The direct costs of living in a sexually harassing environment

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Sexual conflict can lead to individuals evolving behaviours to circumvent preferences of the opposite sex. For example, females have been shown to adjust their behaviours depending on the risk of sexual harassment. In the present study we investigated the effects of sexual harassment in sailfin mollies, Poecilia latipinna, on both females and males depending on the level of male presence to which they were exposed. We exposed females to four levels of male presence (which we assumed to be correlated with intensity of sexual harassment): (1) no harassment (four females); (2) low male presence (one male with three females); (3) moderate male presence (two males with two females); and (4) high male presence (three males with one female). We measured sexual harassment as male sexual behaviours received by the females. The cost of sexual harassment on both males and females was measured as the overall change in body condition after being exposed to a particular treatment. There were three major results. (1) Sexual harassment caused a decrease in male body condition; this is one of the first studies to examine the cost of sexual harassment for males. (2) There are direct negative effects of sexual harassment on female fitness. (3) Male sexual behaviours are not additive, suggesting that there is some nonlinear relationship between the number of males in a population and the degree of harassment females are subjected to. We demonstrate that the social environment can have a direct effect on the body condition of the individuals within that particular environment.

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CONSEQUENCES OF SEXUAL HARASSMENT FOR FEMALES: THE FEMALE PERSPECTIVE

Sexual harassment occurs when males are attempting to coerce females into mating more often than is optimal for the female. For females this can be associated with costs, such as genital damage, increased predator exposure and energy expenditure, and/or a reduction in feeding time and life span (Chilvers et al. 2005; Eady et al. 2007; Ojanguren & Magurran 2007; Kimber et al. 2009; Magurran & Nowak 1991; Rowe et al. 1994). For instance, in Xiphophorus sp. (a group of livebearing fishes), genital bleeding has been documented due to excessive exposure to the male’s gonopodium, a copulatory organ that includes a claw, a hook and several serrae (Clark et al. 1954). Furthermore, poeciliid females often flee from sexually harassing males, causing a reduction in feeding time (Plath et al. 2007; Magurran 2011). Sexual harassment influences an individual’s behaviour within their social environment; females have been shown to adjust their foraging strategies, social structure and group preferences when males are present (Darden et al. 2009; Tobler et al. 2011). For instance, in Anthophora plumipes bees, females alter their foraging preferences when males are present, resulting in reduced foraging efficiency (Stone 1995). Female eastern mosquitoﬁsh, Gambusia holbrooki, prefer larger shoals that contain larger females when
males are present, although this preference disappears when males are removed from the environment (Agrillo et al. 2006). This plasticity in female shoaling preferences can be explained via the dilution effect because larger groups reduce female exposure to sexual harassment (Cappozzo et al. 2008).

Although there are plenty of studies investigating the cost incurred by females due to sexual harassment (i.e. Heubel & Plath 2008; Gerber et al. 2010; Rossi et al. 2010; Tobler et al. 2011; see above), little is known about how the social environment may influence the immediate condition of the individuals within that environment (Smith 2007). Most studies investigate indirect costs on female fitness, but few have looked at the direct, physiological cost for the female (although see Köhler et al. 2011; Córdoba-Aguilar 2009). Female condition may directly correlate with the amount of resources that females can invest into reproduction (Shears 1992); for instance, how many offspring she produces, or the quality of those offspring (Boness et al. 1995; Gay et al. 2009; García-Gonzalez & Simmons 2010). In bruchid beetles (Callosobruchus maculatus), male sexual harassment has been linked to a reduction in the number of eggs laid and in female lifetime productivity; however, it is uncertain whether these results are due to sexual harassment or the cost of mating (Gay et al. 2009). Also, in grey shads (Malusorinus grapsus), females that were sexually harassed produced fewer pups later in the season, suffered from reduced lactation and had slower-growing pups (Boness et al. 1995). In guppies, Poecilia reticulata, sexual harassment results in daughters with smaller bodies and less attractive sons with shorter gonopodia (Gasparini et al. 2012), suggesting that the social environment may directly influence the female’s reproductive output in some poeciliids.

MALE CONSEQUENCES OF PERFORMING HARASSMENT: THE MALE PERSPECTIVE

Males have evolved highly diverse mating strategies to maximize their fitness (Arnqvist & Rowe 2005). Males of some species only exhibit one type of mating behaviour while males of other species show multiple, alternative strategies, often via genetic polymorphisms (Ryan et al. 1992; Hurtado-Gonzales & Uy 2010). These alternative mating behaviours can arise at different points in the male’s development. For instance, in sunfish, Lepomis macrochirus, males start out as female mimics, then, when they have grown large enough to defend their own territories, they become nesting males (Dominey 1980). In other species, a single male can switch from one tactic to another depending on environmental and social cues (Taborsky & Brockmann 2010).

One example of an alternative strategy is sexual harassment, which may be influenced by male–male competition in two ways (Magurran 2011). In Poecilia reticulata, when tested to see how they altered their coercive behaviours in response to an increase in competition, individual males actually decreased their harassment behaviours towards the female (Head & Brooks 2006). However, despite this decrease in harassment behaviours, the overall harassment towards females increased due to the increased number of males present (Head & Brooks 2006). Alternatively, males could increase their sexual behaviours and/or even switch behaviours depending on the level of competition (Evans & Magurran 1999; Evans et al. 2003; Magelllan et al. 2005). Although there is evidence to support both mechanisms, the results appear to vary across species. In fact, studies of sexual harassment from the male perspective have always examined either the form of competition with other males or how vigorous the behaviours are. There are very few, if any, studies addressing the physiological costs of harassing on the males themselves.

In the sailfin molly, Poecilia latipinna, males use two mating strategies; they either court or harass females to gain matings (Constantz 1984). Courtship involves a male swimming in front of the female and displaying his dorsal fin, and the female responds by swimming away or allowing the male to copulate. In sexual harassment, however, males swim up to the female and force copulations. These forced copulations may be less successful for two reasons. First, when males force copulations there is a reduction in the time allowed to transfer sperm; courting males have a longer copulation period, which allows them to transfer more sperm, leading to an increased number of fertilized embryos (Magurran 2011). For instance, in guppies, copulations that follow courtship have longer durations compared with coercive copulations, suggesting females have an influence on copulation duration depending on the attractiveness of the male (Pilastro et al. 2007). Second, forced copulations may cause increased genital damage to the females, causing bleeding and/or scarring (Clark et al. 1954; Langerhans 2011; R. Deaton, unpublished data). Furthermore, males are able to switch between courting and harassing depending on their relative body size compared to the other males in the vicinity (Farr et al. 1986; Travis & Woodward 1988; Makowicz et al. 2010), making this a very dynamic social environment in which to study sexual harassment.

Moreover, little is known about how sexual harassment affects both the female and male simultaneously. The majority of research examining the fitness cost of sexual harassment has only focused on the female (Magurran 2011). There have been few studies to date that have looked at the cost of sexual harassing on the male fitness (i.e. what is the cost for males to increase sexual harassment behaviours under increased sexual competition). To fully understand sexual harassment from an evolutionary perspective, studies are required to include this overlooked variable to get the entire representation of the social environment. To address this, we used a unified approach to examine the cost of male presence (from a female perspective), and the cost of harassing and male–male competition (from a male perspective).

Here, we investigated how sexual harassment influences body condition of female and male Poecilia latipinna when exposed to different social environments. We exposed females to either (1) a treatment with no males present (4:0, females:males, or no male harassment), (2) low male presence (3:1), (3) moderate male presence (2:2) or (4) high male presence (1:3). We measured the direct effects that these environments had on individuals using life-history methods. One prediction of this experiment is that, as the number of males increases in an environment, so will the potential for females to be harassed. To evaluate this, we measured the amount of sexual behaviours a female received when exposed to the different levels of male presence.

If there is an additive effect of the number of males present (i.e. if the number of males correlates with the amount of harassment females receive), we predicted that females in the presence of two or three males would receive double or triple the number of sexual behaviours. We further predicted that there would be a decrease in body condition in both females and males if sexual harassment of females and male competition levels increase, respectively.

METHODS

Study Population

Poecilia latipinna is a small-bodied live-bearer that inhabits backwaters, streams, brooks, small rivers and ponds across the southern Atlantic coast of the United States of America. Study specimens were collected at Comal Springs (29°42’46.86” N, 98°08’8.57” W) in New Braunfels, Texas in 2009, and transported back to Norman, Oklahoma, U.S.A. The transport was conducted in aerated and filtered water in transport coolers to minimize stress.
Fish were separated by sex and maintained in 113.6-litre tanks for 3 months prior to the start of the experiment. This time lapse allowed females that were carrying broods at the time of collection or that retained sperm to give birth without receiving fresh sperm from males (Constantz 1984). Tanks were maintained at 25 ± 2 °C and fish were fed commercial fish flakes ad libitum daily.

**Experimental Design**

Aquarium tanks (37.9 litres), with a filter system and natural gravel on the bottom, were used (N = 10 for each of the four treatments). Each individual was weighed (g) and measured (standard length, mm) and then placed into a random tank. To be able to identify individual fish in each tank, standard length was used to include a large, medium and small individual (all size classes had a difference of ±4–8 mm between each individual) in the set-ups with multiple individuals of each sex. Fish were fed once daily ad libitum with commercial fish flakes and had a weekly 30% water change. Each trial lasted for 24 days and took place during May–September 2009. Trials were staggered in a block design, where each block contained one replicate for each of the four treatments (N = 10 tanks) throughout the testing period. A total of 100 females and 60 males were used in this study.

**Behavioral Observations**

We recorded the sexual behaviours (nips, copulations, courtship displays, and time spent interacting with females; Niemeitz et al. 2002) that each female received. Behavioural recordings were taken daily for 5 min in front of each tank, including the all-female treatment to control for the presence of the observer. The behavioural observations were conducted for 24 days, for a total of 24 behavioural recordings for each tank.

**Life-history Data**

To determine the effects of sexual harassment on body condition, individuals were sacrificed with an overdose of MS222 and preserved in 10% formalin after the last behavioural observations on the final day. Body condition was measured by determining the soluble fat content via ether extractions using the life-history protocol of Reznick & Endler (1982) and Riesch et al. (2010). Specifically, we dissected the reproductive tissue from each individual to determine the reproductive state of the males and females, and then dried both the nonreproductive and the reproductive tissue (including embryos, if applicable) for 10–12 days at 45 °C. Afterwards, all somatic and the combined reproductive and embryonic tissue was reweighed and placed into petroleum ether for a minimum of 6 h. The ether bath was repeated until the solution was clear, indicating the extraction of all nonstructural fats. Once a clear bath was reached, all tissues were dried again and reweighed. This method allowed us to measure the somatic weight, reproductive weight, percentage of fat (used to indicate body condition), reproductive allocation, gonad somatic index (GSI) and fecundity level of females (number of offspring).

**Statistical Analysis**

**Life history**

We determined treatment effects on the gravidity of females using a chi-square test, comparing pregnant and nonpregnant females across all four treatments. All females in the harassment treatments were expected to be pregnant, while the females in the control treatment were expected to have a zero or low pregnancy rate because they had been isolated from males for 3 months prior to the trials. Note, however, that poeciliids can store sperm longer than 3 months (Constantz 1984), so some pregnancies were possible. Life-history traits (lean somatic tissue weight, lean reproductive tissue weight, reproductive allocation and percentage of fat content) were analysed with a multivariate GLM using block as a random factor. Body size measurements (standard length, mm; weight, g) used in the statistical analyses came from the preserved individuals. All variables were controlled for body size, then log and z-transformed (somatic and reproductive tissue) or arcsine-square-root and z-transformed (fat content and reproductive allocation) prior to the GLM. To verify the effects of the treatments, we ran an additional discriminant function analysis (DFA) using treatment as the grouping variable and somatic tissue weight, fat condition and reproductive allocation/GSI as the predicting variables. To control for the dependence of individuals within each tank (hence to avoid pseudoreplication) in life-history traits, we used the largest females and males from each tank to compare across the four different treatments. Note, however, that using another size class of females did not lead to qualitatively different results (see Supplementary Material).

**Behaviours**

We analysed a total of 120 min of behavioural recording for each tank. Because sexual behaviours were autocorrelated, we conducted a principal component analysis (PCA) on the averages of nips, copulations and displays for each tank; using only principal component 1 for further analyses (see Results). A multivariate general linear model (GLM) was used to analyse the overall treatment effect on male behaviours (PC1 and time) using female standard length as a covariate, and month and block as random factors. To investigate how each sexual behaviour varied across the treatments, we used a GLM with standard length as a covariate and PC1 and time as dependent variables. We conducted an additional GLM, similar to the previous one; however, we used data corrected for the number of males present to determine how (on average) each male adjusted his behaviour in the presence of other males.

All statistical analyses were conducted with SPSS v.17.0.0 (SPSS Inc., Chicago, IL, U.S.A.) and InStat v.3.0b (GraphPad Software Inc., San Diego, CA, U.S.A.).

**RESULTS**

**Male—Female Interactions: Does Sexual Harassment Increase with the Number of Males?**

Regression analysis of sexual behaviours (nips, copulations and displays) revealed that all combinations of behaviours were positively correlated with one another (correlations and nips: \( R^2 = 0.609, \ P < 0.001 \); nips and displays: \( R^2 = 0.311, \ P < 0.001 \); copulations and displays: \( R^2 = 0.125, \ P = 0.006 \)); hence we conducted a PCA to resolve this. PC1 explained most of the variation in the behaviours (nips, 94.4%; copulations, 88.6%; displays, 70.0%) and thus was used for subsequent analyses. The treatment (‘sexual harassment environment’) influenced the overall combination of sexual behaviours and time spent interacting with the female (PC1: \( F_2 = 9.53, \ P < 0.001 \); time: \( F_2 = 8.895, \ P < 0.001 \)). Standard length did not affect male behaviours (PC1 and time); therefore, these variables were removed from the model (PC1: \( F_2 = 1.382, \ P = 0.245 \)).

There was a significant increase in the amount of male courtship displays that females received among the treatments (\( F_2 = 19.185, \ P = 0.0001 \); controlling for the number of males: \( F_2 = 10.123, \ P = 0.0001 \), while the number of copulation attempts and nips

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received did not differ between treatments (female perspective: copulations: $F_2 = 2.647, P = 0.092$; nips: $F_2 = 2.491, P = 0.08$; Fig. 1; male perspective: copulations: $F_2 = 0.733, P = 0.485$; nips: $F_2 = 0.803, P = 0.453$; Fig. 2). Standard lengths of the females were positively correlated with the number of copulation attempts and nips that females received (copulations received by females: $F_2 = 5.391, P = 0.024$; copulations attempted by males: $F_2 = 6.303, P = 0.019$; nips: $F_2 = 4.421, P = 0.04$). In addition, the time that males spent interacting with the females was reduced in the moderate treatment, most likely because the two males interacted with each other (Fig. 3).

Consequences of Sexual Harassment for Females: the Female Perspective

There was a significant negative influence of number of males present on female life-history traits (somatic lean tissue: $F_3 = 44.106, P < 0.0001$; reproductive lean tissue: $F_3 = 53.168, P < 0.0001$; fat content: $F_3 = 5.158, P = 0.004$; reproductive allocation: $F_3 = 27.312, P < 0.0001$). In addition, there was a negative relationship between standard length and body fat when individuals were exposed to both the low and high harassment environment (low: $R^2 = 0.07, P = 0.46$; high: $R^2 = 0.129, P = 0.3$; Fig. 4). This relationship was absent in the moderate treatment ($R^2 = 0.023, P = 0.95$). Tukey post hoc tests revealed that reproductive allocation in the no harassment and low harassment environments were significantly lower than in the moderate and high harassment environments ($P < 0.0001$). Furthermore, females in the no harassment treatment had higher body fat content than females in the high harassment treatment ($P = 0.002$; Fig. 4).

The DFA correctly classified 92.5% of the females to treatment (Fig. 5). The variables with the most discriminatory abilities were somatic tissue content (Wilk’s $\lambda$: 0.03, $F_3 = 28.063, P < 0.001$) and reproductive allocation (Wilk’s $\lambda$: 0.383, $F_2 = 19.324, P < 0.001$). There was little variation in standard length and weight between treatments (Table 1). Together, these results suggest that the social environments to which females were exposed greatly influenced their fitness.

Females in the no harassment treatment had a significantly higher rate of pregnancies ($\chi^2 = 22.507, N = 40, P < 0.0001$; Table 2). Only females from the large body-size cohort showed pregnancies; no other females became pregnant during the experiment. This is interesting because the females in the no harassment treatment must have used sperm stored throughout the isolation period. Against our intuition, females that had access to males, showed a much lower rate of pregnancies. In addition, there was no clear pattern in the embryo stages among the four treatments (no harassment, embryo stage (quantity of embryos): 2 (4), 10 (1), 25 (1), 40 (1); low harassment: 2 (1), 10 (1); moderate harassment: 2 (1); high harassment: 2 (1), 35 (1)). Only the no harassment and low harassment treatments had regressing eggs (eggs that are aborted and reabsorbed by the female; Marsh-Matthews 2011; Pires et al. 2011): five females in the no harassment environment (total of 18 regressors) and one female in low harassment environment (total of 5 regressors). Given the low numbers of reproducing females, we were unable to extend this study to the quality and condition of the developing embryos.

**Figure 1.** Mean ± SD sexual behaviours (nipping: low = 3.14 ± 3.01; medium = 4.19 ± 3.12; high = 6.73 ± 5.98; copulations: low = 0.59 ± 0.84; medium = 0.61 ± 0.96; high = 1.68 ± 2.10; displays: low = 0.10 ± 0.12; medium = 0.50 ± 0.62; high = 1.94 ± 1.75) that female sailfin mollies received per day in the three treatments (female:male ratios): 3:1 (■), 2:2 (■) and 1:3 (●), and the expected values for each treatment (○).

**Figure 2.** Mean ± SD sexual behaviours (nipping: low = 3.14 ± 3.01; medium = 2.10 ± 1.56; high = 2.24 ± 1.99; copulations: low = 0.59 ± 0.84; medium = 0.48 ± 0.25; high = 0.70 ± 0.64; displays: low = 0.10 ± 0.12; medium = 0.25 ± 0.31; high = 0.65 ± 0.58) that female sailfin mollies received per day, corrected for the female:male ratio in each treatment: 3:1 (■), 2:2 (■) and 1:3 (●), and the expected values for each treatment (○).

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DISCUSSION

In the present study we investigated the costs of sexual harassment to both females and males depending on the level of harassment/competition environment to which they were exposed. There were three major results. (1) There was a direct effect of sexual harassment on female fitness. (2) Sexual harassing causes a decrease in male body condition. (3) Male sexual behaviours are not additive, suggesting that there is some nonlinear relationship between the number of males in a population and the amount of harassment females are subjected to.

Male—Female Interactions

We found that the sexual harassment environments influenced the frequency of males’ sexual behaviours towards females. On average, females received more sexual behaviours in the presence of two or more males (moderate and high harassment environments). We predicted a linear relationship when females were exposed to two males and to three males; this was only true in the high harassment treatment from the female perspective for all sexual activities and in the moderate and high harassment treatments from the male perspective in copulations and courtship displays. Therefore, our results indicate a nonlinear relationship in the amount of male sexual harassment towards females when females were exposed to different levels of sexual harassment environments.

So why did the two male treatment not have this two-fold increase? It is possible that the split attention hypothesis may explain this (also known as selective attention hypothesis; Driver 2001; Dubios et al. 2008). This hypothesis predicts that an individual’s attention can be focused simultaneously on multiple stimuli rather than on just one stimulus at a time (Dubios et al. 2008). Males were as likely to interact with other males as they were with the female(s) (A. M. Makowicz, personal observations). In the moderate harassment treatment (2:2), one male would chase the second male away from one female, then proceed to interact with that female, or vice versa, when the second male advanced towards the second female. A similar behavioural sequence occurred in the high harassment treatment; however, while two males would be engaging, this left an opportunity for the third male to mate with the female. Although these are just some of the many interactions we observed, future work is needed to understand how multiple males interact with each other in a female limited, socially dynamic environment.

Males, on average, increased copulation attempts when there were larger females present from both the female and male perspective. Males also increased the number of nips at the gonopore but only for the male perspective. The number of courtship displays increased as the level of male competition increased. We hypothesize that males, when in direct competition with several other males, will increase courtship when they are among the largest of the males and reduce their courtship displays when they are among the smallest of the males. Male P. latipinni have been shown to adjust their sexual behaviours when in the presence of another male (Makowicz et al. 2010), although this alteration in male behaviour was only in response to a single male audience. In some
species of poeciliids, persistent courting behaviours may be viewed as an additional form of harassment. However, this is not the case in *P. latipinna*, and excessive courtship is extremely rare in this species. In addition, in this species, male mating behaviours are continuous (Travis & Woodward 1989; Travis 1994; Schlupp et al. 2001), and it is likely that males are able to alter their sexual behaviours depending on the social environment on a temporal and spatial level.

**Consequences of Sexual Harassment for Females: the Female Perspective**

The direct costs for females included a dramatic increase in the level of sexual behaviours they received and a decrease in overall body condition when exposed to a harassing environment, and even more so when that environment was a high harassment environment with multiple males. Females that were exposed to males were more likely to have a lower somatic lean weight, reproductive lean weight, fat content and reproductive allocation than no harassment controls. Other studies suggest that male sexual harassment decreases the amount of resources a female can accrue over time (Plath et al. 2007; Kimber et al. 2009; Makowicz et al. 2010), which may explain the decline in fat content with increasing harassment level in our study. For instance, *P. latipinna* females reduce feeding time when allowed to interact with males (Schlupp et al. 2001) and when exposed only to the visual presence of a male (Plath et al. 2007). It is possible then to associate, within a single species, the results of these previous studies and the results found here in female life-history traits; sexual harassment leads to a decrease in feeding time, which may influence the fat content of females. It would be worth investigating how the visual presence of males alone influences female body condition, although one would predict that habituation would occur, implying that the effects found in Plath et al. (2007) may only be temporary but not very critical to the females’ body condition (Köhler et al. 2011; Tobler et al. 2011). Furthermore, energy expenditure may also affect female body condition such that the energy lost due to fleeing harassing males and the increased energetic cost of finding additional food resources (Amano & Hayashi 1998; Gerber et al. 2010) may lead to reduced body condition. Both factors may be important in explaining weights and fat content throughout the different treatments.

The reproductive output of females across all four treatments was significantly reduced when compared with the no harassment controls. The females that produced the most offspring were females that did not have contact with males. These results suggest that male harassment can actually severely hamper female fitness. Pregnancies in the absence of males must have been the result of stored sperm; corroborating that *P. latipinna* females

**Table 1**

Descriptive statistics for standard length and body weight in female (*N* = 100) and male (*N* = 60) sailfin mollies

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Female</th>
<th>Male</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standard length (mm)</td>
<td>Weight (g)</td>
</tr>
<tr>
<td>No harassment</td>
<td>47.85 ± 5.77</td>
<td>2.69 ± 0.81</td>
</tr>
<tr>
<td>Low harassment</td>
<td>47.85 ± 5.75</td>
<td>2.05 ± 1.07</td>
</tr>
<tr>
<td>Moderate harassment</td>
<td>46.18 ± 5.4</td>
<td>2.42 ± 0.79</td>
</tr>
<tr>
<td>High harassment</td>
<td>43.6 ± 7.68</td>
<td>2.13 ± 1.26</td>
</tr>
</tbody>
</table>

**Table 2**

Numbers of pregnant sailfin mollies in all four treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Pregnant</th>
<th>Not pregnant</th>
</tr>
</thead>
<tbody>
<tr>
<td>No harassment</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Low harassment</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Moderate harassment</td>
<td>1</td>
<td>9</td>
</tr>
<tr>
<td>High harassment</td>
<td>2</td>
<td>8</td>
</tr>
</tbody>
</table>

Data shown are for the largest females (see text for chi-square analysis).
are able to store sperm for longer than 3 months (Constantz 1984). These females did, however, also have the most regressor eggs present, implying that although they are able to store sperm past 3 months, the amount of sperm available after this period may be limited or of low quality. Females may be adjusting their reproductive strategy in response to the availability of males. For instance, in the presence of males, after an isolation period, females may start early processes of yolking up eggs. This may explain why females in the harassment treatments had lower pregnancy rates. Although this was not the case when comparing females in the harassment treatments, there was no difference between the females that had yolking eggs and the females who did not. Even so, females after 24 days should have had embryos of earlier stages. In addition, it was unlikely that females gave birth during the experiment without being noticed by the observer (A.M.). However, since this species is cannibalistic (Hubbs & Schlupp 2008), we cannot completely exclude the possibility that the adults consumed all of the young prior to behavioural observations. Again, this is unlikely and pregnancies would have been noted during the behavioural observations. More research on the effects of offspring production of females exposed to different harassment levels is necessary to understand the unique findings in this study.

Male Consequences of Performing Harassment: the Male Perspective

Males, when exposed to a more competitive environment, became more sexually active and tended to increase courtship displays when there were two other males present. Larger males are more likely to court more than smaller males (Farr et al. 1986), and when males were placed in a priori size classes, the soluble fat content of larger males (range 40–56 mm) was significantly greater than that of smaller males (24–34 mm) (A. M. Makowicz & I. Schlupp, unpublished data). This suggest that there is a direct cost to courting or harassing a female, and both strategies are reflected in the male’s body condition, and/or a direct cost due to male–male interactions (for effects of density on male–male competition, see Jirotkul 1999; Smith & Sargent 2006; Smith 2007).

Here, we showed that the degree of competition had a dramatic effect on male life-history traits. This result is unlikely due to same-sex interactions. When males that were isolated for 40 days were compared to males that were housed in pairs, there was no difference in body condition (I. Schlupp, unpublished data). In P. latipinna, when males are exposed to high competition environments, they may increase testosterone production to increase mating success (Ramm et al. 2005; Ostner et al. 2011; Rangel-Negrín et al. 2011). One hypothesis to explain the significant differences in GSI in males is that male testis size and/or production of testosterone are influenced by sperm competition. Sperm competition has been positively correlated with testis size, and species that are under high sperm competition risks have more variation in testes size (Ramm et al. 2005; Denk & Kempenaers 2006). It would be interesting to test whether testosterone levels are influenced by or have an influence on male mating strategies
like courtship or harassment because in medium-sized males these behaviours are very plastic. To test this hypothesis, testosterone levels, testis size and sexual behaviours of each male exposed to different competition environments would have to be investigated further.

In summary, this study demonstrates that the social environment can have a direct, negative effect on the body condition of males. To test the hypothesis, testosterone can have a direct, negative effect on the body condition of males. To test this hypothesis, testosterone levels, testis size and sexual behaviours of each male exposed to different competition environments would have to be investigated further.

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