

TABLE 10

Results of the χ^2 tests

Mothers of type	Discrepancy between the observed and the expected distributions of phenotypes in the offspring		
	χ^2	P	Discrepancy
M	0.073	> 0.70	No
MN	22.545	< 0.001	Significant
N	1.628	> 0.10	No

5. SUMMARY

1. A sample of the population of Bosnia and Hercegovina (Yugoslavia) consisting of 616 cases of disputed paternity is examined.
2. An excess of $L^M L^N$ heterozygotes is found to exist.
3. The evidence is presented that the excess of heterozygotes is due to the excess of homospecific deliveries among MN mothers.

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HERITABILITY OF SPOT-NUMBER IN SCILLONIAN STRAINS OF
THE MEADOW BROWN BUTTERFLY (*MANIOLA JURTINA*)

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1. DATA

In the first of a long series of papers (which have been summarised by Ford (1964)) on the variability of spot-numbers in *Maniola jurtina*, Dowdeswell and Ford (1952) suggested that the stability of the frequencies of the spot-phenotypes in colonies of this grass-feeding, univoltine insect was maintained over wide areas by selective forces which were independent of considerable differences in climate, soil, etc. Attempts to demonstrate the heritability of

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spot-number in stocks obtained from the Winchester region and from other areas in England and Cornwall failed, since, in the laboratory, larvae reared from the egg succumbed to a bacterial disease, usually in the third instar.

McWhirter and Scali (1965) reported that the normal bacterial micro-

TABLE 1
Comparisons of spot-number of female progeny with mid-parent value in Scillonian strains of Maniola jurtina

Brood	Parents	Mid-parent	Spot-number of female progeny										Total	Spot-average	
			0	1	2	3	4	5	6	7	8	9			10
A	2-6	4	-	-	1	-	2	-	-	-	-	-	-	3	3.3
B	10-7	8.5	-	-	2	-	5	2	10	4	10	-	-	33	6.12
C	2-6	4	1	1	1	-	1	-	1	-	1	-	-	6	3.5
D	0-10	5	-	1	1	-	3	2	-	-	-	-	-	7	3.6

floras of larvae vary greatly according to their venue. In general, larvae from the Isles of Scilly thrive in laboratory conditions. The following data have been obtained from parents caught *in copula* in the Isles of Scilly or from Scillonian specimens reared from the fifth instar of the larval stage and mated in the open air; progenies were brought up in a cool laboratory, with temperature fluctuating about 15° C. (see tables 1 and 2).

If heritability is judged by the usual method of linear regression it is barely significant in the male progeny at 0.14; in the female progeny, however, it would be estimated at 0.63 ± 0.14 . On these small numbers

TABLE 2
Comparisons of spot-number of male progeny with mid-parent value in Scillonian strains of Maniola jurtina

Brood	Parents	Mid-parent	Spot-number of male progeny										Total	Spot-average	
			0	1	2	3	4	5	6	7	8	9			10
A	2-6	4	-	-	-	-	4	-	2	-	-	-	-	6	4.3
B	10-7	8.5	-	-	-	-	5	1	10	-	4	-	-	20	5.85
C	2-6	4	-	-	-	-	1	-	-	-	-	-	1	2	7.0
D	0-10	5	-	-	-	-	6	-	4	-	2	-	-	12	5.3

N.B.—Spot-values in tables of heritability are for both wings and so are double those given in the usual tables of flying populations.

there are serious objections to the use of this method. Inspection shows that the heritability of spot-number in female progeny far exceeds that in males. Further, the spot-phenotype of the parents has resulted from the interaction of their genotypes with influences of the natural environment, while the progenies were reared in a laboratory. If, however, the variance ratio of spot-number "within broods" and "between broods" is calculated, not only is another estimate of heritability made available, but also this estimate is free from the objections mentioned.

Tables 3 and 4 present the ratios of "between brood" and "within brood" variances of female and male progenies and confirm the high significance of heritability in the females and its apparent non-significance

in males. Further resolution of the inter-brood mean square in table 3 follows from the solution of the simultaneous equations:

$$24.72 = \frac{N^2 - \sum n_1^2}{N(k-1)} \sigma_B^2 + \sigma_A^2 \quad (1)$$

$$3.59 = \sigma_A^2 \quad (2)$$

where N is the total number of observations, n_1 is the number of observations within broods, σ_B^2 is the inter-brood variance, k is the number of broods and σ_A^2 is the intra-brood variance.

$$\text{Hence} \quad \sigma_B^2 = 2.55 \quad (3)$$

Now, since the parents of the broods were randomly sampled from large wild populations and since there is no indication from many copulations

TABLE 3
Variance ratio of female broods of Maniola jurtina

Sources of Variation	Sums of squares	d.f.	Mean square	Variance ratio
Between broods	74.15	3	24.72	6.89
Within broods	161.40	45	3.59	—
Total	235.55	48	—	P < 0.01

TABLE 4
Variance ratio of male broods of Maniola jurtina

Sources of Variation	Sums of squares	d.f.	Mean square	Variance ratio
Between broods	11.21	3	3.74	1.55
Within broods	86.56	36	2.40	—
Total	97.77	39	—	N.S.

observed that any kind of assortative mating (*qua* spot-number) takes place in the Isles of Scilly, it is reasonable to suppose that f (the co-efficient of inbreeding) is virtually nil. Thus the equations listed by Jinks and Broadhurst (1965, at p. 100) can be simplified and

$$\sigma_B^2 = \frac{1}{4}D_R + \frac{1}{16}H_R + E_2 \quad (4)$$

$$\sigma_A^2 = \frac{1}{4}D_R + \frac{3}{16}H_R + E_1 \quad (5)$$

$$\sigma_T^2 = \frac{1}{2}D_R + \frac{1}{4}H_R + E_1 + E_2 \quad (6)$$

where D_R and H_R are respectively the random mating form of the additive and dominance components of variation (as defined by Mather, 1949).

With the present limited material E_1 (non-heritable component of variation within broods) and E_2 (non-heritable component of variation between broods) are not analysed further, but it may be noted that the variance-ratio method does not distinguish the component E_c (variance due to the common environment of parents and their broods) from E_2 .

Using Mather's notation (which is translatable into that used by Falconer (1967) by equating D_R with $2V_A$; H_R with $4V_D$; E_c with V_{Ec}) the regression on mid-parent values yields an estimate of heritability based on

$$\frac{\frac{1}{2}D_R + E_c}{\frac{1}{2}D_R + \frac{1}{4}H_R + E_1 + E_2} = 0.63 \pm 0.14 \quad (7)$$

while the variance ratio method (assuming $f = 0$) gives an estimate of heritability based on double the full-sib contribution

$$\frac{\frac{1}{2}D_R + \frac{1}{8}H_R + 2E_2}{\frac{1}{2}D_R + \frac{1}{4}H_R + E_1 + E_2} = \frac{2\sigma_B^2}{\sigma_A^2 + \sigma_B^2} = \frac{5.1}{3.59 + 2.55} = 0.83 \quad (8)$$

These two ratios, of course, are estimates of heritability only if E_c and E_2 are zero, respectively.

2. DISCUSSION

It may be inferred from these estimates that in the present material H_R , due to dominance effects, or E_2 , the common environmental variation among full-sibs, is appreciable, while E_c , in view of the drastic change of environment between the P and F_1 generations, is negligible. Ordinary evolutionary processes would be expected to maximise E_c in the case of mobile animals, even in an insect which is unlikely to have developed positive feed-back from socio-genetic interaction. Micro-ecological studies of the choice of immediate environment by females, when laying eggs, and by larvae would be needed to estimate the significance of E_c in the field.

McWhirter (1957) has analysed samples from many British populations and shown that male and female spotting is strongly correlated; the spot-average is normally one higher in males than in the corresponding females. The effect of the spot-genes seems to be sex-controlled so as partially to inhibit their action in the males when passed through that sex to the F_2 generation. Further experiment is needed to analyse this situation which indeed is well known in other species of the Lepidoptera (Ford, 1964); there, however, the type of sex-control is more often an absolute rather than a partial inhibition of effect in one sex.

Sudden inter-seasonal changes of spot-distribution have occasionally been observed in England and Scilly. These have been interpreted as being due to disturbance of the normal selective forces after exceptional changes in the ecology. In one case an elimination of high-spotted females on the island of Tresco was found to be 61 per cent., with 95 per cent. confidence limits at 81 per cent. and 19 per cent. (Dowdeswell, Ford and McWhirter, 1960). The evidence of heritability of spot-numbers indicates that this approach is correct. Similarly the great stability of spot-distributions over periods exceeding 50 years and within areas extending over thousands of miles, which has been described by Dowdeswell and McWhirter (1967), should also be due, as suggested by them, to stabilising selective forces. The type of sex-control and the genetic background against which the spot-genes operate could well vary from area to area throughout the wide geographic range of the insect. Whether the pre-imaginal characters which are subject to selection are controlled by the spot-genes in the same way in all colonies is not yet known.

3. SUMMARY

1. The heritability of spot-number in the Meadow Brown Butterfly, *Maniola jurtina*, is here estimated for the first time by two methods.
2. According to one, it is 0.63 ± 0.14 in female progeny reared at about 15°C .; according to the other it is 0.83 in female progeny under the same conditions.
3. The reasons for this divergence are discussed.

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FREQUENCIES OF HAPLOIDS IN SPRING OIL-SEED RAPE (*BRASSICA NAPUS*)

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HAPLOIDS from the genus *Brassica* were reported first by Morinaga and Fukushima (1933) in the species *B. napella*, which Olsson (1954) has since shown to be in all respects identical to *B. napus*. These haploids were highly sterile and occurred fairly frequently in rape fields. Morinaga stated that "Half a day's excursion through the rape field, when the flowers are passing away, will suffice to find dozens of such haploid individuals". In Sweden Olsson and Hagberg (1955) found seven haploids in winter varieties of oil-seed rape over a four year period, but the frequency of haploids was low. Only three haploids were obtained from a 6000 square metre (about 1½ acre) propagation field of the Svalöf variety Matador after "careful and thorough investigation". These marked differences in frequency of haploids may have been determined either by environmental or by genetical factors.

In 1967 haploids were recognised at flowering time in plots of four spring varieties of oil-seed rape, *B. napus* L. ssp. *oleifera* (Metzger) at Cambridge. They were easily identified by their small, pollen-sterile flowers and very poor seed set; the stomatal guard cells from the underside of leaves from these plants were also shorter than those from diploids. Estimates of plant populations were made from counting the number of plants in 40-ft lengths of rows from two plots of each variety (all plants were counted in the small plot of the Canadian variety, Target). A much higher frequency of haploids occurred in Target than in the considerably larger populations of the other three varieties of European origin (table 1).