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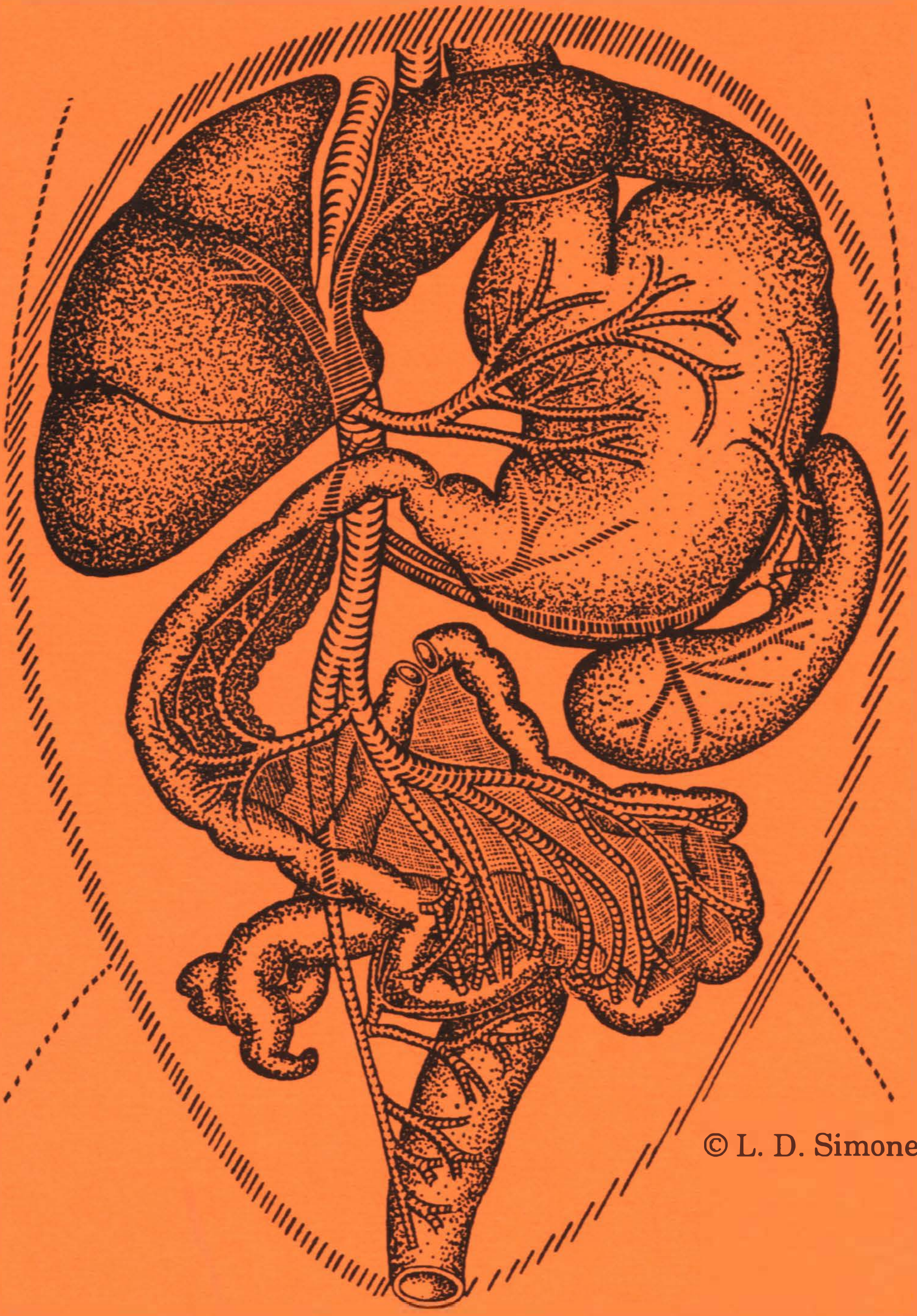

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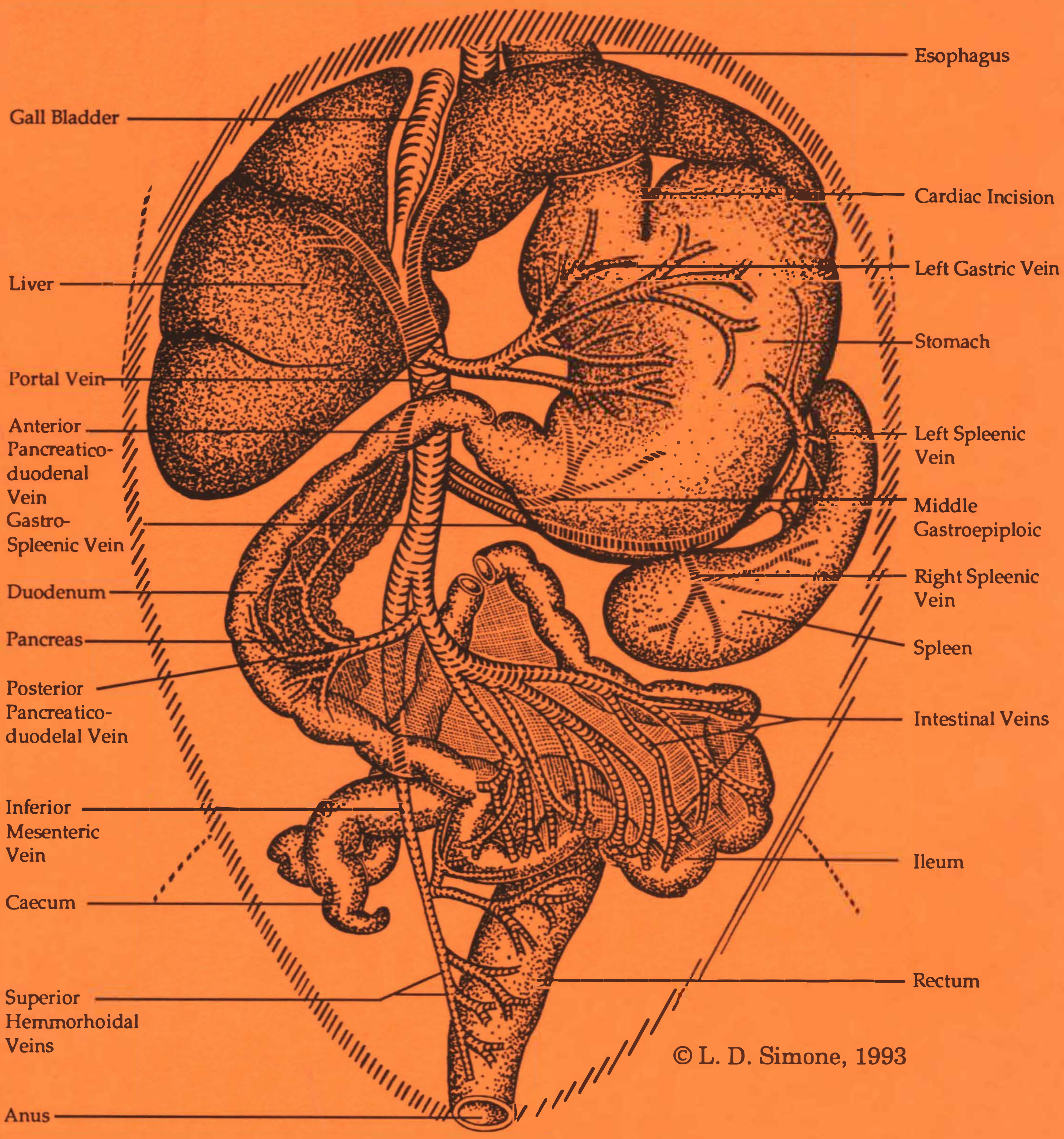

Cover Illustration: Diagram of the Portal System of *Felis domestica* (Domestic Cat). The mesenteries and a portion of the intestine are removed to reveal various veins which drain major abdominal organs, such as the stomach, pancreas, spleen and intestines. Ultimately, these veins lead to the portal vein which carries deoxygenated blood directly to the liver, where it mixes with oxygenated blood from the hepat artery. Blood percolates through a labyrinth of capillaries and sinusoids of the liver lobules passing phagocytic Kupffer cells and hepatocytes. Here it is processed and modified before returning to the heart via the hepatic veins and inferior (posterior) vena cava. Thus, life sustaining nutrients as well as drugs or toxic substances, which are absorbed by the digestive system, pass through the liver before circulating throughout the body.

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Kettlewell and the Peppered Moths Reconsidered

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Introduction

Industrial melanism in the peppered moth, *Biston betularia*, is perhaps the most widely used example of natural selection in introductory college textbooks. The case dramatically illustrates how directional selection can cause an adaptive mutation to spread quickly through a population. The genetic basis for melanism is relatively simple (autosomal dominance) and the selective agent (predatory birds) is easily understood by students. Finally, the elegant experiments carried out by H.B.D. Kettlewell beginning in the 1950s provide an excellent case study for discussing how scientists test their ideas.

Unfortunately Kettlewell's work is rarely presented in a way that challenges students to think critically about the process of science. As a result, students are deprived of an opportunity to learn about how successful scientists identify problems, propose hypotheses, design methods of testing, and persuade skeptical colleagues of the validity of explanations. This article attempts to present industrial melanism within a framework for active learning[1].

The Phenomenon of Industrial Melanism

Wing coloration is an important adaptation in moths. In *B. betularia* and related species, females rarely fly (Kettlewell, 1973). Males fly during the night and rest on tree trunks and other vertical surfaces during the day. Both females and males rest with their wings open and they usually will not move unless disturbed. Thus cryptic wing coloration provides protection against predators. In many species, moths have light colored wings that provide camouflage against lichen covered tree trunks. This cryptic coloration is so effective that the moths are often nearly invisible to humans standing only a few feet away. Because their wing coloration often contrasts with the background on which they rest. melanic individuals are more likely to be eaten by predatory birds. Of course, not all trees have uniformly light colored bark. Birch trees, for example, are common in British forests. The black patches on the otherwise white bark of these trees provide camouflage for dark moths. For this reason, among others, melanic individuals are usually found at low frequencies in natural populations.

As a result of the industrial revolution many areas in Britain were heavily polluted (Kettlewell, 1959, 1973; Bishop and Clark, 1980; Bishop and Cook, 1975; Ricklefs, 1979). Smoke from burning coal killed the lichens and caused trees and other surfaces to darken with soot. In some industrial areas one could blacken a white handkerchief simply by rubbing it against a tree trunk. In such polluted areas the selective pressure on moth populations is reversed. Melanic individuals are protected by their cryptic coloration and the more conspicuous light colored moths are at a selective disadvantage. Photographs of light and dark moths side by side on a sooty tree trunk dramatically illustrate the advantage of having dark colored wings (Kettlewell. 1956). As a result of directional selection, melanic individuals almost completely replaced the light colored variety in several local populations.

Industrial melanism is not restricted to the peppered moth. Over 100 species of British moths (out of a total of 780) exhibit this type of evolutionary change (Kettlewell, 1973). It is not surprising that Kettlewell and other scientists chose to study *B. betularia*, however, for it is an excellent experimental organism. It is common, easy to capture and breed, and it is broadly distributed in both urban and rural environments.

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[1] A complete teaching module based upon this case study, including suggestions for classroom and laboratory exercises, is available from the author.

Competing Hypotheses of Industrial Melanism

During the late nineteenth century changes in the wing coloration of British moths were noted by collectors, and industrial melanism was recognized as a striking evolutionary phenomenon by professional biologists. This interest continued during the early twentieth century, particularly in England. Leading evolutionary theorists such as J.B.S. Haldane and R.A. Fisher wrote brief commentaries about it. Experimental biologists also turned attention to the changes in wing coloration. In a widely publicized series of experiments conducted during the 1920s the British entomologist J.W. Heslop Harrison (1927) fed larvae of two different species of moths (*Selenia bilunaria* and *Tephrosia bistortata*) leaves impregnated with manganese sulfate or lead nitrate. An unexpectedly high proportion of the descendents of these larvae had dark wings. According to Harrison, industrial melanism was the result of an increased mutation rate induced by chemical substances found in air pollution. Harrison published his results in the widely read journal, *Nature*, and he presented his claims as a proof of inheritance of acquired traits. Attempts to replicate these experiments failed, and Harrison was criticized on theoretical grounds by Fisher, who pointed out that his explanation required a mutation rate several orders of magnitude greater than any previously reported. Nonetheless, Harrison continued to argue for his neo-Lamarckian theory and he later became a persistent critic of Kettlewell. Because he was a distinguished member of the British scientific community, Harrison's ideas could not simply be ignored. Therefore, this controversy formed an important part of the historical and social context of Kettlewell's research.

A decade after Harrison published the results of his experiments, the geneticist E.B. Ford presented an alternative, neo-Darwinian explanation. According to Ford, industrial melanism could be explained on the basis of rare mutations and natural selection. Melanic moths occasionally occurred in populations as a result of mutation, but usually they were quickly eliminated by selection. However, in polluted areas melanism proved adaptive, gained a selective advantage, and rapidly spread through the population. Ford did not conduct experiments to test his hypothesis, and his explanation left a number of important questions unanswered. What exactly was the cryptic advantage of melanism? Could predators actually distinguish between melanic and non-melanic moths? Could natural selection account for the rapid increase in melanic individuals in polluted areas? These were the questions to which Kettlewell turned when he began to work with Ford during the 1950s.

Henry Bernard David Kettlewell (1907-1979) studied both zoology and medicine at Cambridge University. During the 1930s and 1940s he practiced anesthesiology at a number of hospitals in and around London. Throughout this period he also published a number of entomological papers and after the war he worked on a locust control project in South Africa. In 1952 he was awarded a fellowship to carry out research in genetics with Ford at Oxford University. The following year he gave up medicine for good and spent the rest of his life as a research fellow at Oxford. Such a brief biographical sketch provides few clues to the success of Kettlewell's research. To account for this we need to consider more closely the unique historical context within which he carried out the experiments.

The Modern Synthesis and the Oxford School of Ecological Genetics

Among evolutionary biologists the period between about 1920 and the late 1940s has become known as the "modern synthesis." During this period there was a consolidation of ideas about how the process of evolution does and does not occur. Ideas that had been widely held at the turn of the century — inheritance of acquired traits and various mutation theories — were largely abandoned. This change occurred gradually, but by the end of World War II a broad consensus emerged that a combination of Mendelian genetics and natural selection could adequately explain most or all evolutionary phenomena. Both the destruction of competing theories and the construction of a neo-Darwinian theory were carried out by a loose coalition of theoreticians (R.A. Fisher, J.B.S. Haldane, Sewell Wright), geneticists (Theodosius Dobzhansky, E.B. Ford, G. Ledyard Stebbins), and naturalists (Ernst Mayr, G.G. Simpson).

This traditional interpretation of the modern synthesis has been greatly expanded by historians (Provine, 1971; Mayr and Provine, 1980; Smocovitis, 1992; Cain, 1993). Two points are particularly important for understanding Kettlewell's work. First, we now recognize that the the modern synthesis was not simply an intellectual achievement, but also an important social movement. During the synthesis period evolutionary biologists were quite consciously involved with building a research community around evolutionary studies. For the leaders of the synthesis, evolutionary biology was to become a distinctive discipline capable of holding its own against the aggressive rise of molecular biology. Secondly, we now recognize that despite the connotation of unity implied by the term "synthesis" there were sharp disagreements within the movement. Cooperation occurred among evolutionary biologists, but so did competition. Thus, the new research community of evolutionary biologists, was, in fact, a very loose coalition of often competing research schools.

One of the most important of these smaller communities was the group of "ecological geneticists" led by E.B. Ford at Oxford University (Ford, 1980, 1981). Working with Ford was a group of outstanding evolutionary biologists: Kettlewell, A.J. Cain, P.M. Sheppard, and C.A. Clarke. Ford also had a long working relationship with R.A. Fisher, and all of the Oxford ecological geneticists were heavily influenced by his ideas. What characteristics defined this Oxford school of ecological geneticists? **(1)** Perhaps most important, they were experimentalists who worked in the field rather than the laboratory. Kettlewell was quite critical of arm-chair theoreticians and laboratory experimentalists — to test evolutionary hypotheses, the geneticist had to work in nature's laboratory. **(2)** Second, this group was particularly interested in genetically based polymorphisms (Ford, 1940). A polymorphism is the occurrence of two or more distinct forms in a population. The Oxford school believed that polymorphism almost always occurs in natural populations, and that these polymorphisms are maintained by a balance of conflicting selective agents. For example, Kettlewell believed that although melanism might be disadvantageous in rural areas as cryptic coloration, it might be adaptive as a means of regulating body temperature. Therefore, the number of melanic individuals within a local population would depend upon a balance of selection for temperature regulating mechanisms and against non-cryptic wing coloration. **(3)** Third, the Oxford group advocated the "supergene" concept, an idea put forward in the 1920s by the British cytogeneticist C.D. Darlington (Ford, 1980). According to this view, natural selection acted on chromosomal rearrangements to perpetuate favorable combinations of genes. Adaptive gene complexes (supergenes) composed of genes located near one another on a chromosome would tend to be inherited as a unit. In the case of industrial melanism, Kettlewell believed that this selection for closely linked, adaptive, modifying genes would eventually lead to increased fitness and increased dominance of the supergene that controlled wing coloration. **(4)** Finally, the Oxford group accepted Fisher's belief that selection pressure can be very great in nature. Because of Fisher's influence, Kettlewell was pre-disposed to discover rapid evolutionary changes caused by the heavy hand of natural selection on populations of moths.

Kettlewell's Experiments

Background Choice

Kettlewell believed that the evolution of industrial melanism depended upon a moth being able to correctly choose a background that matched the color of its wings. Indeed, he claimed that the rapid population changes in wing coloration could not have occurred without background choice (Kettlewell, 1973). This behavior must be genetically determined, he believed, because any error in background choice would be fatal. Moths would not have time to learn the correct behavior. Although skeptical of laboratory experiments, Kettlewell designed a simple test of his hypothesis. He lined a large cider barrel with overlapping strips of black and white cloth. In the evening he released equal numbers of dark and light winged moths in the barrel. The top of the barrel was then covered with a sheet of glass and a white cloth. In the morning, the resting position of each moth was recorded. Kettlewell obtained the following results (Table 1):

Table 1. Resting positions of moths on background of barrels.

	Dark Winged Moths	Light Winged Moths
Black Background	38	20
White Background	21	39
		$\chi^2 = 10.9$, $P \cong 0.001$

After completing the barrel experiments in 1954 Kettlewell formulated his "contrast-conflict theory" of background choice. According to this theory moths used a variety of tactile, visual, and olfactory cues to assess the background on which they landed. If the background did not match the color of its wings, the moth would take flight again. Beginning in 1957 Kettlewell attempted to test background choice in the field. Moths resting on trees were collected along with small samples of bark. Correct or incorrect choice of background was then determined visually by Kettlewell and his co-workers. Kettlewell realized that biases could effect the way that he scored the moths' choices. Believing as strongly as he did in the contrast-conflict theory, he might tend to score borderline cases as correct choices.

Even so, in the field investigations Kettlewell found no statistically significant tendency for moths to choose correct backgrounds. Despite these negative results, he continued to believe in the importance of background choice.

The background choice experiments are never presented in textbooks, presumably because the results were ambiguous. However, they provide an excellent topic for class discussion. It might be useful to ask students whether or not Kettlewell was justified in holding a hypothesis in the face of negative evidence. At what point should a scientist abandon a hypothesis? What function might this weakened hypothesis have served in Kettlewell's research?

Selection Experiments in the Laboratory

One of the most controversial aspects of Kettlewell's early research was his claim that birds selectively prey upon non-cryptic moths (Kettlewell, 1973; Tinbergen, 1958). In an early experiment Kettlewell released equal numbers of dark and light winged moths in a large, outdoor aviary (6 yds x 18 yds). In the enclosure were light and dark tree trunks. After the moths had come to rest on the tree trunks, Kettlewell released a pair of Great Tits. During the first two hours none of the moths were eaten, even those which had come to rest on contrasting backgrounds. However, once the birds learned that moths are food, they actively searched for conspicuous prey. Inconspicuous moths were less often eaten, although they too, were taken, particularly if they happened to be resting near a conspicuous individual.

From this experiment, Kettlewell was convinced that birds could act as selective agents, but selective predation was a learned behavior. The birds had to form a "hunting image" for specific types of food before they could effectively exploit it. Apparently other biologists were unconvinced (Kettlewell, 1973; Tinbergen, 1958). Both ornithologists and entomologists were skeptical that birds would actively search for specific food items. In response to this criticism Kettlewell enlisted the aid of the ethologist Niko Tinbergen who spent two days observing selective predation of moths in the field. Tinbergen observed that birds discovered conspicuous moths approximately three times as often as inconspicuous moths resting on the same tree trunk. Motion picture films and still photographs of predation by birds provided dramatic evidence to support Kettlewell's claim about selective predation (Kettlewell, 1956).

Mark-Release-Recapture Experiments

Textbook accounts present Kettlewell's research as a classic illustration of controlled experimentation. In actuality, the historical case is more complex than this idealized version would suggest.

In 1952-53, Kettlewell carried out a series of mark-release-recapture experiments in a polluted woodland at the Christopher Cadbury Bird Reserve near Birmingham. The results of this research were published in 1955 (Kettlewell, 1955). In this early paper he also reported observational studies of crypsis conducted in an unpolluted forest in Dorset. However, he did not include results from mark-release-recapture experiments in unpolluted environments. These experiments, conducted in 1954 in the Deanend Wood in Dorset, were described in a second article (Kettlewell, 1956). There are several plausible explanations for Kettlewell's decision to publish the two sets of experiments separately. Perhaps he was concerned about priority. Industrial melanism was an important problem, and he undoubtedly did not want to be "scooped" by another investigator. Like most creative and ambitious scientists, Kettlewell was willing to go out on a limb; he frequently published incomplete reports and put forward speculative hypotheses. This, too, may explain why he rushed the early report into print. Practical problems may also have convinced him to publish the original uncontrolled experiment. Finding comparable woodlands in polluted and unpolluted areas of England was difficult. Furthermore, his experiments required facilities for breeding moths and electricity to power the mercury vapor lamps that he used to recapture the moths. Conducting large field experiments is labor-intensive. Working with little assistance from others, it was impossible for Kettlewell to conduct mark-release-recapture experiments simultaneously in two places. Breeding hundreds of moths to be released also posed practical problems. All of these factors may have prevented Kettlewell from conducting a controlled experiment in 1952. But the early paper gives little indication that it was written as a preliminary report. Nowhere in the paper did Kettlewell discuss the need for a control. It seems likely that Kettlewell initially believed that the uncontrolled experiment in a polluted woods was sufficiently compelling to support his hypothesis. Perhaps criticism of the early experiments forced Kettlewell to reconsider his argument and to expand the scope of his research. This possibility is supported by Kettlewell's claim that the results of his initial experiments faced considerable skepticism from other biologists.

Although Kettlewell modified his techniques during successive experiments, the basic design remained unchanged. Following methods pioneered by Fisher and Ford, he marked the underside of the wings of male moths with a dot of paint. Only males were used because the more sedentary females are difficult to recapture. After marking, large numbers of light and dark winged moths were released in the evening. Every evening during the next week, males were recaptured using mercury vapor lamps and pheromone traps (i.e. traps containing virgin females). Table 2 below summarizes the results of experiments conducted in the two different environments, with the number of recaptures expressed as a fraction of the total number of moths released.

	ENVIRONMENT	
MOTHS	Polluted Woods (Birmingham)	Unpolluted Woods (Dorset)
Light Wings	18/137 (13%)	62/496 (12.5%)
Dark Wings	136/447 (27.5%)	34/488 (7%)

Table 2. Recaptured male moths from two different field experiments

If we consider only the first column in the table, we can place ourselves in the position of a reader of Kettlewell's first paper. How might these results be explained? Natural selection favoring melanism is one possibility. But Kettlewell, himself, recognized that the data could also be explained by: 1) melanic moths being more attracted to female pheromones, 2) melanic moths being more attracted to mercury vapor lamps, 3) light colored moths being more likely to migrate from the study area, 4) light colored moths being less viable for reasons other than predation (Kettlewell, 1973). That Kettlewell was able to recognize these possibilities and take them seriously highlights the importance of skepticism and criticism in science. As a teacher, I have found that presenting the data from the Birmingham site and asking students to provide several possible explanations for them, is an excellent exercise in critical thinking.

Taking the data from both environments together provides a much more convincing argument for natural selection. Assuming that recapture rates reflect rates of selection by predators, cryptic individuals have approximately twice the survival rate of conspicuous moths. Using this data, together with observational evidence of selective predation by birds, Kettlewell provided a convincing argument for the evolution of industrial melanism by natural selection. For all intents and purposes, his explanation has become a "fact" that all students learn in introductory biology courses. Both historically and pedagogically, however, this biological fact is embedded within a complex context that includes the elimination of rival explanations, the social and intellectual development of a discipline of evolutionary biology, cooperation and competition among scientists, the choice of an ideal species for experimentation, and the design of an elegant set of experiments — prompted, in part, by criticism from Kettlewell's contemporaries.

Reconsidering the Significance of Kettlewell's Experiments

Kettlewell's mark-release-recapture experiments were brilliantly conceived demonstrations of evolution in action. Discussing these experiments with students is particularly useful for showing that evolutionary hypotheses can be tested experimentally, and that properly designed field experiments rival the rigor of more easily controlled laboratory experiments. But to leave the discussion there robs students of the opportunity to further explore the process of science. In retrospect, we see that Kettlewell probably did not set out to do a controlled experiment — at least not initially. Documenting the reason or reasons that he did not do so would require a level of historical analysis that goes well beyond the scope of this paper. However, by setting up the historical problem for students, the instructor can initiate a fruitful line of questioning:

- What practical problems did Kettlewell face in carrying out his experiments?
- What assumptions did he make in carrying out the original experiment?
- How convincing would the results of this experiment be to a skeptic such as J.W. Heslop Harrison?
- And what about Harrison's experiments?
- How might a Darwinian interpret the results that Harrison used in support of a neo-Lamarckian theory of evolution?

These questions are not trivial. By posing such problems we can challenge students to go beyond memorization of terms and definitions. Perhaps we can demythologize science and make its process more understandable to the general student population. Like many other historical case studies, the story of Kettlewell and the peppered moths illustrates the social nature of science, the give-and-take between competing scientists, the cooperation within small research communities, the complex interplay between theory and experiment, and the inevitable problems and dead ends that are parts of every process of discovery.

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