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FINE TUNING THE PEPPERED MOTH PARADIGM

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The trouble with classic examples of evolution is that they continue to evolve. Once an example of a major principle becomes widely accepted, it gets put into a museum cabinet for public display. Ineluctably, new information accumulates outside the cabinet, but it can't get in because the cabinet is locked. Ultimately the new information demands attention. Interested parties call for revisions. To follow that route requires understanding the true nature of the problems and the remedies. Curators of museum displays, working with limited resources, may decide that some of the old classics have been around long enough, and rather than adjust to vague controversies, it is simpler to replace a flawed display entirely than to fix it, much like discarding an old car that needs too much work to keep it running. Let's get a new one. Such are the prescriptions, at least from some quarters (e.g., Coyne 1998, Sargent et al. 1998), about the classic textbook example of evolution by natural selection: industrial melanism in peppered moths.

Sargent et al. subvert the traditional explanation for industrial melanism by presenting an equivocal analysis of the evidence. Coyne laments that our "prize horse" of examples is in bad shape in his review of a recent book, *Melanism: Evolution in Action*, by Michael E. N. Majerus (1998). Although Majerus assesses the bulk of the literature and controversy that has accumulated since Kettlewell's (1973) *The Evolution of Melanism*, he could hardly agree less with Coyne or with Sargent et al. that the basic story is built on a house of cards. Majerus argues convincingly that industrial melanism in the peppered moth remains among the most widely cited examples of evolution by natural selection for two reasons: First, the basic story is easy to understand. Second, the evidence in support of the basic story is overwhelming.

Majerus has done considerably more than write a book about industrial melanism. His ambitions were broader, although more modest than the title suggests. The book is divided into 10 chapters with some general features of melanism, genetics, and evolution spread across the first 4. The last 4 chapters catalog examples of melanism in various Lepidoptera, and in ladybird beetles, with a call for future research as the book's climax. Readers interested specifically in industrial melanism in peppered moths, however, can skim or skip all of those chapters and focus on the middle two. Indeed, chapters 5 and 6 should be read carefully by all teachers of evolutionary biology. Certainly not all active workers in this field would agree with Majerus' analysis in its entirety, nor necessarily endorse his interpretations and speculations, but his account will illustrate that the classic story is still being written and revised as research continues. What Majerus tells us is that this is a work in progress.

Early History

Majerus' treatment of the early history is thorough. Until about the middle of the last century peppered moths were effectively monomorphic throughout the United Kingdom. The common name derives from the typical phenotype (the "type" specimen) which is covered in white scales "peppered" with black over the body and wings. Melanic forms have conspicuously more black scales than do typicals; those uniformly covered in black are called *carbonaria*. Intermediates are also known; these range between the two extremes, and are collectively called *insularia*. The phenotypes result from multiple alleles at a single locus that approximate a dominance hierarchy with the *carbonaria* allele as top dominant and typical as recessive (Lees and Creed 1977). Because *insularia* is fairly uncommon in most regions where industrial melanism has been studied, it has received relatively little attention in general treatments of the subject. Throughout this discussion melanic refers to *carbonaria* unless otherwise specified.

It's not certain when and where the first melanics appeared, but the traditional history begins in Manchester, circa 1848. That melanics have also appeared elsewhere prior to this in the UK, and later than this in Europe and in North America, suggests that the Manchester melanic was not a unique event. By the turn of the century, most specimens of peppered moths examined in the vicinities of British industrial centers were melanics, reaching proportions as high as 98%. With only one generation per year, the nearly complete reversal in phenotype frequency, from monomorphic pale to almost monomorphic black, was astonishingly rapid.

Majerus has always paid proper homage to J. W. Tutt, who in 1896 spelled out the basic story much as it is taught today. Few other reviewers have recognized Tutt as the author of the classical explanation of the evolution of melanism in peppered moths by natural selection. A notable exception is Berry (1990) who reprinted the essentials of Tutt's account. Indeed, it was Tutt who suggested that the "speckled" form of the peppered moth gains protection from predators by its resemblance to lichens. In manufacturing regions, however, where the lichens have been destroyed by pollution and the surfaces of trees blackened by soot, the peppered forms have fallen victim to bird predators while the formerly rare black forms of this moth species have increased in numbers because they escape the attention of birds and pass their traits on to their "children." It is curious that Kettlewell, who championed this account, practically to the letter, scarcely acknowledges Tutt as its author other than to say Tutt "preferred an explanation on the basis of natural selection." Perhaps it's just as well that Majerus sidesteps this historical slight. The subject has been treated elsewhere (Owen 1997).

From Tutt's time until a half-century later when Kettlewell rekindled interest in this subject, little actual work was done. Majerus reminds us that in 1924 Haldane calculated the selection coefficients necessary to account for the spread of melanic peppered moths, and he also reviews the several papers by Heslop Harrison written during the 1920s that challenged a Darwinian explanation. 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. All of this work was severely criticized by contemporaries who attempted to repeat the experiments, but failed to reproduce the results. Whatever the correctness of that work might be, none of it has proved relevant to peppered moths. Nevertheless, modern reviewers (e.g., Sargent et al. 1998) continue to resurrect these arguments as if they are worthy of serious consideration in this context. It certainly is true that peppered moth caterpillars (larvae) develop different colors in response to environmental stimuli (they come to match the colors of the twigs of their host plants) (Poulton 1890), but it has never been demonstrated that environmental stimuli experienced at any stage in development can induce melanism in adults. The Mendelian inheritance of the melanic forms of adult peppered moths has been repeatedly demonstrated (see Creed et al. 1980 for an analysis of published data reporting 12,569 progeny from 83 families). Clearly, the recent attempts to extend induction arguments to the evolution of melanism in peppered moths are unfounded.

Predation Experiments

The Kettlewell era of peppered moth research began in the early 1950s when he initiated experiments to test Tutt's hypothesis that selective predation by birds drove the evolution of melanism (Kettlewell 1955a, 1956). Majerus criticizes the design of these experiments, but misses the mark in identifying solutions.

Kettlewell's stated objective was to determine whether or not birds ate cryptic moths at rest on their normal backgrounds, and whether, in the case of polymorphic moth species, the birds ate them selectively. His experiments included 3 main aspects: 1) quantitative rankings of camouflage effectiveness (degree of conspicuousness as judged by human observers) of pale and melanic peppered moth phenotypes placed on various backgrounds; 2) direct observations of predation by birds on moths placed onto tree trunks; 3) recapture rates of marked moths released onto trees in polluted and unpolluted woodlands.

Majerus points out that recent work on birds shows that their ability to see into the UV spectrum indicates that the visual acuity of birds is greater than that of humans, and that we should bear this in mind when undertaking experiments on rest site selection by moths, or predation on moths by birds. Kettlewell did not have benefit of this information, nor did he argue that we see as well as birds, but he did demonstrate convincingly that the moths adjudged most conspicuous by humans were the first moths to be eaten by the birds. His initial work was done in an aviary so the order of consumption could be followed. His conclusion that conspicuous insects are more vulnerable to predation than are inconspicuous insects was in complete agreement with the corpus of work that had already been published on the adaptive coloration of animals (see review by Cott 1940), and was consistent in direction with the population frequency data that documented melanic peppered moths were common in habitats blackened by industrial soot and rare in unpolluted habitats.

Among the criticisms of Kettlewell's original predation experiments (and these were first raised by Kettlewell, himself) is that the numbers of moths he released on trees created

artificially high densities, and that the moths were put onto the trunks of trees which may not be where they actually pass the day exposed to predators. Inasmuch as the high density problem was addressed by others in follow-up studies (e.g. Clarke and Sheppard 1966, Bishop 1972), Majerus' strongest criticism of these experiments is that Kettlewell used the wrong part of the tree. As to where peppered moths actually do take up daytime resting sites, Majerus himself reports by far the greatest number of sightings among moth workers. In his 34 years of moth hunting, Majerus has discovered 47 peppered moths at rest by day in the wild. (The large samples of peppered moths used to calculate melanic frequencies in local populations come from operating light traps and assembling [pheromone] traps at night. It's rare, indeed, to find a peppered moth away from a trap by day even where the species is abundant.) Majerus separates into categories the position on trees where the moths were located (trunk, trunk/branch joint, branches). While the trunk/branch joint was the most common site, his data indicate that the moths do not all rest in the same place. As Clarke et al. (1994) put it: "Moths habitually resting in only one place will be habitually sought there." Mikkola (1984), based on his observations of moths kept in captivity, suggested that peppered moths hide by day on the underside of branches in the canopy. Grant and Howlett (1988) showed that captive moths move to whatever end of their holding pen light enters (if the light enters from the bottom of the pen, the moths will sit on the floor). Perhaps Mikkola's conclusion is correct, but perhaps his evidence is an artifact of his apparatus. In truth, we still don't know the natural hiding places of peppered moths.

Majerus sees it as "crucially important" to learn the natural resting place of peppered moths if we are to assess fitness differences between the morphs based on crypsis. This seems reasonable; however, in his call for future research Majerus proposes using "two large flat transportable surfaces to act as artificial backgrounds to place the moths upon" with surfaces made to match the colors of the moths. He then proposes conditioning birds to feed from these boards, then putting pale and melanic moths on the boards to record how long it takes birds to find and eat them. I fail to understand how such an experiment will tell us anything that hasn't already been demonstrated repeatedly: namely, that conspicuous moths are easier to find. If the fault with Kettlewell's experiments is that he did not use the right parts of trees to release his moths, I cannot imagine how the use of feeding trays is an improvement. Cook (1998) correctly reminds us that Kettlewell's complementary experiments in polluted and unpolluted woodlands compared the relative success of different moths on the same parts of trees in different areas, not different parts of trees in the same area.

Morph Specific Behavior. Kettlewell proposed that pale and melanic forms of peppered moths actively seek out *different* resting sites. To test this idea, he put typicals and *carbonaria* into a barrel lined with black and white strips of card, and he recorded where they had settled. (The moths are active at night, but remain motionless, unless disturbed, during the day.) From these "barrel" experiments, Kettlewell (1955b) reported morph specific behaviors: *carbonaria* tended to settle on black, and the typicals tended to settle on white. Kettlewell suggested that the moths accomplish this by comparing the darkness of their body scales to the surface reflectance of the immediately available substrates and that they come to rest where the contrast between the scales and the substrate is least "conflicting." The gene causing melanism would therefore have a

pleiotropic effect on the behavior if moths used the "contrast/conflict" mechanism in background selection. This would facilitate the evolution of melanism because newly arisen melanic variants would automatically rest on available matching surfaces.

Kettlewell didn't actually test the contrast/conflict mechanism; however, Sargent (1968) attempted to do so by painting the scales of black and white moth species in contrasting colors. The species he used were not fooled by this treatment, thus Sargent concluded that the behavioral differences between the species had a genetic basis. Kettlewell dismissed Sargent's work and conclusions as irrelevant to peppered moths, not because he used different species, but because he used two different *monomorphic* species: one monomorphic white, the other monomorphic black. The correct test for morph specific behavior within populations requires that a *polymorphic* species is used, not separate species with different evolutionary histories. Grant and Howlett (1988) attempted to resolve the contrast/conflict controversy by repeating Sargent's experiments with polymorphic peppered moths caught near Liverpool, England. They found no evidence that typicals and *carbonaria* prefer to rest on different backgrounds. Majerus presents a skewed discussion of this work; despite a conspicuous absence of support that morph-specific behaviors exist, he speculates nevertheless about the possible mechanism that might account for the behavioral polymorphism as if it had been established. He does explore explanations for the contradictory results from various "barrel" experiments by other workers, including the possibility that Kettlewell's source of typicals and *carbonaria* came from different regions of the UK where the populations were essentially monomorphic for one variant or the other. If Kettlewell had in fact used moths from such populations, then his experiments suffered from the same problem as did Sargent's.

Moth Behavior and Predation Experiments. The most relevant aspect about moth behavior that we have learned from Kettlewell's barrel experiments and the experiments they inspired is that the moths "clamp down" at dawn. By the time birds begin to forage, night-flying moths have assumed their daytime resting positions, and in the case of peppered moths, they remain motionless unless disturbed. It is important to understand this in evaluating Kettlewell's predation experiments. Moths released during daylight hours do not behave normally, and if prompted to fly, they will settle quickly on just about the first thing they encounter. In my view, the greatest weakness of Kettlewell's mark-release-recapture experiments is that he released his moths during daylight hours. Kettlewell devotes considerable discussion to "release problems" created because he wanted to avoid having moths turned loose under the cover of darkness from flying directly into his traps before they had been exposed to predators that hunt by vision. It would have been much better had he released marked moths after dark on nights when traps were intentionally shut off. Such moths could then select their own hiding places and would either survive or fail to survive the following day before trapping begins. This solution might seem obvious and easy to recommend, but it's not easy to do. The return rate two days after release drops off enormously as a result of either mortality or dispersal from the trapping area. To get enough data for statistical comparisons requires releasing many moths, and to rear them from the egg stage requires feeding fresh leaves to thousands of caterpillars the year preceding the experiment. Few who haven't fed large numbers of growing caterpillars can appreciate how

labor intensive the task is. Still, the experiment should be done. And it should be done using only lab-bred specimens, not mixtures of lab-bred and wild-caught. (This is another potential source of error in Kettlewell's procedures; but see Bishop 1972).

Despite design problems, Kettlewell's predation experiments are still instructive. He used the same procedures in two distinctly different places, a habitat disturbed by pollution and an unpolluted habitat, and he got complementary results. His data, in both directions, were in complete accord with the directions predicted by the incidence of melanism in the regions. So, if he was wrong to use the trunks of trees in Birmingham, he was consistently wrong to use the trunks of trees in Dorset. If he was wrong to release the moths during the daylight hours in Birmingham, he was consistently wrong to release the moths at the same time in Dorset. His data, however, show that the variable of regional pollution made a significant difference as to which phenotypes of the moths better survived the conditions imposed by the experiments.

Kettlewell's aren't the only experiments that show this. Majerus recounts five other studies, using variously modified experimental designs, that corroborate fitness differences between the morphs in polluted and unpolluted regions. He also reviews some exceptions. Hindsight has enabled us to find fault with all of these experiments to varying degrees and has helped us to suggest future work. It is not true, however, that these experiments are so seriously flawed that their conclusions are invalid. The conclusion that conspicuous moths are more readily eaten by birds than are inconspicuous moths has been repeatedly confirmed. The findings from the grand bulk of the predation experiments are in qualitative agreement with the direction of changes in melanic frequencies documented among geographically separated populations of peppered moths.

Geographic and Temporal Variation in Melanism

Kettlewell's indelible legacy includes the national surveys he organized to document melanic frequencies in peppered moth populations throughout the UK. Majerus reviews Kettlewell's several approaches, but clearly his most effective method was to recruit amateur collectors. The results, illustrated by pie charts positioned on maps of the UK, show that high melanic frequencies corresponded well to the distribution of industry (Kettlewell 1958, 1973). The exceptions to the prevailing pattern have been accounted for by incorporating migration into the picture. On this point there has been mild debate because migration rates have been based on imprecise dispersal studies (chiefly involving adult males), and estimations of gene flow extracted from models which have attempted to apply selection coefficients based on predation studies. In addition, some data from lab broods hint that pre-adult viability differences may complicate the dynamics of frequency changes. Majerus argues the case well, but other opinions exist. The subject of genetic subdivision among *Biston* populations could benefit enormously from a molecular approach. These familiar techniques have been applied to almost everything that moves, except, it seems, to peppered moths!

Among Kettlewell's recruits to the cause of collecting population data is Cyril Clarke,

who began sampling at his home near Liverpool in 1959 (Clarke et al. 1994). Over the 40 years that followed, Clarke has collected over 18,000 specimens at this single location. Clarke's meticulously detailed records document a decline in melanic frequency from above 90% to below 10% in concert with a decline of atmospheric pollutants (SO₂ and soot) following the Clean Air Acts. The most recent national survey, organized by Denis Owen in 1996, 40 years after Kettlewell's first survey, shows convincingly that similar declines in melanism have occurred everywhere in the UK (Grant et al. 1998). Parallel changes in melanism have also occurred in the North American subspecies of the peppered moth, *Biston betularia cognataria*, again in concert with changes in regional levels of pollution (Owen 1962, Grant et al. 1996, 1998). While minor geographic anomalies within countries can be attributed to gene flow, the similarity of patterns between the British Isles and North America indicate parallel evolutionary changes that cannot be explained by anything other than selection acting independently on similar phenotypes in widely separated populations of the same species. On both continents, high frequencies of melanism and subsequent reductions correlate well to the same key factor: atmospheric pollution from regional industrial development and urbanization.

The Role of Lichens. Kettlewell most certainly subscribed to Tutt's view that typical peppered moths gain protection from birds by their resemblance to lichens, but he also allowed that other backgrounds could lend protection to typicals. "That the wild *B. betularia* population of Rubery [the polluted woodland devoid of lichens] contained as much as 10.14 per cent typicals is, in my opinion, due to the advantage of this form in the surrounding birch woods of which there were many in the neighborhood" (Kettlewell 1955a). As the story of melanism has been recounted and abridged, lichens were kept and birches were forgotten. Thirty years later Clarke et al. (1985) mentioned that the steady increase in the frequency of typicals in their area was occurring without any noticeable increase in lichens on the trees. They added however that regional reductions in the soot component of atmospheric pollution meant that the surface reflectance from tree bark, even in the absence of lichens, would be lighter. Grant and Howlett (1988) further suggested that well documented increases in abundance of silver birch trees following the establishment of "smokeless zones" in the region presented significantly modified habitats. In review, Clarke et al. (1994) cautioned "...that the role of lichens...has been overstated. This is not to suggest that where lichens do occur *betularia* ignore them as refugia; instead, our findings show that typical peppered moths are not dependent on the presence of lichens to thrive." The rise and fall of melanic peppered moths in southern Michigan also occurred in the absence of lichen succession (there the lichens remained abundant); but the changes in melanic frequencies were consistent with declines in levels of atmospheric pollution, including suspended particulates (Grant et al. 1996). Reflectance from the surface of tree bark is strongly negatively correlated with atmospheric levels of suspended particles (Creed et al. 1973). In no case have the authors who have questioned the importance of lichens offered this as evidence against selective predation on the moths by birds. Crypsis, it would appear, is equally convincing in the absence of lichens (see Fig. 2, Clarke et al. 1994, or Fig. 5, Grant and Howlett 1988). Yet, the mere suggestion that lichens might not be so important as we once thought is either dismissed as anecdotal (as Majerus has done in his book), or taken as evidence against predation as an important factor in the evolution of peppered moths (as Sargent et al. and Coyne

have done in their reviews). Both reactions place too much attention on the importance of lichens. Kettlewell's view wasn't nearly so extreme.

Evolution of Dominance

Kettlewell argued that the first melanics weren't quite as dark as they became over generations as the result of an evolution of dominance through the accumulation of background modifiers that affect the expression of a gene that produces a favorable phenotype. Majerus reviews Kettlewell's experimental work in this area, and cites problems others have had with replication. He omits from the discussion that dominance as a property of the allele rather than modifiers seems the only reasonable explanation in regions where the allele has never been common (at least not in modern times; see West 1977). Majerus also speculates that dominance may be breaking down as selection against the *carbonaria* allele continues, although there is no evidence for this. Whether Kettlewell was right or wrong about the evolution of dominance, it bears little on the basic story of industrial melanism. We do have, however, a rare opportunity to test Haldane's (1956) theory that modifiers might accumulate as an allele "sweeps" to fixation. Incidentally, both Majerus and Kettlewell incorrectly attribute this version of the theory of the evolution of dominance to Fisher instead of Haldane (see Orr 1991 for a clear distinction).

Indisputable Evidence for Natural Selection

Textbook accounts of industrial melanism too often dwell in the past. They begin with pre-industrial England and end with Kettlewell. As a footnote they might add that melanism has been on the decline in recent years following clean air legislation. Yet, it is the record of the *decline* that is by far the strongest. During the last century and the early part of this one few people kept records about morph frequencies, so our picture of the rise and spread of melanism is sketchy. Documentation for the decline in melanic frequencies is vastly more detailed (e.g., Clarke et al. 1994, Cook et al. 1999, Grant et al. 1996, 1998, Mani and Majerus 1993, West 1994). No other evolutionary force can explain the direction, velocity and the magnitude of the changes except natural selection. That these changes have occurred in parallel fashion in two directions, on two widely separated continents, in concert with changes in industrial practices suggests the phenomenon was named well. The interpretation that visual predation is a likely driving force is supported by experiment and is parsimonious given what has been so well established about crypsis in other insects. Majerus allows that the basic story is more complicated than general accounts reveal, but it is also true that none of the complications so far identified have challenged the role assigned to selective predation as the primary explanation for industrial melanism in peppered moths. Opinions differ about the relative importance of migration and other forms of selection. It's essential to define the problems, to question assumptions, and to challenge dogma. This is the norm in all active fields of research. Majerus has succeeded admirably in communicating this excitement to the reader. I would add this: Even if all of the experiments relating to melanism in peppered moths were jettisoned, we would still possess the most massive data set on record documenting what Sewall Wright (1978) called "...the clearest case in which a conspicuous evolutionary process has been actually observed."

Certainly there are other examples of natural selection. Our field would be in mighty bad shape if there weren't. Industrial melanism in peppered moths remains one of the best documented and easiest to understand.

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