

SU835074, at mvl, 19.vii.2015 (Robert Eadie); Titchwell RSPB, West Norfolk (VC 28), TF 74, at mvl in a small woodland at edge of coastal marshes, 22.vii.2015 (Paul Cobb); and finally again at Tyrwaun, Pwll, on 1.viii.2015 (Ian K. Morgan).

The species is associated with deciduous oak trees *Quercus* spp. and it is of interest therefore that the Bursledon record was made beneath such a tree. However, for Titchwell Paul Cobb informs me that “so far as I know there is no oak whatsoever in that little wood, I certainly didn't see any, and no oak woodland (or woodland including oak) within 2½ miles, and very little in the way of hedgerow oaks”. There are oaks in the general vicinity of the location of the Welsh records, though Ian Morgan tells me that there are none within 500 yards of the actual site.

It is unclear from the limited information currently available whether these reports relate to primary immigrants, residents that have recently established themselves as a result of immigration or longer-term residents that have simply been overlooked. That said, primary immigration is significantly less likely in Wales and together with the fact that Carmarthenshire may not be the best recorded county for lacewings this might suggest an overlooked population. On the other hand, immigration from Europe is far more likely to be the original source of any population that is established in Hampshire, Sussex or East Anglia. The 2013 report of a female from Martlesham was noted at the time as being coincident with moth movements. Sean Clancy, who maintains the definitive national record of immigrant moths, tells me that for 2015 insect immigration was at an exceptional and sustained level throughout July, with high numbers of a wide range of immigrant species including *Eublemma parva*, *Spodoptera exigua*, *Heliothis peltigera* and *Macroglossum stellatarum* in particularly unprecedented numbers. In association with these were records several exceptional immigrant rarities, most notably the second and third UK records of *Aedia funesta* and the fourth and fifth UK records of *Stegania cararia*, both these species occurring around the time of the first record of the lacewing and the fifth and sixth UK records of *Callopietria juvenina* which arrived during the period between the second and third lacewing records.

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### **A Response to some criticisms of the ‘Selection Theory’ of industrial melanism**

I have followed with great interest the recent fiery exchanges between Dr Geoffrey Fryer and Professor Laurence Cook in the pages of *The Linnean*, on the subject of industrial melanism. However, given the rather exasperated tone of Cook's (2014) last reply, I feel I must step into the breach and place myself firmly upon his side. This debate has been a long running one, and a great many of the arguments and hypotheses advanced today have their roots in the late nineteenth century (eg. Tutt, 1891). Yet the importance of this question has not diminished, nor is it confined to a narrow academic context. Across the world, the rise and fall of the melanic form of *Biston betularia* is

held aloft as a textbook example of natural selection in action, and is taught to millions in schools as such. It is highly important, therefore, not only that the available evidence and the conclusions drawn from it are thoroughly discussed and criticised, but that this information continues to be brought before the entomological public.

The orthodox explanation for the widespread occurrence of melanism among various species of Lepidoptera after the Industrial Revolution might conveniently be termed the “selection theory”. It holds that industrial pollution, such as soot and smoke, brought about a general blackening of the environment in areas possessed of heavy industry, which caused natural selection, via differential avian predation, to favour darker variations of cryptic, day-resting species of Lepidoptera. However, Fryer (2012, 2013) claims that the hitherto obscure observations of the naturalist George Porritt (1848-1927) refute this. He argues, from Porritt’s work, that many, if not all, of the species which became melanic are not exposed to predation by birds. He asserts that the rapid rate at which some species became melanic and the subsequent spread of melanic individuals into clean, unpolluted countryside, are facts which are incompatible with a selection-driven, background mismatch process. Rather, Fryer suggests that the phenomenon is better explained though the induction of melanic mutations by mutagens present in the pollution itself, and cites the experiments of Harrison and Garrett (1926). In contrast, Cook (2013, 2014) maintains that there is no evidence of melanic mutations being induced in any species, and that were this the case it would have undoubtedly been noted by breeders during the nineteenth century. Further, he contends that the notion of induction cannot be reconciled with the fact that, in *B. betularia*, with the decline of heavy industry and the subsequent decline in levels of pollution, the numbers of the dark *carbonaria* form declined while the intermediate *insularia* form temporarily increased in abundance, which is highly suggestive of the levels of pollution differentially affecting the fitnesses of the two forms. The work of Kettlewell (1973) and Majerus (1998) together, he argues, provide extremely strong evidence that industrial melanism is produced through selection-driven Darwinian evolution.

It is my firm opinion that, given due consideration of the evidence before us, it is impossible to accept that industrial melanism in the Lepidoptera was brought about by the induction of melanic mutations. Indeed, the dismantling of the “selection theory” would seem to be essential if Fryer’s alternative is to be erected in its place. It is my intention here, therefore, to deal with what I see as the two major thrusts of his assault against it.

Firstly, I must address the point rolled out by Fryer again and again throughout both of his articles that differential predation by birds cannot explain the occurrence of industrial melanism because birds are simply not predators of the species involved. He writes that: “[...] as Porritt made absolutely clear, some species hide by day and are not subjected to any predation by birds”; there is “scant unequivocal evidence to support it [avian predation]” (Fryer, 2012); “the species concerned were never exposed to selection”; “Porritt [...] found little to suggest that moths were much taken as food by diurnal birds”; “[s]ome species which became melanic were certainly not even exposed to natural selection [...] as they spend the day completely hidden from

potentially predatory birds”; “as adult moths they are almost never exposed to *any* selective predation” (Fryer, 2013). Again and again this assertion is made and it is unclear to me whether Fryer in fact subscribes to the same view as the American naturalist Waldo McAtee (1883-1962), who fiercely contended that Lepidoptera were never eaten by birds at all (Forbes, 2011). In any case, the suggestion seems to me to be nonsensical and I think it can be shown to be so purely theoretically. When we consider the colouration of British moths, the first thing which must surely strike us is how drab the overwhelming majority of them are. Most often we encounter what might well be called *natural* tones; browns, blacks, creams etc. So, why are they not often clad in the bright and gaudy colours of many of their day-flying relatives? Simply, as they are nocturnally active, they must sit still throughout the whole of the day and consequently rely upon *crypsis* for protection. Were they dazzling yellow or bright red in colour they would stand out a mile wherever they chose to rest and would undoubtedly be picked off as an easy meal by predators. Indeed, anyone who doubts the fact that moths are coloured in such a way that they are not easily seen is invited to wander into a woodland in summer and try to find as many as possible by searching alone. Run a moth trap in that same woodland by night and swarms of moths will descend. It takes years of field experience to be able to find appreciable numbers of moths by searching and, I am sorry to say, the advent of powerful MV moth traps has been to the detriment of the abilities of modern-day lepidopterists in this area, compared with our Victorian and Edwardian predecessors.

I must confess that this may not be a very convincing argument for some people, for it is certainly not an experimental one. However, it is my view that no one who has studied moths can deny that the form, pattern and colouration of their wings have been driven relentlessly by predation. Indeed, once it is accepted that birds would almost certainly eat obvious moths then all else follows; predation of moths by birds must still then occur, constantly honing and refining cryptic patterns and colours to an ever changing environment. Indeed, Fryer (2013) all but accepts this when, discussing selection experiments on *Biston betularia*, he writes, “[m]oths displayed on a background that renders them conspicuous will be taken more frequently than those displayed on a background against which they are inconspicuous, so results are always predictable.”

As I say, such an abductive argument may not satisfy some, but it is bolstered by the fact that it does not stand alone. Many authors have discussed the role of predation by birds on Lepidoptera and provided evidence for it; Barrington (2012) discusses the role of avian predation on *Coenonympha tullia*; Collenette (1935) lists page after page of recorded incidences of birds preying on butterflies; Majerus (1998) and, particularly, Kettlewell (1973) provide yet more evidence that this is a real phenomenon and a greatly powerful one in the evolution of butterflies and moths.

Fryer also cites some specific examples of species which are supposedly not exposed to avian predation and it is only proper to examine these individually. He asserts that the “females of *Apocheima pilosaria* and *Agriopus marginaria* [became melanic], neither of which [...] are *exposed* [my italics] to predation by birds by day” (Fryer,

2013). I simply refute this outright. The females of the former are apterous and during the day hide on the trunks of trees while the males “may be found on fences and tree-trunks” (Skinner, 2009); just the sort of places which would become blackened by soot and smoke and where colour mismatches would no doubt be prominent to would-be predators. The females of *A. marginaria* have their wings much reduced in size so that they are also flightless. Skinner (2009) states, “[t]he male... is more readily found sitting on the stems of bushes and the lower branches of trees. The flightless female may be found, sometimes commonly, by searching the trunks of oak and other trees”. Tutt (1902) confirms this view; “the females of *H. marginaria* [old genus] are to be found freely on tree-trunks”. Again, the trunks and branches of trees are the areas which would typically become blackened by industrial pollution, as described in detail by Kettlewell (1973), and upon which any pale coloured moth would be *highly* conspicuous. Fryer (2013) then cites *Colostygia multistrigaria* which, he writes, “spends the daylight hours hidden among grasses and other vegetation and is ‘absolutely out of evidence until dusk’, so its colour is irrelevant to protection”. Tutt (1901) states that “*Larentia multistrigaria* [old genus] usually rests at the foot of palings, &c., in its haunts, where it is almost hidden by the herbage.” Typically, this moth is of a mottled grey colour which would be extremely difficult to spot among vegetation *but* were that vegetation to become darkened by industrial pollution it would be very different; anything pale would undoubtedly become prominent. Fryer (2013) asserts that the adults of *Odontoptera bidentata* are “so well hidden that they are almost entirely free from predation by birds” and again, this is simply not true. From the literature I can find two general resting positions ascribed to this species; Tutt (1901) says that “[o]ne finds the species that simulate dead leaves hanging on bushes – [...] *Odontoptera bidentata*, &c. These are much less rarely taken on the trunks” while Skinner (2009) states that it is “[f]ound frequently at rest on walls and fences” and Kettlewell (1973) supports this view to an extent; “*G. bidentata* [old genus]... is normally a trunk-sitter”. In either case, all of these species of moths rest during the hours of day in places which are *not* so tremendously inaccessible or well hidden that a bird engaged in searching for food could not possibly find them. Furthermore, it seems elementary that melanic individuals would most certainly possess a cryptic advantage in an industrially polluted environment, where the trunks and foliage of trees and the ground-level vegetation, among which these species rest, are blackened.

Repeatedly, Fryer denigrates the ingenuity and searching ability of birds and magnifies the cryptic patterns and hiding abilities of moths. Can he not see that the one cannot be without the other? The only reason moths possess such exquisite cryptic patterns and conceal themselves so well is because of the selective pressure of predators! Such a misunderstanding leads to absurd statements from Fryer (2013) such as “*Odontoptera bidentata* and other *cryptic* [my italics] species that are essentially immune from it [predation]”; I would be fascinated to know how Fryer proposes these species gained their cryptic colouration if they are immune from predation. The argument that moths hide during the day in such a way that they are not preyed upon significantly by birds and that, hence, selective predation by birds

could not be the “central driving force” (Cook, 2013) of industrial melanism, is simply incompatible with the evidence before us.

Fryer also writes about the speed at which some species underwent changes in colouration during and after the Industrial Revolution and asserts that the populations of many species became melanic at a rate far in excess of the traditionally cited example, *Biston betularia*. He then dismisses differential predation as effecting this change by simply stating that “[s]election takes longer”. I am not a great admirer of sweeping generalisations and I think that this particular one is not justifiable under any circumstances. Selection, like all biological processes, is a dynamic one, and dependant on an enormous number of variables; for example, individual anatomy and the particular habits of the species in question. I have no doubt that the species involved did become melanic at different rates from one another, but this in no way disproves that the change was brought about by selection; indeed, it is what should be reasonably expected. Take, for example, *Apocheima pilosaria* and *Agriopis marginaria*: Fryer (2012) states that not only did these species become melanic more rapidly than *B. betularia* but the females did so quicker than the males, in some five or six years. Perhaps this is not so surprising when we consider the fact, already alluded to, that the females of these species are flightless. Perhaps their reduced mobility hinders their ability to conceal themselves during the day and, given a background which makes them highly conspicuous, the selective pressure upon the females could be slightly greater than upon the males? It must also be borne in mind that these species are on the wing (so to speak) in the winter and the deciduous trees upon which they rest are devoid of any leaves. At this time of year, bird populations are under great strain themselves to find enough food and whatever insect life is available will be most assiduously searched for. Therefore, the increased exposure against the blackened bark and branches, and the heavy selective pressure of hungry winter birds might explain the increased rapidity with which these species became melanic.

In spite of any arguments as to why this might have occurred, Fryer still contends that the change occurred too quickly to have been brought about by natural selection. Let us examine this view mathematically. Suppose there exists an isolated population of moths in an area of woodland where a dominant, melanic allele *A* occurs at a frequency of one percent. This would mean that initially something like two percent of the population would display a melanic phenotype. Then we introduce industrial pollution to our woodland. Assuming we have three different genotypes - *AA* and *Aa* which are melanic individuals and *aa* which are typical individuals – it is possible to calculate the relative proportions of each genotype (and hence, the frequency of each allele) in subsequent generations given a particular selection coefficient, *s*, against the *aa* genotype. Where the frequencies of alleles *A* and *a* are *p* and *q*, respectively, the frequency of each genotype in the next generation, after selection, is  $p^2/W_{mean}$  for *AA*,  $2pq/W_{mean}$  for *Aa*, and  $(q^2(1-s))/W_{mean}$  for *aa*, where  $W_{mean}$  is the mean fitness of the population  $(1-sq^2)$ . From this I have calculated that, given an *s* value of 0.6 for *aa*, within six generations melanic individuals would comprise approximately 85% of the entire population. In addition, I have run several simulations on the University

of Washington's excellent PopG genetic software which yielded a slightly more conservative estimate of around 90% of the population being melanic after ten generations, given an  $s$  value of 0.6 for  $aa$  (based on a population size of 1000). This computer program more realistically takes into account the effects of genetic drift. For a univoltine species of Lepidoptera each generation would translate into a single year.

The figure of  $s=0.6$  (a 'selective disadvantage' of 60%) is not unreasonable, given that Kettlewell (1973) talks about regularly occurring selective advantages of 30 to 60 percent. Simply to state "[s]election takes longer" is entirely unjustifiable, for the rate at which it operates is entirely dependant on the degree of the selective advantages or disadvantages of the traits involved; that is to say, the greater the pressure of natural selection the greater the speed of the evolutionary change.

I believe that the argument advanced by Fryer in his two papers, and by many before him, that industrial melanism is due to the induction of mutations by pollution, is fundamentally based upon a dissatisfaction with the idea of its having been brought about by differential avian predation and the perceived inability of natural selection to accomplish it. I hope that I have successfully refuted these notions here and in so doing demolished the very basis for the mutagen theory.

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