

THE INHERITANCE OF WING COLOUR IN LEPIDOPTERA.

III. *MELANISM IN BOARMIA CONSORTARIA* (VAR. *CONSOBRINARIA*, BKH.).

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(With Plate XIII.)

THE inheritance of melanism in *Tephrosia consonaria*¹ was described in a recent communication, and further experiments with a similar form of *Boarmia abietaria* will appear shortly. The work here detailed was carried out with the melanic form of *B. consortaria* (the Pale Oak Beauty). The three melanic varieties just mentioned are peculiar, because their origin is confined to the South of England. Black specimens of *T. consonaria*, as well as those of *B. consortaria* first appeared in the same oak-wood in Kent, and were not found far from that neighbourhood until recently. Also the melanic form of *B. abietaria* occurs only in Surrey, and occasionally in the New Forest. In none of these three species did the melanism originate in the industrial districts of the North. Lately, a melanic form of *T. extersaria* has arisen in Kent.

In all accounts of the progressive spread of melanism, great stress is laid on the fact that the melanic varieties have been found chiefly in the "Black Country" of England, and in a similar district round Crefeld in Germany. The deposit of soot and chemicals on the trees etc. in these districts is supposed to give to the melanic varieties a survival value, on account of their colouring, which there becomes protective. There seem to be grave objections to this theory. In the first place some typically melanic varieties have arisen in the rural districts of the South (as is the case with the three species just mentioned), and other varieties are found in equally rural parts of the North and West. Secondly, most melanic moths are night flying, only occasionally being seen sitting on trees,

¹ Onslow, H., *Journal of Genetics*, Vol. ix. No. 1, p. 53, Dec. 1919.

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palings, etc. in the daylight; and at night all moths are melanic. It is true that a species like *Gnophos obscurata* has a white form confined to the chalk district of Lewes, and a dark form common in the New Forest, where the insect is said to rest on cut peat; but the contrast between the colour of chalk cliffs and that of peat hags is much greater than between urban and rural districts. Geological formations, moreover, have been able to exert their influence for a much greater period than the works of man. It would be dangerous to say that the black colour of the melanic forms has no protective value, but it is hardly credible that it can be the chief, or only factor in their rapid appearance and increase.

It might at first sight appear that if a new form is dominant, as is the case in most melanic varieties, nothing else would be required to ensure that it gradually replaced the type form. It has however been shown on mathematical grounds¹, that if a dominant character is introduced into a normal population, in which mating takes place at random, the proportion of this form in the second generation will be double what it was in the preceding one, but this proportion will afterwards have no tendency whatever to increase. Some other factor which favours the variety at the expense of the type form must therefore be postulated.

It appears much more reasonable to suppose that the black colour has little or nothing to do with the matter, but that the real cause lies in a constitutional hardiness, which is correlated with melanism. The black colour is such a striking feature that far too great an effect is likely to be attributed to it. Doncaster², who first made this suggestion, has observed that the banded variety of *Angerona prunaria*, var. *sordidata*, is less hardy than the type, and Bowater³ states that the melanic variety of *Odontoptera bidentata* is also the hardier. In the experiments here recorded, as well as in those dealing with *T. consonaria*, var. *nigra*, and other melanic forms, the general impression is that the melanics seem to be earlier, stronger and larger than the type forms. Moreover, there is often a slight excess of melanics in most crosses.

Some explanation is certainly necessary to account for the fact that melanic varieties occur with such frequency in urban and industrial districts. If however it be supposed that many species have "sporting," giving melanic varieties, which are hardier and more robust than the type insects, it follows that these melanics will increase rapidly at the expense of the feebler form, wherever the struggle for existence is

¹ Hardy, G. H., *Science*, N. Y., Vol. xxviii. N. S. No. 706, p. 49, July 10, 1908.

² Doncaster, L., *Ent. Rec.* Vol. xviii. p. 219, 1906.

³ Bowater, W., *Journal of Genetics*, Vol. iii. p. 299, 1914.

severest. These conditions could not be better fulfilled than in the manufacturing areas, where the woods and vegetation upon which the larvae feed have been largely destroyed and elsewhere contaminated with a chemical deposit.

E. Goodwin originally found the melanic form of *B. consortaria* in the same oakwood in North Kent in which he took the black form of *T. consonaria*. There is a mention of the Kentish form by R. South¹, which is referred to var. *humperti*, Humpert. The second line of the forewings is, however, edged with white, and there is a white sub-marginal line in the English form, but both markings are lacking in var. *humperti*. All the melanic specimens bred in these experiments had the white lines more or less well developed. E. A. Cockayne reports taking a typical ♀ at Oxshott in 1914, which had evidently paired with a melanic ♂, because the ova deposited produced about equal numbers of both forms. A virgin melanic ♀ was taken at Oxshott by the same observer in 1919. These melanics he refers to var. *consobrinaria* Bkh. There are at least two other references to captures at Oxshott, where a large proportion of melanics are said to occur every year, and another specimen was taken at Chislehurst, so that it seems to have soon spread. Mr L. W. Newman tells me that in 1916 he received a dark ♀ captured at Oxshott, which in the following year produced a number of specimens, all dark like their parent, and yet considerably lighter than the melanic form. It appears therefore that either the melanic specimens at Oxshott vary considerably, or else an intermediate form must exist. Two of these dark Oxshott insects are shown in Plate XIII, Figs. 3 and 9.

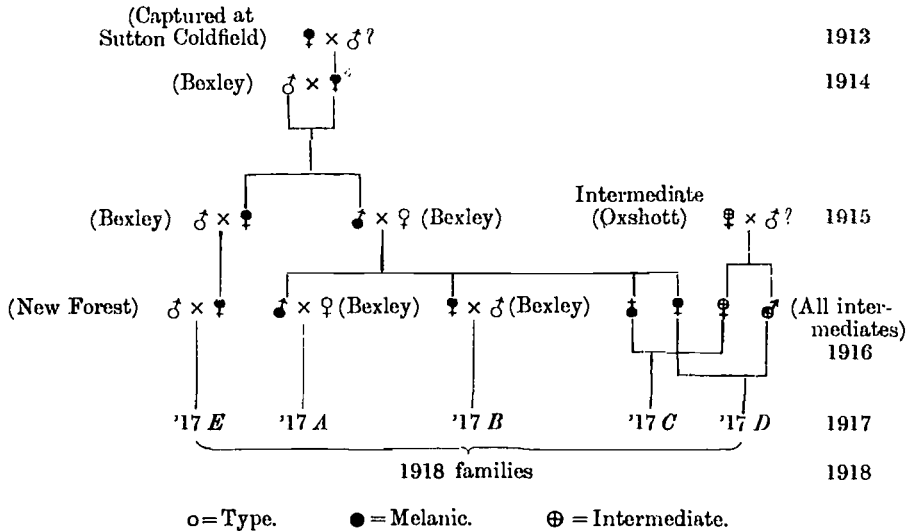
The original melanic stock which supplied material for these experiments was a melanic ♀ from Mr Newman captured at Sutton Coldfield in 1914. This appears to be the first record in Britain of a specimen of the melanic variety being taken outside Surrey. Though all the Surrey specimens may have spread from the original mutant in the Kentish oakwood, it is hardly likely that a specimen could have reached Warwickshire, unless by the aid of man, so it seems legitimate to suppose that this race must have originated *de novo*; this time, be it observed, in the close proximity of Birmingham. The pedigree on the next page gives the parentage of the families dealt with in this paper.

It will be seen that Mr Newman paired two of the intermediate Oxshott insects with two melanic specimens of the Sutton Coldfield strain, and two of the latter strain were paired to type insects. Three of the resulting families are shown on p. 344 (i.e. '17 A, '17 B, '17 D).

¹ South, R., *Moths of the British Isles* (F. Warne, 1909).

GENEALOGICAL TABLE.

B. consortaria and var. *consobrinaria*.



Family '17 C came from a pairing of an intermediate ♀ (Oxshott) × melanic ♂ (Sutton Coldfield). Instead of producing the expected 50 per cent. melanic, it gave only 4 melanics and 63 type. As this result is quite unlike any of the later broods obtained, it has not been entered in the tables, on account of the possibility of confusion before the ova were sent. Moreover, I have not seen the parents, and there is always the chance that the ♂ parent may have been a dark intermediate and not a melanic. It should be mentioned that Mr Newman reported getting 4 per cent. melanics from pairings between the original melanics and type insects.

It is quite possible that some of the specimens in '17 C and '17 D may have been intermediate like one of their parents, but as they were most of them used for breeding, the specimens were rubbed, and it was impossible to judge them accurately. One of the 1918 families, however, '18 L, instead of producing equal numbers of melanics and types, as was expected, gave melanics and a distinct intermediate form, which was a peculiar dark brown, quite unlike all other specimens. This form is illustrated in Plate XIII, Figs. 4 and 10. Comparison between Figs. 3 and 9 and Figs. 4 and 10 shows the latter to be not unlike the dark variety from Oxshott, though slightly paler, forming as it were a link

with the types. The type specimens (Figs. 1, 2, 7 and 8) all vary appreciably. The females are certainly greyer than the males, many of which have a pale buff line giving the whole insect a slightly yellow appearance. The darkest type specimen bred is shown in Fig. 8. There were only a few insects as dark as this, but there is always the possibility that they may have been specimens of the dark intermediate form. A number of pairings were carried out with the 1917 families, crosses being made with the melanic strain and a race of type insects from pupae collected in the New Forest. The average appearance of these insects, one of which is illustrated in Fig. 2, is much the same as that of the types extracted from the melanics, a typical specimen of which is shown in Fig. 7. The melanics were all of a deep grey with a white sub-marginal line, as shown in Figs. 5, 6, 11 and 12. There was some variation, certain insects being even paler than Fig. 11, but they were all without exception quite distinct from both type and intermediate specimens, chiefly owing to the lack of any pattern, even in the palest insects. This difference, though very distinct soon after emergence, when all records were made, gets much fainter after the insects have been dried some months.

The larvae proved very hardy, especially the melanic race. They were fed entirely with oak, upon the hard, older leaves of which they thrived remarkably well. They were kept in the usual glass breeding cylinders, and in the spring of 1919 over a thousand insects emerged.

The result of mating together melanics, both of which were evidently heterozygous, was as follows:

Melanic × *Melanic*.

DR × *DR*.

Family	Imagines					
	Melanic			Type		
	Male	Female	Totals	Male	Female	Totals
'18 G	19	15	34	12	10	22
'18 H	3	12	15	3	5	8
'18 I	10	11	21	2	2	4
'18 J	23	27	50	13	8	21
Totals	...		120 (69%)			55 (31%)
Expectation			131.25			43.75

Unfortunately, no matings could be made with homozygous melanics¹,

¹ Through the courtesy of Prof. J. W. H. Harrison, who has bred this species extensively, I am enabled to say that in 14 broods of melanic by melanic, he obtained 662 melanic ♀♀ and 653 melanic ♂♂, but no types.

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as all the melanics in the previous year had been paired to types. Several matings of this description have however now been made, and the results will be known next summer. The expected ratio of 3:1 is not very closely approached in the above table, there being an excess of nearly 6 per cent. of types, which is unusual. The numbers are however not very large, but clearly the divergence is due principally to family '18 G, which from the ratio of the offspring might almost belong to the DR × RR type of mating.

The result of mating heterozygous melanics by type was as follows :

		<i>Melanic × Type.</i>								
		<i>DR × RR.</i>								
		Imagines								
					Melanic			Type		
Family	Bred by	Female	×	Male	Male	Female	Totals	Male	Female	Totals
1914	E. Cockayne	Type (Oxshott)	×	♂?	18	25	43	21	19	40
'17 A	Ova from	Type	×	Melanic	1	7	8	14	8	22
	L. Newman	(Bexley)		(Sutton Coldfield)						
'17 B	"	Melanic	×	Type	12	5	17	4	8	12
	"	(Sutton Coldfield)		(Bexley)						
17 D	"	Melanic	×	Dark Intermediate	14	14	28	10	3	13
	"	(Sutton Coldfield)		(Oxshott)						
'17 E	H. O.	Melanic	×	Type	10	8	18	11	14	25
	"	(Sutton Coldfield)		(New Forest)						
'18 Z*	H. O.	?	×	?	11	18	29	11	9	20
'18 B	H. O.	Type	×	Melanic	7	5	12	7	3	10
	"	(ex '17 C)		"						
'18 C	H. O.	Type	×	Melanic	4	10	14	4	9	13
	"	(ex '17 A)		"						
'18 D	H. O.	Type	×	Melanic	49	64	113	60	49	109
	"	(ex '17 C)		"						
'18 E	H. O.	Type	×	Melanic	5	3	8	5	2	7
	"	(ex '17 C)		"						
'18 F	H. O.	Melanic	×	Type	24	22	46	23	25	48
	"	"		(ex '17 E)						
'18 M	H. O.	Type	×	Melanic	4	6	10	9	6	15
	"	(New Forest)		"						
'18 N	H. O.	Melanic	×	Type	16	18	34	18	13	31
	"	"		(New Forest)						
'18 L	H. O.	Melanic	×	Type	35	27	62	43	17	60
	"	"		(New Forest)						
Totals					442 (51%)			425 (49%)		
<i>Expectation</i>					433.5			433.5		

* The ova from this pairing were given to Mr W. Moore, who very kindly reared them for me and showed me the resulting specimens. The identity of the parents, however, has unfortunately been lost.

The melanics were all bred from one or other of the 1917 melanic × type or melanic × intermediate pairings, shown in the pedigree. In

five cases the type parents come from 1917 pairings of melanic × type, which are indicated in brackets, and in all other cases they come from wild pupae. The expected ratio of half and half is seen to be approached very closely, and there is probably little doubt that the previous table would not have shown such a wide divergence, had the numbers been as considerable. The last family in the table, '18 *L*, the numbers of which have been printed in italics, produced, not melanics and types, but melanics and intermediates (see Plate XIII, Figs. 4 and 10) in equal numbers. As has been said, this dark form, though slightly darker than the Oxshott strain, was probably introduced by it, since the melanic ♀ parent came from (Oxshott) ♀ × (Sutton Coldfield) ♂. A number of further matings have, however, been carried out with this form, and the results, if they prove of any interest, will be published in due course.

Attention should perhaps be called to the curious inverse relationship between sex and colour in some of the above matings, there being an excess of one sex in the melanic offspring, and an excess of the other sex in the type offspring. This occurs in families 1914, '17 *A*, '17 *B*, '17 *E*, '18 *D* and '18 *M*, there being as a rule an excess of melanic ♀♀ and of type ♂♂ when the ♀ parent is a type, and an excess of melanic ♂♂ and type ♀♀ when the ♀ parent is melanic. It is quite probable that this relationship may be fortuitous, as it does not occur in nearly all the families. Nevertheless, '17 *A*, '17 *B*, and '17 *E* are all descended from the same strain of melanic parents, and in both the families '18 *M* and '18 *D*, the melanic parent comes from '17 *E*.

A small number of type insects were also paired together, and as was expected, they all gave nothing but types.

Type × Type.

RR × RR.

Family	Bred by	Female ×	Male	Imagines					
				Melanic			Type		
				Male	Female	Totals	Male	Female	Totals
'17 <i>T</i>	Ova from L. Newman	Type × (Bexley)	♂ ?	—	—	—	8	6	14
'18 <i>A</i>	H. O.	Type × (ex '17 <i>A</i>)	Type (ex '17 <i>C</i>)	—	—	—	62	43	105
'18 <i>Q</i>	H. O.	Type × (ex '17 <i>D</i>)	Type (New Forest)	—	—	—	45	23	68
'18 <i>K</i>	H. O.	Type × (ex '17 <i>B</i>)	Type (ex '17 <i>D</i>)	—	—	—	43	45	88
		Totals	—	—	—	—	275

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The breeding of the above parents may be found from the genealogical table. The ♀ parent of '18 *Q* was selected, as being one of the darkest types, similar to Fig. 8, Plate XIII. Both parents of '18 *K* were the same shade, nevertheless only a few per cent. of the offspring approached the same depth as their parents.

It can be concluded, therefore, that in the case of *B. consortaria*, as in that of *T. consonaria*, the melanic variety is a simple mendelian dominant.

My thanks are due to Mr L. W. Newman for supplying me with my original material. I am also indebted to Professor Harrison, Professor Doncaster and Professor Punnett for help in the preparation of this paper, and to Miss Helen Moodie for her constant care of the larvae.

DESCRIPTION OF PLATE XIII.

Boarmia consortaria and var. *consobrinaria*. Natural size.

1. *B. consortaria* ♂. Type, bred from type × melanic.
2. *B. consortaria* ♂. Type (New Forest).
3. *B. consortaria* ♂. Dark intermediate from Oxshott.
4. *B. consortaria* ♂. Dark brown intermediate from family '18 *L*.
5. Var. *consobrinaria* ♂. Melanic.
6. Var. *consobrinaria* ♂. Melanic.
7. *B. consortaria* ♀. Type, bred from melanic × melanic.
8. *B. consortaria* ♀. Type.
9. *B. consortaria* ♀. Dark intermediate from Oxshott.
10. *B. consortaria* ♀. Dark brown intermediate from family '18 *L*.
11. Var. *consobrinaria* ♀. Melanic.
12. Var. *consobrinaria* ♀. Melanic.

