The melanism of Adalia bipunctata around the Gulf of Finland as an industrial phenomenon (Coleoptera, Coccinellidae)

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Samples collected in and around Helsinki reveal that the melanism of *Adalia bipunctata* (L.) has a uniform level of 10–12% of melanic beetles in, and falling to zero or near zero roughly 15 km from the city. In Finland, melanism mainly occurs in the towns, the northernmost melanics being from the town of Oulu (65°N). In Leningrad, U.S.S.R., 300 km E of Helsinki, melanism reaches 85% in the city centre and declines to a level of 50% first at a distance of 12–40 km (published Soviet data). In two towns — Tallinn and Narva — in Estonia, U.S.S.R., on the southern side of the Gulf of Finland the melanic percentages are 27% and 20% respectively.

The concept of thermal melanism, resulting in a negative relationship with sunshine, does not explain the low-level melanism of Helsinki because there tends to be, as a mesoclimatic effect of the coast, *more* radiation available in areas with higher proportions of melanism, and also higher average temperatures because of the "heat island" effect of the city. The melanism of *A. bipunctata* has many similarities with that of *Oligia strigilis* (L.) (Lepidoptera, Noctuidae), a species which has been used as an indicator of air pollution. Several findings suggest that in this area *Adalia bipunctata* shows industrial melanism, although the mechanism leading to selective advantage of the melanic forms remains unknown.

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1. Introduction

The selection acting in favour of melanism in the two-spot ladybird, Adalia bipunctata (L.), has been subject to intense, scientific debate since the early 1970s. Creed (1966, 1971, 1974) and Lees et al. (1973) noted positive correlations between local air pollution and melanic frequencies in Great Britain. However, pursuing a theory developed by Lusis (1961), Benham et al. (1974) found that climatic effects could account for the geographical variation in this area. Recently, Brakefield & Lees (1987) argued that the decline in the melanic frequencies in the Birmingham area from 1960 to 1978 followed from "an influence on thermal melanism via the effect of smoke in reducing sunshine".

Since the mid-1970s, climatic factors have been postulated to influence geographical patterns of the melanism of *A. bipunctata* in Great Britain (Muggle-

ton et al. 1975, Muggleton 1979), Norway (Bengtson & Hagen 1975, 1977), Czechoslovakia (Honek 1975) and Italy (Scali & Creed 1975). From the Netherlands, Brakefield (1984a–c, 1985) has given strong evidence regarding the effects of climatic factors on the reproductive activity of melanic beetles. Zakharov & Sergievsky (1983) consider atmospheric pollution to be the most important cause for the melanism of *A. bipunctata* in the Leningrad area.

Other factors studied include selective predation (Muggleton 1978, Brakefield 1984b, 1985), sexual selection involving frequency-dependent mating or female preference (O'Donald & Muggleton 1979, Majerus et al. 1982, O'Donald & Majerus 1985), isolation (Muggleton 1978), and thermal properties of the forms (Brakefield & Willmer 1985). Brakefield (1984c) observed non-random mating, but not assortative mating or frequency-dependent mating systems.

Locality		Total	4-m.	6-р.	Melanics	Melanic % ± S.D.	
1.	Helsinki, Taivallahti	62	3	6	9	14.5	4.47
2.	Helsinki, Kyläsaari	74	5	4	9	12.2	3.80
3.	Helsinki, Sea Harbour	102	9	3	12	11.8	3.19
4.	Espoo, Tapiola	74	7	1	8	10.8	3.61
5.	Helsinki, Ilmala	115	6	5	11	9.5	2.74
6.	Helsinki, Zoological Mus.	171	9	9	18	10.5	2.35
7.	Helsinki, E Herttoniemi	90	9	0	9	10.0	3.16
8.	Helsinki, Mellunmäki	91	4	5	9	9.9	3.13
9.	Helsinki, Kulosaari	85	2	3	5	5.9	2.55
10.	Vantaa, church	58	0	1	1	1.7	1.71
11.	Espoo, Kuitinmäki	92	0	1	1	1.1	1.08
12.	Espoo, Kivenlahti	61	0	0	0	0	

Table 1. Samples of Adalia bipunctata from the Helsinki area with the numbers of the melanic forms quadrimaculata (4-m.) and sexpustulata (6-p.) given separately. The samples are given in order of frequencies (except no. 5).

Sergievsky & Zakharov (1983) in the Leningrad area and Klausnitzer & Schummer (1983) in Eastern Germany could not, in accordance with several other authors, observe any seasonal change in the phenotype frequencies. The latter authors noted that this was also true in Berlin, where Timofeef-Ressovsky (1940) published his classic data on seasonal change. Muggleton (1978) and Sergievsky & Zakharov (1983) have emphasised that many factors are likely to be involved and that geographical differences in the gene pools of *A. bipunctata* may help to explain the differences in the results of different authors.

The aim of this paper is to present the first data on the frequency of melanic forms of A. bipunctata in Finland and to analyse the data in relation to certain climatic variables and to air pollution. The melanism of A. bipunctata is also compared with that of Oligia moths, see below. Further, the results are compared with data from the geographically closest areas where comparable data have been obtained — the Leningrad area (Sergievsky & Zakharov 1983, Zakharov & Sergievsky 1983) and the coast of Estonia (unpublished data from I. A. Zakharov), both in the U.S.S.R.

2. Material and methods

All the material collected during three days, August 4–6, 1982 (Table 1; Fig. 1), i.e. in the latter part of the eclosion period of the univoltine beetle, were adults (the few unhatched pupae seen were not sampled). A. bipunctata has not been plentiful enough since 1982 to allow further sampling. This has probably been caused by yearly application (except in 1982!) of insecticide (malasin) against aphids on garden roses. Rosa

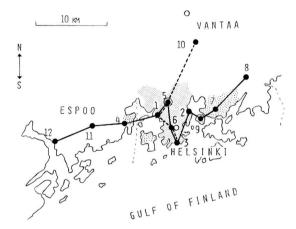
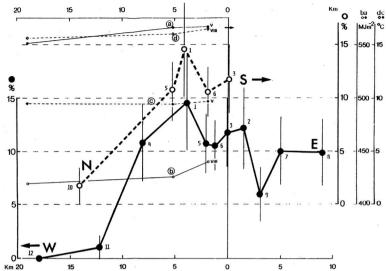


Fig. 1. Map of the Helsinki area showing the sampling places with the same numbering as in Table 1 (closed symbols), the two transects of Fig. 2, S-N (interrupted line) and W-E (continuous line) and the three stations where the physical measurements were made (open symbols). Densely inhabited areas are shaded.

rugosa, the main feeding substrate of the beetles, was not sprayed, but because garden roses are much more sensitive to aphids, the spraying of them may be decisive in the development of the entire aphid population of the roses. Nevertheless, the range of variation within years and within seasons of the melanic frequencies remains unknown.

The beetles were collected from *Rosa rugosa* and, in one case (sample no. 8), from *Sambucus racemosa* by shaking them into an insect net — i.e. the samples were collected randomly (visual collecting could be non-random). The polymorphic forms were classified according to Creed (1966). In addition to the field data, the material in the Zoological Museum of the University of Helsinki was examined.

Fig. 2. The frequencies of melanic Adalia bipunctata from the Helsinki area on transects from S to N (open circles and interrupted line; scale on the right; cf. Fig. 1) and from W to E (closed circles and continuous line). The small numbers indicate samples (cf. Fig. 1, Table 1) and the vertical bars show standard deviations. The horizontal axis denotes kilometres to the west, east and north from the Sea Harbour of Helsinki (sample 3). For an S-N transect, cf. Fig. 1, mean monthly values for May (closed symbols) and August (open symbols) of solar radiation (small circles) and of temperature (small quadrats) are given; the scales are on the far right. Note the large difference in radiation between the months, caused by different day lengths.



The melanic frequencies on a south-north transect were compared with records of solar radiation (Kulmala 1982) and mean monthly May and August temperatures on approximately the same transect (unpublished materials of the Finnish Meteorological Institute; Fig. 2). Unfortunately, comparable data were not available for the west-east transect shown in Fig. 2. The decrease in solar radiation caused by air pollution has not been measured in the seasons when the adults of *A. bipunctata* are active — in late July to September or (after overwintering) in May-June.

The melanic frequencies of *A. bipunctata* were also compared with the melanic allele frequencies (see Mikkola 1975) of *Oligia strigilis* (L.) (Lepidoptera, Noctuidae), which were available from a recent examination of the melanism of *Oligia* moths in the Helsinki area (Mikkola et al. 1982; Fig. 3). *O. strigilis* was chosen over *O. latruncula* (D. & S.) because the latter shows, unlike *O. strigilis* and *A. bipunctata*, definite melanism, though on a low level, in the rural areas.

3. Results

3.1. Field collection

Of the 1075 Adalia bipunctata beetles, collected as 12 samples, 92 (8.6%) were melanic. Of these 92, 54 (58.7%) were of the form quadrimaculata (black with four red spots; cf. Fig. 4) and 38 (41.3%) of the form sexpustulata (black with six red spots). There was no sharp distinction between the forms. 980 red beetles were of f. typica, and only three (0.28%) were of additional forms (f. annulata, f. rubiginosa and one undetermined). The distribution of the two melanic forms in the samples was rather heterogeneous.

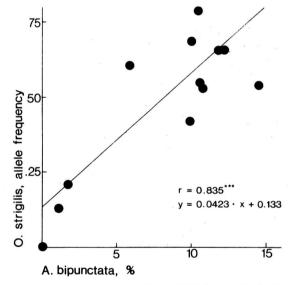


Fig. 3. Correlation between the melanic frequencies in the Helsinki area of *Adalia bipunctata* (L.) and of the noctuid moth *Oligia strigilis* (L.) (as allele frequencies). The latter data are from the years 1980–1982 (Mikkola et al. 1982), except for one point from 1975; the maximal distance between corresponding data of *Adalia* and *Oligia* is 1.5 km.

A fairly uniform level of melanism was observed in the entire city area, including samples 4 and 8, about 20 km apart (Figs. 1–3): in seven out of 12 samples the percentage was about 10% to 12%. The three samples with a melanic frequency less than 2% were collected outside the city area, to the north and west of it.

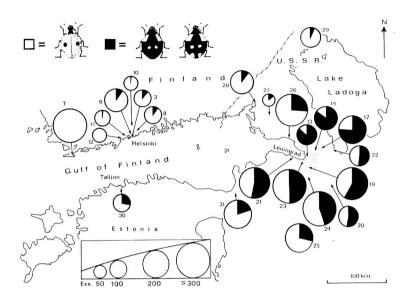


Fig. 4. The melanism of Adalia bipunctata from selected localities around the Gulf of Finland. The black sector of the diagrams shows the melanic frequency. For the data, see Table 1 and 2, and text (the localities indicated with the same numbers as in the tables). Sample size shown as indicated in the scheme inserted. T = Tvärminne in the 1940s (see text).

The apparently higher proportion of sample 1 (14.5%) does not deviate significantly from the others (compared with sample 5 with 9.5%, $\chi^2 = 0.99$, n.s.) neither does the slightly lower value of sample 9 (5.9% as compared with sample 6 with 10.5%, χ^2 = 1.50, n.s.). At distances greater than 10 km from the city area, the percentages fall significantly (the difference between sample 11 with 1.1% and sample 3 with 11.8%, $\chi^2 = 8.82$, P < 0.01, and that between sample 10 with 1.7% and sample 6 with 10.5%, Fisher's exact test, P = 0.023). In the west, no melanics were obtained in a sample of 61 beetles collected 18 km from the city. In spite of several efforts, no beetles were found east of the city, and south of sample 3 (zero point of the kilometre scale of Fig. 2) only scattered islands exist.

3.2. The museum material

The material examined consists of samples chosen by collectors and allows only a very limited examination of frequencies. Because the melanic morphs are relatively rare they are expected to be overrepresented, and therefore their absence or presence in the samples is noteworthy.

Of the 457 museum specimens available 165 are melanic, but 105 originate in Helsinki itself and 14 more in its environs. The oldest dated melanic ladybird had been collected in Helsinki in the year 1915.

The melanic forms seem to be quite strictly limited to the towns throughout Finland. The northern-

most melanics come from the towns of Kuopio (3 beetles; 63°N) and Oulu (4 beetles, 2 of f. *quadrimaculata* and 2 of *sexpustulata*; 65°N). The northernmost red beetles originate at Kemijärvi (67°N) (omitting *A. frigida* (Schneider), which is commonly held as a separate species).

It appears that the melanic forms may occur at a low frequency in rural areas, too, particularly in southwestern Finland: from Villnäs, a manor house in Askainen, there are 13 melanic ladybirds. Otherwise, only single melanics are found in the rural areas, the northernmost one being from Kontiolahti (62°45′N). In general, the species is quite infrequent in rural areas. From the well-collected Tvärminne Zoological Station in southwestern Finland there were 10 ladybirds, all red ones. In addition, the collection of the station itself included 6 local specimens, all typicals, but had 4 melanics from Helsinki as models. Therefore we conclude that the melanic form has never been found there (cf. Palmén 1944 cited below).

3.3. Data from the Leningrad area and from Estonia

Fig. 4 and Table 2 show selected data from the neighbouring areas of the U.S.S.R. From the values of 80–87% in the city area of Leningrad, a uniform plateau of over 70% extends mainly to the northeast: at a distance of 22 km 75.8%. In the east, the frequency is 51.5% at a distance of 40 km on the shore of Lake Ladoga. To the south and southwest, the decline

Table 2. Samples of Adalia bipunctata from the Leningrad area and Estonia, U.S.S.R. SZ = Sergievsky & Zakharov 1983, ZS = Zakharov & Sergievsky 1983, Z = unpublished data from I. A. Zakharov. The samples are arranged in order of percentages.

Locality, distance and direction from centre of Leningrad, source		Time of collection	Total	% melanics \pm S.D.			
The Leningrad area:							
13.	Leningrad University (0 km, Z)	21.7.1982	135	86.7 ± 2.93			
14.	Mechnikovskiy str. (8 km ENE, SZ)	1976–77	167	85.1 ± 2.76			
15.	Nakhimov str. (4.5 km W, SZ)	May 1977	118	83.1 ± 3.45			
16.	Shuvalovskoye gr.y. (10 km NNE, SZ)	September 1976	127	77.2 ± 3.72			
17.	Vsevolozhsk (22 km NE, ZS)	August 1980	223	75.8 ± 2.89			
18.	Troytskoye field (12.5 km SSE,SZ)	July 1975	276	71.0 ± 2.73			
19.	Moskovskiy park (9 km S, SZ)	August 1975	281	59.1 ± 2.93			
20.	Tosno (54 km SE, ZS)	August 1980	125	57.6 ± 4.42			
21.	Old Peterhof (35 km W, Z)	2.8.1980	274	54.0 ± 3.01			
22.	Petrokrepost (40 km E, ZS)	August 1980	134	51.5 ± 4.32			
23.	Sold. Korzun str. (12 km SSW, SZ)	July 1980	310	50.0 ± 2.84			
24.	Gatchina (44 km SSW, ZS)	1975–78	1337	44.7 ± 1.36			
25.	Luga (120 km SSW, ZS)	August 1980	214	29.0 ± 3.10			
26.	Komarovo (40 km WNW, Z)	20.8.1980	283	26.5 ± 2.62			
27.	Lake Glubokoye (90 km NW, ZS)	May 1976	46	15.2 ± 5.29			
28.	Vyborg (120 km NW, Z)	15.8.1980	157	9.6 ± 2.35			
29.	Lodeynoye field (200 km N, ZS)	August 1977	130	6.2 ± 2.12			
Esto	onia:						
30.	Tallinn (300 km WSW, Z)	19.8.1982	89	27.0 ± 4.70			
31.	Narva (135 km WSW, Z)	24.7.1984	228	20.2 ± 2.66			

is steeper: 59.1% at 9 km, and 50.0% at 12 km. Some industrial towns have their own peak of melanism, e.g. point nos. 8, 12 and 35. To the northwest, the frequencies decline to a level of about 10% nearly 100 km from the city centre. In the town of Vyborg, a melanic frequency of 9.6%, a level similar to Helsinki, is observed.

In the Estonian towns Tallinn (the capital) and Narva, the frequencies were higher than in Helsinki, 27.0% and 20.2%, respectively (point 6 of Table 1 with 10.5% compared with Tallinn, $\chi^2 = 11.68$, P < 0.001, and with Narva, $\chi^2 = 6.75$, P < 0.01). It remains unknown if the frequencies drop to zero in the areas around these towns or around Vyborg.

4. Discussion

4.1. Application of different hypotheses

The present data from the Helsinki area (Table 1), together with the extensive records from the Leningrad area and Estonia (Table 2, Sergievsky & Zakharov 1983, Zakharov & Sergievsky 1983, Zakharov oral comm.; cf. Fig. 4), allow some specula-

tions to be made about the selection favouring the melanic forms in the populations of the two-spot ladybird, *Adalia bipunctata*, around the Gulf of Finland. A drawback is the scarcity of measurements of physical variables.

The following alternatives will be examined as explanations for melanism around the Gulf of Finland:

- 1. Climatic melanism, according to which the melanic frequencies would not be connected with air pollution or its consequences.
- 2. Thermal melanism, according to which the melanics gain an advantage (because of more efficient absorption of radiation) in the regions of low sunshine, caused by air pollution. Actually, we would regard the effects of mesoclimatic changes caused by air pollution as a kind of industrial melanism (cf. Creed 1971).
- 3. Strict industrial melanism, according to which the frequencies could be explained by levels of air pollution irrespective of climatic phenomena, namely by direct selective effects of air pollution on populations. The cause could be an unknown physiological mechanism connected to the black colouration (pleiotropism). Muggleton (1978) and Brakefield (1985)

have suggested that selective predation may also be involved, even if *A. bipunctata* is aposematically coloured.

4. The "heat island" hypothesis, according to which the proportion of melanics would increase with increasing temperature (cf. Scali & Creed 1975). This would be a consequence of the "heat island" effect of big cities (warming up of the stony mass of a city during the day).

Climatic melanism. In and around Helsinki, the major climatic curves (isotherms) run parallel to the coast, i.e. there is a maritime effect. The main phenomena are: (1) the sea produces in the spring and early summer a cooling, in the summer a stabilizing, and in the autumn a warming effect and (2) a narrow strip of coast receives more insolation throughout the year than inland areas because of the frequent lack of cloudiness over the sea (cf. Fig. 2; note that the oblique incidence of the radiation causes the strip to be broader than the actual cloudless zone).

Fig. 2 suggests that in May the strong insolation near the sea (curve a) has almost entirely been neutralized, with respect to temperature, by the cooling effect of the sea (c). In August the temperature rises more clearly towards the sea (d), as expected from the stronger insolation (b). In June and September, potential months for the activity of ladybird adults, the conditions are similar to those in May and August, respectively (see Kulmala 1982).

The lack of climatic data from the Sea Harbour of Helsinki (point 3 and zero line of Fig. 2) and from east and west of the city makes it difficult to differentiate between the stronger insolation and the "heat island" effect of the city. At point 3 of Fig. 2 the temperature curves would presumably, if the data were available, show quite a steep drop in May because of the cooling effect of the sea. The similarity of the ladybird sample from the Sea Harbour with those from the inner parts of the city, as well as the similarity of the decline of the melanic frequencies to the north and west of the city suggest that the ambient temperature or other climatic variables do not influence the frequency of melanics.

Thermal melanism. In Helsinki, the area of highest melanic frequencies corresponds quite closely with that of the highest temperatures and highest insolation (see above). The absence of thermal melanism is supported by data from Leningrad and its environs (Sergievsky & Zakharov 1981, 1983, Zakharov & Sergievsky 1983). There the melanism is at a considerably higher level than in Helsinki, in

spite of a more continental climate with a sunnier and warmer summer. In Leningrad, variations occur irrespective of the climatic variables, namely both high and low frequencies on the sea coast and in the inland areas, depending on the distance and direction to the city centre.

The following facts, emphasised by Zakharov & Sergievsky (1983), support the idea that reduction of sun radiation, due to increased smoke levels influences melanism (and also industrial melanism, but not the "heat island" idea): (1) The melanic frequencies are highest to the northeast of the city, corresponding to the distribution of pollutants by the prevailing winds (W and SW); (2) during the industrial depression, after World War II, the melanism of A. bipunctata at Peterhof (35 km W of the city centre; site 21) remained at a lower level for several years. Fact (1) could also be explained by transportation of the beetles by the prevailing winds and corresponding gene flow to that direction, but this does not explain fact (2).

Industrial melanism. A comparison between melanic frequencies in Helsinki and Leningrad reveals a large difference, about 10% and 85%, respectively. This corresponds well with the numbers of inhabitants, 0.5 and 4.0 (with environs, 0.8 and 4.5) millions, respectively. The pollution level of Leningrad must be several orders of magnitude higher than in Helsinki but, unfortunately, no data are available. Why the capital of Estonia, Tallinn, only 80 km south of Helsinki and with 440 000 inhabitants, and the smaller town of Narva (74 000 inhabitants) have higher levels of melanism than Helsinki remains open to speculation. It may be that the principal source of energy used for heating is different: in Leningrad, coal; in Estonia, coal and so- called oil shale; and in Helsinki, heating in power plants with centralised gas cleaning.

The decrease of melanism in A. bipunctata from the city centre of Helsinki outwards corresponds well with that in the noctuid moth Oligia strigilis (L.) (r = 0.835, see Fig. 3). The melanism of Oligia moths accurately describes the level of total dustfall (Mikkola 1975, Mikkola et al. 1982). O. strigilis shows melanism mainly in larger towns and industrial centres (see also Mikkola 1979), corresponding to A. bipunctata. In central Helsinki the melanism of these two species shows a clear difference: while that of A. bipunctata remains on an even level of 10–12%, that of O. strigilis rises continuously towards the centre, where it reaches ca. 90% (gene frequency ca. 0.80).

The melanism in the beetles and moths may have quite a different origin, since the former are day-active, aposematically coloured predators which feed on aphids, while the latter are night-active, protectively-coloured insects which rest in the daytime in exposed positions (see Mikkola 1984a) and have herbivorous larvae. Since the major climatic variations occur perpendicular to the coast, but the decline of melanism also occurs parallel to the coast and away from the city, the basic cause seems to be the same — air pollution. More thorough comparisons are needed before this hypothesis can be proven.

It is extremely difficult to distinguish between thermal melanism and direct industrial effects, and the points presented mainly fit the former, too. The fact that the melanism of *Adalia* remains at a high level also on the sunnier coastal areas of Helsinki and Leningrad (see below) cannot, however, be explained on the basis of thermal melanism.

"Heat island" hypothesis. Scali & Creed (1975) noted that in Italy, the proportion of melanic ladybirds increased with increasing temperature. This phenomenon has not been observed elsewhere. However, the "heat island" effect of the big cities supports many cases of ladybird melanism well and is not easily distinguished from the effects of air pollution.

Three samples available from the westernmost part of the Leningrad centre, Vasilevskiy Island (one of them is no. 15, Table 2), do not support the idea of "heat islands". As in the Sea Harbour of Helsinki, the cooling effect of the sea must be pronounced, particularly early in the season. Similarly three samples from the northeastern coast of the Gulf of Finland (sample no. 26 of Table 2 is one of them), with relatively high melanic frequencies, are from similar mesoclimatic conditions as the Sea Harbour of Helsinki. Thus, it seems that the high melanic frequencies from coastal areas cannot be explained by the "heat island" effect.

In Leningrad the clear difference in the melanic frequencies between the northeastern and southwestern directions, at a distance of some 20 to 50 km from the centre, does not support the "heat island" hypothesis because at the northeastern side, where melanic frequencies are higher, the mean temperatures are expected to be lower rather than higher than in the surrounding areas due to higher smoke levels. Zakharov & Sergievsky (1983) connect this hypothesis with hibernating conditions, but the same argument holds true against the idea.

4.2. Geographical considerations and the movements of the ladybirds

As several authors have pointed out, different mechanisms may act in different geographical areas. Perhaps the most striking example of the genetic differences of the polymorphisms is that in Great Britain only two specimens out of 6000 were of the form sublunata (Creed 1966), whereas in Central Asia this is the main component of melanism (Sergievskiy & Zakharov 1981). We have made a comparison with the geographically closest areas, expecting that the gene pools and selective regimes would be similar.

In Norway, Bengtson & Hagen (1975, 1977) found a correlation as high as 0.93 between the melanism of *A. bipunctata* and an oceanity index. A weak point in their conclusion is that they did not have samples from the oceanic islands off Bergen. If these populations were paler instead of darker than those of Bergen, the melanism may be of industrial origin.

Brakefield (1984b) regards A. bipunctata as a fairly local animal, but Creed (1966, p. 69) gave data on the long-range migrations of the species in the British Isles. In Finland, the species has been seen among migrating insects in the outer archipelago (May 21, 1984). It has also been observed in the socalled insect drifts on sea shores which indicate migrations (maximally over 50 beetles/0.25 m²; Palmén 1944; all typicals, Palmén oral comm., cf. considerations about the Tvärminne area above). The migrations of A. bipunctata are probably more marked than has been believed. If the flights occur on a few favourable days, and not necessarily every year, they would be difficult to detect; but they may nevertheless be significant from the gene flow point of view.

Zakharov & Sergievsky (1983) emphasise that A. bipunctata is a strictly synanthropic species, the populations of which are isolated from each other in the city centre of Leningrad, but are continuous in the outskirts of the city. According to them, it is entirely absent in natural areas; this might be true for Finland as well. Further south, in the more densely inhabited areas, the populations of Adalia bipunctata may be continuous over wide areas.

The peculiarity of the situation in the Helsinki area — an even level of melanism in the city area and probably a steep drop outside it — may be better understood against this background: the ladybird populations in the city area are far larger than those in the surroundings, and the migrations spread genetic ma-

terial outwards. The use of insecticides against aphids is a factor of which the effects are unknown from the melanism point of view.

4.3. Conclusions

The two noctuid species, Oligia latruncula (D. & S.) and O. strigilis (L.), show strong industrial melanism in and around Helsinki (e.g. Mikkola 1975), but in the peppered moth, Biston betularius (L.), only weak traces of the evolution of melanism have been observed (Douwes et al. 1976, Mikkola 1984b). In the two-spot ladybird, Adalia bipunctata, the melanism in Helsinki is roughly at the same level as in Eastern Germany, in the north-west of the Netherlands, and in southern London. It is, however, only half of the level of Tallinn, 80 km south, and less than 1/5 of that of Leningrad, about 300 km E, or of the south-eastern Netherlands (see Klausnitzer & Schummer 1983, Brakefield 1984a, Creed 1966, Sergievskiy & Zakharov 1983). These extreme examples show that the level of melanism in a single species cannot be predicted on the basis of the level of air pollution and the geographical position.

Around the Gulf of Finland, the concentration of melanism in A. bipunctata in the city areas, irrespective of the climatic gradients, points to an industrial origin of the phenomenon. The two other alternative hypotheses — the thermal melanism and the "heat island" effect of the towns — almost opposite to each other, do not explain the distribution of melanic frequencies either.

The maintenance of the polymorphism may partly be dependent on population dynamic parameters, such as qualitative mating systems (heredity proved, O'Donald & Majerus 1985), and genetic phenomena such as homozygous disadvantage. Geographical comparisons reveal that in different areas the populations may react differently to the actual environmental conditions.

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