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Melanism in the two spot ladybird: the nature and intensity of selection

BY E. R. CREED

Department of Zoology, University College, Cardiff

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Intraseasonal changes in the melanic frequency of *Adalia bipunctata* have been recorded in and around Berlin and Birmingham; in the latter place a steady decrease in frequency has also occurred over several years. Estimates of the intensity of natural selection have been made from the observed changes in frequency. Selection against black individuals in winter, and against red ones in summer, appears to be higher in Berlin (52% against black heterozygotes in winter and 33% against red homozygotes in summer) than in Birmingham (24 and 9% respectively); there are indications that mean maximum summer temperature and mean minimum winter temperature influence the intensity of selection, as do local smoke pollution levels, but not sulphur dioxide (as with *Biston betularia*). In some parts of the ladybird's geographical range, increased mating activity of the black individuals may also be important.

INTRODUCTION

It has long been recognized that melanism in the peppered moth, *Biston betularia* (L.), is associated with strong selective pressures; Haldane (1924) demonstrated that a 50% advantage of the melanic form over the typical was necessary to account for the spread of *carbonaria* during the latter half of the nineteenth century. Ford (1937) suggested that melanic moths are favoured by physiological selection, in addition to any visual selection by birds, which Kettlewell (1955, 1956) later so convincingly demonstrated in *B. betularia* to be operating against melanics in a rural area and typicals in a polluted one. Confirmation of a strong component of selection which is independent of crypsis has been obtained by Lees & Creed (1975).

In contrast with the various moth species which have been investigated, melanism in the two spot ladybird, *Adalia bipunctata* (L.), cannot be convincingly explained in terms of any form of visual selection, for the insect is distasteful and avoided by many potential predators (Frazer & Rothschild 1960). On the other hand, in Britain the melanic frequency of *A. bipunctata* shows a far greater association with areas having much atmospheric pollution (Creed 1966, 1971*a*) than it does in *B. betularia* (Kettlewell 1965). The transition from some polluted to unpolluted areas is characterized by steep clines in melanic frequency in the ladybird, and furthermore, a decline in frequency has been observed in Birmingham at the same time as a fall in smoke levels (Creed 1971*b*). Based mainly on continental

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European samples, Lysis (1961) not only found an association with polluted conditions, but also suggested that humid maritime conditions favoured the melanics. Scali & Creed (in preparation), working on Italian material, have also found a strong climatic influence, but it is clearly due to temperature rather than humidity; cold conditions favour the red ladybirds, and hot conditions favour the black ones. This is in accord with what is perhaps the most convincing evidence of strong selection operating on the melanism in this species; that is to say, Timofeeff-Ressovsky's (1940) observations on the seasonal fluctuations in melanic frequency of a population in Berlin. The black forms were selectively eliminated in winter, though they increased during the summer.

This paper sets out to analyse the data at present available in an attempt to elucidate both the intensity and the nature of the selective forces. Timofeeff-Ressovsky & Svirezhev (1966) have already re-examined the Berlin observations, but with a model which does not result in a stable equilibrium. This does not lead to any major quantitative differences between their results and the values calculated in this paper, except where there are inconsistencies between the raw data and calculated frequencies, and consequently the selection coefficients, in their paper. There are also a number of inconsistencies between the data that they present and the data in the original paper (Timofeeff-Ressovsky 1940). I have therefore based my own calculations entirely upon the samples as recorded in the earlier paper.

SEASONAL FLUCTUATIONS IN FREQUENCY

Potsdam and Berlin

Extensive sampling at different times during the year has been carried out in Potsdam by Meissner (1907*a, b*, 1909, 1910, 1912), in addition to the observations in Berlin of Timofeeff-Ressovsky (1940). Both sets of results show that red individuals reach a high frequency in spring and early summer, but are less common by autumn. Meissner's results suggest that the frequency of red may go on increasing until June or July, when the adults of the first new generation of the year emerge; unfortunately, the sampling was spread over several years and the change in frequency cannot be followed in detail for any one of them.

Timofeeff-Ressovsky collected samples in both spring and autumn of several years; from the seasonal change in frequency and making certain assumptions, it is possible to estimate the intensity of selection. First, it is assumed that there are three generations per year, and these are treated as non-overlapping. Secondly, it is necessary to make assumptions about the selective differential between black heterozygotes and black homozygotes; if they were equivalent, then a polymorphism could not be maintained in this species without frequency dependant selection. Black individuals are at a disadvantage during winter, and possibly during the spring also, and the homozygotes are taken to have twice the disadvantage that the heterozygotes have. On the other hand, both are assumed to have an equal advantage over red (homozygous) individuals during the summer. This results in a

state similar to heterozygous advantage over a range of selective values, producing a stable, though fluctuating, polymorphism.

Thus the selection coefficient, s , against black heterozygotes in winter is given by

$$s = \frac{BB + BR - RR(BB' + BR')/RR'}{2BB + BR},$$

where BB , BR and RR denote the frequencies of black homozygotes, black heterozygotes and red homozygotes in autumn, and BB' , BR' and RR' the corresponding frequencies in spring. If a value for s of greater than 0.5 is indicated, the black homozygote would be lethal and a value of $BB = 0$ should be entered to avoid a negative survival rate.

During summer, and assuming random mating (see below), the frequencies of the three genotypes can be found in terms of the gene frequencies of the parents (black allele, p ; red allele, q) and the selection coefficient, t , against the red homozygotes:

$$BB = p^2/(1 - tq^2),$$

$$BR = 2pq/(1 - tq^2),$$

$$RR = (1 - t)q^2/(1 - tq^2).$$

Trial values of t may be inserted to give the best fit with the observed change in frequency over the summer months, the new gene frequencies being calculated for each generation. However, the initial value of BB in the spring, and the proportion of black individuals which are homozygous, will depend on the intensity of selection, s , during the winter. Similarly, the value of BB in the autumn, which is required to calculate s , will depend on the intensity of selection, t , during the summer. It is therefore necessary to solve for s and t iteratively, making an initial guess as to the relative values of BR and BB . In practice, two cycles of iteration result in little further change in the estimated values of s and t .

A weighted mean percentage of red and black individuals in spring and autumn in Berlin may be derived from tables 2 and 3 of Timofeeff-Ressovsky (1940). The mean frequency of black individuals in spring is 37.54%, and in autumn it is 60.48%, giving a value of 0.33 for t (against red in summer) and 0.52 for s (against black heterozygotes in winter); this implies lethality of the black homozygotes in winter. If black homozygotes were exactly equivalent to the heterozygotes, that is if dominance extends to all characters, $s = 0.61$ and $t = 0.27$; however, under these circumstances a stable polymorphism would not result.

Timofeeff-Ressovsky (1940, table 2) gives details of the proportions of red and black individuals that have survived the winters of 1933–4, 1936–7, and 1937–8 in the crevices of a wall where they hibernated. The total of the insects for these three winters is entered under 1929–30 in Timofeeff-Ressovsky & Svirezhev (1966), together with further data for 1930–1 and 1932–3, which are not mentioned in the earlier paper. Dividing black individuals into heterozygotes and homozygotes in the same proportions as were found in the analysis based on change in frequency the value of s for the three later years combined (i.e. the original data) is 0.54; the

same value is, of course, obtained for the supposed 1929–30 winter figures. Taking all six winters at their face values, $s = 0.51$ for the total.

Birmingham

Collections have been made at a number of sites in Birmingham during the period 1961–70 (Creed 1966, 1971 *a, b* and unpublished). At no one site has it proved possible to obtain samples regularly throughout the season and over several years. However, the frequencies at Hall Green and Aston Church, in the city of Birmingham, and at Maw Green, Walsall, have always been similar to one another. The

TABLE 1. MELANIC FREQUENCY IN SAMPLES CAUGHT AT DIFFERENT TIMES IN THE SAME YEAR AT HALL GREEN AND ASTON CHURCH, BIRMINGHAM, AND MAW GREEN, WALSALL

		time interval between samples months	early sample		late sample	
			size	frequency	size	frequency
Hall Green	1962	3	38	57.9	58	34.5
	1965	3	33	21.2	28	35.7
	1967	2	159	28.3	31	41.9
	1968	1	54	31.5	21	19.0
	1970	1	65	24.6	30	30.0
Aston Church	1964	1	39	41.0	23	43.5
	1967	1	196	21.9	125	27.2
	1969	2	111	25.2	36	36.1
Maw Green	1964	1	65	35.4	115	41.7
	1967	1	106	34.0	67	26.9
	1969	1	81	24.7	48	25.0

mean percentage of melanics, based on the total caught at the three sites in any year, has decreased by 2.27 per year over this period ($r = 0.94$; $P < 0.001$). However, the frequency of melanics in samples caught early in the year has usually been less than the frequency in later samples. Based on occasions when two samples have been caught at the same place in one year (see table 1), the increase in the percentage has averaged 1.47 per interval of one month between samples (in practice, 4–6 weeks was taken as one month, 7–11 weeks as two months). Assuming three generations, or three such intervals, per breeding season and a fairly steady rate of change, this represents an increase of 4.41 per summer, and a decrease of $2.27 + 4.41 = 6.68$ per winter. These estimates may be used to derive values for s and t in an identical manner to that applied to the data for Berlin.

Starting with an arbitrary frequency of red at 70% in spring (the mean value over the period of study was 71.4%), the selection against black heterozygotes, to account for the increase in frequency of red during winter, is given by $s = 0.244$. The subsequent decrease in frequency of red in summer is accounted for by $t = 0.086$.

Pairs of samples, with an interval between collections of at least one month, have been obtained from a number of other British sites during the course of a year. The magnitude of the changes in frequency are not strictly comparable because melanics are much more common at some of these sites than at others. However, the mean increase in melanic percentage, allowance being made for differences in sample size, is 1.1 per month, which is similar to the figure for Birmingham.

NON-RANDOM MATING

Meissner (1907*a, b*; and 1909) recorded the elytral colours of each mating pair encountered on his daily collections in Potsdam. Lusiš (1961) records the total numbers of each of the four possible combinations of red and black males and females, together with the total numbers of each colour seen, at localities in Moscow and Riga; he compared the observed numbers with those expected on a random basis and found a considerable excess of black individuals among the mating pairs. Since 1969 I have also recorded the colours of all mating pairs that I have encountered in Britain and Western Europe. It is thus possible to compare the ratio of observed to expected numbers of black ladybirds among mating pairs at several widely separated localities. For Meissner's data the expected figures may be calculated on a daily basis, and then the observed and expected figures summed for all days; this avoids bias due to small sample sizes on some days and fluctuations in melanic frequency during the period of observation. Lusiš gives the total observed and expected for each set of samples; I have added together all the Moscow observations, and, separately, all those for Riga.

In none of my own samples have I found many copulating pairs; however, for each sample containing such a pair it is possible to calculate a set of expected values for each possible mating combination, based on the observed frequency of adults (i.e. ignoring individuals which later hatch from pupae in the sample). The observed and expected values may then be summed for several localities, regardless of differences in the melanic frequency at each.

Table 2 summarizes the results for Moscow, Riga, Potsdam, western continental Europe and Britain. There is no indication that the combination within each group of mating individuals are other than random, but in all cases black is more frequent within this group than in the populations at large. The excess of black individuals, whether measured as the frequency of red and black individuals (χ^2 with one degree of freedom), or as the frequency of red-red, red-black and black-black pairs (χ^2 with two degrees of freedom) is formally significant in Moscow and Riga, but not elsewhere. A comparison between populations may be made from the apparent deficiency of red individuals amongst the mating pairs. If R_o and B_o are the proportions of red and black observed in the mating pairs, and R_e and B_e are the proportions based on the summed expectations from the total adult populations, the apparent deficiency of red individuals, d , is calculated as

$$d = (R_e - R_o)/R_e B_o.$$

A deficiency would arise if black individuals mate more often than do red ones, or if black individuals tend to remain longer *in copula* than the red ones. The former might be construed as a selective advantage for the blacks and, in effect, increases the value of t , the selection against red in summer, whereas the latter might well constitute a selective disadvantage. The results (see table 2) are consistent with a very low value of d in much of Western Europe, but a steady increase from Potsdam eastwards.

TABLE 2. OBSERVED (o) AND EXPECTED (e) OCCURRENCE OF MATING PAIRS OF *A. BIPUNCTATA*

(Expected numbers are based on the frequencies in the wild populations.)

		mating pairs				comparison between observed and expected, χ^2		relative deficiency of red, d
		red red	red black	black black	total	mating pairs	red vs. black	
Moscow	o	273	81	9	363	34.29	31.93	0.45
	e	308.0	52.4	2.7	363.1			
Riga	o	860	1347	571	2778	52.42	50.84	0.17
	e	998.8	1329.4	449.4	2777.6			
Potsdam	o	60	90	44	194	1.35	1.02	0.10
	e	63.5	92.8	37.7	194.0			
W. Europe	o	16	16	11	43	0.61	0.00	0.01
	e	14.8	18.5	9.7	43.0			
Britain	o	111	44	5	160	1.14	0.21	0.06
	e	115.2	38.6	6.2	160.0			

DISCUSSION

The nature of the data available means that fairly wide limits must be placed on the estimate of selection operating in Birmingham. However, it appears that there is clearly a greater advantage relating to black individuals in summer, and to red in winter, in Berlin than in Birmingham. The seasonal reversal of selection, together with the difference in selective values between the two cities, suggest that some climatic factor may be important; there is also a strong indication in both areas that urbanization is responsible for an increased melanic frequency compared with neighbouring rural areas. Around Birmingham the melanic frequency falls to less than 10% well before open country is reached. In July 1973, the melanic frequency at Geltow, on the outskirts of Potsdam, was 15.2% (sample size 105). The melanic frequency in Potsdam in June and July of 1906–8 was between 30 and 45%, while in Berlin the mean frequency during the 1930s was 37.5% in April, rising to 60.5% in October. If temperature is implicated as a selective factor, then the 'heat island' effect of large towns (Chandler 1962) may contribute to the difference in frequency between urban and rural areas; in Britain, at least, local

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pollution conditions seem to be the most important single factor (Creed 1971*a, b*, 1974; Lees, Creed & Duckett 1973).

The part played by temperature may be more clearly investigated with the Berlin data (see table 3); values of s and t may be calculated for each summer and each winter season for which initial and final frequencies are known, and these

TABLE 3. ACTUAL NUMBERS AND MELANIC FREQUENCY OF *A. BIPUNCTATA* OBSERVED AT THEIR PLACE OF HIBERNATION IN BERLIN

(The figures are derived from tables 2 and 3 of Timofeeff-Ressovsky (1940).)

	spring				autumn			
	black	red	total	black (%)	black	red	total	black (%)
1930	176	428	604	29.1	783	461	1244	62.9
1931	334	443	777	43.0	622	494	1116	55.7
1933	213	351	564	37.8	1414	668	2082	67.9
1934	172	304	476	36.1	708	529	1237	57.2
1936	—	—	—	—	528	305	833	63.4
1937	31	41	72	43.1	578	405	983	58.8
1938	216	333	549	39.3	432	448	880	49.1
Total	1142	1900	3042	37.5	5065	3310	8375	60.5

TABLE 4. ESTIMATES OF THE SELECTIVE COEFFICIENT, s , AGAINST HETEROZYGOUS BLACK *A. BIPUNCTATA* DURING WINTER, ASSUMING SELECTION AGAINST HOMOZYGOUS BLACK TO BE TWICE AS GREAT

	period	s	sample size		lowest daily mean min. temp.
			autumn	spring	°C
Berlin	1930-1	0.477	1244	777	-3.6
	1933-4	0.666	2084	476	-5.9
	1936-7	0.487	833	72	-5.6
	1937-8	0.462	983	549	-2.9
	1930-8	0.524	8375	3042	-4.1
Birmingham	1962-70	0.244	582	947	+0.1

values may then be compared with summer and winter temperatures (tables 4 and 5). Although the estimates of s and t are not equally reliable as a result of different sample sizes and of the assumptions that must be made in some cases as to genotype frequencies of the black individuals, regression calculations have been weighted only according to sample sizes; the harmonic mean of spring and autumn sample sizes has been taken as the weight, in that it is roughly proportional to the joint variance. A positive correlation is in general obtained between t and measurements of summer temperature; the higher the temperature, the greater is the selection against red. This conforms with Marriner's (1926) observation that black *A. bipunctata* can better withstand high temperatures than can red ones.

The best correlation, though not formally significant, was with the highest mean

monthly maximum temperature for the relevant year ($r = 0.65$; $0.2 > P > 0.1$). This positive correlation (figure 1a) is also in agreement with the trend shown between Berlin and Birmingham; if the value for Birmingham (the mean of the lowest monthly value for each winter) is also included, the regression becomes formally significant ($r = 0.81$; $0.05 > P > 0.02$).

Conversely, the best correlation found with s is the lowest mean monthly

TABLE 5. ESTIMATES OF THE SELECTIVE COEFFICIENT, t , AGAINST RED *A. BIPUNCTATA* DURING SUMMER

	year	t	sample size		highest daily mean max. temp.
			spring	autumn	°C
Berlin	1930	0.43	604	1244	25.0
	1931	0.22	777	1116	23.2
	1933	0.41	564	2082	29.8
	1934	0.31	476	1237	25.2
	1937	0.26	72	983	23.7
	1938	0.18	549	880	24.6
	1930-8	0.33	3042	8375	25.1
Birmingham	1962-9	0.09	947	582	19.7

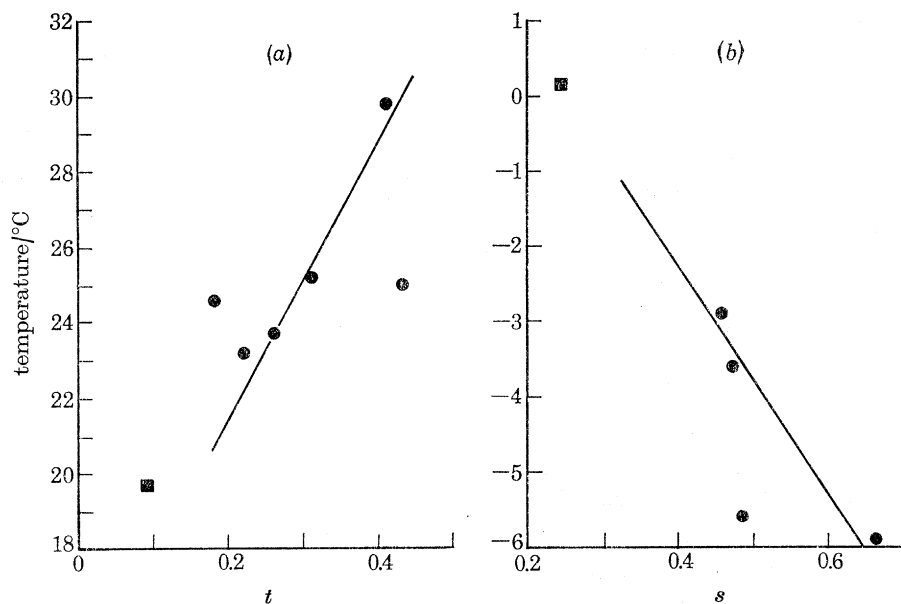


FIGURE 1. (a) The relation between estimates of the selection coefficient, t , against red *A. bipunctata* in summer and the highest monthly mean maximum temperature (see table 5). (b) The relation between estimates of the selection coefficient, s , against heterozygous black *A. bipunctata* in winter and the lowest mean monthly minimum temperature (see table 4). In each case the regression line is calculated from the Berlin results (●), and does not include the point for Birmingham. (■).

minimum temperature in winter (figure 1*b*). Again, the regression from the Berlin data alone does not reach formal significance ($r = 0.92$; $0.1 > P > 0.05$), but it does so when the value for Birmingham (the mean of the highest monthly value for each year) is also included ($r = 0.97$; $0.01 > P > 0.001$). Thus there is some evidence that black individuals survive cold conditions less well than do red ones, though Meissner's observations (see above) suggest that the length of the winter, as opposed to its severity may also be important.

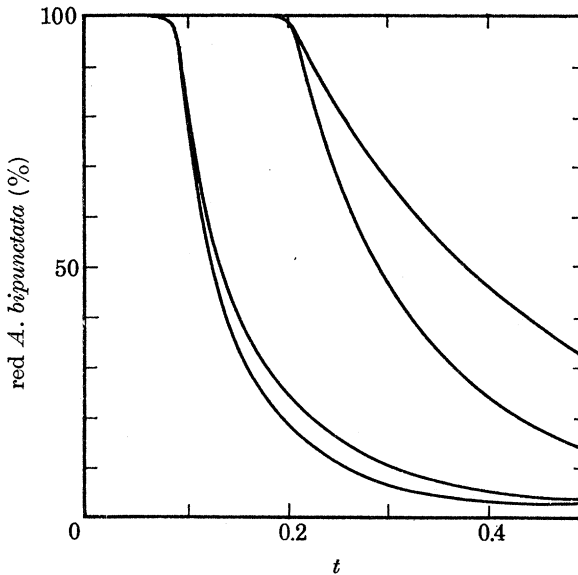


FIGURE 2. Expected equilibrium frequency of red *A. bipunctata* with different intensities of selection (t) against red individuals in summer near Birmingham (lower pair of curves; $s = 0.244$) and near Berlin (upper pair of curves; $s = 0.5$). The top curve of each pair represents the frequency of red in spring, and the lower one the autumn frequency.

If one assumes that the selection coefficient, s , of about 0.5 against black heterozygotes in winter (with black homozygotes being lethal) applies to Geltow, as well as to Berlin, then a stable melanic frequency of 15% early in the season will be maintained by a coefficient, t , of 0.24 against red homozygotes in summer. The melanic frequency would rise from 14.3% (gene frequency 7.1%) to 26.2% (gene frequency 13.9%) by the end of the summer. Thus the survival of red homozygotes in summer ($1 - t$) in the relatively rural area of Geltow is 0.76 compared with 0.67 in Berlin. Assuming that selection due to different causes is multiplicative in effect, the reduction in survival of red individuals resulting from the urbanization is $0.67/0.76 = 0.88$, corresponding with a selection coefficient of 0.12.

Similarly in Britain, equilibrium frequencies corresponding to different values of t may be calculated on the assumption that $s = 0.24$, as was found in Birmingham; the results are shown graphically in figure 2. Melanic frequencies of less than 20%

will occur when t is less than 0.1. On the outskirts of Birmingham, with less than 10% melanics, a value of about 0.09 is indicated; this compares with the value of 0.086 derived from the change in frequency of Hall Green, Aston Church and Maw Green, and suggests that the melanic frequencies at these three sites may continue to fall even if the pollution conditions now remain constant.

If a survival of red individuals of 0.88, being the value calculated as due to the effects of urbanization in Berlin, is imposed in addition to the selection of $(1-t) = 0.91$, the resulting net survival is 0.80 (in other words, $t = 0.2$); this corresponds with a melanic equilibrium frequency of about 75%, being very close to the mean frequency of 75.5% found by Hawkes (1927) in Edgbaston, Birmingham, in 1920–7. The melanic frequency in Edgbaston has not decreased by as much as in other parts of Birmingham. In 1960–1 it was 59.5% (sample size 173), whereas in 1969 it was 50.6% (sample size 172). For an equilibrium frequency of 55%, the net survival of red individuals per generation in summer would be about 0.87. In other words, a change in selective intensity in Birmingham, and probably elsewhere in Britain, leads to a much larger change in the equilibrium melanic frequency than would a similar change in selection in Berlin (see figure 2); this is a direct consequence of the different magnitude of selection in favour of red individuals during the winter.

Elsewhere in Britain the melanic frequency rises to about 95%. Ignoring the possibility that s may be somewhat different in Manchester and Glasgow compared with Birmingham, figure 2 suggests that t reaches a maximum value of about 0.4 in the most heavily smoke polluted areas. If the survival of red in the absence of pollution is 0.91 in Britain, then this value corresponds with a relative survival of 0.66 as a result of pollution or other urban influences. These estimates of selective intensity are summarized in table 6.

It has seemed appropriate to distinguish two types, or phases, of selection acting against the red homozygotes: one that varies with local pollution levels, and one that varies, in part at least, with summer temperature. Although non-random mating (see above) may contribute to this second phase of selection, there are difficulties in accounting for it all in this manner. The deficiency of red individuals, d , among mating pairs, though not significant, is greater in Potsdam than in Britain; similarly, mean summer temperature is higher in Potsdam and selection against red homozygotes also appears to be higher in the rural area around Potsdam than on the outskirts of Birmingham. A considerably higher value of d is obtained in Moscow, which is again somewhat hotter in summer than Potsdam; the lower melanic frequency in Moscow could result from an increased advantage of red individuals in winter. However, Riga, where d has a value intermediate between Potsdam and Moscow, has a lower mean July temperature than either. Thus there is no conclusive evidence as to the importance of non-random mating.

A generally greater activity level of black individuals than of red at a given temperature (Benham, Lonsdale & Muggleton 1974) might be expected to favour black forms in areas where summer air temperatures are relatively low. Published

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distribution data (Lusis 1961; Creed 1971*a*) do not support this conclusion; indeed, Scali & Creed (in preparation) have found a strong positive correlation between melanic frequency and mean temperature in Tuscany.

Lusis (1961) pointed out that the black forms would be better able to absorb reduced levels of solar radiation than would the red, and that the presence of smoke in the atmosphere above large cities would therefore place the red forms at a disadvantage. Benham *et al.* (1974) carried out a regression analysis of melanic frequencies in Britain against mean annual sunshine levels as estimated from a 1:2000 000 scale map (Bickmore & Shaw 1963). They obtained a correlation of -0.59 and discount the possibility that smoke may have a more direct selective

TABLE 6. ESTIMATES OF THE SURVIVAL OF RED *A. BIPUNCTATA* RELATIVE TO BLACK INDIVIDUALS DURING SUMMER: MELANIC FREQUENCIES ARE FOR APRIL IN BERLIN, JULY IN GELTOW AND THROUGHOUT THE SUMMER IN BRITAIN

	pollution intensity	selection due to:		net survival of reds ($1-t$)	melanic frequency
		pollution	temperature		
Berlin	+	0.88	0.76	0.67	38
Geltow	-	1.00	0.76	0.76	14
Birmingham (1920-7)	+	0.88	0.91	0.80	75
Birmingham (Edgbaston)	+	0.96	0.91	0.87	55
Birmingham (outskirts)	-	1.00	0.91	0.91	5
Manchester + Glasgow	++	0.66	0.91	0.60	95

effect. I have already discussed these two alternative arguments (Creed, 1971*a*), and will not repeat here my earlier reasons for thinking that smoke is having a direct selective effect, other than to point out that a correlation of 0.74 was obtained in a regression of melanic frequency against mean summer smoke levels at 69 sites in Britain.

Although a significant regression neither proves cause nor effect, it may indicate the nature of the relation between variables. Nine ladybird sampling sites in Scotland may be closely matched with sunshine recording stations (Meteorological Office 1963); the data are included in table 7. The correlation between melanic frequency and mean annual sunshine is given by $r = -0.56$ ($0.2 > P > 0.1$), which is very close to the value obtained by Benham *et al.* However, the correlation with mean January sunshine ($r = -0.59$; $0.1 > P > 0.05$) is far higher than with mean July sunshine ($r = +0.08$; $0.9 > P > 0.8$). There can be little direct exposure to sunshine during January, when the ladybirds are hibernating in crevices and any activity would be disadvantageous. For 14 sites in England between latitudes 52° and 54° N, the correlation with mean July sunshine is -0.45 ($0.2 > P > 0.1$).

Of the Scottish collecting sites, 13 may be matched by locality, and reasonably closely by year, with pollution recording stations (Warren Spring Laboratory 1963-70) (see table 6). The correlation between melanic frequency and mean summer

(April to September) smoke levels is given by $r = 0.89$ ($P < 0.001$). For 16 sites in the west Midlands, and centred on Birmingham, where the smoke derived from the combustion of coal might be expected to be relatively uniform qualitatively, though certainly not quantitatively, the correlation is somewhat lower ($r = 0.72$; $0.01 > P > 0.001$), but so also is the range of melanic frequencies (0–56 %, compared with 4.5–95 % in Scotland).

TABLE 7. MELANIC FREQUENCIES IN *A. BIPUNCTATA*, MEAN SUMMER SMOKE CONCENTRATION AND MEAN HOURS OF BRIGHT SUNSHINE AT COLLECTING LOCALITIES IN SCOTLAND

locality	ladybirds			smoke		sunshine/h d ⁻¹		
	year	sample size	melanics (%)	year	$\mu\text{g m}^{-3}$	Jan.	July	annual
Bathgate	1972	22	86.4	1970	38	—	—	—
Dumbarton	1967	152	75.0	1966	81	—	—	—
Dumfries	1965–8	66	9.1	—	—	1.39	4.94	3.55
Dundee	1966/7	111	4.5	1966/7	44	1.70	5.09	3.69
Edinburgh	1968	341	89.7	1968	76	1.42	5.44	3.64
Falkirk	1967/8	73	60.3	1967/8	31	—	—	—
Glasgow								
Kelvinside	1966	250	95.2	1966	80	0.95	4.96	3.20
Provanmill	1967/8	123	86.2	1967/8	76	—	—	—
Govanhill	1967	101	92.1	1967	70	—	—	—
Greenock	1967	138	76.8	1966	58	0.83	5.14	3.34
Haddington	1967/8	60	8.3	1967	10	—	—	—
Kilmarnock	1967/8	155	58.1	1967/8	35	1.38	5.08	3.62
Kirkcaldy	1966–8	82	1.2	—	—	1.35	5.14	3.66
Paisley	1967	104	88.5	1967	60	1.01	5.07	3.32
Perth	1966–8	174	32.8	—	—	1.32	5.25	3.59
Stirling	1966–8	131	4.6	1966/7	22	—	—	—

None of the foregoing account excludes the possibility that there may be some additional, constant, selective differential between red and black; that is to say, one which does not vary geographically. Furthermore, the possibility cannot be excluded that some factor in addition to, or even instead of, temperature may contribute to the difference in selection that is manifest between Berlin and Birmingham; for example, local abundance of predominantly red and of predominantly black species belonging to the same assemblages of Müllerian mimics could influence the melanic frequency in the polymorphic ladybird species.

Komai & Hosino (1951) found that the frequencies of the colour morphs and the presence of the elytral ridge in the ladybird, *Harmonia axyridis* (Pallas), were very different in samples collected from pine trees (var. *conspicua* 12.0 %, presence of elytral ridge 4.2 % in 1950) compared with samples from other habitats (on wheat in 1950: var. *conspicua* 61.9 %, presence of elytral ridge 40.7 %) at Sanagé in Japan; the latter frequencies were typical for the region as a whole, while those on the pine trees were unlike anywhere else in Japan. Although Komai & Hosino

describe this phenomenon in terms of an isolate rather than as a result of selection, there was no geographical separation; other possibilities are that strong selection is taking place in the pine tree habitat of an otherwise continuous population, or differential habitat preference in being exercised by the morphs. A similar situation to that at Sanagé was not observed elsewhere in that species, nor has any evidence of such local differentiation been found in *A. bipunctata*. While changes in frequency within one habitat and during one season, such as have been recorded in Birmingham, could result from a progressive migration to a preferred habitat, the cyclical change in Berlin, observed at the place of hibernation, and the directional change in Birmingham must result from natural selection. If this selection varies according to habitat within one population, then the estimates of its intensity must be regarded as mean values for that population.

Considerable geographic variation in the proportions of the two melanic forms, *quadrimaculata* and *sempustulata*, indicate qualitative differences in selection between places with the same overall melanic frequency; one such qualitative difference, relating to the properties of coal and hence of the resulting smoke, has already been tentatively considered (Creed 1971*a*). In a later paper it is intended to examine the extent to which pollution and temperature can be used to explain the variations in melanic frequency found elsewhere in Europe.

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REFERENCES

- Benham, B. R., Lonsdale, D. & Muggleton, J. 1974 Is polymorphism in two-spot ladybird an example of non-industrial melanism? *Nature, Lond.* **249**, 179–180.
- Bickmore, D. P. & Shaw, M. A. 1963 *The atlas of Britain and Northern Ireland*. Oxford: Clarendon Press.
- Chandler, T. J. 1962 London's urban climate. *Geogr. J.* **128**, 279–302.
- Creed, E. R. 1966 Geographic variation in the two-spot ladybird in England and Wales. *Heredity* **21**, 57–72.
- Creed, E. R. 1971*a* Melanism in the two-spot ladybird, *Adalia bipunctata*, in Great Britain. In *Ecological genetics and evolution* (ed. E. R. Creed), pp. 134–151. Oxford: Blackwell Scientific Publications.
- Creed, E. R. 1971*b* Industrial melanism in the two-spot ladybird and smoke abatement. *Evolution* **25**, 290–293.
- Creed, E. R. 1974 Two-spot ladybirds as indicators of intense local air pollution. *Nature, Lond.* **249**, 390–392.
- Ford, E. B. 1937 Problems of heredity in the Lepidoptera. *Biol. Rev.* **12**, 461–503.
- Frazer, J. F. D. & Rothschild, M. 1960 Defence mechanisms in warningly-coloured moths and other insects. *Proc. 11th int. Congr. Ent.* **3**, 249–256.
- Haldane, J. B. S. 1924 A mathematical theory of natural and artificial selection. *Trans. Camb. phil. Soc.* **23**, 19–40.
- Hawkes, O. A. M. 1927 The distribution of the ladybird *Adalia bipunctata* L. (Coleoptera). *Entomol. mon. Mag.* **63**, 262–266.
- Kettlewell, H. B. D. 1955 Selection experiments on industrial melanism in the Lepidoptera. *Heredity* **9**, 323–342.

- Kettlewell, H. B. D. 1956 Further selection experiments on industrial melanism in the Lepidoptera. *Heredity* **10**, 287–301.
- Kettlewell, H. B. D. 1965 A 12-year survey of the frequencies of *Biston betularia* (L.) (Lep.) and its melanic forms in Great Britain. *Entomol. Rec. J. Var.* **77**, 195–218.
- Komai, T. & Hosino, Y. 1951 Contributions to the evolutionary genetics of the lady-beetle, *Harmonia*. II. Microgeographic variations. *Genetics* **36**, 382–390.
- Lees, D. R. & Creed, E. R. 1975 Industrial melanism in *Biston betularia*: the role of selective predation. *J. Anim. Ecol.* **44**, 67–83.
- Lees, D. R., Creed, E. R. & Duckett, J. G. 1973 Atmospheric pollution and industrial melanism. *Heredity* **30**, 227–232.
- Lusis, J. J. 1961 On the biological meaning of colour polymorphism of ladybeetle *Adalia bipunctata* L. *Latvijas Entomologs* **4**, 3–29.
- Marriner, T. F. 1926 A hybrid coccinellid. *Entomol. Rec. J. Var.* **38**, 81–83.
- Meissner, O. 1907a Die relative Häufigkeit der Varietäten von *Adalia bipunctata* L. in Potsdam (1906). *Z. wiss. InsektBiol.* **3**, 12–20, 39–45.
- Meissner, O. 1907b Die relative Häufigkeit der Varietäten von *Adalia bipunctata* L. in Potsdam (1907). *Z. wiss. InsektBiol.* **3**, 309–313, 334–344, 369–374.
- Meissner, O. 1909 Die relative Häufigkeit der Varietäten von *Adalia bipunctata* L. in Potsdam (1908). *Z. wiss. InsektBiol.* **5**, 231–242.
- Meissner, O. 1910 Die relative Häufigkeit der Varietäten von *Adalia bipunctata* L. (1908–9). *Z. wiss. InsektBiol.* **6**, 98–101.
- Meissner, O. 1912 Zur Statistik und Biologie von *Adalia bipunctata* L. *Ent. Z. Frankf. a. M.* **26**, 82–83, 87–88, 90, 94–95.
- Meteorological Office 1963 *Averages of bright sunshine for Great Britain and Northern Ireland 1931–60*. London: H.M.S.O.
- Timofeeff-Ressovsky, N. W. 1940 Zur Analyse des Polymorphismus bei *Adalia bipunctata* L. *Biol. Zbl.* **60**, 130–137.
- Timofeeff-Ressovsky, N. W. & Svirezhev, Yu. M. 1966 Adaptive polymorphism in populations of *Adalia bipunctata* L. *Problemy. Kibern.* **16**, 136–146. (English translation: *Probl. Cybern.* **16**, 161–174.)
- Warren Spring Laboratory 1963–70 *The investigation of air pollution: annual summaries* Ministry of Technology.