Descended from Darwin

Insights into the History of Evolutionary Studies, 1900–1970

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Chapter 12

H. B. D. Kettlewell's Research, 1934–1961

The Influence of J. W. Heslop Harrison*

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Introduction

H. B. D. Kettlewell is best known for what has long been regarded as *the* classic demonstration of natural selection, his pioneering field studies of the phenomenon of industrial melanism in the early 1950s. Brief synopses and textbook accounts, as well as popularizations by scientists (including Kettlewell), historians, philosophers, textbook and popular writers since have collectively led to the development of a legend surrounding his investigations. In a previous paper Rudge (2006) drew attention to how the legend overstates the role E. B. Ford played in Kettlewell's investigations while simultaneously diminishing or ignoring the important roles played by E. A. Cockayne and P. M. Sheppard, among others. Aside from distorting the historical record, this legend is pernicious in that it downplays the phenomenon of industrial melanism as an area of active inquiry, ignores the existence of alternative theories that might account for the phenomenon, and depicts Kettlewell's initial investigations as largely unproblematic. These latter charges are perhaps best illustrated with reference to the fate of Kettlewell's most vocal contemporary critic, J. W. Heslop Harrison.

The following essay critically appraises the historical accuracy of how Harrison and his work have been depicted according to the legend surrounding Kettlewell's investigations with reference to both the published record and Kettlewell's private correspondence. As will be shown below, the feud between Kettlewell and Harrison is far more complicated than is typically recognized. A concluding section draws several general morals regarding how science is and should be depicted.

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The Phenomenon of Industrial Melanism

The Legend

By the mid-nineteenth century it was widely recognized that a dramatic increase in air pollution associated with the industrial revolution in Britain and continental Europe was having a profound effect on the flora and fauna of the surrounding countryside. Anecdotal accounts drew attention to a general decline of wildlife, particularly among bird populations. Trees in affected areas were becoming visibly darker as the lichen that normally covered their surfaces died off and was replaced by a gradual accumulation of soot. Naturalists and amateur lepidopterists also discovered a curious increase in the frequency of previously dark (melanic) forms in many moth species in these areas. This latter trend came to be referred to as *the phenomenon of industrial melanism* owing to widespread speculation that it was either a direct or indirect consequence of industrial pollution.

According to the legend that now surrounds Kettlewell's research, the phenomenon of industrial melanism attracted widespread interest among academics, who seized upon it as an example of natural selection taking place before their eyes. An influential paper written by J. B. S. Haldane (1924) further heightened this interest. In his paper, Haldane calculated the selection coefficient of the gene responsible for the melanic form in polluted situations would have to be much greater than that of the gene associated with the pale form, given the apparent speed of its spread in the Manchester area by 1901 from the time it was first discovered in 1848.

J. W. Tutt is generally acknowledged as the first to account for the phenomenon in terms of natural selection, and in particular *crypsis*, or how well the insect matches its background (Tutt, 1890, 1896). He pointed out that a dark moth is normally at a tremendous disadvantage in unpolluted environments because dark coloration against a pale lichen-covered tree trunk or other resting site would make the moth very conspicuous to visual predators. In a polluted environment, dark coloration would actually be advantageous because it presumably makes the moth less easy to see by visual predators when it rests on a soot-darkened tree trunk or other resting site.

Breeding experiments by E. B. Ford and others (Ford, 1937, 1940a) led to widespread speculation on the part of geneticists that the dark form in industrial melanic species might be "hardier" than the pale form. Precisely what these workers meant by hardier seems to have varied with the worker, some identifying it in terms of a tendency for black forms to emerge earlier in the year and at lower temperatures (Bowater, 1914). Ford's own preliminary experiments testing for the possibility of viability differences between the two forms raised under stress (e.g., reduction of available food) suggested to him that the gene for dark coloration also made the moth less vulnerable to toxins in the soot, possibly as the result of heterozygote superiority. Ford (1937, 1940a) concluded that the dark form was becoming more common due to this physiological advantage. To account for why the spread was limited to the vicinity of industrial areas, he drew attention to the obvious handicap of being dark in rural areas (similar to Tutt and others previously):

> In my opinion, melanic forms have spread in industrial areas owing, primarily, to selection for characters other than colour. The action of the genes producing melanism as one of their effects may sometimes give the organism a physiological advantage. That such

> favourable factors have not become widely established may be due to the handicap of black coloration, which, in normal circumstances, would render some species very conspicuous. On the other hand, melanism, as such, may at least be no longer a drawback in the blackened countryside of many manufacturing districts, in which, furthermore, the number of predators may be reduced. Here, then, the insects may be able to avail themselves of the other benefits conferred by these genes. (Ford, 1937, p. 487)

H. B. D. Kettlewell is hailed on the legend as providing definitive proof in the early 1950s of the second part of Ford's explanation, namely that birds selectively prey upon moths with reference to their relative conspicuousness as they rest on pale lichen-covered and soot-darkened surfaces (Kettlewell, 1955a, 1956a). Kettlewell worked with the most famous example of the phenomenon of industrial melanism, the peppered moth, *Biston betularia*. Kettlewell documented that birds prey upon the moth and further that they do so differentially with reference to how well the moth matches its background in a series of elegant field experiments conducted in a polluted and an unpolluted forest. To establish this, Kettlewell used a technique called mark-release-recapture (previously pioneered by Fisher and Ford, 1947), in which he marked large numbers of moths and released them into well-circumscribed woods. He then over the course of the next few days attempted to recapture as many as possible using a combination of mercury vapor lamp and assembling traps. In each setting he predicted if one form of the moth was at an advantage compared to the other (for instance it was less likely to be seen by avian predators), the recapture rate of that form should be greater than the recapture rate for the other. This is precisely what Kettlewell found (after ruling out some possible alternative explanations). Kettlewell also directly observed that, when presented with a choice, the birds of his study tended to capture the more conspicuous form of the moth, namely, the pale form in the polluted setting and the dark form in the unpolluted setting. Indeed, Kettlewell's results were regarded as so definitive that he and others began to downplay the importance of Ford's first selective force (the alleged physiological advantage of the dark form) to the point where Kettlewell is now regularly depicted as having set out to test *Tutt's* explanation (e.g., Grant, 2005).

Depictions by scientists who work on the phenomenon are generally careful to acknowledge that Kettlewell's investigations were not as definitive as the above paragraph suggests. They acknowledge that some of the assumptions underlying Kettlewell's investigation (e.g., the assumption that moths rest on tree trunks by day) have been called into question, and indeed the phenomenon itself is more complicated than Tutt's explanation suggests (e.g., other selective factors such as sulfur dioxide concentrations) and might play a role in the spread of the melanic gene (Cook, 2000; Majerus, 1998). This being said, nearly all emphasize that research by Kettlewell and multiple workers since has qualitatively confirmed the basic outlines of Tutt's explanation (Grant, 1999; Majerus, 2005).[1]

Problems with the Legend

The legend as described above departs from historical accuracy in a number of ways, some of which are more or less innocuous depending upon the intended audience. Textbooks routinely neglect to mention that the peppered moth has two melanic forms, *carbonaria* and *insularia*, not one. Most also privilege the mark-release-recapture experiments while minimizing the arguably more important role played by strictly observational techniques (Rudge, 1999, 2003). Numerous discrepancies between simplified textbook accounts written for introductory students and those written for professional scientists had led some (with an obvious agenda) to openly question whether the phenomenon is as well understood as textbooks would have us believe, and further that there is a conspiracy by textbook writers to hide this (e.g., Wells, 2000).[2] Judith Hooper (2002) in the first book-length popularization of Kettlewell's work all but explicitly claims that he committed fraud.[3]

The legend as depicted in textbooks is particularly pernicious with reference to its depiction of the process of science. Textbook accounts present the phenomenon of industrial melanism as if it were no longer the object of active research. They ignore the existence of alternative theories that might account for the phenomenon. They imply Kettlewell's work was a logical consequence of *Tutt's* (not Ford's) theory and suggest further that his results were regarded as unproblematic and greeted with universal acclaim (Rudge, 2000). These issues are particularly poignant when one considers the fate of Kettlewell's most vocal critic, J. W. Heslop Harrison.

J. W. Heslop Harrison[4]

James William Heslop Harrison (1881–1967)[5] was a notable field naturalist and considered a pioneer in studies on genetics, sex, and evolution in moths, roses, and willows. His fame and later infamy rests primarily with a series of botanical, entomological, and biogeographic discoveries, many of which ultimately were shown to have been fabricated by Harrison and his students.[6]

Harrison was particularly influential in natural history circles, being a member of the editorial board of *The Entomologist* from 1924 until his death, and the founder and editor of *Vasculum*, a local natural history journal he started in 1915. He was elected a Fellow of the Royal Society of Edinburgh (FRSE) in 1924, and a Fellow of the Royal Society (FRS) in 1928, just a few years prior to the first public suspicions his work on the induction of melanism might be fraudulent.

Harrison began his career as a schoolteacher at Middlesbrough High School where he served as science master for 12 years. Even during this early period he distinguished himself as a prolific scientific researcher, despite heavy teaching responsibilities. In midcareer Harrison accepted a prestigious Department of Scientific and Industrial Research (D.S.I.R.) award, which led to an association with Armstrong College at the University of Durham, an affiliation he retained (in one capacity or another) for the next 40 years. He became a lecturer in Zoology in 1920, a reader in Genetics in 1926, and ultimately a professor in Botany in 1927. Harrison retired in 1946 as an emeritis professor, first of the University of Durham (and later the University of Newcastle upon Tyne). Despite changes in the nature of his position, Harrison maintained an active interest in school biology throughout his life as a member of the Durham University school examinations board, for which he served as secretary for the years 1940 to 1950. He was also a founder of the Northern Naturalists' Union in 1924 and was well known for his encouragement of young entomologists throughout his career.

A number of striking parallels can be drawn between Harrison and Kettlewell. Both traced their boyhood love of natural history to the encouragement of their mothers and adult mentors.[7] Both agonized over and ultimately chose to leave established careers in midlife to pursue their lifelong interest in natural history, despite the substantial financial hardship this presented for them and their families. Both were regarded as particularly gifted field naturalists, renowned for their encyclopedic knowledge.[8] And both had reputations as less than ideal scientists, a failing their colleagues and friends traced to strong convictions and a general tendency to regard criticisms of their work as personal attacks.[9]

The most striking similarity between these men, of course, is that both became famous (infamous) in part as a result of their respective work on melanism in moths. Kettlewell's fame stems from a series of field experiments conducted in the early 1950s, which are often regarded as among the most definitive demonstrations of natural selection.[10] Kettlewell has more recently become infamous among adherents of intelligent design, who draw attention to well-known technical problems in the original design of Kettlewell's investigations (identified by Kettlewell and others since) as compromising the value of industrial melanism as an example of natural selection (e.g., Wells, 2000).[11] Judith Hooper, the first to write a book-length popularization of Kettlewell, all but explicitly accuses him of fraud (Hooper, 2002, pp. 298–299; but see Rudge, 2005). Harrison likewise became famous for a series of experiments he conducted on moths, experiments in which he systematically raised pale moths on polluted foliage and observed what appeared to be an increase in the incidence of melanism among their offspring.[12] These investigations made him famous because they were widely interpreted as striking evidence of the possibility of the inheritance of acquired characteristics, a theory that had long been discredited as a result of the work of August Weismann and others. Later, the design and execution of Harrison's investigations was called into question, ultimately leading to charges of fraud. We should note that in Kettlewell's case, the charges of fraud were only recently raised by a popular science writer with the apparent aim of selling a book in the face of at least eight field studies since that have confirmed the basic outlines of Kettlewell's explanation (Majerus, 2005). In Harrison's case, by contrast, the charges were leveled by multiple scientists during his own lifetime, several of whom tried, but were unable to reproduce his remarkable results.

Harrison's Role According to the Legend

Given that the two men were contemporaries, belonged to several of the same entomological circles, and actively pursued the phenomenon of industrial melanism as a major focus of their research, it is only natural to consider what effect Harrison's earlier research and its subsequent reception had on Kettlewell's investigations.

Standard portrayals of Kettlewell's work typically either exclude any mention of Harrison's research or depict it as wholly discredited (sometimes misleadingly as a result of Kettlewell's investigations). It is altogether understandable that contemporary scientific research articles on the phenomenon of industrial melanism would omit reference to Harrison's work, given its status as being completely discredited. Most review articles and book chapters written by scientists that briefly review the history of research on the phenomenon of industrial melanism that do mention Harrison's research are completely dismissive:[13] For instance, Berry (1977) writes,

> The proof that the spread of melanic moths in industrial areas was the result of natural selection through bird predation dates only from the work of H. B. D. Kettlewell in the early 1950s. Before this it was frankly not believed that birds could be discerning enough to select between morphs. For example, White (1876) cited climatic factors in the Scottish Highlands; Merrifield (1894 and earlier) believed that melanism was the result of temperature during development; Tutt (1899) argued (but did not prove) that in wet areas, particularly where soot was present, melanic moths were better concealed and "natural selection" augmented by "hereditary tendency" favored them. Ford (1937, 1940[a]) suggested that increased viability of some melanic mutants would result in their spread in industrial areas once their cryptic disadvantage had disappeared. But the most important red herrings were produced by Heslop Harrison (reviewed 1956). He fed caterpillars of the Early Thorn (*Selenia bilunaria*) and Engrailed (*Ectropis bistortata*) moths on leaves impregnated with lead nitrate and manganese sulphate, and produced a number of melanic offspring from them. He attributed this to the direct results of the salts on the "soma" (i.e., bodies of the moths), which in turn affected the "germ plasm." Unfortunately for himself, Heslop Harrison chose species which possessed recessively inherited melanics. Hughes (1932) repeated the experiments and bred 3,265 individuals under conditions identical to those of Heslop Harrison, and obtained no melanics. Heslop Harrison proved no more than that heterozygotes are common in wild populations. In neither of the species he studied intensively are industrial melanics found. (Berry, 1977, pp. 120–121)

And in a more recent encyclopedia entry, Grant similarly notes,

> From Tutt's time until H. B. D. Kettlewell rekindled interest in this subject over half a century later, little fieldwork was done. In 1924, J. B. S. Haldane calculated the selection coefficients necessary to account for the spread of melanic peppered moths; however, during the same period, J. W. Heslop Harrison challenged the Darwinian explanation for the changes observed in moth populations. Harrison argued from his experimental work on certain other Lepidoptera that melanism can be induced in adults by feeding larvae contaminated leaves. Other workers also exposed pupae to noxious fumes and reported darkening of the wings of the adults. These experiments, however, were severely criticized by contemporaries who attempted to reproduce the experiments but failed to reproduce the results. Whatever the correctness of that work might be, none of it has proven relevant to *B. betularia*. Although the larvae develop different body colors in response to environmental stimuli (they come to match the colours on the twigs of their host plants), it has never been demonstrated that environmental stimuli experienced at any stage in development can induce melanism in the adult stage of this species. On the contrary, the Mendelian inheritance of the melanic forms of adult peppered moths has been demonstrated repeatedly. (Grant, 2005, pp. 1–2)

Following the lead of scientific publications, textbooks and popular accounts of the phenomenon of industrial melanism likewise omit any mention of Harrison's work.[14] Accounts written by historians and philosophers of science who have considered the history of this episode tend to present Harrison's previous research primarily to set a context for making sense of Ford and Kettlewell's later work on the subject. For instance, Hagen (1996) mentions Harrison's work as follows:

> In a widely publicized series of experiments conducted in the 1920s, the British entomologist J. W. Heslop Harrison fed caterpillars leaves coated with toxic compounds

> commonly found in soot. For example, in one experiment, caterpillars captured in a non-polluted forest were fed leaves coated with lead nitrate. After pupation, 53 light-winged moths and 3 dark-winged moths emerged from cocoons. All of the caterpillars in the control group, which were fed unpolluted leaves, developed into light-winged moths. Harrison concluded that these results were due to mutations induced by chemical pollutants. Because the dark wings were inherited by many descendants in his experimental moths, Harrison claimed he had documented a case of the inheritance of acquired traits. Publishing his experimental results in the prestigious journal *Nature*, Harrison presented his theory as a clear-cut alternative to natural selection. . . . Later attempts to replicate Harrison's experiments failed, and his explanation for industrial melanism was criticized by Darwinians. For example, the prominent theoretical biologist R. A. Fisher pointed out that Harrison's explanation required a mutation rate much higher than any previously reported. Nonetheless, Harrison continued to argue for his Lamarckian theory. Because he was a distinguished member of the British scientific community, his ideas could not be simply ignored. Therefore this controversy set the stage for later research on industrial melanism. A decade after Harrison published the results of his experiments, the geneticist E. B. Ford presented an alternative explanation. (Hagen, 1996, pp. 2–3)

And in an article devoted specifically to a discussion of the history of Kettlewell's work, Hagen (1999) writes,

> Both Darwinian and non-Darwinian explanations were proposed to explain the rapid change in wing color. During the 1920s, the entomologist J. W. Heslop-Harrison published experimental data supporting his claim that chemicals in soot caused widespread mutations from the light winged to the dark winged form. Because these mutations were supposedly passed on to subsequent generations, Harrison claimed that he had documented a case of the inheritance of acquired traits. Other biologists failed to replicate Harrison's results, and R. A. Fisher pointed out that Harrison's hypothesis required a mutation rate far higher than any previously reported. Because he based his claims on flawed experimental data and used results to argue for a discredited neo-Lamarckian theory, Heslop-Harrison provided the perfect foil for Kettlewell's later experiments. (Hagen, 1999, p. 41)

Rudge (1999) similarly discusses Harrison's work as follows:

> Later experimental investigations, such as those conducted by Merrifield (1890) and Weismann (1882) suggested that the rise in melanic forms was due to the direct operation of some factor in the environment, such as temperature or humidity. The most influential proponent of such a view was Heslop Harrison, who proposed on the basis of breeding experiments that magnesium salts (or some other pollutant) had mutagenic properties (Harrison 1920 a, b, 1926, 1927). Harrison's account was significant in drawing the attention of the scientific community to the possibility that industrial melanism required a different or more specific explanation than the phenomenon of melanism in general. Other experimental investigators, such as Hughes (1932) and Thomsen and Lemeche (1933) attempted to reproduce Harrison's results using larger populations, but none was able to duplicate his results. (Rudge, 1999, p. 13)

Harrison's work, when mentioned, is restricted primarily to that of setting a context within which to make sense of Kettlewell's work. It is depicted as an alternative explanation for the phenomenon of industrial melanism. It is an alternative that is fundamentally flawed theoretically (to the extent that it appears to rest upon a Lamarckian theory of inheritance), flawed in terms of its experimental design, and flawed in terms of its execution. At most, Harrison on this standard portrayal is depicted as a "perfect foil" for Kettlewell's later experiments.

As easy as it is to dismiss Harrison as someone whose outdated ideas were simply a distraction that preceded Kettlewell's work, the relationship between these two men and their research was more complex. The two were acquaintances for decades prior to Kettlewell's research in the early 1950s; as were Harrison and E. B. Ford. Their common interest in industrial melanism was undoubtedly a topic of conversation during the crucial period when Kettlewell began his fieldwork on the subject. And indeed, as will be shown below, it was Harrison's ongoing conflict with *Ford* that lay behind the very public feud Kettlewell had with him upon the initial publication of Kettlewell's results.

Reasons for Reappraising Harrison's Role

After briefly summarizing Harrison's research on melanism during the 1920s and the reaction of the scientific community to his controversial results, this section considers what effect, if any, Harrison (and his results) had on the conduct of Kettlewell's later investigations in the early 1950s. The section concludes by considering the impact of Harrison's lengthy 1956 critique of Kettlewell's initial work on subsequent research on the phenomenon of industrial melanism.

Harrison's Investigations on the Induction of Melanism

Harrison began his research on the induction of melanism in 1917, while he was still a high school teacher at Middlesbrough, and continued them sporadically over the course of the next 20 years amidst numerous other projects.[15] His first paper on the subject discusses the "vexed question of melanism" within the context of a long paper devoted to the genetics of the geometrid genus *Oporinia* (Harrison, 1920). Within it Harrison openly questions Tutt's theory that the dark form is becoming more common in industrial areas indirectly by the natural selection, and in particular differential selection by birds with respect to how conspicuous the moth appears when it rests on surfaces darkened as a result of increased humidity or the deposition of soot. His critique harps on what he regards as peculiar differences between local populations of species exhibiting the trend, differences which suggest the need for multiple separate explanations. He disputes that tree and rock surfaces really are darker in polluted areas with reference to his own observations. He points out that dark insects can escape detection even when backgrounds are not darkened owing to increased humidity or soot, owing to suitable choice of resting site. He notes melanism appears to be a trend even in unpolluted areas. And, if this were not compelling enough, he draws attention to some fairly systematic observations he made of a situation where differential selection by birds should occur, always with negative results:

> To demonstrate that the effect of natural selection is quite negligible as a factor in progressive melanism, I carefully studied the case of *Polia chi*, which in the Team Valley produces about 50% each of the typical and of the melanic forms grouped under the name *olivacea*, and near Middlesbrough about 10% of dark and 90% of pale forms. For several years and on every day during their season–rain or fine–either my wife or my brother

> carefully noted the positions of the insects resting on three walls: (1) old and dark in parts, proceeding from Birtley to Newcastle; (2) old light yellow sandstone, proceeding to Burnmoor; (3) mixed new greyer sandstone and old reddish ones leading to Chester-le-Street. On these three walls I have seen up to three hundred examples daily, so that the present test is not confined to a few insects; in the evening full particulars would be given to me and sometimes alone and sometimes accompanied with my brother I would go over the ground and investigate the fate of insects observed earlier in the day. Never was there any diminution of numbers in which more *olivacea* vanished than type *chi*; as a matter of fact we used to consider it a marvellous thing if a single one had disappeared. (Harrison, 1920, p. 235)

Presuming at this point that the reader is in agreement that natural selection is not the cause, Harrison points out that whereas mechanical and physical distresses have been demonstrated to produce darker coloration, the cause of action appears to be their interference in some process happening at a highly specific time during the development of the insect. Drawing attention further to the fact that in the affected districts, the melanic form appears to breed true, Harrison concludes that some other cause is needed, one that would in addition account for continuous melanism in polluted localities. An obvious candidate, to Harrison's mind, are the metallic salts insects in the affected localities are commonly exposed to by virtue of air pollution and the deposition of soot on their food plants. He concludes this "may" be the cause of melanochroism (the induction of melanism), and points out further that in the genus studied, the inheritance of melanism does not appear to be Mendelian.

The results of Harrison's direct attempts to induce melanism in moths were first published in 1925–1926 with the assistance of Frederick Charles Garrett (Harrison & Garrett, 1925–1926). Within the paper they describe a series of experiments aimed at inducing melanism in nonmelanic species of lepidoptera from unaffected areas, the Early Thorn, *Selenia bilunaria,* and the Engrailed Moth, *Tephorsia biostortata* Goeze, chosen primarily with reference to the authors' previous experience raising them in captivity.[16] The experiments essentially involved feeding larvae on polluted foliage, which was either initially contaminated as a result of being taken from polluted environs or artificially "charged" by placing leaf-bearing twigs into dilute solutions of two common contaminant metallic salts (lead nitrate and manganous sulphate). In each case, they began by inbreeding multiple generations of moths to ensure that a melanic gene, if recessive, was not present. They then divided the resulting progeny into control and experimental groups, the latter being fed on polluted foliage. Harrison and Garrett's most striking results were found among the *Selenia bilunaria* moths fed on leaves contaminated by lead nitrate. No differences were found among the progeny of experimental and control treatments that constituted the first generation, but by the second, which emerged in 1923, melanics began to appear only among the offspring of the experimental group (see Table 12.1). Harrison and Garrett drew great attention to the fact that the ratios of the melanics appearing within the experimental group did not conform to an expected Mendelian ratio of 3:1 that would have occurred if the result were simply due to the segregation of a recessive melanic gene.[17] They further noted that subsequent cross pairing of induced melanics yielded all black offspring, which again is suggestive that a genetic change has occurred. They reported similar results for the other treatments used and concluded from the fact that melanism is unknown in *Selenia bilunaria*, a very common species, that they had indeed induced melanism as a result of their treatment.

Table 12.1. Showing *Selenia bilunaria* families in which induced melanism appeared.[18]

		Females		Males	
Family	Treatment	Types	Melanics	Types	Melanics
1923 AL	Lead	15	—	11	1
1923 BL	Lead	11	—	18	2
1923 LL	Lead	6	2	11	1
1923 DM	Manganese	7	2	5	6

In a follow-up paper presented to the Royal Society, Harrison (1928) shared further research aimed at establishing whether it was the metal or the acid radical contained in solutions used in the previous experiments that was responsible for inducing melanism, ultimately concluding that the metal and not the acid radical was responsible. He reported once more finding some melanics among the progeny of *Selenia bilunaria* used in the experiment, and also breeding results that confirmed (at least to his satisfaction) that this change was not merely somatic, but an inherited variation.

Harrison ended the paper with the two altogether curious conclusions, one denying that he was claiming his results were evidence of Lamarckian inheritance, and a second denying that his work was intended as a solution to the problem of industrial melanism:

> No claims are made here or elsewhere that we are concerned with a Lamarckian effect. Coupling the work described above with that discussed in the 1926 paper (Harrison & Garrett, 1926), it is almost certain that the result has been produced by direct action on the germ plasm of the metallic compound administered with the food. This, I have already pointed out . . . affords a new principle of evolution and would suffice to account for evolutionary progress in a variety of forms, both animal and plant, in Nature and in the hands of man. (Harrison, 1928, pp. 345–346)
>
> In view of the possibility of criticism in this direction, it should be made clear that the present work is not regarded as solving the problems of industrial melanism, although it is claimed that some light has been thrown on the matter. (Harrison, 1928, p. 346)

These caveats (expressed in this paper and in other places) confounded friends and critics alike.[19] If one identifies Lamarckian inheritance with the passing on to offspring of characters newly acquired by parents during the course of their lives, Harrison's results clearly seem to be evidence for the existence of Lamarckian inheritance, and even he conceded as much in connection with similar studies conducted on the egg-laying instincts of the saw-fly *Pontania salicis* Christ.[20] What Harrison appears to have had in mind is that his results provided an account for how variations arise in nature, what he referred to as a new principle of evolution that would account for the *origin* of mutations.[21] And, related to this, the point of his investigations attempting to document that ingestion of metallic salts could induce melanism was not to solve the entire problem of industrial melanism (which presumably would include an account of its spread), but simply to account for how the first *carbonaria* gene responsible for excess melanin production arose.[22]

Reactions to Harrison's Investigations

Reaction to Harrison's amazing results was swift. Some, such as Julian Huxley and H. G. Wells, greeted Harrison's work with acclaim as providing evidence of the possibility that chemical stimuli could induce mutations similar to Hermann Joseph Muller's well-known experiences with radiation in fruit flies in the 1920s:

> Besides X-rays, it seems that chemical influences can produce mutations. An interesting example of this was found a few years ago by Heslop Harrison, an English biologist. It concerns the black or "melanic" varieties of moth that are occasionally found in the wild.
>
> About a century ago the first recorded examples of a dark or "melanic" variety of the peppered moth *Amphildasys betularia* were caught in England, and for years afterward the variety remained rare. Collectors were keen, so that it is unlikely that the variation first appeared much before the date of discovery or that its rarity was only apparent. It gradually became commoner, until by the beginning of this century it was in some districts more abundant than the normal type. Where it was common in industrial regions and near big cities; in the country-side it remained rare. Other species of moth in similar localities gradually followed suit. . . . Moreover, wherever the breeding behaviour has been tested, the two forms have always been found to differ in one Mendelian gene only, dark being almost always dominant to light. No help in escaping the notice of enemies seems to be conferred upon these moths by their dark colour; it is not a protective variation.
>
> Now all green things in industrial districts are coated with a grime that is rich in poisonous metallic salts. It occurred to Harrison, struck by the coincidence between the distribution of black moths and of industrial smoke, that this might be the cause of the change. Accordingly he made the caterpillars of various moths eat tiny quantities of heavy metals, especially lead and manganese, with their food. His suspicion was justified; in the metal-fed cultures a few mutants with black wings appeared. Moreover, the colour, once it had been produced, bred true even without further metal feeding. The chemical agencies had induced permanent changes in the germ-plasm.
>
> Here, then, we have proof that environmental factors, X-rays or chemical substances, can actually induce mutation in animals. This must be distinguished very clearly from the Lamarckian method of inheritance . . . The Lamarckian method was directly adaptive; the individual responds in a favourable way to some factor in its surroundings and the response is supposed to be inherited. But in these actually proven methods of modification there is no direct adaptive response. The experimental agents simply knock the germ-plasm about, so to speak. They produce random mutations, not adaptive responses. (Wells, Huxley, & Wells, 1931, pp. 595–596; emphasis in original)

It is striking to note in the above passage that the authors downplay the possibility that the melanic form existed prior to industrialization, and further that they outright denied the melanic form was adaptive in the affected districts. It was the absence of an adaptive effect that led them to conclude that Harrison's results were *not* the result of Lamarckian inheritance.

Most did not interpret Harrison's results in this way, even when one restricts one's attention to those who believed Harrison had indeed experimentally demonstrated an example of induced melanism. E. A. Cockayne (1880–1956), Kettlewell's mentor for at least 20 years (1930–1950) prior to Kettlewell's formal association with E. B. Ford at Oxford, extolled Harrison's work. In a commentary on Harrison's paper published in *The Entomologist's Record and Journal of Variation*, the ever-critical Cockayne wrote,

> This paper is of the greatest importance to biologists, *because it clearly proves that acquired characters can be transmitted*, and shows how they may arise through changes in environment, and so throws fresh light on the processes of evolution. It is of special interest to lepidopterists, because it goes far to explain the rapid increases in melanism, which has taken place in the recent past, and is still taking place today. Every criticism has been anticipated and met by the most careful precautions. . . .
>
> A convincing part of the proof is that melanics first appeared in non-Mendelian ratios, and that once they had appeared they bred as recessives or dominants like the similar melanic forms of the same species found in industrial areas. The artificial production of a dominant, as well as recessives, is most important because it disposes of the least suspicion that melanism was latent in the strain used. The insect with a black streak on the costa, which had all black offspring, proves that a germinal mutation was caused by the food of the larvae. It is to be hoped that similar experiments will be carried out by independent workers; speedy confirmation of results, which prove that acquired characteristics may be inherited, a subject of acute controversy for many years, is in the highest degree desirable [*emphasis* added].[23]

As alluded to above, the vast majority who followed Harrison's work were far less charitable in their assessments of the value of his research. A prominent critic among them was Kettlewell's mentor at Oxford, E. B. Ford, who had nothing but contempt for Harrison as a scientist.[24] Ford regularly discussed Harrison's work in his periodic reviews of research on industrial melanism during the time period of interest in the present essay (Ford, 1937, 1940a, 1940b, 1955).[25] Ford's summaries drew attention to the objections of prominent scientists such as Fisher (1933) and Haldane (1935). The most comprehensive of his critiques appeared in Ford's (1955) *Moths*, within which the results of Kettlewell's historic investigations were also first published:

> It has been claimed by Harrison that the increase of melanism in manufacturing districts is due to the chemical induction of mutation. He found that the soot coating the leaves and bark in such areas contains salts of lead and manganese and suggested that these substances, when eaten by larvae, caused the mutation of genes responsible for an excessive production of the black pigment melanin. The difficulties of this view are insuparable. Obviously it is subject to the identical double criticism just leveled at that based upon simple cryptic colouring [it does not account for melanism in rural districts, nor does it throw light on the "extraordinary physiological difference" between the pale and dark forms]. But there are other objections to it at least as weighty. Thus those who have supported it do not appear to have considered the mutation-rate involved, which would have to be much greater than the maximum so far produced even by the use of penetrating radiation. Indeed the objections to all theories of evolution which are supposed to work by controlling mutation are extremely cogent (see Ford 1948, Chapter 3). Furthermore, such a concept throws no light upon the curious dominance relation to which attention has already been directed (page 188): that is to say, only genes dominant or semi-dominant in effect have taken part in the recent spread of melanism.
>
> Harrison has several times attempted to demonstrate experimentally the production of melanic varieties by mutations due to salts of lead and manganese. His results are subject to criticism on several different grounds. First, they have been repeated by two independent workers [Hughes, 1932; Thomsen & Lemeche, 1933], who failed to confirm them though they used larger numbers than he. Secondly, he worked principally on the Early Thorn . . . in which the melanism he studied is recessive. This was a most unfortunate choice of material, for it required the use of extremely rigorous controls to

> make sure that the gene concerned was not present in the heterozygous state: controls which R. A. Fisher has shown to be inadequate. Had a species in which the dark form is dominant been employed, no such difficulty would have arisen. Thirdly, Harrison was thereby investigating a phenomenon which seems never to have occurred: the spread of recessive melanism. Thus his interpretation, which caused considerable controversy in past years, need no longer be considered. (Ford, 1955, pp. 196–197)

Impact on Kettlewell's Initial Research

What impact, if any, did Harrison and the controversies surrounding his research on the induction of melanism have on Kettlewell's research? According to a surviving letter by Kettlewell, they first began corresponding around 1934,[26] about the time that Harrison had completed the last of his empirical studies on the induction of melanism, but prior to the start of Kettlewell's association with E. B. Ford in 1937.[27] Thus, while it appears unlikely that his association with Kettlewell influenced the direction of Harrison's research, it most certainly opens up the possibility that conversations with Harrison may have influenced the course of Kettlewell's later work.

Among the early letters that survive is one written in connection with a talk Harrison gave at the South London Entomological Society, which Kettlewell arranged. In it, Harrison refers to some experiments Kettlewell presumably was conducting with the aid of E. A. Cockayne on melanism:

> I was disappointed not to be able to see your collections, & to lose the chance of talking over matters of common interest. However, I do not consider myself to blame in any way. Your Selenia cross interests me as I performed that operation several times. In introducing melanism from one of the species in a Tephrosia experiment, parallel to yours, & then in introducing melanism (dominant) from one species and melanism (recessive) from another, I obtained amazing results.[28]

The quoted passage above appears to refer to crossbreeding experiments later published as Cockayne and Kettlewell (1949), in which they discuss a number of crosses aimed at elucidating the genetics of the Lunar Thorn, *Selenia tetralunaria*, a species that, like the peppered moth, has larvae whose melanin production is strongly influenced by environmental factors (Majerus, 1998, p. 67). Cockayne and Kettlewell were at this time involved in multiple studies that demonstrated the effects of environmental factors on larval and pupal coloration.

Kettlewell himself authored a paper demonstrating that a prolonged pupal period in the Bordered Straw, *Heliothis peltigera*, and the Scarlet Tiger Moth, *Panaxia dominula*, could result in a darkening of resultant adults (Kettlewell, 1944). Kettlewell's conclusion makes it quite clear that he did *not* interpret these results as providing evidence of the possibility of acquired inheritance, but rather that phenotypic traits are the product of both genes and the environment:

> Once again the concept of Professor Goodrich has been clearly shown that "no single part or character is completely 'acquired' or due to inheritance alone. Every character is the product both of the factors of inheritance and of environment and can only be reproduced when both are present." (Kettlewell, 1944, p. 81)

The above quotation notwithstanding, there is evidence that Kettlewell took an interest in Heslop Harrison's work around the time of his famous investigations in the early 1950s, as indicated in the following letter from Kettlewell to Harrison, written on November 2, 1954:

> You may remember me as someone who has corresponded with you sporadically from time to time over the last twenty years. I am working here on Industrial Melanism in the Lepidoptera, and am at present rereading your excellent papers most of which are in the Journal of Genetics. I am writing to ask you two things.
>
> In view of the fact that I am constantly having to refer to your papers, is it possible you could spare me any of your earlier reprints. Secondly, could you be so good as to give me the references to your paper of Observations of *Polia chi* sitting on a wall, and their predation. E. B. Ford quotes it in his paper in *Biological Reviews*, Vol. 12, 1937, p. 461, but unfortunately gives the wrong reference, and I have spent two days in the Radcliffe Library unsuccessfully.
>
> I should so much have liked to discuss this work I have been doing for the last two or three years with you, as no body, to my knowledge, has done anything since the work you did. I am using *Biston betularia*, and its two melanics, *carbonaria* and *insularia*. (I have at last been able to show that these melanics ARE NOT allelomorphs) as my guinea pig, and am undertaking the following lines of enquiry. Leaf washings each month from the same tree in various parts of England. As I think you point out among your papers the solid precipitation from the atmosphere is entirely different than the SO2 measurements. I found a correlation between the month of the year and the amount of pollution (obviously), and also between the greenfly count. I feed back this pollution to 1:1 broods, which genetically should produce half black half white, and there is some evidence [that the melanics have a superior condition (?) [rest of line indecipherable]
>
> . . . which were most instructive. I undertook, following aviary experiments at Madingly, Cambridge, [indecipherable] a large mark-release experiment at Birmingham (where typical forms about 8%–10% of the population), and succeeded in getting back about 30% of my carbonaria, but only about 13% of my typical. We actually witnessed birds taking them off the tree trunks, having previously scored them for crypsis. I am mentioning these things to you in case you can make any suggestion, or know anyone working on parallel lines.[29]

The introductory tone of the letter suggests that Kettlewell was using it to broach the subject of industrial melanism for the first time, well after he completed the initial Birmingham trials in the summer of 1953. While it is tempting to take Kettlewell at his word that he was willing to keep an open mind about the results of Harrison's research at this late date, it seems far more plausible to interpret him as simply being polite toward an older, well-respected entomologist with whom he must have had multiple dealings in connection with numerous publications Kettlewell had already published, starting in 1943 in the *Entomologist*, an entomological journal for which Harrison served on the editorial board.[30] The letter also draws attention to the one and only investigation Harrison had conducted that was at issue with reference to Kettlewell's investigations, namely his attempt to determine whether birds prey upon *Polia chi* at all; and if so, is it done selectively with reference to how conspicuous the moth is on its resting site (quoted above).

After Harrison sent the reprints, possibly with a cover letter that has not survived,[31] Kettlewell replied,

> It was most unfortunate that I happened to be away when your reprints arrived, and as it was not certain how long I should be down south, I did not have my letters sent on

> to me. I am extremely sorry that this has necessitated your writing to me a second time, and please forgive me for giving you this additional trouble. First of all, I want to thank you very much indeed for sending me these reprints which I value very much, and for the trouble you went to give me the references. I am a bit worried about the *Polia chi* findings. Unless they were in sufficient concentration only casual predation would take place surely? and in your last paragraph it appears that this in fact did take place, and even though this was in the order of 1% it would have considerable selective effects on the two phenotypes. With my *betularia* releases in Birmingham, I did not get marked predation until I had released many hundreds into the wood where I was working. I shall be hoping to send you reprints of this work in the next few months . . .
>
> I was most interested in what you had to say in your letter of the 17th, particularly in regard to your population which has turned from its melanic state to one containing a majority of pale individuals. I find that it is very difficult to understand in terms of crypsis if the lichens have not at the same time returned to the tree trunks, which is unlikely I think. At the same time, I expect you will agree that melanic insects may not have a cryptic advantage in an industrial area if their habit is to sit on birch trunks?[32]

Kettlewell's letter is striking in that it makes no mention of the numerous reservations he, Ford, and others such as Philip Sheppard had about Harrison's research on the induction of melanism.[33] Kettlewell instead understandably took direct issue with Harrison's previous selection experiment on *Polia chi* (quoted above), which stood in direct opposition to the findings of his Birmingham investigations.

Harrison's response at this point was entirely cordial:

> I need scarcely say that I still hold my original view that the matter of industrial melanism is one of recurrent mutations brought about by a melanogene in industrial smoke. Still I am no bigot in favor of a one factor solution. Hence I have continued and expanded my outdoor experiments and observations. All the best + good wishes, Yours sincerely, J. W. Heslop Harrison[34]

Kettlewell politely responded in kind:

> I still remember the pleasant lunch we had together on my short visit which I wish so much could have been extended as I had a great deal more to discuss with you. I am very much looking forward to seeing your forthcoming paper. Although we may not agree on the fundamental causes of the spread of Industrial Melanism, I think it is most important that we should keep in contact because after all, apart from your pioneering work, so few people have worked on this line, which surely we must both agree is one of the most exciting and profitable roads of research open to biologists . . .
>
> I will send you a copy of a paper I have coming out in the December number of *Heredity*. I particularly want you to see it because it is the companion experiment to the reprint I am sending you which has already come out in *Heredity*.[35]

The correspondence so far gives no evidence that Harrison had read or reacted to a critical discussion of his investigations in (1955) *Moths*, where (as quoted above) Ford used part of a chapter devoted to research on melanism to summarize numerous concerns Ford and others had previously raised about Harrison's research.

Nor did he apparently dispute Kettlewell's brief critique of his anecdotal attempt to observe selective predation among *Polia chi* (quoted above), in which Kettlewell summarized concerns previously raised by Ford and Fisher:

> How low this may be under certain conditions may be seen from data provided by Heslop Harrison (1919–20) who kept daily observations on *Polia chi* (Agrotidæ), and its dark form, which took up positions in a state of nature on three types of wall in the Newcastle district. The frequency of the latter (= *olivacea*) was 10 per cent. in one locality and 50 per cent. in another. He examined "up to 300 examples daily" and "never was there any diminution in numbers in which more *olivacea* (= the 'melanic') vanished than type *chi*. As a matter of fact, we used to consider it a marvellous thing if even one had disappeared." He quotes this "to demonstrate that the effect of natural selection is quite negligible as a factor in progressive melanism."
>
> I am afraid I cannot agree with this. In the first place *olivacea* is not a melanic in the sense that the whole pattern has been obliterated, for this remains present in a darker olive-grey tint (= it is a "melanochronic" J. W. H. H.). For this reason, sitting on stone walls (and not tree trunks) as they do, both forms are inconspicuous against the same backgrounds. Secondly, in the absence of concentrations, predation may have been at a very low level, though highly selective, and however small an advantage (0.1 per cent. or less) selection is able to use that advantage and spread a gene through the population at a calculable rate (which is not a linear one) and which depends upon the population's size. Consequently there is, theoretically, no limit set to the smallness of an advantage which can be used in selection, and one involving one out of three hundred individuals indicates quite a considerable selective influence (Fisher, 1930). Fortunately, in the present series of experiments the values are of a much higher order and the effects of natural selection on industrial melanics for crypsis in such areas can no longer be disputed. (Kettlewell, 1955a, pp. 340–341)

Harrison's ire, instead, appears to have been initially provoked by a passage in Kettlewell's *Discovery* paper, to wit:

> We are now able to answer some of those questions which inevitably arise in analyzing an occurrence of this magnitude [i.e., the spread of industrial melanics]. In 1926 Prof. Heslop Harrison put forward a suggestion that certain salts of manganese and lead, present in air pollution, were responsible for inducing the black mutations. In 1928 he read his now well-known paper to the Royal Society, whose purpose was to show that this induced melanism was inherited according to Mendel's Law. The battle over the inheritance of acquired characters was thus started again, this time on the grounds of "industrial melanism." Nevertheless, in the idea that the change was a case of inherited "acquired characters" was rejected for two reasons. Firstly, Heslop Harrison's experiments were carried out on the larvae of *Selenia bilunaria*, Esp. and the melanic moths which he produced were shown to be recessive and less viable than normals, a situation unknown in "industrial melanism," as pointed out at the time by E. B. Ford; secondly, if induced melanism was responsible for the rapid spread of melanics, the mutation rate would have to be raised to a degree hitherto unknown in any other organism. That was the argument of R. A. Fisher in 1933. The direct effect of pollution on the insect could, therefore, not be accepted as being the principal cause of the spread of "industrial melanism." (Kettlewell, 1955b, p. 509)

In what must have been an angry reply,[36] Harrison apparently took great issue with the above appraisal of his work, pointedly refuting the idea that he was a Lamarckian on the subject of industrial melanism. He apparently also took this occasion to let Kettlewell know that he was about to publish a rebuttal in the *Entomologist's Record and Journal of Variation*. Kettlewell attempted to placate Harrison in his reply:

> I am so glad to receive your letter. Many thanks for it and also for the copy of the *Vasculum*. I fully endorse what you say about people in our position becoming hostile to each other because of failure to agree over scientific matters. I must hasten to say, however, that I am very disturbed to hear that what I wrote in *Discovery* met with your disapproval, and the first thing I did when I returned here today from my East Coast field work was to go through a copy of this article. I can't help feeling that you have implied more into my criticism of your earlier experiments than was meant, and I certainly never suggested that you held Lamarckian views over the subject of industrial melanism. If you look at this paper of mine again, you will see that I have said that you "put forward a suggestion that certain salts . . . were responsible *for inducing* the black mutations." The fact that I mentioned the word "mutations" shows that I was thinking of their effects on the germ-plasm and the reason I criticised your conclusions was that you produced a non-recessive melanic in your stock. Furthermore, it would appear from your paper in the *Vasculum* that you believe that the cause of industrial melanism is directly due to larvae ingesting food plus pollution, thereby causing a change in their germ-plasms. I gather from this that you think this happens in a high percentage of cases which would produce a mechanism quite different from the normal mutation rate, which is in the order of let us say 1 in a 100,000 or 1 to 106. If having read this you now cast your mind back to my paper in *Discovery*, you will see this is exactly the criticism I have made. May be that you do not like my referring to this situation as "inheritance of acquired characters" because, and I will agree, this phrase is usually confined to Lamarckian philosophy? In any case, I am very sorry if it has in any way offended you. I understand that your paper will be coming out in the *Entomologist's Record* and I look forward greatly to seeing it.[37]

Harrison's Critique of Kettlewell's Research and Its Impact

Harrison's aforementioned article (Harrison, 1956), the first paper he had published on the subject of industrial melanism for over two decades, was a lengthy critique of Kettlewell's work as discussed in Ford's *Moths* and Kettlewell's popular article written for *Discovery*. Reading Harrison's paper, it is hard to escape the conclusion that Kettlewell's brief references to longstanding published concerns surrounding Harrison's work was simply a pretext for Harrison to publicly rebut longstanding criticisms of his critics, particularly E. B. Ford.

Harrison criticized Ford's and Kettlewell's accounts for misrepresenting his views, attributing views to him that he did not hold, and ignoring previous work of Harrison and researchers on the Continent, such as Warnecke.[38] Two thirds of Harrison's paper was devoted to a critique of Kettlewell's recent experiments. He faulted Kettlewell for studying a single species (*Biston betularia*) rather than studying many species of diverse habits and habitats. He drew attention to multiple discrepancies between the recapture figures quoted in Ford's *Moths*, Kettlewell's *Discovery* article, and Kettlewell's 1955 *Heredity* article, pointing out further that within one and the same paper, the numbers were not consistent. Harrison disputed Ford and Kettlewell's contention that melanic forms sporadically arise by mutation, pointing out that if so, someone in either the U.K. or continental Europe surely would have found one previous to 1850 (the date of the first recorded example of a specimen of the melanic form, *carbonaria*, near Manchester). Kettlewell's investigations did not focus on the cause of industrial melanism (as was done in Harrison's previous investigations), nor did Harrison find Kettlewell's investigations of the spread to be particularly convincing. He questioned Kettlewell's use of an oakwood, instead of a birch forest, given that the silvery trunks of birch would remain relatively light despite the absence of lichens and the presence of heavy pollution. He pointed out that it was difficult to interpret Kettlewell's results in the absence of greater detail regarding the types of trees present, the relative numbers of *betularia* released on each type of tree, and also detail regarding how it chose its resting site. He drew attention to the potential confounding effects of local populations of insects, particularly wild female *betularia*.

Harrison additionally objected to the use of strong lighting from the top left in photographs used in Kettlewell's *Discovery* article, which had the effect of heightening the contrast between the two forms when they rest on lichen-covered and soot-darkened trunks. Ford's use of photographs was even worse, in that a photograph intended to illustrate the camouflage value of the pale form features a clean piece of bark, not one encrusted with lichen. Harrison further claimed his own observations of *betularia* suggest that typical is the more conspicuous regardless of whether the bark is lichen covered or sooty, and further that in a polluted area he had no problem sighting specimens of *carbonaria* from distances of over 20 yards. Finally, he reiterated his criticisms of Kettlewell and Ford's overemphasis on the role of bird predation, pointing out that his own observations of chaffinches preying upon moths leads him to believe that they take moths indiscriminately. He further disputed Ford's claim that bat predation had no role in that they take prey on the wing. Bat predation can be considerable; moreover, observers have observed bats prey on moths when resting on walls.

Harrison's article must have been devastating to Kettlewell.[39] It was the first lengthy critique of his work by a well-respected scientist, and went well beyond polite disbelief expressed by others about the magnitude of bird predation actually observed by Kettlewell in previous reviews of Ford's (1955) *Moths* (Allen, 1955; Minion, 1955). Kettlewell apparently sent a letter to Ford asking what to do, to which Ford replied,

> I have not seen the article in the *Entomological Record* to which you refer. Heslop Harrison has not the first glimmerings of a scientist, and now he is in his dotage. I suppose it may be worth while to publish some reply, though it is generally much better to ignore criticism. Of course, they are hoping you will rise to the bait, and the thing that puts them back in their place most is silence. When Goldschmidt published a violent attack on me, I took a convenient opportunity of smashing him when I happened to be writing seven years later. You ask me to look into, and to deal with, this matter; but surely, having regard to the speed of publication, the fact that you will be in the best position to answer it, it had much better await your return. I would, of course, deal with anything that was urgent, but it will be so much better that you say what you want to yourself (if anything should be said at all), and the matter cannot possibly be affected by a delay of three or four weeks.[40]

Presumably with Ford's assistance, Kettlewell wrote an extended reply to Harrison's diatribe that was published the following December (Kettlewell, 1956b). In it, Kettlewell emphasized he did not regard his experiments as decisive, nor that by virtue of them, the story of industrial melanism was completely solved.[41] While fully admitting bats prey on moths, Kettlewell denied that bats were visual predators and as such, even if they destroyed thousands of moths, they did not do so selectively with respect to color. Kettlewell dismissed Harrison's anecdotal claims about the relative conspicuousness of the moths, drawing attention to the large numbers of moths he used in his own systematic scoring experiments (used to assess how conspicuous moths were against different backgrounds). Kettlewell further traced Harrison's concerns regarding discrepancies in figures provided in his papers and requests for additional detail regarding relative numbers of species of trees to Harrison's lack of care in reading the papers. Nearly half of Kettlewell's rebuttal was devoted to defending his claim (and Ford's) that Harrison's views were Lamarckian. He drew attention to multiple passages within Harrison's writings in which Harrison either espoused a Lamarckian perspective or equivocated, first denying that his view was Lamarckian and then concluding later that the evidence on balance favored a Lamarckian interpretation. Kettlewell concludes his reply by reviewing the research findings of multiple scientists, previously summarized by Ford, who openly questioned Harrison's results.

Kettlewell's reply, in short, called into question Harrison's abilities as a scientist. In later correspondence and radio appearances, following Ford's lead, Kettlewell became ever more dismissive of Harrison's work:

> I read Heslop Harrison's original papers some years ago, and it was clear that the experiments were faulty (in relation to the conclusions drawn). In spite of this, I think they deserve quotation, accompanied of course by indication of their fallacy. Some of Dr. Ford's writings, in particular, give the impression that until recently nothing was done about melanism, whereas it is very, very many years since a committee was set up by the Royal Society or the Ent. Soc. (I forget which) to study the matter. Perhaps the committee did nothing effective, but at any rate, the importance of the phenomenon was realized.[42]

Kettlewell's derogatory comments about Harrison's work were not restricted to his private correspondence. He made similar remarks, publicly, as indicated in the following transcript of a radio broadcast.

> BLACK: Just to give the historical background. It was at the turn of the century that Mendel published—that Mendel's papers were in fact, published, so that at the time when these were first discovered, this system of inheritance wasn't even known about.
> KETTLEWELL: That is quite correct. Even though Darwin, of course, must have lived during the beginnings of industrial melanism. Now to continue the history I think the next step we can say is that Professor Heslop Harrison, about 1926, did a series of big-scale experiments, and came to the conclusion that the origin of industrial melanics—the blacks—was the direct effect of a substance, or substances, which he called melanogenic agents, in the air pollution, on the germ plasm of the insects. And he then went on to show that these black forms which were produced went on breeding according to Mendel's law. In other words, he really was claiming the inheritance of an acquired character.
> BLACK: Would this be Lamarckism?
> KETTLEWELL: Well yes, or probably more correctly, Buffanism (?) Nevertheless, whatever you call [it] . . . his experiments have been repeated both on the Continent and in this country, and very large numbers of insects have been used, but nobody has ever repeated his work with success.

> BLACK: You express that, Dr. Kettlewell, with great great scientific caution. What you're really trying to say is that Professor Heslop Harrison's work was not true—not correct.
> KETTLEWELL: No, I'm saying that his interpretation of his conclusions have not been verified by anyone else. Well now, as a theory which one could put forward to—as an alternative. I prefer it because one hasn't got to invoke any new laws of nature, and one can use the long established ones that have been accepted. I would suggest that what we are seeing in this rapid spread of industrial melanism is by the effects of natural selection—choosing those moths which are blacker because the average background in England of trees and trunks and rocks, has slowly, in the last hundred years, got darker, and this has been brought about of course, by air pollution, the dimunition in the numbers of lichens, with the result that the tree trunks in all industrial areas and far beyond, particularly in England to the east, because of the prevailing south-westerly wind—the trunks are very much darker than they were a hundred years ago.[43]

And in a reply to a direct question about Harrison's work, Kettlewell specifically denied that he ever even felt the need to directly test Harrison's work, as this would be unnecessary:

> In regard to your request for a reprint on any experiments I undertook as a repeat of Professor Heslop Harrison's work, I myself, of course, have not done any because others have repeated his experiments on such a large scale, always with a negative result; also I think it is not necessary to do more. Furthermore, I think it fair to say that the whole body of biologists are completely satisfied that the origin of the melanics in his experiments arose from the fact that they were recessive in inheritance, and that therefore the most likely explanation is that they were in his stock the whole time. I am, however, enclosing a reprint of a short paper I wrote giving my views on his work after he had made certain observations on my conclusions in the August number of the *Entomologists' Record* (1956).[44]

And again,

> Thank you very much for your letter in which you quote a paragraph from Grogan's "The Living World." My immediate comment is how very shrewd he was in 1948 to state that there was really no evidence that industrial melanism was an acquired characteristic. Following up on statements of Heslop Harrison about 1926 a large number of people fell for the belief that this was so. I can assure you that there is not a shred of evidence in favour of his views. In fact, I think I can say we have clearly shown that industrial melanism can be accounted for in the same way as the speed or elimination of any other character. This is brought about, as you suggest, by natural selection.[45]

The passages above provide evidence that Kettlewell completely dismissed Harrison's views that melanism was induced by contaminants in the soot. This being said, several of the concerns voiced by Harrison in his critique of Kettlewell's work may have affected the course of subsequent research by others, either by directly identifying previously unrecognized problems, or indirectly by inviting the scientific community to exercise greater scrutiny. Indeed, much of the history of research on industrial melanism since Kettlewell's pioneering research has been motivated by perceived problems in his original investigations, from assumptions surrounding the actual resting sites of moths to concerns about the relative densities of moths used and how moths were released (Majerus, 1998). Majerus's most recent study is largely an attempt to assess whether bat predation is a factor (Majerus, 2007). And, curiously enough, there are still a few scientists who continue to research the possibility that melanism might be induced by pollutants (Sargent, Millar, & Lambert, 1998; but see Cook, 2000; Grant, 1999). Clearly Kettlewell's 1950 investigations did not "solve" the problem of industrial melanism. Attending to the role played by Harrison reveals that the phenomenon of industrial melanism is and remains an area of active inquiry, that there were alternative accounts for the phenomenon, and further that there were a host of design and interpretive problems associated with Kettlewell's original research, like any scientific investigation.

Summary and Conclusions

The preceding analysis of the published record and private correspondence strongly suggests neither Harrison nor his research on melanism played an important role in the conduct of Kettlewell's initial investigations. There is no evidence that Kettlewell was at any time sympathetic to what was generally regarded as a Lamarckian alternative offered by Harrison, and indeed the only references to Harrison's work contained in Kettlewell's initial papers on the subject reiterate concerns previously raised by E. B. Ford and others. The only investigation Harrison had conducted that was even relevant to Kettlewell's work was his largely anecdotal attempt to observe whether moths are differentially preyed upon by birds. Aside from perhaps drawing Kettlewell's attention to the importance of making systematic observations of bird predations using a species that was indeed regarded as an example of industrial melanism, it's unclear Harrison had any effect on the design, execution, or even initial interpretation of Kettlewell's results.

Harrison's impact on Kettlewell's work rests primarily in his lengthy 1956 critique of Kettlewell's investigations. Whereas Kettlewell and Ford were inclined to dismiss it as the ravings of someone whose outdated ideas had been thoroughly discredited, Harrison's critique was significant in drawing attention to numerous problems in the design and interpretation of Kettlewell's results, problems that with historical retrospect can be seen to have guided subsequent research.

The preceding overview of Harrison's work and analysis of its potential impact on Kettlewell also reveals numerous flaws in the legendary portrayal of Kettlewell's research, flaws many of which ultimately trace their origin to Ford's portrayal of both Kettlewell's and Harrison's research. On the standard portrayal, the phenomenon of industrial melanism is depicted as a problem that was "solved" by Kettlewell's early investigations in the 1950s, rather than an active area of research. The standard portrayal typically ignores the presence of alternative theories that might account for the phenomenon, such as Harrison's, and further presents Kettlewell's results as definitive when in point of fact they were the object of controversy from the moment they were first published. In short, and perhaps not surprisingly, the legend surrounding Kettlewell's research is fundamentally misleading with respect to its depiction of science as a process. When one contrasts the certainty surrounding the phenomenon of industrial melanism as depicted in standard accounts with articles written by scientists who work on the phenomenon, one can certainly appreciate why some with an obvious agenda would mistakenly question whether it should still be regarded as an example of natural selection and further interpret these differences as an indication of a conspiracy by textbook writers to prop up the phenomenon of industrial melanism as an example of natural selection (e.g., Wells, 2000).

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Notes

1. Over the past seven years Michael Majerus has conducted an extensive set of investigations repeating Kettlewell's original work that have been specifically designed to address problems that have raised over the years. Although these investigations were restricted to a repeat of Kettlewell's Dorset experiments (the unpolluted wood) because owing to clean air legislation, no part of Britain currently has a rising *carbonaria* frequency, Majerus's results reaffirm Kettlewell's basic conclusion, namely that selective bird predation is responsible for the decline of *carbonaria* in the unpolluted area studied (Majerus, 2005, 2007).
2. See Rudge (2002) for an extensive critique of Wells's analysis of the phenomenon of industrial melanism and Kettlewell's work on it.
3. See Rudge (2005) for an extensive critique of Hooper's argument; and also Young and Musgrave (2005) for a careful statistical analysis of Kettlewell's data that undermines her specific allegations that he fudged his data.
4. In the text and endnotes that follow manuscripts and correspondence from archives are referred to by the following convention: FA (The E. B. Ford Archive, Bodleian Library, University of Oxford), KA (The H. B. D. Kettlewell Archive, property of Wolfson College, Oxford, deposited in the Bodleian Library, University of Oxford), and SP (The Philip M. Sheppard Papers, American Philosophical Society Library). Following the name of the archive, the endnote subsequently identifies the Box, Folder, and Item consulted. (Correspondence is between the scientist whose papers have been placed in the archive and the person whose name is used to identify the box/folder, unless otherwise indicated.)
5. Biographical details regarding Harrison's life are taken from Peacock (1968) unless otherwise noted.
6. See Sabbagh (1999) for a careful examination of charges of fraud surrounding J. W. Heslop Harrison's botanical work on the Isle of Rhum [Rum] during the 1940s.
7. Peacock draws attention to the pivotal role played by Harrison's mother "[a woman who] loved plants and had the green fingers of a born gardener. She was one of the few to whom he [Harrison] would entrust his moths if he had to be absent from home. It was from her

that Harrison inherited his bent towards natural history" (1968, p. 243). Peacock also draws attention to the important roles played by Harrison's uncle, the Rev. J. E. Hull, M.A., D.Sc. (Hon. Durham) "a true and lonely scholar who, in his country parishes in Northumberland, wrought and wrote as an authority on the lore and language of Northumbria and its natural history, with especial regard to the spiders and mites" and Charles Robson, a "working man naturalist" neighbor during his youth who took him under his wing and helped him obtain a Ray Society grant early in his career (Peacock, 1968, p. 243). Kettlewell similarly acknowledges the pivotal role played by Timothy Tams of the British Natural History Museum "into whose safe keeping I was firmly put by my mother in 1919 and who has continued to help my coworkers and myself for over fifty years" (Kettlewell, 1973, p. xxi).

8. "Harrison was a field naturalist par excellence. If slight misquotation be allowed it could be said 'the range of the mountains and islands were his pastures and he searched after every green and winged thing.' To novices his powers of observation and knowledge of plant and insect life savoured of magic; professionals, too, could not forebear to cheer" (Peacock, 1968, p. 262). "Bernard Kettlewell was the finest living ecologist of the Lepidoptera. Moreover, he was blessed with the good luck, which ought to attend devoted field workers. On one occasion he found himself surrounded by numbers of the Bath White butterfly (*Pontia daplidice*) in South Cornwall and had a specimen of this and another fabulously rare species the Short tailed Blue (*Everes argiades*), in his net at the same time" (Ford, 1979, p. 166).
9. "[Harrison's] great failing as a scientist, however, as even his friends agreed, was to become so convinced of the rightness of his theories and views that he either ignored reasoned criticism, or perceived it as a personal attack" (Salmon, 2000, p. 217; see also Marren, 1999). "Kettlewell was an exciting person to be with, full of lore and anecdotes. He was the best naturalist and almost the worst professional scientist I have ever known. Writing research papers with him was traumatic; as an experienced clinician he made rapid diagnoses and refused to be diverted by what he regarded as irrelevant evidence. I learned an enormous amount from Bernard Kettlewell, and was enthused by him at a crucial time in my life when I was in danger of becoming a closet biologist" (Berry, 1988, p. 2). Harrison's reputation as a scientist was, of course, also sullied by allegations of fraud (see note 5 above); a charge that to my knowledge (contra Hooper, 2002, pp. 298–299) has never seriously been leveled by any scientist or historian at Kettlewell (see Rudge, 2005).
10. Technically the evidence that the phenomenon of industrial melanism in the peppered moth is an example of natural selection is the unidirectional increase in the frequency of *carbonaria* in the vicinity of manufacturing centers during the industrial revolution (both in Europe and the United States) and its altogether predictable decline after the advent of Clean Air legislation (Grant, Owen, & Clarke, 1995). Kettlewell's field experiments were important in establishing that differential predation by birds was the primary selective agent.
11. As noted in the previous footnote, none of these problems calls into question whether industrial melanism is an example of natural selection. At most, they raise questions regarding the extent to which it has been established that differential bird predation is indeed the selective agent.
12. Kettlewell also conducted numerous experiments that involved raising pale and dark moths on polluted foliage, but these were done only with an eye to assessing whether the melanic form was hardier. The following exchange illustrates Kettlewell's purpose:

    KETTLEWELL: I get my air pollution sent down from the filters of the Festival Hall of Great Britain in London. I use it, you see, for feeding back to my stock, to try various experiments—viability differences between the back [*sic*] and white forms.

    BLACK: Well, wait a minute, Dr. Kettlewell, you're going back to Professor Heslop Harrison's work, when you are feeding air pollution to the moths. You're trying to see whether it changes them.

    KETTLEWELL: Not, that is not so, the . . . [*sic*] take place we should have discovered it. But our object in doing this is to see if either the black or the white forms are hardier when feeding on the appallingly dirty leaves caterpillars have to if they are to survive in an industrial area.

(KA, Box 3, BBC #1, Transcript of London Calling Asia—The Searching Mind (November 1, 1957).

13. A notable exception is Majerus (1998, pp. 103–104). He points out the influential role Harrison's work played in raising the possibility that the increase in melanic forms might be accounted for in terms of the ingestion of metallic salts in the fallout from air pollution, and Majerus goes so far as to allow that Harrison's work "affected" later writings on the subject of melanism, but does not elaborate beyond drawing attention to the strong and adverse reaction to Harrison's work felt by E. B. Ford, who was Kettlewell's mentor at Oxford, and a vocal proponent of R. A. Fisher's panselectionist agenda.
14. Of 31 American biology textbooks published from 1972 to 1996, I found only one that so much as mentioned Lamarck's theory of the inheritance of acquired characteristics in connection with its discussion of industrial melanism, and this was only to emphasize that the phenomenon is not an example (Campbell, 1987, pp. 426–427).
15. Date taken from Harrison (1926), the first paper he wrote detailing his experiments on the induction of melanism and consistent with all but his last paper on the subject, in which he asserted his work on melanism had actually commenced starting in 1903 (Harrison, 1956).
16. They also reported similar results in a smaller pilot study involving a related species, *Tephrosia crepuscularia*.
17. For example, Brood 1923 BL had 11 females and 20 males, all typical save two of the males. The disparity of the ratio of typicals to melanics is 29:2, not the 3:1 ratio one would expect if this were the result of a hidden recessive melanic gene.
18. This is a slightly simplified version of Table I on page 249 of Harrison and Garrett (1925–1926).
19. See Peacock, 1968, pp. 253–255.
20. Harrison's own words clearly admit this conclusion:

    > Clearly such evolution as is pictured at work here is not of the Lamarckian order; most likely the influences at work act directly and simultaneously on soma and germ alike, or even on germ plasm alone, and indeed, the latter view obtains concrete support from the *Selenia bilunaria* work. If, however, the germ plasm can be influenced in the matter [*sic*], the step to admitting the truth of the Lamarckian doctrine is but slight, and one almost involuntarily made, when it is realized how easy it would be for chemical action registered in the soma to be communicated by some method, whether by means of the blood stream or otherwise, to the germ plasm. Add to this the fact that a direct demonstration of a genuine Lamarckian effect has been made, and one is forced to admit that Lamarckism itself has received very powerful support, both directly and indirectly, from the work described above. (Harrison, 1927b, p. 125)

21. Note the distinction Harrison makes in the following:

    > In 1917 I commenced certain experiments (*Entomologist*, May 1926) at Middlesbrough in which, as a result of spraying the food of certain Geometrid larvae with a solution of manganese sulphate, melanic imagines were developed. Coupling these results with investigations into the spermatogenesis of the same insects, it became perfectly clear that, in the development of melanism and its inheritance, the course of events must have been the very reverse of the phenomena covered by the phrase 'inheritance of acquired characters'; the effect must have been marked first in the germ plasm to manifest itself somatically in the following generation. In other words, we are concerned with an entirely new principle of evolution. (Harrison, 1927a, p. 104)

22. "In itself, neither Lamarckian nor the opposed view is [a satisfactory account of industrial melanism]. Natural selection cannot create and therefore demands the existence of a population including wholly melanic individuals on which it can work." (Harrison, 1927a, p. 104). "To be precise, I looked upon the experiments then, *as I do now*, as illustrating induced melanism" (Harrison, 1956, p. 173).

23. Taken from Cockayne, 1926b (the insect with a black streak was found among Harrison and Garrett's experiments with *Tephorsia biostortata* Goeze, not discussed above). Cockayne's response is all the more remarkable when one considers that just a few pages earlier in the same issue, he railed against similar work by the German chemist Karl Hasebroëk, who likewise attempted to induce melanism by exposing larvae to gaseous pollutants, methane and ammonia (Cockayne, 1926a). Among his criticisms was that Hasebroëk used species that have not produced melanic forms in industrial areas, the very charge E. B. Ford would later level with great effect against Harrison's work.
24. "Harrison's letter (returned herewith) really fills one with contempt. He is not a *scientist* at all. Clearly he does not comprehend the real thing: the man who is simply full of curiosity and longing for the answers to problems, without minding whence they come—from himself or another—so long as they are valid. His attitude is fortunately rare in this country but I find it very common among foreigners, especially when Jewish" (KA Box 17, Ford, E. B., Ford to Kettlewell, January 9, 1948).
25. Ford also regularly critiqued Harrison's work in multiple editions of his well-known *Ecological Genetics*, first published in 1961.
26. "You may remember me as someone who has corresponded with you sporadically from time to time over the last twenty years" (KA, Box 19, Heslop Harrison, Kettlewell to Heslop Harrison, November 2, 1954).
27. Throughout his career, Kettlewell repeatedly told the story of his first chance meeting with Ford at Rannoch. The Kettlewell archive contains an early letter that appears to refer to this encounter: "Dear Kettlewell, Dowdeswell and I are immensely grateful to you for your kindness to us at Rannoch the other day. . . . Yours sincerely, E. B. Ford [P.S.] I don't know if you are still at Rannoch, so it seems best to write you at your home address." (KA Box 17, Ford, E. B., Ford to Kettlewell, July 20, 1937).
28. KA, Box 19, Heslop Harrison, Heslop Harrison to Kettlewell (May 6, 1947).
29. KA, Box 19, Heslop Harrison, Kettlewell to Heslop Harrison (November 2, 1954).
30. In a previous letter written to Cyril Clarke, Kettlewell refers to Harrison as "notoriously unreliable and very difficult to pin down to statements" (KA, Box 13, Clarke, Cyril A., Kettlewell to Clarke, December 13, 1951).
31. The following oblique reference to it is mentioned in another letter from Kettlewell to Cockayne: "I am going up to Scotland next Thursday for ten days' stalking, and I am hoping to take the opportunity of calling on Heslop Harrison on the way back, which should be elucidating . . . I have been having some considerable correspondence with him lately. I think he sounds slightly crazy" (KA, Box 14, Cockayne, E. A., Kettlewell to Cockayne, December 3, 1954).
32. KA, Box 19, Heslop Harrison, Kettlewell to Heslop Harrison (November 29, 1954).
33. M.S. #65 Philip Sheppard Papers Series I, Box 17: Muspratt, Vera, Kettlewell to Muspratt (September 2, 1952).
34. KA, Box 19, Heslop Harrison, Heslop Harrison to Kettlewell (April 19, 1956).
35. KA, Box 19, Heslop Harrison, Kettlewell to Heslop Harrison (April 20, 1956).
36. Brief extracts from this letter, received by Kettlewell in early June, are contained in Kettlewell, 1956b, pp. 279–280.
37. KA, Box 19, Heslop Harrison, Kettlewell to Heslop Harrison (June 19, 1956).
38. This latter criticism continues to be leveled at Kettlewell and Ford—see Owen, 1997.
39. "If you want a few moments of light reading see the 'shoot down' we have had in the July issue of the *Entomologist's Record* (Heslop Harrison). He has not progressed since 1926 except that he now seems to have developed a Persecution mania" (SP, Series I, Box 13, "Kettlewell folder #1 1952–60," Kettlewell to Sheppard, dated September 9, 1956).
40. KA Box 17, Ford, E. B., Ford to Kettlewell, August 31, 1956.
41. Kettlewell's remark contrasts with Ford's less guarded conclusion (which was presumably what Harrison was referring to): "Though much more work of a similar kind remains to be

done, the mystery surrounding the selective elimination of normal and melanic Lepidoptera has thus been solved" (Ford, 1955, p. 204).

42. KA, Box 10, Bowden, S. R., Bowden to Kettlewell, June 7, 1957.
43. KA, Box 3, BBC #1, Transcript of London Calling Asia—The Searching Mind, November 1, 1957.
44. KA, Box 10, Bersin, Th., Kettlewell to Bersin, May 14, 1959.
45. KA, Box 2, Research & Equipment #5, Kettlewell to Josephine, June 12, 1961.

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