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The cleverest man I never met

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Peter Medawar who was himself a brilliant scientist said that J. B. S. Haldane was the cleverest man he had met. For my part I never came face to face with Haldane. I feel, though, that I have some connection with him through my kinsman William Bateson who coined the term 'genetics'. This Bateson died before I was born but he was talked about a great deal in my family and it was on the strength of what I learned about him that I set my heart on becoming a biologist, though in the end I became a behavioural biologist not a geneticist. William Bateson met Haldane several times and commented extensively on one of Haldane's papers, especially Haldane's Rule paper which appeared in *Journal of Genetics* in 1922 (Cock and Forsdyke 2008). Thus, I do have a connection with Haldane through my kinsman.

I heard a lot about Haldane from John Maynard Smith whom I knew well. The intellectual relationship between Haldane and Maynard Smith was strong. Haldane regarded Maynard Smith as one of the few people who understood his papers. While Haldane and Maynard Smith were good friends, the relationship was surprisingly impersonal at least to modern eyes. Maynard Smith said that he continued to call Haldane 'Prof.' and Haldane called him 'Smith' until they finally parted. Maynard Smith told me about Haldane's explosive temper which he had experienced himself. After the person to whom he directed his anger left the room feeling hurt and upset sometimes for days on end, Haldane would immediately return contentedly to his thoughts and his pipe, having put the unpleasant encounter totally out of his mind. In one way they differed intellectually. Haldane saw Darwinian evolution as a fascinating puzzle which he would think about from time to time but it was only one of a range of challenges he considered. For Maynard Smith's part adaptation raised almost every question that he sought to answer.

*Prof. Patrick Bateson passed away on 1 August 2017, and this article is published posthumously.

Beanbag genetics

Ernst Mayr (1963) criticized the view that evolutionary process could be usefully explained by what he called 'beanbag genetics'. The term came from the early geneticists' practice of keeping coloured beans in bags as a way of tracking Mendelian ratios. Mutation, or more generally the replacement of one allele by another, was the exchange of one kind of bean for another. Mayr disliked the way the great founders of population genetics, Haldane, Fisher and Wright, treated genes as independent entities to simplify their mathematical analyses. He wrote: 'Work in population and developmental genetics has shown, however, that the thinking of beanbag genetics is in many ways quite misleading. To consider genes as independent units is meaningless from the physiological as well as the evolutionary view point.'

Haldane (1964) was quick to respond to Mayr. He gave many examples of how the beanbagers had proved successful in understanding evolutionary processes. He conceded that the approach did not explain the physiological interactions of genes and the interaction of genotype and environment but went on: 'The beanbag geneticist need not know how a particular gene determines resistance of wheat to a particular type of rust, or hydrocephalus in mice, or how it blocks the growth of pollen tubes in tobacco, still less why various genotypes are fitter, in a particular environment, than others. If he is a good geneticist he may try to find out, but in so doing he will become a physiological geneticist. If the beanbag geneticist knows that, in a given environment, genotype *P* produces 10 per cent more seeds than *Q*, though their capacity for germination is only 95 per cent of those of *Q*, he can deduce the evolutionary consequence of these facts, given further numbers as to the mating system, seed dispersal, and so on.' Haldane complained that Mayr's arguments were always verbal rather than algebraic. He wrote that he had complete mistrust of verbal arguments in evolutionary theory where algebraic arguments were possible. Mayr (1982) subsequently maintained his original critique, emphasizing the importance of the interactions between genes that muddies the theoretician's algebra.

Another great biologist, C. H. Waddington (1953, 1968), took the same position as Mayr. He regarded the mathematical treatments of Fisher and Haldane as drastically oversimplified, taking no account of developmental processes. He emphasized that the study of these processes, which he called epigenetics, was crucial for understanding evolution. Haldane had dealt with this point when responding to Mayr. Moreover, he and Waddington were much closer together intellectually than might at first have seemed. They had jointly published an important paper together (Haldane and Waddington 1931) and independently Haldane wrote a piece that could easily have been written by Waddington. He wrote, 'What is inherited is not a set of characters, but the capacity for reacting to the environment in such a way that, in a particular environment, particular characters are developed', (Haldane 1949).

The difference between the Mayr–Waddington position and that of Haldane and other population geneticists has been discussed extensively by Rao and Nanjundiah (2011). In part the difference in positions between the epigeneticists and the population geneticists, which persists to the present day, boils down to whether Darwinian evolution acts on genotypes or on phenotypes. Genetic determinism has largely disappeared as an overt issue but remains covertly in the writings of many biologists (see Noble 2016; Bateson 2017).

Kin, groups and Darwinian evolution

I am a behavioural biologist and have not been a close follower of Haldane's thinking about genetics. However, one of his quips is well known in my field. After an informal calculation made in a London pub, he declared that he would lay down his life for two brothers or eight first cousins (later published in Haldane 1955). Individuals will often put themselves at risk and do things that are bad for their health in the production and care of offspring. Bill Hamilton generalized this point to collateral relatives and in an extensive theoretical argument produced a much-quoted rule for what is known as 'kin-selection' Hamilton (1964). Hamilton argued that self-sacrificial behaviour would tend to evolve when $C < rB$, where C is the fitness cost to the actor; r, the genetic relatedness between the actor and the recipient; and B, the fitness benefit to the recipient.

The overall fitness of an individual is known as its 'inclusive fitness'. Hamilton's formulation holds if the difference between the presence and the absence of the self-sacrificial tendency is associated with a difference in a single gene. If it were two genes, presumably Haldane, by his self-sacrifice, would have needed to save at least four brothers or 64 first cousins. Some caution is required, therefore, when evolutionary arguments are applied without thought being given to developmental biology. Hamilton (1996) recognized that the value of r was not simply based on a genealogical closeness but could depend on overall similarities. The gene-based approach assumes that the products of crucial genes do not interact. If they do, as seems highly likely in many cases, the calculation of genetic similarity (r) is affected and will tend to have a much lower value than would be calculated from simply knowing, say, that the actor and the recipient were cousins (Bateson 2014).

Major controversy has been stimulated by some theorists questioning whether kin -selection has ever occurred and favouring instead a form of group selection (Nowak and Highfield 2011; Nowak *et al.* 2010). The threat to what had been regarded as a well-established principle evoked a furious rejoinder from a large contingent of evolutionary biologists and behavioural ecologists (Abbot *et al.* 2011). Birch (2014) suggests that the critics of kin -selection based their argument on a special version of the theory, derived from game theory, and their adversaries based theirs on a general version derived from the partial regression coefficients for a statistical formulation of the evolutionary process. Instead of chiding each other for being confused the theorists should start listening to what has been proposed by their opponents. My sense is that while the special version is probably incorrect, the general version does describe what may have happened in evolution, subject to no interactions occurring between the genes necessary for the expression of altruistic behaviour.

In the most recent edition of a justifiably famous text book, Davies, Krebs and West (Davies *et al.* 2012, p. 428) wrote: 'The new group selection approach tells us that cooperation is favoured by: increasing group benefits; reducing individual cost; and increasing the proportion of genetic variance that is between-group as opposed to within-group. However, this is mathematically equivalent to the prediction from Hamilton's rule that altruism is favoured by high B, low C and high r.'

In one sense they and others before them (e.g. Grafen 1984; Gardner and Grafen 2009) were certainly right in that cooperating groups are likely to be much more closely related to each other than they are to members of groups that do not cooperate so effectively. In another sense, though, they missed the point that the character that makes one group more likely to survive than another is a property of the whole assemblage and not of the component individuals if, as I believe, Darwinian evolution acts on the phenotype rather than on the genotype.

Spalding and behavioural imprinting

One of Haldane's contributions impacted my own field of research which has been on behavioural imprinting in birds. The field had been made famous by Konrad Lorenz in the 1930s. Sometimes he paid credit to his mentor the zoologist Oskar Heinroth, but more frequently he described himself as the 'discoverer' of imprinting. Haldane (1954) published a short piece prior to reprinting an article by Douglas Spalding (Spalding 1873). Spalding acted as a tutor to Bertrand Russell's brother and was much loved in the Russell family. He died from tuberculosis when still a young man. In his short life he carried out experiments on imprinting some 60 years before Lorenz. Why should Haldane have been interested in this fact? The answer may be provided by an observation of Desmond Morris. He had stood in for his research supervisor, Niko Tinbergen, at a small elegant conference in Paris on instinct organized by Pierre-Paul Grassé in 1954. The conference was attended by prominent European ethologists headed by Konrad Lorenz, by the critics of ethology, and by Haldane together with his wife Helen Spurway. Morris noticed that Haldane and his wife kept themselves apart from Lorenz and his wife. Morris asked them, what was the matter? Spurway revealed that she had an affair with Lorenz (Kohn 2004). The affair, which started in 1949 and lasted for fully a year, had been conducted, it seems, with Haldane's awareness and even approval (Burkhardt 2005, p. 390). The political and emotional aspects of the affair were intriguing. Lorenz had been an ardent supporter of the Nazi regime in Germany, and Haldane and his wife were Marxists at the opposite end of the political spectrum. Haldane may have entered into the history of imprinting as a result of the ideological differences and as a way of exacting revenge on Lorenz, for his affair with Helen Spurway, by puncturing his pride about being the discoverer of imprinting. Whatever Haldane's motives were at the time, his historical research has been important for those of us who have studied behavioural imprinting. Subsequently Haldane and Spurway were highly critical of Lorenz's view that behaviour was either learned or instinctive, and, in doing so, made substantial contributions to behavioural biology (Griffiths 2004).

Conclusion

I wish that I had known Haldane, even though the experience of meeting him might have been challenging. His thinking was as wide as it was deep and would have provided stimulation and profit to any biologist. Haldane and Waddington, another hero of mine, did meet, worked together, and shared much more in common than might have seemed at first. The controversy over beanbag genetics stemmed from a misunderstanding about the benefits of what can be learned by simplifying the developmental process. Haldane was clear about the value of a developmental approach and his writing complemented that of many ethologists and comparative psychologists who were abandoning the old learned/instinctive dichotomy. Again Haldane foreshadowed the enormous growth of interest among behavioural biologists in the evolution of cooperation and self-sacrificial behaviour. And this was only a fraction of what he was thinking about. Altogether he was a very remarkable man.

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