The Peppered Moth

Decline of a Darwinian Disciple
Biston betularia betularia
carbonaria
By 1895, 98% of Mancunian population were black

1896: Tutt proposes differential bird predation is the agent responsible

Haldane (1924) showed: *carbonaria* 1.5 times as fit as f. *betularia* to account for rise

1950s: Kettlewell’s predation and mark/release/recapture experiments gave reciprocal results.
Prologue

- Kettlewell demonstrated correlation between *carbonaria* frequencies and pollution levels
- Peppered moth becomes the foremost example of Darwinian evolution in action
- Over the next 40 years, further details of the case were investigated. None seriously undermined Kettlewell’s interpretation
The declines of the melanic moth

- Following anti-pollution laws, *carbonaria* began to decline on both sides of the Atlantic
- From 1998, the reputation of the peppered moth, as an example of Darwinian evolution in action, became tarnished
Plan

• The decline in reputation
• Are the criticisms justified?
• The status of the peppered moth as an example of evolution
• Fraud and conspiracy theory
• A personal view of the peppered moth
• What needs to be done
Melanism: Evolution in Action

- Aim: critically appraise melanism in animals and ‘update Kettlewell’.
- Two chapters concern the peppered moth.
Components of the text book story

- Two forms
- Genetic control
- Fly at night, rest by day
- Birds finding moths on tree trunks, eat them
- Bird predation depends on moth crypsis
- Level of crypsis depends on pollution
- Frequencies depend on selection/migration balance
Coyne’s review in *Nature*

- 5th Nov. 1998: review titled *Not black and white*
- ‘…. For the time being we must discard *Biston* as a well-understood example of natural selection in action…’
- Robert Matthews (*Sunday Telegraph* 14/3/99): ‘Scientists pick holes in Darwin moth theory’
Scientists pick holes in Darwin moth theory

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.

Scientists now admit that they do not know the real explanation for the fate of Biston betularia, whose story is recounted in almost every textbook on evolution.

According to the standard account, only one version of

by ROBERT MATTHEWS
Science Correspondent

ation-free trees, while the black type continued to thrive in areas unaffected by industry. Experiments have also shown that neither moth chooses resting places best suited to its camouflage.

Most damning of all, despite 40 years of effort, scientists have seen only two moths resting on tree trunks — the key element of the standard story and Kettlewell’s experiments.

According to Michael Majerus, a Cambridge University expert on the moth, Dr Kettlewell tried to confirm the standard story simply by
Matthews

- ‘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.’
Donald Frack

• 1999: Peppered moths in black and white. Posting to ‘Anticreation List’, anticreation@talkorigins.org

• Commented on Coyne’s review of my book
Moth-eaten Statistics:
A Reply to Kenneth R. Miller

Jonathan Wells
Discovery Institute
April 16, 2002

Second Thoughts About Peppered Moths

The True-Origin Archiv
Exposing the Myth of Evolution

Second Thoughts about Peppered Moths
This classical story of evolution by
natural selection needs revising
• Second thoughts about the peppered moth
• Darwinism in a flutter
• The moth that failed
• Staple of evolutionary thinking may not be a textbook case
• Moth-eaten statistics
• The Piltdown moth
• Goodbye, peppered moths; a classic evolutionary story comes unstuck
OF Moths and Men
INTRIGUE, TRAGEDY & THE PEPPERED MOTH

‘A riotous story of ambition and deceit.’
Dava Sobel, author of Longitude and Galileo’s Daughter

JUDITH HOOPER
Grant on Hooper

• Grant (2002, *Science*): ‘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 on Hooper

• Coyne (2002, *Nature*): 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’.
Coyne on Hooper

• Coyne concludes: ‘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 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.’
The peppered moth’s place in evolution

• Does it provide proof of biological evolution?
• Does it provide proof of Darwinian evolution (evolution through selection)?
• Is the main agent of selection differential bird predation?
Biological evolution

• Defined as changes in heritable material (i.e. genes) through time.

• Changes in the frequency of the *carbonaria* gene provides irrefutable proof of biological evolution
Darwinian evolution

- Facts:
  - Forms inherited according to Mendel’s laws
  - Form frequencies have varied in both time and space
  - Correlation between form frequencies and pollution levels
  - Changes too rapid to be due to random genetic drift.
Darwinian evolution

• These facts prove that selection has had a role

• Even Hooper cannot find an alternative, which she grudgingly admits: “It is reasonable to assume that natural selection operates in the evolution of the peppered moth” [Hooper, 2002, p. 312].
Are birds involved?

- 8 other studies
- Many of these addressed criticisms of Kettlewell’s methods
- None undermined the qualitative conclusions of Kettlewell
- Alternative theories (mutagenic pollutants, inherent physiological advantage) do not fit the data
- Only agent that has empirical support is bird predation
Summary

• The case of the peppered moth provides irrefutable proof of biological evolution through the process of natural selection. While there is strong circumstantial evidence that differential bird predation is the main agent of selection, the evidence is only circumstantial.
The nature of criticisms

- Scientific criticisms of artificiality (e.g. ‘bird-table effect’, not natural frequencies, translocated moths may behave differently, etc.
- Pseudo-scientific criticisms.
- Data fudging and/or fraud.
Pseudo-scientific criticisms

• E.g. moths frying
• E.g. bats eat more adult moths than do birds
Predation by bats

<table>
<thead>
<tr>
<th>Form</th>
<th>Flew and lost from view</th>
<th>No flight within 10 min</th>
<th>Caught by bats</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>carbonaria</em></td>
<td>114</td>
<td>35</td>
<td>51</td>
</tr>
<tr>
<td><em>betularia</em></td>
<td>107</td>
<td>39</td>
<td>54</td>
</tr>
</tbody>
</table>
Hooper’s accusations of fraud?

- Ford to Kettlewell, 1st July: ‘It is disappointing that the recoveries are not better … However, I do not doubt that the results will be very worth while ….’
- Hooper’s translation of this passage: ‘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’.
Comments on and alternatives to fraud

- Increase in recaptures does **not** coincide with arrival of letter
- Many factors can alter moth trap catches
- Increase is from 0.117 to 0.267
- Coincided with three fold increase in releases
- Matt Young (in press) has since shown that increase is not statistically significant, and that the increase correlates to reductions in moonshine
- Could predators have been satiated, leading to increase survival of released moths?
Resting site selection

- Kettlewell’s 1954 experiments in cider barrels
- Proposed contrast/conflict hypothesis
- Failure to replicate
- Failure to change behaviour by manipulation
Kettlewell’s barrel experiments

<table>
<thead>
<tr>
<th></th>
<th>f. betularia</th>
<th>f. carbonaria</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black</td>
<td>20</td>
<td>38</td>
<td>58</td>
</tr>
<tr>
<td>background</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White</td>
<td>39</td>
<td>21</td>
<td>60</td>
</tr>
<tr>
<td>background</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>59</td>
<td>59</td>
<td>118</td>
</tr>
</tbody>
</table>
## Howlett/Majerus cylinders

<table>
<thead>
<tr>
<th></th>
<th>betularia</th>
<th>insularia</th>
<th>carbonaria</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black side</td>
<td>58</td>
<td>30</td>
<td>70</td>
<td>158</td>
</tr>
<tr>
<td>White side</td>
<td>20</td>
<td>7</td>
<td>14</td>
<td>41</td>
</tr>
<tr>
<td>Floor</td>
<td>21</td>
<td>5</td>
<td>36</td>
<td>62</td>
</tr>
<tr>
<td>Totals</td>
<td>99</td>
<td>42</td>
<td>120</td>
<td>261</td>
</tr>
</tbody>
</table>
Explaining the data

- Howlett model shows different background selection will depend on form frequencies
- Grant and Howlett (1988), Jones (1993) provide data showing differences in preferences in different populations
- Kettlewell may have used pale and black moths from different populations, with different behaviours
The horse’s mouth

• Misquoted, misrepresented, had words falsely attributed to me

• My view: Tutt’s hypothesis is correct

• My reasons are based on both assessment of all published work, and experience
The next steps

• ‘Proof’ of differential bird predation

• The genotype - phenotype link
Genotype - phenotype link

- Nachman et al (2003): association analysis of lab mice candidate genes to show mutation responsible for adaptive melanism in rock pocket mice
- Similar approach with peppered moth, using candidate genes from *Drosophila, Manduca* or *Papilio*
- Show whether melanic mutants are all the same
Predation experiment

• Aim: predation experiment avoiding criticisms of artificiality

• Therefore: low density, natural frequencies, correct resting positions, moths select resting positions at night, observe predation, know origin of moths
Experimental procedure

• 1 hectare plot near Cambridge
• 103 randomised release points
• Caged releases at dusk (12 per night, natural frequencies)
• Removal of cages at dawn
• 4 hours observation + scoring disappearance
• Moths used are: i) light trap males, ii) pheromone trap males, iii) bred males iv) bred females
Natural resting sites of peppered moths (1964-2001)

<table>
<thead>
<tr>
<th></th>
<th>f. betularia</th>
<th>f. insularia</th>
<th>f. carbonaria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Exposed trunk</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Unexposed trunk</td>
<td>2</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td>Trunk/branch join</td>
<td>11</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Branches</td>
<td>9</td>
<td>5</td>
<td>8</td>
</tr>
</tbody>
</table>
## Resting sites in trees (2002-2003)

<table>
<thead>
<tr>
<th>Location</th>
<th><em>betularia</em></th>
<th><em>insularia</em></th>
<th><em>carbonaria</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Exposed trunk</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unexposed trunk</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Trunk/branch joint</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Branches (&gt; 5 cm diameter)</td>
<td>7</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Branches/twigs (&lt; 5 cm diameter)</td>
<td>6</td>
<td>2</td>
<td>0</td>
</tr>
</tbody>
</table>

+ two mating pairs (one *bet.* female x *carb.* male, the other both *bet.*), both on the side/underside of branches with a diameter > 5 cm.
The Peppered Moth Matters

• 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”.
Endnote

• Darwinian evolution does not stand or fall on the peppered moth case, but in my view, the peppered moth is still one of the best examples of evolution in action through natural selection.

• The critics of the peppered moth case should stick to topics they know something about. Their creationist faiths belong in religious education classes, not biology lessons.
• Finally, lest anyone doubts it, I stand by my view, 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’.