Andrew Pomiankowski

Sexual Evolution

Born in London in 1959, I graduated in Zoology from the University of Oxford, spent a year diversifying at Harvard (philosophy, history, film studies) and then took my D. Phil. at the University of Sussex. I returned to Oxford as a Junior and then Senior Research Fellow at Keble College. Since 1990, I have been a Royal Society Research Fellow at University College London, where I was recently promoted to Reader in Genetics. My research interests span the whole of evolutionary biology, with some dabbling in developmental biology and genetics. Most of my work has concerned the evolution of sex and its consequences. — Address: Department of Biology, UCL, Gower Street, London WC1, UK.

It is always sad to leave. Life at the Wissenschaftskolleg has been so easy. The sun is still shining through the trees into my office in the Villa Jaffé. How much easier it is to think creatively in beautiful surroundings. I will miss many things. *Frühstück* at the Winterfeldtmarkt before doing the weekend shopping. People-watching, with coffee and cake, at the Wiener Konditorei in Roseneck. I wonder why so many German women like to paint themselves a strange orange colour and where do they buy those clothes (men included)? What a shame the Gemäldegalerie is moving from Dahlem to Museum Island, where it will lose its unique away-from-it-all atmosphere. Opera, music, the film festival (mercifully not dubbed), the unending building site, my aerobics class with 12 lithe *Frauen,* swimming in the lakes every other evening and another beautiful view from my tree-bound apartment at the back of Villa Walther.

In my first few months at the Kolleg, I became viscerally aware of Germany's darker side. The Nazi past is everywhere in Berlin, both monumental and trivial. I was particularly glad to attend some of the Hannah Arendt meeting at the Einstein Forum and to hear a discussion of many of the issues that had preoccupied me. This was followed up by further discussion at one of the Thursday evening dinners.

The work with my colleagues in the evolutionary biology *Schwerpunkt* (Steve Frank, Yoh Iwasa and Mark Pagel) went exceedingly well, and I present a few highlights below. To my surprise, the no-book library was wonderful, I have never read so much so quickly. This amazing service is likely to become redundant in just a few years, since I can now get about twenty-five per cent of the journals I want on the Web (try http://www.janet.idealibrary.com, if only the Wissenschaftskolleg was a registered user!). I also had some interesting diversions into vision research with Mandyam Srinivasan, even leading to setting up a secret laboratory in the Villa Jaffé. However, our stalk-eyed flies never behaved as they were supposed to, so the mysteries of their stereo vision remain. I feel more ambiguous about the *Dienstags-Kolloquia.* Many of the presentations were excellent and I learnt a lot. But is it really necessary to read a paper? What's wrong with visual aids? Let's have clearly stated hypotheses, evidence and conclusions. I feel that in these respects the humanities lag well behind the sciences.

An attempt was made to bring the humanities and sciences together with the Biology and Culture group. But this was not entirely successful. I'm not sure why. Despite the enthusiastic contributions from Heinrich von Stietencron and Bernard Williams, few attended, particularly from the humanities. Was this a real lack of interest or the many other attractions of Berlin nightlife?

Human imprints

The most fascinating discovery I made all year came about by chance. In May, the journal *Nature* published an article on the social behaviour of girls suffering from Turner's syndrome. These individuals have lost one of their sex chromosomes and have only a single X chromosome (women usually have two Xs). What was so striking about this report was the finding that individuals whose single X chromosome came from their mother were much more socially disruptive than individuals whose single X came from their father.

This is an example of imprinting: a gene showing different expression when paternally or maternally inherited. But what was really puzzling about this example was the way it jarred with the standard 'conflict' explanation of imprinting. The `conflict' hypothesis predicts that paternally inherited genes should be more aggressive and resource-demanding than maternally inherited genes, the reverse of the pattern observed.

On discussing this problem with Yoh Iwasa, we realised that this was not the only counterfactual. A similar pattern of an aggressive maternal X was known in mice (again uncovered in single X individuals). We have now proposed a new hypothesis to account for the patterns observed, namely that X-linked imprinting serves to control sex-specific genes expression. In turn, this has forced us to find another new explanation for the evolution of dosage compensation.

I don't want to go into these scientific arguments in depth; time will tell whether we are correct. But it is amusing to note how science works. The mouse example was well known. Yet it had been dismissed by leading exponents of the `conflict' hypothesis; it had to be wrong because it did not tie in with the theory. Unfortunately the reverse was true: another `ugly fact destroying a beautiful theory'. But I don't blame my colleagues for hanging on. There is little point changing your mind until a better theory comes along.

It is also amusing to recount how the Kolleg reacted. The findings were widely reported in the press as a clear demonstration of the genetic basis underlying sex differences. As males always get their single X from their mothers, this may explain why males on average score lower on tests of social skills. The most common reaction I heard was — well isn't that obvious, of course there must be a genetic basis to sex differences in behaviour. Others seemed shocked, what about the environment, surely it was just another wild claim by a scientist desperate for publicity and grants. The old division genes vs. environment rumbles on, but at last we have a sound example. I can't see the point in seeking explanations outside science before taking a good look at the evidence.

Mate choice

The main topic I worked on this year was sexual selection. This work was done in collaboration with Yoh Iwasa, an extension of joint work going back to 1989. Our pattern of working together has been short intensive meetings, a burst of e-mailing to complete manuscripts, followed by quiescence and the shelving of half-thought-out projects. We have always had many more things to work on than we could complete. A year at the Wissenschaftskolleg has made this problem greater than ever. But some matters have been cleared up.

I now feel that we have a much better understanding of how mate choice contributes to speciation. Sexual characteristics like male songs, colour patterns and courtship displays are highly variable. Closely related species often differ markedly in their sexual traits but hardly at all in their ordinary, non-sexual traits. I recommend looking at the ducks in any of the lakes surrounding the Wissenschaftskolleg in the Spring. What evolutionary force generates this diversity?

One of the major forces causing the evolution of female mate preferences for male sexual ornaments is Fisher's runaway process. Fisher suggested that the advantage of female preference lies in the choice of a male who will father attractive sons. If females on average prefer a particular male trait, for example a long tail, then males with that trait have higher fitness because they get more matings. Females with the preference are also fitter, because their sons tend to inherit long tails and so also enjoy a mating advantage. As a consequence, both the preference and the male trait will increase in strength together.

Fisher formulated his idea in the 1930s. He interestingly suggested that runaway would occur in a boom-bust manner, as female preferences came and went through evolutionary time. In 1995, we provided the first mathematical treatment of this possibility, showing that runaway naturally leads to continual evolutionary change under very general conditions (rapidly increasing selection against further exaggeration of male traits and costly female preference). Runaway causes semi-stable exaggeration of a preference for a male ornament. Then preference slowly declines (as it is costly) until eventually runaway in another direction is triggered, and the whole process repeats itself.

We extended our analysis to the more realistic situation where there are several different preferences for different male traits (e.g., song, dance, long tail, coloration). With multiple preferences and multiple ornaments, the number of possible states increases greatly. So rather than simple cycles, we find a complex switching between different sexual phenotypes through evolutionary time. The analysis shows that the relative stability of different traits varies. Some change very frequently, others are stable through evolutionary time.

The point of our modelling is to allow predictions to be made about how separate populations evolve under sexual selection. The model predicts that small environmental differences are quickly amplified into large population differences in sexual characters. So the sexual phenotypes of separate populations will diverge within a short period of time. Since sexual preferences will cause sexual isolation, this diversity will lead to speciation if the two populations come into contact.

Cuckoos

One of the more peculiar sights of animal behaviour is that of a host bird (e.g., dunnock, warbler) rearing the chick of the European cuckoo. The parasite chick is much larger than the host adult, and looks and acts nothing like the host's own young. Moreover, the host behaves in this solicitous manner even though the cuckoo chick has killed all its brood. Hosts show no glimmer of recognition that they are being duped. Why not?

With Mark Pagel, who visited intermittently as a guest of the Rektor, I investigated models to explain how cuckoo hosts evolve to accept parasite chicks. Our approach was to find an explanation in terms of natural selection for non-ejection of parasites, to show that selection can favour what at first glance appears to be severely maladaptive behaviour.

Using game theory models we found that non-ejection can evolve in the presence of cuckoos that retaliate against hosts that eject their nestlings. First consider how cuckoos evolve. Retaliation by cuckoos is favoured so long as it is easy for them to detect whether a host has ejected their chicks and if their retaliatory behaviour creates new opportunities for them to parasitise nests. Both conditions appear to be met in the European cuckoo which regularly revisits its nests in which it lays its eggs. Retaliation is probably a simple extension of normal cuckoo behaviour of depredating nests that do not contain cuckoo eggs (Wyllie 1981). This behaviour forces the host to re-lay thereby creating a new opportunity for the cuckoo.

Now consider the host. Non-ejection of the cuckoo chick can evolve if it brings future benefits. Our hypothesis is that hosts can recoup the costs of rearing the cuckoo's chick by enjoying a reduced rate of parasitism of their second clutch. This requires that non-ejectors have sufficient time to rear a clutch of their own following the rearing of a cuckoo nestling. The breeding dates of cuckoos and some of their hosts supports this possibility. Also it must be the case that hosts who eject the cuckoo's chick suffer. This requires that they are re-parasitised at relatively high rates. The one piece of experimental data shows that this is the case.

The role of theory in this area is to open up discussion. It is surprising how little attention the problem has attracted. Most cuckoo biologists have sidelined the problem. Our theoretical treatment makes distinct predictions that ought to stimulate empiricists. The next question we need to address is why hosts often discriminate against cuckoo eggs whilst accepting cuckoo chicks. We started work on this with Yoh Iwasa. Finally we also suspect that there are many other examples where retaliatory parasites select for a lack of host response. Now we have a good understanding of one system, it should be easier to know how to interpret other cases where pathogens became virulent in response to attack by the immune system or where hosts appear to tolerate pathogens without response.