



Forum

Why do males care for their competitor's offspring? A response to Székely et al.



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Székely et al.'s article in this issue (Székely et al. 2013) claims several shortcomings of our recent study (Kamel & Grosberg 2012) of male parental care and paternity in a marine snail, advising caution on several fronts about the reliability and interpretation of our data. Our original paper had three main goals: (1) to determine whether males were the exclusive postzygotic caregivers in *Solenosteira macrospira*, (2) to estimate the costs of egg carrying, and (3) to characterize the distribution of paternity both within and across males. Briefly, we found that only males carry offspring in this species; care is costly for males, and care-giving males are often not the genetic sires of the offspring they carry on their shells. The points Székely et al. raise were all discussed by us in the original paper and in the supplementary material published with the paper, or are not directly relevant to our findings. We comment on these points below.

DO CARE-GIVING MALES GAIN FITNESS THROUGH RECIPROCAL MATINGS?

Contrary to Székely et al.'s claim that we should have considered that males may reciprocally benefit from mating with promiscuous females, we do clearly address the possibility of 'reciprocal matings' as a way in which males may gain more paternity than evidenced by the offspring on their own shells. In the discussion of the original paper (page 1171) we wrote, 'However, it should not be forgotten that each caring male is likely to sire young in the subsequent mixed-paternity clutches a female produces, which should presumably improve the cost:benefit ratio of care. Indeed, it is possible that having offspring on other males' shells might be an effective form of bet-hedging from the focal male's perspective'.

Székely et al. further state that we did not sample the male population exhaustively enough to detect large numbers of 'reciprocal' paternities. We agree. Our aim was to estimate paternity, not to estimate lifetime reproductive success for individual males, as desirable as that might be. For our paternity studies, we sampled 15 males from the population, which constitutes a small absolute number of snails (for example, we sampled 287 individuals to calculate population allele frequencies) with respect to the entire population. Given that populations are very large (see

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Table 1 in the supplementary material published with our paper), it would be highly unlikely to find a caring male's genotype on another male's shell. Nevertheless, we did perform this analysis on our sample, and, as expected, found no evidence for this outcome. The referees of the paper asked us to eliminate this analysis from our paper, because of its inevitably weak power in a population that potentially contained thousands of individuals.

DO CARING MALES' OFFSPRING HAVE A FITNESS ADVANTAGE?

Second, Székely et al. propose that a caring male may actually assist his own offspring by caring for other eggs and embryos. However, given that all cannibalism occurs within capsules it is difficult to imagine how males might assist their own offspring's survival. In our paper we unambiguously state that there is no evidence that the caring male's offspring are less likely to die, given that paternity is equally low among early stage and late-stage embryos. Indeed, the only difference in paternity occurred among the hatchlings that were crawling around the caring male's shell. The tendency for hatchlings located on the male to be offspring of that male may be the result of differential survival or of a tendency for hatchlings to remain longer on a related male.

In any case, the issue of whether a caring male's offspring might have an advantage over foster offspring is an interesting one, which we extensively discussed in our paper. However, because of strict word limits in *Ecology Letters*, we based our discussion on available evidence, rather than on presently groundless speculation about the existence of 'pheromones'. We wrote (page 1171): 'Females may mate with many males to maximise phenotypic and genetic variance among siblings, thereby increasing the scope for cannibalistic selection among offspring within capsules to yield the fittest survivors (Elgar & Crespi 1992). The fact that most surviving hatchlings were sired by a single male is consistent with a particular paternal genotype winning out over others. However, we also found evidence of last male sperm precedence, because caring males sired proportionally more offspring in a given clutch than any other fathers did individually. This simple numerical advantage could have also lead to the increased representation of the caring male's genotype in the hatchlings. Temporal increases in female promiscuity might also explain this pattern of high paternity among hatchlings. Given that the hatchlings represent the most advanced stage of development, the capsules we sampled were laid early in the season when females had potentially mated with fewer males. Paternity could then be higher simply by virtue of decreased sperm competition. However, paternity of the caring male was low among late-stage embryos as well; the increase occurred after offspring became cannibalistic. For now, we can only speculate as to why more of the caring male's offspring emerge as the survivors. It might be that fathers can skew hatching success in favour of their own young or that females choose a high-quality male to mate with last. Alternatively, this pattern could be generated by an age effect: older sperm could result in poorer offspring survival, so the offspring of the last male to mate would have higher survival, by virtue of being fertilised by younger sperm (Blount et al. 2001)'.

IS IT BETTER TO CARE FOR THAN ABANDON OFFSPRING?

Third, Székely et al. suggest that if finding a new mate is difficult, because of low population densities or heavily male-biased adult sex ratios, a male's best option may be to care for extrapair offspring rather than abandon them. As we wrote in both the Results and the supplementary material, natural population densities of *S. macrospira* are high and there is no detectable bias in the sex ratio. Furthermore, the sheer degree of promiscuity of both females and males (males carried clutches of up to five females on their

shells), and the fact that all males in the population carry egg capsules, are strong evidence that individuals are not mate limited in this population. Again, we directly addressed the question of why males carry foster offspring in the original paper (page 1171): 'The relationship between paternity and parental care also reflects the evolutionary history of a species. The simplest explanation here might be that, unlike in many other organisms (Kaitala & Kaitala 2001; Neff & Gross 2001), males cannot avoid caring for offspring. Throughout most of the reproductive season, virtually all males are covered with capsules; there does not appear to be a subset of cheater males that acquires copulations without providing the requisite caring behaviour. Interestingly, with the exception of *S. macrospira* and its congeners, all other cantharid gastropods attach their eggs to hard substrates in the intertidal (Houston 1978). The habit of attaching eggs to conspecifics may have evolved due to the limited availability of rocky substrate in intertidal areas of the northern Gulf of California, or as a way for adults to mitigate risks of predation or thermal stress on developing offspring in these warm, shallow, subtropical and tropical habitats. Males would be the primary targets for oviposition, given their proximity during copulation, and because conspecific females and heterospecifics would have no incentive to allow attachment of egg capsules. An inability for males to perceive or improve their paternity could underlie the persistence of this trait (Maynard Smith 1977; Westneat & Sherman 1993)'.

ARE THE DATA RELIABLE?

Fourth, Székely et al. suggest that while our results are remarkable, they are questionable because of a lack of important methodological details and quality control. This claim misrepresents the analyses we actually performed and reported. Either we explicitly discussed these so-called 'quality control' issues in our paper or such protocols are pro forma parts of any sound study of parentage. To put any doubts to rest, we did not use any microsatellite loci for parentage analysis that contained null alleles, and all loci conformed to Hardy–Weinberg equilibrium in the sampled population. To determine whether genotyping errors might affect our estimates of parentage, we ran the analyses in the sibship reconstruction program COLONY (Wang 2004) five times, varying the genotyping error rate. Results were consistent across error rates, indicating that our data are robust. We also analysed the data using different (and more conservative) methods of assigning parentage (Neff et al. 2000) and obtained results consistent with those produced by COLONY.

In the end, we agree with Székely et al. that many intriguing behavioural, ecological and evolutionary questions remain to be addressed in this system, none of which will be easy to answer experimentally or in the field. What is clear is that the pattern of parental care exhibited by *S. macrospira* represents an extreme example of the coexistence of high levels of female promiscuity, low paternity and costly male care, and emphasizes the still unresolved roles of natural and sexual selection in the evolution of male parental care.

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