UNIVERSITY OF SOUTHAMPTON

ALTERNATIVE FORAGING STRATEGIES OF THE WHITE ADMIRAL BUTTERFLY (*LADOGA CAMILLA* L.) AND THE BROAD BORDERED BEE HAWK MOTH (*HEMARIS FUCIFORMIS* L.) ON HONEYSUCKLE (*LONICERA PERICLYMENUM* L.)

Submitted by

BARRY WINSTON FOX

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ABSTRACT

FACULTY OF SCIENCE

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ALTERNATIVE FORAGING STRATEGIES OF THE WHITE ADMIRAL BUTTERFLY AND THE BROAD BORDERED BEE HAWK MOTH ON HONEYSUCKLE

by Barry Winston Fox

Foraging strategies of two Lepidoptera, *Ladoga camilla* L. (Nymphalidae: Limenitinae) and *Hemaris fuciformis* L. (Sphingidae: Macroglossinae) were compared in Bentley Wood, a 40 year old British lowland plantation forest. They were found to be the most dominant members of a guild of 34 moths and 1 butterfly feeding on *Lonicera periclymenum* L. Ovipositing females of *L. camilla* and *H. fuciformis* discriminated between conspecific host plants in which *L. camilla* females preferred to oviposit on host growing in shade in contrast to *H. fuciformis* females which preferred to oviposit on host growing in sun.

Natural oviposition foliage of the two Lepidoptera differed in terms of toughness, trichome density, foliage secretion but not in nutrient quality. First instar *L. camilla* caterpillars suffered a decrease in caterpillar survival due to foodplant secretion when feeding on host foliage growing in open sun while 1st instar *H. fuciformis* caterpillars showed no change in caterpillar survival when feeding on shade host foliage.

First instar caterpillars of both species removed leaf trichomes before feeding bouts. *L. camilla* 1st instar caterpillars also constructed silk platforms, a defence refuge and an aerial latrine preventing frass drop. All surviving 1st instar *L. camilla* caterpillars feeding on secretory *L. periclymenum* foliage were able to construct a defence refuge but all 1st instar *L. camilla* caterpillars suffering mortality failed to construct their defence refuge.

A possible explanation is that the compelling evolutionary strategy of *L. camilla* 1st instar caterpillars in constructing a defence refuge immediately after emergence, and prior to caterpillar growth, creates an energy drain. Under the constraint of foliage secretion, this energy drain may cause starvation and caterpillar fatalities. Female *L. camilla* butterflies avoided secretory host foliage in the field by ovipositing only on non-secretory shade growing foodplants.

In contrast, *H. fuciformis* 1st instar caterpillars have evolved a successful feeding strategy on secretory host foliage by vein cutting which may reduce secretion flow. Both *L. camilla* and *H. fuciformis* 1st instar caterpillars maintain strict foraging pathways on their foodplant leaf surface, possibly, to avoid tarsal rupture of leaf secretory canalicular network.

The results of this study indicate that hypotheses of evolution of lepidopteran host selection should take into consideration conspecific host plant discrimination rather than interspecific host plant discrimination.

This study has shown that the survival of both *L. camilla* and *H. fuciformis* in British woodland requires contrasting degrees of shade. Sunny clearings provide suitable *L. periclymenum* growth for *H. fuciformis*. *L. camilla* requires plantations, shaded woodland and rides which allow penetration of sufficient sunlight to promote *L. periclymenum* growth but not too much sunlight to create secretory foliage.

In the memory of my parents,

Edith (1898-1959) and Harold (1904-95),

and for my family,

Jo, Debby, Dani and Jim,

with love.

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Chapter One

Introduction

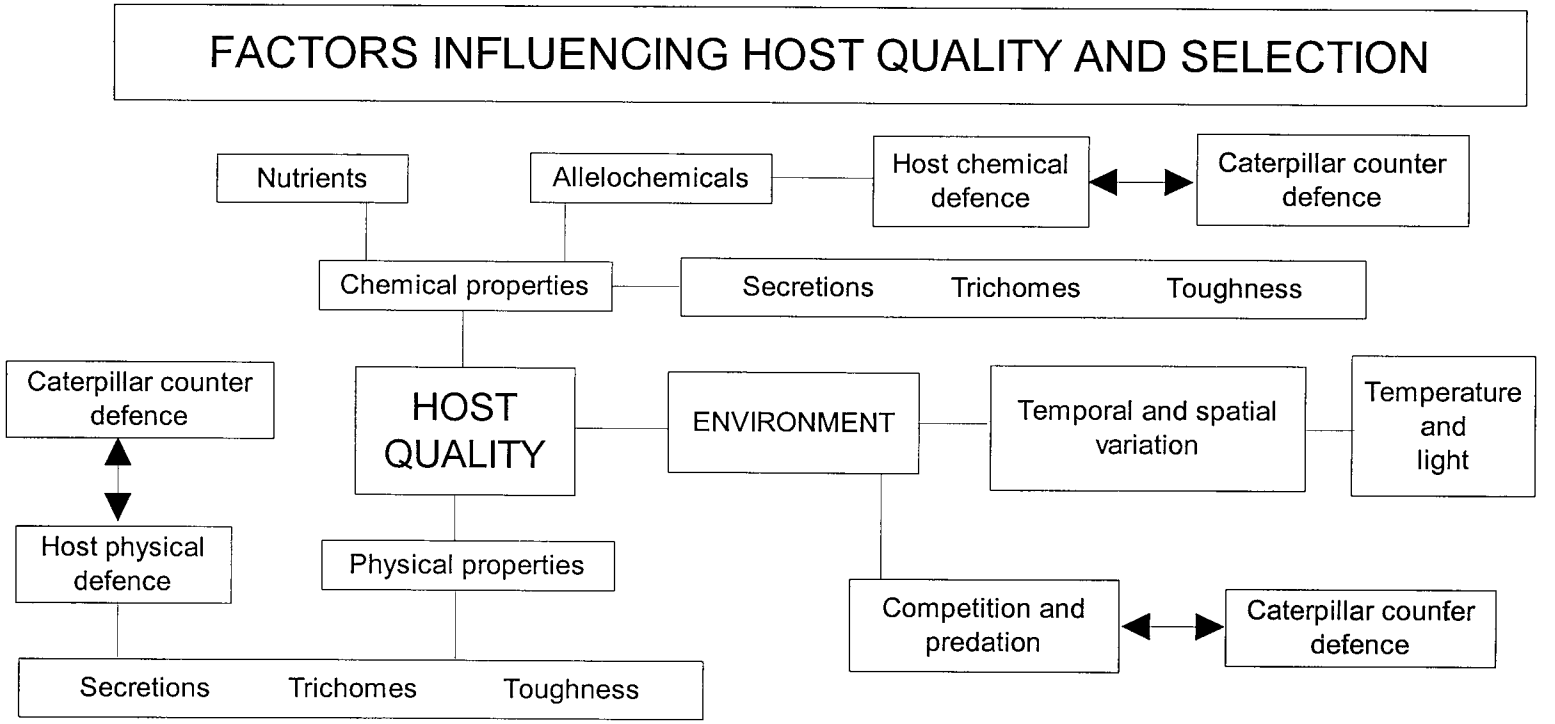
Aims - oviposition behaviour - host quality - defence - adaptation

1.1 Aims.

The ultimate aim of this study is to determine why female *Ladoga camilla* L (White Admiral) butterflies only oviposit on their host, *Lonicera periclymenum* L. (Honeysuckle), when host foliage is growing in shade. This question has puzzled lepidopterists in the UK for many years (Pollard, 1993). An equally important question is why female *Hemaris fuciformis* L. (Broad-bordered Bee Hawk) moths oviposit on the same host as *Ladoga camilla,* only when host foliage is growing in sunny habitats. The ecological principles governing the answers to both questions are probably the same and therefore the ecology of both Lepidoptera will be studied. In addition to *L. camilla* and *H. fuciformis,* several other species of Lepidoptera are known to use *Lonicera periclymenum* as a caterpillar food resource (Emmet and Heath, 1991). A limited study of the complete lepidopteran guild foraging on *L. periclymenum* will also be carried out. Host quality will be investigated and compared between habitats. Growth rate and survival of *L. camilla* and *H. fuciformis* caterpillars will be compared between natural oviposition foliage and other related foodplants.

Host selection and caterpillar performance within local populations of phytophagous insects have been the centre of ecological debate concerning the evolution of interactions between plants and insects. Lepidoptera has been a well used insect group for the study of oviposition behaviour since Ehrlich's and Raven's (1964) paper on coevolution of butterflies and plants. Behavioural studies of butterflies and moths have featured greatly in the reviews and papers of Gilbert (1975 and 1977). However, little is known concerning the extent of conspecific foodplant discrimination in natural populations and few field studies have quantitatively demonstrated such discrimination. Even fewer studies have explained this discrimination in terms of behavioural ecology of lepidopteran caterpillars (Mackay, 1985). This type of discrimination may have evolved in response to variable foodplant quality which is a central theme in terms of investigation and analysis in the present study of *L. camilla* and *H. fuciformis*. Chapter One of this study concentrates on the behavioural and ecological factors of oviposition behaviour and caterpillar performance as they influence preference for plants and their architecture (plant parts) in both butterflies and moths (Figure 1.1). These aspects of oviposition behaviour are major issues of most of the field and experimental work carried out in this study involving the lepidopteran host, *L. periclymenum.*

Fig. 1.1 Factors influencing host quality and selection in Lepidoptera.



This study doe not assume that foraging behaviour of Lepidoptera rests solely with the ovipositing female. It will explore the potential capabilities of a freshly emerged first instar caterpillar to search and distinguish between favourable and unfavourable parts of a leaf surface just as a foraging female butterfly has to distinguish between favourable and unfavourable plant species during oviposition. The foraging strategies of *L. camilla* and *H. fuciformis* on their conspecific foodplant, *L. periclymenum,* their caterpillar performance and behavioural traits will be examined and compared with other guild members and, finally, with oviposition foliage.

Both these species of Lepidoptera are uncommon in the UK and could be classified as vulnerable species since their woodland habitat is constantly changing due to forestry management and human pressures. If oviposition requirements of Lepidoptera are not fully understood, inappropriate forestry and conservation management may cause vulnerable species to become endangered and, ultimately, locally extinct.

1.2 Oviposition behaviour and caterpillar performance in Lepidoptera.

1.2.1 Introduction.

The major factors frequently used in hypotheses explaining the evolution of host specificity in phytophagous insects are allelochemicals, nutritional chemistry, plant morphology, natural enemies, and feeding techniques. The important ecological and evolutionary problem is to understand how these factors interact with each other (Thompson and Pellmyr, 1991). In this respect the present author has attempted to show a network of possible pathways of interactions which influence foodplant quality and hence host selection by discriminating female Lepidoptera (Figure 1.1).

1.2.2 Host detection.

The study of insect-plant relationships has long focused on the process by which phytophagous insects locate and examine their host plants. Since Thorsteinson's classic review (1960), significant advances have been made in explaining behavioural and sensory mechanisms by which insects recognise their hosts and reject unsuitable plants. Recent progress in isolating and identifying chemicals responsible for controlling the behavioural stages which take place during recognition have clarified many of the important issues (Jaenike, 1990).

The precise behavioural sequence used by females when choosing plants for oviposition varies among species. The results of some studies implied that females obtained cues and made choices at three different stages when searching for a potential foodplant: choice of habitat in which to search for host plants, choice of specific plants on which to land within a habitat, and the decision

to oviposit or not after landing on a plant (Papaj and Rausher, 1987; Renwick and Radke, 1980). In choosing a habitat or an individual plant on which to alight, females in some lepidopteran species have been shown to use the amount of sunlight hitting plants or some indicator of diffused sunlight (Grossmueller and Lederhouse, 1985; Scherer and Kolb, 1987).

Previous reviews dealing with oviposition behaviour in Lepidoptera include a comprehensive account of butterfly oviposition by Chew and Robbins (1984), a discussion of the evolution of oviposition behaviour and host preference by Thompson and Pellmyr (1991). Ramaswamy (1988) analysed the behavioural steps and the quality of sensory stimuli in host detection by moths, and Feeny *et al.* (1983) reviewed the chemical aspects of butterfly oviposition. Singer (1986) discussed the consequences of oviposition choice by butterflies and compared the methods and terminology used in the study of oviposition preferences. Courtney and Kibota (1990) and Jaenike (1990) discussed the factors affecting acceptance of potential host plants by ovipositing insects. Renwick (1989) provided a general outline of chemical factors influencing oviposition and Stadler (1992) reviewed in detail the behavioural responses of insects to plant secondary compounds. Renwick and Radke (1987, 1988) discussed the influence of chemical factors affecting oviposition by Lepidoptera and their presence on oviposition stimuli.

Most work on oviposition behaviour is based on the idea that female Lepidoptera, when given a choice of potential hosts, exhibited a hierarchy in their preferences (Courtney *et al., 1*989; Singer, 1982; Thompson, 1988a; Wiklund, 1981). When confronted with a choice of foodplants, a female will lay most eggs on her most preferred plant species, most preferred habitat and most preferred part of the plant. Fewer eggs will be laid on her next preferred plant, and so on. Using this criterion, specificity is the number of plant species on which a female will oviposit when offered all plants in a simultaneous choice trial. However, Singer (1982 and 1984) suggested that insects meet plants one at a time rather than simultaneously, and therefore, used different techniques for evaluating preference and specificity. He proposed that the length of time over which a female refuses all hosts except one as the index of specificity. In both views of preference a host shift involves either a change in the preference hierarchy or the use of a foodplant lower in the hierarchy in the absence of the most preferred foodplant.

The problem with closed arena type experimental design is that ovipositing females do not encounter foodplants in their natural environment where there maybe a variation in foodplant quality with which females are capable of discrimination. Indeed, the degree of variable quality of foodplant may be undefined which introduces another variable into the specificity of choice. Stress resulting from close confinement of ovipositing females may also introduce another variable. Studies in which females have been observed individually (Singer, 1982; Thompson, 1988a; Wiklund, 1981) have shown variation among females within populations.

In this study of *L. camilla* and *H. fuciformis,* observation and recording of female oviposition preference for host foliage was confined to natural populations where competition between Lepidoptera and other insects was unlikely due to an excess of food plant.

1.2.3 Chemistry of host choice.

Renwick (1989) showed that for some species of Lepidoptera the concentrations of particular chemical compounds determined the relative preference of females for potential foodplants, whereas in other species the relative proportions of compounds determined the female's response.

In the buckeye butterfly, *Junonia coenia* (Nymphalidae), which feeds on plants rich in iridoid glycosides, females oviposited preferentially on agar discs with the highest concentrations of these compounds when presented with discs ranging in concentration from 0 to 1% (Pereyra and Bowers, 1988). In contrast, *Heliothis subflexa* (Noctuidae) responded to extract leaf washings, but no dosage response was apparent, at least in tests using olfactometers (Mitchell and Heath, 1987). *H. virescens* females showed that they were capable of choosing between cotton and groundcherry even when olfaction and vision were prevented, which indicated that contact chemoreception and mechanoreception alone allowed discrimination in this species (Ramaswamy *et al.*, 1987).

In *Hadena bicruris* (Noctuidae), which lays its eggs in the white flowers of *Silene latifolia*, search behaviour and orientation to the flowers were induced by a dose-dependent response towards the floral volatiles (Brantjes, 1976). After floral visits, a moth approached non-fragrant white objects, but alighted only in the presence of olfactory stimuli. Other floral odours experienced during initial feeding may also lead to oviposition behaviour, but these other odours were overridden by the foodplant odour.

Swallowtail butterflies have been studied intensively for the combinations of plant compounds that induce oviposition. For the species studied so far (*Papilio polyxenes* in North America, *Papilio xuthus* and *Papilio protenor* in Japan), the oviposition response of females after contact with impregnated filter paper depended upon the relative proportions of several plant compounds (Feeny *et al.*, 1989; Honda, 1986; Nishida *et al.,* 1987). Individual compounds induced either weak oviposition responses or no responses at all. Also, *P. polyxenes* females appeared to use a combination of contact stimulants and volatiles in choosing hosts. Using artificial plants made from wire branches and sponge leaves, Feeny *et al.* (1989) found that females laid more eggs on model plants treated with a combination of contact stimulants and volatiles from carrot leaves than they did on plants treated only with contact stimulants.

As in swallowtail butterflies, pine beauty moths, *Panolis flammea* (Noctuidae), in free flight cages preferred particular ratios of concentrations of plant compounds, beta- and alpha-pinene, when choosing plants for oviposition (Leather, 1987). Yellow peach moths, *Conogethes punctiferalis* (Pyralidae), were attracted to and oviposited on ripe host fruits on the basis of fruit volatiles. Attraction was increased when the volatiles of particular mould fungi were present, indicating that unacceptable substrates may be rendered acceptable by mould infection (Honda *et al.*, 1988).

A combination of chemical stimulants and deterrents induced the use of a plant species by ovipositing *Pieris* (Pieridae) females. Water soluble compounds other than glucosinolates appeared to be mainly responsible for foodplant choice in *Pieris rapae* (Renwick and Radke, 1988). Specific cardenolides were recently identified in crucifers as chemical deterrents to *Pieris brassicae* and *P. rapae* oviposition (Renwick *et al.*, 1989). *Erysimum cheiranthoides* contained both oviposition attractants and deterrents for oviposition by *P. rapae* (Renwick and Radke, 1987), but the effect of the deterrents overcame the effect of the attractants. Conspecific discrimination between foodplant quality by ovipositing female Lepidoptera has also been suggested. Nitrogen fertilisation of plants affected oviposition in *P. rapae* in different experiments. Some experiments, using potted plants in small plots, have shown that females oviposited preferentially on plants augmented with nitrogen fertiliser (Myers, 1985). Recently, however, Letourneau and Fox (1989) found that nitrogen addition had a positive effect on egg densities in small scale trials using potted plants but had no effect on egg densities in larger scale trials with field grown plants. Changes in nitrogen levels are often accompanied by changes in other chemical constituents of plants (e.g. sugars, secondary compounds), which complicates the interpretation of the effects of nitrogen, alone. By sampling neighbouring pairs of ragwort (*Senecio jacobaea*) plants, one of which had an egg mass, the other of which did not, van der Meijden *et al.* (1989) found that cinnabar moths, *Tyria jacobaea* (Arctiidae), selected plants with a high concentration of both organic nitrogen and sugars. Plants rich in only nitrogen or sugars, or poor in both, proved less likely to attract oviposition. The varying results of these studies may be due to the different ways in which nitrogen levels interact with other plant compounds under various ecological conditions.

In general, most studies have shown that host location and acceptance depended on a wide variety of sensory cues. After an insect alights on a plant, contact perception of both physical and chemical characteristics of the leaf or other plant surface, have been shown to be important stages in determining the suitability for oviposition. The sensory receptors involved are present on the tarsi, antennae, proboscis, and ovipositor of Lepidoptera. The final acceptance or rejection of a site for oviposition then depends on central nervous system processing of the information provided by the various sensory inputs received by the insect. This usually involves balancing an array of positive and negative signals from the plant. Often the insect must respond to non-plant stimuli, such as eggs, other insects and pheromones. The outcome of host evaluation behaviour may depend to a large degree on physiological factors such as motivation or age of the female. Learning also plays

a role in recognition of suitable sites or avoidance of unfavourable situations for oviposition, and either learned or genetic associations may result in an insect's preferences.

1.2.4 Oviposition preference and caterpillar performance.

An important working hypothesis on the evolution of oviposition behaviour is that females will choose plant species that maximise caterpillar survival and growth. Most studies concerning preference and performance comparison in Lepidoptera have concentrated on producing mean oviposition preferences rather than determining mean survival and growth rates of caterpillars from a single female (Courtney *et al.*, 1989; Rausher, 1981, 1982; Singer, 1982, 1983; Williams, 1983). However, Via (1986) suggested that the more important evolutionary question is how variation in preference and performance is distributed among individuals. A study of *E. editha* (Singer *et al.*, 1988) showed that both preference and performance varied within a population of this butterfly, when some individuals preferred and displayed a faster caterpillar growth rate on *Collinsia parviflora* than on *Plantago lanceolata*. Also, some individual females tended to oviposit on the plant species on which their caterpillars reached the greatest weight during the first ten days after oviposition.

Ovipositing females of some Lepidoptera choose foodplants specifically because these plants harbour ant species that protect the caterpillars from predators or parasitoids (Pierce and Elgar, 1985; Thomas, 1977a, 1977b). In some species, such as *Ogyris amaryllis* in Australia, ovipositing females actually choose a plant species of lower nutritional value rather than other available plants because that species is attended by particular ant species (Atsatt, 1981). In contrast, each of the five species of Maculinea (Lycaenidae) in Europe is tended in later instars by different species of Myrmica ant. Females oviposited regardless of the presence of ants, and the early instars developed on the plants in the absence of ants (Thomas *et al.*, 1989).

The present study concerning caterpillar performance and oviposition preference of *L. camilla* and *H. fuciformis* will reveal another unusual method of caterpillar defence against predation, which is only effective if *L. camilla* females oviposit on the appropriate type of foodplant (Chapter Seven). Further examples where good caterpillar performance was not necessarily reflected by oviposition preference are well documented and can result from several factors. For instance, the preferred plant may be rare. *E. editha* in coastal California preferred to oviposit with better caterpillar performance on *Scrophularia californica* than on *Diplacus aurantiacus*. *Diplacus*, however, was more abundant and received more eggs than *Scrophularia californica* (Williams, 1983; Williams *et al.*, 1983). Also, a plant commonly chosen for oviposition which results in poor caterpillar growth rate, may be innovative to a habitat, and selection may not have had sufficient time to favour females that avoid that plant species. For example, *Pieris napi* in Colorado oviposited on seven cruciferous hosts, including two recently introduced species that are lethal to caterpillars (Chew, 1977; Rodman and Chew, 1980). A host plant may be favourable for caterpillar growth under some

conditions only, but it may sometimes grow in a habitat unfavourable for flight of ovipositing females or for caterpillar growth (Rausher, 1979). Females may oviposit preferentially on plants that allow their offspring to sequester particular secondary plant compounds for defence (Eisner and Meinwald, 1987; Grant *et al.*, 1989).

1.2.5 Discrimination of host quality by ovipositing females.

The ability of ovipositing females to discriminate between conspecific foodplants using foodplant nitrogen has already been mentioned. Previous work has shown that the ovipositing females of some lepidopteran species are able to discriminate not only among plant species but between genotypes of plant species. That is, plants of the same genus or species differing in their microhabitat, size and architecture (plant parts) and physiological condition brought about by their temporal and spatial properties (e.g. Beach and Todd, 1988). The present study concerning contrasting foraging strategies and oviposition preference of *L. camilla* and *H. fuciformis* will, in part, examine the ability of these two Lepidoptera to discriminate between the different plant parts of *L. periclymenum* (Chapter Five).

In both the pipevine swallowtail (*Battus philenor*) (Papaj and Rausher, 1987; Rausher and Papaj, 1983a, 1983b) and the zebra swallowtail (*Eurytides marcellus)* (Damman and Feeny, 1988), the particular plants chosen by ovipositing females sustained a higher caterpillar survival than plants rejected by those females. In contrast, Wilkund (1977) found that *Leptidea sinapsis* (Piridae) females landed on plant species in proportion to the plants' density, indicating that plant architecture (plant parts) was a factor guiding oviposition.

Learning may influence pre-alighting choices and post-alighting choices in plant discrimination. After naive females of *B. philenor* landed upon a number of plants in an experimental enclosure, they learned to land more often on large young plants than on large old plants. These large young plants were found to be more likely to elicit an ovipositional response after landing than were old large plants (Papaj and Rausher, 1987). *B. philenor* females also showed their ability to discriminate conspecific leaf shape which they used as cues in choosing host plants (Rausher, 1978).

When resource competition or cannibalism is likely, mechanisms in females may evolve to recognise and avoid conspecific egg loads or caterpillars on hosts. Such conditions may arise when host plant species or the parts fed upon are of limited availability (Shapiro, 1981: Thompson, 1983). Recognition and avoidance of conspecific eggs have been demonstrated with several lepidopteran species (Benson, 1978; Williams and Gilbert, 1981; Shapiro, 1981; Wiklund and Ahrberg, 1978; Rothschild and Schoonhoven, 1977). Both visual and chemical cues were employed in *P. brassicae* (Rothschild and Schoonhoven, 1977). In this case, deterrence persisted for seven weeks under laboratory conditions. A coevolutionary consequence of egg-load

assessment is the evolution of egg-mimicking structures in some *Heliconius* hosts (Williams and Gilbert, 1981).

All possible patterns of egg distribution relative to plant density have been observed. At one extreme, females of some species sometimes lay more eggs on plants in patches than on isolated plants. For example, *Euphydryas ancia* females make sharper turns and fly shorter distances between landings when encountering host plants within patches than on isolated plants. In one year of a three year study, this behaviour resulted in an aggregation of females and eggs within host patches (Odendaal *et al.*, 1989). Harassment by males, however, served somewhat as a counterbalance to this aggregation in other years because it caused females to fly further and sometimes to leave a patch altogether. In *L. sinapis* (Pieridae), females landed on plants at random and the distribution of their eggs among potential host plants species corresponded to the relative densities of these plants within a community (Wiklund, 1977). At the other extreme, *P. napi,* often oviposited on relatively isolated plants (Courtney, 1988; Shapiro, 1975). *P. rapae* appeared to spread eggs among plants by laying few eggs within any one patch regardless of plant density (Cromartie, 1975; Jones, 1977).

Chew and Robbins (1984) interpreted oviposition on relatively isolated plants by suggesting that there was a greater likelihood of encountering isolated plants if females regularly moved between nectar plants and oviposition sites. Also, there was a potentially higher probability of encountering isolated plants if females always chose the nearest plant from a random point. Isolated foodplants receiving more sun than plants within patches were more likely to reach fruition and act as hosts for species which specialise in inflorescence oviposition such as the microlepidopteran species, *Ypsolopha dentella* (Yponomeutidae) (pers. obs., B. W. Fox).

Grazing type behaviour of caterpillars favours females capable of finding patches in which caterpillars can move among plants, and favours caterpillars capable of finding new host individual plants (Thompson, 1982, 1988a, 1988b). Although Lepidoptera whose caterpillars feed on a single plant throughout the caterpillar period are often aggregated on large hosts, some grazing Lepidoptera show quite different patterns of distribution. In Sweden, for example, *P. napi* and *Pontia daplidice* (Pieridae) preferred to oviposit on rosettes or on seedlings of their host plants when they were abundant (Forsberg, 1987). The smaller plants, nearer to the warm ground, supported faster caterpillar growth rates than larger plants.

The availability of nectar for adult butterflies can greatly affect how females distribute their eggs among potential host plants. Nectar and pollen sources have been shown to influence the pattern of movement of adult females (Douwes, 1968; Ehrlich and Gilbert, 1973; Futuyma, 1983; Gilbert and Singer, 1973; Murphy *et al.*, 1984; Sharp *et al.*, 1974). Murphy (1983) found that *Penstemon newberryi* shrubs near nectar plants were more likely to receive eggs from *E. chalcedona* than were plants far away from nectar sources. In contrast, *A. cardamines* females minimised feeding

time by using a broad spectrum of plants for nectar in the caterpillar foodplant habitat (Wiklund and Ahrberg, 1978). The availability of nectar may sometimes result in oviposition on hosts that are relatively unsuitable for caterpillar growth. Courtney (1981) found that, among several cruciferous hosts, *A. cardamines* laid most of their eggs on plants that also provided the females with nectar, even though these plants were not very good for caterpillar growth. In contrast, Odendaal *et al.* (1989) found no correlation between the distribution of females and that of nectar plants in *E. anicia*; and, in *L. sinapis*, females actually searched for nectar and host plants in different habitats (Wiklund, 1977).

Closely related species or genera of Lepidoptera sometimes differ in the plant parts they choose for oviposition. Heliconiine butterflies, for example, include genera that specialise on old leaf tissue and others that specialise on new shoots (Benson, 1978). *Depressaria* includes species in which females oviposit almost exclusively on flowers or floral buds and other species that oviposit both on floral buds and leaves (Thompson, 1983). The *Depressaria* species that are more flexible in their choice of oviposition sites are those that feed on plants that are relatively small and flower more irregularly than related potential host plants.

The selection of various plant parts by ovipositing females can influence how an interaction evolves between a particular insect species and its host plant. Attack on some plant parts may have very little effect on plant fitness (e.g. old leaves), whereas attack on other parts (e.g. meristems, flowers) may greatly affect plant survival or reproduction. *Tyria jacobaeae* (an Arctiidae moth) was released in North America and Australia in an attempt to control its foodplant, *Senecio jacobaea* (ragwort). Laid in batches of 30-40 eggs on the underside of the lower leaves of its foodplant, its caterpillars rapidly defoliate its poisonous foodplant (Emmet and Heath, 1983).

Even within the general category of a plant part (e.g. leaves), females can be highly selective in where they lay their eggs. For example, eggs of leaf-mining moths are sometimes aggregated among leaves within host plants. Leaf age, damage by other herbivores, and position on a plant all influence choice by ovipositing females (Auerbach and Simberloff, 1989; Bultman and Faeth, 1986; Simberloff and Stiling, 1987). Some butterflies are more likely to lay their eggs on the underside of leaves rather than the upper-side of leaves (Moore, 1986; Higashuira, 1989; Williams, 1981) or those receiving high levels of sunlight (Grossmueller and Lederhouse, 1985).

A special case of egg placement is oviposition away from the host, notably by dropping eggs during flight. This behaviour appears to be related to host abundance (Wiklund, 1984) or polyphagy. Under such circumstances, the reduction of search time in laying each egg may compensate for failures of some first instar caterpillars reaching their host leaves. Oviposition away from the host is also common among species that over-winter as eggs and feed on herbaceous hosts. Wiklund (1984) proposed that such behaviour might in some cases result from selection for enemy - free space. However, females of a British butterfly, *Argynnis paphia*, having located its caterpillar

foodplant, lays its eggs singly, usually three to five feet up on a mossy side of a tree trunk that has its caterpillar foodplant (*Viola* spp.) growing underneath (Heath *et al.*, 1984); the *A. paphia* caterpillar, after emergence, partially eats its egg shell and then immediately goes into winter diapause still on the tree trunk and usually under moss. Moss growing amongst its foodplant is also favoured as an over-wintering diapause refuge by *Eurodryas aurinia* (Nymphalidae) as observed by the author during the present fieldwork.

The quality of lepidopteran foodplants varies with age and a number of studies have shown oviposition preference synchronous with foodplants at their period of optimal quality in terms of nutrient content and leaf toughness. Williams *et al.* (1983), in a study of the coevolution of *Euphydryas chalcedona* butterflies and their caterpillar foodplants, found seasonal timing of caterpillar feeding activity and caterpillar growth rates were closely related to the availability of any *Scrophularia californica* leaves and high-quality *Diplacus aurantiacus* leaves. The faster growth rate of caterpillars on the more nutritious *Scrophularia* foodplant may facilitate completion of their life-cycle before *Scrophulari* senesces in mid-summer. Preszler and Price (1993) found that early abscission of mined leaves was an important mortality factor of a *Phyllonorycter* species (Gracillariidae) on *Salix lasiolepis* foodplant and that Faeth (1990) suggested that oviposition preference selects leaves which are less likely to abscise early.

The presence of complex phenolic compounds or tannins may render lepidopteran foodplants unpalatable due to increased toughness and making metabolic nitrogen unavailable. Concentration in the spring of feeding caterpillars of the winter moth, *Operophtera brumata*, rather than later period feeding, was found to be due to increasing amounts of tannins in its foodplant *Quercus robur* (oak). Feeny (1970) suggested that oak leaf tannins were a defensive mechanism against other herbivores and pathogens. Schultz *et al.* (1982) examined seasonal trends of leaf quality of *Acer saccharum* (sugar maple) and found total nitrogen and water contents declined and toughness increased through the growth season. However, leaf quality was found to be highly variable in space and time and this heterogeneity of quality of potential oviposition sites may reduce caterpillar survival.

In contrast to Lepidoptera which prefer early season foodplant foliage, there are other species which, for reasons other than nutrient quality or palatability, prefer poor quality older leaves. Such Lepidoptera are those which construct leaf shelters or barriers as defence mechanisms against potential predators and require tough leaves for their construction which they also have to use for food. Hunter (1987) suggested that *Diurnea fagella* (Oecophoridae) was found more often on damaged or regrowth leaves of its oak foodplant, in spite of poor caterpillar growth and survival on these leaves. Constructing shelters was more important than caterpillar growth rate. This conclusion by Hunter (1987) may have an important bearing on the final conclusion of the present study (Chapter Eight).

1.2.6 Egg batch size.

Several hypotheses have been proposed on the ecological conditions that favour oviposition in clusters rather than singly (Chew and Robbins, 1984). Some mathematical models have suggested that clutch size should generally decrease as the number of females ovipositing in a patch increases (Parker and Begon, 1986; Parker and Courtney, 1984; Skinner, 1985) or, under some conditions, as caterpillar competition increases (Ives, 1989).

Clutch size varies considerably between related species, among populations within species, and sometimes even among females within a population. In two related species of *Colotis* (Pieridae), one species located eggs singly near the main trunk, whereas the other species oviposited in clusters of about 30 on the lower leaf surface (Larsen, 1988). *P. brassicae* and *P. rapae* used the same host plant but laid their eggs in batches and singly, respectively. This variance may be linked to ecological specialisation on high and low density stands of the host (Davies and Gilbert, 1985). In a transcontinental experiment, *P. rapae* females from a population in Britain were more likely to lay more than one egg after alighting than were females from a population in Australia flown under the same experimental conditions (Jones, 1987). *Aporia crataegi* (Pieridae) females in Morocco vary in their average clutch size with host species, and two other butterflies appeared to vary clutch size depending on host plant density (Courtney, 1984). In *B. philenor*, where clutch size apparently varied between hosts (Tatar, 1989), individuals in at least some populations adjusted clutch size according to host quality (Pilson and Rausher, 1988).

1.3 Defensive attributes of foodplants and caterpillars.

1.3.1 Introduction.

There are several possible 'battles' in operation when caterpillars are observed feeding on their foodplants even if they are not obvious to the naked eye. Before caterpillars arrive on the scene, some lepidopteran foodplants have already established anti-herbivore strategies which involve both chemical and physical defence mechanisms. Plant secretions may prove both a physical barrier by impeding mandibular action and caterpillar mobility, and a chemical barrier because secretions may contain toxins. Foodplant trichomes or hairs which exist in a multitude of forms may be found on all plant parts of many foodplants and are responsible for most of the impediment to caterpillar mobility but they can also be secretory on occasions.

Simple trichomes are often a mechanical barrier to feeding and seem to be characteristic of foodplant species that are relatively poorly defended by secondary chemicals (Denno and Donnelly, 1981; Coley, 1983). Trichomes are frequently the basis of plant resistance to insect attack (Beck, 1965; Chapman, 1977). There are also developmental, seasonal and habitat

differences of trichomes on a single plant species (Wellso and Hoxie, 1982), and it may well be that insects are responsible for the evolutionary pressures that have produced these patterns (Southwood, 1986).

Leaf toughness is regarded as a defence mechanism against insect herbivory which trees may have evolved to prevent defoliation by aerial herbivores such as caterpillars. The toughness of the cuticle is a further and physical barrier to feeding (Tanton, 1962; Grime *et al.*, 1968); Coley (1983) concluded that, with water content, it was the most important predictor of leaf palatability for 24 trees of tropical rain forest.

The present study involving a comparison of the foraging strategies of two Lepidoptera, *L. camilla* and *H. fuciformis*, will, in part, investigate their techniques used in coping with the defence mechanisms of their conspecific foodplant, *L. periclymenum.* This chapter will conclude with examples of foodplant defence and caterpillar adaptation.

1.3.2 Trichomes (glandular and non-glandular).

An advantage of plant surface defence mechanisms is that caterpillars encounter the defence without rupturing the leaf surface. A major disadvantage is that only the leaf surface is protected. The interior remains vulnerable to miners, which may, as a result, be protected from predation by the plant's external defence mechanisms. However, restricted mobility of a miner makes it vulnerable to parasitoid attack. Gravid lepidopteran females may be aided or deterred in oviposition by trichomes (Levin, 1973; Southwood, 1986). Glandular trichome secretions may be removed by wind and rain or evaporate, creating the necessity of continuous replenishment, although some trichomes may produce a single burst of liquid which destroys the mechanism (Chapter Six). Certain types of specialised glandular trichomes found on leaves are regarded as extrafloral nectaries and by the digestive glands of some insectivorous plants (Juniper, 1986).
There are also developmental, seasonal and habitat differences (Wellso and Hoxie, 1982), and it may well be that insects are responsible for the evolutionary pressures that have produced these patterns (Southwood, 1986).

Caterpillar survival must involve successful foraging or feeding techniques which circumvent or neutralise these defence mechanisms as well as protecting themselves from predation from birds and other insects such as parasitic diptera. Caterpillars may neutralise non-glandular trichomes by mowing or swiping before feeding (Hulley, 1988). The leaf midrib may be especially protected by dense zones of trichomes which hinder caterpillars retreating from predator attack or inhibit the construction of tents and hibernacula. After trichome removal, caterpillars may cover the sharp stumps with a platform of silk (Chapter Four). Trichomes appear on both leaf surfaces although *L. periclymenum* foodplant contains a greater density on the underside of leaves. The resistance of a

maize cultivar to *Chilo partellis* caterpillars has been attributed to the high density of trichomes on the lower as well as upper leaf surface (Kumar, 1992).

Trichomes may be used as anchorage for eggs or for straining ovipositing females (Callahan, 1957). Navasaro and Ramaswamy (1991) studying oviposition behaviour of *H. virescens* females showed that trichome shape but not secretary behaviour influenced oviposition success. Trichomes may influence the ease or difficulty of caterpillar attachment to the leaf feeding surface, the 'attachment hurdle' as Southwood (1973) calls it. Stork (1980) showed that on cabbage varieties the mustard beetle (*Phaedon cochleariae*) could adhere best to glossy leaves and least well to glaucous leaves; on the latter the adhesive setae were unable to become closely attached because of the tubes and plates of wax.

The Mexican bean beetle (*Epilachna varyvestis*) was observed to fall off leaves of cultivars with long trichomes (Van Duyn *et al.*, 1972), but for some other insects on other plants hairs seem to provide a 'foothold' and aid attachment to a plant. *Heliothis zea* lays more eggs on the upper hairy surface of the corn leaf, than upon the glabrous underside (Ditman and Corey, 1933). Callahan (1957) observed that ovipositing moths grasped either a leaf vein or a hair when ovipositing and he showed that the weight they could support whilst clinging to a surface was greater on a hairy than a smooth surface. Robinson *et al.* (1980) noted that *Heliothis* laid fewer eggs on the cotton leaves that were smooth.

Simple impedance by trichomes has been demonstrated on cotton, where Smith *et al.* (1975) showed that the rate of travel of first instar caterpillars of the pink bollworm (*Pectinophora gossypiella*) was more than six times faster on smooth leaves than on those with pubescence (any type of cuticular prominence). On wheat, the leaf beetle (*Oulema melanopus*) was found to oviposit less on pubescent cultivars (Schillinger and Gallun, 1968; Lampert *et al.*, 1983). These differences between insects are probably due to size and form and are influenced by the length, density and alignment of pubescence (Southwood, 1986). In some cases hooked hairs penetrate the cuticle of insects causing death or severe damage (Johnson, 1953).

Glandular trichomes or sticky hairs are present on many plants especially insectivorous plants where their role in trapping insects has long been recognised (Joel, 1986; Juniper, 1986). These exudates vary in their viscosity and frequency with weather and time of day; they have been found to block the spiracles and, more generally, adhere to the caterpillar preventing it from moving (Kreitmer and Sorensen, 1979). The exudates of the glandular trichomes of *Stylosanthes* trap and poison cattle-ticks (Sutherst *et al.*, 1982). Two types of glandular trichomes are present on the leaves of various *Solanaceae.* It has been shown that the effects of these trichomes complement each other both through the behaviour of the animal and directly (Tingey and Gibson, 1978; Tingey and Laubengayer, 1982).

In addition to their mechanical effects the exudates or secretions of glandular trichomes often have physiological or behavioural effects on animals. More than one type of glandular hair is found in *Urtica, Nicotiana, Solanum* (Thurston and Lersten, 1969; Akers *et al.*, 1978; Tingey and Laubengayer, 1982), and components of the exudates have been found to be toxic and leading to changes in caterpillar behaviour (Rabb and Bradley, 1968; Thurston, 1970; Beckman *et al.*, 1972; Duffey and Isman, 1981; Roberts *et al.*, 1981; Dimock and Kennedy, 1983). Various compounds have been identified as the active components; for example alkaloids, phenols, a tridecanone and a farnesene. Recent advances in chemical instrumentation have allowed the identification of minute traces of complex organic molecules in trichome secretions (Duffey, 1986; Gregory *et al.*, 1986).

Plant hairs can also influence the access of penetration of the leaf surface by an insect herbivore. This has been shown with the early instars of grasshopper *Melanoplus* on *Artemisia ludoviciana* (Smith and Grodowitzi, 1983). These grasshoppers are also adversely affected by the contents of glandular trichomes (Knutson, 1982).

Trichomes are often indigestible being composed of cutin and both glandular and non-glandular trichomes can pass through the insect gut without being digested and may provide a significant non-nutritive bulk (Smith and Kreitner, 1983). Passage through the gut may occur without loss of trichome shape and they may be used for constructional purposes by caterpillars (see Chapter Four). In contrast, glandular trichomes, when digested may benefit specialist species such as the grasshopper *Hyposchlosa alba* which is monophagous on *Artemisia ludoviciana* (Knutson, 1982; Smith and Kreitner, 1983), but may inhibit growth in less adapted species (Duffey and Isman, 1981). Glandular trichomes may provide a chemical barrier and the gregarious caterpillars of the ithomiid butterfly, *Mechanitis isthmia*, spin a fine silk 'scaffolding' over the tops of trichomes; they then feed on the edges of the leaves (Rathcke and Poole. 1975). This caterpillar method of neutralising trichomes is very similar to the technique used by *L. camilla* 1st instar caterpillars (Chapter Four).

1.3.3 Secretion from internal repositories.

Plant secretions can be produced by the rupture of internal leaf defences as well as external cuticular trichomes. Internal defences can include thickened cell walls, specialised cellular receptacles, intercellular pockets, and canal networks. Tannins and alkaloids may be dispersed throughout these cellular structures. The leaves of sugar maple, *Acer saccharum*, for example, are toughened by bundle sheaths that form a lignified fibrous encasement around vascular traces (Hagen and Chabot, 1986). Many canicular structures ooze copious secretions when damaged which is a function of their large size and pressurised contents. Phloem can act as a secretion from damaged leaf veins in cucurbits (Dussourd and Denno, 1991). This method of plant secretion may play a vital role in the defence of *L. periclymenum,* the foodplant of *L. camilla* and *H. fuciformis*, which is a major theme of the present study (Chapters Six-Eight).

Internal defences may be dispersed, patchy or canalicular or intermediate depending on the location and density on the leaf. Large veins are major components of the canalicular system but usually too tough for penetration by 1st instar caterpillars (Chapter Six). Even relatively small veins, still visible with the naked eye, are rarely tackled by young caterpillars. The canalicular system becomes vulnerable to young caterpillars at about the 100 microns size (using study observations of *L. camilla* and *H. fuciformis* caterpillars feeding on *L. periclymenum*). However, observations of freshly emerged *H. fuciformis* 1st instar caterpillars foraging on the foodplant leaf surface indicated that they were capable of locating and preferred penetrating the canilicular system in the size range 70-50 microns. Their detection and location mechanism of the canalicular system is open to debate but it is unlikely to be visual. Olfactory, acoustic (sound of moving phloem) or vibrational (moving phloem) mechanisms are more likely. However, Dussourd (1993) provides evidence for behavioural stimulation of trench cutting with *T. ni* caterpillars. This species did not normally cut trenches (a linear type incision on a leaf surface without complete detachment) when feeding on *Plantago lanceolata*. Yet, a minute quantity of sap from another plant species, applied to caterpillar mouth parts, caused immediate trench cutting on *Plantago* in many caterpillars.

Dispersed or evenly distributed defences may cause the caterpillar to avoid the leaf altogether or, due to dispersion causing dilution of secretion, become ineffectual. Large repositories may effectively deploy adhesives as well as toxins in high concentrations and large quantities, enough to deter caterpillar feeding when encountered. However, small first instar caterpillars attacking leaves with small cavities may be unaffected by patchy defences (Dussourd, 1993).

Canal systems solve many of the problems of dispersed and patchy defences. When ruptured, canals release secretion precisely at the site of attack, immediately on injury. In canal networks large volumes of secretion are capable of being produced due to a downward pressure gradient towards the rupture. Secretions may, as an alternative to defensive toxicity, simply prevent caterpillar feeding due to 'gumming up' mandibles, especially with small first instar caterpillars (Chapters Six-Eight). Secretions may also cover receptors preventing food recognition. Non-articulated and articulated laticifers differ in vulnerability to attack. Damage to either structure causes the release and concentration of secretion at a distinct point that can be subsequently avoided by the herbivore. This caterpillar counter-defence strategy is probably the method used most successfully by *H. fuciformis* 1st instar caterpillars in the present study (Chapter Four). But in species with non-articulated laticifers, secretion pressures are rapidly restored proximal (close-to), but not distal (far away), to a rupture (Dussourd and Denno, 1991). The distal section containing several branches is then highly vulnerable to attack. Not only are the branches isolated from the main canal system, but they are also partially drained of fluid and any remaining secretion is diluted with water. Systematic attacks on canals may therefore severely reduce the effectiveness of phloem as a defence. As a result, caterpillars may utilise this weakness by cutting veins or by feeding on damaged tissue.

Secretions that require air or oxygen to gel, such as phloem sap (Alosi *et al.*, 1988) may be completely ineffective against caterpillars that come into contact with fluids inside the leaf such as miners. In contrast, rapidly gelling secretions would impede the movement of mandibles and retard feeding ability. Dussourd (1993) provides experimental evidence that a cabbage looper caterpillar, *Trichoplusia ni*, cuts trenches across veins specifically to deactivate canal systems in host plants and thereby prevent the outflow of secretion during feeding.

Extrafloral nectaries are normally glandular trichomes which exude solutions of sugars and are usually found on leaves. They are capable of attracting and retaining insect parasitoids, which tend to suppress the populations of phytophagous insects (Gilbert, 1975,1977). There is a complete range of modifications from simple extrafloral nectaries (Elias and Newcombe, 1979), through special 'pearl' or 'Beltian' bodies (O'Dowd, 1980) to elaborate structures on all parts of plants (Huxley, 1980). Extrafloral nectaries often attract ants to leaf surfaces which may then defend the leaf from potential insect herbivores.

Canal systems deliver fluids to sites of damage caused by caterpillars in order to prevent further attack. Specialist species like *H. fuciformis* may have evolved a successful strategy which circumvents this plant defence mechanism. However, other lepidopteran species feeding on the same foodplant may be unable to do so due to some physical adversity like small size or weak mandibular power. In which case, the weaker species may then choose to feed on the foodplant where it may be growing in a weakened state such as habitats deficient in light and warmth. Under these circumstances the foodplant may be unable to produce sufficient phloem pressure to create a problem for the weaker forager.

1.3.4 Caterpillar counter-adaptation to foodplant toxins.

Caterpillar foodplants may contain toxins which may be a permanent component of leaves or may be induced through feeding damage of plant tissue. Erhlich and Raven (1964) proposed a new theory of biochemical coevolution which suggested that some caterpillar foodplants evolve to produce secondary compounds or toxins as a defence against phytophagous predators like caterpillars. The theory then proposes that some caterpillar species adapt to the toxin threat by becoming capable of neutralising the toxins through the chemical procedure of sequestration or complexing. The next stage in this theory is that the foodplant then revises its chemical synthesis to produce new toxins which results in a counter-response of chemical circumvention by the caterpillar. The discovery that a small number of lepidopteran species were capable of storing plant toxins to prevent their own predation provided support for this theory (Rothschild, 1972). Secondary compound production by plants may be energy consuming and which may weaken its primary metabolic pathways. One way in which this energy cost might be reduced is if the plant only

produced toxins at the time of caterpillar feeding damage in the form of an induced defence mechanism (Edwards and Wratten, 1983).

Toxic plant compounds cover a wide range of chemistry and include both protein and non-protein amino acids, cyanogenic glycosides, alkaloids and peptides apart from simple compounds like hydrogen cyanide in laurel leaves. An example of the biochemical coevolution theory involving a lepidopteran species which sequestrates the toxin as an anti-predator device is the interaction between milkweeds, monarch butterflies and blue-jays (Rothschild, 1972). Milkweed (*Asclepias curassavica*) produces several toxic glycosides which are sequestered and stored safely by the feeding monarch (*Danaus plexippus*) caterpillar. The toxins are transferred to the adult butterfly during ecdysis and predatory blue jay birds are caused to vomit when attempting to feed on the butterfly. As a result, blue jays learn to avoid not only further monarch butterflies but also any other butterfly which has the same warning coloration (which includes four other aposematic danaid species). Other examples of aposematic Lepidoptera are the British tiger moth, *Arctia caja*, and the cinnabar moth, *Tyria jacobaeae,* which feed on the toxic foodplants, *Senecio vulgaris* and *S. jacobaea*, respectively.

An example of wound-induced changes in the acceptability of tree foliage to Lepidoptera was demonstrated by Gibberd *et al.* (1988). The Mediterranean brocade moth, *Spodoptera littoralis*, found acceptability of artificially damaged foodplant was significantly reduced compared with undamaged foliage. Reduced palatability occurred within six hours of damage and persisted for at least seven days with birch and 14 days in alder. A mechanism for induced plant defence was proposed by Ryan (1979) who showed that some plants were able to respond quickly to insect attack by the production of specific proteins which are proteinase inhibitors and were able to deter further feeding.

1.4 Conclusion.

The present-day foraging strategy and feeding techniques employed by a lepidopteran species may be the result of an energy balance of many of the processes referred to in this introduction which affect caterpillar performance. This strategy was probably shaped by local circumstances of microclimate in which a lepidopteran foodplant grows. In the following study of the of foraging strategies of *L. camilla* and *H. fuciformis* on their conspecific foodplant, *L. periclymenum,* their caterpillar performance and behavioural traits will be examined and compared with other guild members and, finally, with each others oviposition plants. The aims of the study will be approached on the model of host selection in which ovipositing females are capable of discriminating between conspecific foodplants. Indeed, this introduction has provided evidence that ovipositing female Lepidoptera can identify their foodplants by recognising characteristic and varying concentrations of mixtures of chemical compounds and not through visual taxonomy. The 'chemical fingerprint' of a foodplant species is most likely to vary between plant parts due to heterogeneity of defence

mechanisms, between habitats and between seasons due to variations in microclimate which control the kinetics and energetics of biochemical synthesis. Therefore, an ovipositing female is most likely to distinguish between plant parts as well as between plant species.

Following page.

Study species.

Plate 1.1a *L. camilla* p. 1-20

Plate 1.1b *H. fuciformis* p. 1-20

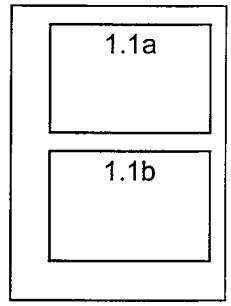


Plate 1.1 The Study Species

Chapter Two

Bentley Wood Study Site

Location - history - geology - vegetation - management - monitoring

2.1 Introduction

This study concerns the ways in which Lepidoptera have evolved to forage on a particular host, *L. periclymenum,* in different habitats of a British lowland commercial forest, Bentley Wood. Previous ecological studies of Lepidoptera in woodland (Lederer, 1960; Waring, 1990) have shown that similar groups of lepidopteran species may have evolved to forage with different strategies in different locations and habitats, indicating the importance of habitat structure.

There are several examples of lepidopteran species displaying different foraging strategies in southern European habitats compared to their UK locations. For example, *Papilio machaon* (Swallowtail butterfly) is restricted to wetlands and fens and feeds on a single foodplant, *Peucedanum palustre* (Milk Parsely), in the UK. In other areas of Europe this species is more catholic in foraging strategy, feeding on a range of Umbellifers in different habitats (Warren, 1949). Also, *Maculinea arion* (Large Blue butterfly), tolerated a wider range of habitat in southern Europe than it did in Britain before it became extinct (Thomas, 1980a).

Intraspecific variation of oviposition habitat in different habitats in a small country like the UK may be considerably less likely but still a possibility. Therefore, the author regards a detailed description of the study site as important to the understanding and interpretation of study data, not only when comparing different habitats within Bentley Wood, but, with other sites and habitats in other areas of the UK.

2.2 Location of Bentley Wood.

Bentley Wood is located on the Hampshire - Wiltshire border, 11 km east of Salisbury, 5 km south of the A30 trunk road, 45 km from the M3 and 129 km from London (G.R.: SU 250300).

2.3 Physical features of Bentley Wood.

2.3.1 Soils

Over the northern part of the wood, plateau drift, deep brown earth, soils overly chalk along with rendzinas. Surface water gleys and imperfectly drained brown earths cover most of the rest of the wood with the odd pocket of valley gravel (Figure 2.1).

2.3.2 Physiography

Bentley Wood is gently undulating with slightly steeper slopes along the north eastern boundary, the whole wood having a generally south facing aspect.

2.3.3 Elevation

Bentley Wood rises steadily from 50 m along the southern boundary to 130 m at the north western boundary.

2.3.4 Mean Annual Rainfall

The mean annual rainfall for Bentley Wood was 80 cm (32 inches) over the period, 1960-80 (Forestry Commission: unpublished data).

2.4 Management history of Bentley Wood.

The ancient Celtic name of the wood, The Forest of Penchet, suggests that Bentley Wood was one of the primeval forests of England and may be regarded as a site of primary woodland (Rackham, 1993). Before complete afforestation in the 1950s Bentley Wood's history was that of a typical ancient countryside estate forest used for growing timber (coppice with standards and a few plantations) including woodland pasture and open areas of grassland. The site of Bentley Wood is shown as part of a more extensive area of woodland in the Domesday Book in the year 1086.

The wood belonged to the Norman Court Estate for several centuries until the estate was dissolved and the wood was purchased by the Forestry Commission in 1952. Shortly before this purchase over 90% of the wood was clear-felled by timber merchants and the remaining scrub woodland was subsequently cleared by the Forestry Commission. However, 100 + year old oaks are still found on the perimeter of Bentley Wood in addition to a single oak plantation planted in 1937. In 1983 Bentley Wood was purchased by a Charitable Trust using funds provided by the late Lady Colman, who lived in the nearby village of Winterslow. Today, Bentley Wood continues to be managed on a commercial basis with amenity and conservation taken into consideration.

In 1984 Bentley Wood was designated a Site of Special Scientific Interest (SSSI) by the Nature Conservancy Council (now English Nature) because of its outstanding diversity of Lepidoptera. Over 400 macro-moth species have been recorded in the wood and its environs during the period 1980-95 (unpublished records of P. Waring, B. W. Fox and J. Williams). In good years over 40 butterfly species can be seen flying along the rides and clearings and 35 species are regular breeders.

Over 300 species of ground flora, 74 species of Gramineae, 63 species of trees, shrubs and climbers, and 205 species of fungi have been recorded over the last ten years. In the same period 96 species of birds have been recorded in the wood including 11 raptors (unpublished Bentley Wood Natural History Records).

2.5 Plantation composition.

2.5.1 Original composition (1952-59).

The plantation system was planted by the Forestry Commission in the 1950s with 85 % mixed conifers and broadleaf species and 15% pure conifer or pure broadleaf (Figure 2.2). The plantation crop was established on fertile land which had carried a tree crop of a more open broadleaf woodland type with coppice for several centuries. *Fagus sylvatica* (Beech) was the dominant broadleaf species in the northern chalk soils whilst *Quercus robur* (Oak) was the dominant broadleaf on the heavier clay soils to the south. The trees were notch planted, with mixtures consisting mainly of 3 rows of conifers to 3 rows of broadleaves, but with some areas of 3 rows x 2 rows and occasional broadleaf groups in a conifer matrix. The predicted clear-fell time for the conifers is about 2010 although several line thinnings have already taken place in addition to the odd clear-fell. The final target density for the oaks is about 125 per hectare.

The last Forestry Commission planting took place in 1983 with two pure Corsican pine plantations. At this period the overall timber composition in the wood was as follows:

Picea abies (Norway spruce) 37 %; *Quercus robur* (oak) 24 %; *Fagus sylvatica* (beech) 17 %; *Pinus sylvestris* (Scots pine) 6 %; *Pinus nigra* (Corsican pine) 6 %; *Pseudotsuga menziesii* (Douglas fir) 4 %; mixed broadleaves 3 %; other species 3 %.

The area of woodland containing plantations of oak and conifer mixture was 61% (342.6 ha) with 38 % (212.4 ha) of the woodland area containing a beech and conifer mixture.

2.5.2 Plantations today.

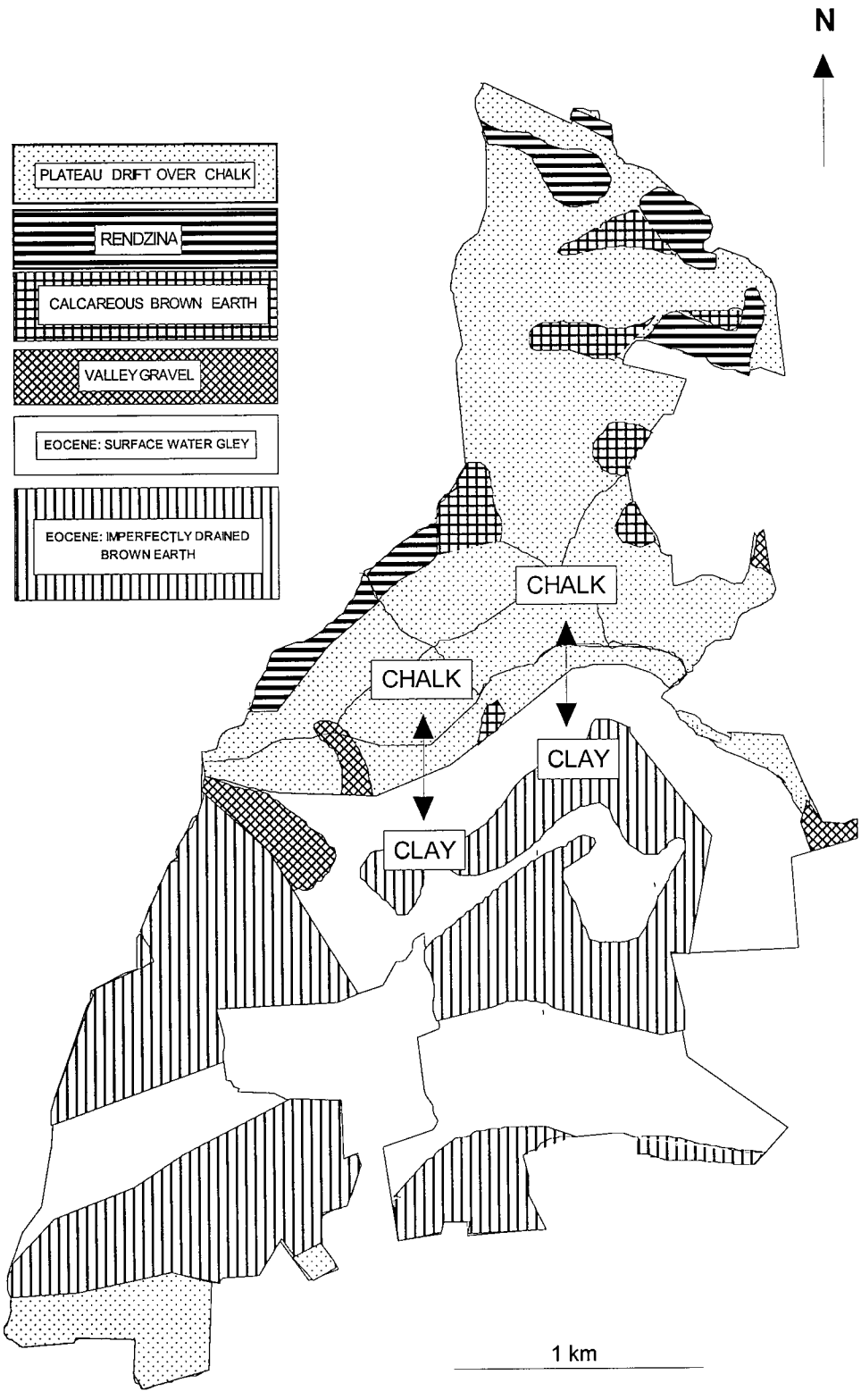
2.5.2.1 Plantation vegetation surveys (Tables 2.1-2).

Periodic thinning of the nursery conifer crop and broadleaf species for commercial firewood and paper manufacture allowed more light to penetrate the plantations which has enabled the growth of scrub species and climbers like *L. periclymenum* although this lepidopteran host was found mainly in the oak dominant southern areas of Bentley Wood (Table 2.2 and Figures 2.2). Hazel was present in many of these plantations as regeneration from the old coppice areas which featured strongly in Bentley Wood before afforestation. Hawthorn was a frequent scrub species inside the plantations especially in areas where hawthorn thickets existed before clearance. Today, there are more scrub species like sallow, birch, aspen and hazel growing in the oak plantation areas than are growing in the beech dominant areas to the north. The beech canopy allows less light to penetrate than oak foliage which may help to explains the greater density of *L. periclymenum* in the southern oak areas of the wood. A substantial number *L. periclymenum* drapes were found climbing up dead scrub species which accounts for the transient nature of this climber. Each winter's gales readily destroy the fragile structure of these dead tree supports and creates a survival problem for diapause *L. camilla* larvae which overwinter in *L. periclymenum* drapes.

The lack of herbaceous plant species in the beech dominant plantations, as found in the ground vegetation survey using the Domin Scale of ground cover abundance (Table 2.3), reflects how little light penetrated the plantation canopy even after one or two forestry thinnings had taken place in plantations A-F and K.

Hazel scrub was found to be a major support of *L. periclymenum* drapes (tree supports for *L. periclymenum* are examined in Chapter Three). Plantations C, E and K, all dominated by beech, contained very little scrub growth (3 %, 6 % and 11 %, respectively) with a total lack of *L. periclymenum* drapes. The other two beech dominant plantations, A and B, contained much more scrub species (47 % and 33 %, respectively) but still contained few *L. periclymenum* drapes (3 and 6, respectively). In contrast, the two oak dominant plantations H and J which contained a moderate number of scrub species (13 % and 22 %, respectively) contained the highest number of *L. periclymenum* drapes (36 and 62, respectively). However, another oak dominant plantation, G, contained a very high proportion of scrub species (50 %) but a complete lack of *L. periclymenum* drapes. The difference between plantations G and H-J was that plantation G was

Fig. 2.1 Bentley Wood soil type.



on chalky soil while the other two plantations were on acid clay soils. Thus, the main three plantation factors which create good numbers of *L. periclymenum* drapes are

- a light penetrating canopy (e.g., oak dominant plantations)
- a high proportion of supporting scrub species (e.g., hazel and silver birch) and
- an acid soil (e.g., clay or imperfectly drained brown earth with high moisture content).

Plantation F, containing mixed broadleaf (10 % oak, 6 % beech and 5 % ash) growing on neutral to acid soil, contained 34 % scrub species which supported 24 *L. periclymenum* drapes. All these plantations except D, a sycamore coppice, contained a nursery crop of conifers which help the growth of the broadleaf timber species.

The plantation ground vegetation cover (Table 2.3) was dominated by leaf litter and mosses. Mosses were most abundant in oak dominant plantations and were found to be a good indicator for *L. periclymenum* growth. Moss cover abundance appeared to be proportional to *L. periclymenum* density in plantations.

2.5.2.2 Recent management in Bentley Wood (1984-95).

In 1992 three thousand hardwood trees were planted in areas of storm damage caused by the 1987 and 1991 gales. Since 1984 the present owners, Bentley Wood Trust, with the aid of the Woodland Grant Scheme, have carried out ride widening, coppice restoration and other conservation plans which have improved the wood considerably for Lepidoptera. Forestry management tasks have been implemented in such a way as to minimise adverse impact on lepidopteran colonies.

Lederer (1960), in his study of *L. camilla* in German woodland sites, found this species of butterfly reluctant to re-establish itself in new areas after well established colonies were lost or reduced through forestry management. However, recent butterfly records from Bentley Wood have indicated that *L. camilla* has recovered from thinning operations in plantations carried out over the last five years (Section 4.5 and Figure 4.2 in Chapter Four). Loss of *L. camilla* oviposition sites is inevitable during forestry thinning operations. Selective thinning carried out gradually in widely dispersed areas, has minimised the loss of *L. camilla* oviposition sites in Bentley Wood. One of the aims of this study is to identify the type of woodland habitat best suited to *L. camilla* and *H. fuciformis* so that supportive forestry and conservation management may be carried out in future.

In the northern part of Bentley Wood 90 % of the conifers (planted as a nursery crop to broadleaf species) have been removed. However, clumps of conifers have been left for the benefit of bird species which prefer a conifer or mixed conifer-broadleaf habitat. Some areas which were originally intended as pure beech final crop have been clear-felled and are being allowed to regenerate,

naturally, with the help of small numbers of replanted oak, wych elm and cherry. Some scrub planting has been carried out on the edges of new clearings and widened rides to achieve a layered effect between high forest and swiped ride margins. Some of these clearfells were prematurely created to increase the age diversity of the wood which increases biodiversity.

Since the early 1980s a substantial number of small clearings and open areas have been created to diversify the predominantly plantation forest (Figure 2.3). Box junctions (ride junctions with wide margins), scalloping (small clearings along rides) and the creation of new rides have been successfully integrated with forestry management to minimise expense. Such management has created a range of shade which has helped to increase the numbers of many species of butterflies.

Hazel coppicing has been initiated in several areas to provide suitable habitats for insects and flora which benefit from successional ground vegetation. Fritillary species of butterfly have benefited considerably from such management and Bentley Wood colonies have been used to regenerate fresh colonies in other woodland areas.

2.6 *L. periclymenum, L. camilla* and *H. fuciformis* monitoring sites in Bentley Wood.

2.6.1 Location of *L. periclymenum* monitoring sites (Table 2.1; Figure 2.4).

L. periclymenum drape density was recorded in 10 plantations and along 39 butterfly transect ride and clearing sections. The results of *L. periclymenum* density in comparison with stock trees in plantations are shown in Table 2.2 and ride drape density is shown in Table 4.1 (Chapter Four). The plantations chosen for recording *L. periclymenum* density in the period 1992-94 included 5 beech-conifer, 3 oak-conifer, 1 mixed broadleaf-conifer and 1 sycamore coppice. The recording site locations are shown in Table 2.1 and Figure 2.4. All plantations adjacent to transect sections were of a similar age (40-45 years old) except the sycamore coppice (plantation D) which was planted in 1970. Examples of tree frequency and stand distribution in sample plots are shown in Appendices 5 and 6 with the results in Table 2.2.

Fig. 2.2 Plantation structure and compartment numbers: based on Forestry Commission stock map (1982)

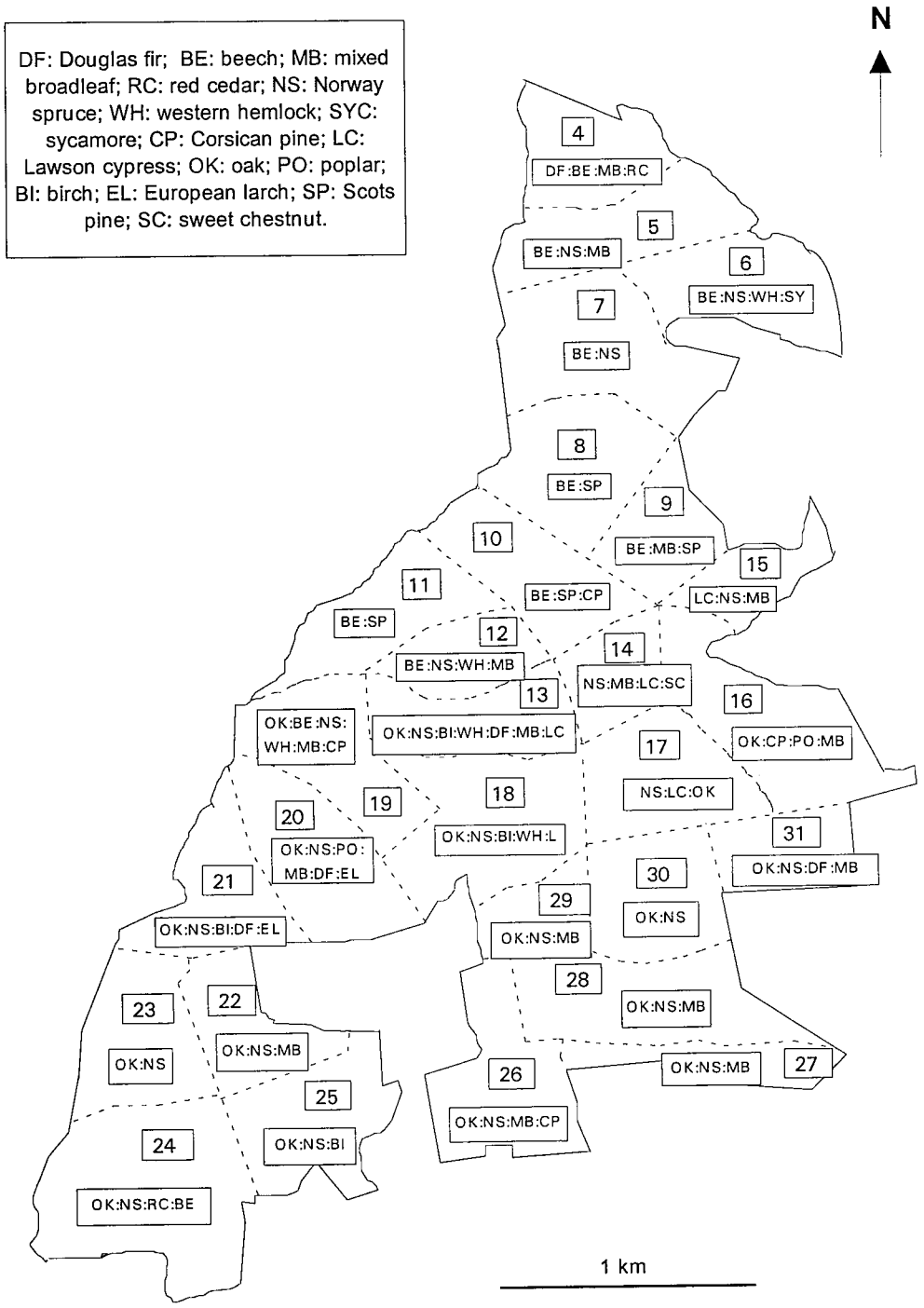


Fig. 2.3 Bentley Wood: clearings and major rides (1995).

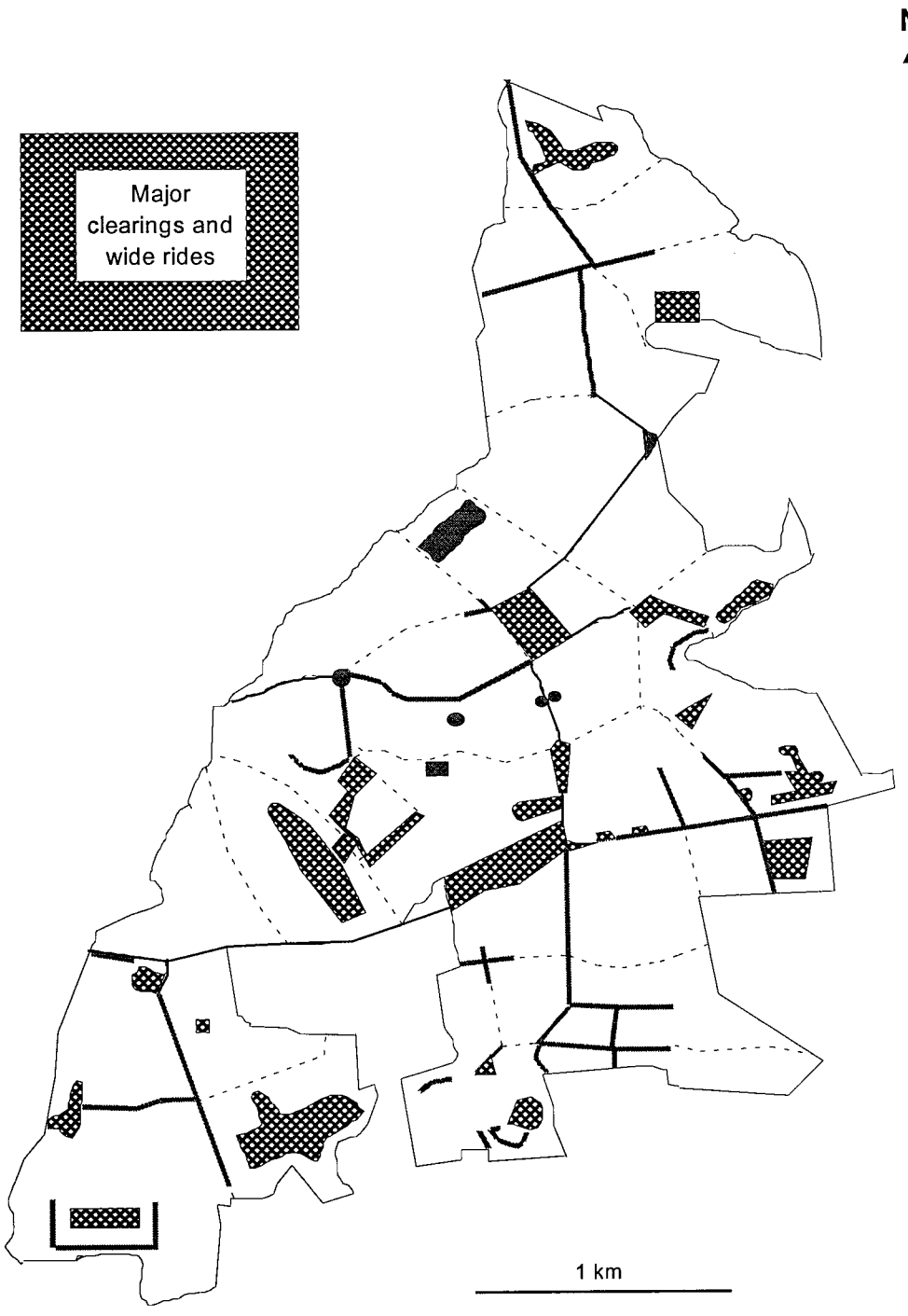


Plate 2.1

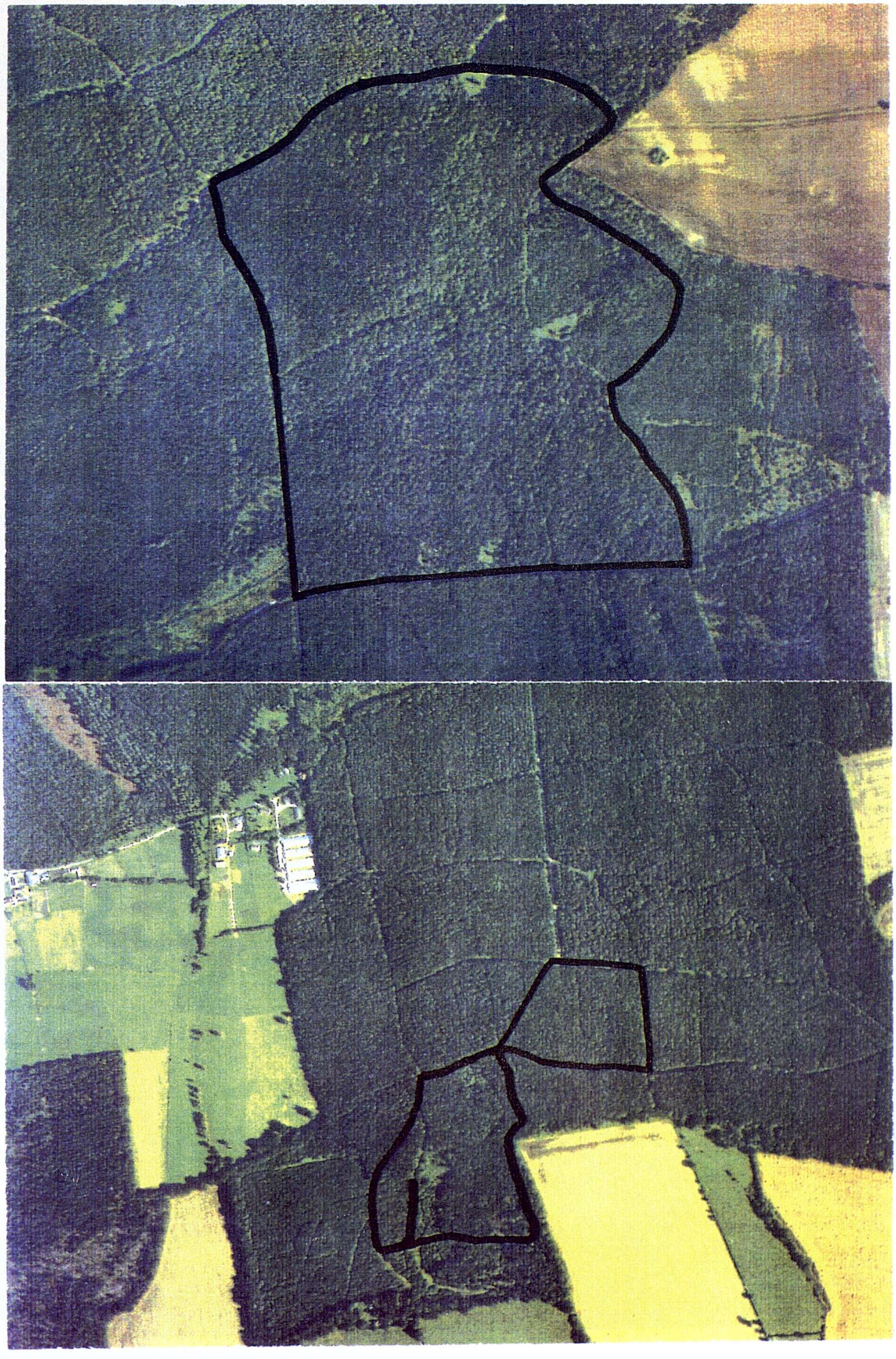
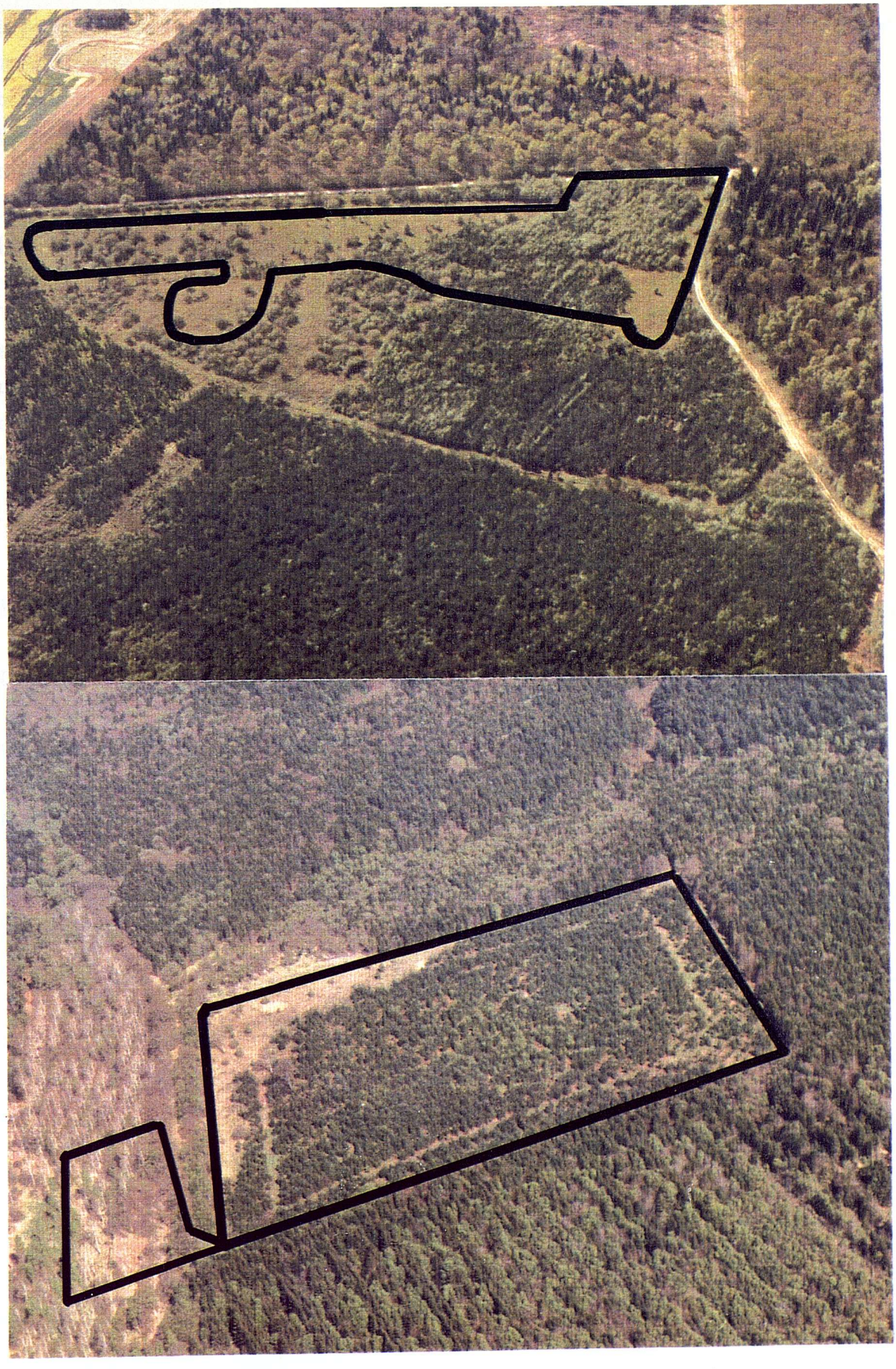


Plate 2.2



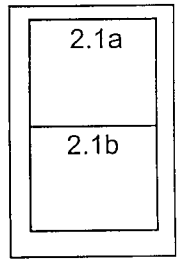
2.6.2 Location of *L. camilla* monitoring sites in Bentley Wood (Plates 2.1-2: Figure 2.4).

L. camilla monitoring sites were located on the four butterfly transect routes which were established in Bentley Wood in the 1980s to monitor the effect of forestry and conservation management on butterfly populations. In total, 39 transect sections were used to monitor *L. camilla* numbers over the period 1986-95 and cover a wide range of woodland habitat including plantation rides and clearings. Transect data is discussed in Chapter Four.

2.6.3 Location of *H. fuciformis* monitoring sites in Bentley Wood.

There was no transect monitoring of *H. fuciformis* since their presence at ground level was extremely infrequent and their overall abundance was too low to produce meaningful transect counts. However, their main oviposition sites were located and recorded in detail and are discussed in Chapters Four and Five. In general, the main oviposition sites were found in the southern half of Bentley Wood where host plants are most abundant (Figure 2.4).

Previous pages



Date of photographs: 1991.

Plate 2.1a *L. camilla* monitoring site (I): North transect (1 cm = 50 m). p. 2-10
Plate 2.1b *L. camilla* monitoring site (II): South transect (1 cm = 45 m). p. 2-10
Both areas are potentially good sites for *L. camilla* but poor sites for *H. fuciformis.*

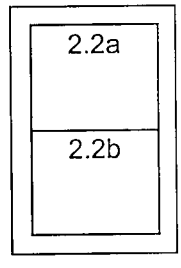


Plate 2.2a *L. camilla* monitoring site (III): East transect (1 cm = 25 m). p. 2-11
Plate 2.2b *L. camilla* monitoring site (VI): Barnridge transect (1 cm = 25 m).
p. 2-11

Table 2.1 *L. periclymenum* plantation monitoring sites. (See Figure 2.4 for site locations in Bentley Wood.)

Monitoring site	Forestry block	Map reference	Area of block (ha)	Planting date	Intended final crop
A	4	253317	21	1958	Beech
B	5	251315	23	1958	Beech
C	5	253314	23	1958	Beech
D	6	256313	2	1970	Sycamore
E	8	252306	27	1956	Beech
F	15	257299	12	1961	Mixture
G	13	250297	16	1959	Oak
H	29	250288	13	1955	Oak
J	28	250286	32	1954	Oak
K	9	254301	7	1954	Beech

2.7 Conclusion.

The massive clear-fell of Bentley Wood in the 1945-55 period and subsequent forestry cleaning operations probably destroyed the vast majority of lepidopteran oviposition sites then existing in Bentley Wood. The surrounding pockets of ancient woodland and the mixed conifer and broadleaf plantations, as opposed to pure conifer stands, may have contributed to its present day recovery as a prime lepidopteran site. However, the most important factor must be the conservation management carried out by the present owners of Bentley Wood over the last decade. Its future success will depend on the long-term plans for sustainable management after restoration. Such plans must target those species of butterfly which are normally associated with short turf habitat but which are still present in small numbers in Bentley Wood. Future management should also include ecological research in Lepidoptera and emphasise integration of forestry and conservation management. The results of the present study, hopefully, will provide information for appropriate habitat management which may help to sustain *L. camilla* and *H. fuciformis* in future.

Fig. 2.4 Bentley Wood: *L. periclymenum* and *L. camilla* monitoring sites along 4 butterfly transects and inside plantations (A-K).

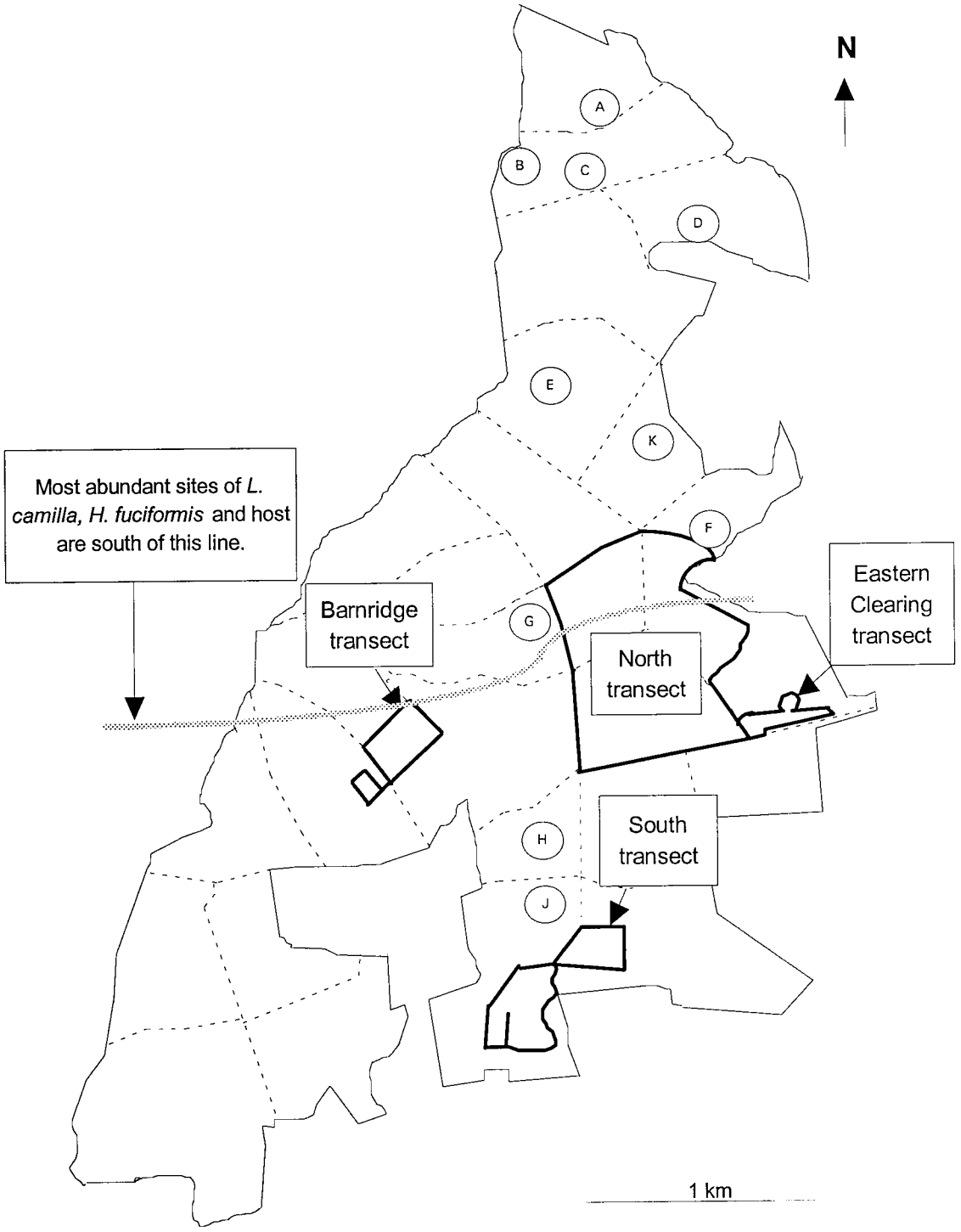


Table 2.2 Vegetation structure of plantation monitoring sites (A-K): number of trees in sample area (0.2 hectare).

		A	B	C	D	E
Norway spruce	*Picea abies*	59	67	131	0	0
Douglas fir	*Pseudotsuga manziesii*	10	0	0	0	0
Scots pine	*Pinus sylvestris*	0	0	0	0	53
Corsican pine	*Pinus nigra*	0	0	0	0	0
Lawson cypress	*Chamaecyparis lawsoniana*	0	0	0	0	0
Beech	*Fagus sylvatica*	75	94	57	0	293
Wych elm	*Ulmus glabra*	0	0	0	0	0
Oak	*Quercus robur*	8	11	4	0	1
Silver birch	*Betula pendula*	55	10	1	0	20
Aspen	*Populus tremula*	1	0	0	0	0
Ash	*Fraxinus exelsior*	0	0	0	1	0
Sweet chestnut	*Castanea sativa*	0	0	0	0	0
Field maple	*Acer campestre*	0	0	0	0	0
Sycamore	*Acer pseudoplatanus*	0	0	0	160	0
Sallow	*Salix caprea*	25	31	1	0	6
Hawthorn	*Crataegus monogyna*	17	0	0	17	5
Blackthorn	*Prunus spinosa*	0	0	0	1	0
Hazel	*Corylus avellana*	28	46	4	17	22
Elder	*Sambucus nigra*	0	0	0	2	0
Wild privet	*Ligustrum vulgare*	0	0	0	1	0
Honeysuckle	*Lonicera periclymenum*	3	6	0	0	0
Total		281	265	198	199	400

		F	G	H	J	K
Norway spruce	*Picea abies*	88	100	307	208	0
Douglas fir	*Pseudotsuga manziesii*	0	0	0	0	0
Scots pine	*Pinus sylvestris*	0	0	0	0	61
Corsican pine	*Pinus nigra*	0	0	0	0	6
Lawson cypress	*Chamaecyparis lawsoniana*	31	0	0	0	0
Beech	*Fagus sylvatica*	20	0	0	0	97
Wych elm	*Ulmus glabra*	3	0	0	0	0
Oak	*Quercus robur*	36	281	335	316	5
Silver birch	*Betula pendula*	15	36	54	53	11
Aspen	*Populus tremula*	0	0	9	27	0
Ash	*Fraxinus exelsior*	19	0	63	0	8
Sweet chestnut	*Castanea sativa*	7	0	0	0	2
Field maple	*Acer campestre*	5	0	0	0	0
Sycamore	*Acer pseudoplatanus*	0	0	0	0	0
Sallow	*Salix caprea*	2	0	27	63	0
Hawthorn	*Crataegus monogyna*	71	335	18	9	9
Blackthorn	*Prunus spinosa*	0	9	0	0	0
Hazel	*Corylus avellana*	27	18	9	45	2
Elder	*Sambucus nigra*	1	0	0	0	0
Wild privet	*Ligustrum vulgare*	2	9	0	0	0
Honeysuckle	*Lonicera periclymenum*	24	0	36	62	0
Total		351	788	858	783	201

Table 2.3 Ground vegetation survey of *L. periclymenum* monitoring sites (plantations A-K; Domin Scale). Sample sites F, H, and J contained most aerial L. periclymenum drapes (Table 2.2).

Rating	A	B	C	D	E
1	Leaf litter	Leaf litter	Leaf litter	Leaf litter	Leaf litter
2					
3				Lichens	
4	Mosses/lichens	Mosses/lichens	Mosses/lichens	Bracken/ferns	
5	Bracken/grasses /bramble	Bracken/grasses	Bracken/grasses /bramble	Grasses/mosses /bracken	Bracken

Rating	F	G	H	J	K
1	Leaf litter	Leaf litter	Leaf litter	Leaf litter	Leaf litter
2	Mosses	Dog's mercury	Mosses	Mosses	
3	Nettle/lichens	Mosses			Dog's mercury
4	Bracken/grasses	Nettle	Bracken/ferns	Grasses	Bracken/ferns
5	Bramble/ferns	Ferns/bracken /viola sp.	Grasses	Bramble/ferns	Grasses/mosses /bracken

Key Rating	Frequency	Ground cover (%)
1	Dominant	80-100
2	Abundant	60-79
3	Frequent	40-59
4	Occasional	20-39
5	Rare	1-19

Chapter Three

Lonicera periclymenum - an important host?

Host ecology - lepidopteran status - guild structure - foraging strategies host specificity - habitat

3.1 Introduction

3.1.1 What is an important lepidopteran food plant?

The importance of *Lonicera periclymenum* as a caterpillar food resource for Lepidoptera was determined by answering the following questions:

- How many lepidopteran species use *L. periclymenum* as caterpillar host?
- How many adult Lepidoptera use *L. periclymenum* as a nectar source?
- How many specialist Lepidoptera feed on *L. periclymenum*?
- How many of these Lepidoptera are rarities?
- How stress tolerant is *L. periclymenum* ?
- Is *L. periclymenum* foliage available at unusual times of the year?
- Does *L. periclymenum* allow a wide range of caterpillar foraging strategies?
- Does *L. periclymenum* grow and attract Lepidoptera in a wide range of habitat?

3.1.2 Lepidopteran status and popularity of *L. periclymenum* as a lepidopteran host.

Phytophagous literature for UK Lepidoptera (Emmet and Heath, 1991; Bradley *et al.,* 1973; Skinner, 1984; South, 1977) frequently quoted *L. periclymenum* or *Lonicera* spp. as a lepidopteran food plant. Emmet and Heath (1991) listed ten Lepidoptera feeding on *Lonicera* spp. and 6 Lepidoptera feeding on *L. periclymenum,* itself.

National rarity or status data for macro-moth species was obtained from Waring (1996). Waring's status list was based on the number of 10 km squares within the UK in which the species has been reported at least once since 1980. Using this technique the rarest national species are given Red Data Book (RDB) designation and are found in 15 or fewer 10 km squares. Nationally scarce species

are found in the range 16-100 10 km squares, local species in the range 101-300 10 km squares, and common species are found in more than 300 10 km squares. It is important to note that species can be found to be abundant where they occur and yet have a very restricted national distribution. On the other hand, some species are found sparingly for various reasons but maybe found in most areas of the country.

3.1.3 Ecology of *Lonicera periclymenum.*

Lonicera periclymenum belongs to the *Caprifoliaceae* family which contains about 200 species of evergreen and deciduous flowering shrubs and woody climbers. *L. periclymenum* is found throughout Britain in all vice counties (Grime *et al.*, 1990) and throughout Wiltshire (Fuller, 1995) growing wild in woodland and hedgerows on both acidic and basic soils.

In the theory of botanical strategy *L. periclymenum* is regarded as having an intermediate strategy between stress-tolerant and ruderal (Grime *et al.*, 1990). A ruderal species is a plant which lives in disturbed sites and is generally characterised by a high relative growth rate during the seedling phase and an early onset of reproduction. The theory of botanical strategy argues that stress-tolerant species will succeed in habitats of stress where resource availability is brief, unpredictable and limited. Forestry plantations, where *L. periclymenum* is often found in Bentley Wood, could be described as stressful habitats since light, nutrients and water are in great demand by plantation trees and scrub growth.

The ability of *L. periclymenum* to be stress-tolerant in habitats like shaded plantations and ruderal in woodland clearings of high sunlight availability creates the potential for a good lepidopteran host with the possibility of a wide range of foliage quality. This variation of host quality may influence lepidopteran phenology (flight periods) and foraging strategies. For instance, a lepidopteran species may feed on nutrient rich leaf material in clearings and race through the caterpillar stage of metamorphosis especially in warm, sunny, climes. However, another lepidopteran species may have evolved in shaded habitats and be unable to tolerate host foliage growing in sunny woodland areas. Inner shaded areas of commercial plantations may produce slow photosynthesis and foodplant having poor nutrient quality. Acid soils, often found on clay and in conifer plantations, as in the southern half of Bentley Wood, contain nitrogen in the form of the ammonium ion which is only slowly oxidised to the more useful nitrate ion by root bacteria (Salisbury and Ross, 1985). These conditions may also help to produce lepidopteran foodplants of poor quality in forestry plantations. In this study foodplant quality of *L. periclymenum* is determined and compared between shade and open sunny habitats (Chapter Six).

By nature a woodland clearing normally contains no trees or supporting structures for climbing plants like *L. periclymenum.* In commercial forests a clearing is usually a transient stage area where young

saplings are planted or allowed to regenerate from natural seed in the soil. However, stumps and damaged timber of varying heights are frequently found in woodland clearings after windblow which adequately support climbers like *L. periclymenum*. In Bentley Wood the majority of present cleared areas were caused by the gales of 1987 and 1991 rather than conservation management. In addition, such clearings contained prostrate or ground *L. periclymenum* growth inter-twined with other herbaceous plant growth where predation from other insects is probably more likely than in aerial growths. As a result, oviposition by *L. camilla* and *H. fuciformis* will be compared between aerial and ground growing foodplant. It has been suggested (Grime *et al.,* 1990) that stress-tolerant plants are generally characterised by having strong anti-herbivore defences which protect the living foliage and often remain operational after senescence, retarding the breakdown of litter by decomposing organisms. This behaviour may explain the dense accumulation of litter found under plantation trees at all times of the year, and which is often used by pupating Lepidoptera. Lepidoptera preferring shaded plantations as oviposition sites may have evolved counter adaptation techniques against plant defence mechanisms which are not displayed by lepidopteran species feeding on their hosts growing in sunny clearings.

Since *L. periclymenum* is shade tolerant (Grime *et al.,*1990), this climber may be expected to succeed in both shade and sunlight areas of woodland. Since plant defence mechanisms are regarded as energy consuming and compete for energy with other types of plant growth, there may be a variation in plant defence mechanisms in shade growth compared to sun growth. In turn, this variation may have influenced the foraging behavioural patterns of Lepidoptera so the interactions between Lepidoptera and *L. periclymenum* will be studied in habitats of contrasting shade such as plantations and open clearings.

3.1.4 Availability of *L. periclymenum* at unusual times of the year.

Host availability is very important to foraging Lepidoptera especially if a particular host is available at an unusual time of the year. This importance applies to host inflorescence as well as host foliage. Post-diapause caterpillars may find host foliage availability in early spring, late winter or even mid-winter essential to survival since mild periods in winter may induce occasional feeding. Small pre-diapause lepidopteran caterpillars may find difficulty in accumulating fat reserves prior to diapause (Leather *et al.*, 1993). The availability of early season host foliage during warm periods may help survival of caterpillars which are living at latitudes close to their northern limit as is the case with several British lepidopteran species (Thomas, 1980a).

3.1.5 Foraging strategies and caterpillar feeding behaviour on *L. periclymenum.*

Plant defence mechanisms and parasitoid predation help to shape foraging patterns and feeding techniques of lepidopteran caterpillars (Rhoades, 1985). Large numbers of lepidopteran species

feeding on the same foodplant would indicate that *L. periclymenum* is unlikely to employ a plant defence technique which is based on a toxic secondary chemical. This hypothesis would be further supported if a large proportion of guild members feeding on *L. periclymenum* are generalists since generalists are not normally able to neutralise plant toxins (Harborne, 1989).

The variety of feeding strategies illustrated by lepidopteran caterpillars is very limited especially when compared with the number of lepidopteran species. Consequently, it is logical to conclude that the same evolutionary driving forces have shaped these feeding strategies for all species of Lepidoptera. Since nearly all Lepidoptera are phytophagous, feeding strategies of caterpillars must be influenced to a great extent by the properties or defence mechanisms of the food plant. The same food plant might be expected to exhibit the same defence mechanisms irrespective of predatory species. However, variations in host defence mechanisms may arise through environmental variation of abiotic factors such the degree of available sunlight.

Physiological adjustments made by the host plant to cope with possible variation in temperature and sunlight may determine and alter food plant quality. Coley *et al.* (1985) predicted that plants growing in resource-poor microhabitats protect their foliage by producing long lived foliage with constitutive defences and those plants growing in resource poor environments protect their foliage with short lived foliage using induced defences. Variable foodplant quality may, in turn, influence caterpillar and adult lepidopteran foraging behaviour. Some species of Lepidoptera may prefer to feed on hostplant growing in shade because shade host quality favours the caterpillar's feeding technique and metabolism.

From the point of view of feeding caterpillars the reasons for variation in food plant quality are irrelevant. What is important is how the caterpillars, themselves, cope with variable host quality. Investigation of these host-caterpillar interactions may reveal clues about the food plant defence mechanisms. For example, if the majority of the lepidopteran guild feeding on *L. periclymenum* prefer to do so when the plant is growing in the shade, then foodplant quality may be more unpalatable when *L. periclymenum* is growing in contrasting conditions such as in full sun. In any event, such investigations may reveal important host defence mechanisms and the ability of Lepidoptera to counter-adapt to these mechanisms.

3.2 Method and materials.

3.2.1 How many Lepidoptera use *Lonicera periclymenum* as a larval food plant?

Aerial and ground *L. periclymenum* growth was examined in rides, clearings and plantations throughout Bentley Wood for the presence of lepidopteran eggs and caterpillars. Searching for caterpillars and eggs was carried out by hand. Other methods such as beating and suction

sampling were not employed as a record of the microhabitat of the leaf surface on which the caterpillars were feeding was also required.

During the period 1993-94, over 500 drapes of aerial growing *L. periclymenum* were examined in various habitats of Bentley Wood and a similar number of non-climbing plants were examined in a number of clearings.

The seasonal period of examination covered January to December although most fruitful searching took place in the period March-August in both years. During these months at least two days (five days in the peak April-June period) in every week were spent in the field examining *L. periclymenum* drapes in rides, clearings and plantations. A fair comparison of habitat oviposition preference was affected by examining an equal number of *L. periclymenum* drapes in each of the three main habitats.

Night searching for caterpillars proved successful in April and May especially for Noctuidae and Geometridae macro-moth species. All 31 compartments in Bentley Wood were searched during the two year period although most of this searching took place in the southern half of the wood where *L. periclymenum* was most abundant.

A systematic approach was used for searching each drape of *L. periclymenum* for caterpillars or eggs. In plantation drapes each leaf was examined prior to and after expected caterpillar emergence periods. Ride and clearing drapes were searched as thoroughly as practically possible. The presence of lepidopteran imago and pupae on *L. periclymenum* foliage was not accepted as proof of feeding on *L. periclymenum*. The presence of fresh feeding damage (leaf incisions which had not had time to turn brown) was used as a good indicator of the presence of foraging caterpillars. In sunny locations the presence of sticky globules of secretion on the leaf surface was another indicator and rolled up leaves indicated the presence of leaf rollers occupied by micro-moth caterpillars. Twisted leaves were carefully scrutinised as they often indicate the presence of leaf miners. Both upper and lower leaf surfaces were examined for the presence of lepidopteran foraging.

Unidentifiable specimens in the field were reared through to adult in captivity and eventually identified. Only 4 % of caterpillars died in captivity (excluding parasitised specimens) and were unable to be identified. Parasitoid caterpillars rarely died before the final instar which allowed identification. Approximately 10 % of all caterpillars and eggs (N = 495) found in the field were parasitoid. The adult parasitoid specimens were identified by Mark Shaw (Edingburgh Museum) and the results appear in the appendix.

The adult and other stages of Lepidoptera were identified by using various texts and lepidopteran specialists. Macro-Lepidoptera were identified using mainly Skinner (1984) and Tortricoid moths were identified using Bradley *et al.* (vol. I, 1973; vol. II, 1979). Identification of macro-lepidopteran eggs and caterpillars was aided by the use of Carter and Hargreaves (1986) and Stokoe (1948). Specialist lepidopterists who helped with identification were Stephen Palmer and John Langmaid (micro-Lepidoptera), and Adrian Riley (Rothamsted Experimental Station) and Barry Goater (macro-Lepidoptera).

The majority of the micro-moth caterpillars were reared in petri dishes lined with filter paper. The larger caterpillars were reared in 500 cm^3 clear plastic boxes. Freshly cut *L. periclymenum* foliage from the original location was supplied every day although leaf rolls were not disturbed. Each box was labelled with specimen number, date of capture and various other data as required.

3.2.2 Which habitats favour *L. periclymenum* growth?

Rides, plantations and clearings throughout Bentley Wood were thoroughly examined and searched for foraging caterpillars on *L. periclymenum* drapes during the period 1993-94. The number of *L. periclymenum* drapes were counted in 0.2 hectare sample plots in 10 plantations covering both the oak and beech dominant areas of Bentley Wood. The sample plots were chosen by simply walking into the central area of each plantation to avoid ride side influence and marking the centre of each plot with a pole. In total, 5 beech-conifer plantations, 4 oak-conifer plantations and one sycamore coppice were chosen for sampling.

In total, 39 ride sections (established butterfly transect sections) were used for counting *L. periclymenum* drapes growing on the plantation perimeter of both sides of each section. These ride sections covered both beech dominant and oak dominant areas of Bentley Wood and included all orientations. All Bentley Wood clearings (13 ranging from 0.4 to 10 hectares) were searched for both aerial and ground *L. periclymenum* drapes in central and perimeter areas.

3.2.3 Larval feeding techniques of Lepidoptera foraging on *L. periclymenum.*

Each caterpillar foraging site was examined and classified into four categories: external feeders (no shelter on leaf surface), leaf rollers (leaves tied together with silk containing caterpillar resting site), leaf miners (internal feeder) and leaf web (caterpillars feeding externally inside a silk-foliage shelter). Plants used by nectaring adult Lepidoptera were recorded together with their proximity to oviposition sites.

3.2.4 Recording oviposition site character for *L. camilla* and *H. fuciformis.*

Recording oviposition site character for *Ladoga camilla* and *Hemaris fuciformis* was carried out in greater depth than other species as they were the major study species and details of method and results appear in Chapter Five.

3.3 Results

3.3.1 How many *Lepidoptera* use *Lonicera periclymenum* as a larval food plant? (Table 3.1; Fig. 3.1)

During the period 1993-94, 35 species of Lepidoptera were discovered and identified using *L. periclymenum* as a caterpillar food resource in Bentley Wood (Table 3.1). This guild of Lepidoptera consisted of one butterfly, *Ladoga camilla*, and 33 species of moths which included 18 macro- and 15 micro-moths.

The micro-moths were represented by 6 families:

- Tortricidae (9 spp.)
- Yponomeutidae (2 spp.)
- Gracillariidae (1sp.)
- Pyralidae (1 sp.)
- Gelechiidae (1 sp.)
- Oecophoridae (1 sp.)

the macro-Lepidoptera represented 5 families:

- Noctuidae (10 spp.)
- Geometridae (6 spp.)
- Sphingidae (1 sp.)
- Lymantriidae (1 sp.)
- Nymphalidae (1 sp.)

The two most frequently occurring species foraging on *L. periclymenum* in the period 1993-94 were *Ladoga camilla* (33 % of oviposition sites) and *Hemaris fuciformis* (21 % of oviposition sites) (Fig. 3.1). The next four dominant species were all micro-moths, three of which belong to the Tortricidae family: *Archips podana* (10 % of oviposition sites), *Ditula angustiorana* (5 % of oviposition sites), and *Pandemis cerasana* (5 % of oviposition sites). The fourth micro-moth was *Phyllonorycter trifasciella* (7 % of oviposition sites), a member of the Gracillariidae family, the only leaf miner or internal feeder.

Plate 3.1

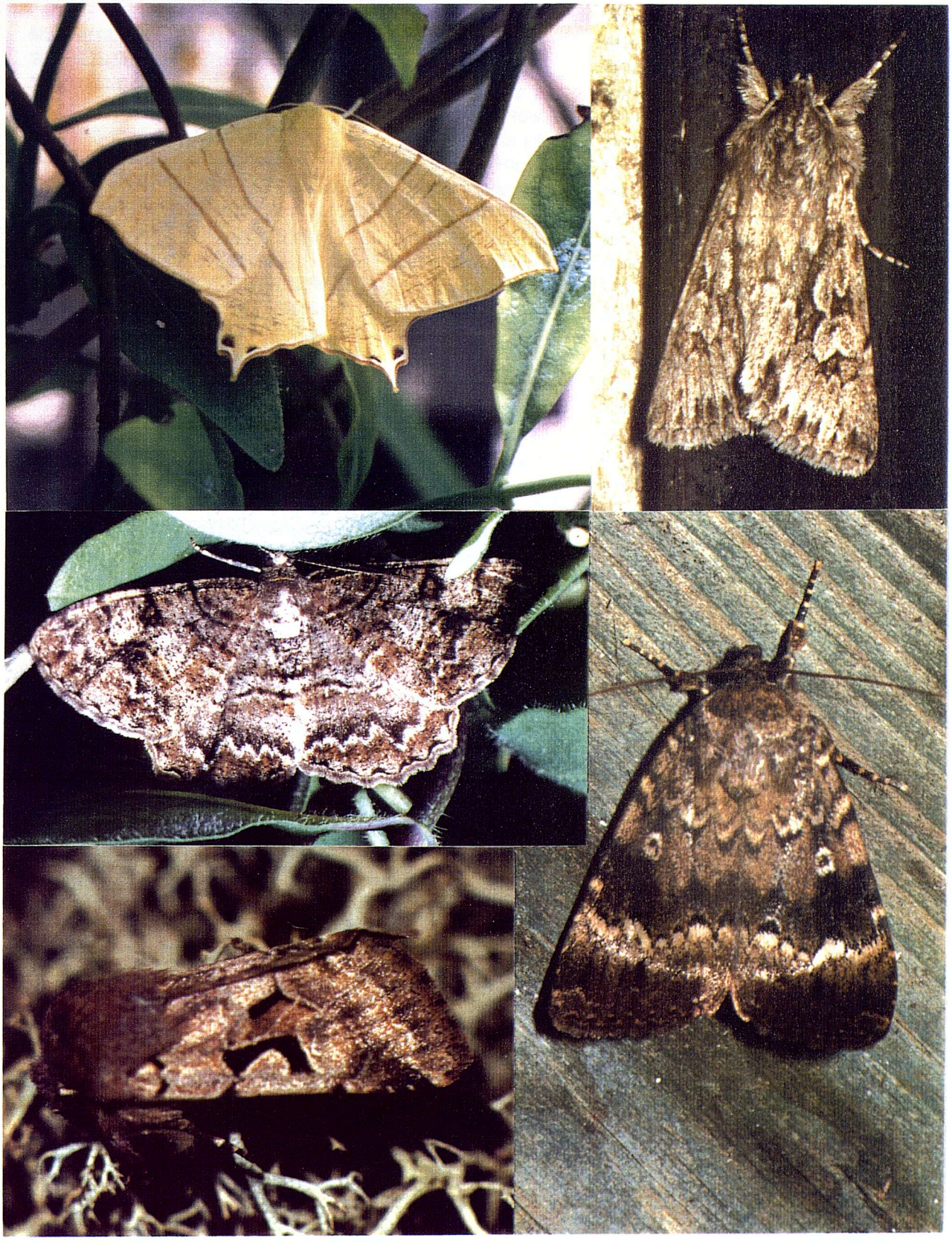


Table 3.1 Lepodopteran guild foraging on *L. periclymenum* in Bentley Wood (1993-94; egg sites; N = 554). Over 90 % of oviposition sites (leaves) were occupied by a single egg.

Family	Genus	Species	Macro/micro	Frequency
NYMPHALIDAE	LADOGA Moore	camilla (Linn.)	MACRO	185
SPHINGIDAE	HEMARIS Dalm.	fuciformis (Linn.)	MACRO	123
TORTRICIDAE	ARCHIPS Hb.	podana (Scop.)	Micro	53
GRACILLARIIDAE	PHYLLONORYCTER Hb.	trifasciella (How.)	Micro	37
TORTRICIDAE	DITULA Steph.	angustiorana (Haw.)	Micro	25
TORTRICIDAE	PANDEMIS Hb.	cerasana (Hb.)	Micro	25
YPONOMEUTIDAE	YPSOLOPHA Latr.	dentella (Fabr.)	Micro	15
GEOMETRIDAE	APEIRA Gistl	syringaria (Linn.)	MACRO	12
TORTRICIDAE	PANDEMIS Hb.	corylana (Fabr.)	Micro	11
GEOMETRIDAE	ALCIS Curt.	repandata (Linn.)	MACRO	11
NOCTUIDAE	PHLOGOPHORA Treit.	meticulosa (Linn.)	MACRO	9
LYMANTRIIDAE	EUPROCTIS Hb.	similis (Fuessl.)	MACRO	6
NOCTUIDAE	BRACHIONYCHA Hb.	sphinx (Hufn.)	MACRO	6
NOCTUIDAE	XYLOCAMPA Guen.	areola (Esp.)	MACRO	5
GELECHIIDAE	ATHRIPS Billb.	moufetella (Linn.)	Micro	4
NOCTUIDAE	AMPHIPYRA Ochs.	pyramidea (Linn.)	MACRO	3
TORTRICIDAE	GYPSONOMA Meyr.	dealbana (Frol.)	Micro	2
TORTRICIDAE	LOZOTAENIA Steph.	fosterana (Fabr.)	Micro	2
NOCTUIDAE	ORTHOSIA Ochs.	gothica (Linn.)	MACRO	2
TORTRICIDAE	OLETHREUTES Hb.	lacunana ([D & S.])	Micro	2
NOCTUIDAE	ORTHOSIA Ochs.	stabilis ([D. & S.])	MACRO	2
TORTRICIDAE	ARGYROTAENIA Steph.	xylosteana (Linn.)	Micro	2
NOCTUIDAE	NOCTUA Linn.	comes (Hb.)	MACRO	1
TORTRICIDAE	PANDEMIS Hb.	heperana ([D & S.])	Micro	1
NOCTUIDAE	ORTHOSIA Ochs.	incerta (Hufn.)	MACRO	1
YPONOMEUTIDAE	YPSOLOPHA Latr.	nemorella (Linn.)	Micro	1
PYRALIDAE	UDEA Guen.	prunalis ([D. & S.])	Micro	1
OECOPHORIDAE	CARCINA Hb.	quercana (Fabra.)	Micro	1
GEOMETRIDAE	OURAPTERYX Leach	sambucaria (Linn.)	MACRO	1
NOCTUIDAE	COSMIA Ochs.	trapezina (Linn.)	MACRO	1
GEOMETRIDAE	ECTROPIS Hb.	bistortata (Goeze)	MACRO	1
GEOMETRIDAE	CHLOROCLYSTA Hb.	truncata (Hufn.)	MACRO	1
NOCTUIDAE	LACANOBIA Billb.	oleracea (Linn.)	MACRO	1
GEOMETRIDAE	CROCALLIS Treit.	elinguaria (Linn.)	MACRO	1

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Examples of adult macro-Lepidoptera feeding on *L. periclymenum.*

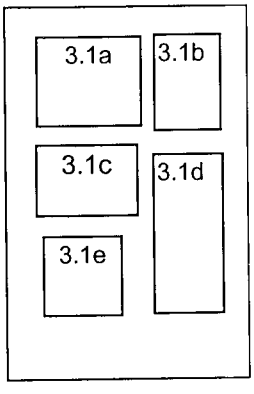


Plate 3.1a *Ourapteryx sambucaria* (swallowtail moth). p. 3-9
Plate 3.1b *Xylocampa areola* (early grey). p. 3-9
Plate 3.1c *Alcis repandata* (mottled beauty). p. 3-9
Plate 3.1d *Amphipyra pyramidea* (copper underwing). p. 3-9
Plate 3.1e *Orthosia gothica* (Hebrew character). p. 3-9

3.3.2 National status of Lepidoptera foraging on *L. periclymenum* (Table 3.2).

The rarest national species of the lepidopteran guild was *H. fuciformis* which is classified as notable (Nb). All other macro-moth members of the lepidopteran guild foraging on *L. periclymenum* are regarded as either local or common. All the micro-moth members are regarded, nationally, as common (Bradley *et al.*, 1979). The single butterfly, *L. camilla*, is mainly restricted to southern England where it is found in most woodlands containing broadleaf trees (Emmet and Heath, 1991) and may be regarded as locally common (Thomas, 1986).

3.3.3 Host specialisation of Lepidoptera foraging on *L. periclymenum* (Table 3.2; Fig. 3.3).

Only one species, *L. camilla*, is regarded as monophagous under natural conditions. Eight species (24 %) are regarded as oligophagous and the other 25 species (73 %) are regarded as polyphagous by Emmet and Heath (1991). One of the specialists (monophagous or oligophagous), *Gypsonoma dealbana*, was not indicated as a *Lonicera* spp. feeder by Emmet and Heath (1991) and Bradley *et al.* (1979).

Hemaris fuciformis is normally regarded as oligophagous since it is occasionally found foraging on *Symphoricarpos rivularis* (snowberry), which was confirmed by this study in Bentley Wood. However, less than 1 % of eggs and caterpillars were found on this food resource during the period 1993-94, possibly because there was only a single bush of this species found in the whole of Bentley Wood during four years of field work.

3.3.4 *L. periclymenum* as a nectar resource.

Lonicera periclymenum was rarely observed being used as a nectar source by adult Lepidoptera. Plantation *L. periclymenum* drapes were rarely found to reach the inflorescent stage and no adult Lepidoptera were observed nectaring on this plant inside plantations. However, ride-side and aerial clearing drapes frequently produced inflorescence but normally too late in the season for *H. fuciformis*. Inflorescence structure only allow adult Lepidoptera with long probosci to reach the nectar and *H. fuciformis* were occasionally observed nectaring on *L. periclymenum* drapes growing in full sun. *H. fuciformis* was mainly observed nectaring on *Rhododendron ponticum* and *L. camilla* was always observed nectaring on *Rubus fruticosus* (bramble) and no other nectar source.

Table 3.2 Life history traits of lepidopteran guild foraging on *L. periclymenum* in Bentley Wood (1993-94). Data based on Emmet & Heath, vol. 7(2) (1991).

Species	Status [a]	Ophagousy [b]	Strategy [c]	Habitat
L. camilla	Local	Monophagous (L)	External	Woods
H. fuciformis	Notable	Oligophagous (L)	External	Woods
A. podana	Common	Polyphagous	Leaf roller	Woods/gardens
P. trifasciella	Common	Oligophagous (L)	Leaf miner	Woods
D. angustiorana	Common	Polyphagous	Leaf roller	Widespread
P. cerasana	Common	Polyphagous	Leaf roller	Woods/gardens
Y. dentella	Common	Oligophagous (L)	Leaf web	Woods/gardens
A. syringaria	Local	Oligophagous (L)	External	Woods/heaths
P. corylana	Common	Polyphagous	Leaf roller	Woods/gardens
A. repandata	Common	Polyphagous	External	Woods/gardens
P. meticulosa	Common	Polyphagous	External	Widespread
E. similis	Common	Polyphagous	External	Widespread
B. sphinx	Common	Polyphagous	External	Woods/gardens
X. areola	Common	Oligophagous (L)	External	Woods/gardens
A. moufetella	Common	Oligophagous (L)	Leaf web	Woods/gardens
A. pyramidea	Common	Polyphagous	External	Woods
G. dealbana	Common	Oligophagous (-L)	Leaf roller	Woods
L. fosterana	Common	Polyphagous	Leaf roller	Woods
O. gothica	Common	Polyphagous	External	Woods
O. lacunana	Common	Polyphagous	Leaf roller	Widespread
O. stabilis	Common	Polyphagous	External	Woods
A. xylosteana	Common	Polyphagous	Leaf roller	Woods/gardens
N. comes	Common	Polyphagous	External	Widespread
P. heperana	Common	Polyphagous	Leaf roller	Widespread
O. incerta	Common	Polyphagous	External	Woods
Y. nemorella	Common	Oligophagous (L)	Leaf web	Woods
U. prunalis	Common	Polyphagous	Leaf roller	Woods/gardens
C. quercana	Common	Polyphagous	Leaf web	Widespread
O. sambucaria	Common	Polyphagous	External	Widespread
C. trapezina	Common	Polyphagous	External	Woods/wet areas
E. bistortata	Common	Polyphagous	External	Woods/gardens
C. truncata	Common	Polyphagous	External	Widespread
L. oleracea	Common	Polyphagous	External	Woods/gardens
C. elinguaria	Common	Polyphagous	External	Widespread

a: status based on occupancy of 10 km grid system (see text).
b: (L) indicates that Emmet & Heath, vol. 7(2), (1991) quoted *Lonicera* spp. as a previously known foodplant. (-L) indicates that *Lonicera* spp. was not quoted for an oliphagous or monophagous species.
c: an external feeder is a caterpillar exposed to natural enemies and not bound to any sort of shelter; a leaf roller is a caterpillar which rests and goes through ecdysis inside a rolled up tube of leaf material; a leaf miner is a caterpillar which feeds under the leaf cuticle; a leaf web species is a caterpillar which feeds and rests inside a silk shelter on foodplant foliage.

Fig. 3.1 Dominant Lepidoptera foraging on *L. periclymenum* in Bentley Wood (1993-94; egg site frequency; N=554).

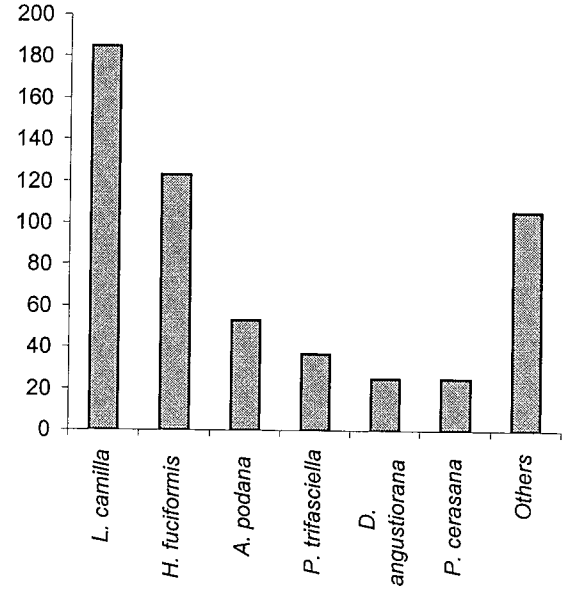
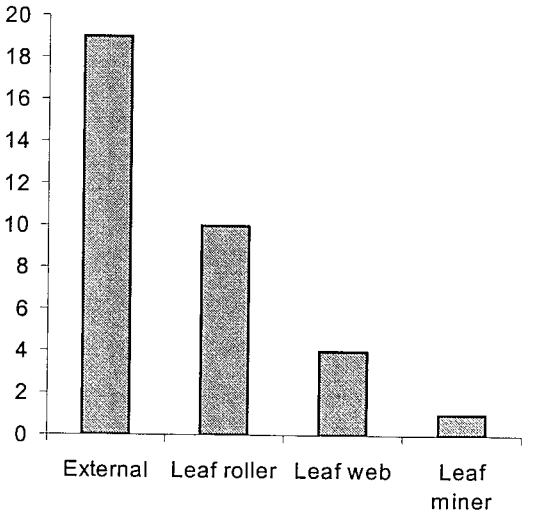
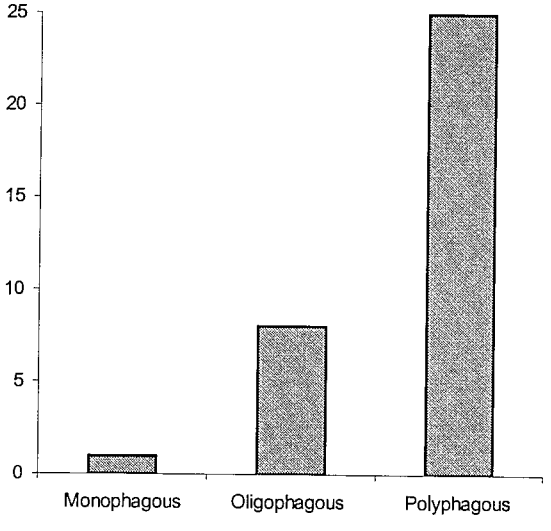


Fig. 3.2 Caterpillar foraging strategies on *L. periclymenum* in Bentley Wood (1993-94: spp. frequency; N=34).





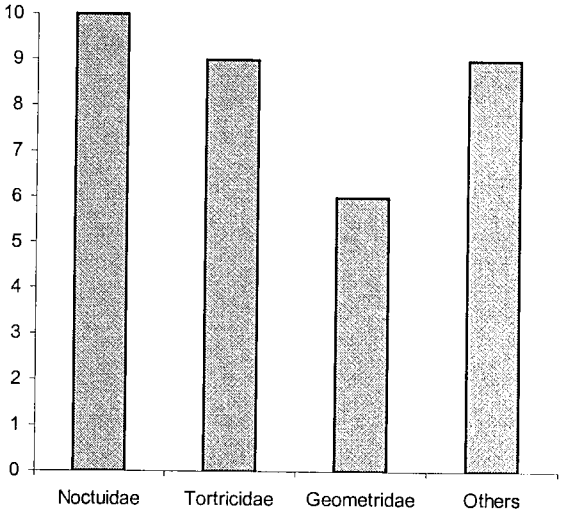


Fig. 3.3 Ophagousy of Lepidoptera foraging on *L. periclymenum* in Bentley Wood (1993-94; spp. frequency; N=34).

Fig. 3.4 Family structure of Lepidoptera foraging on *L. periclymenum* in Bentley Wood (1993-94; spp. frequency; N=34).

3.3.5 Habitat preference for Lepidoptera foraging on *L. periclymenum* (Table 3.3; Figs. 3.5-7).

3.3.5.1 Which habitats favour *L. periclymenum* growth?

There was a great variation in the density of *L. periclymenum* drapes found growing in different areas and habitats of Bentley Wood. In general, there was a much higher density of *L. periclymenum* drapes in the southern half of the wood which had a mainly clay soil structure compared to chalk in the north. In the beech dominant northern plantations and ride systems only 23 drapes were found growing in an area of 160 hectares. In contrast, in the oak dominant southern areas of Bentley Wood *L. periclymenum* was found abundant in most of the three main habitats, plantations, rides and clearings. A survey of *L. camilla* oviposition sites (Table 4.1, Chapter Four) showed the outer 5m strip of plantations to contain *L. periclymenum* drapes in abundance (up to 160 drapes along a 250 m transect section) in areas of clay soil.

Lonicera periclymenum drape density in plantations depended on soil type and plantation timber species. Table 3.3 shows the number of *L. periclymenum* drapes together with timber species found growing in a 0.2 hectare sample areas in ten plantations. A combination of basic soil and beech dominance was associated with low density and thin *L. periclymenum* growth in contrast to acid-neutral soil and oak canopy where drape density was high and of vigorous growth. The few *L. periclymenum* drapes growing in the beech plantations were found in small cleared pockets such as extraction tracks where trees had died or fallen or removed for vehicular access during thinning operations.

The total number of *L. periclymenum* drapes found growing in four beech dominant plantations (A, B, C, and E) was 9, and the corresponding number in four oak dominant plantations (F, G, H, and J) was 121. All plantations were approximate the same age having been planted in the period 1954-58.

Plate 3.2

Table 3.3 Vegetation structure of 10 Bentley Wood plantations (A-K): number of trees in 0.2 hectare sample plot.

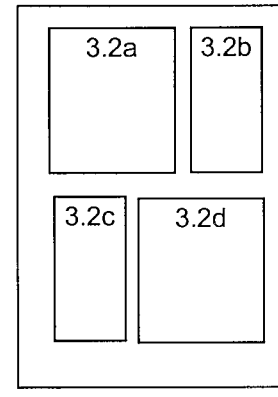
Plantation	A	B	C	D	E
L. periclymenum drapes	3	6	0	0	0
Stock trees	281	265	198	199	401
Dominant broadleaf	Beech	Beech	Beech	Sycamore	Beech
Dominant conifer	N. spruce	N. spruce	N. spruce	None	S. pine
Soil pH	Basic	Basic	Neutral	Neutral	Basic

Plantation	F	G	H	J	K
L. periclymenum drapes	24	0	36	62	0
Stock trees	351	788	858	783	195
Dominant broadleaf	Mixed	Mixed	Oak	Oak	Beech
Dominant conifer	N. spruce	N. spruce	N. spruce	N. spruce	N. spruce
Soil pH	Neutral	Basic	Acidic	Acidic	Neutral

Previous page.

Examples of caterpillar species feeding on *L. periclymenum.*

Plate 3.2a *Brachionycha sphinx* (sprawler). p. 3-15
Plate 3.2b *Alcis repandata* (mottled beauty). p. 3-15
Plate 3.2c *Ypsolopha dentella* (honeysuckle moth). p. 3-15
Plate 3.2d *Apeira syringaria* (lilac beauty). p. 3-15



3.3.5.2 Which habitats favour Lepidoptera foraging on *L. periclymenum*? (Figs. 3.5-7)

Using 1993 field data (Fig. 3.5) the first 22 dominant lepidopteran species of the guild ovipositing on *L. periclymenum* were used to compare oviposition preference between the three types of habitat: rides, plantations and clearings. Just over half (51 %) of the oviposition sites were found in rides between plantations, 29 % of oviposition sites were found in inner plantation zones and 20 % of oviposition sites were found in clearings (Fig. 3.5). With respect to species preference, the ride system was the most favoured habitat accommodating 20 species, with plantations and clearings containing 13 and 11 species, respectively. Only 5 out of 22 species (23 %) were found ovipositing in all 3 habitats while the other 17 species preferred one or two of the three habitats.

Data from 1994 field work, using the same survey areas for all three habitats as 1993, showed a greater preference of oviposition sites for plantations. Just over half (54 %) of the oviposition sites were found in plantations, 29 % of oviposition sites were found in rides and 17 % of oviposition sites were found in clearings (Fig. 3.6). With respect to species preference, plantations was the most favoured habitat accommodating 14 species, with rides containing 10 species and clearings were again found to be the least favoured habitat with 6 species. Only 3 out of 18 species (17 %) were found ovipositing in all 3 habitats while the other 15 species preferred one or two of the three habitats.

Species comparison of oviposition site preference for *L. camilla, H. fuciformis,* other macro-Lepidoptera and micro-Lepidoptera for the combined totals of the two years of data (1993-94) are shown in Fig. 3.7. Contrasting oviposition habitat preference was most clearly illustrated by *L. camilla* and *H. fuciformis. L. camilla* was never found ovipositing on sun host foliage and preferred shaded plantations and partially shaded ride systems. In contrast, *H. fuciformis* was never found ovipositing in plantations and preferred *L. periclymenum* drapes growing in clearings and south facing rides.

There was no statistically significant difference of oviposition habitat preference between other macro-Lepidoptera and micro-Lepidoptera (χ^2 = 1.2; df = 2; NS at p = 0.05). Both these sets of lepidopteran species preferred to oviposit in plantations and rides and disfavoured clearing host foliage.

Fig. 3.5 Habitat of oviposition sites of all Lepidoptera foraging on *L. periclymenum* (1993; N = 320).

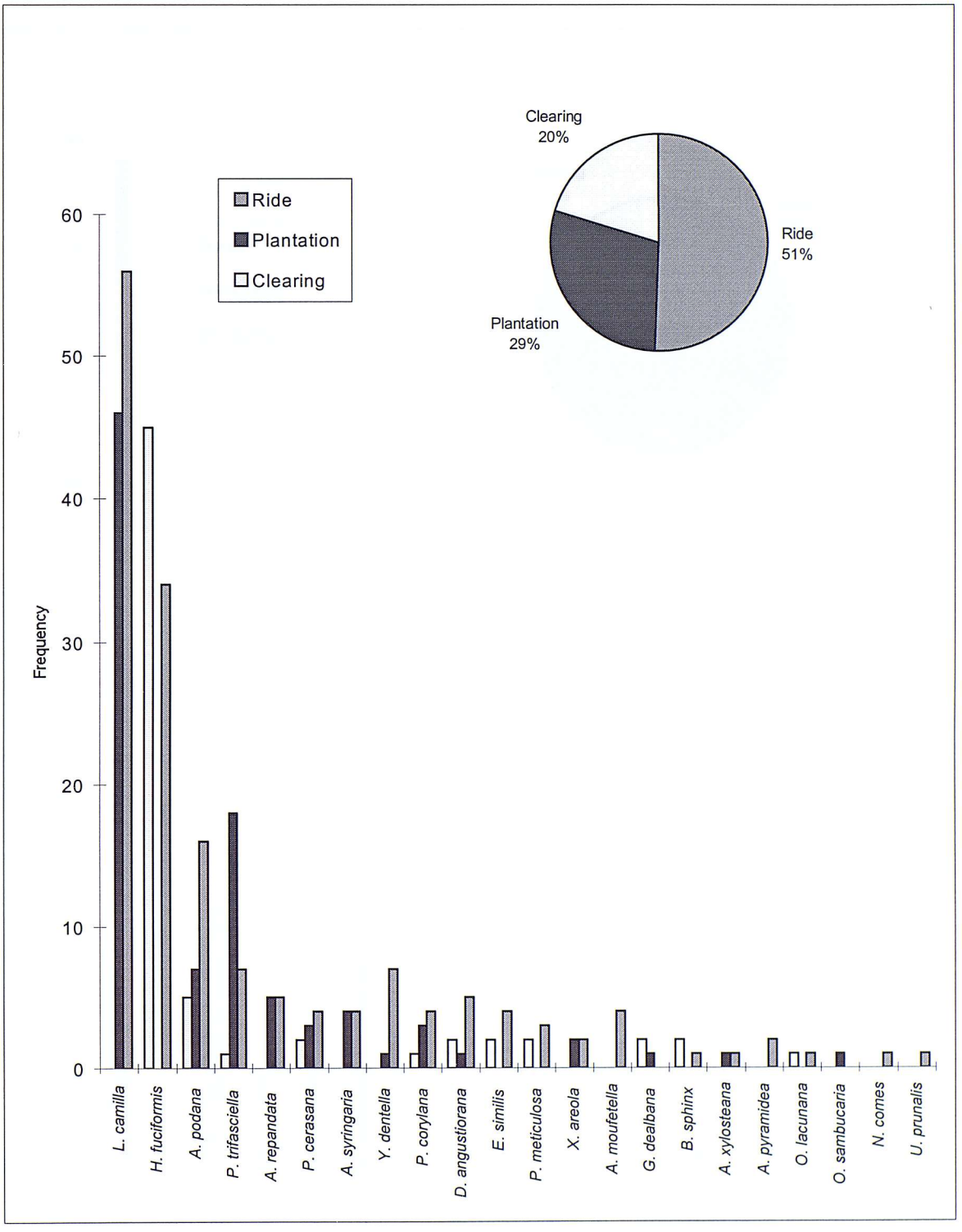


Fig. 3.6 Habitat of oviposition sites of all Lepidoptera foraging on *L. periclymenum* (1994; N = 175).

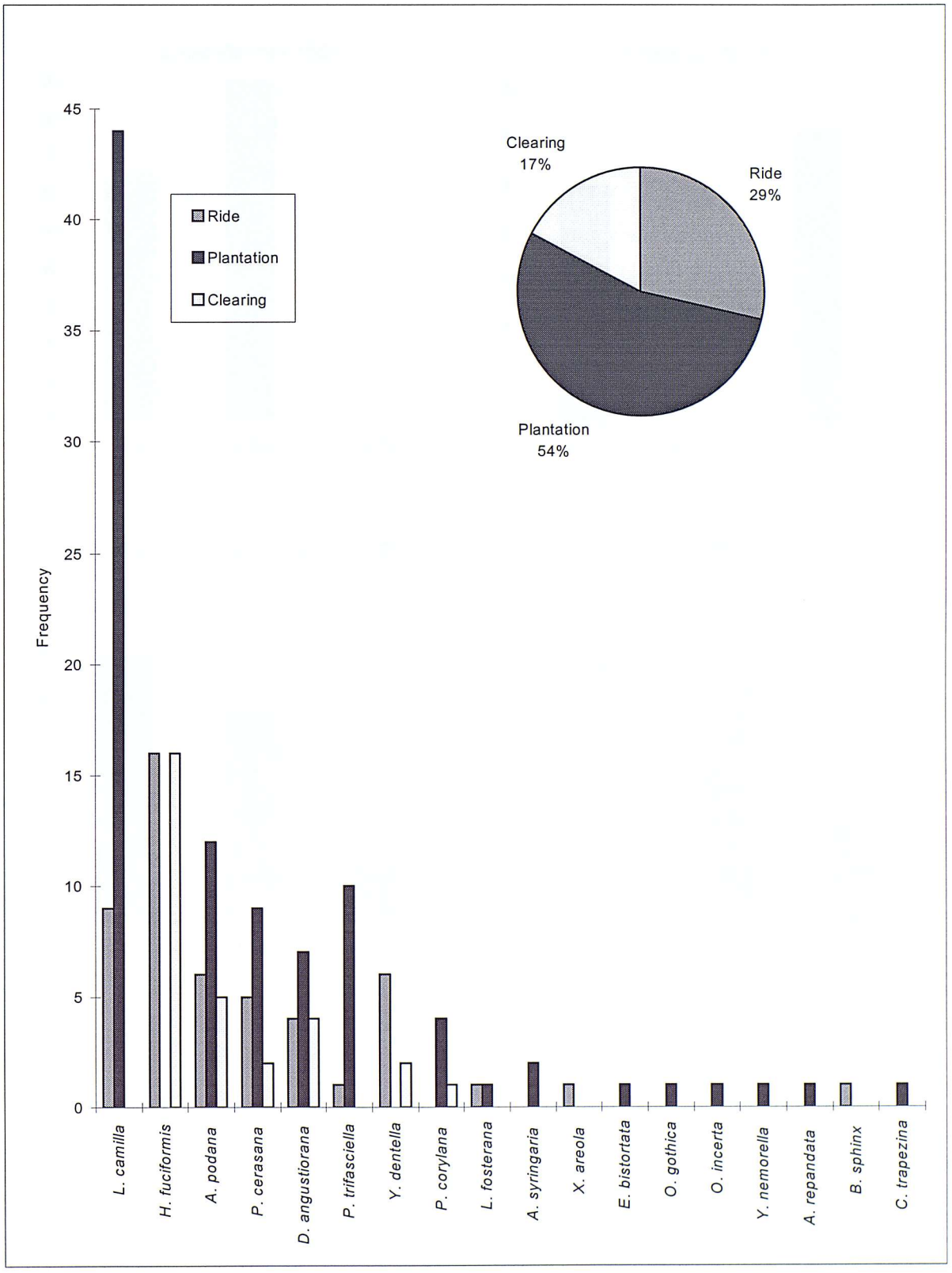
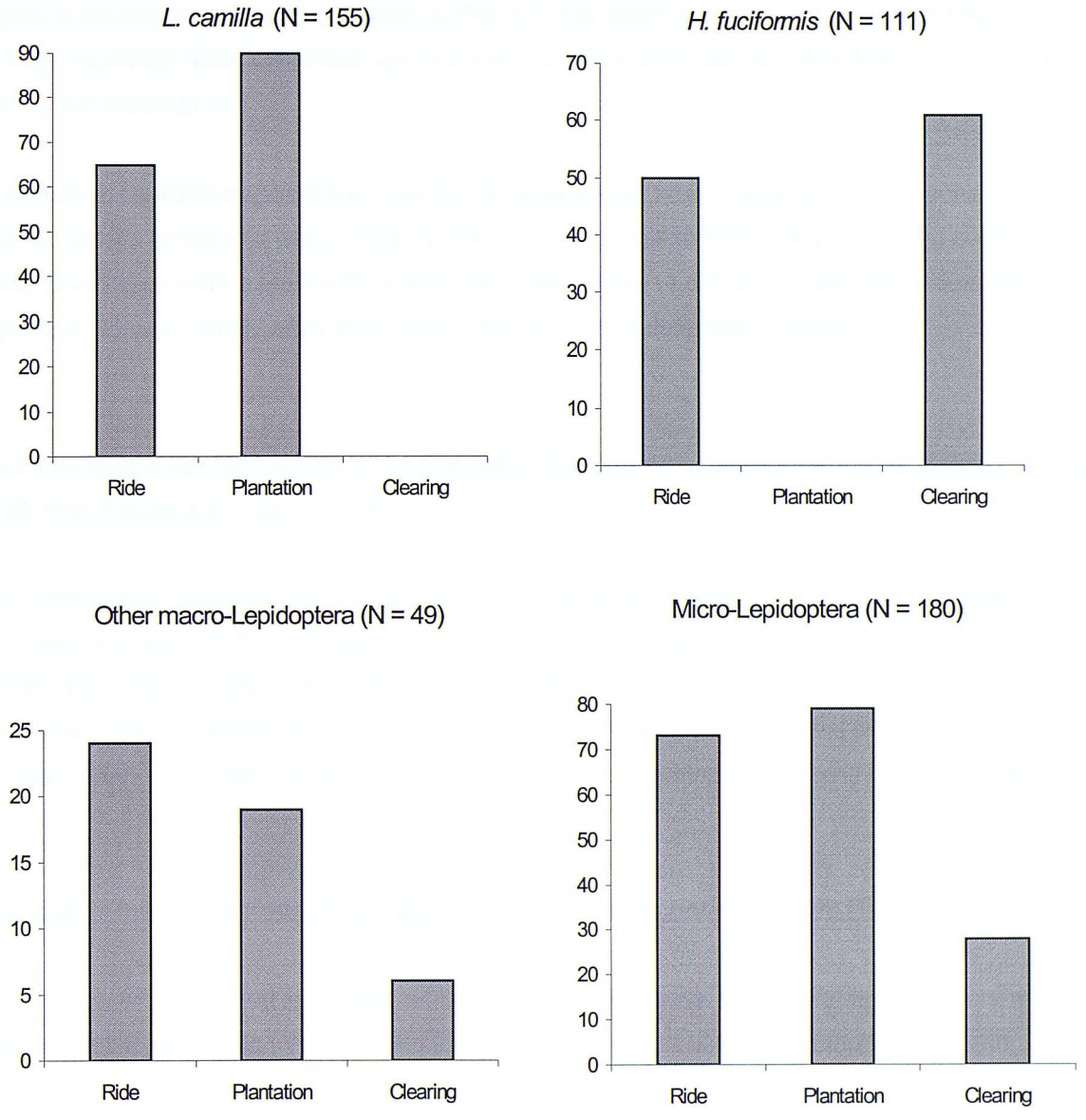


Fig 3.7 Habitat comparison of oviposition sites of Lepidoptera foraging on *L. periclymenum* (number of eggs found in each habitat during the period 1993-94).



3.3.5.3 Comparison of tree species supporting oviposition host foliage (Fig. 3.8).

A total of 11 species of trees were found supporting lepidopteran oviposition site host foliage. With regard to the 9 most dominant Lepidoptera (Fig. 3.8) oak was the most commonly used tree with 43 % of all oviposition sites. Other tree species were Norway spruce (22 %), silver birch (18 %), hazel (13 %) and sallow (4 %).

H. fuciformis favoured oviposition on oak and Norway spruce host drapes (93 % of oviposition sites) while *L. camilla* favoured a wider range of oak, silver birch, and Norway spruce (85 % of oviposition sites). Dead trees were a feature of several oviposition sites (11.5 % of all 1993 oviposition sites) especially Norway spruce, silver birch and hazel (94 % of all dead tree supports).

3.3.6 Larval feeding techniques of Lepidoptera foraging on *L. periclymenum* in Bentley Wood 1992-1994 (Table 3.2; Figs. 3.2, 3.9).

The predominant caterpillar feeding technique was the external feeder (19 spp., 56 %), followed by leaf rollers (10 spp., 29 %), with leaf webs (4 spp., 12 %) and a single leaf miner (3 %). All the external feeders were macro-Lepidoptera and all the leaf rollers were micro-Lepidoptera of which 90 % were members of the Tortricidae family. The single leaf miner, *P. trifasciella,* was the smallest adult moth and caterpillar (final instar) species of the complete guild of Lepidoptera foraging on *L. periclymenum.*

3.3.7 Larval feeding periods of Lepidoptera foraging on *L. periclymenum* (Table 3.4).

Host foliage, when growing in shaded habitats such as plantations, was available for all months of the year. In the winter months (Nov-Feb) the foliage was in the form of rosettes (short shoots with relatively low leaf density; Plates 5.2a-c in Chapter Five) which slowly opened throughout this period. This type of growth starts shooting in late Autumn in contrast to *L. periclymenum* drapes growing in open clearings in full sun which produced bud burst in April creating large enough leaves for foraging Lepidoptera in May.

Table 3.4 shows the monthly periods when caterpillars of each species were found in Bentley Wood. Additionally, an indication of wintering diapause species is given in which caterpillars were found inside an aerial cocoon amongst *L. periclymenum* foliage. A large proportion of the complete guild of Lepidoptera foraging on *L. periclymenum* were winter diapause caterpillars (38 %, N = 34) and a large proportion of these diapause caterpillars were polyphagous (85 %; N = 13). No species of the winter diapause group was found preferentially ovipositing in clearings compared with rides and plantations in 1993. In the same year only *H. fuciformis* and *G. dealbana* were found preferentially ovipositing on

host plant growing in clearings and in 1994 only *H. fuciformis* was found preferentially ovipositing in clearings (Figs. 3.5-7).

Fig. 3.8 Tree species supporting oviposition sites for Lepidoptera foraging on *L. periclymenum* (N = 260).

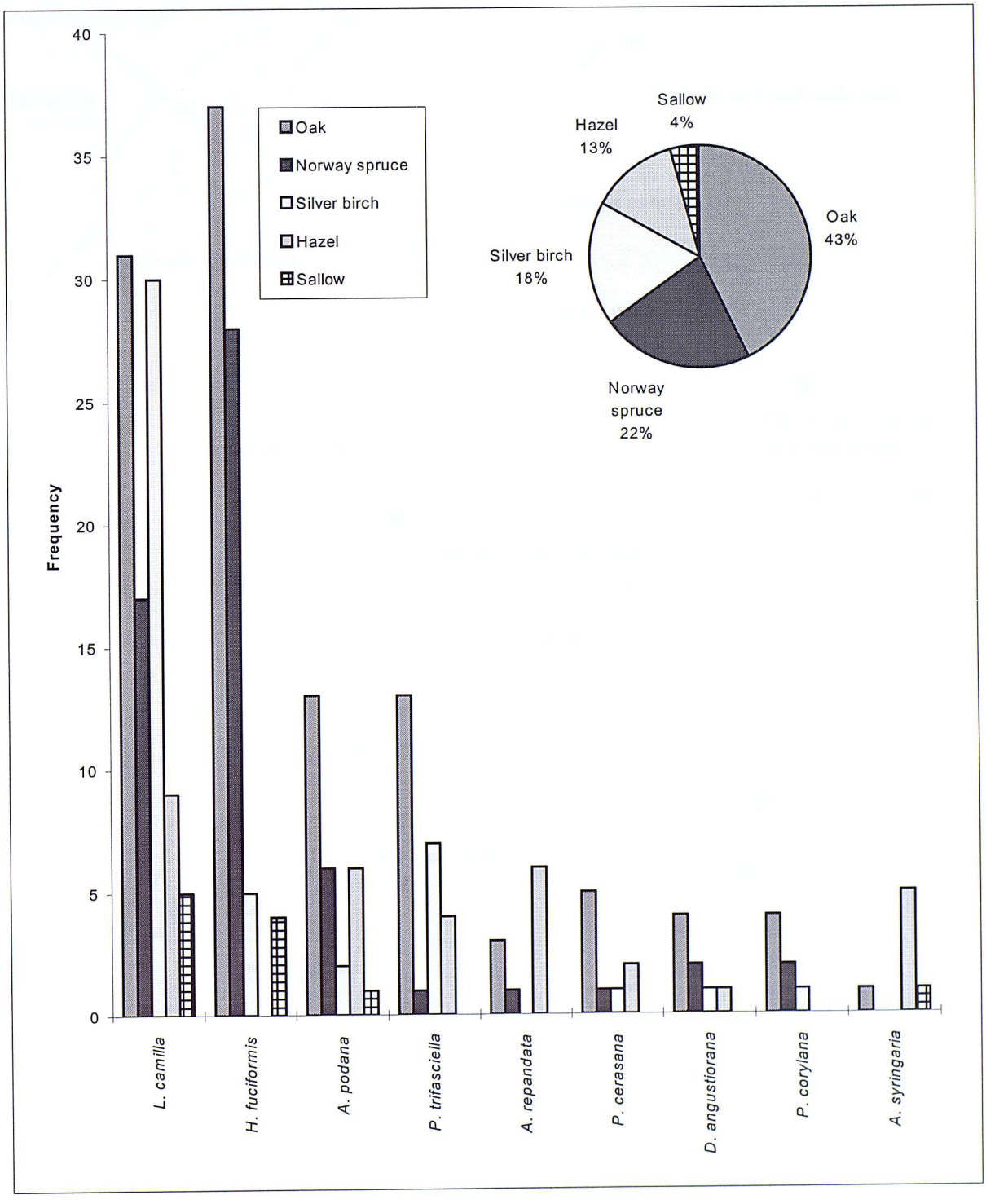


Fig 3.9 Four feeding techniques used by iepidopteran larvae on *L. periclymenum* foliage. Majority of Lepidoptera were external feeders and leaf rollers.

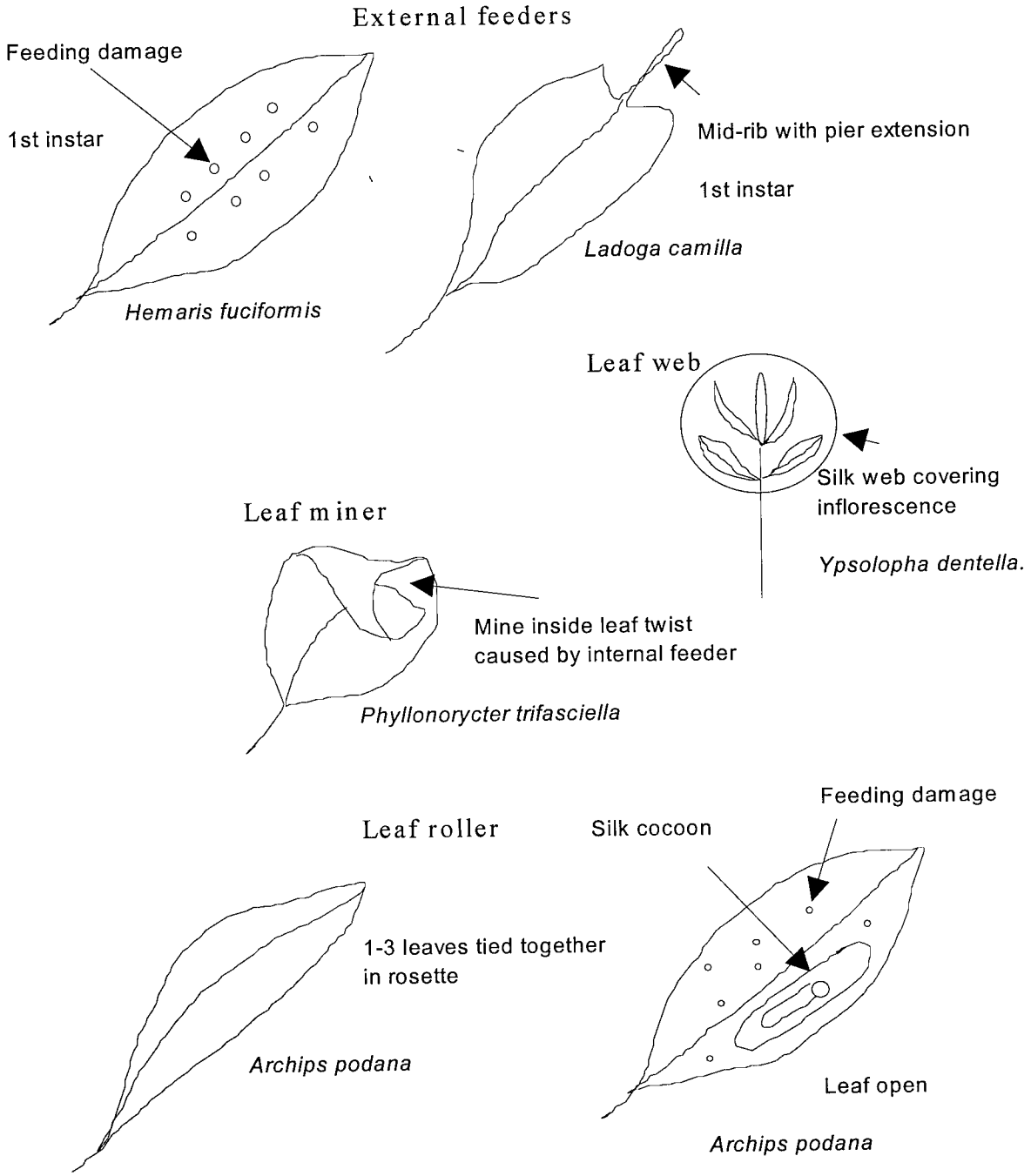


Table 3.4 Periodic utilisation of aerial *L. periclymenum* foliage by foraging Lepidoptera in Bentley Wood. Foliage use includes oviposition sites, larval feeding, pupation in leaf roll or web and hibernaculum construction (larval field observations in Bentley Wood).

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec
Host availability												
Host foliage (shade)	•	•	•	•	•	•	•	•	•	•	•	•
Host foliage (sun)				•	•	•	•	•	•	•		
Lepidoptera												
A. podana [d]	•	•	•	•	•	•	•	•				
A. xylosteana [d]		•	•	•	•	•	•	•			•	•
C. quercana [d]	•	•	•	•	•	•	•	•			•	
C. truncata [d]	•	•	•	•								
D. angustiorana [d]	•		•	•	•	•	•	•	•	•	•	•
E. simllis [d]				•	•	•	•					
G. dealbana [d]	•	•	•	•	•	•	•	•			•	•
L. camilla [d]		•	•	•	•	•	•	•	•	•	•	
L. fosterana [d]	•	•	•	•	•	•	•		•		•	•
O. sambucaria [d]		•	•	•	•	•	•	•	•	•	•	
P. cerasana [d]	•	•	•	•	•	•	•	•	•		•	•
P. heperana [d]		•	•	•	•	•				•		•
U. prunalis [d]	•	•	•	•	•	•	•	•	•	•	•	•
A. moufetella			•	•	•	•						
A. pyramidea				•	•							
A. repandata			•	•	•	•	•					
A. syringaria			•	•	•	•	•	•	•	•		
B. sphinx				•	•	•						
C. elinguaria			•	•	•							
C. trapezina				•	•							
E. bistortata				•	•							
H. fuciformis					•	•	•	•				
L. oleracea				•	•							
N. comes	•	•	•	•								
O. gothica				•	•							
O. incerta				•	•							
O. lacunana				•	•	•	•					
O. stabilis				•	•							
P. corylana				•	•	•	•					
P. meticulosa				•	•	•						
P. trifasciella			•	•	•	•	•	•	•	•	•	
X. areola			•	•	•	•						
Y. dentella				•	•	•	•	•				
Y. nemorella				•	•	•	•	•				

d: larval diapause during winter period inside leaf roll or hibernaculum.

3.4 Discussion

3.4.1 Importance of *L. periclymenum* as a lepidopteran larval food plant.

A lepidopteran guild of 34 species feeding on a single food plant from a two year study period is unusually large and must qualify *L. periclymenum* as an important lepidopteran host. Although only one species, *H. fuciformis*, is regarded as a national rarity and 73 % of the guild are regarded as polyphagous (Emmet and Heath, 1991), the majority of the guild were found feeding in commercial plantations in Bentley Wood, a habitat normally regarded as of poor quality for foraging Lepidoptera (Mitchell and Kirby, 1989). However, the presence of *L. periclymenum* in plantations improves the habitat for foraging Lepidoptera. Waring (1990) compared various woodland habitats in Bernwood Forest (Oxfordshire) and found that 138 moth species were found foraging on native weed species in conifer plantations.

It is possible that further field work would have revealed more generalist and the odd specialist species foraging on *L. periclymenum* in Bentley Wood. The only specialist lepidopteran species feeding on *L. periclymenum* in woodland (Emmet and Heath, 1991), which was not found in this study was *Phyllornorycter emberizaepenella.* Its absence is puzzling considering its close relative, *P. trifasciella*, was regularly found ovipositing in Bentley Wood in plantations. Another puzzling result of this study was the absence of evidence of foraging Lepidoptera on ground growing *L. periclymenum* foliage in contrast to other woodland areas where lepidopteran caterpillars have been found feeding on ground *L. periclymenum* foliage (pers. comm., P. Waring and D. Owens). A possible explanation is that female Lepidoptera prefer to oviposit on aerial host but choose ground host foliage in the absence or shortage of aerial *L. periclymenum* drapes.

This study failed to produce evidence of another moth which is normally found feeding on *L. periclymenum* in woodland (Emmet and Heath, 1991). *Trichopteryx carpinata* (early tooth-striped; Geometridae) was abundantly found as the adult in Bentley Wood plantations but was never found as caterpillars feeding on *L. periclymenum.* However, the caterpillars were found feeding on *Salix* spp. in the vicinity of *L. periclymenum* drapes indicating its preference for the former foodplant. *Phyllonorycter emberizaepenella,* a leaf miner specialist on Caprifoliaceae spp. including *L. periclymenum,* was probably overlooked (pers. comm., J. Langmaid). In conclusion, *L. periclymenum* has been shown to be an important caterpillar food resource for Lepidoptera especially for species requiring early season foodplant foliage in plantations.

3.4.2 Habitat preference for *L. periclymenum growth.*

L. periclymenum growth was found to exist in all three major habitats, clearings, rides and plantations in Bentley Wood. Clearings contained both ground foliage and aerial growing *L. periclymenum* drapes on various supports including isolated standard trees and broken stumps. *L. periclymenum* abundance differed markedly between plantation type and the vast majority of *L. periclymenum* growth in plantations were aerial drapes.

Beech dominant plantations in the northern part of Bentley Wood did not favour *L. periclymenum* growth in comparison with oak dominant plantations. This contrast in *L. periclymenum* density may be due to the dense beech canopy created by a 50 year old plantation preventing light penetration (Rackham, 1993). The lack of sunlight in beech plantations may also explain the shortage of scrub and herbaceous species at ground level under the beech canopy (Chapter Two). The few drapes which existed in beech plantations were found in small pockets of dappled sunlight created by fallen trees or timber extraction tracks made by forestry vehicles.

The oak dominant plantations allowed more light penetration than beech plantations throughout the growing season. Plantation oaks (unlike single specimens in open situations) contain little lateral branching in the canopy (and even less lower down the tree) allowing greater light penetration than in plantation beeches of similar age. Plantation oaks proved ideal supports for climbing *L. periclymenum* growth. Even when oak dominant plantations contained three times the density of stock trees than beech plantations (Table 3.3), *L. periclymenum* density in oak plantations was found to be greatly in excess of *L. periclymenum* in beech plantations. However, plantation oaks isolated after windblow quickly attained lateral branching and increased foliage. Observations in Bentley Wood after the major gales of 1987 and 1991 showed that three years after isolation in open sites, *H. fuciformis* oviposition sites were being abandoned at the same time as the *L. periclymenum* foliage became heavily shaded by increased density of oak foliage. Circumstances which disfavoured *L. periclymenum* growth were a combination of dense canopy foliage as associated with beech, and dry surface soil as associated with chalk sub-soil character.

Only in areas of extreme shade, as found in the occasional 40 year old pure conifer plantation, was there a complete lack of *L. periclymenum* growth. Pure *Pinus nigra* (Corsican pine) plantations, 14 years old and 5-7 m tall, contained considerable aerial *L. periclymenum* growth which was occasionally used by ovipositing *L. camilla,* indicating that certain types of conifer plantations can also accommodate Lepidoptera. An interesting difference between *L. periclymenum* foliage growing in heavily shaded areas with open sunny sites was that shaded growth was available at most times of the year and especially in the winter months. In contrast, *L. periclymenum* foliage growing in open sunny sites behaved more 'deciduously' with foliage appearing in spring. This difference in habitat

growth behaviour of *L. periclymenum* may have important implications with some species of Lepidoptera whose diapause caterpillars spend their winter months in host foliage.

3.4.3 Habitat preference for Lepidoptera foraging on *L. periclymenum.*

Both 1993 and 1994 field data showed that the vast majority of ovipositing Lepidoptera (80 % and 83 %, respectively) favoured *L. periclymenum* drapes growing in ride systems and plantations rather than sunny clearings. Only one species, *H. fuciformis,* disobeyed this tendency and this species was never found foraging in plantations and its oviposition sites were only found on rides which were south facing rides or box junctions (open cross-tracks) and clearings where *L. periclymenum* grew in sunny locations. In contrast, *L. camilla* females were never found ovipositing in the central zones or south facing perimeters of clearings and its ride oviposition sites were always shaded and facing north.

Ride widening operations can prove detrimental to lepidopteran species feeding on *L. periclymenum* in ride systems. Figs. 3.5-7 show a marked decline in the number of oviposition sites found in rides between the field study years of 1993 and 1994. This decline was mainly due to the loss of *L. camilla* caterpillars during intensive ride widening operations initiated in Bentley Wood in late 1993 in areas containing the main *L. camilla* colonies. The ratio of *L. camilla* oviposition sites found between plantations and rides during the years 1993 and 1994 were 1:1 and 5.5:1, respectively. A more sympathetic ride widening policy involving a gradual removal of ride side vegetation carried out over a period of years may have had less detrimental effect.

3.4.4 Larval feeding techniques used by Lepidoptera foraging on *L. periclymenum.*

The majority of lepidopteran species feeding on *L. periclymenum* were either external feeders (56 %) or leaf rollers (29 %). A large proportion of the guild foraging on *L. periclymenum* wintered as diapause caterpillars (38 %) in leaf rolls (micro-Lepidoptera) or hibernacula (*L. camilla*). These diapause caterpillars need host foliage in the winter months which explains why their oviposition sites occurred mainly on shade foliage which was always available during this time of the year in contrast to sun growing foliage in clearings which produced new leaf growth in spring.

Most of these diapause caterpillars constructed silk platforms (Chapters Four and Six) which may be a caterpillar technique used to buffer themselves from the leaf cuticle. Another common feature of most guild species during their feeding periods was their habit of puncturing leaves during feeding with small circular holes which occurred mainly in the 1st and 2nd instar stages. When caterpillar feeding occurred on host foliage which had been growing in open sunny habitat, these small feeding damage holes produced globules of sticky secretion which was mainly absent when foliage from shaded host growth was being attacked. *L. camilla* caterpillars always fed on shaded host foliage

found as spindly growths in plantations and shaded rides and its unusual caterpillar feeding technique is described in depth in Chapter Four.

3.4.5 Summary

The most outstanding foraging characteristic of Lepidoptera feeding on *L. periclymenum* was their oviposition preference for host foliage growing in shade which was most typically illustrated by the butterfly, *L. camilla.* In contrast, *H. fuciformis* was the only member of the guild which preferred to oviposit on host foliage growing in sunny open clearings and rides. This contrasting foraging behaviour between *L. camilla* and *H. fuciformis* may indicate some important difference in foraging strategy which has evolved through variation in foodplant quality in the different habitats. As a result, one of the major aims of the remaining part of this study will be a comparative detailed study of the foraging behaviour of these two Lepidoptera which may explain the reason for their difference in habitat preference of oviposition sites.

Chapter Four

Life history of Ladoga camilla and Hemaris fuciformis

Life history - classification - distribution - behavioural ecology - habitat

4.1 Introduction

There have been no previous autecological studies of *H. fuciformis* in the UK and the rest of Europe. However, several lepidopteran texts (Newman, 1965; Pittaway, 1993) contain useful information on general habitat and behavioural ecology. The only study of *L. camilla* in the UK was carried out by Pollard (1979) in Monks Wood in Cambridgeshire and emphasised population dynamics. The only other study of *L. camilla* in Europe was carried out by Lederer (1960) during the 1939-51 period in which he compared the behavioural ecology of *L. camilla* with *Limenitis populi* L. in four separate sites in Germany. The life history of both *L. camilla* and *H. fuciformis* has been compiled in the multi-volume publication, The Butterflies of Great Britain and Ireland (Emmet and Heath, vols. 9 (1983), 7(I) (1990), 7(II) (1991)).

This chapter emphasises habitat preference of oviposition site and the unusual behavioural traits of *L. camilla* and *H. fuciformis* and compares field and behavioural data from previous studies with the present study. Unfortunately, the scarcity and difficulties in studying adult *H. fuciformis* in the field prevented any study of population dynamics but its caterpillar feeding behaviour, which is more important to this particular study, is investigated.

4.2 Classification

4.2.1 *Ladoga camilla* L.

Classification of the White Admiral butterfly is in some confusion. Most authors classify it as a Nymphalidae butterfly belonging to a Palaeartic and Oriental genus, *Limenitis* Fabricius, which contains three species. Moore, in 1898, separated the White Admiral from the other two species on account of its hairy eyes and gave it the genus, *Ladoga.* However, some authors still retain it in *Limenitis* including Higgins (1975) who also places it in the subfamily Limenitinae. Emmet and Heath (1990) and more recent British publications use the genus, *Ladoga.* The other two members of the *Limenitis* genus are *Limenitis reducta* (Southern White Admiral) and *Limenitis populi* (Poplar Admiral), both of which are found in southern Europe but not in Britain. *L. camilla* is found as far

south as northern Spain and northern Italy. More southern and warmer latitudes are taken over by *L. reducta.*

4.2.2 *Hemaris fuciformis* L.

Hemaris fuciformis (Broad-bordered Bee Hawk moth) is a day flying member of the Sphingidae (Macroglossinae) family. It belongs to a moderate-sized Holarctic genus with two resident species in the British Isles, *H. fuciformis* and *H. tityus* L. These two species are characterised by the wings having areas free of scales which are shed on the first flight after emergence. A third member the genus, *H. croatica*, is found in the mountainous areas of south-east Europe. *H. fuciformis* extends its range eastwards to north-west India.

4.3 Distribution.

4.3.1 *Ladoga camilla* L.

In the early 1900s *L. camilla* was restricted to southern England, especially Hampshire and adjoining counties (Emmet and Heath, vol. 7(1), 1990). During the period 1930-50 the butterfly spread northwards as far as Lincolnshire and has maintained this distribution in recent years. However, its stronghold is still the southern central counties of Dorset, Hampshire, Sussex, Surrey, Wiltshire, Berkshire, Buckinghamshire and Oxford (Thomas, 1986).

Its county status in Wiltshire varies according to location and habitat (Figures 4.1a-d). In the late 19th century the butterfly was regarded as scarce in northern Wiltshire but by 1935 it was locally common (Fuller, 1995). In the area of Bentley Wood in southern Wiltshire the annual reports of Salisbury Natural History Society refer to its status as locally common in the 1930s and very common in the 1970s. During in the last decade it has been recorded from 55 woodlands in Wiltshire ranging in size from Bentley Wood (688 hectares) to smaller woods of 11 hectares (Fuller, 1995). In the southern neighbouring county of Hampshire the late 1980s was a poor period for *L. camilla*. In the same county 1990 turned out to be a very bad year in every locality except Pamber Forest where the population increased reaching enormous numbers in the summer of 1992, only to fall dramatically in the following year (Goater, 1992). The New Forest, only 30 km away from Bentley Wood, was a prime site for *L. camilla* in the pre-1900s but only a few butterflies are seen there at present. *L. periclymenum* was once common in inclosures but heavy grazing and conifer planting has reduced its numbers (Oates, 1996).

Fig. 4.1a Distribution of *L. periclymenum* in Wiltshire (1994).

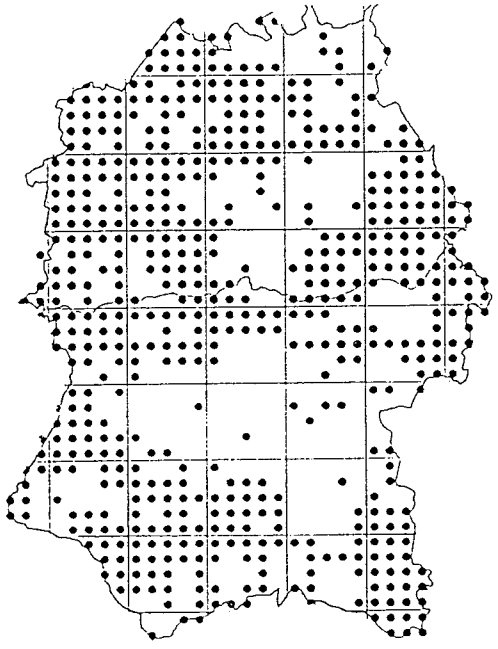
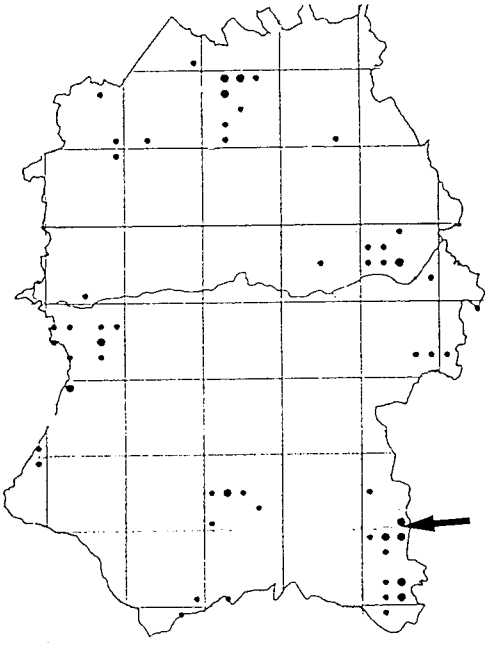


Fig. 4.1b Distribution of *L. camilla* in Wiltshire (1982-95; ● major sites, • minor sites).



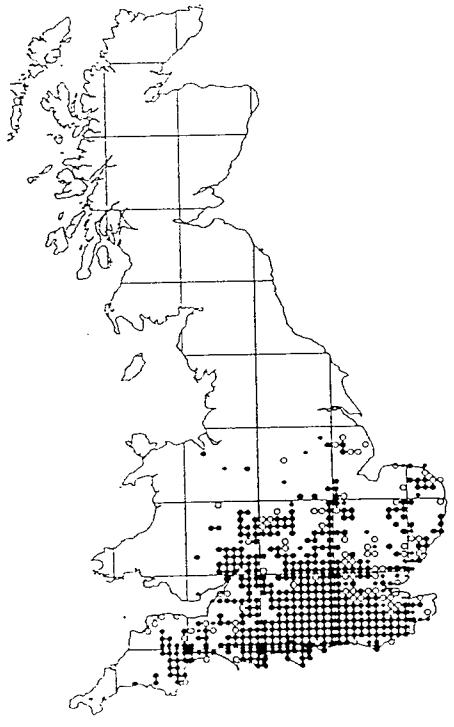


Fig. 4.1c Distribution of *L. camilla* in Britain (o sites before 1970; ● sites 1971-88).
L. camilla and *H. fuciformis* are both absent from Ireland.

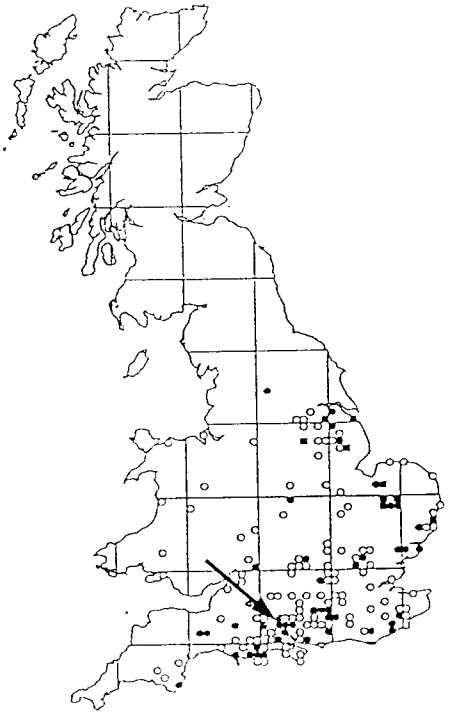


Fig. 4.1d Distribution of *H. fuciformis* in Britain (o sites before 1980; ● sites 1981-96).

4.3.2 *Hemaris fuciformis* L.

In Britain *H. fuciformis* is found as far north as a line from the Mersey to the Humber and is absent from Scotland and Ireland. It is local and uncommon and has become scarcer in recent years (Emmet and Heath, 1983). In Dorset in the early part of this century Tatchell (1926) found the moth "very common at Studland from the beach going north towards Shell Bay, also a few to be met with at Windmill and Coombe Woods".

The 1996 version of the National Recording Network for the Rarer Macro-moths (Waring, 1996) described the national status of *H. fuciformis* as notable (Nb; found in 31-100 10 km squares of the national grid). In the neighbouring county of Hampshire this moth was recorded as fairly common in all larger woods in the early part of the 20th century but declined in the post-1940 period and was regarded as scarce in the early 1970s (Goater, 1974). However, the moth appears to have made a slight recovery in Hampshire in the last 20 years (Goater, 1992). A lepidopteran survey of Bentley Wood in 1983 by Waring (1983) found only two specimens of the adult moth during the complete flight period. In a *H. fuciformis* caterpillar search in Bentley Wood in 1988, along ride systems, in which the author participated, no clear evidence of foliage feeding damage was found. However, personal observation of *H. fuciformis* in Bentley Wood over the last five years by the author indicates an increase in numbers during this period.

4.4 Life history

4.4.1 *Ladoga camilla* L.

Most British authors state that *L. camilla* oviposits singularly on the marginal area of the upper surface of a *L. periclymenum* leaf (Thomas, 1985: Chinery, 1989; Emmet and Heath, 1990) and that the butterfly is monophagous. The adult insect nectars mainly on *Rubus fruticosus* (bramble). *L. camilla* is normally monovoltine in both the UK and in southern Europe. In the latter area, its close relative, *L. reducta*, is bi- and sometimes tri-voltine (Chinery, 1989). The caterpillar over-winters inside a hibernaculum made from stitching leaf sections together with silk chords. Thomas (1985) describes the caterpillar as "ridiculously easy" to locate due to its conspicuous feeding damage (Section 4.6).

Lederer's (1960) behavioural study of *L. camilla* in Germany revealed a curious caterpillar behavioural trait which involved the construction of a leaf midrib tip extension from faecal pellets immediately following emergence from the egg (Section 4.6). Also, Thomas (1985) is the only author to mention the appearance of "seeping" of secretion from nibbled leaves by fully grown

Plate 4.1

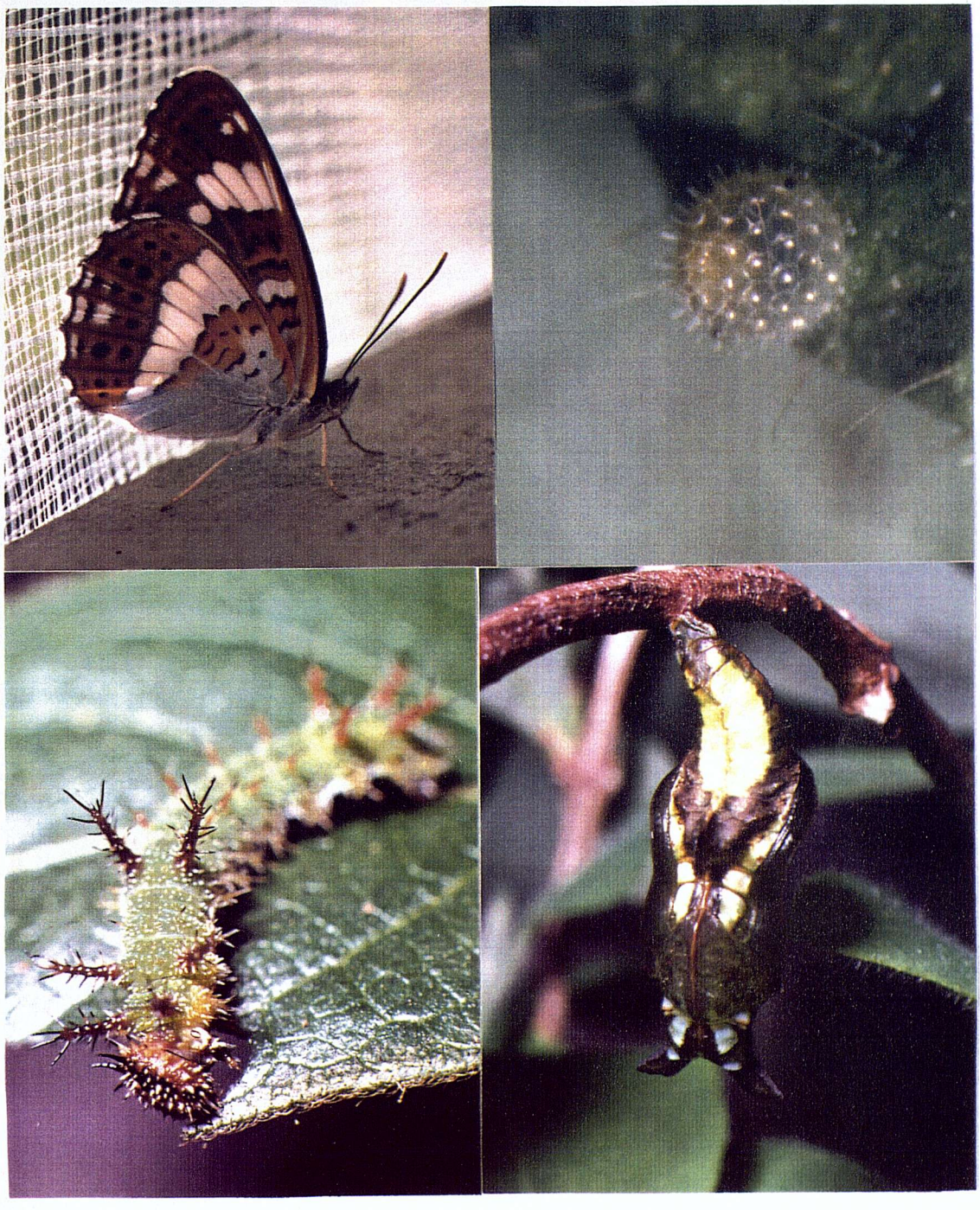


Plate 4.2

caterpillars (Section 4.6). The spectacularly shaped pupa (Plate 4.1) is normally found suspended from *L. periclymenum* foliage.

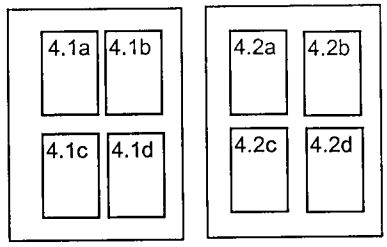
4.4.2 *Hemaris fuciformis* L.

Most authors state that *H. fuciformis* oviposits singularly on the lower surface of a leaf of its foodplant which is usually *L. periclymenum.* Unlike *L. camilla, H. fuciformis* does oviposit on other hosts and may be regarded as oligophagous. *Symphoricarpos rivularis (Snowberry) and Galium* spp. are occasionally used in the UK (Newman, 1965). In southern Europe the moth frequently oviposits on *Lonicera xylosteum* and *Lonicera tatarica* as well as *L. periclymenum* (Pittaway, 1993). Tutt (1902) includes *L. caprifolium* and *Symphoricarpos racemosus* as additional food plants. Although Newman (1965) states that, in the wild, *H. fuciformis* prefers *L. periclymenum* to *S. rivularis* as host species the author has observed *H. fuciformis* ovipositing on *S. rivularis* for several years even though the oviposition bush was surrounded by suitable unused *L. periclymenum* drapes.

The adult moth, which is a bumble-bee mimic, often nectars on the same nectar sources that bees use. Most authors agree that *Rhododendron* spp. are its favourite nectar source. However, the author has observed the moth ignoring cultivars in preference for *Rhododendron ponticum,* the species found in British woodland. Other nectar sources include *Ajuga reptans* (bugle), *Lychnis flos-cuculli* (ragged robin) and *Rhinantus crista-galli* (yellow rattle) (Newman, 1965). The author provides the only record for *H. fuciformis* nectaring on its own oviposition food plant in Bentley Wood in June 1994. In southern Europe and in the lower alpine valleys the moth is bivoltine, but elsewhere only a single brood appears each season (Newman, 1965). However, there have been rare partial second broods in Britain (Pittaway, 1993). The caterpillar pupates in a fragile cocoon just below the soil surface where it over-winters (Emmet and Heath, 1983).

Previous pages.

Plate 4.1a Adult *L. camilla* (x2). p. 4-5
Plate 4.1b Egg of *L. camilla* (x25). p. 4-5
Plate 4.1c Final instar caterpillar of *L. camilla* (x3). p. 4-5
Plate 4.1d Pupa of *L. camilla* (x3). p. 4-5
Plate 4.2a Adult *H. fuciformis* (x3). p. 4-6
Plate 4.2b Final instar caterpillar of *H. fuciformis* (x2). p. 4-6
Plate 4.2c Pupa and cocoon of *H. fuciformis* (x2). p. 4-6
Plate 4.2d Egg of *H. fuciformis* (x30). p. 4-6



4.5 Habitat.

4.5.1 *Ladoga camilla* L.

The butterfly is associated with extensive woodlands in which it is found ovipositing on thin spindly growths of its only food plant, L. periclymenum, in partly shaded areas, according to most authors. Vigorous bushy plants in sunny clearings are never used and it is typical of long abandoned coppices and deciduous forests where the canopy has almost closed (Thomas, 1986). It is found in many small woods and almost all large ones in its stronghold areas where it is locally common but seldom abundant. Transect monitoring data from Bentley Wood indicate a population increase over the last eight years and the butterfly has been seen in most parts of the wood in large numbers in recent years.

The fluctuations in population density of *L. camilla* at local sites may indicate population dynamics which are very sensitive to changes in weather and, possibly, local site management. Pollard's population study in Monks Wood (Pollard, 1979), using k-factor analysis, explained the 1930-50 national expansion of *L. camilla* on high June temperatures during the expansion period because low temperatures produces prolonged caterpillar and pupal growth which increases mortality through bird predation.

Figure 4.2 compares the index of abundance (total number of butterflies counted on a transect on 25 occasions during the period April to September; Pollard, 1993) for *L. camilla* for the period 1986-95 from four Bentley Wood transects with Picket Wood which is situated in north Wiltshire. Although the North and South transects are slightly longer than East and Barnridge transects, *L. camilla* is more abundant on the first two transects than the latter pair. South and North transects are mainly rides with 50 year old plantations on either side while East and Barnridge transects are mainly tracks passing through clearings or rides with a plantation on one side only. The clearings contain copious amounts of ground *L. periclymenum* growth which do not attract ovipositing female *L. camilla* in contrast to aerial *L. periclymenum* drapes found in plantations. The size of a wood can also influence *L. camilla* populations. Bentley Wood is ten times larger than Picket Wood and is more likely to contain more suitable oviposition habitat than a small wood.

The periodic fluctuations in *L. camilla* numbers is similar for the four most populated transects with the exception of 1995 abundance on the South transect of Bentley Wood. The year index for this transect shows a downward trend from the previous year in contrast to the other three. According to the normal trends South transect should have shown a year index of 3-4 times greater than it did for 1995. The period 1992-95 included a vast amount of plantation thinning on the South transect and ride widening on the North transect. The ride widening removed ride side drapes but had little adverse effect on *L. camilla* numbers in contrast to plantation thinning which removed inner plantation drapes and shows the importance of inner plantation zones to *L. camilla* oviposition

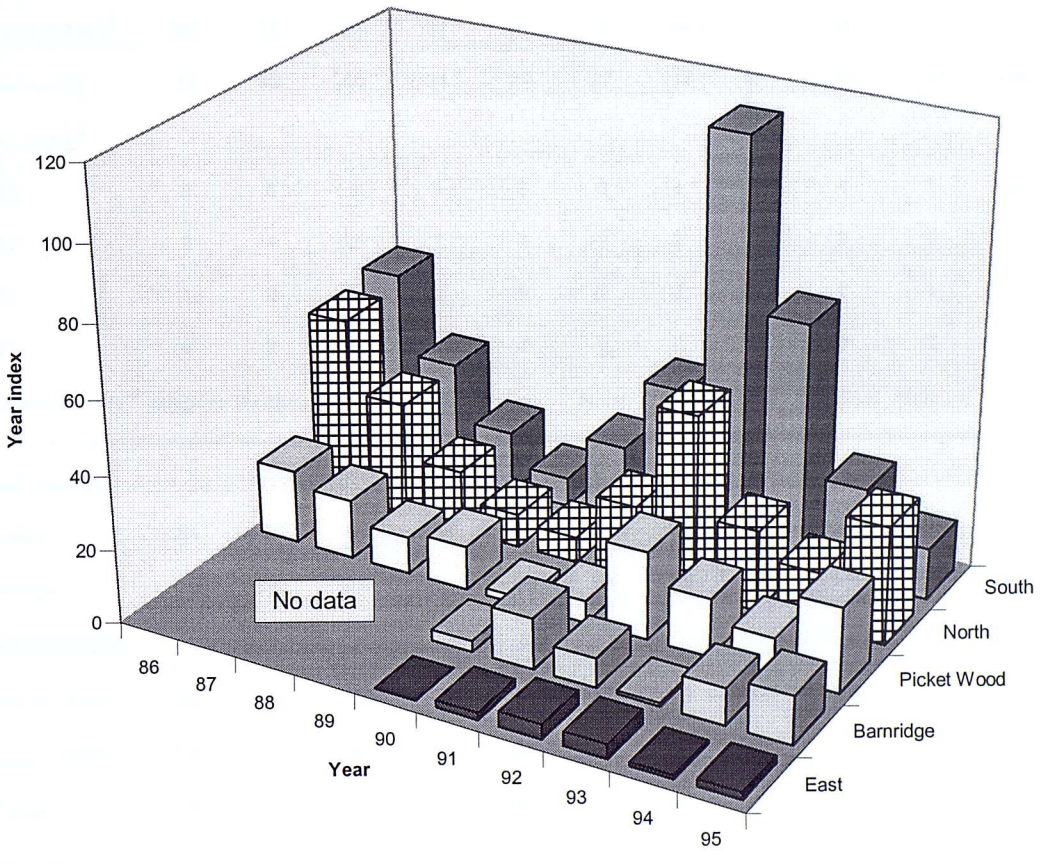
sites. Most of the inner plantation *L. periclymenum* drapes are supported by scrub species (weak growing hazel, birch, and fallen trees) which can be decimated by forestry thinning procedures. Careful felling could prevent most of this damage to *L. camilla* oviposition sites.

Tables 4.1-2 show the main structural vegetation of transect sections including the number of *L. periclymenum* drapes lost through thinning operations. *L. camilla* adults very rarely use any other nectar source than bramble which has to be flowering in full sun. The ideal *L. camilla* habitat is characterised by a number of factors:

- Shade: characterised in Bentley Wood by 40-50 year old mixed oak-conifer plantations after one or two thinnings of conifers containing scrub supporting *L. periclymenum* drapes. (The shade and temperature factors will be quantified with results appearing in Chapter Six).
- Nectar source: large flowering clumps of bramble in full sun (midday) within 100 m of oviposition site.
- Display zone: 10-20 m high vegetation close to oviposition sites in full sun (midday).

Lederer's (1960) German study of *L. camilla* showed the same inclination as did *L. camilla* in Bentley Wood in staying loyal to an ideal site for many years. Marked *L. camilla* in Bentley Wood (an investigation carried out by the author in the present study) have shown their ability to travel long distances (at least 1 mile) in search of nectar sources, but doing so may use up vital energy reserves as well as increasing predation. Second broods of *L. camilla* in autumn are most unlikely due to their behavioural ecology of spending winter in diapause but also due to the lack of suitable autumnal nectar sources (as is the case in the warmer climes of southern Europe). However, adults are occasionally seen in British woods during autumn and the present study will provide evidence that *L. camilla* caterpillars bred in captivity frequently pass through all caterpillar instars and produce adult butterflies in September.

Fig. 4.2 Comparison of *L. camilla* abundance (year index) of 4 Bentley Wood transects with 1 transect from north Wiltshire (Picket Wood) over the period 1986-95.



Year index is the total number of butterflies counted on a transect carried out on 25 occasions during the period April to September.

Table 4.1 Habitat structure of main *L. camilla* oviposition sites in Bentley Wood (North and South transects).

North transect												
Section	N1	N2	N3	N4	N5	N6	N7	N8	N9	N10	N11	N12
Site type [a]	PC	PC	PP	PC	PC	PC	PP	PC	PP	PP	PP	PP
L. periclymenum												
Drapes (1992) [b]	59	108	38	121	36	11	12	17	52	13	82	139
Drapes (1995) [c]	26	35	21	37	32	3	14	7	48	17	115	123
Change (%)	44	32	55	31	89	27	117	41	92	131	140	88
Year index [d]												
1992	9	6	3	4	7	3	4	1	4	1	2	5
1993	2	1	2	1	3	0	2	0	2	0	3	6
1994	1	2	1	0	0	1	2	0	2	1	1	4
1995	9	2	5	2	2	0	0	0	3	2	1	6
Bramble density [e]	Medium	Medium	Medium	Low	Low	None	Low	Low	Medium	Medium	None	High

South transect											
Section	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11
Site type [a]	PC	PC	PP	CC	PC	PP	PP	PP	PP	PP	PP
L. periclymenum											
Drapes (1992) [b]	45	91	160	85	86	62	22	37	105	62	58
Drapes (1995) [c]	8	34	163	60	42	70	20	28	26	19	31
Change (%)	18	37	102	71	49	113	91	76	25	31	53
Year index [d]											
1992	12	15	3	5	2	2	4	4	19	34	13
1993	15	5	3	4	7	1	2	3	10	16	1
1994	0	1	4	0	5	3	1	2	0	7	3
1995	0	2	2	0	0	0	0	4	0	2	4
Bramble density [e]	Low	Medium	Medium	Medium	Medium	Low	Low	Low	Medium	High	Low

a: habitat type either side of transect section, P = plantation, C = clearing.
b: number of aerial *L. periclymenum* drapes within a 5m wide strip of adjacent plantations before thinning.
c: number of aerial *L. periclymenum* drapes within a 5m wide strip of adjacent plantations after thinning.
d: index of abundance of *L. camilla*.
e: abundance of bramble nectar source (visual estimation).

Table 4.2 Habitat structure of low density *L. camilla* oviposition sites in Bentley Wood (Barnridge and Eastern Clearing transects).

Barnridge transect Section	B1	B2	B3	B4	B5	B6	B7	B8	B9
Site type [a]	PC	CC	PC	PC	CC	PP	PP	PP	PP
L. periclymenum									
Drapes (1992) [b]	22	0	5	32	3	33	11	13	36
Drapes (1995) [c]	9	0	4	3	2	37	12	8	25
Change (%)	41	0	80	9	67	112	109	62	69
Year index [d]									
1992	1	0	2	2	0	0	2	1	0
1993	0	0	1	0	0	0	0	0	0
1994	3	0	0	3	0	0	2	0	2
1995	1	1	0	6	1	1	0	1	2
Bramble density [e]	None	Low	Low	Low	Low	Low	Low	Low	None

Eastern Clearing transect Section	E1	E2	E3	E4	E5	E6	E7
Site type [a]	PP	CC	CC	CC	CC	PC	PC
L. periclymenum							
Drapes (1992) [b]	77	10	17	24	13	55	22
Drapes (1995) [c]	34	12	16	28	16	62	25
Change (%)	44	120	94	117	123	113	114
Year index [d]							
1992	2	0	0	0	2	0	0
1993	1	0	0	3	0	0	0
1994	1	0	0	0	0	0	0
1995	0	0	1	1	0	0	0
Bramble density [e]	Medium	Medium	Medium	Low	Medium	Low	Low

a: habitat type either side of transect section, P = plantation, C = clearing.
b: number of aerial *L. periclymenum* drapes within a 5m wide strip of adjacent plantations before thinning and ride margin widening.
c: number of aerial *L. periclymenum* drapes within a 5m wide strip of adjacent plantations after thinning and ride marging widening.
d: index of abundance of *L. camilla.*
e: abundance of bramble nectar source (visual estimation).

4.5.2 *Hemaris fuciformis* L.

Most authors describes the habitat of *H. fuciformis* as sunny spots in woodland rides and clearings. Emmet and Heath (1990) simply describe its habitat as woodland rides. Pittaway (1993) describes its habitat in Britain as sunny glades in open woodland. In northern Europe and further south, it displays a marked preference for sand- and chalk-hills lightly overgrown with conifers and shrubby honeysuckles, such as *L. xylosteum* and *L. tartarica*, where it is often extremely abundant (Pittaway, 1993). Tutt (1902) describes its habitat as woodland rides and clearings and the moth "loves the flowers of rhododendrons in the large private parks of the South of England".

In Bentley Wood *H. fuciformis* females mainly oviposited on *L. periclymenum* drapes growing in full sun and, more rarely, on ride-side plantation drapes providing they were facing south. South facing isolated drapes growing on wide ride margins were found to be very popular but, rare, as these growths only appear on supporting trees with little lateral growth and broken tree trunks or large stumps. A main conservation problem for *H. fuciformis* is that ideal oviposition sites rarely remain ideal for periods longer than 2-3 years under natural conditions as aerial *L. periclymenum* drapes eventually become shaded by the supporting tree foliage and female *H. fuciformis* rarely oviposit on host leaves not facing south and in full sun (Chapter Five). Artificial sites which retain their attraction to ovipositing *H. fuciformis* for several years can be created quite easily by pollarding young trees or piling up dead timber to support foodplants in suitable woodland clearings (actions carried out by the author during the present study). The gales of 1987 and 1991 created ideal habitat for *H. fuciformis* which can be summarised as having the following characteristics:

- Shade: none other than that created by the *L. periclymenum* drape; ideal support is broken stump or pollarded oak or small birch, 1.5-2.5 m high, in full sun.
- Nectar source: flowering rhododendron bushes (not cultivars), 1.5 - 4 m high, situated in full sun at midday.
- Display zone: 15-20 m vegetation in full sun (plantation oaks are ideal).

Although ground growing *L. periclymenum* was abundant in Bentley Wood clearings, it was never found to be used by ovipositing *L. camilla* and *H. fuciformis* in this study. In woodland where suitable aerial *L. periclymenum* drapes are scarce, *H. fuciformis* has been recorded ovipositing on this type of foodplant growth (pers. comm., P. Waring). Ground oviposition sites for *H. fuciformis* may be less desirable than aerial drapes and their use by ovipositing *H. fuciformis* probably indicates a declining quality of habitat and foodplant for *H. fuciformis.*

Like *L. camilla,* adult *H. fuciformis* flies and oviposits at the warmest times of the day and rarely below an air temperature of 18 °C. The first three instar caterpillars feed during day and night periods although 4th and 5th (final) instar feed rapidly and mainly at night. The pre-pupation period (during which the caterpillar turns from green to purple-brown and its behaviour becomes

more violent when disturbed) can take 2-5 days whilst the caterpillar clears its gut and constructs a thin brown cocoon of silk surrounded by soil and leaf bits (personal observation by the author in Bentley Wood and assay). The feeding behaviour of the caterpillars is described in Section 4.6 of this chapter and also Chapter Seven.

4.6 Unusual behavioural traits of *L. camilla* and *H. fuciformis* caterpillars.

4.6.1 Introduction.

L. camilla and *H. fuciformis* caterpillars, mainly in the 1st instar, displayed unusual behavioural traits when feeding on *L. periclymenum* leaves. These traits included silking (laying platforms of silk over leaf surface parts; Plates 4.3a-b), trichome swiping (mandibular cutting of trichomes involving a swiping motion of the head), defence refuge construction, hibernaculum construction, latrine construction and unusual techniques of feeding. All of these traits were displayed by *L. camilla* caterpillars but only trichome swiping and an unusual feeding technique were displayed by *H. fuciformis* caterpillars.

Some of these unusual behavioural traits may have evolved during the early evolutionary period of caterpillar - foodplant interactions as counter adaptations against foodplant defence mechanisms. These caterpillar behavioural traits will be discussed in relation to caterpillar feeding and variable foodplant quality in Chapters Six, Seven and Eight.

4.6.2 *L. camilla* caterpillar behavioural traits.

Caterpillar emergence normally took about 2-3 minutes followed by the consumption of the egg shell in about 45 minutes. Once the freshly emerged 2 mm long caterpillar had consumed most of the egg shell, its first journey was to travel to the leaf tip via the marginal edge of the egg leaf (30 out of 33 caterpillars observed carried out this procedure; the other 3 caterpillars crossed the leaf laminal zone towards the midrib). All caterpillar travelling took place on the adaxial (upper) leaf surface. Occasionally, the first move was towards the leaf petiole via the margin but the caterpillar normally reversed direction near the petiole and travelled back along the margin to the leaf tip. At this stage few caterpillars were observed crossing the laminal zone towards the midrib before reaching the leaf tip for the first time. Those which did, immediately travelled towards the leaf tip via the leaf midrib. In doing so, these caterpillars experienced considerable difficulties in negotiating midrib trichomes. The first swiping or mowing of trichomes took place at this time. The swiping motion involved mandibular grasping of the trichome (near its base) followed by a lateral shaking of the head. (The same motion was carried out by freshly emerged 3 mm long 1st instar *H. fuciformis* caterpillars but with apparently more power.) First contact of *L. camilla* caterpillars with the

leaf tip area, about 25 minutes after consuming the egg shell, resulted in immediate silking of the leaf tip. During the next four hours, the caterpillar intermittently rested in the typical rest posture (Plate 4.4a) of head protruding beyond leaf tip with anal claspers anchored to the silk scaffold, and travelled up and down either side leaf margin, silking all the time.

The first feed or mandibular penetration of the leaf took place after 4-5 hours of emergence on either side of the leaf tip and over the following 3-4 hours the leaf tip was shaped into an arrow head. After 7-8 hours following emergence (activity was not interrupted by daylight or nightfall) the construction of the midrib extension or 'pier' as this study calls it was started. Later evidence will prove that this 'pier' extension acts as a defence refuge.

Initial construction of the 'pier' (Plates 4.4a-c) consisted of the caterpillar reversing its normal overhang position with head outermost on leaf tip to deposit faecal pellets or frass on the leaf midrib tip followed by pushing the frass pellet, using its head, onto the very edge of leaf tip and bonding it into position with caterpillar 'glue' and silk using the arrow headed shaped leaf tip as an anchor point for the silk. Eventually, the pier extension grew as the building procedure was repeated until the pier was completed after about 24 hours after emergence, when the pier was about the same length as the caterpillar (2.0-2.5 mm). For most of the remainder of the 1st instar and most of the 2nd instar, the caterpillar would spend its resting periods, head foremost, located on the pier although, by this time, the joint between pier and midrib was indistinguishable due to multi-layered silk (Plate 4.4b-c). From a sample of 9 piers chosen randomly, length, number of frass bits, and period of completion was 2.43 ± 0.28 mm, 23.6 ± 3.9, 2.0 ± 0.2 days, respectively (mean ± S.E.).

During the construction of the pier the caterpillar, as part of its feeding procedure, begins to make incisions from the marginal part of the leaf towards the midrib which results in the leaf taking on the appearance of a series of 'flags' attached to the leaf midrib (Figure 4.3). However, rarely are there more than two 'flags' on either side of the midrib in existence at any one time. The reason for this situation is that the caterpillar eventually cuts each flag into bits, silks them together, and suspends the tiny bundle of silked leaf bits from the midrib with a silk chord. This bundle of leaf bits was used as a latrine (Plate 4.3c). Once the pier was completed, further defecation was frequently carried out by the caterpillar pointing its anus at the suspended latrine and shooting frass bits, at great speed, into the latrine bundle of leaf bits. The latrine would grow in size (but still remain relatively small) and be regularly maintained, adjusted for position, added to with additional leaf bits, and, of course, accumulate in frass bits. As the caterpillar carried out the latrine servicing, minute particles of sticky secretion, exudating from the sliced epidermal leaf cells, would cause frass bits to stick to all parts of the caterpillar's abdomen. Occasionally, the caterpillar would use these frass bits to service its pier extension. All ecdyses took place on the midrib where the caterpillar could anchor its anal claspers to the silk platform in order create leverage for moulting. The frass bits inside the pier eventually attract fungal growth which can completely cover the pier extension and other areas of

the leaf midrib (Plate 4.3b).

Under normal circumstances, *L. camilla* caterpillars remained feeding on the same leaf for 2-3 weeks before venturing onto an adjacent leaf during their second and third instars. However, they always returned to their original leaf pier refuge to rest and digest food. If disturbed during these periods of resting, caterpillars would assume a characteristic "z" shaped posture (Plate 4.4a). The original leaf was rarely consumed beyond two thirds of the midrib length.

Soon after ecdysis into the 3rd instar, in all cases under natural conditions in the field and sometimes in captivity during bioassay, the *L. camilla* caterpillar started to construct its hibernaculum (Plate 4.5a-d) in which it would spend its winter diapause. Hibernaculum construction usually started at the end of August in Bentley Wood and was completed by most caterpillars by mid-September. Some caterpillars used their existing feeding leaves for this purpose, others used a fresh leaf. The caterpillar's first task in constructing the hibernaculum was to swipe all trichomes clear of the chosen leaf petiole and its junction with the main stem. The petiole was then bonded to the main stem with a figure of 8 silking action using a multitude of silk layers (Plate 4.5d). The leaf was then cut perpendicularly from the central marginal area to the midrib. Sometimes the upper unused portion of the leaf was left attached, other times it was completely removed. The two laminal sides of the midrib were then silked together, the silk joints taking place marginally and at the upper midrib end. During these operations the caterpillar gradually constructed a platform of silk on top of the midrib swiped trichome stumps to which it anchored itself using its anal claspers, always with its anal end pointing towards the petiole, the only open end of the hibernaculum.

Under natural conditions, the post-diapause caterpillar emerged in March during mild days to nibble the nearest leaf margin near the petiole or scrape the mesophyll layer of the laminae. Cold spells would send the caterpillars back into their hibernacula. The 3rd, 4th and final instars simply 'chomped' (consumed rapidly on any part of the feeding leaf) without any of the pre-diapause caterpillar precision in carefully selecting particular parts of the feeding leaf. Pupation took place aerially with the pupa normally suspended from a *L. periclymenum* stem. The amount of sticky secretion produced by feeding damage of *L. camilla* caterpillars on host shade foliage was extremely small and was most noticeable in the latrine.

This account of *L. camilla* 's feeding technique took place on natural *L. periclymenum* oviposition foliage, that is, host foliage growing in shade. The following account of the caterpillar feeding technique of *H. fuciformis* also took place on natural *L. periclymenum* oviposition foliage, that is, host foliage growing in full sun.

4.6.3 *H. fuciformis.*

The life-style of 1st instar *H. fuciformis* caterpillars is far less complex than *L. camilla* but shares the traits of trichome swiping and producing a distinctive feeding pattern. The egg is situated on the abaxial leaf (underside) lamina where trichomes were found to be most dense in shade and sun hostplant foliage. Some caterpillars, before leaving the freshly opened egg shell, swiped nearby trichomes by leaning out of the shell. After consuming its egg shell the caterpillar wanders around the leaf laminae before coming to rest on the abaxial midrib. In contrast to *L. camilla* all feeding takes place on the abaxial leaf surface. The first feed takes place after about 2 hours when the caterpillar, with its anal claspers attached to the leaf midrib, leans over and appears to inspect the leaf cuticle for a few seconds before biting a circular hole about 1 mm in diameter. This procedure is repeated up and down either side of the midrib, accompanied by trichome swiping of the midrib and laminal leaf zones. During the 1st instar the size of the feeding damage holes increase from 1 to 2 mm in diameter, reaching 3-4 mm in the 2nd instar, before 'chomping' in late 3rd and final instars (5 in all, as with *L. camilla*).

In the first few feeding bouts sticky globules of secretion appear on the leaf at the feeding damage hole location. At this caterpillar stage the time interval between mandibular penetration of leaf lamina and production of sticky globules was in the range 10-15 minutes. However, microscopic observation of the hole showed a sudden surge of secretion first appearing from the damaged epidermal layer 3-5 minutes after mandibular penetration. A few seconds before the appearance of this initial surge of secretion, the caterpillar would suddenly turn away indicating that the caterpillar was able to predict or expected the secretion and wished to avoid it. Comparison of hole size with amount of secretion gave the impression that the smaller holes produced more secretion and the amount of secretion diminished as the number of holes in the leaf increased. Later instars (3-5) produced little or no secretion when feeding on fresh leaves of sun growth *L. periclymenum.*

H. fuciformis 1st instar caterpillars did not reveal the same techniques as *L. camilla* with faeces disposal but they still showed a similar and great reluctance to allow frass pellets to come in contact with the laminal areas of the leaves on which they were feeding. *H. fuciformis* caterpillars usually ejected their frass into the void below the leaf (which never took place with 1st instar *L. camilla* caterpillars). Occasionally, a caterpillar would remove a faecal pellet from its anus with its mouth before tossing it into space below the leaf in contrast to 1st instar *L. camilla* caterpillars which never allowed frass to drop below the leaf on which it was feeding. A more quantitative record of feeding behaviour of *L. camilla* and *H. fuciformis* appears in Chapter Seven.

Fig. 4.3 Sequential feeding pattern produced by 1st and 2nd instar *L. camilla* larva.

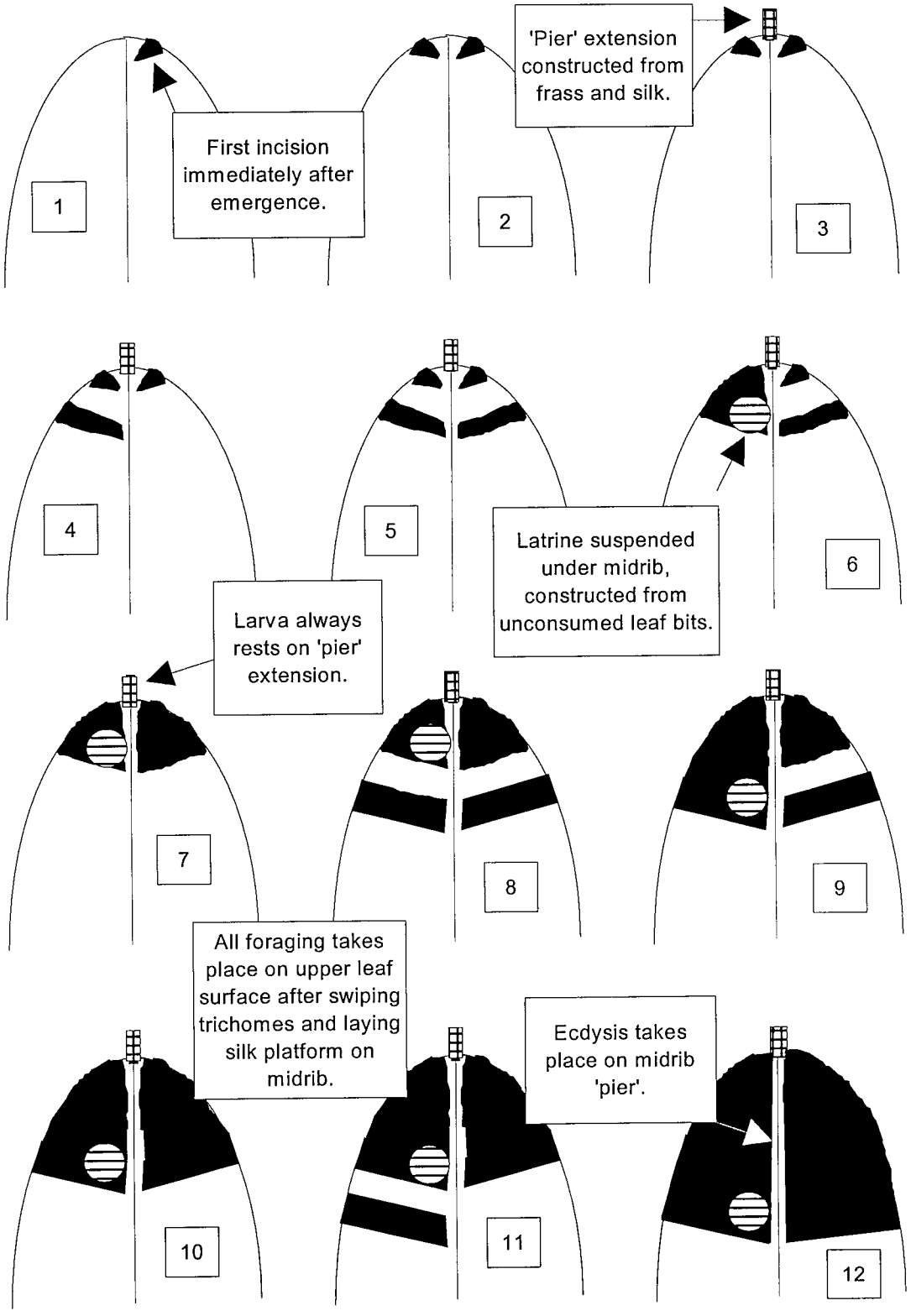


Plate 4.3

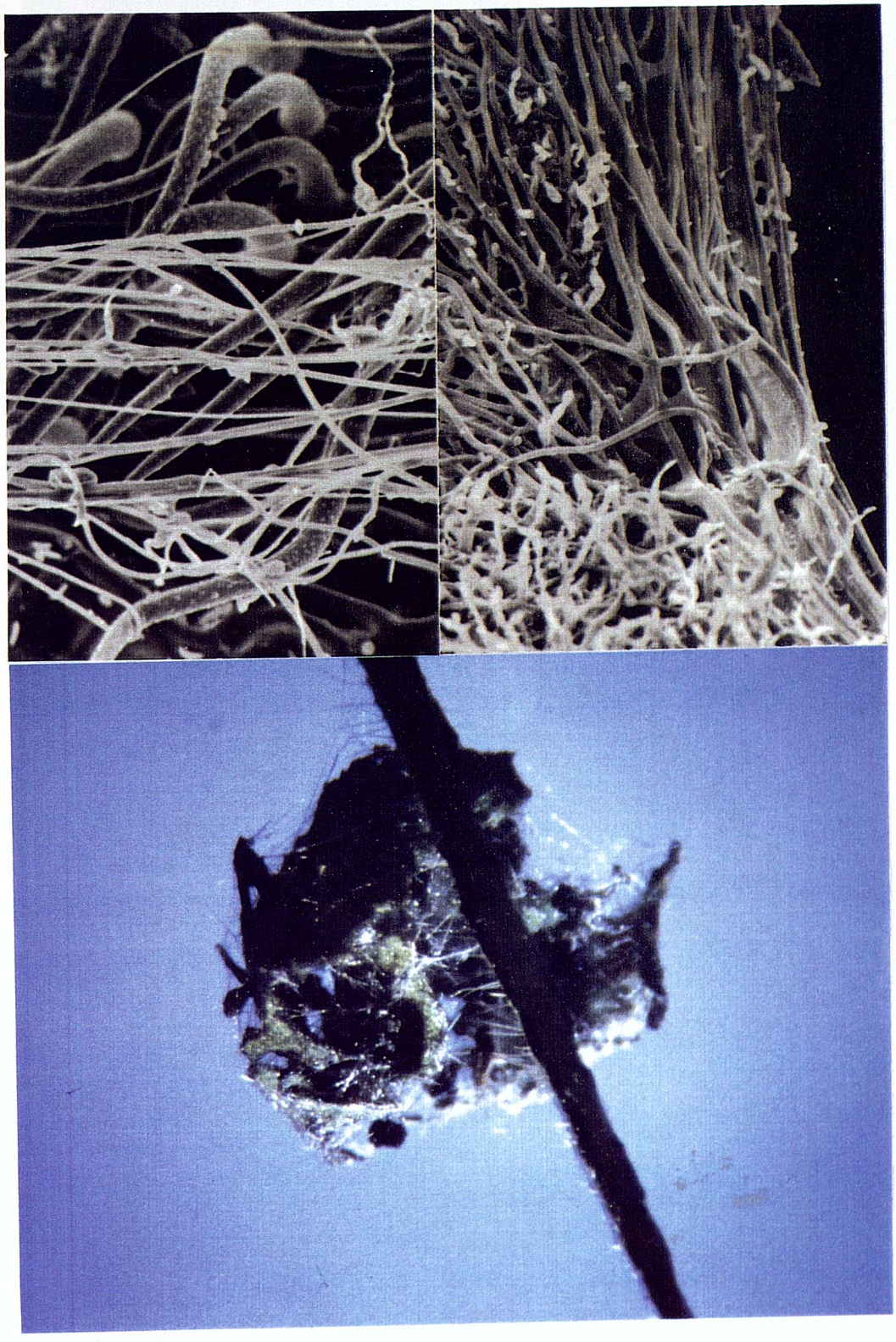


Plate 4.4

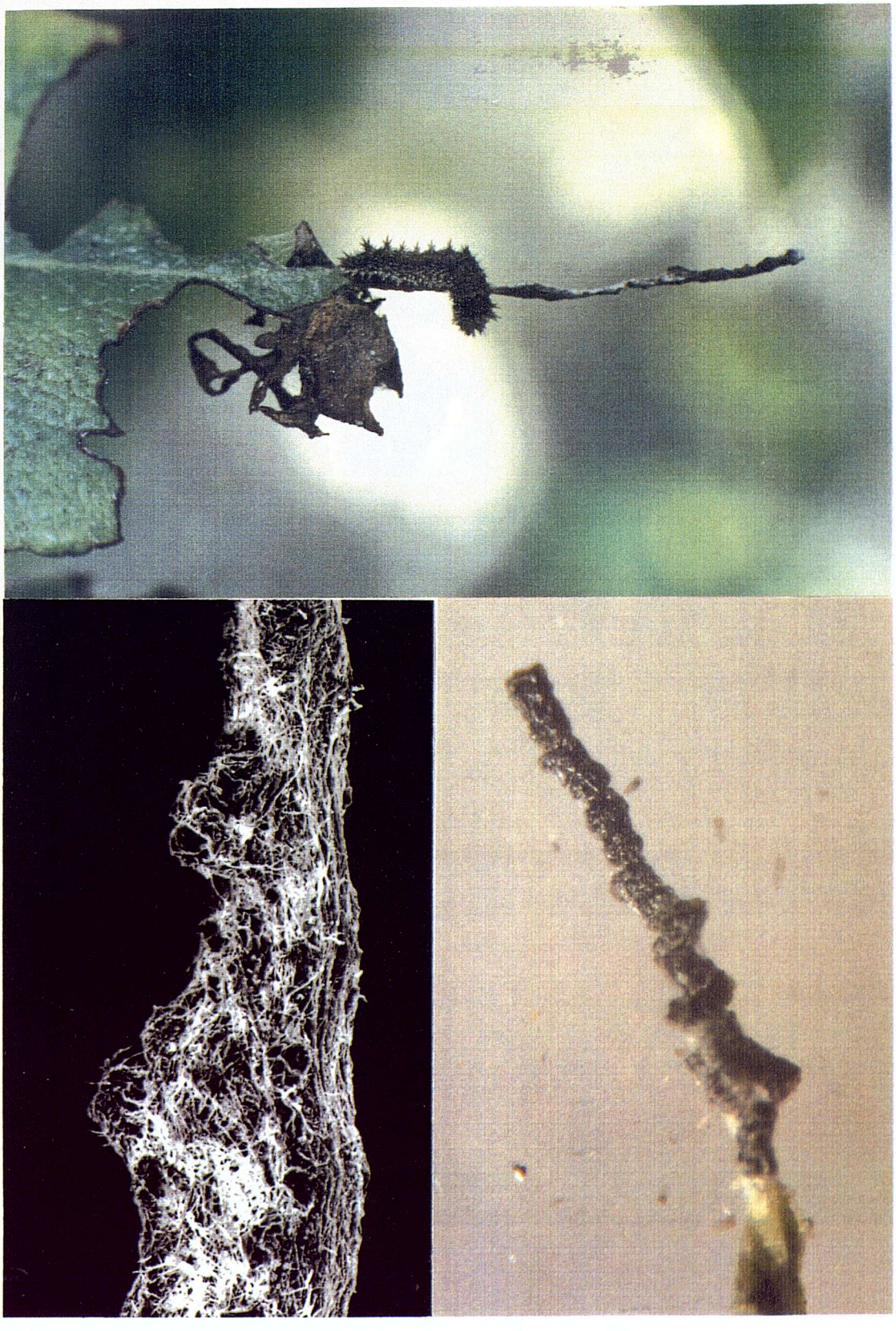


Plate 4.5

Previous pages (Plates 4.3-4.5; pp. 19-21).

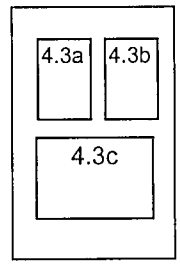


Plate 4.3a Scanning electron micrograph of early silk platform construction by *L. camilla* 1st instar caterpillar (x300). p. 4-19
Caterpillar silk is shown flattening the upright nature of unicellular trichomes located on *L. periclymenum* midrib.

Plate 4.3b Scanning electron micrograph of late silk platform construction by *L. camilla* 1st instar caterpillar (x400). p. 4-19
The silk platform has completely covered the trichomes; caterpillar 'glue' and fungal hyphae can also be seen

Plate 4.3c Aerial latrine of *L. camilla* 1st instar caterpillar (x10). p. 4-19
The latrine, constructed from leaf bits interwoven with silk, is shown suspended under the leaf midrib. Frass bits (faecal pellets), shown stuck in the latrine, are 'fired' into the latrine by the 1st instar *L. camilla* caterpillar from a position on the midrib. No frass is allowed to fall below the caterpillar feeding position during the 1st instar.

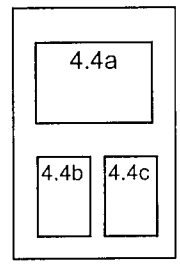


Plate 4.4a Normal foraging pattern by *L. camilla* caterpillars (1st-2nd instar; x8). p. 4-20
The 2nd instar lava is displaying its defence posture immediately above its latrine. The joint between the midrib tip and the defence refuge is 2 cm from the end of the 'pier' and can be seen more clearly in Plate 4.4c.

Plate 4.4b Scanning electron micrograph of part of *L. camilla* 1st instar refuge (x100). p. 4-20
The smooth right hand side of the refuge is the upper part of the refuge which contains a thicker layer of silk where the caterpillar rests. The jagged edge is caused by frass bits on the lower part of the refuge covered by a thin layer of silk.

Plate 4.4c Completed *L. camilla* defence refuge attached to leaf tip (x50). p. 4-20
The joint between the contrasting dark coloured refuge of frass bits can be seen against the green living tissue of the midrib tip.

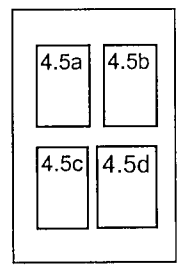


Plate 4.5a Early stages of *L. camilla* hibernaculum construction (x10). p. 4-21
The 3rd instar caterpillar has severed the leaf midrib and silked the outer exit which is slowly pulling the two upper leaf laminae together. The caterpillar is in the act of constructing the inner silk platform base.

Plate 4.5b Completed and occupied pre-diapause *L. camilla* hibernaculum construction (x10). p. 4-21
The hibernaculum is now complete and the unused parts of the leaf have been discarded in this case. The marginal areas of the leaf laminae have been silked together. The caterpillar always faces into the hibernaculum.

Plate 4.5c Occupied post-diapause *L. camilla* hibernaculum construction (x5). p. 4-21

Plate 4.5d Scanning electron micrograph of silked petiole joint between *L. camilla* hibernaculum and *L. periclymenum* stem (x30). p. 4-20
The caterpillar clears the petiole and stem of trichomes before reinforcing the petiole with silk. The petiole joint is surprisingly strong and stretches rather than snaps when force is artificially applied.

4.7 Discussion

4.7.1 Habitat

Most authors agree that *L. camilla* females prefers to oviposit on *L. periclymenum* growing in shade while *H. fuciformis* females prefer their oviposition sites in sunny areas of woodland. However, visual estimation of shade is rather inaccurate and a quantitative measurement of oviposition site shade will be attempted in this study, the results of which are discussed in Chapter Five.

It is likely that both *L. camilla* and *H. fuciformis* are existing in Britain on their northern range limit, resulting in populations which will be sensitive and fluctuate according to changing weather conditions. Changing management regimes in woodland may also affect the degree of shade and density of *L. periclymenum* drapes. However, the general impression from field work is that their numbers have increased in Bentley Wood over the last eight years. The main reason for this increase was probably the creation of clearings from windblow damage caused by the gales in southern Britain in 1987 and 1991 which destroyed many trees in Bentley Wood. The windblow damaged trees and broken stumps produced suitable supports for *L. periclymenum* drapes to grow in full sun which produced the type of host foliage preferred by ovipositing *H. fuciformis*.

4.7.2 Unusual behavioural traits of *L. camilla* and *H. fuciformis* caterpillars.

No author in Britain has referred to silking, trichome swiping and the construction of defence refuge and latrine by *L. camilla* caterpillars. However, Lederer (1960), in his comparative study of *L. camilla* with *L. populi* in Germany, described the construction of the leaf midrib extension by 1st instar *L. camilla* caterpillars from faecal pellets and silk but did not refer to its function as a defence refuge but simply an extension of the leaf midrib.

Available evidence supporting the argument that the function of the pier extension is a refuge or defence refuge for 1st instar *L. camilla* caterpillars is compelling. *L. camilla* 1st instar caterpillars always return to rest on the pier after feeding, silking and trichome swiping activities. Thus, the caterpillar returns to the pier and no other location on over one hundred occasions during the first instar period under its own volition and without undue stress. Danger, simulated or real, when threatened, always caused the caterpillar to return to the pier with haste. Also, the pier may have been constructed as a favourable platform for defence against parasitoid flies. Time lapse video recording showed a fly attacking a 1st instar *L. camilla* caterpillar. The tape showed a 'tug-of-war' in which the fly, using its labella, was trying to pull the caterpillar off the pier, while the caterpillar resisted by holding onto the pier silk platform with its anal claspers. The labella itself was longer than the caterpillar, so the applied force to dislodge the caterpillar must have been substantial. However, the caterpillar survived as the fly eventually released its hold on the caterpillar. The

fly may have been attracted to the feeding zone of the caterpillar, initially, by the smell of the small amount of secretion (shown later to contain sugars including fructose which has a fruity smell) produced in the leaf bits of the suspended latrine. The latrine may act as a decoy zone for potential predators as well as a frass disposal unit. Obviously, increasing amounts of smelly secretion will increase the chances of predation. *L. camilla* females may have evolved to oviposit on shade *L. periclymenum* foliage because of its limited amount of secretory potential compared with sun host foliage.

Like Lederer's (1960) German site observations, field observations in Bentley Wood have produced a small number of instances where the pier was constructed on the leaf margin and not at the usual leaf tip location. The explanation behind this unusual pier location may be associated with adverse leaf quality since close observation of the leaves revealed abandoned half-constructed piers at the usual tip location, often accompanied with small amounts of sticky secretion. The reaction of *L. camilla* caterpillars to adverse foodplant quality is investigated and discussed in Chapter Seven.

Lederer (1960) did not refer to the use of swiped trichomes as additional building material for the construction of the midrib extension although he did mention the general silking of the leaf surface. Emmet and Heath (1990) referred to the construction of a "cushion" of faecal pellets by *L. camilla* :

> "Early in the first instar, the caterpillar constructs a 'cushion' of faecal pellets, spun together with silk and this may be used as a resting site. Later, the cushion falls away and the caterpillar rests on the projecting midrib."

Presumably, this reference relates to what this study has called a latrine due to the observation from video recording of caterpillars shooting faecal pellets into the suspended mixture of leaf bits and silk from a nearby caterpillar position on the leaf midrib.

The patterns of feeding damage by both *L. camilla* and *H. fuciformis* caterpillars are well known and recorded by lepidopterists (Lederer, 1960; Emmet and Heath, 1990; Thomas, 1986; Waring, 1988) but trichome swiping by both *L. camilla* and *H. fuciformis* has not been previously recorded.

Methods used by other insects to overcome trichome defences of foodplants have been noted previously. Rathcke and Poole (1975) showed how the ithomid butterfly, *Mechanitis isthmia* Bates, neutralised the trichome defence of a species of *Solanum* by spinning a "silken scaffolding" on the tips of the trichomes. Hulley (1988) reported caterpillars of a sphingid moth, *Erinnyis ello* L., eating trichomes before feeding on the foodplant *Cnidoscolus urens* (L.) Arthur, and recorded caterpillars of a South African noctuid moth, *Pardasena* sp. nr *diversipennis* Gaede, mowing paths of trichomes before feeding on the leaves of a small shrub, *Solanum coccineum* Jacq.

L. camilla caterpillars may be very unusual in that they swipe trichomes, occasionally eat them

(although undigested in 1st and 2nd instar; pers. obs.), use them as building material and use the trichome stumps as anchorage in constructing a platform of silk. This constructional ability in addition to the carefully constructed foraging pathways used by *L. camilla* caterpillars may indicate a strong reluctance to make contact with the host leaf cuticle when unprotected from sharp caterpillar tarsi by a silk platform. Although displaying a different feeding technique, 1st instar *H. fuciformis* caterpillars indicate a similar reluctance to make contact with the laminal area of the foodplant leaf cuticle on sun growing foliage. The feeding damage holes created by *H. fuciformis* caterpillars on sun foodplant foliage exude a sticky secretion. The feeding technique used by *H. fuciformis* caterpillars may be directed at minimising the adverse effects of this type of plant defence mechanism. At the same time, *L. camilla* caterpillars may have evolved a different strategy of counter-adaptation against secretion which works most effectively on shade growing host foliage.

The following chapter, Chapter Five, will examine the microhabitat of both *L. camilla* and *H. fuciformis* in more detail in order to confirm that these two Lepidoptera oviposit on their *L. periclymenum* host in different habitats of shade which may create a variance in host properties. The quality of host foliage growing in shade and sun will then be examined and compared in Chapter Six. Chapter Seven will test the hypothesis that the respective feeding strategies adopted by *L. camilla* and *H. fuciformis* work best, in terms of caterpillar fitness, when feeding on their natural habitat conspecific foodplants and, therefore, reveal the ability of these two Lepidoptera to discriminate between host plants during oviposition.

Chapter Five

Habitat requirements of L. camilla and H. fuciformis.

Habitat - microhabitat - food plant architecture - light - temperature

5.1 Introduction

5.1.1 Essential environmental factors.

A habitat or 'address' is a description of where an organism is found in the environment and the term micro-habitat was coined by ecologists as a more precise description for small insects which lived only in very restricted areas and locations of their food plants (Chapman and Reiss, 1992). Elton (1927) regarded the ecological niche as a role within a community and a more modern approach of niche theory is concerned particularly with resource competition between species. The present study does not intend to establish any possible competition between the guild of Lepidoptera foraging on *L. periclymenum* although there is limited evidence that competition for this food resource may exist in areas of Bentley Wood where *L. periclymenum* drapes are scarce.

Community interactions can take place between completely different animals. Deer, for example, can indirectly effect the egg laying potential of *L. camilla* butterflies. Surveys carried out in 1973 and 1993 in Monks Wood National Nature Reserve (Cambridgeshire) showed that a substantial proportion of potential egg-sites of *L. camilla* had been removed by Muntjac deer, *Muntiacus reevesi* (Pollard and Cooke, 1994). In Bentley Wood, the two main deer species are Fallow (*Dama dama)*, and Roe (*Capreolus capreolus).* Although this study did not record browsing heights of these two species of deer, oviposition sites of *L. camilla* and *H. fuciformis* on *L. periclymenum* are probably within the range of these deer. However it is unlikely that *L. periclymenum* suffers greatly from deer browsing in Bentley Wood as there are many alternative food sources such as young coppice growth and other plantation trees (Putman, 1986).

A complete account of the niche of a butterfly or moth would therefore not only include the choice of caterpillar food plant, but other details of its biotic and abiotic environment such as shade, temperature, copulation requirements, other animals feeding on the same food plant, nectaring plants and predators. Chapters Three and Four referred to general habitat preference of Lepidoptera foraging on *L. periclymenum.* This chapter is concerned with a more detailed comparative examination of habitat preference between *L. camilla* and *H. fuciformis* which includes details of shade, temperature and foodplant architecture of oviposition sites.

5.1.2 Food plant architecture

Plant architecture and leaf morphology can play important roles in the foraging behaviour of caterpillars as well their predators such as birds. Some foraging bird species consistently changed their foraging pattern from favouring upper leaf surfaces in beech which housed 15 % of the beech lepidopteran caterpillars, to favour lower leaf surfaces in sugar maple which housed 62 % of the maple lepidopteran caterpillars (Holmes and Schulz, 1988). *L. camilla* caterpillars may have adopted a foraging pattern on its foodplant leaf surface in order to avoid recognition by birds. Pollard (1979) attributed bird predation of *L. camilla* caterpillars as a major factor in the population dynamics of the species.

Plant architecture and density influence colonisation by predators (Letourneau, 1990) and plant characteristics affect the searching efficiency of various insect predators. For example, trichomes impede the progress of predators (Scopes, 1969) and smooth surfaces increase the tendency of predators falling off the plant (Carter *et al.*, 1984). If trichomes impede predators then ovipositing female Lepidoptera may locate their eggs on a leaf surface according to its trichome distribution. In this part of the study the exact location of the egg on the leaf surface will be determined and the trichome distribution of the leaf surface will be examined in Chapter Six.

The orientation of the egg leaf was measured as an attempt to indicate the possible use of the sun's sky location as a means of homing onto or selecting an appropriate leaf in the *L. periclymenum* drape for oviposition. Initial thoughts indicate a random approach by ovipositing female *L. camilla* and *H. fuciformis* towards their selected egg leaf. However, if oviposition occurs in a regular time slot (normally in the time period 10.00 - 13.00 for both species at normal June - July temperatures), then the female adults may be using the sun's location in the sky as a homing beacon in locating its foodplant.

5.1.3 Shade and temperature

The first aim of this part of the study is to confirm the preference of oviposition sites of *L. camilla* and *H. fuciformis* according to shade or diffused sunlight using a more accurate method of measurement (hemispherical photography) than simply a visual impression of habitat light availability between plantation, ride, and clearing sites. Since light and temperature are often closely related, one or the other may normally suffice. However, several studies have shown that photoperiod (length of daylight), intensity of light, wavelength of light and temperature can all trigger separate mechanisms in plant biology which, in turn, may affect nutritional quality and caterpillar growth rate (Stamp and Bowers, 1990a and 1990b). Consequently, oviposition site temperature was also recorded in this study.

5.2 Methods and materials

5.2.1 Habitat preference of oviposition sites.

These details are given in the methods and materials section of Chapter Three (Section 3.2).

5.2.2 Food plant architecture of oviposition sites.

The field methodology used for searching for lepidopteran caterpillars and eggs has already been described in Chapter Three. For both species, egg and caterpillars were easily identified in the field (Chapter Four). In addition, this visual evidence of recognition was further supported by characteristic feeding damage patterns on foodplant leaves (Chapter Four). Field work was carried out in the period 1992-94 when the following parameters were measured and recorded for *L. camilla* and *H. fuciformis* oviposition sites.

- Habitat type: ride, clearing or plantation.
- Spring and summer host foliage.
- Species of tree supporting *L. periclymenum.*
- Height of eggs above ground level.
- Position of eggs on leaf (distance of egg from leaf tip/midrib/margin, upper/lower surface).
- Position of egg leaf along shoot (measured from base).
- Dimensions of egg leaf.
- Number of eggs on each leaf.
- Number of leaves holding eggs in each rosette of *L. periclymenum* on drape.
- Number of egg rosettes per drape of *L. periclymenum.*
- Leaf density of egg leaf (number of leaves touching a 5 cm diameter sphere centred on egg).
- Structure of egg leaf shoot (short shoot rosette growth or long shoot radial growth).
- Horizontal distance of egg leaf from main vertical tree support of *L. periclymenum.*
- Number of leaf pairs on egg shoot and location of egg leaf pair.
- Orientation of egg leaf shoot and egg leaf tip (compass bearing).

All parameters were measured and recorded in the field without the need of specialist equipment other than a magnifying lens, rulers, tapes, compass and recording material. The initial aim was to find at least 50 and preferably 100 replications per species for each oviposition character.

5.2.3 Shade factor of oviposition site (diffused light site factor; Table 5.7, Figures 5.2-3).

The diffused light site factor was measured by taking hemispherical photographs using an 180° wide angle or fish-eye lens. The lens was attached to a Nikkon 35 mm camera and placed horizontally (using spirit levels) on the ground facing up to the sky. The camera was rested on a sand-bag for careful levelling and the shutter released using a cable as low shutter speeds are often necessary inside plantations. The delay shutter mechanism was used to allow for the retreat of the field worker so that he would not be captured in the photograph.

The black and white print was analysed using an IBAS (integrated visual analysis system) machine (Barrie *et al.*, 1990). Analysis of the photograph involves calculating the relative amounts of white area (equivalent to sky space) and black area (equivalent to shaded space). Grey areas of the photograph are designated either black or white according to degree of greyness and this difficult part of the calculation is adequately processed by the computer analysis system. A total of 29 *H. fuciformis* and 33 *L. camilla* oviposition sites were randomly chosen for photography. All sites were photographed during the oviposition periods for both *L. camilla* and *H. fuciformis* (July and June, respectively) after locating *L. periclymenum* drapes containing eggs.

5.2.4. Oviposition site temperature.

Site temperatures were measured in two ways. Maximum and minimum shade daily temperatures were recorded throughout the year at a site on the boundary of Bentley Wood. In addition, oviposition site mean temperatures were calculated from measuring the change of optical activity of an acidified sucrose solution over a known period of time. This method was employed to determine seasonal variation of habitat temperatures during the period August '94 to June '95.

An acidified sucrose solution undergoes hydrolysis or inversion which changes the optical rotatory power of the solution. For a given concentration of sucrose and hydrochloric acid the rate at which this change in rotation takes place is dependent on temperature. The experiment was calibrated by measuring the optical rotation change at fixed temperatures in the laboratory before use in the field. The measured change in rotation of plane polarised light indicated a mean temperature sustained in the field for a given period of time. During the laboratory calibration experiments, calculated temperatures were producing results with a degree of accuracy of ± 1° C. Further details of procedure are given in the Appendix.

In this study replication was achieved by attaching 10 bottled samples of the acidified sucrose solution to the *L. periclymenum* drapes of an oviposition site as close to the actual egg leaf as possible. The samples were left at their locations for periods ranging from 3-7 days. The optical rotation of the

solutions was measured using a portable Griffin polarimeter immediately upon acidification of the sucrose prior to placement at their locations and at the end of experimental period. The mean temperature was calculated from first order reaction kinetics. For seasonal comparison, experimentation was carried out on 4 occasions during the year: mid-summer (August), autumn (October), mid-winter (February) and June (oviposition period). The same locations were used for each period.

5.3 Results

5.3.1 Habitat preference of oviposition sites (Table 5.1; Figure 5.1).

Throughout four years of fieldwork *H. fuciformis* was never found to oviposit in plantations or other very shaded areas of *L. periclymenum* foliage. In contrast, *L. camilla* was never found to oviposit in open sunny clearings containing *L. periclymenum.* In ride systems *H. fuciformis* normally oviposited on south facing marginal host foliage while *L. camilla* only oviposited on north facing rides. The ride side locations for *H. fuciformis* were always associated with the availability of sun for most of the day. Typical ride side locations were box junctions, wide rides and the south facing sides of west-east orientated rides.

The oviposition frequency data illustrated in Table 5.1 shows that *L. camilla* preferred to oviposit in plantations whereas *H. fuciformis* preferred to oviposit in clearings. In addition, there was also a highly statistically significant association between *L. camilla* and *H. fuciformis* and their oviposition frequencies on spring and summer foliage ($\chi^2 = 7.1$, df = 1, $P < 0.01$). Both Lepidoptera preferred to oviposit on *L. periclymenum* rosette foliage which had started growing in spring (in the case of *H. fuciformis*) or winter (in the case of *L. camilla*) rather than the foliage which had started growing in early summer. Both types of *L. periclymenum* growth were present at the time of oviposition although the summer growth was limited in quantity.

All oviposition sites were located on aerial growing drapes of *L. periclymenum.* Ground growing *L. periclymenum* foliage (< 0.3 m high), although inspected continuously throughout the respective oviposition periods in the appropriate habitats, was never used by ovipositing females of both species. Indeed, adults were never observed foraging on ground foliage. Both aerial and ground *L. periclymenum* foliage existed in abundance in the southern areas of Bentley Wood.

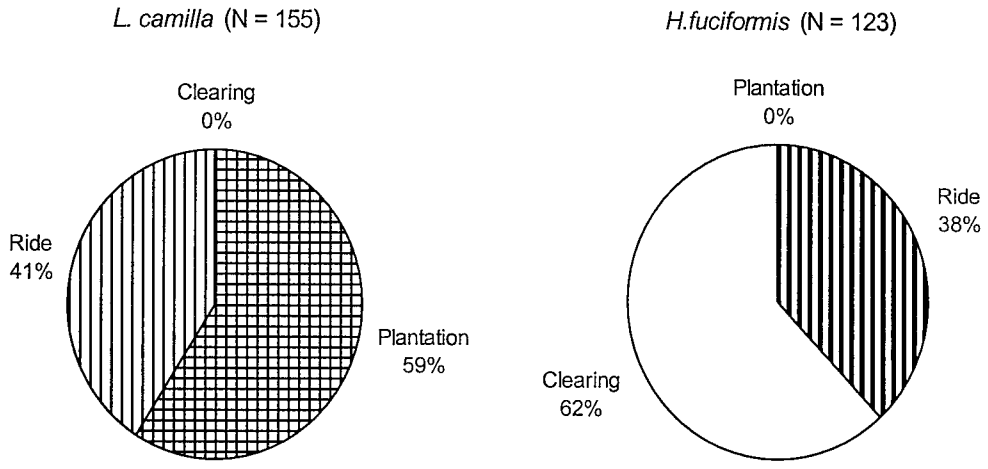
Table 5.1 Habitat oviposition preference of *L. camilla* and *H. fuciformis* (egg numbers). Oviposition foliage for both species was aerial growth (> 1 m height above ground level).

	L. camilla '93	*L. camilla* '94	*H. fuciformis* '93	*H. fuciformis* '94
Plantation	47	44	0	0
Ride	55	9	31	16
Clearing	0	0	60	16
Shaded site [a]	102	53	31	16
Open site [b]	0	0	60	32
Spring growth [c]	77	45	87	23
Summer growth [d]	25	8	4	9

a: shaded site = plantation + ride sites.
b: open siteas = clearing sites.
c: spring growth is *L. periclymenum* rosettes (short shoots, < 0.3 m, dense foliage, slow growth in winter-spring period).
d: summer growth is *L. periclymenum* long shoots (> 1m, rapid growth in May-June).

Plate 5.1

Fig. 5.1 Habitat oviposition preference of *L. camilla* and *H. fuciformis* (% frequency 1993-94).



5.3.2 Oviposition preference for tree species supporting *L. periclymenum* drapes (Table 5.2).

Table 5.2 shows the number of *L. periclymenum* drapes supported by various tree species associated with oviposition sites of *L. camilla* and *H. fuciformis,* and comparison is made with other Lepidoptera foraging on *L. periclymenum*. Oak and Norway spruce were the main plantation stock timber in the southern half of Bentley Wood. The other tree species were mainly scrub species (hazel and birch) which have naturally regenerated and were normally in their juvenile stage. Ovipositing *L. camilla* females favoured oak and silver birch *L. periclymenum* drapes whereas *H. fuciformis* females preferred oak and Norway spruce drapes. The majority of other Lepidoptera (micro-and macro-moths) favoured *L. periclymenum* drapes growing on oak.

Previous page.

Plate 5.1a Typical *L. camilla* oviposition site in open plantation.
Weak spindly *L. periclymenum* shaded drapes (right hand side) are used for oviposition. p. 5-7

Plate 5.1b Typical *H. fuciformis* oviposition site in open clearing.
Vigorous bushy *L. periclymenum* drapes with an abundance of flowers in sunny clearings and rides are used for oviposition. p. 5-7

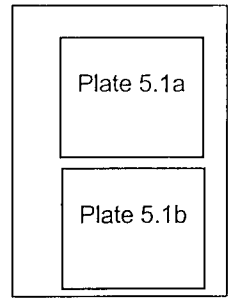


Table 5.2 Comparison of oviposition sites of *L. camilla* and *H. fuciformis* with other Lepidoptera: supporting tree species of *L. periclymenum* oviposition drapes (frequencies).

	Oak	N. spruce	Birch	Hazel	Sallow	Others
L. camilla	31	17	30	9	5	10
H. fuciformis	37	28	5	0	4	5
Other Lepidoptera	60	22	16	28	2	3

Association

L. camilla vs. *H. fuciformis* $\chi^2 = 29.4$, df = 5, $p < 0.01$.			positive / negative			
L. camilla vs. Other Lepidoptera $\chi^2 = 40.8$, df = 5, $p < 0.01$.	negative / positive			negative / positive		
H. fuciformis vs. Other Lepidoptera $\chi^2 = 58.7$, df = 5, $p < 0.01$.	negative / positive		positive	negative / positive		

Table 5.2 also shows the positive and negative associations between tree species and oviposition sites. There is a statistically highly significant association between certain tree species and *L. camilla* and *H. fuciformis* ($p < 0.01$). *L. camilla* preferred ovipositing on *L. periclymenum* drapes supported by silver birch in contrast with *H. fuciformis* which disfavoured this drape support.

There are also highly significant associations when *H. fuciformis* and *L. camilla* are separately compared with the other group of Lepidoptera ($p < 0.01$). The Other Lepidoptera group of species preferred to oviposit on drapes supported by oak, silver birch and hazel relative to *H. fuciformis.* A similar preference for oviposition sites was shown when *L. camilla* was compared with the Other Lepidoptera group.

5.3.3 Food plant architecture of oviposition sites (Tables 5.3-6).

5.3.3.1 Leaf density (Table 5.3)

Both *L. camilla* and *H. fuciformis* females oviposited on *L. periclymenum* of similar leaf density ($p > 0.05$). That is between 5 and 6 leaves were within a sphere of 5 cm radius centred on the egg leaf, for both species. This relatively dense group of leaves is referred to as a rosette in this study and the first leaves of these rosettes appear during the months of November and December in shade growth in contrast to sun growth rosettes whose first leaves appear in April (Plates 5.2a-c). This type of foliage is referred to as spring growth (Table 5.1) in contrast to summer growth which starts to shoot in the May-June period. Summer growth is rapid growth, non-rosette type, producing long shoots of over 1 m length and not favoured by ovipositing females of both *L. camilla* and *H. fuciformis.*

5.3.3.2 Shoot length (Table 5.3)

The *L. periclymenum* shoot containing the egg leaf for *H. fuciformis* was twice as long as the shoot for *L. camilla* ($p < 0.01$).

5.3.3.3 Leaf pairs on egg shoot (Table 5.3)

The mean number of leaf pairs on the egg shoot for *H. fuciformis* was greater than the *L. camilla* number of leaf pairs ($p < 0.01$).

5.3.3.4 Position of the leaf containing eggs on the *L. periclymenum* shoot (Table 5.3).

L. camilla females preferred to oviposit mainly on the second pair of leaves counted from the stem whereas *H. fuciformis* females preferred the second or third leaf pair ($p < 0.01$).

5.3.3.5 Number of eggs per egg leaf (Table 5.4).

Both *L. camilla* and *H. fuciformis* oviposited singly ($p > 0.05$) and the rare occasions when two eggs were found on one leaf were due to different females as emergence usually occurred at different times. Lederer (1960) found a similar egg distribution with mainly 1, rarely 2, and exceptionally 3 eggs per leaf.

Table 5.3 Oviposition site architecture of *L. camilla* and *H. fuciformis* (I).

	L. camilla	*H. fuciformis*	t	df	p
Leaf density [a]					
Mean	5.1	5.4			
Standard error	0.1	0.2			
Sample size	258	142			
t test			1.25	239	NS at 0.05
Shoot length [b]					
Mean (mm)	47.2	89.5			
Standard error	5.2	9.8			
Sample size	53	32			
t test			3.82	49	< 0.01
Leaf pairs on shoot [c]					
Mean	3.3	4.9			
Standard error	0.2	0.2			
Sample size	53	32			
t test			6.11	65	< 0.01
Egg leaf location [d]					
Mean	2.3	3.6			
Standard error	0.1	0.2			
Sample size	53	32			
t test			5.75	69	< 0.01

a: number of leaves within a sphere of 5 cm radius centred on the egg leaf.
b: length of shoot (mm) bearing the egg leaf.
c: number of leaf pairs on the egg leaf shoot.
d: location of egg leaf pair numbered from base of egg shoot.
t = t test (assuming unequal variances) comparing sample means of *L. camilla* and *H. fuciformis.*
df = degrees of freedom.
p = significance level of t-test.

5.3.3.6 Number of egg leaves per rosette (Table 5.4 and Plate 5.2b).

Both *L. camilla* and *H. fuciformis* females used one leaf only per rosette for oviposition ($p > 0.05$).

5.3.3.7 Number of egg rosettes per drape (Table 5.4).

Both *L. camilla* and *H. fuciformis* females used one or two rosette per *L. periclymenum* drape for oviposition ($p > 0.05$).

5.3.3.8 Height of egg leaf (Table 5.5)

The mean height of the egg leaf above ground level for both *L. camilla* and *H. fuciformis* was 1.4-1.6 m ($p > 0.05$). *L. periclymenum* drapes normally reached 5 m above ground level.

5.3.3.9 Overhang: distance of egg leaf in drape from supporting tree trunk (Table 5.5).

The mean overhang distance (horizontal distance of egg leaf from main tree trunk supporting *L. periclymenum* drapes) for both *L. camilla* and *H. fuciformis* was found to be in the range 0.5 - 0.6 m ($p > 0.05$). The available overhang distance for *L. periclymenum* foliage was normally in the range 0 - 2 m but the outer range varied considerably according to the density of adjacent growing vegetation.

5.3.3.10 Orientation of the egg leaf shoot (Table 5.5).

Both *L. camilla* and *H. fuciformis* females oviposited on *L. periclymenum* leaves on shoots which pointed in the compass bearing range 170 - 190 ° ($p > 0.05$). The available orientation for *L. periclymenum* foliage was normally in the range 0 - 360 °.

5.3.3.11 Orientation of the egg leaf tip (Table 5.5).

Both *L. camilla* and *H. fuciformis* females oviposited on *L. periclymenum* leaves which pointed in the compass bearing range 190 - 200 ° ($p > 0.05$). The available orientation for *L. periclymenum* foliage was normally in the range 0 - 360 °.

5.3.3.12 Egg leaf dimensions (Table 5.6)

Both *L. camilla* and *H. fuciformis* females oviposited on *L. periclymenum* leaves which were of similar length ($p > 0.05$) but slightly different in width ($p < 0.05$). During the period of oviposition for both Lepidoptera, spring shoot growth contained leaves in the range 6-8 cm long and 3-4 cm wide for the

larger leaves. There were, also, small leaves available, 2-3 cm long and 1-2 cm wide (usually the first basal pair of rosettes).

5.3.3.13 Egg location on egg leaf (Table 5.6).

The location of the egg on the *L. periclymenum* leaf was completely different between *L. camilla* and *H. fuciformis*. *H. fuciformis* oviposited on the abaxial (underside) leaf laminae (100 %) in contrast to *L. camilla* which oviposited on the adaxial (upper side) leaf laminae (100 %) within 2 mm of the leaf margin without exception.

Table 5.4 Oviposition site architecture of *L. camilla* and *H. fuciformis* (II).

	L. camilla	*H. fuciformis*	t	df	p
Number of eggs per egg leaf.					
Mean	1.06	1.07			
Standard error	0.03	0.03			
Sample size	96	85			
t test			0.20	179	NS at 0.05
Number of egg leaves per rosette.					
Mean	1.12	1.16			
Standard error	0.04	0.05			
Sample size	86	73			
t test			0.78	144	NS at 0.05
Number of egg rosettes per drape.					
Mean	1.25	1.66			
Standard error	0.14	0.24			
Sample size	69	44			
t test			1.50	72	NS at 0.05

t = t test (assuming unequal variances) comparing sample means of *L. camilla* and *H. fuciformis*.
df = degrees of freedom.
p = significance level of t-test.

Table 5.5 Oviposition site architecture of *L. camilla* and *H. fuciformis* (III).

	L. camilla	*H. fuciformis*	t	df	p
Height [a]					
Mean	1.49	1.54			
Standard error	0.03	0.03			
Sample size	102	91			
t test			0.97	189	NS at 0.05
Overhang [b]					
Mean	0.47	0.55			
Standard error	0.03	0.03			
Sample size	102	91			
t test			1.90	189	< 0.06
Orientation (A) [c]					
Mean	186	170			
Standard error	10	11			
Sample size	102	91			
t test			1.159	190	NS at 0.05
Orientation (B) [d]					
Mean	190	194			
Standard error	9	9			
Sample size	102	91			
t test			0.48	191	NS at 0.05

a: height (m) of egg leaf above ground level.
b: horzontal distance (m) of egg leaf from tree trunk supporting *L. periclymenum* drape.
c: compass bearing (degrees) of egg leaf shoot.
d: compass bearing (degrees) of egg leaf tip.
t = t test (assuming unequal variances) comparing sample means of *L. camilla* and *H. fuciformis.*
df = degrees of freedom.
p = significance level of t-test.

Table 5.6 Oviposition site architecture of *L. camilla* and *H. fuciformis* (IV).

	L. camilla	*H. fuciformis*	t	df	p
Leaf length [a]					
Mean	4.96	4.74			
Standard error	0.11	0.12			
Sample size	102	91			
t test			1.35	184	NS at 0.05
Leaf width [b]					
Mean	2.24	2.07			
Standard error	0.06	0.05			
Sample size	102	91			
t test			2.10	191	< 0.05
Egg location (A) [c]					
Mean	0.14	0.40			
Standard error	0.01	0.03			
Sample size	102	91			
t test			18.57	145	< 0.01
Egg location (B) [d]					
Mean	1.82	1.82			
Standard error	0.08	0.08			
Sample size	102	91			
t test			0.03	190	NS at 0.05

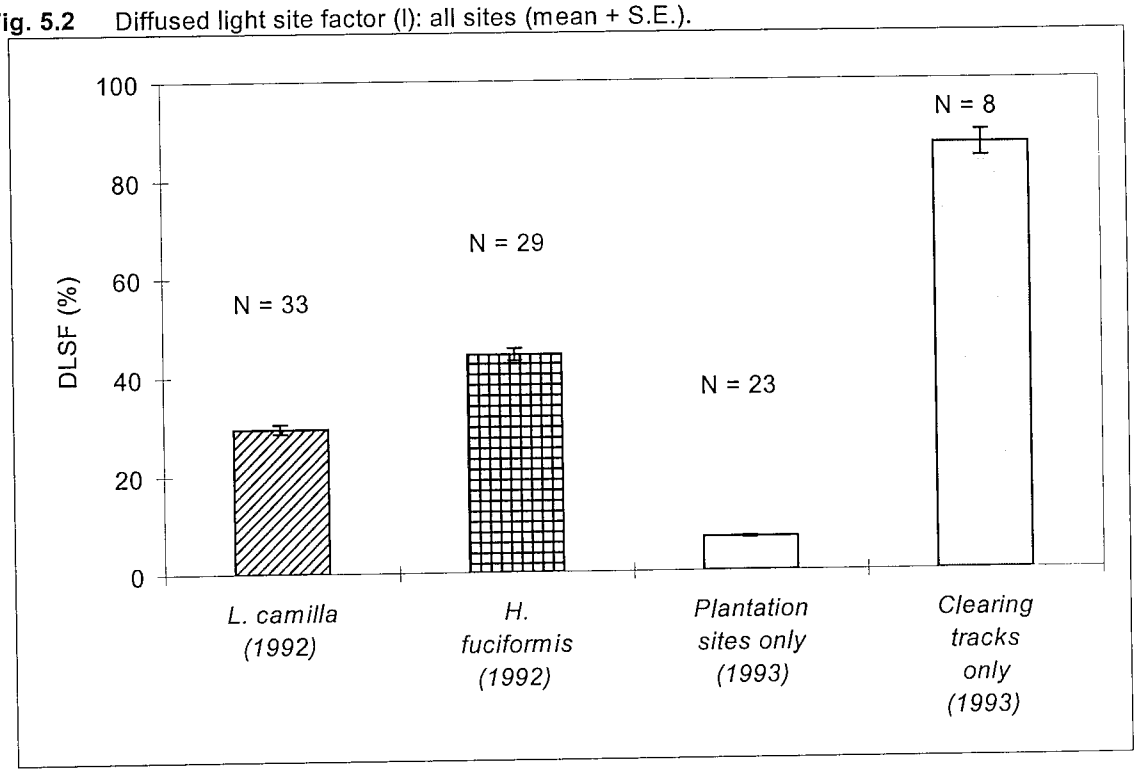
a: length (cm) of egg leaf including petiole.
b: width (cm) of egg leaf.
c: egg distance (cm) from leaf margin: adaxial lamina for *L. camilla*, abaxial lamina for *H. fuciformis*.
d: egg distance (cm) from leaf tip.
t = t test (assuming unequal variance) comparing sample means of *L. camilla* and *H. fuciformis*.
df = degrees of freedom.
p = significance level of t-test.

Plate 5.2

5.3.4 Shade factor of oviposition sites (Table 5.7; Figures 5.2-3).

H. fuciformis females preferred to oviposit on *L. periclymenum* growing in relatively sunny areas in contrast to *L. camilla* females which preferred to oviposit on shaded *L. periclymenum* foliage ($p < 0.01$).

Fig. 5.2 Diffused light site factor (l): all sites (mean + S.E.).



5.3.5 Temperature of oviposition sites. (Table 5.8; Figure 5.4).

H. fuciformis oviposition sites produced higher temperatures than *L. camilla* oviposition sites during every recording period ($p < 0.01$).

Previous page.

Plate 5.2a Typical *H. fuciformis* oviposition *L. periclymenum* drape showing 1st and 2nd caterpillar instar feeding damage in dense rosette. p. 5-16

Plate 5.2b Typical *L. camilla* oviposition *L. periclymenum* rosette containing few leaves. p. 5-16

Plate 5.2c Typical *L. camilla* oviposition *L. periclymenum* drape with weak spindly growth and few rosettes. p. 5-16

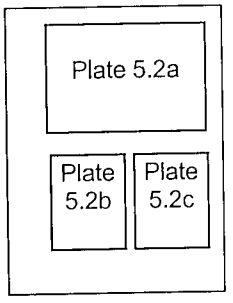


Table 5.7 Shade factor of *L. camilla* and *H. fuciformis* oviposition sites (DLSF).

	H. fuciformis	*L. camilla*
Mean DLSF (%)	44.3	29.5
Standard Error	2	1.7
Range	39.2	40.1
Minimum value	26.3	11.8
Maximum value	65.5	51.9
Number of sites	29	33

DLSF (Diffused light site factor)
DLSF is the percentage of hemispherical diffused sky-light penetrating foliage canopy directly above oviposition site.

DLSF mean difference

$t = 5.7$; d. of f. = 57; $p < 0.01$

Fig. 5.3 Diffused light site factor (DLSF) of oviposition sites (II).

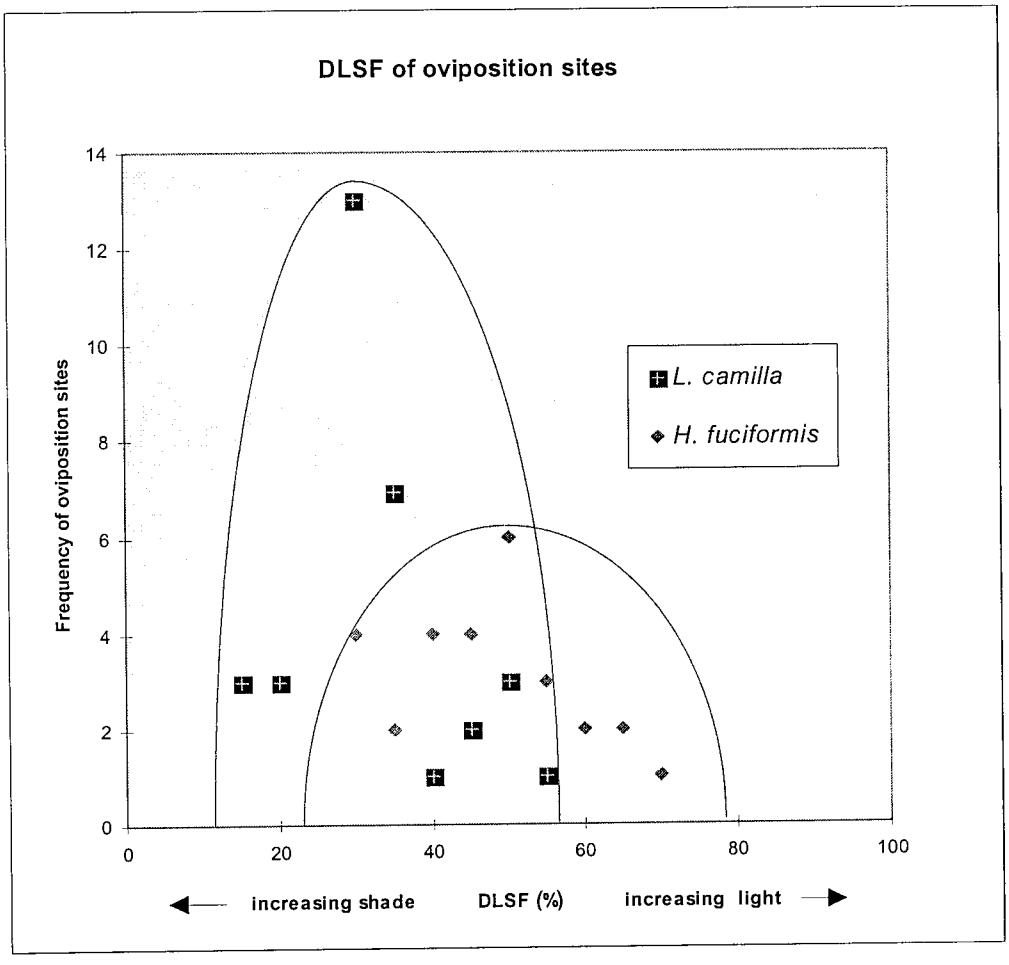
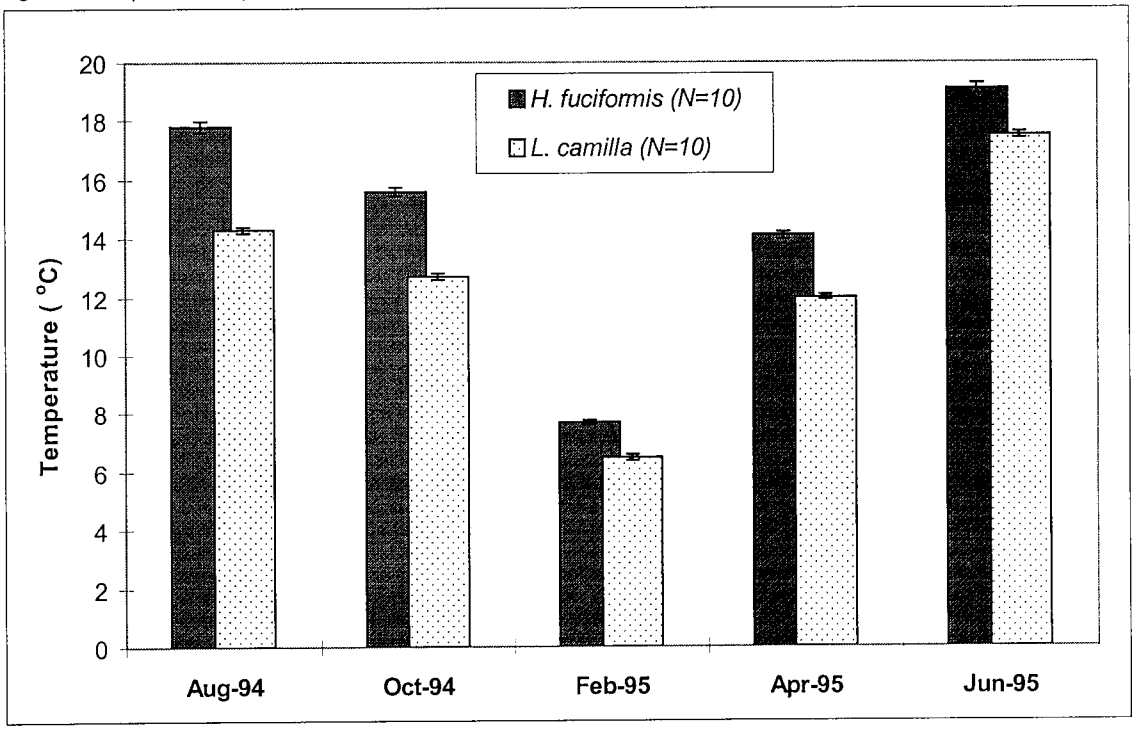


Table 5.8 Seasonal temperature of oviposition sites (mean + S.E., °C) using the sucrose method in comparison with maximum-minimum temperatures (thermometers were located in open shade). Recording periods varied between 3-7 days.

	Aug '94	Oct '94	Feb '95	Apr '95	Jun '95
Sucrose [a]					
L. camilla (N=10)	14.3 ± 0.2	12.7 ± 0.2	6.5 ± 0.1	12.0 ± 0.1	17.5 ± 0.1
H. fuciformis (N=10)	17.8 ± 0.2	15.6 ± 0.2	7.65 ± 0.1	14.1 ± 0.1	19.1 ± 0.2
Max. - min. [b]					
Max. range	26.0 -19.0	19.0 - 13.0	12.0 - 9.0	22.0 - 10.0	29.0 - 25.0
Min. range	12.0 - 7.0	11.0 - 1.0	6.0 - - 4.0	6.0 - 3.0	12.0 - 9.0

a: hydrolysis of sucrose and recording change in optical rotation.
b: maximum-minimum mercury thermometer.
The difference in temperature (sucrose method) between oviposition sites was statistically significant ($p<0.01$) for all 5 recording periods.

Fig. 5.4 Temperatures (mean ± S.E.) of oviposition sites (sucrose hydrolysis method).



5.4 Discussion

5.4.1 Habitat preference of oviposition sites (shade and temperature).

The results (Figure 5.1) show a clear difference in preference of oviposition sites between ovipositing females of *L. camilla* and *H. fuciformis.* The quantitative results obtained from hemispherical photography confirm the earlier visually estimated results of habitat shade. This distinction has been characterised in terms of shade, temperature and habitat. *L. camilla* females preferred to oviposit on shaded host foliage which is mainly found in plantations and shaded parts of rides. *H. fuciformis* females preferred to oviposit on host foliage which grows in the relatively warmer and sunnier habitats of Bentley Wood. The fact that *H. fuciformis* was never seen foraging in plantations and *L. camilla* was never seen foraging in central clearing areas throughout three years of field work helps to compound the clear discrimination of conspecific foodplants by the two Lepidoptera.

There are no other native examples of specialist lepidopteran species coexisting in the same locality which oviposit on the same foodplant but in totally different microclimates. Indeed, there is no other native butterfly which oviposits in a shadier habitat than *L. camilla* (Thomas, 1986). The only British butterfly to resemble *L. camilla* for ovipositing on host growing in shady vegetation is *Pararge aegeria* (Speckled Wood) which is a multi-voltine graminivorous specialist. In spring and early autumn this species oviposits most eggs on sunlit plants growing in open sites but in midsummer eggs were deposited on shaded plants growing in closed woodland. Temperature is considered to be a major factor because higher temperatures improved the chances of first instar survival due to rapid growth rate with less chance of predation (Shreeve, 1984). Lederer (1960), in his 1940-55 German study of *L. camilla,* also found females preferring to oviposit in shaded woodland and "rarely" in sunny clearings.

The temperature factor may be a reason why *H. fuciformis* prefers to forage in warmer habitats since its caterpillar passes through all instars in 4-5 weeks in the field and high temperatures would increase caterpillar growth rate. Since *L. camilla* caterpillars oviposition sites in plantations were found to be cooler than *H. fuciformis* oviposition sites during each recording period (Figure 5.4), the construction of a hibernaculum by *L. camilla* may be an attempt to reduce the adverse effects of a low temperature winter environment.

5.4.2 Preference for tree species supporting *L. periclymenum* drapes.

The results of this section of the habitat survey reflect the catholic choice of the main supporting vegetation the host species, *L. periclymenum*. Although the association statistics show positive relationships, they may be simply reflecting the presence of the most common trees in the areas of *L. camilla* and *H. fuciformis* oviposition drapes.

L. camilla, relative to *H. fuciformis,* may have favoured host drapes supported by birch simply because birch was more commonly found as a tree in plantations than clearings and, equally important, its relatively low foliage density (especially in weak plantation growth) allows sufficient penetration of light to sustain weak plantation *L. periclymenum* growth.

The positive associations shown by the Other Group of Lepidoptera (the remainder of the guild other than *L. camilla* and *H. fuciformis*), which showed a relative oviposition preference for oak, birch and hazel foodplant supports, may also simply reflect the relative abundance of drape support trees or they may reflect a clever lepidopteran strategy where bivoltine species oviposit on the early growth of *L. periclymenum* for the first brood and then use the support tree as the second brood foodplant. Several moth species belonging to the guild found foraging on *L. periclymenum*, which are regarded as polyphagous, are known to feed on oak, birch and hazel and were occasionally found doing so in this study, although only in small numbers since examination of these foodplants was not a study priority.

Gales in southern England in 1987 and 1991 extended the amount of sunny clearings suitable for *H. fuciformis* in the south western area of Bentley Wood. Here, large sections of oak-conifer plantations suffered considerable damage with areas of total clearance interspersed with broken tree stumps and isolated groups of oak containing few lower branches due to their previous growth inside the middle of plantations. The oaks and the broken stumps quickly attracted *L. periclymenum* drapes which were soon colonised by *H. fuciformis* and caused, probably, the highest abundance of this insect since the great clear-fell of Bentley Wood in 1950-53. However, by 1995, there had been rapid growth of foliage on the lower sections of the trunks causing *H. fuciformis* to desert many of their original sites, thus illustrating the transient nature of habitat suitability.

5.4.3 Food plant architecture of oviposition site.

5.4.3.1 Introduction.

Firstly, a group comparison is made between *L. camilla* and *H. fuciformis* oviposition site preference of statistically similar and statistically different architectural characteristics.

Similar architectural characteristics.

- Leaf density.
- Number of eggs per egg leaf.
- Number of egg leaves per rosette.
- Number of egg rosettes per drape.
- Height of egg leaf above ground level.

- Overhang distance of egg leaf from main support.
- Orientation of egg leaf and egg leaf shoot.
- Egg leaf length.

Different architectural characteristics.

- Shoot length.
- Leaf pairs on shoot.
- Egg leaf location along shoot.
- Leaf width
- Egg location on leaf.

5.4.3.2 Leaf density (similar), shoot length (different) and number of leaf pairs on egg shoot (different).

Variation in foliage density of oviposition foodplant may be a direct result of different climatic factors associated with shade and temperature. However, ovipositing lepidopteran females may choose the relatively denser foliage sites for oviposition since they may provide better protection against avian and parasitoid predation. Dense foliage allows a minimum of movement which reduces the possibility of detection. At the time of oviposition there was a considerable range of leaf density of *L. periclymenum* available but both *H. fuciformis* and *L. camilla* chose the denser rosettes. *H. fuciformis* females oviposited on longer shoots containing more leaf pairs probably because *L. periclymenum* was more vigorous in growth than shade growth.

5.4.3.3 Egg leaf location (different), egg leaf width (different), egg leaf length (similar), egg location on leaf (different) and height of egg leaf (similar).

H. fuciformis females normally chose the 3rd or 4th leaf pair from a shoot containing 5 leaf pairs while *L. camilla* females chose the 2nd or 3rd leaf pair from a shoot containing 3 leaf pairs. Both Lepidoptera chose leaves for oviposition of similar dimensions even though smaller and larger leaves were available at each oviposition site. *H. fuciformis* females were observed having not a little difficulty in the act of oviposition on the chosen leaf. Indeed, they oviposit with wings in motion, rarely alighting on the leaf surface. In contrast, female *L. camilla* appeared to take careful probing with their ovipositor after alighting on the leaf surface. Ground growing *L. periclymenum* was observed to grow much smaller and lower density leaf foliage than aerial drapes and female *H. fuciformis,* which are relatively heavy moths, would have great difficulty in ovipositing on such a small leaf surface which may explain their reluctance to oviposit on this type of *L. periclymenum* foliage.

Leaf quality in terms of nutrients, toughness and trichomes may vary along a shoot and ovipositing females may be able to detect variation in these factors. However, having observed the difficulty which *H. fuciformis* females experience in gripping their chosen egg leaf, it is understandable why they do not choose the 1st and 2nd leaf pairs which are normally much smaller than the 3rd and 4th leaf pairs. In addition, they would not be able to bend their relatively thick abdomen sufficiently to make ovipositor contact with the abaxial leaf surface. In contrast, *L. camilla* oviposit on the adaxial leaf surface and like most butterflies they have a more flexible abdomen which they use to probe and carefully select the marginal leaf zone.

The two Lepidoptera used a different approach when selecting their respective egg leaves. *H. fuciformis* females fly directly to their chosen leaf and rarely reject it in favour of another. *L. camilla* females usually inspect several leaves, remaining for a few seconds on each leaf, starting at the lower plant area and working upwards before final selection.

Oviposition was carried out at about 1.5 m above ground level with little variation between *L. camilla* and *H. fuciformis* and all the other species of Lepidoptera feeding on *L. periclymenum.* The height range of *L. periclymenum* foliage available was normally in the range 1 - 5 m above ground level. On several occasions, *L. camilla* and *H. fuciformis* females were observed foraging at heights above 3m going through the motions of ovipositing on suitable leaves. Subsequent examination of these leaves by climbing the tree immediately after the adult female had flown away did not reveal any eggs. Is it possible that these females were about to oviposit but detected some undesirable element on the leaf? If so, was this undesirable element associated with the chemical nature of the leaf surface? A limited number of tall *L. periclymenum* drapes were pulled down to head height and examination of these drapes revealed little, if any, feeding damage by any insect in the higher regions of the plant. It is possible that upper regions of *L. periclymenum* drapes acquire some degree of unpalatability due to the effect of direct sunlight more evident in the upper regions of the foodplant.

Grossmueller and Lederhouse (1985) examined the oviposition pattern of *Papilio glaucus* and found over 97 % of eggs were laid below 3 m on host tree species. Suggested explanations included higher caterpillar body temperatures at lower host levels due to reduced wind speed, resulting in increased caterpillar growth rate. Also, lower oviposition sites were mainly found on host saplings which might have higher nutrient content.

Pollard and Cooke (1994) concluded that browsing by Muntjac deer, *Muntiacus reevesi*, had removed a substantial proportion of potential egg-sites of *L. camilla* in a Cambridgeshire wood. Foodplant areas close to ground level (< 0.5 m) may suffer from other foraging insects as well as mammals which force Lepidoptera into foraging in the central foodplant zones of *L. periclymenum.*

5.4.3.4 Egg density on host: number of eggs per egg leaf (similar), number of egg leaves per rosette (similar) and number of egg rosettes per drape (similar).

Both *L. camilla* and *H. fuciformis* normally oviposited one egg per leaf per rosette. Between 1 and 2 rosettes per drape were found with eggs. In the case of *L. camilla,* drapes with more than one egg had been oviposited by different females (different emergence dates) but the same *H. fuciformis* female occasionally oviposited two eggs on the same drape or different females may have oviposited one egg within a short time of each other. Lederer's (1960) 1940-55 German study of *L. camilla* revealed far more variability in egg location on leaves especially in "isolated populations". His conclusion was that this variability was "due to genotypical, and not phenotypical factors, as continuous inbreeding may occur in a small, isolated population of *camilla*".

Deviation from normal oviposition density on *L. periclymenum* drapes was scarce but one notable exception was discovered in the case of *L. camilla.* in the northern part of Bentley Wood where *L. periclymenum* drapes were extremely scarce in the beech-conifer plantations and adjacent rides. On this occasion a single *L. periclymenum* drape supported by a mature broad-leaved sallow, *Salix caprea*, was found to contain 9 egg rosettes with a total of 12 eggs. Only 3 caterpillars survived to post-diapause period and only one caterpillar survived to pupation stage. This situation was repeated in the following two years but with reduced egg numbers and no pupation. Reasons for this high mortality are unknown but most caterpillars succumbed during the diapause period as several hibernicula were found empty and other caterpillars were found dead in their hibernicula. One possibility is that the 3rd instar caterpillars, prior to diapause, did not accumulate sufficient fats due to lack of available food to survive during the diapause period. Unlike post-diapause caterpillars, pre-diapause *L. camilla* caterpillars do not normally leave their egg foodplant, even in times of food shortage as illustrated by this example.

Lederer (1960), in his German study of *L. camilla,* found a more variable egg location with 62 % and 23 % of eggs located on the abaxial (underside) leaf surface in 1942 and 1943, respectively. In addition, 30 % of females of an "isolated" population of *L. camilla* deposited their eggs on the tips of leaves compared with 9 % in another population with the majority using the leaf margin. In the present study 100 % of females located their eggs on the leaf margin within 2 mm of the leaf edge.

5.4.3.5 Overhang of egg leaf from main tree support (similar) and orientation of egg leaf shoot and egg leaf (similar).

Measuring orientation of egg leaf and overhang leaf distance was an attempt to detect any specific line of approach in flight towards the potential egg leaf using the sun as a homing beacon. The overhang distances for egg leaves for both *L. camilla* and *H. fuciformis* egg leaves were found to be in the horizontal range 0.4-0.6 m from the main tree support. The available overhang distance for *L. periclymenum* drape foliage was normally in the range 0-2 m. Thus, both *L. camilla* and *H. fuciformis*

females normally preferred to oviposit on the outer canopy foliage of *L. periclymenum* drapes. Insect predators frequently used the main tree trunk supports as pathways from ground to aerial foliage so oviposition on outer canopy leaves may simply be a method of avoiding predation.

The orientation of both *L. camilla* and *H. fuciformis* egg shoots and egg leaves was found to point almost due south in the range 170-200 ° while the available orientation of *L. periclymenum* shoots and leaf tips was normally spread through the range 0 - 360 °. Since oviposition normally took place in a restricted period of daylight (usually 10-14.00 hours) when the sun was positioned south in the midday sky, it is possible that ovipositing females approached their potential oviposition foliage using the sun as a guide.

Grossmueller and Lederhouse (1985) examined the oviposition pattern of *Papilio glaucus* and and found over 50 % of eggs had westward exposures and only 7.6 % faced northward. Similar to *H. fuciformis* moths, *P. glaucus* displayed heliophilic behaviour. It is possible that certain frequencies of light, most prevalent in bright sunlight, reflecting back off south facing host leaves help to stimulate oviposition in a searching female (Scherer and Kolb, 1987). Also, strong sunlight may induce volatile chemicals to stimulate olfactory sensors.

Lederer (1960), in his 1940-55 German study of *L. camilla,* found that removing antennae from adult butterflies prevented re-location of their normal oviposition sites and concluded that females located their oviposition foliage primarily by olfactory sensors, and optical detection was of secondary importance.

5.4.3.6 Summary.

The most outstanding distinguishing factor between the habitat requirements of *L. camilla* and *H. fuciformis* has been shown to be the oviposition site preference of *L. camilla* for shade host foliage in contrast to sun host foliage by *H. fuciformis.* Field observations of the appearance of *L. periclymenum* foliage with and without caterpillar feeding damage indicate possible important differences in host quality between the two habitats. Mid-summer host foliage in plantation drapes appear less vigorous with little inflorescence and only spindly host growths are used by ovipositing *L. camilla* females. In contrast, sunny clearing host growth was found to be far more vigorous, eventually, full of inflorescence, and evidently preferred by *H. fuciformis* ovipositing females. Feeding damage of host foliage caused by *H. fuciformis* 1st instar caterpillars always produced secretion of sticky colourless globules. In contrast, 1st instar *L. camilla* caterpillar feeding damage rarely produced host secretion. These observations indicate the possibility of variation in host quality between the two oviposition habitats.

Why do *L. camilla* females prefer to oviposit on host foliage which appears to be less healthy than the abundant host foliage growing in sunny clearings? How would *L. camilla* caterpillars behave when

feeding on sun foliage and how would *H. fuciformis* caterpillars behave when feeding on shade foliage? How does host quality vary between the two habitats of clearing and plantation? Answers to these questions will be the concluding aims of this study. Chapter Six will cover experimentation and analysis of important host quality characteristics. Chapter Seven will deal with bioassays involving caterpillar transfer experiments.

Chapter Six

Quality of oviposition foliage

Trichomes - toughness - nutrients - secretion

6.1 Introduction

The review of plant defence mechanisms and host quality in Chapter One indicated the importance of interactions between leaf cuticle and feeding caterpillars. Cuticular structure in terms of trichome type and density, foliage toughness, possible secretion, and host nutrient quality all featured strongly in these interactions. In this chapter these host foliage characteristics are investigated and measured where appropriate. Comparison of leaf quality between natural oviposition foliage of *L. camilla* and *H. fuciformis* is emphasised. The quality of treatment foliage in assay is analysed to confirm that any variation reflects natural habitat variation. *Symphoricarpos rivularis* and *Lonicera caprifolium*, used as additional bioassay treatments, are also examined for leaf quality.

The results of the micro-habitat requirement survey (Chapter Five) revealed that the eggs of *L. camilla* and *H. fuciformis* were oviposited in different locations on the respective host leaf surface. *L. camilla* uses the adaxial leaf margin whereas *H. fuciformis* oviposits on the abaxial laminal area of the *L. periclymenum* leaf. There are a number of possible reasons which may influence ovipositing females in their choice of egg location. Trichome density, leaf toughness and secretion may be contributory factors. These qualities of *L. periclymenum* leaves were measured in order to ascertain any evidence that they had influenced the oviposition location and feeding behaviour of *L. camilla* and *H. fuciformis* caterpillars. Ovipositing females may search for a location on the leaf surface which is devoid of trichomes indicating a possible nuisance value to egg attachment and early instar feeding ability.

There were four main objectives for the measurement of trichome density, leaf toughness, nutrient quality and foodplant secretion:

- comparison of oviposition foliage between *L. camilla* and *H. fuciformis*
- comparison of oviposition foliage with random sampled foliage
- comparison of treatment foodplants used in transfer bioassays (Chapter Seven)
- determination of any variation in seasonal host quality.

6.2 Method and materials

6.2.1 Determination of trichome structure, density and distribution.

Two *L. periclymenum* shoots (rosettes) were removed from each of five *L. periclymenum* drapes found in the two habitats of shade (plantations) and open sun (clearings). Different plantations and different clearings were used for each of the five drapes. Where possible the two shoots were removed at different heights of the drape within the range 0-3 m. The leaves were removed from the shoots and placed in a bag, shaken, and working samples of 20 leaves were randomly removed from each bag for each habitat. *L. periclymenum* foliage (shade, sun and ground), *S. rivularis* and *L. caprifolium*, used as treatments in bioassays, were obtained in a similar manner. Oviposition foliage (leaves containing eggs) were examined for trichome density prior to use in bioassay.

Trichome density measurements were based on the number of trichomes counted in a cuticular sample area of dimensions 5 x 0.5 mm. For the determination of trichome density variation over the leaf cuticle and egg location, three different locations were used for trichome density measurement on the leaf cuticle of both abaxial and adaxial leaf surfaces (midrib, laminae, and margin) for comparison with trichome density of egg location. As there were two margins and laminae on either side of the midrib of each leaf surface, alternative locations were used for trichome measurement for each leaf in the sample. In addition, a trichome count was made at the egg location on oviposition foliage for the two Lepidoptera. The results of 1994 trichome densities on *L. periclymenum* foliage showed that the trichome density measurement on the abaxial midrib central area was a good indicator of overall leaf trichome density. Consequently, in the 1995 comparison of foodplant trichome density this leaf location was used alone for measurement of trichome density.

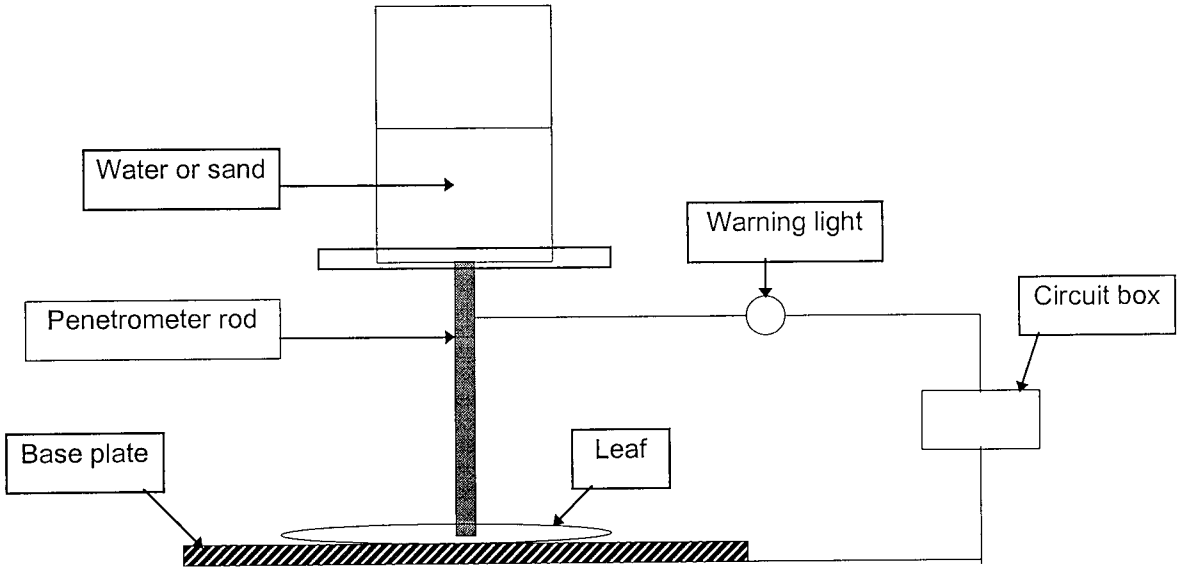
Optical and scanning electron microscopy and associated photography were used to study the leaf cuticle for variation in trichome type and the influence of trichomes on caterpillar behaviour. The leaf cuticle was investigated by scanning electron microscope (SEM) in the magnification range of 40 to 20 k. Leaf sections up to 1 cm long were fixed with araldite on 12 mm diameter aluminium stubs which were then coated with gold-palladium alloy in preparation for the SEM. Associated photographs were taken with the SEM camera using 120 (62 mm wide), 125 ASA, Ilford FP4 black and white negative film.

Optically, the leaf epidermis was examined at a magnification range 10 to 40 using a MEIJI TECHNO (model SKC) microscope. Associated photographs were taken with PENTAX SPOTMATIC and PRAKTICA (MTL 50) 35 mm cameras using both black and white (Ilford FP4), and colour negative (Kodak Gold) film, and colour transparency (Kodak Ektachrome) film.

6.2.2 Determination of leaf toughness.

In this study leaf toughness is regarded as the ability of a penetrometer rod to penetrate a leaf. A penetrometer was constructed in which the leaf under examination was placed on an aluminium base. The tip of the penetrometer rod was placed touching the leaf at a selected location and the penetrating pressure of the rod was increased by adding mass in the form of water or sand to a container attached to the top of the rod. When the tip of the penetrating rod pierced the leaf and came in contact with the base plate an electric circuit was completed. The moment of cuticular penetration was immediately registered electronically by an indicator light. More details of the penetrometer are given in Appendix 4.

Fig. 6.1 Penetrometer apparatus (diagrammatic) used for measuring leaf toughness.



Each leaf examined for toughness was penetrated in four different locations (twice either side of the midrib) and the unit of toughness is regarded as the total mass (g) of rod and contents required to penetrate the leaf in the four locations. Apart from the first experiment which measured any variation of toughness over the leaf surface, the unit of mass quoted in tables for each leaf tested is the sum of the four individual position values. This procedure was adopted to smooth any toughness variation on the leaf surface and avoid having to take means of means in statistical analysis of results. Large or major veins were avoided in leaf toughness measurements as they were considerably more tough than leaf laminae which were the only leaf parts eaten by the early instar caterpillars. Where possible a 20 leaf sample was selected for toughness measurement in the same way as the sample selection method used for trichome density measurement (Section 6.2.1). The leaves were obtained from Bentley Wood, stored in a cold box during transit, and examined for toughness on the same day to avoid possible moisture content change. For the seasonal change in toughness objective 3 samples of *L. periclymenum* leaves were collected in early April and at later periods from both shade (plantation) and open sun (clearings) habitats to

determine any possible seasonal variation. A sample batch of 10 leaves was used for experimentation.

6.2.3 Determination of foodplant nutrient quality.

Foodplant nutrient quality determination was restricted to the analysis of total carbon, total nitrogen and the water content of foodplant samples. The carbon and nitrogen content of foodplant samples was determined using a Carlo Erba elemental analyser on powdered, oven- dried foodplant leaves.

Leaf samples collected in Bentley Wood were stored in a cold box during transit to avoid moisture loss and weighed within two hours of collection. Leaves were then kept in an oven for 48 hours in the temperature range 70 ° - 80 ° C. Afterwards, the dried leaves were reweighed giving the water content, crushed, homogenised and ground into a fine powder. Only 1-2 milligrams of each sample were used in the elemental analyser. Between 5 and 10 samples of each foodplant were prepared for analysis. Each sample contained all the leaves from one rosette (4-10 leaves) where possible. Where bioassay foodplants were in short supply fewer leaves were taken. Samples were taken in the months April, May, June and July for possible seasonal variation.

6.2.4 Determination of foodplant secretion.

In the 1994 bioassay secretion was recorded on a daily basis as simply present or not when feeding caterpillars and foodplant foliage were examined. The presence of secretion on the leaf received 1 unit and its absence received 0 units. The presence of secretion flowing from foliage damaged by caterpillar feeding was easily identified and noticed as a colourless (later turning to a pale yellow semi - solid) viscous liquid. The daily secretion units were summed for the total caterpillar period (instar 1-5).

In 1995 bioassays the amount of feeding damage secretion was recorded by estimating the fraction of leaf area feeding damage producing secretion. In the case of *H. fuciformis* feeding damage the fraction of feeding damage holes exhibiting secretion flow was determined. For example, a daily inspection of caterpillar feeding damage producing no sign of secretion received 0 units, observable secretion in only a few of the holes present received 1 unit, observable secretion in about half of the holes present received 2 units and observable secretion in most of the holes present received a maximum of 3 units. For the *L. camilla* 1995 bioassay a similar procedure was adopted.

In contrast to *H. fuciformis*, *L. camilla* feeds by cutting strips of foliage ("flags") and observable secretion in only a small fraction of linear strip feeding damage received 1 unit, observable

secretion in half of the linear strip feeding damage received 2 units and observable secretion in most of the linear strip feeding damage received a maximum of 3 units. The daily secretion units were summed for the total caterpillar period (instar 1-5).

6.3 Results

6.3.1 Trichome structure.

Scanning electron micrographs and optical microscopy showed the presence of two basic types of trichomes on the cuticle of *L. periclymenum* leaves and inflorescence. The most abundant trichome was found to be a simple unicellular trichome (Plate 6.1) which was originally thought to be non-glandular as the pointed tip revealed no signs of glandular head cell structure. Scanning electron micrographs of these trichomes which had been cut and removed from the leaf midrib by *L. camilla* caterpillars showed them to be hollow and, eventually, a small number was found with globules of sticky secretion attached to the trichome tip (Plates 6.2, 6.4). These unicellular trichomes varied in length from 120 μm, found mainly on inflorescence, to 600 μm, found mainly on the underside of leaves. Their basal diameter was found to be in the region 25-35 μm. The shorter unicellular trichomes were often erect but occasionally appeared in relatively small hooked clusters. The taller unicellular trichomes were also mainly erect but occasionally curved and curled (Plate 6.1b). These unicellular trichomes were also covered with micropapillate surface sculpturing which is readily seen in Plates 6.3a-b. The unicellular trichome exudes secretion via its tip which is fractured through the build up of pressure inside the trichome. High magnification (SEM) micrographs revealed trichomes after secretion with tips containing jagged holes (Plate 6.3b) in contrast to the conical shaped tips of unfractured trichomes (Plate 6.3a).

The second type of trichome was a typical glandular trichome with a multicellular stalk and head. This type of trichome was mainly found on inflorescence and, to a much lesser extent, on the petioles, laminae, margins and mid-ribs of leaves. Their length varied in the region 150-250 μm and their stalk diameter was similar to the simple trichome, 20-30 μm. These trichomes were normally found erect and they secreted via holes in their heads after cuticular penetration by physical contact with foraging insects.

6.3.2 Distribution and density of trichomes on *L. periclymenum* foliage.

6.3.2.1 Trichome density and distribution on oviposition leaf (1994) (Table 6.1; Figures. 6.2-3)

No (typically glandular) trichomes were found on leaf laminal area containing eggs for both *L. camilla* and *H. fuciformis*. The density of this type of trichome on other parts of the *L. periclymenum*

leaf was very low (normally < 1 per sample area). The highest density of the multicellular trichome was found on the inflorescence and flower stalk of *L. periclymenum*.

The highest density of trichomes was found on the abaxial leaf surface from both shade and sun *L. periclymenum* leaves. Here, in the case of shade *L. periclymenum* oviposition leaves, which showed the overall highest density of trichomes, the marginal and midrib zones were found to be almost twice as dense as the laminal zones. With both *L. camilla* and *H. fuciformis* oviposition leaves the midrib and laminal zones of the adaxial leaf surface contained trichomes with a density much lower than the actual density of trichomes at the egg location.

H. fuciformis females oviposited on *L. periclymenum* leaves which had an overall lower density of unicellular trichomes than the oviposition leaves of *L. camilla. H. fuciformis* females chose the abaxial lamina for egg location which had a trichome density as high as anywhere on the leaf.

L. camilla females chose the adaxial marginal zone for egg location which was one of the higher density zones on the adaxial leaf surface, but of considerably lower trichome density than any of the abaxial leaf zones.

The oviposition leaf for both *L. camilla and H. fuciformis* contained fewer multicellular trichomes than the random sample leaves from both sun and shade foliage. Indeed, there were no multicellular trichomes found in the sample areas surrounding the egg for both Lepidoptera.

6.3.2.2 Trichome density of oviposition foliage compared to non-oviposition foliage (1995) (Table 6.2).

There was a statistically significant difference ($p < 0.01$) in trichome density between oviposition foliage of *L. camilla* and *H. fuciformis* and also between non-oviposition foliage of *L. periclymenum* randomly sampled from their shade and sunny habitats. There was no statistical difference ($p > 0.05$) in trichome density between oviposition and non-oviposition foliage from the same habitat.

6.3.2.3 Trichome density of bioassay (1995) foodplants (Table 6.3).

In both 1995 *L. camilla* and *H. fuciformis* caterpillar survival bioassays there was a statistically significant difference ($p < 0.01$) of trichome density between sun and shade *L. periclymenum* foliage. The magnitude of this difference (2-4 times greater trichome density on shade foliage) reflected the magnitude previously found on natural oviposition foliage (6.3.2.2).

6.3.3 Foliage toughness (Tables 6.4-6).

6.3.3.1 Variation of toughness at different locations on the leaf cuticle (Table 6.4).

There was no statistically significant difference ($p > 0.05$) of toughness between the four locations on the cuticle of the sample of *L. periclymenum* leaves irrespective of habitat (sun or shade) origin. There was a statistically significant difference ($p < 0.01$) of toughness between shade and sun *L. periclymenum* foliage. Sun foliage was approximately 1.5 times tougher than shade foliage.

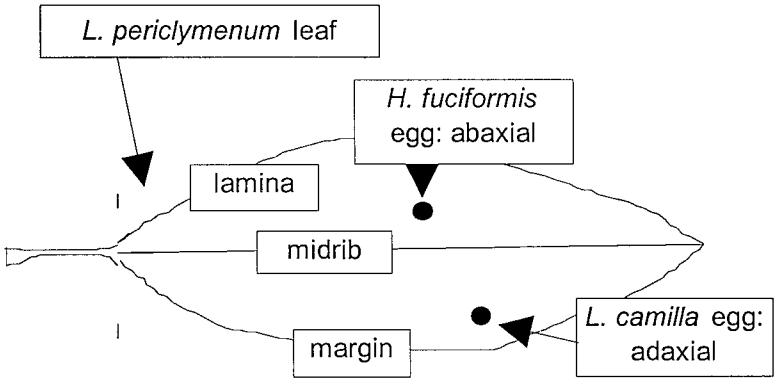
6.3.3.2 Leaf toughness: seasonal variation (Table 6.5).

The toughness measurements for both shade and sun *L. periclymenum* foliage indicate no significant change during the April-June period. However, the *L. camilla* oviposition foliage, taken in late June to early July is statistically significantly ($p < 0.01$) tougher than any shade sample taken earlier. A similar situation arose with sun *L. periclymenum* foliage. Sun foliage including oviposition foliage of *H. fuciformis* was statistically significantly tougher than the corresponding shade and *L. camilla* oviposition foliage for each sampling date ($p < 0.01$).

6.3.3.3 Leaf toughness: bioassay foodplants (Table 6.6).

The difference in toughness between oviposition (control) foodplant and the corresponding toughness of treatment *L. periclymenum* foodplant for both *L. camilla* and *H. fuciformis* bioassays was similar to the naturally previously determined foliage differences. The greatest toughness value was shown by *Symphoricarpos rivularis* treatment used in the *L. camilla* 1995 bioassay and previously used in the *H. fuciformis* 1994 bioassay.

Table 6.1 Trichome density distribution of *L. periclymenum* (I): egg leaf (mean + S.E.; 95 % C.L. = 95 % confidence level range of mean). Based on the number of trichomes found in a sample area of dimensions, 5 x 0.5 mm, counted at 3 locations on each leaf surface, and the egg location.



	H.fuciformis (N=32)		L. camilla (N=53)	
	Unicellular trichome	Multicellular trichome	Unicellular trichome	Multicellular trichome
Egg location	11.2 ± 1.8	0	7.9 ± 0.7	0
95 % C.L.	14.7-7.6	-	9.2-6.6	-
Adaxial				
Midrib	3.3 ± 0.8	1.1 ± 0.5	2.1 ± 0.6	0
95 % C.L.	4.9-1.7	-	3.2-1.0	-
Lamina	1.5 ± 0.3	0.06 ± 0.04	1.6 ± 0.4	0
95 % C.L.	2.2-0.9	-	2.2-0.9	-
Margin	7.9 ± 1.4	0.47± 0.24	14.0 ± 0.7	0
95 % C.L.	10.6-5.2	-	15.4-12.6	-
Abaxial				
Midrib	11.2 ± 2.4	0.06 ± 0.06	22.6 ± 1.4	0
95 % C.L.	15.9-6.5	-	25.3-22.8	-
Lamina	9.7 ± 1.6	0.13 ± 0.09	13.2 ± 1.3	0
95 % C.L.	12.9-6.5	-	15.7-10.7	-
Margin	10.0 ± 1.9	0.09 ± 0.05	24.9 ± 1.4	0
95 % C.L.	13.7-6.3	-	27.6-22.2	-

Fig.6.2 Trichome density distribution (I): egg leaf of *L. camilla* (N=53).

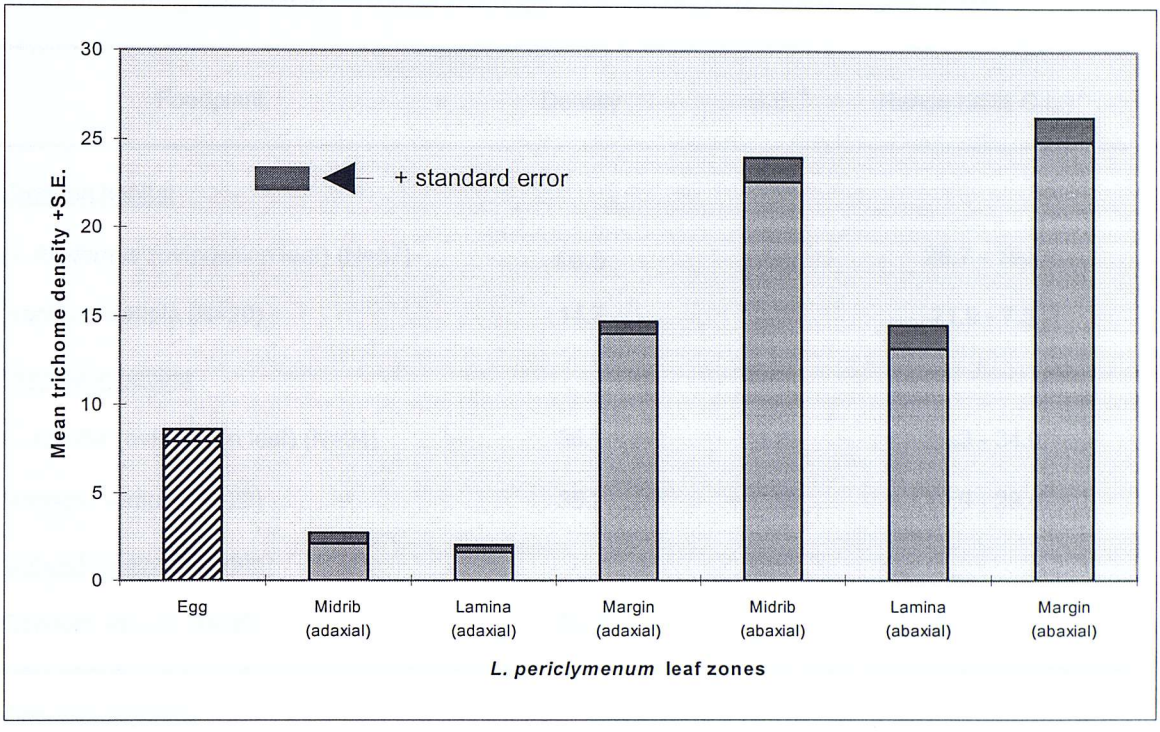


Fig.6.3 Trichome density distribution (II): egg leaf of *H. fuciformis* (N=32).

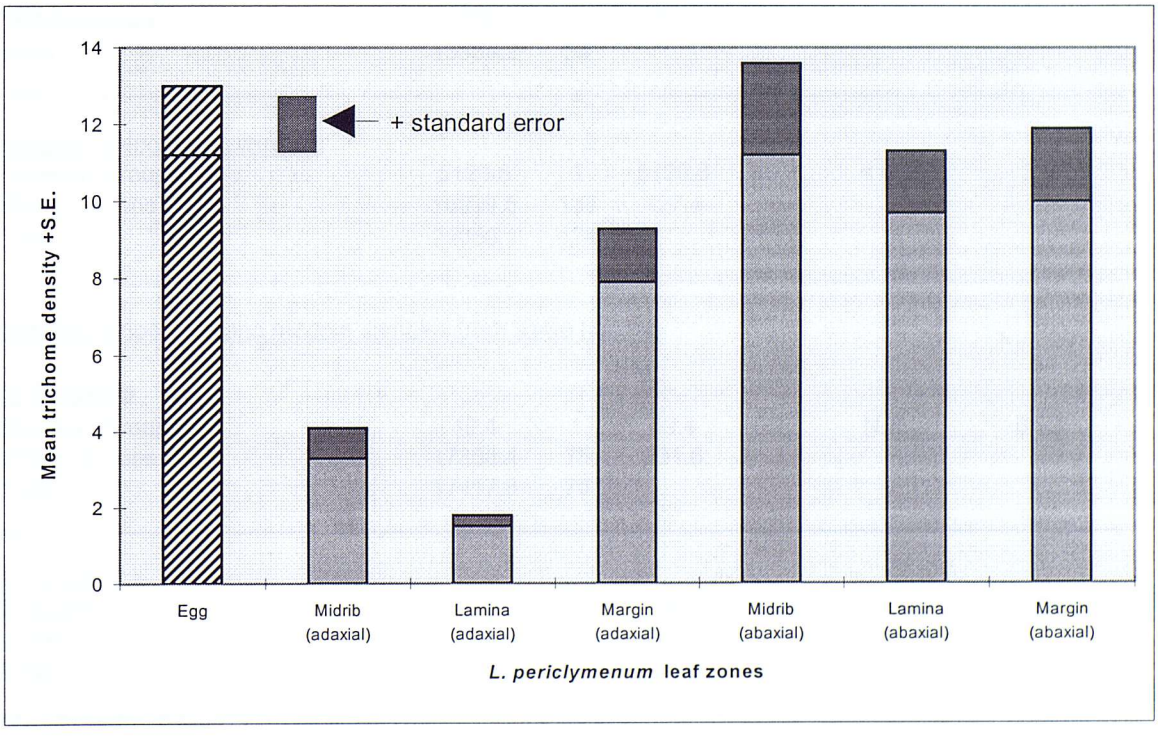


Table 6.2 Trichome density of *L. periclymenum* (II): egg leaf compared with random sample. Trichome density units: mean number of trichomes on 5mm length of central abaxial midrib.

Foodplant	Density	S.E. [a]	Range (95% C.L.) [b]
Clearing habitat			
H. fuciformis (oviposition leaf) (N=57)	16.5	1.96	26.7 - 18.8
Random sample (N=20)	14.7	3.65	21.9 - 7.5
Plantation habitat			
L. camilla (oviposition leaf) (N=94)	36.1	1.09	36.3 - 34.0
Random sample (N=20)	35.2	2.92	40.9 - 29.4
Ground foliage (clearing)			
Random sample (N=20)	23.0	2.71	28.3 - 17.7

One-way ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit (p=0.01)*
Between non-oviposition samples.						
Between Groups	4231.4	2	2115.7	10.9	< 0.01	5.0
Within Groups	11106.8	57	194.9			
Total	15338.2	59				
Between oviposition samples.						
Between Groups	5120.6	1	5120.6	40.2	< 0.01	3.9
Within Groups	16939.5	133	127.4			
Total	22060.1	134				
Between oviposition and random samples from same habitat.						
H. fuciformis						
Between Groups	49.4	1	49.4	0.21	N.S. [c]	6.99
Within Groups	17368.4	75	231.6			
Total	17417.8	76				
L. camilla						
Between Groups	16.5	1	16.5	0.14	N.S.	6.87
Within Groups	13572.5	112	121.2			
Total	13588.9	113				

a: standard error; b: 95 % confidence level range of mean; c: not significant at p = 0.05.

Table 6.3 Trichome density of *L. periclymenum* (III): egg leaf compared with bioassay foodplants. Trichome density units: mean number of trichomes on 5mm length of central abaxial midrib.

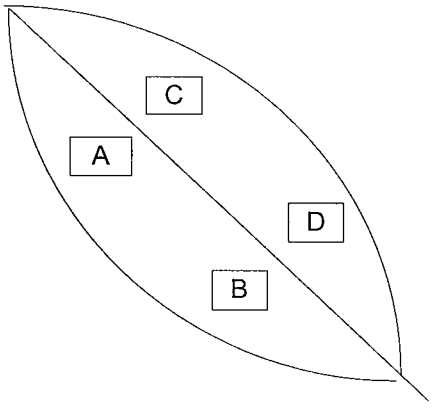
Foodplant	Density	S.E. [a]	Range (95% C.L.) [b]
H. fuciformis bioassay.			
L. periclymenum: sun (N=9)	15.1	4.5	23.9 - 6.3
L. periclymenum (shade) (N=11)	55.2	4.8	64.5 - 45.9
L. periclymenum (ground) (N=11).	41.8	4.0	49.6 - 34.0
L. caprifolium (N=10)	0	0	-
L. camilla bioassay.			
L. periclymenum (shade) (N=14)	35.9	3.1	41.9 - 29.9
L. periclymenum (sun) (N=12)	15.2	4.1	23.3 - 7.1
L. periclymenum (ground) (N=11).	19.4	2.2	23.7 - 15.1
L. caprifolium (N=12)	0	0	-
S. rivularis (N=12)	0	0	-

One-way ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit (p=0.01)*
Between *H. fuciformis* foodplants.						
Between Groups	8102.7	2	4051	19.78	< 0.01	3.34
Within Groups	5736.2	28	204.9			
Total	13839	30				
Between *L. camilla* foodplants.						
Between Groups	3162.2	2	1581	11.96	< 0.01	3.28
Within Groups	4493.1	34	132.2			
Total	7655.3	36				

a: standard error; b: 95 % confidence level range of mean.

Table 6.4 Leaf toughness of *L periclymenum* (I): leaf surface variation (mean ± S.E.). Toughness unit is the mass (g) required to cause a penetrometer rod to penetrate foodplant leaf. The following data was obtained by penetrating the leaf surface at four different locations (A-D).



	Mass (g) required for penetration of leaf			
	A	B	C	D
L. periclymenum (shade) (N=20)	145 ± 6	152 ± 7	143 ± 6	141 ± 5
L. periclymenum (sun) (N=20)	228 ± 10	231 ± 11	232 ± 11	227 ± 12

2-way ANOVA

Source of Variation	*SS*	*df*	*MS*	*F*	*P-value*	*F crit*
Habitat samples	215138.0	1	215138.0	130.47	< 0.01	6.86
Leaf locations	962.2	2	481.1	0.29	NS (>0.05)	4.80
Interaction	546.8	2	273.4	0.17	NS (>0.05)	4.80
Within	187975.4	114	1648.9			
Total	404622.3	119				

Table 6.5 Leaf toughness of *L. periclymenum* (II): seasonal variation (mean + S.E.). Toughness unit is the mass (g) required to cause a penetrometer rod to penetrate foodplant leaf. The following data was obtained by penetrating the leaf surface at four different locations and table data is the sum of the four readings.

Date	Shade foliage (N=20)	Sun foliage (N=20)
03.04.95	757 ± 20	-
05.04.95	700 ± 41	-
08.04.95	798 ± 29	-
11.04.95	743 ± 30	1094 ± 40 [a]
24.04.95	750 ± 18	905 ± 23 [b]
02.05.95	771 ± 24	873 ± 39 [c]
Oviposition foliage (bioassay control) (N=54)		
	L. camilla (July '95)	*H. fuciformis* (June '95)
	1099 ± 47	1395 ± 49 [d]

Statistical difference between toughness of shade and sun foliage.

a: $t = 7.05$, d. of f. = 38, $p < 0.01$.
b: $t = 5.18$, d. of f. = 38, $p < 0.01$.
b: $t = 2.00$, d. of f. = 38, $p < 0.05$.
d: $t = 4.35$, d. of f. = 52, $p < 0.01$.

Table 6.6 Leaf toughness (III): bioassay foodplants (mean + S.E.). Toughness unit is the mass (g) required to cause a penetrometer rod to penetrate foodplant leaf. The following data was obtained by penetrating the leaf surface at four different locations and table data is the sum of the four readings.

Foodplant	*L. camilla*	*H. fuciformis*
Oviposition foliage (control) (N=54)		
L.periclymenum	1099 ± 47	1395 ± 49 [a]
Treatments (N=10)		
L.periclymenum (sun foliage)	1609 ± 106	-
L.periclymenum (shade foliage)	-	830 ± 70
L.periclymenum (ground foliage)	963 ± 83	792 ± 60
L. caprifolium	860 ± 20	749 ± 35
S. rivularis	1934 ± 71	-

a: there is a significant difference between the toughness of *H. fuciformis* and *L. camilla* oviposition leaves:
$t = 4.35$; d. of f. = 106; $p < 0.01$.

6.3.4 Foliage nutrients (C, N, H_2O) (Tables 6.7-8).

6.3.4.1 Comparison of nutrient quality between sun and shade *L. periclymenum* foliage.

The four sampling periods of April-July produced no statistically significant difference ($p > 0.05$; 95 % confidence level of mean) in the total carbon and total nitrogen content between shade and sun *L. periclymenum* foliage. The first three sampling periods of April-June produced no statistically significant difference ($p > 0.05$; 95 % confidence level of mean) in the water content between shade and sun *L. periclymenum* foliage but there was a statistically significant difference ($p < 0.05$; 95 % confidence level of mean) in the water content between shade and sun *L. periclymenum* foliage for the July sample (*L. camilla* bioassay).

6.3.4.2 Seasonal variation in nutrient quality (Tables 6.7-8).

The carbon and nitrogen content of both shade and sun *L. periclymenum* foliage showed a statistically significant decrease ($p < 0.05$; 95 % confidence level of mean) between the sampling periods April and May. There was no statistically significant change ($p > 0.05$; 95 % confidence level of mean) in the water content for the same samples in the same sampling periods.

6.3.4.3 Nutrient quality of bioassay foodplants (Tables 6.7-8).

There was no statistically significant difference ($p > 0.05$; 95 % confidence level of mean) in carbon and nitrogen content between sun and shade *L. periclymenum* foliage in both *L. camilla* and *H. fuciformis* bioassays. There was no statistically significant difference ($p > 0.05$; 95 % confidence level of mean) in the water content between sun and shade *L. periclymenum* foliage in the *H. fuciformis* bioassay but in the *L. camilla* bioassay the sun *L. periclymenum* treatment foliage was statistically significantly lower ($p < 0.05$; 95 % confidence level of mean) in water content. The water content of *S. rivularis* in the *L. camilla* bioassay was almost 20 % lower than any other bioassay foodplant.

Table 6.7 Foodplant nutrient quality (I): total carbon and total nitrogen (% mean + S.E.).

Foodplant	Date	Carbon (%)	Nitrogen (%)
L. periclymenum (shade) (N=8)	April '95	48.3 ± 0.2	3.66 ± 0.11
L. periclymenum (sun) (N=8)	April '95	48.6 ± 0.2	3.42 ± 0.06
L. periclymenum (shade) (N=5)	May '95	45.4 ± 0.2	2.82 ± 0.15
L. periclymenum (sun) (N=5)	May '95	46.4 ± 0.3	2.92 ± 0.04
Bioassay (*H. fuciformis*)			
L. periclymenum (shade) (N=10)	June '95	45.5 ± 0.2	2.44 ± 0.08
L. periclymenum (sun) [a] (N=10)	June '95	46.6 ± 0.6	2.51 ± 0.11
L. periclymenum (ground) (N=8)	June '95	44.9 ± 0.1	1.98 ± 0.06
L. caprifolium (N=8)	June '95	46.5 ± 0.3	2.17 ± 0.17
Bioassay (*L. camilla*)			
L. periclymenum (shade) [b] (N=10)	July '95	44.5 ± 0.5	2.15 ± 0.07
L. periclymenum (sun) (N=10)	July '95	46.1 ± 0.5	1.80 ± 0.05
L. periclymenum (ground) (N=5)	July '95	45.5 ± 0.3	2.28 ± 0.10
L. caprifolium (N=5)	July '95	45.7 ± 0.2	2.42 ± 0.10
S. rivularis	July '95	45.5 ± 0.2	2.09 ± 0.04

a: *H. fuciformis* oviposition foliage.
b: *L. camilla* oviposition foliage.

Table 6.8 Foodplant nutrient quality (II): water content (% mean + S.E.).

Foodplant	Date	H_2O (%)
Non-oviposition foliage		
L. periclymenum (shade) (N=5)	April '95	73.3 ± 0.9
L. periclymenum (sun) (N=5)	April '95	73.9 ± 0.8
L. periclymenum (shade) (N=5)	May '95	73.2 ± 0.3
L. periclymenum (sun) (N=5)	May '95	73.3 ± 0.3
Bioassay (*H. fuciformis*)		
L. periclymenum (shade) (N=5)	June '95	74.6 ± 0.3
L. periclymenum (sun) [a] (N=38)	June '95	74.8 ± 0.3
L. periclymenum (ground) (N=5)	June '95	71.2 ± 0.2
L. caprifolium (N=5)	June '95	78.2 ± 1.8
Bioassay (*L. camilla*)		
L. periclymenum (shade) [b] (N=57)	July '95	76.0 ± 0.3
L. periclymenum (sun) (N=5)	July '95	68.1 ± 0.5
L. periclymenum (ground) (N=5)	July '95	67.3 ± 0.5
L. caprifolium (N=5)	July '95	77.7 ± 0.9
S. rivularis (N=10)	July '95	51.9 ± 0.5

a: *H. fuciformis* oviposition foliage.
b: *L. camilla* oviposition foliage.

6.3.5 Foliage secretion (Tables 6.9-10; Figures 6.4).

6.3.5.1 Introduction.

Secretion was produced from *L. periclymenum* foliage from three different sources. Two sources involved trichomes (unicellular and multicellular) and a third source issued from the leaf epidermis. This study can only offer a superficial explanation of the mechanism behind the activation of secretion. General field observation showed the production of secretion globules at the point of caterpillar feeding damage on most *L. periclymenum* foliage which was growing in open sunny clearings or rides but very rarely on foliage growing in shade. Multicellular trichome secretion was easily artificially induced by breaking the head cuticle with a pin. Only rarely was natural activation of secretion from this trichome observed in the field from foraging insects. Artificial induction of secretion from the unicellular type of trichome proved impossible through physical contact and natural induction via physical contact with foraging insects was never observed. However, a SEM micrograph of the entrance of a micro-moth (*A. podana)* leaf roll (Plate 6.4a) showed unicellular trichomes exudating secretion which may have been activated by physical contact with the caterpillar or secretion may have been induced by damage to leaf tissue caused by micro-climatic stress inside the leaf roll. SEM micrographs also showed unicellular trichomes producing very slow pulses of secretion which produced bulging cuticles, and after release, very viscous spherical globules which hardened as they flowed slowly down the outside cuticle of the trichome (Plates 6.2a-b). Using the size of the secretion globule and trichome from Plates 6.4c, the volume ratio of secretion globule to trichome volume is approximately 1400:1. Secretion from caterpillar feeding damage on *L. periclymenum* sun foliage occasionally produced crystallisation of a fibrous nature (Plate 6.4b).

6.3.5.2 Secretion during *L. camilla* bioassays (Figure 6.4-5).

In both 1995 and 1994 *L. camilla* bioassays only *L. periclymenum* sun foliage treatment produced substantial secretion from caterpillar feeding damage with very small amounts from *L. periclymenum* shade and *L. periclymenum* ground foliage treatments. Most of the total instar secretion was produced in first instar feeding damage with decreasing amounts in later instars (Tables 6.9-10). *L. caprifolium* and *S. rivularis* did not produce secretion.

6.3.5.3 Secretion during *H. fuciformis* bioassays (Figure 6.4-5).

In the 1995 *H. fuciformis* bioassay only *L. periclymenum* sun foliage produced substantial secretion from caterpillar feeding damage with statistically significantly ($p < 0.05$) smaller amounts from *L. periclymenum* shade and *L. periclymenum* ground foliage treatments. Again, most of the total instar secretion was produced in first instar feeding damage with decreasing amounts in later instars (Tables 6.9-10). *L. caprifolium* produced a minute amount of secretion in the first instar. In the 1994

bioassay *S. rivularis* did not produce secretion whereas *L. periclymenum* sun foliage produced secretion in the 1st and 2nd instars only.

6.3.5.4 Field evidence of *L. periclymenum* secretion in plantations.

Observation of secretion from caterpillar feeding damage on *L. periclymenum* foliage growing in sunny clearings was common with *H. fuciformis* caterpillars. In contrast, *L. periclymenum* secretion from shaded foliage in plantation *L. camilla* colonies was never observed. However, during early spring, before bud-burst canopy extension, a few examples of small amounts of secretory feeding damage were observed from micro-moth caterpillars foraging in leaf rolls and external feeders. However, as the plantation canopy closed to create more shade no further secretion was observed in this type of habitat.

Following pages: Plates 6.1-4.

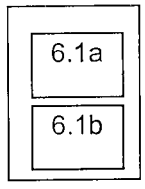


Plate 6.1a Scanning electron micrograph of unicellular trichomes (linear) on *L. periclymenum* leaf midrib (abaxial; x 400). p. 6-20

Plate 6.1b Scanning electron micrograph of unicellular trichomes (curled) on *L. periclymenum* leaf midrib (abaxial; x 450). p. 6-20

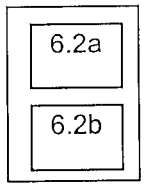


Plate 6.2a Scanning electron micrograph of unicellular trichomes on *L. periclymenum* leaf margin (adaxial) loaded with secretion (x 200). p. 6-21

Plate 6.2b Scanning electron micrograph of unicellular trichomes on *L. periclymenum* leaf lamina (abaxial) with released secretion (x 100). p. 6-21

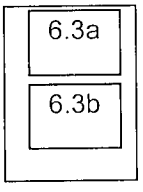


Plate 6.3a Scanning electron micrograph of unicellular trichome tip (intact) on *L. periclymenum* leaf lamina (abaxial; x 7400). p. 6-22

Plate 6.3b Scanning electron micrograph of unicellular trichome tip (burst) on *L. periclymenum* leaf lamina (abaxial) after secretion release (x 12600). p. 6-22

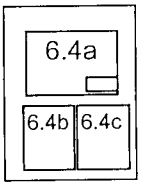


Plate 6.4a Scanning electron micrograph of leaf roll entrance of *Archips Podana* showing secretion (outer abaxial surface; x 20). p. 6-23

Inset: leaf roll of *Archips podana.* p. 6-23

Plate 6.4b Scanning electron micrograph of secretion with crystallisation on *L. periclymenum* leaf lamina (adaxial) at point of *H. fuciformis* caterpillar feeding damage (x 80). p. 6-23

Plate 6.4c Globule of secretion from unicellular trichome on *L. periclymenum* lamina (abaxial) showing partial solidification after two days following secretion (x 25). p. 6-23

Plate 6.1

Plate 6.2

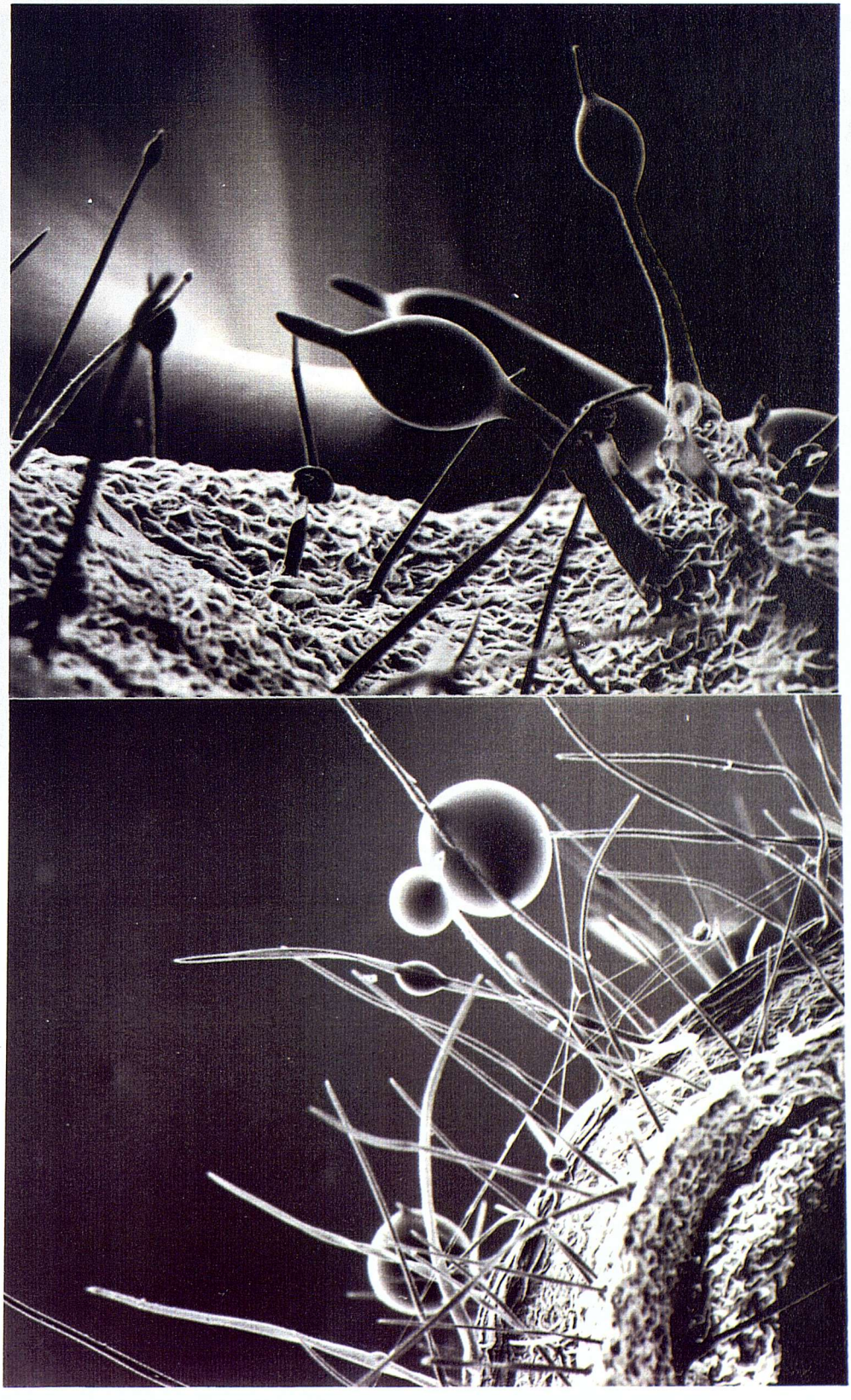


Plate 6.3

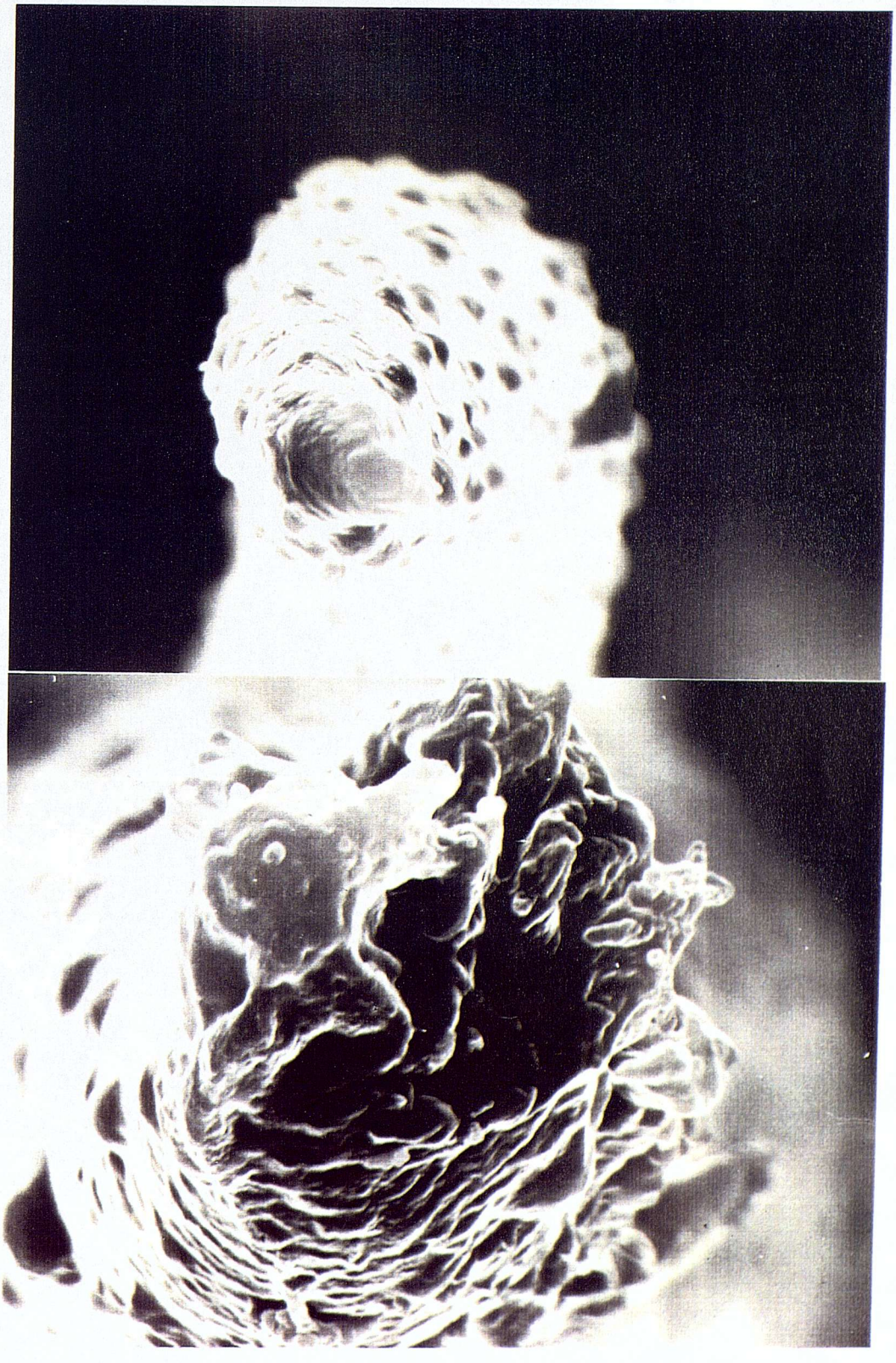


Plate 6.4

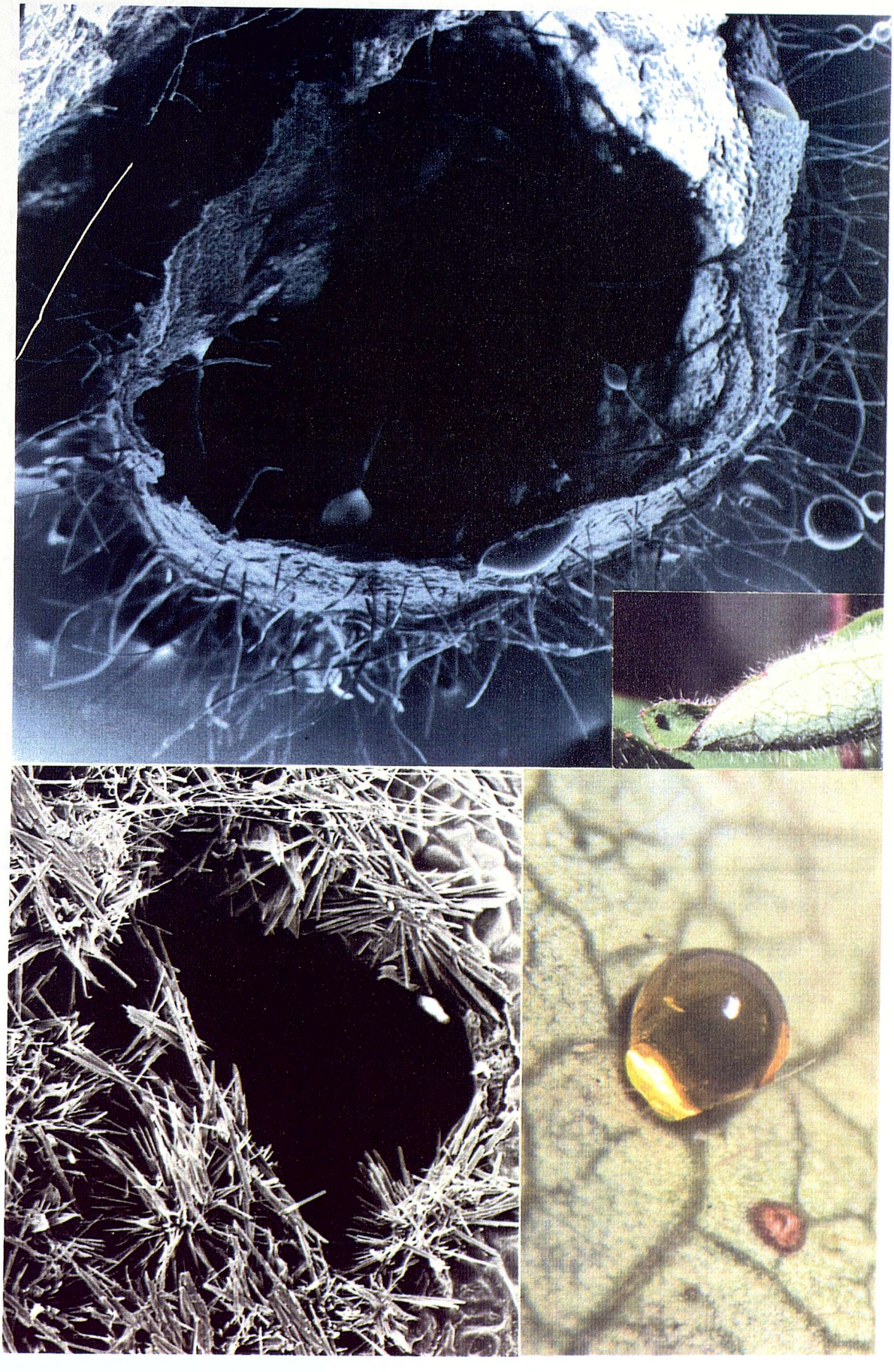


Table 6.9 Foodplant secretion (I): *L. camilla* bioassay (mean + S.E.).
Unit of secretion (1994): daily presence on feeding leaf = 1 unit; absence = 0.
Unit of secretion (1995) was based on the fraction of total area of feeding damage producing secretion: no secretion = 0; 0 - 0.25 = 1; > 0.25 < 0.75 = 2; > 0.75 = 3.
Secretion was measured each day and table values are sample mean totals per instar.

	Instar					
Foodplant treatment	1	2	3	4	5	1-5
1995 bioassay						
L. periclymenum (shade) (N=14)	0.1 ± 0.1	0.1 ± 0.1	0	0	0	0.3 ± 0.2
L. periclymenum (sun) (N=12)	9.8 ± 1.9	3.1 ± 1.6	0.3 ± 0.3	0.3 ± 0.3	0	15.1 ± 3.2
L. periclymenum (ground) (N=11)	0.6 ± 1.1	0	0	0	0	0.6 ± 1.1
L. caprifolium (N=11)	0	0	0	0	0	0
S. rivularis (N=11)	0	0	0	0	0	0
1994 bioassay						
All *L. periclymenum* treatments.						
Shade foliage (N=10)	0	0.2 ± 0.2	0.0	0.1 ± 0.1	0	0.3 ± 0.2
Sun foliage (total) (N=22)	5.8 ± 0.8	2.4 ± 0.6	0.7 ± 0.5	0.9 ± 0.6	0	8.0 ± 2.0
Sun foliage (egg only) (N=10)	7.6 ± 1.2	2.8 ± 1.1	1.3 ± 0.8	0.5 ± 0.5	0	9.0 ± 3.1
Sun foliage (transfer larvae only) (N=12)	4.3 ± 0.9	2.1 ± 0.7	0	1.3 ± 1.3	0	6.7 ± 2.9

Mann-Whitney U-test for difference between *L. periclymenum* sun (egg and transfer) foliage (1994) 1st instar: $U=28.5$; $P < 0.05$.
In the 1994 bioassay some *L. camilla* larvae (N=10) were fed on *L. periclymenum* (sun) foliage immediately after emergence. Others (N=12) were alllowed to feed on *L. periclymenum* (shade) foliage for 24 hours before transfer to *L. periclymenum* (sun) foliage for the remainder of their larval growth. Shade *L. periclymenum* bioassay treatment was always natural oviposition foliage.

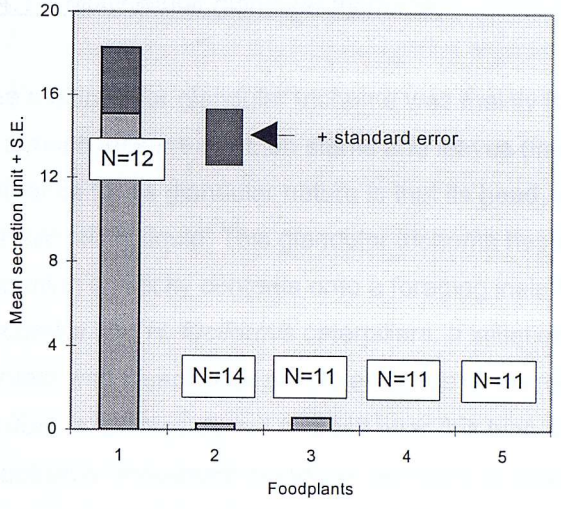
Table 6.10 Foodplant secretion (II): *H. fuciformis* bioassay (mean + S.E.).
Unit of secretion (1994): daily presence on feeding leaf = 1 unit; absence = 0.
Unit of secretion (1995) was based on the fraction of total area of feeding damage producing secretion: no secretion = 0; 0 - 0.25 = 1; > 0.25 < 0.75 = 2; > 0.75 = 3.
Secretion was measured each day and table values are sample mean totals per instar.

	Instar					
Foodplant treatment	1	2	3	4	5	1-5
1995 bioassay						
L. periclymenum (sun) (N=9)	9.1 ± 1.2	8.4 ± 1.1	5.4 ± 1.2	0.8 ± 0.4	0	23.8 ± 2.5
L. periclymenum (shade) (N=11)	4.4 ± 1.1	0.8 ± 0.3	0.1 ± 0.1	0	0	5.3 ± 1.1
L. periclymenum (ground) (N=11)	3.0 ± 0.9	1.8 ± 1.0	0.1 ± 0.1	0	0	4.9 ±1.8
L. caprifolium (N=10)	0.5 ± 0.3	0	0	0	0	0.5 ± 0.3
1994 bioassay						
L. periclymenum (sun) (N=9)	0.77 ± 0.04	0.46 ± 0.04	0	0	0	0.65 ± 0.03
S. rivularis (N=15)	0	0	0	0	0	0

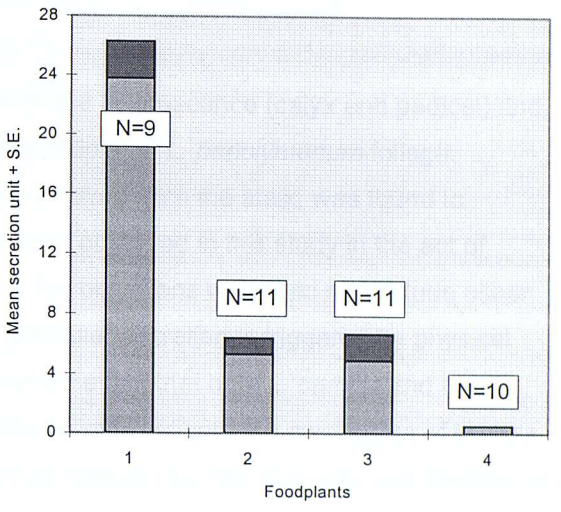
Mann-Whitney U-test for difference between *L. periclymenum* (sun and shade foliage, 1995) 1st and 1-5 instars: U = 11.1; P < 0.05 and U = 18.5; P < 0.05; respectively.

Fig. 6.4 Food plant secretion per instar from bioassay caterpillar foodplant feeding damage.
Unit of secretion (1994): daily presence on feeding leaf = 1 unit; absence = 0.
Unit of secretion (1995) was based on the fraction of total area of feeding damage producing secretion:
no secretion = 0; 0 - 0.25 = 1; > 0.25 < 0.75 = 2; > 0.75 = 3.

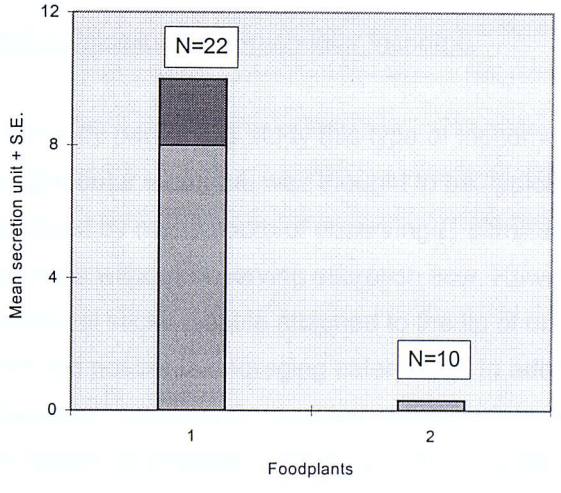
L. camilla bioassay (1995)



H. fuciformis bioassay (1995)



L. camilla bioassay (1994)



Foodplants

1: L. periclymenum: (sun foliage)

2: L. periclymenum: (shade foliage)

3: L. periclymenum: (ground foliage)

4: L. caprifolium

5: S. rivularis

6.4 Discussion

6.4.1 Effect of trichomes on oviposition strategy.

6.4.1.1 Multicellular glandular trichome.

The multicellular glandular trichome was mainly found on the inflorescence (calyx and pedicel) and, to a much lesser extent, on stems and leaves (including petiole) of *L. periclymenum* foliage. Evidence for its glandular nature is that its head, when removed from the stalk, was found to contain sticky liquid. This glandular trichome has only been observed in this study in the act of secreting its sticky contents onto a foraging insect on a few occasions which did not include either *L. camilla* and *H. fuciformis* caterpillars. If initiation of glandular secretion is triggered by physical contact with insect, lack of field evidence of secretion and the fact that both *L. camilla* and *H. fuciformis* females do not oviposit near this type of trichome may indicate the awareness of insects of possible unpleasant glandular secretory characteristics. Indeed, the fact that only one member of the 34 Lepidoptera (*Ypsolopha dentella* Fabr.) found feeding on *L. periclymenum* specialises by feeding on the glandular trichome dense areas of host inflorescence, also supports this hypothesis.

6.4.1.2 Unicellular non-glandular trichome.

In the early part of this study this type of trichome, which has all the typical structural properties of a non-glandular trichome, was thought to be, typically, non-glandular. This assumption was reinforced by many hours of observing *L. camilla* and *H. fuciformis* caterpillars swiping these trichomes without observing secretion flow. However, field observations eventually showed the occasional sticky globule attached to the tip of unicellular trichomes on *L. periclymenum* leaves which did not contain foraging caterpillars. In addition, lepidopteran leaf-rolls of micro-moth caterpillars occasionally revealed secretion from this type of trichome. Scanning electron microscopy of chopped trichomes from *L. camilla* piers and mid-rib silk platforms showed these trichomes to have internal vascular structures. Schnepf and Klasova (1972) referred to the "oil secreting hairs" of *L. periclymenum* but made no reference to secretion of the unicellular trichome. However, in contrast to the impedimentary effects, this study has never revealed any adverse effects of the unicellular trichome secretion on the foraging behaviour of *L. camilla* and *H. fuciformis* caterpillars.

Both *L. camilla* and *H. fuciformis* females chose oviposition sites of trichome density which were intermediate between minimum and maximum available densities. Eggs of both Lepidoptera were found to be within 1 mm of unicellular trichomes and often surrounded by them. The ovipositing females of both species had the opportunity of laying their eggs on leaf parts which were almost devoid of these trichomes but they always rejected this opportunity. The egg site location chosen by *L. camilla* females is most unusual in Lepidoptera. With no exception in this study, the eggs

were always laid within 2 mm of the adaxial margin, about half way along between base and leaf tip which was a relatively long way (15 caterpillar lengths at emergence time) from the first feeding position near the leaf tip.

Impedimentary influence of the unicellular trichome was shown by transferring freshly emerged 1st instar *L. camilla* caterpillars onto dense trichome sites of *L. periclymenum* leaves. The caterpillars found mobility on top of the trichomes almost impossible. They were forced to cut a path through the jungle of trichomes using their mandibles. However, this activity was only possible if the caterpillars had purchase of the leaf cuticle with their anal claspers. Without such purchase caterpillars would hang onto trichomes with their thoracic legs until, in many cases, they would fall off the leaf. In some cases they remained in the same position for 24 hours without making any lateral movement. Considering this impedimentary influence of the unicellular trichome, it is puzzling why *L. camilla* females did not locate their eggs on the laminal areas of the leaf surface close to the leaf tip which would have allowed the 1st instar caterpillars to avoid most of the trichomes. Perhaps, *L. camilla* females had more important factors to consider involving caterpillar survival on the leaf cuticle.

H. fuciformis females located their eggs on the abaxial laminae of host leaves. In contrast to the shade host foliage of *L. camilla*, the abaxial laminal site of sun *L. periclymenum* foliage contains fewer trichomes but they are even less dense on the adaxial leaf surface. *H. fuciformis* 1st instar caterpillars revealed little difficulty in coping with the unicellular trichomes they encountered during feeding bouts. They appeared to be stronger than 1st instar *L. camilla* caterpillars with a more vigorous lateral swiping motion of their heads as they mowed pathways through the trichomes. However, they also had difficulties in coping with very dense areas of trichomes during a transfer experiment but, in contrast to *L. camilla* caterpillars, they quickly negotiated a pathway to a suitable feeding location.

The midrib and other major veins were protected to a greater degree than the laminal areas by housing a greater density of unicellular trichomes which were swiped clean by both species of caterpillar before using them as pathways. Again, *L. camilla* 1st instar caterpillars went one stage further by laying down a platform of silk which completely covered the trichome stumps (Chapter Four).

Unlike ovipositing *L. camilla* females, *H. fuciformis* did not completely alight on the leaf surface during the act of oviposition. With wings in full motion and tarsi skidding over the adaxial leaf surface, *H. fuciformis* females gave the impression that their intention was to locate the egg anywhere on the abaxial leaf surface with little thought to possible trichome adversity. In contrast, *L. camilla* females alighted on the adaxial leaf surface and spent several seconds probing with their ovipositor prior to oviposition.

Although *L. camilla* 1st instar caterpillars reveal a greater difficulty in coping with dense areas of unicellular trichomes compared to *H. fuciformis* 1st instar caterpillars, under natural conditions, female *L. camilla* locate their eggs on the leaf surface in such a position as to avoid the most dense areas of trichomes and, hence, alleviate their adverse effect on movement.

Further evidence of caterpillar - foodplant leaf surface interactions will be made in the following chapter based on observations during caterpillar survival bioassays.

6.4.2 Effect of foodplant nutrients on oviposition strategy.

The quality of a caterpillar's foodplant can affect its feeding rate and therefore the quantity eaten which, in turn, can affect caterpillar survival. Feeding rates of *L. camilla* and *H. fuciformis* caterpillars will be one of the aims of feeding rhythms considered in Chapter Seven. The results of the analysis of *L. periclymenum* foliage showed little difference in total carbon, total nitrogen and water content between shade and sun host foliage for *L. camilla* and *H. fuciformis* respectively. These factors, alone, cannot explain why *L. camilla* caterpillars spend approximately four months feeding in the caterpillar stage (excluding diapause) compared with 4-5 weeks in the case of *H. fuciformis* caterpillars. The nutritive quality of foodplants is rarely optimal in terms of meeting nutritional requirements. Total carbon and nitrogen in *L. periclymenum* was at its highest values in early season growth in April. This optimal nutrient period, especially in the case of total nitrogen, was used by post-diapause *L. camilla* caterpillars but pre-diapause caterpillars fed on host foliage at its lowest nutrient level in July and August. *H. fuciformis* caterpillars fed on its host in its mid-nutrient level in June. Thus, *L. camilla* caterpillars utilise the advantage of high nitrogen content foodplant in their post-diapause period when caterpillar mass increase is greatest and consume their foodplant at its lowest nitrogen content in pre-diapause period when rapid caterpillar mass increase is not required.

This seasonal trend of decrease in leaf nutrients shown in this study for *L. periclymenum* is similarly reflected in many plants (Slansky and Scriber, 1985). For example, total nitrogen in oak foliage can decrease from 5-2 % in the period April-August compared to 3.7-1.8 % for *L. periclymenum* for the same period as shown in this study. There is normally a similar decrease in water content of plants during the year (e.g., oak: 75-60 %). In this study the water content of *L. periclymenum* showed a limited decrease of 74-68 %. Nutrient contents of caterpillar foodplants may show important variation according to conditions of temperature and shade. In this study sun *L. periclymenum* growth showed a slight increase in the region of 0.5-1.0 % in total carbon over shade growth for each of the four sampling months April to July. A similar comparison between habitat foliage for total nitrogen showed no overall difference as was the case with water content with the exception of the lastsampling period (July) when sun foliage showed a decrease of 8% compared to shade growth.

H. fuciformis caterpillars feeding on sun *L. periclymenum* foliage in June utilise the higher ambient temperature which increases their growth rate but at the possible expense of predation from birds and parasitoid wasps which may locate the caterpillars more easily in open vegetation.
In comparison, *L. camilla* caterpillars feed at lower temperatures in shady conditions producing lower growth rates but with less exposure to predation.

6.4.3 Effect of leaf toughness on oviposition strategy.

Leaf toughness is a major constraint in caterpillar foraging and many lowland tropical leaves are protected from caterpillars by being tough (Coley, 1983). However, any one leaf is not uniformly tender or tough. The first penetrometer examination of *L. periclymenum* foliage showed that there was no difference in toughness between the main laminal areas of leaves. However, the major vein system was purposely avoided in toughness measurement throughout all examinations of foliage since the main aim was to compare the toughness of laminal areas of shade and sun *L. periclymenum* and other bioassay foodplants. Penetrometer measurements of the major veins showed that they were 2-3 times more tough than the laminal zones which is reflected by the reluctance of the first three instars of both *L. camilla* and *H. fuciformis* caterpillars to feed on these leaf parts. Indeed, both species utilised the major midrib strength by using this part of the leaf as a major pathway during foraging operations. *L. camilla* 1st instar went further and extended the midrib tip by constructing a refuge as previously described in Chapter Four.

Unfortunately, the penetrometer method of measuring toughness used in this study was unable to measure the toughness of very small leaf zones (e.g., 2 mm^2) which are probably crucial to the successful feeding strategy of *L. camilla* 1st instar caterpillars. This caterpillar, immediately after emergence, has to penetrate the marginal leaf tip areas of its feeding leaf in order to construct its defence refuge. Inability to carry out this task may result in fitness decline and ultimate demise. This possibility is explored in the caterpillar survival bioassays referred to in Chapter Eight. In contrast *H. fuciformis* 1st instar caterpillars make their first penetration of the leaf surface in the less tough areas of the leaf laminal zones The smaller and probably weaker mandibles of *L. camilla* 1st instar caterpillars are more suited to the less tough foliage of *L. periclymenum* shade oviposition foliage. Mandibular strength may also be a crucial factor in coping with foodplant secretion which is considered in the following section.

Leaf quality tends to decline as leaves age, with nitrogen and water concentrations decreasing and fibre and toughness increasing (Scriber and Slansky, 1981). In this study *L. periclymenum* sun foliage produced its greatest toughness value from the latest sampling period in June (36% higher than the first sampling period in April). Similarly, *L. periclymenum* shade foliage produced its highest toughness in the last sampling period in July (47 % higher than the first sampling period in

April). During each sampling period *L. periclymenum* sun foliage was more tough than shade foliage.

6.4.4 Effect of leaf secretion on oviposition strategy.

Sticky secretion has been shown to originate from three sources in *L. periclymenum* foliage - unicellular and multicellular trichomes, and epidermal cells ruptured through caterpillar feeding damage. The former source of secretion, via multicellular glandular trichomes, appears to be effective in deterring lepidopteran caterpillars from foraging in parts of the hostplant where this type of trichome is concentrated (inflorescence). Secretion flow is triggered from this type of trichome by physical contact rupturing the trichome head cell.

The unicellular trichome is typically non-glandular but, on rare occasions, which are not necessarily triggered by the presence of insects on the leaf cuticle, secretion has been observed from the ruptured tip of the trichome. The main effectiveness of this type of trichome as a hostplant anti-predator mechanism has been shown to be through its impedimental character against caterpillar mobility.

The main source of sticky secretion is via the ruptured epidermal cells of the *L. periclymenum* foliage during caterpillar feeding and possibly by tarsal rupturing of the leaf cuticle. Early instar caterpillars of *H. fuciformis* and *L. camilla* were observed to leave a trail of secretion on sun foliage *L. periclymenum* laminal areas when artificially placed there.

Explanation of this type of secretion may involve the rupture of the canalicular network by tarsal or mandibular damage. High turgid pressure may force secretion through the ruptured cells causing foraging caterpillars to stop feeding. The multicellular and unicellular trichomes of *L. periclymenum,* as they are both potentially glandular, may be also part of a canalicular network (Mahlberg *et al.*, 1984),

Foodplant secretion causing a decline in caterpillar survival has been observed with several species of Lepidoptera from other studies. Dussourd (1993) devised an experiment to test the effect of plucked leaves (causing depressurised latex canals) of the laticiferous foodplant *Lactuca serriola* (= *scariola*, Asteraceae) on the caterpillar survival of yellow-striped armyworms (*Spodoptera ornithogalli*) and cabbage loopers (*Trichoplusia ni*). *Spodoptera ornithogalli* caterpillars of all instars survived well on plucked leaves, showing rapid growth and development in contrast to survival on live leaves. In the latter case only a few early instar caterpillars successfully moulted to their next instar. Dead first and second instar caterpillars were often found with their mandibles stuck together with dried latex, sometimes still glued to the leaf at the feeding point. However, the cabbage loopers survived well on both plucked and live leaves of their foodplant by employing a

successful adaptation strategy. The first instar caterpillars fed between leaf veins and avoided the possibility of rupturing the latex canal system.

Further evidence from bioassay studies for the adverse effect of secretion and the way in which *L. camilla* and *H. fuciformis* caterpillars adapt to secretion will be examined and discussed in Chapter Seven.

Chapter Seven

The effect of foodplant quality on caterpillar survival

Caterpillar growth - adaptability - feeding rhythms - activity traits

7.1 Introduction

7.1.1 Concluding aims of study.

The survey of habitat requirements of *L. camilla* and *H. fuciformis* (Chapter Five) established that *L. camilla* females preferred to oviposit on *L. periclymenum* growing in shade. In contrast *H. fuciformis* females preferred to oviposit on *L. periclymenum* growing in open woodland which received considerable sunlight. *H. fuciformis* was chosen as a reference species because out of the total lepidopteran community feeding on *L. periclymenum*, *H. fuciformis* showed the greatest contrast to *L. camilla* in oviposition habitat preference.

Investigations into the quality of *L. periclymenum* foodplant (Chapter Six) between shade and sun growth revealed a significant difference in terms of secretion, toughness, trichome density but not nutrients. The final stage of this study reveals how the caterpillars of both species cope with feeding on their foodplant which has been growing in alien habitats. That is, *L. camilla* caterpillars will be forced to feed on *L. periclymenum* foliage which has been growing in the sunny habitat of *H. fuciformis* and *H. fuciformis* caterpillars will be forced to feed on its foodplant which has been growing in the shady habitat of *L. camilla.* In addition to these two habitat forms of *L. periclymenum*, other foodplants will be used which have been selected for various characteristics which were shown to be important in the results of the quality of oviposition foliage (Chapter Six).

The main purpose of the no-choice assays (caterpillars are forced to attempt to feed on a given foodplant with no alternative foodplant available) was to determine how an important characteristic of a foodplant affected caterpillar survival and the ability to carry out evolutionary behavioural traits such as refuge and hiberniculum construction, and trichome swiping. The ideal situation would have been when an individual foodplant or treatment exhibits a single outstanding characteristic in force in contrast to all other characteristics which would have been negligible in force. Using natural foodplants as opposed to artificial food makes this ideal situation difficult to attain. Artificial food would not have allowed *L. camilla* and *H. fuciformis* to display their evolutionary leaf - caterpillar interactions which are important features of their behavioural ecology. Thus, bioassay foodplants were chosen if they exhibited an important character in strength compared to other, weaker, characteristics. Previous study had shown that sun foliage of *L. periclymenum* was outstandingly strong in sticky secretion produced by caterpillar feeding damage but of lower trichome density

compared to shade foliage of *L. periclymenum* which produced negligible secretion but was of high trichome density. Replication of strong sticky secretion in alternative, palatable, foodplants was impossible. However, it was possible to replicate palatable foodplants which had no trichomes (*S. rivularis* and *L. caprifolium*). In addition to physical attributes which affected foodplant quality, chemical attributes in the form of nutrient composition also affects foodplant quality so all these features were measured in the foodplants used and will have be considered before drawing conclusions from assay results.

The assays took place in two stages. The first stage was carried out in 1994 when *L. camilla* caterpillar survival was compared using the two forms of *L. periclymenum* foliage - sun growth and shade growth (natural oviposition foliage). In addition, caterpillar survival of *H. fuciformis* was compared using sun growth *L. periclymenum* foliage (natural oviposition foliage) and *Symphoricarpos rivularis*. The latter foodplant was chosen because, in contrast to sun foliage *L. periclymenum, S. rivularis* lacks secretory properties when damaged and is devoid of trichomes. Also, this foodplant is unlikely to contain any unusual toxic secondary compounds as *S. rivularis* has been recorded as a rare natural foodplant of *H. fuciformis*.

The 1995 assay included a wider range of food plant and foodplant quality. *L. camilla* caterpillar survival was compared between three types of conspecific host, *L. periclymenum* foliage shade and two sources of sun foliage - aerial growth (natural oviposition foliage) and ground foliage which, for some unknown reason, was never used as natural oviposition foliage by either *L. camilla* or *H. fuciformis*. Two additional foodplants were used: *Lonicera caprifolium* and *Symphoricarpos rivularis* on account of their total lack of trichomes and non-secretory foliage.

The results of the 1994 bioassay experiments revealed unusual 1st instar behavioural traits involving foraging caterpillars and foodplant leaf surface structure. To gain more knowledge in this area of interaction, the feeding rhythms of the 1st instar caterpillars were investigated using time-lapse video recording.

Successful adaptation to alien foodplants or foodplants with abnormal qualities may require metabolic adjustment and the ability to carry out unusual evolutionary behavioural traits under stressful circumstances. Feeding techniques or mechanisms evolved on a particular foodplant having specific qualities may not succeed on alien foodplants or when the normal foodplant qualities change.

7.1.2 Summary of foodplants used in bioassays.

7.1.2.1 Bioassay: 1994.

L. camilla

L. periclymenum (shade) natural oviposition foliage vs. *L. periclymenum* (aerial sun) foliage. No - choice experiment.

H. fuciformis

L. periclymenum (sun) natural oviposition foliage vs. S. rivularis foliage. No - choice experiment.

7.1.2.2 Bioassay: 1995

L. camilla

L. periclymenum (shade) natural oviposition foliage vs. *L. periclymenum* (aerial sun) foliage vs. *L. periclymenum* (ground sun) foliage vs. *L. caprifolium* foliage vs. *S. rivularis* foliage. No - choice experiment.

H. fuciformis

L. periclymenum (sun) natural oviposition foliage vs. *L. periclymenum* (aerial shade) foliage vs. *L. periclymenum* (ground sun) foliage vs. *L. caprifolium* foliage. No - choice experiment.

7.1.2.3 Summary of aims of bioassays for *L. camilla* and *H. fuciformis*

The main aim of assays was to compare caterpillar growth rate and adaptability when feeding on oviposition foodplant with *L. periclymenum* from alternative habitat and other foodplants which differed in trichome density, toughness and secretion. Caterpillar adaptability in this study is defined as the ability to adopt a healthy growth rate measured in terms of length of instar period, mortality frequency, maximum caterpillar length, pre-ecdysis period, refuge construction (*L. camilla* only), pupal mass (*H. fuciformis* only), diapause frequency (*L. camilla* only) and feeding rhythm traits.

7.2 Method and materials

7.2.1 Measurement of caterpillar growth rate.

To make sure that any abnormal caterpillar growth or behavioural traits recorded were the result of feeding on alien foodplant rather than bioassay technique, caterpillar growth rate was not measured by the usual techniques associated with transfer assay experiments.

Caterpillar growth rate is normally measured by using the index G.R. = G/TA where G = fresh or dry weight gain of animal during feeding period; T = duration of feeding period (days); and A = mean fresh or dry weight of animal during the feeding period (Waldbauer, 1968). Other indices are used such as consumption index and digestibility and efficiency index.

In all cases the daily weight of the animal is measured which necessitates the continual removal and replacement, in the case of lepidopteran caterpillars, of test specimen from the feeding surface of the plant. This procedure may impair any important cuticular - caterpillar interaction and introduces further variables to the test arena if natural food, as opposed to artificial bait or pellets, is the source of caterpillar food. In this study these interactions are considered as an important part of caterpillar survival and the basic assumption is that caterpillars of both *L. camilla* and *H. fuciformis* do not forage randomly on the leaf surface. Therefore, the following bioassays did not involve continual removal and replacement of caterpillars from the leaf surface. The growth rate was measured by recording instar period length.A previous study which used caterpillar length as a measure of caterpillar growth rate was that undertaken by Rausher and Papaj (1983b) on the pipevine swallowtail (*Battus philenor*) in which a separate experiment had shown that caterpillar length and biomass were highly correlated.

Separate caterpillar instars were identified according to caterpillar appearance, body length and head width. Imminent ecdysis between instars was identified by cessation of feeding, bulging thorax and head down posture. Length measurements were recorded every day and at the same time of day for each instar.

7.2.2 Source of foodplants.

All *L. periclymenum* foodplants used in all bioassays were obtained directly from natural growth located in suitable areas of Bentley Wood. Control (oviposition foliage containing eggs) foodplant rosettes were taken as cuttings from their natural drapes, stored in rain water and kept at 5 °C prior to their use in experiment. Shade and sun growth *L. periclymenum* used as treatment foliage was obtained in a similar manner from their respective habitats in Bentley Wood. Shade growth *L. periclymenum* was obtained from plantation drapes which had been used by ovipositing female *L. camilla,* and sun growth *L. periclymenum* was obtained from clearing drapes which had been used by ovipositing female *H. fuciformis.* The cuttings were always in the form of rosettes taken at the time of natural oviposition in their respective habitats in Bentley Wood. All oviposition *L. periclymenum* drapes were aerial growth. Ground growing *L. periclymenum* foliage was obtained from open sunny clearings in Bentley Wood. It was used as a treatment foodplant because both *L. camilla* and *H. fuciformis* were never found naturally ovipositing on *L. periclymenum* in this habitat and inclusion as a bioassay treatment may reveal possible explanations. *L. caprifolium* treatment foliage was grown from seed obtained from natural sources and cuttings of leading shoots were

used in bioassay experiments. *S. rivularis* cuttings used as treatment foliage were obtained from a mature plant growing in Bentley Wood.

The food plant shoot, in the form of a rosette, was placed in a test tube of rain water (pH in the range 5 - 7) for storage prior to, and during, bioassay. The cutting having been removed a short time earlier (no longer than 24 hours) from its drape growing in Bentley Wood. Earlier experimentation with *L. periclymenum* cuttings had shown that cuttings can last for several months in water and still produce leaf secretion, in the case of sun foliage, when prompted through leaf damage of the epidermis.

In the 1994 bioassay the control consisted of a replication of 10 rosette shoots of oviposition foliage taken from plantation shade growth with each shoot containing a single egg. The treatment consisted of 22 rosette shoots taken from drapes growing in full sun in clearings. Ten of the 22 caterpillars emerged from eggs which had been artificially attached to the sun foliage leaves at the usual *L. camilla* egg location on the upper margin. The other 12 replicates had caterpillars transferred to the sun foliage treatment leaf 24 hours after emerging and feeding on their natural oviposition egg leaf. The purpose of this variation in treatment was to determine possible acclimatisation to alien sun secretory foliage after spending 24 hours immediately after emergence feeding on natural non - secretory foliage.

7.2.3 Source of *L. camilla* and *H. fuciformis* eggs.

All *L. camilla* and *H. fuciformis* caterpillars and eggs used in bioassay were obtained from natural oviposition sites in Bentley Wood. Eggs were obtained in batches so that embryonic development was at a similar stage and emergence occurred simultaneously for bioassay experimentation. When necessary eggs were stored for short periods at 5 °C.

7.2.4 Bioassay environment.

Since one of the main aims of bioassay experimentation was to observe feeding rhythms and behavioural traits on natural foodplants, the use and re-production of natural conditions as far as possible was attempted for bioassay environment. The natural 24 hour temperature cycle was reproduced by using a bioassay room with no artificial heating or lighting and maintained with outdoor temperatures, light and humidity through open windows in a well ventilated room. The bioassay laboratory was situated approximately 500 m from Bentley Wood and transport of materials from the natural habitat to bioassay arena was achieved quickly and with little disturbance. Temperature (maximum and minimum) and humidity were recorded daily and natural photoperiod was used. All foodplant cuttings were used in bioassay within 24 hours of their removal from their natural locations.

7.2.5 Growth rate indicators used during bioassay experimentation.

7.2.5.1 Instar period length.

Caterpillar growth rate was measured by recording the length of instar period in days. Ecdysis was identified by temporary cessation of feeding, bulging thorax and head down posture (Plates 7.1b-c).

7.2.5.2 Caterpillar length.

Caterpillar length was recorded on a daily basis as an indicator of caterpillar development and approaching ecdysis. In the pre-ecdysis period caterpillar length remains constant in the early instars and decreases in the later instars for both *L. camilla* and *H. fuciformis*.

7.2.5.3 Foliage secretion.

In the 1994 bioassay secretion was recorded on a daily basis as simply present or not when feeding caterpillars and foodplant foliage were examined. The presence of secretion on the leaf received 1 unit and its absence received 0 units. The presence of secretion flowing from foliage caterpillar feeding damage was easily identified and noticed as a viscous colourless liquid (later turning to a pale yellow solid). The daily secretion units were summed for the total caterpillar period (instar 1-5).

In 1995 bioassays the amount of feeding damage secretion was recorded by estimating the fraction of leaf area feeding damage producing secretion. In the case of *H. fuciformis* feeding damage the fraction of feeding damage holes exhibiting secretion flow was determined. For example, a daily inspection of caterpillar feeding damage producing no sign of secretion received 0 units, observable secretion in only a few of the holes present received 1 unit, observable secretion in about half of the holes present received 2 units and observable secretion in most of the holes present received a maximum of 3 units.

For the *L. camilla* 1995 bioassay a similar procedure was adopted. In contrast to *H. fuciformis*, *L. camilla* feeds by cutting foliage strip sections ("flags") and observable secretion in only a small fraction of linear strip feeding damage received 1 unit, observable secretion in about half of the linear strip feeding damage received 2 units and observable secretion in most of the linear strip feeding damage received a maximum of 3 units. The daily secretion units were summed for the total caterpillar period (instar 1-5).

7.2.5.4 *L. camilla* refuge construction.

In the 1995 bioassay the length of leaf midrib (created by feeding caterpillars stripping laminae either side of midrib after refuge construction) and midrib extension (refuge or defence pier) were measured on a daily basis. As this construction must involve considerable expenditure of energy at a crucial period of caterpillar growth, its measurement and rate of construction was considered to be a possible indicator of any stress created by abnormal foodplant quality. This measurement was restricted to *L. camilla* only since *H. fuciformis* did not participate in leaf appendage construction.

7.2.5.5 Pre-ecdysis period.

Ecdysis in arthropods is the periodic moulting and shedding of the cuticle in the course of caterpillar growth. There are 5 such caterpillar moults or ecdysis in the development of both *L. camilla* and *H. fuciformis* caterpillars, the final ecdysis producing pupae. The timing and mechanism of ecdysis is controlled by hormones (Harborne, 1988). Juvenile hormone is required only during the first ecdysis of caterpillar development while the moulting hormone is required at every ecdysis stage. Both hormones must be present at the right time and in the right amount for normal caterpillar development and are normally synthesised by secondary metabolism of foodplant material. Alien or abnormal foodplant sources may interfere with hormonal production and cause abnormal ecdysis resulting in abnormal instar periodicity and overall caterpillar growth. With both *L. camilla* and *H. fuciformis* the act of ecdysis takes 3 - 6 minutes. Pre-ecdysis period is the period between temporary cessation of caterpillar feeding and the terminal instar moult. This period was recorded in bioassay as a possible additional indicator of caterpillar survival and adaptability.

7.2.5.6 Pupal mass (1995 *H. fuciformis* only).

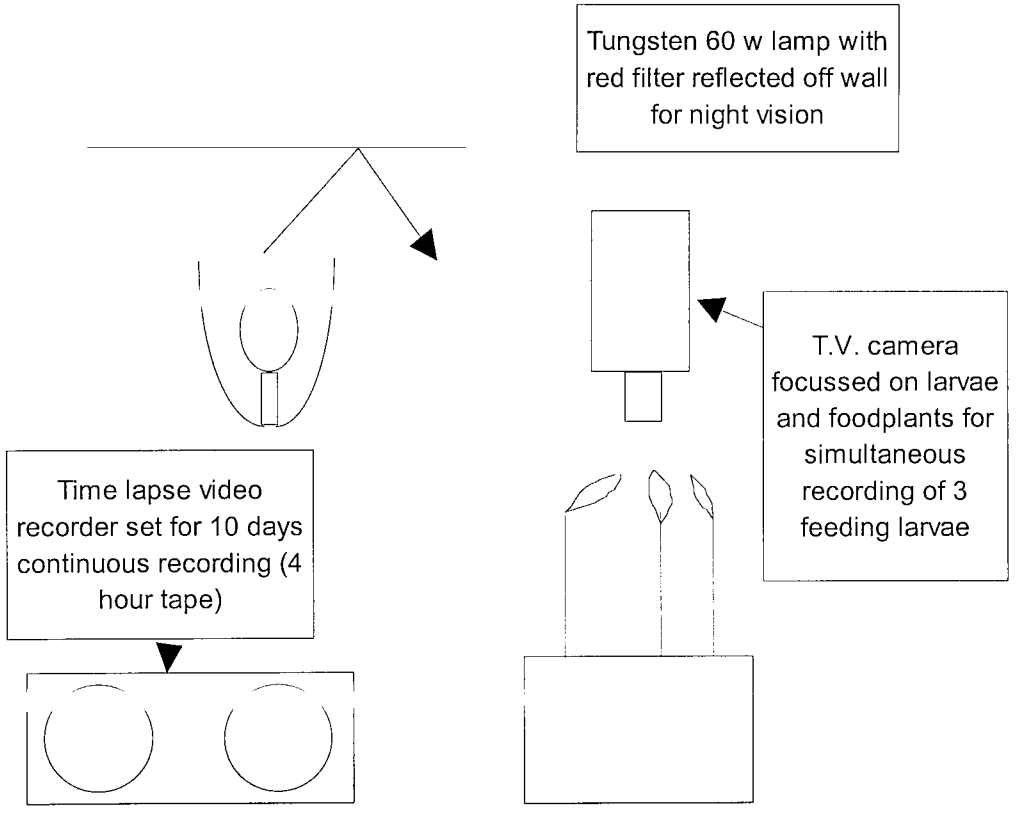
H. fuciformis pupal mass was recorded as a survival indicator two months after pupation. Pupae were carefully removed from their cocoon, weighed, and replaced. The cocoons were re-sealed to avoid predation. Pupal mass measurement was not attempted in the case of *L. camilla* pupae as this measurement would have entailed the destruction of the cremaster (anal silk joint to supporting vegetation).

7.2.6 Measurement of feeding rhythms.

In this study caterpillar feeding rhythm was measured as the relative amounts and periodic sequence of time spent in carrying out individual foraging traits on the leaf surface during caterpillar development. Feeding rhythm measurement was confined to 1st instar periods of *L. camilla* and *H. fuciformis* caterpillars feeding on shade and sun *L. periclymenum* foliage for both species with the additional foodplant of *S. rivularis* for *L. camilla*.

The procedure involved focusing a TV camera (Panasonic: WV - 1550 - B) onto the foodplant leaf holding the feeding caterpillars and recording the picture on a time - lapse video (Panasonic: NV - 8051 - B). The caterpillar foraging behaviour was continuously recorded throughout the 1st instar period. Night - time recording was carried out using a red 60 watt tungsten lamp. The foraging arena and environmental conditions were identical to those of the main bioassay experiments. It was only possible to record the foraging behaviour of 2 or 3 caterpillars simultaneously. Since it was necessary to replicate 2 or 3 different foodplants, only one caterpillar per foodplant was used.

Fig. 7.1 Time lapse video recording arena of caterpillar feeding rhythms.



7.2.7 Bioassay descriptions.

7.2.7.1 *L. camilla*: 1994.

Foodplants.

Control: *L. periclymenum* oviposition foliage (shade); low-secretory, high trichome density.

Treatment : *L. periclymenum* sun foliage; high-secretory, medium trichome density.

Transfer caterpillars compared with non-transfer caterpillars.

Recorded caterpillar survival indicators.

Instar period, caterpillar length, mortality and diapause frequencies.

Bioassay environmental conditions.

Temperature: 16 - 25 °C; humidity: 33 - 45 %; photoperiod: natural.

Statistics.

Sample means and standard error. Mann-Whitney U-test applied to instar periods between control and treatment.

Null Hypothesis (H_o): there is no statistically significant difference between the medians of sample instar periods between control and *L. periclymenum* sun foliage.

7.2.7.2 *L. camilla*: 1995.

Foodplants.

Control: *L. periclymenum* shade (oviposition); low-secretory, high trichome density foliage.

Treatments:

1. *L. periclymenum* sun: high-secretory, medium trichome density foliage.
2. *L. periclymenum* ground: medium secretory, medium trichome density foliage.
3. *L. caprifolium:* low secretory, non-trichome foliage.
4. *S. rivularis:* non-secretory, non-trichome foliage.

Recorded caterpillar survival indicators.

Instar period, caterpillar length, pre-ecdysis period, pier and pier extension (refuge) length, foodplant secretion, mortality and diapause frequencies.

Bioassay environmental conditions.

Temperature: minimum 20.1 ± 0.2 (mean ± S. E.); maximum 24.1 ± 0.2. Humidity: 32.2 ± 0.8.

Statistics.

Sample means and standard error. Kruskal-Wallis K-test was applied to caterpillar survival indicators for difference of sample medians between all foodplants.

Null Hypothesis (H_o): there is no statistically significant difference between the medians of sample caterpillar survival indicators (per instar) between all foodplants; if H_o is rejected the extent of the difference is discussed.

Mann-Whitney U-test was applied to caterpillar survival indicators for difference of sample median indicators between control and *L. periclymenum* sun foliage.

Null Hypothesis (H_o): there is no statistically significant difference between the medians of sample caterpillar survival indicators between control and *L. periclymenum* sun foliage.

7.2.7.3 *H. fuciformis* : 1994.

Foodplants.

Control: *L. periclymenum* oviposition foliage (sun); high-secretory, medium trichome density.
Treatment : *S. rivularis* foliage; non - secretory, very low trichome density.

Recorded survival indicators.

Instar period, caterpillar length and foodplant secretion

Bioassay environmental conditions.

Temperature: 15 - 23 °C; humidity: 31 - 40 %; photoperiod: natural.

Statistics.

Sample means and standard error. Mann-Whitney U-test applied to instar periods between control and treatment. The same Null Hypothesis used for *L. camilla* assay is used for *H. fuciformis* assay.

7.2.7.4 *H. fuciformis* : 1995.

Foodplants with important properties.

Control: *L. periclymenum* oviposition foliage (sun); high-secretory, medium trichome density.
Treatment (1): *L. periclymenum* shade foliage ; low-secretory, high trichome density.
Treatment (2): *L. periclymenum* ground foliage ; low-secretory, medium trichome density.

Recorded caterpillar survival indicators.

Instar period, caterpillar length, pre-ecdysis period, pupal mass and foodplant secretion.

Bioassay environmental conditions.

Temperature.

Mean daily minimum 16.9 ± 0.2 °C; mean daily maximum 21.5 ± 0.2 °C.

Humidity.

Daily mean 32.3 ± 0.6 %

Statistics.

Sample means and standard error. Kruskal-Wallis K-test applied to growth rate characteristics between control and 2 treatments. The same Null Hypothesis used for *L. camilla* assay is used for *H. fuciformis* assay.

Following page.

Plate 7.1a Caterpillar bioassay arena. p. 7-12

Plate 7.1b Appearance of *L. camilla* caterpillar (4th instar) during pre-ecdysis period: head down, bulging thorax (x 4). p. 7-12

Plate 7.1c Appearance of *H. fuciformis* caterpillar (4th instar) during pre-ecdysis period: head down, bulging thorax (x 10). p. 7-12

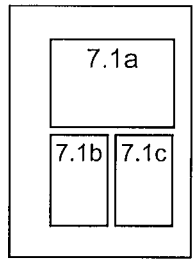


Plate 7.1

7.3 Results.

7.3.1 *Ladoga camilla*: caterpillar survival.

7.3.1.1 Bioassay: 1994 (Table 7.1 and Table 7.7).

The Null Hypothesis (H_0) was rejected ($p < 0.05$) for each individual instar period 1, 2, 3, 4 and also for the total instar period 1-4 between *L. periclymenum* oviposition shade foliage (control) and *L. periclymenum* sun foliage. Instar caterpillar lengths for both control and treatment foodplants were almost identical. Foodplant secretion was negligible in control foliage but considerable in 1st and 2nd instar feeding periods on the treatment sun foliage.

There was no statistically significant difference ($p > 0.05$) between transfer and non-transfer caterpillar instar period in both 1st and 2nd instar for *L. periclymenum* sun foliage. There were too few surviving caterpillars left in other instars for statistical comparison.

Under natural conditions *L. camilla* caterpillars enter diapause during the 3rd instar in contrast to the bioassay results where both diapause and non-diapause were exhibited. There was 100 % non-diapause (caterpillars pupated) with caterpillars feeding on oviposition foliage. In the case of *L. periclymenum* sun foliage 32 % (7 out of 22) of the original sample or 50 % (7 out of 14) of the survivors entered diapause. There were contrasting results in diapause frequency between transfer and non-transfer caterpillars feeding on *L. periclymenum* sun foliage. In the case of transfer caterpillars 50 % (6 out of 12) of the original sample or 67 % (6 out of 9) of the 3rd instar survivors entered diapause. In contrast only 10 % (1 out of 10) of the original non-transfer caterpillars or 20 % (1 out of 5) of the 3rd instar survivors entered diapause.

L. camilla caterpillars feeding on *L. periclymenum* sun treatment foliage suffered 36 % (8 out of 22) mortality with 87 % (7 out of 8) occurring during the 1st instar. Of these mortalities 62 % (5 out of 8) occurred with non-transfer caterpillars and 38 % (3 out of 8) occurred with transfer caterpillars. (Transfer caterpillars were those which had been allowed to feed on natural oviposition foliage for 24 hours before being transferred to sun foliage. Non-transfer caterpillars were forced to feed on sun foliage immediately after emergence.) All surviving *L. camilla* caterpillars after the 2nd instar which had been feeding on sun foliage had successfully completed the construction of a defence refuge in their 1st instar. Of the 14 surviving caterpillars feeding on sun foliage, 10 needed more than one attempt before successfully completing a defence refuge. Of 8 mortalities only 1 caterpillar had successfully completed the construction of a defence refuge.

All control and non-diapause caterpillars feeding on *L. periclymenum* sun foliage pupated normally and produced normal adults in early September in the same year as the assay. However, 71 % (5 out of 7) of the diapause caterpillars did not survive the diapause period whereas the two survivors

produced normal adults. All diapause caterpillars successfully constructed hibernacula. Adult normality was identified by apparently normal flight behaviour and size. Diapause caterpillars had been stored in a well ventilated un-heated out-house during the winter months in which the lowest temperature recorded was -3 °C.

7.3.1.2 Bioassay: 1995.

7.3.1.2.1 *L. camilla*: instar period.(Table 7.2).

The Null Hypothesis (H_o) was rejected ($p < 0.05$) for instars 1 and 1-5 (full caterpillar period) between *L. periclymenum* oviposition shade (control) foliage and *L. periclymenum* sun foliage. For instars 2, 3, 4 and 5 the N.H. (H_o) was accepted ($p > 0.05$). However, the instar period sample means for instars 1-5 showed a greater instar period length for caterpillars feeding on *L. periclymenum* sun foliage.

The N.H. (H_o) was rejected ($p < 0.05$) for each of the five instars and the full caterpillar period when all five foodplants were compared. The lowest sum of instar period sample ranks (R/n) featured the foodplant *L. caprifolium* in instars 1, 2, 3, 4 and 1-5. The greatest sum of instar period sample ranks featured *L. periclymenum* sun foodplant in instars 1, 3, 4, and the full caterpillar period.

In general, *L. periclymenum* sun foliage produced the longer instar periods with one exception and that was the 2nd instar sample feeding on *S. rivularis* (which produced an unusually high proportion of diapause caterpillars). Caterpillars feeding on *L. caprifolium* produced unusually short instar periods in instars 1 to 4.

7.3.1.2.2 *L. camilla*: maximum instar caterpillar length (Table 7.3).

The N.H. (H_o) was accepted ($p > 0.05$) for all five instars periods.

7.3.1.2.3 *L. camilla*: pre-ecdysis period.(Table 7.4).

The N.H. (H_o) was accepted ($p > 0.05$; Kruskal-Wallis K-test) for pre-ecdysis instar medians between all foodplants. The N.H. (H_o) was accepted ($p > 0.05$; Mann-Whitney U-test) for pre-ecdysis instar medians between *L. periclymenum* shade foliage (control) and *L. periclymenum* sun foliage. The highest mean value of pre-ecdysis period was produced by caterpillars feeding on *S. rivularis* during the second instar. This foodplant produced the highest diapause numbers, 82 % (9 out of 11), which occurred during the third instar.

7.3.1.2.4 *L. camilla*: pier and pier extension (refuge) length.(Table 7.5; Figure 7.2).

Pier length (PL).

The pier length was the length of leaf midrib (including refuge) created by feeding *L. camilla* caterpillars during the 1st and 2nd instars. The N.H. (H_o) was accepted ($p > 0.05$; Kruskal-Wallis K-test) for caterpillars feeding on all foodplants during the 1st and 2nd instars. The N.H. (H_o) was accepted ($p > 0.05$; Mann-Whitney U-test) for caterpillars feeding on control and *L. periclymenum* sun foliage.

Pier extension length (PE).

The pier extension or defence refuge was constructed immediately after emergence during the 1st instar. The N.H. (H_o) was rejected ($p < 0.05$; Kruskal-Wallis K-test) for caterpillars feeding on all foodplants during the 1st instar. The greatest sum of ranks (R/n) was produced on *S. rivularis* while the lowest sum of ranks was produced equally by *L. periclymenum* shade and *L. caprifolium* foliage.

7.3.1.2.5 *L. camilla*: foodplant secretion. (Table 7.6).

L. caprifolium and *S. rivularis* never exhibited feeding damage secretion in any instar; *L. periclymenum* shade and ground exhibited minute amounts of secretion in the first two instars. *L. periclymenum* sun foliage produced abundant secretion in the first instar, a mediocre amount in the second instar and minute amounts in the 3rd and 4th instars. Secretion always flowed from caterpillar feeding damage during assay observations and never from trichomes or damaged trichomes.

7.3.1.2.6 *Ladoga camilla* (1994-95): diapause and mortality frequency (Table 7.7).

Mortality.

A similar proportion of *L. camilla* caterpillars mortalities occurred in the 1995 assay (33 %) as occurred in the 1994 assay (36 %) with caterpillars feeding on *L. periclymenum* sun foliage. Caterpillar mortalities normally occurred during the 1st instar period (86 %; 1994-95) and the remainder occurred in the 2nd instar. Nearly all (92 %; 1994-95) mortalities occurred with caterpillars feeding on *L. periclymenum* sun foliage.

Table 7.1 Caterpillar survival: *Ladoga camilla,* 1994. Instar period, caterpillar length and foodplant secretion (mean ± S. E.). Caterpillars feeding on sun foliage were split into two groups: 12 caterpillars were allowed to feed on their natural oviposition foliage for 24 hours before transfer to sun foliage; 10 caterpillars were forced to feed on sun foliage immediately after emergence (non-transfer).

Instar	1	2	3	4	1-4
Lonicera periclymenum : shade foliage (control; N=10)					
Instar period (days)	5.2 ± 0.3	4.5 ± 0.3	3.9 ± 0.2	4.1 ± 0.3	17.7 ± 0.9
Larval length (mm)	3.5 ± 0.1	5.3.± 0.1	7.8 ± 0.2	12.5 ± 0.3	-
Foodplant secretion	0	0.2 ± 0.2	0	0.1 ± 0.1	0.3 ± 0.2
Lonicera periclymenum : sun foliage (total: transfer + non-transfer caterpillars; N=22)					
Instar period (days)	8.6 ± 0.7	6.5 ± 0.5	6.0 ± 0.6	5.4 ± 0.3	24.1 ± 1.4
Larval length (mm)	3.5 ± 0.2	5.2 ± 0.1	7.7 ± 0.2	11.7 ± 0.5	-
Foodplant secretion	5.8 ± 0.8	2.4 ± 0.6	0.7 ± 0.5	0.9 ± 0.6	8.0 ± 2.0
Lonicera periclymenum : sun foliage (non-transfer caterpillars only; N=10)					
Instar period (days)	9.9 ± 1.1	5.5 ± 0.6	6.5 ± 0.3	5.0 ± 0.0	23.5 ± 1.8
Foodplant secretion	7.6 ± 1.2	2.8 ± 1.1	1.3 ± 0.8	0.5 ± 0.5	9.0 ± 3.1
Lonicera periclymenum : sun foliage (transfer caterpillars only; N=12)					
Instar period (days)	7.5 ± 0.8	7.1 ± 0.7	5.3 ± 1.5	6.0 ± 0.6	25.0 ± 2.6
Foodplant secretion	4.3 ± 0.9	2.1 ± 0.7	0	1.3 ± 1.3	6.7 ± 2.9

Mann-Whitney U-test for difference in caterpillar instar period between *L. periclymenum* shade (control) and sun foliage. For instars 2, 3, 4 and 1-4, the total sun foliage sample was used (less mortalities). For instar 1 only the non-transfer caterpillars were used for statistical comparison.

Instar	1	2	3	4	1-4
U value	7.50	25.50	9.50	10.50	5.00
Significance	< 0.05	< 0.05	< 0.05	< 0.05	< 0.05
Degrees of freedom	10 x 10	10 x 15	10 x 7	10 x 7	10 x 7

Diapause.

Under natural conditions *L. camilla* caterpillars normally enter diapause after constructing hibernicula in the early stages of the 3rd instar. Out of a combined assay total of 78 surviving caterpillars 32 % entered diapause exactly as they do under natural conditions. The remainder, 78 %, carried straight through to pupation and adult emergence a few weeks later. In 1994 no caterpillars feeding on natural oviposition foliage entered diapause compared to 30 % in 1995.

Table 7.2 Caterpillar survival (II): *Ladoga camilla,* 1995, instar period (days; mean ± S.E.).

	Instar					
Foodplant	1	2	3	4	5	1-5
1. L. periclymenum (shade)	6.2 ± 0.4	4.9 ± 0.4	3.7 ± 0.3	4.7 ± 0.2	5.5 ± 0.2	25.0 ± 0.5
2. L. periclymenum (sun)	8.2 ± 0.4	7.6 ± 1.9	4.2 ± 0.6	5.7 ± 0.6	5.7 ± 0.3	30.3 ± 1.8
3. L. periclymenum (ground)	6.3 ± 0.2	5.0 ± 0.5	4.1 ± 0.3	4.4 ± 0.3	5.7 ± 0.2	22.2 ± 1.0
4. L. caprifolium	5.2 ± 0.1	3.8 ± 0.3	1.5 ± 0.2	3.6 ± 0.3	7.0 ± 0.4	21.2 ± 0.6
5. S. rivularis	6.3 ± 0.4	8.1 ± 0.7	Diapause			
Kruskal-Wallis K-test for difference between all foodplants.						
K value	29.4	21.6	20.1	11.1	10.53	19.51
Degrees of freedom [c]	4	4	3	3	3	3
Significance (NS at p=0.05)	< 0.01	< 0.01	< 0.01	< 0.05	< 0.05	< 0.01
Greatest sum of R/n [a]	46.5 (2) [b]	44.4 (5)	23.9 (2=3)	26.3 (2)	25.5 (4)	33.6 (2)
Lowest sum of R/n [a]	13.9 (4)	14.3 (4)	6.5 (4)	10.4 (4)	13.8 (2)	11.1 (4)
Mann-Whitney U-test for difference between *L. periclymenum* : shade and sun only.						
U value (lower)	17.5	42.5	39.5	15.5	28.5	7
Degrees of freedom	14 x 9	13 x 8	13 x 8	10 x 6	10 x 6	10 x 6
Significance (NS at p=0.05)	< 0.05	NS	NS	NS	NS	< 0.05

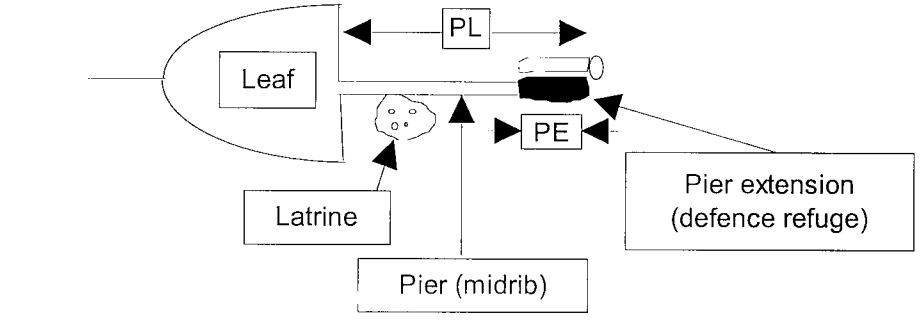
a: the greatest and lowest values of sum of ranks (R) / sample size (n).
b: numbers in parentheses refer to foodplants in the left hand side column.
c: degrees of freedom or sample size allowed for mortalities and diapause larvae: initial sample size for each of the foodplants 1-5 was 14, 12, 11, 11, and 11 respectively.

Table 7.3 Caterpillar survival (III):*Ladoga camilla,* 1995, maximum larval length (mm; mean ± S.E.).

	Instar				
Foodplant	1	2	3	4	5
1. L. periclymenum (shade)	3.5 ± 0.1	4.9 ± 0.1	7.4 ± 0.1	11.9 ± 0.1	21.0 ± 0.1
2. L. periclymenum (sun)	3.0 ± 0.2	5.1 ± 0.1	7.1 ± 0.2	12.8 ± 0.2	22.2 ± 0.2
3. L. periclymenum (ground)	3.1 ± 0.1	4.8 ± 0.2	6.9 ± 0.1	12.0 ± 0.1	21.0 ± 0.4
4. Lonicera caprifolium	3.6 ± 0.1	5.7 ± 0.2	7.3 ± 0.4	11.5 ± 0.4	21.1 ± 0.3
5. Symphoricarpos rivularis	3.1 ± 0.1	4.9 ± 0.1	6.7 ± 0.2	Diapause	Diapause

Kruskal-Wallis K-test for difference between all foodplants, 5th instar:
K=3.1; d. of f. = 3; NS (p=0.05).
Sample size in 5th instar allowed for mortalities and diapause larvae: initial sample size for each of the foodplants 1-5 was 14, 12, 11, 11, and 11 respectively.

Fig.7.2 *Ladoga camilla* pier (PL), pier extension (PE) or defence refuge and latrine construction on *L. periclymenum* foodplant leaf.



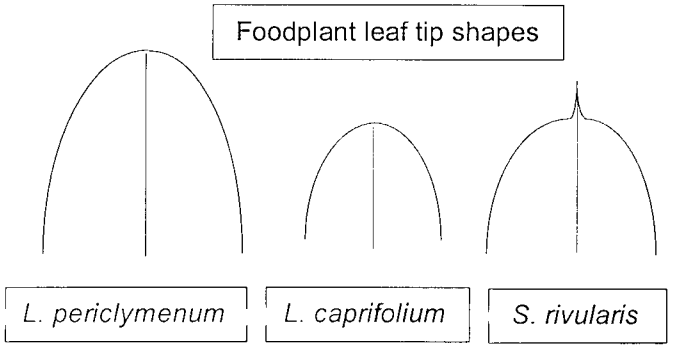


Table 7.4 Caterpillar survival (IV): *Ladoga camilla,* 1995, pre-ecdysis period (days; mean ± S.E.).

	Instar					
Foodplant	1	2	3	4	5	1-5
1. L. periclymenum (shade)	1.4 ± 0.2	1.9 ± 0.2	1.4 ± 0.2	1.6 ± 0.2	1.0 ± 0.0	7.1 ± 0.5
2. L. periclymenum (sun)	0.9 ±0.3	1.5 ±0.4	0.6 ±0.3	1.5 ±0.5	1.1 ±0.1	5.6 ±1.0
3. L. periclymenum (ground)	1.3 ±0.1	1.8 ±0.3	0.5 ±0.2	0.7 ±0.2		4.4 ±0.2
4. Lonicera caprifolium	1.2 ±0.2	1.0 ±0.1	0.6 ±0.3	0.9 ±0.1		3.7 ±0.3
5. Symphoricarpos rivularis	1.1 ±0.2	2.5 ±0.2				
Kruskal-Wallis K-test for difference in pre-ecdysis period between all foodplants.						
K value	5.33	4.83				15.25
Degrees of freedom [c]	4	4				3
Significance (NS at p=0.05)	NS	NS				< 0.01
Greatest sum of R/n [a]	30.4 (2=3) [b]	37.6 (5)				32.1 (1)
Lowest sum of R/n [a]	22.0 (2)	14.7 (4)				11.8 (4)
Mann-Whitney U-test for difference between L. periclymenum: shade and sun only.						
U value (lower)	36.5	41				27.5
Degrees of freedom	13 x 8	13 x 8				10 x 8
Significance (NS at p=0.05)	NS	NS				NS

a: the greatest and lowest values of sum of ranks (R) / sample size (n).
b: numbers in parentheses refer to foodplants in the left hand side column.
c: degrees of freedom or sample size allowed for mortalities and diapause larvae: initial sample size for each of the foodplants 1-5 was 14, 12, 11, 11, and 11 respectively.

Table 7.5 Caterpillar survival (V): *Ladoga camilla*, 1995, pier length (PL) and pier extension length (PE; defence refuge, mm, mean ±S.E.).

	1st instar		2nd instar	
Foodplant	PE	PL	PE	PL
1. L. periclymenum (shade)	2.0 ± 0.1	12.2 ± 0.9	2.1 ± 0.1	21.8 ± 1.6
2. L. periclymenum (sun)	2.2 ± 0.3	11.8 ± 1.5	2.3 ± 0.3	20.6 ± 1.6
3. L. periclymenum (ground)	2.1 ± 0.1	12.7 ± 1.0	2.1 ± 0.1	NFA [d]
4. Lonicera caprifolium	2.1 ± 0.2	10.7 ± 1.0	1.9 ± 0.2	21.0 ± 2.0
5. Symphoricarpos rivularis	3.0 ± 0.3	10.5 ± 0.5	2.8 ± 0.3	22.6 ± 1.8
Kruskal-Wallis K-test: PE/PL difference between all foodplants.				
K value	23.4	4.7		0.32
Degrees of freedom [c]	4	4		3
Significance (NS at p=0.05)	p < 0.01	NS		NS
Greatest sum of R/n [a]	46.6 (5)	35.0 (3)		18.8 (5)
Lowest sum of R/n [a]	26.0 (4=1)	21.1 (4=5)		16.2 (4=2)
Mann-Whitney U-test: PE/PL difference between L. periclymenum (shade and sun only).				
U value (lower)	69.5	48.5	37	31.5
Degrees of freedom	14 x 12	13 x 8	13 x 8	13 x 5
Significance (NS at p=0.05)	NS	NS	NS	NS

a: the greatest and lowest values of sum of ranks (R) / sample size (n).
b: numbers in parentheses refer to foodplants in the left hand side column.
c: degrees of freedom or sample size allowed for mortalities and diapause larvae: initial sample size for each of the foodplants 1-5 was 14, 12, 11, 11, and 11 respectively.
d: NFA = no fixed abode (larvae no longer use refuge).

Table 7.6 Caterpillar survival (VI): *Ladoga camilla,* 1995, foodplant secretion (mean ± S.E.).

	Instar					
Foodplant	1	2	3	4	5	1-5
1. L. periclymenum (shade)	0.1 ± 0.1	0.1 ± 0.1	0	0	0	0.3 ± 0.2
2. L. periclymenum (sun)	9.8 ± 1.9	3.1 ± 1.6	0.3 ± 0.3	0.3 ± 0.3	0	15.1 ± 3.2
3. L. periclymenum (ground)	0.6 ± 1.1	0	0	0	0	0.6 ± 1.1
4. L. caprifolium	0	0	0	0	0	0
5. S. rivularis	0	0	0	0	0	0

Method of quantifying secretion is based on fraction of area of caterpillar feeding damage producing secretion (see Chapter Six).
Sample size for each of the foodplants 1-5 was 14, 12, 11, 11, and 11 respectively.

Table 7.7 Caterpillar survival (VII): *Ladoga camilla,* 1994-95, diapause and mortality frequency.

Foodplant	Diapause	Non-diapause	Mortalities
1995 bioassay			
L. periclymenum: shade (N=14)	3 (21%)	10 (71%)	1 (7%)
L. periclymenum: sun (N=12)	2 (17%)	6 (50%)	4 (33%)
L. periclymenum: ground (N=11)	4 (36%)	7 (64%)	0 (0%)
L. caprifolium (N=11)	0 (0%)	11 (100%)	0 (0%)
S. rivularis (N=11)	9 (82%)	2 (18%)	0 (0%)
1994 bioassay			
L. periclymenum shade (N=10)	0 (0%)	10 (100%)	0 (0%)
L. periclymenum sun (N=22)	7 (32%)	7 (32%)	8 (36%)

Most mortalities occurred during 1st instar (18/21=86%) and remainder in 2nd instar.
Diapause occurred during 3rd instar.

7.3.2 *L. camilla:* feeding rhythm (Table 7.8; Figures 7.3-4).

Four basic activity traits were separately identified by time-lapse video recording of feeding *L. camilla* caterpillars during the 1st instar: refuge construction, cuticular preparation, feeding and resting. Latrine construction is included in the cuticular preparation category for the purposes of this section. Cuticular preparation for *L. camilla* 1st instar caterpillars involved trichome swiping, creating silk platforms and pathways, latrine construction and repair of latrine. All recorded periods of activity traits included time taken for caterpillars to travel the return journey from and to leaf tip refuge. Compared to the overall activity periods this travelling time was relatively short (5-10%). (Resting is regarded as an activity trait.)

The proportions of frequencies of 1st instar caterpillar activity traits between the three foodplants *L. periclymenum* sun and shade foliage and *S. rivularis* was statistically different (χ^2 test for homogeneity, $\chi^2 = 49$; d. of f. = 6; $p < 0.01$). The trait which produced the greatest contribution to the chi squared value was preparation. The *L. camilla* caterpillar feeding on *S. rivularis* carried out less than half the number of preparation tasks as it did on *L. periclymenum* sun and shade foliage. This difference in preparation trait of foodplants was due to the almost total lack of trichomes on *S. rivularis*.

The ratio of preparation, feeding, and resting activity periods (based on fraction of activity to total instar period) between the three foodplants *L. periclymenum* (shade), *L. periclymenum* (sun) and *S. rivularis* were 1 : 1.7 : 6.4; 1 : 2.4 : 4.1; 1 : 4.8 : 13.8, respectively.

For all three foodplants most time was spent resting followed by feeding, preparation and refuge construction in order of decreasing total activity time. However, the *L. periclymenum* sun caterpillar spent about 50% longer during feeding bouts than the *L. periclymenum* shade caterpillar and about 100% longer than the *S. rivularis* caterpillar. Indeed, the *S. rivularis* caterpillar exhibited the shortest mean feeding bout but the highest feeding frequency of all three foodplants.

The *S. rivularis* caterpillar spent approximately half the total cuticular preparation time of the *L. periclymenum* shade and sun caterpillars. The *S. rivularis* and *L. periclymenum* sun caterpillars spent approximately twice as long as the *L. periclymenum* shade caterpillar constructing their refuges.

With resting, feeding and preparation traits the range of time spent in activity bouts was considerable (x 15 to x 100). The periodicity or sequence (regularity) of activity trait was regular in the major middle period of instar but irregular at the beginning and end periods of the 1st instar.

Table 7.8 Larval feeding rhythm (I): *L. camilla* 1st instar activity trait duration (mean ± S.E.) on 3 foodplants: *L. periclymenum* sun and shade foliage, and *S. rivularis*.

	Resting	Feeding	Preparation	Refuge
L. periclymenum (shade)				
Mean duration (minutes: ± S.E.)	14.2 ± 0.7	4.75 ± 0.2	5.52 ± 0.5	1.50 ± 0.2
Minimum duration (minutes)	1	1	1	1
Maximum duration (minutes)	96	18	26	3
Frequency	277	228	110	16
Total activity time (hours)	65.60	18.05	10.12	0.40
Fraction of instar period	0.70	0.19	0.11	0.00
L. periclymenum (sun)				
Mean duration (minutes: ± S.E.)	8.70 ± 0.4	7.24 ± 0.2	4.67 ± 0.4	2.23 ± 0.2
Minimum duration (minutes)	1	1	1	1
Maximum duration (minutes)	57	22	40	6
Frequency	320	221	144	35
Total activity time (hours)	46.42	26.67	11.20	1.30
Fraction of instar period	0.54	0.31	0.13	0.02
S. rivularis				
Mean duration (minutes: ± S.E.)	9.65 ± 0.3	3.62 ± 0.1	3.83 ± 0.4	2.59 ± 0.3
Minimum duration (minutes)	1	1	1	1
Maximum duration (minutes)	32	15	19	7
Frequency	330	301	64	34
Total activity time (hours)	53.07	18.17	4.08	1.47
Fraction of instar period	0.69	0.24	0.05	0.02

Data relates to the behaviour of a single larva for each foodplant during the 1st instar.

Fig. 7.3 *L. camilla* larval feeding rhythm (I): 1st instar sequential periodicity of activity traits on 3 foodplants (*L. periclymenum* sun and shade foliage, and *S. rivularis*).

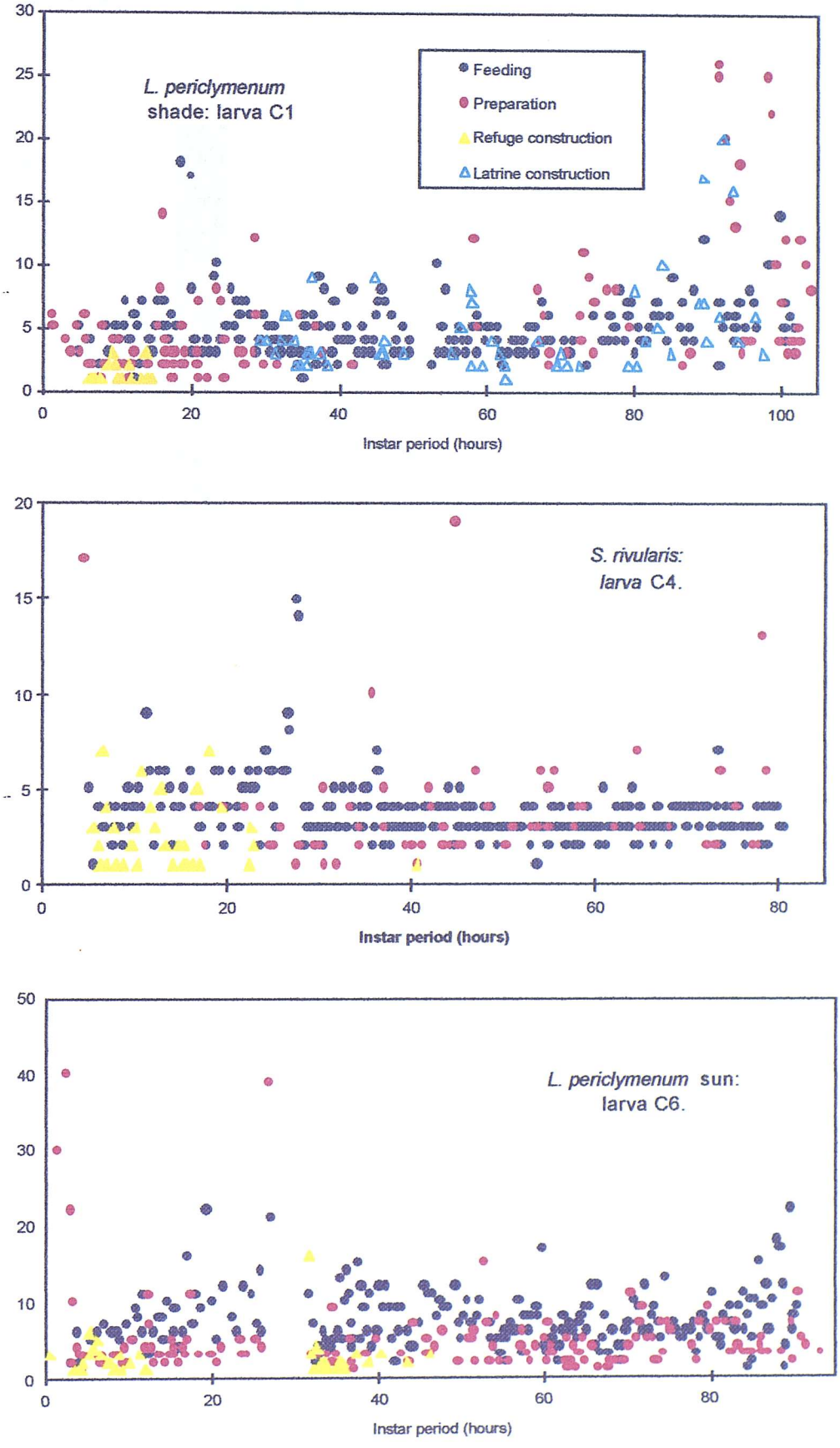
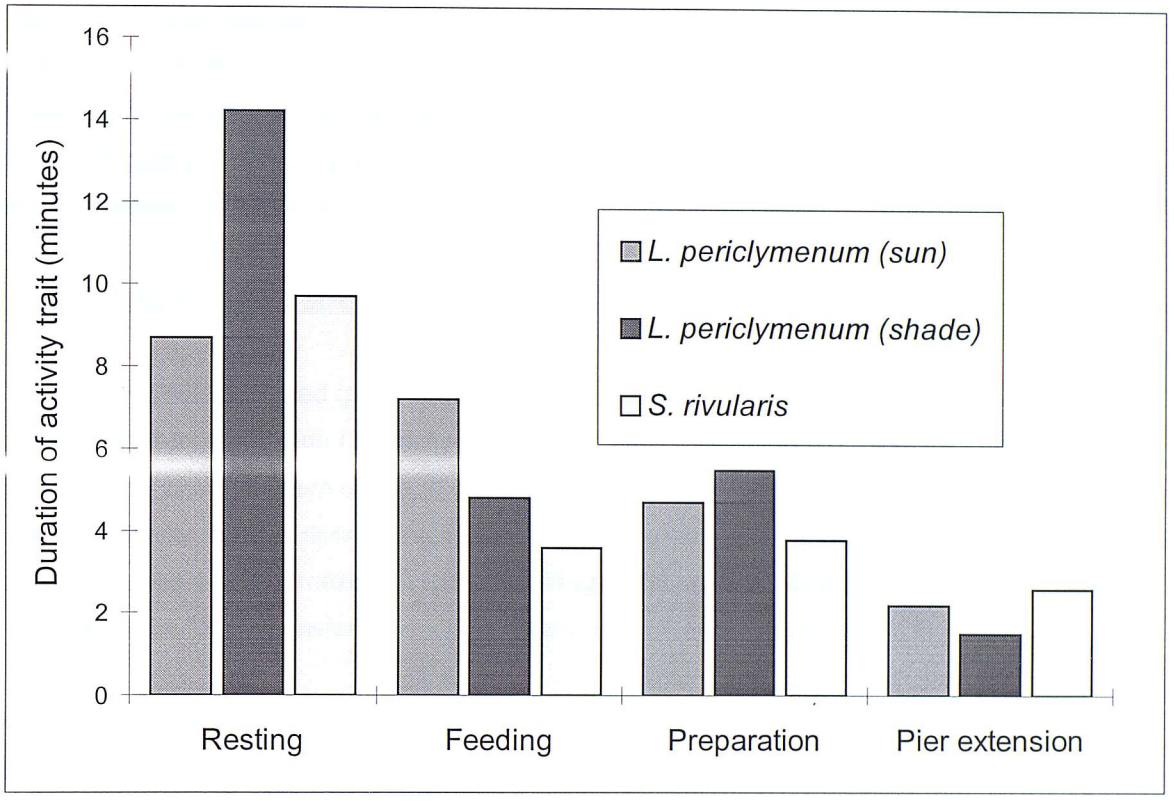


Fig. 7.4 *L. camilla* larval feeding rhythm (II): 1st instar activity trait duration for foodplants *L. periclymenum* (sun and shade foliage), and *S. rivularis*.



7.3.3 *Hemaris fuciformis*: caterpillar survival.

7.3.3.1 Bioassay 1994 (Table 7.9).

The N.H. (H_0) was rejected ($p < 0.05$) for the full caterpillar period of *H. fuciformis* caterpillars feeding on *S. rivularis* compared with *L. periclymenum* natural oviposition foliage. This difference arose due to slight but statistically significant ($p < 0.05$) increased lengths of 2nd and 3rd instar periods of caterpillars feeding on *S. rivularis*. Caterpillar lengths of both foodplant samples were almost identical. All pupae eventually produced normal adults.

7.3.3.2 Bioassay: 1995 (Table 7.10).

The N.H. (H_0) was accepted ($p > 0.05$) for the full caterpillar period (instar 1-5) of *H. fuciformis* caterpillars when feeding on *L. periclymenum* oviposition foliage (control) and the three treatment foodplants, *L. periclymenum* shade, *L. periclymenum* ground, *L. caprifolium* foliage. Each foodplant showed a similar trend of decreasing instar period in the instar range 1-3 before increasing again in the instar range 4-5. The maximum caterpillar length and pre-ecdysis indicators revealed almost identical values for each instar for each foodplant (see mean and S.E. values in Table 7.10).

As expected foodplant secretion values showed a considerable difference between sun *L. periclymenum* oviposition foliage (maximum amount) and the three treatment foodplants, *L. periclymenum* shade, *L. periclymenum* ground, *L. caprifolium* foliage (very small amount).

There was no statistically significant difference ($p > 0.05$) in pupal mass between *H. fuciformis* caterpillars which had been feeding on all four foodplants, *L. periclymenum* oviposition foliage (control) and three treatment foodplants, *L. periclymenum* shade, *L. periclymenum* ground, *L. caprifolium* foliage (0.95 ± 0.04 and 0.85 ± 0.02, 0.89 ± 0.02, 0.89 ± 0.02, (g), respectively).

Table 7.9 Caterpillar survival (VIII)*: Hemaris fuciformis,* 1994, all indicators (mean ± S.E.).

	Instar					
	1	2	3	4	5	1-5
Foodplant: *Lonicera periclymenum* (sun foliage; control; N=9)						
Instar period (days)	4.6 ± 0.2	4.3 ± 0.3	5.1 ± 0.3	6.2 ± 0.2	6.7 ± 0.3	26.9 ± 0.4
Larval length (mm)	6.6 ± 0.1	11.4 ± 0.3	15.7 ± 0.2	22.9 ± 0.2	38.4 ± 0.4	-
Foodplant secretion	0.77 ± 0.04	0.46 ± 0.04	0	0	0	-
Foodplant: *Symphoricarpos rivularis* (N=15)						
Instar period (days)	4.8 ± 0.2	5.3 ± 0.3	5.8 ± 0.2	6.5 ± 0.3	6.6 ± 0.2	28.9 ± 0.5
Larval length (mm)	6.6 ± 0.1	11.5 ± 0.1	16.0 ± 0.2	22.3 ± 0.2	37.7 ± 0.4	-
Foodplant secretion	0	0	0	0	0	-
Mann-Whitney U-test for difference of instar periods between foodplants.						
Instar	1	2	3	4	5	1-5
U-value	55	32.5	10.5	62.5	-	28.5
Degrees of freedom	9 x 15	9 x 15	9 x 15	9 x 15	-	9 x 15
Significance (p=0.05)	NS	NS	NS	NS	-	$p < 0.05$

Table 7.10 *Caterpillar survival* (IX): *Hemaris fuciformis*, 1995, all indicators (mean ± S.E.).

	Instar					
	1	2	3	4	5	1-5
Foodplant: *Lonicera periclymenum* sun foliage (control; N=9)						
Instar period (days)	6.6 ± 0.4	6.3 ± 0.2	5.4 ± 0.3	5.7 ± 0.2	6.7 ± 0.3	30.7 ± 0.6
Larval length (mm)	7.1 ± 0.1	10.9 ± 0.2	15.0 ± 0.4	22.7 ± 0.4	37.1 ± 0.6	-
Pre-ecdysis (days)	2.3 ± 0.5	1.9 ± 0.3	1.3 ± 0.2	1.7 ± 0.2	7.2 ± 0.5	6.4 ± 0.3
Foodplant secretion	9.1 ± 1.2	8.4 ± 1.1	5.4 ± 1.2	0.8 ± 0.4	0	23.8 ± 2.5
Foodplant: *Lonicera periclymenum* shade foliage (N=11)						
Instar period (days)	7.2 ± 0.7	5.4 ± 0.2	5.2 ± 0.4	5.8 ± 0.3	7.4 ± 0.4	30.9 ± 0.8
Larval length (mm)	6.8 ± 0.1	10.8 ± 0.2	15.3 ± 0.2	22.6 ± 0.2	37.1 ± 0.7	-
Pre-ecdysis (days)	1.2 ± 0.2	1.4 ± 0.2	1.3 ± 0.2	1.6 ± 0.2	5.4 ± 0.3	6.5 ± 0.2
Foodplant secretion	4.4 ± 1.1	0.8 ± 0.3	0.1 ± 0.1	0	0	5.3 ± 1.1
Foodplant: *Lonicera periclymenum* ground foliage (N=11)						
Instar period (days)	7.5 ± 0.4	5.9 ± 0.5	5.2 ± 0.3	5.2 ± 0.2	6.4 ± 0.3	30.2 ±1.3
Larval length (mm)	7.1 ± 0.1	10.6 ± 0.2	15.4 ± 0.2	22.4 ± 0.2	37.7 ± 0.5	-
Pre-ecdysis (days)	1.4 ± 0.2	1.8 ± 0.3	1.3 ± 0.1	1.7 ± 0.1	6.3 ± 0.3	6.4 ± 0.3
Foodplant secretion	3.0 ± 0.9	1.8 ± 1.0	0.1 ± 0.1	0	0	4.9 ± 1.8
Foodplant: *Lonicera caprifolium* (N=10)						
Instar period (days)	6.3 ± 0.4	5.2 ± 0.3	5.7 ± 0.5	5.0 ± 0.1	6.1 ± 0.3	28.3 ± 0.9
Larval length (mm)	7.1 ± 0.1	11.2 ± 0.2	15.7 ± 0.3	22.5 ± 0.2	37.4 ± 0.7	-
Pre-ecdysis (days)	1.4 ± 0.4	1.6 ± 0.2	1.4 ± 0.2	1.7 ± 0.1	6.1 ± 0.5	6.7 ± 0.4
Foodplant secretion	0.5 ± 0.3	0	0	0	0	0.5 ± 0.3

Kruskal-Wallis K-test for difference between foodplants.

	Instar	K value	D. of f. [d]	p [e]
Instar period	1-5	4.17	3	NS [c]
Larval length [a]	5	1.21	3	NS
Pre-ecdysis	1-4	5.68	3	NS
Secretion [f]	1-5	18.5	2 [b]	< 0.01
Pupal mass		3.7	3	NS

a: instar maximum larval length; b: L. periclymenum foodplants only; c: not significant ($p > 0.05$);
d: degrees of freedom; e: statistical significance; f: see section 7.2 for secretion units.

7.3.4 *H. fuciformis:* feeding rhythm (Table 7.11: Figures 7.5-6).

Three basic activity traits were separately identified by time-lapse video recording of feeding *H. fuciformis* caterpillars during the first instar: cuticular preparation, feeding and resting. Cuticular preparation simply involved trichome swiping creating clear pathways to and from its resting location which was on the abaxial midrib of the food leaf.

The relative proportions of frequencies of 1st instar caterpillar activity traits between *L. periclymenum* sun (oviposition) and *L. periclymenum* shade foodplants were found to be statistically not significant ($p > 0.05$).

The ratio of preparation, feeding and resting periods (based on fraction of instar period) between the two foodplants were 1.6 : 1 : 6.4, and 1.6 : 1 : 8.4, respectively.

For both foodplants caterpillars spent most time resting and least time feeding. The caterpillar feeding on *L. periclymenum* shade foliage spent more time swiping trichomes but its resting bouts were shorter than the *L. periclymenum* sun caterpillar. The range of all activity trait duration was considerable (x 10 - x 100).

Fig. 7.5. *H. fuciformis* larval feeding rhythm (II): 1st instar activity trait duration on foodplants *L. periclymenum* sun and shade foliage.

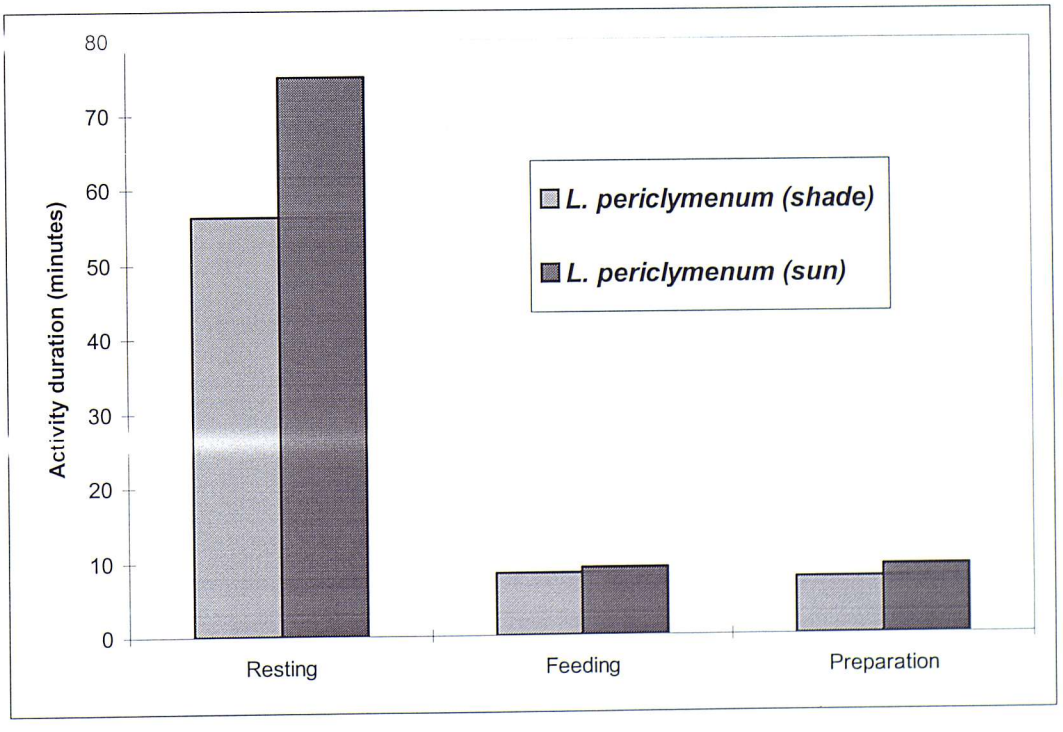
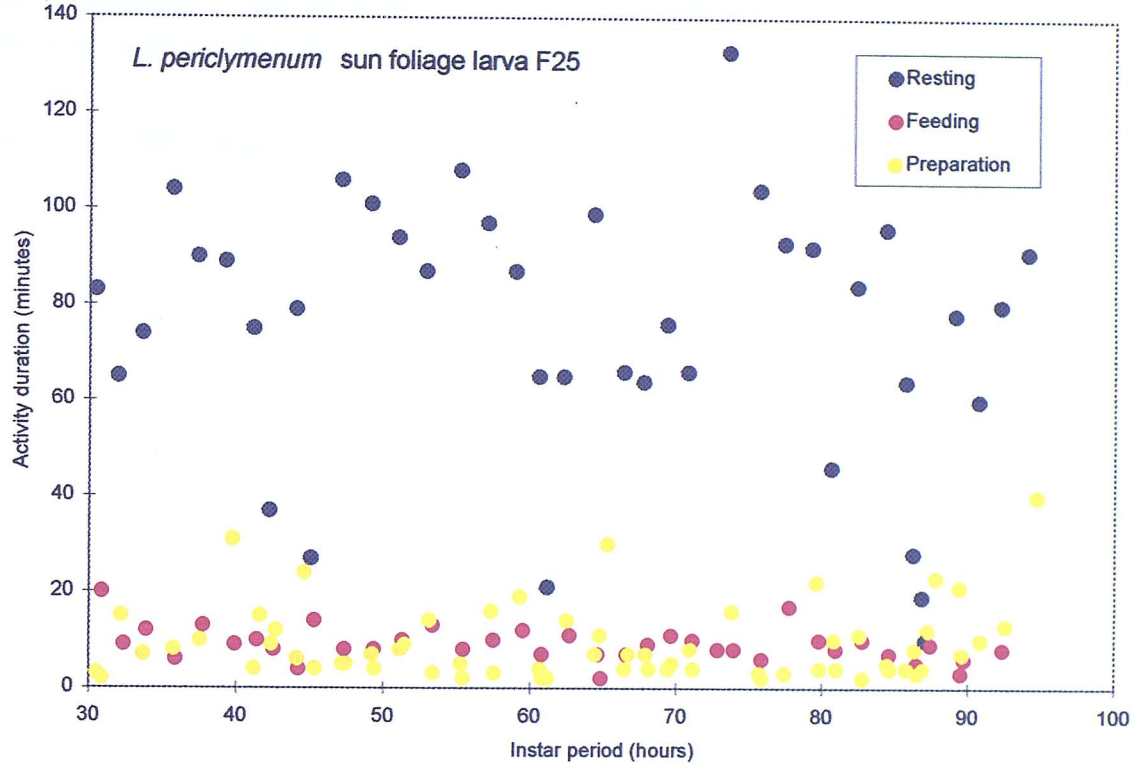


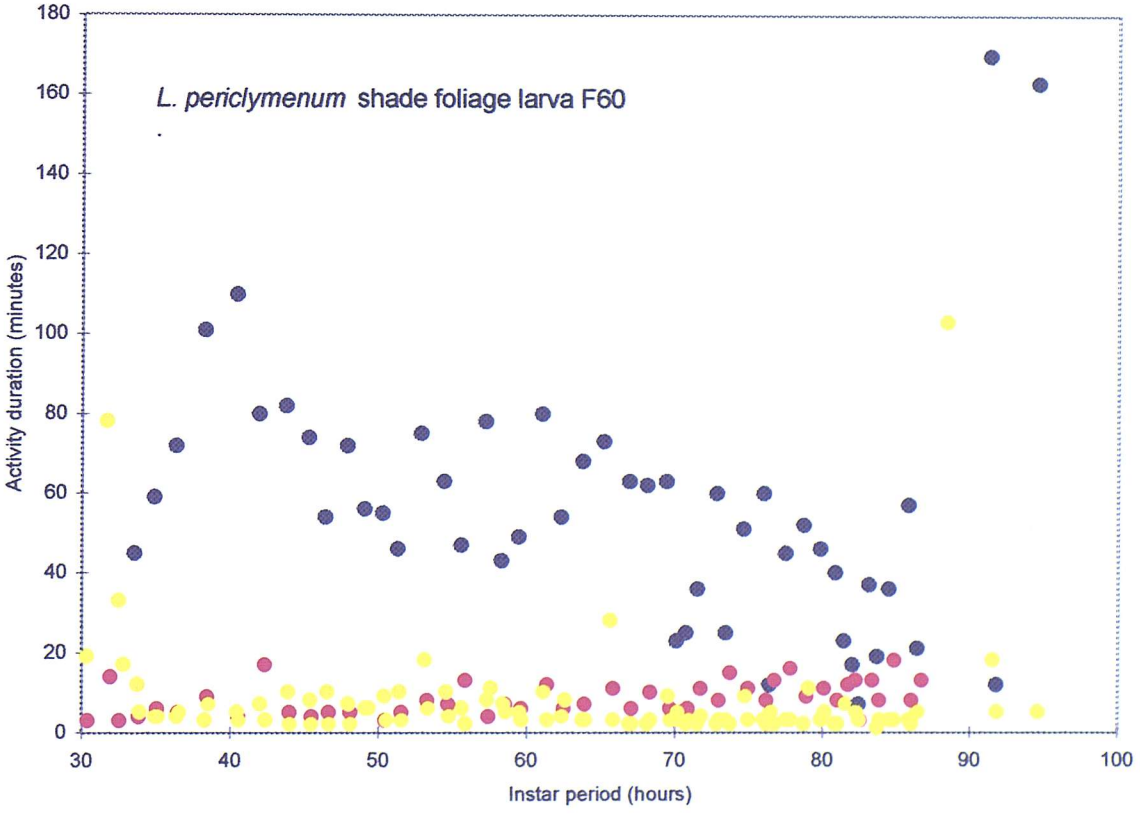
Table 7.11 Larval feeding rhythm (II): *H. fuciformis* 1st instar activity trait duration.

	Resting	Feeding	Preparation
L. periclymenum : shade foliage.			
Mean duration ± S.E. (minutes)	56.3 ± 4.6	8.37 ± 0.6	7.52 ± 1.4
Minimum duration (minutes)	7	3	1
Maximum duration (minutes)	170	18	103
Frequency	49	49	94
Total activity period (hours)	46.02	6.83	11.78
Fraction of instar period	0.71	0.11	0.18
L. periclymenum : sun (oviposition) foliage.			
Mean duration ± S.E. (minutes)	75.1 ± 4.3	9.03 ± 0.6	9.14 ± 1.0
Minimum duration (minutes)	10	2	2
Maximum duration (minutes)	133	20	40
Frequency	40	38	65
Total activity period (hours)	50.05	5.72	9.90
Fraction of instar period	0.76	0.09	0.15

Data relates to the behaviour of a single larva for each foodplant during 1st instar.
χ^2 test for homogeneity of frequencies of traits between foodplants: $\chi^2 = 0.43$;
d. of f. = 2; $p > 0.05$.

Fig. 7.6. *H. fuciformis larval* feeding rhythm (I): 1st instar sequential periodicity of activity traits on *L periclymenum* sun and shade foliage.





7.4 Discussion

7.4.1 Comparison of caterpillar survival of *L. camilla* when feeding on oviposition foliage with alternative foodplants.

7.4.1.1 *L. camilla:* instar period (Tables 7.1-2).

The 1994 *L. camilla* bioassay results showed a reduction in caterpillar survival when *L. camilla* caterpillars fed on *L. periclymenum* foliage which had been growing in open sunny habitats in comparison with caterpillars feeding on oviposition shade foliage. This reduction in caterpillar survival was indicated by increased instar periods and mortalities especially in 1st and 2nd instars. A similar set of results occurred for 1st instar caterpillars in the 1995 bioassay when caterpillar survival was compared between oviposition foliage and *L. periclymenum* foliage growing in sunny clearings. In the 1995 bioassay, for instars 2-5, there was no statistically significant evidence supporting any difference in caterpillar growth when instar period was used as a survival indicator.

However, when all 5 foodplants were compared in the 1995 bioassay, *L. caprifolium* produced the overall shortest early instar periods and *L. periclymenum* sun foliage produced the largest overall instar periods. Unlike *L. periclymenum, L. caprifolium* is devoid of trichomes but since the alternative bioassay foodplant, *S. rivularis,* is also devoid of trichomes, this factor alone cannot explain the short instar periods with *L. caprifolium.* The analysis of bioassay foodplant nutrients (Chapter Six; Tables 6.7-8) showed that *L. caprifolium* contained relatively high water and nitrogen content that may explain the observed short instar periods. Equally, leaf toughness measurements (Chapter Six; Table 6.6) showed that *L. caprifolium* was the least tough foodplant. However, other un-analysed factors such as juvenile hormones may be responsible although the response of a feeding caterpillar to abnormal hormone concentrations usually produces adverse ecdysis effects (Harborne, 1988) which were not observed in the bioassay.

Foodplant secretion levels were shown to be greatest in *L. periclymenum* sun foliage in both 1994 and 1995 bioassays. In the 1995 bioassay alternative foodplants to *L. periclymenum* sun foliage produced negligible secretion although a small number of caterpillars feeding on *L. periclymenum* shade (oviposition) foliage produced small amounts of secretion in feeding damaged areas on the leaf surface. This rare occurrence of secretion on *L. periclymenum* shade foliage was never observed under natural conditions in Bentley Wood except on one occasion when forestry thinning had opened up a plantation which exposed a 4th instar caterpillar and its feeding leaf to sunlight. Also, Thomas (1986) referred to the observation of "seeping nibbled leaves" from a final instar caterpillar feeding on a damaged leaf. This observation supports the observations made in the assays that 4/5th instar caterpillars were able to cope with secretory foodplant. It is possible that a chosen oviposition site by a female *L. camilla* butterfly may be in full shade at the time of

oviposition but, through forestry or natural windblow damage in the winter months, additional sunlight produced secretion in the post-diapause period in spring.

7.4.1.2 *L. camilla*: maximum instar caterpillar length and pre-ecdysis period (Tables 7.3-7.4).

There was no statistically significant difference between foodplants in maximum caterpillar length and pre-ecdysis period for each instar. This result would indicate that the controlling instar size and pre-ecdysis period factors such as juvenile and growth hormones were of a suitable concentration in all bioassay foodplants and a common factor of all CAPRIFOLIACEAE plant species.

7.4.1.3 *L. camilla*: pier and pier extension (defence refuge) length (Table 7.5; Figure 7.2).

Pier length is the length of leaf midrib which is stripped from leaf-tip downwards of laminal foliage on either side of midrib. The fact that there was no statistically significant difference of this factor between all bioassay foodplants for the first two instars indicates a remarkable constant driving force of feeding behaviour character. The only suitable explanation is that any further laminal stripping of the leaf would result in such a bending force which would cause the pier or stripped midrib to collapse under its own weight and assume a vertical position. In such a position rain water would flow down the pier and possibly prevent the caterpillar from foraging properly on the leaf since it is continuously travelling from pier tip (refuge extension) to other parts of the leaf.

There was a statistically significant difference of refuge length between all foodplants. The largest pier extension (Figure 7.2) was produced on *S. rivularis* while the smallest was produced equally by *L. periclymenum* shade (natural oviposition foliage) and *L. caprifolium* foliage. The leaf tip shape of *S. rivularis* (Figure 7.2) was unique in that it had a natural point to begin with. Even so, 1st instar *L. camilla* caterpillars still persisted in constructing a pier extension equal to its own body length which produced the largest overall pier extension.

The presence of foodplant secretion on *L. periclymenum* sun foliage frequently prevented the construction of a normal pier extension (Plate 7.2 and Chapter Four). Other pier extensions were distorted or stunted (Plate 7.3) Some *L. camilla* caterpillars, having failed to construct their defence refuge at the normal leaf tip location (Plate 7.2) attempted to do so at alternative sites on the leaf margin (Plate 7.3a-c) and some caterpillars failed after multiple attempts. Marginal 'pier' extensions or defence refuges were often poor substitutes of the normal leaf tip construction and secretion caused an abundance of frass bits to stick to the caterpillar (Plate 7.3b). Caterpillars suffering early mortality in the 1st instar rarely constructed any section of the refuge (Plate 7.3d).

7.4.1.4 *L. camilla*: foodplant secretion (Table 7.6) and mortality frequency (Table 7.7).

L. caprifolium and *S. rivularis* rarely exhibited feeding damage secretion in any instar; *L. periclymenum* shade and ground exhibited minute amounts of secretion in the first two instars. *L. periclymenum* sun foliage produced abundant secretion in the first instar, a small amount in the second instar and minute amounts in the 3rd and 4th instars. When secretion occurred it always flowed from caterpillar feeding damage during bioassay observations and never from trichomes or damaged trichomes. Caterpillar mortalities normally occurred during the 1st instar period and the remainder occurred in the 2nd instar. Nearly all mortalities (92 %) occurred with caterpillars feeding on *L. periclymenum* sun foliage which also produced the greatest amount of secretion in both 1994 and 1995 bioassays.

7.4.1.5 *L. camilla*: diapause (Table 7.7).

Under natural conditions *L. camilla* caterpillars normally enter diapause after constructing hibernacula in the early stages of the 3rd instar. In the 1995 bioassay 32 % of all caterpillars entered diapause exactly as they do under natural conditions and 78 % carried straight through to pupation and adult emergence a few weeks later. In the 1994 bioassay no caterpillars feeding on natural oviposition foliage entered diapause compared to 30 % in 1995. In the 1995 bioassay no caterpillar feeding on *L. caprifolium* entered diapause in contrast to caterpillars feeding on *S. rivularis* when 82 % entered diapause.

There are several factors which induce diapause in Lepidoptera and other insects such as temperature, photoperiod, nutrient quality, moisture and parasitism (Leather *et al.*, 1993). The analysis of bioassay foodplant nutrients (Chapter Six; Table 6.8) showed that *L. caprifolium* contained the greatest amount of water and *S. rivularis* the lowest amount of water (18 % less than any other foodplant). It is possible that foodplant water content is an important factor in inducing diapause with *L. camilla* caterpillars since all other factors were reasonably constant.

7.4.2 *L. camilla:* feeding rhythm (Table 7.8; Figures 7.3-4).

Five separate activity traits were identified by time-lapse video recording of feeding 1st instar *L. camilla* caterpillars : pier extension construction (defence refuge), cuticular preparation (trichome swiping and silk platform construction), latrine construction, feeding and resting. Third instar caterpillars entering diapause also constructed a hibernaculum. *L. camilla* caterpillars rarely attempted and succeeded in constructing latrines on foodplants other than their oviposition shade foliage.

For each 1st instar caterpillar feeding on the three arena foodplants *L. periclymenum* (shade) acting as control, *L. periclymenum* (sun) and *S. rivularis*, most time was spent resting followed by

feeding, preparation and refuge construction in order of decreasing activity time. However, the *L. periclymenum* sun caterpillar spent nearly 50 % longer during feeding bouts than the *L. periclymenum* shade caterpillar and about 100 % longer than the *S. rivularis* caterpillar. Indeed, the *S. rivularis* caterpillar exhibited the shortest mean feeding bout but the highest feeding frequency of all three foodplants. The *S. rivularis* caterpillar spent approximately half the total cuticular preparation time of the *L. periclymenum* shade and sun caterpillars. The *S. rivularis* and *L. periclymenum* sun caterpillars spent approximately twice as long as the *L. periclymenum* shade caterpillar constructing their refuges.

Leaf toughness measurements (Chapter Six; Table 6.6) showed that *L. periclymenum* sun bioassay foliage was tougher than *L. periclymenum* shade foliage which may explain the longer feeding periods of *L. camilla* caterpillars on *L. periclymenum* sun foliage. However, *S. rivularis* foliage was shown to be the toughest of all bioassay treatment foodplants and yet *L. camilla* caterpillars displayed the shortest feeding bouts on *S. rivularis* foliage. The relatively high feeding frequency of *S. rivularis* caterpillars reflects possible compensatory feeding behaviour as the caterpillars were not consuming enough foodplant nutrient in their relatively short feeding period. The relatively low water content of *S. rivularis* is the most likely explanation behind the short feeding bouts of *S. rivularis* caterpillars. Since most lepidopteran caterpillars obtain their water via their foodplant foliage, large quantities of a relatively dry foliage may cause digestive problems. Since *S. rivularis* contained relatively few trichomes, the relatively short preparation time of caterpillars feeding on this foodplant is understandable. Also, if constructing a silk platform is carried out by *L. camilla* caterpillars to neutralise plant secretion as well as trichomes, then the short preparation time is even more understandable since *S. rivularis* foliage does not produce secretion.

Visual evidence of *L. camilla* caterpillars experiencing great difficulty in trying to construct their pier extensions (defence refuge) on to the leaf tips of *S. rivularis* and *L. periclymenum* sun foliage foodplants was confirmed by the periodicity statistics. The important factor explaining the difficulty is different for each of the two foodplants. Leaf toughness explains the difficulty for the *S. rivularis* caterpillar since freshly emerged *L. camilla* caterpillars were frequently observed having difficulty with what was usually their very first mandibular penetration of their foodplant leaf. Once the leaf was penetrated on the leaf margin, *L. camilla* caterpillars displayed no more difficulties in additional leaf incision at a particular part of the leaf.

The highly secretory nature of *L. periclymenum* sun foliage explains the difficulty *L. camilla* caterpillars experienced in constructing their defence refuge. There was substantial visual evidence of caterpillars being unable to manipulate frass bits into position due to the sticky nature of the foodplant secretion. Caterpillar mobility on the leaf surface, mandibular movement and silking were also prohibited by foodplant secretion.

It is often difficult to explain accurately the relative contributory factors such as foodplant nutrient content, water content, leaf toughness and other foodplant defence mechanisms towards feeding bout periods and frequency. It is possible that all these factors contribute to caterpillar feeding rhythms. However, the fact remains that caterpillar mortalities only occurred on the usually secretory *L. periclymenum* sun foodplant.

7.4.3 Comparison of caterpillar survival of *H. fuciformis* when feeding on oviposition foliage with alternative foodplants.

7.4.3.1 *H. fuciformis*: all caterpillar growth indicators (Tables 7.9-10).

Overall, the results of both 1994 and 1995 bioassays showed little difference in feeding behaviour of *H. fuciformis* caterpillars on the bioassay treatment foodplants compared with *L. periclymenum* sun oviposition foliage. Maximum caterpillar length, pre-ecdysis period and pupal mass indicators revealed almost identical values for each instar for each foodplant. The unexpected slight secretory nature of the 1995 bioassay treatment foodplants *L. periclymenum* shade and *L. periclymenum* ground foliage indicates that the mechanism of secretion in this foodplant species is a reversible process which may be activated by increase in sunlight and temperature and deactivated by reduction of these abiotic factors.

7.4.3.2 *H. fuciformis:* feeding rhythm (Table 7.11; Figures 7.5-6).

Only three basic activity traits were identified by time-lapse video recording for 1st instar *H. fuciformis* caterpillars : cuticular preparation, feeding and resting. Cuticular preparation simply involved trichome swiping creating clear pathways to and from its resting location which was on the abaxial midrib of the food leaf. There was no statistically significant difference between activity trait periods and frequencies between the two treatment foodplants *L. periclymenum* sun and *L. periclymenum* shade foliage. However, visual evidence from time-lapse video recording showed that the *H. fuciformis* 1st instar caterpillar feeding on the non-secretory foodplant, *L. periclymenum* shade foliage, produced larger and fewer feeding damage holes on the leaf laminae. Also, *H. fuciformis* caterpillars feeding on the secretory foodplant foliage indicated that they were able to predict the appearance of secretory liquid a few seconds before it appeared since they always turned away from their feeding location a few seconds (2-5) before the secretory liquid appeared.

No previous caterpillar growth rate studies have been undertaken involving either *L. camilla* or *H. fuciformis*. Rausher and Papaj (1983b) found that ovipositing *Battus philenor* (pipevine swallowtail) butterflies discriminated among conspecific host plants in the field but discrimination had no detectable effect on caterpillar growth rates or on pre-dispersal mortality but did appear to enhance caterpillar survival by increasing caterpillar size at dispersal.

7.4.4 Comparison of feeding behaviour of *L. camilla* and *H. fuciformis* caterpillars.

The overall caterpillar feeding strategies of these two Lepidoptera using the same foodplant are completely different. *H. fuciformis* feeds through all instars and pupates within 4-5 weeks whereas *L. camilla* caterpillars, under natural conditions, feed through the first two instars, enter winter diapause in the 3rd instar, and pupate the following spring. In order to carry out these strategies *L. camilla* females only oviposit on host foliage growing in shade in contrast to *H. fuciformis* whose females only oviposit on host foliage growing in open sunny rides and clearings.

The bioassay results showed that *H. fuciformis* caterpillars achieved the same growth and survival rates on both types of host foliage but *L. camilla* caterpillars suffered a reduction in caterpillar survival with a not insignificant proportion of mortalities when feeding on host foliage growing in open sunny habitats. Also, *L. camilla* caterpillars successfully fed on two new foodplant species, *S. rivularis* and *L. caprifolium*. The outstanding and unique foodplant quality of *L. periclymenum* sun foliage was its ability to secrete a sticky liquid when damaged by feeding caterpillars.

The feeding strategies and behavioural activity traits of *L. camilla* and *H. fuciformis* 1st instar caterpillars on their oviposition leaf showed a remarkable contrast. *H. fuciformis* caterpillars feed abaxially from a position on the central midrib and puncture the laminal areas close to the midrib, without leaving the midrib until near the end of the 1st instar, with a series of small holes which, after a few minutes, display sticky secretion globules (Plate 7.4a-b). In contrast, *L. camilla* 1st instar caterpillars immediately after emergence construct an extension of the midrib tip, adaxially, from frass and silk, and use it as a defence refuge. Their method of cutting the laminal leaf area into a series of strips or 'flags' and constructing an aerial latrine so that there is no visual evidence of frass at ground level is highly unusual. *L. camilla* 1st instar caterpillars feeding on *L. periclymenum* sun foliage which succeeded in completing the construction of their defence refuge, also successfully reached 3rd instar diapause or pupation. In contrast, those caterpillars which failed to complete their defence refuge construction eventually died. Obviously, the completion of the defence refuge by 1st instar *L. camilla* caterpillars is of vital importance to their sequential behavioural character.

The conclusion of this study (Chapter Eight) will provide discussion to support the hypothesis that *L. camilla* females oviposit on their host foliage only if it is growing in shade because sun foodplant foliage, due to its secretory nature, prevents *L. camilla* 1st instar caterpillars from completing their defence refuge construction which may lead to their demise.

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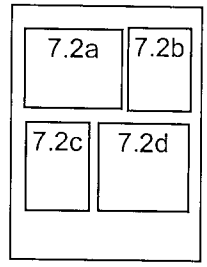


Plate 7.2a Normal feeding pattern of *L. camilla* caterpillar (2nd instar pre-ecdysis period) on non-secretory *L. periclymenum* oviposition foliage. The opposite leaf shows a mine of *P. trifasciella* (very rare to have 2 species on the same rosette). p. 7-39

Plate 7.2b Normal feeding pattern of *L. camilla* caterpillar (1st instar) on non-secretory *L. periclymenum* oviposition foliage (x2). p. 7-39

Plate 7.2c Normal feeding pattern of *L. camilla* caterpillar (1st instar pre-ecdysis period) on non-secretory *L. periclymenum* oviposition foliage (x5). p. 7-39

Plate 7.2d Feeding pattern of *L. camilla* caterpillar (2nd instar) on *S. rivularis* foliage. p. 7-39

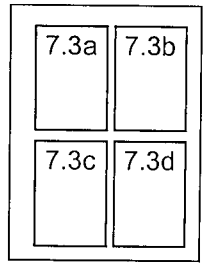


Plate 7.3a *L. camilla* abnormal refuge construction (I) on leaf margin of *L. periclymenum* secretory foliage (x5). p. 7-40

Plate 7.3b *L. camilla* abnormal refuge construction (II) on leaf margin of *L. periclymenum* secretory foliage (x10). p. 7-40

Plate 7.3c *L. camilla* abnormal refuge construction (III) on leaf margin of *L. periclymenum* secretory foliage (x15). p. 7-40

Plate 7.3d *L. camilla* abnormal refuge construction (IV) on leaf midrib tip of *L. periclymenum* secretory foliage (x5). p. 7-40

Plate 7.3e *L. camilla* normal pier and refuge construction on non-secretory *L. periclymenum* oviposition foliage (x5). p. 7-40

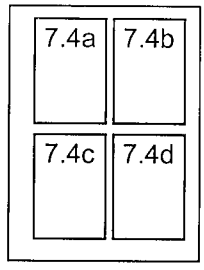


Plate 7.4a Normal feeding pattern (I) of *H. fuciformis* caterpillar (2nd instar) on secretory *L. periclymenum* oviposition foliage (x5). p. 7-41

Plate 7.4b Normal feeding pattern (II) of *H. fuciformis* caterpillar (1st instar) on secretory *L. periclymenum* oviposition foliage (x2). p. 7-41

Plate 7.4c Feeding pattern of *Apeira syringaria* caterpillars (1st instar) on secretory *L. periclymenum* foliage. p. 7-41

Plate 7.4d Rest (alarm) posture of *H. fuciformis* caterpillar (5th and final instar) (x2). p. 7-41

Plate 7.2

Plate 7.3

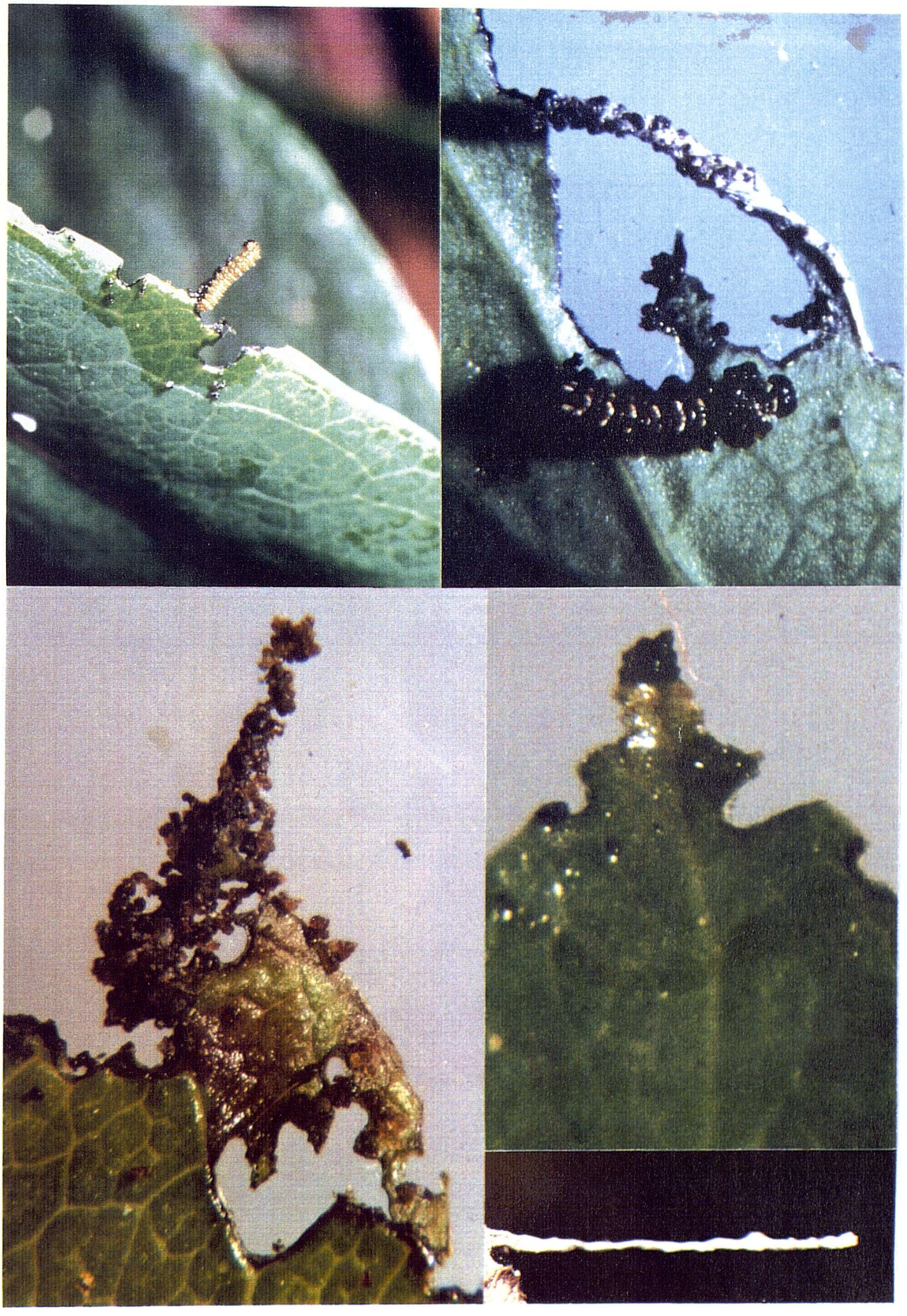
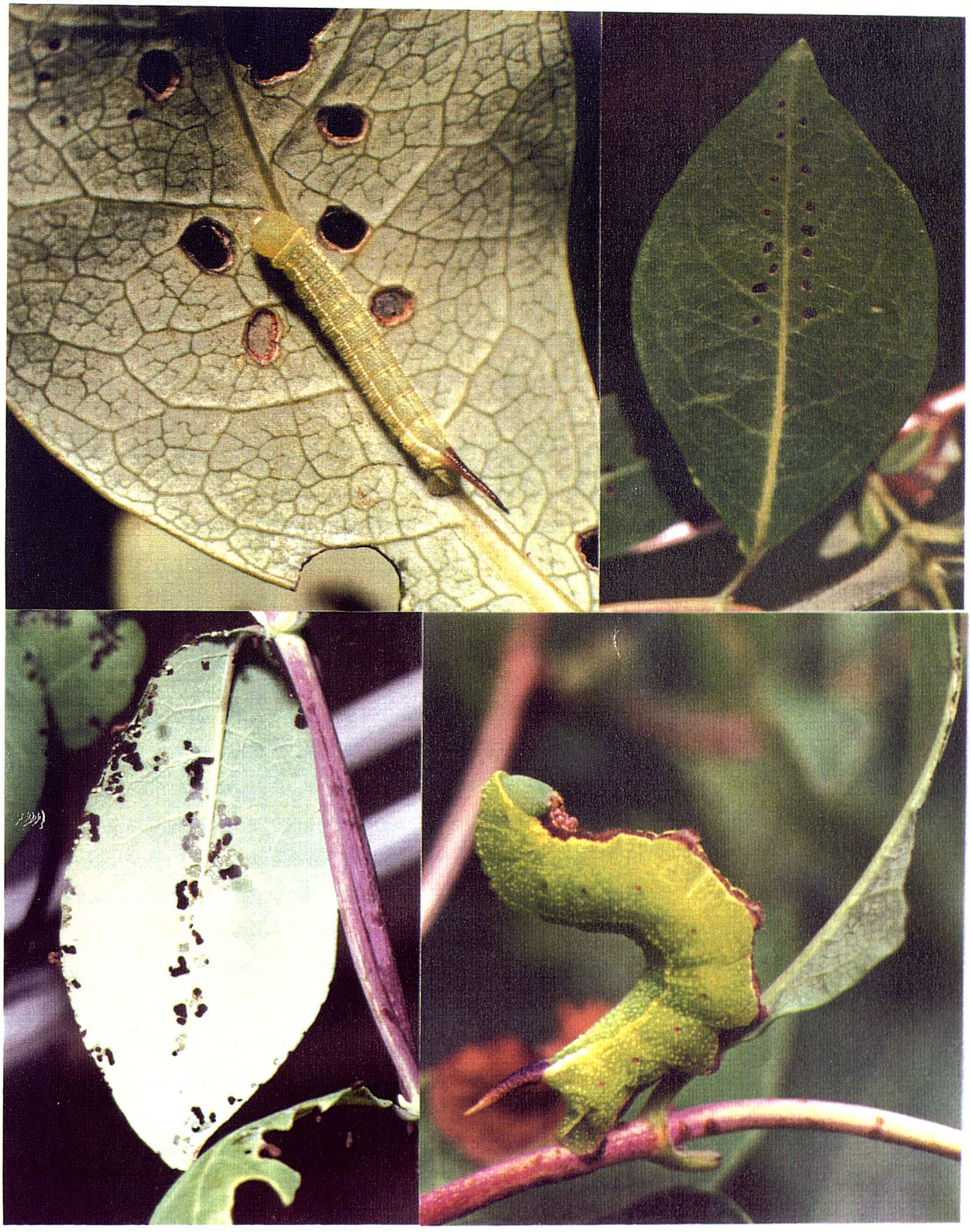


Plate 7.4



Chapter Eight

Conclusion

Adaptation of *L. camilla* and *H. fuciformis* caterpillars to host quality variation

8.1 Introduction

This study has shown that female *L. camilla* and *H. fuciformis* displayed careful discrimination of conspecific foodplants just as many other species of Lepidoptera display equally careful discrimination with regard to oviposition preference between different species of foodplant.

The first part of this study which established host preference in the field (Chapter Three), revealed a large guild of 34 species of Lepidoptera using *L. periclymenum* as a food resource. The majority of guild species showed an oviposition preference for host plants growing in shaded habitat and was typically illustrated by the only butterfly member of the guild, *L. camilla.* In contrast, *H. fuciformis*, a day flying moth, was the only guild member which preferred to oviposit on host foliage growing in sunny open habitat.

Hemispherical photography leading to the calculation of the diffused light site factor for *L. camilla* and *H. fuciformis* oviposition sites confirmed the distinction in habitat shade, and optical rotation measurements of sucrose hydrolysis showed that host plants growing in *H. fuciformis* oviposition sites were subjected to a higher temperature throughout all seasons (Chapter Five). This example of neighbouring sympatry between Lepidoptera ovipositing on conspecific foodplants, within a single woodland habitat, is rare in British Lepidoptera.

There was little difference between *L. camilla* and *H. fuciformis* in the choice of egg location within foodplant architecture with the exception of the position of the egg on the oviposition leaf. Although, Lederer (1960), in his German study of *L. camilla* had shown that egg location on the foodplant oviposition leaf was variable within the upper leaf surface, this study of *L. camilla* in Bentley Wood, showed a marked uniformity involving over 100 examples of egg location within 1 or 2 mm of the leaf margin. This example of phenotypic plasticity of variation in leaf egg location between two widely separated colonies of *L. camilla* may have been due to differing environmental conditions of sunlight and temperature in the two colonies causing a difference in host quality.

Field observation of caterpillar feeding damage of host leaves revealed that *H. fuciformis* 1st instar caterpillars always produced globules of sticky secretion. In contrast, host leaf feeding damage

produced by 1st instar *L. camilla* caterpillars never produced host secretion under natural conditions and very rarely in bioassay.

These differences in host plant reactions to caterpillar feeding damage were regarded as clues indicating a possible difference in host quality caused by differing environmental conditions of microclimate. Alternatively, the observed difference in host secretion between *L. camilla* and *H. fuciformis* caterpillar feeding damage may have been the result of different feeding strategies on the leaf surface. *H. fuciformis* caterpillars may have employed a feeding technique which activated a host secretory mechanism whereas the feeding technique employed by *L. camilla* caterpillars did not activate a host secretory mechanism. Another possibility was that *H. fuciformis* caterpillars had evolved a feeding strategy which successfully circumvented possible adverse effects of host secretion whereas *L. camilla* caterpillars were incapable of neutralising host secretion and through natural selection, ovipositing female *L. camilla* butterflies selected only host plants growing in shaded conditions. Artificial induction of secretion using pin pricks (similar to the 1st instar caterpillar feeding technique of *H. fuciformis*) on *L. periclymenum* foliage growing in shade at the time *L. camilla* were ovipositing in the field, failed to induce secretion but readily did so on *H. fuciformis* oviposition foliage growing in sunny open clearings.

8.2 Caterpillar adaptation to foodplant defence mechanisms.

Vein or canalicular cutting by lepidopteran caterpillars as a method to reduce secretion pressure in leaf tissue has already been discussed (Chapter Six). This method is probably used by *H. fuciformis* 1st instar caterpillars when feeding on their foodplant foliage. Indeed, it is probably the method used by most of the guild species feeding on *L. periclymenum* in sunny habitat which induces secretion. Plate 7.4c (Chapter Seven) shows the feeding damage of 1st instar *A. syringaria* caterpillars feeding on secretory *L. periclymenum* foliage. The feeding damage pattern is not unlike that of *H. fuciformis* 1st instar caterpillars (Plate 7.4b). The feeding holes close to the leaf midrib resemble the feeding damage of *H. fuciformis* caterpillars while the marginal feeding damage resembles the behaviour of *L. camilla* when caterpillars attempt to feed on the leaf margin after rejection of the leaf tip area. Is the feeding pattern of *A. syringaria* the feeding pattern that *L. camilla* would have evolved on secretory foliage had their caterpillars not evolved to construct a defence refuge? However, *A. syringaria* caterpillars have evolved an unusual behavioural trait which could be interpreted as a defence mechanism similar to that of *L. camilla*. Immediately after a feeding bout, they suspend themselves from a thread of silk for periods of 10-30 minutes. This behaviour can be seen by the caterpillar at the bottom of Plate 7.4c which is enlarged in Plate 3.2d (Chapter Three). The silk thread may function like the defence refuge of *L. camilla* which is constructed from silk and frass bits. Could *L. periclymenum* have unusual properties which induce defence mechanisms in its lepidopteran predators?

Lepidopteran foodplants have been shown to display several methods of defence against herbivorous predation which include both chemical and physical mechanisms (Chapter One). Generalist phytophagous lepidopteran species normally feed on host plants which do not induce a chemical method of defence (Harborne, 1989). Since the majority of the lepidopteran guild feeding on *L. periclymenum* are regarded as generalists (Emmet and Heath, 1991), the part of this study which examined host quality concentrated on physical methods of plant defence such as trichomes, leaf toughness, nutrient quality and host secretion. The next section of this study examined unusual behavioural traits of *L. camilla* caterpillars, some of which Lederer (1960) had identified in his German study of *L. camilla* (Chapter Four).

First instar *L. camilla* constructed silk platforms, an aerial latrine, and a 'pier' extension of the leaf midrib in the early stages of the first instar period. Mowing of trichomes or trichome swiping (involving a sideways shearing force with the mandibles) was carried out throughout the first two instars. Swiped trichomes were sometimes consumed (but not digested) and sometimes used together with faecal pellets or frass to construct the 'pier' extension in which silk and a 'glue' were used to bond together the various components. In addition, 1st instar *L. camilla* caterpillars constructed an aerial latrine from silk and leaf bits which was suspended underneath the leaf midrib. This study has provided evidence that the 'pier' extension was used as a defence refuge against possible predation (Chapter Four; Section 4.7.2). The author cannot find another example of this type of anti-predator defence mechanism in lepidopteran caterpillars. However, the general use of enteric discharge and faecal pellets as anti-predator defence mechanisms are well documented in other arthropods including caterpillars of the chrysomelid beetle, *Blepharida rhois*, which employs a sticky moist faecal shield against predator attack (Evans and Schmidt, 1990).

The purpose of the aerial latrine is more difficult to understand. Throughout the whole of the 1st instar and most of the 2nd instar *L. camilla* caterpillars do not allow any faecal pellets to fall below the feeding leaf. This retention of frass is maintained by using frass for defence refuge construction and excess frass is 'shot' into, and absorbed by, the latrine. The latrine may act as a decoy zone for potential predators since lepidopteran frass contains unused nutrients or the frass may contain anti-predator repellent chemicals (Evans and Schmidt, 1990). Alternatively, the latrine may be used as a replenishment store of frass for the defence refuge construction.

Trichome swiping and silk platform construction as methods of neutralising host trichomes by lepidopteran caterpillars are also well documented (Chapter Four; Section 4.7.2). The only unusual behavioural trait which *H. fuciformis* caterpillars share with *L. camilla* caterpillars is trichome swiping. Both species of caterpillars seem reluctant to make tarsal contact with the laminal areas of their feeding leaves early on in their first instar period. *L. camilla* caterpillars create pathways with silk platforms over the upper half of their feeding leaf while *H. fuciformis* caterpillars use the leaf midrib as a major route during feeding bouts when their anal claspers rarely leave the leaf midrib. Occasionally, observation of bioassay feeding periods showed *H. fuciformis* caterpillars wandering

on laminal areas of the feeding leaf on which feeding damage holes were not producing the normal amount of secretion. In contrast, caterpillars were very rarely seen on leaf laminae during periods of high secretion pressure. It is possible that caterpillars are able to detect periods of low secretion pressure which enables them to move freely over leaf zones without the fear of secretion. Host oviposition preference in different habitats may indicate a difference in host qualities which allows their respective feeding strategies to be carried out most effectively. Testing this hypothesis and observing how both species of caterpillars adapted to alternative foodplant foliage was the final aim of this study (Chapter Seven).

Before the main transfer experiments were carried out in 1995 the bioassay foodplants were quantitatively examined for leaf quality in terms of trichome density and distribution, leaf toughness, nutrient quality and leaf secretion (Chapter Six). *L. periclymenum* foliage growing in shaded plantations (*L. camilla* oviposition habitat) exhibited greater unicellular trichome density than host foliage growing in open sunny habitats (*H. fuciformis* oviposition sites). However, both *L. camilla* and *H. fuciformis* females chose egg locations on the leaf surface which had trichome densities midway between the available maximum and minimum values. Field observation of 1st instar caterpillars of both *L. camilla* and *H. fuciformis* showed little difficulty in negotiating leaf trichomes. However, when both caterpillars were forced to negotiate the most trichome-dense parts of host leaves, *L. camilla* caterpillars displayed great difficulty with mobility compared to *H. fuciformis* caterpillars (Chapter Six; Section 6.4.1.2). First instar *H. fuciformis* caterpillars were larger in abdomen and head size and were probably stronger and more able to cope with mowing trichomes. The marginal leaf location of eggs deposited by female *L. camilla* butterflies allowed freshly emerged caterpillars to reach their first feeding location without having to negotiate the most dense trichome areas. This location was always the leaf tip zone (Chapter Four; Figure 4.2) which was first documented by Lederer (1960).

The results of nutrients analysis in *L. periclymenum* oviposition foliage of *L. camilla* and *H. fuciformis* revealed little difference in total carbon, total nitrogen and water content. Carbon and nitrogen levels were found to be highest in early season growth in April. This optimal nutrient period was utilised by post-diapause *L. camilla* caterpillars but pre-diapause caterpillars fed on host at its lowest nutrient level in July and August. *H. fuciformis* caterpillars fed on host at intermediate nutrient levels in June. Thus, *L. camilla* caterpillars utilised the advantage of relatively high nitrogen content foodplant in their post-diapause period when caterpillar mass increase was greatest and consumed their foodplant at its lowest nitrogen level in pre-diapause period when rapid caterpillar mass increase was less important.

For each sampling period *L. periclymenum* sun foliage (*H. fuciformis* oviposition sites) was found to be more tough than host shade foliage (*L. camilla* oviposition sites). For both species, oviposition foliage midribs were the toughest parts of the feeding leaf and were never attacked by 1st instar caterpillars. Indeed, both species used this midrib strength to their advantage as major pathway

routes. *S. rivularis,* one of the alternative foodplant bioassay treatments, was found to be the toughest of all bioassay foodplants and caused *L. camilla* 1st instar caterpillars some difficulty with their first incision of the leaf tip zone. Leaf toughness increased as the summer season progressed and 1st instar *L. camilla* caterpillars fed on oviposition foliage at its highest level of toughness but this problem was compensated by the relatively lower level of toughness of host shade foliage.

8.3 Importance of foodplant secretion on refuge construction and caterpillar survival of *L. camilla*.

Quantitative measurement of foodplant secretion caused by caterpillar feeding damage confirmed earlier qualitative records that host sun foliage of *H. fuciformis* produced considerably more secretion than host shade foliage of *L. camilla.* Under natural field conditions host feeding damage by *L. camilla* caterpillars was never observed to produce secretion. During bioassay and field observation the only foodplant which produced relatively large amounts of secretion from caterpillar feeding damage was *L. periclymenum* sun foliage. With regard to both *L. camilla* and *H. fuciformis* caterpillars, the source of this secretion was always observed to be from epidermal rupture and never from glandular trichomes.

Time-lapse video recording data showed feeding rhythms of *L. camilla* and *H. fuciformis* which contrasted in structure (Chapter Seven; Figures 7.3 and 7.6). First instar *H. fuciformis* caterpillars produced a relatively lower frequency of activity traits with long resting periods whereas 1st instar *L. camilla* caterpillars produced a relatively high frequency of activity traits of short duration. *L. camilla* caterpillars produced different sequential feeding patterns on different foodplants (Figure 7.3; Chapter Seven). Construction of the *L. camilla* refuge was not the only activity trait that proved difficult on alternative foodplants. In many cases, latrine construction was not attempted when 1st instar *L. camilla* caterpillars fed on secretory *L. periclymenum* foliage or *S. rivularis* foodplant.

Instar period length, maximum instar caterpillar length, pre-ecdysis period, pupal mass, duration and frequency of feeding activity traits were used as caterpillar growth and survival indicators in the bioassay experiments (Chapter Seven). Instar period length, feeding rhythm activity traits and pre-ecdysis period all produced discriminatory evidence which indicated that *L. camilla* 1st instar caterpillars suffered a decrease in caterpillar growth rate when feeding on highly secretory host foliage which had been growing in open sunny habitats compared with oviposition, non-secretory, host foliage. This reduction in caterpillar survival was indicated by increased instar periods and mortalities especially in 1st and 2nd instars in both 1994 and 1995 bioassays.

All caterpillar growth rate indicators failed to produce any evidence which showed that *H. fuciformis* caterpillars suffered adverse effects when feeding on non-secretory host foliage compared with secretory oviposition foliage which had been growing in open sunny habitats. Why *H. fuciformis*

females never oviposit on shade foodplant remains a mystery. Does shade *L. periclymenum* foliage produce a repellent secondary compound which is absent in sun foliage? Perhaps *H. fuciformis* females are ignorant of the presence of *L. periclymenum* in plantations since they were never seen foraging in plantations.

Under natural conditions *L. camilla* caterpillars normally enter diapause after constructing hibernacula in the early stages of the 3rd instar. In the 1994 bioassay no *L. camilla* caterpillars feeding on natural oviposition foliage entered diapause compared to 30 % in 1995. In the 1995 bioassay no caterpillar feeding on *L. caprifolium* entered diapause in contrast to caterpillars feeding on *S. rivularis* when 82 % entered diapause. Nutrient analysis of foodplants produced a low water content for *S. rivularis* which was possibly the main reason for inducing diapause. *L. camilla* caterpillars associated a low water content with a deterioration of foodplant quality normally found during senescence and shortly before diapause.

The presence of foodplant secretion on *L. periclymenum* sun foliage frequently prevented 1st instar *L. camilla* caterpillars from constructing their defence refuge. Time-lapse video recording showed that the *L. camilla* 1st instar caterpillar feeding on secretory *L. periclymenum* foliage spent nearly 50 % longer during feeding bouts than the *L. camilla* caterpillar feeding on *L. periclymenum* shade foliage, which may be due to the presence of secretion from ruptured epidermal cells. There was substantial visual evidence of caterpillars being unable to manipulate frass bits into position due to the sticky nature of the foodplant secretion. Caterpillar mobility on the leaf surface, mandibular movement and silking were also prohibited by foodplant secretion.

Those *L. camilla* caterpillars which succeeded in completing the construction of their defence refuge also successfully reached 3rd instar diapause or pupation stage. In contrast, those caterpillars which failed to complete their defence refuge construction eventually died. However, some caterpillars having failed to construct, successfully, their defence refuge at the normal leaf tip location, attempted to do so at alternative marginal sites. Occasionally, several attempts were made before eventual success or failure.

Mortality was probably caused by starvation during the prolonged secretory period of refuge construction. The evolutionary instinct of 1st instar *L. camilla* caterpillars to construct their defence refuge immediately after emergence results in little or no body growth. Energy consumption of caterpillars in refuge construction must be considerable at a most crucial stage of their development. Unfortunately, their persistence to complete their defence refuge at the expense of body growth, can lead to their eventual demise. Those caterpillars which quickly and successfully adapt in constructing their defence refuge when feeding on secretory foodplant subsequently reach a normal adult stage. Those caterpillars which fail to adapt to the adverse nature of secretion or fail to quickly construct a refuge at an alternative site eventually succumb to starvation

Berenbaum *et al.* (1993) investigated the material costs of web spinning behaviour for the parsnip webworm, *Depressaria pastinacella,* and calculated that 18% of ingested nitrogen was incorporated into silk and 82 % into body mass during their final instar. *L. camilla* caterpillars start constructing their refuges during their 1st instar immediately after emergence when their only food supply has been their consumed egg-shells. Any delay in food consumption, such as that caused by sticky secretion from secretory host foliage, probably seriously depletes their low energy reserves. It is not surprising that continued abortive attempts at refuge construction, sometimes over several days, with little or no ingestion of food, caused mortalities.

The purpose of silk production by *L. camilla* caterpillars is debatable. They lay down silk throughout the 1st and most of the 2nd instars only. In addition to using silk to bond their refuge together and construct their latrines, it is densely laid on their main midrib pathway (Chapter Four) after trichome swiping and on other route networks. They grip the silk with their anal claspers during movement and this grip proved strong enough to withstand the pulling force of an attacking house fly during time-lapse video recording of one caterpillar in camera. Bioassay observation showed some 1st instar caterpillars leaving a trail of secretion on a previously undamaged laminal part of a sun *L. periclymenum* leaf. It is possible that their sharp tarsi are capable of rupturing the secretory canals of host leaves when phloem pressure is greatest and laying a silk platform creates a defensive buffer zone. Berenbaum *et al.* (1993) suggested another purpose of silk production in the case of parsnip webworms, which involves detoxification of unmetabolised furanocoumarins (toxins from foodplant) which is excreted in substantial amounts into their webs. Alternatively or additionally, these toxins may retain some of their toxic properties which act as a defence repellent against predators. In a similar way, toxins may be imparted to *L. camilla*'s frass which is collected in the aerial latrine and used as a defensive mechanism.

Although nutrient analysis (Chapter Six) failed to show a decline in nutrient quality of *L. periclymenum* shade foliage compared to sun foliage, drapes found in plantations frequently looked in poor shape due to their spindly appearance and relatively low foliage density. Very few plants were found in flower. The oviposition preference for relatively poor quality host foliage shown by *L. camilla* is probably due to the more important factor for survival of refuge construction. This study has shown that 1st instar *L. camilla* caterpillars can only construct this refuge with certain success by using non-secretory host foliage. Other examples of lepidopteran species choosing nutritionally poor host foliage in preference for host foliage which proves superior for shelter or refuge construction are the leaf tier, *Omphalocera munroei*, a pyralid moth, and another micro-moth, *Diurnea fagella. O. munroei* caterpillars were found to prefer host (*Asimina* spp.) old leaves for leaf tying as they maintained their shape and reduced predation in preference to young leaves (Damman, 1987). Hunter (1987) found *D. fagella* caterpillars more common on damaged or regrowth leaves of oak, even though caterpillar growth and survival on these leaves was reduced compared with nutritionally superior leaves, because caterpillars made their shelters more quickly on these leaves.

This study has shown that *L. camilla* and *H. fuciformis* ovipositing females were able to discriminate between conspecific plants of *L. periclymenum* growing in different microclimates of sunlight and temperature. Their respective host foliage differed in terms of trichome density, leaf toughness and, to a lesser extent, nutrient quality. However, the outstanding discriminating factor in host quality was the ability of *L. periclymenum* foliage to secrete a sticky liquid when growing in the warmer, sunnier, habitat of *H. fuciformis.* The contrasting feeding strategies of the two species proved to be most successful on their respective natural oviposition host foliage. *H. fuciformis* caterpillars have evolved a feeding strategy which successfully avoids the adverse effects of secretion by the simple technique of avoidance and possible reduction of secretion pressure.

Although, this study showed no difference in caterpillar survival of *H. fuciformis* caterpillars when feeding on shade foliage compared with natural oviposition foliage, the higher temperatures of its oviposition sites favour a more rapid caterpillar growth rate which enhances the chances of survival for a non-diapause species. The secretory nature of host foliage growing in warmer sunnier habitats would prevent *L. camilla* 1st instar caterpillars from carrying out their complex behavioural traits especially the construction of their defence refuge. The Bentley Wood colony of *L. camilla* are simply not capable of coping with the problems of secretory host foliage and their lack of an effective feeding strategy against secretion may lead to their demise in habitats where there is no shade. Although some *L. camilla* caterpillars survive secretory foliage, their extended early instar periods would increase predation and possibly increased mortality during diapause. *L. camilla* caterpillars survived by constructing their defence refuge on the leaf margin, an alternative site to the normal leaf tip position. This alternative site may be less susceptible to secretion but, in many cases, this marginal refuge was of poor quality compared to the normal leaf tip construction (Plates 7.2 and 7.3). *A. syringaria* 1st instar caterpillars also found the leaf margin a successful feeding zone (Plate 7.4c). However, the refuge quality factor was relatively unimportant compared to the evolutionary compulsion of having to go through the motions of refuge construction. The limiting quality factor which probably eventually satisfied their evolutionary instinct was refuge length. Once the caterpillars had constructed a make-shift refuge equal in length to their own body size (2-3 mm), other refuge characteristics were considered unimportant. Once completed, *L. camilla* 1st instar were then able to continue feeding for normal body growth even if such growth proved relatively slow on secretory foliage. The variance in adaptability with individual caterpillars is difficult to explain. Greater perseverance in constructing the refuge at the normal location usually increased the risk of mortality.

Perhaps, a slow change of habitat microclimate over a long period of time may enable *L. camilla* to adapt more successfully by natural selection. Studies of *L. camilla* foraging behaviour in warmer climes in southern Europe may provide further evidence of evolving foraging strategies and comparison of present day *L. camilla* colonies at the sites Lederer (1960) investigated over 50

years ago would provide useful information on many aspects of ecology of *L. camilla* and *H. fuciformis.*

The successful foraging strategies of female *L. camilla* and *H. fuciformis* were based on their ability to discriminate between conspecific host plants. This conclusion supports the suggestion made by Rausher and Papaj (1983) that models and discussions of the evolution of host selection behaviour that treat plant species as the unit of discrimination may be seriously flawed because they overlook significant aspects of insect behaviour.

This study has answered the question posed by Pollard (1993) concerning the reason why *L. camilla* females always oviposited on their foodplant growing in shade. Of the four foodplant qualities examined in this study (trichomes, toughness, nutrients and secretion), the lack of foodplant secretion appears to be the best discriminating factor which explains why *L. camilla* females always oviposit on *L. periclymenum* growing in shade.

The identification of the mechanisms by which *L. camilla* and *H. fuciformis* discriminate between conspecific foodplants during oviposition has yet to be resolved. Such mechanisms may explain why *H. fuciformis* females refuse to oviposit on shaded plantation foodplants. Chemical analysis of host secretion may reveal secondary toxins although study evidence points against it. The mechanism of *L. periclymenum* unicellular trichome secretion and why neither *L. camilla* and *H. fuciformis* females rarely oviposit on host foliage growing above 2 metres high are further questions which still remain to be answered.

Appendices

Appendix 1 Scientific and English names of lepidopteran guild whose caterpillars were found feeding on *Lonicera periclymenum* in Bentley Wood.

Genus	Species	English name
LADOGA Moore	camilla (Linn.)	White Admiral Butterfly
HEMARIS Dalm.	fuciformis (Linn.)	Broad-bordered Bee Hawk-Moth
ARCHIPS Hb.	podana (Scop.)	Large Fruit-tree Tortrix
PHYLLONORYCTER Hb.	trifasciella (How.)	-
DITULA Steph.	angustiorana (Haw.)	Red-barred Tortrix
PANDEMIS Hb.	cerasana (Hb.)	Barred Fruit-tree Tortrix
YPSOLOPHA Latr.	dentella (Fabr.)	Honeysuckle Moth
APEIRA Gistl	syringaria (Linn.)	Lilac Beauty
PANDEMIS Hb.	corylana (Fabr.)	Chequered Fruit-tree Tortrix
ALCIS Curt.	repandata (Linn.)	Mottled Beauty
PHLOGOPHORA Treit.	meticulosa (Linn.)	Angle Shades
EUPROCTIS Hb.	similis (Fuessl.)	Yellow-tail
BRACHIONYCHA Hb.	sphinx (Hufn.)	Sprawler
XYLOCAMPA Guen.	areola (Esp.)	Early Grey
ATHRIPS Billb.	moufetella (Linn.)	-
AMPHIPYRA Ochs.	pyramidea (Linn.)	Copper Underwing
GYPSONOMA Meyr.	dealbana (Frol.)	-
LOZOTAENIA Steph.	fosterana (Fabr.)	-
ORTHOSIA Ochs.	gothica (Linn.)	Hebrew Character
OLETHREUTES Hb.	lacunana ([D & S.])	-
ORTHOSIA Ochs.	stabilis ([D. & S.])	Common Quaker
ARGYROTAENIA Steph.	xylosteana (Linn.)	Variegated Golden Tortrix
NOCTUA Linn.	comes (Hb.)	Lesser Yellow Underwing
PANDEMIS Hb.	heperana ([D & S.])	Dark Fruit-tree Tortrix
ORTHOSIA Ochs.	incerta (Hufn.)	Clouded Drab
YPSOLOPHA Latr.	nemorella (Linn.)	-
UDEA Guen.	prunalis ([D. & S.])	-
CARCINA Hb.	quercana (Fabra.)	-
OURAPTERYX Leach	sambucaria(Linn.)	Swallow-tailed Moth
COSMIA Ochs.	trapezina (Linn.)	Dun-bar
ECTROPIS Hb.	bistortata (Goeze)	Engrailed
CHLOROCLYSTA Hb.	truncata (Hufn.)	Common Marbled Carpet
LACANOBIA Billb.	oleracea (Linn.)	Bright-line Brown-eye
CROCALLIS Treit.	elinguaria (Linn.)	Scalloped Oak

Appendix 2 Parasitoids of lepidopteran guild found feeding on *L. periclymenum* in Bentley Wood. Species identified by Mark Shaw (Edinburgh Museum).

Apeira syringaria
Meteorus melanostictus (Capron) (Braconidae: Meteorinae) (x3)
Specialist on *A. syringaria.*
Mesochorus sp. indet. (Ichneumonidae: Mesochorinae) (x1)

Archips podana
Apechthis quadridentata (Thomson) (Ichneumonidae: Pimplinae) (x1)
Campopleginae (Ichneumonidae); possibly *Enytus* sp. (x1)
Campopleginae (Ichneumonidae); probably *Tranosema* sp. (x1)
Macrocentrus linearis (Nees) (Braconidae: Macrocentrinae) (x5)
Itoplectis maculator (Fabricius) (Ichneumonidae: Pimplinae) (x1)
Meteorus ictericus (Nees) (Braconidae: Meteorinae) (x3)
Oedemopsis scabricula (Gravenhorst) (Ichneumonidae: Tryphoninae) (x3)
Tachinidae (x3)

Ditula angustiorana
Ascogaster rufidens (Wesmael) (Braconidae: Cheloninae) (x3)
Glypta sp. (Ichneumonidae: Banchinae) (x2)
Campopleginae (Ichneumonidae); probably *Tranosema* sp. (x1)
Macrocentrus linearis (Nees) (Braconidae: Macrocentrinae) (x1)

Gypsonoma dealbana
Macrocentrus linearis (Nees) (Braconidae: Macrocentrinae) (x1)

Ladoga camilla
Cotesia =(*Apanteles* sensu lato, in part) *sibyllarum* (Wilkinson) (Braconidae: Microgastrinae) (x2)
Specialist on *Ladoga camilla.*

Orthosia stabilis
Eulophus ramicornis (Fabricius) (= *larvarum*) (x1)

Pandemis cerasana
Apophua bipunctoria (Thunberg) (Ichneumonidae: Banchinae) (x2)
Ascogaster rufidens (Wesmael) (Braconidae: Cheloninae) (x4)
Campopleginae (Ichneumonidae); possibly *Enytus* sp. (x2)
Campoplex sp. (Ichneumonidae: Campopleginae) (x1)
Glypta sp. (Ichneumonidae: Banchinae) (x2)
Oedemopsis scabricula (Gravenhorst) (Ichneumonidae: Tryphoninae) (x1)
Tachinidae (x1)

Pandemis corylana
Apophua bipunctoria (Thunberg) (Ichneumonidae: Banchinae) (x2)
Campopleginae (Ichneumonidae); possibly *Enytus* sp. (x1)
Macrocentrus linearis (Nees) (Braconidae: Macrocentrinae) (x1)

Ypsolopha dentella
Copidosoma sp. (Chalcidoidea: Encyrtidae) (x2)
Cladeutes discedens (Woldstedt) (Ichneumonidae: Tryphoninae) (x1)
Very rare; only 5 British previous specimens (with 1 previously known host).

Appendix 3 Habitat temperature measurement using acidified sucrose solution.

Concentration of sucrose solution: 437 g. dm^{-3}

Acidified with hydrochloric acid to produce a 0.1 molar solution of hydrochloric acid.

Volume of acidified sucrose solution used in each sample bottle: 150 cm^3.

Replication for each oviposition site: 10.

Polarimeter used: Griffin Simple Polarimeter; PSH-200-Y.

Calculations based on first order reaction kinetics of the hydrolysis of sucrose:

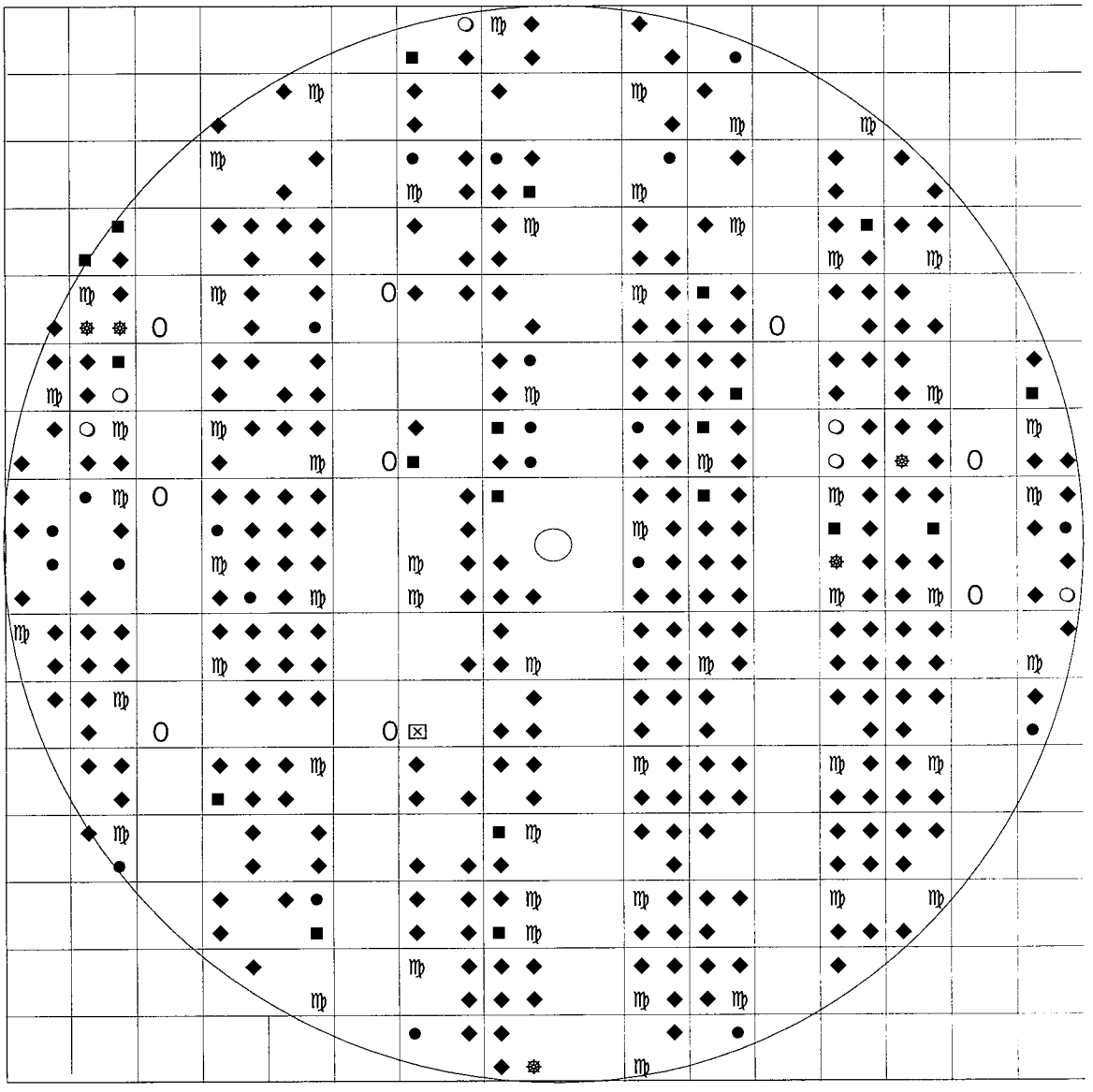
$$\frac{kt}{2.303} = \log_{10} \frac{\alpha - \beta}{\chi - \beta}$$

where k = velocity constant for a given temperature, α, β and χ are the optical rotation values at the start of hydrolysis, end of hydrolysis and at time t of hydrolysis, respectively. In order to calibrate the sucrose 'thermometer', the reaction is carried out in the laboratory at different temperatures and a graph of $-\log_{10} k$ is plotted against 1/T (° K). The value of k is obtained from the above equation. Field values of optical rotation are inserted in the above equation to obtain values of k which may be converted into field temperatures using the above graph. Practice is required to determine the best time periods for the most accurate results for leaving the sucrose solution in the field. The author found 3-4 days were appropriate in summer and 5-8 days in winter assuming normal British seasonal temperatures.

Appendix 4 Penetrometer apparatus.

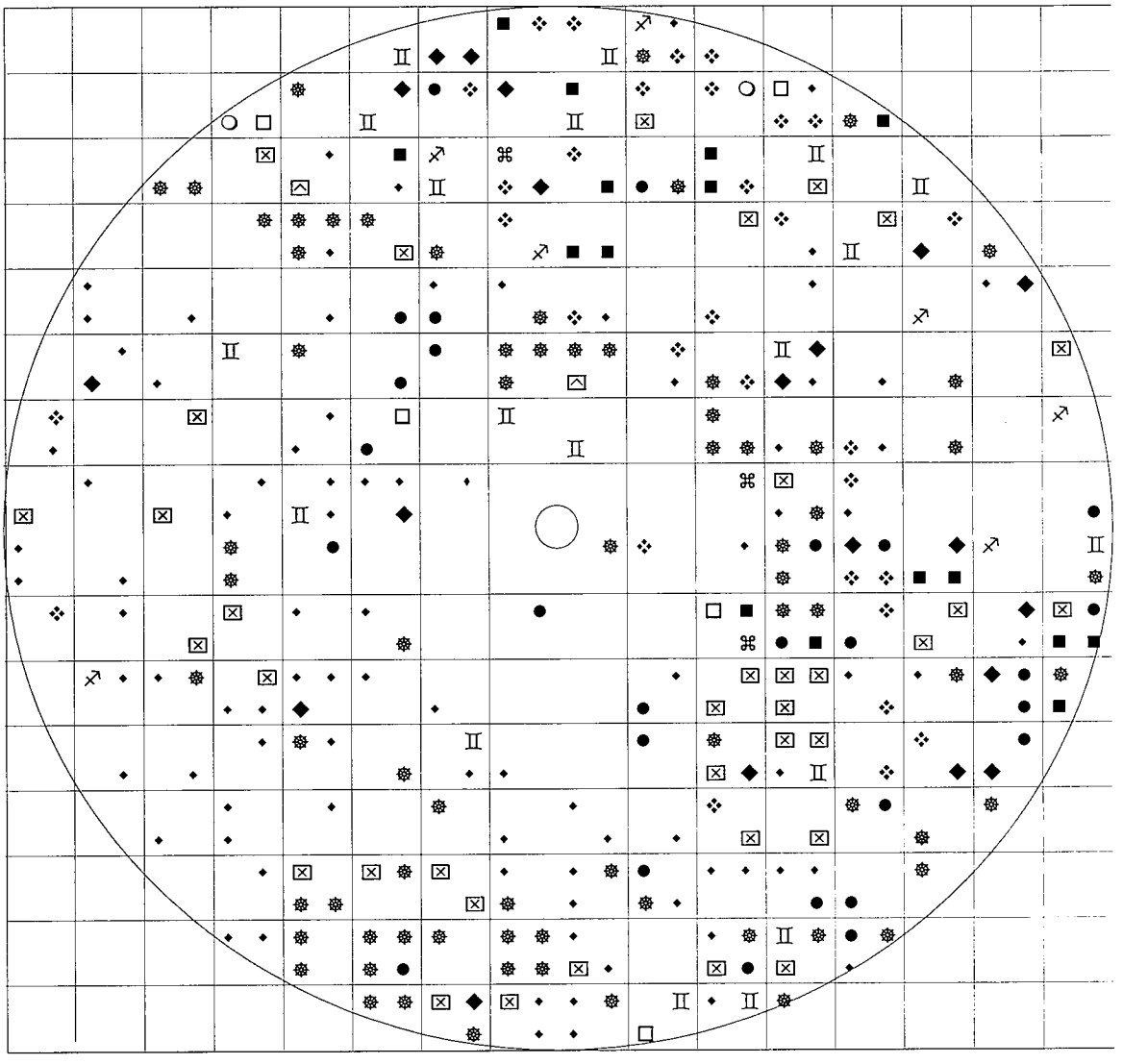
A diagram of the penetrometer apparatus used in this study is found in Chapter Six. The principle of the method used in this study was based on measuring the pressure (produced by adding mass of water or sand to the penetrometer rod) required to produce penetration of the *L. periclymenum* leaf. The moment of penetration was registered by a warning light in the electronic system. The author experimented with various metal rods (welding rods of various metals and sizes proved suitable) before finding the most suitable rod appropriate to the variation of toughness found in *L. periclymenum* and other foodplant leaves. The author will provide a circuit diagram of the electronic system on request.

Appendix 5 Example of tree distribution in beech dominant plantation E (no *L. periclymenum* drapes). Plot size: 24 m radius.



Frequency	Key	
293	◆	beech
22	●	hazel
1	⊠	oak
20	■	birch
6	○	sallow
5	❁	hawthorn
53	♍	Scots pine

Appendix 6 Example of tree distribution in mixed timber plantation F. Plot size: 24 m radius. *24 L. periclymenum* drapes were found on hazel, silver birch, sallow and hawthorn).



Frequency	Key	
88	◆	Norway spruce
20	◆	beech
1	◆	elder
27	●	hazel
3	⌘	wych elm
36	☒	oak
31	❖	Lawson cypress
15	■	birch
2	○	sallow
71	❁	hawthorn
19	Ⅱ	ash
7	➶	sweet chestnut
5	□	field maple
2	⛋	wild privet

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