GEOGRAPHIC VARIATION IN THE TWO-SPOT LADYBIRD IN ENGLAND AND WALES

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1. INTRODUCTION

Two of the most variable species of ladybird in this country are *Adalia bipunctata* and *A. decempunctata.* Hawkes (1920, 1927) drew attention to the differences in frequency of the varieties of *A. bipunctata* in this country, mainly around Birmingham; she found that the black forms predominated in the city while they were less common or rare elsewhere. In London the black forms comprised only a few per cent. of the population. Further information, though figures are not always quoted, may be found in Marriner (1926, 1939*a* and *b*), Bayford (1947), Allen (1957) and Conway (1958).

The insect has also attracted attention in Europe, but more so in some countries than others. It was in this species that Timofeeff-Ressovsky (1940*a*, 1940*b*) demonstrated the action of strong selection in Berlin. He found that the black varieties had a higher mortality than the red during hibernation, but that their relative numbers increased again during the summer. Lusis (1961) has reviewed the distribution of the varieties of *A. bipunctata* in Europe and western Russia and suggests that two conditions tend to favour the black ones: " (1) in places with a maritime, more humid climate the percentage of black forms in the populations of *Adalia bipunctata* L. is as a rule higher than in places with a more continental climate, and (2) in large cities, especially in those with highly developed industry, the percentage of black forms in the adalia-populations is higher than in towns and in the countryside with similar climate." Unfortunately the only figures for the British Isles apparently available to Lusis were those in Hawkes' second paper (1927), and some of these he disregards. He makes no mention of the high frequency of red in London which must have a bearing on the question of industrial centres, quite apart from Britain's maritime climate.

The present survey was started in 1960 since the data then available indicated sharp geographic changes in frequency of the varieties in a not immobile insect in which strong selective forces had been shown to be operating. The results may usefully be compared with those of Lusis and certain important differences emerge.

2. MATERIAL

(i) *Life history*

Adalia bipunctata, in common with most other ladybirds in this country, feeds mainly on aphids throughout its life; the green species seem to be much preferred to the black ones. It overwinters as an adult, quite large numbers often aggregating under the bark of trees or in houses where they may get into crevices, in roller blinds or remain on the walls or ceiling; with the warmer weather they emerge and are to be seen crawling over the window panes. The first eggs are laid in late spring, the exact timing being very variable from year to year, and probably depending mainly on temperature and the availability of food. In the laboratory a complete generation can take as little as a month, but is probably somewhat longer in the wild. The eggs are laid in clusters on the leaves of aphid-infested plants and hatch in about three to seven days; those that do not hatch are eaten by the larvæ that have already emerged. The larvæ feed on the surface of the leaves where they are open to attack by any would-be predators; they are, however, distinctively coloured, being grey-blue with yellowish markings. Though quite different from the adult patterns, the larval colouring is not cryptic and almost certainly serves in a warning capacity. The larvæ pupate in the open, either on the leaves or, if in trees, sometimes on the bark. When unduly disturbed, for example upon excessive movement of the plant. the larvæ and adults will let go their hold and drop off. If picked up and held they expel from the joints of their legs a yellow liquid having a distinctive smell, often described as similar to crushed pea pods (see p. 67). When the pupa is touched it may repeatedly straighten out and close up, or straighten out and remain in that position for some time; the effect of this is to draw attention to itself. The pupa shows no obvious warning coloration. At no stage in the life cycle are any apparent attempts made at concealment.

(ii) *Collections*

1. *Hibernating masses.* Occasionally such aggregations were found; more frequently samples from them were sent by other collectors. For reasons to be explained later, caution has to be exercised in interpreting the figures obtained; data from hibernating insects are included only if the sample is large or if no other data are available for that locality.

2. *Active populations.* Sampling was extended to pupæ as well as to adults. The pupæ hatch with no difficulty in closed containers, but one has to guard against the soft, newly emerged adults being eaten by those that have emerged earlier. Larvæ were only taken when it was impossible to get a sufficient sample, and then only very large ones that were about to pupate.

Although *A. bipunctata* is to be found on a variety of plants, the great majority of samples were collected from lime trees (*Tilia* × *europæa* L.) and patches of stinging nettles (*Urtica dioica* L.). This was done partly to reduce any variation that might be due to different aphid species, though it is almost certain that this possible cause of variation can be ignored, but mainly because on visiting a new and unknown area it proved much easier to find avenues of lime trees or patches of nettle on waste ground than large numbers of roses or other garden plants heavily infested with aphids. It should be mentioned that ideal situations were often found, with aphids in abundance, but apparently devoid of ladybirds. This accounts to a large extent for the absence of samples from such key areas as north Staffordshire and south Cheshire. At Builth Wells, Radnorshire, the ten-spot ladybird, *A. decempunctata* completely replaced *A. bipunctata* on all the lime trees investigated.

(iii) *Varieties*

The varieties most commonly encountered in this country, together with some less common ones, are shown in fig. 1. Lus (1928), working on Russian material concluded that all were controlled by a single multiple allelomorphic series with a dominance order the same as the numbering in fig. 1, *sublunata* being the top dominant of those shown, and with 5-8 grouped together as *annulata*. Timofeeff-Ressovsky (1940*a*) found that Lus's data did not conclusively prove the existence of a single

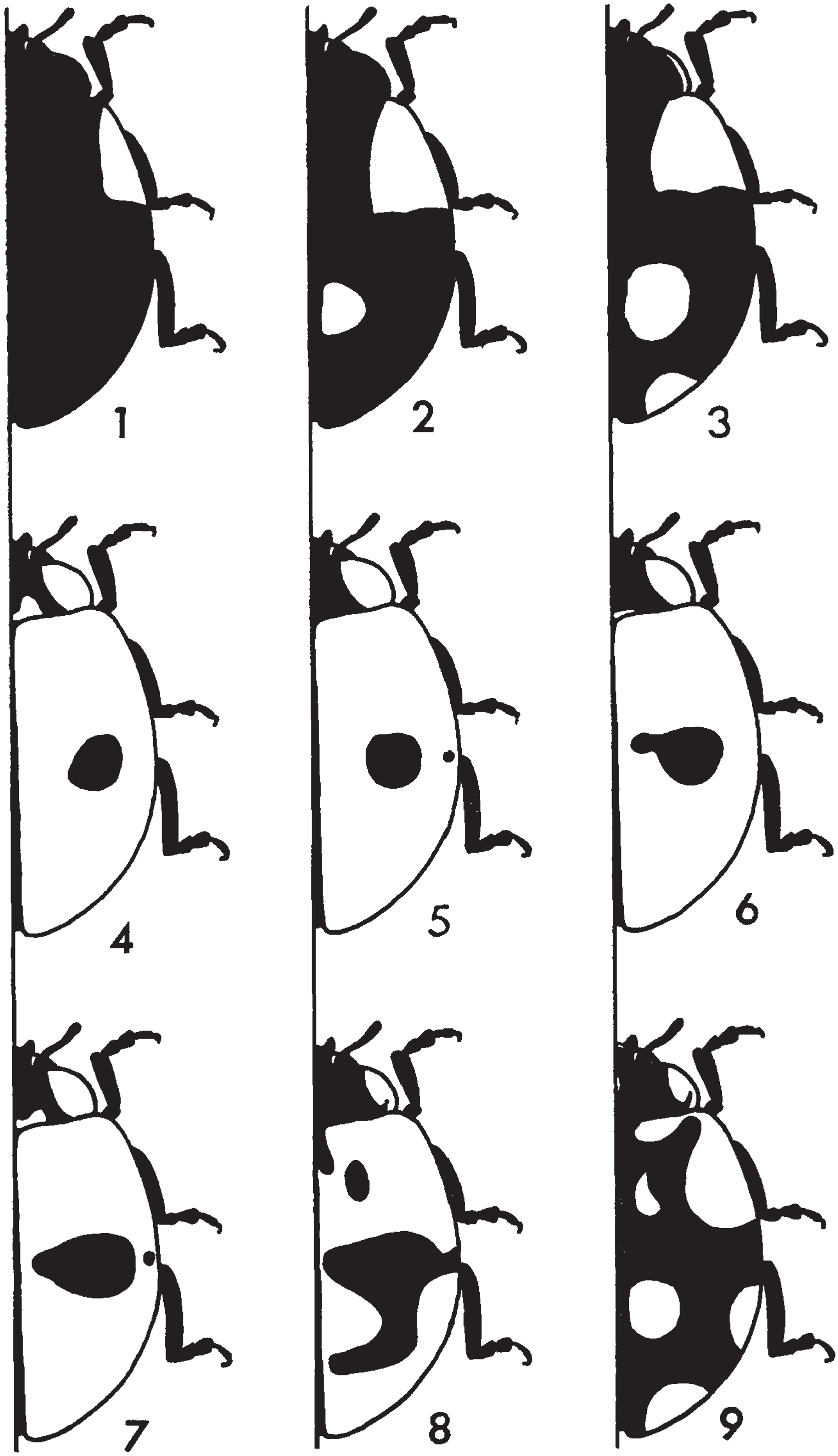

FIG. 1.—Some varieties of *Adalia bipunctata*.

1. *sublunata* 2. *quadrimaculata* 3. *sexpustulata*
4. Typical 5. *stephensi* 6. *rubiginosa*
7. *unifasciata* 8. *annulata* 9. *12-pustulata*

multiple allelic series for all patterns. Preliminary breeding results (Creed, unpublished) do not disagree with the view that *quadrimaculata* and *sexpustulata* are allelomorphic with and dominant to *typica* but they indicate that the control of the forms numbered 5-7, *annulata* and *12-pustulata* is more complicated. In the analysis that follows *sublunata*, *quadrimaculata* and *sexpustulata* are classed together as the melanic or black forms while *typica*, *annulata* and the intermediates are classed as reds. No examples of *12-pustulata* are included in any of the collections, while there were only fifteen *annulata* and two *sublunata* out of a total of about six thousand.

3. INTRASEASONAL STABILITY

Timofeeff-Ressovsky (1940*a*, 1940*b*) found a progressive increase of the melanic forms during the course of the summer and the reverse change during hibernation. The change in frequency of the forms was about 10 per cent. in 1931 and roughly 30 per cent. in 1930 and 1933. Marriner (1926) remarks "... the red varieties predominate in the earlier broods of the year before the hottest weather sets in, whereas, if later, July, August and September, prove fine and hot, then I have found the black forms to predominate."

TABLE 1

A comparison of samples taken at different times in the same year from each locality. In the last column is shown the form which, for the figures available, apparently increased during the period of investigation

Locality	Month	Red	Black	Month	Red	Black	Inc.
Altrincham	July	5	35	Sept.	2	35	Black
Castle Bromwich	June	31	17	July	16	4	Red
Doncaster	July	13	...	Sept.	79	2	Black
Edgbaston, Birmingham	July	4	17	Aug.	11	22	Red
Gloucester	June	17	6	Aug.	24	5	Red
Hall Green, Birmingham	June	16	22	Sept.	38	20	Red *
Henley in Arden	June	73	4	Aug.	58	6	Black
Warwick	June	63	2	July	68	7	Black
Worcester	July	17	5	Sept.	82	14	Red

* = Significant change, $0{\cdot}05 > P > 0{\cdot}02$; none of the others is significant.

If alterations in phenotype frequency are widespread and large, it becomes difficult to compare frequencies between places in which the breeding season is of different length or places sampled at different times of the year. Insufficient data are available for this country, but all relevant figures from the present survey covering 1960-63 are included in table 1. In only one case is there a significant difference, at Hall Green, Birmingham, and it is the red forms that have increased in the course of the summer. The heterogeneity of samples from this locality prevents one from combining them for purposes of statistical comparisons; however, to give an idea of the proportion of black insects for use in the distribution maps, and to prevent a confusion of symbols, the overall percentage of black has been used.

There is no set pattern to the figures in table 1 and certainly no general increase in melanics. The lack of a prolonged heatwave in any of these years may be the explanation, if Marriner's views are correct. It may be that the intervals between observations are not sufficiently long, but since in some cases they represent the limits of the collecting period, it has been felt justifiable to compare samples regardless of the month in which they were taken.

TABLE 2

A comparison of small samples of hibernating ladybirds with samples taken in the field from a nearby locality

Locality	Hibernating		Active		Difference
	Red	Black	Red	Black	
Aldershot . .	10	3	36	3	Not significant
Cambridge . .	23	3	77	2	Not significant
Lincoln . .	12	3	31	...	Significant at 5 per cent.

Rothschild (1962) has suggested that *quadrimaculata* tend to aggregate during hibernation; Allen (1957) implies a similar phenomenon. If this is the case, small samples of hibernating ladybirds would provide a less good estimate of the frequency of black individuals in the population as a whole than would be expected by chance. During the present survey three small samples of hibernating ladybirds were obtained, all from areas in which black was expected to be at a low frequency or absent, but all of which indicated a higher frequency than in surrounding areas. Subsequently, samples of active insects were obtained from as near to the hibernation sites as possible. Details of these collections are given in table 2.

4. GEOGRAPHICAL VARIATION

The results of the survey are given in table 4, and pictorially represented in figs. 2 and 3. While the majority of samples were collected in 1962, some were obtained in the preceding two years and a few in 1963; Conway's (1958) sample from Kingston, Surrey, is also included. In no case has a significant change been detected between years, where data are available (see table 3 which excludes Hall Green where the comparison cannot be made), and all figures for one locality have been combined (including those for Hall Green, Birmingham; see previous section). In table 4 a serial number is given to each locality; these are used on the maps and in the text of the paper, following the locality name, to simplify cross reference.

No single sample of sufficient size for inclusion has been obtained from south-west England. However, a total of just over thirty insects has been examined from Sherborne, Taunton, Exeter, Launceston and Penzance (1); all were of the typical red form. Similarly the

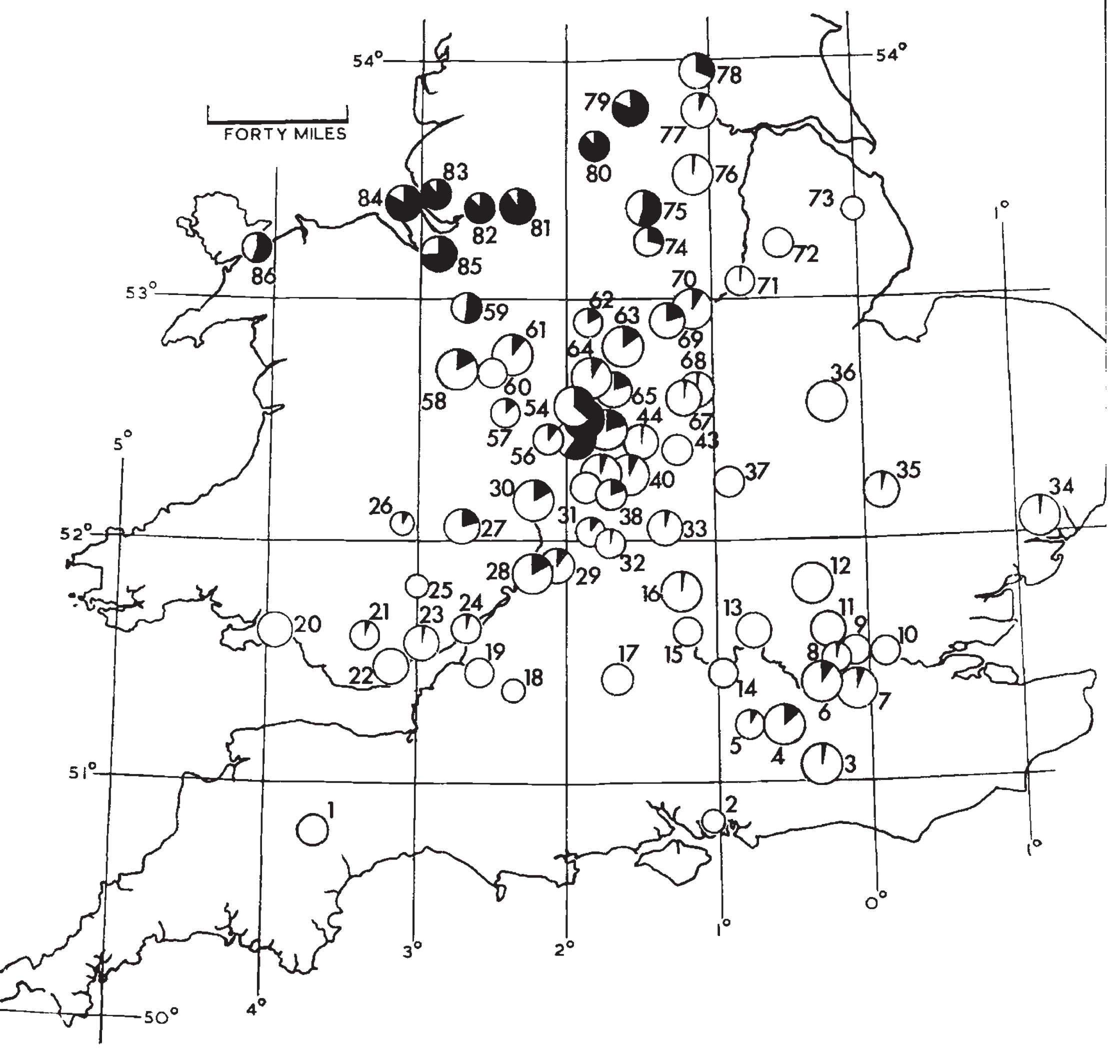

FIG. 2.—Distribution map showing the frequency of the red (white segments) and melanic (black segments) varieties of the Two-spot Ladybird, *Adalia bipunctata*, in England and Wales. For key to numbers see table 4. The four sizes of circle refer to samples of 9-19, 20-39, 40-79 and 80 or more insects, in increasing order.

collection of about forty individuals from the Berkshire and Wiltshire Downs (17) represents several distinct localities.

The distribution maps show an association, but not a coincidence, of the areas having an increased proportion of melanic ladybirds with regions of heavy industry. This is most marked in Birmingham (localities 46-55) and the industrial belt across Lancashire and Yorkshire (localities 75 and 79-84). The area characterised by up to

10 per cent. black in south-east England (3-8), isolated by an otherwise almost entirely red area, suggests some connection with London. The black area is, however, centred probably ten or fifteen miles to the south, and possibly west, of the middle of London, and while Guildford (4), which may almost be described as a country town, has 13 per cent. black, in Hyde Park (9) and the grimiest areas of east London the 67

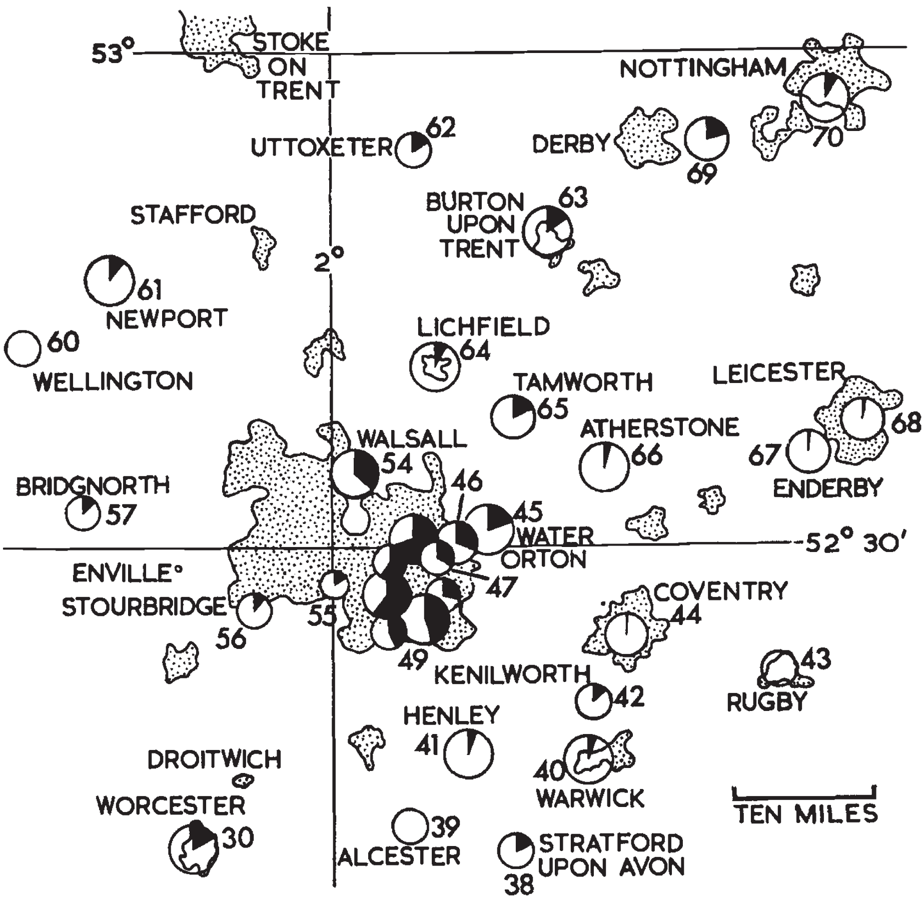

FIG. 3.—Distribution map showing the frequency of the red (white segments) and melanic (black segments) varieties of the Two-spot Ladybird, *Adalia bipunctata*, in the Midlands of England. For key to numbers see table 4. The four sizes of circle refer to samples of 9-19, 20-39, 40-79 and 80 or more insects, in increasing order.

ladybirds found were all red. An apparently similar extension to the south-west is also seen elsewhere; Worcester (30), Hereford (27) and Gloucester (28) all have appreciable proportions of blacks. In the north, Chester (85) lies on the fringe of the industrial belt but Whitchurch (59) and Bangor (86) are well separated from it.

The converse appears also to be true; even in the centre of Coventry (44), only nineteen miles to the east of Birmingham, the black forms are rare, and similarly around Leicester. Sample 68 (3 per cent. black) was collected in the centre of the city; the sample from Enderby (67;

2 per cent. black) came from a village churchyard bordered on one side by open fields. Nottingham (70), a large industrial town, has 9 per cent. blacks. Further to the north there is an absence of blacks from Doncaster (76), and Sheffield (75), at 55 per cent., is much below

TABLE 3

A comparison of samples taken from the same locality in successive years. Only those are included in which the frequency of black is high enough to make the comparison worthwhile

Locality	Year	Red	Black	Total	
Edgbaston	1960 1961 1962	55 15 51	64 39 65	119 54 114	$\chi^2_{(2)} = 5.54$ $0.1 > P > 0.05$
Gloucester	1962 1963	41 107	11 13	52 120	$\chi^2_{(1)} = 3.22$ $0.1 > P > 0.05$
Guildford	1962 1963	101 31	15 3	116 34	$\chi^2_{(1)} = 0.42$ $0.9 > P > 0.8$
Hereford	1962 1963	19 20	6 4	25 24	$\chi^2_{(1)} = 0.41$ $0.9 > P > 0.8$
Maw Green, Walsall	1961 1962	27 51	18 28	45 79	$\chi^2_{(1)} = 0.26$ $0.7 > P > 0.5$
Water Orton	1960 1961 1962	23 19 32	5 9 5	28 28 37	$\chi^2_{(2)} = 3.57$ $0.2 > P > 0.1$
Worcester	1962 1963	100 53	19 9	119 62	$\chi^2_{(1)} = 1.53$ $0.3 > P > 0.2$

the figures of 80-90 per cent. found further to the west. York (78) appears as a possible exception. Although containing heavy industry, it is to the extreme north-east of the area and is over 30 per cent. black. South Wales and Monmouthshire (20-25) represent probably the largest industrial area from which the black forms are almost absent.

5. DISCUSSION

That the two-spot ladybird displays industrial melanism there can be little doubt. It thus provides the first example of this phenomenon to be described outside the Lepidoptera, with the possible exception of *D. melanogaster* in the Caucasus (Dubinin *et al.*, 1934). However, to substantiate this claim fully a number of points have to be resolved. Kettlewell (1958) described the distribution of the melanic forms, *carbonaria* and *insularia*, of the Peppered Moth, *Biston betularia*, and this differs markedly from the present situation; yet both are ascribed, in part at least, to the effects of heavy industry. In addition, a number of

TABLE 4

Details of collections of the Two-spot Ladybird, Adalia bipunctata, *made in England and Wales. The serial numbers refer to the maps (figs. 2 and 3)*

No.	Locality	Red	Black	Total	Black (per cent.)
1	S.W. England	See text		34	0
2	Portsmouth	*ca.* 15	...	*ca.* 15	0
3	Horsham	124	3	127	2·4
4	Guildford	132	18	150	12·0
5	Aldershot	36	3	39	8
6	Kingston-on-Thames *†	95	10	105	9·5
7	Croydon	151	10	161	6·2
8	Southall	24	1	25	4
9	Hyde Park	28	...	28	0
10	East Ham	39	...	39	0
11	Mill Hill *	50	...	50	0
12	Harpenden	92	...	92	0
13	High Wycombe	57	...	57	0
14	Reading	26	...	26	0
15	Wittenham	35	...	35	0
16	Oxford and Elsfield	1058	27	1085	2·5
17	Berks and Wilts Downs	See text		*ca.* 40	0
18	Bath	17	...	17	0
19	Bristol	26	...	26	0
20	Swansea	45	...	45	0
21	Pontypridd	33	2	35	6
22	Cardiff	43	...	43	0
23	Newport, Monmouthshire	40	1	41	2
24	Chepstow	32	1	33	3
25	Abergavenny	17	...	17	0
26	Hay-on-Wye	12	1	13	8
27	Hereford	39	10	49	20·0
28	Gloucester	148	24	172	16·2
29	Cheltenham	56	6	62	10
30	Worcester	153	28	181	15·5
31	Broadway	25	3	28	11
32	Moreton-in-Marsh	26	1	27	4
33	Banbury	75	3	78	4
34	Ipswich	321	8	329	2·4
35	Cambridge	77	2	79	3
36	Peterborough *	100	...	100	0
37	Northampton	23	...	23	0
38	Stratford upon Avon	17	4	21	19
39	Alcester	21	...	21	0
40	Warwick	166	10	176	5·7
41	Henley in Arden	209	14	223	6·3
42	Kenilworth	26	4	30	13
43	Rugby	25	...	25	0
44	Coventry	71	1	72	1
45	Water Orton	74	19	93	20
46	Castle Bromwich	47	21	68	31
47	Alum Rock	14	7	21	33
48	Acock's Green	18	7	25	28
49	Hall Green	See text		...	46
50	Cotteridge	23	17	40	43
51	Edgbaston	121	168	289	58·1
52	Harborne	15	20	35	57
53	Birchfield	30	67	97	69
54	Maw Green, Walsall	78	46	124	37·1
55	Quinton	10	2	12	17
56	Stourbridge	18	2	20	10
57	Bridgnorth	20	3	23	13

Table 4 continued overleaf

TABLE 4 (*continued*)

No.	Locality	Red	Black	Total	Black (per cent.)
58	Shrewsbury	70	13	83	16
59	Whitchurch, Salop	11	12	23	52
60	Wellington	20	...	20	0
61	Newport, Salop	73	9	82	11
62	Uttoxeter	27	5	32	16
63	Burton upon Trent	121	21	142	14·8
64	Lichfield	74	7	81	9
65	Tamworth	34	8	42	19
66	Atherstone	95	5	100	5·0
67	Enderby	48	1	49	2
68	Leicester	39	1	40	3
69	Borrowash	35	9	44	20
70	Nottingham	82	8	90	9
71	Newark	105	1	106	0·9
72	Lincoln	31	...	31	0
73	Louth	9	...	9	0
74	Chesterfield	23	10	33	30
75	Sheffield	21	26	47	55
76	Doncaster	92	2	94	2
77	Selby	41	3	44	7
78	York	31	15	46	33
79	Leeds	7	34	41	83
80	Huddersfield	3	24	27	89
81	Altrincham	7	70	77	91
82	Warrington	4	31	35	89
83	W. Derby, Liverpool	3	25	28	89
84	Hoylake	11	58	69	84
85	Chester	12	39	51	76
86	Bangor *	...	...	*ca.* 40	50+

* Sample consisting entirely of ladybirds taken when hibernating.
† From Conway, 1958.

apparent anomalies in the ladybird distribution have been pointed out and finally there is the question of what other selective agencies may be at work.

The main effect of industry that is relevant here is the production of air-borne pollution. In the case of the Lepidoptera, this may act to a certain extent in a direct manner; it has been suggested that the larvæ of melanic moths may be more tolerant of the toxic deposits on their foodplants than are the larvæ of normal forms (Ford, 1953). However, another action is indirect; lichens are extremely sensitive to industrial pollution and cannot survive on tree trunks in areas where there is any appreciable fall-out. This occurs not only in the industrial areas themselves but also far to the east where the pollution is carried by westerly and south-westerly winds. Lichen-covered tree trunks provide an extremely disruptive background against which the moths are seen when at rest. Trunks without lichen are much more uniform and darker in general appearance; this is enhanced by actual deposits of fall-out. Contrasting differential predation by birds occurs on each background (Kettlewell, 1955, 1956). Easterly winds are by no means uncommon in this country and yet the phenomenon in the moths is found very largely in and to the east of the industrial areas. The south-westerly winds are those that normally bring rain and it is probably polluted rain washing down the trees that kills the lichens in non-industrial areas.

Large-scale predation of the two-spot ladybird has never been reported and no evidence of it has been found during the present work. This does not of course mean that it does not occur; it was denied for a long time that birds predate moths on trees to any appreciable extent, yet Kettlewell and Tinbergen (Kettlewell, 1956) showed conclusively that not only do the birds take the moths but they do it selectively. However, it is doubtful whether the black ladybirds are any more cryptic than the red, even on the most polluted leaves. The red element of the colour pattern in all the varieties in no degree contributes to the concealment of the insect; it is generally regarded as warning coloration, and with good reason. Lane (1960) and Rothschild and Lane (1960) have shown that ladybirds are distasteful to and actively rejected by wasps (*Vespa germanica*) and the Great Tit (*Parus major*), and Rothschild (1961) states that bush-babies and mice " shrink back " from filter paper impregnated with the defensive gland secretions of ladybirds.

Fraser and Rothschild (1960) took a large number of warningly coloured insects and compared their acceptability to a variety of predators including several species of birds, mice, voles, bats, hedgehogs, lizards and toads. The results for the three species of ladybird tested, *Coccinella 7-punctata*, *C. 11-punctata* and *Adalia bipunctata*, are not given separately; however, under the heading ladybirds they received the highest rating for unacceptability, being equal with the Cinnabar moth, *Hypocrita jacobaeæ* L., and the Froghopper *Cercopis vulnerata* Car. This suggests that changes in the background colour due to pollution, which are so important in the Lepidoptera, are here irrelevant. An alternative and more satisfactory possibility is that contact with and ingestion of the toxic substances have a differential effect upon the genotypes. There is no direct evidence for this, but Kalmus (1942), working on *Drosophila*, found that the pale mutants, *yellow*, of both *D. melanogaster* and *D. pseudoobscura* were less resistant than the wild type to spraying with heavy or light petroleum oils, a tar oil emulsion in water, a pyrethrum extract or weak solutions of sulphuric acid. The dark mutant, *black*, of *D. melanogaster* showed a significantly greater survival than the wild type after being sprayed with heavy oil and sulphuric acid. The mutant *ebony* also survived longer than the wild-type after treatment with heavy oil but the difference was not significant.

If it is the pollution that remains on the surface of leaves, and on the aphids that feed on them, that is important, rain will lessen the effect. Fall-out carried down by rain will wash over the surface, but most will fall to the ground; the net result of rain, even in the centre of industrial areas, will be to wash off foreign matter. An important difference between ladybirds and Lepidoptera in this respect is that the caterpillars cannot avoid eating the pollution sticking to the leaves while the ladybirds will have a much lower intake.

The link with industrial pollution appears sufficient to explain most of the major features of the present survey. However, Marriner's (1926, 1939*a*) reports suggest a high frequency of black in non-industrial areas in the extreme north of England. Fig. 2 also suggests a general increase in the proportion of black insects as one move north and west. In the absence of detailed leaf pollution figures, this tendency cannot adequately be analysed. The widespread use of tree-sprays containing creosote and other coal products in fruit-growing areas, particularly Worcestershire, Herefordshire and south-east England, may also temporarily produce conditions very similar to those in industrial areas. This may partly explain the occurrence of melanics in these areas and deserves further investigation. An additional characteristic of large towns which may be relevant is the phenomenon known as a " heat island " (Chandler, 1962). Large collections of buildings act as quite substantial reservoirs of heat and hence the daily cycle of temperature variation may differ considerably in a large town as compared with the surrounding countryside.

Lusis (1961) found that mating of the red and black forms was far from random. He recorded all pairs seen *in copula* in Moscow and Riga: there was a significant excess of black × black crosses and a deficiency of red × red in most localities. The red × black and black × red crosses showed no general tendencies in either direction. Assuming that this reflects the more frequent mating of black with black rather than a longer time taken, red will be placed at a relative disadvantage. Lusis suggests that this may be one reason why the frequency of black increases during the summer. Mating preferences of this type can lead to the maintenance of a balanced polymorphism when for example, the black heterozygote enjoys a net advantage. If there were no such heterozygote advantage a system such as this would lead to the elimination of the red form in the absence of opposing selective forces. Lusis also compared the frequency of red and black insects seen *in copula* with the frequency in the population in which they were found. There was always an excess of black but this was much greater in two out of three localities in Moscow than in any samples from Riga. Lusis ascribes the difference in sexual activity of the two colour forms, at any rate in part, to the increased rate of heat absorption of the black insects. This would be enhanced by the greater temperature excess (over the air temperature) of black as opposed to lighter coloured insects (Digby, 1955), though Digby doubts whether this effect will be large. The difference between the Moscow and Riga figures, together with the absence of any marked increase in the frequency of black in England during the summer as opposed to Berlin, suggest that relative heat absorption may be a more important factor in places with a considerable temperature range, both diurnal and annual, than in places with a less extreme, maritime climate.

If increased activity of the blacks were alone responsible for the preferential mating, an excess of red × black and black × red pairings would also have been expected. That this was not so suggests that there is some form of attraction either by visual or scent stimulus. Ladybirds, in common with many other warningly coloured insects, produce a distinctive scent (Rothschild, 1961); Eisner and Kafatos (1962) have shown that the scent of the males of the aposematic lycid beetle, *Lycus loripes*, acts as a pheromone, promoting aggregation in both sexes of this species. If the apparent non-random grouping in hibernating masses noted above (p. 61) is widespread, it seems likely that the varieties may each produce a different scent.

A further factor influencing the morph frequencies, and counteracting any geographical differences in selective pressures, is gene-flow; this would be much increased by migration. There are periodic reports of immigrations of vast numbers of ladybirds on the south and east coasts of England. The evidence that these insects have in fact crossed the channel is slight. If large numbers breed near the coast and any dispersal occurs, there will tend to be an accumulation along the coastline where further spread is checked. It is the presence of the insects along the coastline that has given rise to the reports of immigration (see also de Worms, 1962). Marriner (1939*a*) described a vast migration of two-spot ladybirds from the south Midlands to the north of England in June 1925. There were no black varieties among the large number he saw near Hexham, in Northumberland; had these insects originated from as near as York there would have been an appreciable proportion of blacks. There seem to be two possible explanations. A large number of observers reported a superabundance of ladybirds along the supposed routes, so either the migrants must have come from eastern England and, although passing through the areas of high blacks, did not mix with them; or else it was an unusually good year for ladybirds, the numbers increasing slightly earlier in the south, and so giving the impression of a northerly movement. Marriner's map shows the migrants as passing through the areas collected by Hawkes (1927); she does not record any startling changes in frequency of the varieties, as would be expected if there was migration from the south of Birmingham through Edgbaston.

A comparison of Hawkes' figures with those obtained in this survey shows that the frequency distribution was very similar then as now; if anything, blacks were somewhat commoner in a number of localities. For example, the frequency at Edgbaston (51) was 67·8-82·0 per cent. black (average 75·5 per cent.) in 1920-27 compared with an average now of 58·1 per cent. At Droitwich (see map, fig. 3) red and black were " almost equal " while slightly further to the south, also in Worcestershire, black was at 9-19 per cent.

The data now available for Britain provide no support for Lusis' view that a maritime, more humid, climate is associated with an increase in the frequency of the black varieties. There is no correspondence between the distribution map (fig. 2) and rainfall or relative humidity. It is true that the eastern counties have, in general, a more continental climate than, for example, Lancashire, but the climate of southern England or South Wales is far from continental. On the other hand, there is strong support for Lusis' view that the percentage of black forms tends to be greater in industrial towns than elsewhere. There are qualitative similarities between fig. 2 and maps showing the annual fall-out of industrial pollution, but the quantitative relationship is less good. This suggests the existence of some further factor, having a geographical basis; in this country it appears increasingly to favour blacks as one moves north. However, of the data quoted by Lusis, one of the most southerly samples, and also non-industrial, that from the Crimea, has a frequency of 58·2 per cent. black—almost as high as the centre of Birmingham. The data of Dobzhansky (1951) and Komai, Chino and Hosino (1956) on the Asiatic Ladybird, *Harmonia axyridis*, which are reviewed in Komai (1956), show the existence of several smooth clines of morph frequencies with no marked local disturbances. The only sharp changes occur where there is a geographical barrier preventing gene-flow, such as the Tugaru Strait between Hokkaido and Honsyu or the Korea Strait separating Japan from the mainland. The type of factor influencing this distribution, whether climatic or otherwise, may well be similar to the non-industrial component of the selective forces acting on *A. bipunctata*.

The existence of industrial melanism in a warningly coloured species is of the greatest interest. In the lepidoptera the melanic forms are associated with a greater degree of crypsis on certain backgrounds, and with various physiological advantages. Melanism in ladybirds results in a reduction of the amount of the warning red pigment displayed with no compensating cryptic advantage, even in heavily polluted districts. The selective forces producing industrial melanism in *A. bipunctata* appear to be entirely of a physiological and not a visual nature. Further work is necessary in the lepidoptera to establish the full extent to which such forces operate there also.

6. SUMMARY

1. A survey was carried out of the frequency of melanic forms of *A. bipunctata*. The survey is based on samples from eighty-three localities in England and Wales. The earliest collection included is that of Conway (1958) from Kingston, Surrey, in 1957. The remainder were collected in 1960-63.

2. The frequency of the red and of the black varieties was recorded for each locality (table 4).

3. In only one locality was a significant change in the percentage of melanics found in the course of a season. It was the reds that increased.

4. In southern and eastern England the black varieties are rare (usually absent, otherwise not more than 3 per cent.) except to the south of London where the melanics sometimes exceed 10 per cent.

5. The industrial areas of the Midlands and Lancashire and Yorkshire are characterised by a high percentage of melanics. Birmingham has 60-70 per cent., the more northerly industrial belt has up to 90 per cent. In the intervening area the percentage drops to probably not more than 10 per cent.

6. Melanics are rare in the coal mining and steel manufacturing area of South Wales.

7. One of the most important factors affecting the frequency of melanics in this country appears to be industrial pollution on foliage. Fall-out in rain is not effective.

8. The melanic forms have no cryptic advantage over the red even in the most polluted areas. In such areas melanic moths enjoy a cryptic and physiological advantage; industrial melanism in ladybirds is assumed to have a mainly physiological basis.

9. There is a strong indication that at least one other geographically varying selective factor is operating; this has not been identified.

10. With the one possible exception of *Drosophila melanogaster*, the two-spot ladybird provides the only example of industrial melanism so far described outside the lepidoptera. It also provides the only example so far described of industrial melanism in a warningly coloured species.

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