



**Universiteit
Leiden**
The Netherlands

Case studies in evolution

Brakefield, P.M.; Shreeve, T.

Citation

Brakefield, P. M., & Shreeve, T. (1992). Case studies in evolution. In . Retrieved from <https://hdl.handle.net/1887/11027>

Version: Not Applicable (or Unknown)

License: [Leiden University Non-exclusive license](#)

Downloaded from: <https://hdl.handle.net/1887/11027>

Note: To cite this publication please use the final published version (if applicable).

The Ecology of Butterflies in Britain

Edited by
Roger L. H. Dennis

Figures prepared by
Derek A. A. Whiteley

Oxford New York Tokyo
OXFORD UNIVERSITY PRESS

1992

Contents

List of contributors

xiii

1 Islands, regions, ranges, and gradients

1

Roger L. H. Dennis

1.1 Butterflies on British islands

1

1.2 Butterfly distributions on the British mainland

9

1.3 Focusing on regional and local issues

17

2 Adult behaviour

22

Tim G. Shreeve

2.1 The significance of behaviour patterns

22

2.2 Regulating body temperature

22

2.3 Finding nutrients

30

2.4 Mate-locating behaviour

34

2.5 Communication and courtship

43

2.6 Behaviour and butterfly biology

45

3 Eggs and egg-laying

46

Keith Porter

3.1 Egg production

46

3.2 Finding and recognizing larval hostplants

58

3.3 Distribution of egg load

64

3.4 Patterns in egg-laying

67

4 Butterfly populations

73

Martin S. Warren

4.1 What is a population?

73

4.2 Measuring and monitoring butterfly populations

73

4.3 The structure of butterfly populations

74

4.4 Natural population fluctuations

81

4.5 Mortality factors affecting population size

88

5	Avoidance, concealment, and defence	93
	<i>Paul M. Brakefield and Tim G. Shreeve with Jeremy A. Thomas</i>	
5.1	Adult defences	93
5.2	The defences of eggs	103
5.3	The defences of larvae	106
5.4	Adaptations to living near ants	109
5.5	Pupal defences	115
5.6	Butterflies and multiple defence mechanisms	118
6	Monitoring butterfly movements	120
	<i>Tim G. Shreeve</i>	
6.1	The components of movement	120
6.2	Variability in butterfly movement	122
6.3	Local movements of butterfly adults	124
6.4	Migration and dispersal	133
6.5	Unresolved issues	138
7	Butterflies and communities	139
	<i>Keith Porter with Caroline A. Steel and Jeremy A. Thomas</i>	
7.1	Biological communities	139
7.2	Resource partitioning and the niche	140
7.3	Interactions between butterflies and other animals	147
7.4	Interactions between butterflies and plants	155
7.5	Diversity, ecological succession, and butterfly communities	171
8	Diversity within populations	178
	<i>Paul M. Brakefield and Tim G. Shreeve</i>	
8.1	Genetic variation, natural selection, and evolution	178
8.2	Polymorphism and wing pattern forms	179
8.3	The development of wing patterns	186
8.4	Enzyme polymorphism	188
8.5	Seasonal polyphenism	188
8.6	Life history variation	191
9	Case studies in evolution	197
	<i>Paul M. Brakefield and Tim G. Shreeve</i>	
9.1	The meadow brown: continuous variation and adaptation	197
9.2	The large heath: evolution of races	209
9.3	The speckled wood: geographic variation in Europe	213

10	An evolutionary history of British butterflies	217
	<i>Roger L. H. Dennis</i>	
10.1	Evolution before glaciers	217
10.2	Evolution with glaciation	221
10.3	The pattern of butterfly arrivals	227
10.4	Butterfly adaptations to Britain's Post Glacial environments	231
10.5	The evolution of subspecies, races, and character gradients	236
11	The conservation of British butterflies	246
	<i>Martin S. Warren</i>	
11.1	Changing butterfly populations	246
11.2	Causes of decline of British butterflies	250
11.3	Early attempts at conservation	257
11.4	The ecological approach to conservation	262
11.5	Strategies for conservation	265
11.6	Future prospects	274
Appendices		
Appendix 1	A check list of British butterflies and their hostplants	275
Appendix 2	Traditional classification of butterfly breeding biotopes in Britain	280
Appendix 3	(a), (b) Summaries of the Joint Committee for the Conservation of British Insects codes on collecting and insect introductions	284
Appendix 4	Useful addresses of societies, journals, specialist books; equipment, livestock, and scientific institutions	287
Glossary		289
Bibliography		300
Index		335

Case studies in evolution

Paul M. Brakefield and Tim G. Shreeve

Genetic variation is all important to evolutionary change. It forms the basis of adaptation to specific or novel environments and also of divergence between populations and speciation. This chapter uses work on three European satyrine butterflies to illustrate the processes involved in such divergence. Firstly, studies of local differences, and of progressive clinal changes between populations are described. These may reflect changes in adaptation to the environment. Secondly, examples of more extensive phenotypic and genetic divergence characteristic of disjunct races or subspecies are discussed. Such divergence may be the prelude to complete reproductive isolation. Once this stage has been reached and genes cannot be exchanged by hybridization between two groups of populations, they have become distinct species. The same processes involved in adaptation to novel environments or in local divergence between populations are also the ultimate basis of speciation events.

Reproductive isolation may involve differences at many genes resulting in the inviability of hybrids. It

may also be associated with more specific changes in the genes underlying the mating systems which lead to successful sexual contacts within a population. Broadly speaking such effects are thought of as involving postmating and premating isolating mechanisms, respectively. In practice most speciation events are likely to involve some combination of both. Unfortunately research on British butterflies has yet to contribute significantly to the understanding of premating isolating mechanisms. Some recent interpretations of the fossil record have described a pattern of comparatively short periods of rapid speciation and adaptive radiation of new lineages interspersed with periods of apparent stasis or relative stability (Eldridge 1987). This pattern of evolutionary change is known as 'punctuated equilibrium'. It is not, however, necessary to invoke any new processes to account for such a pattern. The work on the three species of satyrines has largely been concerned with phenotypic variation in wing pattern.

9.1 The meadow brown: continuous variation and adaptation

The meadow brown *Maniola jurtina* has long been recognized as a particularly variable butterfly comprising a wide range of different forms, races, and subspecies (Thomson 1973). It is a common species, forming more or less discrete populations in a wide variety of grassland habitats throughout Britain and most of continental Europe (Pollard 1981; Brakefield 1982a,b; Heath *et al.* 1984). Adult emergence in Britain ranges from about 100 to 2000 per hectare with an expectation of life of some five to twelve days. The butterfly is rather sedentary in areas of favourable habitat with individuals, on average,

ranging over about one hectare during their lifetime. A wide range of nectar sources are used by adults and larvae feed on a variety of grasses.

In early work on the Isles of Scilly, Dowdeswell *et al.* (1949) noted that the number of small black spots near the margins of the ventral surface of each hindwing of *Maniola jurtina* varies from 0 to 5, rarely six (Fig. 9.1). They chose to use this variation as an index of the fine adjustment and adaptation of populations. Although care is needed in scoring the presence of these small spots (Brakefield and Dowdeswell 1985), hindwing spot-number provides

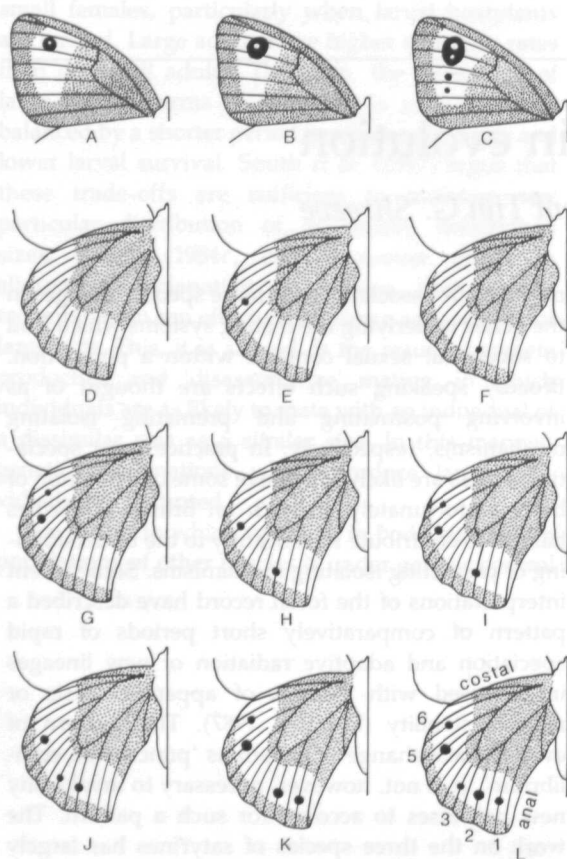


Fig. 9.1 Diagram of variation in the spot pattern on the wing ventral surface of the meadow brown *Maniola jurtina*. Top row shows variation in the forewing eyespot (unshaded area is of brighter fulvous coloration): A, small black eyespot with single white pupil (characteristic of males); B, large spot with single pupil (characteristic of females); C, a more extreme female phenotype showing a very large eyespot with two pupils (f. *bioculata*) and with two additional spots (f. *addenda*). D–L illustrate nine of the thirteen commonly occurring hindwing spot phenotypes: D, nought spot, (0); E, costal 1 (C1); F, anal 1 (A1); G, costal 2 (C2); H, splay 2 (S2); I, costal 3 (C3); J, median 3 (M3); K, splay 4 (S4); L, all 5. Not shown: A2, A3, C4 and A4. The reference numbers of the spots are indicated. Different sized hindwing spots present an idea of changes in relative (not absolute) spot size. (After Brakefield 1990a.)

a simple means of scoring their total area. The size of each individual spot is actually a threshold character in that when it is present it varies in a truly continuous manner; butterflies with no spots represent all individuals below the threshold at which spots are expressed phenotypically. Such quantitative characters are usually jointly determined by the interacting effects of a number of genes or polygenes, each of small effect. The same phenotype can be determined by different combinations of these polygenes. Differences between populations, and the results of processes of natural selection influencing quantitative characters, are usually recorded in terms of the population mean (or spot average) and variance. They cannot be represented in terms of gene frequency changes as is possible for Mendelian characters such as polymorphisms controlled by one or a small number of major genes (see chapter 8). Systems of polygenes which determine continuous variation in phenotypic characters are critical in evolution since they provide the basis for smooth adaptive change.

9.1.1 Field surveys

A large number of populations of *Maniola jurtina* in Europe have now been surveyed to compare the frequency distributions for hindwing spot-number which are referred to as spot frequencies (reviews by Ford 1975; Dowdeswell 1981; Brakefield 1984). Some examples of spot frequencies are shown in Fig. 9.2. Males tend to be more highly spotted than females so that the sexes must be analysed separately (Fig. 9.2a). The following discussion is based on some patterns of variation in the most intensively sampled regions of the species range. The significance of these patterns is discussed in relation to processes which are involved in generating and maintaining them.

The earliest survey work by Ford and his co-workers (Ford 1975) involved populations on the Isles of Scilly archipelago situated off the south-west coast of England (Fig. 9.2). Their study rose to prominence in the 1960s because of the controversy among evolutionary biologists over the relative contribution to geographical and population differentiation of natural selection and adaptation to particular environments on the one hand, and of random genetic drift on the other (discussed further

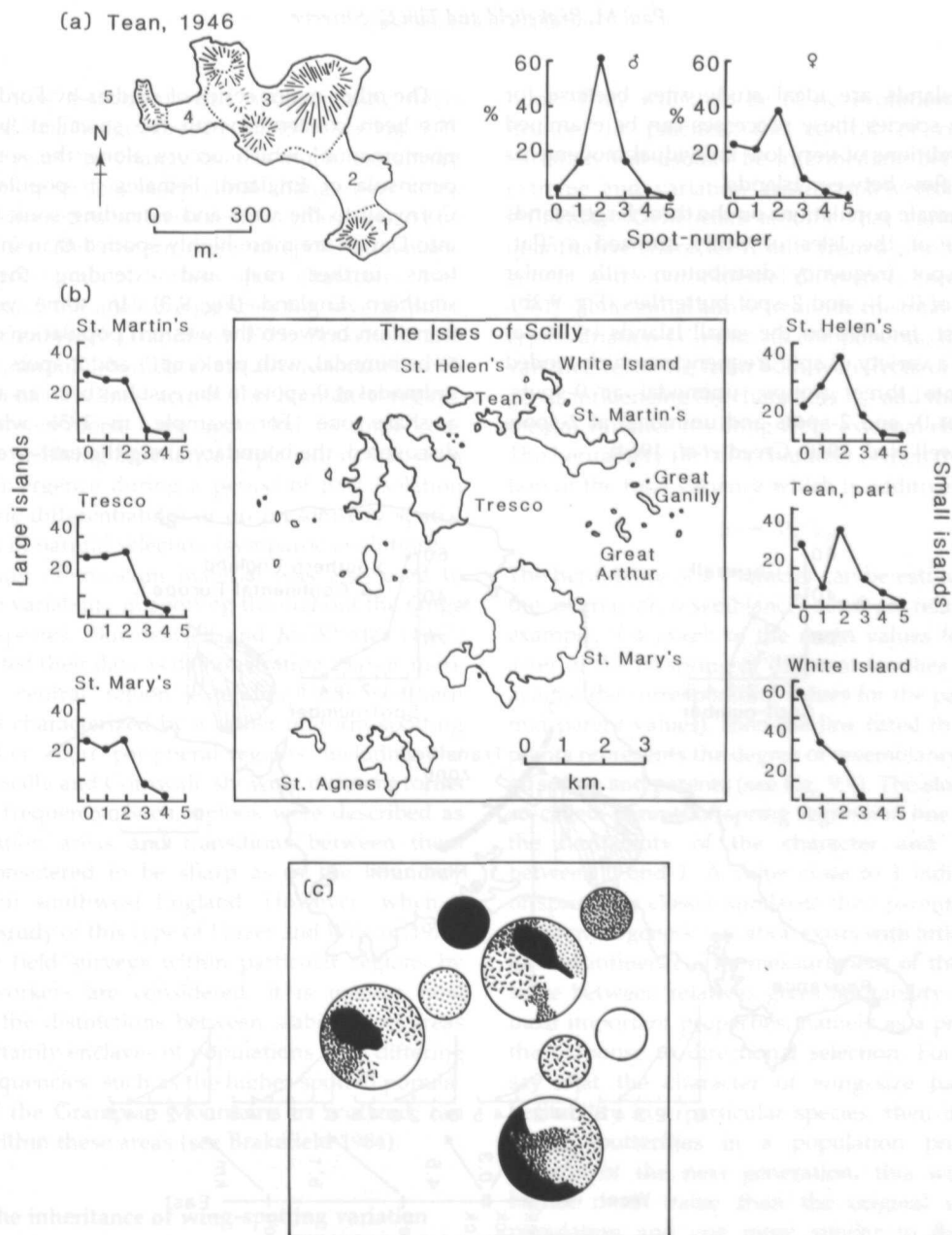


Fig. 9.2 Variation in the number of spots on the ventral surface of the hindwings of the meadow brown *Maniola jurtina* in the Isles of Scilly. (a) A summary of the frequency of males and females with different spot-numbers collected by Ford and his co-workers in their original study on Tean. Note the difference between the sexes. Their mark-release-recapture experiments showed that the population inhabiting areas 1, 3, and 5 of the island were largely isolated from one another by unfavourable habitat in areas 2 and 4. (Adapted from Ford 1975.) (b) Map of the Isles of Scilly showing the spot-frequency distributions for females found on three large islands and on three small islands. (Adapted from Ford 1975.) (c) Diagram of the hypothesis put forward by Ford to account for the dissimilarity among small island populations and the uniformity on large islands. The proposed occurrence of specialized environments on small islands and of mixed habitats on large ones is illustrated by different shadings. (After material in Ford 1975; Berry 1977; Dowdeswell 1981 and Shorrocks 1978.)

below). Islands are ideal study sites because for sedentary species these processes can be examined under conditions of very low individual movements and gene flow between islands.

Most female populations on the three large islands (> 275 ha) of the Isles of Scilly showed a 'flat-topped' spot frequency distribution with similar numbers of 0-, 1-, and 2-spot butterflies (Fig. 9.2b). In contrast, females on the small islands (< 16 ha) exhibited a variety of spot frequencies which tended to fall into three groups: unimodal at 0-spots, bimodal at 0- and 2-spots and unimodal at 2-spots (Dowdeswell *et al.* 1960; Creed *et al.* 1964).

The other major series of studies by Ford's group has been concerned with the so-called 'boundary phenomenon' which occurs along the south-west peninsula of England. Females in populations in Cornwall to the west and extending some distance into Devon are more highly spotted than in populations further east and extending throughout southern England (Fig. 9.3). In some years the transition between the western populations tending to be bimodal, with peaks at 0- and 2-spots, to those unimodal at 0-spots in the east has been an abrupt or a sharp one. For example, in 1956 when first discovered, the boundary along the east-west study

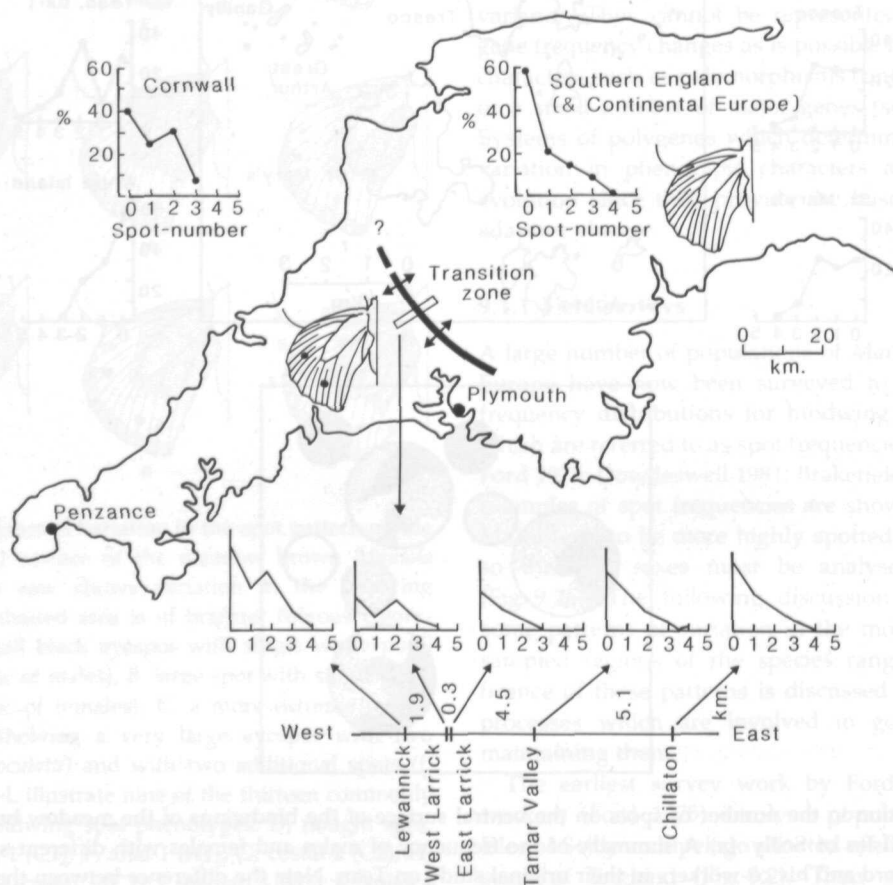


Fig. 9.3 The 'boundary phenomenon' for the hindwing spot-number in females of the meadow brown *Maniola jurtina* across the south-west peninsula of England. The forms of spot-frequency distributions found by Ford and his co-workers to be characteristic of populations in southern England and in Cornwall are illustrated. The zone of the transition between these forms occurred, in some years, along the line indicated. The results of surveying spot-number variation in populations in 1956 along a transect bisecting the transition zone are also shown (inset). (After material in Ford 1975; Berry 1977; and Parkin 1979.)

transect was associated with two adjoining fields separated by a hedge (Creed *et al.* 1959; see Fig. 9.3). In other years the change-over is much less abrupt with a more or less steep clinal change over some tens of kilometres between regions characterized by the western and eastern types of spot frequencies. Male spot-numbers, other spot characters (see below), and the allele frequencies for several polymorphic enzymes (Handford 1973; Brakefield and Macnair, unpublished data) are also associated with fluctuations or clines across the boundary region. These observations have again led to some controversy involving alternative explanations based on either divergence during a period of past isolation (allopatric differentiation) or on present-day spatial changes in natural selection (sympatric evolution).

A study of museum material was also used to examine variability in spotting throughout the range of the species. Dowdeswell and McWhirter (1967) interpreted their data as demonstrating a large, more or less central region extending into southern England characterized by a rather uniform spotting with other, more peripheral regions, including the Isles of Scilly and Cornwall, showing different forms of spot frequency. Such regions were described as stabilization areas and transitions between them were considered to be sharp as in the boundary region in southwest England. However, when a further study of this type of Frazer and Wilcox (1975) and the field surveys within particular regions by other workers are considered, it is unclear how precise the distinctions between stabilization areas are. Certainly enclaves of populations with differing spot frequencies, such as the higher spotted populations of the Grampian Mountains in Scotland, can occur within these areas (see Brakefield 1984).

9.1.2 The inheritance of wing-spotting variation

The evolutionary significance of such survey results can only be assessed with any confidence when the basis of the phenotypic variation in terms of genetic and environmental effects has been rigorously examined. To take an extreme situation, if differences in spot-number depend solely on the environment during development, as for example if temperature alone accounts for the amount of spot pigment synthesized, then the field data will merely reflect the developmental conditions within popula-

tions. They will then be of no evolutionary significance. In practice, the control of continuous variation will usually be intermediate between this extreme and variation arising solely from genetic influences. Geneticists assume that variation in a quantitative character results from a combination of genetic and environmental differences (see Falconer 1981). Their initial aim is to divide the total or phenotypic variation (V_p) into its components, the genetic variance resulting from additive effects of the polygenes influencing the character (V_A) and the environmental variance resulting from external effects (V_E). The heritability (h^2) of a character is then the proportion of the total variance which is additive:

$$h^2 = V_A/V_p.$$

The heritability of a character can be estimated from the degree of resemblance between relatives. For example, if a graph of the mean values for a character of the offspring of different families is plotted against the corresponding values for the parents (i.e. mid-parent values), then the line fitted through the points represents the degree of resemblance between offspring and parents (see Fig. 9.4). The slope of this, so-called, parent-offspring regression line estimates the heritability of the character and can vary between 0 and 1. A value close to 1 indicates that offspring are closely similar to their parents and that substantial genetic variation exists with little environmental influence. The measurement of the resemblance between relatives gives heritability one of its most important properties, namely as a predictor of the response to directional selection. For example, say that the character of wing-size has a high heritability in a particular species, then if only the largest butterflies in a population provide the parents of the next generation, this will have a higher mean value than the original unselected population and one more similar to that of the selected parents. Thus a rapid change will be apparent in the population mean for the character. This type of response is also evident when artificial selection is applied on highly heritable variation in plant breeding or animal husbandry programmes. A heritability of zero, as occurs in the absence of additive genetic variance, precludes a response to any form of selection.

Reliable estimates for heritability in *Maniola jurtina* were obtained by breeding 16 families,

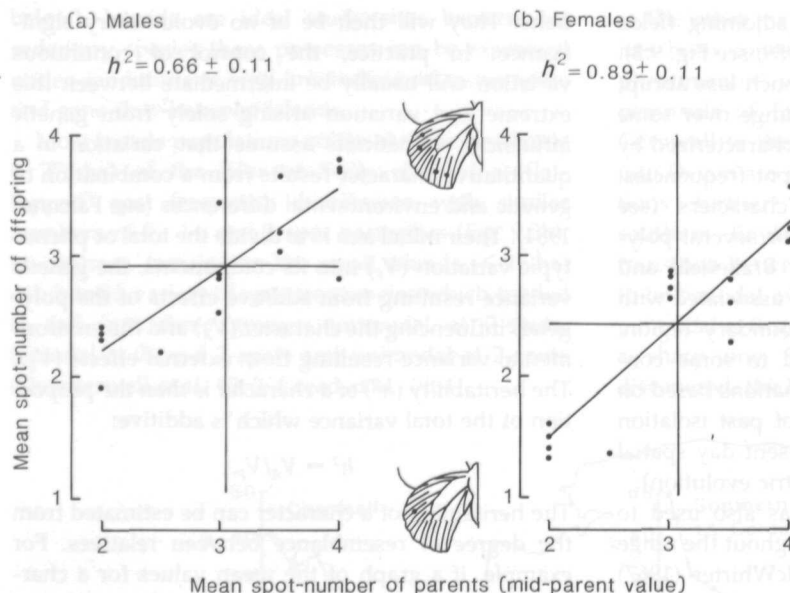


Fig. 9.4 The genetics of variation in the number of spots on the ventral surface of the hindwings of the meadow brown *Maniola jurtina*. The graphs illustrate the family resemblance between offspring of each sex and their parents. The estimates of heritability and their standard errors as given by the indicated regression lines are shown. (After Brakefield 1984; courtesy of Academic Press.)

comprising a total of 1340 butterflies, from a Dutch stock (Brakefield and van Noordwijk 1985). The families and their parents were all reared on growing grasses at similar temperatures and humidities in an unheated laboratory. Parent-offspring regression analyses yielded estimates of heritability (Fig. 9.4). These indicate that there is a fairly high heritability and substantial additive genetic variance for spot-number. However, some caution is necessary in interpreting these estimates since they can only be considered precise for the stock used and the particular conditions in which the butterflies were reared. Indeed it is recognized that such estimates tend to overestimate these parameters in natural populations.

Some additional experiments were performed with one of the families of *Maniola jurtina* to examine further the possibility of direct effects of temperature on spotting during the period of pattern determination in the early pupal stage (see section 8.3). The background to these experiments includes much early work which demonstrated that wing patterns could be altered by subjecting the pupae to extremes of temperature (see Kühn 1926; Köhler and Feldetto 1935). Every pattern element was found to have its particular sensitive period. Lorković (1938, 1943) and Høegh-Guldberg (1971a, 1974) found that prolonged cooling of the pupae of two lycaenids led to effects

on the underside spot pattern. Furthermore, Høegh-Guldberg and Hansen (1977) found that a lower spot-number was sometimes produced in the northern brown argus *Aricia artaxerxes* by subjecting insects, just before or after pupation, to one of more periods of cooling at between 2 and 5 °C for 9–12 hours. Their experimental pupae also yielded some rare forms which may provide an explanation for such aberrations in nature (see chapter 8). The similar experiments to those of Høegh-Guldberg and Hansen on the family of *M. jurtina* failed to detect an environmental effect on hindwing spotting (Brakefield and van Noordwijk 1985). However, this does not preclude the possibility of some more indirect, so far undetected, effect occurring at some earlier stage of development.

The genetical and breeding experiments with *Maniola jurtina* suggest that differences in spot frequency distributions between populations are likely to reflect genetic differentiation, whether arising from random effects or the influences of natural selection. The same is likely to apply to changes which have been detected within populations over a number of generations. Some of these changes (Dowdeswell and Ford 1955; Dowdeswell *et al.* 1957) have been associated with an altered habitat as for example on Tean in the Isles of Scilly where removal of cattle led to more luxuriant vegetation cover and

increased spotting. Other examples have been associated with exceptional droughts or warm and dry summers on islands (Dowdeswell *et al.* 1960; Bengtson 1978) or with climatic changes in England and Italy (Creed *et al.* 1959, 1962; Scali 1972). At lower altitudes in some Mediterranean regions *M. jurtina* shows a modified life cycle with an earlier adult emergence followed by a mid-summer aestivation of females prior to oviposition in late summer (Scali 1971; Masetti and Scali 1972; Scali and Masetti 1975). Scali and his colleagues found that the female spot frequency changed from a 'flat-topped' form to one unimodal at 0 spots over the period of aestivation, indicating a 65–70 per cent selection against 2–5 spotted specimens.

Detailed measurements of variation in the complete spot pattern of *Maniola jurtina* on the ventral surface of both wings revealed the existence of numerous phenotypic correlations. Butterflies of each sex which have more hindwing spots also tend to have larger apical forewing eyespots. These relationships also extend to populations (Brakefield 1984). The forewing eyespot is the most striking and well developed element of the spot pattern, with a white pupil and a large black area which contrast markedly with the background wing colour. It is about twice as large in females as in males and often bipupilled though females usually exhibit fewer and smaller hindwing spots. The eyespot is also extremely variable in size and often in shape within and between populations of each sex. Hindwing spots in females tend to be more often positioned or most heavily expressed towards the costal area of the wing which is closest to the forewing eyespot. These types of phenotypic correlations are probably characteristic of variable species of satyrines and other butterflies (see Frazer and Willcox 1975; Ehrlich and Mason 1966; Mason *et al.* 1967, 1968; Dennis *et al.* 1984) and in *M. jurtina* hindwing spot-number can be conveniently taken as a 'trend' character for the expression of the complete spot pattern. It will be interesting to determine by more detailed genetic analyses or selection experiments whether or not such phenotypic correlations are based on genetic correlations involving common effects of some genes on different spot characters. Studies on the positioning of the hindwing spots have, however, shown that this spot-placing variation is largely independent of spot-number

(McWhirter and Creed 1971). This is emphasized in Scotland where a steep cline of increasing costality in the position of hindwing spots with altitude is not associated with any corresponding change in spot frequency (Brakefield 1984).

Analysis of reared material demonstrates a substantial genetic component in determination of forewing eyespot-size ($h^2 = 0.59\text{--}0.80$; Brakefield and van Noordwijk 1985). The families also revealed evidence for a component of polygenic control for bipupillation of the forewing eyespot (*f. bioculata*), for the shape of the eyespot in males, for the presence of additional spots on the forewing (*f. addenda*) and for the presence of white pupils in the hindwing spots (*f. infra-pupillata*) (Fig. 9.1). Similarly, additive genetic variance exists for the position of the hindwing spots ($h^2 = 0.35\text{--}0.57$). One feature of both hindwing spot-number and spot-placing is that those estimates of h^2 for offspring on their same-sex parent are higher than those on that of the opposite sex (Brakefield and van Noordwijk 1985). In other words, males apparently resemble their male parent more closely than their female parent, and females are more like their female parent. This seems to be due to sexual differences in the inheritance and expression of the characters. Certain of the individual hindwing spots can be characterized as typically female while others are typically male. This will cause a greater resemblance to the same-sex parent in respect of both spot number and spot position.

9.1.3 Wing-spotting and natural selection

This pattern of partial sex-dependence for expression of spotting is of particular interest because it is consistent with a model to account for variability in spot patterns in populations (see chapter 5, Fig. 5.3). This model provides an alternative to the assumption that the spots themselves are 'trivial' or unimportant to the individual. It predicts that visual selection by insectivorous birds and lizards operates differently for males and females of *Maniola jurtina*. These differences in selection are associated with differences in the resource requirements of the sexes and in adult behaviour (Brakefield 1982a). The marked sexual dimorphism in spot pattern is an important component of the model. The large eyespot is frequently hidden when females are at rest,

but as in the grayling *Hipparchia semele* (Tinbergen 1958; chapter 5) it is sometimes exposed when disturbed. Overall, the model predicts that an even wing-spotting will be most advantageous in deflecting attacks by predators to the more active butterflies. Male *M. jurtina* are generally more active than females and have a more evenly expressed spotting.

Mark-release-recapture experiments performed in populations near Liverpool also suggested that the distances moved by butterflies of each sex within a habitat-area increased with spot-number (Brakefield 1984). A particularly clear example of this tendency is illustrated in Fig. 9.5. If such greater dispersal occurs more generally within populations of the species and if it reflects a general increase in activity and frequency of changing behaviour and shifting position, which tends to attract searching predators, then the relationship with spot expression is consistent with the model. Further capture-recapture experiments on other populations and in larger habitat areas would be most useful. Interestingly, there is some evidence for differences in behaviour between two hindwing spotting phenotypes in the

speckled wood *Pararge aegeria* (Shreeve 1987). The selection against spotting, particularly on the hindwing, in inactive butterflies depends on their resting background and the effectiveness of their crypsis (see chapter 5). Circular spots may tend to be more conspicuous in grasslands dominated by linear shapes and thus attract the attention of searching predators (a comparable example is shown in Fig. 5.2).

Many of the components and details of the model require testing, although Bengtson (1978, 1981) working in Sweden found differences in the frequency of wing damage (see Fig. 5.1) between spotted and unspotted females consistent with differences in their activity and consequently in their exposure or 'apparency' to predators. However, the model is of value in the absence of alternative hypotheses about how precisely natural selection influences the phenotypic variation.

An important finding from the breeding programme was that in some larger families there were differences in the timing of adult emergence between the different hindwing spot phenotypes represented

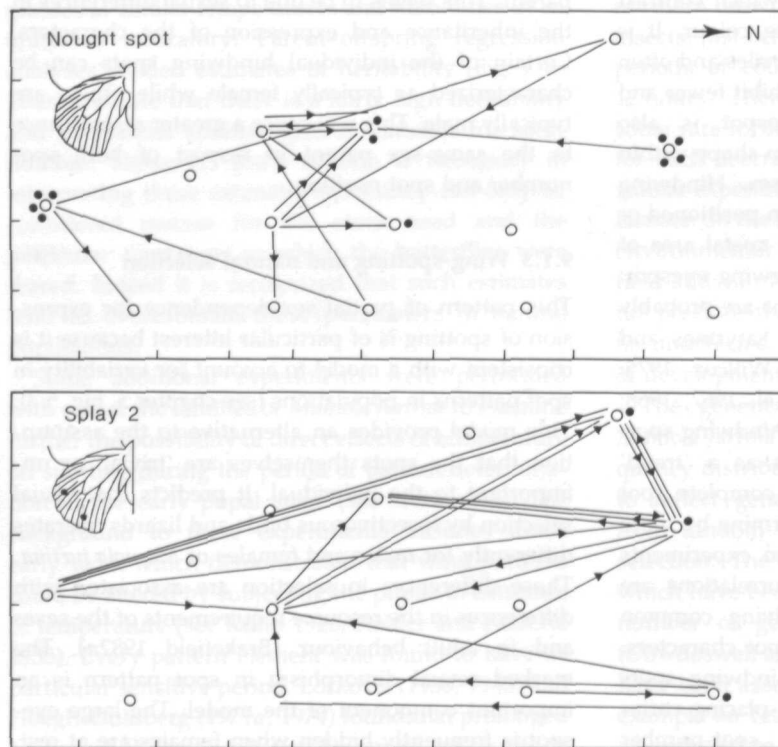


Fig. 9.5 The movements of marked females of two hindwing spot-types of the meadow brown *Maniola jurtina* at Hightown near Liverpool in 1976. Open circles show capture-release sites and closed circles show recaptures at the same site as release. Arrows indicate the direction of moves. Each map (a) and (b) shows 25 movements selected at random from the complete sample for a spot type. Divisions on the edge of each map are at intervals of 15 m. The illustrated patterns of movement are significantly different. (After Brakefield 1979.)

by particular combinations of the hindwing spots. Overall such differences led to declines in spotting during the emergence period. There may be differences in development rates between the phenotypes which result from other (pleiotropic) effects of the spotting genes than those on wing pattern. Such non-visual effects may be critical in the overall selection influencing spotting. These observations are consistent with numerous findings of intra-seasonal changes in spot-number within populations (examples in Creed *et al.* 1959; Dowdeswell 1962; Scali and Masetti 1975; see Fig. 9.6b). When they occur such changes are always in the direction of a declining spot average with time. The species is characterized by extreme geographical variation in the timing and length of emergence. There are consistent differences between populations with a trend towards a more synchronized emergence—beginning later and ending earlier—northwards through England and Wales (Brakefield 1987*d*). There is also a clear trend towards an earlier emergence in years when the month of June is comparatively warm. Figure 9.6a shows that differences in the timing of emergence may also occur in the field between spot types which differ in the positioning of the spots. In Scotland the cline of increasing anality of spotting with altitude may be related to such effects (Brakefield 1984). It is tempting to suggest that spotting is partly related to spatial and habitat-related patterns of variation in timing and length of emergence.

Earlier research on the larvae of *Maniola jurtina* by Dowdeswell (1961, 1962) which involved a comparison of the spotting in adults reared from wild-collected, late-instar larvae with that of flying adults from populations in Hampshire suggested that intra-seasonal changes in spotting could result from differential parasitism by the ichneumonid *Apanteles tetricus*. However, the causal nature of the observed relationship between level of parasitism and spotting has not been demonstrated (Brakefield 1984).

9.1.4 Interpreting geographical variation

With this background information in mind the results of the survey work on the Isles of Scilly and south-west England can be discussed with regard to alternative explanations for the patterns of population differentiation. The spotting of *Maniola jurtina* on the three large islands of the Isles of Scilly is

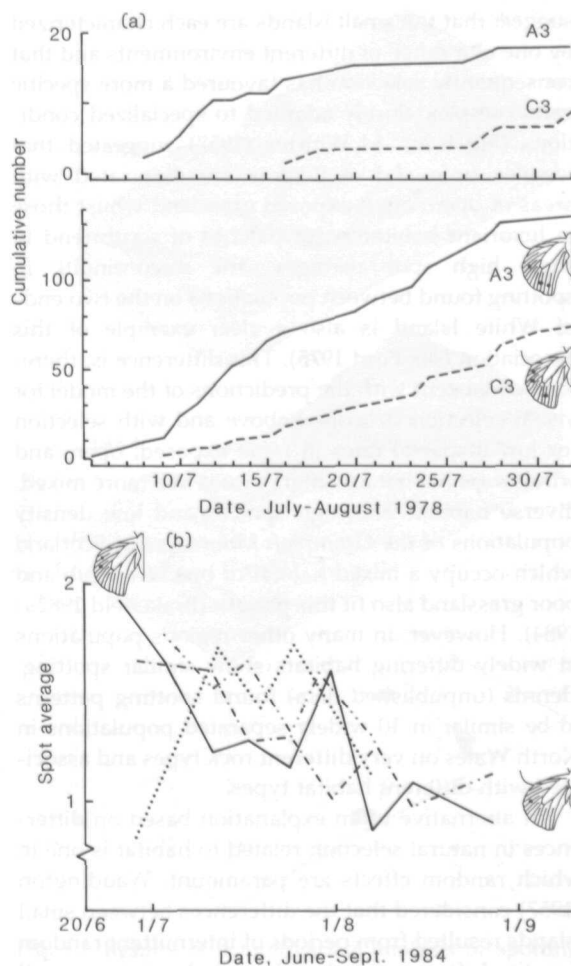


Fig. 9.6 Emergence patterns and hindwing spotting variation in the meadow brown *Maniola jurtina*. (a) Cumulative daily totals of males of two-spot types in fresh condition and captured for the first time in two populations near Liverpool. (b) The intra-seasonal change in female spot average for four populations in the boundary region. Each point is based on about 30 females. (After Brakefield 1979, 1984; Brakefield and Macnair, unpublished data.)

similar whereas the small island populations are more variable tending towards one of three different spot frequencies (Fig. 9.2b). Ford and his co-workers believe that those populations on the large, and diverse islands result from natural selection producing a gene complex simultaneously adapted to a wide range of environments. In contrast, they

suggest that the small islands are each characterized by one of a range of different environments and that consequently selection has favoured a more specific gene complex closely adapted to specialized conditions (Fig. 9.2c). McWhirter (1957) suggested that females unimodal at 0-spots are associated with areas of open, often exposed grassland whilst those in luxuriant habitats with patches of scrub tend to show high spot averages. The discontinuity in spotting found between populations on the two ends of White Island is also a clear example of this association (see Ford 1975). This difference is, therefore, consistent with the predictions of the model for visual selection described above and with selection for low dispersal rates in more exposed, open, and windswept habitat and higher ones in a more mixed, diverse habitat. The high spotted and low density populations of the Grampian Mountains in Scotland which occupy a mixed habitat of bracken scrub and poor grassland also fit this pattern (Brakefield 1982a; 1984). However, in many other regions populations in widely differing habitats show similar spotting. Dennis (unpublished data) found spotting patterns to be similar in 10 widely separated populations in North Wales on very different rock types and associated with different habitat types.

An alternative to an explanation based on differences in natural selection related to habitat is one in which random effects are paramount. Waddington (1957) considered that the differences between small islands resulted from periods of intermittent random genetic drift associated with periods of very small population size known as bottlenecks. A similar reasoning was developed by Dobzhansky and Pavlovsky (1957), who suggested that the small island populations were derived from small founder groups with differing gene frequencies from which relatively stable but different gene pools developed. Such effects do seem to be reflected in frequencies of melanic forms of the spittlebug *Philaenus spumarius* on the Isles of Scilly (Brakefield 1987e, 1990b). However, Ford and his colleagues have countered such hypotheses for *Maniola jurtina* with their observations of a population passing through an extreme bottleneck in size, with no subsequent disruption of spot frequency (Creed *et al.* 1964), and an example of a change in habitat due to the removal of cattle on Tean being associated with one in spotting. Unfortunately recent fieldwork on the Isles of Scilly

found that a switch in land use on smaller, uninhabited islands away from grazing by cattle has led to the spread of bracken scrub through grassland and the extinction or decline of many colonies of *M. jurtina* (Brakefield 1987e).

The studies of the 'boundary phenomenon' in south-west England (Fig. 9.3) also led to alternative hypotheses to account for the population differentiation. Ford and his co-workers consider that their data demonstrate the existence of powerful natural selection which differs on each side of the boundary. Some laboratory experiments with *Drosophila* fruit flies have shown how such disruptive patterns of selection practised on artificial populations may sometimes lead to divergence and effective isolation (see Sheppard 1969). Ford (1975) discusses the boundary phenomenon in relation to sympatric evolution in which distinct races or local forms can arise without isolation past or present. Handford (1973) elaborates on this interpretation, suggesting that there is a switch-over between two co-adapted genetic systems at a critical point in an environmental gradient. Genes are said to be co-adapted if high fitness depends upon specific interactions between them. Oliver's (1972a,b; 1979) hybridization studies provide some evidence of such genetic systems in several species of butterfly. He found various forms of disruption in development and in the relative timing of emergence of males and females in hybrids between geographically well-separated populations of, for example, wall brown *Lasiommata megera*, and small pearl-bordered fritillary *Boloria selene*.

Dennis (1977) discusses evidence, particularly from palaeobotanical studies of pollen, which shows that from about 9500 to 5000 years ago a disjunct or allopatric distribution of *Maniola jurtina* may have occurred in southern Britain. During the warm dry climate of the Boreal period (see Table 10.2), forest cover would have led to populations being restricted to the granite or sandstone upland areas and to the coastal fringe of Cornwall and Devon in the west and to the wide expanse of interconnected calcareous uplands in southern and south-east England. Dennis uses this reasoning to develop the alternative explanation for the boundary phenomenon based on divergence in allopatry originally suggested by Clarke (1970). The boundary is then considered to represent the zone to which two groups of popula-

tions of *M. jurtina* have expanded their range after a period of isolation and divergence. The discreteness of the main population groups may be maintained by some form of selection against hybrids. Alternatively, the boundary zone may be in the process of decay involving a progressive change to a shallow cline, and eventual uniformity and mixing of gene pools. Such a breakdown may be slowed by some present-day changes in selection from east to west and the comparatively low dispersal rate of the species. In practice it is extremely difficult to distinguish between differentiation evolving with or without allopatry, especially without a detailed knowledge of the geological and biological history of the region across which a present day hybrid zone or steep cline occurs (Endler 1977).

The most difficult feature of the boundary phenomenon to account for is the frequent shift in the geographical position of the boundary itself. This may be up to 60 km east or west between generations (Creed *et al.* 1970). Clarke (1970) in suggesting that the boundary region may be a zone of hybridization also postulated that the shifts could result from individuals within this zone being particularly prone to developmental instability. Ford (1975) argues that such instability would lead to a mosaic of populations with differing spot frequencies, which is not found. Recent work by P. Brakefield and M. Macnair (unpublished data) has suggested that progressive declines in spotting during adult emergence (see Fig. 9.6b) in combination with variation between years in the timing of the flight period and/or sampling dates could contribute to such (apparent) shifts in the position of the boundary.

Brakefield and Macnair's research was based on analysis of morphometric data from a grid of over seventy populations covering the whole boundary region. This reveals a more complex pattern of geographical differentiation than the results of Ford and his co-workers obtained by using one or two transects (Fig. 9.7). The morphometric data for each spot-character in males and females showed a series of more or less coincident clines of varying steepness from east to west along the peninsula between 1982 and 1984. The width of the clines was of the order of a few tens of kilometres rather than in single figures. No simple boundary was detected running from north to south across the peninsula. Various types of multivariate analysis of the morphometric data for

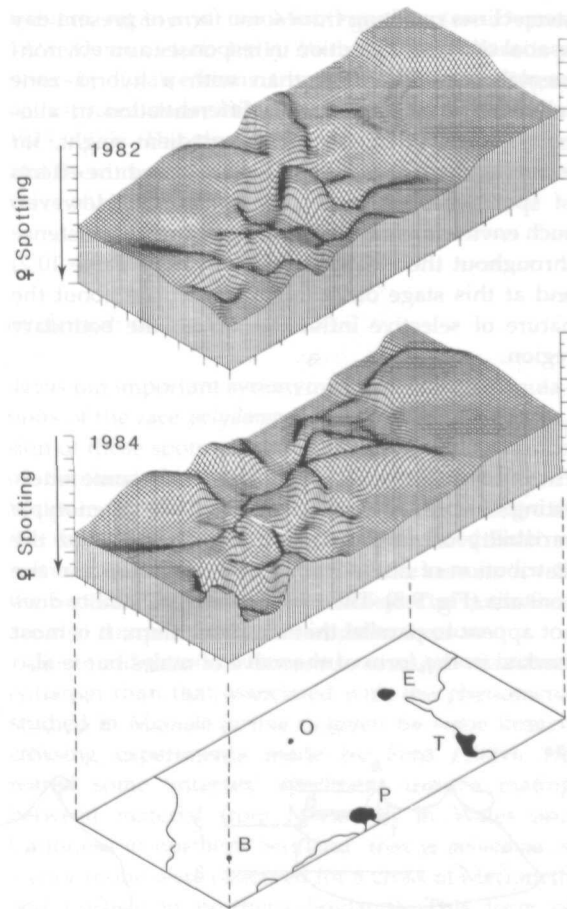


Fig. 9.7 Results of a multivariate analysis of spotting variables in the meadow brown *Maniola jurtina* for a grid of populations covering the boundary region in the south-west peninsula of England in 1982 and 1984. (See also Fig. 9.3.) Pseudo three-dimensional plots for the first principal component over the boundary region. The component is a linear combination of variables and measures the overall extent of development of wing-spotting in females. Note: plot ignores sea areas. Major towns: E, Exeter; T, Torquay; P, Plymouth; O, Okehampton; B, Bodmin. (After Brakefield and Macnair, unpublished data.)

all spot-characters failed to separate the populations into two discrete clusters corresponding to a western and an eastern grouping. Rather, they indicated a single cluster with western populations tending to one side and eastern to the other. Overall these results are more consistent with a pattern of fairly

steep clines resulting from some form of present day spatial change in selection in response to an environmental gradient rather than with a hybrid zone following extensive genetic differentiation in allopatry. Such an environmental gradient might, for example, involve a change in climate and the effects of spot genes on timing of emergence. However, such environmental gradients have been in existence throughout the Holocene (Dennis 1977; Table 10.2) and at this stage one can only speculate about the nature of selective influences across the boundary region.

9.1.5 Variation in genitalia

Thomson (1973, 1975, 1976) has made some interesting studies of another aspect of the phenotypic variability of *Maniola jurtina*. He investigated the distribution of different morphological forms of the genitalia (Fig. 9.8). This geographical variability does not appear to parallel that in spot pattern. It is most marked in the form of the valve of males but is also

evident in the shape of the paired gnathos. Although such characters can be difficult to measure, two main types—the 'eastern' and the 'western'—are distinguished. These differ particularly in the shape of the dorsal process. The change-over between these types apparently occurs along a more or less broad zone running southwards from Sweden, The Netherlands, Belgium and north-east France to south-east France, and the Mediterranean. This region is characterized by a transitional type of valve and is much narrower in the south (Fig. 9.8). Unfortunately the inheritance of the variation in genitalia has not been examined. However, Thomson (1987) has found that changes in allele frequencies at 10 polymorphic enzyme loci (see chapter 8) are associated with the change-over in types of genitalia. This distribution of genitalia types and enzyme variation may reflect some form of hybrid zone or secondary contact between two races or similar entities which diverged in allopatry. Such isolation was probably associated with changing spatial patterns of 'refugia' of favourable habitat occurring in the period of gross

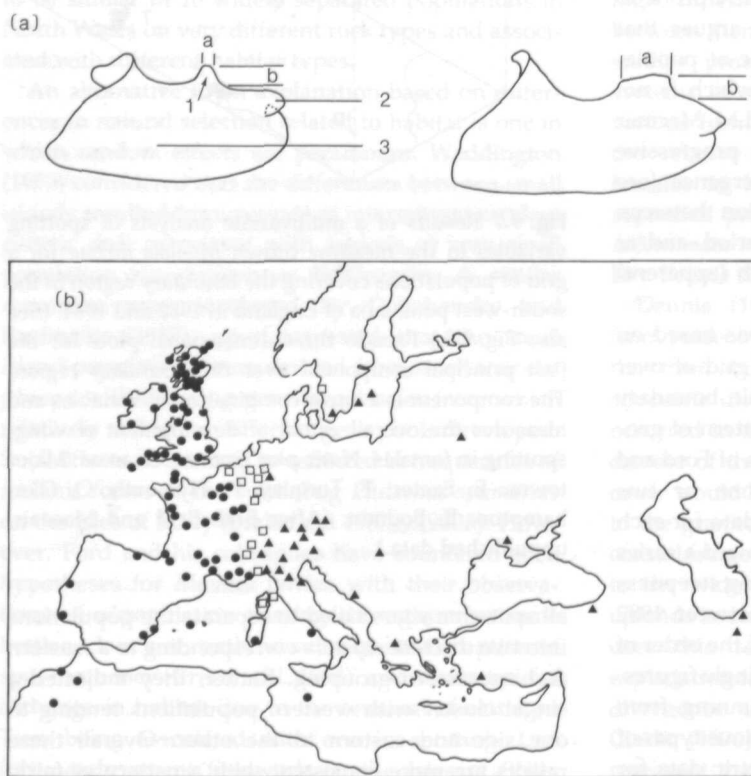


Fig. 9.8 Geographical variation in male meadow brown *Maniola jurtina* genitalia forms over Europe. (After Thomson 1973, 1975, 1987; courtesy of G. Thomson.) (a) The two principal forms of the valve of the male genitalia: left, 'western' form; right, 'eastern' form. 1, dorsal process; 2, distal process; 3, valve. The simple coefficient $b-a$ gives positive values when populations are 'western' and negative when values are 'eastern'. (b) The distribution of ▲, 'eastern', ●, 'western', and ◻, transitional male genitalia forms.

climatic fluctuations of the glacial advances and retreats of the Pleistocene (see section 10.5). Thomson considers that both the eastern and western types of valve originated from ancestral populations in western Asia (Iran). These populations are represented today by a so-called 'primitive' valve structure. The two main types of valve may, however, have originated independently in the eastern and

western regions of the Mediterranean (see Dennis 1977; Dennis *et al.* 1991). Within Britain there is a diversity of valve forms, transitional types tending to be restricted to dry calcareous landscapes (Thomson 1973, 1975). This diversity occurs at individual sites and there may also be an element of seasonality in valve shape (Shreeve 1989).

9.2 The large heath: evolution of races

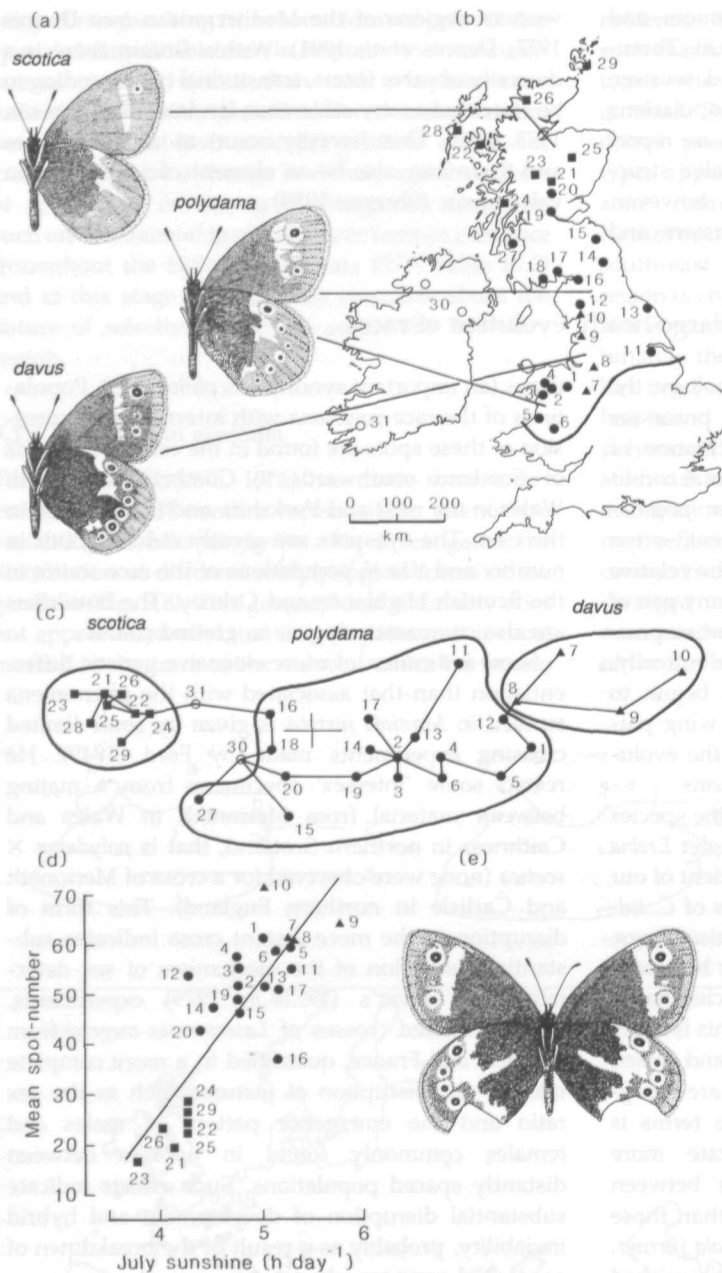
Apart from the variation in genital morphology, the study of *Maniola jurtina* has examined processes involved in microevolution and the adaptation of local populations to particular environmental conditions. The differences examined between populations have been rather limited in extent, often concerning gradual or clinal changes in the relative frequency of different spotting types with any pair of populations differing in mean number, size, or position of spots. Research on another satyrine butterfly, the large heath *Coenonympha tullia*, has begun to examine more substantial differences in wing pattern which are probably associated with the evolution of races in different geographical regions.

Coenonympha tullia is a northern or alpine species and together with the small mountain ringlet *Erebia epiphron* probably represents the most ancient of our butterfly fauna (see section 10.3). Colonies of *C. tullia* are confined to peat mosses, lowland raised bogs, damp acid moorland, and upland blanket bog from sea-level up to at least 800 m. The species has a disjunct distribution in Britain, although this is likely to be partly due to major losses of lowland raised bogs. Several major races or subspecies are recognized by taxonomists. The use of these terms is somewhat imprecise but they implicate more distinctive and far-reaching differences between populations inhabiting different regions than those involving hindwing spot pattern in *Maniola jurtina*. The races of *Coenonympha tullia* are distinguished principally on the basis of development of the submarginal rings of eyespots especially on the ventral surface of both wings (Fig. 9.9). These are most striking in populations inhabiting some of the peat mosses of England from lowland Cumbria to Shropshire. This phenotype, which is also characterized by a comparatively dark ground colour, is known as

davus (an important synonym is *philoxenus*). Populations of the race *polydama* with intermediate expression of these spots are found in the central lowlands of Scotland southwards to Cumbria and North Wales in the west and Yorkshire and Lincolnshire in the east. The eyespots are greatly reduced both in number and size in populations of the race *scotica* in the Scottish Highlands and Orkney. The butterflies are also comparatively pale in ground colour.

Some indication of more extensive genetic differentiation than that associated with the phenomena studied in *Maniola jurtina* is given by some limited crossing experiments made by Ford (1949). He reared some 'intersex' specimens from a mating between material from Merioneth in Wales and Caithness in northern Scotland, that is *polydama* × *scotica* (none were observed for a cross of Merioneth and Carlisle in northern England). This form of disruption in the more distant cross indicates substantial disruption of the mechanism of sex determination. Oliver's (1972*a,b*; 1979) experiments, which included crosses of *Lasiommata megera* from England and France, quantified in a more complete manner the disruption of features such as the sex ratio and the emergence pattern of males and females commonly found in hybrids between distantly spaced populations. Such effects indicate substantial disruption of development and hybrid inviability, probably as a result of the breakdown of coadapted gene complexes.

A detailed morphometric analysis of material from British collections of *Coenonympha tullia* has been done by Dennis and Porter over the last decade or so. Their latest results (Dennis *et al.* 1986) describe a multivariate analysis of records of spot presence and measurements of spot size and wing area in samples from thirty-one localities in the British Isles



(Fig. 9.9b). A non-metric two dimensional scaling plot (see p. 6) produces three clusters corresponding to populations of the three phenotypes associated with the described subspecies (Fig. 9.9c). The clusters to the left and right of Fig. 9.9c include samples from the north of Scotland and from Shrop-

Fig. 9.9 Variation in wing-spotting among British populations of the large heath *Coenonympha tullia*. (Redrawn from sources in Dennis *et al.* 1986; courtesy of *Entomologist's Gazette*.) (a) Examples of the ventral spotting to illustrate the degree of variation from north to south in Britain. (b) Sites from which population samples were obtained for morphometric analysis. (c) A non-metric scaling plot of the male populations for some fifty spot variables; most of the geographical variation can be accounted for in a single dimension. Lines join nearest neighbour populations from single linkage cluster analysis of the same data. Clusters specify traditional subspecies. (d) Relationship between the mean spot-number (index of spot development) for the samples of males and the mean daily hours of sunshine in July at the sites. The fitted regression line is shown. (e) A male of the race *davus* collected at Whixhall Moss, Shropshire, shows symmetrical damage to the hindwings likely to have resulted from the partial evasion of an attack by a bird or lizard. Forty per cent of the males sampled in 15 of the populations given in (b) had symmetrical wing damage to the hindwings.

shire, Cheshire, and Cumbria, respectively. The larger, central envelope comprises the geographically more heterogeneous group covering the region from the central lowlands of Scotland to northern England with North Wales. The two Irish collections appear to be somewhat intermediate between *scotica*

and *polydama*. It is interesting that the position within the *polydama* envelope tends to reflect the geographical order either southwards from Scotland or westward into North Wales. This relationship can be seen more clearly within the array for the Scottish Highlands and lowland English mosses.

These findings suggest several possible evolutionary explanations. For example, the local disjunct distribution of *Coenonympha tullia*, throughout much of its range, may tend to mask what is essentially a pattern of equivalent clines in spotting extending both northwards and westwards from the lowland English mosses in response to an environmental gradient. At the other extreme, the three phenotypes may correspond to three (or four) groups of populations which have diverged genetically from each other during a past period of allopatry and isolation. If so, why is there evidence of clinal change within each race? This could represent a common response to similar environmental gradients within each region. The occurrence of intersexes when distant populations are crossed is consistent with this type of explanation. One can then ask whether the divergence in spotting patterns reflects:

- (1) a by-product of more general genetic differentiation unrelated to adaptation processes;
- (2) pleiotropic effects of selected differences in genes controlling spotting unrelated to the spotting phenotypes *per se*; or
- (3) an integral component of adaptation to differences in the environment inhabited by each race.

A further possible complication is that the heterogeneous grouping of populations with intermediate phenotypes could represent a zone of mixing or introgression between the races with extreme phenotypes produced by a spread and mixing of populations resulting from recent human activities.

Unfortunately, as Endler (1977) has emphasized, it is very difficult to distinguish between hypotheses involving past allopatry and differentiation with secondary contact and those concerning responses to present-day selection regimes and environmental gradients (see preceding section). This applies to *Coenonympha tullia* since it is difficult to speculate about the likely historical changes in distribution of the population groupings in relation to both ecological and climatic constraints. If future work demonstrates more profound ecological differences,

and confirms the major genetic differentiation between populations of the lowland mosses and those of the Scottish Highlands, then the hypothesis involving secondary introgression becomes more attractive. The often patchy distribution of colonies of *C. tullia* even in regions where it is relatively well distributed makes it rather difficult to distinguish real discontinuities in distribution and gene flow between populations. The northern and southern races of the brown argus, which are now usually given the taxonomic status of species (*Aricia agestis* and *A. artaxerxes*), provide a particularly interesting example of well separated population groupings associated with both genetically controlled differences in wing pattern and other morphological characters and with ecological differences especially in larval hostplants (section 10.5).

The model described in the previous section relating variation in spotting between meadow brown butterflies to differences in adult activity patterns and exposure to vertebrate predators can be applied to *Coenonympha tullia* (Brakefield 1979, 1984; Dennis *et al.* 1984, 1986). The basic components suggest that the combination of a habitat with mixed vegetation and high sunshine experienced by the lowland Shropshire populations will favour the evolution of eyespots for deflection of predator attacks. Figure 9.9e illustrates a specimen from Whixhall Moss in Shropshire with symmetrical damage to the hindwing consistent with deflection by the eyespots of an attack by a bird or lizard away from the body of the insect (see also Fig. 5.1). At the other extreme it can be argued that in northern Scotland a comparatively homogeneous moorland habitat and a cooler climate which reduces adult activity will favour smaller eyespots which enhance crypsis. Analogous to the scenario for *Maniola jurtina*, large eyespots in these conditions might attract predators to resting insects which were for the most part incapable of escape. It is also noteworthy that when other species of heaths on the continent are considered, for example, *Coenonympha arcania*, *C. doris*, *C. gardetta*, and *C. vaucheri*, populations at lower altitudes show a more pronounced spotting than those of more mountainous regions.

Dennis *et al.* (1986) found a close positive association between spotting in *Coenonympha tullia* and the duration of bright sunshine in the adult flight period (Fig. 9.9d). Although there are statistical associations

with other climatic variables, that with sunshine is the highest and most consistent with geographical changes in levels of adult activity. An increase in activity with more frequent changes in behaviour and position could in turn shift the balance of selection on wing pattern towards an emphasis on more highly developed spotting functioning primarily in the deflection of attacks by predators. Interestingly, in the *scotica* phenotype the pupils of small spots are silver in colour which may tend to increase their conspicuousness in sunshine by reflective effects. Significant positive correlations between spotting and sunshine have also been found for *Maniola jurtina* in Britain (Brakefield 1979) suggesting that this may be a more general relationship. Dennis *et al.* (1986) summarize the incidence of wing damage in their material of *C. tullia* which was consistent with failed attacks by predators (see chapter 5). There was evidence of a high level of predation by birds, with 43 per cent of males and 58 per cent of females bearing at least one damage mark. They had noted earlier (Dennis *et al.* 1984) that the pattern in the positioning of such damage was consistent with the hypothesis that larger wing spots are the best decoys.

Dennis *et al.* point out that certain populations of *Coenonympha tullia* in Britain, including some with well expressed spots, are associated with grassland habitats at the margins of woodlands or where substantial invasion by birch scrub has occurred. These are habitats where the abundance of foraging birds and heterogeneity of resting backgrounds are greater than in uniform grassland. Interestingly an additional spot frequently occurs at the anal border of the hindwing in populations near Witherslack, Cumbria which is the most wooded locality. This is consistent with the influence of the strongest directional selection for spotting. Shapiro and Cardé (1970) described an increase of spotting in some woodland satyrines of the genus *Lethe* in an area of New York State USA. Brakefield (1979, 1984) suggests that there may be a general tendency for woodland satyrines to be more heavily spotted, possibly because their resting backgrounds tend to be more heterogeneous and less dominated by the linear shapes of grasslands. However, this does not seem to apply to the dry season forms of tropical species which are inactive and rely on a resemblance to dead leaves for survival (see Fig. 5.2). Dennis *et al.* (1986) suggest that more

numerous and larger eyespots are favoured in conditions of changing light and shade because butterflies may be less able to monitor, and therefore avoid, approaches by predators and that the low light levels necessitate more contrasting spots to divert predator attention.

Although some interesting explanations of geographical variability in wing pattern have been given to some butterflies such as large heaths, it must be emphasized that tests for the entire chain of causal mechanisms are still required. Evidence that birds can select for small differences in wing pattern or details such as eyespots is discussed in chapter 5. In common with most research on variation in wing patterns where visual selection by predators is implicated, we need to know much more about the precise incidence and mechanics of feeding by predators on living Lepidoptera in the wild. In *Coenonympha tullia* we also need to know much more about its ecology before we can be more confident about our adaptive explanation for variation in wing pattern. There are no quantitative data describing the postulated differences in activity levels between populations of different regions, although they could be readily obtained.

The other major area for which empirical data must be obtained before we can be more definite about the role of natural selection in the observed spatial differentiation of wing pattern is the mode of control of the phenotypic variation. There is no information from breeding work about the inheritance of spotting variation in *Coenonympha tullia*. Indeed Turner (1963) suggested that the distribution of the races of *C. tullia* is to some extent correlated with temperature: for example, on Islay in the Western Isles, Scotland, which has a mean annual temperature comparable to that of Shropshire, a small proportion of individuals approach the *davus* phenotype, with many more of intermediate spotting development. Dennis *et al.* (1986) confirmed the close statistical correlations between spotting and temperature variables for July. Although such effects are quite consistent with the model of selection developed above, there is a need to establish that the development of spotting is insensitive to such direct environmental effects (see previous section and chapter 8).

9.3 The speckled wood: geographic variation in Europe

The studies of *Maniola jurtina* illustrate clinal variation and microevolution, and those of *Coenonympha tullia*, evolution and differentiation in isolation. More substantial variation, in wing pattern and seasonal polyphenism (see section 8.5) is exhibited by the speckled wood *Pararge aegeria* in Europe. This is discussed below in relation to the evolution and maintenance of distinct forms within a continuous distribution.

Within its whole range (Fig. 9.10) *Pararge aegeria*, occupies a variety of habitats, including forest, grassland, and wasteland. Some geographic regions

are characterized by a gradual change of the wing phenotype, but there are also more abrupt changes despite an apparently continuous distribution. There are also differences in the life histories of populations from different areas (Thompson 1952; Robertson 1980; Wiklund *et al.* 1983; Shreeve 1985; Nylin *et al.* 1989; E. Lees, personal communication) which may not coincide with changes in the adult phenotype. This whole pattern of variation is not easily explained by either clinal variation in response to present-day environments or by adaptation to past isolation but rather by some combination of the two.

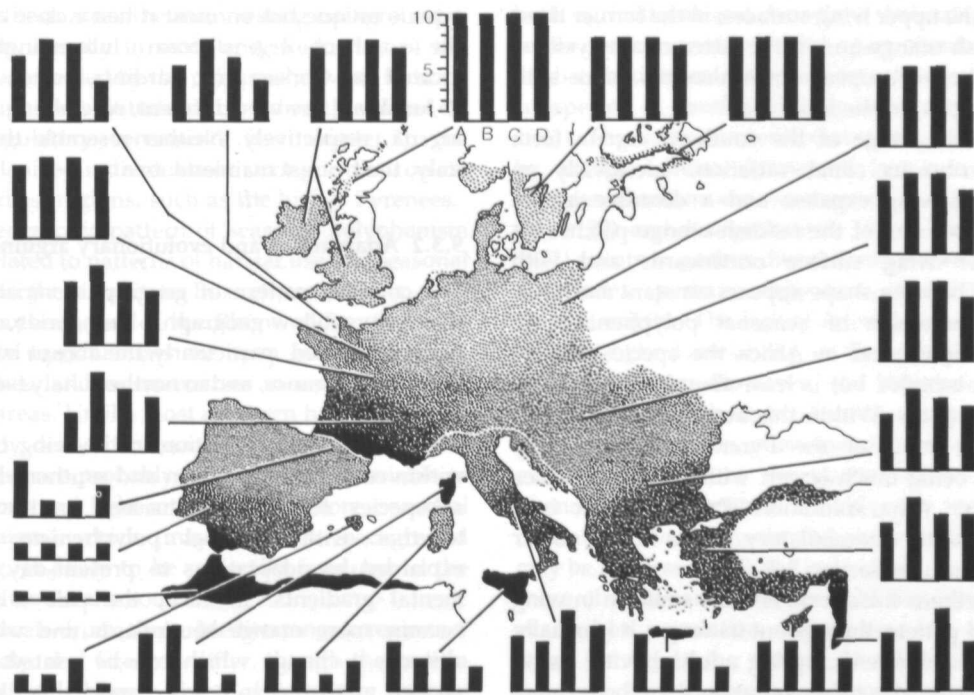


Fig. 9.10 Geographic variation in the phenotype of the speckled wood *Pararge aegeria* in Europe. The three main forms, *P. aegeria aegeria* in Iberia and North Africa, *P. aegeria tircis* over most of Europe, and *P. aegeria italica* restricted to the Italian peninsula, are clinally variable. Most Mediterranean island forms resemble adjacent mainland forms, but those from Sicily, Crete, and Cyprus are probably unique. Size, wing shape, pattern, and colour of the various forms are represented on an arbitrary scale from 1 to 10 by histograms. A. Size: 1, smallest (Africa), 10, largest (Scotland); B. wing shape (forewing angularity): 1, most indented (Africa), 10, least indented (northern Europe); C. pattern (dorsal pale patches): 1, most extensive (Africa), 10, least extensive (Scotland); D. dorsal patch colour: 1, most orange (Africa), 10, pale cream colour (Scotland). Subspecies *tircis* is the most seasonably variable. Distribution in eastern Europe is not well documented but may extend to the Ural mountains and Pripyat marshes.

9.3.1 Species, subspecies, and geographic variation

The three species within the genus *Pararge* (see Higgins and Riley 1983) are distinguished by their wing shape and colour. *P. aegeria*, which occurs throughout mainland Europe, western Asia, North Africa, and Madeira is the smallest and most variable species. *P. xiphia*, is the largest and darkest species and is restricted to Madeira. *P. xiphioides*, which occurs on the Canary Islands is intermediate in size and colour between *P. xiphia* and *P. aegeria*. Numerous races of *P. aegeria* have been described by various authors as varieties or subspecies (e.g. Verity 1916; Gaede 1931), but two subspecies are universally recognized, *P. aegeria aegeria* from southern Europe and *P. aegeria tircis* from northern Europe. They are distinguished by the colour of the pale areas on the upper wing surfaces; in the former these are reddish orange and in the latter creamy yellow. The southern European form also has more scalloped margins on the forewing.

Within the range of the southern *aegeria* form there is obvious clinal variation, specifically an increase in wing expanse and a decrease in the intensity and size of the reddish orange patches on the upper wing surface northwards and with altitude. The wing shape appears constant and there is little indication of seasonal polyphenism. In southern Spain and in Africa the species is continuously brooded but is least abundant in the dry summer months. Within this area individuals from the higher parts of the Pyrenees are strikingly different, being much larger, with more hair-scales and darker wing coloration. Presumably it is a response to thermoregulatory needs in the cooler environment (see section 2.2).

The northern *tircis* form is more uniform in wing shape and pattern throughout its range. It is usually seasonally polyphenic, spring adults having larger and more extensive pale wing areas than those flying in summer. This variation is more extreme in the north. However, populations in eastern Finland, central Sweden, and probably north-western Russia have only one generation a year (Wiklund *et al.* 1983), and may therefore be less variable (see also section 8.5). Although coloration is one of the features which distinguishes *tircis* from the southern European *aegeria*, this coloration is variable. At low altitude in southern parts of its range it is similar in

colour, but not pattern, to the southern form. At northern latitudes and at high altitude in southern areas the phenotype of *tircis* is very similar to that found in southern Britain.

Individuals from peninsular Italy are different from those of all other mainland European areas, both in wing shape and pattern, though this phenotype is also located on certain Aegean islands, in Syria, and Lebanon. This similarity of Italian and Middle-Eastern races was first commented on by Verity (1916) but Larsen (1974) disputes this view. He points out that current geographic distribution patterns cannot support any inferred similarity between Italian and Middle-Eastern races. The phenotype does not extend into the Alps but does occur along the northern Dalmatian Coast.

On each of the Mediterranean islands the phenotype is unique but on most it has a close affinity to the southern *aegeria* form. Interestingly, those located on Corsica and Sardinia, which are only 25 km apart, are very different, resembling *tircis* and *aegeria*, respectively. Neither resemble those from Italy, the nearest mainland area.

9.3.2 Adaptations and evolutionary arguments

The complex pattern of geographic variation does not always follow geographic boundaries and is not easily explained, particularly the abrupt boundaries in southern France, and in northern Italy (see Dennis *et al.* 1991).

However, clinal variation in the wing coloration within each of the northern and southern European subspecies follows a consistent pattern which, together with seasonal polyphenism, can be explained by adaptations to present-day environmental gradients. In each, the pale wing areas become more orange southwards and with lower altitude, a change which can be related to background matching. In a woodland habitat in Britain more than one half of individuals are damaged in a manner which is consistent with having been attacked by birds (Shreeve 1985). An examination of populations in 25 different sites in France reveals a similar incidence (Shreeve, unpublished data). Therefore, an appropriate form of crypsis may substantially enhance survival (see chapter 5). When settled in a potentially active state, the butterfly basks with open wings and when the general wing

pattern matches that of the background the butterfly is difficult to detect. Although the effectiveness of the various colour forms on different backgrounds needs to be tested, orange coloration probably affords better crypsis in drier southerly, low-lying, habitats. A reduction in the contrast between dark and light wing areas of *aegeria* may decrease conspicuousness in more open habitats where the contrast between light and shade is less extreme than in densely wooded areas. This may also account for the development of orange coloration on the upper surfaces of individuals from the Isles of Scilly, described by Howarth (1971) as subspecies *insula*. Observations of the species in France (Shreeve, unpublished data) demonstrate that in southern areas individuals spend more time resting on bare earth and dead leaf litter than on vegetation, but in more northern areas the main resting background is vegetation, usually in woodland. Reduction of the wing area occupied by the pale patches with increasing latitude and altitude can be directly related to thermoregulatory constraints (see chapter 2), the most melanized individuals occurring in the coolest and cloudiest regions, such as the higher Pyrenees.

The geographic pattern of seasonal polyphenism can be related to patterns of habitat use and seasonal changes in these habitats. In southern regions, such as the southern part of the Rhône valley, the most frequently used habitats are open evergreen forest and ditches, and water-courses in very open agricultural areas. Unlike most northern habitats, which are chiefly dense deciduous and coniferous woodland, these are probably less seasonally variable in both colour and light intensity. Therefore, seasonal polyphenism, which may enhance background matching, is likely to be generally favoured in the north but not in the south.

Individuals from three Mediterranean regions—Spain, Italy, and Greece—differ, though they are in similar climatic zones. Three explanations may be offered to account for these differences. Firstly, they may all originate from a single source in the southern range of the species, variation between these geographic areas being related to local adaptation to differences in climate, predators, and habitat. Secondly, the present distribution of forms may be the result of colonization by distinct forms from two or more areas since the last major ice retreat some 15 000 years ago, each adjusting to current condi-

tions. Thirdly, variation may be the consequence of phenotypic plasticity with different environmental and/or climatic conditions producing different phenotypes (see section 8.5).

At present it is impossible to provide a definitive explanation for the pattern of variation throughout Europe or to provide an accurate post-Pleistocene framework of range expansion (see Dennis *et al.* 1991; section 10.5). However, it is possible that the species has spread from more than one geographic area. Examination of museum material and field work in July 1987 and 1988 reveals an apparent absence of phenotypes intermediate between *Pararge aegeria aegeria* and *P. aegeria tircis* in their main contact zone in southern France. In the Rhône valley the former subspecies is located in agricultural areas at low elevation and the latter at higher elevation in both agricultural and woodland habitats, the two forms occurring some 1–2 km apart. Similar patterns of distribution are recorded for other species and subspecies in southern Europe (see Dennis *et al.* 1991). This lack of intermediates may be explained by abrupt habitat differences but a comparison between chromosome numbers of *P. aegeria aegeria* ($N = 27$) and *P. aegeria tircis* ($N = 28$) (Robinson 1971) points to genetic dissimilarity between the two subspecies, perhaps indicative of different geographic origins. The lack of intermediates may then indicate hybrid inviability or the existence of premating barriers. However, the degree of genetic differentiation of these two forms is not quantified. It is possible that the phenomenon may be a more extreme example of the genital valve boundary phenomenon described for *Maniola jurtina*. The distance between *aegeria* and *tircis* is not great and may be traversed by flying individuals. Furthermore, these observations were made at the driest time of year when population density was low and damp areas for egg-laying scarce. At other times, particularly in spring, population density may be higher and with more abundant and widespread suitable larval resources, the distance between *aegeria* and *tircis* may be less.

The distribution of the various forms of *Pararge aegeria* is currently changing. In southern France there is some evidence that the southern European form is expanding its range northwards (Robertson, personal communication) perhaps in response to changes of landuse. In Sweden there are two

geographically separate races of different origin, a univoltine race from Finland and a bivoltine race from Denmark, the latter being recent colonists (Nordstrom 1955).

Pararge aegeria aegeria is a recent colonizer of Madeira, being first found on the island in 1967 by Høegh-Goldberg (Oehmig 1980). The impact of this colonizer on the endemic *P. xiphia* is of considerable interest. Lace and Jones (1984) suggest that it may replace the endemic species, citing the disappearance of *P. xiphia* from low-lying areas in the south of the island as tentative evidence of the 'taxon cycle' (Wilson 1961; Ricklefs and Cox 1972). In this cycle a recent colonist is supposed to be competitively superior to a resident species because the invading organism has escaped from its natural enemies whereas the resident has a suite of enemies. This effect is presumably thought to outweigh the closer adaptation of the resident to the environment.

More recent work (Owen *et al.* 1986; Jones *et al.* 1987; Shreeve and Smith, in press; Lace and Jones, in press) provides evidence of limited habitat partitioning and overlap and of potential competitive interactions between the two species. Because *Pararge xiphia* is more active in cool, and *P. aegeria* in warm temperatures (Shreeve and Smith, in press), the distribution of the two species changes with the season. *P. xiphia* tends to be most abundant in cool, high altitude laurel forest in summer but more dispersed into more open, lower pine forest and agricultural areas in winter. *P. aegeria* tends to be more common in low altitude warm habitats. Although there may be interactions between individuals of the two species in relation to mate-location (Lace and Jones, in press), competitive displacement of adults is unlikely as the larger endemic species tends to occupy canopy layers and the colonizer ground layers while engaging in patrolling and perching (see chapter 2). There is a possibility that interactions during development, perhaps via shared natural enemies have an effect on the dynamics of any interaction between the two species: larvae of both species can occur on the same foodplant (*Brachypodium sylvaticum*) when the two occur together. Whilst the exact nature of the interaction between these two species remains in doubt, changes in agri-

cultural practices may well have caused the loss of *P. xiphia* from low-lying areas before colonization of the island by *P. aegeria aegeria*.

The time of origin and establishment of *Pararge xiphia* on Madeira is not known. It is probable that this species, and *P. xiphioides*, are derived from *P. aegeria* or *P. aegeria*-like ancestors possibly from North Africa or southern Europe, the isolated populations then evolving into distinct, reproductively isolated species. The marked dissimilarity of these species from *P. aegeria* imply a relatively long period of isolation. However, the strength of past and present selection on the adult phenotype is not known; intense selection can cause rapid change and phenetic differentiation in isolation can be rapid (Dennis 1977). If change has been rapid it is possible that divergence of wing pattern of the different island species has occurred over a few thousand generations, though differences of other features of both island species, such as genitalia (Higgins 1975), larval morphology (Shreeve, personal observation), behaviour, and thermoregulation (Shreeve and Smith, in press; A. Smith, T. Shreeve, and M. Z. Baez, unpublished data) suggest a longer period of isolation (see section 10.5). Some of the Mediterranean island races are probably of more recent origin than the Atlantic island species. They may be the result of either recent colonization events, as perhaps in the case of the Balearics, or originate from earlier Pleistocene invasions.

Pararge is not unique in its complex pattern of variation and probable diverse origin of geographic races. Other equally complex patterns occur, for example in species of *Melanargia* (Higgins 1969; Descimon and Renon 1975; Wagener 1982; Mazel 1986; Tilley 1986), *Erebia* (Lorković and de Lesse 1954), *Lysandra* (de Lesse 1960, 1969, 1970), and *Hipparchia* (de Lesse 1951). In *Erebia* there are identifiable hybrid zones.

In this chapter studies of three species have been examined in detail to illustrate the processes of divergence, differentiation, and the formation of reproductively isolated forms of species. These issues are put into the wider historical perspective in chapter 10.