SELECTION AGAINST THE MELANIC MORPHS OF *ADALIA BIPUNCTATA* (TWO-SPOT LADYBIRD): A REVIEW AND SOME NEW DATA

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SUMMARY

Work on the nature of the factors selecting against the melanic morphs of *Adalia bipunctata* is reviewed.

New data are presented showing that there is normally one generation per year in Great Britain and that the cyclical changes in morph frequency observed in Berlin may not occur in Great Britain.

The roles of migration and selective predation in limiting the spread of the melanic morphs are discussed and evidence is presented to show that predation by birds on ladybirds occurs more frequently than previously supposed.

In conclusion it is proposed that the melanic frequency of a population is the result of the interaction of a number of factors whose importance varies from locality to locality.

1. INTRODUCTION

THE polymorphism found in *Adalia bipunctata* L. (two-spot ladybird) has been studied for many years and it is established that some populations contain a large proportion of melanic morphs. There are several melanic and non-melanic morphs and these are under the control of a number of alleles at a single locus with the melanic morphs being dominant to the non-melanics (Lusis, 1928, 1932). The melanic morphs have a black background coloration with red spots in contrast to the non-melanics which are red with black spots. Intermediates are rare but when they do occur can be classified by reference to the forms depicted by Lusis (1932). The nature of the factors maintaining this polymorphism in Great Britain has been the subject of recent discussion (Creed, 1971a, 1975; Muggleton, Lonsdale and Benham, 1975) and for the most part this discussion has concentrated on those factors that advantage the melanic morphs. Yet, in spite of the fact melanics are dominant and have been present since at least 1696 (Hammond, 1975), populations with high frequencies of melanics are uncommon and throughout most of the range of this circumboreal species high frequencies of typicals are found. Indeed, high melanic frequencies are characteristic only of populations from the climatic extremes of the species range in Europe and Asia (*i.e.* from north-west Europe, southern Europe and central Asia). Fig. 1 shows the frequency of the melanic morphs in all samples for which there are published data.

From the generally low frequencies of melanics in most populations it is clear that in most localities the melanic morphs must be at a considerable disadvantage. Recent evidence from urban areas, where high melanic

frequencies occur as a result of smoke in the atmosphere, shows that when the smoke levels are reduced there is a rapid decrease in melanic frequency (Creed, 1971*b*; Bishop, Cook and Muggleton, 1978*a*) which must be the
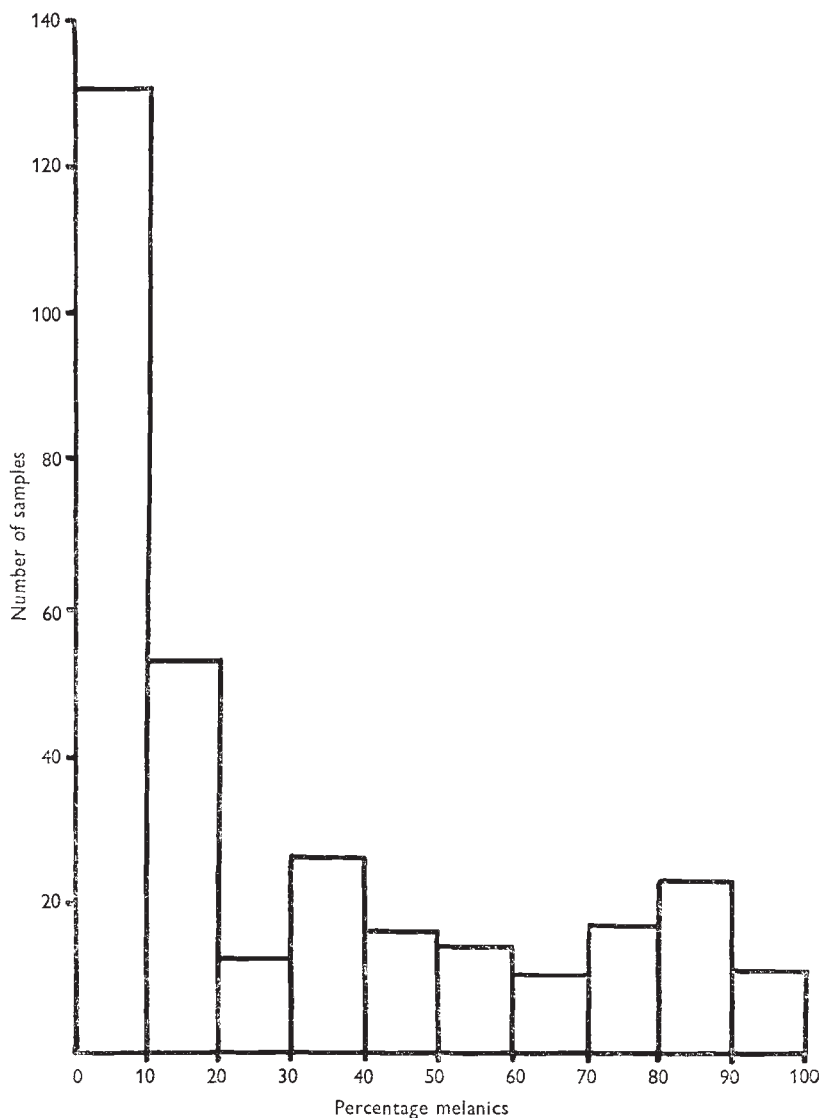

Fig. 1.—The percentage of the melanic morphs of *Adalia bipunctata* in *321* samples from Europe and Asia. Data from published sources mentioned in the text.

result of intense selection against the melanic morphs.   Knowledge of the selective disadvantage of the melanics is essential to our understanding of this polymorphism.   In this paper I shall review the work on this subject and suggest some additional factors which may be involved.

2. The nature of the disadvantage of the melanic morphs

(i) *Selection during the winter*

Timoféeff-Ressovsky (1940), working in Berlin, found significant changes in morph frequency between spring and autumn, with the non-melanic being the commoner morphs in the spring and the melanics being the commoner morphs in the autumn. By examining hibernating ladybirds he was able to show that mortality of melanics during the winter was greater than that of the non-melanics. In the course of the summer melanic frequencies increased. Timoféeff-Ressovsky concluded that these seasonal variations in morph frequency were the result of selection taking place in opposite directions in winter and summer. More recently Timoféeff-Ressovsky and Svirezhev (1966, 1967) have re-analysed these results and suggested that the balance between the two opposing selective factors could in itself maintain the polymorphism. They have termed this " adaptive polymorphism " to distinguish it from polymorphism maintained by heterozygote advantage. This suggestion has been challenged by Creed (1975) who claims that their model does not result in a stable equilibrium and that heterozygote advantage must be present at some stage. On the other hand, Haldane and Jayakar (1963) point out that a polymorphism can be maintained by selection in opposite directions in a situation where the opposing selective forces are large, and Hedrick (1973) has shown that, in a situation analogous to that of *A. bipunctata* in Berlin, cyclic environmental variation can maintain a stable polymorphism.

Lusis (1961) suggested that the greater changes in body temperature experienced by the melanic morphs as a result of their more rapid heating and cooling may account for the winter mortality found by Timoféeff-Ressovsky. Other authors have also suggested that temperature may play a part in selecting against melanics during the winter (Creed, 1975; Scali and Creed, 1975). Creed (1975) has found a non-significant correlation between lowest mean monthly temperature in winter and selection against melanics in Berlin, but he points out that length of winter may be an important factor. Scali and Creed (1975) have found a positive correlation between melanic frequency and altitude in Northern Italy and have suggested that this is related to the colder temperatures at higher altitudes. Data given by Lusis (1973) suggests that a similar relationship may occur in some parts of Central Asia. Scali and Creed (1975) also found a positive correlation between mean annual temperature and melanic frequency, but they point out that this relationship does not apply throughout the range of *A. bipunctata*. Indeed, in Great Britain there is a significant negative correlation between melanic frequency and mean winter temperature ($r = 0.508$, $n = 32$) although this may be related to the correlation between mean winter temperature and annual sunshine hours at the same sites ($r = 0.662$, $n = 32$). In Great Britain sunshine levels appear to be one of the major factors determining morph frequency (Muggleton *et al.*, 1975).

The extent to which cyclical changes in morph frequency occur elsewhere than in Berlin is not known. Both Hawkes (1920) and Marriner (1926) remarked that the non-melanic morphs were commoner earlier in the season at the localities in England where they made their observations, but from their data it is not possible to tell whether this was due to increased mortality of melanics during the winter. Data collected by Creed (1975)

in Birmingham between 1962 and 1970 show neither significant differences in morph frequencies between samples nor any uniform trend, although this may be because the time between early and late samples was short.   Table 1 shows the melanic frequencies at six sites I have sampled in spring and late summer for two or more consecutive years.   At all these sites there are non-significant changes in melanic frequency between samples and taken

TABLE 1

Melanic frequencies in the earliest and latest samples collected at six sites in southern England. In each case the animals sampled in late summer are the offspring of those sampled in the spring.

| Locality | Date | Numbers | | % melanics |
		Non-melanics	Melanics	
Avonmouth	7 May 1976	102	12	10·5
	7 Sept 1976	102	6	5·6
	2 June 1977	82	8	8·8
	10 Sept 1977	41	3	6·8
Cheltenham	6 May 1976	47	2	4·1
	17 Sept 1976	47	2	4·1
	1 June 1977	57	0	0
	11 Sept 1977	50	1	2·0
Gloucester	6 May 1976	118	18	13·2
	6 Sept 1976	49	10	17·0
	19 May 1977	32	1	3·0
	10 Sept 1977	64	8	11·1
Nottingham	19-30 May 1976*	320	8	2·4
	21-30 Sept 1976*	161	4	2·4
	25 May 1977	104	2	1·9
	26 Aug 1977	42	1	2·3
Staines (a)	26 April 1975	42	4	8·7
	13 Sept 1975	40	2	4·8
	16 April 1976	27	3	10·0
	12 Sept 1976	29	4	12·1
	12 April 1977	19	1	5·0
	20 Aug 1977	31	3	9·7
Staines (b)	15 May 1976	208	12	5·5
	19 Sept 1976	23	0	0
	13 May 1977	50	6	10·7
	21 Aug 1977	70	2	2·8

* Animals marked in the course of mark-recapture experiments.

together there is no evidence of a uniform trend.   At only one locality, Gloucester, is the pattern consistent with the changes observed in Berlin. Samples collected in the U.S.S.R. (Lusis, 1973), Czechoslovakia (Honek, 1975) and Norway (Bengston and Hagen, 1975) also show no significant differences or trends.   It is, of course, possible that Berlin is one of the few places where the balance between summer and winter selection results in a polymorphism and that in other localities selection by one or other factor results in a population containing a majority of one morph.   If this is true, then localities in Great Britain with high frequencies of non-melanics should show correspondingly high selection against melanics during the winter.

That this cannot be found suggests that selection against melanics in Great Britain may be taking place in another season.

(ii) *Selection during the summer*

Muggleton *et al.* (1975) suggested that the greater heat absorption and activity of the melanic morphs would put them at a disadvantage during the summer months as a result of overheating and desiccation and Hodek (1973) points out that for many polymorphic ladybirds there is a tendency for increases in melanic frequency to be associated with increasing humidity. The relationship between high melanic frequencies in *A. bipunctata* and high humidity has been stressed by Lusis (1961) and, more recently, by Bengston and Hagen (1977). The existence, however, of high melanic frequencies in areas where sunshine levels and temperatures are considerably in excess of those in north-western Europe (*e.g.* northern Italy, the Crimea and in hot and dry regions of central Asia) suggests that melanics are able to tolerate conditions of high temperature and low humidity. Additional support for this suggestion comes from the findings of Hawkes (1920) and Marriner (1926) that in captivity the melanics can withstand high temperature better than the non-melanics. The possibility cannot be ignored, however, that the genetic constitution of the melanics differs from place to place or that local adaptations may have occurred. The former may certainly be true of the Central Asian populations where the majority of the melanics are of the form *sublunata* which is uncommon in Europe; other morphological and genetic differences have led Lusis (1973) to consider these Central Asian populations as a subspecies of *A. bipunctata*.

(iii) *Generation time*

In Berlin the increase in melanics took place during the course of three successive generations in the summer (Timoféeff-Ressovsky and Svirezhev, 1966), and it may be supposed that the frequency of melanics increases from generation to generation. In localities where there were fewer generations a year the increase in melanics during the summer would not be so great unless the selective advantage per generation was larger. Table 2 shows

TABLE 2

Percentage of A. bipunctata *found copulating in samples from southern and eastern England during 1976. (1) and (2) indicate the first and second halves of the month*

	% in cop.	Sample size
April	11·5	192
May (1)	22·4	1640
May (2)	24·7	1246
June (1)	17·5	620
June (2)	10·4	308
July	0	1261
August	0	111
September	0	588

the percentage of mating pairs found in samples collected in southern and eastern England between April and September 1976. These data indicate that there was only one period of mating activity and hence only one generation in this long, hot summer. Data collected from Kew, in southern England, between 1964 and 1968, confirm this finding (Eastop and Pope, 1969). Klausnitzer (1971) states that in central Europe *A. bipunctata* has at most two generations a year and in Norway there is only one generation (Ellingsen, 1969). If *A. bipunctata* is a univoltine species in England the ability of the melanics to increase during the summer months will be much reduced and one of the advantages of the melanic morphs will be largely eliminated.

(iv) *Migration*

Creed (1966, 1971*a*) has proposed that melanic frequencies may be low in certain isolated industrial towns because the selective advantage of the melanics in these localities is counteracted by gene flow from the surrounding non-melanic populations. In order to demonstrate this it would be necessary to know the level of the selective advantage of the melanics and the migration rate for specific localities. While such information is not available, it is possible to come to some general conclusions about migration rates. Data collected in the course of four mark-recapture experiments (Muggleton, in preparation) show that over periods of several weeks movement of more than a few metres are rare. Although reports of ladybird migrations are common, in Great Britain at least, *A. bipunctata* is rarely involved (Muggleton and Benham, in preparation). The picture of *A. bipunctata* as a rather immobile species is reinforced by the steep clines in morph frequency which are invariably associated with areas of high melanic frequency (Creed, 1971*a*; Muggleton, unpublished). Similar clines are associated with the melanic polymorphism of the moth *Gonodontis bidentata* and have been ascribed to the low migration rates of this species (Bishop and Cook, 1975). Indeed, comparing the pattern of melanism of *A. bipunctata* in the industrial north-west of England with that of melanism in both *G. bidentata* and *Biston betularia* it is apparent that the pattern is much more like that of the less mobile *G. bidentata* than of the much more mobile *B. betularia* (Bishop *et al.*, 1978*a*). Thus it is probable that at least in areas of high melanic frequency a lack of migration is reducing the spread of the melanic morphs. This, in turn, suggests that the existence of low melanic frequencies in isolated industrial towns cannot be explained in terms of migration and that an explanation for it must be sought elsewhere (see Muggleton *et al.*, 1975).

(v) *Selective predation*

In contrast to the other melanic polymorphisms in invertebrates, the possibility that selective predation is a factor maintaining the polymorphism in *A. bipunctata* has been ignored on the assumption that ladybirds are aposematic and avoided by vertebrate predators. This assumption has arisen as the result of experiments in which birds and other vertebrates have been offered ladybirds as food in laboratory experiments. While the early experiments of this kind were often inconclusive (Pocock, 1911; McAtee, 1912; Heikertinger, 1932) the more recent work of Frazer and

Rothschild (1960) showed that when ladybirds, including *A. bipunctata,* were offered to a variety of vertebrates they were invariably rejected as food. However, these results conflict with the many reports of predation on lady-birds by birds and other vertebrates (Heikertinger, 1932; Hodek, 1973; Klausnitzer, 1971).   I have located records of 19 species of birds which have been found to reject ladybirds as food in laboratory experiments, whereas there are published records of 121 bird species having eaten ladybirds, mostly in natural conditions, and these include six of the species found to reject ladybirds in laboratory conditions.   Heikertinger (1932) was able to list some 40 European birds, most of which occur in Great Britain, as having been recorded as eating ladybirds, or having ladybirds found in their stomachs or droppings.   My own examination of 38 gm of dried House Martin (*Delichon urbica*) droppings collected from under a nest in Northenden, Manchester, by M. V. Hounsome in 1976 showed them to consist almost entirely of the remains of five species of ladybird (*Adalia bipunctata, A. 10-punctata, Coccinella 7-punctata, C. 11-punctata* and *Propylea 14-punctata*).   In spite of being fed on ladybirds the young were reared successfully.

TABLE 3

Numbers of previously frozen melanic and non-melanic A. bipunctata *taken during predation experiments*

	Numbers taken		Numbers left		Relative survival of melanics
Locality	Non-melanic	Melanic	Non-melanic	Melanic	
Woodchester Park, Glos., July 1975	1	3	49	47	0·96
Nottingham, July-August 1976	12	16	39	35	0·9
Chobham Common Surrey, Oct-Nov 1976	3	6	27	24	0·89
Nottingham, June 1977	7	7	18	18	1·0

In view of the quite different situations experienced by birds in experi-mental and natural surroundings this conflict of results is not surprising. For example, the reaction of a caged well-fed bird used to a limited number of prey species is unlikely to be the same as that of its wild counterpart, which may not only be hungry but may also be faced with a large number of prey species in a short time, of which only a few are distasteful.   Under these conditions it seems inevitable that the experimental birds will avoid ladybirds more readily.   Thus laboratory experiments have only a limited value, which is to identify species that are potentially distasteful.   The extent to which this distastefulness is a deterrent to predation under natural conditions can only be determined by observation of wild animals.   Undoubtedly, ladybirds are distasteful and warningly coloured, but there can be little doubt that the results obtained by Frazer and Rothschild (1960) are misleading to the extent that they imply a far greater protection of ladybirds by their scent and colour than actually exists.

A selective predation experiment, carried out in July and August 1976 in Nottingham, during which frozen ladybirds were glued to the twigs of apple trees in life-like positions in the same manner as has been used for

selective predation experiments with the moths *Biston betularia* and *Gonodontis bidentata* (Bishop, 1972; Bishop, Cook and Muggleton, 1978*b*) showed that 28 per cent of the ladybirds were taken ($n = 102$) and that the relative survival of melanics compared to typicals was 0·9. An experiment using the same trees in June 1977 showed the same predation rate but on this occasion equal numbers of melanics and non-melanics were taken ($n = 50$). An experiment done on pine trees on Chobham Common, Surrey, showed 15 per cent predation ($n = 60$) and a relative survival rate for the melanics of 0·89. A further experiment, again on apple trees, but this time at Woodchester Park in Gloucestershire, was carried out by Papeeta Mackenzie and Judith Prince as part of a field course project and on this occasion the predation rate was only 4 per cent ($n = 100$). Mackenzie and Prince believed their low predation to have been the result of the specimens thawing before the experiment and thus becoming unpalatable. In the other experiments the ladybirds retained their distinctive scent for the 24-hour period during which they were exposed to predation. These experiments show that ladybirds (at least our frozen specimens, which are not known to be perceived by birds differently from live ones) are taken more readily by birds than would have been expected from the observations of Frazer and Rothschild on live ladybirds (1960). Indeed, the predation rates are not far removed from those found in the selective predation experiments mentioned above, using moths which are cryptic and palatable. The average predation rate in these experiments with moths was 33 per cent and ranged from 18 to 50 per cent.

Fifty-one fragments of *A. bipunctata*, each large enough to have come from a single ladybird, were recovered from the House Martin droppings mentioned above. Of the 26 left elytra, 20 were from melanics and of the 25 right elytra, 24 were from melanics. The mean melanic frequency from left and right elytra is 86·3 per cent which does not differ significantly from the expected melanic frequency for the Northenden area (Bishop *et al.*, 1978*a*). Thus the House Martins appeared to have taken the morphs randomly, but this may not be surprising for a bird which captures its prey on the wing.

Nevertheless, although their protection is imperfect, it is hard to escape the conclusion that ladybirds do form an assemblage of Müllerian mimics. For while polymorphism is common amongst the Coccinellidae, the majority of species are red with black spots and they share the same distinctive scent (Rothschild, 1961). Given this fact and the existence of predation it may well be that the scarcer melanics are not recognised as ladybirds in the majority of situations where red species will predominate. It is interesting to note that in Great Britain there are some species of ladybird which are always black with red spots. The commonest of these is *Exochomus quadri-pustulatus* which is very similar in size and colour pattern to the *quadrimaculata* morph of *A. bipunctata*. This species is associated with pine trees and in such habitats can be one of the commonest ladybirds. It may be that in such areas the melanic morphs of *A. bipunctata* will be better protected against predation as predators will be accustomed to finding black ladybirds, and this may explain the unexpectedly high frequencies of melanism in *A. bipunctata* found by Creed (1966) to the south-west of London where pine and *E. quadri-pustulatus* are particularly abundant. Edmunds (1974) has suggested that the melanic morphs of *A. bipunctata* may be cryptic against certain backgrounds

and the dark bark of pine trees certainly offers a background against which melanic ladybirds are difficult to see. *A. bipunctata*, however, rarely occurs on pine trees and the selective predation experiment carried out on pine trees on Chobham Common shows a disadvantage to the melanic morphs.

3. DISCUSSION

At present there seems to be no factor which can be positively identified as selecting against the melanic morphs. While the results from Berlin indicate that selection there is taking place during the winter, these results do not appear to be repeated elsewhere, although given the wide range of climates experienced by the species this may not be surprising. If, however, selection against the melanic morphs during the winter is general, then the existence of a univoltine life cycle in many regions may have prevented the build-up of melanics in areas where the advantage to them during the remainder of the year is marginal.

The similarity of the predation rates on moths and ladybirds in predation experiments suggests that both cryptic and aposematic coloration can offer similar levels of protection from vertebrate predators. That avian predation on ladybirds can be considerable must now be accepted and suggests that in some areas selective predation could be involved in the polymorphism of *A. bipunctata*. In a similar way Kettlewell's finding (Kettlewell, 1956), against the opinion of the day, that *B. betularia* on tree trunks were commonly eaten by birds led to the elucidation of the polymorphism in that species.

Throughout this paper no attention has been given to the fact that there are several melanic morphs of *A. bipunctata*, two of which are common in Great Britain, and this reflects the habit of previous authors of placing all the melanic morphs in one category. From the little that is known of the distribution of the melanic morphs it appears that their proportions in samples vary geographically and it is probable that these different melanic morphs are responding differently to some of the selective factors. Such a difference in response would add to the difficulty of analysing the polymorphism and future work should indicate which melanic morphs are concerned.

In conclusion, it is evident that the factors selecting against melanics are not the same throughout the range of the species. That a number of selective factors may be acting on the polymorphism should not be surprising, indeed this may be true for most of the widespread polymorphsims which have been studied. The literature on *Cepaea nemoralis* contains many accounts indicating the nature of selective agents in particular areas (Cain and Sheppard, 1954; Lamotte, 1959; Arnold, 1968; Jones, 1973) which often conflict with the findings from other parts of the species' range. The same is true for the spittlebug *Philaenus spumarius* where selective predation by birds, climate, parasites and effects of air pollution (Owen and Wiegert, 1962; Halkka, Raatikainen and Vilbaste, 1975; Harper and Whittaker, 1976; Creed, pers. comm.) have all been suggested as selective agents. These examples all refer to colour polymorphisms, but the same multiplicity of selective factors has also been proposed for some enzyme polymorphisms. Latitude, substrate, temperature, and frequency dependent selection have all been suggested at the alcohol dehydrogenase locus of *Drosophila melanogaster* (Vigue and Johnson, 1973; Pipkin, Rhoades and Williams, 1973; Morgan, 1975; Kojima and Tobari, 1969).

There has, however, been a tendency to overlook the possible complexity
of selective factors and to search instead for some single factor which will
explain the entire picture. Such an approach leads to difficulties in explain-
ing why similar morph frequencies are found in widely differing habitats or
localities. Thus the fact that a particular selective factor does not seem to
be important in one locality has been taken as evidence that nowhere else
is it important (*e.g.* the climatic selection *v.* selective predation controversy in
Cepaea nemoralis). This type of argument has been applied to the poly-
morphism in *A. bipunctata* by Scali and Creed (1975) who compare the
situation in central Italy to that in Great Britain. Such difficulties are
avoided if the polymorphism is considered as being the result of the inter-
action of a number of selective factors whose relative importance may differ
from one locality to another. This argument may be applied to the poly-
morphism in *A. bipunctata*. It is probable that throughout the range of the
species the melanic morphs of *A. bipunctata* have an advantage over non-
melanics in terms of their more efficient absorption of solar radiation
(Lusis, 1961; Muggleton *et al.*, 1975). Over much of the range, however,
this advantage may be counteracted by varying combinations of other
factors including winter mortality, selective predation, number of generations
per year, migration rate and perhaps a disadvantage of melanic homozygotes.
High melanic frequencies may occur in high, as well as low, sunshine areas.
In high sunshine areas the melanic frequency will depend on the extent to
which selection against melanics counteracts their thermal advantage. In
low sunshine areas it is probable that their thermal advantage will always be
in excess of the disadvantages.

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