Male harassment reduces short-term female fitness in guppies

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Summary
Males can maximise their fitness by copulating with as many females as possible. Although this behaviour may have negative consequences for the females involved, females can also benefit from multiple mating. For example, multiple mated female guppies produce more, larger and fitter offspring. It is not clear if these fitness benefits are a direct result of multiple mating, or the product of female choice — either pre or post copulatory — for better quality males. To answer this question, individual virgin female guppies were exposed to different combinations of males: just one male; three males, one at a time; and three males presented simultaneously. Mating activity was more intense in the three-at-a-time treatment but did not differ between the other two. This increased attention did not affect gestation time nor offspring size, but significantly reduced the number of offspring produced. This reveals that male harassment causes a direct reduction in female short-term fitness.

Keywords: sexual conflict, multiple mating, fecundity, Trinidadian guppy, Poecilia reticulata.

Introduction
Traditional sex roles have been defined on the basis of the relative parental investment of males and females (Trivers, 1972; Arnold, 1994). The optimal number of partners is predicted to be higher for the sex with the higher potential reproductive rate (Clutton-Brock & Vincent, 1991). This asymmetry

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leads to sexual conflict (Gavrilets et al., 2001; Chapman et al., 2003; Parker, 2006) in which female resistance to mating typically evolves to counteract persistent and indiscriminate copulations by males (Johnstone & Keller, 2000). However increasing numbers of studies on virtually every taxonomic group suggest that polyandry is the norm rather than the exception (Birkhead, 2000).

As males of most species provide only sperm (i.e., genes), any benefits that females gain from multiple mating must be purely genetic (Jennions & Petrie, 2000; Hosken & Stockley, 2003). By copulating with several males, females can exert a form of postcopulatory (cryptic) choice allowing only the best available sperm to fertilise the eggs (Eberhard, 1996; Birkhead & Möller, 1998). Other genetic benefits involve biasing paternity towards those males with the most ‘competitive’ sperm (Keller & Reeve, 1995; Yasui, 1997) or avoiding genetically incompatible partners (Tregenza & Wedell, 2000; Colegrave et al., 2004). Another possibility could be that females mate multiply just to ensure fertilization avoiding the risk of infertile or sperm depleted males (García-González, 2004; Uller & Olsson, 2005).

The Trinidadian guppy (Poecilia reticulata Peters) has become a classic model organism for testing hypotheses about sperm competition, sexual selection and speciation (Houde, 1997; Magurran, 2005). Guppies exhibit marked sexual dimorphism, and an ovoviviparous reproductive system in which females store sperm and give birth to live young. Male guppies relentlessly court females using sigmoid displays. Females evaluate male attractiveness on the basis of colour patterns, and thereby exercise pre-copulatory mate choice (Houde, 1997). This female discrimination, combined with brief periods of receptivity (when females are virgin or shortly after parturition), means that most displays do not lead to consensual copulation. Sneaky mating, i.e., transfer of sperm with a thrust of the gonopodium (a modified anal fin), allows males to copulate with unresponsive females. Not all multiple mating is attributable to males however. Receptive females will solicit and accept copulation from several different males. This promiscuous mating system results in high levels of multiple paternity in laboratory experiments (Becher & Magurran, 2004) as well as in natural populations (Kelly et al., 1999; Neff & Pitcher, 2002).

Multiple mated female guppies have been demonstrated to produce more offspring of a larger size and with better antipredator skills (Evans & Magurran, 2000; Ojanguren et al., 2005). The simultaneous increase in fecundity