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Forum

Why do males care for their competitor's offspring?

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A fundamental pattern in animal behaviour is that females care for the young, whereas males either court females or fight for access to them. However, in a number of taxa as diverse as insect, fish, frog and bird species, only males care for the young. The occurrence of exclusive male care has been an enigma for evolutionary biologists since the time of Darwin (1871) because it is not clear why males should devote themselves to caring for offspring on their own instead of attempting to secure additional mates. Nevertheless, the clear prediction emerges that males who care for young should attempt to minimize the risk of cuckoldry: why after all should they raise another male's offspring?

A recent paper by Kamel & Grosberg (2012) reports an extraordinary breeding behaviour in a marine snail, *Solenosteira macrospira*, inferred by genetic analysis of wild-caught individuals. Here we focus on this paper and derive broad implications for studying behaviour as a whole. Shortly after copulation in this marine snail, females deposit their egg cases on the shell of the male with whom they last mated, and this male cares for the eggs until the young snails hatch. This is essential to offspring survival, but highly costly to the male: he looks after the eggs for up to 1 month and the egg masses represent approximately 40% of an average male's wet mass. Individuals experimentally manipulated to carry a full burden of eggs lost on average 8% of body mass over 2 weeks relative to those with no egg masses.

Males, however, carry mostly other males' offspring on their shells. On average, only 24% (range 1–61%) of offspring were sired by the caring male. Moreover, females appear to be extremely promiscuous, with an average clutch being fathered by 13 different males. Thus, it seems that male snails of this species work very hard to rear their rivals' offspring.

How could such a striking and seemingly maladaptive behaviour persist in a wild population? First, males may reciprocally benefit from mating with promiscuous females. If paternity loss in the carrying male's own clutch is compensated for by paternity gain in other males' clutches, everybody is a winner. To test this would require paternal sibships to be identified not only within young cared for by particular males, but also over all of the offspring combined. Kamel & Grosberg do not report this analysis, although it seems unlikely that the male population could have been sampled exhaustively enough to detect large numbers of 'reciprocal' paternities.

Second, a carrying male may actually assist his own offspring by caring for other eggs and embryos. *Solenosteira macrospira* embryos are cannibalistic, and devour both unhatched eggs and fellow embryos. Therefore, nonpair young may provide fodder for the parenting male's offspring. Parenting males may also boost their own young's viability (or reduce that of extrapair young) by secreting pheromones or selecting habitats in which their own

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young have a survival edge. Kamel & Grosberg's findings are consistent with these explanations, since the paternity of the caring male was higher among hatchlings than among the eggs or late-stage embryos. However, this could easily be tested experimentally, for instance by allowing females to mate with two males, depositing the resulting capsules in equal numbers on the shells of both males, and then comparing embryo survival of the caring male's own offspring and those sired by the other male.

Third, the male's best option may be to care for the young rather than abandon the female with the fertilized eggs. If finding a new mate is difficult, for instance because population density is low or the adult sex ratio is heavily male biased, a male's best option may be to put up with extrapair offspring and care for them. Finding a mate is not always a trivial task, and studies of natural populations suggest that males and females can have vastly different mating opportunities owing to persistent biases in adult sex ratios (Kosztolányi et al. 2011). To test this experimentally, one would need to manipulate mating opportunity by reducing the density of breeding animals or changing the adult sex ratio around a focal pair.

Kamel & Grosberg's results are remarkable, although we fear that important methodological details are lacking. Parentage analysis is an imperfect science that involves numerous assumptions, some of which have not been addressed in their paper. For example, microsatellites are prone to nonamplifying 'null' alleles, which can lead to the false exclusion of true fathers (Dakin & Avise 2004). It is, therefore, standard practice in paternity studies to report tests for Hardy–Weinberg equilibrium and to discard any loci showing evidence of null alleles prior to parentage analysis. Unfortunately, Kamel & Grosberg instead report *F* statistics, which are primarily informative in the context of population subdivision, despite all of the genotyped snails having apparently been sampled from a single location (Bahia de las Chollas, page 1168).

Genotyping errors are also extremely difficult to eliminate from all but the smallest of data sets, yet even a modest rate of 1% can lead to around 20% of paternities no longer being assigned (Hoffman & Amos 2005). Although it seems unlikely that genotyping errors would have such a dramatic effect on sibship reconstruction as conducted by Kamel & Grosberg, careful quality reporting would nevertheless have been a valuable addition to the paper, since high-profile findings arguably merit a commensurately greater burden of evidence.

Caveats set aside, this work highlights two major issues. On the one hand, a seemingly maladaptive breeding system can exist if one carefully considers the natural history of a species in question, and works through the costs and benefits to the key players, in this case the males. On the other hand, while humankind spends vast sums on exploring the solar system and outer space, the behaviour and ecology of the vast majority of organisms on our planet remain unknown. Consequently, to explain biological diversity and to obtain the most benefits from biodiversity for humankind, it is not sufficient to investigate traditional model organisms such as mice, *Drosophila* and *Caenorhabditis* in controlled laboratory environments. Instead, researchers need to reach out towards lesser-studied creatures that may well live in inaccessible environments.

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