Selective Bird Predation on the Peppered Moth

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Brief history of the peppered moth debacle

The material basis of evolution began to be investigated at the end of the 19th century. J.W. Tutt studied melanism in moths in relation to natural selection. He was the first to suggest that the rapid increases in melanic moths that had been occurring in industrialized England during the late 19th Century were due to natural selection. He was particularly interested in the peppered moth *Biston betularia*, and argued that the rise in melanism was due to preferential bird predation against sooty vs. unpolluted resting sites on bark [1,2].

Others were skeptical of predation as a means of producing such rapid evolution, especially the Mendelians who believed that saltational mutation could be more efficacious (e.g., [3,4]. H.B.D. Kettlewell, with help from Niko Tinbergen and a movie camera, was the first to show conclusively that peppered moths were indeed eaten by birds. When moths were at rest, those that matched their backgrounds least well were the most vulnerable [5,6]. In his experiments Kettlewell often used high densities of reared insects. These were placed on tree trunks and observed, or marked, released and subsequently recaptured; most of his estimates of selection came from the latter type of experiment. Later, dead moths were used (Clarke and Sheppard [7] and others) which were attached in a range of positions on different types of tree trunk.

These procedures all have potential drawbacks [8,9]. Densities may be too high to be realistic. Investigators may not place moths where they would rest naturally. Reared insects, which were often used, may not behave naturally once released for mark-recapture studies. For these reasons resting behaviour, substrate quality and design of the experiments began to be scrutinised critically [10-13]. Majerus himself [8] was among the more outspoken critics, and his forthright analysis of possible procedural defects was enough to make a reviewer of his book doubt that the peppered moth provided a well understood case of natural selection [14], much to Majerus' own dismay [9].

Appearing as it did in an influential journal, Coyne's review helped to set off an anti-evolutionist outpouring on the internet and the printed page (e.g., [15]). JD Morris of the Institute of Creation Research wrote "What a wonderful time to be a creationist, when even the supposed best proof of evolution in action is so flimsy that it cannot stand the test of truth" (www.icr.org/article/what-about-the-peppered-moth/).

Similar comments appeared even in reputable newspapers such as the Daily Telegraph, where it was stated that the experiments were "now thought to be worthless" [16]. A popular book later appeared alleging that the original peppered moth selection experiments of Kettlewell had been fraudulent [17]. The fraud allegation in particular has since been shown to be quite groundless [18-20], but today, a casual enquirer can be forgiven for believing that the selective basis for industrial melanism in moths has been utterly discredited. Of course, this was the last thing Majerus, or indeed Coyne had intended [21].

Majerus therefore resolved to carry out an experiment that would take account of perceived weaknesses in earlier work and consolidate the case for selective predation. He wished to ensure that the density of settled moths was not too high and that they settled in positions they chose themselves. The moths used should be from the locality of the experiment. It should be possible to compare behaviour of the different sexes and of individuals raised for the purpose or caught in different ways. Kettlewell had been accused of modifying his design during the course of an experiment [15,17], so Majerus chose to publish details of his experimental methods while the predation experiment itself was underway [9].

The attacks on the classic peppered moth story were promulgated almost entirely by people who never studied the peppered moth themselves. It is notable that no new fieldwork had ever been done that disproved the classical explanation.

More detailed accounts of the history of the rise and current eclipse in belief in the predation theory of the peppered moth industrial melanism are available in a variety of other publications [9,22-26].

References

- 1 Tutt, J.W. 1896 *British Moths*. London: Ludgate Hill: George Routledge & Sons, Ltd..
- 2 Tutt, J.W. 1899 A Natural History of the British Lepidoptera. A Text-book for Students and Collectors. London: Swan Sonnenschein & Co..
- 3 Bateson, W. 1900 Collective enquiry as to progressive melanism in moths -memorandum from the Evolution Committee of the Royal Society. *Entomological Record and Journal of Variation* **12**, 140
- 4 Bateson, W. 1913 *Problems of Genetics*. New Haven, Connecticut: Yale University Press.
- 5 Kettlewell, H.B.D. 1955 Selection experiments on industrial melanism in the Lepidoptera. *Heredity* **9**, 323-342
- 6 Kettlewell, H.B.D. 1956 Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* **10**, 287-301
- 7 Clarke, C.A. & Sheppard, P.M. 1966 A local survey of the distribution of industrial melanic forms in the moth *Biston betularia* and estimates of the selective values of these in an industrial environment. *Proc. Roy. Soc. Lond. B* **165**, 424-439
- 8 Majerus, M.E.N. 1998 *Melanism. Evolution in Action*. Oxford: Oxford University Press.
- 9 Majerus, M.E.N. 2005 The peppered moth: decline of a Darwinian disciple. In Insect Evolutionary Ecology. (eds Fellowes, M.D.E., Holloway, G.J. & Rolff, J.), p. 371-96. Wallingford, Oxon.: CABI Publishing.
- 10 Mikkola, K. 1984 On the selective forces acting in the industrial melanism of *Biston* and *Oligia* moths (Lepidoptera: Geometridae and Noctuidae). *Biol. J. Linn. Soc.* **21**, 409-421
- 11 Liebert, T.G. & Brakefield, P.M. 1987 Behavioural studies on the peppered moth *Biston betularia* and a discussion of the role of pollution and lichens in industrial melanism. *Biol. J. Linn. Soc.* **31**, 129-150
- 12 Howlett, R.J. & Majerus, M.E.N. 1987 The understanding of industrial melanism in the peppered moth (*Biston betularia*) (Lepidoptera: Geometridae). *Biol. J. Linn. Soc.* **30**, 31-34
- 13 Sargent, T.D., Millar, C.D. & Lambert, D.M. 1998 The 'classical' explanation of industrial melanism. *Evol. Biol.* **30**, 299-322

- 14 Coyne, J.A. 1998 Not black and white. Review of "Melanism: Evolution in Action" by Michael E.N. Majerus. *Nature* **396**, 35-36
- 15 Wells, J. 2000 Icons of Evolution: Science or Myth? Why Much of What We Teach About Evolution is Wrong. Washington, D.C.: Regnery Press.
- 16 Matthews, R. 1999 Scientists pick holes in Darwin moth theory. Daily Telegraph
- 17 Hooper, J. 2002 *Of Moths and Men. An Evolutionary Tale. The Untold Story of Science and the Peppered Moth.* London: Fourth Estate.
- 18 Grant, B.S. 2002 Sour grapes of wrath. Science 297, 940-941
- 19 Rudge, D.W. 2005 Did Kettlewell commit fraud? Re-examining the evidence. *Public Understanding of Science* **14**, 249-268.
- 20 Cook, L.M. & Turner, J.R.G. 2008 Decline in melanism in two British moths: spatial, temporal and interspecific variation. *Heredity* **101**, 483-489
- 21 Coyne, J.A. 2002 Evolution under pressure. Review of Judith Hooper: "Of Moths and Men: Intrigue, Tragedy and the Peppered Moth. *Nature* **418**, 19-20
- 22 Grant, B.S. 1999 Fine tuning the peppered moth paradigm. Evolution 53, 980-984
- 23 Marec, F. 2002 Role of the sex chromosome W in sex determination in Lepidoptera. Grant proposal.
- 24 Cook, L.M. 2003 The rise and fall of the *carbonaria* form of the peppered moth. *Q. Rev. Biol.* **78**, 399-418
- 25 Mallet, J. 2004 The peppered moth: a black and white story after all. *Genetics Society News* **50**, 34-38
- 26 Majerus, M.E.N. 2009 Industrial melanism in the peppered moth, *Biston betularia*: an excellent teaching example of Darwinian evolution in action. *Evolution: Education and Outreach* 2, 63-74 (DOI: 10.1007/s12052-008-0107-y).