

THE *MEDIONIGRA* POLYMORPHISM OF *PANAXIA DOMINULA* IN 1969

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1. INTRODUCTION

THE Scarlet Tiger Moth, *Panaxia dominula* L. (Lepidoptera Hypsidae) is a warningly coloured diurnal species which usually occurs in clearly defined colonies in association with its chief larval food plant the Comfrey, *Symphytum*, Cook (1961). It is univoltine, the imagines flying throughout July and in early August. Details of the habits and ecology of the moth can be obtained from Fisher and Ford (1947) and from Ford (1967).

The *medionigra* polymorphism in this species affects spotting on both the forewing and the hindwing and is controlled by a single major gene such that the heterozygote *medionigra*, though variable, is visibly distinct from both the rare homozygote, *bimacula*, and the normal form, *dominula* (see Fisher and Ford, 1947, for illustrations of all three forms). The polymorphism has been found to occur naturally at a single locality, the marsh at Cothill in Berkshire. Several artificial colonies containing *medionigra* have, however, been established using material brought originally from Cothill (Sheppard and Cook, 1962), and Sheppard (1956) has introduced the gene at a known frequency into a previously existing colony of *dominula* at Sheepstead Hurst, Berkshire. This is only a mile away from the Cothill colony but is isolated from it (Sheppard, 1951).

At Cothill the polymorphism has been studied continuously since 1939 and at Sheepstead Hurst since 1949. Fluctuations in population size and in the frequency of *medionigra* in both colonies up to 1968 have been recorded in several places (Fisher and Ford, 1947; Sheppard, 1951, 1953, 1956; Ford, 1965; Ford and Sheppard, 1969). The purpose of this paper is to give additional information for the 1969 season.

2. OBSERVATIONS

The method of marking, releasing and recapture used by Fisher and Ford (1947) was employed to evaluate the population size at both localities. The captures were scored by using the criterion that the presence of any central spot on the hindwing, whether black or yellow, indicated *medionigra*. Details of gene frequency, population size and survival rate in the colonies at both Cothill and Sheepstead Hurst are included in table 1.

Thirty-eight *medionigra* at Cothill and twenty-five at Sheepstead Hurst were captured during the 1969 season. These were used to measure the visible effects of the *medionigra* gene before they were released into the population. The hindwing spot of this genotype is in some individuals black with a yellow penumbra while in others the area of black scales is reduced or even absent, leaving a spot which is entirely yellow (Ford, 1965). The colour of the spot was recorded for each of the 63 *medionigra* captured and measurements were taken of its maximum and minimum diameters; these two values have been multiplied to give an estimate proportional to the area of the spot on each hindwing, and an average of left and right has been

calculated. At the same time the forewing was scored for the presence, absence or reduction of the yellow mid-spot.

Table 2 contains a summary of these observations.

TABLE 1
Gene frequency, population size and survival rate at Cothill and Sheepstead Hurst

	Cothill					Sheepstead Hurst				
	<i>dominula</i>		<i>medionigra</i>		total	<i>dominula</i>		<i>medionigra</i>		total
	male	female	male	female		male	female	male	female	
Captures	246	262	20	18	546	219	290	8	17	534
<i>medionigra</i> gene-frequency	3.5 per cent.					2.3 per cent.				
Estimated seasonal population size	5712					2942				
	male	female	total			male	female	total		
Daily survival rate	0.72	0.70	0.71			0.76	0.83	0.79		

TABLE 2
Medionigra at Cothill and Sheepstead Hurst in 1969
Estimates of hindwing spot area are the product of the largest and smallest diameters of the spot

(a) Cothill	Male		Female	
	Yellow	Black	Yellow	Black
Hindwing spot colour				
Total 38	13	7	8	10
Mean area of hindwing spot \pm standard error	3.3246 \pm 0.4188 mm. ²	2.7214 \pm 0.4975 mm. ²	1.2453 \pm 0.1182 mm. ²	2.5780 \pm 0.3011 mm. ²
Mid-spot on forewing absent	0	3	0	5
Mid-spot on forewing reduced	2	2	0	1
(b) Sheepstead Hurst	Male		Female	
Hindwing spot colour	Yellow	Black	Yellow	Black
Total 25	7	1	12	5
Mean area of hindwing spot \pm standard error	2.0017 \pm 0.1234 mm. ²		1.4043 \pm 0.1100 mm. ²	1.9440 \pm 0.2954 mm. ²
Mid-spot on forewing absent	0	0	0	0
Mid-spot on forewing reduced	2	0	2	0

3. DISCUSSION

At Cothill the population size of *dominula* from 1962 to 1967 was so small and the number of recaptures was so low that the method of marking, releasing and recapture could not be employed to assess its size (Ford and Sheppard, 1969). In 1968 a slight increase to 978 became apparent and this was continued, to a much greater degree, in 1969 with an estimated value of 5712, its highest level for ten years. A smaller increase in population

size from 1968 to 1969 occurred at Sheepstead Hurst. It has previously been noticed that the numbers in these two colonies do not fluctuate synchronously (Ford, 1965).

Dowdeswell, Fisher and Ford (1949) have used the average daily survival rate, calculated when obtaining numerical estimates of populations, to compare the survival of a species (*Maniola jurtina*) in different environments. Sheppard (1951) has since applied this type of comparison to *Panaxia dominula* at Cothill and Sheepstead Hurst. He found that, in general, the survival rate at Sheepstead Hurst was higher than at the other colony, and that females have a higher survival rate than males at both places. The values he obtained at Cothill, from 1947 to 1950, were mainly lower than the average value for both sexes of 0.84 calculated by Fisher and Ford (1947) over the six years, 1941 to 1946. In 1969 at Cothill a daily survival rate for both sexes of 0.71 (0.72 males, 0.70 females) was obtained, while at Sheepstead Hurst the equivalent value was 0.79 (0.76 males, 0.83 females). These values are consistent with Sheppard's finding that *dominula* has a higher survival rate at Sheepstead Hurst.

It has been shown that fluctuations in the frequency of *medionigra* at Cothill have been due to selection, varying in intensity and direction from year to year (Fisher and Ford, 1947). No significant relationship between these fluctuations and those in population size have been found (Sheppard, 1951; Williamson, 1960). However, from 1962 to 1968 at Cothill population size and gene frequency were both at a low level and during this time a total of seven *medionigra* were captured. As a result it was possible to estimate gene frequency in only two of these eight seasons, 1965 and 1968, when values of 1.1 per cent. were obtained. At Sheepstead Hurst, Sheppard (1965) introduced the *medionigra* gene at a frequency of 0.2 per cent. in 1954 and since then it has been greater than this value in seven of the eleven years in which it has been estimated, with a maximum of 1.4 per cent. in 1967 (Ford and Sheppard, 1969).

In both colonies a sharp increase in gene frequency occurred in 1969; to 3.5 per cent. at Cothill, its highest value for twelve years, and to 2.3 per cent. at Sheepstead Hurst, a higher value there than at any time since the introduction of *medionigra* in 1954. Ford and Sheppard (1969) have indicated that some of those *medionigra* with a yellow spot on the hindwing are difficult to separate from *dominula*. This is particularly true of individuals that are at all worn. It is therefore possible that some error due to inconsistent scoring of *medionigra* at both colonies in 1969 has been introduced by the change of observers in that season. However, if gene frequency in 1969 is calculated using only those individuals with some black scales in the central hindwing spot, values of 1.56 per cent. and 0.56 per cent. are obtained for Cothill and Sheepstead Hurst respectively. These are higher than the estimates reported by Ford and Sheppard (1969) for 1968, which included insects with yellow hindwing spots. They also mention that only three of the ten *medionigra* at Sheepstead Hurst in the three years, 1966 to 1968, had black hindwing spots and these represent a gene frequency over the three years of 0.21 per cent., compared with 0.56 per cent. in 1969. It thus seems that errors due to inconsistent scoring in 1969 were not large enough to have a major effect on gene frequency estimates, and therefore it may be assumed that the increases observed in that year are real.

Ford and Sheppard (1969) conclude that *medionigra* is becoming dominant

for its visual effects at Cothill and recessive at Sheepstead Hurst. They draw attention to the larger black hindwing spots at Cothill and to the fact that individuals with small yellow hindwing spots are commoner at Sheepstead Hurst. Selection experiments in the laboratory for these visual effects of *medionigra* have forestalled the changes observed in nature; in three generations Ford (1960) was able to alter the expression of *medionigra* towards *dominula* in one direction and towards *bimacula* in the other.

The sixty-three *medionigra* captured in 1969 made it possible to compare its expression in a number of individuals at both colonies in the same season. Confirmation that *medionigra* is becoming dominant at Cothill and recessive at Sheepstead Hurst was obtained from two sets of observations:

- (a) At Cothill eight *medionigra* were found to have the mid-spot on the forewing missing and in five more it was reduced in size. Eleven of these thirteen insects had a black spot on the hindwing. In contrast at Sheepstead Hurst no *medionigra* were found to have the mid-spot on the forewing missing and in only four was it reduced; none of these four had black hindwing spots.
- (b) A higher proportion of *medionigra* at Cothill had black scales in their hindwing spots; 17 out of 38 compared with six out of 25 at Sheepstead Hurst. This difference is not significant, however, ($\chi^2(1) = 1.97$, $P > 0.05$), and it will be interesting to see if this trend is continued in the next few years.

In addition, comparisons of the area of the hindwing spot between localities lend some support to the above evidence. These comparisons fall into four classes, according to the colour of the spot and sex (table 2). For 1969 only three of these comparisons are possible since one class at Sheepstead Hurst, males with a black hindwing spot, consists of but a single individual. It will be seen from table 2 that the remaining classes are small, and in order to compare them the *t*-test has been used for both between-colony comparisons and for those within each colony. It might be expected that the average area of the hindwing spots would be greater at Cothill as Ford and Sheppard (1969) have indicated. One of the three possible comparisons for 1969, between males with a yellow hindwing spot, does show significantly larger spots at Cothill. The other two comparisons are, however, inconclusive (table 3 (b)). Further measurements of this character are required in succeeding seasons.

Comparisons of hindwing spot area made within the two colonies show two trends (table 3 (a)):

- (a) Males tend to have larger hindwing spots than females. This may be a function of wing size since measurements of specimens from bred stock indicate that males have longer forewings than females. It is unlikely that *medionigra* is partially sex controlled.
- (b) Black spots, at least in females, tend to be larger than yellow spots. This might be expected if the hypothesis is accepted that black spots are an indication of a tendency to dominance in *medionigra* and yellow spots to recessiveness.

Ford and Sheppard (1969) have given reasons why the long lasting study of the *medionigra* polymorphism of *dominula* should continue; events in 1969 have emphasised this necessity. At Cothill, following a slight increase in

1968, giving an estimated population of 978, the numbers have at last shown a striking increase to an estimated value of 5712, after a period of six years when they had varied from 216 to 625 during the entire season. In addition, it seems that the frequency of *medionigra* at Cothill is rising again and in the next few seasons it may be possible to ascertain some of the factors responsible for the changing selective value of *medionigra*. The contrasting tendencies to dominance of *medionigra* at Cothill and to recessiveness at Sheepstead Hurst also require further study.

TABLE 3

Comparisons of the area of the hindwing spot in various classes of medionigra

(a) Within colony comparisons

Class	Comparison	d.f.	<i>t</i>	Significance
Cothill male	Black and yellow	18	-0.8886	N.S.
Cothill female	Black and yellow	16	+3.7593	P < 0.002
Sheepstead Hurst female	Black and yellow	15	+2.1476	P < 0.05
Cothill Black	Male and female	15	+0.2617	N.S.
Cothill Yellow	Male and female	19	+3.8033	P < 0.002
Sheepstead Hurst Yellow	Male and female	17	+3.4651	P < 0.01

(b) Between colony comparisons

Class	Comparison	d.f.	<i>t</i>	Significance
Yellow male	Cothill and Sheepstead Hurst	18	+2.2633	P < 0.05
Yellow female	Cothill and Sheepstead Hurst	18	-0.9584	N.S.
Black female	Cothill and Sheepstead Hurst	13	+1.3263	N.S.

4. SUMMARY

1. This paper describes the colonies of the Scarlet Tiger Moth (*Panaxia dominula*) at Cothill and Sheepstead Hurst, Berkshire in 1969.

2. In that season the estimated population size at both colonies had increased. At Sheepstead Hurst it was 2942 and at Cothill it had risen to 5712 after a period of scarcity, the totals varying from 216 to 625 during the period 1962 to 1967. This change had been foreshadowed in 1968 when the numbers were estimated as 978.

3. The daily survival rate of *dominula* at Sheepstead Hurst (0.79) was higher than at Cothill (0.71).

4. The frequency of the *medionigra* gene at both colonies had increased in 1969; to 3.5 per cent. at Cothill and to 2.3 per cent. at Sheepstead Hurst, its highest level there since the introduction of *medionigra* in 1954.

5. Evidence supporting the view that *medionigra* is becoming dominant for its visual effects at Cothill and recessive at Sheepstead Hurst was obtained.

6. Comparisons of the area of the central hindwing spot between colonies indicate that at Cothill these spots are larger than at Sheepstead Hurst. Within the colonies, differences between male and female, and between black and yellow hindwing spots were also found.

7. The need to continue the study of the *medionigra* polymorphism is emphasised.

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ENVIRONMENTAL AND GENOTYPE-ENVIRONMENTAL COMPONENTS OF VARIABILITY. VII. SIMULTANEOUS PREDICTION ACROSS ENVIRONMENTS AND GENERATIONS

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1. THE BASIS OF PREDICTION

In this series of papers (Bucio Alanis, 1966; Bucio Alanis and Hill, 1966; Perkins and Jinks, 1968*a* and *b*; Bucio Alanis, Perkins and Jinks, 1969; Perkins, 1970) we have shown that the means of a pair of inbred lines (P_1 and P_2) and their F_1 in any environment j , can be described by the equations,

$$\begin{aligned} P_{1j} &= \mu + [d] + (1 + \beta_d)\epsilon_j \\ P_{2j} &= \mu - [d] + (1 - \beta_d)\epsilon_j \\ \text{and } F_{1j} &= \mu + [h] + (1 + \beta_h)\epsilon_j \end{aligned}$$

The conditions under which these equations hold are that

$$\begin{aligned} g_d &= \beta_d \epsilon_j \\ \text{and } g_h &= \beta_h \epsilon_j \end{aligned}$$