GENETIC CONTROL OF THE MELANIC FORMS OF THE MOTHS *DIURNEA FAGELLA* AND *ALLOPHYES OXYACANTHAE*

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SUMMARY

The melanic forms, *dormoyella* of the moth *Diurnea fagella* and *capucina* of the moth *Allophyes oxyacanthae*, are both controlled by single genes, completely dominant in expression to the respective typical phenotypes. The intermediate form of *A. oxyacanthae* is not inherited at the same locus as *capucina*. Distortions in the melanic: typical segregation ratios among the female progeny of some of the families of *A. oxyacanthae* indicate viability differences between the sexes which could possibly result in a difference between the relative fitnesses of heterozygous and homozygous *capucina*.

1. INTRODUCTION

THE melanic forms which increased in frequency in many moth species during the last century have almost always been found to be inherited at a single locus, with complete dominance of the melanic phenotype over the paler typical phenotype (Bowater, 1914; Onslow, 1921; Lees, 1974). In many species distinct forms, intermediate in darkness between the melanic and typical phenotypes, occur and in both *Biston betularia* (Clarke, and Sheppard, 1964; Lees, 1968) and *Phigalia pilosaria* (Lees, 1974) these are controlled at the same locus as the melanic forms. However, in both *P. pilosaria* (Lees, 1971) and *Gonodontis bidentata* (Kettlewell, 1959) there are "dark typical" forms which seem to be under polygenic control.

The work described in this paper was carried out to investigate the genetic control of f. *capucina* of *Allophyes oxyacanthae* and f. *dormoyella* of *Diurnea fagella*. Dr D. R. Lees (personal communication; Kettlewell, 1973) has reared families of *A. oxyacanthae* and obtained evidence that *capucina* is inherited as a single gene. No previous work on the genetics of the melanic forms of *D. fagella* seems to have been published.

2. GENETIC CONTROL OF THE FORMS OF *D. fagella*

In the typical form the forewings are white or pale yellow and are overlaid with a speckling of black scales. In *dormoyella*, the wings are mainly black, with a fine scattering of white scales, a thin transverse white line and a white fringe on the outer margin of the wing. The rest of the body is also affected by the darkening. In addition there is an intermediate (or "dark typical") form which is clearly distinct from *dormoyella* but which tends to overlap with the typical phenotype. In this intermediate form, dark speckling of the typical pattern is increased and there is a brown band across the middle of the forewing.

The parentage and progeny of the families, which were all reared on beech (*Fagus sylvatica*), are shown in table 1. If *dormoyella* is controlled by a single dominant gene, then the melanic offspring of F/1/73 must have been heterozygotes. A cross between two melanics from this family produced a segregation of *dormoyella* and typical (F/1/74) not significantly different from the expected 3 : 1 ratio, indicating that *dormoyella* is inherited as a simple Mendelian dominant. The segregations of approximately 1 melanic : 1 non-melanic in F/2/74 and F/3/74 are consistent with this suggestion.

The segregation of intermediates and *dormoyella* in F/2/74 indicates that the phenotypes are clearly distinct. The variability in the intermediate phenotype suggests that it may represent polygenic darkening of the typical phenotype.

3. GENETIC CONTROL OF THE MELANIC FORMS OF *A. oxyacanthae*

In the typical form the forewings are light brown or brown, with paler oval markings and areas of green scales. In *f. capucina* the ground colour of the wings varies from chocolate-brown to blackish-brown and there are no green scales, although there may be a few scattered yellow scales. There is a distinct form, referred to as "intermediate" by Kettlewell (1973), which has uniform pale brown forewings with the areas of green scales of the typical form replaced by yellow scales.

The parents and progeny of the families, which were fed on hawthorn (*Crataegus monogyna*), are shown in table 2. The larvae were all reared under the same conditions in a cool, unheated room and fresh foliage was always present in the rearing containers.

In 1973, six crosses of *capucina* × typical were reared. Of these, five families (0/1, 0/3, 0/5, 0/11 and 0/13) segregated for *capucina* and typical; in each family the ratio of *capucina* : typical was not significantly different from 1 : 1 (table 2). Two crosses were of melanic male × typical female, while the other three crosses were melanic female × typical male. The segregation of *capucina* and typical in both sexes in each family indicates that the inheritance of the *capucina* form does not involve *X* or *Y* linkage. The other family, 0/6, produced 25 offspring, all *capucina*, indicating that *capucina* is controlled by a single dominant gene and that the melanic parent of 0/6 was homozygous. This was confirmed by the segregation of *capucina* and typical in the five *capucina* × *capucina* crosses in 1974. In each family the segregation ratio was not significantly different from 3M : 1T. In table 2 the segregation ratios for each family, and for the total progeny of several families involving the same type of mating, are tested against the expected segregation ratio (1 : 1 or 3 : 1).

Examination of the variation in the darkness of the melanics in the families suggested that this was continuous. The melanic progeny of a "light" *capucina* parent showed a similar range in variation to the progeny of a "dark" *capucina* parent. Kettlewell (1973) states that a melanic form, darker than *capucina*, is spreading in some areas but all of the *capucina* seen in the *British Museum* (N.H.) Lepidoptera Collection were within the range of variation observed in the 22 families reported here. A similar range of darkness of the *capucina* phenotypes was observed in the *capucina* × typical families as was seen in the *capucina* × *capucina* families, indicating that *capucina* homozygotes are not darker than the heterozygotes.

TABLE 1
Origin of parents, and progeny of families of Diurnea fagella reared in this study

Family	Male parent	Female parent	Progeny of the families						χ^2
			Dormoyella		Typicals		Intermediates		
			Males	Females	Males	Females	Males	Females	
F/1/73	Melanic ex Stroud	Typical ex Stroud	3	1	2	0	0	0	—
F/1/74	Melanic ex F/1/73	Melanic ex F/1/73	16	8	4	1	0	0	0.56 ($\times 3 : 1$)
F/2/74	Unknown	Intermediate ex Savernake	10	8	0	0	17	7	0.60 ($\times 1 : 1$)
F/3/74	Typical ex Trelleck	Melanic ex Trelleck	22	26	28	26	0	0	0.25 ($\times 1 : 1$)

TABLE 2
Families of Allophyes oxyacanthae reared in this study

Family	Male parent	Female parent (Expected 1 : 1)	Progeny				χ^2
			Melanics		Typicals		
			Males	Females	Males	Females	
(a) Melanic $\times$ Typical crosses which segregated.							
0/1/73	Typical ex Oxford	Melanic ex Risca	23	22	25	30	1.00
0/3/73	Typical ex Oxford	Melanic ex Cardiff	26	25	24	30	0.09
0/5/73	Typical ex Oxford	Melanic ex Abercanaid	6	5	6	7	0.17
0/11/73	Melanic ex Oxford	Typical ex Swansea	10	9	11	8	0.00
0/13/73	Melanic ex Oxford	Typical ex Oxford	41	49	46	50	0.19
0/21/74	Melanic ex 0/1/73	Typical ex 0/3/73	25	17	19	27	0.18
0/22/74	Typical ex 0/3/73	Melanic ex Mountain Ash	52	58	35	53	2.44
0/25/74	Melanic ex 0/3/73	Typical ex 0/1/73	26	37	21	22	3.77
0/27/74	Typical ex Mountain Ash	Melanic ex 0/1/73	30	33	33	29	0.01
0/31/74	Melanic ex 0/1/73	Typical ex 0/3/73	26	16	28	35	4.20
0/32/74	Typical ex 0/3/73	Melanic ex 0/1/73	16	14	17	16	0.14
0/33/74	Typical ex 0/15/73	Melanic ex 0/15/73	8	5	9	7	0.31
0/35/74	Melanic ex 0/3/73	Typical ex 0/1/73	20	23	18	14	1.61
0/37/74	Typical ex Mountain Ash	Melanic ex 0/1/73	33	40	35	24	1.49
Total progeny			342	353	327	352	0.19
(b) Melanic $\times$ Melanic crosses which segregated. (Expected 3 : 1)							
0/23/74	Melanic ex 0/3/73	Melanic ex 0/1/73	51	54	17	20	0.12
0/24/74	Melanic ex 0/3/73	Melanic ex 0/1/73	52	49	17	15	0.06
0/26/74	Melanic ex 0/3/73	Melanic ex 0/1/73	49	55	19	21	0.59
0/28/74	Melanic ex 0/1/73	Melanic ex 0/3/73	30	24	6	10	0.17
0/29/74	Melanic ex 0/13/73	Melanic ex 0/11/73	56	45	12	21	0.01
Total progeny			238	227	71	87	0.04
(c) Other crosses. (Expected ratio for 0/6 and 0/15, 1 : 1)							
0/4/73	Melanic ex Risca	Melanic ex Abercanaid	46	32	0	0	—
0/6/73	Melanic ex Risca	Typical ex Oxford	13	12	0	0	23.04
0/15/73	Intermediate ex Oxford	Melanic ex Risca	24	23	38	30	3.48

The male parent of 0/15 was the only intermediate used as a parent in the matings. This specimen had uniform pale brown forewings with scattered yellow scales. The absence of green scales distinguishes the intermediate form from the normal range in variation of the typical phenotype, while the reflectance of the forewing clearly distinguishes the intermediate and *capucina* phenotypes. The forewing reflectances of a sample of six *capucina* and six typicals from 0/15 and 0/13, and of the intermediate parent of 0/15, were measured using an S.E.I. exposure photometer. For *capucina*, the range in reflectance was from 5.0 per cent to 7.0 per cent and for typical the range was from 10.7 per cent to 18.0 per cent. The reflectance of the intermediate form was 10.1 per cent.

The segregation in 0/15 was not significantly different from a 1 : 1 ratio of *capucina* : typical ($X^2_1 = 3.48$, $0.1 > P > 0.05$). None of the progeny of 0/15, nor of 0/33, which resulted from a mating between two offspring of 0/15, resembled the intermediate male parent of 0/15. The failure of intermediates to segregate in either 0/15 or 0/33 indicates that this form is not controlled by another allele at the *capucina* locus. If the intermediate form were controlled by an allele, recessive to both *capucina* and typical, then $\frac{1}{4}$ of the offspring of 0/33 would be expected to have been intermediate. The results indicate that the male parent of 0/15 was genotypically "typical" and that the intermediate phenotype was produced by modifiers or environmental effects.

4. DISCUSSION

The results for *dormoyella* and *capucina* are in agreement with Ford's (1937) suggestion that industrial melanism in the Lepidoptera will usually involve completely dominant melanic genes. Surveys in southern Britain indicate that both of these forms reach their highest frequencies in urban and industrial areas (Steward, 1977*b*). Ford (1937, 1940) suggests that melanic heterozygotes may have some physiological advantage over typicals but estimation of relative fitnesses of the genotypes from the results of laboratory rearing involves many problems.

For *A. oxyacanthae*, considering the totalled results for both sexes, there is no evidence of any consistent deviation from the expected 1 *capucina* : 1 typical segregation ratio among the progeny of the 14 crosses of *capucina* $\times$ typical (table 2a). Similarly, the five crosses of heterozygous *capucina* $\times$ heterozygous *capucina* (table 2b) show an overall segregation ratio not significantly different from the expected ratio of 3 *capucina* : 1 typical. However, if the segregation ratio within each sex is examined, there is evidence of important viability differences between the sexes.

The segregation ratio within each sex was tested against an expected 1 *capucina* : 1 typical ratio for each of the 14 crosses of heterozygous *capucina* $\times$ typical. The heterogeneity of the results for different families, calculated as the sum of the individual X^2 values, minus the X^2 value for the total progeny of the 14 families, was, for the females, $X^2_{13} = 22.39$ ($0.05 > P > 0.02$), and for the males, $X^2_{13} = 5.30$ ($0.98 > P > 0.95$). There is significant heterogeneity in the female segregation ratios of these families, although the pooled results show an almost exact 1 *capucina* : 1 typical ratio. Kettlewell (1973) has emphasised the need to consider the genetic origin of the moths used as parents when examining distortions in segregation ratios.

The largest deviations from the expected 1 : 1 ratio, among the female progeny, occur in 0/25, which shows an excess of melanic females, and in 0/31, which shows an excess of typical females. There is evidence that the provenance of the moths affects the distortion in the female segregation ratio. Thus 0/25 and 0/35 both resulted from the mating, 0/3 *capucina* × 0/1 typical, and both produced more melanic females than typical females. 0/31, 0/21 and 0/32 resulted from the mating, 0/1 *capucina* × 0/3 typical, and each contained more typical females than melanic females. The total progeny resulting from these two types of matings are shown in table 3. In both cases the deviation from the expected 1 : 1 segregation ratio, among the female progeny, is significant. In contrast, the male progeny show no significant deviation from a 1 : 1 ratio. The segregation ratio among the female progeny resulting from mating (a) in table 3 is significantly different

TABLE 3

Capucina : typical segregation ratios among the male and female progeny resulting from three types of mating: (a) 0/1 *capucina* × 0/3 typical; (b) 0/3 *capucina* × 0/1 typical; (c) 0/3 *capucina* × 0/1 *capucina*. The results which were combined to calculate the male and female segregation ratios are not significantly heterogeneous. The expected *capucina* : typical segregation ratios are for matings (a) and (b), 1 : 1 and for (c), 3 : 1

Families	Total progeny				Segregation ratios (<i>capucina</i> ÷ typical)		χ^2_1 (against expected ratio)	
	<i>capucina</i>		typical		Males	Females	Males	Females
	Males	Females	Males	Females				
(a) 0/21, 0/31, 0/32	67	47	64	78	1.05	0.60	0.03	7.20**
(b) 0/25, 0/35	46	60	39	36	1.18	1.67	0.42	5.51*
(c) 0/23, 0/24, 0/26, 0/28	182	182	59	66	3.09	2.76	0.01	0.26

* $0.05 > P > 0.01$ ** $0.01 > P > 0.001$.

from that among the males from the same families ($X^2_1 = 4.26, 0.05 > P > 0.02$) and from that among females resulting from the other type of *capucina* × typical mating ($X^2_1 = 12.47, P < 0.001$).

The mating, 0/3 *capucina* × 0/1 *capucina* (table 3c), will combine the genotypes resulting from the two types of *capucina* × typical mating and in these families neither males nor females show any significant deviation.

However, if the expected ratio of heterozygous *capucina* : typical among the progeny of these families is assumed to be 2 : 1, then it can be seen that the estimated ratio of homozygous *capucina* : typical for the females is 0.76 : 1 and for the males is 1.09 : 1. It is again the females which show the largest distortion. This indicates that, although the combined results for both sexes may show close agreement with the expected segregation ratio, there may be important viability differences between males and females. These will have to be taken into account in any attempt to calculate relative fitness values for the melanic and typical genotypes from the rearing data. The expected ratio of heterozygous *capucina* : typical will itself be dependent on estimates of the relative fitnesses of these genotypes. Clarke and Sheppard (1963) have also found viability differences between the sexes in families of the moth, *Biston betularia*.

The differences between the segregation ratios among the female progeny

of the two types of *capucina* × typical mating in table 3 correspond with differences between the resting site selection behaviour of *capucina* from these families (Steward, 1977a). The *capucina* offspring of the parental families, 0/1 and 0/3, also showed different resting behaviour (Steward, 1976). Analysis of the resting site selections of *capucina* from different families indicates that, while genetic differences between families seem to influence this behaviour, the variation cannot be explained as simply being the result of differences between the melanic alleles segregating in the families 0/1 and 0/3 (Steward, 1977a).

For *Diurnea fagella*, the small amount of rearing carried out so far neither demonstrates nor excludes viability differences between the melanic and typical genotypes. In F/1/74, the ratio of males : females is significantly different from 1 : 1 ($X^2_1 = 4.17$, $0.05 > P > 0.02$). Both F/1/74 and F/2/74 show a deficiency of females suggesting that viability differences between the sexes may also be important in this species.

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