# Evolution: Inbreeding, Multiple Mating and Embryonic Aid

**Females frequently mate with more than one male, but it is rarely clear why. In species where related individuals frequently meet, multiple mating may allow females to avoid fertilising their eggs with sperm from a close relative. A new study suggests that promiscuous females do indeed suffer lower costs of inbreeding, but that this is because of interactions between embryos.**

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Just when you think things cannot get any weirder, they do and evolution seems to excel in amazing its students. One example of this bizarreness was discussed in these pages last year [1]. In that instance, male and female ants were found to be distinct genetic units, essentially separate species [2]. That is strange enough, but another seemingly weird case has recently come to light [3], in which females carrying at least some outbred embryos have lower spontaneous abortion rates and give birth to more offspring in non-aborted broods. The implication is that outbred offspring somehow save their inbred half-siblings from death. The new findings both shed light on the enigmatic reasons for female multiple mating and open up a whole new raft of questions about what on earth is going on.

Until quite recently, females were generally assumed to be monogamous [4]. We now know this is not true for most species, and yet it remains unclear why females should mate with multiple males [5,6]. Matings inevitably have costs, including time and energy as well as risks of disease and predation. A single copulation has the potential to provide more than enough sperm for full female fertility, so what are females up to mating more than once? One possible reason is that they do this to avoid using the sperm of genetically incompatible males [7,8]. Not all genetic combinations work well, and females can reap reproductive benefits by avoiding the production of offspring with unfavourable gene combinations.

One situation likely to produce offspring with a poor genetic constitution is inbreeding. Inbreeding increases the chances that deleterious recessive alleles will be expressed and that favourable heterozygous gene combinations will be lacking in offspring [9,10]. As a result, if the likelihood of inbreeding is reasonably high, but females cannot discriminate siblings from non-siblings, or run the risk of not mating at all if they do not copulate with a brother, then they may choose to mate with several males to defray inbreeding costs. These costs could be offset if some degree of bias in sperm use in favour of unrelated males is possible, or if females can subsequently reduce their investment in those embryos that have inherited low fitness gene-combinations. Female field crickets appear to be able to bias sperm use in favour of unrelated males [11,12]. and Jeanne and David Zeh [3] have now described another situation where polyandry can defray inbreeding costs, although in this case, differential fertilisation success does not appear to be involved.

Figure 1. A female harlequin beetle riding pseudoscorpion (*Cordylochernes scorpioides*) with developing embryos visible in the brood sac surrounding her abdomen.

Photo courtesy of Jeanne Zeh.

The pseudoscorpion (*Cordylochernes scorpioides*) is a tiny arachnid with an unusual lifestyle. Females brood their babies and the offspring draw nutrients from their mothers (Figure 1) who ride around the forest on the backs of large harlequin beetles until they come to a suitable habitat (decaying fig trees), where they decamp and begin reproducing. This mode of colonization of an ephemeral habitat has the potential to increase the risk of inbreeding, especially because, once on the dead trees, the psuedoscorpions must wait two to three generations for the beetle larvae to develop to adulthood before they can once more hitch-a-ride on an adult beetle to the next fallen tree [13]. As a result, even though neutral DNA markers show very high levels of heterozygosity [14], the potential for individuals to find themselves marooned with a bunch of close relatives is high.

Jeanne Zeh [15] had previously shown that female pseudoscorpions have higher offspring viability when they mate with several males, but in their latest study [3], the Zehs assigned females to treatments that all involved two matings, but which differed in whether they were to unrelated or related males, or one of each. They found that, when a female mated with her two brothers, the rate of whole brood abortions was around 40% and that this was reduced in treatments that included a non-sib mate. Additionally, females mating with their brothers had fewer offspring in the broods that did not abort.

This pattern is just what you would expect to find if inbred and outbred males have an equal probability of fertilising eggs, but that inbred embryos are less viable. When the Zehs examined the paternity of embryos, however, they found that related males actually sired a disproportionately high number of offspring. This makes it much harder to understand what is going on: if siblings have an advantage in sperm competition over unrelated males, females mating to both types should have much lower numbers of surviving offspring than females mating to just unrelated males.

The only plausible explanation for the pattern is that, in broods containing out-bred offspring, something happens to stop brood abortion and facilitate embryo survival. Hence, if females do happen to copulate with a brother, by re-mating with an unrelated male they can defray some of the costs of inbreeding in this species, and of course, by mating with many males, females increase the likelihood of mating with a non-sib. This still does not explain why related males are more successful in sperm competition, nor how the 'rescuing' effect of unrelated males could work.

One possible explanation for the rescue effect might be that embryos signal their health to the mother, and a few healthy embryos provide enough signal for females not to abort and to maintain a reasonable food supply. This would require that females cannot selectively abort unhealthy, inbred, embryos. Alternatively, perhaps females can only carry a fixed number of embryos and above that number, abortion is the optimal option. This would then require brothers to be involved in manipulating their sisters such that they over-invest in offspring, and again the fitness consequences of too large a brood would have to be substantial because of the long-term fitness costs of brood abortion. Finally, is it possible that the pattern detected is a side-effect of something else and does not serve as an mechanism to avoid costs of full-sib matings in the wild? Perhaps embryos do signal their health, but in the forests of central and south America, selection for this has nothing to do with inbreeding? What seems strange in any case is that females abort at all since this has substantial long-term fitness costs, and tends to increase the chance of future abortions [16]. Why not produce one sub-optimal brood and then at least avoid the cycle of abortion and non-receptivity? By avoiding abortion a female stays in the mating game and can seek more males, hopefully including a non-sib, next time around.

Although Jeanne and David Zeh [3] do not discuss the possibility, one explanation for the second, intuitively strange finding that related males have higher success in sperm competition may be that females somehow give priority to the sperm of their brothers because their ecology means that males may frequently be limited by mating opportunities, so that females can gain inclusive fitness benefits by allowing their brothers to mate with them even if it slightly reduces the fitness of their offspring [17].

This and other studies (for example [12,13]; see discussion in [18]) have some pretty startling implications. They suggest that, even in organisms like insects that are characterised by large population sizes, the probability of inbreeding can be sufficiently large to create significant selection pressures. A major challenge for evolutionary ecology in the next few years will to determine how structured invertebrate populations actually are, a challenge. because pedigrees of free-living insects are hard to come by. The take-home message? Perhaps it is just that the outcomes of organic evolution are diverse and sometimes a little strange, and as H.S. Thompson [19] repeatedly reminded us: "when the going gets weird, the weird turn pro".

**References**

1. Sykes, E.M., and West, S.A. (2005). Evolution: revenge of the clones. Curr. Biol. *15*, R547–R549.
2. Fournier, D., Estoup, A., Orivel, J., Foucaud, J., Jourdan, H., Le Breton, J., and Keller, L. (2005). Clonal reproduction by males and females in the little red fire ant. Nature *435*, 1230–1234.
3. Zeh, J.A., and Zeh, D.W. (2006). Outbred embryos rescue inbred half-siblings in mixed paternity broods of live-bearing females. Nature *439*, 201–203.
4. Birkhead, T.R., and Moller, A.P. (1992). Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press.
5. Jennions, M.D., and Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. Biol. Rev. Camb. Philos. Soc. *75*, 21–64.
6. Hosken, D.J., and Stockley, P. (2003). Benefits of polyandry: A life history perspective. Evol. Biol. *33*, 173–194.
7. Zeh, J.A., and Zeh, D.W. (1996). The evolution of polyandry I: Intragenomic conflict and genetic incompatibility. Proc. Roy. Soc. Lond. B *263*, 1711–1717.
8. Tregenza, T., and Wedell, N. (2000). Genetic compatability, mate choice and patterns of parentage. Mol. Ecol. *9*, 1003–1027.
9. Falconer, D.S. (1981). Introduction to Quantitative Genetics. Longman.
10. Keller, L.F., and Waller, D.M. (2002). Inbreeding effects in wild populations. Trends. Ecol. Evol. *19*, 395–420.
11. Bretman, A., Wedell, N., and Tregenza, T. (2004). Molecular evidence of post-copulatory inbreeding avoidance in the field cricket *Gryllus bimaculatus*. Proc. Roy. Soc. Lond. B *271*, 159–164.
12. Tregenza, T., and Wedell, N. (2002). Polyandrous females avoid costs of inbreeding. Nature *415*, 71–73.
13. Zeh, J.A., Zeh, D.W., and Bonilla, M.M. (2003). Phylogeography of the harlequin beetle-riding psuedoscorpion and the rise of the Isthmus of Panama. Mol. Ecol. *12*, 2759–2769.
14. Zeh, D.W., Zeh, J.A., and May, C.A. (1994). Charomid cloing vector meets the pedipalp chelae: single-locus minisatellite DNA probes for paternity assignment in the harlequin beetle-riding pseudoscorpion. Mol. Ecol. *3*, 517–522.
15. Zeh, J.A. (1997). Polyandry and enhanced reproductive success in the harlequin-beetle-riding pseudoscorpion. Behav. Ecol. Sociobiol. *40*, 111–118.
16. Zeh, J.A., and Zeh, D.W. (2001). Spontaneous abortion depresses sexual receptivity in a viviparous arthropod. Anim. Behav. *62*, 427–433.
17. Parker, G.A. (1979). Sexual selection and sexual conflict. In *Sexual selection and reproductive competition in insects*, M.S. Blum and A.N. Blum, eds. (London: Academic Press), pp. 123–166.
18. Tregenza, T., and Hosken, D.J. (2005). Mate choice: been there done that. Curr. Biol. *15*, R959–R961.
19. Thompson, H.S. (1994). Better than Sex (London: Black Swan Books).

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