individual matured in the tank had the largest effect on all male life history traits, but weak effects on female phenotypes. Our results suggest that interactions with other juveniles outweighed males' experiences of the adult social environment. Future studies should consider how juvenile-juvenile interactions may affect male and female life history traits differently.

SIRE SIZE CLASS EFFECTS ON AGE AND SIZE AT MATURITY

Sire size class affected both male and female life history traits. For females, sire size affected both age and size given age, suggesting that there are heritable factors affecting female life history traits. Such factors clearly cannot be Y-linked. Previous studies on female mollies have not reported an effect of sire size class on life history traits, but have reported family-level effects, suggesting that these traits are heritable (Trexler and Travis 1990). However, this previous work suggested that environmental treatments were more important in determining female life history traits than family-level variation. Here, we find the opposite pattern. Sire size class accounted for more variation, and had a larger effect size, than social environment for all female traits that were measured. Females with large sires tended to mature later than females with intermediate or small sires. However, females from intermediate sires were the largest in size given age at maturity. This indicates that there may be a significant heritable component to female age and size at maturity in some environments.

For males, size, but not age, at maturity was affected by the sire size class. However, the direction of these effects was surprising, based on previous work in mollies (Travis 1994a,b) and related species (Kallman et al. 1973; Schreibman and Kallman 1977; Kallman and Borkoski 1978; Bao and Kallman 1982; McKenzie et al. 1983; Kallman 1989; Zimmerer and Kallman 1989; Lampert et al. 2010) that showed a strong, Y-linked component to male size at maturity. A heritable component to male age and size at maturity was also reported for sailfin mollies reared under different abiotic conditions (Trexler and Travis 1990; Trexler et al. 1990). As predicted from previous empirical work, we found that males with intermediate-size sires were longer at maturity than males from small sires. However, males from large sires did not differ in size from males with small or intermediate sires. This suggests that the heritability of male size, especially the strength of Y-linked effects, could be altered when males experience different social environments during ontogeny. Our results could also mean that males used as sires in this experiment may have been less uniform in size genotypes than expected. If social environments, whether through juvenile-juvenile interactions or responses to adult-juvenile ratios, have stronger effects on determining the length of the juvenile period than Y-linked genotypes, then the size of a wild-caught male may not reflect the size of his sire.

Our social environment results show that life history differences were driven by variation in being in the presence of adults or juveniles during the juvenile period. Given that all sires were collected in the fall, and overwinter mortality of juveniles is high (Trexler et al. 1992), it is likely that all sires were born that year and spent the summer as growing juveniles. The most drastic seasonal variation we see in social environment is of the size of adult males in the populations, which did not affect life history traits in this study. Therefore, it is unlikely that differences in sire size in our source population are due to differences in seasonal social environments in the population. However, we did not see the expected strong effects of sire size class on male life history traits. Therefore, our sire size class factor is likely confounded with environmental history, age, and potentially genotype.

We did not find any sire size class by social environment interactions on male or female life history traits. This suggests that social environment does not generate interactions that could maintain adaptive variation in molly life histories. Instead, we found independent effects of social environment and sire size class on life histories. However, our statistical power to detect interactions was low because of our relatively small number of sires. If there are differences in sensitivity to social environment among families, this would further complicate the issue of identifying genotypes from phenotypes.

Social environment may be a powerful influence on the development of traits in both males and females that warrants further attention. Furthermore, by assessing both male and female traits together, we found that males and females may respond to social environment in similar directions, but differing magnitudes. However, the differences we observed in life history phenotypes did not match the predictions of sexual selection theory. Social environment may be a powerful modulator of phenotypes even in species with a genetic basis to alternative life history phenotypes, but these differences appear to be better explained by perceived mortality cues as predicted by life history

theory, not by differences in perceived sexual selection mating environments.

AUTHOR CONTRIBUTIONS

ECL collected life history measures, analyzed the data, and wrote the first draft of the manuscript. All authors contributed to the design of the experiment and provided comments on the manuscript.

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DATA ARCHIVING

All data used in this study are archived on Dryad (https://doi.org/10.5061/dryad.2rbnzs7ms).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Covariance estimates for random effects of male life history phenotypes.
Table S2. Covariance estimates for random effects of female life history phenotypes.
Table S3. Results from post hoc comparisons of social environments for male age (A), length (B), and mass (C) at maturity.
Table S4. Results from post hoc comparisons of maturation order for male age (A), length (B), and mass (C) at maturity.
Table S5. Results from post hoc comparisons of father size effects for male length (A) and mass (B) at maturity.
Table S6. Results from post hoc comparisons of father size effects for male length (A) and mass (B) at maturity in models where age was a covariate.
Table S7. Slopes for relationship between (A) male age and length at maturity, and (B) male age and mass at maturity for males that matured in different orders.
Table S8. Differences in growth rates for male length (A) and mass (B) between maturation orders.
Table S9. Results from post hoc comparisons of social environments for female age (A), length (B), and mass (C) at maturity.
Table S10. Results from post hoc comparisons of maturation order for female age (A), length (B), and mass (C) at maturity.
Table S11. Results from post hoc comparisons of father size effects for female age at maturity.
Table S12. Results from post hoc comparisons of father size effects for female length (A) and mass (B) at maturity in models where age was a covariate.
Table S13. Slopes for the relationship between female age and length at maturity (A) and female age and mass at maturity (B) for females reared in different social environments.
Table S14. Differences in growth rates for female length (A) and mass (B) between social environments.
Table S15. Slopes for relationship between female age and length at maturity for females that matured in different orders.
Table S16. Differences in growth rates for female length between maturation orders.
Figure S1. Mass at maturity for males (A) or females (B) that were exposed to three juveniles (N_{males}=50, $N_{females}$=61), three adult females (N_{males} = 42, $N_{females}$ = 62), a small adult male and two adult females (N_{males} = 48, $N_{females}$ = 54), or a large adult male and two adult females (N_{males} = 35, $N_{females}$ = 59) as their social environment during development.
Figure S2. Mass at maturity for males (A) or females (B) that were offspring of small (N_{males} = 53, $N_{females}$ = 73), intermediate (N_{males} = 64, $N_{females}$ = 77), or large (N_{males} = 58, $N_{females}$ = 86) sires.
Figure S3. Mass at maturity for males (A) or females (B) that were the 1st (N_{males} = 16, $N_{females}$ = 85), 2nd (N_{males} = 14, $N_{females}$ = 74), 3rd (N_{males} = 40, $N_{females}$ = 50), 4th (N_{males} = 50, $N_{females}$ = 27), or 5th (N_{males} = 55) individual to mature in their tank.
Figure S4. Length (A), and mass (B) at maturity given age at maturity for males (a, c) or females (b, d) that had small (N_{males} = 53, $N_{females}$ = 73), intermediate (N_{males} = 64, $N_{females}$ = 77), or large (N_{males} = 58, $N_{females}$ = 87) fathers.
Figure S5. The predicted relationship (±95% CI) between age and mass at maturity for males (A) or females (B) that matured in different orders.
Figure S6. The predicted relationship (±95% CI) between age and mass at maturity for females reared in different social environments.