

## FREQUENCY AND SELECTION IN THE INDUSTRIAL MELANIC MOTH *ODONTOPTERA BIDENTATA*

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### SUMMARY

Data are presented on morph frequency, selective return and date of emergence of morphs in the polymorphic melanic moth *Odontoptera* (= *Gonodontis*) *bidentata* (CL.). They come from three sites along the Mersey in industrial northwest England, and are used to test predictions from an earlier survey. There has been no decline in melanic frequency over the period studied. Non-melanics returned to traps less frequently than melanics at a site where the melanic frequency is high, agreeing with an earlier result. This suggests selection against non-melanics. Emergence starts later to the east of the region than to the west, and melanics emerge later than non-melanics. The late emergers must include heterozygotes as well as homozygotes. These results are discussed in relation to the question of how the polymorphism is maintained.

### 1. INTRODUCTION

The Scalloped hazel moth, *Odontoptera* (= *Gonodontis*) *bidentata* (Cl.) has a melanic form *nigra* which reaches a high frequency in northern England. The frequency apparently increased in the nineteenth century (e.g., Wright, 1911, Bowater, 1914). In a survey in the early 1970s it was at its highest level of 70-80 per cent in Leeds and Manchester, and declined westward along a transect from Manchester to Liverpool and Birkenhead running parallel to and north of the river Mersey (Bishop *et al.*, 1978a). Along the transect the frequencies rise to local peaks in the industrial towns and fall in the suburban and semi-rural areas between (fig. 1). At the Manchester end there was a sharp drop in frequency from 80 per cent in central Manchester to 15-30 per cent 15 km to the south in Cheshire.

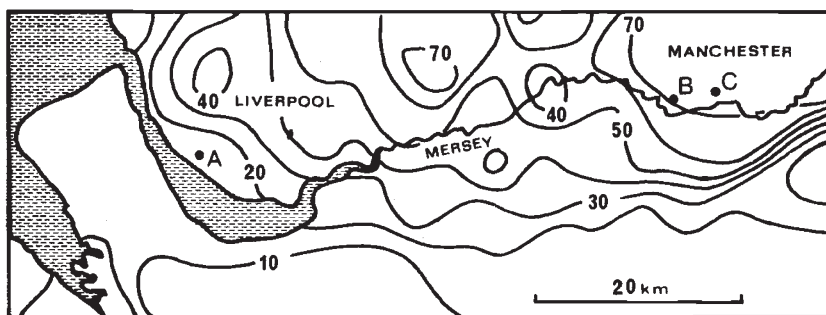


FIG. 1. Map showing the Mersey valley with the positions of Liverpool and Manchester. Contours represent per cent *nigra* morph in the moth *O. bidentata* estimated by Bishop *et al.*, 1978a. The sites discussed in the present paper are A: Aigburth, B: Didsbury, C: Heaton Moor.

The pattern suggests that the dark morph is an industrial melanic, directly affected by conditions in the old, and at one time heavily polluted, industrial centres. It has a pattern of distribution corresponding more closely with these sites than that of the Peppered moth *Biston betularia*, which has a melanic frequency of over 90 per cent throughout the region. Unlike the Peppered moth, however, it appears to be secretive in its resting behaviour and therefore less likely to be exposed to selective predation (Bishop *et al.*, 1975, but cf. Mikkola, 1983, who considers that the role of selective predation may have been over-emphasized in *B. betularia*).

When trying to find clues as to the factors maintaining the polymorphism (Bishop *et al.*, 1978a) we made the following observations. The average distance of movement appears to be much lower than that of the Peppered moth. There is less evidence of selective elimination on adults than in the Peppered moth, although the average rate of returns of typicals did appear to be lower than that of melanics in Manchester, where the melanic frequency was high. Date of emergence of adults was on average later in Manchester than further west in Warrington and Liverpool, where the frequencies of *nigra* were lower. This will have the effect of reducing gene flow between neighbouring areas. In Manchester the date of emergence appeared to be bimodal, the second mode having the higher frequency of melanics, and we speculated that this contained most of the *nigra* homozygotes.

Since the time of the survey the amount of smoke pollution of the atmosphere has progressively declined. Corresponding declines in melanic frequency have been recorded in *B. betularia* in and to the south of Birmingham (Lees, 1981) and in the same species on the Wirral peninsula (Clarke and Sheppard, 1966, Whittle *et al.*, 1976, summarised by Bishop and Cook, 1980).

We now have additional records for *O. bidentata* collected over several years in Manchester by L.M.C. and J. Delf, and in Liverpool by the late J. A. Bishop and T. J. These have been examined for evidence of change in morph frequency with time and for confirmation or otherwise of selective elimination and of differential emergence time of the morphs.

## 2. MATERIALS AND METHODS

Moths were collected at two sites in the Manchester area and one in Liverpool. In Manchester these were at Heaton Moor (National Grid Reference 33 882918) and Didsbury (Nazarene College, G.R. 33 840910), and in Liverpool at Aigburth (G.R. 33 388857). All the sites lie just north of the Mersey valley (fig. 1). In the first survey these sites produced *nigra* frequencies of 68 per cent at Heaton Moor, from a small sample of 19 individuals in 1972, 67 per cent at Didsbury in 1974 ( $N = 306$ ) and 12 per cent at Aigburth from 1971-75 ( $N = 923$ ). Trapping was by assembling trap using caged females to attract males, or occasionally by mercury vapour light trap. Light traps are very much less efficient than assembling traps for this species, the difference in efficiency being greater than in *B. betularia*. The numbers caught varied greatly from year to year. Whenever possible insects were scored, marked and released. Recaptures were used to estimate population size and survival rate.

## 3. RESULTS

(i) *Frequency in successive years*

The total numbers caught throughout the collecting period are shown in table 1. There is no evidence of a trend in frequency at any of the sites.

TABLE 1

*Numbers of nigra and non-nigra individuals of the moth Odontoptera bidentata caught in successive years at three sites along the Mersey valley*

Site	Year	nigra	non-nigra	per cent nigra
Heaton Moor	1972	13	6	68.4
	1977	85	56	60.3
	1978	438	186	70.2
	1979	108	41	72.5
	1980	110	46	70.5
	1981	3	4	42.8
	1982	35	19	64.8
Didsbury	1974	182	95	65.7
	1979	109	47	69.9
	1981	154	109	58.6
	1982	32	15	68.1
Aigburth	1971	4	31	11.4
	1972	7	40	14.9
	1973	33	239	12.1
	1974	67	421	13.7
	1975	14	117	10.7
	1977	41	286	12.5
	1978	71	404	14.9
	1979	61	310	16.4
	1980	53	387	12.0

In order to test this, taking into account changes in sample size from year to year the method used by Lees and Creed (1975) and in the earlier survey was employed. Values of  $\chi^2$  were calculated for the  $2 \times 2$  tables representing pairs of successive years. The signed square root of  $\chi^2$  was then found, which is a normal deviate indicating whether a significant increase or decrease has occurred. Only two of these values were significant (Heaton Moor, 1977-78,  $\chi = 2.29$  and Didsbury, 1979-81,  $\chi = -2.32$ ). The 17 values were summed, squared and divided by 17 to give a  $\chi^2$  value of 0.016 (df = 1,  $P > 0.9$ ). There is therefore no evidence of a progressive change in morph frequency. No change was seen in the earlier survey, where 26 sites were compared over time intervals of a year or two. There is also no indication from the data that the difference in frequency between the sites may be declining. Similarly, Lees (1981) found no consistent decline in the frequency of melanics in the moth *Phigalia pilosaria* on a transect where the frequency of melanic *B. betularia* had declined.

(ii) *Selection on adults*

Where animals were marked and released recapture data are obtained, which may be tested for differential return of the moths. The recapture

results have been analysed by the method of Manly (1973) to produce estimates of the fitness of non-*nigra* relative to *nigra*. Previously, results were obtained for three sites in Liverpool and two in Manchester. Estimates are now available for later years at the Aigburth site in Liverpool and for Heaton Mersey and Didsbury. They are presented together with the earlier ones in table 2. The combined estimate at Heaton Moor was obtained by adding the small amount of information available for 1977, 1979 and 1982 to the large sample for 1978.

TABLE 2

*Estimates of selective recapture for sites in Liverpool and Manchester. The fitness of non-nigra relative to nigra is shown, calculated by the method of Manly (1973). Data marked with an asterisk have been published previously.*

Site	Year	per cent <i>nigra</i>	Fitness	Standard error
Aigburth	1974*	13.7	1.34	0.22
	1975*	10.7	0.83	0.10
	1977	12.5	1.02	0.16
	1978	14.9	0.8	0.14
	1979	16.4	3.46	2.08
	1980	12.0	1.28	0.35
	combined	13.8	0.99	0.07
Cressington Park	1970*	15.6	0.89	0.06
Broadgreen	1969*	44.6	0.98	0.12
Wythenshawe	1974*	47.1	1.06	0.05
Didsbury	1981	58.6	0.94	0.13
Heaton Moor	1978	70.2	0.77	0.15
	1977-82	68.9	0.82	0.14
Rusholme	1973*	79.5	0.74	0.11

The Aigburth data have been tested for heterogeneity by summing the  $\chi^2$  values from each year and taking from the sum the  $\chi^2_1$  calculated as we have done above. This provides  $\chi^2_3 = 9.06$ , which is not significant. The data have therefore been pooled by a method given by Manly (1972) to give a combined estimate of 0.99. Using this value for Aigburth, there is only one site in the seven for which the estimate is greater than unity (Wythenshawe) and only one which is significantly different from unity (Rusholme;  $\chi^2_1 = 6.07$ ,  $P < 0.05$ ). Combining the data to test the trend produces  $\chi^2_1 = 3.91$ , which is just significant at the 5 per cent level. For the heterogeneity test,  $\chi^2_6 = 8.35$  ( $P > 0.05$ ). We conclude, tentatively, that the data show overall slight selection against typicals, although this is mostly due to the large effect at Rusholme.

### (iii) *Date of emergence*

Data on numbers trapped per day are available at Aigburth and Heaton Moor for four years from 1977 to 1980. Recording of day of capture commences on 18 May each year except 1980, a leap year, when it starts on 17 May. The pattern of emergence usually involves a rapid increase in numbers over the first ten days, followed by a slower decline, so that there is a tail of emergence extending into July. It was suggested (Bishop *et al.*, 1978a) that the tail may in fact contain a second peak of emergence. This

is difficult to detect, however, and in comparing the sites we have transformed the data by taking the logarithm of the day of emergence in order to make allowance for the assymetry of the distribution. The values shown in table 3 are obtained. Analysis of variance shows that the difference in emergence time between sites is very significant ( $F = 2188.6$ ), but that there is also significant variation between years ( $F = 820.6$ ). The annual pattern of emergence shows some resemblance between sites, 1980 being the most advanced season of the four.

TABLE 3

*Mean and 95 per cent confidence intervals for data of emergence at two sites, based on the logarithm of day of emergence. The first day scored is 18 May for 1977-79 and 17 May for 1980.*

Site	Year	Mean	Confidence intervals
Aigburth	1977	10.5	4.3-25.6
	1978	12.9	4.0-41.4
	1979	21.9	9.9-45.6
	1980	8.5	2.5-28.7
Heaton Moor	1977	26.7	12.9-55.6
	1978	20.9	10.3-42.2
	1979	28.6	14.7-55.3
	1980	16.0	4.1-63.4

The proposition we suggested was that the later emergence in Manchester was due, in part at least, to the later emergence of *nigra* individuals, which are at a higher frequency there, and in particular to late emergence of *nigra* homozygotes. In order to examine this we may compare the frequency of *nigra* and non-*nigra* in the first three-quarters of the season's emergence, as compared with the final quarter. When that is done for the published data from 1973 to 1975 the frequency of *nigra* is higher in the last quarter in eight out of nine cases. The overall tendency for the final quarter to have a higher frequency of *nigra* is very significant ( $\chi^2_1 = 10.54$ ). These results are shown in table 4.

The later results also indicate that *nigra* emerges later than non-*nigra* (table 4). For the five sets of data for the Manchester area the  $\chi^2_1$  measuring the trend is 2.05 ( $P > 0.1$ ). For Aigburth the equivalent value is 3.09. Combining these data from the two areas we get  $\chi^2_1 = 5.02$ , which is significant ( $P < 0.05$ ). It may be argued that since we are interested in testing whether the frequency increases, rather than that it deviates, the one-tailed criterion should be used. The significance of the difference would be increased. If *nigra* were selected then its frequency might go up progressively through the season. This would not account, however, for the higher frequency of the melanics at the end of the season at Aigburth.

The suggestion that emergence is bimodal is difficult to confirm or to contradict, owing to the erratic nature of the capture pattern from day to day. This irregularity is almost certainly a consequence in part of fluctuation in weather conditions. Even in the largest set of results, for 1978, the pattern may be bimodal but is not certainly so. The data are therefore not presented here.

TABLE 4

Totals for nigra and non-nigra caught in the first three-quarters and the final quarter of the emergence in each season. Results in the upper part of the table are from the earlier survey.

Site	Year	1st three-quarters			final quarter		
		nigra	non-nigra	% nigra	nigra	non-nigra	% nigra
Aigburth	1974	47	363	11.5	5	26	16.1
	1975	8	98	7.5	6	30	16.7
Warrington	1973	53	47	53.0	16	8	66.7
Chorltonville	1974	65	25	72.8	11	7	61.1
Wythenshawe	1974	223	277	44.6	84	67	55.6
	1975	43	60	41.7	7	4	63.6
Didsbury	1974	145	83	63.6	59	19	75.6
Rusholme	1973	109	32	77.3	88	18	83.0
	1974	75	22	77.3	47	12	79.7
Didsbury	1979	81	39	67.5	28	8	77.8
Heaton Moor	1977	60	41	59.4	25	15	62.5
	1978	316	145	68.5	119	38	75.8
Aigburth	1979	78	31	71.6	30	10	75.0
	1980	85	34	71.4	25	12	67.6
	1977	28	222	11.2	16	64	16.9
	1978	49	312	13.6	22	92	19.3
Aigburth	1979	38	223	14.6	23	87	20.9
	1980	42	287	12.8	11	100	9.9

#### 4. DISCUSSION

The maintenance of polymorphism in industrial melanics is not fully understood. The correlation of melanic frequency with areas of industrialisation indicates that selection favouring melanics acts in these areas. In *B. betularia* the fact that the insect almost certainly spends part of its life on exposed surfaces during the day, the evidence from artificial selection experiments and the decline in melanic frequency after introduction of smoke control all suggest that visual predation plays a part. Mani (1982) developed a theoretical model in which visual selection, non-visual difference in fitness between melanics and non-melanics (demonstrated by Creed *et al.*, 1980), and migration (demonstrated by Bishop, 1972) combine to produce a plausible representation of the known geographical pattern of morph frequency.

In *O. bidentata* it is known that the moths tend to be more secretive in their resting position (Bishop *et al.*, 1975). Nevertheless, experiments indicated that non-nigra individuals were at a disadvantage in areas of high nigra frequency, and there is evidence of late emergence of nigra (Bishop *et al.*, 1978a, b). We therefore proposed as a tentative hypothesis that non-nigra suffers selective predation in urban industrial areas, probably at a lower level than *Biston*, and that nigra homozygotes emerge later than the rest of the population. The homozygotes would then have a more limited choice of mates. If the time gap were right, they would be at a mating disadvantage, because some were unable to obtain mates. Migratory powers appear to be much weaker than in *Biston*. This pattern of selection and migration could account for the fact that in *O. bidentata* the frequency varies over smaller distances than in *Biston*. Mani (1981) has investigated the general properties of systems with a time lag in emergence of one

morph. If balance is achieved in this way then, just as spatial pattern is on a smaller scale than in *Biston*, so it might be expected that morph frequency should change more rapidly when environmental changes modify the selective pattern.

The results discussed here were collected to test the model outlined above. The model is neither completely endorsed nor contradicted. There is no change in frequency with time. On the other hand, tests for selection produced apparent selection against non-*nigra* at a second site (Heaton Moore) at which *nigra* is at a high frequency, the level of selection being very similar to that observed before at Rusholme. There is confirmation that *nigra* makes up a larger fraction of the later than of the earlier emergence period. This is true in Liverpool, however, where *nigra* homozygotes are 1 per cent or less of the population, as well as in Manchester where they are a substantial minority. The later period must therefore contain heterozygotes as well as melanic homozygotes, although not necessarily in random proportions. Late emergence was discussed by Mani (1981) on the assumption that the delayed section was homozygous. The effects of differential emergence are complex, however, depending on the length of the delay, asymmetry in delay between the sexes and the effect it has on mating behaviour. It is possible that the emergence pattern plays a part in generating the differences in frequency distribution between *O. bidentata* and *B. betularia*.

Note added in proof: For 1983 at Heaton Moor, there were 111 *nigra* : 46 non-*nigra*, giving a melanic frequency of 70.7%.

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