BOOKS: EVOLUTION

Sour Grapes of Wrath

Bruce S. Grant

Mark Twain once quipped that reports of his death had been exaggerated. Recent reports exaggerate the death of industrial melanism as an exemplar of natural selection. The latest is Judith Hooper's *Of Moths and Men*, which promises "the untold story of science and the peppered moth." 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. This is unfortunate. Hooper is a gifted writer. In places, her prose is quite enjoyable, even brilliant. But, sadly, the book is marred by numerous factual errors and by misrepresentations of concepts and controversies.

The fundamental problem is Hooper's failure to clearly distinguish the evidence for natural selection and the mechanism of selection. A dead body with a knife in its back is evidence that a murder has been committed. An inability to establish beyond reasonable doubt the guilt of the leading suspect does not mean that the murder did not occur.

Population geneticists define evolution as a change in allele (gene) frequency. Adult peppered moths come in a range of shades from mottled gray (pale) to jet black (melanic). We know from extensive genetic analysis that these phenotypes result from combinations of multiple alleles at a single locus. Changes in the percentages of the phenotypes in wild populations are well documented. The changes continue and are observable even now. The steady trajectory and speed of changes in allele frequencies indicate that this evolution results primarily from natural selection. J. B. S. Haldane's original calculation of a selection coefficient was estimated from the number of generations it took for the melanic phenotype to effectively replace the pale phenotype during the 19th century. More detailed records document recent changes. For example, near Liverpool, England, the melanic phenotype declined from 93 to 18% in 37 generations (one generation per year); this change is consistent with a 15% selective disadvantage to genotypes with the dominant (melanic) allele.

We have amassed enormous records of changes in allele frequency in peppered moth populations that cannot be explained in the absence of natural selection. But what is the mechanism of selection? Even the answer "we have no clue" would not invalidate the conclusion that selection has occurred. Fortunately, the circumstances have left clues.

Geographic and temporal variations in the incidence of melanism correlate with atmospheric levels of SO_2 and suspended particles. (The correlations are not perfect; gene flow by migration spreads alleles, even into populations where they are deleterious.) Light reflectance from tree bark declines as suspended particles increase. Across a range of backgrounds, the pale and melanic phenotypes are differently conspicuous to the human eye. As early as 1896, J. W. Tutt suspected that birds were selectively eating conspicuous phenotypes in habitats variously modified by industrial fallout; H. B. D. Kettlewell first tested Tutt's idea in the 1950s.

It is on Kettlewell and his experiments that Hooper focuses her attention. In a biography more akin to character assassination than to objective disclosure, she portrays Kettlewell as an insecure misfit so driven to please his "boss," E. B. Ford, that he is suspected (by Hooper) of fudging his data. She bases her case on experimental design changes that Kettlewell himself described in his papers and on a sudden increase in the recapture rate of marked moths released in polluted woodlands. Several obvious things that Hooper left unexamined affect the size of moth catches, and her case is unconvincing. In addition, she presents it as if the very evidence for natural selection in peppered moths depends on the validity of Kettlewell's experiments. But even the evidence for bird predation does not depend on them.

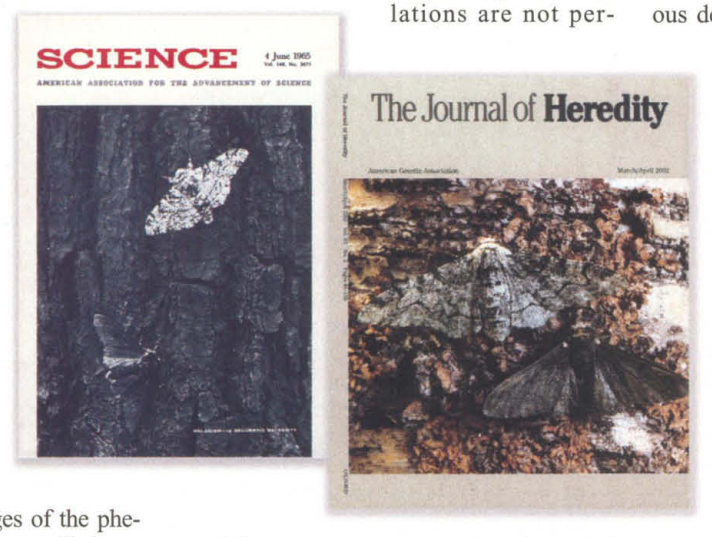
Of Moths and Men
Intrigue, Tragedy and the Peppered Moth
by Judith Hooper
Fourth Estate, London, 2002. 397 pp. £15.99. ISBN 1-84115-392-3.

Of Moths and Men
The Untold Story of Science and the Peppered Moth
Norton, New York, 2002. 397 pp. $26.95, C$38.99. ISBN 0-393-05121-8.

Fortunately, science assesses the correctness of work by testing its repeatability. Kettlewell's conclusions have been considered in eight separate field studies, of various designs, performed between 1966 and 1987. Some of the design changes—such as reducing the density of moths, randomly assigning moths to trees, altering locations on trees where moths were positioned, and positioning killed moths to control for differences in viability and dispersal—were made to correct deficiencies identified in his original experiments. L. M. Cook's regression analysis of fitness estimates from these experiments plotted against phenotype frequencies at their various locations shows the studies to be remarkably consistent (*1*).

Other mechanisms of selection have been proposed. An inherent physiological advantage of melanic over pale phenotypes is consistent with the rise and spread of melanism, but the widespread decline in melanism that followed the Clean Air Acts obviates that interpretation. Although the possibility remains that physiological differences might be facultative (changing with conditions), so far no experimental work supports this idea. To date, only selective predation by birds is backed by experiment.

Hooper's book turns bizarre when she showcases American biologist T. D. Sargent as a wounded iconoclast whose career was stultified because Kettlewell dismissed his



Fateful contrasts. For peppered moths in both Britain and North America, the melanic phenotypes that became predominant in industrial environments have declined substantially since the enactment of clean air legislation.

CREDITS: (LEFT) PHOTOGRAPH, H.B.D. KETTLEWELL; (RIGHT) PHOTOGRAPH, B. GRANT/COURTESY *J. HEREDITY* AND OXFORD UNIV. PRESS

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work. She argues that Sargent is now under attack because he questions the "classical explanation" for industrial melanism. Hooper garbles the controversy regarding background selection by moths, and she entertains Sargent's protracted speculation about phenotypic induction. (He has offered no evidence that melanism is an induced character in adult peppered moths.) But most egregious is Sargent's assertion that studies in North America falsify the classical explanation. The history of melanism in American peppered moths—which are conspecific with Kettlewell's moths, not a separate species as Hooper indicates—closely parallels what has occurred in Britain, and melanism is correlated in like manner with levels of atmospheric pollution (*2*). The American studies corroborate rather than contradict the classical explanation.

The case for natural selection in the evolution of melanism in peppered moths is actually much stronger today than it was during Kettlewell's time. Textbook accounts should be expanded to reflect this newer information, and they should not cite *Of Moths and Men* as a credible resource.

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BOOKS: ENVIRONMENT

Gold from Green Paths

David Pearce

I recently asked a well-known carbon trader if he had any idea of the total number of carbon trades that had taken place to date. He replied, "Around 350 up to 1998." Why had he stopped counting in 1998? "Because there were too many after that to count." In a carbon trade, an entity subject to a constraint (externally or self-imposed) on carbon dioxide emissions secures the required reduction in emissions through a third party. An electric utility might, for example, continue its own emissions at their current level but reduce net emissions elsewhere by paying for an afforestation program or an energy efficiency project. The utility gains because it is cheaper to cut emissions in other regions, especially in developing countries. It gets the paper "credits" for the carbon reduction. The environment gains because emissions are reduced. The host country gains because new technology and employment are generated by the investment. Such a trade is an instance of "market creation," a mechanism for paying for an environmental service to the mutual gain of the trading parties. My carbon trader had lost count of the trades because they have multiplied in anticipation of the implementation of the Kyoto Protocol. But many of the trades also reflect corporate "social responsibility," the notion that corporations should take on self-regulation to improve their image as environmentally concerned and to meet ethical goals.

Carbon trading is just one of the many good examples of environmental market creation that ecologist Gretchen Daily and journalist Katherine Ellison discuss in *The New Economy of Nature*. Citrus growers may compensate the owners of surrounding forests for maintaining those trees to protect the microclimate in the groves. Farmers and hydroelectric companies may pay the owners of upstream forests to retain tree cover for regulating water supply and avoiding reservoir sedimentation. Wetland owners may be rewarded for the filtering of water supplies and the regulation of effluent. Local communities may collect part of ecotourists' expenditure in return for protecting wildlife against poachers. The possibilities are endless.

The highly readable and openly journalistic book maximizes the chances politicians, entrepreneurs, and venture capitalists will pick up the theme that paying for the environment works. The authors give a slightly misleading impression that the initiatives are mainly American and very recent. Europe already has nascent official carbon trading schemes. Scandinavian countries pay for technology improvements in Baltic power stations to reduce the impacts of acid rain. Peugeot, based in France, has a US$12 million investment in forest conservation in Brazil. But the principles are the same: the environment generates services that have an economic value. Paying for those services provides an open recognition of the worth of those environments, and the resulting prices provide incentives for conservation. Although Daily and Ellison focus on developments since the 1980s, the origins of the approach go back to the 1960s, which saw both an important theoretical essay by Nobel prize winner Ronald Coase (*1*) and the original essay on tradable permits by Canadian economist J. H. Dales (*2*). Environmental economists have advocated market solutions for the past three decades.

The New Economy of Nature
The Quest to Make Conservation Profitable
by Gretchen C. Daily and Katherine Ellison
Shearwater (Island Press), Washington, DC, 2002. 270 pp. $25. ISBN 1-55963-945-8.

Daily and Ellison's account is full of fascinating mini-biographies of some of today's leading players, though there are many others who could have been included in the gallery of market-creation advocates. The authors are rightly cautious of some of the ventures they discuss. As in any field of business, there will be successes and failures. Some other caveats might have been included. Trades work when the trading partners are institutionally and politically stable. (The decimation of biodiversity in central Africa, for example, is unlikely to be the subject of market solutions.) And the massive extent of global illegal logging dwarfs the well-intentioned attempts at timber certification whereby consumers pay a little extra for sustainably managed timber.

But the truth is that everything has to be tried, and solutions based on mutual self-interest probably have a better chance of working than moralistic appeals to do the "right thing." *The New Economy of Nature* is a good place to start this learning process.

References
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Investing in a living river. The residents of Napa, California, accepted higher taxes to pay for natural flood protection. Levees and dams along the Napa River were removed so that high waters will spill over onto the historical floodplain.

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