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ESSAY

A gene mutation which changed animal behaviour: Margaret Bastock and the *yellow* fly

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In 1956, Margaret Bastock published the first demonstration that a single gene could change a behaviour pattern. A Ph.D. student with Niko Tinbergen, Bastock's work was partly inspired by discussions between Tinbergen and the American evolutionary biologist, Ernst Mayr. In this essay, the genesis of Bastock's work is outlined, including reference to archival correspondence between Mayr and Tinbergen, and she is given the credit for developing the study of how a mutation can affect a behaviour pattern. Her paper is described and put into contemporary context, including an analysis of its impact in the 1960s and beyond. Finally, the implications of this study for modern investigations into the genetic bases of behaviour, from behavioural ecology to neuroscience, are discussed.

Keywords: *Drosophila*; *yellow* mutant; Bastock, Margaret; Mayr, Ernst; Tinbergen, Niko; history of science; behaviour

Virtually all science that relates to behaviour, be it behavioural ecology, evolutionary biology or neuroscience, is now based on the assumption that genes can directly affect behaviour. Few people, however, realize that the first clear demonstration of a relation between a single gene and a behaviour was published 50 years ago, in an article in the December 1956 issue of *Evolution*: 'A gene mutation which changes a behavior pattern'. Furthermore, this boldly titled article was not the product of an American molecular biology laboratory, but came from the heart of postwar ethology: Niko Tinbergen's animal behaviour group in Oxford, U.K.

This study, by Tinbergen's Ph.D. student Margaret Bastock (Fig. 1), examined the effects of the *yellow* mutation on courtship in *Drosophila melanogaster*, and heralded the beginning of a shift towards the kind of reductionist, causal explanations of behaviour that are commonplace today. Looking at the place of this article in the history of the study of behaviour shows parts of the path that took science from then to now. It also reveals some of the strengths and weaknesses of our predecessors, both of which may cast light on our current ideas and approaches.

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Bastock, who was 31 years old at the time, was a mature postgraduate in Niko Tinbergen's animal behaviour laboratory in Oxford (Kruuk 2003); as with so many people of her age-group, her academic career had been severely affected by World War II. In Bastock's case, her undergraduate studies had been interrupted while she worked for the BBC during the war, before returning to Oxford to complete her degree in Zoology. She joined Tinbergen's laboratory as a Ph.D. student, and became a member of the recently founded St Anne's college. Among her many research interests, she worked on displacement activities as evidence of conflicting drives within animals; together with Desmond Morris and Martin Moynihan, she wrote an important paper on the subject which continues to be cited (Bastock et al. 1953).

Most people in Tinbergen's team studied vertebrates (birds or sticklebacks) and aimed to understand behaviour in its natural context. Bastock's doctoral research, which she had begun by 1950, was very different: it focused on a fly, was a classic laboratory study (we still know little about what *Drosophila* get up to in the wild, Reaume & Sokolowski 2006) and directly investigated the role of genes in behaviour. Despite these differences in approach and interest, Bastock was a key member of the Tinbergen laboratory's 'Hard Core': a group of students and postdoctoral researchers who would meet every Friday evening at Tinbergen's house (Burkhardt 2005; Manning 2005). This

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Figure 1. Margaret Bastock, in the late 1950s. © Aubrey Manning. Reproduced with permission.

informal grouping was a focus for much of the excitement and dynamism that characterized the Oxford group, as ideas and recent discoveries were debated late into the night.

Up until the 1950s, evidence for a genetic basis to behaviour generally came from observations of the differences between strains or breeds (e.g. Keeler & King 1942). Bastock's research used the power of *Drosophila* genetics and the behavioural outlook of the Tinbergen group to take a step beyond this relatively simple approach and to identify a behavioural change with an alteration in a single gene.

Bastock's work followed on from two previous investigations of the role of genes in *Drosophila* behaviour, both relating to mutations affecting body colour. The *yellow* mutation, which gives the fly's cuticle a golden hue, was part of the first wave of mutants to be described at the dawn of genetics by the Morgan laboratory (Kohler 1994); Morgan's student, Alfred Sturtevant, soon noticed that the courtship behaviour of *yellow* males tended to be less successful than that of their wild-type counterparts (Sturtevant 1915). After World War II, Jim Rendel, working at Waddington's Institute of Animal Genetics in Edinburgh, U.K., reported similar findings on *yellow* mutants in *Drosophila pseudoobscura* (Rendel 1945), and went on to look at the effect of *ebony* and *vestigial* mutations on mating in *D. melanogaster* (Rendel 1951). However, none of these studies provided any insight into why these mutant males were less successful; the relation between genotype and behavioural phenotype remained elusive. Tinbergen's laboratory, with its emphasis on detailed analyses of behaviour, was the right place for such a relation to be studied.

The inspiration for Bastock's pioneering work apparently came from the leading American evolutionary biologist, Ernst Mayr. At the end of 1946, Tinbergen had made a 3-month visit to the U.S.A., at Mayr's invitation. Two of the main consequences of this visit and the subsequent correspondence between the two men were Tinbergen's growing interest in evolutionary problems and his decision to follow Mayr's suggestion of studying the behaviour of *Drosophila* (Burkhardt 2005) (Mayr himself had just published a study on 'the nature of the isolating mechanisms between *Drosophila pseudoobscura* and *Drosophila persimilis*', Mayr 1946). In a letter written to Mayr on 4 September 1950, Tinbergen outlined Bastock's project and described his hope that he would continue with *Drosophila* work, before concluding 'You see, I took your advice to heart' (Tinbergen 1950a).

Interestingly, Tinbergen, Mayr and Bastock all approached the idea of studying *Drosophila* from different angles. For Mayr, the main question was the role of behavioural 'isolating mechanisms' in evolution. Tinbergen, on the other hand, was keen to develop a new tool for the comparative study of behaviour. Margaret Bastock's vision went beyond both these approaches, as she sought to investigate the role of a gene in behaviour. This was particularly bold, at a time when the nature of the gene was still unknown, and in some quarters its physical reality was still disputed (Morange 1999).

THE STUDY

The ethological tradition, which Tinbergen and Lorenz had established over the previous two decades, often focused on producing an 'ethogram': an extensive account of the behaviours that could be seen in a given context. Together with her fellow student Aubrey Manning (whom she married in 1959), Bastock therefore came up with a description of *Drosophila* courtship. Their interpretation, published in 1955, at around the same time Bastock received her Ph.D., was based on the drive-focused view of behaviour that predominated at the time (Bastock & Manning 1955).

Dividing courtship into three phases based on distinctive male behaviours, orientation, vibration and licking, Bastock & Manning (1955) argued that each phase corresponded to an increasing level of excitation. As the male became more excited, another courtship element would be added until, in the final phase prior to mating, he would perform all three elements. One obvious weakness was that the model emphasized the role of male behaviour, which is much easier to identify than that of the female. However, this is still an acknowledged gap in our understanding of *Drosophila* behaviour (Billeter et al. 2006), and Bastock, to her credit, did attempt to address this fundamental issue in her 1956 article by studying female responses to different types of male.

Bastock & Manning's (1955) choice to focus on their three-level operational description of courtship behaviour contrasted with the descriptive, category-rich analyses provided a few years earlier by Spieth (1952) in his survey of courtship in over 100 species and subspecies of *Drosophila*. Their model was also very different from the caricature of field-influenced ethology that many of today's students might imagine was carried out in Tinbergen's laboratory. Above all, the three-level model lent itself to quantitative