SELECTION EXPERIMENTS ON INDUSTRIAL MELANISM IN THE *LEPIDOPTERA*

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1. THE SPREAD OF MELANISM

In view of the extremely rapid spread of melanic forms of at least fifty species of Lepidoptera in the industrial areas of Britain, experiments were carried out with the following objects. To ascertain : (i) Whether the black and pale forms are to an appreciable extent at an advantage on their appropriate backgrounds. (ii) If so, whether the difference can be evaluated. (iii) Whether birds and other visual predators search for and eat resting moths. (iv) If that be established, whether the insects are taken selectively, and in the order of conspicuousness that is registered by the human eye.

The importance of these questions will be appreciated from the following facts. The industrial melanism of the Lepidoptera is the most striking evolutionary change ever actually witnessed in any organism, animal or plant. Its current explanation (p. 2) assumes selective elimination by predators. Yet after more than twenty-five years of observation and constant enquiry, I have found no single instance in this country in which anyone has witnessed a bird detecting and eating a moth belonging to a protectively coloured (or " cryptic ") species when sitting motionless on its correct background. Nevertheless, the effective concealing patterns found in great numbers of these insects (those affected by industrial melanism and others) seem explicable only on the assumption that predators hunting by sight are of serious danger to them. I determined, therefore, to subject this matter to experiment and precise observation on a scale not so far attempted. Since for this purpose it was necessary to use large numbers of specimens, I decided to concentrate upon a single species, which could act as a test case for this aspect of the theory of industrial melanism ; and also in assessing the importance of predators as selective agents in the solution of the cryptic patterns of the Lepidoptera. The insect I chose for this work was the Peppered Moth, *Biston betularia* L., Selidosemidæ, the most famous example of industrial melanism, and the first to be detected. I accordingly reared this insect on a large scale in order to provide the experimental material that was required.

There is no question of dealing in this paper with other aspects of Industrial Melanism, such as the character and behaviour-differences associated with melanic and non-melanic insects, nor with air pollution. This latter topic involves a consideration of the degree of contamination of foliage in different areas of Britain, and its effect on larvæ, with the viability differences associated with the typical and the melanic forms. These subjects will be dealt with elsewhere.

2. THE EXPLANATION OF INDUSTRIAL MELANISM

The current explanation of industrial melanism was suggested by Ford (1937). Since a knowledge of it is essential to the purpose of this paper, it is necessary to summarise it for the benefit of those unacquainted with the subject. Briefly, it may be said that industrial melanism is ascribed to a change between selective advantage and disadvantage, due to industrialisation. It was noticed (i) that the species affected by this phenomenon rest fully exposed on tree trunks, walls or fences, apparently protected from predators by a concealing pattern. (ii) In nearly all of these, the melanics are unifactorial and not recessive (it is probable, and in some instances certain, that the quantity of melanin is greater in the homozygotes than in the heterozygotes). (iii) There was much somewhat anecdotal evidence, though derived from independent sources, that the successful melanics are more viable than the normal forms, which, nevertheless, until recently they have nowhere succeeded in displacing. This difference in viability was suggested by an excess of black varieties above expectation in segregating families. It should here be noticed in parenthesis that the type of metabolism involved in excess melanin production does not necessarily confer superior viability. Recessive melanics are known as rare varieties and these, though often as black as the darkest " dominants ", are much less hardy than the pale forms.

In view of these considerations, it was suggested that all genes conferring a physiological advantage had spread through the species, unless responsible also for some counter-balancing disadvantage, such as the destruction by excess melanin formation of the concealing pattern upon which the safety of the insect depends. Such melanics, though physiologically at an advantage, were therefore unable to establish themselves until the blackened vegetation of industrial areas provided an environment in which black colouring is no longer a handicap, perhaps even an asset, to concealment. Here, therefore, they have spread ; though the equally well protected, but relatively inviable, recessive melanics have not done so.

One aspect of this explanation, the superior viability of the industrial melanics, was soon established by experiment (Ford, 1940). The other, the selective action of predators in destroying the pale or blackish moths on inappropriate backgrounds, has remained unproved, and it is this which is studied in the present paper.

3. THE GENETICS OF MELANISM IN *BISTON BETULARIA*

In about fifty species showing industrial melanism, the black forms are more or less complete dominants (their heterozygotes cannot be distinguished from the homozygotes). Several have no dominance, and a few are multifactorial. *Biston betularia* represents the usual condition for such species in which melanism is unifactorial and dominant. There are, however, a few points of special interest in regard to its genetics.

This species is normally whitish grey with a sprinkling of black dots: a colour-pattern which conceals it extremely well on light bark, especially when lichens are present. It has two melanic forms. One, *carbonaria*, is completely black except for a small white dot at the base of each forewing and another where the antennæ approximate to the head. This is the famous industrial melanic of the species which has spread in such a spectacular fashion in industrial areas. It is now a complete dominant, but was probably not so when first found in the middle of last century. At that time there appears to have been in many of the heterozygotes (we do not know the appearance of the homozygotes) some trace of the pale markings. These are never seen now in districts where *carbonaria* constitute all but a small fraction of the population. It appears, therefore, that the gene-complex has been selected to produce the complete dominance of this form at the same time as it has become common during the last one hundred years. This matter is at present being subjected to genetic tests, which are not the subject of this paper. The other melanic form of *B. betularia* is less complete, being dark with a sprinkling of white scales. It is known as *insularia* and is much less common (for relative frequencies, see p. 334), though it has certainly spread in and outside industrial areas. It cannot be distinguished phenotypically in the presence of the *carbonaria* gene. It, too, seems to have become blacker during the last fifty years or so. It was long in doubt whether or not these forms were allelomorphs. I have, however, lately demonstrated that they are at separate loci, with no evidence of linkage.

4. THE NATURAL HISTORY OF THE MOTH

B. betularia has a long period of emergence, from early May to early August. It flies at night from late dusk till dawn. The male only comes to Mercury Vapour light freely, the female but rarely. Assembling to newly hatched females in nature takes place between 9 p.m. and midnight (G.M.T.), but will continue until dawn to caged females. By day the moth rests on tree trunks and boughs, on which it takes up its position at dawn. It hatches normally at dusk, thus avoiding visual predators on the first day of its imaginal life, before being free to choose its correct background.

5. METHOD OF SCORING THE MOTHS ON THEIR BACKGROUNDS

It must be emphasised that the relation of insects to backgrounds does not merely involve a simple colour-difference such as black on white or black on black. The complicated pattern of the typical cryptic insects melts into a surprising number of backgrounds, but only if they are light coloured or have a variegated pattern. For the purpose of analysis, the following system was devised :—

In the first instance, *at two yards distance*, the question had to be answered : is the insect conspicuous or inconspicuous on its background? Surprisingly, in nearly every case this was found to be capable of immediate solution without difficulty. To obtain the degree of divergence as between insect and background, the following method was found satisfactory. After making the initial decision at two yards, if the insect was judged " conspicuous " one walked away from it until a point was reached where it became inseparable from its background, be it *carbonaria* on lichen covered oak trunk in Devon (50 yards), or a typical *betularia* on a Birmingham oak trunk (40 yards). In each case a value of −3 was given, and anything visible *over 30 yards* was awarded this. In trial experiments, with several observers taking part to test at which spot the moth disappeared into its background, a marked degree of agreement and uniformity was reached. The readings for degrees of conspicuousness were decided at the following distances :—

" *Conspicuous* " *insects (on incorrect background)*

30 yards and over	−3	Taken in the shade in average daylight.
20-30 yards	−2	
10-20 yards	−1	

Similarly, decisions in the direction of inconspicuousness were decided :—

" *Inconspicuous* " *insects (on correct background)*

2 yards	+3	Taken in the shade in average daylight.
5 yards	+2	
10 yards	+1	

In practice, it soon becomes unnecessary to pace the distance of each insect (a difficult procedure anyway in an aviary cage), and even after as short a schooling as one day, the independent scoring of others, taken at two yards, seldom diverged by more than plus or minus one unit.

6. RESULTS OF SCORING MOTHS ON THEIR BACKGROUNDS

The scorings of Dr R. A. Hinde and myself for sixteen insects assessed separately are given in table 1.

TABLE 1

Results obtained by two observers in scoring black and typical B. betularia *independently*

Phenotype *	Black (*carbonaria*) = C	Pale (*typical*) = T
Dr Hinde	+2 +2 −3 +3 −2 −2 +3 −2 −1 +3	+3 −2 +3 −3 +2 +1
H. B. D. K. .	+2 +3 −3 +3 −3 −2 +3 −3 −2 +3	+3 −3 +2 −3 +1 +2

* Throughout this paper the three phenotypes of *B. betularia* : *carbonaria, typical* and *insularia* are designated by the letters C, T and I respectively.

This experimental design was decided on to give the least error in judging which of the six possible scores were applicable. The same method of scoring was used for both aviary and field experiments, the insects being released on trunks of different species of trees relative to their proportions within the wood. From the scoring alone (quite apart from what subsequently happened), it was possible to get some idea of the state of the average background.

Thus 651 male and female *betularia* were released in a circumscribed wood in the Birmingham district, where the melanic form comprised about 90 per cent. of the population. These consisted of 171 *typical*, 416 *carbonaria*, and 64 *insularia*. There were 33 release points, being the trunks and boughs of three birch trees and thirty oaks. The proportion of birch to oak being not more than 1 : 10 in this wood.

The following scoring was obtained :—

TABLE 2

Background scoring for betularia *and its melanics in a wood near Birmingham (males and females)*

Score (birch throughout in brackets)	+3	+2	+1	−1	−2	−3	No. of inconspicuous insects		No. of conspicuous insects		Total releases ♂s & ♀s		Averag[e] score pe[r] insect
Typical on oak .	3	5	9	7	44	86	17	11%	137	89%	154	171	−2·11
,, birch .	(10)	(6)	(1)	(0)	(0)	(0)	(17)	100%	(0)	0%	(17)		(+2·53
Carbonaria on oak .	184	127	47	7	1	0	358	98%	8	2%	366	416	+2·33
,, on birch	(8)	(8)	(5)	(4)	(7)	(18)	(21)	42%	(29)	58%	50		(−0·54
Insularia on oak .	21	5	10	8	9	3	36	64%	20	36%	56	64	+0·85
,, on birch .	(5)	(2)	(1)	(0)	(0)	(0)	(8)	100%	(0)	0%	(8)		(+2·50

From table 2 it can be seen that the degree of crypsis (protection due to camouflage) as judged by the human eye varies greatly according to background and phenotype. On the oaks of Birmingham, the *carbonaria* are nearly always extremely well protected, but the reverse is shown for the *typical*, and the scoring of one is inversely proportional to that of the other. Birches, with their areas of black on light trunks, offer suitable crypsis to all phenotypes, which no oak trunk can possibly do. *Insularia*, though varying from light to dark, is seldom very conspicuous on any background, but is less perfectly concealed than *carbonaria* on dark trunks and than the *typical* form on light ones.

As a comparable experiment to this, I am able to quote one small release undertaken near Torcross, Devon, where all the trees and rocks are covered with lichen and algæ, and where no dark backgrounds similar to those found in the Midlands, were found. 128 *betularia* were released, 45 *typical* and 83 *carbonaria*. They gave the following scorings :—

TABLE 3

Background scoring for betularia *and melanic on Devon coast*

Score	+3	+2	+1	−1	−2	−3	Total conspicuous insects		Total in-conspicuous insects		Average score per insect
Typical	29	11	5	0	0	0	0	0%	45	100%	+2·53
Carbonaria	0	0	4	2	25	52	79	95%	4	5%	−2·46

This shows a reversal of the situation found in the Birmingham district, and in the location where I worked, there appeared to be no available resting sites for *carbonaria* other than those which were nearly always very conspicuous.

This method of scoring, then, appeared to be satisfactory as a means for our gauging background differences. It was, therefore, imperative to find whether bird predators, in the first instance, in confinement, appreciated the same set of values as decided by man, and finally to repeat, if possible, their reactions in the wild.

7. AVIARY EXPERIMENTS

(i) *General features of the aviary*

Due to the kindness of Dr Hinde and others, I was permitted to use the outdoor aviaries at the Research Station, Madingley, Cambridge. I chose a pair of nesting Great Tits (*Parus major*) which were in a wire netting frame approximately 18 yards by 6 yards, and 7 feet in height. The supports of the cage were made of dark larch and spruce trunks with the bark still present. There were 13 of these and in addition 20 other resting sites were introduced, making 33 in all (15 light and 18 dark).

There were also four horizontal poles. All the original construction trunks could be referred to as being lichen-free and with dark coloured bark, but among the introduced " furniture " birch and lichened trunks were included, and as variable an assortment of natural backgrounds as possible. The three forms of *betularia* were released on these.

(ii) *Method of introduction to birds*

The tits, having been driven to the far end of the cage, were screened off with a large sheet. The releasing was then carried out on selected trunks and boughs, each of which had a number, and the scoring was assessed in the manner previously described. The sheet was then taken down and the tits given the freedom of the aviary. From then on the investigation was conducted in two ways. Firstly, direct observation of the behaviour of the tits was kept from a distance through glasses. Secondly, at intervals the cage was entered and an inventory taken of the remaining moths.

(iii) *Results of the findings of aviary experiments*

In the first experiment, equal numbers of typical *betularia* and *carbonaria* were released on to the trunks and scored as being either on

TABLE 4

Order of predation by two great tits (Parus major) *in aviary experiment* (*A/16*)

Phenotype	Site No.	Score at commencement +	Score at commencement −	Score after 20 minutes +	Score after 20 minutes −	Score after further 20 mins. +	Score after further 20 mins. −	Score after 1½ hr.
Carbonaria	birch, light	+3		present		present		taken
”	pine, dark	+3		”		”		”
”	tarred post, dark	+3		”		”		”
Typical	elder bough, light	+1		”		”		”
”	elm bough, light	+1		”		”		”
Carbonaria	elm bough, dark	+2		”		taken		...
”	birch, light		−3	”		”		...
”	lichened birch, light		−2	”		”		...
”	birch, light		−3	”		”		...
”	lichened birch, light		−2	”		”		...
Typical	birch trunk, light	+3		”		”		...
”	elm trunk, dark		−3	”		”		...
Carbonaria	elm trunk, dark	+2		taken		...		...
”	birch trunk, light		−3	”		...		...
Typical	post, dark		−3	”		...		...
”	birch, light	+2		”		...		...
”	tarred post, dark		−1	”		...		...
No. of insects taken	...	...		5		7		5
No. of insects left	...	17		12		5		0
Total score left	...	+20	−20	+16	−13	+11	−0	0
Total score taken	...	...		+ 4	−7	+9	−20	+11 −0
Per cent. score taken	...	...		+25%	−53·85%	+45%	−100%	...

correct (+3) or incorrect (−3) backgrounds. Five were on correct and five on incorrect. The release was undertaken at 3 p.m. By 5 p.m. none had been taken. By 6 p.m. all those on incorrect backgrounds had been eaten as well as two scored as “ correct ” ; three remaining untouched, 2 *carbonaria* and 1 *typical*, all on correct backgrounds. The following day this was repeated using 18 *betularia*, 6 of each phenotype placed on backgrounds giving an equal score plus and minus for each phenotype. After a half hour, they had all been taken except two, one being a *typical* (+3), and one an *insularia* (+2). It was suggestive that the tits were becoming specialists on *betularia*, and subsequently they were seen to be searching each tree trunk eagerly one at a time immediately after admission, thereby defeating the object of the experiment. I decided, therefore, to try and widen their feeding interests and this was done by introducing into the cage at the same time as the *betularia* release, a number of other moths and insects in a proportion comparable to what was then occurring in nature, as judged by the local sample taken in my Mercury Vapour traps. These, of course, included individuals showing other types of colouration as well as cryptic. This proved successful, and in all further aviary experiments the introduction of other species of insects was carried out at the same time as that of *betularia*. In experiment A/16, 17 *betularia* (9 *carbonaria* and 8 *typical*) were released with the total score plus and minus in equality. The results are shown in table 4. For the purpose of statistical analysis it is accepted that it would have been more satisfactory if after each time the insect was taken it had been replaced by a similar phenotype. Experimentally this was impossible, nor in view of what happened was it necessary. It can be seen from table 4 that after two periods of 20 minutes each, when the tits were left alone, all 8 of the conspicuous insects had been taken with the score of -20, but in this time only 4 of those on correct background with a score of $+9$ had been eliminated, leaving five with a score of $+11$ untouched. A small series of similar experiments were conducted in each case with comparable results, except when pouring rain caused movement on the part of the insects and these experiments were abandoned.

An attempt was made to observe directly the order in which the *betularia* were taken by viewing from a distance through field glasses. The speed at which the two birds worked, however, in so limited a space made it impossible for accurate record to be kept. They would scan the trunks from nearby twigs, then fly and snatch the selected insect and frequently carry it down to the ground in order to eat it. At no time did I see a moth with warning colouration taken, but an Eyed Hawk, *S. ocellata* (showing " deflective coloration ") was eaten after one aborted attack.

It would appear then from these observations that birds, in this case, Great Tits, do in fact eat stationary cryptic insects including melanic forms, but in the first instance only after two hours of being in close proximity to them did they begin to do so. After an initial experience, however, they were quick to learn and took freely both light and black forms of *betularia*. Secondly, they took these in an order of conspicuousness similar to that gauged by the human eye. This is in accord with the Laboratory findings of Sumner (1934), who showed that predators failed to recognise camouflaged individuals in the same way as man. If the same could be shown in the field, it would provide the missing data needed to substantiate the current explanation of industrial melanism. Moreover, it would be possible to explain the stability in which complicated cryptic patterns are held, and at the same time to determine the relative selective values of light and black forms for crypsis in a given environment.

8. EXPERIMENTAL RELEASES IN AN INDUSTRIAL AREA

(i) *Choice of site*

B. betularia is not a colony insect, and in the course of its life the males, no doubt, and to a very much smaller extent the females, must frequently travel many miles from their origin. This is an entirely different state of affairs to that found in *Panaxia dominula*, the colony insect previously used by Fisher, Ford, Sheppard and others, for developing their technique for mark-release experiments (Fisher and Ford, 1947 ; Sheppard, 1955). Accordingly, it was of considerable interest to see whether their methods could be applied to this more usual state of affairs, that in which a species has a continuous range, and without having to resort to C. H. M. Jackson's "multiple square technique", as used by him in tsetse fly studies with all the labour it involves (C. H. M. Jackson, 1940). The site chosen, therefore, was of the greatest importance, and a wood with as many natural barriers as possible surrounding it, such as fields, rivers, or moorlands, was desirable. It is necessary to remember that the object of the experiments was to subject as many individuals as possible to maximum predation for as long a time as they could be exposed. For all these reasons, I chose a wood (or part of it) in the Christopher Cadbury Bird Reserve, near Rubery, Birmingham. This interesting Reserve is typical indigenous oak wood, with a fair sprinkling of large birch trees and an undergrowth of bracken, intersected by rides. No dead wood had been cut from the trees for years, hence this place boasts of a large bird population including the following trunk and bough feeders :—

Woodpeckers, *Picus viridis*, *Dryobates major*, *D. minor*.
Nuthatch, *Sitta affinis*.
Tree Creeper, *Certhia familiaris*.
Tits, *Parus caeruleus*, *P. major*, *P. ater*.
Flycatchers, *Muscicapa striata*, *M. hypoleuca*.

Nevertheless it must be judged an industrial area, being heavily polluted by smoke from the midlands.

I decided to use a peninsula of woodland, three sides of which were surrounded with fields and gardens, and which lay in a hollow in the hills. The fourth side continued into the main area of the reserve. The whole wood had sundry other copses almost exclusively consisting of birch, in its immediate neighbourhood. As stated, the proportion of birch to oak was less than 1 : 10, and none of the trunks or boughs had any lichen or algæ growing on them, having long since disappeared as the result of pollution (Eustace W. Jones, 1952). I decided, then, to undertake my releases in this peninsula of woodland and to surround the area as far as possible with assembling traps containing virgin females, as well as two Mercury Vapour lights. The assembling traps were of two kinds, one made of perforated zinc which allowed males to enter but not to escape, and the other were muslin cages at which I and two others collected assiduously throughout the night. Each trap contained one virgin female of each phenotype in case of scent differences. As the result of this,

TABLE 5

Release Experiment figures for Biston betularia (*males only*)
Rubery, near Birmingham, 1953

The letters C, T, I, stand for *carbonaria*, *typical* and *insularia* respectively throughout this paper

Date (1953)	Releases			Totals	Catches			Totals	Recaptures			Totals
	C	T	I		C	T	I		C	T	I	
25.6	10	12	10	*32*	8	0	1	*9*	...	...	...	...
26.6	0	0	0	*0*	127	15	7	*149*	3	1	1	*5*
27.6	33	11	15	*59*	34	5	1	*40*	1	0	1	*2*
28.6	37	21	5	*63*	23	3	3	*29*	2	0	2	*4*
29.6	0	0	0	*0*	55	10	1	*66*	5	4	0	*9*
30.6	68	26	8	*102*	37	3	2	*42*	1	0	1	*2*
1.7	90	21	3	*114*	76	9	2	*87*	19	2	2	*23*
2.7	74	21	3	*98*	75	13	4	*92*	28	6	0	*34*
3.7	68	15	0	*83*	77	11	10	*98*	25	3	1	*29*
4.7	67	10	2	*79*	66	9	2	*77*	23	2	0	*25*
5.7	0	0	0	*0*	73	3	5	*81*	16	0	0	*16*
Totals	**447**	**137**	**46**	**630**	**651**	**81**	**38**	**770**	**123**	**18**	**8**	**149**

	Catches			Totals
	C	T	I	
Wild Birmingham population	528	63	30	621
Per cent. phenotype . .	*85·03*	*10·14*	*4·83*	
Release after one day of self-determination	25	2	2	
Per cent. phenotype . .	*5·72*	*1·48*	*4·35*	
Per cent. return of releases .	*27·5*	*13·0*	*17·4*	

the whole area must have been flooded with female scent from dusk to dawn, and this was probably responsible for holding the males in the wood. As previously stated the three phenotypes were released on the trunks and boughs as early as possible in the day, scored, then visited later in the day and absent individuals recorded.

(ii) *Method of release*

In all the experiments, whether in the field or the aviary, boughs and trees selected for release-sites, were each given a number. In the wood, the proportion of such trees belonging to different species bore direct relationship to their estimated frequency in the locality.

Each insect, having been marked on its under-side with a small dot of quick drying cellulose paint with a colour-position for each day, was shaken from its box on to the bough or trunk. They generally wandered about for a few moments, and rapidly took up the optimum

TABLE 6

Comparative methods of collecting (with exception of first night).
Mercury Vapour Light and Assembling

Phenotypes	26th June			27th June			28th June			29th June			30th June			1st July		
	C	T	I	C	T	I	C	T	I	C	T	I	C	T	I	C	T	I
M.V. Light— Totals	90	12	6	16	3	1	14	2	1	17	2	0	17	1	1	44	6	2
Recaptures	2	1	1	1	0	1	1	0	1	1	0	0	1	0	0	9	2	2
Assembling— Totals	37	3	1	18	2	0	9	1	2	38	8	1	20	2	1	32	3	0
Recaptures	1	0	0	0	0	0	1	0	1	4	4	0	0	0	1	10	0	0

Phenotypes	2nd July			3rd July			4th July			5th July			Totals	Percentage
	C	T	I	C	T	I	C	T	I	C	T	I	C T I	C T I
M.V. Light— Totals	45	7	4	41	6	7	33	8	1	45	0	1	433	*56·89*
Recaptures	16	3	0	13	2	1	10	2	0	5	0	0	75	*50·33*
Assembling— Totals	30	6	0	36	5	3	33	1	1	28	3	4	328	*43·11*
Recaptures	12	3	0	12	1	0	13	0	0	11	0	0	74	*49·67*

Phenotypes	Total Captures			Recaptures		
	C	T	I	C	T	I
M.V. Light— *Totals*	362	47	24	59	10	6
Percentage	*83·60*	*10·85*	*5·55*	*78·67*	*13·33*	*8·0*
Assembling— Totals	281	34	13	64	8	2
Percentage	*85·68*	*10·36*	*3·96*	*84·40*	*10·81*	*2·71*

position available. We have recently been able to show, experimentally, that black and light *betularia* are able to appreciate contrast differences between themselves and their backgrounds, and hence they tend to come to rest in the optimum positions offered by an available resting site (Kettlewell, 1955). Having done this, they did not move again. The position of the paint marks, being on the underside which is not exposed by day, excluded the possibility of an additional risk of attack by predators. It was important to see that the sun did not shine on the moths, and each one of them, having settled, was scored by the method described previously.

TABLE 6A

Captures at light and by means of assembling, showing the equivalence of the methods, for which $\chi^2_{(2)} = 1{\cdot}09$, *for which* $P = 0{\cdot}\text{—}0{\cdot}5$

(with the exception of first night)

	Captures		Total	χ^2
	at light	assembling		
carbonaria . . .	362	281	643	0·094
typical . . .	47	34	81	0·042
insularia . . .	24	13	37	0·957
	433	328	761	1·093

(iii) *Release results*

Six hundred and thirty *betularia* males (*carbonaria* 447, *typical* 137, *insularia* 46) were released. Out of a total of 770 caught (*carbonaria* 651, *typical* 81, *insularia* 38) 149 were recaptures (*carbonaria* 123, *typical* 18, *insularia* 8), HENCE THE RELATIVE RECOVERY VALUES FOR THE THREE PHENOTYPES OF MY RELEASES WERE *carbonaria* 27·5 per cent., *typical* 13·0 per cent., *insularia* 17·4 per cent. (see table 5).

Twenty-nine individuals were recaptured after forty-eight hours' absence, and therefore after at least twenty-four hours of self-determination. They gave survival values of *carbonaria* 5·72 per cent., *typical* 1·48 per cent., *insularia* 4·35 per cent. of the initial release.

Of the 770 caught, 621 were local insects not released by us. They comprised *carbonaria* 528, *typical* 63, *insularia* 30, giving a frequency of *carbonaria* 85·03 per cent., *typical* 10·14 per cent., *insularia* 4·83 per cent. for Rubery insects (see table 7).

In regard to the method of collecting, after the first night (there having been no release on the 25th), 433 males were taken at Mercury Vapour light, and 328 by assembling, with practically identical phenotype frequencies at both (see table 6A). This demonstrates the random nature of the samples collected. No one phenotype had behaviour differences as between attraction to light and assembling, always remembering that there were equal numbers of each female phenotype in all the assembling traps. The detailed results are shown in tables 5 and 6.

9. ECOLOGICAL OBSERVATIONS AND DATA

All three phenotypes of *Biston betularia* are cryptic. In attempting to decide their relative selective values in the Birmingham area we have three sets of figures to take into account :—

(i) Scoring values as gauged by human standards.
(ii) Direct observation as to what happened to the individuals so scored.
(iii) Recapture figures which provided data over longer periods.

TABLE 7

Daily totals of wild-caught Birmingham specimens

Date	C	Per cent.	T	Per cent.	I	Per cent.	Total
25.6.53	8	*88·9*	0	*0*	1	*11·1*	9
26.6.53	124	*86·1*	14	*9·7*	6	*4·2*	144
27.6.53	33	*86·84*	5	*13·6*	0	*0*	38
28.6.53	21	*84*	3	*12*	1	*4*	25
29.6.53	50	*87·7*	6	*10·5*	1	*1·8*	57
30.6.53	36	*90*	3	*7·5*	1	*2·5*	40
1.7.53	57	*89·06*	7	*10·94*	0	*0*	64
2.7.53	47	*81·04*	7	*12·07*	4	*6·89*	58
3.7.53	52	*75·36*	8	*11·59*	9	*13·05*	69
4.7.53	43	*82·69*	7	*13·40*	2	*3·85*	52
5.7.53	57	*87·69*	3	*4·62*	5	*7·69*	65
Totals	**528**	**85·03**	**63**	**10·14**	**30**	**4·83**	**621**

(i) *Scoring values*

The insects, having been released on to thirty-three trees, being a sample of the only trunks and boughs available in this wood, were then scored. Of 366 male and female *carbonaria* released on oak, 358 (97·83 per cent.) were gauged as inconspicuous, and 8 (2·17 per cent.) otherwise. Conversely, of 154 *typical* which took up their positions on oak, only 17 (11·1 per cent.) were judged inconspicuous as shown in tables 2 and 2A.

TABLE 2A

The concealment (or otherwise) of B. betularia *and its melanic* carbonaria *on oak trunks near Birmingham, as gauged by Man*

	Conspicuous	Inconspicuous	Total
carbonaria	8	358	366
typical	137	17	154
	145	375	520

The other melanic form, *insularia*, because of its small numbers, need not be considered in detail here. Releases of 50 *carbonaria* on to birch trees, which were in proportion to their frequency in the wood, gave this melanic conspicuous to inconspicuous in approximate equality. Thus it appeared that in this locality typical *betularia* were at an approximate disadvantage of 40 per cent.

(ii) *Direct observations*

After the first day of release it was noticed that some of the *betularia* were disappearing from one or two positions so observation of these sites was maintained continuously from a distance through field glasses. H. M. Kettlewell first observed a bird fly up out of the bracken, snatch a *betularia* and return to the ground, the whole incident being over in a flash. Subsequently we were able to watch this bird, a Hedge Sparrow (*Prunella modularis*) regularly at work and to score the order in which it took the phenotypes. At a somewhat later date moths began to disappear from another series of trees, and I and others witnessed a Robin (*Erithacus rubecula*) at work, particularly in the late afternoon. This bird was observed in a similar way to the Hedge Sparrow, flying on to the twigs and bracken near to the trees whence it viewed the trunks and branches, making occasional excursions to pick up *betularia*. This it frequently did on the wing, always returning to the ground to eat them, and there subsequently I found wings and remains as an additional check to what had happened. It came as a surprise to us to find the Robin and the Hedge Sparrow behaving in this way, and there were most certainly other birds at work, unseen by us. I give below (table 8) a record of the few occasions when there was no doubt of the order in which these birds took their insects.

TABLE 8

Direct observations of the predation of B. betularia *by two species of birds*

Robin	Oak	4th July 1953 Order of take
typical	−3	1
carbonaria	+1	2
typical	−3	3
typical	−2	4
carbonaria	+3	
carbonaria	+3	Not taken by 7 p.m.

Robin	Oak	2nd July 1953 Order of take
typical	−3	1
typical	−3	2
carbonaria	+3	3
typical	−3	4
carbonaria	+3	
carbonaria	+2	Not taken by 7 p.m.

Hedge Sparrow	Oak	1st July 1953 Order of take
typical	−3	1
typical	−3	2
carbonaria	+3	3
typical	−1	4
carbonaria	+3	
carbonaria	+2	Not taken by 7 p. m.

From this it would appear that when a conspicuous insect had been found, it at once put other insects in the immediate vicinity at a disadvantage because of the birds' active searchings. This is corroborated by the increased predation which took place on those trees which harboured a moth with the score of −3 compared with trees where no such conspicuous individuals existed. Nevertheless, on oaks there were nearly always one or more *carbonaria* left which had been overlooked.

Total figures for male releases show that while 62·57 per cent. of *carbonaria* survived per day during observation (see table 9) only

TABLE 9

Observation release for 7 days (males only)

Score	*Carbonaria* +3	+2	+1	−1	−2	−3	Total
25.6.53	3	3	2	0	0	0	8
27.6.53	11	15	5	1	1	0	33
30.6.53	17	20	15	6	2	0	60
1.7.53	43	28	6	0	0	4	81
2.7.53	47	14	3	1	0	6	71
3.7.53	24	18	12	0	2	3	59
4.7.53	29	14	7	0	1	3	54
Total release before midday (seven days)	174	112	50	8	6	16	366
Total missing (seven days) up to 5 p.m.)	65	35	20	3	3	11	137
Per cent. missing .	37·35	31·25	40	37·5	50	68·75	37·43
Per cent. survival .	*62·45*	*68·75*	*60*	*62·5*	*50*	*31·25*	*62·57*
Release escapes .	...	...	...	...	...	...	44
Per cent. escapes = activity	...	...	...	...	...	...	10·75

45·79 per cent. of the *typicals* did so (table 10). *Insularia* had a 57·14 per cent. survival rate for the comparatively few insects under observation (table 11). Furthermore, there is evidence that the birds took the individuals within each phenotype with regard to their degree of crypsis. Of the 508 males released for observation over seven days, 210 had disappeared at the end of the day for one reason or another.

(iii) *Recapture figures*

It is evident from table 5 that we recaptured more than twice as many *carbonaria* as *typical* relative to the number released. This can be accounted for in one or more ways.

(i) That the melanics were attracted to light more freely than the *typicals*.

(ii) That the *typicals* had a shorter span of life than the *carbonaria*.
(iii) That the *typicals* wander or migrate more than the melanics.
(iv) That there was a differential predation between the phenotypes.

TABLE 10

Observation release for seven days (males only)

Score	*Typical*						Total
	+3	+2	+1	−1	−2	−3	
25.6.53	1	0	0	2	2	2	7
27.6.53	1	1	0	0	3	6	11
30.6.53	2	2	2	5	6	7	24
1.7.53	2	0	2	0	3	11	18
2.7.53	2	1	0	3	8	11	25
3.7.53	3	0	1	0	2	7	13
4.7.53	0	0	0	0	3	6	9
Total release before midday	11	4	5	10	27	50	107
Total missing up to 5 p.m.	4	2	3	5	13	31	58
Per cent. missing .	36·36	50	60	50	48·15	62	54·21
Per cent. survival .	*53·64*	*50*	*40*	*50*	*51·83*	*38*	45·79
Release escapes .	...	...	...	...	...	...	9
Per cent. escapes = activity	...	...	...	...	...	...	6·67

In regard to the first, we were able to show that an equal relative percentage of each form came both to light and assembling traps, which excludes behaviour differences in these directions. In regard to the life span, most wild caught insects were mark-released except for weak individuals, and when possible their numbers were subsidised by laboratory-bred specimens which were released at the same time. Many more of the *typicals* than *carbonaria* were bred ones and hence were in their first day of imaginal life, nor in regard to the wild individuals was there any evidence of a diminution of hatchings which would lead to the using of older moths, with a consequent shorter expectation of life (see table 7). Furthermore, the length of life of the two forms does not differ appreciably when bred and kept in the laboratory. The question of a different life span can therefore be excluded.

The possibility of a differential migration or dispersal rate taking place between the *typicals* and the melanics, must also be considered.

A comparison of the relative proportion of marked phenotypes taken at traps situated at the periphery of the release area to those caught at traps which were placed two hundred yards or more distant, shows

TABLE 11

Observation release for seven days (males only)

Score	*Insularia*						Total
	+3	+2	+1	−1	−2	−3	
25.6.53	2	0	1	3	0	0	6
27.6.53	3	1	4	1	3	1	13
30.6.53	4	3	0	0	1	0	8
1.7.53	1	0	1	0	0	1	3
2.7.53	3	0	0	0	0	0	3
3.7.53	0	0	0	0	0	0	0
4.7.53	1	1	0	0	0	0	2
Total release before midday	14	5	6	4	4	2	35
Total missing up to 5 p.m.	6	2	2	1	2	2	15
Per cent. missing	33·33	50	33·33	25	50	100	42·36
Per cent. survival	*66·67*	*50*	*66·67*	*75*	*60*	*0*	57·14
Release escapes	...	...	...	...	...	...	6
Per cent. escapes = activity	...	...	...	...	...	...	17·39

no difference in the frequencies of the three forms. One must, therefore, accept that the figures represent selective differences. Moreover, having in mind the state of the tree trunks, the results of the observation-release and, lastly, the frequent witnessing of the selective nature of the predation undertaken by two species of birds, it is fair to assume that this is the correct interpretation.

10. DISCUSSION

On the, of course unverified, assumption that in the Manchester area *carbonaria* occupied 1 per cent. or less of the *betularia* population in 1848 and 99 per cent. or more of it in 1898, Haldane (1924) showed that *carbonaria* has a selective advantage of about 30 per cent. over the *typical*. This, of course, might not be entirely due to crypsis, in fact it almost certainly would not be so. That the wild *B. betularia* population of Rubery 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 neighbourhood. This is to some degree borne out by the fact that, within a mile and a half of the centre of Birmingham, where there are few birch trees and nearly all the tree trunks are black, the frequency of *carbonaria* is still higher, being 93·18 per cent., with *typical* 4·54 per cent., *insularia* 2·28 per cent., in a total of 176 (Bowater and others).

I am not aware of previous attempts to discover the selective advantages of melanic insects by mark-release recapture experiments. To the obvious criticism that the releases were not free to take up their own choice of resting site for the first day, I must answer that there were no other alternative backgrounds available for an insect that has to spend its days on trunks and boughs in this wood. I admit that, under their own choice, many would have taken up position higher in the trees, and that since the surface area of a tree increases proportional to the distance up the trunks and boughs, in so doing they would have avoided concentrations such as I produced. Tinbergen (1952), de Ruiter (1952) and others have shown the importance to cryptic insects of avoiding too high a density level, but this is no argument against the findings for the *relative* advantages of the three forms. It must be accepted, however, that, under natural conditions, predation, though selective, might take place at a lower tempo.

How low this may be under certain conditions may be seen from data provided by Heslop Harrison (1919-20) who kept daily observations on *Polia chi* (Agrotidæ), and its dark form, which took up positions in a state of nature on three types of wall in the Newcastle district. The frequency of the latter (= *olivacea*) was 10 per cent. in one locality and 50 per cent. in another. He examined " up to 300 examples daily " and " never was there any diminution of numbers in which more *olivacea* " (= the ' melanic ') " vanished than type *chi*. As a matter of fact, we used to consider it a marvellous thing if even a single one had disappeared." He quotes this " to demonstrate that the effect of natural selection is quite negligible as a factor in progressive melanism."

I am afraid I cannot agree with this. In the first place *olivacea* is not a melanic in the sense that the whole pattern has been obliterated, for this remains present in a darker olive-grey tint (= it is a " melanochroic " J. W. H. H.). For this reason, sitting on stone walls (and not tree trunks) as they do, both forms are inconspicuous against the same backgrounds. Secondly, in the absence of concentrations, predation may have been at a very low level, though highly selective, and however small an advantage (0·1 per cent. or less) selection is able to use that advantage and spread a gene through the population at a calculable rate (which is not a linear one) and which depends upon the population's size. Consequently there is, theoretically, no limit set to the smallness of an advantage which can be used in selection, and one involving one out of 300 individuals indicates quite a considerable selective influence (Fisher, 1930). Fortunately, in the present series of experiments the values are of a much higher order and the effects of natural selection on industrial melanics for crypsis in such areas can no longer be disputed.

II. SUMMARY

1. Industrial melanism in moths is the most striking evolutionary phenomenon ever actually witnessed in any organism, animal or plant.

2. In order to account for its success, a theory has been assumed in which an inter-relation exists between the superior viability of certain melanics and predation by birds which eliminate resting moths selectively.

3. It has been considered probable that those individuals are principally destroyed which do not effectively match their backgrounds: so favouring black forms in areas polluted by soot.

4. In general, predation by birds has been thought to be responsible for the evolution of concealing colour-patterns in moths.

5. In spite of exhaustive observations, however, no evidence of such a selective elimination has, up to now, ever been produced. This paper supplies it.

6. The work has been conducted on the pale cryptically coloured moth *Biston betularia*, and its two melanic forms : the extreme black *carbonaria*, and the less extreme and rarer *insularia*. Both are unifactorial and dominant. They are not allelomorphs.

7. To the human eye, *carbonaria* proved much the better concealed on the lichen-free tree trunks, blackened by pollution near Birmingham, but this advantage was reversed in favour of the pale form in unpolluted country. *Insularia* possessed an intermediate advantage in both places.

8. The three forms were exposed to the attacks of birds (*Parus major*) in an experimental aviary, where their selective elimination on incorrect backgrounds was first demonstrated.

9. Corresponding work was then carried out in a wood near the industrial area of Birmingham, where the proportions of the three forms occurring naturally are, *carbonaria* 85 per cent., *typical* 10 per cent., *insularia* 5 per cent.

10. 630 male *B. betularia* (447 *carbonaria*, 137 *typical* and 46 *insularia*) were released in this wood. The moths were each identified by a mark on the underside, invisible when the insect was at rest.

11. The released insects were recaptured by assembling to females and at light traps. Of 149 which were recovered, the proportions were *carbonaria* 27·5 per cent., *typical* 13·0 per cent., *insularia* 17·4 per cent. This indicates their relative survival rates, as other agencies affecting their recapture could be excluded.

12. Birds, *Erithracus rubecula* and *Prunella modularia*, were seen frequently to inspect the trees from the undergrowth and capture the resting moths.

13. They did so generally without alighting and with great rapidity. Consequently, the act can only be detected in large-scale planned experiments. It is for this reason that it has not been previously observed.

14. Three sets of figures, the camouflage efficiency as scored by man, the differential survival at the end of day (as the result of predation) and, mark-release results, each show that the more conspicuous moths (in the Birmingham district, the *typicals*) were principally taken. Consequently birds act as selective agents, as postulated by evolutionary theory.

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