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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 analysis, which was at the heart of Bastock's project. These quantitative data were to be used to address the links between behaviour, genetics and evolution. As Bastock put it in the Introduction to her 1956 article (page 421), the two questions that interested her were how a gene that affects behaviour produces such an effect ('this is of considerable genetical interest' she wrote), and what part such a gene might play in evolution ('this is of considerable evolutionary interest').

To investigate the function of different components of courtship, Bastock first looked at the role of wing vibration and of visual signals in wild-type flies by removing male wings and using *antennaless* females, and by placing flies in the dark. Wingless males and *antennaless* females both showed lower fertilization levels, suggesting that vibration was an important aspect of successful wild-type courtship. She then turned her attention to *yellow* courtship, having first eliminated genetic background effects by crossing her wild-type and *yellow* lines for seven generations, and then studying the F2 offspring of a final cross between the two lines. This crucial step (which had been suggested by Mayr in a letter to Tinbergen, Mayr 1950) not only enabled her to be certain that the effects were due to the *yellow* mutation (or 'closely linked genes' as she rightly put it), they also reveal a degree of genetical clear-thinking that is still sometimes lacking in studies of the genetics of behaviour.

To quantify courtship, Bastock used an ingenious procedure. With a grant from the Nuffield Foundation, she bought a reel-to-reel tape recorder, and then spoke into a microphone and described what the flies were doing, in time to a metronome that ticked every 1.5 s, for 100 ticks (2.5 min). The tapes were then transcribed and turned into numerical data, presented either as a simple diagram (Fig. 2), or as tables showing the percentage of each observation period spent in orientation, vibration and licking. The results showed that *yellow* males performed significantly fewer bouts of vibration and licking than wild-type males, and that the average duration of these behaviours was shorter. As Bastock pointed out, this was the first time that a single gene had been shown to control the frequency of a behaviour.

Despite this apparently clear result, Bastock astutely recognized that there might not be a direct relation between the mutation and the 'deficient' courtship of the *yellow* male. 'A male's courtship behavior is never an entirely automatic process,' she wrote; 'it is determined, at least in part, by the stimuli received from the courted object. It is therefore quite possible that a female, reacting against the changed appearance or scent of a yellow male, may either fail to give attractive stimuli or give instead repelling stimuli. Thus the male's deficient courtship behavior may be explained simply as a different reaction to different stimuli, and there may be no fundamental difference between the two males in this respect at all' (Bastock 1956, page 427).

A possible source for questioning the apparent predominance of a male effect was Ernst Mayr, who in late September 1950 wrote to Tinbergen about Bastock's work: 'I am somewhat surprised that he [*sic*] seems to find the males so almost exclusively responsible. I didn't make a very detailed examination myself but, on the basis of casual observation, I gained the impression that the frequency of attempted copulations by yellow males was about as great as that of wild type males' (Mayr 1950).

However, Bastock's keen awareness of the interaction between the sexes, and of the difficulty of identifying a particular character solely with one partner, was undoubtedly the product of the attention to behavioural detail that was characteristic of Tinbergen's work. It must have been influenced, even unconsciously, by the widespread study of bird behaviour in Oxford, in which assumptions about the 'automatic' nature of behaviour, even in insects, would have been less strong. This relatively subtle view of the nature of 'instinct' which

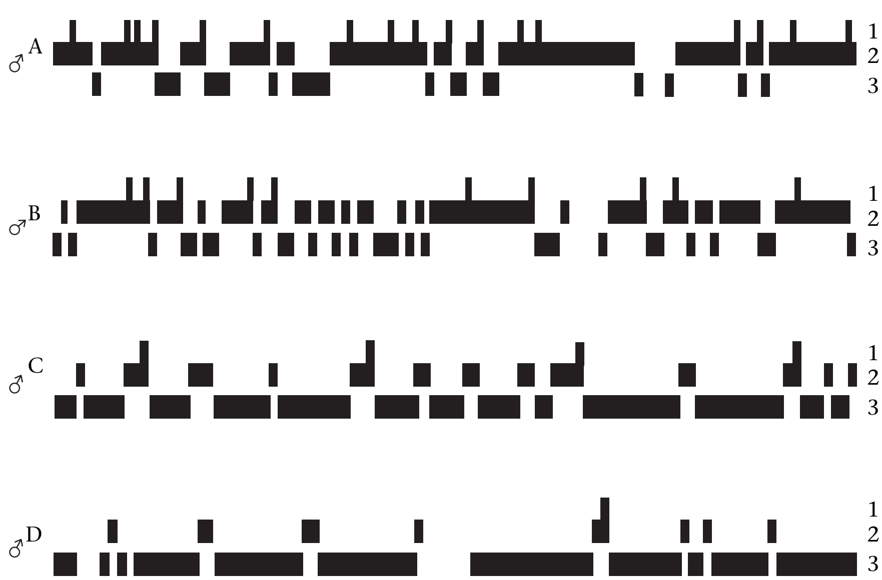


**Figure 2.** Figure 2 from Bastock (1956), showing three courtship behaviours (1: licking; 2: vibration; 3: orientation) performed by four male *Drosophila melanogaster* flies. © Society for the Study of Evolution. Reproduced with permission.

prevailed in Tinbergen's group would prove to be important when criticisms of the very concept began to arise (see below; Griffiths 2004).

To test her hypothesis that females might be discriminating against *yellow* males, Bastock studied the behaviour of females in response to courtship by wild-type and *yellow D. melanogaster* males. There were no significant differences in the responses of the females to the two types of male, suggesting that whatever effect the *yellow* gene was inducing, it was not altering the observable behaviours of the female. Returning to the more obvious interpretation that *yellow* was directly and pleiotropically affecting male behaviour, Bastock interpreted the shorter bouts of vibration shown by *yellow* males as evidence that the mutation had lowered their 'sexual motivation', which in turn could occur through a peripheral change in some sense organ detecting stimuli from the female. To illustrate her point she presented a diagram showing how regular fluctuations in 'motivation' could lead to different bout lengths of behaviours, assuming that the thresholds of 'motivation' required to perform each behaviour were constant (Fig. 3).

Finally, Bastock discussed her findings in terms of the evolution of behaviour, analysing how such a character might spread in a population, in particular if a group of individuals were isolated. The two questions she had posed at the outset, the genetic control of a character and its evolutionary impact, were answered in the results of her study and in her discussion of their implications. In so doing, she also satisfied both Mayr, by looking at the role of potential behavioural 'isolating mechanisms', and Tinbergen, by integrating her findings with those on other *Drosophila* species, in a comparative framework. Strikingly, however, she did not try to interpret *Drosophila* courtship and mating behaviour in terms of sexual selection, except in the broadest sense of one sex potentially discriminating against members of the other.

As it happens, the exact link between the *yellow* mutation and the behavioural phenotype studied by Bastock remains unclear. Over the last half century, a number of explanations have been put forward, including pleiotropic effects of *yellow* on both catecholamine biosynthesis (Burnet et al. 1973) and cuticle strength (Wilson et al. 1976). A more direct effect now seems probable: Drapeau et al. (2006) have suggested that the effect of *yellow* on male wing extension is produced by a 300-bp regulatory region that exerts its influence during larval life. They even speculated that *yellow* might be a target of one of the key genes involved in *Drosophila* courtship, *fruitless*.

Although this brings us closer than Bastock could ever have imagined to the relation between mutation and mating phenotype, she would doubtless have been amused and amazed to discover that, half a century later, we still do not know exactly what is going on. Having finished her Ph.D., Bastock continued to work on *Drosophila* for some years, and went on to write an influential book on courtship behaviour (Bastock 1967). Together with Manning, she moved to Edinburgh in the early 1960s, where she eventually studied child development and aggressive behaviour. She died of cancer in 1982.

## THE CONSEQUENCES

The importance of Bastock's work can be seen from its title: this was the first time that a single gene had clearly been shown to affect a behaviour. By fusing the ethological rigour of the Tinbergen tradition with the genetic outlook that was beginning to dominate biology, Bastock helped create the context that led to the development of the gene-centred view of behaviour that currently predominates in behavioural ecology and indeed virtually all studies of behaviour. More directly, by showing that a single gene could have a relatively straightforward effect on a complex behaviour, Bastock's study of *yellow* paved

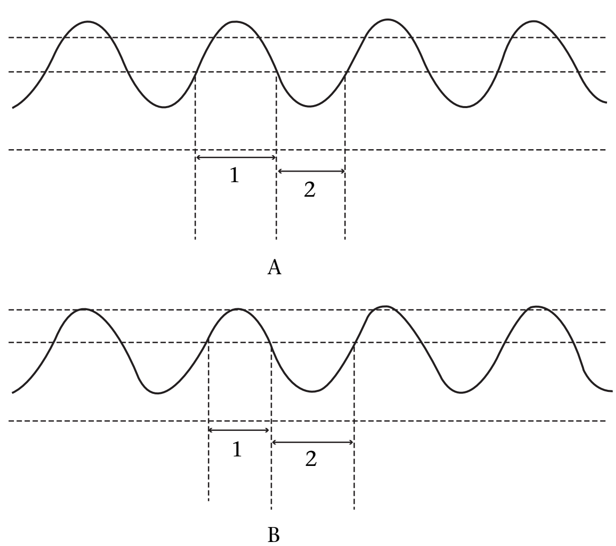


**Figure 3.** Figure 7 from Bastock (1956), showing her interpretation of her data on courtship patterns in terms of fluctuating levels of sexual motivation. When average motivation is high, courtship is typical of wild-type males (A); when it is low, courtship is typical of *yellow* males (B). Bout durations of vibration and licking (1) and of orientation (2) are indicated. © Society for the Study of Evolution. Reproduced with permission.

the way for the development of *Drosophila* neurogenetics, which began a decade later in Seymour Benzer's Caltech laboratory and which has had such a major influence on the genetic study of behaviour, and, more generally, on neuroscience (Greenspan 1990; Roberts 2006).

Benzer implicitly acknowledged this debt in the opening paragraph of his first article on *Drosophila* behaviour (Benzer 1967), in which he highlighted Aubrey Manning's recent review of the literature (Manning 1965). But there was no explicit recognition of Bastock's work: none of the 190 citations of Bastock's article to be found in the ISI Web of Science database are directly from Benzer's laboratory. This is because Benzer's group did not study mating behaviour, but focused instead on novel phenotypes such as phototaxis, circadian rhythms or learning, all of which were more amenable to screening for new mutants than mating behaviour. As Benzer's ex-students and ex-postdocs subsequently turned their attention to courtship, Bastock's article was eventually cited (e.g. Hall 1978; Quinn & Greenspan 1984). However, the immediate citation impact of the study was on those, primarily in the U.K. and principally in Edinburgh, Sheffield and Birmingham, who worked on *Drosophila* sexual behaviour, and on those who were proselytising for the new discipline of behaviour genetics (e.g. Fuller 1960).

One explanation for the relative lack of interest shown in Bastock's work in the 1960s may lie in its theoretical framework. In the 1950s, ethology's early emphasis on drives, motivation and instinct, partly borrowed from psychology and enjoying an intuitive validity, was the subject of growing criticism. Lorenz's notion of drives was attacked by Lehrman (1953), while Hinde (1960) similarly questioned the usefulness of 'energetic' models of motivation. Lehrman's (1953) critique, and in particular his arguments against Lorenz's distinction between learned and instinctive behaviours, was rapidly adopted by the Tinbergen group, suggesting a degree of observational and genetic sophistication (Griffiths 2004).

In his letters to Mayr describing Bastock's work, Tinbergen used drive concepts, talking of 'the mating drive' and a 'sub-drive' (presumably male wing vibration, Tinbergen 1950a, b). Strikingly, Bastock, writing after Lehrman's (1953) paper had been published, did not use this terminology in her article. However, she still relied on the 'energetic' conceptual framework, as shown particularly clearly in her model of fluctuating motivation leading to different behavioural durations (Fig. 3). Although this merely reflects contemporary theoretical developments (in this respect Bastock was simply of her time) it may have altered the way her paper was viewed even 5 years later. While her results still stood, regardless of her interpretation, what had become an old-fashioned theoretical framework must have rapidly aged the article in the eyes of many. This is, of course, the fate of all science: in general, it is our interpretation of the facts that changes as science progresses, not the facts themselves.

Although behaviour genetic work carried on in Tinbergen's group after Bastock had completed her Ph.D. research, in particular through Aubrey Manning and Bastock's Ph.D. student Stella Crossley, it was not oriented towards the single-gene approach highlighted in the study of *yellow*, and which proved so productive in the hands of Benzer. Instead, the focus was on the evolutionary implications of various aspects of courtship (this issue had been a major part of the Introduction and Discussion of Bastock's article), identification of the sensory modalities involved, and comparisons with other species, with selection being the main genetic tool (e.g. Manning 1965; Bastock 1967; Ewing & Manning 1967; for a personal account see Manning 1989). While this was more in keeping with the holistic approach cultivated by Tinbergen, it is surely the case that, from a purely heuristic point of view, the single-gene mutational approach favoured by Benzer has so far proved more productive.

One of the reasons that the search for identifiable genes involved in behaviour did not go much further in Tinbergen's laboratory might have been that the 'Maestro' (as Tinbergen was called by his students) was not particularly interested in the question. True, he enthusiastically described Bastock's work to Mayr in September 1950: 'A graduate student of mine is now studying the reproductive isolation between *Drosophila melanogaster* wildtype and yellow mutant and finds some very interesting things about the causes; in short, the mutant male has some differences in degree of strength of mating drive and of strength of a sub-drive, as compared with the wild-type male […] I think it gives some interesting facts on the effect of a relatively simple mutation on behaviour' (Tinbergen 1950a).

Tinbergen also light-heartedly claimed that he did not understand the genetic studies that he supervised (Kruuk 2003). More tellingly, in a long review entitled 'On aims and methods of ethology' (Tinbergen 1963), written by Tinbergen to celebrate Lorenz's 60th birthday, genetics is raced over in one brief paragraph, and Bastock's work is not cited at all. In fact, Tinbergen never cited Bastock's article, even when writing on such apparently related topics as his 1965 address on 'Behaviour and natural selection' (Tinbergen 1973).

This relative lack of interest in genetic studies of behaviour probably helps explain why Tinbergen missed out on one of the most important developments in the study of behaviour that took place in the 1960s, which gave rise to behavioural ecology. Although he was part of the informal discussion that coined the term 'kin selection' in the mid-1960s (Kohn 2004), Tinbergen later admitted to Bill Hamilton that he appreciated the importance of Hamilton's theoretical explanations of the evolution of social behaviour only after another of his Ph.D. students, Richard Dawkins, had published *The Selfish Gene* in 1976, by which time Tinbergen had both retired and won the Nobel Prize (Kruuk 2003).

This apparent blind spot in Tinbergen's outlook was not surprising when it came to understanding the mathematical detail of Hamilton's (1964a, b) dense papers (Maynard Smith also found it difficult, Kohn 2004), but it is striking that the relatively simple idea of studying a mutant seems to have left little trace on Tinbergen's work, even though the research was carried out by his student. *The Tinbergen Legacy* (Dawkins et al. 1991), which contains papers celebrating the impact of Tinbergen's life and work, accurately reflects this attitude, and does not refer to either behaviour genetics in general or the work of Bastock in particular.

In a way, this is quite understandable: 15 years ago, the focus was on the promise of behavioural ecology, which was rightly seen as one of the main consequences of Tinbergen's work. The framework of most studies in behavioural ecology is genetically reductionist, in that they assume that there is a relation (however indirect) between phenotype and genotype; the emphasis, however, is on estimating the evolutionary impact of that relation, rather than investigating its nature. In other words, behavioural ecology has generally centred on only the second of the two questions that Bastock addressed in her 1956 article: how genes affect behaviour, and what are the evolutionary consequences.

Half a century on, Margaret Bastock's work is beginning to look particularly prescient. As Owens (2006) has recently pointed out, behavioural ecology now finds itself increasingly needing to test the assumptions of its adaptive models by searching for the genetic bases of the observed behaviours. Insights into potential candidate genes may well come from model organisms such as the fly. *Drosophila* has already provided a number of striking examples in which genes that affect complex behaviours, such as circadian rhythms, learning and foraging, have turned out to have homologues that exert similar effects in other species (Rosato & Kyriacou 2001; Reaume & Sokolowski 2006). The same may even be true of the genes involved in courtship (Kyriacou 2002). Furthermore, studies of sexual selection and the ways the two sexes interact and attempt to manipulate each other have recently begun to return to *Drosophila* (e.g. Crudgington et al. 2005). They should be able to fulfil the unstated promise of Bastock's work and provide a rich theoretical context for understanding how individual genes interact to produce a behaviour of such profound evolutionary significance.

Whether or not the future identification of the genes underlying many animal behaviours will be directly enriched by the study of mutants, Bastock's work can serve as a model and as a salutary reminder of the kind of rich science we should aspire to. Her 1956 paper was characterized by clear-minded genetic analysis, rigorous behavioural observations, and an acute awareness of the importance of pleiotropy; these are precisely the features that will be decisive in future explanations of the evolution of behaviour. Both Margaret Bastock and Niko Tinbergen would surely have been pleased with this development, and with the long-term influence of their thinking and outlook on behaviour and the natural world.

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