The Ecology of Butterflies in Britain

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Avoidance, concealment, and defence

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Fluctuations in abundance are a regular feature of butterfly populations. Most of these changes can be related either to the performance of egg-laying females (chapter 3) or to survival at each stage of the life cycle (chapter 4). Every stage differs in size, form, location, mobility, duration, and usually in its season of occurrence. Because of these differences each offers a different reward to a specific type of natural enemy, and presents it with particular problems of finding and handling. The different life stages, therefore, have different enemies. Those of the earliest stages tend to be arthropod predators and parasitoids, whereas later, larger and often more mobile stages tend to be difficult for these small enemies to handle. In contrast, vertebrate predators are not usually the major enemies of eggs and small larvae because they offer small reward to these consumers compared to the energetic cost of finding them. They tend to be the most important enemies of the larger stages. Predators and parasitoids can be divided into two major groups: generalists, which use many types of food, and specialists, which attack particular species or groups of related species. All life stages of butterflies are vulnerable to both types of enemy.

To escape from natural enemies each stage has its own suite of defences (Fig. 5.7). These can be divided into primary and secondary defence mechanisms. The function of the former is to avoid detection. They may involve four main categories:

(1) adjustments of the timing of appearance;
(2) changes in habitat use or location;
(3) behavioural or morphological adaptations; and
(4) mimicry or resemblance to an inedible food item.

Secondary defence mechanisms, on the other hand, enhance the ability to escape from an enemy once it has been detected. These commonly include mechanisms that:

(1) make it difficult for the enemy to handle the prey;
(2) confuse or startle the predator or parasitoid; and
(3) cause distastefulness or toxicity.

This chapter discusses the effectiveness of these mechanisms in each of the various stages of butterfly life cycles.

5.1 Adult defences

5.1.1 The predators of adults

Of all the stages in the life cycle, the adult butterfly is the most active, whilst at the same time comprising the smallest number of individuals. Because of their generally conspicuous feeding, mate-location and egg-laying activities, adult butterflies have a unique set of problems in evading predators. Not only must they avoid predators when active but also when inactive, either during unsuitable weather conditions or when roosting. Predators may be more numerous in favourable habitats which support high densities of adults than in less favourable habitats where the reward for any particular predator is low. The most common predators of adults are vertebrates, most of which hunt in specific sites at particular times. Therefore, the risks for an adult differ with location and time of day.

Weather affects the activity of adults and predators in different ways. Cool weather inhibits butterfly activity while increasing the energetic requirements of warm blooded predators, but warm weather can act inversely. There is some evidence that survival rates of butterflies, such as the meadow brown *Maniola jurtina* (Brakefield 1982*b*), are lower when the flight seasons are hot and dry. Work on the monarch *Danaus plexippus* and sulphur butterflies (*Colias* spp.) in North America suggests that longer and more intensive periods of adult activity, likely to be associated with such conditions, may lead to more rapid wing wear and exhaustion of energy reserves (Watt *et al*. 1974; Brown and Chippendale 1974).

Although invertebrates such as spiders and dragonflies can take substantial numbers of butterflies (see Moore 1987), birds and lizards are recognized as their principal predators. There are, however, remarkably few observations of actual predation taking place (e.g. Ford 1945; Brockie 1972; Bengtson 1981). In studies of selective predation on the black and pale forms of the peppered moth *Biston betularia*, Kettlewell (1973) released the moths and directly observed their predation by birds. However, in these experiments there are problems of interpretation, as there was a higher density of released moths than would occur in the wild, and the resting positions on trees of many of the released moths were unnatural (Brakefield 1987*a*). Direct observations of predation on other species are rare. However, Chai (1986) has made careful observations of jacamar birds taking a variety of butterflies in flight in Costa Rica. Brower and Calvert (1985) estimated that orioles and grosbeaks took over two million butterflies or nine per cent of an overwintering colony of *Danaus plexippus*. Melling (personal communication) showed that 90 per cent of meadow pipit *Anthus pratensis* droppings on a Northumberland moor contained wing-scales, most probably of the large heath *Coenonympha tullia*, and perhaps of the small heath *C. pamphilus* and *Maniola jurtina*.

Another approach to collecting information about predation by birds and lizards is by examining wing damage. Sometimes butterflies are captured with clear impressions of beak-marks on the wings (Fig. 5.1). Usually the evidence is less clear cut. Many workers have discussed the analysis of different patterns of wing damage; some of which are probably consistent with predator attacks (see Bowers and Wiernasz 1979; Robbins 1980, 1981). However, the interpretation of data describing such damage is fraught with difficulties, especially because damage is indicative of a successful escape from a predator and not of mortality due to a predator. It is impossible to relate the data directly to the ratio of successful to unsuccessful attacks. Chai's (1986) observations of jacamars suggest that successful attacks may frequently outnumber, or even far outweigh, unsuccessful ones which result in wing damage. It is also difficult to use wing damage data to compare the levels of predation in different populations or on different morphs. The incidence of wing damage will depend on the length of time that individuals are exposed to predators as well as on the rates of predator attacks for each of the activity states of the butterfly. Edmunds (1974*a*) emphasizes similar problems when comparisons are made between species. Nevertheless, the almost universal incidence of wing damage (of a form consistent with vertebrate predator attacks) in large samples of butterflies from a wide variety of species is convincing evidence for the general importance of mortality due to vertebrates, especially birds.

5.1.2 Camouflage as a defence against vertebrates

Studies of butterfly mating and courtship show that the general colour of the wings, including ultraviolet reflecting areas, are important in communication between the sexes and the discrimination of mates (see section 2.4), but there is little evidence that the *details* of pattern play any substantial role in mate-location or mate-choice (Silberglied 1984). The general distribution and amount of dark melanin pigments and pale pigmentation on the wings of many butterflies is involved in thermoregulation (see chapter 2). Thus sex and climate play a role in wing pattern evolution. However, when the details of wing pattern elements and of their arrangement are considered, then undoubtedly the influences of visual predators are the most important factors shaping their evolution and general diversity.

It has recently been demonstrated by Bowers *et al*. (1985) for a North American fritillary, *Euphydryas chalcedona*, that bird predation can bring about rather subtle differences in colour pattern in a natural population of the butterfly. They demonstrated differences in colour pattern between 309 butterflies that had been attacked and eaten by birds (leaving detached wings), and a representative sample of 296 live butterflies from the same popula-

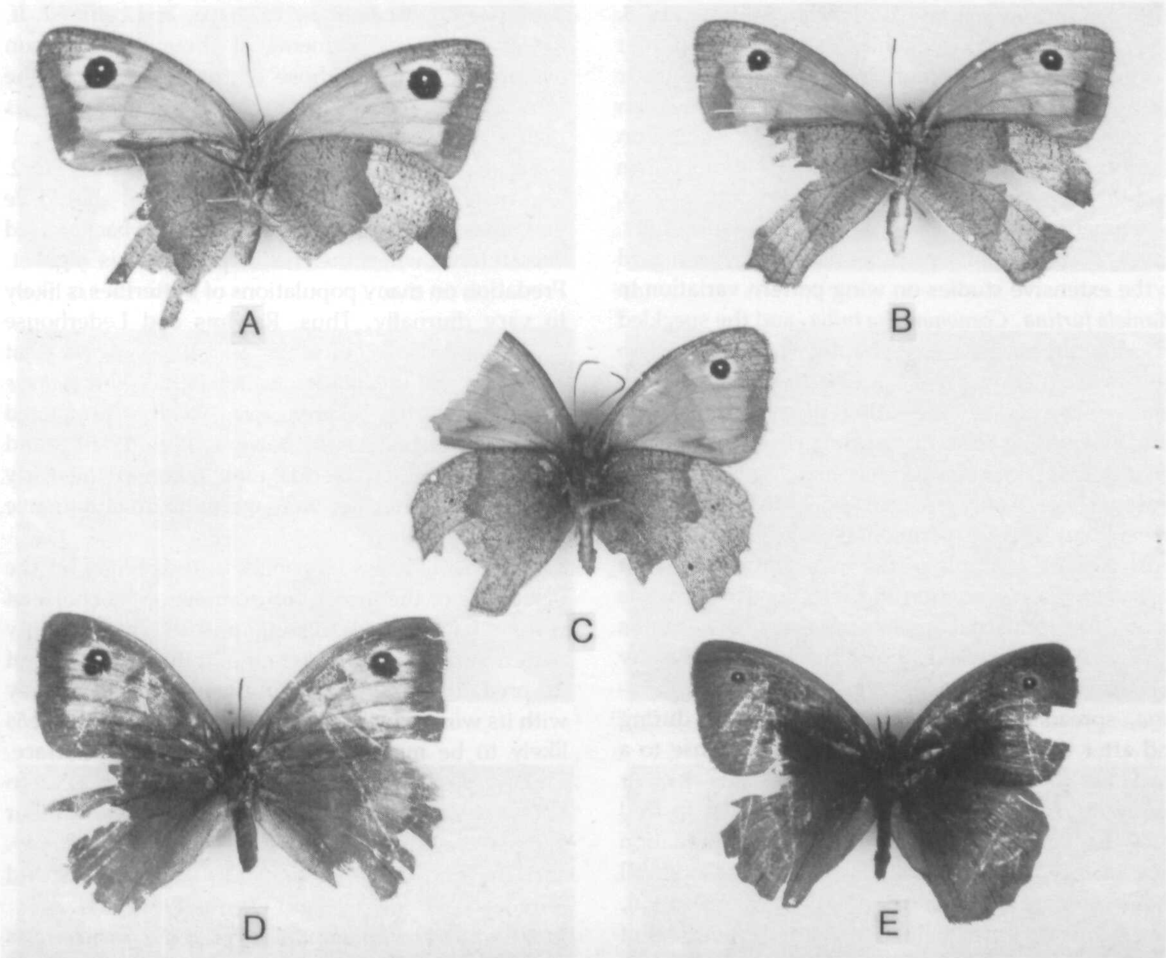


Fig. 5.1 Examples of wing damage found in wild-caught butterflies. Part of a sample of 29 meadow brown *Maniola jurtina* collected along a line of poplar trees on a coastal dyke on Goeree Overflakee in The Netherlands (A, B, and C show the ventral surface; C and E are males). Some of the specimens show clear evidence of partial evasion of attacks by vertebrate predators. Many insectivorous birds were feeding along the dyke. D and E have clear imprints of the bills of birds. C has had the one forewing tip cleanly cut off by a bird. The symmetrical damage to the hindwings of A and B is consistent with attacks by birds on butterflies at rest with their wings closed.

tion. In particular, birds attacked the palest individuals, independent of their age, and they also took proportionately fewer males.

The colour and pattern of the wings of many species can be described as camouflaged, thus enhancing the ability of the species visually to resemble its resting background making it difficult to be detected by a predator. Where species with such cryptic wing surfaces have been tested or bioassayed for palatability to vertebrate predators there has been little or no evidence of any chemical defence or distastefulness. Such studies have involved a wide variety of butterflies, usually in comparisons with warningly-coloured or aposematic species protected by a chemical defence (reviewed by Brower 1984; see Bowers and Wiernasz 1979).

The adaptive significance of cryptic coloration has been demonstrated by numerous experimental studies using a variety of organisms (Endler 1978, 1980, 1986). Such work has usually shown that colour forms which more closely resemble their resting backgrounds have a higher survival rate than more conspicuous ones. Although two studies on European species have involved colour dimorphism in butterfly pupae (Baker 1970; Wiklund 1975), experiments have not been performed with adults. These would be most valuable not least with regard to the extensive studies on wing pattern variation in *Maniola jurtina*, *Coenonympha tullia*, and the speckled wood *Pararge aegeria* (see chapter 9). Indeed, these studies frequently invoke a selective influence on relative crypsis of the different phenotypes by visually-hunting predators as the major process producing geographical variation in wing pattern. At present there is only circumstantial evidence for this rather than direct experimental demonstration. The most striking example of the association of habitat with changes in predation and selection for crypsis is given by industrial melanism in many moths (reviewed by Brakefield 1987*a*). Black forms of many species, including the peppered moth *Biston betularia*, spread through most cities in Britain during and after the industrial revolution in response to a blackening of their resting backgrounds by air pollution. They are more difficult for birds to find than the paler, wild-type forms. Many predation experiments, beginning with those of Kettlewell (1973) involving direct observation of predation, have confirmed the qualitative switch in survival of the forms from rural to industrial environments. Some present-day declines in the frequencies of the dark forms are associated with reduced air pollution and changes in resting backgrounds.

Crypsis involves a variety of components of colour and pattern, which have only recently been fully recognized. It involves being inconspicuous to a predator which effectively does not recognize the received image as being potential prey. Endler (1978) provides a useful definition: 'a pattern is cryptic if it resembles a random sample of the background perceived by the predator at the time and age, and in the microhabitat where the prey is most vulnerable to visually-hunting predators'.

Crypsis is maximized in relation to colour and pattern when the image of the insect represents a random sample of the components of its resting background. This randomness must extend to components of colour, size, shape, and contrast. If, for example, the elements of the pattern are on average larger than those of the background, the insect will stand out even if these same elements match it in terms of colour, shape, and contrast. Examples of these effects are illustrated in Fig. 5.2. The matching of insect and background should be maximized with respect to the resting background encountered when the risk of predation is highest. Predation on many populations of butterflies is likely to vary diurnally. Thus, Rawlins and Lederhouse (1978) and Lederhouse *et al*. (1987) found that predation on the black swallowtail *Papilio glaucus* occurred during evening or weather-prolonged roosting. Kingsolver (in Bowers, *et al*. 1985) found that predation on pierids took place in the early morning as butterflies were warming up and unable to fly.

The effectiveness of crypsis also depends on the behaviour of the insect, for example on its choice of resting background, resting posture, and activity pattern, and on the behaviour and hunting tactics of its predators. If a butterfly always rests inactively with its wings closed then the ventral wing surface is likely to be more cryptic than the dorsal surface. Thus, crypsis is not merely an attribute of pattern but is an interaction between the insect's colour pattern, resting background, behaviour, and activity, and the behaviour of predators (see Dennis and Shreeve 1989; Shreeve and Dennis 1991).

A frequent component of cryptic colour patterns is the presence of disruptive markings or bands crossing the wings and bisecting their edges. These are thought to function in breaking up the outline of the insect when at rest (see Cott 1940). They are particularly well developed in the admirals, including *Ladoga camilla* in Britain. This species has white bands crossing both dorsal and ventral wing surfaces. They contrast most highly with the background colour on the dorsal surface which is exposed in dorsal basking behaviour (see chapter 2). Silberglied *et al*. (1980) examined the proposed function of disruptive bands in a tropical nymphalid, *Anartia fatima*, a study made on the assumption that the white band was conspicuous rather than a normal part of the background. Silberglied and co-workers, captured individuals in a natural population releasing them again after either painting out the white band or adding a black 'control' stripe over

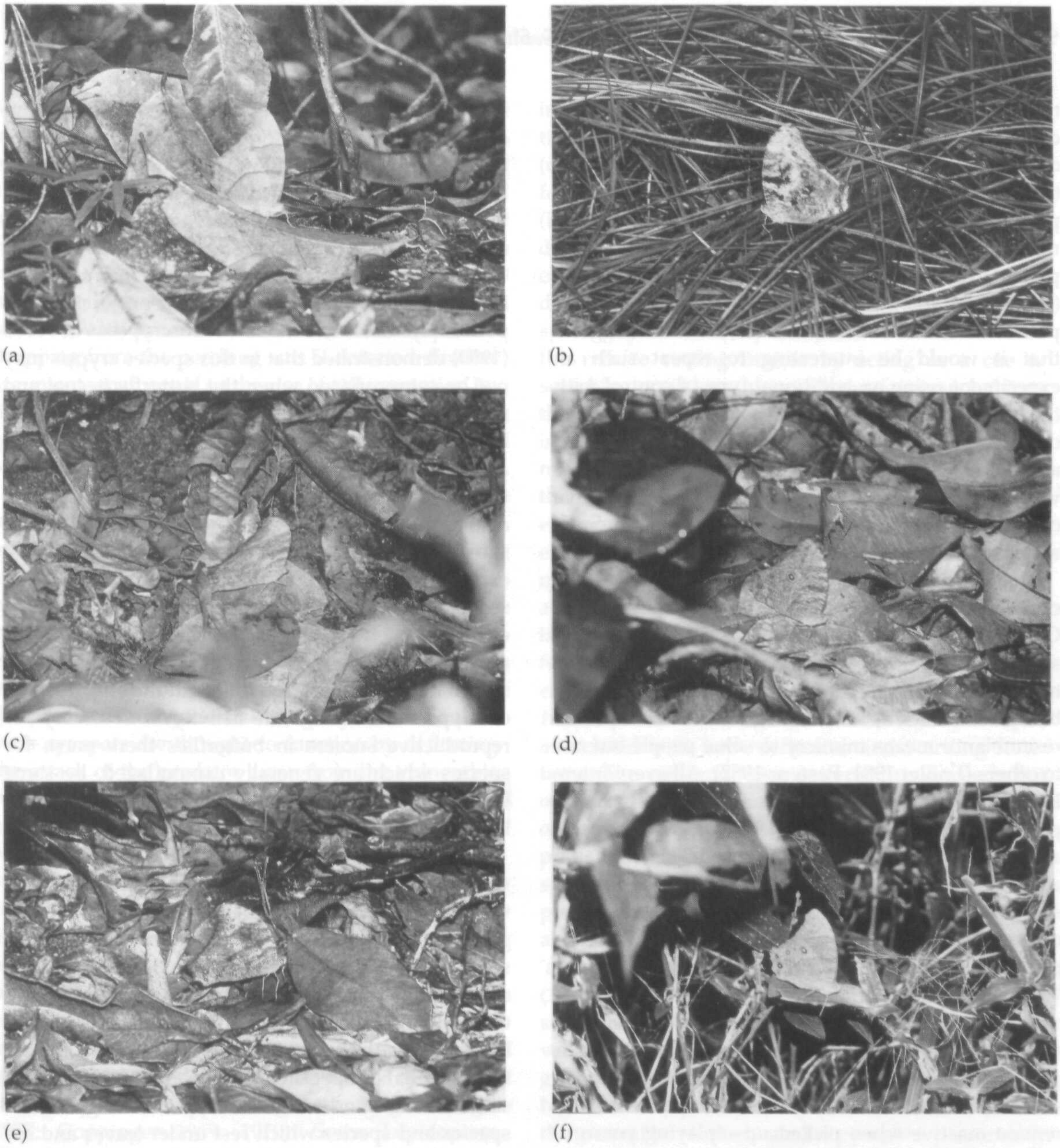


Fig. 5.2 Some components of crypsis illustrated by seasonal forms of the evening brown *Melanitis leda* taken from the Shimba Hills of Kenya. The three on the left are representative of the excellent background matching of the brown-coloured dry season form of the butterfly when in its usual resting place among dead brown leaves on the forest floor. (b) Shows an individual of the dry season form resting on the floor of a conifer plantation. There is an obvious loss of crypsis due to a mismatching between the shape and size of the butterfly and the background of dead pine needles. The matching, in terms of the generally brown colour of the wings and the needles, remains close. The four individuals shown of the dry season form illustrate the characteristic variability in the details of the colour pattern in this form which may reduce the chance of a predator developing a search image for it. (d) and (f) are of the wet season form with a finely striated pattern and submarginal eyespots. The latter may be prominent to a searching predator when this form is at rest on dead brown leaves because of the absence of this type of feature in the background (d). When this form is at rest among the carpeting green herbage typical of the wet season (f), crypsis is poor because of a mismatch in colour and the eyespots probably serve a deflective function.

the dark ground colour. Unfortunately there was no difference in survival or in the incidence of wing damage between the experimental and control butterflies. There is therefore, no direct evidence supporting a disruptive function. The lack of positive results may have been due to the conversion of the pattern to that of a locally aposematic species (Waldbauer and Sternburg 1983) or from one cryptic pattern to another (Endler 1984). Endler suggests that it would be interesting to repeat such an experiment using an additional type of control with the band painted out as before but with an additional one of similar dimensions and colour pattern painted along the wing edge. This would help to determine whether such a band is conspicuous and disruptive or represents a normal part of the background. Such an experiment could be done with *L. camilla*.

The above discussion of crypsis has referred to cases of a general resemblance to the background. Cott (1940) and others make a distinction between such general resemblance and examples of specific resemblance to a particular component of the background such as leaves, twigs, and so on. Specific resemblance means mimicry to some people but not to others (Endler 1981; Pasteur 1982). All overwintering adults in Britain (e.g. comma, *Polygonia c-album*, peacock, *Inachis io*, brimstone, *Gonepteryx rhamni*) are leaf-mimics, in pattern and colour, if not shape, and resemble the background of their overwintering sites. To some extent they have other, secondary, defence mechanisms which operate when the primary mechanism of leaf-mimicry fails. Vane-Wright (1986) documents the hissing sound produced by wing-rubbing in overwintering *I. io*. This may startle a predator or even mimic the sound of a predator, such as a weasel or owl. Dennis (1984*a*) describes the way in which disturbed adult *G. rhamni* remain inactive when picked up—'playing possum' (thanatosis)—with a rigid body and tucked in legs. This behaviour may make prey recognition less likely. In this, and other overwintering species, the chance of predators failing to recognize the adult as prey may be enhanced by wing-toughness. This behaviour may also cause handling problems for the predator, thus facilitating escape.

The resting posture of a butterfly may be a compromise between crypsis and other behaviours. The grayling *Hipparchia semele* may provide an example. Findlay *et al*. (1983) demonstrated the importance of resting posture, involving body-orientation and wing-tilting, in relation to exposure to incident solar radiation and thermoregulation. Longstaff (1906) believed that the behaviour of tilting the closed wings closer to the ground aided concealment by minimizing the shadow. Observations by Findlay *et al*. suggest that thermoregulation is the primary function but they did not exclude the possibility of interactions with crypsis. Shreeve (1990) demonstrated that in this species crypsis may not be compromised when the butterfly is cool and most vulnerable to predation. In cool conditions the butterfly basks on the warmest substrates available and it is these against which the hindwing phenotype is most cryptic. When the butterfly is fully active and warm, it tends to settle on other substrates against which it is less cryptic and exploits other defence mechanisms, such as secondary flash coloration involving the forewing eyespots together with evasive flights. In most cases movement by a resting butterfly will tend to attract a searching predator and so diminish the effectiveness of crypsis. Since daytime activity is necessary for reproductive success in butterflies there must, for species which are generally camouflaged, be some balance between effective crypsis at rest and a breakdown of crypsis during spells of activity.

Endler (1984) measured and compared the cryptic wing patterns of a community of North American woodland moths with that of their resting backgrounds from analysis of photographs of each species taken at rest in nature. He showed that moths are on average more cryptic at the period of their normal flight time on their normal resting backgrounds than on other backgrounds available in their habitats. Specialist species which rest on a single background are more cryptic than generalist species and species which rest under leaves and are not visible from above are not very cryptic. It would be fascinating to apply this technique to butterfly communities such as those of grasslands or woodlands in Britain or to the satyrine species, discussed in chapter 9, which have variable wing patterns.

The vulnerability of a resting individual may also be related to the microclimate and position of its roosting site. At night, ground temperatures are generally lower than at sites higher in the vegetation. Sites near the ground are also more humid than those higher up. Thus any individual which roosts in high vegetation remains potentially active for longer in the evening and is likely to become active earlier in the day than one which roosts low down. Therefore, the use of particular roosting sites can influence how long an individual is exposed to predators when it is inactive. Dennis (1986*a*) suggested that the wall brown *Lasiommata megera* roosted in high positions to enable evening and early morning activity and also to facilitate escape, by dropping from the perching site, if detected. Similar arguments may apply to the use of tall vegetation by the orange-tip *Anthocharis cardamines* and prominent grass stems by species such as the Glanville fritillary *Melitaea cinxia* (Willmott 1985).

If crypsis is not successful in overcoming the prey-recognition of a searching predator then some butterflies may have a second line of defence which can be effective even if they are unaware of the predator and cannot or do not escape by flight. For example, small, often not fully differentiated, eyespots on the margins of the wings of many species may be components of crypsis except when the predator is very close. If the prey is located then such eyespots are thought to function by deflecting the attack of the predator away from the vulnerable body towards the wings (see Fig. 5.2). The butterfly may then escape, albeit having lost a portion of wing-tissue. The relatively thin wing-margins of such species may facilitate escape (Dennis *et al*. 1984). Erratic flight, exhibited by many species, will also reduce the probability of any further attack. Many British butterflies exhibit submarginal spots on the ventral wing surface which is exposed when at rest. More fully differentiated and larger eyespots are often hidden at rest. They may be suddenly or quickly exposed on disturbance, startling or confusing a predator and causing it to withdraw (Blest 1957; Coppinger 1969, 1970). Some Lepidoptera show this type of 'flash' display associated with patches of bright colour rather than eyespots, though large eyespots are frequently associated with bright patches of colour. The striking eyespot pattern of *Inachis io* is of this type and may be exposed by suddenly opening and closing the wings. This display is also associated with an audible scraping or hissing sound made by the inner margins of the forewings rubbing against the costal margin of the hindwings.

Predation by birds has been implicated as an important selective influence on intraspecific variation in *Maniola jurtina* and *Coenonympha tullia* (chapter 9). Figure 5.3 illustrates a model developed for *M. jurtina* but it is more widely applicable (Brakefield 1984). The balance of selection on the development of wing spots is considered to depend on interactions between several factors. In habitats dominated by linear shapes (i.e. uniform grassland) spots may be relatively conspicuous and so increase the risk to resting insects by acting as a cue to searching predators. In more heterogeneous habitats this constraint may be lessened. More active individuals which frequently change their position may tend to attract predators through movement. In this type of situation the deflective function of eyespots may be paramount. The more strongly expressed ring of submarginal spots exhibited by male *M. jurtina* is consistent with their higher activity levels than females (Brakefield 1982*a*). The larger and more contrasting forewing eyespot of females is hidden at rest. It may sometimes be exposed on disturbance in a similar way to that of *Hipparchia semele* (Tinbergen 1958). It may then be associated with both deflective and startling functions. The optimum spot pattern thus depends not only on the nature of resting backgrounds but also on insect activity rhythms and their exposure to predators. The model for species showing variable spot patterns suggests that shifts occur between populations in the balance between 'passive' crypsis and reliance on eyespots in deflection and other 'active' anti-predator functions. Work by Young (1979, 1980) on Neotropical *Morpho* butterflies suggests that those species with well-developed, ventral eyespot rings feed on rotting fruit on the ground and are thus exposed to a particular type of high intensity predation. Species that seldom rest on the ground have much smaller eyespots, presumably because larger ones would disrupt their crypsis when at rest on foliage.

Another probable type of deflective device occurs in several British hairstreaks. These have wing tail filaments at the anal edge of the hindwing. A strong clue to their deflective function comes from research on more fully developed systems of this type occurring in many tropical lycaenids (Fig. 5.4). In the most striking examples, longer pairs of tail filaments and well-marked radiating lines occur together with small eyespots close to the anal corner. This is the

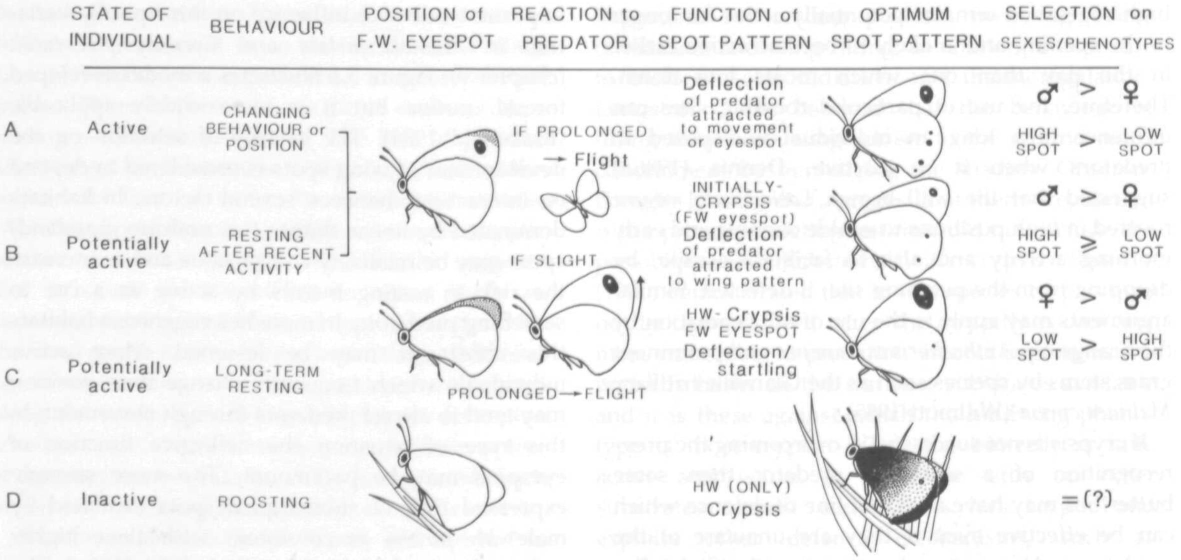


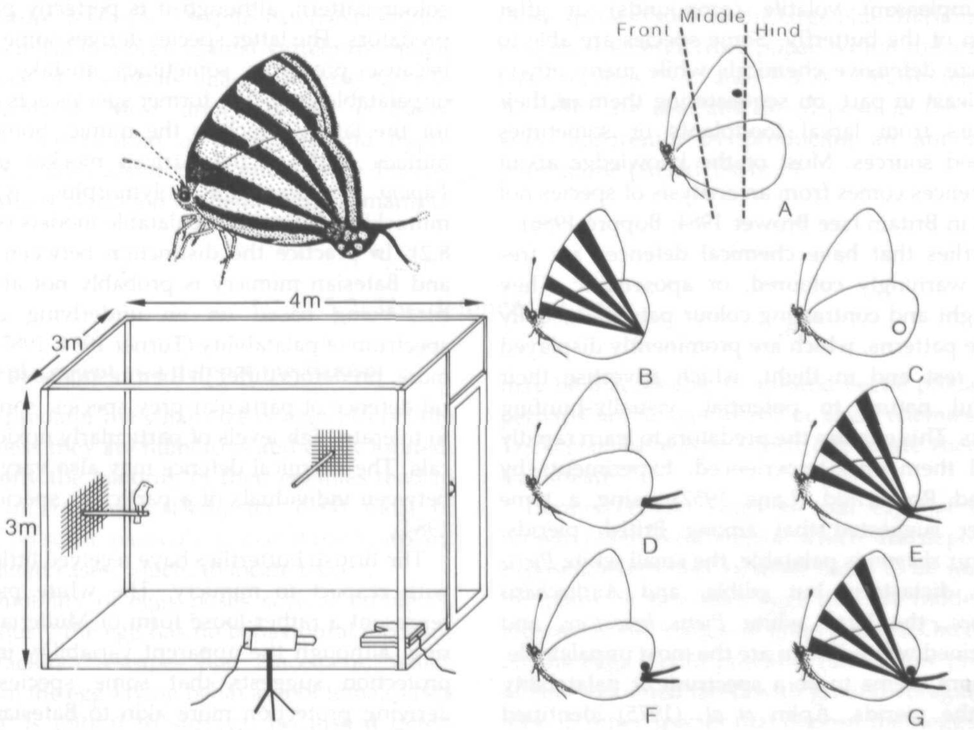
Fig. 5.3 A model to account for the phenotypic variation in the pattern of wing spotting in the meadow brown *Maniola jurtina* and other satyrinae. Four activity states are labelled A to D on the left. An outline of butterfly behaviour and of the proposed mechanism of visual selection involving predators follows for each state, from left to right. The final column indicates predictions about the relative fitness of the wing pattern of the sexes and of spotting phenotypes of *M. jurtina* in relation to the model. (After Brakefield 1984; courtesy of Academic Press.)

so-called 'false-head' pattern considered to involve false antennae and eyes with the radiating lines attracting attention towards this image. The field studies of Robbins (1980, 1981) provide strong support for the effectiveness of the false-head in combination with associated patterns of adult behaviour on alighting from flight in deflecting predator attacks away from the body and true head. Riley and Loxdale (1988) have demonstrated that the twisted structure of the tail, as in the tropical butterfly *Arawacus aetolus*, better simulates antennal movement in air currents than an untwisted form, thus accentuating false-head deception. A recent experimental study by Wourms and Wasserman (1985) involving analysis of video recordings of the responses of captive jays to pierid butterflies painted with different combinations of the various elements of the false-head system provides especially compelling evidence for the proposed functional components of the pattern. Figure 5.4 includes a subset of their data which demonstrates that a small eyespot in the outer-anal part of the hindwing produces a significant increase in attacks to this wing area (i.e. deflections). This element and other components of the pattern also changes the way in which the butterfly is handled by the bird. Butterflies with the complete pattern were more likely to escape during handling by the predator.

The false-head device of the British woodland hairstreaks is far less developed than in other species with wing-tails. It presumably has some deflective function at very short distances while complementing crypsis at longer distances. It may also be poorly developed in British species because of constraints imposed on escape by cool weather and the tensile strength of a tail filament (R. Dennis, personal communication). Butterflies with longer tails may be more vulnerable to capture and less able to escape when inactive in cool conditions.

5.1.3 Chemical defences and warning coloration

The adults of many species of butterfly are protected by a chemical defence often involving more than one type of compound. Two important groups of noxious chemicals are cardenolides and pyrrolizidine



Type	Wing marking	Areas of attacks (%)			Areas of handling (%)		
		Front	Middle	Hind	Front	Middle	Hind
A	Controls	49	35	16	51	35	14
B	Lines	41	34	25	25	32	43
C	Eyespots	59	4	37	28	33	39
D	Tails	33	26	41	33	26	41
G	Complete	36	32	32	16	19	65

Fig. 5.4 An experimental analysis of some anti-predator functions of butterfly wing markings during feeding by birds. The components of the 'false-head' pattern were analysed by Wourms and Wasserman (1985). This wing pattern is commonly found in lycaenids including the tropical species *Arawacus aetolus* which is illustrated. Eyespot, convergent lines, tail and anal-spot components were painted on white *Pieris rapae* in the combinations A to G as indicated. The dead butterflies were fed singly to five blue jays *Cyanicitta cristata* using special presentation devices in aviaries of the design shown. The positioning on the wings of feeding attacks by the birds and the birds' subsequent handling of the butterflies in their bills was recorded on videotape for later analysis. A subset of the results of this analysis is shown in the table below. The difference in the areas of the wings attacked between the painted butterflies and the unpainted controls (type A) was only statistically significant for butterflies having an added eyespot. All such differences were significant when the location of strike points during handling was analysed. (After Wourms and Wasserman 1985, courtesy of the Society for the Study of Evolution; Robbins 1981, courtesy of the *American Naturalist* and Chicago University Press.)

alkaloids. The defence may act either before (as in many unpleasant volatile compounds) or after ingestion of the butterfly. Some species are able to synthesize defensive chemicals while many others rely, at least in part, on sequestering them or their precursors from larval foodplants or sometimes adult food sources. Most of the knowledge about such defences comes from an analysis of species not resident in Britain (see Brower 1984; Boppré 1986).

Butterflies that have chemical defences are frequently warningly coloured, or aposematic. They have bright and contrasting colour patches, usually in simple patterns, which are prominently displayed both at rest and in flight, which advertise their distasteful nature to potential, visually-hunting predators. This enables the predators to learn rapidly to avoid them once experienced. Experiments by Lane and Rothschild (Lane 1957) using a tame flycatcher suggested that among British pierids, *Gonepteryx rhamni* is palatable, the small white *Pieris rapae* is distasteful but edible, and *Anthocharis cardamines*, the large white *Pieris brassicae*, and green-veined white *P. napi* are the most unpalatable. Thus, there seems to be a spectrum of palatability among the pierids. Aplin *et al*. (1975) identified probable noxious chemicals—glucosinolates—in different life stages of *P. brassicae* and, at lower concentrations, in *P. rapae*. They also occur in their brassica foodplants. Work is lacking on other groups in Britain such as the fritillaries and nettle-feeding nymphalids which may have some chemical protection and associated warning coloration.

Many brightly coloured insects show striking similarities in colour pattern to other species. Such similarities are characteristic of the phenomenon of mimicry (reviewed by Turner 1984). Two basic forms of mimetic resemblance have long been recognized. Müllerian mimicry occurs between two or more species (called a mimicry ring), each of which is warningly coloured and protected by some noxious compounds. Müllerian mimics exhibiting the same warning coloration derive mutual benefit in terms of lower mortality. Their resemblance to each other increases the efficiency of predators in learning to avoid the unpalatable prey because their rate of encounter with that particular colour pattern will be higher than if each of the different prey species had different colour patterns. In contrast, Batesian mimicry involves one (or more) species that exhibit warning coloration and another that has the same colour pattern, although it is perfectly palatable to predators. The latter species derives some protection because predators sometimes mistake it for the unpalatable prey. The former species acts as a model for the latter, which is the mimic. Some Batesian mimics, such as the African mocker swallowtail *Papilio dardanus* are polymorphic, with forms mimicking different unpalatable models (see section 8.2). In practice the distinction between Müllerian and Batesian mimicry is probably not always clear cut, being based on an underlying continuous spectrum of palatability (Turner 1984; 1987). Furthermore, predators differ in their response to the chemical defence of particular prey species; some are able to tolerate high levels of particularly noxious chemicals. The chemical defence may also vary in quality between individuals of a particular species (Brower 1984).

The British butterflies have received little attention with respect to mimicry. The white pierids may represent a rather loose form of Müllerian mimicry ring, although the apparent variability in chemical protection suggests that some species may be deriving protection more akin to Batesian mimicry (see above). The satyrine marbled white *Melanargia galathea* may also be a Batesian mimic of pierids, as it has a similar colour pattern and behaviour to the chemically defended pierids (Dennis and Shreeve 1988). The classic studies of mimicry in butterflies have concerned tropical species, especially *Papilio* spp. in Africa and Asia, and *Heliconius* spp. in South America (Turner 1984, 1987). Müllerian mimicry in Britain is probably best illustrated by groups of day-flying burnet moths (Rothschild 1984), bumble-bees (Plowright and Owen 1980), wasps, and ladybird beetles (Brakefield 1985). Hoverflies are also good examples of Batesian mimics of bees (Heal 1982).

Predators such as spiders (Moore 1987) and dragonflies, and parasites such as ceratapogonid midges (Lane 1984) are likely to cause substantial mortality in many populations of adult butterflies. In many cases they are able to eat with impunity species that are highly unpalatable or toxic to birds. Some form of visual recognition is likely to be employed by stalking or hunting predators such as crab spiders and hornets. However, it seems unlikely to involve details of wing patterns. There is little knowledge of what appears warningly coloured or cryptic to such species, but this may provide a fertile area for future research. Despite extensive knowledge of chemical defences against vertebrate predators the role of chemicals against invertebrates is little understood. Most understanding is based largely on identification of chemicals and hypothetical inferences about their effects (see Brower 1984). A partial exception is chemomimetic manipulation of ants which probably includes adults of those species (such as the large blue *Maculinea arion*) that must emerge from pupae within the ant colony (see sections 5.4 and 7.3.3). *Ogyris* females in Australia are also able to oviposit in the midst of ants, apparently by producing an ant dispersal pheromone (Atsatt 1981*a*,*b*).

5.2 The defences of eggs

5.2.1 Egg-placement as a defence mechanism

To a large predator the small size of eggs offers little reward unless they are numerous and easily located. Consequently the majority of their enemies tend to be other invertebrates (Dempster 1984) most of which rely on scent, particularly that of the hostplant and, in limited cases, touch, to locate food.

The immobility of eggs poses several problems, most obviously the egg has no behavioural mechanisms to facilitate escape. Egg placement, which results from the egg-laying behaviour of females (see chapter 3), is critical to survival because it determines their availability to particular types of predators and parasites. Among the grass-feeding butterflies (Satyrinae and some Hesperiidae) there is considerable variation in the placement of eggs (Wiklund 1984; Table 5.1). Most of those species (e.g. *Maniola jurtina*, *Melanargia galathea*) which use open habitats that are maintained by grazing herbivores, tend to attach their eggs either to the basal parts of hostplants or they drop them on the ground, on litter, or in vegetation adjacent to suitable grasses. By contrast those species (e.g. Lulworth skipper *Thymelicus acteon*, *Pararge aegeria*) associated with grasses growing in areas where grazing is infrequent tend to attach their eggs higher on hostplants. While egg placement by such species may have evolved partly in relation to grazing, the pattern of placement exposes eggs of different species to different enemies. Eggs on the ground or in litter are vulnerable to free-roaming generalists, such as some beetles, bugs, and ants, but those attached to leaves may be more vulnerable to more specialist enemies. For instance, the eggs of the small skipper *Thymelicus sylvestris* and *T. lineola* which are placed in the rolled leaf sheaths of flowering stems of several grasses may be inaccessible to ant and beetle predators but perhaps not to specialized or small enemies such as *Trichogramma* wasps which can locate them in the leaf sheath.

Dennis (1983*c*) suggests that eggs of the wall brown *Lasiommata megera* which are deposited on exposed leaves may be more likely to be washed off the plant by rain than eggs that are hidden in the recesses at the margin of grass clumps. Once washed off the eggs would probably have a low probability of survival when faced with ground-foraging predators. In other species that deposit their eggs on leaf-litter such a position for the egg may be advantageous. Both the pearl-bordered fritillary *Boloria euphrosyne* and small pearl-bordered fritillary *B. selene* lay eggs on dry leaves adjacent to hostplants as well as on the plants themselves. By placing eggs in a variety of microclimates they may ensure a variable period of egg development. Such a strategy could be a form of risk spreading, exposing eggs (and emergent larvae) to enemies for a variable time and also to different suites of enemies. Eggs on plants may be less exposed to free-roaming and ground-dwelling predators while those on the ground or on the hostplant may be more likely to escape from parasitoids and predators which locate their prey by searching the larval hostplant.

Eggs that are attached to a substrate have a form of defence which is unavailable to those more generally scattered by females. Ants can be important predators of many eggs, but attached eggs may pose problems of removal. For instance, eggs of *Pararge aegeria* on the underside of the leaves of cocksfoot grass *Dactylis glomerata* are more easily levered off by individual foraging workers of the ant *Lasius niger* than are those attached to the underside

Table 5.1 Egg placement of British grass-feeding butterfly species in relation to possible grazing effects

Species	Egg-placement	Height (cm)	Hostplant sites	Vulnerability to grazing
Carterocephalus palaemon	Attached singly to leaf underside	5–20	Ungrazed edges	Low
Thymelicus sylvestris	Small batches within rolled leaf sheaths	10–30	Ungrazed woodland and scrub edges	High
Thymelicus lineola	Small batches within rolled leaf sheaths	10–30	Ungrazed woodland and coastal marshes	High
Thymelicus acteon	Small batches within rolled leaf sheaths	10–30	Ungrazed grassland	High
Hesperia comma	Attached singly to leaf blades, stems and shoots	0–2	Grazed and broken areas of chalk grassland	Medium
Ochlodes venata	Attached singly to leaf blades	5–20	Ungrazed edges, open grassland	High
Pararge aegeria	Attached singly to leaf underside	1–25	Ungrazed woodland in sun and shade	Low
Lasiommata megera	Attached singly, mostly to leaf underside and basal shoots	1–25 (most low)	Recess areas in sun	Medium
Erebia epiphron	Attached singly to leaf blades	1–5	Grazed moorland	High
Erebia aethiops	Attached singly to blades within tussocks	5–20	Ungrazed areas of damp grassland	Low
Melanargia galathea	Unattached, dropped by settled female	0	Field and woodland edge sites, some sites grazed	Low
Hipparchia semele	Attached singly in low-medium density patches, on shoots, roots and litter	0–2	Dry dune-slacks, scree, downland	Medium
Pyronia tithonus	Attached singly to leaf blades	5–20	Sheltered tall, shaded, edges	Low
Maniola jurtina	Attached singly or dropped in basal plant parts	0–5	Various, includes tall and short grassland	High
Aphantopus hyperantus	Unattached in basal plant parts	0–5	Open, part shaded, tall grassland	Low
Coenonympha pamphilus	Attached singly to leaf blades	0–5	Short, grazed grassland	High
Coenonympha tullia	Attached singly to leaf blades	5–20	Ungrazed or part grazed moorland and mosses	Low

See Appendix 1 for hostplants.

of wood false-brome *Brachypodium sylvaticum* (Shreeve, personal observation). This is probably because the wider spaced and less prominent veins on the leaves of *B. sylvaticum* permit firmer attachment than do the closer, more pronounced veins of the former. However, strength of attachment may not always be of significance in deterring ants; they are reported eating through the top of eggs of *Maniola jurtina* and leaving the base (Brakefield, personal observation). Strength of attachment and the nature of the substrate to which the eggs are attached may also be critical to the survival of eggs of species with a long, overwintering egg stage, such as the white-letter hairstreak *Satyrium w-album*, purple hairstreak *Quercusia quercus*, and high brown fritillary *Argynnis adippe*.

5.2.2 Physical and chemical defences of eggs

Egg placement is important for escaping detection but egg colour or contrast is only relevant to visually-hunting enemies. This relationship between egg colour, placement, and the method of detection by natural enemies may partly explain why long-lived eggs are placed singly and tend to be visually cryptic (as in black hairstreak *Satyrium pruni* and in *Argynnis adippe*). Such eggs may well be apparent to invertebrate predators but these have minimal winter activity. Eggs of many species which are laid singly and develop directly, tend to resemble the general background colour and pattern of the area in which they are deposited. Similarly, clustered eggs with no secondary defences, which offer a rich reward to all types of enemies, are often located on leaf undersides, where they are difficult to detect by eye because of their position and, when newly laid, their green colour. This minimizes predation from those predators that detect their prey visually.

The surface structures and shapes of eggs are highly complex (see Table 3.1). Those of some, such as the Pieridae are finely ribbed and elongate, while those of the Lycaenidae are reticulated and doughnut-shaped. Although this complexity is probably significant structurally and also important in the control of water balance (Hinton 1981; see chapter 3), it is possible that it may facilitate escape from parasitoids and perhaps predators. The commonest egg parasitoids are the minute Chalcid wasps, usually species of *Trichogramma*, which may be as small as 0.25 mm long. Before laying their eggs these wasps first assess the size of the host egg, usually by walking from the apex to the base (Schmidt and Smith 1987). Then they use the surface of the host egg for a foothold as they insert their ovipositor. It is possible that some surface structures and egg shapes may prevent certain parasites assessing egg size correctly or gaining a foothold before inserting their ovipositor. Surface patterns and structures may also provide a limited form of defence against the piercing mouthparts of bugs and the biting jaws of beetles, and in combination with egg chemistry provide some form of protection from fungal attack.

Egg clustering is described as an adaptation which increases the probability of individual eggs escaping detection by predators and parasitoids (i.e. Fisher 1930; Stamp 1980; Chew and Robbins 1984); firstly, because it may increase the time predators have to search before encountering any of the prey items, thereby increasing the chance that individual enemies move elsewhere, and secondly, because the clustering of eggs has sometimes been associated with the evolution of distastefulness and warning-coloration in this and in later stages (see below). Birds are not generally believed to be major predators of eggs but it is known that those of *Pieris rapae* and *P. brassicae* are eaten by the house sparrow *Passer domesticus* and garden warbler *Sylvia borin*. Baker (1980) reports that 20 per cent of eggs of *P. rapae* can be taken by these birds but fewer *P. brassicae* are consumed. This difference is related to the advantages and disadvantages of clustering in the presence or absence of egg-toxins. Eggs of *P. brassicae*, but not *P. rapae*, contain allylisothiocyanate, an irritant compound, making them unpalatable (Aplin *et al*. 1985). Clustering by *P. brassicae* enhances the effect of this compound because fewer eggs within batches will be eaten once a predator experiences the protective chemical. The eggs of *P. rapae* which are not protected in this way probably rely on a combination of dispersal, scarcity, and greater crypsis for protection.

Egg-clusters may protect eggs from parasitoids and predators by their spatial arrangement. Innermost eggs of large masses are less accessible to parasitoids and invertebrate predators and those in the centre of single layer clusters escape attack because of the searching and host-locating patterns of their enemies (analogous to the 'edge-effect' of butterfly egg-laying in chapter 3). No British species lays its eggs in strings as does the map butterfly *Araschnia levana* on mainland Europe. Such an arrangement may minimize the chance of detection by invertebrate predators because an egg string occupies the same area as a single egg when viewed from above. It is therefore harder to find than a batch which covers a larger area of leaf. It may also make the handling of the eggs more difficult once detected.

5.3 The defences of larvae

5.3.1 The enemies of larvae

Larvae are potentially mobile, and like all stages their basic problem is to avoid being eaten or parasitized. They are the growth stage and have the additional problem of needing to consume food without being detected, a behaviour which can render them conspicuous by their association with hostplants, by their feeding damage, and frass. As larvae consume food they increase in size, and their value to particular enemies changes throughout their growth. Thus large larvae tend to have different enemies to newly emerged larvae. Additionally, the larval stage is the overwintering form of many species, a quiescent period with its own unique problems.

Most larvae have multiple defence mechanisms to cope with a variety of enemies, but however effective any particular defence mechanism is against one class of enemy there may be others with alternative strategies that cannot be circumvented. For example, ichneumonid and braconid wasps are common larval parasitoids, which usually lay their eggs in the host body by inserting the ovipositor through the larval cuticle. Others lay their eggs on the host body and the emergent larvae then burrow through the cuticle. Larvae may have defences, either physical (i.e. spines and hairs) or behavioural (e.g. wriggling) which lessen the chance of successful parasitoid egg-laying, but Tachinid flies, that have larvae which are also parasitic may invade the host by an alternative mechanism. Some species lay their eggs on the hostplant and larvae consume these eggs when they ingest the leaf material. Eggs then hatch in the larval gut and penetrate the gut wall to develop within the host body cavity. Once a parasitoid has penetrated the larval body it may fail to develop further because of the additional defence of encapsulation. In this process the developing eggs or larvae of the parasitoid become melanized by the haemocyte cells that surround them, restricting their oxygen and nutrient supplies.

Different enemies search for prey items at different times of day, for example birds are daytime searchers and some mammals are crepuscular. Therefore, the activity of a larva can influence its exposure to different kinds of enemies, as can its position on the hostplant, since different enemies may search different parts of a plant.

5.3.2 Larval concealment

Among British butterfly species some form of crypsis in the larval stages is extremely common. This may extend from appearance to behaviour. For example, the larvae of the purple emperor, *Apatura iris*, resemble the leaf on which they feed, but the effectiveness of this crypsis is dependent on the orientation of the larva. All of the Satyrinae and grass-feeding Hesperiidae are cryptically coloured and counter-shaded, being green or brown (Table 5.2). Those species which are green tend to be located in the wetter environments where the background grass-colour throughout the larval period is green, but those of drier habitats, such as *Hipparchia semele*, are brown in colour. Inconspicuousness in these species is also maintained by behaviour—most rest during the day in the basal parts of grasses, adopting night-time or crepuscular feeding. This behaviour may prevent their detection by visually-hunting predators, but may also minimize their risk to diurnal-feeding herbivores and day-time active invertebrates which locate their prey by searching the hostplant or detecting feeding damage. Inconspicuousness may also be enhanced by manipulating the hostplant, for example, large skipper *Ochlodes venata* larvae construct a tube of leaves from which they emerge only to feed. All of the Hesperiidae enhance their inconspicuousness by

Table 5.2 The colour of larvae of grass-feeding British butterflies in relation to their resting sites, feeding times, and the general nature of their habitats and hostplants

Species	Larval colour	Resting site	Feeding	Significance of colour
Carterocephalus palaemon	Grass-green striped dark green, white	In tube of rolled leaf blade	Day and night	Cryptic when feeding, concealed at rest
Thymelicus sylvestris	Pale green striped dark green	In tube of rolled leaf blade. Old larvae out of tube	Day and night	Cryptic when feeding, concealed at rest. Old larvae cryptic at rest
Thymelicus lineola	Pale green striped dark green and yellow	In tube of rolled leaf blade	Day	Cryptic when feeding, concealed at rest
Thymelicus acteon	Pale green striped cream, dark green	In tube of folded leaf	Day and dusk	Cryptic when feeding, concealed at rest
Hesperia comma	Olive-green	In spun tent of leaves	Day	Cryptic when feeding, especially on *Festuca ovina*. Concealed at rest
Ochlodes venata	Blue-green striped dark green and yellow	In tube of folded leaf blade	Day	Cryptic when feeding, concealed at rest
*Pararge aegeria**	Pale green, striped dark and light green	Leaf underside near feeding site	Day and night	Cryptic at all times especially on pale leaves of *Brachypodium sylvaticum*
Lasiommata megera	Bluish-green, striped white	Vertical, near feeding site	Night	Cryptic at all times especially on dark green plants
Erebia epiphron	Olive-green, striped white buff tails	Within tussocks	Night	Cryptic when at rest, less so when moving to feeding sites
Erebia aethiops	Grey-green, striped light green	Basal plant parts	Night, some day feeding	Cryptic when at rest, especially against *Molinia caerulea*
Melanargia galathea	Variable, brown to lime-green striped dark green, pink tails	Basal plant parts	Night	Different forms may be cryptic when at rest, dependent on composition of resting site
Hipparchia semele	Dark, striped brown, white, yellow	Basal plant parts and dry litter	Night, some day feeding	Cryptic when at rest on brown and bleached dead leaves and roots
Pyronia tithonus	Green-grey or green-brown, striped dark green	Low parts of hostplant clumps	Day, then night	Cryptic when resting on dark coloured grasses
Maniola jurtina	Bright green striped pale and darker green	Basal plant parts	Day, then night	Cryptic when at rest

Table 5.2 (*cont.*)

Species	Larval colour	Resting site	Feeding	Significance of colour
Aphantopus hyperantus	Pale brown striped pink and dark brown	Low leaf blades	Night	Cryptic at rest, against dry leaf sheaths and dead leaf blades
Coenonympha pamphilus	Grey-green, striped white, pink tails	Low parts of hostplant	Day	Cryptic at all times, especially on reflective grasses
Coenonympha tullia	Dark green striped dark and light green	All parts of upright leaf blades	Day	Cryptic at all times, stripes resembling leaf veins

* Excludes first instar larvae.

Note: many larvae may feed at different times of day in the final instar. In such circumstances crypsis may break down but individuals may gain some protection by their relative scarcity, reducing the likelihood of particular predators forming an effective search image.

ejecting their frass some distance away from their feeding site with the aid of an anal comb. This may render them less conspicuous to those enemies that rely on vision to detect their prey and also to those which associate the scent of frass with prey items.

Most of these palatable larvae have a secondary defence mechanism that can be employed when they are detected. If disturbed when at rest on a leaf, these larvae will release their grip on the plant, drop to the ground, and roll into a ball. Such behaviour is probably effective and involves little risk in losing the hostplants that are low growing and frequently abundant. This secondary defence mechanism may also be effective against some parasitoid attacks. All violet-feeding fritillaries rest away from their hostplants, a behaviour which may be related to the searching patterns and recognition methods of some generalist enemies that search damaged hostplants. However, this behaviour may also be related to thermal constraints on activity (see p. 92).

Those larvae (e.g. *Anthocharis cardamines* and swallowtail *Papilio machaon*) which feed on high growing parts of their hostplants cannot wander from the hostplant when not feeding, and must rely on crypsis or some other mechanism to avoid detection. Second and later instars of *A. cardamines* are greenish-white in colour and counter-shaded. They resemble the seed-pods of the cruciferous hostplants on which they feed and their counter-shading enhances their crypsis when seen from different angles. First instar larvae are orange and conspicuous; thus the probability that they are recognized by egg-laying females is increased and larval competition reduced (see chapter 3). When larvae of *A. cardamines* are small, visually-hunting predators are not important as most deaths at this stage are related to larval competition (see chapter 7) and the mechanical problems of chewing through a developing seed-head (Courtney and Duggan 1983). Larger larvae are often consumed by birds and therefore cryptic coloration reduces the chances of detection.

5.3.3 Chemical and physical defences of larvae

Small larvae of *Papilio machaon* closely resemble small bird droppings, but after the third instar they are remarkably different in coloration, with green and black stripes. This pattern is cryptic at a distance but conspicuous and warningly-coloured when seen at close quarters. Presumably predation by visual-hunters (like birds) is important at all stages but for various reasons mimicking a non-food item may be ineffective when larvae are large, the advantage of warning-coloration relative to crypsis being greater for large larvae than small. Size itself may not be the most important factor in determining the relative advantages of the different defence mechanisms. After the first moult all the larval stages of *Polygonia c-album* increasingly resemble bird-droppings. All larval stages of *Papilio machaon* have a secondary defence mechanism involving a large, orange organ (the osmaterium) which is extruded from behind the head when the larva is disturbed. This organ gives off a smell when extruded which has been described as being like pineapple (Dempster *et al*. 1976) and unpleasant or acrid (Frohawk 1934; Thomas 1986). The secretions of this organ (isobutyric and 2-methylbutyric acids) are probably an irritant, and are effective against ants (Eisner and Meinwald 1965). In the related North American *Eurytides marcellus* these secretions are also effective against small salticid spiders (Damman 1986), but not against larger spiders or wasps, which also attack *P. machaon* (Dempster *et al*. 1976). These secretions may not be effective against some birds. Although reed bunting *Emberiza schoeniclus*, sedge warbler *Acrocephalus schoenobaenus* and bearded tit *Panurus biarmicus* take larvae (Dempster *et al*. 1976), aviary experiments with great tits *Parus major*, done by Jarvi *et al*. (1981), and with *P. major* and blue tits *P. caeruleus* by Wiklund and Jarvi (1982) revealed that members of these species were unwilling to eat larvae and rejected those they pecked. Both intact larvae and those without osmateria were avoided, and Jarvi *et al*. and Wiklund and Jarvi concluded that warning-coloration alone was sufficient for protection. However, these experiments were not done in the field where predatory birds may show different behaviours.

Larvae which feed on noxious plants are able to accumulate or sequester plant chemicals which can be used in defence. Such a mechanism is most effective if larvae are warningly-coloured. Larvae of *Pieris brassicae*, for example, are conspicuous and feed on the upper leaves of their cruciferous hostplants. Their gregarious behaviour may enhance defence because it provides a more effective visual warning. Living in aggregations may also enhance escape from parasitoids and invertebrate predators which are not deterred by chemical defences (see below and p. 105). However, Stamp and Bowers (1988) document the effect of predatory wasps on gregarious larvae of the moth *Hemileuca lucina*. Those larvae harassed by wasps move to less favourable sites in cool microclimates, where they grow more slowly. In such circumstances escape from wasps may expose larvae to different enemies and also affect larval fitness.

Some aggregations of larvae (e.g. marsh fritillary *Eurodryas aurinia*, *Aglais urticae*) may defend themselves by spinning webs; such structures may entangle or prevent access of some small enemies. Clustering of dark-coloured larvae may also speed up development by elevating body temperature within the cluster (see p. 10), minimizing the time that larvae are exposed to attack. All nymphalid larvae (and those of some other species) show a jerking response if lightly touched. This may be effective against a wide range of predators and parasitoids, and in clustering species disturbing one individual sets off a chain reaction in the whole cluster. This could be triggered by mechanical disturbance of the substrate on which larvae are settled or perhaps by the release of an alarm-pheremone.

In the nettle-feeding larvae and some satyrines, disturbance also causes the larvae to regurgitate their stomach contents. Nettles themselves are defended from herbivores by hairs which secrete acids when touched, but the leaves apparently have no chemicals which can be used by larvae for defence. However, the gut contents of the nymphalids which feed on this plant are distasteful (Shreeve, personal observation) and perhaps provide some defence from avian predators. Spines on the larvae of these and other species may also make handling by predators difficult, acting as a physical irritant and also increasing the effective size of the larvae. They may also prevent penetration by some parasitoids by their length, particularly when they form an effective mesh over the whole body (e.g. late larvae of *Inachis io*).

5.4 Adaptations to living near ants

Ants are so dominant in most terrestrial biotopes that numerous organisms have evolved ways of living alongside them. Adaptations range from simple protective devices, such as thick or toughened skins, to special organs such as nectaries (Hölldobler and Wilson 1990). The latter secrete sugars or amino acids, and in return for this food, ants not only exempt the organism from attack but protect or even cultivate it (Donisthorpe 1927; Way 1962; Heads and Lawton 1984). Butterflies are among the many insects that possess such devices; ants incessantly tend certain lycaenids through the whole pupal period and during all larval instars, except usually the first. It is impossible to determine how widespread this relationship is among the Lycaenidae, for only a small proportion of species has been observed undisturbed in the wild when young. Nevertheless, regional studies suggest that the vast majority will prove to have a relationship at least somewhere within their geographical ranges (e.g. Geiger 1987; Thomas and Lewington 1991). Since over one-third of the world's 18 000 butterfly species belong to this family, an association with ants must therefore be regarded as a major feature of butterfly ecology.

This strange phenomenon was first noticed 200 years ago in a continental lycaenid, Reverdin's blue *Lycaeides argyrognomon*, and by 1793 it had also been reported for the green hairstreak *Callophrys rubi* and silver-studded blue *Plebejus argus* (Hinton 1951). On present knowledge, the larvae or pupae of 16 out of 17 British Lycaenidae are known to attract ants in captivity, and an association in the wild has been observed in 14 species (Table 5.3); there is little doubt that the rest live with ants in some parts of Europe, if not in Britain. Most of the important adaptations that enable larvae and pupae to live with ants had been described by the end of the nineteenth century. These, and more recent discoveries, are reviewed by Hinton (1951), Malicky (1969), and Cottrell (1984). The commonest adaptations are illustrated in Figs 5.5 and 5.6 and are described below; their ecological significance, and the additional adaptations of aphytophagous species, are described in chapter 7.

The dorsal nectary organ (DNO) or honey gland has been described by many authors; Kitching and Luke (1985) give photographs from the chalk hill blue *Lysandra coridon* (see Fig. 5.6), Adonis blue *L. bellargus* and common blue *Polyommatus icarus*. It consists of a large slit-like depression across the top of the larva's seventh abdominal segment, surrounded by slightly raised lips that are clearly visible through a hand lens (Fig. 5.6a). The slit leads down to a sac into which collect liquid secretions from four glands situated deep in the body of the larva. The whole organ is surrounded by curious knob-like mechanoreceptors on the outside (Fig. 5.6b). Ants drum these and the lips of the slit, beating them very rapidly for long periods with their antennae. In response, the slit opens, exposing a droplet of liquid honeydew, which is squeezed out as the sac is raised. In many species, there are short hairs pointing inwards round the edge of the slit, which holds the droplet in place. This, however, is often unnecessary, for the honeydew is highly attractive to ants and generally drunk the moment it appears. Droplets from the Provence chalk hill blue *Lysandra hispana* have been analysed, and found to consist of a 13–19 per cent sugar solution, containing glucose and sucrose, with traces of trehalose, protein, and the amino acid methionine (Maschwitz *et al*. 1975). This represents a 6–10 fold concentration by this gland of the normal sugars found in the larval haemolymph. The secretions of *P. icarus* are very similar, as are those of *Jalmenus evagoras*, an Australian hairstreak studied by Pierce (1984). However, Pierce also found high concentrations of the amino acid serine in the honeydew, and at certain times of day the concentration of sugars reached 55 per cent. This also varies with diet: *J. evagorus* females preferentially oviposit on specimens of their foodplant that have high concentrations of nitrogen in their leaves, and the resulting larvae secrete particularly attractive secretions for ants (Baylis and Pierce, 1991); *P. icarus* secretions are richest when larvae are fed on their natural foodplants (Fiedler 1990*a*). The DNO usually appears first in the second or third larval instar, and is particularly active in full grown larvae just before pupation. It is absent or rudimentary on some British Lycaenidae (Table 5.3) and is absent from all pupae.

Tentacle organs are curious, finger-like organs that occur as a pair either side of the larval honey gland, one segment further back (the eighth). They are normally kept retracted within the body, but are periodically everted, being blown up in unison by haemolymph, each unrolling from the centre (Figs 5.5a,b; 5.6c,d). As the tip finally unfolds, a group of spiny hair-like threads springs out to form a rosette around the tip; in some species these rotate. The structure of these 'tentacles' differs from species to species, but many look rather like a chimney sweep's brush (Clark and Dickson 1956). After a second or

Table 5.3 A summary of the relationships between British Lycaenidae (including Riodininae) and ants

Species	Larva						Pupa				
	Honey gland	Tentacles	Cupola	Sound produced in captivity	Attraction to ants in captivity	Relationship observed in the wild	Cupola	Sound organ observed	Sound heard in captivity	Attraction to ants in captivity	Observed tended by ants in wild
Hamearis lucina	×	×	✓								
Thecla betulae	×	×	✓		✓	✓	✓			✓	✓
Quercusia quercus	×	×	✓		✓		✓	✓	✓	✓	✓
Satyrium pruni	×	×	✓		✓		✓	✓			
Satyrium w-album	✓	×	✓		✓	✓	✓	✓	✓		
Callophrys rubi	†	×	✓		✓		✓	✓	✓	✓	✓
Lycaena phlaeas	×	×	✓		✓		✓	✓	✓		
Lycaena dispar	×	×	✓		✓	✓	✓				
Maculinea arion	✓	×	✓	✓	✓	✓	✓			✓	✓
Cupido minimus	✓	×	✓	✓	✓	✓	✓			✓	
Lysandra coridon	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓
Lysandra bellargus	✓	✓	✓	✓	✓	✓	✓			✓	✓
Celastrina argiolus	✓	✓	✓		✓	✓			✓	✓	
Aricia artaxerxes	✓	✓	✓		✓	✓	✓		✓		
Aricia agestis	✓	✓	✓		✓	✓	✓		✓	✓	✓
Polyommatus icarus	✓	✓	✓		✓	✓	✓	✓	✓	✓	✓
Plebejus argus	✓	✓	✓		✓	✓	✓		✓	✓	✓

×, no organ present, but the absence of a tick does not necessarily mean that no organ or relationship exists.

†, rudimentary organ.

Based on Hinton (1951); Downey (1966); Malicky (1969); Kitching and Luke (1985); Baylis and Kitching (1988); P. J. DeVries, personal communication; N. W. Elferrich, personal communication; J. A. Thomas, unpublished data.

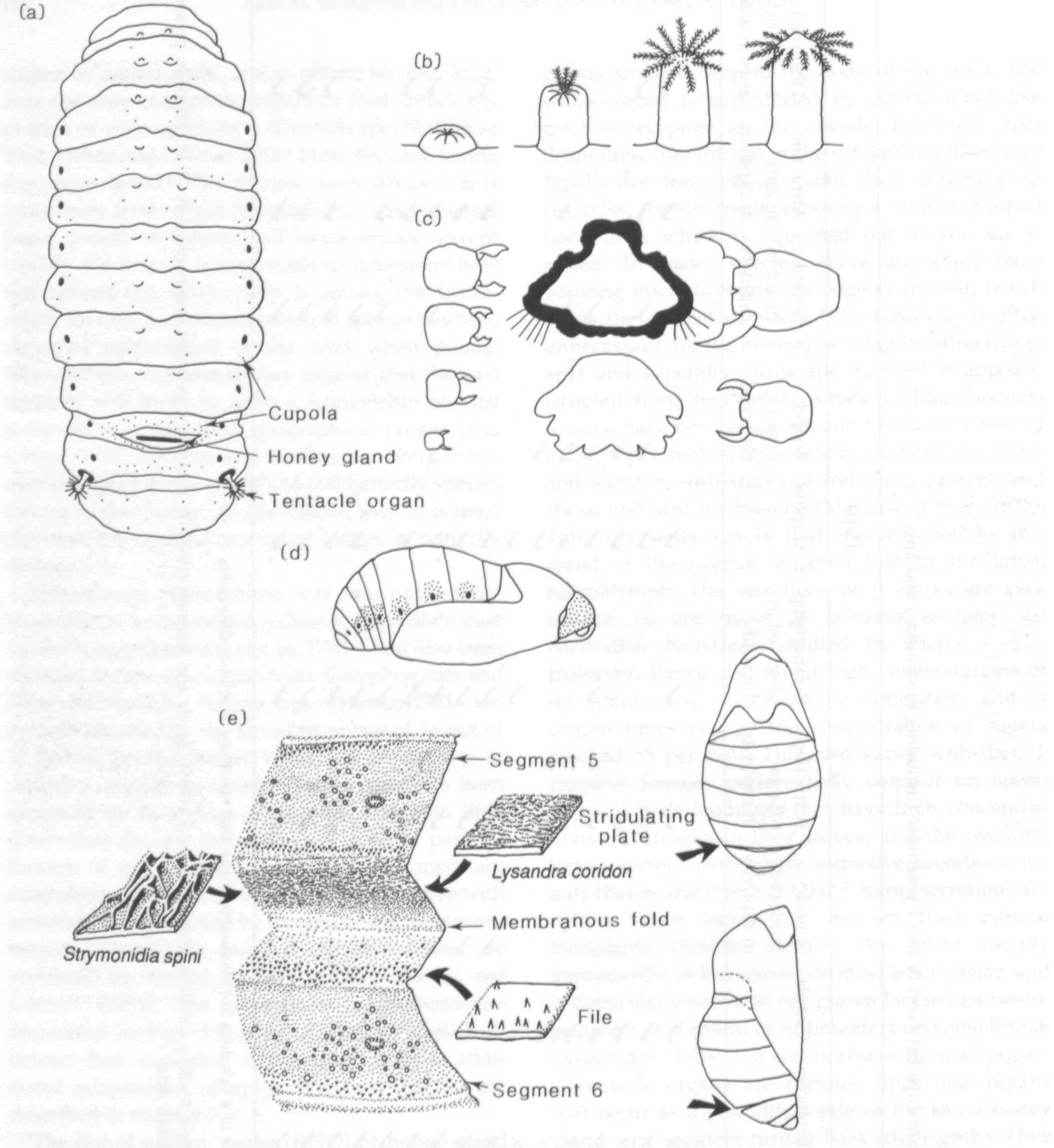


Fig. 5.5 Organs on the larvae and pupae of Lycaenidae and Riodininae that enable them to live in association with ants. (a) Dorsal view of the final larval instar of the chalk hill blue *Lysandra coridon*, showing the honey gland, everted tentacle organs, and cupola. (b) Stages in the eversion of a tentacle organ. (After Malicky 1969; courtesy of *Tijdschrift voor Entomologie*.) (c) Cross-section of a typical lycaenid larva showing thick integument and fringe of hairs (top), and cross-section of other families of butterfly larvae (bottom). The heads of various European ants are shown in outline on both sides. (After Malicky 1969; courtesy of *Tijdschrift voor Entomologie*.) (d) Distribution of cupola on a typical lycaenid pupa. (After Malicky 1969; courtesy of *Tijdschrift voor Entomologie*.) (e) The stridulating organ of a lycaenid pupa. Enlargements are shown of the stridulating plate of the two species, *Lysandra coridon* and the blue-spot hairstreak, *Strymonidia spini*. (After Downey 1966; courtesy of the Lepidopterists' Society, USA.)

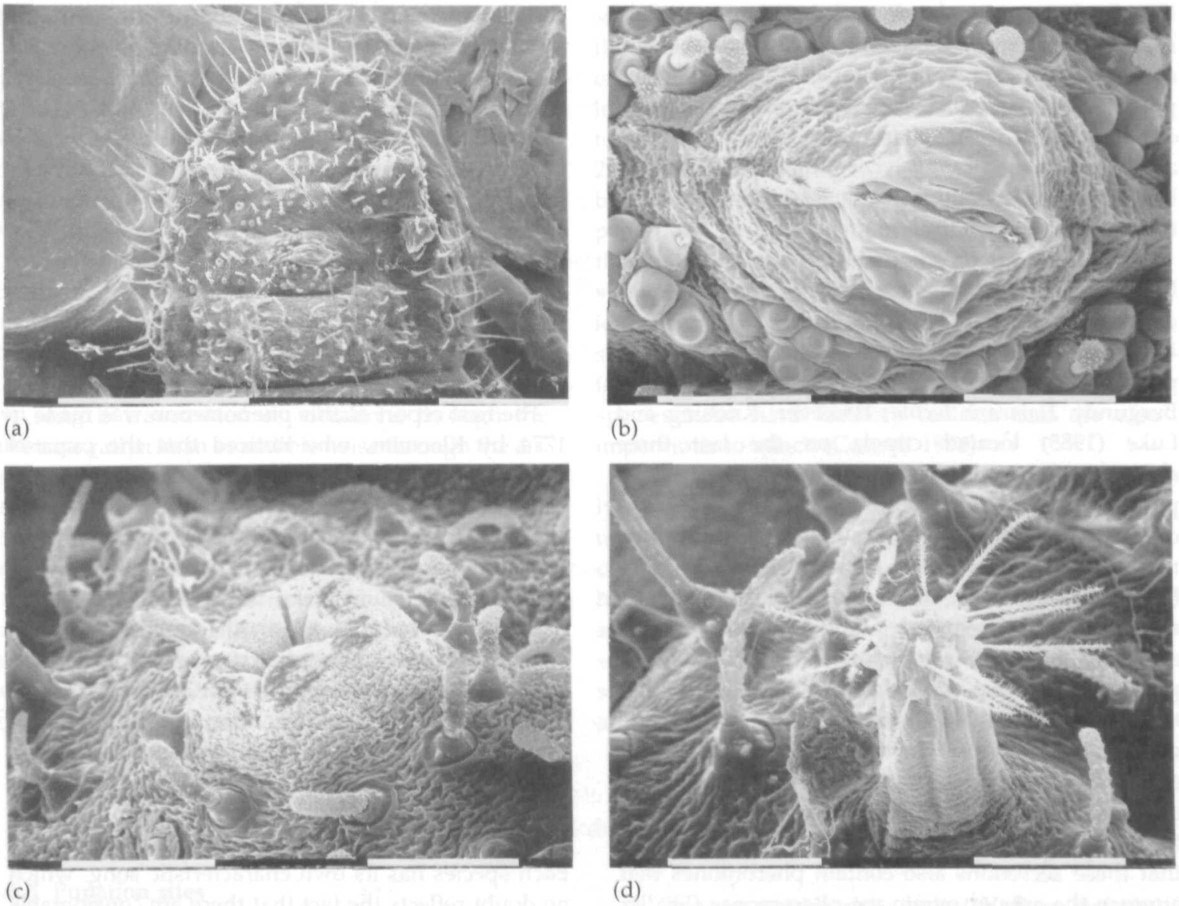


Fig. 5.6 Scanning electronmicrographs of organs on the larvae of the chalk hill blue *Lysandra coridon* that enable them to live in association with ants. (Courtesy of Barbara M. Luke.) (a) The last four segments (6–9) of a full-grown larva of *L. coridon*, showing a central honey gland on section 7 and two everted tentacles on section 8. Scale bar: 1 mm. (b) Close up of the honey gland of *L. coridon*. Note the knob-like mechanoreceptors surrounding this organ, which probably detect the drumming of the ant's antennae. Scale bar: 0.1 mm. (c) The tentacle organ of *L. coridon*, just beginning to unroll outwards from the centre. Scale bar: 0.1 mm. (d) The tentacle organ of *L. coridon*, fully everted. Scale bar: 1 mm.

two, the tentacles are withdrawn into the body by a special muscle attached to the cuticle on the lower side of the larva.

There has been much argument about the function of this organ, which may well differ from species to species. Ants seldom touch everted tentacles, and often seem oblivious to them. However, there is no doubt that the tentacles are everted much more frequently—every two or three seconds—when a larva is moving from one part of its foodplant to another, and also when the ants have wandered a little way off (Thomas, personal observation). The consensus is that they release a cocktail of volatile pheromones which alarm and activate the ants (Fiedler 1988; Fiedler and Maschwitz 1988*a*; De Vries 1988). Ants that are not already milking the caterpillar are whipped up into a frenzy when the tentacles are extruded, and are then more prone to investigate nearby objects, which brings them into contact with the larva. It is possible that this organ also releases pacifying pheromones to supplement those secreted by the pore cupola (see below) and thus further reduce the danger that the ants might attack the larva itself; there is little doubt that agitated ants are more prone to attack other potentially dangerous organisms in the vicinity that do not have pacifying pheromones. Tentacle organs are not possessed by all lycaenid larvae (Table 5.3) but, if present, usually appear in the second, third, or fourth instar, depending on the species.

Pore cupola are the commonest organ on lycaenid larvae and the only secretory organ found on pupae or first instar larvae; 52 out of 53 European Lycaenidae and Riodininae tested by Malicky (1969) possessed them, the exception being the Duke of Burgundy *Hamearis lucina*; however, Kitching and Luke (1985) located cupola on the last three abdominal segments of *H. lucina*, and have published a convincing photograph. These organs consist of specialized hairs that have become modified and reduced to form microscopic pores (Fiedler 1988). They are found in clusters mainly around the DNO, spiracles, and head of the larva and pupa (Fig. 5.5a,d). It is now certain that they too produce secretions, as larvae that possess neither tentacles nor eversible glands are coated in a mixture of amino acids, of which serine was the main component in one Australian lycaenid that has been analysed (Pierce 1984). In addition to producing a film of food over the body, there is strong evidence that these secretions also contain pheromones that appease the ants or mimic ant pheromones (Fiedler 1990*a*). The latter pay great attention to those parts of the body where cupola are concentrated, and in some cases spend as much time licking the cupola as they do in milking the DNO (Thomas, J. A., personal communication).

A few other ant-attracting organs have been described in butterfly larvae, including 'dish organs', which are saucer-like depressions found on the thorax of some riodinines and lycaenids, and along the dorsal midlines of species of *Aphnaeus* (Cottrell 1984). These secrete a fluid that attracts ants and which presumably contains sugars or amino acids for, if not removed, it becomes mouldy.

Since pupae do not feed, they are unable to secrete large quantities of food to attract ants, and merely possess pore cupola. But they compensate by having the additional ability to produce sounds (Høegh-Guldberg 1971*b*; Downey and Allyn 1973). The stridulating organ usually lies on the dorsal side of the abdomen, in the groove between the fifth and sixth segments back from the head. Here there is a large V-shaped fold of exoskeleton that penetrates deep into the body of the pupa (Fig. 5.5e). Closer examination reveals that the posterior wall of this fold contains a series of hard projecting teeth while the opposite side, nearest the head, has a toughened surface that is criss-crossed by an intricate pattern of tubercules, ridges, and reticulations, together known as the stridulating plate. Thick muscles are attached to the membrane connecting these two plates, which draw the teeth across the stridulating plate in a rapid series of contractions.

The first report of this phenomenon was made in 1774 by Kleeman, who noticed that the pupa of *Callophrys rubi* made squeaking noises when disturbed (Downey 1966). This species, and *Quercusia quercus* (Thomas and Lewington 1991), are among the few lycaenids that have stridulations that are clearly audible to the human ear. Since then, stridulating organs have been found on the pupae of a large number of blues, coppers, hairstreaks, and riodinines, including several species that live in Britain (Table 5.3). Moreover, recent recordings of live lycaenid pupae suggest that all the European species can emit noises which, when amplified, sound rather like the drumming of a woodcock or the drilling of a woodpecker (N. W. Elfferich, personal communication). Each species has its own characteristic song, which no doubt reflects the fact that there are considerable differences between the patterns on the stridulating plates of different species, as well as in the size and spacing of the teeth (Fig. 5.5e from Downey 1966). However, this organ has not been found on all pupae that sing, and some other device must be present, for example, on alcon blue *Maculinea alcon* pupae, which produce powerful and frequent noises.

Elfferich has recorded the songs of many European Lycaenidae, and has made tapes of pupae from within ant nests. Ants themselves communicate to one another by stridulating, and it is extraordinary to hear pupae emitting bursts of song and seemingly being answered by the ants. This becomes particularly frenzied just before the adult butterfly emerges. It seems likely that these songs, like pheromones, simultaneously alarm and pacify ants, so that they are on hand in an agitated state near the pupa, ready to attack enemies but not the pupa itself (Wilson 1971). Predators may even associate pupal sounds with unpleasant encounters with ants (Brower 1984). It has recently been discovered that some—possibly many—larvae also stridulate to attract ants (De Vries 1988, 1991*a*,*b*). For example, some riodinines have vibratory papillae: small hard blades that project forward from the front edge of the prothorax and which vibrate very rapidly against a hard patch or the epicranium on each downstroke and against two hardened horns on the upbeat. Similar low amplitude sounds are produced by some lycaenid larvae, including *Lysandra bellargus*, *Cupido minimus* and all the European *Maculinea* (De Vries 1991*a*; De Vries, Cocroft and Thomas, unpublished data). In all cases, the song is transmitted as vibrations through the substrate rather than as audible noise through the air. Singing is particularly pronounced when the larvae are on the move, and probably reinforces the tentacular organs, where present, in agitating and hence attracting ants.

All the above organs serve to agitate, attract, pacify, and feed ants at various times during the larval and pupal periods. However, ants are dangerous and unpredictable; even workers from the same colony will often attack each other if they become severely agitated. The bodies of lycaenid larvae have therefore evolved other adaptations with which to enhance their chances of survival. Nearly all larvae, including all British species, have an exceptionally tough and rubbery outer skin (integument) that is 20–60 times thicker than the integument in other butterfly families (Fig. 5.5c). Although this can be penetrated by prolonged attacks, it is not pierced if the ant nips the larva or tries to pick it up; at worst a small nick is made in the side. A few tropical Lycaenidae that live in close association with aggressive species of ant have an armour of stout hairs modified to form studs over the dorsal surface, whilst *Liphyra* species have hard leathery cuticles that are also impervious to attack (Cottrell 1984).

The characteristic 'woodlouse-like' shape of the lycaenid larva also helps to protect it (Fig. 5.5a). The mouth parts, legs, and other organs that cannot be cushioned, if they are to function properly, are kept hidden beneath a flattened body, the edges of which are fringed with stout downward-pointing hairs that seal off the vulnerable underside. All that the ant can see is the humped dorsal surface, with its array of attractants, agitants, and protective devices.

5.5 Pupal defences

5.5.1 Pupation sites

Pupae are relatively large and immobile. Their position results from site selection by the prepupal larvae and this is influenced by predictable patterns of hostplant seasonality, weather, and the duration of the pupal stage. However, unpredictable events and enemies are the major mortality factors. Of the 11 resident species that overwinter as pupae (Table 5.4), most pupate low in the vegetation. This includes those larvae that feed on the high parts of their foodplant, as for example *Anthocharis cardamines*, *Papilio machaon*, green hairstreak *Callophrys rubi*, holly blue *Celastrina argiolus*. High and exposed pupation sites could increase mortality through several effects, especially winter loss of aerial parts, and long-term conspicuousness to predators. Some individuals of *A. cardamines* and *P. machaon* may sometimes pupate high up but in such cases the pupation site is sheltered and the pupae cryptic.

Detection of, and access to, pupae of some species (e.g. *Ochlodes venata*, red admiral *Vanessa atalanta*) by predators is minimized as a result of their being concealed, for instance contained within rolled or folded leaves or within a loose tent of silk spun by the final larval stage before pupation (e.g. *Thymelicus sylvestris*, silver-spotted skipper *Hesperis comma*). However, silk may also prevent the access to pupae by some parasitic insects. When a predator encounters a pupa that is attached to a substrate, it must be able to remove it in order to consume the whole. Baker (1970) found that predation by birds on *Pieris brassicae* and *P. rapae* differed. The more firmly attached pupae of *P. brassicae* are less frequently eaten. However, *P. brassicae* pupae are protected chemically (containing sinigrin), more so than are *P. rapae* (Aplin *et al*. 1975) and this is also likely to influence predation by birds (see p. 105).

Many species pupate on or near the ground, influencing the ease with which they can be detected. *Hipparchia semele* buries itself in sites with

Table 5.4 The usual pupation sites and major defences of British butterfly species, including common breeding migrants

Species	Pupal position and height				Form of visual protection		
	attached	suspended	litter	buried	background matching	resemblance to plant parts	
						dead	live
Species with overwintering pupae							
Pyrgus malvae	Low in cocoon of foodplant					+	
Papilio machaon[1]	Low				+	+	+
Leptidea sinapis	Low				+	+	+
Pieris brassicae[1]	Low				+	+	+
Pieris rapae[1]	Low				+	+	+
Pieris napi[1]	Low				+	+	+
Anthocharis cardamines	Low				+	+	
Callophrys rubi[2]	Low		+	+	+	+	
Celastrina argiolus[1,2]	Low		+		+	+	
Pararge aegeria[1]		Low			+		+
Species which form pupae at other times of the year							
Carterocephalus palaemon		Low in loose grass tent				+	
Thymelicus sylvestris		Low in cocoon in grass tent					+
Thymelicus lineola		Low in cocoon in grass tent					+
Thymelicus acteon		Low in cocoon in grass tent					+
Hesperia comma		Low in cocoon in grass tent					+
Ochlodes venata		Low in cocoon in grass tent					+
Erynnis tages			In silk web				+
Colias croceus	Low				+		+
Gonepteryx rhamni		Low			+		+
Thecla betulae[2]			+	+	+		
Quercusia quercus[2]			+	+	+		
Satyrium w-album[2]	High				+		+
Satyrium pruni[2]	High				Resembles bird dropping		
Lycaena phlaeas	Low				+		+
Lycaena dispar		Low			+	+	
Cupido minimus[2]		Low	+	+	+	+	
Plebejus argus[2]				+			
Aricia agestis[2]			+	+	+		
Aricia artaxerxes[2]			+	+	+		
Polyommatus icarus[2]			+	+	+		
Lysandra coridon[2]			+	+	+		
Lysandra bellargus[2]			+	+	+		
Maculinea arion[2]				+			
Ladoga camilla		High			+		+
Apatura iris		High			+		+
Vanessa atalanta		Low			+		
Cynthia cardui		Low			+		
Aglais urticae		Low			+		

Species	Pupal position and height				Form of visual protection		
	attached	suspended	litter	buried	background matching	resemblance to plant parts	
						dead	live
Nymphalis polychloros		High			+		
Inachis io		Low			+		
Polygonia c-album		Low			+		
Boloria selene		Low	+		+		
Boloria euphrosyne		Low	+		+		
Argynnis adippe	Low in loose tent of vegetation						+
Argynnis aglaja	Low in loose tent of vegetation						+
Argynnis paphia		Low			+	+	
Eurodryas aurinia		Low			+		
Melitaea cinxia	Low in loose tent of vegetation					+	
Mellicta athalia		Low			+		
Lasiommata megera		Low			+		+
Erebia epiphron	Low in loose tent of foodplant						+
Erebia aethiops			+	+	+		
Melanargia galathea			+		+		
Hipparchia semele				+	+		
Pyronia tithonus		Low			+		+
Maniola jurtina		Low			+		+
Aphantopus hyperantus			In loose cocoon		+		
Coenonympha pamphilus		Low			+		+
Coenonympha tullia		Low			+		+

[1] Has one or more generations per year and pupates at other times.

[2] Ant attended, pupae may be buried by attendant ants.

Low < one metre; high > one metre.

Background matching refers to resemblance to pupation site background; those species which also have a resemblance to plant parts have a general resemblance to the coloration of specific sites where they pupate.

loose soil before pupating underground, or moves under stones where detection is impossible. The larvae of *Celastrina argiolus* and *Quercusia quercus* also move to underground sites to pupate, burying themselves in ground cracks or under leaves and moss (Thomas 1986) and in the latter species being taken into ant's nests (Heath *et al*. 1984). With the exception of the lycaenids, other ground-pupating species are located on the soil surface or among litter, relying on background matching for protection (Table 5.4). Most lycaenid larvae pupate in sites where ants frequently occur (see section 5.4).

5.5.2 Defences from visually-hunting predators

Pupae of British species are nearly always extremely cryptic. They are located in hidden sites and/or rely on background matching or resemblance to a non-food item. Like larvae, the colour of pupae is related to the types of enemies normally associated with pupation sites and the types of protection that the pupae can use after detection. Some, such as that of *Satyrium pruni*, resemble bird droppings and occur in sites where such droppings would be found, for example on the upper surfaces of twigs or leaves. Others which pupate within green vegetation, such as *Lasiommata megera* and *Pararge aegeria* are green in colour and are suspended from the underside of green grass blades which they generally resemble. Equally common is some form of brown or black colour often enhanced with elaborate shading and highlights or spangling with gold spots (e.g. *Aglais urticae*) which resembles dry vegetation. Even in those species which appear to have strikingly obvious pupae when seen close to, as in *Eurodryas aurinia* and the heath fritillary *Mellicta athalia*, individuals closely resemble the resting background when seen from a distance. In the case of *E. aurinia* the pupae are white with black and orange markings, resembling the underside of bleached leaves of dead vegetation. Both these species may appear warningly-coloured when seen close to.

In the three British *Pieris* species, and in *Anthocharis cardamines*, *Papilio machaon*, and *Leptidea sinapis*, pupal colour is variable. This variation, or polyphenism, is under environmental control (e.g. Smith 1978, 1980; and see pp. 188–91), individuals of these and related species tending to be of the colour form which best matches their resting background (Wiklund 1975; West and Hazel 1982). This phenomenon is probably of importance to pupal survival at different times of the year. Individuals least likely to survive detection will be those which contrast with their background and the ability to vary colour enhances survival when backgrounds vary in colour, especially with season (see section 8.5).

5.5.3 Secondary mechanical defences of pupae

Independent of primary defences, pupae have a range of structural and behavioural characteristics which can deter attacks, particularly by pupal parasites. Many satyrine and nymphalid pupae are capable of restricted movement, and will jerk when disturbed. Although this jerking can prevent attack by vertebrate predators it is probably of more importance to escape parasitoid attacks. It is most rapid when pupae are touched by parasitoids and slowest when they are gripped in a manner similar to a bird or rodent attack (Cole 1959). Newly formed pupae of *Aglais urticae* were found to be easily stabbed by Ichneumonid species (*Apechthis* spp.) but older pupae, because of their rapid vibration and hard burnished cuticle make it impossible for the parasitoids to grip the pupa or press the ovipositor through the cuticle. Similarly, newly formed pupae of *Pararge aegeria* were stabbed by *Apechthis resinator* but the smooth waxy cuticle and slight abdominal movements of pupa 24 hours old or more prevented attack. Not all pupae are so protected. While a smooth cuticle may prevent or hinder attack by making the parasitoid itself vulnerable to disturbance or attack if handling time per pupa is long, rough surfaced pupae can be more vulnerable. Pupae of *Pieris brassicae* have a cuticle which facilitates grip by parasites, being easily handled and penetrated by species of *Apechthis* (Cole 1959) and by *Pimpla instigator* (Picard 1922). However, a rough cuticle, especially if associated with spines, may deter vertebrate predators.

5.6 Butterflies and multiple defence mechanisms

All stages have a variety of natural enemies, which may be specialists or generalists. Most defence mechanisms, such as crypsis, are effective against a variety of enemies. Because every stage is liable to be attacked by a variety of enemies, which differ in their prey-locating and handling mechanisms, butterflies have multiple primary and secondary defence mechanisms (Fig. 5.7). Adaptations which reduce attacks by generalist enemies are usually less specific and less highly evolved than those which operate against specialist enemies. A small adjustment may prevent attacks by some of the former because these enemies have prey-locating and handling mechanisms which cope with a variety of prey items. More complex adaptations are required to circumvent specialist attacks since the biology of these enemies is more closely tied to the biology of a limited number of prey types.

The defence mechanisms of the stages of particular species are related to the predictability of enemies. The most effective defences will, therefore, be those that reduce the probability of attacks from enemies which have the potential to cause the most mortality. These enemies may not be of significance in all years (see Chapter 4) and their activity is in part related to the abundance and activity of other members of the community in which the butterfly species lives.

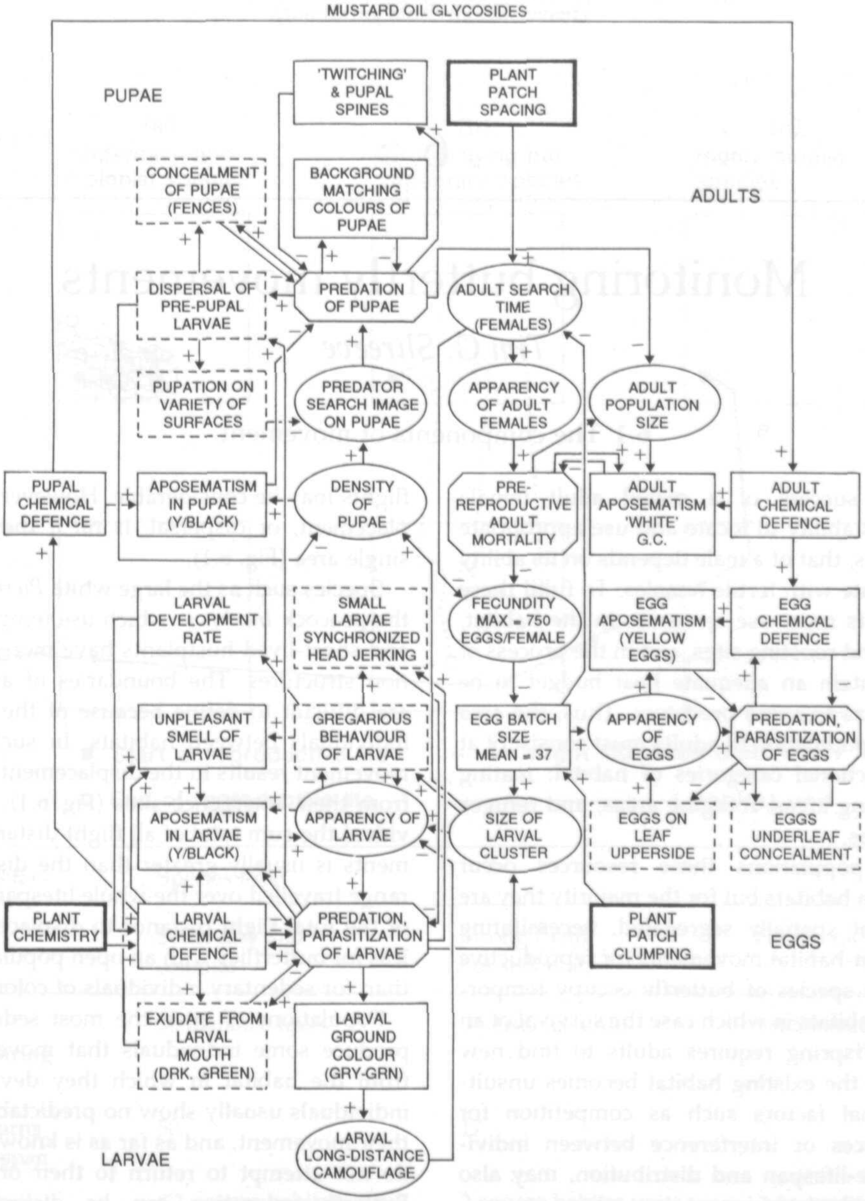


Fig. 5.7 A hypothetical model for some of the morphological, physiological, behavioural, and ecological consequences (i.e. various defences) of cluster egg-laying in the large white, *Pieris brassicae*. Influences and responses associated with climate (e.g. reduction of desiccation by underleaf egg placement), hostplant quality, and size (e.g. starvation and egg-load assessment by females) are excluded. Boxes with bold outlines, hostplant–habitat precursors of cluster egg-laying; boxes, morphological and physiological adaptations; boxes with pecked outlines, behavioural adaptations; octagons, predation and/or parasitization; ellipses, other variables. For the interpretation of signs, see **process-response models** in the glossary. (Data from J. Feltwell 1981*a*,*b*, and personal communication; B. O. C. Gardiner, personal communication; Aplin *et al*. 1975; Rothschild *et al*. 1977.) Chemical defence is transmitted from larvae, through pupae and adults, into the next generation of eggs. Pupae typically conceal themselves by background colour matching, but are also distasteful to predators. Most overwintering British pupae are brown and the summer pupae are green. However, Rothschild *et al*. 1977, believe that the bright green diapause (overwintering) pupae of the reared Cambridge strain are aposematic. (After R. L. H. Dennis)