Review

Does being wrong make Kettlewell wrong for science teaching?

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Biology textbooks, almost without exception, introduce students to evolutionary theory with reference to the phenomenon of industrial melanism, long regarded as the classic example of natural selection. Its status as an icon among biology teachers and the public stands in stark contrast to ongoing debates among scientists which reveal that this phenomenon is nowhere near as well understood as textbooks would have us believe. The 'classic' account of the phenomenon of industrial melanism, associated with the work of H B D Kettlewell and recounted in texts and the popular media, is reviewed. Several major discrepancies are identified that have led some to conclude that it should be removed from textbooks altogether. It is argued that these problems actually augment the value of discussing the phenomenon of industrial melanism, and Kettlewell's work in particular, for the teaching of evolutionary biology. The 'classic account' has several advantages that make it particularly useful as an introduction to the concept of natural selection. Discussing some of the details so often omitted from texts can potentially enhance student understanding about the nature of science as a process.

Key words: Depictions of science, Natural selection, Industrial melanism.

The classic textbook account

Almost all introductory biology textbooks illustrate the concept of natural selection with reference to a fairly standard account of the phenomenon of industrial melanism in the peppered moth, *Biston betularia* (e.g. Beck *et al.*, 1991; Campbell, 1987; Campbell *et al.*, 1994). It is helpful to analyse this account with reference to three components:

- The description of the phenomenon itself.
- The explanation of the phenomenon.
- The evidence for the correctness/validity of this explanation.

The phenomenon of industrial melanism

Textbooks generally introduce the phenomenon of industrial melanism with reference to how it was first discovered in the peppered moth, *Biston betularia*. The peppered moth has two forms: a light form, f. *typica*, which has a pale speckled appearance, and a dark or melanic form, f. *carbonaria*, which is nearly soot black. As its name suggests, *typica* was the most common form of the moth throughout the British Isles and Continental Europe until around the middle of the nineteenth century when this situation began to change. The burning of coal, coke, and oil, associated with the industrial revolution, killed off the lichen cover of the unpolluted countryside downwind of manufacturing sites, visibly darkening the surfaces of trees and rocks with a blanket of soot. By the late nineteenth century, naturalists began to notice that previously rare melanic (dark) forms of many moth species, most notably the peppered moth, were becoming much more common in soot darkened areas. The *phenomenon of industrial melanism* refers to this rapid rise in the frequency of melanic forms in several moth species associated with the advent of industrial pollution. Figure 1 is often used to illustrate this correlation between melanic forms and areas downwind of industrial sites.

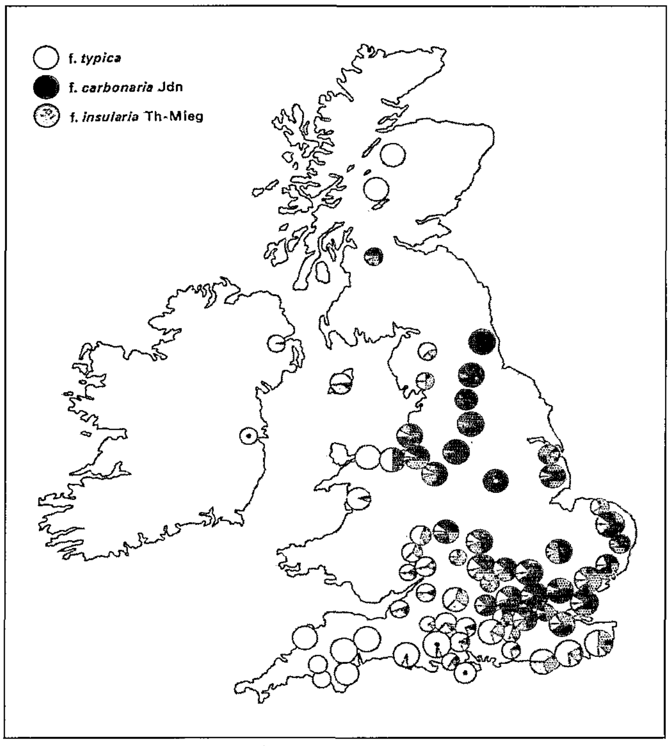

Figure 1 A frequency map of Biston betularia *and its two melanics, f.* carbonaria *and f.* insularia *comprising more than 30 000 records from 83 centres in Britain (Reproduced from Kettlewell (1973), by permission of Oxford University Press).*

The explanation

Textbook authors point out that the *typica* and *carbonaria* phenotypes of the peppered moth are controlled by a single gene, *carbonaria*, which is completely dominant to the recessive typica *allele*. They then explain the spread of *carbonaria* allele in terms of natural selection, and in particular, *crypsis*, or the protective value of colour in hiding the moth against visual predators when it rests on its 'correct' or matching background. According to this standard account, peppered moths fly at night, spending most of the day motionless on the surfaces of tree trunks in plain view. In polluted woods, *carbonaria* is at an advantage compared to *typica*, because its dark colouration camouflages it against soot-darkened backgrounds. This provides it with a better chance of escaping avian predators, and thus a greater chance of surviving and reproducing, than the pale form which is not so protected (see Figure 2). In unpolluted environments, the reverse is true. The pale form of *typica* camouflages it against lichen-covered backgrounds, which gives it a greater chance of escaping avian predators in contrast to *carbonaria* which is much more conspicuous (see Figure 3). Thus, over time (and in the presence of migration), one can appreciate why *typica* would come to predominate in populations living in rural environments, and *carbonaria* in polluted settings.

***Figure** 2 Plate of* Biston betularia L. f. typica *and its melanic f.* carbonaria *on polluted Oak trunk (Birmingham) (Reproduced from Kettlewell (1973), by permission of Oxford University Press).*

The evidence

Many textbooks do not include evidence in favour of the above explanation, preferring instead to illustrate the relevant contrast using photographs of the two forms of the moth on lichen-covered and soot-darkened backgrounds. Of those that do, most make reference to a series of mark-release-recapture experiments conducted by H B D Kettlewell in the early 1950s (Kettlewell, 1955, 1956). They point out that he released large numbers of dark (*carbonaria*) and pale (*typica*) moths in polluted and unpolluted settings and attempted to recapture them over the course of several nights. In the polluted setting, he was able to recapture twice as many *carbonaria* as *typica*, which led him to conclude that more *carbonaria* had escaped avian predation since their release. In the unpolluted setting, Kettlewell found the reverse to be true. Some textbooks go on to mention that since the advent of clean air legislation, the frequency of *carbonaria* has predictably declined.

Problems with the classic account

In a recent comprehensive review of research on melanism, Michael Majerus (1998) recounts several deficiencies of the above account (see also Majerus, 1989; Sargent *et al.*, 1998). While some of the simplifications textbooks adopt might be considered superfluous detail (e.g. neglecting to mention that the speckled colouration pattern of the pale form, *typica*, in the peppered moth represents a highly complex pattern) others are more serious.

Sins of omission

Textbook accounts omit reference to the fact that melanic forms were known to be present in many British moth species prior to

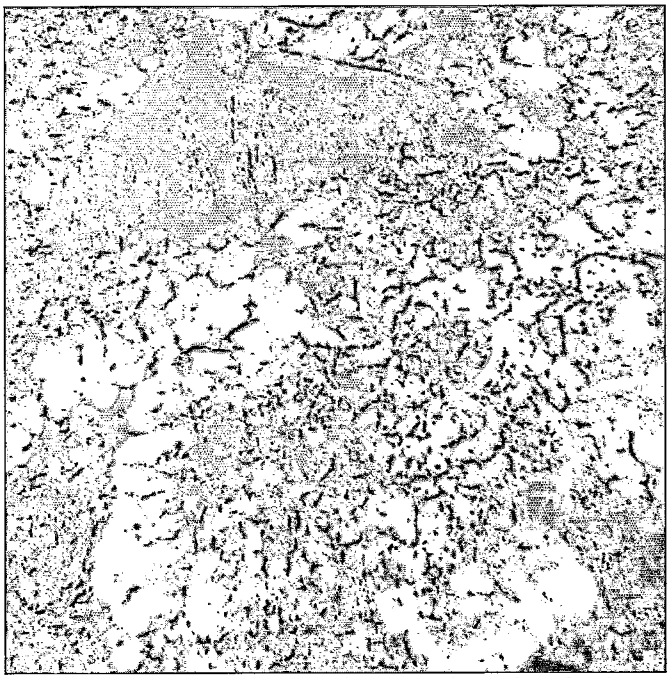

***Figure** 3 Plate of* Biston betularia L. f. typica *and its melanic f.* carbonaria *on lichened Oak trunk (Dorset) (Reproduced from Kettlewell (1973), by permission of Oxford University Press).*

the industrial revolution. This is particularly misleading in that it tacitly suggests melanism has evolved in all moth species by the same mechanism (Majerus, 1989). They also fail to mention the fact that *Biston betularia* was known to exhibit a range of melanic forms between *carbonaria* and *typica*, referred to as f. *insularia*, whose genetics and distribution were less well understood. (Allchin (accepted) has raised concerns that this omission may reinforce dualistic thinking.) They also ignore any reference to the fact that frequencies of *carbonaria* as high as 80% were recorded in *rural* East Anglia.

The explanation textbooks provide makes no reference to other non-selective explanations for the phenomenon extant at the time of Kettlewell's study. Nor do they mention the fact that Kettlewell worked under a model that invoked two selective forces for why the *carbonaria* gene was becoming more common, *crypsis*, and an alleged physiological advantage, of which the latter was initially proposed as the more important (Rudge, 1999). Nor do they indicate the possibility of other factors (e.g. heterozygote advantage, the possibility that the moths might choose their resting sites) being at work.

As mentioned above, textbook accounts generally do not provide any evidence in favour of the above explanation and, when they do, they omit many of the details. Kettlewell's investigations, for instance, included predation experiments using captive birds, ancillary observational studies, background choice experiments, and an extensive survey of *Biston betularia* frequencies throughout the British Isles. Those textbooks that do recount the details of his famous mark-release-recapture experiments omit the details of how he came to his interpretation that his results substantiated claims about differential avian predation by ruling out other possible explanations. Most draw attention to the dramatic contrast between the results of the field experiments in the polluted and rural settings taken with hide observations of wild birds preying on moths by Kettlewell and Niko Tinbergen that fellow scientists found so compelling. However, some misleadingly suggest that the experiment carried out in the unpolluted area was conducted as a control for the experiment done in the polluted setting (Rudge, 1999; but see Hagen, 1999).

Perhaps most damaging of all, textbook accounts provide no indication of the controversies surrounding Kettlewell's investigations and subsequent work. The relevance of Kettlewell's mark-release-recapture experiments as evidence of differential bird predation, for instance, depends upon several details regarding the ecology and behaviour of the moths and birds. Kettlewell's interpretation of his initial experiments assumes that predation by birds reflects their behaviour in nature, rather than being an artefact of the relatively large numbers of moths he used. Clarke and Sheppard (1966) repeated Kettlewell's experiments (with similar results) largely out of a concern that birds that normally never prey on the moth might do so when the moth is present at high densities. Kettlewell's investigations (and subsequent experimental field work since) also rely on the assumption, noted above, that the moths really do spend most of the day on tree trunks and other resting sites in plain view. This assumption has never been reliably documented, despite nearly 40 years of intense effort to learn more about the ecology and behaviour of the moth (Howlett and Majerus, 1987). Some recent studies suggest the moth might actually rest in the shade on the undersides of the boughs of trees (Mikkola, 1984). Majerus (1998) includes photographs taken of live moths in positions they were found by day (Plates 3a, b, c, d, and Figure 6.1a and b), only one of which (Figure 6.1a) was on a tree trunk. If it is indeed the case that the moth does not rest on tree trunks in plain view, this would seriously undermine the value of Kettlewell's experiments (and numerous subsequent studies) by calling into question whether the all important colour differences between the different forms are visible to birds at all[1].

The above considerations suggest that textbook accounts may be misleading to the point of raising serious concerns about the continued use of the phenomenon of industrial melanism as an example of natural selection. The simple and clear-cut manner by which textbooks recount the story of how industrial melanism was first discovered and studied by Kettlewell strongly suggests that the scientific community regards this example as a particularly well documented and well understood example of natural selection. Its choice as one of a very few examples included further suggests it is one of the best if not the best documented example of natural selection. Many textbooks explicitly refer to it as such (e.g. Campbell, 1987 p. 426; Curtis and Barnes, 1985 p. 530). The absence of details regarding the controversies surrounding both the phenomenon and Kettlewell's work further suggest that there is widespread consensus among scientists who study this phenomenon regarding its explanation and the evidence offered in support. Wells (1999), an outside commentator on these problems, takes issue in particular with the continued use of photographs of pale and dark moths on soot-darkened and lichen-covered backgrounds. The reader is never told that these photographs usually depict frozen specimens that have been pinned to the respective surfaces, nor is there any indication that the depiction is only a conjectured resting site of the moth for which there is little reliable evidence (Sargent *et al.*, 1998)[2].

The import of problems with the classic account

Clearly the oversimplifications of the classic account render it technically false, but the reader should be aware that there is widespread disagreement among scientists regarding the import of the foregoing problems. Majerus (1998), in particular, cautions that in his view 'the huge wealth of additional data obtained since Kettlewell's initial predation papers (1955, 1956) does not undermine the basic qualitative deductions from that work'. Almost all of those who have actually done research on melanism agree that the phenomenon of industrial melanism is a well-documented example of evolutionary change and, further, that as an example of directional change it undoubtedly reflects the action of natural selection. Most would also claim that there is reliable evidence for the claim that differential bird predation is the most important of the selective factors at work (Cook, 1998; Grant, 1999; Majerus, 1998; but see Sargent *et al.*, 1998). There is some evidence that suggests heterozygote advantage or some physiological advantage associated with the melanic gene that allows it to better tolerate SO_2 concentrations might play an important role (Berry, 1990). There is evidence to suggest migration has been more important than has been previously recognised (Mani and Majerus, 1993). A distinct, yet minority opinion, also decries the lack of attention paid to the possibility that industrial melanism might be induced by pollutants in the environment (Lambert *et al.*, 1986, Sargent *et al.*, 1998; see Ford, 1964 and Grant, 1999 for critiques of these claims). The bottom line appears to be that the explanation for why melanic forms have become more common may hinge crucially upon specific details associated with each affected species (Majerus, 1989). In other words, despite the frequency with which it has occurred in different moth species (and other animal groups), there is probably no general explanation that will account for the trend in all groups, and in the case of *Biston betularia*, different accounts may be required to explain the trend in different populations (e.g. the anomalous East Anglia population noted above).

Cognisant that resolution of the controversies surrounding the phenomenon of industrial melanism will depend on further scientific work, the question remains, what should science teachers and textbook writers make of these developments? Majerus (1989) suggests many of the outstanding questions about industrial melanism represent outstanding opportunities for teachers and students to conduct original and valuable research, particularly in the case of species other than *Biston betularia* that have been the object of less scientific attention. There is something to be said for this approach, given the ease with which students can collect frequency data using inexpensive moth traps, the relative simplicity of design predation and genetics experiments can take, and the ubiquity of the phenomenon. One can hardly dispute that actually doing science is the ideal way to learn about the design, execution, and interpretation of the results of scientific investigations. Nevertheless, one can question whether this approach represents a realistic alternative, particularly for precollege students, given the extended nature of several of the projects Majerus suggests and the scientific training it presupposes teachers have.

This controversy is part of a more general problem regarding the depiction of science for the purposes of science teaching. The problems associated with how to portray the scientific study of the phenomenon of industrial melanism reflect a fundamental tension between the pedagogical task of introducing unfamiliar concepts and the need to accurately reflect the nature of science. Recourse to the history and philosophy of science, rather than just depicting science as a body of established knowledge, provides one avenue by which this tension can be negotiated without overwhelming the student with superfluous detail or unnecessarily undermining confidence in the method of science.

Pedagogic advantages of the classic account

While some simplifications may reflect time and space constraints, teachers and textbooks omit many details out of a well intentioned and steadfast conviction that students cannot understand science in all its complexity. Introductory students need simple, straightforward descriptions and explanations in order to make sense of new terms and unfamiliar concepts. While some of the popularity of the classic account of industrial melanism reflects history[3] and the fact that new textbooks often adopt familiar examples taken from older texts, it is fair to say that much of its ubiquity reflects several pedagogic advantages afforded by this particular example.

Heuristics

One would be hard pressed to find another example of natural selection that is as straightforward as the classic textbook account of industrial melanism. It makes intuitive sense and refers only to elements teachers may readily presume introductory students have some familiarity with (i.e. birds, moths, pollution, and predation). The selective mechanism (bird predation) plays on the general view of natural selection as a struggle for existence. Moreover, the visual character of this example makes the spread of the melanic form and the selective differences between the two types of the moth in polluted and unpolluted settings easy to depict. Students can readily appreciate the visual contrast between dark and pale moths on lichen-covered and soot-darkened backgrounds as well as how birds preying upon moths might attend to these differences. Many other examples of natural selection are much more difficult to visualise (e.g. the evolution of pesticide resistance in insects).

It is important to note, at the risk of belabouring the obvious, that these heuristic advantages of the classic textbook account stem from its simplicity and the dramatic contrast afforded by the juxtaposition of photographs of the two forms of the moth taken from different settings. The inclusion of information on *insularia* or the removal of photographs from the account would seriously undermine the advantages of this example.

Content

Similar remarks apply with regard to content. The relative simplicity and the absence of extraneous elements in the classic textbook account make it a particularly good vehicle with which to teach the concept of natural selection. It discusses the replacement of one form by another in terms of the spread of a single gene and one effect of that gene on fitness. Students can readily appreciate why and how visual differences between the moth in polluted and unpolluted settings would place the dark form at an advantage in one, and the pale form at an advantage in the other. Thus it is particularly helpful in clarifying that relative fitness is a function of the fit between an organism and its environment rather than some reified property the organism possesses (Brandon, 1990). Most other examples refer to more complex processes (e.g. heterozygote advantage in the case of sickle cell anemia) or appeal to effects of the environment on fitness that are less intuitive (e.g. snail banding patterns). Also, as a result of its popularity, many students already have some familiarity with this particular example from experiences outside the classroom. Meaningful student learning is largely a function of the restructuring of existing knowledge, therefore the advantage of using familiar examples is clear. Again, it can be argued that the addition of further detail, such as the possibility that other selective factors are at work, compromises the value of the classic account as a particularly lucid illustration by which to introduce the concept of natural selection

In addition to explicating what a concept means, teachers often use a particular illustration to educate students about that example. It is here that the debate among the scientists noted above is particularly relevant. Coyne's (1998) point regarding the use of the classic account of the phenomenon of industrial melanism in introductory biology textbooks seems to be that textbook discussions of natural selection should mention or refer only to those examples that are well documented. Continuing to include the phenomenon of industrial melanism as the example of natural selection constitutes a grave disservice to students, because by including it we tacitly suggest to students that it is a well understood example when it is not.

There are other examples of natural selection that are better understood (e.g. the evolution of beak size in the Galapagos Finches (Grant and Grant, 1989), see Endler, 1986 for other examples). It is also fair to say that textbooks and teachers who use the phenomenon of industrial melanism should indicate that the phenomenon of industrial melanism may involve the operation of selection for factors other than colour, and that it continues to be the object of ongoing research. Is it really the case that a textbook should never include scientific claims that are either suspect or known to be false? In the case of physics, the answer is decidedly no. We continue to educate students in Newtonian mechanics in full recognition that Newton's equations are technically false. One might argue that in the case of Newtonian physics, students are learning equations that are approximately true and moreover that such a step is necessary for them to understand and fully appreciate Einsteinian and post-Einsteinian developments. The same could be said of the classic account of industrial melanism. While technically false, the classic account is an approximately true story about how and why the phenomenon of industrial melanism has occurred that will no doubt be the background against which any more successful account will be based. The vast majority of students in high school and college do not go onto careers in evolutionary biology; for those that do, there is plenty of time in graduate school to learn the subtleties of this particular example. The many constraints on teachers and textbooks with regard to the time and space they can devote to the topic of natural selection, not to mention heuristic considerations, rally against the further stipulation that the accounts they provide must be true or command consensus among scientists. The problem is not that textbooks and teachers are knowingly perpetuating falsehoods, but rather the uncritical and unreflective attitude students (and teachers) take towards the information gained from such sources. Rather than presenting the phenomenon of industrial melanism as a subject that was settled by three field experiments by Kettlewell in the 1950s, both teachers and students could profit from thinking about this phenomenon as the object of ongoing scientific attention (Grant, 1999).

Process

These considerations point to another, often neglected, advantage afforded by the overly simplistic textbook account of industrial melanism. It has long been recognised that students should be learning about the nature of science as a process (DeBoer, 1991). Teachers can use the pithy description of Kettlewell's initial work associated with the standard account to introduce students to how scientific claims are developed and tested in science. Kettlewell's experiments are elegant in their simplicity and involve only a minimal amount of mathematics. Having a simple, clear-cut example of how scientific claims are investigated provides a wonderful introduction to the process of science. Inclusion of the many interpretive problems now associated with Kettlewell's experiments conversely limits their value in introducing the logic of science by making the results ambiguous.

A role for the history and philosophy of science

Teachers and textbook writers are, of course, familiar with the above tension. Unfortunately many interpret this as a debate that must be decided one way or the other: either we must focus on pedagogical considerations of how to make science accessible to introductory students *or* we must provide students with an accurate description of the nature of science and what we know about the world. Most teachers choose the former, and it is hard to blame them given the stress placed on preparing students for standardised tests on isolated concepts, limitations of time and resources, and their own lack of scientific training. Textbooks, which often define the curriculum for science classes, further the perception that learning science is a matter of memorising a set of idealised claims and definitions. While teachers recognise that they should be educating students about the complexities of science, one can well appreciate why for many this seems to be a luxury that they cannot afford.

However, this is a false dilemma. There are ways of teaching science that can both provide students with simple, accessible illustrations of scientific concepts and also share some of the complexities of the actual practice of science. Part of the solution will depend upon revising standardised tests to focus less on content, along with the refinement of teacher training programs to involve more on the actual practice of science. Part will also depend upon the development of superior instructional materials and lesson plans that go beyond just teaching the basics. It is here that the use of history and philosophy of science, as illustrated by work on industrial melanism, can play a pivotal role.

It has long been recognised that discussing scientific debates with reference to their historical and philosophical contexts provides an excellent vehicle with which to promote active learning about how scientific claims are developed and evaluated (Matthews, 1994; Monk and Osborne, 1997). Hagen (1993, 1996) illustrates how Kettlewell's investigations can be used to promote active learning. Discussing the history of work on the phenomenon of industrial melanism in a broader context can further help students become aware of how patterns in nature are discovered, how models are used to explain those patterns, and how such models are evaluated.

Patterns in nature

The history of work on the phenomenon of industrial melanism provides students with a wonderful example of how a curious pattern was discovered in nature by lepidopterists, naturalists, and amateur moth collectors. The teacher can discuss with students how discoveries of rare dark forms of certain moths such as f. *carbonaria* in the peppered moth, *Biston betularia,* were initially identified as occasional accidents of nature. It can then be pointed out how the increasing frequency with which these forms were found led individuals who found them to notice a pattern in their distribution: an odd association with areas downwind of industrial sites. The beauty of this example is that recognition of the pattern does not depend upon a previous scientific context per se.

Models

Discussing the history of work on the phenomenon of industrial melanism also provides teachers with an opportunity to discuss how models are developed and used in science. From a constructivist perspective, meaningful learning involves the restructuring of previous knowledge (Novak and Gowin, 1998). Teachers must elicit what the students already know about a subject if they are to correct antecedent understandings and/or misconceptions students bring in to the classroom. Students without previous training in evolutionary biology often have strong intuitions that closely resemble Lamarckian or mutationist perspectives (Bishop and Anderson, 1990). In the case of the phenomenon of industrial melanism, there are excellent historical precedents to both these perspectives — both Lamarckian and mutationist interpretations of the phenomenon were seriously entertained as potential explanations (e.g. Cooke, 1887; Heslop-Harrison, 1927). Teachers can likewise discuss this example with reference to natural selection, and, as noted above, the phenomenon of industrial melanism is a particularly helpful illustration precisely because it provides a straightforward and intuitive example of this otherwise unfamiliar and difficult concept.

The evaluation of models

In the presence of three distinct models offered as explanations of the pattern, students can consider whether one model might be a better explanation than another. Here recourse to the evidence that historically led Kettlewell and other biologists since to dismiss Lamarckian and mutationist theories is one important avenue by which meaningful learning can take place. Discussing the variety of observational and experimental studies Kettlewell used to discredit other models and support his own illustrates to students how models are tested in science. The almost unique advantage of early work on the phenomenon of industrial melanism for teaching in this regard is that Kettlewell's (1955, 1956) investigations were elegant in the simplicity of their design and involve a minimal amount of mathematical reasoning. These aspects make discussion of experimental work in this context much more accessible to students than experimental and observational studies used in support of other examples.

Monk and Osborne (1997) point out that successful use of history and philosophy of science in teaching requires some sense of closure to the discussion. High school students are notorious for dualistic thinking and a need for knowing what the 'right' answer is; a phenomenon not unknown among college students. Teachers who are convinced their students have such limited intellectual capabilities should, in my opinion, feel free to end the discussion by pointing out that on balance the evidence favours Kettlewell's interpretation by minimising or omitting details of the outstanding problems noted above. The phenomenon of industrial melanism is an example of evolution by natural selection and the suggested requirement students must have complete knowledge of all the outstanding scientific questions surrounding this particular example is overstated.

The problem with such an approach is not that it leaves students uninformed about our current understanding about the phenomenon of industrial melanism. The problem is that it perpetuates a stereotype of science as a body of knowledge. Students would be much better served if they left our classrooms with some questions that left them thinking, rather than a tidy answer to be forgotten once the test is over. Discussing some of the contemporary controversies surrounding the phenomenon of industrial melanism with students will help them better appreciate the nature of science, the tentative nature of scientific knowledge, and the complexity of the process of science.

It is the presence of discrepancies between the classic textbook account and what is actually known that makes the phenomenon of industrial melanism so valuable for the purposes of science teaching. By contrasting the oversimplified version with a richer account of the history of work on the phenomenon, teachers can drive home the differences between science as it is depicted in textbooks and the practice of actual research. The fact that our current understanding contrasts markedly from the classic account makes it all the more intriguing. Indeed one could argue that if there were only slight differences between the two accounts, the distinction would be too subtle to be appreciated by the vast majority of students. Thus, the current controversies surrounding the phenomenon of industrial melanism, far from undercutting its importance, actually augment its value for the teaching of evolutionary biology.

This example can also help disabuse students of identifying experimental work as the hallmark of science. By pointing out the importance of ecological and life history data to ongoing debates about the evolution of melanism, teachers can highlight the complex interplay between observational and experimental studies in the life sciences.

Conclusion

The presence of discrepancies between textbook accounts and what is actually known about the phenomenon of industrial melanism is an instance of a more general problem in science education regarding how science should be depicted. This example vividly illustrates a fundamental tension between making new concepts accessible to students with limited science backgrounds and providing them with an accurate portrait of science in all its complexity. It is disputed that this tension represents a dilemma that must be decided one way or another. By reviewing both the classic account and discussing how and why it oversimplifies what is known about the phenomenon and Kettlewell's work on it, teachers can help students gain insight into the many complexities inherent to the process of science that are so often lost in textbook accounts.

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Endnotes

1. Kettlewell was aware that the moths had only rarely been found to rest in exposed positions on tree trunks in nature. See Majerus (1998) for a comprehensive discussion of the effect that resting on the underside of lateral branches or in the canopy would have on the story.

2. Critics of evolutionary theory have had a problem with this example well before the aforementioned problems regarding our understanding of the phenomenon of industrial melanism became widely known. They have repeatedly claimed that the phenomenon of industrial melanism is not evidence of evolution because it has not led to the creation of a new species. This criticism reflects a misunderstanding — biologists use the term evolution to refer to both macro- and micro-evolutionary processes. Whereas the first refers to the origin and extinction of taxa, the latter is used to refer to changes in gene frequencies over time. The phenomenon of industrial melanism, as exemplified by *Biston betularia*, refers to the rapid rise in frequency of the *carbonaria* gene in areas downwind of manufacturing centres. It is clearly an example of microevolution, and we should note that this would be true even if the change turns out not to have been the result of the process of natural selection. Moreover, to the extent that the phenomenon demonstrates how a trait can become established in a population, the phenomenon of industrial melanism provides circumstantial evidence for how reproductive barriers leading

to the development of new species can be established, and therefore indirect evidence of the possibility of macroevolutionary change.

3. The phenomenon of industrial melanism was seized upon by Haldane (1924) and Ford (1960, 1964) as one of a very few examples of evolutionary change that had been observed by man. Ford and other members of the Oxford School of Ecological Genetics drew attention to the example with reference to ongoing debates about the evolution of dominance, and how rapidly natural selection can produce evolutionary change (Hagen, 1999). Its initial importance to scientific debates notwithstanding, much of the credit for why this example has become so common is a direct reflection of Kettlewell's own lobbying efforts. Kettlewell practically made a second career out of popularising the phenomenon as 'Darwin's missing evidence' in a series of articles, his treatise (1973), and numerous public lectures. Particularly important in this regard are two films devoted to the topic of evolution in action that featured his work on the phenomenon of industrial melanism, which he loaned out to organisations all of over the world.

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