

The Peppered moth: decline of a Darwinian disciple

Michael E.N. Majerus

Reader in Evolution, Department of Genetics, University of Cambridge

Delivered to the British Humanist Association, at the London School of Economics, on Darwin Day, 12th February 2004.

{Text links to powerpoint presentation, with slides indicated by PP numbers }

PP1

Introduction

The rise of the melanic moth

The rise of the black, *carbonaria* form of the peppered moth, *Biston betularia*, in response to changes in the environment caused by the industrial revolution in Britain, is probably the best known example of evolution in action. The reasons for the prominence of this example are three-fold. First, the rise was spectacular, occurred in the recent and well-documented past, and was timely, the first record of an individual of *carbonaria* being published by Edleston (1864), just five years after the *Origin of Species* (Darwin, 1859). Second, the difference in the forms had visual impact. Third, the major mechanism through which *carbonaria* rose is easy to both relate and understand.

The story, in brief, is this. The non-melanic peppered moth is a white moth, liberally speckled with black scales (**PP2**). In 1848, a black form, f. *carbonaria* (**PP3**), was recorded in Manchester, and by 1895, 98% of the Mancunian population were black (**PP4**). The *carbonaria* form spread to many other parts of Britain, reaching high frequencies in industrial centres and regions downwind.

In 1896, the Lepidopterist, J.W. Tutt, hypothesized that the increase in *carbonaria*, was the result of differential bird predation in polluted regions. Bernard Kettlewell obtained evidence in support of this hypothesis in the 1950s, with his predation experiments in polluted and unpolluted woodlands. The results of this work showed that in polluted woodland, the pale form was more heavily predated than was *carbonaria*, the reverse being the case in the unpolluted woodland. It was the reciprocal nature of Kettlewell's data in the two woodlands, allied to mark-release-recapture work in the two woods, and extensive survey work showing a strong positive correlation between *carbonaria* frequency and industrial pollutants (**PP5**), that made the case so persuasive. It became the classical example of **Darwinian evolution in action**.

Over the next 40 years, many other studies were carried out on the peppered moth in Britain, across Europe, in the United States and Japan. These unearthed many other details of the peppered moth's biology, but none seriously undermined the veracity of Tutt's hypothesis, or Kettlewell's evidences. Perhaps the zenith of the peppered moth's popularity as an example of Darwinian evolution came in 1996, when, reporting work

carried out in England and the United States showing that the same changes in melanic frequencies had occurred on both sides of the Atlantic, *The New York Times* depicted the peppered moth on the front page of its science section, and devoted 74 column inches to it.

The peppered moth in decline

Yet, since Kettlewell's experiments, the black peppered moth has suffered two declines (**PP6**). First, following the enactment of anti-pollution legislation during the 1950s and subsequently, *carbonaria* frequency has declined dramatically in Britain, and elsewhere.

Second, the reputation of the peppered moth as an example of Darwinian evolution in action, has suffered a severe decline. The cause of this decline can be sourced to the publication in 1998 of my book on melanism, or more specifically, a review of it in *Nature* by Professor Jerry Coyne.

It is the second of these declines that this paper addresses (**PP7**).

First I shall relate how the decline in the peppered moth's reputation came about.

I shall briefly discuss whether criticisms of the story are justified and consider the peppered moth's status as an example of evolution.

I shall also consider accusations of fraud and conspiracy theory aimed by some commentators at Kettlewell, Ford and evolutionary biologists in Britain.

Thereafter, I will give a personal view of why I feel reasonably qualified to discuss the behaviour, ecology and evolution of the peppered moth, and briefly give my own view of the rise and fall of the black peppered moth.

Finally, I will suggest two major pieces of work that are needed. If achieved, they should clarify some of the current uncertainties in the case, and may redeem the reputation of the peppered moth as an example of evolution in action.

'Melanism: Evolution in Action'

Melanism: Evolution in Action (**PP8**), was commissioned by Oxford University Press to be published 25 years after Kettlewell's book on melanism, *The Evolution of Melanism*.

The mandate that I was given (**PP9**) was to critically appraise the phenomenon of melanism amongst animals in an evolutionary context and to 'update' Kettlewell. In the book, two chapters are devoted to the peppered moth. The first describes the basic peppered moth story and particularly Kettlewell's work. The second dissects the story, looking at each of the seven component parts of the basic story (**PP10**), critically assessing the evidence for each, and discussing additional factors pertinent to the case, such as UV visual sensitivity by birds, and morph-specific resting site selection by peppered moths.

Coyne's review and the Sunday Telegraph article

Professor Coyne's review of *Melanism: Evolution in Action* (**PP11**) was published on 5th November 1998, under the title *Not black and white*. I read the review with mounting dismay. Generally the review was positive. Indeed, Coyne wrote: 'Occupying a quarter of the book, the *Biston* analysis is necessary reading for all evolutionists, as are the introductory chapters on the nature of melanism, its distribution among animals, and its proposed causes'.

However, the message from the review was that the peppered moth case is fatally flawed as an example of Darwinian evolution. Coyne writes: '....for the time being we must discard *Biston* as a well-understood example of natural selection in action....'.

The passage that caused me most personal concern was: 'Majerus concludes, reasonably, that all we can deduce from this story is that it is a case of rapid evolution, probably involving pollution and bird predation. I would, however, replace "probably" with "perhaps".' I checked my own book to see where I had concluded "probably". I could not find the word in this context.

Coyne's review was followed up by an article in *The Sunday Telegraph* by Robert Matthews, entitled *Scientists pick holes in Darwin moth theory* (**PP12**). This article begins: (**PP13**) 'Evolution experts are quietly admitting that one of their most cherished examples of Darwin's theory, the rise and fall of the peppered moth, is based on a series of scientific blunders. Experiments using the moth in the Fifties and long believed to prove the truth of natural selection are now thought to be worthless, having been designed to come up with the "right" answer.'

This opening was a surprise to me. I know most of those who have experimented with the peppered moth, and do not know any who would subscribe to this view. Moreover, if evidence were obtained that seriously undermined the qualitative accuracy of the case, it would be of such importance in academic circles that I can not imagine any scientist speaking of it 'quietly'. The Matthews article numerous scientific inaccuracies, misquotations and misrepresentations, but then many press reports, particularly of science, are. However, one would not expect misrepresentation in a book review in *Nature*. I leave judgement of whether Coyne's 1998 review was a misrepresentation of my book to Donald Frack (**PP14**), an American scientist, who has long wrestled in the United States with creationists and intelligent design advocates (Box 1).

Box 1 Extracts from an article posted by Donald Frack on the anticreation@talkorigins.org web site, 30th March 1999

‘A while back creationists on the lists I subscribe to, and elsewhere in the “real” world and cyberspace, began crowing over the death of the peppered moth as “an example of evolution”. The references cited are a book review by Jerry Coyne in Nature of Michael Majerus’s *Melanism: Evolution in Action*, and a later article from interviews with Majerus and Coyne in the on-line version of The Telegraph. These documents have been quite literally flaunted to show that evolutionists have been the willingly blind victims of everything from poor research to outright fraud, and that this famous example of natural selection has been abandoned by “knowledgeable scientists”.

.... ‘I finally became fed up with this newest creationist claim, and the fact that no one seemed to refer to the actual book upon which Coyne’s review was based, but simply to the review itself. To evaluate the situation I located the seemingly notorious book by Majerus at UC Riverside.

.... ‘I opened Majerus’s book anticipating a bashing for Kettlewell.From twenty years of reading anti-pollution literature, as well as advocacy of non-mainstream science views, I think I can pretty often see the attack coming in the form of qualifying with “supposed evidence”, etc. and confrontational discussions throughout the text. I expected this from Majerus.

.... ‘Throughout the chapter “The Peppered Moth Story”, Majerus gives not the slightest hint of the bomb I was waiting for. His discussion of Kettlewell’s experiments, and those of others, are so fairly and complimentarily done that I was amazed at the thought that he was about to destroy it all.How was Majerus going to unhinge the discussion in “The Peppered Moth Story Dissected”? And why did he lead his readers on so cruelly without a hint that they were being given trash data? I read to the end of the second chapter like it was a whodoneit.

.... ‘If you’re waiting for the punch line, here it is. There is essentially no resemblance between Majerus’s and Coyne’s review of it. If you pick through the book, you might be able to argue for Coyne’s accuracy – but only at the expense of completely ignoring the majority of the text and all of Majerus’s intent. If I hadn’t known differently, I would have thought the review was of some other book.’

'Of Moths and Men'

Following the Matthew's article, many papers on the peppered moth appeared (PP15). On the anti-evolution side were titles such as (PP16) *Second thoughts about peppered moths, Darwinism in a flutter: Did a moth show evolution in action?, The moth that failed, Staple of evolutionary teaching may not be a textbook case, Moth-eaten statistics, The Piltdown Moth, and Goodbye peppered moths.*

Then came the publication of *Of Moths and Men: Intrigue, Tragedy & the Peppered Moth* (Hooper, 2002) (PP17), which is, according to the front cover, 'A riotous story of ambition and deceit'.

This book, which purports to give 'the untold story of science and the peppered moth', is essentially an attack on the peppered moth, those who have worked on the evolution of melanism in this species, Lepidopterists in general and Kettlewell and Ford in particular. As Grant (2002) puts it in reviewing the book for *Science* (PP18), 'What it delivers is a quasi-scientific assessment of the evidence for natural selection in the peppered moth (*Biston betularia*), much of which is cast in doubt by the author's relentless suspicion of fraud'.

Coyne (2002) in a review in *Nature* goes further (PP19). He criticizes her 'flimsy conspiracy theory', her theme of 'ambitious scientists who will ignore the truth for the sake of fame and recognition', by which 'she unfairly smears a brilliant naturalist', and

her lack of criticality when she champions Ted Sargeant's 'phenotypic induction' theory, as 'she conveniently glosses over the simple and unassailable fact that the light and dark alleles of *Biston* segregate as Mendelian variants when tested under uniform experimental conditions'. Coyne concludes (**PP20**): 'This issue matters, at least in the United States, because creationists have promoted the problems with *Biston* as a refutation of evolution itself. Even my own brief critique of the story [his 1998 review] has become grist for the creationists' mill. By peddling innuendo and failing to distinguish clearly the undeniable *fact* of selection from the contested *agent* of selection, Hooper has done the scientific community a disservice.'

Coyne's reference to the United States is interesting. The anti-Darwinian lobby has had considerable success in the USA in ensuring, through legislation and litigation, that creationism and intelligent design theories are given equal time to Darwinian evolution in biology teaching in schools. In Britain, we may have thought that we were immune to such action. However, now there are a number of schools in this country, both independent and state funded, in which Creationism and Intelligent Design theory is taught in biology. In these schools attacks on the peppered moth story are used as evidence against Darwinian evolution.

This is despite the fact that the peppered moth case is an integral part of the national syllabus. For example, the Oxford, Cambridge and RSA Examinations Board (OCR) syllabus for GCSE Biology 2003, contains under the subsection on evolution: 'Describe

how the process of natural selection may result in changes within a species, as illustrated by the peppered moth’.

Coyne’s ‘at least in the United States’ is too parochial. The peppered moth story matters – period!

Hooper’s book, *Of Moths and Men* is so littered with errors, misrepresentations, misinterpretations and falsehoods that it is impossible to innumerate them all here. The writings of Wells and some of the other critics of the peppered moth story are similarly plagued. However, they cannot be simply dismissed, as many of the readers of these critics are not armed with the knowledge of evolutionary biology, genetics and ecological entomology necessary to perceive the errors and manipulations within these works. Their writings are lively and readable, and their arguments can be persuasive to those with limited or no training in evolutionary genetics or entomology. Furthermore, few of their readers will have the time to refer to original and review papers on the peppered moth written by those who have worked with the peppered moth, to judge the veracity of the words of people such as Hooper and Wells.

The peppered moth’s place in evolution

Three important questions of the peppered moth case should be addressed (**PP21**):

- i) Does it provide proof of biological evolution?
- ii) Does it provide proof of Darwinian evolution?

iii) Is the main agent of evolution differential bird predation?

Evidence for biological evolution

Biological evolution may be defined as a change in the frequency of an allele through time (**PP22**). The *carbonaria* form of the peppered moth differs from *f. betularia* with respect to the alleles of a single gene. The frequency of the *carbonaria* allele did increase during the nineteenth and first half of the twentieth centuries, and is now declining. This is irrefutable evidence of biological evolution.

Evidence of Darwinian evolution

We may take certain observations of the peppered moth as fact (**PP23**).

- i) From numerous breeding experiments, both published and unpublished, it is incontrovertible that the forms of the peppered moth are inherited according to Mendel's laws of inheritance.
- ii) The frequencies of *f. carbonaria* and *f. swettaria* (the melanic form of the peppered moth in North America), have varied both temporally and spatially.
- iii) There has been and is a correlation between *carbonaria* frequency and pollution levels, particularly sulphur dioxide levels.
- iv) The observed changes in the frequencies of forms of the peppered moth, both in the nineteenth century, and currently are too rapid to be accounted for by random genetic drift.

These factual observations are sufficient to provide evidence that natural selection has had a role in the rise and fall of *carbonaria*.

As Coyne (2002) points out (**PP24**), even Hooper (2002) cannot find an alternative to selection to cause the striking directional changes observed in the peppered moth. He highlights that: ‘Hooper’s grudging admission of this fact occupies but one sentence: “It is reasonable to assume that natural selection operates in the evolution of the peppered moth” [Hooper, 2002, p. 312].’

Is the agent of evolution differential bird predation?

This question is more difficult to address (**PP25**). Critics of Tutt’s differential bird predation hypothesis rely heavily on design flaws in Kettlewell’s experiments in the 1950s. Hooper for example, bases much of her case on design changes that Kettlewell described himself. Wells takes valid criticisms made by evolutionary biologists – e.g. Brakefield, Clarke, Cook, Creed, Grant, Howlett, Sheppard and myself – out of context, and reinterprets them without consideration of the known natural history of the moth, or, for that matter, of practical and logistical expediency. Despite their detailed (if somewhat selective) dissection of Kettlewell’s work, neither Wells, nor Hooper assesses the eight subsequent independent field predation studies. They fail to comment on variations in the methodologies used, many of which were designed to correct for precisely the

deficiencies in Kettlewell's procedures that they argue under-mine the peppered moth case.

These eight studies, and indeed Kettlewell's, consistently show that the fitness of a morph is correlated to concurrent changes in the frequencies of the forms in a particular area. Were I giving my view of each of the procedures in each of these nine studies, including my own, I would certainly criticize each for artificiality in some respect. However, the cause of the artificiality varies between studies – using dead moths, moths at unnatural frequencies, moths at unnatural densities, not allowing moths to take up natural resting sites, and so on. Reviewing all these studies, it is difficult to believe that the artificiality in each case just happen by chance to provide results that support Tutt's bird predation hypothesis. Yet this is what some critics would have us believe.

Other mechanisms have been proposed to account for the rise in *carbonaria*. These include direct mutagenic effects of pollutants (Harrison, 1927; Sargeant *et al.*, 1998), which may be dismissed on the basis of the wealth of data, spanning almost a hundred years, showing Mendelian segregations of the forms of the peppered moth, when reared under controlled conditions, and that *carbonaria* has an inherent physiological advantage, which is difficult to reconcile with the recent decline in *carbonaria*. Neither has any empirical support from studies of the peppered moth. Indeed, at present, only the agent of differential bird predation has any experimental support.

In summary (**PP26**), the situation is this. The case of the peppered moth provides irrefutable proof of biological evolution through the process of natural selection. While there is considerable circumstantial evidence that differential bird predation is the main agent of selection, the evidence is only circumstantial.

The nature of criticisms of the peppered moth case

What then can we say of criticisms of the peppered moth story and of Kettlewell's experiments in particular? The criticisms seem to me to have differing tones and can thus be split into three categories (**PP27**).

- i) Cogent scientific criticisms of artificiality (e.g. 'bird-table effect, morphs not released at natural frequencies, translocated moths may have different behaviours, bred and wild caught moths may act differently).
- ii) Pseudo-scientific criticisms (e.g. bats predation is probably higher than bird predation).
- iii) Data fudging and/or fraud.

Criticisms of artificiality in Kettlewell's experimental procedures

Many criticisms have been aimed at the experiments conducted by Kettlewell in the 1950s. Some of these were first noted by Kettlewell himself; others by scientists who worked on peppered moths. Most could have some validity. The major criticisms have been:

- i) The densities of moths in Kettlewell's predation and mark-release-recapture experiments were too great.
- ii) Kettlewell released moths onto tree trunks. The sparse evidence that exists suggests that although some peppered moths naturally rest in exposed positions on tree trunks, this is not their preferred resting site.
- iii) In his mark-release-recapture experiments, Kettlewell released moths during the day. Peppered moths prompted to fly during the day will settle on the first substrate that they encounter, and generally remain still thereafter. Thus, moths released during daylight will not select the same sites as those that settle at the end of night flight. It is improbable that the degree of crypsis secured by Kettlewell's released moths would have been as high as that of moths in the wild.
- iv) Kettlewell used mixtures of wild-caught and laboratory bred specimens, which may have behaved differently.

In addition, many later workers glued dead moths onto trees in 'life-like' positions, selecting sites that maximized their crypsis. I have tried to do this by very carefully gluing moths onto birch tree trunks, and releasing a similar number of live moths onto the

trunks soon after dawn. A class of students then assessed the degree of crypsis of the moths by walking towards the trunks and saying when they could see any moth. For all forms, the live moths were more cryptic than the glued moths.

The only criticism that can be aimed at all the predation studies conducted to date is that the moths available for predation did not take up their own resting positions during the pre-dawn flight that characterizes this species. This criticism should be addressed in future predation experiments.

Pseudo-scientific criticisms

It has been pointed out that most of the critics of the peppered moth case as an example of evolution in action (with the notable exception of Sargeant) have never worked on the moth, nor are most experienced field biologists or trained in evolutionary genetics. Thus one of the problems with many of these critics is that they do not have a thorough understanding of how selection operates, nor any understanding of the moth itself. A trivial example illustrates the latter point (**PP28**). Kettlewell (1955a) wrote of releasing moths for his experiments, that: 'It was important to see that the sun did not shine on the moths'. He does not say why this was important. However, Hooper (2002) comes up with a reason, writing: 'He scored each moth.... – after making sure that the sun did not shine directly on the insect, which would have fried it'. This is not the reason. Any experienced lepidopterist knows that night active cryptic moths that rest on bark by day avoid the sun to reduce shadow effects and over-heating. Most rest on the north-facing

side of trees or in full shadow. However, a moth in a position that becomes directly sunlit as the day progresses does not 'fry'. It simply moves across the bark ahead of the sun.

Although Hooper's lack of evolutionary and ecological knowledge is revealed on numerous occasions in both *Of Moths and Men*' and in an e-mail that she sent to me prior to the publication of the book (Hooper to Majerus, 16th November 2000), there is a persuasiveness to much of the pseudo-scientific nonsense that she peddles. One example, concerning the predation of moths by bats, will serve as illustration.

Bats vs birds

The questions that Hooper asked me about bat predation in her e-mail are given verbatim in (Box 2).

Box 2 Extract from an e-mail from Judith Hooper to Mike Majerus, 16/11/00, asking questions about the peppered moth.

‘11. BAT PREDATION: In Kettlewell’s time, various people who challenged him (including Heslop Harrison) said that bat predation was a more likely source of selection than bird predation. Kettlewell himself admitted that bats accounted for 90% of the mortality of the moths but said that this didn’t matter because it wasn’t selective—ergo, even if only 10% of the predation was by birds hunting by sight, that 10% is what makes the difference and drives evolution. It seems to me that there are several flaws in this reasoning.

‘a) If you had only 10% of moth mortality effected by birds hunting selectively (and 90% by bats, totally random) wouldn’t you see a different statistical outcome? How would you get the robust 2:1 and 3:1 advantages that Kettlewell got in 3 different experiments?

‘b) Wouldn’t it be wrong to ASSUME that bat selection was totally random? Would a good scientist need to do an experiment to rule out selective predation by bats, esp. if bats were responsible for 90% of adult mortality? Isn’t it possible that one genotype might be more palatable, or smell different, or something? Of course, this would have been a problem for Kettlewell’s model, because bats hunt at night, preying on moths that are flying, so crypsis against tree trunks would not be the issue. You’d be back to square one.

‘I’d love to hear your thoughts on this?’

Question 12 was a similar enquiry relating to pre-adult mortality.

My responses were given in a lengthy telephone conversation the following Sunday. I do not remember precisely what I said, but my preparatory notes on her e-mail are that Kettlewell's reasoning is correct, that the two forms are unlikely to differ in palatability or smell, but that scale types and pigments might affect sonar. I also explained Kettlewell's reasoning, and the flaw in Hopper's, in detail, by theoretical example. My example is cited by Hooper (2002).

'Say three hundred eggs are originally laid. Once you get to the adult stage, maybe you have ten left. Of these more than half are killed by things not hunting by sight, so say you have four moths left – two typical and two *carbonaria*. You must be prepared to say that none of the mortality prior to this is due to selection on colour pattern, no pleiotropic effects of alleles, no differences in palatability, no greater energetic costs in producing black pigment and so on. If so, then despite 296 moths being killed up to that point, if those two typicals are eaten by birds, you've increased *carbonaria* by a hundred per cent at one go.'

Hooper (2002) then asks 'Can we really be sure that bat predation is *not* selective, that there is not some yet unidentified difference between melanics and typicals that makes one morph more vulnerable to bats? Certain night-flying moths can dodge or jam bat sonar, according to several studies, and it is not known whether this ability is equally distributed'.

This passage is nonsense. Following this line of reasoning, the assumptions that we would have to make are that not only could bats distinguish between the forms by sonar, smell or taste, but that the form that was taken more would vary geographically, and that the variation was correlated to pollution levels.

The test of Hooper's question about the 'need to do an experiment to rule out selective predation by bats', is not difficult to address. So I did it.

Non-selective predation of peppered moths by bats

Four hundred laboratory reared male peppered moth were released sequentially between 11 pm and 3 am over five nights, 20 m from a mercury-vapour light, in the grounds of the Genetics Field Station, Cambridge, being attended by pipistrelle bats. Equal numbers of *f. betularia* and *f. carbonaria* were released. The moths, which had all eclosed earlier on the day of release, were kept individually in Perspex boxes. These were numbered randomly and moths were released in numerical order. The bats were flying above the trap, taking moths flying in the area. Up to seven bats were observed feeding at a time. At 10 min intervals, five boxes were laid on the ground and opened. Moths were watched as they took flight, and followed by eye, with the help of night glasses, until they were lost from view, or were seen to be caught by a bat. The results are given in **PP29**. There is no significant difference in the numbers of the two forms that were caught by the bats. Bats do catch and eat peppered moths flying at night, but they do so randomly with respect to the forms of the moth.

Data fudging and/or fraud?

One of the most damaging criticisms of Kettlewell's work is the reported increase in recapture rates that occurred in Birmingham from 1st July 2003. Hooper (2002) notes that after recaptures running in the low single digits for the first six days [in fact it was five days – see Kettlewell, 1955a], on the morning of 1st July, 23 marked moths were recaptured, and the increased recapture rates were maintained thereafter. She ties in the increase in recapture rates with a letter from E.B. Ford to Kettlewell dated 1st July, in which Ford wrote (**PP30**): 'It is disappointing that the recoveries are not better ... However, I do not doubt that the results will be very worth while' Hooper gives her own translation of this passage as: 'Now I do hope you will get hold of yourself and deliver up some decent numbers.' Hooper makes large of 1st July. She writes: 'what happened between the last day of June and the first day of July 1953 to turn the tide', implying of course, that it was the arrival of Ford's letter.

Three points should be made (**PP31**).

First, while I do not know when Kettlewell received Ford's letter, it is notable that the recapture rates had certainly risen on the night before Ford wrote the letter. Kettlewell was certainly disappointed by the low initial recapture rates, and increased the number of marked moths released on 30th June, not after receiving Ford's letter.

Second, from my own experience of moth trapping over 40 years, I am aware that moth trap catch sizes vary greatly, both in respect of total catch and for individual species. The variations are not always predictable. Factors such as temperature, cloud cover, and wind speed can have a very marked effect, as can something as innocuous as a slight repositioning of a trap, a point made by Coyne (2002).

Third, the increase in recapture rates is not as great as Hooper implies. Kettlewell's own work shows that the number of recaptures declines very rapidly after the first night. If the recapture levels for the two nights following days when no moths had been released (nights of 26/27th June and 29/30th June) are excluded, the average proportion of released moths recaptured up to the night of 30th June/1st July is 0.117. Thereafter the proportion is 0.267. This is certainly an increase. Hooper writes: 'The average number released prior to 30 June was 30.8, while the average for 30 June-4 July was 92.5. Was this why he recaptured more? Or was there some other reason as well?'

Well, there may have been. First, Matt Young has recently shown that the changes in recapture rates are not statistically significant, while he, working with Ian Musgrave, has also shown that the changes present correlate inversely to levels of moonshine.

Second, the three fold increase in the number of moths released may have effectively flooded the area with moths, to an extent where the predators of the peppered moth in the area were at least partially satiated, leading to an increase in the survival of the released moths and so to increased recapture rates. Despite criticizing the high densities of

Kettlewell's releases, Hooper does not seem to have considered the possible effects of this flaw in Kettlewell's procedure in any great depth, nor indeed that it could answer her own question.

It is interesting, but perhaps not surprising, that Hooper does not try to answer her own question. Most anti-evolution critics of the peppered moth story seem keen to simply discredit the peppered moth case and in particular Kettlewell. They do not seem prepared to seek alternative explanations or interpretations of data. Those that do offer alternatives, tender such ill-conceived hypotheses, based on the most tenuous evidence, and frequently showing little understanding of genetics, evolutionary processes, or the behaviour of the subject material, that they can be rapidly dismissed. However, in the wealth of data that has been accumulated on the peppered moth, there are inconsistencies. Critics of the peppered moth case are quick to stress these inconsistencies, and aim accusations of fudged data or fraud. They rarely seek a scientific explanation of inconsistencies. Kettlewell's work on morph-specific resting site selection provides an example (PP32).

Morph specific resting site selection?

Kettlewell (1955b) reports the results of experiments carried out in 1954 on background recognition in the peppered moth. In this experiment, Kettlewell lined a large cider barrel with alternate black and white strips of cloth or rough paper, all of identical texture (PP33). A sheet of glass was placed on top of the cylinder and was then covered with

white muslin. The barrel was situated outside, but out of direct sunlight. Each evening, up to six peppered moths of the same sex, with *carbonaria* and *betularia* in equality, were released into the barrel. At dawn, the resting positions of the moths were scored. Moths that rested on the floor or across two backgrounds (80 of 198) were excluded from analysis. The results (**PP34**) showed a significant difference in the behaviour of the forms, almost two-thirds of *carbonaria* resting on black surfaces and two-thirds of *betularia* resting on white.

Kettlewell (1955b) proposed that a peppered moth, after landing on a surface, but before clamping down, will select a position where it is out of the sun, where it can align its body with a groove in the bark, and where the contrast between the colour of the substrate and the moth's circumocular tufts is minimised.

Various authors have subsequently investigated resting site selection in the peppered moth using a range of experimental approaches, including attempted replications of Kettlewell's experiments, and various manipulations of the circumocular tufts of moths. Resting site preferences have been reported in some studies (e.g. **PP35**) but not in others. However, none has found morph-specific resting site preferences within a population.

The failure to replicate Kettlewell's results has brought veiled accusations of fraud by Kettlewell. However, neither Wells, nor Hooper attempts to take the various data sets at face value and seek a biological explanation to reconcile variations in them. Yet such an explanation exists (**PP36**).

In 1989, Rory Howlett and I modelled the rise of a mutant allele, unlinked to the colour pattern locus, that induced a preference for peppered moths to select dark homogeneous backgrounds, rather than pale heterogeneous backgrounds, to rest upon. We assumed that the fitness of *carbonaria* would be increased by the expression of such an allele, and that of *betularia* would be reduced by it. The model showed that the allele would only increase in frequency in populations in which *carbonaria* was already common. I then argued that this might account for the morph-specific resting site selection reported by Kettlewell (1955b). This hypothesis is based upon the premise that a heritable preference to prefer to rest on dark homogeneous substrates would have evolved in regions with high *carbonaria* frequency, but not where *carbonaria* is rare, as Howlett's model suggests. Where *carbonaria* is rare, moths would retain the ancestral resting site choice, which Majerus assumes is for pale heterogeneous surfaces. There is some support for these assumptions, both Grant and Howlett (1988) and Jones (1993) finding variation in the resting site preferences of moths from different populations, with preferences for dark backgrounds being found in all populations with high melanic frequency. The thesis is then that the moths that Kettlewell used in his barrel experiments were drawn from different populations, the f. *carbonaria* from an industrial population and the f. *betularia* from a rural one.

The source of the moths that Kettlewell used in his barrels is not known, despite exhaustive enquiries (Majerus, 1998), so it is not possible to verify this explanation. However, were this explanation correct, it would explain the disparity between

Kettlewell's results and those of others, without having to resort to unverifiable accusations of fraud.

A personal view from the horse's mouth!

It is dangerous to open ones mouth, to put pen to paper, or to start tapping away at the keyboard (**PP37**). If you have opinions and offer these to others, you run the risk of being misquoted, misrepresented when your words are taken out of context, or indeed having words falsely attributed to you.

Over the peppered moth, I have suffered all three. Some of these misrepresentations are repeated over and over again in anti-Darwinian literature, possibly because citing a Cambridge University evolutionary geneticist appears to give authority to the subjective private agendas of pseudo-scientists or journalists.

Some of the interpretations and statements falsely attributed to me should, I feel, be exposed, for some damage science, or the reputation of individual scientists, or the public's image of how good science is generally conducted.

Good science is conducted largely through observation, hypothesis formation, prediction and experimentation. Much of the work on the peppered moth has been conducted in this way. An impressive array of evidence has been accumulated. Many of the experiments, particularly those conducted in the field, are not without their flaws. Moreover, predicted

outcomes have not always been realized. However, if you wade through the 200+ papers written about melanism in the peppered moth, it is difficult to come to any conclusion other than that natural selection through the agent of differential bird predation is largely responsible for the rise and fall of *carbonaria*.

That said, my own conviction that bird predation is largely responsible is not based purely on empirical data from experiments published in the literature. I 'know' that Tutt's differential bird predation hypothesis is correct because I 'know' about peppered moths. For those who have never seen a peppered moth in the wild, which is almost everybody, for those with anti-Darwinian agendas, and for scientists, well-trained in rigour, stringency and experimental controls, for differing reasons this statement must seem insufficient if not heretical. However, I stick by it.

The biography of the great geneticist Barara McLintock was titled 'A Feel for the Organism' (Keller, 1993). I think that I have a feel for some organisms.

My credentials are these:

I caught my first butterfly when I was four (Majerus, 1994).

I learnt the basics of Mendelian genetics when I was ten (Berry, 1990).

For 45 years I have bred, collected, photographed and recorded moths, butterflies and ladybirds in Britain, across Europe and latterly around the world.

I have run one or more moth traps almost nightly for 40 years.

This experience has given me something of a feel for the organisms that I observe.

I bred my first broods of the peppered moth in 1964, following Ford's (1955) advice on careful separation of broods and writing notes on all procedures used.

I found my first peppered moth at rest in the wild in the same year (Howlett and Majerus, 1987).

As far as I am aware, I have found more peppered moths at rest in their natural resting position than any other person alive. I admit to being, in part, a moth man.

In the first chapter of *Of Moths and Men*, Hooper (2002) assassinates the character of 'moth men', who have 'stunted social skills of the more monomaniacal computer hackers, going about with misbuttoned shirts and uncombed hair, spouting taxonomic Latin. She cites Ted Sargeant, who considers moth collectors to be weirder than butterfly collectors. According to Hooper, Sargent is awed by moth enthusiasts who 'can go up to a streetlight and start naming these things Its an extraordinary talent'.

But it isn't extraordinary. Hundreds of thousands of children across the world can recognize hundreds of different Pokemon characters, and provide details of their characteristics, their evolutionary potential and their powers in contest. How is this different to a 12 year old who can recognize several hundred species of macromoth, know when they fly, and what their larvae feed upon. Calling out names to a group around a moth trap, the names I use are in English, not Latin, for I learnt them, out of interest and fascination, when I was a child, and the English names were easier.

I know the peppered moth, and I know that J.W. Tutt was essentially correct in his explanation of the rise of *carbonaria*. However, for those who do not 'know' the peppered moth, whether they are scientists, teachers or members of the public, this should not, indeed, it must not be enough. So, what is needed to prove whether changes in frequencies of the peppered moth are indeed the result of differential bird predation? And, can the declining reputation of the peppered moth be reversed?

Two evidences for proof

In my view, two pieces of evidence are critical (**PP37**). The first is that birds eliminate a greater proportion of one form than the other to an extent consistent with monitored changes in the frequencies of the forms. The second is that a connection should be made between the genotype and phenotype.

The genotype – phenotype link

Taking the second point first, it is an unfortunate omission that the multiple allelic gene that controls melanism in the peppered moth in Britain has not been identified and sequenced. The critical step of connecting genotype with phenotype has thus not been accomplished in this classical case of Darwinian evolution in action. However, this step has recently been accomplished in another case of adaptive melanism involving crypsis (Nachman *et al.*, 2003) (**PP38**). The rock pocket mouse, *Chaetodipus intermedius*, varies in coat colour. Strong correlations between coat colour and substrate have been shown

for this and related species in the South-western United States. The most obvious correlations occur where black volcanic lava rocks abut white sandy soils. The similarity of the dorsal pelage of mice and their substrate is adaptive, providing cryptic protection against birds of prey, particularly owls. Nachman *et al.* (2003), using candidate genes from the many that affect coat colour in laboratory mice, identified, by association analysis, the mutation causing melanism in a population of mice on a lava bed in Arizona. The mutation is in the melanocortin-1-receptor gene (*MC1R*). Other mutations of this gene are known to be associated with melanic phenotypes in jaguars, *Panthera onca*, and jaguarundis, *Herpailurus yaguarondi*. In these species showing melanic polymorphism in the wild, morph frequencies appear to be at equilibrium. Work on a system with an established genotype-phenotype characterisation, and in which the frequencies of forms are changing directionally, i.e. under selection, would allow changes in adaptive mutations to be tracked. The peppered moth is the obvious candidate species. A similar association analysis, using candidate genes from *Drosophila*, *Manduca sexta* or *Papilio glaucus*, should be rewarding. It could provide the genotype – phenotype link in the most celebrated example of Darwinian evolution in action.

A new predation experiment

To determine whether changes in *carbonaria* frequency can be accounted for by differential bird predation requires a predation experiment that avoids the suggested flaws in those carried out by Kettlewell and others (**PP39**). Such an experiment was designed in 2001. The design took account of the criticisms aimed at previous experiments,

plausibility of procedure and methods of statistical analysis. Initial testing of release procedures, the trees that peppered moths rest upon in the area, the visibility of subjects during experiments and levels of predation was undertaken in 2001 to assess feasibility.

The experimental design (**PP40**) involves releasing both forms of moth, at natural frequencies and low densities, into cages around tree branches at dusk, removing the cages dawn and observing any predation on the moths.

The experiment, because of the constraints of low density and natural frequencies will take at least five years.

New data on the natural resting sites of peppered moths

The work has already yielded one interesting piece of data. The slowest accumulating data set that I have is of the resting positions of peppered moths I have found in the wild since 1964. This data set, first published in 1987 (Howlett and Majerus, 1987), has continued to build. The set up to 2001 is given in (**PP41**), and consists of just 59 moths, a rate of 1.55 moths located per year. While constructing or removing release sleeves in the trees, I have found, by eye a considerable number of moths, 27 of which have been peppered moths (**PP42**). The rate of find has thus risen to 13.5 moths per year.

Furthermore, all of these moths were more than 2 m above ground, most were in the upper half of the trees that they were on and only five were on the main trunks of the trees.

Critics of the peppered moth have often pointed to a statement made by Clarke *et al.* (1985): ‘.... In 25 years we have only found two *betularia* on the tree trunks or walls adjacent to our traps, and none elsewhere’.

The reason now seems obvious. Few people spend their time looking for moths up in the trees. That is where peppered moths rest by day.

Endnote

The case of the peppered moth matters (**PP42**). Our earth faces huge problems of overpopulation, diminishing resources, loss of habitats and species extinctions. More than ever before, biologists with an understanding of the complexities of ecological systems are needed. **Darwinian evolution is fact.** And as the great Russian/American geneticist, Theodore Dobzhansky famously said, “nothing in biology makes sense except in the light of evolution”. Only through understanding of the complexities of natural systems do we have a hope of successfully addressing the monumental problems we face.

(**PP43**) If molecular analysis does provide the link between genotype and phenotype, and if the predation experiment does supply evidence fulfilling the predicted differences in bird predation of the forms to account for the current rate of decline in *carbonaria*, will the anti-evolution lobby be convinced, and redeem the reputation of the peppered moth as the exemplar par excellence of evolution in action? Sadly, I doubt it.

(PP44) For my part, lest anyone doubts it, I stand by my view, given in the conclusion of Chapter 6 of *Melanism: Evolution in Action* (Majerus, 1998, p. 155): *'My view of the rise and fall of the melanic peppered moth is that differential bird predation in more or less polluted regions, together with migration, are primarily responsible, almost to the exclusion of other factors'*.

References

- Berry, R.J. (1990) Industrial melanism and peppered moths (*Biston betularia* (L.)). *Biological Journal of the Linnaean Society* 39, 301-22
- Brakefield, P.M. (1990) A decline of melanism in the peppered moth, *Biston betularia* in the Netherlands. *Biological Journal of the Linnaean Society* 39, 327-34.
- Clarke, C.A., Mani, G.S., and Wynne, G. (1985) Evolution in reverse: clean air and the peppered moth. *Biological Journal of the Linnaean Society* 26, 189-99.
- Cook, L.M. (2000a) A century and a half of peppered moths. *Entomologist's Record and Journal of Variation* 112, 77-82.
- Cook, L.M. (2000b) Changing views on melanic moths. *Journal of the Linnean Society* 69, 431-441.
- Cook, L.M., Rigby, K.D. and Seaward, M.R.D. (1990) Melanic moths and changes in epiphytic vegetation in north-west England and north Wales. *Biological Journal of the Linnaean Society* 39, 343-54.
- Coyne, J.A. (1998) Not black and white. *Nature* 396, 35-36.

Coyne, J.A. (2002) Evolution under pressure. *Nature* 418, 19-20.

Darwin, C.R. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray: London.

Edleston, R.S. (1864) No title (first *carbonaria* melanic of moth *Biston betularia*). *Entomologist* 2, 150.

Ford, E.B. (1955) *Moths*, No. 30, New Naturalist Series. Collins, London.

Frack, D. (1999) Peppered moths – in black and white. Posting to ‘Anticreation List’, anticreation@talkorigins.org, 30th March 1999.

Grant, B.S. (2002) Sour grapes of wrath. *Science* 297, 940-941.

Grant, B., and Howlett, R.J. (1988) Background selection by the peppered moth (*Biston betularia* Linn.): individual differences. *Biological Journal of the Linnaean Society* 33, 217-32.

Grant, B., Owen, D.F., and Clarke, C.A. (1995) Decline of melanic moths. *Nature* 373, 565.

Grant, B.S., Owen, D.F., and Clarke, C.A. (1996) Parallel rise and fall of melanic peppered moths in America and Britain. *Journal of Heredity* 87, 351-357.

Hooper, J. (2002) *Of Moths and Men: Intrigue, Tragedy & the Peppered Moth*. Fourth Estate, London, 377 pp.

Howlett, R.J., and Majerus, M.E.N. (1987) The understanding of industrial melanism in the peppered moth (*Biston betularia*) (Lepidoptera: Geometridae). *Biological Journal of the Linnaean Society* 30, 31-44.

Jones, C.W. (1993) *Habitat Selection in Polymorphic Lepidoptera*. Ph. D. thesis, Cambridge University.

Keller, E.F. (1993) *A Feel for the Organism: The Life and Work of Barbara McClinton*. W.H. Freeman: Basingstoke.

Kettlewell, H.B.D. (1955a) Selection experiments on industrial melanism in the Lepidoptera. *Heredity* 9, 323-42.

Kettlewell, H.B.D. (1955b) Recognition of appropriate backgrounds by the pale and black phases of the Lepidoptera. *Nature* 175, 943-4.

Kettlewell, H.B.D. (1956) Further selection experiments on industrial melanism in the Lepidoptera *Heredity* 10, 287-301.

Kettlewell, H.B.D. (1973) *The Evolution of Melanism*. Clarendon Press, Oxford.

Majerus, M. E. N. (1989) Melanic polymorphism in the peppered moth *Biston betularia* and other Lepidoptera. *Journal of Biological Education* 23, 267-84.

Majerus, M. E. N. (1998) *Melanism: Evolution in Action*. Oxford, Oxford University Press, 338 pp.

Matthews, R. (1999) Scientists pick holes in Darwin moth theory. *The Sunday Telegraph*, March 14, 1999.

Nachman, M.W., Hoekstra, H.E. and D'Agostino, S.L. (2003) The genetic basis of adaptive melanism in pocket mice. *Proceedings of the National Academy of Science* 100,

Tutt, J.W. (1896) *British Moths*. George Routledge.

Wells, J. (2000) *Icons of Evolution: Science or Myth? Why Much of What We Teach About Evolution is Wrong*. Regnery Press, Washington, D.C.

Wells, J. (2001) Second thoughts about peppered moths: This classical story of evolution by natural selection needs revising. *The True Origin Archive*, <http://trueorigin.org/pepmoth1.htm>.

Wells, J. (2002) Moth-eaten statistics: A reply to Kenneth R. Miller. *Discovery Institute: Centre for Renewal of Science and Culture – Article Database*,

<http://www.discovery.org/viewDB/index.php3?command=view&id=1147&program=CR>

[SC](#)

Yoon, C.K. (1996) Parallel plots in classic of evolution. *New York Times: Science Times*, 12th November, pp C1, C7.