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, “melanistic” 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 melanic must have had about 50% higher survival than typical mottled forms to explain the rapid rise in melanin gene frequency. In the last half of the 20th century, field experiments at 16 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 melanin and the degree of urbanization and smoke pollution. This relationship becomes even more convincing when one considers the considerable declines in frequency of melanin 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 melanin (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 outline 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 sympathy with the supposed selection 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.” Notably, this maverick view was not based 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 ‘probable’ with ‘pure’” – 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 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: “... so, 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”. Hooper’s argument amounts to an allegation of fraud. Initially, in a 1993 field experiment, Kettlewell was getting poor recaptures. If this had continued, the evidence for evolution in the peppered moth certainly have been a failure, but the recapture rates suddenly went up soon after. Kettlewell received an encouraging letter from the archaeological geneticist E. F. Ford. Hoover searched the meteorological data for 1993, but found no evidence for a sudden change in weather to explain the increase in recaptures. Therefore, according to Hoover, the increase in recapture rates were highly suspicious. At first, Hoover asks, mildly (p. 118) “Is it possible that [Kettlewell] made modifications in his experimental design?”

Although she doesn’t directly answer this rhetorical question, Hoover 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 bleak. All the 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 perfectly fits with most non-lepidopterists’ general experience. To me, a geneticist with co-authors in the field, the convincing evidence for the case is just as convincing in non-specialist personal experience.

The convincing evidence for the case is that 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. 1989, 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 experiments 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 distasteful species. The mimic therefore remains unmolested by visual predators that have learnt to avoid the distasteful species. Far fewer field experiments have been done to test for this 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 color pattern matching in unrelated species, and in such a geographically coherent manner. I can conclude this article with some of the background information that makes us 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 them 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 current, 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 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 defunct power station achieved new post-coal-era fame on the cover of Pink Floyd’s ‘Animals’ LP). As a child, my “moth chief” was always black from soot-stained nose, 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 soot bomb hit me (an actual event), 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 and wood as fuels ensures that London has remarkably clean air. The soot on most buildings has long since been cleansed off, and the trees have all shed 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 50 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.

Recently, reversals of melanism in industrial areas have been dramatic, and again not just confined to the peppered moth. The marbled beauty moth Cycraea domesticus, 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, rocks, rocks etc.” From the 1990s onwards, this pretty, greenish-grey moth has been a common visitor to my home in Highbury, north-central London, on summer evenings. But I have never seen a melanin. It would be hard to explain the resemblance of the typical adult Cycraea pattern to the mottled grey-green encrusting lichens on these surfaces other than as a camouflage adaptation, and to deny that the melanic form is a response to the grimy surfaces on which the moth rests, 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 much 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. This is 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, 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 photo, a pale form rests on a sooty background. Reprinted, with permission, from HBD Kettlewell, 1956, Heredity 10: 300.
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What and who do you believe?


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 tracible 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 any one. 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 art and not science. The presence of N’s (which should not be present) is a result of the errors in the sequencing process itself. He suggested that there may be many more N’s than currently estimated.

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 compared 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!