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Support for a pluralistic view of behavioural evolution

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Invited reply

Support for a pluralistic view of behavioural evolution

Empirical studies conducted since the late 1980s have supported three seemingly incongruous theories of behavioural evolution: good genes sexual selection; sexual conflict; and parental effects (which relates to differential allocation theory, the social constraints hypothesis and indirect genetic effects). Priest *et al.* (2008*a*) presented the first evidence that sexual conflict and parental effects are mechanistically linked. Long *et al.* (2009) argue that this study might be confounded by methodological and statistical problems. Here, we address their concerns.

The Long *et al.* (2009) comment highlights the myriad ways culture conditions and experimental methodologies can confound the sources of variation in fitness. Long *et al.* (2009) argue that our conclusion is not sufficiently supported because we did not control for sperm incapacitation, did not account for larval density effects and used inappropriate statistical methods. Their central argument is that increased sperm incapacitation in the mating treatment vials could have reduced larval competition to such an extent that it increased the resulting daughters' fitness.

Sperm incapacitation is an important concern. We have known since the 1960s that additional bouts of mating can temporarily decrease egg viability in fruitflies (David 1963). However, sperm incapacitation would had to have been greater than 40 per cent in the mating treatment vials to overcome the 40 per cent greater level of egg production in these vials. Prout & Clark (2000) found that additional bouts of mating and exposure to Acps temporarily reduce egg viability by only 13 and 35 per cent, respectively, for the same *DTA* males and sons of *tudor* females used in Priest *et al.* (2008*a*). In addition, none of the 210 mating treatment females was sterilized by mating with the sterile males, unlike the finding of Snook & Hosken (2004).

Even if sperm incapacitation had occurred, it would only have influenced our results if it had altered larval densities enough to change the fitness of daughters. When larval density is high, between-vial variation in larval density can have a critical influence on the fitness of adult fruitflies (Ashburner *et al.* 2005). However, egg and larval densities are not important sources of variance in daughters' fitness at 30–65 eggs per vial (Priest *et al.* 2008*a*,*b*), the range of egg densities in which we have conducted our study. That our study was conducted in ideal conditions was an important component of our argument that population growth rate, not lifetime reproductive success, is the appropriate measure of daughters' fitness.

Long *et al.* correctly point out that there is an assumption of statistical independence in ANCOVA between a covariate and a dependent variable. However, as our results indicate, there was little effect of the egg density covariate on daughters' fitness. Moreover, within each of the mating treatments, egg density was equally weakly correlated with daughters' fitness, indicating that the covariate did not lead to an artificial ANCOVA result.

The larger question, to which Long *et al.* only partially allude, is the relative importance of mating-induced parental effects in behavioural evolution. It is often considered that studies supporting sexual conflict or good genes sexual selection might be nullified by parental effects (Gil *et al.* 1999). This is simply not the case. The general support for sexual conflict and good genes sexual selection is conclusive. What we do not understand is how sexual conflict, good genes and maternal effect processes act in conjunction during behavioural evolution. In some systems, parental effects appear to amplify genetic effects on offspring traits (Kotiaho *et al.* 2003) or strengthen sexual selection driven by mate choice (Bluhm & Gowaty 2004). In other systems, parental effects and good genes processes that increase offspring fitness might be balanced by fitness losses resulting from sexual conflict (Head *et al.* 2005; Priest *et al.* 2008*b*). Systems in which sexual conflict, good genes and maternal effect processes act in different ways are particularly interesting case studies because they might help us explain how counter-intuitive behaviours are maintained in the population. Our paper shows that the agents that drive sexual conflict in fruitflies, mating and Acps, may stimulate parental effects, which improve the fitness of offspring (Priest *et al.* 2008*a*). These results indicate that we may need to adopt a more pluralistic view to understand behavioural evolution.

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The accompanying comment can be viewed on page 26 or at http://dx.doi.org/doi:10.1098/rsbl.2008.0325.

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