



The direct costs of living in a sexually harassing environment

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ARTICLE INFO

Article history:

Received 1 March 2012
 Initial acceptance 3 April 2012
 Final acceptance 10 December 2012
 Available online 24 January 2013
 MS. number: A12-00165R

Keywords:

body condition
 fitness
Poecilia latipinna
 sailfin molly
 sexual harassment
 social environment
 sexual conflict

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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Sexual conflict is widespread throughout polygynous sexual organisms (Arnqvist & Rowe 2005). It occurs when individuals of one sex invest less into reproduction and increase their fitness through frequent matings, while individuals of the other sex invest more into reproduction and their fitness is dependent on the amount of resources they can acquire (Parker 1979). Interactions between males and females have resulted in the evolution of behaviours that benefit one sex while having a fitness cost on the other sex, such as mate guarding and sexual harassment. Additionally, male and female interactions have led to the evolution of alternative mating strategies (Henson & Warner 1997). For instance, if females directly choose one particular male strategy, they could indirectly select for multiple male strategies if males gain a benefit from circumventing this choice (Henson & Warner 1997), potentially leading to an evolutionary arms race (Dawkins & Krebs 1976). Persistent male behaviours have evolved to overcome a female's mate choice, and thus her resistance to mating with unwanted males. Therefore, female resistance may also impose dramatic fitness costs on females (Arnqvist & Rowe 2005).

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

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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 (Stearns 1992); for instance, how many offspring she produces, or the quality of those offspring (Boness et al. 1995; Gay et al. 2009; Garcia-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 seals, *Halichoerus grypus*, females that were sexually harassed pupped 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; Magellan 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 1989; 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 *P. 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.

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