
Andrew Pomiankowski

Sex and Evolutionary Conflicts*

Participants and Programme

Anne Atlan, Institut Jacques Monod, Paris

Co-occurrence of sex ratio drive and suppressor in natural populations of Drosophila simulans

Eörs Szathmáry, Collegium Budapest

Some major transitions and models of population structure

Yoh Iwasa, Wissenschaftskolleg zu Berlin

Genomic imprinting

Jack Werren, University of Rochester

Wolbachia

Steve Frank, Wissenschaftskolleg zu Berlin

Germ-soma and symbionts

Mike Wade, University of Chicago

Speciation and genomic conflicts

Ichizo Kobayashi, University of Tokyo

Selfish genes and the evolution of sex

Graham Bell, McGill University, Canada

Experiments on the effect of sex on fitness and the spread of transposons in sexual and asexual populations

Andrew Pomiankowski, Wissenschaftskolleg zu Berlin:

Mafia cuckoos

Peter Hammerstein, Humboldt University, Berlin:

Games between the sexes

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Laurence Hurst, University of Bath:
Male mutation rates

Also in attendance

Andreas Herz, Humboldt University, Berlin
Hanspeter Herzel, Humboldt University, Berlin
Bernd Ronacher, Humboldt University, Berlin
Sahotra Sarkar, Wissenschaftskolleg zu Berlin
Paul Ward, University of Zurich, Switzerland

Introduction

In recent years there has been a great deal of interest in the idea that some genetic elements may be 'selfish'. Most genes have a functional role in cellular or organismal processes. In contrast, selfish genetic elements can be defined as those having characteristics that enhance their own transmission relative to the rest of an individual's genes and are either neutral or detrimental to the organism as a whole. Potential examples include supernumerary B chromosomes, meiotic drive genes, transposable elements and sex-ratio distorting symbionts. The concept that such elements are selfish or parasitic, although widely accepted, is still controversial.

Selfish genetic elements are of interest in evolutionary biology for two reasons. First, they illustrate clearly how selection can favour genetic elements, even if they are detrimental to the organism or population. As a result, they are relevant to the 'levels of selection' controversy. Second, selfish elements may promote evolutionary change in the genetic structure of a species. Indeed, selfish elements and the intragenomic conflict resulting from them are probably involved in the evolution of such fundamental biological phenomena as sex and sex determination, recombination rates, chromosome structure and organelle inheritance.

The theoretical evolutionary biology group (Steve Frank, Yoh Iwasa and Andrew Pomiankowski) decided to organise a seminar on 'Sex and Evolutionary Conflicts' to discuss new developments in our understanding of selfish genetic elements. The meeting was organised in a somewhat unusual fashion. We asked participants to present a short paper on their current research and, in addition, to lead a discussion on a topic of general interest. Both aspects worked very well. It led to some unusually stimulating and productive discussions. Two of the participants wrote

to me after the meeting to say it was the best conference they had ever attended. The following report gives a general background to the subject matter discussed at the meeting.

General themes

Organisms are designed by natural selection to transmit their genes to future generations. Most genes within an organism act in a co-operative manner because the common good benefits individual genes. However, conflict arises at reproduction because not all offspring inherit the same set of genes from their parents, nor are all genes transmitted in the same way. There is always room for some genes to exploit the common good even if this is detrimental to the rest of the genome.

Conflict within an organism, or intragenomic conflict', has two main causes. The first is that organisms are composed of multiple genetic entities: sex chromosomes, autosomes, organelles, transposable elements, plasmids and a variety of intracellular symbiotic genes. These genes do not share the same interests because they have different modes of inheritance. To give a simple example from mammals (eg, humans, mice), genes in mitochondria are passed on only through the female lineage, from mother to sons and daughters, they are never passed on by males. In contrast, genes in the nucleus are passed on equally by both sexes; sons and daughters inherit nuclear genes from their mother and father. This leads to conflict between these different groups of genes over the sex ratio of offspring.

The second cause of conflict is sexual reproduction. Sexual mixing is preceded by meiosis. This is a form of reduction division in which only half the nuclear genes segregate in each gamete. Human beings, for instance, have two copies of each chromosome, but only one copy segregates into each egg or sperm. If meiosis is fair, each allele or chromosome segment is inherited by half the gametes. However, there is strong selection for genes to subvert meiosis and transmit themselves to more than half of the competent gametes that go to make up the next generation.

Genes that cause intragenomic conflict have come to be called 'selfish genetic elements' (or selfish DNA, ultraselfish genes, genetic parasites etc.). Such elements enhance their own transmission to future generations while being either neutral or harmful to the fitness (survival or fertility) of the individuals that carry them. Harm can arise as a side effect of selfish behaviour. For example, transposable elements increase their own fitness by inserting extra copies elsewhere in the genome. But as a

side effect, insertions often cause mutations. Harm can also arise because selfish genetic elements actively destroy or disable competitors. For example, a number of selfish mitochondria and other symbionts gain by killing male offspring and re-directing resources to female offspring.

These deleterious effects favour countermeasures. Most genomes contain suppressors that limit the activity of selfish genetic elements. Suppression can be so strong that it obscures evidence of the underlying intragenomic conflict. Anne Atlan (Paris) gave us a very good example of this from her own work on the fruit fly *Drosophila simulans*. By chance, crosses were made between flies from different coastal and inland geographic locations in Africa. These crosses revealed the presence of meiotic drive genes in several populations causing odd sex ratios in the hybrid crosses. Normally the effect of these meiotic drive genes is not seen, because they are totally repressed in their own populations.

There is also selection on selfish genetic elements to reduce the harm they cause to their hosts, especially where the reproductive interests of host and element overlap. For example, many transposable elements have mechanisms that restrict transposition (the creation of extra copies within an individual) as element number increases. Such a restriction is necessary as the harm caused by transposable elements increases exponentially with the number within a genome.

A general theme that emerged later in the seminar was the similarity of concepts used to understand social interactions between separate organisms and those applied to the evolution of cooperation and conflict between genes within an organism. A number of familiar concepts were discussed at the meeting including: kin-selected altruism directed at related genes, reciprocity between partners that frequently interact, the suppression of deleterious competition between genes by communal policing, coevolutionary arms races between different elements and the evolution of an optimal trade-off between virulence (damage to the organism) and transmission to future generations. All apply to interactions between genes in separate organisms and genes within the same organism.