The peppered moth: a black and white story after all

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Perhaps the most famous example of natural selection is the story of industrial melanism in the peppered moth. Recently there has been a sudden outbreak of disbelief in this classic story, even though no new experiments or even reanalyses of earlier data have been performed. Here I argue that these recent critiques almost entirely lack substance – a careful examination of all the data shows that evidence for natural selection on the peppered moth could hardly be bettered.

Peppered moth melanism – the classic story of natural selection in the wild

Among a number of examples of natural selection in nature, industrial melanism in the peppered moth has been perhaps the most iconic. The peppered moth story was, at least until recently, a key demonstration of natural selection used in almost every textbook of evolution. Briefly, in the industrial revolution, "melanic" or black forms of the peppered moth (*Biston betularia* – family Geometridae) became much more common than the typical pale form in polluted areas of Britain and elsewhere. From the 1890s onwards, biologists argued that the moths, which rest with their wings open on tree bark, are adapted in wing colour to the prevailing background (Fig. 1). This is a form of camouflage, because bird predators would be able to find the moths if they didn't match their background visually. When the trees are dark and sooty, the moths are better off being black; when the trees are soot-free or lichen-covered, they are better off pale and mottled.

JBS Haldane calculated long ago that the melanics must have had about 50% higher survival than typical mottled forms to explain the rapid rise in melanic gene frequency. In the last half of the last century, field experiments at 35 sites were performed by a number of scientists. These experiments directly demonstrated how bird predation affected the survival of adult moths, and demonstrated that the strength of natural selection was of the same order as that required by Haldane's calculations (Fig. 2). There is good geographic evidence for a tight correlation across Britain between the frequency of melanism and the degree of urbanization and smoke pollution. This relationship becomes even more convincing when one considers the considerable declines in frequency of melanism since the clean air acts of the late 1960s in Britain. These reversed selection pressures must have been of a similar order to those implicated in the original rise of melanism (Clarke et al. 1985). The peppered moth story is remarkably complete: it combines an easily-appreciated, visual form of selection, knowledge of the genes involved (albeit in the Mendelian, pre-molecular sense; see also True 2003 for an update on research towards understanding the evo-devo and molecular genetics of melanism), direct experimental demonstration, geographic correlation with the purported ecological causes, and direct observation of increase and decline of the phenotype in synchrony with the supposed selective agent – soot on tree bark.

The peppered moth story – refuted?

Today, suddenly, doubt that peppered moth melanism is due to bird predation is surfacing, and the story is even being dropped from textbooks. Serious scientists and the lay public alike are convinced by apparent new evidence that the story was false all along. This change in opinion dates only from the last few years. Why? This sudden change in our views of the peppered moth story is baffling, especially, as I will show, no actual new data have been produced to refute the earlier experimental work.

The seeds of doubt were probably sown by the maturation of the British ecological genetics school, considered by Lewontin to have resulted from a "genteel upper middle class fascination with snails and butterflies". It became more difficult to justify more basic studies of natural selection; people were beginning to be interested in the wrinkles and exceptions as well. My colleague Steve Jones (1982) epitomised this phase of the peppered moth story with a commentary entitled "More to melanism than meets the eye": he and others began to argue that non-visual selection could be important as well as camouflage. Mike Majerus's recent book "Melanism" (1998), which contains a long discussion of the peppered moth story, continues very much in this vein. This is hardly surprising. Writing about work mainly done in the 1950s to 1970s, Majerus needed a new angle to discuss in the 1990s. He therefore carefully laid out some unsolved problems about the exact mechanisms of selection. However, neither Majerus nor Jones, nor indeed any serious scientist knowledgeable about the field at this stage doubted the central idea that natural selection was caused by bird predation. To quote Majerus (p. 116): "In my view, the huge wealth of additional data obtained since Kettlewell's initial predation papers does not undermine the basic qualitative deductions from that work".

Differential bird predation of the *typica* and *carbonaria* forms, in habitats affected by industrial pollution to different degrees, is the primary influence on evolution of melanism in the peppered moth". These critics merely argued that other factors, such as thermal ecological effects of the same genes, might be involved as well, and might explain some of the scatter around the overall geographic and temporal trends in the evolution of melanism.

However, more aggressive criticism soon appeared in the scientific literature. Ted Sargent et al. (1998) argued that "there is little persuasive evidence, in the form of rigorous and replicated observations and experiments to support this explanation [i.e. bird predation as the agent of selection] at the present time." Notably, this maverick view was based not on new experiments, but on a sceptical re-evaluation by two Americans and a New Zealander of the largely British data.

The biggest bombshell, however, was dropped in a review of Majerus' book by Jerry Coyne (1998). Some quotations: "Majerus concludes ... that all we can deduce from this story is that it is a case of rapid evolution, probably involving pollution and bird predation". Note the contrast with the Majerus quotation above. Coyne continues: "I would, however, replace 'probably' with 'perhaps'. ... one senses [Majerus] is making a virtue of necessity. My own reaction resembles the dismay attending my discovery ... that it was my father and not Santa who brought the presents on Christmas Eve." "... for the time being we must discard *Biston* as a well-understood example of natural selection in action, although it is clearly a case of evolution".

This single book review, published in the journal "Nature", was enormously influential, and it was widely and in many cases wilfully misread as a rejection of the best-documented case of natural selection by a major evolutionary biologist. This was not intended at all. Coyne's statement, quoted above, was unfortunately worded. He meant, I think, that understanding of the causes ("action") of natural selection were still obscure, rather than that the rapid rise and then fall of melanism in the peppered moth was anything other than an excellent example of natural selection (Coyne 2002). But the damage was done: citations of Coyne's (1998) review, especially the part about Santa, soon appeared in anti-evolution literature. Recently, I found over 200 websites using search terms "Coyne, peppered", consisting mainly of creationist diatribes, or of evolutionary biologists' attempts to rebut the anti-evolution literature on this topic.

More recently, Judith Hooper's (2002) history of the peppered moth story has reopened this can of worms, and indeed prominently cites Coyne's review. Hooper's well-written, racy story of the British ecological genetics school, and of Bernard Kettlewell in particular, appeals particularly to laymen and was widely reviewed and discussed in media such as the London broadsheet newspapers. Kettlewell performed the prototype field experiments on the peppered moth, and Hooper's argument amounts to an allegation of fraud. Initially, in a 1953 field experiment, Kettlewell was getting poor recaptures. If this had continued, the experiment would certainly have been a failure, but the recapture rates suddenly went up soon after Kettlewell received an encouraging letter from the ecological geneticist EB Ford. Hooper searched the meteorological data for 1953, but found no evidence for a sudden change in weather to explain the increase in recaptures. Therefore, according to Hooper, the increase in recapture rates were highly suspicious. At first, Hooper asks, mildly (p. 118) "Is it possible that [Kettlewell] made modifications in his experimental design?" Although she doesn't directly answer this rhetorical question, Hooper has convinced herself a score of pages later (p. 136): “what had passed unnoticed by their peers for at least a decade, was that Bernard had done a little tweaking … in Birmingham in 1953”.

Hooper’s book is an excellent read, but I feel that this particular allegation, based on such slender evidence, is unfair. Hooper’s outlook is strongly influenced by friendly relations with Ted Sargent who, according to Hooper, had his career ruined by his iconoclastic views on the peppered moth. The possibility that opinions of Sargent might be largely a result of his failure to perform successful experiments to back up his negative take on bird predation does not seem to have occurred to Hooper. In any case, as Cook (2000) has demonstrated, even if Kettlewell was a fraud (and there is no good evidence that this was the case; see above), the other 30-odd experiments on survival of adult moths in the field done by different scientists are convincing on their own (Fig. 2).

One reason the melanism/bird predation story may be so prone to attack is that it is so neat and easy to understand. It’s too good to be true! At the same time it perhaps doesn’t gibe with most non-lepidopterists’ personal experiences. To me, a geneticist working on Lepidoptera, the convincing evidence for the class-ical explanation comes not just from the field experiments, but on the background natural history evidence from over 70 moth species, and in multiple geographic areas (Lees 1981, Clarke et al. 1985, Cook et al. 1986, Grant et al. 1998, Majerus 1998).

Experiments can prove selection at one time and in one place, but cannot prove the overall evolutionary hypothesis; for this, we must generalise from the experi-ments using comparative natural history data.

I am involved in another case of this kind. “Mimicry” is the situation where the wing pattern of one species of butterfly or other insect is a copy of that in a second distasteful species. The mimic thereby remains unmolested by visual predators that have learnt to avoid the distasteful species. Far fewer field experiments have been done to test for the selective advantage of mimicry than have been done on melanism in the peppered moth, yet I find the argument for mimicry in butterflies, proposed by Henry Walter Bates on the basis of extensive South American butterfly collections in 1862, absolutely convincing. It is almost incredible that anything other than visual predation could cause such perfect colour-pattern matching in unrelated species, and in such a geographically coherent manner. I conclude this article with some of the background information that makes industrial melanism so convincing.

The environmental backdrop of industrial melanism

I have never worked specifically on the peppered moth, but I know the species well and have trapped it and other moths with melanic polymorphisms in both industrial and non-industrial areas. I have also done serious field experiments on mimicry in *Heliconius* butterflies. Thus I feel qualified to comment on this topic.

For those readers who have never experienced coal-era industrial pollution, it may seem unlikely that environmental changes over the last couple of centuries can have been great enough to lead to rapid evolution of melanism and its recent, equally rapid decline. My own experiences suggest that there have been plenty. I spent part of my childhood in London during the 1960s. Our heating system was originally a messy coal-fired stove in the basement around which we huddled for warmth, although my parents soon installed in gas-fired central heating. Towering over our street was the tall chimney of the nearby hospital incinerator, which periodically released foul-smelling black vapours. Electricity was then provided by the coal-fired Battersea Power Station across the river, with its four giant chimneys belching smoke over our area (a photograph of this now derelict power station achieved new post-coal-era fame on the cover of Pink Floyd’s “Animals” LP). As a child, my handkerchief was always black from soot-stained snot, due to constant inhalation and subsequent condensation of sooty particulates on my mucous membranes. The walls of our house, and in fact the surfaces of every building or tree were covered in black grime and soot. My parents warned me not to put my head out of the open window of the then coal-fired steam trains in case a “smut”, or large clot of soot coming out of the smokestack, went in my eye. I was present in some of the last great “London Fogs” (more properly called “smogs”), when the air was so full of soot and other pollutants that it turned dark at midday, and visibility was down to a few feet. Today, the situation has radically changed: apart from the odd sulphurous inversion layer due to car exhaust, our windy and rainy climate together with a ban on coal or wood as fuels ensures that London has remarkably clean air. The soot on most buildings has long since been cleaned off, and the trees have all sloughed their black bark.

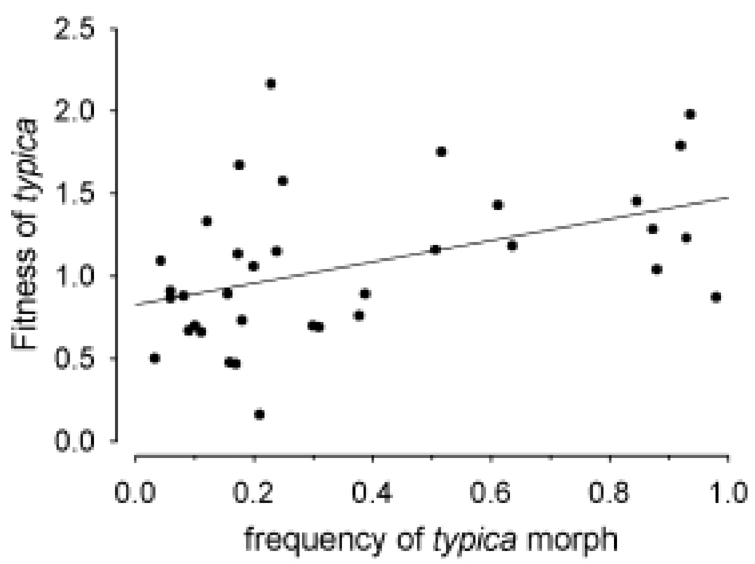
As a small child I don’t remember seeing many moths in Central London, but in the 1970s, when I went “mothing” with a friend in Hull in industrial E. Yorkshire, I was surprised to find it almost impossible to identify the local moths. Many of their colour patterns had been obliterated by melanism. This was particularly true of smaller noctuids (such as the “minors”, *Oligia* spp. – Noctuidae) and geometrids. Although experimental work has been done mostly on the peppered moth, over 70 other British moths show (or rather showed) industrial melanism (Lees 1981); this is not generally appreciated from the text-book accounts. Meanwhile, moths were much more distinguishable at other places I visited, such as rural Hampshire and Kent where the trees were covered in crustose and foliose lichens rather than soot, and the moths were usually brown, grey and mottled instead of uniformly black.

Fig. 1. Industrial melanism in the peppered moth. Dark forms of the British peppered moth (*Biston betularia*), as well as many other species of moth, became common in the middle of the 19th century near centres of industrial pollution. Soot coated the trunks and branches of trees, and killed lichens. In the photos, a pale form rests on a sooty background (above) and a dark form against a soot free background (below). Reprinted, with permission, from HBD Kettlewell, 1956, Heredity 10: 300.

Recently, reversals of melanism in industrial areas have been dramatic, and again not just confined to the peppered moth. The marbled beauty moth *Cryphia domestica*, for example, was said to have melanic forms that “predominate in London” (Skinner 1984: 122). The moth “may be found during the day on walls”, and its larvae feed “on lichens … growing on walls, roofs, rocks etc.” From the 1990s onwards, this pretty, greenish-grey noctuid has been a common visitor to my home in Highbury, north-central London, on summer evenings. But I have never seen a melanic. It would be hard to explain the resem-blance of the typical adult *Cryphia* pattern to the mottled grey-green encrusting lichens on these surfaces other than as a camouflage adaptation, and to deny that the melanism “predominating” earlier was a response to the grimy surfaces on which the moth rested, until recently, in London.

For the peppered moth there are controversies too complicated to go into here about the importance of lichens, settling position and background matching by the moth. Lichens are generally absent or at least different in industrially polluted regions. To me, the arguments are largely irrelevant to the question of visual predation. The peppered moth doesn’t do exact background matching, but the melanic moth is clearly less visible on a black sooty background, and the pale form is less visible on a non-sooty, mottled background, whether or not there are lichens, whether or not the moth rests on the tree trunks or on branches higher up. This is as true for birds as it is for humans (see Lees 1981). All that is required for us to know is that the moths rest on bark (they do), and that the bark gets darker in industrially polluted sites (it does, or at least,

Figure 2. Relative fitness of adult *typica* (normal, pale form) compared with ***carbonaria*** (melanic form) in 35 field experiments with the peppered moth, *Biston betularia*. The survival data are plotted against the frequency of *typica* in the population, and the trend shows that adults of each form tend to have higher survival in areas where its own form is most abundant, as expected under the industrial melanism hypothesis. The equation for the best-fitting line is $y = 0.83 + 0.65x$; $r2 = 0.20$, $P=0.007$). The data are from Cook (2000); see also Lees (1981). Laurence Cook has told me he doesn't believe the simple regression analysis performed here is sensible, as different groups of experiments were done in very different ways and with different sample sizes. However, I am merely using this regression as a conservative heuristic tool to display the data, because I believe it shows the results clearly. Cook's own (2000) sample-size-weighted analysis of the data after log-transforming the relative fitness values gave similar results ($P < 0.001$).



did), and that birds find it harder to detect melanics on sooty backgrounds, and easier on an unpolluted backgrounds (extensive experiments prove they do).

What and who do you believe?

So, disbelieve the peppered moth story if you must. But if you do want to disbelieve it, make sure your sources are good. Don't just take it from the Daily Telegraph, Hooper's book, Ted Sargent's critiques, Coyne's review, or word of mouth. Ask yourself: in what direction does the weight of experimental, geographic, temporal evidence, and maybe also a little common sense, lead? Read Laurence Cook's papers reviewing the evidence, especially Cook (2000). Look at Fig. 2. I believe that if you do this, you will conclude that the peppered moth story is about as convincing an example of natural selection by bird predators as you could possibly hope to find.

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UCL Prize Lecture in Clinical Science

Given by Sydney Brenner . 1st October 2003

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This year's UCL Prize Lecture in Clinical Science was given by Sydney Brenner, one of the founding fathers of molecular biology. In his introduction to the talk, the chair paid tribute to Brenner by suggesting that the citation of his work on nematodes for his Nobel Prize last year was merely the excuse given by the committee for awarding the prize, and that it could equally have been given for any one of a number of major discoveries he has made. Amongst these are the discovery of mRNA, the triplicate nature of the genetic code and also his championing the fugu fish as an ideal candidate for genome sequencing. Given the obviously colossal intellect to which the audience was treated, it is perhaps not too trite to draw the parallel with Einstein who received his Nobel Prize for neither one of his two theories of relativity, nor for his work on quantum theory, but for his much overlooked work on Brownian motion.

Brenner's wide-ranging talk covered the history of molecular biology, its modern day failings and potential, and its obligations to humanity. Obviously his own personal history played an essential part, and it was recounted with constant humour, starting with his observation that each successive organism he has worked on (bacteria, phage, nematodes, fish and humans) has eaten the previous one.

His message about molecular biology was salutary, containing elements of hope and praise as well as serious warnings. The starting point was the observation by a physicist in the very early days that molecular biology was useless because it had not cured anyone. Brenner retorted that neither had it killed anyone, which certainly could not be said about physics. He then went on to discuss how to rectify the former failing without falling into the latter trap.

There was criticism of some of the more simplistic approaches to the human genome, starting with the fact that the sequence in the database is to some extent an abstraction, being a mosaic of the two copies from each of several individuals, while on the other hand having no real handle on the actual genetic diversity of the human species. This diversity, he suggested, might be crucial in the search for gene-disease associations, more so than the study of individuals.

Obtaining the genome sequence was of course the easy part; now we need to identify the functions of all the encoded proteins, a task more complex than merely treating each as a potential drug target. Indeed we probably need to reconsider the very nature of the gene and look rather at the entire range of physiological functions, several of which may be encoded by the same gene. That said, Brenner remains sceptical about some of the recent high throughput methods for screening genomes and advocated a return to proper experimental biology and the search for the minimum genetic information required for a phenotype rather than the maximum.

Concerning the ethics of molecular biology Brenner is unequivocal in his desire to see insurance companies denied genetic information, drawing a firm distinction between present health condition as shown by such indicators as blood pressure, and the probabilistic predictions about future health that might be obtained from genotyping. When it comes to the desire to improve humanity through genetic engineering he pointed out how feeble such an approach is when contrasted with the age old method of improving our brains. Conditions such as obesity are going to be countered far more successfully by persuading people to eat healthily than by prescribing either pills or gene therapy. Finally he pointed out that we in the West should not monopolise the benefits of molecular biology and should remember the universality of man when deciding what diseases need urgent research.

While addressing all these serious issues, Brenner's playful sense of humour shone through. A favourite example was his suggestion that rather than humans possessing a gene for language, chimpanzees might possess a language suppressor gene; if the former is the Chomsky gene then the latter must be the Chimpsky gene!