Biston betularia f. *typica*

f. *carbonaria*

Prologue

- First f. *carbonaria* in Manchester in 1848
- By 1895, 98% of Mancunian population were black
- 1896: J.W. Tutt proposes differential bird predation is the agent responsible
- J.B.S. 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

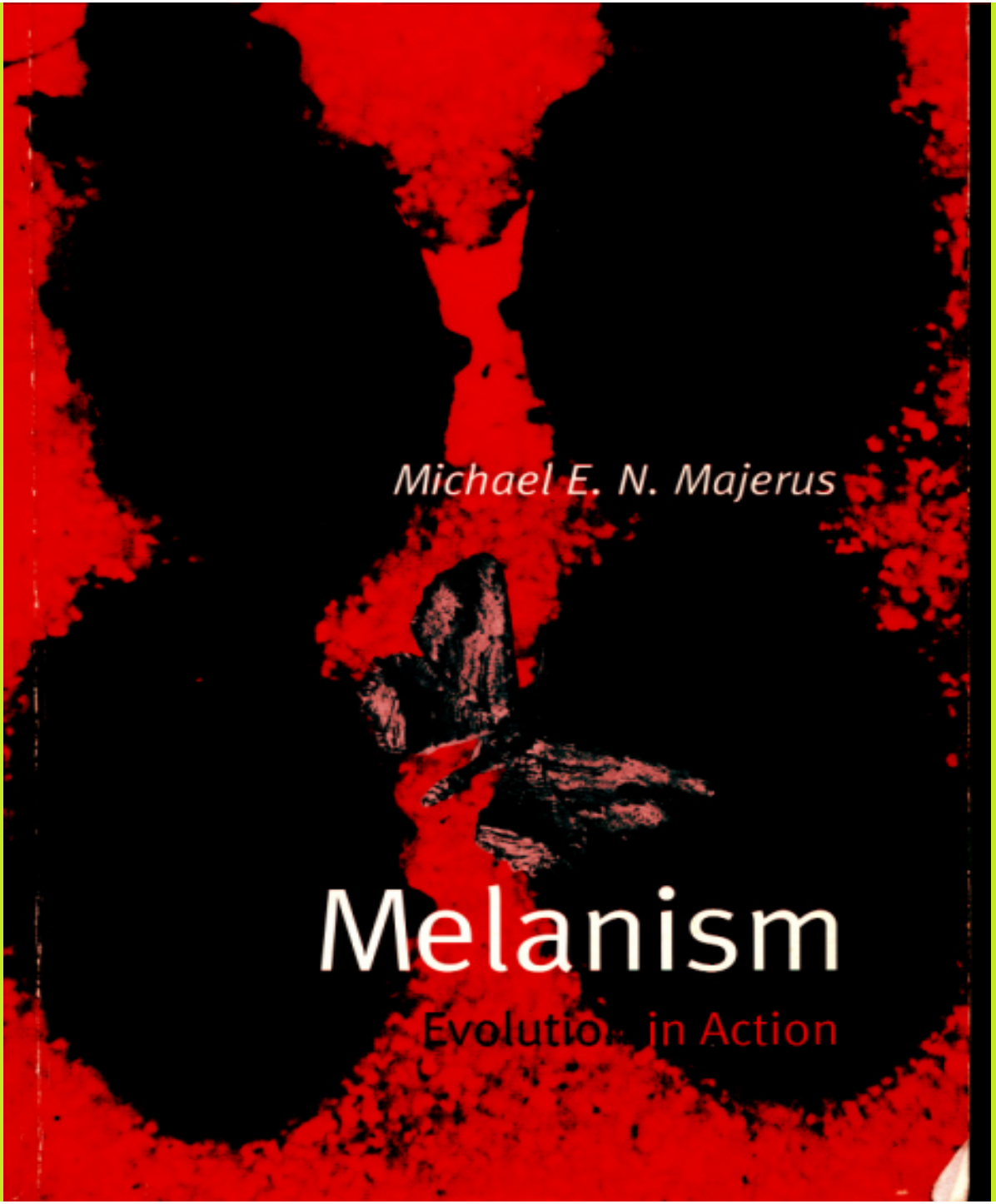
- Kettlewell demonstrated correlation between *carbonaria* frequencies and pollution levels
- Peppered moth becomes the foremost example of Darwinian evolution in action
- In next 40 years, other *Biston* details were investigated. None seriously undermined Kettlewell's qualitative interpretation

The declines of the melanic moth

- Following anti-pollution laws, *carbonaria* began to decline on both sides of the Atlantic
- Zenith of peppered moth's popularity came in 1996, in the New York Times
- From 1998, the reputation of the peppered moth, as an example of Darwinian evolution in action, has declined

Plan

- Briefly explain the reasons for this decline in reputation
- Describe what I have been doing for the last seven years
- Give results of one set of field observations and two experiments
- Make a few concluding remarks


Michael E. N. Majerus
Melanism
Evolution in Action

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…'*
- As Donald Frack put it: *There is essentially no resemblance between Majerus's book and Coyne's review of it. If I hadn't known differently, I would have thought the review was of some other book.*"

But the damage had been done:

March 1999, Robert Matthews in the Sunday Telegraph

The black variety is to the left of the white peppered moth

Scientists pick holes in Darwin moth theory

by ROBERT MATTHEWS
Science Correspondent

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

tion-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

- *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*

2002

Of Moths and Men

JUDITH HOOPER

Magpie

Yellow Shell

Orange Moth

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*

Orange Moth

Peppered Moth

Magpie

JUDITH HOOPER

Orange Moth

Orange Moth

Barred Umber

From the Fly-sheet

- "*Of Moths and Men* is … a fascinating psychological dissection of the ambitious scientists who will ignore the truth for the sake of fame and recognition".

Many judgements on Hooper's book

- E.g. Bruce Grant, Bryan Clarke, Lawrence Cook, James Mallett, Paul Brakefield, David Rudge, myself, and even Jerry Coyne (*Nature, 2002)* who 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*.'

Hooper's first sentence

- *"To begin at the beginning, the Lepidoptera are divided into two orders: the butterflies (Rhopalocera) and the moths (Heterocera)."*

Did Kettlewell commit fraud?

- Rudge (2005) examined Hooper's evidence that Kettlewell committed scientific fraud

  He concludes, "*that Hooper does not provide one shred of evidence to support this serious allegation*".

  He points out that among the scientists who have worked on peppered moths over the last 50 years, none, not even Kettlewell's severest critics have ever suggested he committed fraud.

New work to address problems

- In 2000, in response to Coyne, Matthews, et al. I conceived two parts of the work I am going to describe: i) gain evidence on where peppered moths rest by day; ii) check the qualitative accuracy of Kettlewell's work
- The third piece of work, an experiment on predation by bats, derives specifically from Hooper's book.

Main predation experiment

- Aim: Is differential bird predation sufficient to explain any changes in frequency in the forms of the moth observed over a period of years?
- From previous survey work, it was known that *carbonaria* frequency was declining.
- N.B. Not possible to replicate Kettlewell's reciprocal design as there is nowhere that *carbonaria* is increasing.

Improvements in protocol (1)

- Experiment designed to improve on flaws in Kettlewell's protocol, i.e. that:
    - i) The densities of moths were too great, and he used too few release sites
    - ii) Moths were released onto tree trunks, when Kettlewell knew that peppered moths usually rest under lateral branches
    - iii) Moths were released during the day, and so might not have selected sites that would maximize their crypsis
    - iv) Kettlewell used mixtures of wild caught and lab bred moths, which might behave differently
    - v) Kettlewell used translocated moths that might have had different behaviours as a result of local adaptation.

Improvements in protocol (2)

- My design, piloted in 2001, and published in 2005, involved:
  - i) Doing the experiments in the wild, at low frequency (<10 per hectare per night), with any moths left at the end each predation run being recovered.
  - ii) Releasing moths in their natural resting positions (initially 103 release sites in a 1 hectare experimental site)
  - iii) Release moths at dusk, into restricted arenas at their natural resting sites, so that they chose resting positions at the end of their night flight. (Arenas removed just before sunrise.)
  - iv) Using male moths that were moth-trap caught, pheromone-trap caught or lab-bred, and lab-bred females.
  - v) Only use moths from Cambridge, within 5km of the experimental site.

Improvements in protocol (3)

- In addition, I:
    - vi) Released moths at the frequencies that they occurred at in the previous year at a site 1.9km from the experimental site.
    - vii) Ran the experiment during the months that the moth is naturally on the wing.
    - Predation scored by direct observation or absence after 4hrs.
- Only changes during experiment: i) the number of release sites has dropped to 97 due to storm damage, and ii) the experiment ran for six years, rather than five, due to low frequency of *carbonaria* in 2003

Parts of the experimental site

Predation of peppered moths by bats

- Hooper (2002, page 270) raises the question of bats as predators of peppered moths. She states that, "*Kettlewell himself admitted that they {bats} probably accounted for 90% of the predation of adult moths*."
- By phone, in 2000, she pointed out to me that Kettlewell had "*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*". Hooper thought that there were flaws in this argument and asked me about this.
- I said I agreed with Kettlewell and explained why (Hooper, 2002, p. 270). But not understanding how selection operates, Hooper didn't get it, and concludes, '*Can we really be sure that bat predation is not selective….?*'

A batty predation experiment

- Despite the extreme logical gymnastics and unrealistic assumptions one would have to perform if bat predation were to be responsible for industrial melanism in the peppered moth, I decided to do an experiment to test whether bats do prey on *typica* and *carbonaria* differentially.
- The design was simply to release equal numbers of the forms near moth-traps where pipistrelle bats were feeding and watch which were eaten

Predation by bats

Form	Flew and lost	Did not fly	Caught by bats
a) Camb. 2003			
carbonaria	114	35	51
typica	107	39	54
b) Camb. 2004			
carbonaria	104	43	53
typica	117	36	47
c) New Forest 2005			
carbonaria	100	39	61
typica	95	32	73
d) Leeds 2005			
carbonaria	126	31	43
typica	132	31	37

Conclusion

- Across the four runs, 208 *carbonaria* were eaten, while 211 *typica* were eaten, with no significant difference between sites or runs.
- **There is no evidence of differential bat predation of the *tyipca* and *carbonaria* forms of the peppered moth.**

Where peppered moths rest by day (1)

- During the main predation experiment, I have had occasion to spend a great deal of time carefully scrutinizing the trunks, branches and twigs of a limited set of trees at the experimental site. During this time I have found 135 peppered moths, resting in what I have no reason to presume are not their freely chosen natural resting sites.

Where peppered moths rest by day (2)

- The position of each moth was scored for resting site (trunk, branch, twig); height above ground; on trunks, north or south half; on branches, top or bottom half. Sex and form of each moth was also recorded.

Where peppered moths rest by day (2001-2006)

	Trunks	Branches	Twigs	Totals
Males	28	40	11	79
Females	20	30	6	56
Totals	48	70	17	135

Where peppered moths rest by day (3)

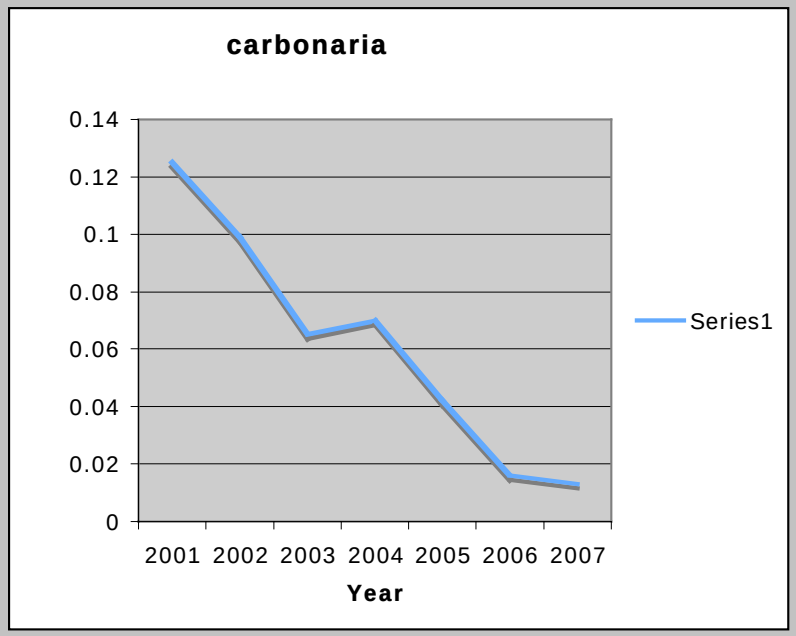
- Results (2001-2006) are that:
  - i) The majority (50.4%) of moths rest on lateral branches
  - ii) That of the moths on lateral branches, the majority (89%) rest on the lower half of the branch
  - iii) That a significant proportion of moths (37%) do rest on tree trunks
  - iv) That of those that rest on trunks, the majority (86.8%) rest on the north, rather than the south half.
  - v) That a minority of moths (12.6%) rest under or among twigs
  - vi) That there was no significant difference in the resting sites of males and females.
  - vii) There was no significant differences in the resting sites used by *typica*, *carbonaria* or *insularia* forms.

Peppered moths at rest

Can you see it?

Predation (1): Form frequencies

- F. *carbonaria* frequencies by moth trapping at Maddingley Wood (1.9km from experimental site).
- Form frequencies given exclude f. *insularia*, which had a frequency of 0.063-0.109, with no pattern of consistent change in direction.



Predation (2) Experimental data

Numbers of the two forms available for predation and predated (2002-2007).

Year	Numbers available for predators		Numbers eaten	
	typica	*carbonaria*	*typica*	*carbonaria*
2002	706	101	162	31
2003	731	82	204	24
2004	751	53	128	17
2005	763	58	166	18
2006	774	34	145	6
2007	797	14	158	4

Proportion of *typica* taken = 0.212: proportion of *carbonaria* taken = 0.292.

Predation (3) the predators

- A number of species of bird were seen to take the moths
- These included robins, hedge sparrows, a lesser-spotted woodpecker, great tits, blue tits, blackbirds, starlings, wrens and magpies

Predation (4) seln coefficients

Selection coefficient against *carbonaria* compared to *typica*

Year	Expected selection against *carb.* based on form frequency differences between years	Observed selection against *carb.* from selection experiment
2001	0.239	Not done
2002	0.337	0.252
2003	-0.096	0.046
2004	0.435	0.469
2005	0.63	0.299
2006	0.13	-0.061
2007	prediction	0.306

- Average selection against *carb.* from form frequency data = 0.286
- Average selection against *carb.* from predation experiment = 0.219

- Correlation coefficient for expected compared to observed for years 2002-2006 = 0.75169

Predation (5) Conclusion

- I conclude that differential bird predation here is a major factor responsible for the decline in *carbonaria* frequency in Cambridge between 2001 and 2007.
- So Tutt's hypothesis stands, and is, once again, supported.

Why do anti-evolutionists care about the peppered moth?

- "…. *Even today that persists as a slightly tricky problem if you are trying to persuade somebody who doesn't believe in this evolution stuff and wants you to show him an example – they are hard to find in terms of everyday observation.*" (Adams 2002)
- But 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.

Hooper on moth men

- “*Moth men have stunted social skills of the more monomaniacal computer hackers, going about with mis-buttoned shirts and uncombed hair, spouting taxonomic Latin*”

Darwinian evolution cannot NOT happen

- Organisms produce many more reproductive cells than ever give rise to mature individuals
- Population sizes remain more or less constant
- **Therefore**, there must be a high rate of mortality
- The individuals in a species show variation
- **Therefore**, some variants will succeed better than others, and those individuals with beneficial traits will be naturally selected to be the parents of the next generation
- There is a hereditary resemblance between parents and offspring
- **Therefore**, beneficial traits will be passed to future generations

Holmes' dilemma

- "What is the meaning of it Watson? What object is served by this circle of misery and violence and fear? It must tend to some end, or else our universe is ruled by chance, which is unthinkable. But what end? There is the great standing perennial problem to which human reason is as far from an answer as ever." (Doyle, His Last Bow: The Adventure of the Cardboard Box)

THE PROOF OF EVOLUTION

- We need to address global problems now. To do so with any chance of success, we have to base our decisions on scientific facts: and that includes the **fact** of Darwinian evolution.
- The peppered moth is perhaps the most visually impacting and easily understood example of Darwinian evolution in action. It should be taught. It is, after all, **The Proof Of Evolution**


Thank you