the mouse retina. J. Comp. Neurol. *499*, 797–809.
12. Vaney, D.I. (1990). The mosaic of amacrine cells in the mammalian retina. In Progress in Retinal Research, N.N. Osborne and G.J. Chader, eds. (Oxford: Pergamon Press), pp. 49–100.
13. Oesch, N., Euler, T., and Taylor, W.R. (2005). Direction-selective dendritic action potentials in rabbit retina. Neuron *47*, 739–750.
14. Fried, S.I., Munch, T.A., and Werblin, F.S. (2005). Directional selectivity is formed at multiple levels by laterally offset inhibition in the rabbit retina. Neuron *46*, 117–127.
15. Ozaita, A., Petit-Jacques, J., Volgyi, B., Ho, C.S., Joho, R.H., Bloomfield, S.A., and Rudy, B. (2004). A unique role for Kv3 voltage-gated potassium channels in starburst amacrine cell signaling in mouse retina. J. Neurosci. *24*, 7335–7343.
16. Tukker, J.J., Taylor, W.R., and Smith, R.G. (2004). Direction selectivity in a model of the starburst amacrine cell. Vis. Neurosci. *21*, 611–625.
17. Borg-Graham, L.J., and Grzywacz, N.M. (1992). A model of the directional selectivity circuit in retina: Transformations by neurons singly and in concert. In Single Neuron Computation, T. McKenna, J.L. Davis, and S.F. Zornetzer, eds. (London: Academic Press), pp. 347–376.
18. Tjepkes, D.S., and Amthor, F.R. (2000). The role of NMDA channels in rabbit retinal directional selectivity. Vis. Neurosci. *17*, 291–302.

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Mating Behaviour: Promiscuous Mothers Have Healthier Young

A small marsupial has thrown new light on the question of why females typically mate with several males: promiscuous female antechinuses have many more surviving offspring because males that are successful in sperm competition also sire healthy offspring.

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The myth of the coy and chaste female is all but shattered. We now know that in most animals females are surprisingly promiscuous. Surprising, because it has often been difficult to see the benefits of female promiscuity. While males typically have the potential to fertilise the eggs of a large number of females, female reproduction is usually limited by material resources rather than by access to sperm or willing males. Males of some species do provide benefits such as food or access to a territory in exchange for sex, but in most cases females seem to get little more than sperm from their mates. That many females nonetheless mate with several males is puzzling because sexual encounters inevitably carry costs — they take time and energy and involve risks of disease or even harm by males [1].

The key to understanding female promiscuity may be that by mating around, females acquire sperm from several mates. This would be to their advantage if, for some reason, sperm from more suitable sires were more likely to fertilise the eggs. The simplest way this could occur is if males carrying better genes win out in sperm competition with inferior rivals, either because they are able to produce ejaculates with larger numbers of sperm or because the individual sperm they produce are better [2,3]. Alternatively, rather than simple ejaculate competition, promiscuous females might be able to store and use sperm from males with good genes and reject sperm from others based on signals they receive during mating or from the ejaculates themselves [4]. A new study from Australia [5] has provided the clearest evidence yet that promiscuous females can indeed exploit differences in male fertilisation success to improve the genetic quality of their young.

The antechinus is a small carnivorous marsupial similar to a shrew with some dramatic reproductive tactics. During their winter breeding season, males show a dedication to mating that includes copulations lasting between five and 14 hours and that ends with the entire male population dying from their exertions [6]. In an elegant new study, Fisher *et al.* [5] mated wild-caught female brown antechinuses (*Antechinus stuartii*, Figure 1) either three times to the same male or to three different males. They found that, when mated females were released back into the wild with their pouch young, the proportion of offspring that survived to weaning was three times higher for polyandrous (mating with several males) females than for monandrous (mating with one male only) females.

A similar effect was seen when females were kept under less stressful conditions in the laboratory. Offspring from the two groups showed no differences in survival until a few weeks before weaning when many of the monandrous females' offspring died despite milk still being available. The size of the difference in survival between the two groups reveals a truly staggering benefit of taking multiple mates; just the magnitude of this effect is informative because it is impossible to conceive of any costs of mating that could outweigh such a large advantage. Promiscuity definitely pays for these females.

So, are these huge benefits of taking multiple mates really genetic effects? A key piece of evidence revealed by this study is that males that are good at winning in competition for fertilisations have offspring that are much more likely to survive. Fisher *et al.* [5] showed this by genetically determining the paternity of offspring of females that had mated to three males. They then mated other females to only one of the males each and found that offspring of males with more competitive ejaculates had a much better chance of survival than offspring of males that were poor sperm competitors. This is, of course, just what you would expect if polyandrous females have offspring that survive well because males with competitive sperm also carry good genes.

Brown antechinuses are especially well suited for this type of study because females tend to have just one reproductive bout (fewer than 10% survive to produce a second litter). This is crucial, because a persistent problem with attempts to determine whether males that are good at winning in sperm competition also produce good offspring has been that the quality of offspring does not only depend on the genes they inherit. Females can influence the quality of their offspring through their investment in the eggs and any care they provide while the offspring are growing up. To complicate things further, these maternal effects can, in turn, be under male influence. Often, females must trade-off current reproduction against future reproduction; any investment in current reproduction will have a negative effect on future reproduction. In many species, females invest more in their offspring when they have mated to a relatively attractive male [7], for instance, field crickets lay eggs faster after mating to a dominant male [8].

Males, of course, benefit if they can somehow make their mates invest as much as possible in current reproduction since they may not be in a position to father any future offspring with the same female. As a consequence, males of many species appear to have evolved ways to induce greater reproductive investment, both in terms of number and resources per offspring, from their mates [4]. This causes problems for studies setting out to investigate potential benefits of polyandry. Even though a few studies have found that polyandry seems to improve offspring survival, it is difficult to be sure just how much of this effect is due to genetic quality of the offspring and how much is due to male influence over female investment in reproduction. Studying antechinuses gets around this problem, because the single reproductive bout means there is no trade-off between current and future reproduction; females are expected to invest maximally in their first and only litter regardless of what males they mate with. This means that we can be confident that the difference in the quality of offspring of polyandrous and monandrous females is almost certainly due to the genes they inherit from their fathers and not to a difference in maternal investment.

Figure 1. A female antechinus with suckling young (Photo courtesy of A. Keszei).

The big remaining question is how such enormous differences between the genetic quality of males can persist in a population. Natural selection has proved capable of the subtlest refinements to organisms so it is difficult to understand why there should be lots of males with genes that make offspring several times less likely to survive than those of other males. Such bad genes should be rapidly weeded out by selection. Fisher *et al.* [5] suggest that the answer may lie in the extreme reproductive physiology of this species, with males ending sperm production one month before mating starts [9]. Perhaps ageing sperm accumulate mutations [10] that harm young? Further study is clearly needed — it is not easy to understand why genetic damage to sperm would only manifest when offspring are more than 50 days old. The challenge for the future is to understand the genetic mechanism by which antechinuses benefit so strikingly from polyandry and to design tests for other species that can also separate the effects of genes and of maternal investment.

References

1. Arnqvist, G., and Rowe, L. (2005). Sexual Conflict (Princeton, N.J.: Princeton University Press).
2. Harvey, P.H., and May, R.M. (1989). Out for the sperm count. Nature *337*, 508–509.
3. Keller, L., and Reeve, H.K. (1995). Why do females mate with multiple males - the sexually selected sperm hypothesis. Adv. Study Behav. *24*, 291–315.
4. Eberhard, W.G. (1985). Sexual Selection and Animal Genitalia (Cambridge, Massachusetts: Harvard University Press).
5. Fisher, D.O., Double, M.C., Blomberg, S.P., Jennions, M.D., and Cockburn, A. (2006). Post-mating sexual selection increases lifetime fitness of polyandrous females in the wild. Nature *444*, 89–92.
6. Lee, A.K., Woolley, P., and Braithwaite, R.W. (1982). Life history strategies of dasyurid marsupials. In Carnivorous Marsupials, *Volume I*, M. Archer, ed. (Sydney: Royal Zoological Society of NSW), pp. 1–11.
7. Sheldon, B.C. (2000). Differential allocation: tests, mechanisms and implications. Trends Ecol. Evol. *15*, 397–402.
8. Bretman, A., Rodríguez-Muñoz, R., and Tregenza, T. (2006). Male dominance determines female egg laying rate in crickets. Biol. Lett. *2*, 409–411.
9. Kerr, J.B., and Hedger, M.P. (1983). Spontaneous spermatogenic failure in the marsupial mouse Antechinus stuartii Macleay (Dasyuridae, Marsupialia). Austral. J. Zool. *31*, 445–466.
10. Siva-Jothy, M.T. (2000). The young sperm gambit. Ecol. Lett. *3*, 172–174.

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