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Polymorphic Müllerian mimicry and interactions with thermal melanism in ladybirds and a soldier beetle: a hypothesis

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It is argued that groups of similarly coloured species of coccinellids are Müllerian mimicry rings. This is based on a synthesis of the literature about the nature of their biology and aposematic colour patterns, their highly developed chemical defence and the responses of bird predators to them. The system of multiple mimicry 'rings' is illustrated for the Dutch coccinellid fauna. Some polymorphic species, including *Adalia*, exhibit red forms and black melanic forms which are apparently components of different putative mimicry rings. A similar reasoning is put forward with regard to the orange and the black forms of the soldier beetle *Cantharis livida.* Hypotheses involving spatial variation in comimics, as have been developed to account for some other cases of polymorphic Müllerian mimicry, predict that sympatric polymorphic species exhibiting similar sets of phenotypes will show parallels in their geographical variation. This is tested for *A. bipunctata* and *A. decempunctata* in The Netherlands. On this local scale there is no parallel variation; *A. bipunctata* exhibits marked geographical differentiation whereas *A. decempunctata* shows a general uniformity in morph frequency. Observations on their population biology show that only in *A. bipunctata* is there a major spring period of adult reproduction on shrubs exposed to direct sunshine. Previous work has demonstrated an influence of thermal melanism in this period of the life cycle. It is suggested that local responses in species such as *A. bipunctata* may reflect a partial 'escape' from stabilizing aposematic selection. The basis of a steep cline found in *C. livida*, which opposes one in *A. bipunctata*, is unknown and unlikely to be related to mimicry. There is some evidence that the polymorphism is influenced by non-random mating. When species and communities of coccinellids are considered on a wide geographical scale many observations about their colour patterns and spatial variation, especially those of Dobzhansky, support an interaction between selection favouring mimetic resemblance and forms of climatic selection, especially thermal melanism. The polymorphism in *Adalia* is discussed in relation to a system of multiple mimicry rings and to Thompson's recent theoretical treatment of the maintenance of some polymorphisms for warning coloration by a balance between aposematic and apostatic selection. This becomes more tenable in coccinellids because of evidence that bird predators show a variable response to them. Frequency-independent selection arising from thermal melanism can provide the basis of spatial variation in equilibrium points. An alternative to such a hypothesis is one in which differences in unpalatability between species of coccinellids are emphasized (after experiments of Pasteels and colleagues). Some less unpalatable species such as *Adalia* may have responded to periods of prolonged disruptive selection acting in a frequency-dependent way to promote polymorphic mimicry associated with different modal colour patterns and intermediate in nature between classical Batesian and Müllerian mimicry. The likely occurrence of a supergene controlling polymorphism in some coccinellids is consistent with such an explanation.

KEY WORDS:—Coccinellidae – Cantharidae – *Adalia* – warning coloration – Müllerian mimicry – mimicry rings – melanic polymorphism – morph-ratio cline – thermal melanism – Batesian mimicry.

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INTRODUCTION

Surveys of the geographical variation in morph frequency in organisms which exhibit polymorphisms with similar ranges of phenotypes can provide novel insights into the way in which selection influences genetic variation. For example, surveys of shell colour and banding polymorphism in the snails *Cepaea hortensis* and *C. nemoralis* led to the formulation of hypotheses about the way in which predators hunting by sight can maintain visual polymorphism through introducing frequency-dependent effects (Clarke, 1962a, b) and in so doing, exert apostatic selection. Such studies have also involved examples of industrial melanism in moths and some other insects (see Lees, 1981, for a recent review). Examinations of the response of different species to particular gradients in air pollution have been especially enlightening. Thus, comparative surveys of some moths have provided strong evidence that spatial variation is strongly influenced by differences in such biological parameters as gene flow and adult resting behaviour (e.g. Bishop, Cook & Muggleton, 1976, 1978). During a five-year investigation of the dynamics of the melanic polymorphism in the two-spot ladybird *Adalia bipunctata* (L.) (Coleoptera, Coccinellidae) in The Netherlands (Brakefield, 1984a) samples of the ten-spot ladybird *A. decempunctata* (L.) and a soldier beetle *Cantharis livida* (L.) (Coleoptera, Cantharidae) were also obtained from many sites. Forms which are predominantly red or black are found in each of these species. The work on *A. bipunctata* provided evidence that thermal melanism involving differences in the absorption of solar radiation between non-melanics and melanics influences the polymorphism and in particular the timing and intensity of adult reproduction (Brakefield, 1984b, c; Brakefield & Willmer, 1985).

In the first part of this paper I argue that groups of similarly coloured species of coccinellids are probably Müllerian mimicry 'rings'. The possible relevance of this to polymorphism in species of *Adalia* and, more generally, in other coccinellids is explored. Muggleton (1978) has suggested that coccinellids form an assemblage of Müllerian mimics. He also pointed out the possibility of a relationship between a local abundance of monomorphic species which are predominantly black and a high frequency of melanic *A. bipunctata* to the southwest of London. The second part of the paper examines the basic population biology and geographical variation of the three beetles studied in The Netherlands. The results are then discussed in relation to hypotheses of polymorphic Müllerian mimicry and thermal melanism. In contrast to the comparatively recent evolution of high frequencies of melanics in moths exhibiting industrial melanism, the polymorphisms in the beetles appear to have been established for a long time. Thus, Hammond (1975) records that a collection made in the 1690s around London by L. Plukenet includes melanic specimens of both *A. bipunctata* (four of five) and *C. livida* (one of two). Furthermore, many of the complete range of non-melanic and melanic phenotypes found in the genus *Adalia* are common to the different taxa (see for example Lusis, 1973). These phenotypes probably share homologous developmental pathways and the polymorphisms are therefore unlikely to be of a transient nature.

HYPOTHESES FOR MÜLLERIAN MIMICRY IN COCCINELLIDS

Adalia bipunctata is a highly polytypic species with a distribution covering almost all of the Palearctic (it also occurs in the Nearctic). *Adalia decempunctata* is confined to Europe, the Near East and N Africa (Lusis, 1973). The present discussion is restricted to European populations. Adult *Adalia* have typically aposematic patterns of shiny red and black. Common forms are illustrated in Fig. 1 including the melanic *quadrimaculata* (*A. bipunctata*) and *bimaculata* (*A. decempunctata*). A further melanic form of *A. bipunctata* is *sexpustulata* which has six red marks. Other forms of these species are generally rare in W Europe. The black pigments are melanins and the red-yellow ones, carotenoids (Britton, Goodwin, Harriman & Lockley, 1977). The tough cuticle, long lifespan, habit of laying eggs in batches and aggregative behaviour (e.g. during hibernation, see Brakefield, 1985) of adult coccinellids are all characteristic attributes of aposematic insects.

The *typica* form of *C. livida* is predominantly testaceous or orange but has prominent black antennae, eyes and posterior femora. The melanic form, *rufipes* (Herbst.), has long black elytra but the head, thorax and forelegs are orange (see colour plates in Linssen, 1959; Sandhall, 1975). As in coccinellids the elytra represent most of the visible dorsal cuticle. Cantharids differ from coccinellids in being quite soft bodied and elongate (rather than half-spherical like). They are usually larger; *C. livida* is 11–14 mm long. They are similarly conspicuous insects when at rest on flowers or foliage and are also easy to capture.

Chemical defence

Coccinellids have been shown to exhibit lethal properties if injected (i.v.) into guinea-pigs and cats (Frazer & Rothschild, 1960; M. Rothschild, personal communication). The most important chemicals so far identified in ladybird beetles are a group of closely related alkaloids (Pasteels *et al.*, 1973; Mueller, Thompson & DiPardo, 1984, and references therein). These include adaline (in *Adalia* species), propyleine (*Propylaea quatuordecimpunctata*), coccinelline and precoccinelline (*Coccinella* species). Some cocinellid genera (e.g. *Adonia, Calvia* and *Harmonia*) are characterized by alkaloids of a higher molecular weight, suggesting a different structure (Pasteels *et al.*, 1973). Both non-melanics and melanics in *A. bipunctata* and *A. decempuncata* were found to contain adaline. Three of the hydropyridoquinolizine alkaloids of lower molecular weight, including precoccinelline, have also been found in an Australian soldier beetle,

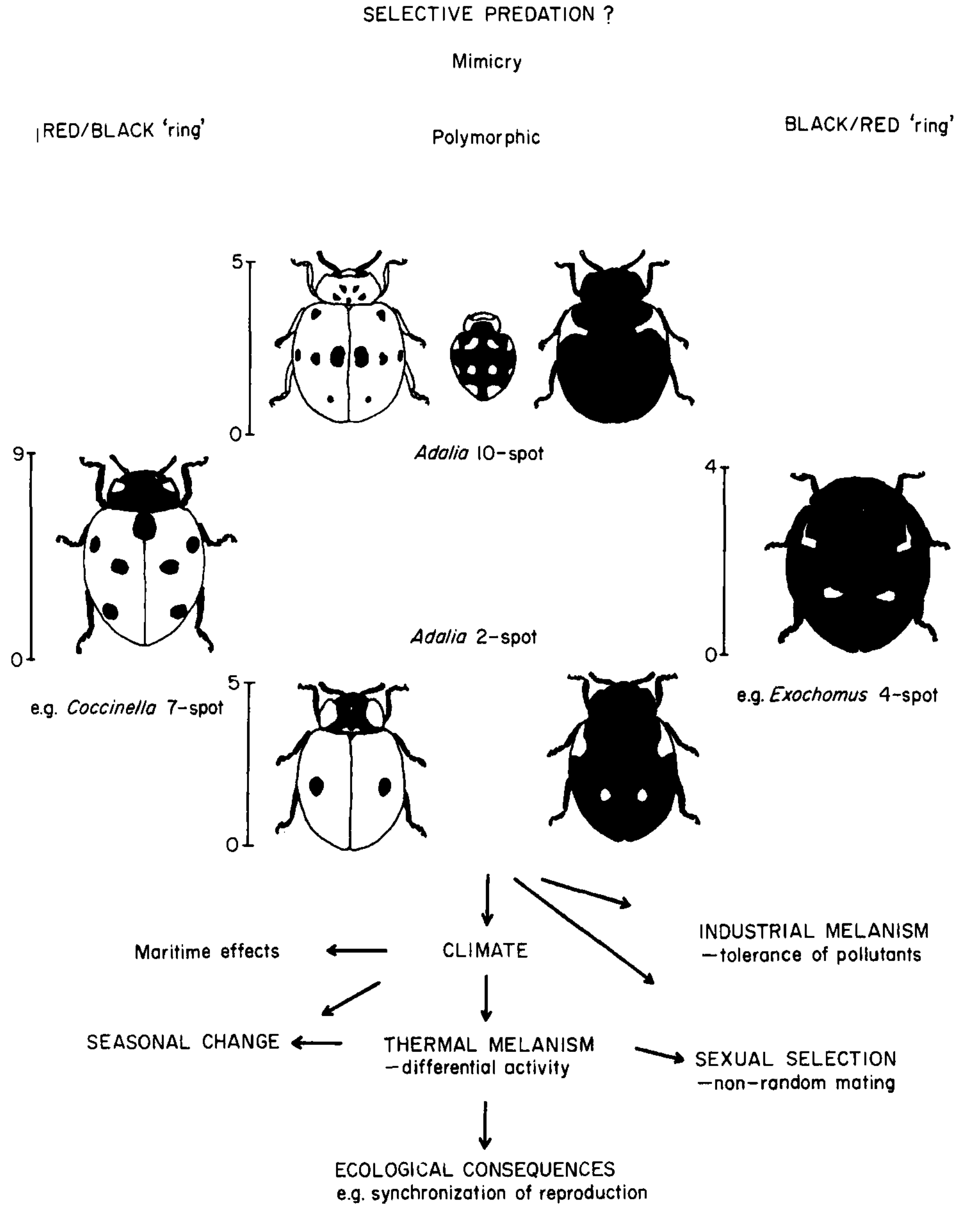

Figure 1. The most abundant melanic and non-melanic forms of *Adalia decempunctata* (form *decempustulata* in reduced size) and *A. bipunctata* together with examples of monomorphic coccinellid members of Müllerian mimicry rings (red areas of the beetles are depicted in white and size scales are in millimetres). An indication of selective factors which have been considered to influence the polymorphism in *A. bipunctata* is given.

Chauliognathus pulchellus (Moore & Brown, 1978). This common occurrence in two unrelated groups of beetles is believed by Moore and Brown to reflect convergence. Coccinellids also contain high concentrations of histamine (Frazer & Rothschild, 1960) and at least one species feeding on *Aphis nerii* stores cardiac glycosides (Rothschild, Euw & Reichstein, 1973; Rothschild & Reichstein, 1976). Volatile substances, pyrazines and quinolenes, have also been identified in coccinellids and cantharids (Rothschild, 1961; Moore & Brown, 1981; Rothschild, Moore & Brown, 1984). In addition, an acetylenic compound, dihydromatricaria acid, occurs in the haemolymph and defensive secretions of at least two cantharids (Meinwald, Meinwald, Chalmers & Eisner, 1968; Moore & Brown, 1978). These components of the characteristic odour and bitter taste of the beetles almost certainly serve warning functions as cues in the earlier phases of a multiple-line defence (see for example Rothschild, 1961, 1984a). Coccinellids exude a pungent, oily substance from the leg joints when molested, which, in some but not all species, contains yellow haemolymph (Happ & Eisner, 1961; Kay, Rothschild & Aplin, 1969). Cantharid beetles possess eight pairs of dorsal scent glands on the abdomen (Meinwald *et al.*, 1968). The alkaloids, histamines, cardiac glycosides, acetylenic acids, pyrazines and quinolenes are all associated with toxic or repellant qualities in a range of aposematic insects including Danaid and Papilionid butterflies, and Arctiid and Zygaenid moths (see Brower, 1984; Rothschild, 1984b). The secretions and odours which probably enable some of the beetles and other insects to survive predator attacks may have played an important role in the evolution of warning coloration (Sillén-Tullberg & Bryant, 1983).

Feeding experiments performed by Morgan (1896), Pocock (1911), Morton Jones (1932), Frazer & Rothschild (1960), Meinwald *et al.* (1968) and Pasteels *et al.* (1973) have in general provided strong evidence that warningly coloured coccinellids, including *A. bipunctata*, and cantharids are well or partially protected from bird predators. These experiments have sometimes also involved other vertebrates, especially reptiles and amphibia. Morton Jones' experiments, in which recently killed beetles were exposed on trays amongst other aposematic and cryptic species to wild birds at a woodland edge in America are particularly well documented and noteworthy. The rather small scale experiments of Pasteels *et al.* suggested that there were differences among individual captive quails in their reaction to moderately protected species of coccinellids including *A. bipunctata*. The general conclusion reached from these experiments is to some extent countered by the many observations based on analyses of stomach contents or excrement, of birds feeding on *Adalia* spp., other warningly coloured coccinellids and cantharids (see Heikertinger, 1932; McAtee, 1932; Muggleton, 1978). Some birds may have breached the toxic defence mechanisms (cf. for example Rothschild & Kellett, 1972; Fink & Brower, 1981). In any case coccinellids may be a regular food item for some species. For example, redstarts and tree sparrows commonly eat coccinellids (Buxton, 1950; Kristin, 1984) and observations have been made of some urban blue tits feeding them to nestlings (R. J. Cowie & S. A. Hinsley, pers. comm.). In birds which take coccinellids, including *Adalia* spp., on the wing, such as swifts (Owen, 1955) and house martins (Muggleton, 1978), the colour patterns may play no part. In other birds the feeding is probably irregular and infrequent or occurs predominantly in periods of food scarcity. For example, Kluyver (1933) found that of 4490 beetles eaten by wild starlings in The Netherlands only two were coccinellids while *A. decempunctata* can be a substantial component of the winter diet of titmice in oak woodland (Betts, 1955). However, some coccinellids, including *A. bipunctata*, overwinter conspicuously and in clusters at exposed hibernacula and yet may not suffer high predation from birds (see Brakefield, 1985, and discussion in Copp, 1983). The chemical defence probably also provides some protection against wasps and ants (Lane, 1960; Happ & Eisner, 1961; Pasteels *et al.*, 1973; but see Morton Jones, 1932). Some observations on the responses of other predatory invertebrates to coccinellids are detailed by Heikertinger (1932).

Pasteels *et al.* (1973) failed to detect alkaloids in those coccinellids lacking aposematic coloration which involves a bright and contrasting pattern. Furthermore, their experiments with captive quails showed that three such species, including *Aphidecta obliterata*, were edible. The fact that the quails rejected several species with aposematic coloration and which contained alkaloids is particularly interesting since these birds are very insensitive to toxic insects (see Rothschild & Kellett, 1972). This also applies to Frazer & Rothschild's (1960) experiments with young cuckoos (see for example Rothschild, 1981).

Müllerian mimicry rings

The problem of relating the defensive chemistry of an aposematic insect and the results of feeding experiments, which must always involve some element of artificiality, to the actual advantage accrued in nature in terms of enhanced protection has long been recognized and discussed from different viewpoints. Rothschild & Kellett (1972) emphasized the facts that no protective mechanism can be absolute and the enormous variation found in the reaction of predators to extracts or whole insects. Warningly coloured insects which lacked protection either from chemical defence or appropriate models would be expected to suffer a higher total mortality than those gaining such protection. The observations reported above with regard to coccinellids and cantharids provide strong overall evidence that the warning colour of these beetles is associated with a high or moderate degree of unpalatability and related chemical protection from most or many bird predators. They are then likely to be involved in mimetic relationships. Many coccinellids are monomorphic and can usually be assigned to one of a number of putative Müllerian mimicry groups. Such mimicry 'rings' comprise an assemblage of unpalatable species which share the same or similar warning 'signal'. Examples of systems of two or more mimicry rings have been studied in *Heliconius* butterflies and *Bombus* bumblebees (Papageorgis, 1975; Plowright & Owen, 1980). Some coccinellids are also the models for palatable Batesian mimics. Wickler (1968) illustrates two examples from the cockroach genus *Prosoplecta* in the Philippines.

All communities of coccinellids with a high species diversity can probably be described in terms of a series of mimicry rings. I will illustrate this with respect to the most abundant species and genera in The Netherlands (and more widely in Europe; see Gunst, 1978, and Linssen, 1959). These species or genera are nearly all represented in the list of Pasteels *et al.* (1973) of those with alkaloids (none were shown to lack them). Many coccinellids are red or orange-red on the dorsal surface with a number of black spots or marks. In The Netherlands they include species of *Coccinella, Anatis, Adonia* and *Hippodamia. Coccinella septempunctata* (Fig. 1), *C. quinquepunctata* and *C. undecimpunctata* are likely to be especially significant in mimetic associations because of their abundance and wide distribution. Other species are black with a small number of red marks on the elytra or pronotum. These include *Chilocorus renipustulatus, C. bipustulatus, Exochomus quadripustulatus* (Fig. 1) and *E. nigromaculatus.* Other probable mimicry rings are those of species which are a shade of yellow with black marks (e.g. *Thea vigintiduopunctata*, *Tytthaspis sedecimpunctata* and *Anisosticta novemdecimpunctata*) and brown with yellow spots or marks (e.g. *Calvia quatuordecimguttata*, *Halyzia sedecimguttata*, *Myrrha octodecimguttata* and *Neomysia oblongoguttata*).

Although the colour patterns of coccinellids tend to fall into a small number of modal groups, representing the putative mimicry rings, the similarity in pattern between the group members is not generally as close as that characteristic of the *Heliconius* and *Bombus* systems. This applies especially to variability in the expression of marks on the elytra (see Fig. 1). Resemblance is expected due to stabilizing selection exerted by visual predators (e.g. Benson, 1972; and see Mason, 1976). Such selection could be weaker on coccinellids due to the presence of a lower 'load' from Batesian mimics (cf. Plowright & Owen, 1980), lower levels of visual predation or the way in which the vertebrate predators perceive the warning 'signals' (see also discussion in Turner, 1984). To provide a measure of protection the resemblance between the species does not have to be close enough to cause misidentification by the predator, merely close enough to remind it of a past experience with similar prey. Two aposematic forms probably have to be very similar to gain 'full mutual protection' and never be discriminated by predators (see Sillén-Tullberg, Wiklund & Jarvi, 1982, 1983; Paxton & Harvey, 1983). In many cases coccinellid comimics are unlikely to achieve this. Some of the main mimicry rings may more appropriately be described as two or more subrings within which species gain a greater mutual protection than exists between those of different ones. This might be the case in the red/black ring (Fig. 1) for species with 'few' spots and those with 'many'. However, there is probably no sharp division between these groupings or members of other possible subrings (see below).

Müllerian mimicry and polymorphism

The common forms of species of *Adalia* appear to be components of different putative mimicry rings (see also Lusis, 1973, for an account of polymorphism in other taxa of *Adalia*, particularly *A. tetraspilota*). The *typica* forms and dark forms resemble the red/black and black/red species groups, respectively (Fig. 1). The evident close similarity in the colour pattern of *quadrimaculata* melanic *A. bipunctata* and *Exochomus quadripustulatus* is particularly striking. The common intermediate melanic form *decempustulata* of *A. decempunctata* (Fig. 1) resembles *Synharmonia conglobata*, *Propylaea quatuordecimpunctata* and *Coccinella hieroglyphica* in The Netherlands. There is some variability in ground-colour from red-orange to pink to pale yellow in these species but their pattern tends to give a lattice-work effect and they probably represent a further mimicry ring or subring. Other species of coccinellids with similarly striking ranges of phenotypes to *Adalia* are likely to be polymorphic between different mimicry rings (see for example figures in Dobzhansky, 1933; A. Honek in Hodek, 1973; Houston & Hales, 1980).

A similar reasoning can be put forward with regard to *C. livida* since there are numerous monomorphic species of *Cantharis* in N Europe which are either predominantly orange or black. Common species include *C. pallida* (orange) and *C. rustica* (black) (see Linssen, 1959).

There may be little, if any, overlap in habitat preference between the members of particular groups of putative comimics in the Coccinellidae. However, in some instances such overlap is substantial and in others, the species may share some bird predators because their habitats are within the range over which the birds forage. In The Netherlands, *A. bipunctata* is abundant on various deciduous shrubs and trees and *A. decempunctata* is common on lime trees, *Tilia* spp. (see Results section). Several of the black/red species frequently occur in the same or adjacent habitat area as *Adalia.* This applies especially to *E. quadripustulatus* which is widely distributed and often abundant. Together with *S. conglobata*, it is also sometimes found in or close to overwintering groups of *Adalia* at hibernacula on trees (Brakefield, 1985). *Exochomus quadripustulatus* in Britain is more closely associated with conifers (J. Muggleton, pers. comm.) which are not favoured by *Adalia.* Thus, the extent of habitat overlap in regions where these species occur is probably less than in The Netherlands, although *Adalia* is sometimes abundant on birch trees, *Betula* spp., within areas of conifers (personal observations).

The species of *Adalia* and the red/black coccinellids in The Netherlands are members of the subfamily Coccinellinae (Gunst, 1978). The monomorphic black/red species are of the subfamily Chilocorinae which is considered to have diverged from the Coccinellinae early in the evolution of the family (Sasaji, 1968). Thus many cases of similar colour patterns are likely to reflect a common ancestry. If mimicry is involved, the melanic forms of *Adalia* provide the most extreme examples of convergent evolution in W Europe. The patterns of inheritance of colour polymorphism in species of coccinellids are usually consistent with single series of multiple alleles (review by Komai, 1956; an exception involving two pairs of complementary genes is given by Sasaji & Akamatsu, 1979). It is probably appropriate to describe the polymorphisms in species of *Adalia* as homologous although there are important differences. For example, the *quadrimaculata* (Fig. 1) and *sexpustulata* phenotypes do not apparently occur in *A. decempunctata.* Lus (1928, 1932) showed that in *A. decempunctata* the dominance order is *typica* > *decempustulata* > *bimaculata* (the extreme melanic, Fig. 1) whilst in *A. bipunctata* it is *sublunata* (*bimaculata*-like) > *quadrimaculata* > *sexpustulata* > *typica* > *simulatrix* (similar to *A. decempunctata typica*) > *decimpustulata* (*decempustulata*-like). Thus the common and extreme melanic alleles in Europe and elsewhere are dominant in *A. bipunctata* and recessive in *A. decempunctata.* With respect to the extent of melanization and dominance order the coccinellids *Harmonia axyridus* (review in Komai, 1956; and see Sasaji, 1981) and *Coelophora inaequalis* (Houston & Hales, 1980, and references therein) are comparable to *A. bipunctata* and *A. decempunctata*, respectively. This apparent lack of any strong bias towards dominance of melanism contrasts with industrial melanics in moths (review by Lees, 1981) and the presumed recessive nature of ancestral colour patterns in race formation in *Heliconius* butterflies arising from an evolutionary 'sieve' mechanism (see Turner, 1984). Recessive melanics are found in laboratory stocks of other species of beetle, for example *Tribolium castaneum* (Sokoloff, 1966).

The frequent occurrence of polymorphism indicates that the mimicry rings in coccinellids are generally not as distinct genetically as those of *Heliconius* where mutations of at least two major genes are usually needed to switch a pattern characteristic of one ring to the spectrum of protection afforded by another ring.

In the aposematic moth *Zygaena ephialtes*, mutations at two gene loci are necessary for a comparable change in pattern although it has been suggested that a phenotype resulting from an allelic substitution at only one locus derives partial protection from exhibiting a pattern element of each ring (Sbordini *et al.*, 1979). Such genetic complexities are believed by Turner (1977) to contribute to a lack of (further) convergence of mimicry rings within multiple systems. However, in bumblebees and coccinellids phenotypic differences between discrete rings can be the result of allelic substitution at single gene loci (Owen & Plowright, 1980; also cf. *H. doris*, Turner, 1971) although in some coccinellids such loci may actually be groups of tightly linked loci (Komai, 1956; and see Discussion below).

The operation of stabilizing selection means that colour and pattern polymorphism is not predicted in Müllerian mimics. A species is expected to converge on the colour pattern which is the most protected due to the combination of its abundance and associated distasteful qualities. There are, however, a number of exceptions whose study has given some insight into how polymorphism may be maintained. Cases of allopatric polymorphism and differentiation, often with zones of intergradation, which are associated with the presence or absence of appropriate models in different geographical regions are most readily understood (reviews in Turner, 1977; Sbordoni *et al.*, 1979). A particularly interesting example involving a morph-ratio cline occurs in *Bombus melanopygus* (Owen & Plowright, 1980). Moving south on the west coast of America along a transect of about 600 km the dominant allele for red abdominal colour is progressively replaced to fixation by the black allele. Owen and Plowright convincingly suggest that the cline is a response to spatial changes in the distribution of *Bombus* comimics. Examples of apparently stable sympatric polymorphisms extending over wide geographical regions are less common. The African *Danaus chrysippus–Acraea encedon* and *encedana* complex of warningly coloured butterflies is comparatively well studied (e.g. Owen, 1971; Gordon, 1984a) but not fully understood. In some geographical regions there is no rank correlation in the abundance of the four parallel forms in these species. It has been suggested or shown that the polymorphism in *D. chrysippus* (and therefore in *A. encedon*) is influenced by variation in cardiac glycoside storage (Rothschild, Reichstein & Euw, 1973; Rothschild *et al.*, 1975; Brower, Gibson, Moffitt & Panchen, 1978), Batesian load (see for example Brower *et al.*, 1978), sexual selection (e.g. Smith, 1984), racial hybridization (Gordon, 1984b) and differential parasitism (Gibson, 1984), each of which may show spatial and temporal variation. Populations of *Heliconius doris* and *H. eanes* commonly have forms in different mimicry rings (Turner, 1971; Papageorgis, 1975). Papageorgis suggests that these species may have become polymorphic because their vertical flying ranges in the S American rainforest encompass the narrower, overlapping ones characteristic of those mimicry rings within which they have representative forms. However, she does not examine whether polymorphism based on such habitat heterogeneity can be stable. She speculates that there could be an associated behavioural polymorphism. *Heliconius numata* exhibits less striking polymorphism involving subrings within its 'tiger pattern' mimicry ring. Its polymorphism has been accounted for through variation in the abundance and species composition of its comimics which occur in localized concentrations throughout its range (Brown & Benson, 1974). A polymorphism in *Bombus* *rufocincus* is phenotypically similar to that of *B. melanopygus* but genetically more complex. It is apparently maintained within certain regions of N America by the earlier emergence from hibernation of the 'models' of each form (Plowright & Owen, 1980). The earlier emergence serves to reinforce predators against the warning patterns of each form. Plowright and Owen show mathematically that such a system based on temporal separation, which they call 'serial mimicry', can produce stable polymorphism.

In coccinellids temporal separation or heterogeneity in the abundance of comimics seems unlikely to account for colour polymorphism because of the generally long expectation of life of the beetles. However, some species, particularly of the red/black ring in Europe, are characterized by irregular invasions or large scale migrations (discussion in Hodek, 1973). Seasonal differences in their availability to predators may also occur, particularly during the period of hibernation when certain species are found in exposed hibernacula (see below).

Spatial changes in the relative abundance of the groups of comimics of the non-melanic and melanic morph classes of *Adalia* could lead to geographical variation in melanism involving morph-ratio clines. They seem unlikely, however, to be able to account for strongly localized areas of extreme morph frequency, such as that found within a few kilometres of a smokeless fuel plant in S Wales (Creed, 1974). Hypotheses involving spatial variation in comimics lead to the important prediction that sympatric polymorphic species exhibiting similar sets of phenotypes will show parallels in their geographical variation. The correspondence between this prediction and the geographical variation of *A. bipunctata* and *A. decempunctata* in The Netherlands is examined below.

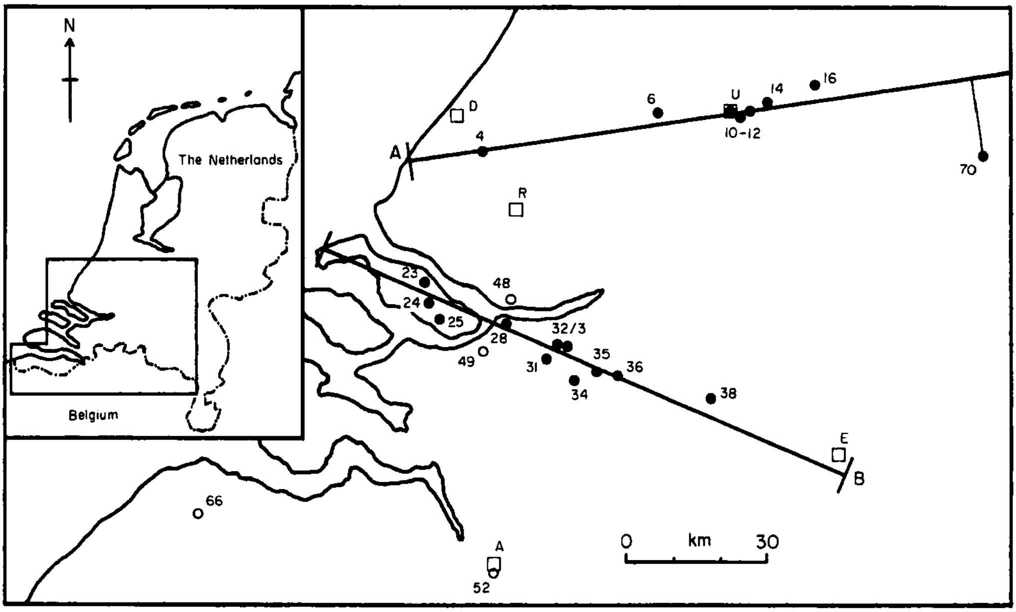

Figure 2. Map of the sampling sites for *Adalia decempunctata* and *Cantharis livida*. Site numbers are indicated. The central axes of transects A and B are shown. Open circles indicate non-transect sites. Some major cities are shown by squares: A, Antwerp; D, Den Haag; E, Eindhoven; R, Rotterdam; U, Utrecht.

METHODS

The distribution of sites in south and central Netherlands where samples of *A. decempunctata* and *C. livida* were obtained is shown in Fig. 2 (with the addition of Antwerp in N Belgium). Most sites were along two transects running approximately eastwards from the coast. The many additional sites throughout The Netherlands and N Belgium at which *A. bipunctata* were collected are shown in Brakefield (1984a: fig. 1).

Basic population biology was examined by sequential sampling of adults and of prepupae and pupae at a number of the study sites, usually in several different habitats. Tests showed that sampling of pupae of *A. bipunctata* was random with respect to morph class (Brakefield, 1984a). Some samples of *A. bipunctata* and *C. livida* from shrub habitats where a high sampling intensity was possible represented counts rather than collections.

The samples of adults were scored for the individual morphs described above. Adult *Adalia* emerging from pupae in the laboratory were scored following complete development of elytral phenotype.

RESULTS

Population biology

Adalia *species*

The life cycles of *A. bipunctata* and *A. decempunctata* in The Netherlands are broadly similar. The periods of summer reproduction and winter hibernation in *A. bipunctata* are described in detail by Brakefield (1984a, 1985). At some sites in some years the main annual reproductive cycle from late April until mid-summer is followed by a partial second generation in late summer or early autumn. *Adalia decempunctata* is less abundant than *A. bipunctata* with a somewhat more restricted distribution. Recruitment of new adults in *A. decempunctata* tends to be later than in *A. bipunctata*. There is also little evidence of any second generation, although three mating pairs collected between mid-July and mid-August included some recently eclosed beetles in which the colour pattern was not fully developed.

Following hibernation, adult *A. bipunctata* are found on low growing shrubs. They disperse to trees, especially limes, *Tilia* spp., from mid- or late May onwards (Brakefield, 1984a, b). The later recruitment of *A. decempunctata* is associated with a lack of substantial early breeding on shrubs (Table 1). The principal spring mating habitats for *A. bipunctata* are on shrubs (Brakefield, 1984a) whilst 80% of all mating *A. decempunctata* ($N = 30$) were found on trees. There was virtually no pre-adult development of *A. decempunctata* on shrubs, almost all pupae being collected on *Tilia* trees (Table 1). Other species of tree, especially oak, *Quercus* spp. (see Betts, 1955), may be more important in other regions of Europe.

Melanic *A. bipunctata* in post-hibernation populations in The Netherlands tend to mate, oviposit and die earlier than non-melanics (Brakefield, 1984b). This leads to an earlier emergence from pupae. It is argued that this earlier reproduction of melanics is a consequence of thermal melanism (Brakefield, 1984b; Brakefield & Willmer, 1985). Nine sequences of samples of pupae of *A. decempunctata* covering the whole period of pupation on *Tilia* trees were

Table 1. Proportions in per cent of adults and pupae of *Adalia bipunctata* and *A. decempunctata* and of adult *Cantharis livida* found in The Netherlands and N Belgium on the plants indicated during the periods of adult activity from 1979 to 1982* (dashes indicate no beetles)

		Trees		Shrubs				Herbs	
	Stage	*Tilia* spp.	Others	*Rosa rugosa*	*Sambucus nigra*	*Crataegus* spp.	Others	*Urtica dioica*	Total *N*
A. bipunctata	Adults	23.3	7.3	52.0	2.5	10.8	3.3	0.6	62 768
	Pupae	54.4	11.9	24.1	7.3	1.0	0.6	0.6	33 513
A. decempunctata	Adults	72.8	7.9	13.2	2.7	3.1	0.3	—	668
	Pupae	98.4	1.5	0.1	—	—	—	—	1421
C. livida	Adults	3.2	—	66.9	29.7	—	—	0.2	1107

* 1978 excluded because only *Tilia* trees were searched except at site 23.

collected. In no case was there clearly more than one peak in numbers, although at site 34 a late sample of 18 was collected on 30 August 1981 on birch trees, *Betula* spp. In 1981 maximum numbers of pupae occurred at sites 10, 11 and 12 during June and at site 34 in July while in 1980 the peak occurred in September at sites 10, 12, 33 and 52 (but in June at site 34). This difference in timing at most sites corresponded to that on *Tilia* in *A. bipunctata* and is attributable to the population biology of the lime aphid *Eucallipterus tiliae* (L.) on which the coccinellids feed (Brakefield, 1984a). Cumulative plots of the emergence of the three morphs of *A. decempunctata* against time were closely similar for each data set. There were no cases of a significant relationship between the percentage frequency of total melanics and time in days. For example, the most complete data set, that for site 10 in 1981, yields a regression coefficient of -0.511 (using arcsin transformation: $F = 2.81$, $\mathrm{df} = 1$ and 7, $P > 0.1$). Heterogeneity χ^2 tests for the samples from each of the nine sites give non-significant values ($P > 0.1$). The three largest individual samples obtained at 5-day intervals at site 12 in June 1981 were similarly homogeneous ($\chi^2 = 5.38$, $\mathrm{df} = 4$, $P > 0.1$) with overall melanic frequencies in sequence of 58.3% ($N = 144$), 63.5% ($N = 96$) and 61.5% ($N = 78$). These analyses therefore suggest that there are no differences in timing of reproductive activity in *A. decempunctata* comparable to those detected in *A. bipunctata*.

Cantharis livida

The general biology of this species and of some other European Cantharids is described by Janssen (1963) (see also Fiori, 1948; Fitton, 1975). In contrast to coccinellids they have a long larval period of 10–11 months and a short adult life of up to a few weeks. Both larvae and adults are active predators of small insects, especially aphids. Adults may also take other foods such as nectar, honeydew and fruit material. Emergence of adult *C. livida* in The Netherlands begins in late May with peak numbers reached in early to mid-June. Numbers then decline rapidly with only odd beetles being found in July. Their distribution suggests that adult movement is rather limited (cf. Brown & Brown, 1984). The majority were collected on shrubs (Table 1) with locally high densities occurring only on several small patches of *Rosa rugosa* (Thunb.) at Zevenbergen W. (site 32) and an area of *Sambucus nigra* (L.) at Willemstad (28). A few other sites with *R. rugosa* supported somewhat lower densities (e.g. 24 and 38). The highest densities all occurred in habitats where there were also very high densities of adults and pupae of *A. bipunctata*, most of the adults being recently emerged. *Cantharis livida* is a much more local species in The Netherlands than the species of *Adalia*.

Spatial and temporal variability

Adalia *species*

Adalia bipunctata exhibits marked geographical variation in The Netherlands (Brakefield, 1984a). The northwest of the country is characterized by low frequencies of melanics (< 15%). In contrast, populations in the southeast have higher than 50% of melanics. Steep clines occur over part of the transition zone between these regions. They are typified by the samples from transect B along which there is an increase over some 20 km from about 10% to 50–55%

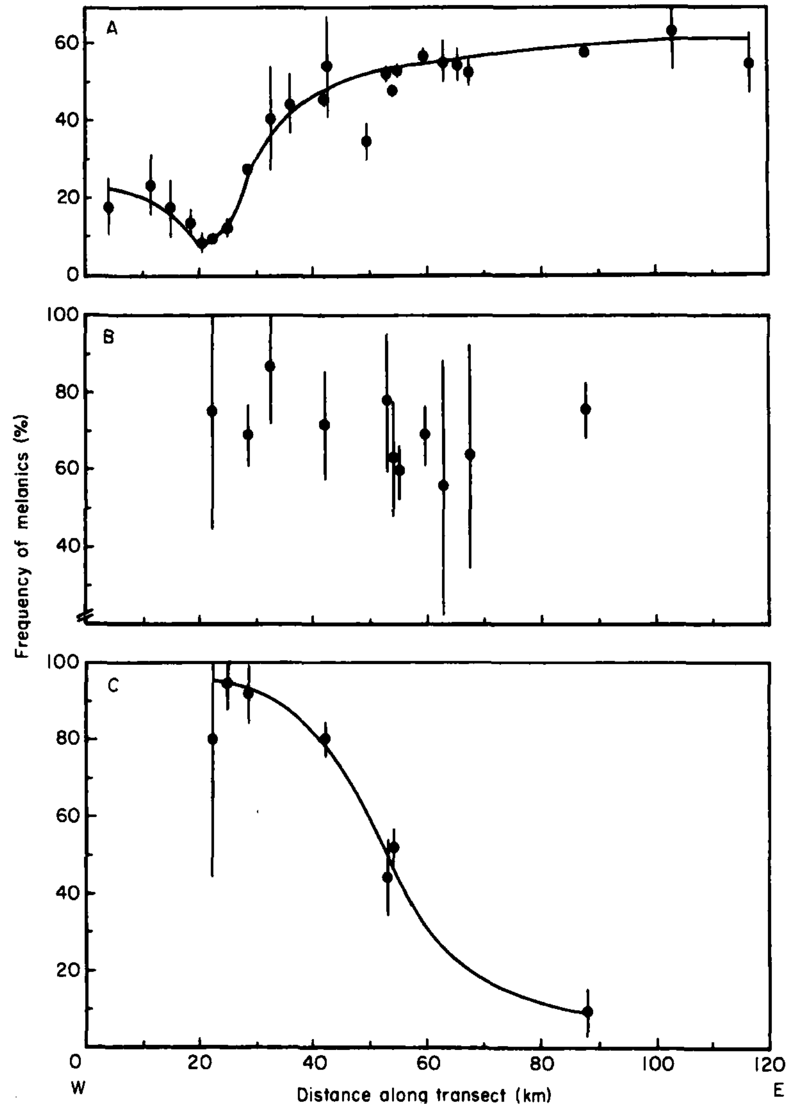

Figure 3. Frequency of the combined melanic forms of: A, *Adalia bipunctata* (from Brakefield, 1984a); B, *A. decempunctata*; and C, *Cantharis livida* along transect B. Vertical ranges show 95% confidence limits and the curves in A and C are fitted by eye.

melanics (Fig. 3A). Transect A is characterized by a much shallower cline (Table 2). It cuts diagonally into the northern edge of the transition zone (see Brakefield, 1984a: fig. 7). The melanic morphs of *A. bipunctata* show parallel clines although those for *quadrimaculata* are probably slightly steeper than for *sexpustulata* (Brakefield, 1984a).

In striking contrast to *A. bipunctata*, *A. decempunctata* shows a general uniformity of morph frequency in the study area. Analysis of the frequency data given in Table 3 shows no significant heterogeneity between sites (minimum $N = 10$, $\chi^2 = 41.34$, df $= 32$; minimum $N = 40$, $\chi^2 = 24.23$, df $= 18$, with $P > 0.1$ for each value). There is also no heterogeneity in the frequency of the

Table 2. Frequency of the melanic forms in the combined samples of *Adalia bipunctata*, *A. decempunctata* and *Cantharis livida* from sites along transect A divided into four sections

		A. bipunctata		*A. decempunctata*		*C. livida*	
Section	Sites	Sample size	% melanic	Sample size	% melanic	Sample size	% melanic
Coast	1–5	4242	3.04	5	(60.00)	7	(0.00)
Utrecht & E	6–10	14614	17.91	573	65.79	10	(0.00)
W of Utrecht	11–17	15808	23.63	787	65.44	27	7.41
Inland	67–70	863	28.16	1	—	24	8.33

two melanic morphs (minimum $N = 10$, $\chi^2 = 16.22$, df $= 14$). The mean frequency of the morphs (with range) for the sites with larger sample sizes are 31.8% (24.0–40.4%) for *typica*, 39.6% (27.9–44.6%) for *decempustulata* and 28.5% (20.2–38.1%) for *bimaculata*. This uniformity is also evident in the central area of transect A (Table 2; $\chi^2 = 2.42$, df $= 8$, $P > 0.1$) and along transect B (Fig. 3B). The only site which exhibits some divergence is Oostburg in the extreme southwest of The Netherlands about 60 km west of Antwerp (see Fig. 2). The single sample of 25 pupae shows a particularly high frequency of

Table 3. Numbers of the non-melanic (*typica*) and melanic forms of *Adalia decempunctata* and *Cantharis livida* collected at sites in The Netherlands and N Belgium in 1978–1982 (minimum = 5 of one species)

Site		*Adalia decempunctata*			*Cantharis livida*	
Name	No.	*typica*	*decempustulata*	*bimaculata*	*typica*	*rufipes*
Delft	4	0	1	1	7	0
Woerden	6	0	0	1	10	0
Utrecht C.	10	195	239	135	—	—
Utrecht E.	11	39	54	28	—	—
De Uithof	12	219	249	154	25	0
Zeist	14	9	14	5	—	—
Amersfoort	16	4	5	4	—	—
Middelharnis	23	2	4	2	1	4
Nieuwe-Tonge	24	2	0	1	2	36
Oude-Tonge	25	42	53	40	4	45
Achthuizen	26	3	11	6	0	2
Willemstad	28	12	14	16	64	257
Oudenbosch	31	5	7	10	56	44
Zevenbergen W.	32	16	12	15	208	224
Zevenbergen E.	33	78	76	39	—	—
Etten Leur	34	43	60	36	—	—
Prinsenbeek	35	4	1	4	—	—
Breda C.	37	4	3	4	—	—
Tilburg	38	33	60	42	78	8
Numansdorp	48	4	7	3	—	—
Dinteloord	49	3	2	3	—	—
Antwerp	52	12	21	17	—	—
Oostburg	66	14	5	6	—	—
Arnhem	70	—	—	—	18	2

non-melanics. The frequency distribution is different from that of Antwerp ($\chi^2 = 7.79$, df = 2, $P < 0.05$) and from all sites further north along transect B ($\chi^2 = 6.67$, df = 2, $P < 0.05$). There is little evidence of frequency changes between years since at only one of six sites is there significant heterogeneity between the pooled annual samples. Furthermore, at this one site, when the single small sample is excluded the remaining two are highly homogeneous.

When variation at individual sites is considered there are no differences between the combined samples of *A. decempunctata* collected on different plants. Furthermore, the pooled samples for all sites show no heterogeneity over the five main plant groupings (see Table 1; $\chi^2 = 11.12$, df = 8, $P > 0.1$) or between all trees and all shrubs ($\chi^2 = 3.37$, df = 2, $P > 0.1$). A similar analysis which considers differences between the pooled samples of adults and of pupae indicates a deficiency of *bimaculata* melanics in pupae at each of six sites (with $P < 0.05$ for values of χ^2 for two sites). The overall morph frequencies for all sites were 28.2, 38.9 and 32.9% in adults and 36.1, 41.2 and 22.7% in pupae for *typica*, *decempustulata* and *bimaculata*, respectively (with $\chi^2 = 28.48$, $P < 0.001$). Since most adults were collected in post-hibernation populations these figures suggest that *bimaculata* are selected against over the reproductive period whilst *typica* are favoured. There is no information about how such selection might operate. The 30 beetles collected *in copula* give no indication of any marked departure from random mating. An alternative explanation is that some behavioural difference results in non-random sampling of adults.

Cantharis livida

The frequency data for each site are given in Table 2. Melanics are at a low frequency along transect A (Table 3) where no populations at a high density were found. There is a steep cline along transect B which is in the opposite direction to that in *A. bipunctata* (Fig. 3C & A). Melanic frequencies of over 80% within 20–40 km of the coast drop sharply to below 10% 90 km inland. No samples were obtained south of transect B (or north of transect A). Therefore the extent of the region of high melanic frequency is unclear. It may be restricted to a relatively small area in the delta region of southwest Netherlands. The more numerous data for Zevenbergen W. and Willemstad collected in 1980 and 1981 show no changes in melanic frequency within seasons or between years ($P > 0.1$ in each case).

Table 4. The frequency of mating pairs (male/female) between the *typica* (*t*) and *rufipes* (*r*) morphs of *Cantharis livida* for the combined samples from the sites indicated. The morph frequencies in mating and non-mating insects are compared by χ^2 using Yates correction for continuity and the selective advantage gained by *rufipes* (*typica* = 1) is indicated

	Pairings				Total mating		Non-mating			
Site	*t/t*	*t/r*	*r/t*	*r/r*	*t*	*r*	*t*	*r*	χ^2	Selective advantage
Zevenbergen W.	2	2	3	9	9	23	199	201	4.72*	2.37
Willemstad	0	1	0	7	1	15	63	242	1.18	3.74

*$P < 0.05$

The samples from Zevenbergen W. and Willemstad included sufficient numbers of beetles found *in copula* for a preliminary statistical analysis (Table 4). The data for Zevenbergen W. indicate that among mating insects pairing is random and non-assortative (e.g. comparison of all like × like against all unlike pairings gives $\chi^2 = 0.56$, $P > 0.1$). An examination of mating and non-mating insects suggests that a mating advantage is gained by melanics at each site. The excess of melanics in mating insects is significant at Zevenbergen W. (Table 4). Ten of the 16 pairs from this site were collected on 2 June 1980. This individual sample also shows a significant departure from random mating ($\chi^2 = 4.48$ with Yates correction, $P < 0.05$). Furthermore, application of Cochran's method (see Everitt, 1977) to detect systematic differences in the proportion of melanics in the mating and non-mating insects at the two sites indicates that overall there is a non-random pattern ($\Upsilon = 2.53$, $P < 0.02$). Thus the mating data although few in number indicate that the polymorphism in *C. livida* may be strongly influenced by non-random mating.

DISCUSSION

Müllerian mimicry cannot account for the difference in the geographical variation of *A. bipunctata* and *A. decempunctata* in The Netherlands. It seems that *A. bipunctata* is responding to some environmental factor whilst *A. decempunctata* is not. The theory of thermal melanism proposed that melanics are favoured in conditions of low sunshine because of a more efficient absorption of solar radiation (Lusis, 1961). The theory is supported for *A. bipunctata* (see Fig. 1) by laboratory measurements (Muggleton, Lonsdale & Benham, 1975; Brakefield & Willmer, 1985) and evidence of field differences in The Netherlands in the timing and intensity of adult reproductive activity (Brakefield, 1984b, c). The clines described in Fig. 3 and Table 2 bisect isobars for hours of sunshine (Brakefield, 1984a) and a negative correlation is also found between melanic frequency and sunshine in Britain (Muggleton *et al.*, 1975). The influence in the spring of thermal melanism on reproductive activity in a population is apparently independent of the frequency of melanics. However, heterogeneity between populations in The Netherlands is evident when comparisons are made of the melanic frequency in different annual generations (Brakefield, 1984b, c, 1985), suggesting that spatial variation in the longer-term effects of thermal melanism occurs. This may be due to the likelihood of a second summer generation or the synchronization with aphid prey cycles, or to thermal effects in other seasons (Brakefield, 1984b; Brakefield & Willmer, 1985). The comparison of the basic population biology of the species of *Adalia* in The Netherlands shows that *A. decempunctata* is much more restricted to trees. In particular, there is no post-hibernation reproductive phase of the life cycle on low-growing shrubs as occurs in *A. bipunctata*. In the shrub habitats beetles are regularly exposed to direct sunshine whereas most of them on trees, especially *Tilia*, are found in shade either beneath leaves or within the canopy. These observations support the hypothesis that due to differences in exposure to sunshine, thermal melanism has a substantially more marked influence on *A. bipunctata* than on *A. decempunctata*. Consequently, only *A. bipunctata* in The Netherlands exhibits a response in melanic frequency to spatial changes in sunshine levels. A similar difference may also occur in Britain where there is substantially more marked geographical variation in *A. bipunctata* (Creed, 1966, 1971a) than in *A. decempunctata.* Data for the latter species from 16 British localities show a rather uniform morph frequency with mean values (plus range) of 53.1% (39–69%) for *typica*, 33.5% (19–48%) for *decempustulata* and 13.4% (6–21%) for *bimaculata* (data of E. R. Creed; D. R. Lees pers. comm. and see Lees, Creed & Duckett, 1973). When compared to The Netherlands these data suggest a generally lower frequency of melanics, especially of the dark *bimaculata*, in Britain.

Shiny, 'black' coccinellids generally have some patches of a bright colour and a higher reflectance (see Brakefield & Willmer, 1985). When forms in which the dorsal surface is completely black occur in polymorphic species they are rare (e.g. Houston & Hales, 1980). If thermal melanism is the overriding selective factor favouring melanism in *A. bipunctata* (and probably some other coccinellids) then completely black cuticles would be expected. Thus the presence of contrasting colour marks suggests that when thermal melanism is operative, there is a compromise with selection promoting warning coloration and mimicry. Similar compromises have been suggested for species of *Heliconius, Bombus* and *Eristalis* (Turner, 1977; Stiles, 1979; Heal, 1982).

Creed's (1966, 1971a) surveys of *A. bipunctata* in Britain showed a general association of industrial regions with high frequencies of melanics. Creed suggested that melanics were more tolerant physiologically to a component of air pollution (see Fig. 1). Further support for the theory of industrial melanism comes from a multiple regression analysis with environmental variables (Lees *et al.*, 1973), a decrease in melanic frequency with declining smoke levels in Birmingham (Creed, 1971b) and findings of high melanic frequency in certain large cities such as Leningrad (Zakharov & Sergievsky, 1983, and references therein). Muggleton *et al.* (1975) have argued that the influence of particulate air pollution on sunshine level suggests that thermal melanism may be an alternative explanation of the observed relationships. A comparison of geographical variation in *Adalia* in The Netherlands in the early 1980s and the distribution of epiphyte growth as recorded in the early 1970s (de Wit, 1983) gives no indication of industrial melanism. For example the large industrial regions without epiphytes around Rotterdam, Amsterdam and Utrecht show very low or intermediate ($\approx 20\%$) frequencies of melanic *A. bipunctata.* The correlations with more recent (October 1976 to October 1980) data for mean annual concentration of sulphur dioxide are not significant: *A. bipunctata*, $r = 0.21$, 41 sites; *A. decempunctata*, $r = 0.48$, 12 sites and *C. livida*, $r = -0.21$, 8 sites (using arcsin transformed percentage melanics and square roots of concentrations for nearby localities; $P > 0.1$ in each case).

Geographical variation in *C. livida* in The Netherlands contrasts with that of both species of *Adalia.* A steep cline occurs on the main transect in the opposite direction to *A. bipunctata* (Fig. 3). The basis of this cline is unknown although most climatic factors show isobars running north–south across the transect (see Brakefield, 1984a). The polymorphism in *C. livida* does not appear to involve spatial variation in thermal melanism. Preliminary data suggest that a general mating advantage to melanics could be a consequence of the thermal advantage of melanics, although the flight period of the insect occurs in June when symptoms of heat stress might be expected in melanics (Brakefield & Willmer, 1985). Adult *C. livida* often occur in the same shrub habitats as *A. bipunctata* but are not found there until after the time when thermal melanism effects on reproduction of the coccinellid have been detected (Brakefield, 1984c). There are other substantial differences in population biology including a much shorter expectation of adult life.

I have argued that within a community of coccinellids the colour patterns of aposematic species which have a chemical defence will be found to conform to a system of multiple Müllerian mimicry rings. Examples are given for the fauna of The Netherlands. My reasoning is based on the biology of coccinellids, the visual similarity between species which in some cases probably reflects convergent evolution and the existence of a number of more or less discrete modal colour patterns. However, experimental proof of the operation of Müllerian mimicry is lacking.

The cantharid beetles of N Europe and probably elsewhere tend to fall into two mimetic assemblages of unpalatable species which are either predominantly orange or black. These assemblages are also likely to involve other coleoptera including the Lycidae. Species such as *C. livida* have forms representative of the colour patterns of each ring. There is no evidence, however, that mimetic relationships influence the local differentiation found in *C. livida* in The Netherlands. Polymorphic populations of this species are widespread. They are found throughout central Europe, northern and central Italy, Hungary and Transylvania with both the melanic and non-melanic forms being generally abundant (W. Wittmer, pers. comm.). Melanics may be less abundant in Britain (Fowler, 1890; R. C. Welsh, pers. comm.).

The prediction that sympatric polymorphic species exhibiting similar sets of phenotypes will show parallels in their geographical variation because of mimetic selection for convergence is not supported for *A. decempunctata* and *A. bipunctata* in The Netherlands. This contrast in their geographical variation is on a very local scale relative to their ranges. The picture may be different when some large geographical regions are considered. Thus Dobzhansky (1924) reports a significant increase in the frequency of several morphs of *A. bipunctata* in central Asia where similar morphs of *A. decempuncta*, which are probably homologous, are frequent. When other polymorphic coccinellids are surveyed on a broad geographical scale, many examples of parallel trends in pairs or groups of species in the occurrence of predominant morphs are apparent (Dobzhansky, 1933). This parallel trend is evident in the area covered by melanic pigment on the dorsal surface and, in many cases, the precise positioning of the black marks. Some examples are repeated in the Old and the New Worlds. Selection related to Müllerian mimicry provides a coherent explanation for the often striking resemblance between the characteristic morphs of different species within particular regions. Dobzhansky (1933) noted the tendency for the centres of light and dark pigmentation to lie in arid and humid regions, respectively (see also reviews by Komai, 1956; A. Honek in Hodek, 1973). The trends in polymorphic species may thus be based on some causal relationship between melanization and humidity (which has no proposed mechanism) or between it and an interrelated climatic factor such as insolation (i.e. thermal melanism). They may also be heightened by mimetic selection related to the species composition, abundance and colour patterns of relatively invariable or monomorphic coccinellids along the gradient. The abundance of such species or potential comimics is likely to change in response to the same climatic factor either through direct effects or, indirectly, through related ecological change. Such a system bears a resemblance to the explanation put forward by Owen & Plowright (1980) for the morph-ratio cline in *Bombus melanopygus* (see above) and more generally to cases of allopatric polymorphism and differentiation associated with presence or absence of appropriate models (reviews in Turner, 1977; Sbordoni *et al.*, 1979).

In conclusion, I believe that hypotheses about Müllerian mimicry and variability in colour pattern in coccinellids are best considered in relation to different scales of distribution. Aposematic species may be monomorphic within a particular mimicry ring throughout their range or polymorphic either between different rings or subrings of a particular one. Different mimicry rings or possibly subrings may predominate in different, broad geographical regions. The ultimate selective factors influencing this differentiation and the relative fitness of the modal colour patterns are likely to be climatic in nature. Selection probably involves interactions between climate and ecology and the effectiveness of aposematism and mimetic resemblance. On a more local scale, such as within The Netherlands, some species because of their particular population biology may respond to certain environmental factors and 'escape' selection promoting convergence of mimetic patterns. This type of response will generate clines in some species but not in others, as is evident for the *Adalia* species in The Netherlands. Such 'escape' is made more likely if the morph(s) concerned resembles the pattern of another ring (as in *A. bipunctata*, see Fig. 1), rather than being unique, since it will continue to derive some mimetic protection.

Edmunds (1969), Thompson (1973, 1974) and Greenwood, Wood & Batchelor (1981) have suggested that some polymorphisms for warning coloration involve a balance between aposematic and apostatic selection. Thompson (1984) shows theoretically how such an interaction between frequency-dependent selection processes can maintain polymorphism. His models apply specifically to single-locus two-allele systems but as he points out such an interaction provides an attractive hypothesis to account for the multiple allelic systems found in coccinellids. Although any Müllerian mimicry will tend to reinforce aposematic selection, this hypothesis is made more tenable because the chemical defence of aposematic coccinellids is not completely effective. This is apparent in the variable response made to them by different bird predators and in the probable seasonal changes in the level of predation by some birds (references above). Overall, coccinellids are probably of moderate unpalatability in comparison to many highly protected species of insects. Aposematic selection by some predators will tend to favour the most abundant or 'apparent' modal colour pattern whilst apostatic selection by others will favour the rarer ones. In Europe, and perhaps most regions, aposematic selection will then favour the red/black morphs of *Adalia* (cf. Muggleton, 1978; see Fig. 1). It is possible that this does not occur in all local habitats, for example in or near extensive conifer plantations where black/red species may be abundant. Temporal heterogeneity may also sometimes occur, for example the black/red species of *Exochomus* and *Chilocorus* in The Netherlands can be abundant in exposed hibernacula on smooth bark of trees such as ash and beech whereas those of most red/black species are more or less hidden (Brakefield, 1985, personal observations; de Gunst, 1978). Other forms of selection associated with thermal melanism may provide alternatives to apostatic selection in

A. bipunctata (Brakefield, 1984b; Brakefield & Willmer, 1985; and see Fig. 1). Frequency-dependent sexual selection can account for the polymorphism in some areas (O'Donald & Majerus, 1984). In *A. bipunctata* in The Netherlands and probably elsewhere, frequency-independent selection arising from thermal melanism can provide the basis of spatial variation in equilibrium points. Forms of climatic selection probably operate similarly in some other species.

An alternative to a hypothesis based on heterogeneity in the reaction of predators is one in which differences in unpalatability between species of coccinellids are emphasized. The experiments of Pasteels *et al.* (1973) suggest that such differences exist and that they are related to the concentration and type of alkaloid bases. Over some wide geographical regions where particular, well-protected species are abundant and 'apparent', for example the ubiquitous and monomorphic *Coccinella septempunctata* in Europe (Pasteels *et al.*, 1973; see Fig. 1), those of more moderate palatability may be influenced by forms of selection more associated with Batesian than Müllerian mimicry. The latter species may include *Adalia* as suggested by the feeding experiments of Pasteels *et al.* Sbordoni *et al.* (1979) show that the yellow form of the burnet moth *Zygaena ephialtes* in S Europe may be an example of this type of system based on a much more abundant model (which also emerges earlier). Some species of coccinellids may have responded to periods of prolonged disruptive selection acting in a frequency-dependent way to promote polymorphic mimicry associated with different modal colour patterns and intermediate in nature between classical Batesian and Müllerian mimicry. The likely occurrence of very tightly linked loci, forming a 'supergene', controlling at least some of the striking visible polymorphisms in coccinellids (Komai, 1956; and Houston & Hales, 1980; Sasaji, 1981) is consistent with such an explanation and would parallel their evolution in well-studied Batesian mimics such as species of *Papilio* butterflies. The evolution of supergenes is not expected or found in Müllerian mimics (for a discussion see Turner, 1984). One of the two major gene loci controlling the northern and southern colour patterns of *Z. ephialtes* may be a supergene and, furthermore, modifier genes probably exist which improve each of the mimetic patterns in their specific genetic background (see Sbordoni *et al.*, 1979; Turner, 1984). Further study of the nature of the major genes determining coccinellid polymorphisms is needed and crosses between allopatric stocks of particular species which exhibit different predominant forms would be of interest to investigate the effect of genetic background on pattern expression. This paper will have served some purpose if future work obtains data which can be used to test some of the hypotheses about mimicry in coccinellids.

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