The moths of war

Once the supreme example of evolution in action, the peppered moth has been hijacked by creationists. It's time to take it back, says **Jaap de Roode**

AT FIRST sight the peppered moth is a rather unprepossessing creature. Surrounded by its more brightly coloured relatives in a moth collection, drab old *Biston betularia* scarcely catches the eye. Yet the peppered moth is more famous – and notorious – than any of its prettier counterparts can ever hope to be.

For decades, the peppered moth was *the* textbook example of evolution in action, unassailable proof that Darwin got it right. Generations of students learned how, during the industrial revolution in England, a dark-coloured mutant appeared and in polluted areas quickly replaced the normal light-coloured form because it was better camouflaged against bird predation. "It is the most simple to understand, visually attractive story of evolution in action," says Michael Majerus, a geneticist at the University of Cambridge.

Recently, though, the peppered moth's status as an icon of evolution has been under threat. Emboldened by legitimate scientific debate over the fine details of the peppered moth story, creationists and other anti-evolutionists have orchestrated a decade-long campaign to discredit it – and with it the entire edifice of evolution. These days you're less likely to hear about the peppered moth as proof of evolution than as proof that biologists cannot get their story straight.

The peppered moth now counts among the anti-evolutionists' most potent weapons. In the past few years it has helped them get material critical of evolution added to high-school science lessons in Ohio and Kansas, although the material has now been removed. In 2000, the authors of the widely used school textbook *Biology* reluctantly dropped the peppered moth in direct response to creationist attacks. "It would be really easy to say it is a fraud, and it would take a long explanation to respond to that," says co-author Kenneth Miller of Brown University in Providence, Rhode Island. The latest edition features the beaks of Galapagos finches instead.

Now, though, biologists are fighting back. Majerus recently finished an exhaustive experiment designed to repair the peppered moth's tattered reputation and reverse the creationists' advances. The preliminary results are out, and Majerus says they are enough to fully reinstate the moth as the prime example of Darwinian evolution in action.

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Flawed work

The textbook version of the peppered moth story is simple enough. Before the mid-19th century, all peppered moths in England were cream coloured with dark spots. In 1848, however, a "melanic" form was caught and pinned by a moth collector in Manchester. By the turn of the 20th century melanic moths had all but replaced the light form in Manchester and other industrial regions of England. The cause of the change was industrial pollution: as soot and other pollutants filled the air, trees used by peppered moths as daytime resting places were stripped of their lichens then stained black with soot. Light-coloured moths that were well camouflaged on lichen-coated trees were highly conspicuous on blackened trees. Melanic moths, in contrast, were less easily spotted by predatory birds and so survived longer, leaving more offspring than the light forms. As melanism is heritable, over time the proportion of black moths increased.

As with all textbook examples, however, this is a simplified account of decades of field work, genetic studies and mathematical analyses carried out by dozens of researchers. It also draws disproportionately on the flawed work of one biologist, Bernard Kettlewell of the University of Oxford.

In the 1950s Kettlewell carried out a series of classic experiments that cemented the peppered moth's iconic status. These were designed to test a hypothesis first proposed by lepidopterist James Tutt that the rise in melanism was a result of natural selection caused by differential bird predation. Though

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Peppered moths exist in two forms, but the darker variety is becoming ever rarer as pollution declines

Tutt put forward the idea in 1896, it was ignored for decades because few ornithologists or lepidopterists believed birds were major predators of moths.

Kettlewell, spurred on by his Oxford mentor Edmund Brisco Ford, thought otherwise. In 1953 and 1955 he carried out experiments in polluted woodland in Rubery, near Birmingham, and unspoiled woodland in rural Dorset. In the mornings he dropped hundreds of marked moths, both light and melanic, on tree trunks, where they quickly took up resting positions. In the evenings he used moth traps to recapture them. In Birmingham, he recaptured twice as many dark as light moths. In Dorset, he found the opposite, recapturing more light moths. The obvious conclusion was that light moths were more heavily predated than dark moths in Birmingham, and vice versa in Dorset.

During these experiments Kettlewell also directly observed robins and hedge sparrows eating peppered moths. As expected, the birds noticed and ate more light-coloured moths on soot-covered trees, and more melanic ones on lichen-covered trees. This was a breakthrough, as hardly anyone in Kettlewell's time believed that birds ate moths. In case anyone doubted his observations Kettlewell recruited his Oxford colleague, ethologist Niko Tinbergen (who would later win a Nobel prize for his work on animal behaviour), to film birds eating moths.

Kettlewell's experiments were quickly accepted as proof that the rise of the melanic moth was a case of evolution by natural selection, and that the agent of selection was bird predation. The peppered moth quickly found its way into textbooks, often accompanied by striking photographs of light and dark moths resting on lichen-covered and soot-stained bark.

In truth, however, there were problems with Kettlewell's experiments. Perhaps the most significant was that he released ▶

"It's a story of birds and moths and pollution and camouflage and lunch and death"

moths onto tree trunks. Although moths occasionally choose trunks as a daytime resting place, they prefer the underside of branches. Kettlewell also let his moths go during the day, even though they normally choose their resting place at night. And he released more moths than would naturally be present in an area, which may have made them more conspicuous and tempted birds to eat them even if they wouldn't normally. These problems were familiar to evolutionary biologists, many of whom tried to resolve them with experiments, but were not given a general airing until 1998, when Majerus pointed out the flaws in Kettlewell's work in his book *Melanism: Evolution in action*.

Majerus had unleashed a monster. In November 1998, *Nature* published a review of his book by evolutionary biologist Jerry Coyne of the University of Chicago (vol 396, p 35). In it, Coyne wrote a sentence that would come back to haunt him: "For the time being we must discard *Biston* as a well-understood example of natural selection in action."

Coyne's motivations were entirely honourable. "I thought I was drawing attention to some problems and was doing the scientific community a service," he says. He did not mean to imply that the peppered moth was not an example of evolution by natural selection, merely that the fine details were still lacking. "I wasn't very clear. The key was *well-understood*."

But to anti-evolution organisations such as the Discovery Institute, Coyne's true intentions were irrelevant. His words were manna from heaven. By selectively quoting him and Majerus they managed to portray the textbook version of events as hopelessly flawed, and with it the entire theory of evolution. In a pincer movement, they also pointed at the textbook pictures – which are often staged with dead specimens – and proclaimed that the science behind those pictures was staged too.

In 2000, in an attempt to rescue the peppered moth's reputation, Majerus embarked on a large experiment designed to iron out the problems with Kettlewell's work. He barely had time to get going, however, before things took a turn for the worse. In 2002, journalist Judith Hooper published a popular science book called *Of Moths and Men: Intrigue, tragedy & the peppered moth* in which she openly accused Kettlewell of manipulating his data to prove his hypothesis. Hooper's book is a roller-coaster tale and brilliantly written. It is not a creationist text, but creationists seized on it anyway as evidence that Kettlewell was a fraud.

No evidence of fraud

He wasn't. As numerous historians and scientists have pointed out, Hooper's book is littered with factual errors, not least the accusation that Kettlewell forged his data. There is no evidence he did so. "Hooper went too far," says Paul Brakefield of Leiden University in the Netherlands. "Anyone who knew Kettlewell would tell you that the last thing he would do was commit fraud." Coyne himself wrote a scathing review of Hooper's book in which he accused her of unfairly smearing Kettlewell and concluded that "industrial melanism still represents a splendid example of evolution in action" (*Nature*, vol 418, p 19). It is fair to say that this accurately represented the views of the vast majority of evolutionary biologists at the time, but by then the damage had been done.

Meanwhile, Majerus was steadily working through his experiment in his own garden in Cambridge. He started by identifying 103 branches that were suitable resting places for peppered moths, ranging in height from 2 to 26 metres, many of them covered in lichen. For seven years, every night from May to August, he placed nets around 12 randomly chosen branches and released a single moth into each net. Around 90 per cent were light-coloured to reflect the natural frequencies of the two forms around Cambridge.

The moths took up resting positions overnight, usually on the underside of the branch. At sunrise the next morning Majerus removed the nets and 4 hours later checked to see which moths were still there. His assumption was that, as peppered moths spend the whole day in their resting position, any that disappeared between sunrise and mid-morning had almost certainly been spotted and eaten by birds.

Because he was able to watch some of the branches from his house through binoculars, he also observed the moths being eaten by many species of bird – including robins, blackbirds, magpies and blue tits. As expected, the birds were better at spotting the dark moths than the camouflaged light ones, he says.

Majerus says his design addresses all the flaws in Kettlewell's experiments. He let moths choose their own resting positions, he used low densities, he released them at night when they were normally active, and he used local moths at the frequencies found in nature.

This August, Majerus presented his preliminary results at a meeting of evolutionary biologists at the University of Uppsala in Sweden. He said that over the seven years, 29 per cent of his melanic moths were eaten compared with 22 per cent of light ones. This was a statistically significant difference.

As in many parts of the UK, pollution in Cambridge has declined since the adoption of clean air acts in the 1950s, and melanic moths are becoming increasingly rare, declining from 12 per cent of the population in 2001 to under 2 per cent today. According to Majerus, his results show that bird predation is the agent of this change. Birds were better at spotting dark moths than light ones, ate more of them and reduced the percentage of black moths over time. "It provides the proof of evolution," he says. He will soon publish his results in a peer-reviewed journal.

Still, Majerus's experiment doesn't satisfy all evolutionary biologists. Even though birds

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Here's why birds find it easier to spot light-coloured moths on a dark background

were responsible for differential moth mortality in the experiment, James Carey of the University of California, Davis, wonders how important they are in nature. He points out that other animals also eat moths, and could have different preferences for dark and light forms. "The question is, does preferential predation by birds matter?" he says. "Unless you know what moths die of in nature, you don't know how important birds really are."

Majerus counters this by saying that there is no evidence that other moth predators preferentially choose dark or light forms. Bats are a major predator, but they hunt by echolocation rather than vision and Majerus has good experimental evidence that they have equal preference for light and dark moths. Even if birds account for only 1 per cent of moth mortality, as long as the other 99 per cent is not selective, bird predation will result in changes in gene frequency. Still, there is an unknown factor remaining: no one yet knows the impact of invertebrate predators such as earwigs and beetles.

Majerus's study also leaves a long-standing problem unsolved. For reasons that are not clear, the frequencies of dark and light moths do not always correlate with the level of pollution. In East Anglia, for example, dark moths have always been relatively common despite low pollution levels.

Biologists feel this can be explained, says Brakefield. Kettlewell himself proposed that peppered moth larvae, which hatch in the tree canopy and hang on silk threads, can be blown long distances by the wind. It's possible that the dark moths of East Anglia arrive on prevailing south-westerly winds from the industrial areas around London, though this idea has yet to be properly tested.

These are legitimate problems that require scientific explanations. But they do not point to a fundamental problem with the peppered moth story, let alone the theory of evolution. Brakefield, Majerus, Coyne and the rest of mainstream biology all agree that the peppered moth was and is a well-understood example of evolution by natural selection. There is no doubt that the peppered moth's colour is genetically determined, so changes in the frequencies of light and dark forms demonstrate changes in gene frequencies – and that is evolution. What's more, the direction and speed at which this evolution occurred can only be explained by natural selection. The agent of selection remains contentious, but bird predation is the only hypothesis with any experimental backing. "There is no controversy among the people who work on peppered moths," says Bruce Grant at the College of William & Mary in Williamsburg, Virginia.

Anti-evolutionists will continue to suggest there is, of course, but as far as Majerus and others are concerned their claims have been debunked and the peppered moth should be reinstated as a textbook example of evolution in action. Not just to teach children either, but also as a direct rebuttal of anti-evolutionism. As Majerus told the conference in Sweden: "The peppered moth story is easy to understand because it involves things that we are familiar with: vision and predation and birds and moths and pollution and camouflage and lunch and death. That is why the anti-evolution lobby attacks the peppered moth story. They are frightened that too many people will be able to understand." ●

Jaap de Roode is a biologist and writer at the University of Georgia in Athens, US