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Melanism in *Adalia* ladybirds and declining air pollution in Birmingham

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The frequency of the melanic forms of *Adalia bipunctata* continued to fall at five sites in the Birmingham conurbation after the earlier decline in the 1960s monitored by E. R. Creed. The decline had levelled off by about 1978. The rate of change in melanic frequency was similar at each site with a more or less constant disadvantage to melanics of about ten percent from 1960 to 1978. The pattern of change shows a close correspondence to the levels of smoke pollution in Birmingham ($r = +0{\cdot}91$) but a weaker association with sulphur dioxide ($r = +0{\cdot}72$). It is argued that this follows from an influence on thermal melanism via the effect of smoke in reducing sunshine. The related *A. decempunctata* shows no changes in melanic frequencies at the same sites. This is consistent with previously inferred evidence for a lack of any influence of thermal melanism in this species. The responses of these ladybird beetles to changing air pollution are compared with that in the moth *Biston betularia*.

INTRODUCTION

Creed (1966, 1971a) showed that the warningly-coloured two-spot ladybird beetle *Adalia bipunctata* (L.) exhibits industrial melanism in Britain, there being a positive correlation between the frequency of melanic forms and the level of smoke pollution but a weaker association with sulphur dioxide. He also (Creed, 1971b) detected a decline of about 15 per cent in the frequency of the melanic forms at six sites in or near Birmingham in the 1960s shortly after the passing of clean air legislation in 1956 and the consequent introduction of smokeless zones. Bishop, Cook and Muggleton (1978) provide support for a similar decline at eight sites in northwest England from a comparison of Creed's (1971a) survey with their own samples, mostly collected in 1976. Creed suggested that smoke has some direct selective influence on melanics. In contrast, Muggleton, Lonsdale and Benham (1975) present an alternative explanation that the correlations arise from the effect of smoke reducing solar radiation reaching the ground. The associated theory of thermal melanism predicts that melanic beetles gain an advantage under conditions of low sunshine because of their more efficient heat absorption than non-melanics (Muggleton *et al.*, 1975; Brakefield and Willmer, 1985). Evidence for influences of thermal melanism on the reproduction of *A. bipunctata* has been obtained by Brakefield (1984a, b).

The decline in melanic frequencies in *A. bipunctata* in Birmingham was substantial some ten years or so before those documented in the peppered moth *Biston betularia* in England and Wales (Lees, 1981; Clarke, Mani and Wynne, 1985; Cook, Mani and Varley, 1986). An understanding of such differences between species in the dynamics of responses to changes in air pollution is likely to provide insights into the underlying causal mechanisms. In this paper we give a more complete analysis of data covering 26 years for *A. bipunctata* from five of Creed's (1971b) Birmingham sites based on samples collected by E. R. Creed (unpublished data) and by ourselves. We also examine corresponding, but more limited data for the 10-spot ladybird *A. decempunctata* (L.). Differences in the responses shown by these beetles and *B. betularia* are discussed in the light of proposed selective processes.

MATERIALS AND METHODS

The data for each of five sites in the Birmingham conurbation (fig. 1) for 1960 to 1978 were

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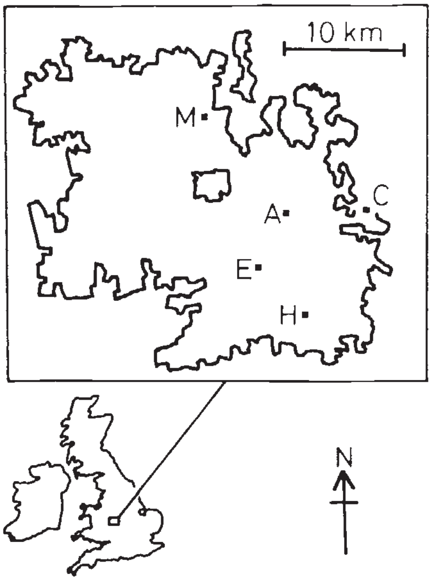

Figure 1 Outline map of the Birmingham conurbation in Great Britain showing the positions of the five sampling sites in this and Creed's (1971*b*) study. A = Aston Church; C = Castle Bromwich; E = Edgbaston; H = Hall Green; M = Maw Green.

abstracted from the late E. R. Creed's records (Creed, 1971b gives details of four small samples from a sixth site). We obtained further samples from the exact localities of the five sites in 1986. Many samples consisted of adults emerging in the laboratory from pupae collected on lime trees, *Tilia* spp., or nettle, *Urtica dioica*. The majority of non-melanics were of the *typica* form. The distinction between the two melanics, *quadrimaculata* and *sexpustulata*, is not always clear, especially in beetles raised from pupae, and in this paper they are grouped together. Data from the same sources for the frequency of the non-melanic (*typica*), intermediate (*decempustulata*) and melanic (*bimaculata*) forms of *A. decempunctata* are also analysed (for illustrations see Brakefield, 1985).

RESULTS

Table 1 presents the data for *A. bipunctata*. Fig. 2 shows that the declines in the frequency of melanics in the 1960s described by Creed (1971b) continued in the 1970s but chi-square comparisons of the combined data for the 3 years 1976 to 1978 against 1986 show that there were no further changes in melanic frequency over this later period ($P > 0{\cdot}1$ for each site). The three geographically well separated sites (fig. 1) with initial frequencies of about forty per cent melanics show a closely similar pattern of changing frequency. Edgbaston and Castle Bromwich with higher and lower melanic frequencies respectively, show a similar rate of decline. Fig. 2 shows that the decline at the five sites is approximately linear over the period 1960 to 1978. An analysis of the data presented in fig. 2 over this period shows no significant differences between the five linear regressions ($F = 1{\cdot}25$, df = 4 and 33, P is NS; range in values of b: $-1{\cdot}38$ to $-2{\cdot}32$ per cent per year with $P < 0{\cdot}05$ for each).

Table 1 Numbers of non-melanic (n-m) and melanic (mel) *Adalia bipunctata* in annual samples from sites in the Birmingham conurbation from 1960 to 1986

	Aston Church		Castle Bromwich		Egbaston		Hall Green		Maw Green	
Year	n-m	mel	n-m	mel	n-m	mel	n-m	mel	n-m	mel
1960	—	—	47	21	55	64	—	—	—	—
1961	—	—	—	—	15	39	5	6	27	18
1962	—	—	—	—	51	65	44	42	51	28
1963	—	—	—	—	2	5	—	—	—	—
1964	36	26	51	17	—	—	30	17	109	71
1965	15	12	—	—	—	—	33	18	41	23
1967	244	77	108	23	—	—	132	58	119	54
1968	4	3	48	5	—	—	54	21	106	38
1969	106	41	40	12	87	91	61	29	97	32
1970	128	33	31	5	—	—	70	25	—	—
1971	29	8	—	—	—	—	51	13	—	—
1972	70	22	186	35	—	—	64	13	—	—
1974	131	19	—	—	—	—	150	36	—	—
1975	—	—	—	—	4	6	—	—	—	—
1976	207	25	—	—	19	6	131	15	71	14
1977	154	24	19	0	114	48	271	33	—	—
1978	31	1	—	—	27	13	—	—	—	—
1986	46	5	2	0	251	84	167	12	85	9

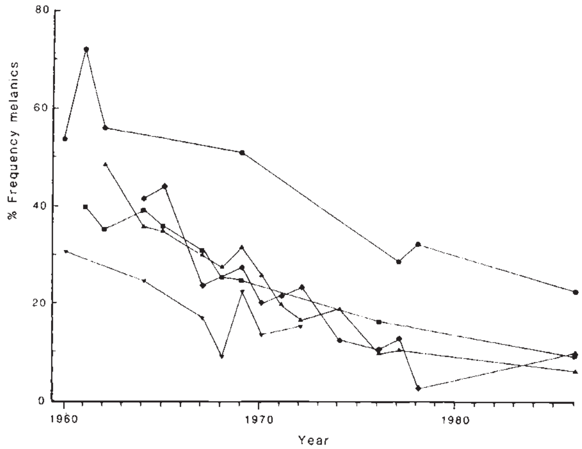

Figure 2 Change in frequency of the melanic forms of *Adalia bipunctata* in the Birmingham conurbation from 1960 to 1986. Sites: ◆, Aston Church; ▼, Castle Bromwich; ●, Edgbaston; ▲, Hall Green; ■, Maw Green. Minimum sample size = 30.

The "common" regression coefficient indicates a decline in melanic frequency of 1·93 per cent per year from an average y-intercept of 45·8 per cent. Application of the method used by Cook *et al.* (1986) shows that this relationship corresponds to a constant selective disadvantage to melanics of about 10 per cent since 1960.

Fig. 3 compares the overall regression of melanic frequency on time with the average levels of smoke and sulphur dioxide at all monitoring sites for Birmingham (Warren Spring Laboratory, 1963–84). Pollution data were abstracted for the months of May, June and July which covers the main perid of adult reproduction (Brakefield, 1984c). Caution must be applied in interpreting these data for two main reasons: (a) lack of continuity of pollution monitoring at particular sites; (b) some heterogeneity in pollution levels between sites. Fig. 3 shows that the fall in the level of smoke is similar to that in melanic frequency in *A. bipunctata* (correlation between frequencies predicted from the common regression line and levels of smoke = +0·91). The amount of smoke also levels off at about the same time as melanic frequency. There is somewhat less parallel with the sulphur dioxide data although the corresponding correlation remains high ($r = +0{\cdot}72$). The pollution data for Birmingham since the implementation of clean air legislation tend to parallel national trends, with more rapid declines in annual emissions of smoke than of sulphur dioxide (see Lees, 1981), although apparently there was also some initial decline of sulphur dioxide in the early 1960s in Birmingham (fig. 3). In general there is some time lag between change in amount of sulphur dioxide and that in melanic frequency with the former continuing to decline to the present day.

The combined samples of *A. decempunctata* show that there is no heterogeneity between sites in morph frequencies ($\chi^2 = 8{\cdot}27$, df = 8, P is NS). Table 2 gives the data for each site combined by decade. There is no evidence for any comparable changes in melanic frequencies in *A. decempuctata* to those in *A. bipunctata* (chi-square comparisons of 1960s × 1970s: P is NS for each site). Edgbaston is the only site at which more than 30 beetles were obtained in 1986. This site shows no heterogeneity over the three decades ($\chi^2 = 1.81$, df = 4, P is NS).

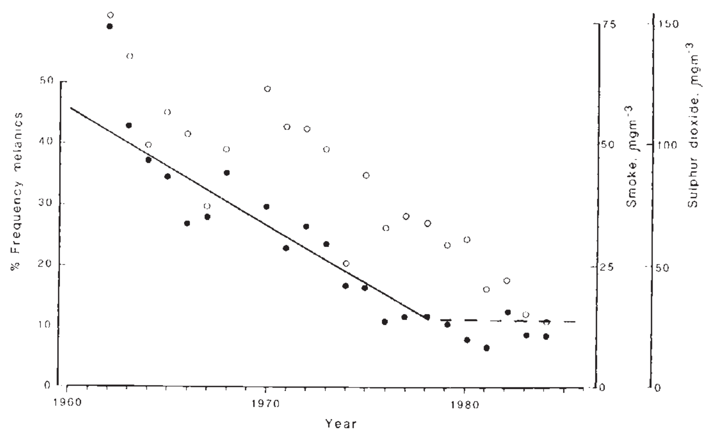

Figure 3 The relationships between the "common" regression slope (solid line) of melanic frequency against time and annual amounts of smoke (●) and sulphur dioxide (○) in May to July in Birmingham. The dashed line indicates the period of more or less stable melanic frequencies.

Table 2 Numbers and percentage frequencies of the non-melanic (*typ.*), intermediate (*dec.*) and melanic (*bim.*) forms of *Adalia decempunctata* in combined samples for each of three decades from sites in the Birmingham conurbation

Site		1960–69			1970–78			1986		
		typ.	*dec.*	*bim.*	*typ.*	*dec.*	*bim.*	*typ.*	*dec.*	*bim.*
Aston Church	*n*	15	5	4	59	19	6	5	2	1
	%	51·7	17·2	13·8	70·2	22·6	7·1	62·5	25·0	12·5
Castle Bromwich	*n*	16	7	3	10	5	1	—	—	—
	%	61·5	26·9	11·5	62·5	31·2	6·2	—	—	—
Edgbaston	*n*	18	9	4	14	9	4	19	9	8
	%	.58·1	29·0	12·9	51·9	33·3	14·8	52·8	25·0	22·2
Hall Green	*n*	42	25	11	89	40	7	4	3	4
	%	53·8	32·1	14·1	65·4	29·4	5·1	36·4	27·3	36·4
Maw Green	*n*	5	3	3	5	1	0	1	1	0
	%	45·5	27·3	27·3	83·3	16·7	0·0	—	—	—

DISCUSSION

Our analysis shows that the decline of melanic frequency in *A. bipunctata* monitored in Birmingham by Creed (1971b) in the 1960s continued until towards the end of the 1970s. Creed points out that data of Hawkes (1927) collected in the 1920s suggest that there was also some reduction in melanics prior to the 1960s. The decrease from 1960 to 1978 was associated with a more or less constant disadvantage to melanics of about 10 per cent compared to the selection regime prior to the decline. It is of a similar timing and pattern to the fall in smoke pollution in Birmingham over the same period (fig. 3). This fall in smoke began in the mid-1950s. The decline in melanic frequency is less similar to the change in levels of sulphur dioxide and supports Creed's (1971a) finding of a substantially weaker association between geographical variation in melanic frequency in *A. bipunctata* and sulphur dioxide than smoke.

At first sight the relationship between falling levels of smoke and melanic frequency is straightforward, but if the strength of selection on melanism tracks the environmental change one might expect that melanic frequency would decrease more rapidly than the amount of smoke. The apparent coincidence in the cessation of changes in melanic frequency and in smoke pollution argues for some selective influence related to continuing environmental change rather than for the initial decrease in pollution triggering a switch from one equilibrium to another, lower one. The decline in melanic frequency appears to be independent of the initial frequency of melanics which varies among the populations. This variability is additional evidence against the existence of two alternative equilibria in Birmingham. The differences in frequency between sites could be associated with local variation in smoke pollution but the pollution data are not good enough to test this.

The data describing the declines in the frequency of melanic *A. bipunctata* in Birmingham cannot in themselves indicate the nature of the selective influence of smoke. However, although we cannot refute the possibility that smoke has some direct selective effect favouring melanics (after Creed, 1966, 1971a, b), there are some other data supporting the hypothesis of a causal association between the effect of smoke in reducing solar radiation and thermal melanism (Muggleton *et al.*, 1975; Brakefield, 1984a, b). This hypothesis predicts that as smoke emissions decline, solar radiation increases at ground level and the thermal advantage of melanics is reduced, via effects on adult fitness, especially reproduction (Brakefield, 1984a, b). Such an effect of lowered smoke pollution on adult reproduction should be detectable in the next generation. No corresponding mechanism has been indicated with regard to direct influences of smoke although a number could be postulated, for example one based on the effect of small particles on the permeability of the cuticle (see Ebeling, 1971).

The lack of any temporal change in morph frequency in *A. decempunctata* paralleling that in *A. bipunctata* is consistent with the operation of thermal melanism rather than a direct influence of smoke. Thus, Brakefield (1985) shows that this species exhibits no geographical variation in The Netherlands, whereas *A. bipunctata* shows steep clines over the same region. He also found that the strictly arboreal habit of this species, in contrast to *A. bipunctata*, predicts that thermal melanism is unlikely to have any significant influence on adult reproduction. Any direct effect of smoke on the polymorphism in *A. bipunctata* might be predicted to operate also on the phenotypically similar polymorphism in the closely related species, *A. decempunctata*.

The substantial decline in melanic frequency in *A. bipunctata* began about 10 years earlier than that in a population of *B. betularia* at West Kirby near Liverpool (Clarke *et al.*, 1985) and more generally in this species in England and Wales (Lees, 1981; Cook *et al.*, 1986). The decline in melanic *A. bipunctata* is associated with a similar selective disadvantage to that estimated at 12 per cent in *B. betularia* (Cook *et al.*, 1986), but the decrease in the *carbonaria* form of *B. betularia* is more closely correlated with sulphur dioxide pollution than smoke. Gaseous pollutants act, at least in part, through effects on the recovery of epiphytic growth on the resting backgrounds of this cryptic moth (see *e.g.* Liebert and Brakefield, 1987). This indirect effect and the later fall in emissions of sulphur dioxide than of smoke could account for the later decline in melanic frequencies in *B. betularia* than in *A. bipunctata*.

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