INHERITANCE OF WING COLOUR IN LEPIDOPTERA.

II. MELANISM IN *TEPHROSIA CONSONARIA* (VAR. *NIGRA* BANKES).

By H. ONSLOW.

(With Plate II.)

In a previous communication[1] the writer described a case of variation in *Abraxas grossulariata*, involving a change in the pigment of the normal ground-colour, from white to yellow. The present note deals with an example of melanism, one of the most remarkable phenomena of variation, because of its recent rapid progress in England and on the Continent. In an article by Bowater[2] evidence is given, showing that the melanic variety of *Odontoptera bidentata*, though somewhat variable in intensity, is dominant to the ordinary pale form. The same author summarises most of the available breeding experiments carried out with other melanic varieties. Though the published evidence is scanty and often obscure, he concludes that melanism may sometimes be recessive, but that it is more frequently dominant to the type form.

Melanism is widely distributed among the Geometridae, and is especially frequent in the sub-family Boarmiinae, a great number of which have melanic forms. Among other species the following are at present being investigated, and the results will shortly be published: *Boarmia abietaria*, *Boarmia consortaria*, and *Tephrosia consonaria*. The last-mentioned species forms the subject of the present communication.

The experiments were planned so that the inheritance of melanism might be studied on a much larger scale than is possible by compiling the published accounts of chance experiments. The primary object, however, was to select two species, preferably closely related, in one of

[1] Onslow, H., *Journal of Genetics*, Vol. VIII. No. 4, p. 209, Sept. 1919.
[2] Bowater, W., *Journal of Genetics*, Vol. III. p. 299, April 1914.

which melanism was dominant, and in the other recessive to the type form. It was then proposed to carry out a chemical study of the metabolism of the adult larvae and the pupae of these two species, in the hope that some light might be thrown on the mechanism responsible for such dissimilar phenomena, and possibly on the wider problem of the chemical aspect of the laws of heredity.

The history of the melanic form of *T. consonaria* (the Square Spot) is not without interest, the most important point being, that it has, as far as I can ascertain, only been found in a single locality, and one moreover which is very far removed from the traditional home of melanic varieties, the Black Country.

In 1892, E. Goodwin first found this form, subsequently described as var. *nigra*[1], in an oak wood at Wateringbury near Maidstone, and it is said to have occurred there every year up to the present. The locality is referred to by various authors as North Kent and West Kent, but I understand the same oak wood is intended. The following interesting details are given[2].

Ova obtained from normal females in the affected district yielded about 10 °/₀ melanic; ova from black females yielded from 30 °/₀ to 75 °/₀ melanic, averaging about 50 °/₀. Black ♀ × black ♂ gave 38 melanic and 4 typical.

Since it is clear from the experiments hereafter recorded that var. *nigra* is a simple Mendelian dominant, these figures require some explanation, because at first sight it might be thought that since normal females give 10 °/₀ melanic, the black form is recessive. If var. *nigra* is dominant, the least number of melanics that could be produced from a type ♀ mated to a melanic ♂ is 50 °/₀, supposing the male to be heterozygous. The only explanation, therefore, is that the females were fertilized by type as well as by melanic males. It is to be expected that black females should give 75 °/₀ melanic, if both parents were heterozygous. Black females giving 30 °/₀ melanic might possibly be heterozygotes paired to a normal male, in which case the expectation would be 50 °/₀, but it seems more probable that here again the females have paired at least twice, that is to say, to a melanic and to a normal male, and that the ova have been fertilized by the spermatozoa of both, which have become mixed in the spermatheca. That males will pair several times is well known. In 1918, for instance, I had two *Abraxas grossulariata* males, var. *varleyata*. One of them paired no less than 9 times,

[1] Bankes, E. R., *Ent. Mag.*, London, Vol. XLI. p. 89, 1905.
[2] Doncaster, L., *Ent. Record*, Vol. XVIII. p. 223, 1906.

though none of the pairings were fertile. The other paired 5 times, the first two pairings being sterile and the last three pairings fertile. The female does not often pair twice, but I have more than once seen this occur, though in breeding the female is usually isolated as soon as fertilized.

The appearance of the type and melanic insects in the following experiments is shown on Plate II. The melanic females are a deep black (figs. 4 and 5), the melanic male is rather browner (fig. 6), the antennae being very slightly pectinated. In both sexes the veins are traced in deeper black, especially noticeable when freshly emerged. The characteristic "square spot" between the second and third submarginal lines is naturally invisible, but usually a pale wedge-shaped marking, more pronounced in the female than in the male, makes its appearance just at the inner margin of the square spot. The only other white marking is a faint wavy line on all four wings, which in the type insect is situated at the outer margin of the square spot. All the type insects, extracted from melanics, were greyer and less ochreous than is usually the case with wild individuals. This is especially noticeable in the female (figs. 1 and 2), in which the speckling is grey and many of the markings black. The males tend to be browner and the markings are slightly blurred and indistinct. Fig. 3 represents one of the darker males, but none of these in any way approached the melanic series.

I am indebted to Mr L. W. Newman for procuring me the melanic ova for experimental purposes, and it is with his permission that I publish the following details. In June 1914 a wild melanic ♀ and several type ♂♂ were taken in the oak wood at Wateringbury. After capture, the ♀ deposited ova, and from the larvae which resulted, three melanic insects emerged in 1915, 2 ♀♀ and 1 ♂. With these, three fertile pairings were obtained, the melanic ♂ pairing twice; the larvae all did well and the following insects emerged in 1916:

	Parentage			Imagines	
Family	Female		Male	Melanic	Type
'15 *C*	*M*	×	*M*	95	—
'15 *A*	*M*	×	*T*	89	1
'15 *B*	*T*	×	*M*	132	3
	Totals	...	...	316	4

The larvae were not kept under experimental conditions, and the four type insects recorded were possibly introduced by accident. The fact that no type insects appeared in families '15 *A* and '15 *B* suggests that the melanic parents were homozygous for the melanic factor. If this were so, the original captured ♀ must have paired with a wild melanic ♂.

Fig. 1 gives a schematic representation of the history of the strain, showing how the 1918 families were descended from the original stock. Each family is labelled with a distinctive letter, and the year in which the ova were laid.

GENEALOGICAL TABLE

of *T. consonaria* and var. *nigra.*

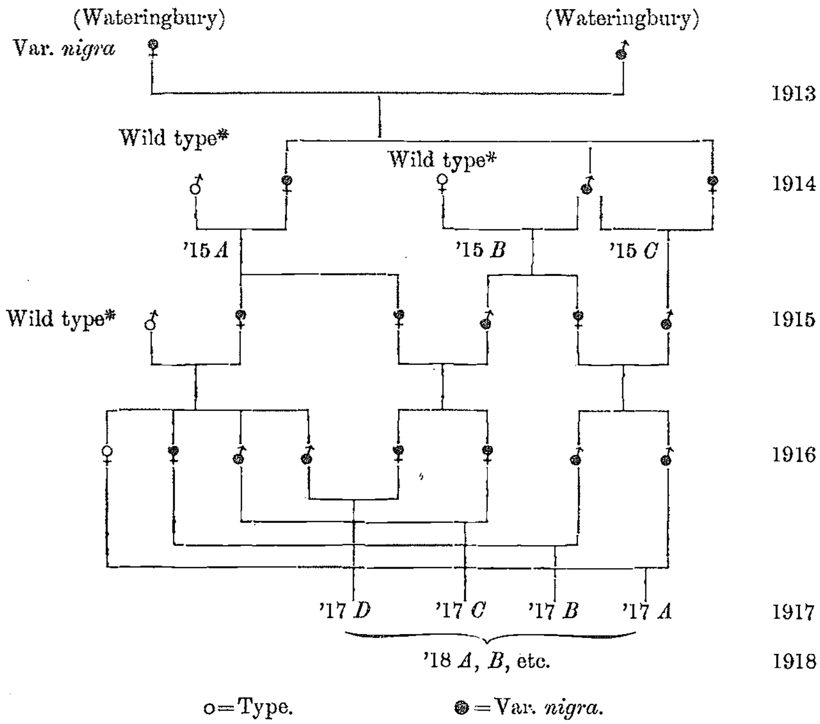

Fig. 1. Schematic representation of the relationship of the 1918 families of *T. consonaria* and var. *nigra* to the original stock.

* Captured in the same oak wood at Wateringbury.

In 1918 a sufficient number of insects were obtained to make all the necessary pairings. The larvae are very hardy and remained almost free from dysentery and other diseases. The species seems to withstand a certain amount of inbreeding without showing any ill effects. The eggs were kept in metal boxes, in which the young larvae were allowed to remain a fortnight. They were then transferred to the ordinary type of glass breeding cylinders. Since the larvae will only eat the tenderest oak leaves, sycamore (*Acer pseudoplatanus*) was largely used towards the end of June, when the larvae commence "feeding-up." It is, however, sometimes possible to get a supply of adventitious oak shoots, from trees which have been stripped some time previously by any small Geometer. The pupae were allowed to remain in the leaf-mould and sand in which they pupated, until the following spring. Over one thousand insects emerged in 1919, and are shown in the following tables. When the type insects used for pairings were not extracted from melanics, they came from wild pupae collected in Buckinghamshire.

The result of pairing two melanics, at least one of which was homozygous, was as follows:

Melanic × *Melanic* [*DD* × *DD* (*R*)].

		Imagines					
		Melanic			Type		
Family	Bred by	Male	Female	Totals	Male	Female	Totals
'15 *C*	L. W. Newman	—	—	95	—	—	—
'18 *M*	H. O.	47	51	98	—	—	—
	Total			193	—	—	—

The result of pairing two melanics, both of which were heterozygous, was as follows:

Melanic × *Melanic* [*DR* × *DR*].

		Imagines					
		Melanic			Type		
Family	Bred by	Male	Female	Totals	Male	Female	Totals
'17 *B*	H. O. ...	9	7	16	3	4	7
'17 *C*	H. O. ...	3	5	8	1	1	2
'17 *D*	H. O. ...	5	5	10	2	—	2
'18 *L*	H. O. ...	30	22	52	13	11	24
'18 *R*	H. O. ...	13	12	25	3	1	4
	Totals ...			111 (74 °/$_{o}$)			39 (26 °/$_{o}$)
	Expectation			*112·5*			*37·5*

The percentage of types to melanics is very close to the expected ratio 75 : 25.

The result of mating homozygous melanics to types should give nothing but melanics. The result was, however, as follows:

Melanic × *Type* [*DD* × *RR*].

	Parentage				Imagines: Melanic			Imagines: Type		
Family	Female	×	Male	Bred by	Male	Female	Totals	Male	Female	Totals
'15 *A*	*M*	×	*T*	L. W. Newman	—	—	89	—	—	1
'15 *B*	*T*	×	*M*	L. W. Newman	—	—	132	—	—	3
'17 *A*	*T*	×	*M*	H. O.	3	7	10	—	—	—
'18 *B*	*M*	×	*T*	H. O.	54	27	81	1	—	1
'18 *K*	*T*	×	*M*	H. O.	3	4	7	—	—	—
'18 *T*	*M*	×	*T*	H. O.	9	6	15	—	—	—
				Totals	...	...	334			5

Five types are recorded. Four of them occurred in the pairings made by Mr L. W. Newman, that is to say, before the larvae were kept under experimental conditions, and had possibly strayed from some other source. The percentage of types included in the later families is less than 1 per cent.

The type parents of families '15 *A* and '15 *B* above were captured in the same wood as the original melanic ♀. The type parents of '17 *A* and '18 *T* were extracted from melanics. The type parents of '18 *B* and '18 *K* were wild insects from pupae collected in Buckinghamshire.

The result of pairing heterozygous melanics with types, either way, gives almost exactly 50 °/₀ melanic and 50 °/₀ type, as follows:

Melanic × *Type* [*DR* × *RR*].

	Parentage				Imagines: Melanic			Imagines: Type		
Family	Female	×	Male	Bred by	Male	Female	Totals	Male	Female	Totals
'18 *A*	*M*	×	*T*	H. O.	43	27	70	32	38	70
'18 *C*	*T*	×	*M*	H. O.	15	17	32	12	17	29
'18 *G*	*M*	×	*T*	H. O.	13	12	25	10	18	28
'18 *H*	*M*	×	*T*	H. O.	7	8	15	9	9	18
'18 *I*	*T*	×	*M*	H. O.	6	3	9	6	10	16
'18 *N*	*M*	×	*T*	H. O.	12	8	20	2	8	10
'18 *Q*	*T*	×	*M*	H. O.	4	9	13	3	8	11
'18 *V*	*M*	×	*T*	H. O.	13	20	33	4	22	26
				Totals ...	...		217 (51 °/₀)			208 (49 °/₀)
				Expectation	...		*212·5*			*212·5*

The type parents of families '18 *A*, *C*, *G*, *H*, *I*, *V* were wild type insects. Those of families '18 *N* and '18 *Q* were types extracted from melanics. In this and the previous cases reciprocal crossings were obtained, but it appears to make no difference which parent was melanic and which type. The sexes have also been separated in each family, but the proportions appear to have no significance.

The result of pairing two types together is to produce nothing but types, whether the parents are extracted from melanics or not, as follows:

Type × *Type* [*RR* × *RR*].

		Imagines					
		Melanic			Type		
Family	Bred by	Male	Female	Totals	Male	Female	Totals
'17 *E*	H. O.	—	—	—	4	8	12
'18 *F*	H. O.	—	—	—	58	53	111
'18 *O*	H. O.	1	1	2	50	40	90
'18 *P*	H. O.	—	—	—	23	33	56
			Totals ...	2			269

In family '17 *E* both parents were wild types; in family '18 *F* the ♂ parent was an extracted type; in families '18 *O* and '18 *P* the ♀ parents were extracted types. In this case again less than 1 °/$_o$ of melanic insects have been included accidentally[1]. The eggs are so exceedingly small that it is extremely easy to transfer one inadvertently to the wrong box in the hairs of the brush.

The evidence from the above experiments, which include over 1,400 insects, shows that the melanic variety of *T. consonaria* behaves as a simple Mendelian dominant with regard to the pale type form. Moreover the melanics are a perfectly definite class and show no tendency to vary in either direction.

In conclusion I should like to express my thanks to Mr L. W. Newman for supplying me with the material, and some of the details mentioned above, and to Miss Helen Moodie for her care of the larvae, to which the size of the families is entirely due.

[1] (Note added Nov. 25, 1919.) Professor J. W. H. Harrison, whose work on this species will be published shortly, tells me he has had occasional melanics from pure type pairings, and *vice versa*, which could not be attributed to accident, as they occurred in single test broods. With the possible exception of the 1915 broods (p. 55) I have been unable to exclude the possibility of error.

DESCRIPTION OF PLATE II.

Tephrosia consonaria and var. *nigra*. $1\frac{1}{2}$ times natural size.

1. *T. consonaria* ♀. Type, bred from var. *nigra*.
2. *T. consonaria* ♀. Type, bred from var. *nigra*.
3. *T. consonaria* ♂. Type, from *T. consonaria* ♀ × var. *nigra* ♂.
4. Var. *nigra* ♀.
5. Var. *nigra* ♀.
6. Var. *nigra* ♂.

PLATE II