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Fifty per cent and all that: what Haldane actually said

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In 1924, J. B. S. Haldane used the observation of increasing melanic frequencies in peppered moths (*Biston betularia* L.) to illustrate strong selection in a natural population. Since the phenomenon was first observed, there has been criticism and misinterpretation of work on industrial melanism in moths coming from a number of directions, increasingly on the Internet. Haldane's calculation, its reception and his other interests in peppered moths are reviewed. An example of Internet comments attributing opinions to him, and their origin and background, are discussed.

ADDITIONAL KEYWORDS: *Biston* – melanism – peppered moth – selection.

INTRODUCTION

The change in frequency of melanic forms of the peppered moth (*Biston betularia* L.) following industrialization and smoke pollution in northern British cities has long been considered to be a clear case of adaptation to changing environmental conditions. The black form, *carbonaria*, behaves as a Mendelian dominant. In industrial locations it was less conspicuous than the pale typical form on blackened daytime resting surfaces. Birds eat these moths. It seems natural to conclude that they were camouflaged and that differential predation changed the frequencies. Nevertheless, from the time they were first observed and studied, dissenting voices have criticised all parts of this story. When first reported in the 19th century, genetic principles were unknown; therefore, it is unsurprising that alternative explanations were considered, such as the transforming effect of pollutants. After the genetic basis was clearly demonstrated, this suggestion continued to be put forward with surprising tenacity (e.g. Lambert *et al.*, 1986; Fryer, 2013). The possibility of appreciable predation was questioned at an early stage (Porritt, 1907) and recently by Fryer (2013), despite evidence that it could occur (Kettlewell, 1973; Cook *et al.*, 2012).

Until the 1960s, experimental investigation and assembly of survey data relating to this story was largely the work of Bernard Kettlewell (1973). E. B. Ford gave him the opportunity to do so. Based together in Oxford, they would have discussed the planning and results. Otherwise, Ford's chief contribution was earlier, when he examined survival in breeding experiments with various species and discussed the origin of heterozygote advantage (Ford, 1937, 1945). He was not primarily interested in selective predation. Soon, however, critics argued that the two of them connived to massage the evidence for it (Hooper, 2002). Wells (2000) had gone further, claiming that all the work was fraudulent, as do numerous creationist Websites. Several rebuttals of these claims were later published (e.g. Grant, 2002; Young, 2004; Rudge, 2005, Majerus, n.d.).

Reports suggesting that Ford and Kettlewell used calculations made by J. B. S. Haldane without acknowledgement have become associated with the name of Gary Botting. Given that the allegation is available at several sites on the Internet, it is useful to examine his role more fully. In doing so, we outline Haldane's various interests in the peppered moth.

HALDANE AND THE PEPPERED MOTH

J. B. S. Haldane (1924) developed ways to measure selection on two or more alleles in populations, initiating a major section of early theoretical population genetics. He first showed the change expected over a single generation of random mating for a given amount of

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selection. Numbers of alleles were expressed as ratios, rather than relative frequencies, but in other respects his methods continue to be used. If 1 + s dominant alleles contribute to the next generation for every recessive allele, then s is the selection coefficient. If the frequency of dominant alleles in generation n is q_n then $q_{n+1} = (1 + s)q_n/[1 + s.q_n(2 - q_n)]$. The difference in frequency between successive generations is $q_{n+1} - q_n$. To see the effect of selection over several generations, we might repeatedly sum the differences the required number of times, varying the selection coefficient for each such run to obtain a good match. Without modern calculators, that would be laborious. Instead, Haldane integrated his difference equation to estimate the mean selection over the required number of generations. A modern calculation for this process was derived by M. G. Bulmer (Clarke & Murray, 1962) and is to be found in Manly (1985).

To illustrate the effect of selection on a dominant gene, Haldane used the changing frequency of *carbonaria* in peppered moths in Manchester. He pointed out that the change could not be attributable to environmental effects because, if it were, 'it would be impossible to obtain true breeding recessives' as had by that time been done. There is one generation per year. The literature suggested to Haldane (1924: 26) a frequency of perhaps 1% in 1848 and 99% 50 generations later; he concluded that whatever caused this change, 'the fertility of the dominants must be 50% greater than that of the recessives'. That figure has been widely reported. The curve of increasing frequency is illustrated by Kettlewell (1958, 1959, 1965, 1973), although he gives the final value as 95%, rather than 99%. In the first three of these papers, the advantage is quoted as 30 or 33%, later changed to 50% (in his book, Kettlewell explains the difference as a mistake on his part). Likewise, it is 30% in Ford (1964), revised to 50% (Ford, 1975).

In practice, we observe the frequency only of the dominant phenotype, *carbonaria*, rather than gene frequency. Comparing phenotypes in successive generations, starting from generation 0, the melanic advantage over n generations could be estimated as $1 + s = \{[Q_n(1 - Q_o)]/[Q_o(1 - Q_n)]\}^{(1/n)}$, where Q is the frequency of the melanic phenotype. This procedure does not allow for the changing ratio of dominant to recessive alleles in heterozygotes, but reflects what we actually see.

Figure 1 shows selection required to move a population from 1% *carbonaria* to different final frequencies in 50 generations. The upper curve represents the iteration and the integration methods, which are almost coincident, the lower curve the phenotype method (a calculation by Van't Hof *et al.*, 2016, gives a curve lying between). Over much of the frequency range, the allele and phenotype calculations agree, but near the endpoint they diverge. To get >90% *carbonaria*, a small increase in frequency requires a large increase in fitness, but values of 15–30% are more plausible than 50%. Van t'Hof *et al.* (2016) found a selective advantage of up to ~20% when they also included data on the degree of linkage disequilibrium along the *carbonaria* chromosome. Calculations are bound to be notional when there are extreme frequencies and imprecise data. The important point is that the selection was substantial. Estimates from more complete sequences of frequencies during the declines in industrial regions provide figures in the 20–30% range, this time for disadvantage to *carbonaria* (Cook & Turner, 2008).

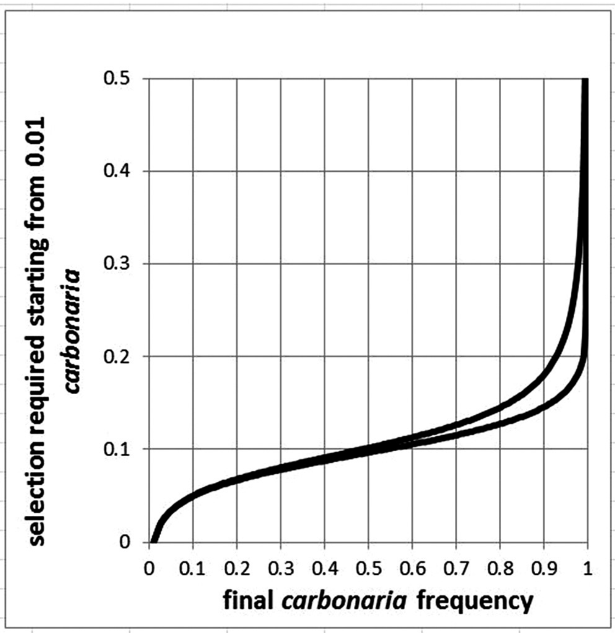

Figure 1. Selective advantages required to shift a frequency of 1% *carbonaria* in the peppered moth to a range of final values over 50 generations. Upper curve, calculated from allele frequencies; lower curve, from phenotype frequencies.

Another interest of Haldane was the way in which different selection in different places, together with migration, might generate spatial clines in gene frequency (Haldane, 1948). When relevant data became available, this paper influenced Bishop (1972) in his examination of how *carbonaria* frequency changed across north Wales, and the Welsh cline was a model system for May *et al.* (1975) when extending the theoretical analysis. The peppered moth was used by Haldane (1957) when he quoted Kettlewell (1956) as showing that in the course of selection as much as half of a population could be removed by predators. The resulting losses are a cost, setting a limit to the number of other characters that can be selected at the same time (sometimes called Haldane's dilemma).

A more detailed consideration of melanic peppered moths occurred at a Royal Society discussion meeting on the dynamics of natural populations, organized by E. B. Ford. Haldane (1956) referred to topics debated since the early observations, namely, the possibility that melanics were intrinsically fitter than typicals, accounting for their increase in frequency, that the expression of melanism may have evolved to increase dominance and that melanic heterozygotes may be fitter than homozygotes. Evolution of expression and non-visual fitness differences are not convincingly established for the peppered moth, but the possibility influenced thinking about the architecture of the genome. With regard to the last topic, Haldane pointed out that although selection was strong in Manchester, and that by the end of the 19th century the melanic frequency was very high, it was still not fixed, thus suggesting an equilibrium resulting from heterozygote advantage. The alternative was that typicals migrated into the area. That was rejected at the time. Later evidence, including a weak pattern of isolation by distance at microsatellite loci and wind dispersal of eclosing larvae, which suspend themselves on silk threads, indicates much greater movement than formerly believed (Liebert & Brakefield, 1987; Saccheri *et al.*, 2008). Many of the apparent anomalies in frequency distribution can be accounted for if densities are generally relatively low and migration high.

More data now exist relating to the rapid decline in melanic frequency since the 1960s. The largest sequence is from the Clarkes' site on the Wirral between 1959 and 2002 (Clarke *et al.*, 1990, and elsewhere; Cook, 2018). During that period, the melanic frequency fell from 94.2 to 2.7%. This can provide evidence on heterozygote advantage, because during the melanic decline the fraction heterozygous must become progressively greater. If the allele frequency of typical is estimated as the square root of the frequency of the typical phenotype then there would have been ~40% heterozygous melanics at the start and 98% by the end. Estimates of selective advantage to typicals made by comparing typical frequencies in successive generations assume the two melanic genotypes to have equal fitness. If, in fact, heterozygotes were fitter than *carbonaria* homozygotes, we should therefore expect a decline in the estimated typical fitness. Over the period of the survey, the yearly estimated advantage fluctuates widely, but the trend in relation to heterozygote frequency, and to date, is upward rather than downward. Improvement in the environment could be involved (Clarke *et al.*, 1985). Immigration of typicals, which were at a high frequency a few kilometres away, might also have contributed. Heterozygote advantage is not indicated. Testing for it in the few examples of temporal change then available was introduced by Philip Sheppard (Clarke & Sheppard, 1963, 1966).

BOTTING AND THE PEPPERED MOTH

In 1960, Gary Botting's exhibit on hybridizing silk moth species won first prize for biological science at the United States National Science Fair. As a result, he was sponsored to go on a world lecturing tour, which in 1961 took him to India, where he (and his travelling companion, another prize winner), met Haldane and Helen Spurway. This encounter ended in broad farce, when the American sponsors and some of the Indian hosts prevented the two young scientists from taking up a dinner invitation with Haldane, on the one hand, because there was a fear of Haldane teaching them some Marxism (see also Haldane, 1964), and on the other hand, because Haldane's abrasive style had become increasingly irritating. A thoroughly furious Haldane then announced a hunger strike and resigned from the Indian Statistical Institute. This episode was well publicised at the time and is reported in the Wikipedia entries on Botting, Haldane and Spurway (1, 2, 3). It is described with wit and elegance by G. Botting (in Botting & Botting, 1984) and in abbreviated form in the introduction by T. Gagnon to the poetry collection by Botting (2016). Botting's original account provides a sympathetic portrait of the ailing, injured and soon-to-be terminally ill Haldane.

During Botting's visit, Haldane, knowing that he was (at that time) a devoted missionary for the Jehovah's Witnesses, invited him out birdwatching at dawn in Kolkata zoo, to observe the great diversity of birds flying above the river; Haldane remarked on the impossibility of shipping all those species on Noah's Ark. This is well referenced in the Wikipedia entries (2, 3), citing both Botting & Botting (1984) and Gagnon (in the book by Botting 2016). For his part, Botting severed his relationship with the Witnesses long ago and now broadly accepts evolutionary theory (1).

Some further reports in Wikipedia, however, appear to be citing conversations with Botting for claims that are not in either of these two sources. Thus, under Spurway (3), and with reference only to Hooper, there is: 'Decades later, E. B. Ford and Bernard Kettlewell … attempted to capitalize on the supposed evolutionary adaptation of the peppered moth. Kettlewell apparently fudged his data to obtain results that approximated Haldane's 1924 statistical calculations.' Under E. B. Ford (4), we have: 'Haldane, who did not like Ford, was of the opinion that Ford and Kettlewell had attempted to capitalise on the supposed evolutionary adaptation of the main two variants of the peppered moth, for which Haldane, as early as 1924, had predicted the statistical probability of rate of change from light to melanic forms as an example of classic Mendelian genetics.' Under Kettlewell (5): 'J.B.S. Haldane was of the opinion that Kettlewell had attempted to capitalize on Haldane's own observations, made as early as 1924 …

In 1961, Haldane and his graduate student (and later [sic] wife) Helen Spurway told Canadian lepidopterist Gary Botting that they questioned Kettlewell's data since it too "nicely" approximated Haldane's 1924 statistical calculations.' In both cases, the Botting and Gagnon sources appear to be credited. The entries on Kettlewell, Spurway and Ford all refer to eating live moths to test their palatability. This strengthens the impression that similar extra material has been inserted into the pre-existing texts, with some of the material about eating moths being derived apparently from Hooper.

As a clarification of what is said in the original published sources, Gary Botting (personal communication, 2019) has explained why discussions with Haldane and Spurway moved to debating industrial melanism, which Botting had been aware of from the popular science and entomological literature, especially Kettlewell (1959) (later condemned by the Witnesses as 'apocryphal'). At that time, Botting regarded industrial melanism not as evidence for Darwinian evolution, but as evidence of the very rapid evolutionary change needed in the Witness's account of the Flood, to get around the problem of accommodating all the world's species on the Ark.

Botting (Botting & Botting, 1984) therefore countered Haldane with the established orthodox proposal that only two of each 'kind' of organism had been carried on the Ark, and that these had then proliferated and speciated. 'Kind' here is something like a whole Linnaean genus, or a modern family or even suborder. This is now regarded as scientifically ridiculous, but depending on one's Biblical chronology (Witnesses do not use the Ussher estimate) there may be an allowed time of many thousands of years (Botting & Botting, 1984). As Botting recalls, 'Haldane laughed heartily at my suggestion that rapid adaptation across a species over a period of 50 years (let alone 5000!) was "proof" of the [Witness's] version of post-Deluge speciation' (G. Botting, personal communication, 2019).

This part of the conversation between Botting and the Haldanes does not appear in any of the hard-copy sources, but is variously in the Wikipedia entries (2–5). By their nature, these entries are anonymous, potentially ephemeral and perhaps scrambled by the ongoing editing and counter-editing that is essential for Wikipedia. 'Editors' cannot necessarily be distinguished clearly, and they are also obliged to use pseudonyms. We can, however, treat them as a valid base for discussion, considering that much of the scientific literature is now published only on-line (albeit in a more stable form) and that the often significant contribution of the referees is frequently anonymous.

Two of Haldane's reported statements (above) are of interest: that he felt the work of Ford and Kettlewell had 'capitalised' on his paper of 1924, and that he (and Spurway) felt that Kettlewell's results were 'too neat a fit' to Haldane's 1924 estimate of the strength of selection in favour of the melanic. These statements are confirmed by Botting (personal communication, 2019). They appear in Wikipedia, juxtaposed or welded to suggestions of fraud apparently quoted from Hooper (2002). It is important to note that the various Wikipedia pages (2–5) were originated between 2002 and 2008, and therefore all post-date Hooper. Furthermore, despite the conflated wording of the Spurway entry, there is no explicit suggestion that Haldane thought the results were fraudulent, a point also confirmed by Botting (personal communication, 2019), 'certainly there was no talk of "fraud" or "fudging the data" '.

These two statements are discussed separately below.

Haldane's work 'capitalized' by Kettlewell and Ford

Here, there is a difference between US English and UK English usage. In UK usage, the allegation is serious and negative, implying illegitimate use of someone's ideas or results. In US usage, 'capitalize' merely denotes using someone's ideas or results as a platform or starting point for further developments and is a neutral or positive observation rather than a complaint. Botting & Botting (1984: 73, footnote) use 'capitalize' in this exact way only a few pages on from a discussion of the question of speciation. The statement that Kettlewell and Ford's work followed Haldane's estimate of strong natural selection is true and accepted both at that time and now, and the Ford–Kettlewell publications cite Haldane. On balance, Haldane may simply have drawn Botting's attention to his contribution; alternatively, perhaps he felt that the wider world had not fully appreciated his work. Ford and Kettlewell tended to see the whole matter in a very wide context and to think of the question as founded in entomology and natural history pre-dating Haldane's mathematical contribution.

Kettlewell's 'too nice' approximation to Haldane's estimate

The estimates Kettlewell had from his predation experiments do not measure selection in the same way as Haldane's estimate based on generational change; other influences on life expectancy would also be involved. Haldane was aware of this, as confirmed by Hooper (2002: 177–178), where he is quoted as writing to Kettlewell in 1956: 'One would want to know what the extra mortality of T [typical] is per day, and also what fraction of eggs are laid on the various days of life, and what fraction of successful copulations by males take place on the various days of life.' Later, Haldane (1964) wrote of the spread of *carbonaria*: 'I calculated that it conferred a selective advantage of about 50 per cent on its carriers. … Kettlewell has now made it probable that, in one particular wood, the melanics have at least double the fitness of the original type.' And in a valedictory piece published after his death, he wrote of the selection estimate in his 1924 calculation, 'This was regarded as ridiculously high, but 30 years later Kettlewell found a slightly higher figure in field studies' (Haldane, 2017).

Botting (personal communication, 2019) recalls Haldane as saying that he felt 'the significance of Kettlewell's results confirming his calculations of 30 years earlier as "too pat", which Helen interpreted as "too nice" in the sense of too convenient for Haldane to feel comfortable with the results'.

It is here not entirely simple to figure out what Haldane and Spurway actually meant. Haldane could not have been complaining of 'too good a fit' in the conventional sense used for examples, e.g. involving Mendelian ratios in which there is a suspicious recurrence of χ^2 values with exceptionally high probabilities, because this is not that type of data. It would be suspicious if the two relevant values of the selection coefficient were the same to several decimal places, but clearly they are not; Kettlewell's estimate is detectably larger than Haldane's. The suggestion of 'fudged' data (in the Spurway entry) is clearly derived from Hooper.

We suggest that the most likely explanation is that Haldane was taking the view that he had taken when writing to Kettlewell in 1956 (above), that his estimate of selection subsumed many more factors than the visual bird predation estimated by Kettlewell, and that any attempt to claim that Kettlewell had vindicated Haldane's estimate would be simplistic. The aim of Kettlewell–Ford was rather to show that birds were a selective agent selecting in the appropriate direction. Overall, there is also the possibility that Haldane was being humorous, as was his wont, and it would not be surprising if he was also feeling irked by Ford and his friends; the mutual distrust at a personal and political level is no secret.

CONCLUSION

The scientific questions

The various accounts of the Haldane–Botting meeting are irrelevant to any questions about the validity of the overall scientific interpretation of work on industrial melanism, because this depends on the multiple replication of experiments on selective predation; flaws in any one set have a minimal effect on the overall interpretation.

The question of fraud

The Wikipedia accounts do not explicitly claim that Haldane said that the Ford–Kettlewell work was fraudulent; and Haldane made no such claim.

Haldane's views

These are historically important, given Haldane's scientific stature and the fact that he was expressing them so soon after the publication of the Ford–Kettlewell experiments. Haldane was, to judge from subsequent events over 'the dinner', in an irritable frame of mind, perhaps made worse in some way by Ford and Kettlewell's work. Given that Haldane and Ford did not get on, this is not surprising, but it is likely that of much greater significance was his interest in natural selection as a complex phenomenon worthy of theoretical elucidation.

Haldane was a polymath, a popularizer and a stimulator of other scientists, who made brief, insightful contributions in a wide variety of fields. Although he did no direct work on peppered moths, the 1924 paper provided the basic methodology for many subsequent studies. His contributions on heterozygote advantage and on dominance and its origins were influential. Although, or perhaps because, the peppered moth seems such a clear example of adaptive response, the work has always attracted criticism. This is healthy, as is public discussion of science within the multiple-editing system of Wikipedia. Wanton allegations of fraud are not healthy, because it is possible to allege that any piece of empirical work is fraudulent and it is extremely difficult for scientists to defend themselves if 'guilty until proved innocent'. Fortunately, this has not happened in the present case. However, such allegations can rather easily become embedded. An example concerns discussions of how settling behaviour by peppered moths might influence selection by predators. These were picked up by critics unfamiliar with the field and led to a spate of negative comment, including claims that the work was worthless (Wells, 2000; see Young, 2004; Cook *et al.*, 2012 and elsewhere). Such attacks have continued to the present. As new information has become available, new objections have been invented, now reaching the point where the same story is run twice in the same year on the same site under different authorship (Hunter, 2016; Wells, 2016).

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