

### Book Review

*Genomic Imprinting and Kinship* by David Haig. Rutgers University Press, New Brunswick, NJ, 2002.

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The gene-centred approach to evolutionary biology that became popular in the 1970s led to re-examination of apparent shared interests of both parents caring for young or the mutually beneficial interactions of parent and offspring. The traditional image of human parenthood had been one of complete harmony between the mother and her child both before and after birth. Evolutionary theory in the hands of the Robert Trivers and, subsequently, David Haig cast doubt on this blissful picture. In sexually reproducing species, parents are not genetically identical to their offspring. Consequently, offspring may require more from parents than parents are prepared to give, creating the possibility of a conflict of long-term interests. Trivers called this 'parent-offspring conflict', a term that refers strictly to a conflict of reproductive interests, emphatically not to conflict in the sense of overt squabbling. The parent may sacrifice some of the needs of its current offspring for others that it has yet to produce; the offspring maximises its own chances of survival. Haig developed the thesis brilliantly in relation to the unborn mammalian foetus. Parent and offspring “disagree” about how much the offspring should receive, battling it out hormonally across the placental wall.

The results of such evolutionary conflicts of interest were sometimes portrayed as a form of arms race, with escalating foetal manipulation of the mother being opposed by ever more sophisticated maternal counter-measures. However, limits must be encountered in the course of evolution. If the offspring is too aggressive in its demands it will kill its mother and, of course, itself. Likewise, if the mother is too mean, her dependent offspring will not thrive and she might as well have not bred. Moreover, mutually beneficial communication often occurs between parent and offspring.

In recent years evolutionary conflict theory has been given a new twist. Conflict may occur between parents in determining the character of their offspring through a mechanism known as “genomic imprinting” (not to be confused with behavioural imprinting of the Konrad Lorenz type). Some of the genes coming from one parent may be dominant to those of the matching alleles coming from the other by a

suppression process that has now been well described. When genomic imprinting surfaced as a phenomenon, it was natural that David Haig should have seized on the parental asymmetries for further explorations of evolutionary conflict. He suggested that the parent who wins the battle of allelic suppression passes on his/her characteristics to the offspring.

This book reprints a number of Haig's essays presenting his ideas about the impact of asymmetries introduced by genomic imprinting on conventional kinship theory. Haig is always stimulating, but whether he is right is quite another matter. For my part, I am not convinced that attempting to squeeze genomic imprinting into the box of evolutionary conflict will stand the test of time. Even though Haig provides some linking commentaries, the essays are not easy to read, partly because much of the theory he develops is still inchoate. The attractive thing about him is that he is so full of ideas, but Haig's playful style easily leads to misunderstanding. Some of his proposals have been dissected mercilessly by critics. Haig complains: "I sometimes feel that I should have employed a competent lawyer before submitting each of my papers to check not only my intended meaning, but also how my words might be construed by a hostile prosecutor." Perhaps he should because his thinking is by no means always clear. Haig writes that a female's paternally derived alleles should be selected to *prefer* greater allocation to current reproduction than should her maternally derived alleles. How is a gene meant to express a preference? An image that grew out of a teleological account of evolution does not translate well into the mechanistic language needed to understand evolutionary process or indeed development.

The question is whether the individual that is able to dominate the genes of its partner is more likely to leave copies of its genes behind than another individual of the same sex that doesn't. Its offspring will share more of its characteristics than would have been the case without genomic imprinting. But what about the grand-offspring? If the answer is that they will not because of re-segregation, then where is the advantage of genomic imprinting? This line of questioning leaves out of account any counter-measures that might be employed by the opposite sex if there were an advantage. To be fair, Haig has his own doubts about conditional, parent-specific patterns of expression. The question is whether mutual adaptation and counter-adaptations of maternal and paternal genomes are as elaborate and common as those between males and females. Or, asks Haig with characteristic honesty, is genomic imprinting just an oddity? His preferred answer is somewhere between common and odd. The problem is how do we find out. He admits that the answer won't be uncovered by the usual methods of behavioural ecology.

Undoubtedly, some fascinating phenomena need explaining. Barry Keverne and his colleagues have found that in primates paternally expressed genes are found in the so-called emotional brain and maternally expressed genes are found in the so-called executive brain. Rather than treat this as another battle between the sexes, albeit internalised, as Haig would have it, other explanations may prove more tractable. Many arguments against too much out-breeding can be advanced, but one of the most

compelling is the break-up of co-adapted gene complexes. It is possible that in the first generation of hybrids, no problems arise because they all have the necessary complement of genes, but in the F2s the genes will have re-segregated and the problems begin. I used to suppose that finding the right balance between inbreeding and outbreeding, minimising the costs of both, is best achieved by careful mate choice. However, genomic imprinting achieves the goal of minimising at least one of the costs of outbreeding by ensuring that all the genes that are required for building an intricate structure such as the brain come from one parent. The more that this happens, the more it will add evolutionary momentum to imprint the important genes needed for that structure from the parent that had already acquired dominance. The linking process could involve the genes of either parent so long as those that work together are held together. The effects are likely to be especially great in the case of genes that are regulatory and expresses early in development. The young organism is particularly likely to be disrupted by the lack of co-ordination between regulatory genes, just as it especially likely to be disrupted by environmental agents. The idea is, then, that genomic imprinting reduces the costs of outbreeding. Whether or not this conjecture is correct, the ways in which genomic imprinting has been co-opted for specific uses will attract theorists for years to come.