Aspects of the ecology of the Lepidoptera associated with heather *Calluna vulgaris*

by

Carol Fielding B. Sc. (Dunelm)

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Department of Biological Sciences,
University of Durham.

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I certify that all material in this thesis which is not my own work has been identified and that no material is included for which a degree has previously been conferred on me.

Abstract

Aspects of the ecology of the assemblage of lepidopteran herbivores associated with heather (*Calluna vulgaris*) were investigated on northern heath and blanket bog habitats in the northern Pennines, England. The results of a literature search revealed 86 macrolepidopteran species to feed as larvae on *Calluna* in Britain although only 26 of these were recorded during this study. Information on the instar development of 15 species is presented. An investigation of the phenology of larval utilisation of the *Calluna* plant revealed spring and autumn peaks in macrolepidopteran species richness. This pattern is related to the different life-cycles exhibited by the Geometridae and Noctuidae families. The effect of altitude on the relationship between macrolepidoptera and *Calluna* was investigated along an altitude gradient from 290 to 650m. Approximately three species were lost for every 100m rise in altitude, of which one species was a Geometridae and two were of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae families. There was no observed decline in the species richness of Noctuidae species on *Calluna* with altitude. The density of Lepidoptera species varied greatly within the altitudinal distribution with individual species exhibiting increases and decreases in density with elevation. There was an absence of upland specialists with the majority of Lepidoptera species present at higher altitudes also recorded at lower altitudes. The species richness of the lepidopteran fauna varied little between *Calluna* stands of different ages, although individual species exhibited preferences for different aged stands. An abundant geometrid species was found to remove 50% of the current year's foliage in mature aged stands. The lepidopteran herbivores on *Calluna* were compared and contrasted with those on *Vaccinium myrtillus*. During the spring *V. myrtillus* had a higher density of lepidopteran larvae than *Calluna* which mainly consisted of microlepidopteran species. Species richness of Lepidoptera on the two plant species was similar. There was evidence for certain lepidopteran species of disparities in larval development on the two plant species.

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Chapter One

Introduction

The natural distribution of heather (*Calluna vulgaris*) and its habitat management creates an ideal opportunity to investigate the effects of altitude and plant age on the guild of insect herbivores associated with the plant.

In Britain *Calluna* occurs over a wide altitude range extending from sea level to approximately 1,000m and being present in almost every 10km square (Gimingham 1960; Webb 1986). Over large areas it is the vegetative dominant on heathland and moorland; Bunce (1987) estimated there to be approximately one million hectares of almost pure heather in Britain with a further 1.3 million hectares containing varying amounts of heather. The upland moorland habitats are prevalent in the north of Britain as well as north Wales, Exmoor and Dartmoor. *Calluna* is a dwarf shrub and is one of the most intensively studied of British plants (Gimingham 1989). Although certain aspects of the avian fauna associated with such habitats have been well studied, *e.g.* red grouse (Hudson 1986; Lance and Lawton 1990), there is relatively little known of the invertebrate communities.

The Lepidoptera are generally one of the most abundant groups of insect herbivores on woody shrubs such as *Calluna* (Lawton and Schröder 1978) and they are the most diverse taxon of leaf feeding insects in ecosystems throughout the world (Strong *et al.* 1984). There is a relatively large number of Lepidoptera listed as feeding on *Calluna* (Webb 1986) with nearly all of the species found in the uplands being moths rather than butterflies (Pearsall 1950). Although this order of insects has been the focus of strong amateur and academic interest, the species associated with moorland plants such as *Calluna* have been relatively little studied, although the basics of their life-cycle and distribution are documented. A few of the species have been investigated in greater detail, including butterfly species such as the Silver-studded Blue (*Plebejus argus*) and species that are of economic interest such as the Winter Moth (*Operophtera brumata*) or rare, *e.g.* the Northern Dart (*Xestia alpicola*).

The primary aim of this study is to investigate the effects of altitude on the lepidopteran fauna associated with *Calluna* (Chapter 7). Many authors have noted the general decline in the diversity of invertebrates with altitude (*e.g.* Greenslade 1968) although more recent studies have found no such relationship (Lawton *et al.* 1987). Previous work by Coulson (1988) recorded a significant decline in the species richness of Lepidoptera on moorland and peatland habitats although the investigation was not

specifically of the fauna associated with heather. For poikilothermic insects the most important change with altitude is likely to be temperature, with the lapse rate of temperature with altitude in Britain being among the sharpest in the world (Taylor 1978). The lower temperatures at higher altitudes affect the ability of insects to complete their growth and development. Species compensate by increasing the length of their life-cycle and decreasing the number of generations within a year. For example the oak eggar (*Lasiocampa quercus*), which as its name suggests feeds on oak foliage, has a one year life-cycle but the race of the species that feeds on *Calluna*, the northern eggar (*L. q. callunae*), has a more northern and higher altitude distribution and takes two years to complete its life-cycle. The changes found in biological organisms with altitude are likely to duplicate those found in movement from a southern to more northern geographical position in Britain.

In areas such as the north-east Pennines where red grouse (*Lagopus lagopus scoticus*) are abundant, *Calluna* moorland is managed by burning. This produces discrete stands of the plant of an even age within a patchwork of stands of a wide range of ages (Plate 1.1). These circumstances inspire investigations as to the relationship between different aged patches of the plant and its lepidopteran fauna (Chapter 8). The age gradient of the *Calluna* plant was divided by Watt (1955) into four stages which he entitled the pioneer, building, mature and degenerate phases and there has been much subsequent investigation of the physical, chemical and vegetational aspects of this cycle (Barclay-Estrup 1970, 1971; Barclay-Estrup and Gimingham 1969; Gimingham 1972). The gradient ranges from the young heather seedlings of the pioneer phase to degenerate plants of up to 30-40 years of age. The invertebrates on heather of different phases have previously been investigated by Miller (1974) and Barclay-Estrup (1974) who found higher diversity in stands and on plants of pioneer and degenerate age. These studies investigated broad patterns among invertebrates with no detailed examination of the Lepidoptera. The efficient management of moorlands aims to burn on a 12-15 year cycle or before the heather reaches a height of 30cm (Muirburn Working Party 1977). This prompts questions about the effect of a truncated age gradient of *Calluna* on the lepidopteran fauna associated with the plant. The extent of *Calluna* dominated habitats are currently in decline (Mowforth and Sydes 1989) which emphasizes the need to extend our knowledge of the invertebrates associated with such habitats.

In a temperate climate such as occurs in Britain there are likely to be seasonal changes in the diversity of herbivorous insects on plants. The most renowned illustration of this is the study of Feeny (1970) which documents the patterns of seasonal change in the Lepidoptera on oak (*Quercus robur*). The majority of larvae were found to coincide their feeding with the bud burst of oak in spring in order to exploit the leaves at their most nutritious before nutrient levels fell and tannin levels rose. Chapter 5 investigates similar patterns in the lepidopteran fauna on *Calluna* which,

Plate 1.1.

Photograph showing a view of a patchwork of *Calluna vulgaris* stands of a wide range of ages at Waskerley (500m), County Durham. The darker coloured areas towards the back of the picture represent recently burnt areas in which regeneration of *Calluna* has not yet begun.

unlike oak, is evergreen, hence it is feasible that insects could feed throughout the year on its foliage.

A plant that grows in close proximity with *Calluna* is bilberry (*Vaccinium myrtillus*) and after heather this is the second most common flowering plant on moorlands in Britain (Pearsall 1950). In order to set some of the findings of the lepidopteran fauna associated with *Calluna* into perspective some comparisons were undertaken with bilberry (Chapter 9).

A fundamental aspect of this study was the examination of the growth and development of the individual lepidopteran species (Chapter 6) so that development could be related to such factors as altitude and plant species. As a prelude to the rest of the study Chapter 4 attempts to answer some basic queries about the relationship between Lepidoptera and *Calluna*. For example, how many of the potential number of Lepidoptera species that could have been found were actually recorded?

The study was undertaken on heather moorlands in the northern Pennines that are described as being of two main types, namely northern heath and blanket bog with the former merging into the latter at an altitude of approximately 500m. Previous work on the invertebrates of blanket bog are summarised by Coulson and Whittaker (1978). Studies of the invertebrates of northern heath are less abundant but include the work of Coulson and Butterfield (1985) and Usher and Gardner (1988). Some of the information gathered on the invertebrates of lowland heathlands is also pertinent to this study (Gimingham *et al.* 1979; Webb 1986; Webb 1989).

Lepidoptera have been referred to as 'micro' and 'macro' species throughout this work. This division is frequently used although there is little basis to it in terms of natural classification (Scoble 1991). However this distinction has been adhered to because of its convenience since many of the identification guides and sources of reference use these terms. All of the species discussed in this work are in the infraorder Heteroneura of the sub-order Glossata (Scoble 1991). Within the Heteroneura, superfamilies Nepticuloidea to Pterophoroidea are the microlepidopteran and Hesperoidea to Noctuoidea the macrolepidopteran species. Lepidoptera pass through the egg, larval, pupal and adult stage during their life-cycle with the larval and pupal stages being alternatively known as the caterpillar and chrysalis. The majority of the feeding is done in the larval stage during which there are a number of moults in order to accommodate the increasing body size.

Calluna vulgaris (L.) Hull has generally been denoted as *Calluna* throughout this study since it is a monospecific genus. Heather refers specifically to this species without including the genus *Erica*. *Vaccinium myrtillus* has been referred to as *V. myrtillus* or bilberry and the term *Erica* has been used to incorporate all the species in this genus in Britain. The term moorland has been used to encompass both northern heath and blanket bog habitats.

Chapter Two

Study areas and sample sites

2.1. Location and characteristics of study areas

The study areas are located in north-east England in the counties of Durham and Cumbria and are mainly within the confines of Weardale and Teesdale. The sites lie along an approximate east-west transect from the lee side of the Pennines towards the east coast of Britain. The study areas are Waldridge Fell, North Plantation, Waskerley Moor, Middle End, Chapel Fell and Moor House and some of their characteristics are listed in Table 2.1.

All of the study areas, with the exception of Waldridge and Moor House, comprise areas of moorland which are primarily managed for red grouse. Management for this purpose requires that the *Calluna* dominated vegetation is burnt on a rotational basis, to provide regeneration of younger, more nutritious *Calluna* which is more desirable for the red grouse population (Watson and Miller 1970). Small areas of vegetation of 20-30m width are burnt which results in small *Calluna* patches of differing ages. As the plants regenerate from a single burning event the stands of the plant tend to be relatively even-aged. Management by controlled burning is not currently practised at the higher altitude sites of Chapel Fell and Moor House. This is because the burning of blanket bog tends to lead to the loss of *Calluna* in favour of *Eriophorum* (Coulson *et al.* 1992). The lack of burning together with the growth structure of the plant on the deeper waterlogged peats means that the plant stands tend to be less even-aged than on northern heath.

There is free-range grazing by sheep in all the study areas with the exception of Waldridge. The two study areas of Waldridge and Moor House are additionally managed as nature reserves.

The two habitats used to define the study areas in Table 2.1 are northern heath and blanket bog. These correspond to the *Calluna-Vaccinium* northern heaths and *Calluna-Eriophorum* wet heaths in the classification of heath communities given by Gimingham (1972). The decrease in temperature and the increase in rainfall with rising altitude reduces the decomposition of the plant material. Together with the intrinsic low decay rate of the plants (Coulson and Butterfield 1978), this leads to the formation of peat. The vegetation changes on blanket bog with *Calluna* co-dominant with *Eriophorum* rather than being the dominant species as on northern heath. A detailed description of the blanket bog community at Moor House is given by Heal and Smith (1978).

Table 2.1. The characteristics of the study areas. The geology is of Carboniferous age with CM = Coal Measures, MG = Millstone Grit and LS = Limestone Series with information taken from the maps of the Geological Survey. Land use is coded as NR = nature reserve, RD = management for red grouse, SG = free range sheep grazing and habitat as NH = northern heath and BB = blanket bog (Gimingham 1972). Within the study areas were a varying number of sample sites which are numerically coded. More detailed information about the individual sample sites is given in Tables 2.2 and 2.3.

Study area	Grid Reference	Geology	Land use	Habitat	Sample sites
Waldridge Fell, Durham.	NZ2449	CM	NR	NH	WD1
North Plantation, Weardale.	NZ0845	CM	SG, RD	NH	NP2-9
Waskerley Moor, Weardale.	NZ0245	MG	RD, SG	NH	WK10-28
Middle End, Teesdale.	NY9730	LS	RD, SG	NH	ME29-30
Chapel Fell, Teesdale.	NY8634	LS	RD, SG	BB	CF36-37
Moor House, Teesdale.	NY7433	LS	SG, NR	BB	MH32, MH33

All the study areas, with the exception of Waldridge, are set within extensive areas of *Calluna* dominated moorland in Weardale and Teesdale. Waldridge is relatively isolated, being a remnant of lowland heathland and it represents a small island of *Calluna* habitat in comparison to the other fieldsites. As a result Waldridge has been excluded from some of the discussions in the following chapters. North Plantation also differs slightly in the range of its vegetation diversity compared to the other study areas, as it is partially surrounded by woodland.

The sampling of the Lepidoptera associated with *Vaccinium myrtillus* was conducted at the three study areas of North Plantation, Middle End and Chapel Fell which together spanned the altitude range. The use of these three study areas was determined by the fact that these were the only areas where there was an extensive cover of bilberry.

Throughout this work the geographical delimitation of the study has been discussed with regard to County Durham. This is not entirely correct as one of the study areas, Moor House, was a few miles within the borders of Cumbria but the abbreviation has been used for simplification.

2.2. Description of sample sites

Patches or stands of *Calluna vulgaris* were selected from within the study areas to be sample sites. A stand is defined as an area of vegetation which is relatively homogeneous with respect to age, structure and composition of the *Calluna* and other vegetation. Within a fire managed moorland environment, the margins of a stand are easily defined by the different lapse times since burning of surrounding patches. On the blanket bog sites where there was no burning, patches of *Calluna* were selected of an area roughly equal to the northern heath stands. Stands were chosen to be as similar and moderate as possible with regard to factors such as slope, aspect and grazing pressure. Individual stands have been numerically identified, with the study area denoted by the first two letters of the classification (Table 2.1). The same criteria were used for the selection and identification of the *Vaccinium myrtillus* stands.

The altitude, slope, and aspect of each sample site have been calculated using the 1:25,000 Ordnance Survey maps (Tables 2.2 and 2.3).

2.3. Description of *Calluna* at sample sites

The life-history phase, age, height, and wet and dry aerial standing crop of *Calluna* at each of the sample sites are given in Table 2.2.

Table 2.2. The characteristics of each *Calluna* sampling site. The altitude, aspect and slope of each site has been calculated from the 1:25,000 Ordnance Survey maps. Columns 5-9 describe the characteristics of the *Calluna* plants and stand. The life-history phase of the *Calluna* stand is described as P=pioneer, B=building, M=mature or D=degenerate after Watt (1955). SS denotes the stand to have a steady state structure as defined by Smith and Forrest (1978). The details of the stem age and height and the standing crop estimations are discussed in the text. Standing crop figures are for the biomass of *Calluna* vegetation and dashes indicate that no measurements were obtained for that sample site. Sample size equals *n*.

Sample site	Altitude (metres asl)	Aspect	Slope (degrees)	Life-history phase	Maximum stem age (years) (*n*)	Mean stem height ± SE (cm) (*n*)	Mean wet standing crop ± SE ($g/0.25m^2$) (*n*)	Mean dry standing crop ± SE ($g/0.25m^2$) (*n*)
W1	120	E	2	M	26 (6)	41 ± 1.4 (44)	542 ± 48 (7)	276 ± 24 (7)
NP2	290	SE	3	M	12 (5)	29 ± 0.7 (56)	749 ± 28 (5)	367 ± 27 (5)
NP3	290	W	3	B	14 (5)	36 ± 1.2 (15)	636 ± 38 (10)	318 ± 13 (10)
NP4	290	SE	3	D	22 (5)	47 ± 1.4 (10)	-	-
WK10	360	NE	3	D	28 (6)	27 ± 0.8 (38)	758 ± 67 (10)	401 ± 37 (10)
WK11	360	NE	4	B	10 (5)	28 ± 0.5 (10)	482 ± 12 (10)	230 ± 7 (10)
WK12	360	NE	2	M	19 (5)	33 ± 1.2 (11)	-	-

Table 2.2. (continued).

Sample site	Altitude (metres asl)	Aspect	Slope (degrees)	Life-history phase	Maximum age (years) (*n*)	Mean stem height ± SE (cm) (*n*)	Mean wet standing crop ± SE ($g/0.25m^2$) (*n*)	Mean dry standing crop ± SE ($g/0.25m^2$) (*n*)
WK13	360	NE	3	B	10 (5)	23 ± 0.9 (10)	-	-
WK14	360	NE	3	B	13 (5)	39 ± 0.7 (11)	-	-
WK15	360	NE	2	M	17 (5)	43 ± 2.1 (10)	-	-
WK16	400	E	4	M	19 (6)	35 ± 1.1 (48)	639 ± 31 (7)	349 ± 22 (7)
WK17	400	NW	3	M/D	15 (5)	38 ± 1.2 (10)	-	-
WK18	400	level	0	M	21 (5)	49 ± 2.3 (10)	-	-
WK19	450	NE	6	B	8 (5)	26 ± 1.3 (10)	408 ± 39 (10)	202 ± 19 (10)
WK20	450	NE	8	M	15 (8)	27 ± 0.9 (38)	791 ± 30 (9)	412 ± 13 (9)
WK21	500	SW	3	B/M	10 (8)	26 ± 1.1 (38)	713 ± 41 (10)	345 ± 19 (10)

Table 2.2. (continued).

Sample site	Altitude (metres asl)	Aspect	Slope (degrees)	Life-history phase	Maximum age (years) (*n*)	Mean stem height ± SE (cm) (*n*)	Mean wet standing crop ± SE ($g/0.25m^2$) (*n*)	Mean dry standing crop ± SE ($g/0.25m^2$) (*n*)
WK22	500	SW	3	M	21 (5)	34 ± 1.3 (12)	-	-
WK23	500	SW	3	B	12 (5)	21 ± 0.6 (10)	421 ± 35 (10)	171 ± 10 (10)
WK24	425	SE	2	M	15 (5)	38 ± 1.5 (10)	-	-
WK26	500	NW	3	M	14 (5)	33 ± 1.0 (12)	-	-
WK27	500	NW	3	B	11 (5)	26 ± 0.7 (10)	-	-
ME29	470	SW	4	M	17 (5)	37 ± 1.0 (10)	-	-
MH32	550	NE	2	SS	21 (5)	24 ± 0.6 (52)	384 ± 34 (9)	138 ± 15 (9)
MH33	650	SE	2	SS	17 (5)	20 ± 0.6 (47)	387 ± 30 (10)	159 ± 12 (10)
CF37	650	level	0	SS	13 (5)	10 ± 0.4 (15)	-	-

Table 2.3. The characteristics of each *Vaccinium myrtillus* sample site. The altitude, aspect and slope have been calculated from the 1:25,000 Ordnance Survey maps.

Sample site	Altitude (metres asl)	Aspect	Slope (degrees)
NP5	290	SE	3
NP6	290	SE	3
NP7	290	SE	3
ME30	470	SW	4
CF36	650	W	4

The measurement of the aerial standing crop of *Calluna* has been taken at a limited number of twelve sites, which is a consequence of the time involved in collecting such data. These measurements were obtained during late September and early October 1989. Ten quadrats of $0.25m^2$ area were examined from each sample site with the quadrat randomly placed by being thrown blind. The plant stems from within the quadrat were cut at their base so that the stems were removed in one piece which helped to minimise the number of cut surfaces exposed for water loss. For the same reason all vegetation was carefully sealed in a plastic bag before removal to the laboratory. It was occasionally difficult to distinguish between root and stem material as decumbent stems often grow adventitious roots. This problem was limited by excluding stems with secondary roots around their entire circumference but including those with roots on one side as these probably represent decumbent rather than buried stems. The wet weight of each sample was taken to the nearest gram after all litter, dead material and vegetation of other plant species had been discarded. An estimation of the dry aerial standing crop of *Calluna* per $0.25m^2$ was achieved by taking approximately one third of the material in each sample and drying it to constant weight at 100°C. The factor of difference between the wet and dry weights of the subsample was then used to calculate the total dry weight per $0.25m^2$.

Multiple regression analysis of the effect of stand age and altitude on the dry aerial standing crop of *Calluna* vegetation shows a significant decline with increasing altitude ($P<0.0001$) but no change with the age of the *Calluna* stand ($P>0.05$) (Table 2.4). The decline in aerial standing crop with increasing altitude can be explained by a number of factors. On the blanket bog habitat at higher altitudes, *Calluna* is co-dominant with *Empetrum nigrum* and *Eriophorum vaginatum* whereas at lower altitudes it occurs in relatively pure stands. On the wet heath sites *Calluna* also changes its growth form, with increased exposure causing stems to become decumbent and gradually buried by peat and moss and for growth to be dwarfed and prostrate. The effect of exposure and/or lack of vigour due to waterlogging is illustrated by the low height of the *Calluna* at Chapel Fell (mean ± SE = 10 ± 0.4cm Table 2.2). Grant and Hunter (1962) found a similar decline in aerial standing crop and a change to a more prostrate growth form at higher altitudes. Wallèn (1987) also notes the low aerial standing crop of *Calluna* in mire conditions. The lack of a significant effect of stand age on the aerial standing crop is unexpected. Aerial biomass of *Calluna* generally increases rapidly through the pioneer and building phases with a levelling out in the mature and degenerate phases (Bellamy and Holland 1966; Chapman *et al.* 1975). There were no stands of pioneer age sampled but there was an age range from 8 to 28 years representing building to degenerate phased stands.

From the ten samples of *Calluna* vegetation taken from each sample site for standing crop estimations, the base of the oldest (thickest) stems were removed for a length of approximately 2cm. These pieces of severed stem were softened by soaking in

Table 2.4. The results of multiple linear regression analysis of the effects of altitude (m) and age (years) of *Calluna* stands on the dry aerial standing crop (g/0.25m^2) and stem height (cm) of the *Calluna*. The regression equation is shown in addition to the coefficient of determination (R^2) and the significance of the regression. The significance level is taken at $P<0.05$ and for the stepwise regression the probability of F-to-enter was set at 0.05.

Analysis	Regression equation	Total R^2	$F_{[d.f.]}$	P
Stepwise regression of age (years) and altitude (m) vs. the dry standing crop of the *Calluna* stand (g/0.25m^2).				
Step 1. enter altitude	Dry standing crop = (-0.345 ± 0.0753) altitude + 421	17%	$21.1_{[1, 105]}$	<0.0001
Stepwise regression of age (years) and altitude (m) vs. the height of the *Calluna* stand (cm).				
Step 1. enter altitude	Height = (-0.040 ± 0.0024) altitude + 46.5	33%	$269_{[1, 545]}$	<0.0001
Step 2. enter age	Height = (-0.038 ± 0.0025) altitude + (0.169 ± 0.0636) age + 42.8	34%	$140_{[2, 544]}$	<0.0001

a mixture of 50:50 70% alcohol and glycerol and thin sectioned using a microtome. The lignin in the sections was stained using phloroglucinol and the annual growth rings counted using a binocular microscope. The number of growth rings were assessed for the oldest stem of at least five samples from each sample site. From these counts the mean, maximum and standard deviation of the oldest stem age was calculated for each stand (Appendix A). The age of the stand has been taken as the maximum age of the stems examined (Table 2.2) since this indicates the minimum lapse of time since burning. Inaccuracies in the predicted age are likely to arise from the difficulty of locating the oldest stems in a vegetation stand. The maximum age equates to the age of the plant stand from regeneration after burning rather than the time since burning. These two measurements are not synonymous because the lapse of time between burning and the initiation of *Calluna* regeneration varies depending on factors such as the age of the original stand at the time of burning (Hobbs and Gimingham 1987). The blanket bog sites at the higher altitudes, although previously burnt more than 40 years ago, are not presently managed by burning. At these sites, the *Calluna* tends to be in a 'steady state system' where the rejuvenation of stems as they become buried by accumulating peat and moss results in the mean age of the stems remaining relatively constant (Smith and Forrest 1978; Wallèn 1980).

Watt (1955) divided the age gradient of *Calluna* into four groups which he described as the pioneer, building, mature and degenerate phases. During the progression through these phases there are changes in primary production, standing crop, illumination, nutrient levels and diversity of plant species (Barclay-Estrup 1970, 1971; Barclay-Estrup and Gimingham 1969; Gimingham 1972). The ages at which individual plants pass from one phase to the next depends to some extent on environmental conditions. Since many of the stands used in this study are even aged, whole stands can be classified as belonging to a developmental stage (Table 2.2). The relationship between the age in years and life-history phase of the *Calluna* stands is illustrated in Figure 2.2. There are some inconsistencies in the age assigned to some of the stands. For example, the age of the NP2 stand as shown from the counts of the growth rings does not satisfactorily correspond with the phase description.

The height of the stand is the mean height of the *Calluna* plants above the ground and not the mean length of the stems. These two measurements are not equivalent as older stems become decumbent and on the wetter peat sites a sprawling growth form tends to develop (Gimingham 1972). The height of *Calluna* is significantly related both to the age ($P<0.0001$) and altitude ($P<0.0001$) of the stand, with these two variables together explaining 34% of the variation in height (Table 2.4). There is a decrease in stem height of approximately 4cm per 100m increase in altitude and an increase in height of 10cm per 10 years of extra age. The decrease in stem height with altitude is the result of the increased incidence of prostrate growth forms at higher altitudes (Grant and Hunter 1962).

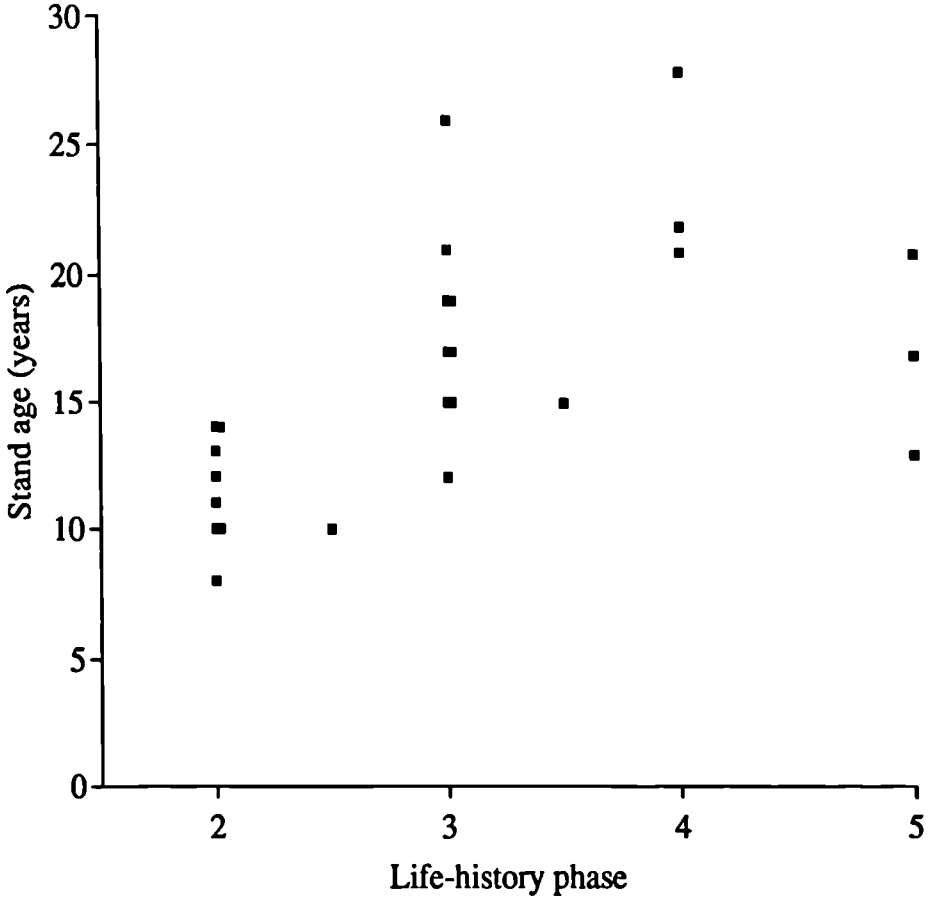

Figure 2.2. The age of the *Calluna* stands in relation to their designated life-history phase. The age of the stand has been taken as the maximum stem age derived from counts of the growth rings as discussed in the text. The phases of the stands are denoted as 2 (building), 3 (mature) and 4 (degenerate) as described by Watt (1955). Those stands which have a steady state age structure have been plotted as phase 5. The data are from Table 2.2. The pioneer phase would be phase 1 except no stands of this age were sampled. Two of the stands, WK17 and WK21, are described as being midway between two phases in Table 2.2 and have been plotted as such.

2.4. Annual use of sample sites

The annual utilisation of study areas and sample sites varied as the emphasis on different aspects of the study changed. Waldridge ceased to be used during 1990 because of its unrepresentativeness in terms of its management and small size, however in the same year, sampling at Middle End and Chapel Fell became extensive. Chapter 3 discusses the sampling methods and their use at individual sample sites in different years.

Chapter Three

Methods of sampling Lepidoptera

3.1. General objectives

The sampling methods were selected primarily for their ability to collect the larval stage of the lepidopteran life-cycle. This is because the mobility of the adult phase means that its presence cannot be equated with that of the entire life-cycle. The larval phase is relatively easy to collect and identify compared to the egg and pupal phase, although identification is not so simple as for the adults.

3.2. Identification of Lepidoptera

The identification of adult Lepidoptera was relatively simple with the use of such photographic guides as Skinner (1984). Identification of the larval stage was more difficult. A number of species display a range of larval colour forms and appearance may change dramatically between instars. The available guides for lepidopteran larval identification either include only a proportion of the British fauna (Carter and Hargreaves 1986; Brooks 1991) or are of limited value because of their descriptive nature (*e.g.* Stokoe and Stovin 1948). Larval identification was therefore initially accomplished by rearing individuals through to the more easily identifiable adult stage.

3.3. Sampling techniques

3.3.1. Berlese funnel extraction

The Berlese funnels used were as described by Southwood (1978), with a heat source above the *Calluna* herbage driving the animals downwards towards a collecting jar. This method relies on the mobility of the invertebrates and it is not therefore suitable for the extraction of eggs and pupae from vegetation. There were twenty funnels available for use with a total depth of 80cm and a circumference of 130cm at their widest part.

The sample sites from which quadrat samples were collected for Berlese funnel extraction were stratified into ten 15x15m squares. On each sampling occasion a single $0.125m^2$ area of *Calluna* vegetation was removed from each of the ten squares. A quadrat of side 33.3cm enclosing an area of $0.125m^2$ was used to select *Calluna*

vegetation. The quadrat was positioned randomly by being thrown blind by the operator, with repositioning if it fell in an area with less than 80% *Calluna* cover. The vegetation enclosed by the quadrat was cut at its base using garden shears and removed in one piece. The selected vegetation was carefully handled to prevent animals being lost and placed in plastic bags which were sealed for return to the laboratory.

The limited number of Berlese funnels meant that two 0.125m^2 vegetation samples had to be placed in each funnel. Therefore the density estimates are for the mean number of larvae per 0.25m^2 of vegetation with five replicates for each sampling occasion. The vegetation was positioned in the funnel and was left *in situ* for seven to ten days. Generally the collecting jar was checked daily and the animals were extracted live from the funnel. When frequent inspection of the collecting jar was impractical, a quantity of 70% alcohol was placed in its base to prevent losses from predation and cannibalism.

The limited number of Berlese funnels meant that only 12 of the total number of 25 sample sites could be surveyed by this method (Table 3.1). The emphasis changed annually on which sites were sampled although some, namely NP2, WK10, WK16, WK20, MH32 and MH33, were sampled every year for continuity. Berlese funnel extraction is relatively time consuming in comparison to other sampling techniques. Approximately one hour is needed for the collection of samples from a single site with additional time required for the processing of samples in the laboratory. Generally sample sites were sampled every two weeks (Appendix B).

There is a significant relationship between the number of species found by Berlese funnel sampling at a site and the number of sampling occasions ($F_{[1,11]}=74$, $P<0.0001$) with approximately one extra species found for every 2.7 extra sampling occasions (Figure 3.1). This relationship is what would be expected both because a greater number of samples increases the chance of recording rare species and because a greater number of sampling occasions allows sampling to coincide with the larval periods of more Lepidoptera species. There is no relationship between the number of sampling occasions and the age ($F_{[1,10]}=0.009$, $P>0.05$) or altitude ($F_{[1,10]}=3.8$, $P>0.05$) of the sites.

3.3.2. Sweep-netting

A sweep-net sample consisted of ten sweep strokes with the interval between them being one pace by the operator, and the net being swept in alternate directions through the heather at each pace. After ten sweepstrokes the net was checked and all animals removed. This action was repeated ten times so that on any sampling occasion 100 sweepstrokes were taken. The net had a semi-circular mouth with the straight side of 36cm length forming the edge which was swept through the vegetation.

Table 3.1. The utilisation of sampling by Berlese funnel extraction at each of the 25 individual sample sites during each of the three years of the study (1989-1990).

Sample site	Years sampled		
	1988	1989	1990
WD1	X	X	
NP2	X	X	X
NP3			
NP4			
WK10	X	X	X
WK11			X
WK12			
WK13			
WK14			
WK15			
WK16	X	X	X
WK17			
WK18			
WK19			X
WK20	X	X	X
WK21	X		X
WK22			
WK23			
WK24			
WK26			
WK27			
ME29			X
MH32	X	X	X
MH33	X	X	X
CF37			X

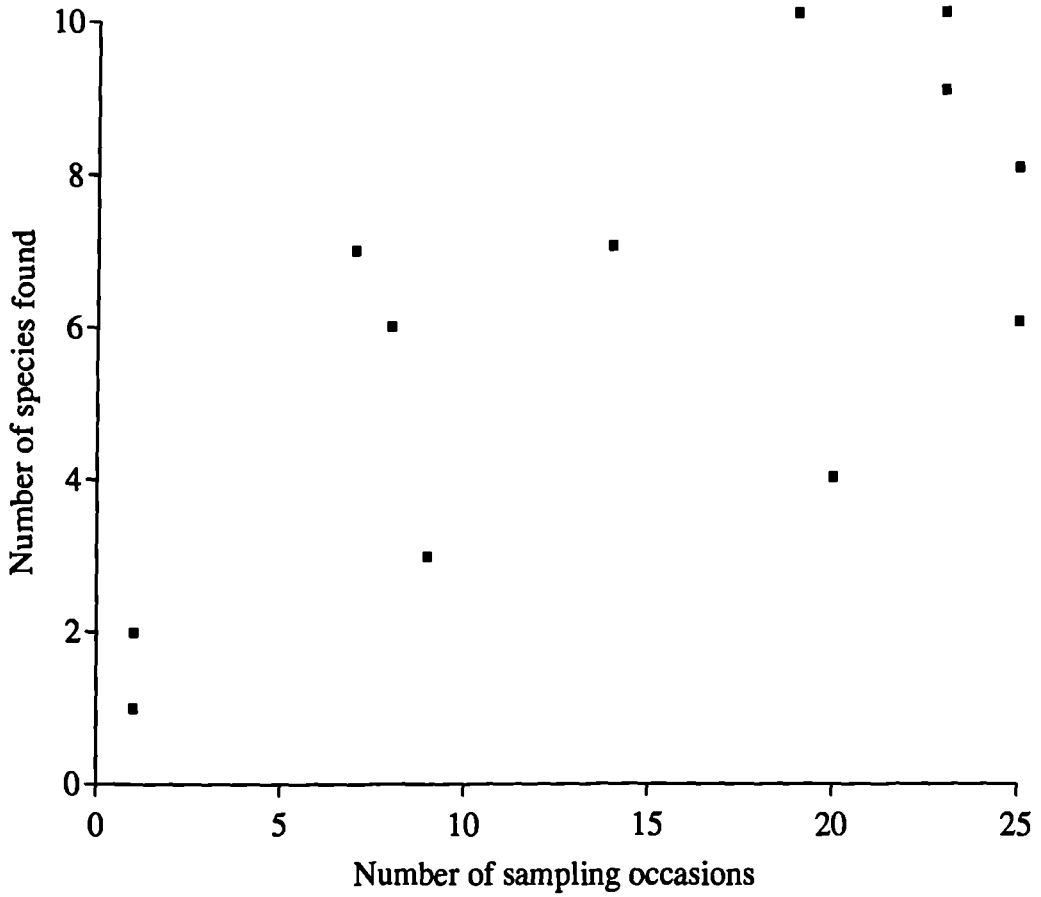

Figure 3.1. The relationship between the number of macrolepidoptera species recorded by Berlese funnel sampling and the number of sampling occasions at each sample site. Data are the records of the larval stage found feeding on *Calluna* during the years 1988 to 1990. Regression gives: $Y=(0.370\pm0.043)X$, $R^2=87\%$, $F_{[1,11]}=74$, $P<0.001$, $n=12$.

The efficiency of capture of invertebrates from plant material using a sweep-net is subject to many sources of variation including temperature (Romney 1945; Saugstad *et al.* 1967), wind velocity (Romney 1945; Hughes 1955), wind direction (DeLong 1932), the time of day (Fewkes 1961; Saugstad *et al.* 1967; Sage 1991), animal behaviour (Day 1991) and inadvertent bias on the part of the operator (Carpenter and Ford 1936). In order to try and minimise the effect of these biases, sampling in extreme weather conditions was avoided and sampling was carried out by a single operator. Samples were collected between 9.00 and 18.00 hours but sites were sampled in a different order on each day to restrict the effect of diurnal changes in larval abundance. The sweep-net will only collect those insects occurring in the upper strata of the vegetation and with increasing height it samples a decreasing proportion of the vegetation.

Sweep-netting gives a relative rather than absolute measure of density, although it allows information to be gathered on seasonal fluctuations and the degree of aggregation of animals (Beall 1935).

The advantage of sweep-netting is that it is quick and easy to use with the sampling of a site possible within 15 minutes. This relative rapidity allows a large number of *Calluna* stands to be sampled in a single day. Sweep-netting is primarily a method to collect lepidopteran larvae although it can be used to capture the adult (*e.g.* Latheef *et al.* 1991), egg and pupal phases when present on herbage.

A total of 29 sample sites were examined by sweep-netting during the 1990 fieldseason, with Waldridge and Chapel Fell being excluded. The growth form of *Calluna* was too prostrate at Chapel Fell to allow sweep-netting and all sampling had ceased at Waldridge before 1990 when sweep-netting was initiated. Individual sample sites were generally sampled every two weeks although many of the sites were sampled on a more frequent basis (Appendix C).

The relationship between the number of sweep-net sampling occasions and the number of Lepidoptera species found as larvae by this method at each sample site is shown in Figure 3.2. There is a significant regression between the two parameters ($F_{[1,22]}$=175, P<0.0001) with 89% of the variation in the number of species caught by this method explicable by the number of sampling occasions. There was approximately one extra species found at a sample site for every additional 1.8 sampling occasions. The reasons for this relationship are the same as for Berlese funnel sampling. The number of sweep-net sampling occasions is not related to either the age ($F_{[1,21]}$=0.001, P>0.05) or altitude ($F_{[1,21]}$=0.10, P>0.05) of the site.

3.3.3. 'Searching'

For some species of Lepidoptera the most successful method of collection was to visually search for the larvae. This was especially true of larger species, such as the Fox Moth (*Macrothylacia rubi*), where the densities were low but the caterpillars

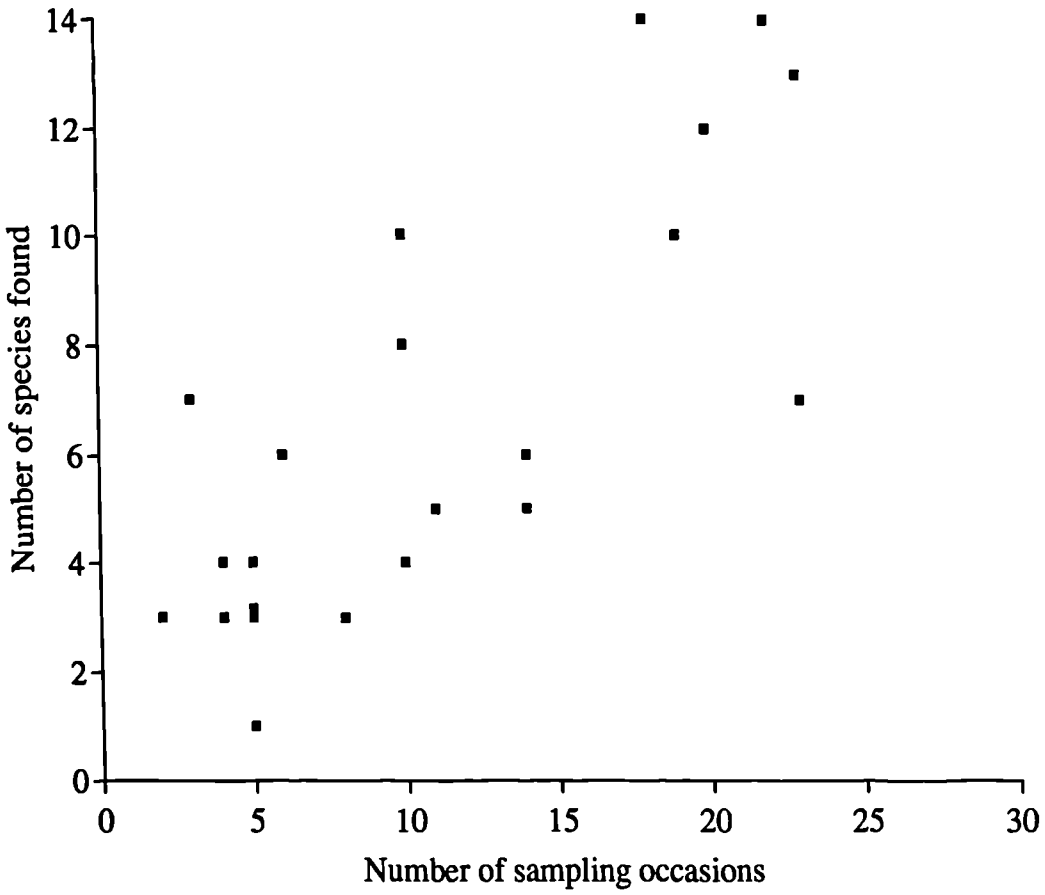

Figure 3.2. The relationship between the number of macrolepidoptera species recorded by sweep-netting and the number of sampling occasions at each individual sample site. The data are for the records of the larval stage found feeding on *Calluna* during the years 1988 to 1990. Regression gives: $Y=(0.56\pm0.042)X$, $R^2=89\%$, $F_{[1,22]}=175$, $P<0.0001$, $n=23$. The regression line was calculated so the y-axis intercept passed through the origin.

themselves were relatively conspicuous. It was also applicable where the behaviour of species made the use of other sampling methods difficult. For example, the later instars of the July Highflyer (*Hydriomena furcata*) construct larval cocoons by tying together the plant shoots with silk which reduces the efficiency of sweep-netting.

(a) 'Quantitative searching'

An attempt was made to quantify the use of visual searching in order to allow comparisons between sites. This was achieved by concentrated searching for larvae during five minute intervals with two or four replicates during each occasion. The use of this method tended to be restricted to certain periods of the year, in order to coincide with the larval periods of selected Lepidoptera species (Appendices D and E). It was mainly used for investigations of the abundance and distribution of *Hydriomena furcata* (Appendix D) and *Macrothylacia rubi* (Appendix E) larvae although the occurrence of all species was recorded.

(b) 'Found'

Many individual Lepidoptera were found during the pursuit of activities at the sample sites. This method of collection was not quantitative, but added to the pool of data on areas such as the development of species and the presence of species at certain altitudes.

3.3.4. Light trapping

A Heath light trap powered by a 12 volt car battery was set up at selected sample sites. Public disturbance meant the light traps were only placed at certain locations, namely, North Plantation (290m), Waskerley (500m) and Chapel Fell (650m). In comparison to the other sampling techniques used, this method almost exclusively captures the adult stage. Adults were required to obtain eggs and to provide confirmation of some of the larval records. Light trapping provided evidence of the presence of some Lepidoptera species noted by the literature to feed on *Calluna* which were not recorded by any of the other sampling methods (Chapter 4). The trap was set to make live catches with the majority of the animals released.

There are limitations to using a light trap for the collection of quantitative results because of the large temporal and spatial variations in the expected catch caused by factors such as the lunar cycle, wind velocity and trap position (Southwood 1978).

3.4. General conclusions on sampling

The proportions of each of the stages of the lepidopteran life-cycle found by each of three main sampling methods are shown in Table 3.2. The majority of the animals collected by each method were in the larval stage which was to be anticipated since sampling methods were selected for this ability. The pupae and adults collected by Berlese funnel extraction represent larvae pupating in the collecting jar and adults emerging from pupae attached to the vegetation in the funnel. A comparison of the number of lepidopteran larvae found by each of the three main quantitive methods, shows a greater number captured by sweep-netting compared to Berlese funnel extraction with both of these methods more successful in numeric terms than quantitive searching (Table 3.3). The different numbers of larvae collected by these methods is partially a result of the frequency of their use. The greater numbers of larvae collected by sweep-netting compared to Berlese funnel extraction is despite the fact that the first method was only employed during the final year of the study compared to three years of Berlese funnel extraction. This is a reflection of the rapidity of sweep-net sampling which allows both a greater number of sampling occasions and a greater number of sites to be sampled.

It became apparent during the progress of the study that the sampling techniques varied in their capture efficiency for the larvae of the different lepidopteran taxonomic groups and species. The percentage of the four taxonomic groups caught by each sampling technique are shown in Table 3.3. It illustrates that searching captures the conspicuous 'Others' larvae whereas very few Noctuidae larvae are found by this method. This is probably a consequence of their nocturnal habits and the fact that they tend to be well concealed on the vegetation or in the litter layer beneath the plants. The percentage of larvae of the abundant species that were caught by each sampling method is shown in Table 3.4. For example, *Eupithecia nanata* although well represented in sweep-net samples, was never found in Berlese funnel samples. Therefore different conclusions as to its abundance would have been derived if sampling had been exclusively by the latter method. The varying sampling efficiencies for different species are probably a consequence of the behaviour and size of the species. For example, as already mentioned *Hydriomena furcata* builds a cocoon amongst the *Calluna* foliage in the later larval instars which reduces the efficiency of capture by sweep-netting. Smaller species such as *Eupithecia nanata* may have lower efficiencies in the Berlese funnel samples as a result of desiccation before the larvae reach the base of the funnel and the collection jar.

It is evident from the results of Figures 3.1 and 3.2 that the number of samples taken at any sample site are an important determinant of the number of species of larval Lepidoptera found at that site. There is no correlation between the number of sweep-net and Berlese funnel samples taken at sample sites (r=-0.25, d.f.=8, P>0.05).

Table 3.2. The percentages of the four stages of the lepidopteran life-cycle found by each of the three methods of quantitative sampling. Miscellaneous methods of capture such as accidental finding and egg batches derived from adults have been excluded. Descriptions of each of the three sampling methods are provided in the text. Data are for the 26 macrolepidopteran species found feeding as larvae on *Calluna* during the study.

Sampling method	Life-cycle stages			
	Eggs	Larvae	Pupae	Adults
Berlese funnel extraction	0	94%	4%	2%
Sweep-netting	<1%	99%	<1%	<1%
Quantitative searching	0	99%	0	<1%

Table 3.3. The percentages of the four taxonomic groups of the Lepidoptera found by the various quantitative sampling methods of Berlese funnel extraction, sweep-netting and quantitative searching. Individuals found by miscellaneous methods such as accidental finding have been excluded. The four taxonomic groups are the 'Others', Geometridae, Noctuidae and Micros with the 'Others' comprising the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. The total number of larvae collected by each method is denoted by *n*.

Sampling method	*n*	Taxonomic group			
		'Others'	Geometridae	Noctuidae	Micros
Berlese funnel extraction	768	<1%	51%	29%	19%
Sweep-netting	1529	2%	69%	25%	4%
Quantitative searching	322	60%	36%	<1%	4%

Table 3.4. The percentages of larvae of the abundant macrolepidoptera species captured by each of the sampling methods. The miscellaneous category includes sampling methods such as 'found' and derivation from eggs laid by adults. Only the 17 species of which more than 10 larvae were caught are included. The data for *Eulithis populata* and *E. testata* are combined.

Taxonomic group & species	Percentage of larvae found by: Berlese funnel	Sweep-netting	Quant. search	Misc.
'Others'				
Trichiura crataegi	0	0	7	93
Lasiocampa callunae	0	5	8	87
Macrothylacia rubi	1	6	70	23
Pavonia pavonia	0	18	4	78
Phragmatobia fuliginosa	17	17	6	61
Geometridae				
Entephria caesiata	16	49	11	24
Eulithis species	8	3	0	89
Hydriomena furcata	35	27	11	27
Operophtera brumata	4	93	1	2
Perizoma didymata	21	47	0	32
Eupithecia satyrata	0	92	8	0
E. nanata	0	99	0	1
E. goossensiata	8	92	0	0
Ematurga atomaria	14	64	6	16
Noctuidae				
Lycophotia porphyrea	19	75	0.2	6
Diarsia mendica	95	0	0	5
Anarta myrtilli	4	82	0	14

However there is also no correlation between the species richness of Lepidoptera estimated by the two methods of sampling for the ten sites where both methods used (r=0.39, d.f.=8, P>0.05) (Figure 3.3) even when two sample sites with a low species richness (WK11 and WK18) were excluded (r=0.28, d.f.=6, P>0.05). The accumulation of species with successive sampling occasions is shown in Figure 3.4.

Figure 3.5 shows the total number of macrolepidoptera species found as larvae on *Calluna* during each of the three years of the study and the number of these species that had not been recorded in previous years. In 1989 and 1990, six and seven new species were found respectively, in addition to species found in previous years of the study. Not all species found in one year were found in subsequent years. There is no correlation between the year in which a species was first found and the abundance of the species in that year, with abundance measured as the total number of individuals found (r=-0.019, d.f.=23, P>0.05) (Figure 3.6). This suggests that species which were not recorded until the later years of the study are not necessarily just the 'rarer' less abundant species. The fact that new species continued to be recorded even in the third year of the study is probably a consequence of the addition of new sampling methods and sample sites. There was a increase in the number of individuals found in each of the three years of the study (Figure 3.5).

None of the methods used to sample larval Lepidoptera were highly efficient and all had disadvantages. However, in the absence of 'ideal' methods, the available methods had to be utilised.

3.5. The calculation of densities from samples

The distribution of the data and hence the spatial distribution of the caterpillars was estimated by the calculation of χ^2 (Equation 1). This uses the relationship between the mean and variance of the number of larvae in samples to test whether the distribution of the data was significantly different from random.

Equation 1.

$$\chi^2 = \frac{s^2 (n-1)}{\bar{x}}$$

s^2 = variance, $\bar{x}$ = mean, n = sample size.

A table of percentage points of the χ^2 distribution (Pearson and Hartley 1966) was used to test departure from the Poisson series. Significant departure from the Poisson series can occur in two directions, either χ^2 values can be less than expected and a regular distribution of the larvae is suspected or it can be greater than expected indicating a contagious distribution (Elliot 1977).

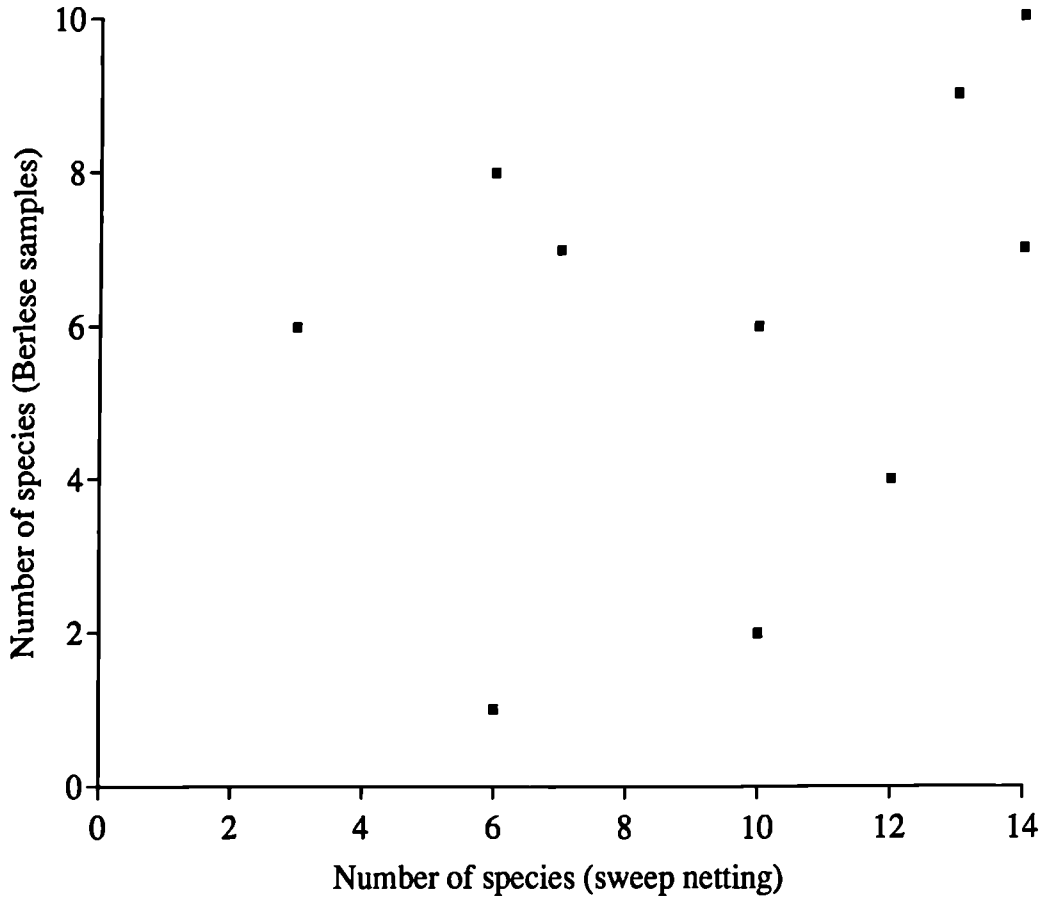

Figure 3.3. The relationship between the number of macrolepidoptera species recorded at each individual sample site by Berlese funnel and sweep-net sampling. Correlation gives: r=0.339, n=10, P>0.05. Data are for the ten out of the total number of 25 sample sites where both sampling methods were utilised.

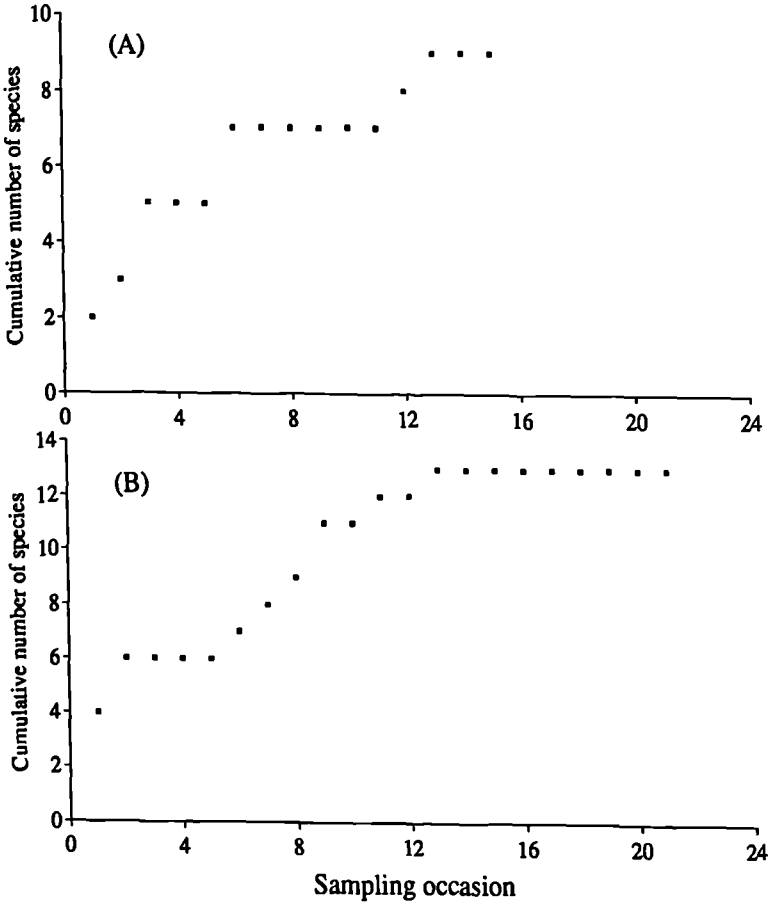

Figure 3.4. The accumulation of macrolepidoptera species with successive sampling occasions by two different sampling techniques. (A) Berlese funnel sampling (B) Sweep-netting. All data are records of the larval stages of the species found on *Calluna* at sample site WK16 at 400m. The sweep-net data are for 1990 only whereas the Berlese funnel data consists of data collected from 1988 to 1990.

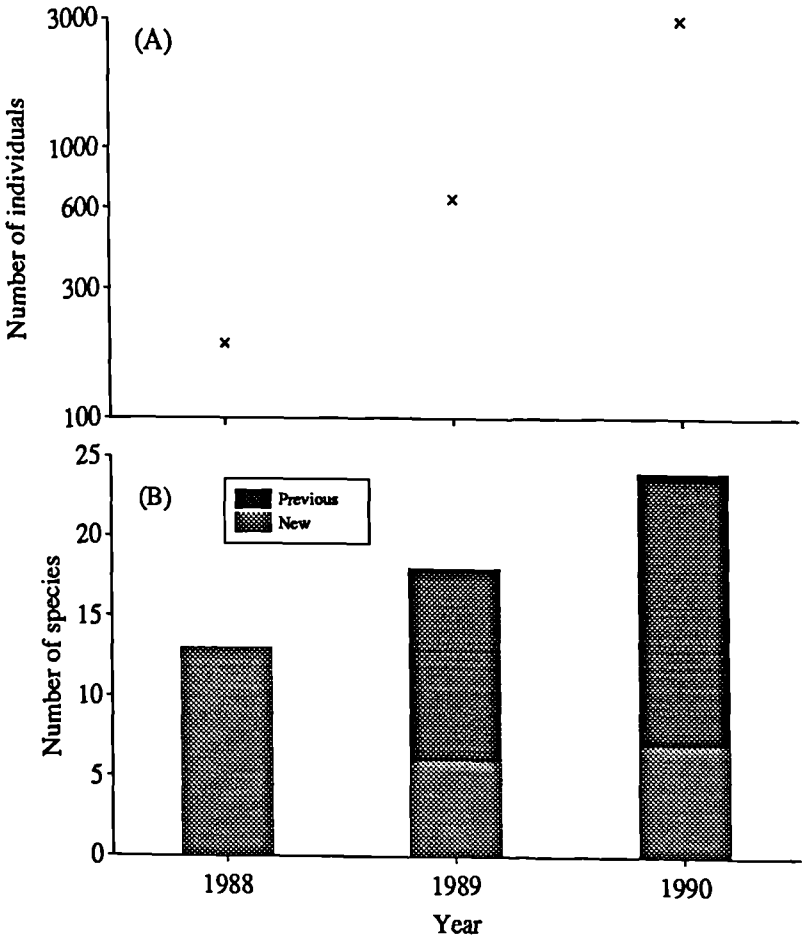

Figure 3.5. (A) The number of macrolepidopteran larvae found during each of the three years of the study. The *y*-axis is shown on a logarithmic scale. (B) The number of macrolepidopteran species recorded during each of the three years of the study. Species recorded in any one year are divided into those found in previous years of the study and new, *i.e.* previously unrecorded, species. Not all of the species recorded in any year were found in subsequent years.

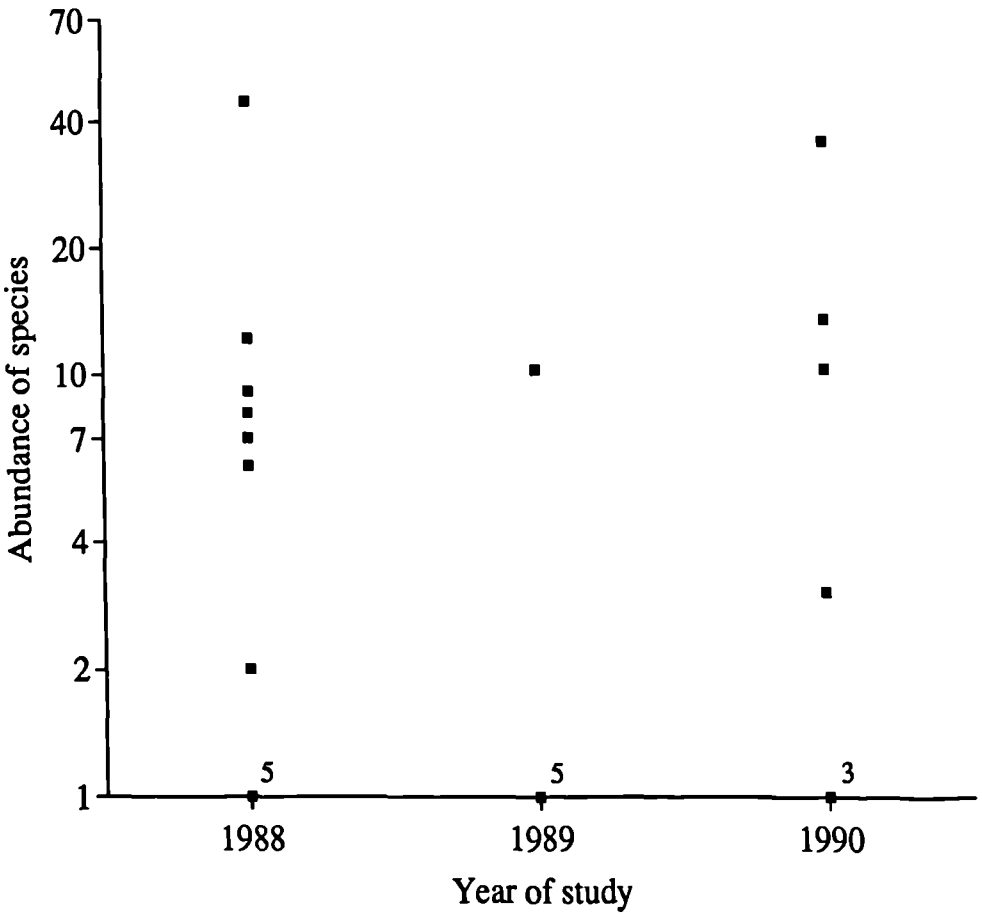

Figure 3.6. The relationship between the year in which a macrolepidopteran species was first recorded and the abundance of that species in that year (r=0.019, d.f.=23, P>0.05). The abundance has been measured as the total number of larvae of that species found during the year. Data for the two *Eulithis* species have been combined. The y-axis is shown on a logarithmic scale. The numbers by the points on the x-axis represent the number of points of equal value.

The data were transformed depending on their distribution.

(a) Randomly distributed data were considered to be normally distributed if mean=variance=10 but since all the density values were less than this, then a square root transformation is used. As many of the counts were zero the transformation was modified to $\sqrt{x+0.5}$.

(b) Contagiously distributed data conforming to the negative binomial distribution were logarithmically transformed. As some of the counts were zero the transformation was modified to $\log(x+1)$

(c) Regularly distributed data was not found to be represented in any of the samples.

Chapter Four

The Lepidoptera associated with Ericaceae

4.1. Introduction

As a preliminary to a more complex study of the relationships between *Calluna vulgaris* and its associated Lepidoptera, some simple questions can be asked. For example, how many lepidopteran species are associated with the plant in Britain and how does this compare to other plants such as bilberry (*Vaccinium myrtillus*).

The number of phytophagous insects associated with plant species is known to be determined by factors such as the plants' geographical range, architecture, chemical composition and its duration of residence in the British Isles (Strong *et al.* 1984).

There are a number of different types of association between Lepidoptera and foodplants such as *Calluna* (Ward 1988). The most obvious involves the dependence of the larval stage of the lepidopteran life cycle on plants for food. However, if the adult stage feeds it may use different plant species compared to the larvae, and in a few species, the plant species on which the adult lays its eggs are different from those which are required by the larvae *e.g. Mellicta athalia* (Warren *et al.* 1984). In this section the relatively well researched and documented association between the lepidopteran larvae and their foodplants is discussed.

Species of the family Ericacea are widespread and abundant in Britain being especially dominant on moorland and heathland habitats. They are characterised by woody shrubs such as *Calluna, Erica* and *Vaccinium* species which as well as being taxonomically related also occur in the same ecological habitats. This study is concerned with the Lepidoptera fauna associated with *Calluna* although some comparative work was done on *Vaccinium myrtillus* (Chapter 9). The genus *Erica* is very similar to *Calluna* in its morphology although the extent of the distinction between the two genera by phytophagous insects is unknown. Authorities differ in whether *Erica* species are more (Stubbs 1983) or less (Bannister 1965; Moss 1968) nutritious than *Calluna.*

Webb (1989) estimated 40 species of insect to be dependent on *Calluna* for food in Britain and suggested this was the expected figure considering the plant's architecture and geographical distribution.

4.2. The Lepidoptera associated with *Calluna vulgaris*, *Vaccinium myrtillus* and *Erica* species in Great Britain

A list of the British Lepidoptera which feed in their larval stage on *Calluna*, *Vaccinium myrtillus* and *Erica* species has been compiled from the literature (Appendix F). Information was obtained from Stokoe and Stovin (1948), Allan (1949), Bradley *et al.* (1973, 1979), Skinner (1984), Carter and Hargreaves (1986), Goater (1986) and Emmet (1991). Records of foodplants eaten in captivity were excluded. The assignation of Lepidoptera species to foodplants varies for the seven texts, with much of this variation the result of differing levels of comprehensiveness by the authors. A species has been included as feeding on a particular foodplant if it is stated to do so by any of the texts. None of the authors give details of how the foodplant records have been assembled, it is therefore difficult to assess accuracy and it is likely that errors are present (Ward 1988). Other records of lepidopteran foodplants exist, for example South (1961), Brooks (1991) and the individual entries for the plants in the 'Biological Flora of the British Isles' series (Ritchie 1956; Gimingham 1960; Bannister 1965), however these sources are not so comprehensive. Authors tend not to specify individual foodplants for widely polyphagous species, therefore these species are likely to be under-represented in Appendix F. Where personal experience has shown such species to feed on *Calluna* they have been included in Section 4.3. Occasionally authors have specified foodplants by their common name, in these circumstances, 'heath' has been taken to imply *Erica* species, 'heather' is *Calluna* and 'heathers' both *Erica* species and *Calluna*. Additionally most entries for *Erica* do not identify the species hence the genus grouping.

Reference to Appendix F shows that the literature lists 86 lepidopteran species to feed on *Calluna*, 76 on *Vaccinium myrtillus* and 47 on *Erica* species. These figures however must be taken as approximations of the true values given the limitations of the data discussed above.

A summary of the results of Appendix F is given in Tables 4.1 and 4.2. It can be seen that the Geometridae and Noctuidae comprise two of the most numerous families of Lepidoptera on *Calluna*. This is not unexpected as they are the two largest macrolepidopteran families (Daly *et al.* 1981). The other families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae incorporate smaller species numbers and throughout this study they have been merged to form the 'Others' taxonomic group. The microlepidopteran species have been grouped together as 'Micros'. Some typical examples of species in each of these three taxonomic groups are shown in Plates 4.1 to 4.3.

A total of 26 species of Lepidoptera feed on both *Calluna* and *Vaccinium myrtillus* (Table 4.1) which represents 30% of the total number of species on *Calluna* and 34% of those on *V. myrtillus*. A similar calculation for *Calluna* and *Erica* shows 38

Table 4.1. The numbers of species of the four lepidopteran taxonomic groups which are associated with *Calluna vulgaris* or *Vaccinium myrtillus* or both of the plants. All species of Lepidoptera which are stated by the literature (see text) to feed on these two plants in Britain are included. The total number of species associated with each plant is given along with the proportion that is shared with the other plant. The division into feeding specialisation groups has been calculated for Lepidoptera overall, Geometridae, Noctuidae, 'Others' and Micros. 'Others' comprises the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae (see Appendix F for the species which comprise these families).

Species group	*Calluna vulgaris* only	*Vaccinium myrtillus* only	Both plants	Total number of species (% shared) on *Calluna*	on *V. myrtillus*
All Lepidoptera	60	50	26	86 (30%)	76 (34%)
Geometridae	21	14	9	30 (30%)	23 (39%)
Noctuidae	15	17	9	24 (37%)	26 (35%)
'Others'	5	1	6	11 (54%)	7 (86%)
Micros	19	18	2	21 (9%)	20 (10%)

Table 4.2. The numbers of species of the four lepidopteran taxonomic groups which are associated with *Calluna vulgaris* or *Erica* species or both of the plants. All species of Lepidoptera which are stated by the literature (see text) to feed on these two plants in Britain are included. The total number of species associated with each plant is given along with the proportion of that total that is shared with the other plant. The division into feeding specialisation groups has been calculated for Lepidoptera overall, Geometridae, Noctuidae, 'Others' and Micros. 'Others' comprises the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae (see Appendix F for the species which comprise these families).

Species group	*Calluna vulgaris* only	*Erica* species only	Both plants	Total number of species (% shared) on *Calluna*	on *Erica* spp.
All Lepidoptera	48	9	38	86 (44%)	47 (81%)
Geometridae	19	1	11	30 (37%)	12 (92%)
Noctuidae	15	2	9	24 (37%)	11 (82%)
'Others'	4	1	7	11 (64%)	8 (87%)
Micros	10	5	11	21 (52%)	16 (69%)

Plate 4.1.

(A) The upper photograph shows the larvae of the Emperor Moth *Pavonia pavonia* (Saturniidae).

(B) The lower photograph shows the larvae of the Vapourer Moth *Orgyia antiqua* (Lymantriidae).

Plate 4.2.

(A) The upper photograph shows the larvae of a species of the Tortricidae family, the species is unknown.

(B) The lower photograph shows the larvae of the Narrow-winged Pug *Eupithecia nanata* (Geometridae).

Plate 4.3.

(A) The upper photograph shows the larvae of the True Lover's Knot *Lycophotia porphyrea* (Noctuidae).

(B) The lower photograph shows the larvae of the Beautiful Yellow Underwing *Anarta myrtilli* (Noctuidae).

species common to both plants which is 44% of the *Calluna* total and 81% of the *Erica* total. There is no significant difference in the numbers of species in the four taxonomic groups on *Calluna* and *V. myrtillus* (χ^2=1.3, d.f.=3, P>0.05) or *Calluna* and *Erica* (χ^2=2.47, d.f.=3, P>0.05).

As an observation on the methods of compiling foodplant lists a simple comparison was carried out of four of the texts giving macrolepidopteran records (Stokoe and Stovin 1948; Allan 1949; Skinner 1984; Carter and Hargreaves 1986). Of the 65 macrolepidopteran species recorded as feeding on *Calluna* in Appendix F, only 21% of the species were recorded by all four texts as feeding on *Calluna*. The proportion of the species mentioned by one, two and three texts were 26%, 32% and 20% respectively. These figures give an idea of the differing levels of comprehensiveness and accuracy of the authors.

4.3. The numbers of species of Lepidoptera associated with *Calluna vulgaris* in County Durham

Information on the distribution of macrolepidopteran species was obtained from Skinner (1984) and Dunn and Parrack (1986) with the latter authority referring directly to County Durham. The available information on the distribution of microlepidoptera species (Emmet 1991) was less detailed, with reference to the north of England only and not County Durham specifically.

From the total pool of Lepidoptera stated to feed on *Calluna* in Britain only a proportion have a distribution which includes the north-east of England or more specifically County Durham. A number of species such as *Lycia lapponaria scotica* and *Paradiarsia sobrina*, have a more northern distribution, occurring only in Scotland. Alternatively some species such as *Plebejus argus* and *Clorissa viridata* have a distribution which is more southern and western relative to County Durham.

Sixty-three of the 86 species of Lepidoptera stated to feed on *Calluna* in Britain have a distribution that includes County Durham (Appendix F). The difficulties represented by the identification of the microlepidopteran species mean that it is the macrolepidopteran species which have been further discussed in this section.

Forty-seven of the 65 species of macrolepidoptera recorded as feeding on *Calluna* in the larval stage in Britain (Appendix F) are recorded by Skinner (1984) and Dunn and Parrack (1986) as present in County Durham. Of these 47 species, five can be excluded for various reasons from the list of probable captures on *Calluna* in County Durham. *Hydriomena ruberata* and *Abraxas grossulariata* are stated to feed on *Calluna* only in the Hebrides, *Semiothisa brunneata* and *Eurois occulta* occur only as adult immigrants to County Durham and *Lacanobia contiguaria* has only been recorded as a single individual adult in County Durham. Table 4.3 gives the 42 species

Table 4.3. The macrolepidoptera species recorded in the literature as feeding on *Calluna* (see text) and as having a distribution which includes north-east England. Information on distribution was obtained from Skinner (1984) and Dunn and Parrack (1986). The table lists whether the species were recorded during this study as larvae and/or adults. Species marked with an asterisk are those which the literature does not specifically list as feeding on *Calluna* but which were found to do so during the study (see text).

Family & Species	Recorded as adults	Recorded as larvae
LYCAENIDAE		
Callophrys rubi	Yes	No
LASIOCAMPIDAE		
Trichiura crataegi	Yes	Yes
Lasiocampa callunae	Yes	Yes
Macrothylacia rubi	Yes	Yes
SATURNIIDAE		
Pavonia pavonia	Yes	Yes
GEOMETRIDAE		
Scopula ternata	No	No
Idaea straminata	No	No
Scotopteryx mucronata	No	No
Entephria caesiata	Yes	Yes
Eulithis testata	Yes	Yes
* *Eulithis populata*	Yes	Yes
Chloroclysta citrata	No	No
Chloroclysta truncata	No	No
Hydriomena furcata	Yes	Yes
Epirrita filigrammaria	No	No
Operophtera brumata	No	Yes
* *Perizoma didymata*	Yes	Yes
Eupithecia satyrata	Yes	Yes
Eupithecia goossensiata	Yes	Yes
* *Eupithecia assimilata*	No	Yes
Eupithecia nanata	Yes	Yes

Table 4.3. (continued)

Family & Species	Recorded as adults	Recorded as larvae
Alcis repandata	Yes	No
Ematurga atomaria	Yes	Yes
Gnophos obscurata	No	No
Dyscia fagaria	Yes	No
Perconia strigillaria	No	No
LYMANTRIIDAE		
* *Orygia antiqua*	No	Yes
Dicallomera fascelina	Yes	Yes
ARCTIIDAE		
* *Arctia caja*	Yes	Yes
Diacrisia sannio	No	No
* *Phragmatobia fuliginosa*	Yes	Yes
NOCTUIDAE		
Noctua comes	Yes	Yes
Paradiarsia glareosa	Yes	No
Lycophotia porphyrea	Yes	Yes
Diarsia mendica	Yes	Yes
Xestia alpicola	No	No
Xestia castanea	Yes	No
Xestia agathina	Yes	Yes
Anarta myrtilli	Yes	Yes
Papestra biren	No	No
* *Ceramica pisi*	Yes	Yes
Aporophyla lueneburgensis	Yes	Yes
Aporophyla nigra	Yes	No
Lithomoia solidaginis	No	No
Agrochola macilenta	No	No
Agrochola helvola	No	No
Acronicta menyanthidis	No	No
Acronicta rumicis	No	No
Syngrapha interrogationis	No	No

which potentially could have been found during this study and lists whether they were recorded either in the adult or larval stage.

Of the 42 potential species resident in County Durham, 19 were found as larvae during this study with an additional six species found only as adults (Table 4.4). Adult captures because of the mobility of this stage, cannot be regarded as proof of a definite association between the larval phase and *Calluna*. Possible reasons that 23 of the 42 potential species were not recorded as larvae are:

(i) Sampling was not intensive enough to find rare species either in terms of the number of study areas investigated or number of samples taken.

(ii) *Calluna* grows in a number of habitats, of which, northern heath and blanket bog were the main ones surveyed in this study. Other habitats where it exists include coastal heath, scree, and *Betula, Pinus* and *Quercus* woodland (Gimingham 1960). Therefore Lepidoptera species associated with such habitats will have been excluded from the study.

(iii) As a result of the unavailability of large areas of moorland and heathland at lower altitudes in County Durham, all the study areas with the exception of Waldridge Fell were above 250m asl. This meant that species which occur exclusively at lower altitudes were unlikely to be recorded.

(iv) The abundance of insect species varies temporally (MacGarvin 1982; Taylor 1986; Barbosa and Schultz 1987) and although species may be described as common and abundant in the literature, the possibility exists that certain species were not abundant during the period 1988-1990.

(v) The species have been overlooked due to misidentification.

(vi) The literature faunal lists may be in error in assigning certain species as feeding on *Calluna*.

In an attempt to explain why 23 (55%) of the potentially 'available' species were not found as larvae, Table 4.5 classifies them into categories of:

(a) Species recorded by Dunn and Parrack (1986) as rare or uncommon and for which the chances of discovery are small.

(b) Species which Dunn and Parrack (1986) list as occurring in habitats which were not sampled during this study. It is therefore unlikely that these species will be recorded.

(c) Species which Dunn and Parrack (1986) regard as widespread and common in County Durham and which therefore should have been found during this study unless factors (iv), (v) or (vi) above are relevant.

Of the 23 species not found in this study, 9 are classified as rare or uncommon in County Durham and two as restricted to non-sampled habitats (woodlands and coastal limestone sites), leaving 12 species which are widespread and common of which four were recorded as adults during the study.

Table 4.4. The numbers and proportions of the macrolepidoptera species stated by the literature (see text) to feed on *Calluna vulgaris* and to occur in County Durham, which were actually recorded during the course of this study. The calculations are shown for the Lepidoptera overall and for each of the three separate taxonomic groups of the Geometrids, Noctuids and 'Others'. The maximum potential number of species is the number of species stated by the literature to feed on *Calluna* and have a distribution which includes County Durham. Extra species are those species not specifically stated by the literature to feed on *Calluna* but which were found to do so during this study. The total number of species recorded as larvae is therefore the sum of rows two and five and the total number found the sum of rows six and four. 'Others' comprises the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

	Macrolepidoptera	Geometridae	Noctuidae	'Others'
Maximum potential number of species	42	18	17	7
Number of species recorded as larvae	19	8	6	5
Percentage of potential number of species that were recorded as larvae	45%	40%	35%	71%
Number of species recorded only as adults	6	2	3	1
Extra species found as larvae	7	3	1	3
Total number of species recorded as larvae on *Calluna*	26	11	7	8
Total number of species found	32	13	10	9

Table 4.5. The designation of the 23 species of macrolepidoptera which are reputed to feed on *Calluna* and occur in County Durham but which were not found during the course of the study into (a) species recorded by Dunn and Parrack (1986) as rare or uncommon in County Durham (b) species which are listed by Dunn and Parrack (1986) as feeding on *Calluna* in habitats not sampled during the study (c) species which Dunn and Parrack (1986) regard as common and widespread. Species recorded in the adult stage only are marked with an asterisk.

Species	(a)	(b)	(c)
Callophrys rubi			X*
Scopula ternata			X
Idaea straminata	X		
Scotopteryx mucronata	X		
Chloroclysta citrata		X	
Chloroclysta truncata			X
Epirrita filigrammaria			X
Alcis repandata			X
Gnophos obscuratus		X	
Dyscia fagaria	X*		
Perconia strigillaria	X		
Diacrisia sannio	X		
Paradiarsia glareosa			X*
Xestia alpicola alpina	X		
Xestia castanea			X*
Papestra biren			X
Aporophyla nigra			X*
Lithomoia solidaginis	X		
Agrochola macilenta			X
Agrochola helvola			X
Acronicta menyanthidis	X		
Acronicta rumicis			X
Syngraph interrogationis	X		
Total number of species	9	2	12
Proportion of 23 species	39%	9%	52%

In addition to the 19 species found as larvae on *Calluna* during this study that were reported to feed on the plant by the literature, there were 7 unreported species found as larvae on *Calluna*. These species are marked by an asterisk in Table 4.3. There are a number of explanations for these 'unexpected' species:

(a) Some of the species are highly polyphagous in their feeding habits and hence the literature does not specify individual foodplants. This applies to *Orgyia antiqua, Arctia caja* and *Phragmatobia fuliginosa*.

(b) The foodplants of the species are stated by the literature but *Calluna* is not included. Two such species; *Eulithis populata* and *Perizoma didymata* are listed as feeding on *Vaccinium myrtillus* and hence to occur in a moorland/heathland habitat. The other two species are *Ceramica pisi* and *Eupithecia assimilata*, the acknowledged foodplants of which are bracken/broom and currant (*Ribes*) species respectively. Therefore with the exception of *Eupithecia assimilata*, the other three species feed on plants that commonly grow in the same habitats as *Calluna*.

(c) Some of the these species, for example *E. assimilata*, were represented by single or few individuals and they may represent accidental tourists (Moran and Southwood 1982).

Therefore 7 of the 26 species (27%) found as larvae feeding on *Calluna* during the progress of this study were not stated to feed on the plant by the literature. This suggests that an estimate of the number of species associated with *Calluna* as obtained from faunal lists is possibly underestimated by about 25%. This would then give over 100 species of Lepidoptera in total on *Calluna* in Britain.

The Lepidoptera associated with *Calluna* can be discussed with regard to a number of groups:

Group (A) Species said by the literature to feed as larvae on *Calluna* in Britain.

Group (B) Species of Group A stated by the literature to occur in County Durham.

Group (C) Species actually recorded as larvae on *Calluna* during the study. The Group C species are further divided into (i) Species of Group B that were found during the study (C1 species). (ii) Species found on *Calluna* during the progress of the study but not stated by the literature to feed on *Calluna* and hence not included in Group B (C2 species).

The proportion of species feeding as larvae on *Calluna* in Britain that occur in County Durham (B as a percentage of A) and the proportion of species occurring on *Calluna* in County Durham that were actually found during the study (C1 as a percentage of B) can be calculated for the three individual taxonomic groups of geometrids, noctuids and 'Others'. The results are given in Table 4.6 which shows that for each of the three taxonomic groups, 60-70% of the species present on *Calluna* in Britain are found in County Durham. For those present in County Durham, the proportions of the three taxonomic groups actually found (C1 as a percentage of B),

Table 4.6. The numbers of species in the three macrolepidopteran taxonomic groups for the three groups of (A) All species feeding as larvae on *Calluna* in Britain (B) Species of group A stated by the literature to occur in County Durham (C) Species actually recorded as larvae feeding on *Calluna* during the study. Species of group C are further divided into (1) species of group B found during the study and (2) species found feeding as larvae on *Calluna* but not stated to do so by the literature. The proportions are given for the species found in Britain that occur in County Durham (B as a percentage of A), species occurring in County Durham that were actually found (C1 as a percentage of B) and the proportion of group C species that are extra species, *i.e.* not recorded as feeding on *Calluna* by the literature (C2 as a percentage of C). 'Others' incorporates the families of the Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

Taxonomic group	Species group							
	A	B	B as a % of A	C1	C1 as a % of B	C2	C2 as a % of C	C
Geometridae	30	18	60%	8	44%	3	27%	11
Noctuidae	24	17	71%	6	35%	1	14%	7
'Others'	11	7	64%	5	71%	3	37%	8
Total	65	42	65%	19	45%	7	27%	26

shows that a much higher proportion of the species in the 'Others' group were recorded compared to those in the Geometridae and Noctuidae. This fact suggests that the recording of species was most efficient for the 'Others' group. This may be related to the relatively large size and conspicuous habits of these species compared to the Geometridae and Noctuidae. Noctuids tend to have nocturnal feeding habits and may therefore have been missed by sampling.

The number of extra species in relation to the number of expected species in each taxonomic group (C2 as a percentage of C1) shows the same ranking between the three groups (Table 4.6). A proportionally greater number of extra species were found for the 'Others' group compared to the Geometridae and Noctuidae. Again this suggests that the apparency of the different families varies.

4.4. Discussion

Ward (1988) defines a foodplant as being able to support the development of an insect from first instar larva through to an adult, thereby including the ability of the plant to support the pupal stage of the life-cycle. Rarely in the literature is such a rigourous definition applied. Many lepidopteran foodplant records are probably the result of larvae being found on a plant without evidence that a species can support itself throughout the larval period on that plant or indeed even feed on it. The literature sources (*e.g.* Stokoe and Stovin 1948) used in this study give little information about how they define a foodplant, how their records have been compiled or their inclusion criteria. Therefore it must be recognised that most foodplant records assembled from the literature will contain errors. With respect to Appendix F it can be postulated that some of the species listed do not actually feed on *Calluna* but balancing this is a group of species excluded from Appendix F which do feed on the plant. This excluded group includes highly polyphagous species that the literature describes as feeding on 'a wide selection of plants' and species such as *Perizoma didymata* for which the foodplant records are incorrect in not listing *Calluna* as a foodplant.

It is likely that Appendix F does not give an accurate indication of the number of species of Lepidoptera which occur on *Erica* and of the percentage of species common to both *Erica* and *Calluna*. As remarked by Webb (1989) the insect fauna associated with *Erica* is less well known in comparison to *Calluna*. This literature search reported 47 species of Lepidoptera on *Erica* in comparison to the 86 species associated with *Calluna* with 38 species common to both plants. It is perhaps to be expected that *Erica* has a lower species richness of Lepidoptera associated with it as a consequence of its lower abundance compared to *Calluna*. There are 6 species within the *Erica* genus in the British Isles compared to a single species of *Calluna*, although only two, *E. cinerea* and *E. tetralix*, are common.

The literature faunal lists suggest relatively equal numbers of species on *Vaccinium myrtillus* (79) and *Calluna* (86). This contrasts with the study of Niemela *et al.* (1982) in Finland that suggested a higher species richness on *Vaccinium myrtillus* with a minimum of 50 species associated with this plant compared to 30 with *Calluna*.

The results indicate that there is a greater amount of overlap between the fauna of *Calluna* and *Erica* than between *Calluna* and *V. myrtillus*. This may represent a bias of recording or an actual biological phenomena. Holloway and Hebert (1979) used data from Allan (1949) to investigate the levels of similarity between lepidopteran faunas on closely related plants. For *Calluna* the greatest similarity was with *Erica* followed by *V. myrtillus, Genista* and *Ulex*. In contrast, *V. myrtillus* showed a greater level of similarity with *Arctostaphylos* species than with *Calluna*.

The literature search indicated approximately 86 lepidopteran species on *Calluna* in Britain which is relatively high compared to previously quoted figures. Webb (1989) states 40 species of insect to be associated with *Calluna* of which 30 are Lepidoptera and notes this to be the approximate number to be expected considering the architecture and geographical distribution of the plant. Gimingham (1985), although restricting his discussion to heathlands, quotes a figure of about 40 species of phytophagous insects. The total number of phytophagous insects associated with *Calluna* has not been estimated here but even considering the fact that the Lepidoptera often comprise the largest proportion of the total insect fauna on woody shrubs (Southwood 1961; Lawton and Schröder 1978) the total can be estimated as a 100 species or more. What is certain is that previous authors have under-estimated the total insect fauna because they have only considered insects associated with *Calluna* with respect to either heathland or moorland habitats, but rarely both. The list of species feeding on *Calluna* is probably still incomplete. For example, Picozzi (1981) lists the geometrid species *Agriopis marginaria* as feeding on *Calluna*, a behaviour which none of the texts used in this literature search recorded.

Just under 50% of the species recorded by the literature to feed on *Calluna* and to be present in County Durham were actually found as larvae during this study. The proportion of the 'available' species that were actually recorded varied for the different families of the Lepidoptera. It is to be expected that the species richness of phytophagous insects found locally is smaller than the regional pool. Previous studies investigating the phytophagous insects associated with foodplants have also obtained less than the potential number of species (Lawton 1982; MacGarvin 1982) and have noted the difficulty of being able to predict which species will be found (Lawton 1978). Ward (1977) investigating the fauna of juniper (*Juniperus communis* L.) found 15 of the expected 19 native species, and observed that the four species not recorded were relatively rare. The results of the present study suggest that rarity was not the only reason a proportion of species were not found. Other important reasons probably

include temporal variability in the abundance of species and the under representation of certain habitats.

Literature faunal lists have been used frequently in the analyses of how factors such as plant host range, abundance, architectural diversity and taxonomic isolation affect the numbers of phytophagous insects associated with plants (*e.g.* Southwood 1961; Lawton and Schröder 1977; Neuvonen and Niemela 1981; Leather 1986). However there have been criticisms of their use because of their incomplete nature (Kuris *et al.* 1980; Owen 1987) although these claims have been refuted (Lawton *et al.* 1981; Niemela and Neuvonen 1983; Leather 1990). Niemela and Neuvonen (1983) found that the patterns revealed by using data exclusively from the literature were little changed by the addition of records collected from personal experience. Southwood *et al.* (1982) showed the ranking of species richness of insects on different plants was unaffected by whether literature or actual sampling lists were used.

The results of this investigation illustrate some of the weaknesses of published faunal lists for calculating the number of insect species associated with plants. They are likely to underestimate the true figure because the food plants of polyphagous species are not specified in addition to the feeding habits of certain species being under sampled. However balancing these biases is the fact that some species are probably mistakenly said to occur on *Calluna* and as noted by Ward (1988) it is difficult to disprove such records. Of the 26 species recorded as larvae, seven were extra to the literature records. Some of the deficiencies of the published foodplant lists can be compensated for by the use of several different texts rather than reliance on a single author. Although there is the additional problem of one author copying and incorporating the mistakes of earlier sources.

Chapter Five

The phenology of the macrolepidoptera associated with *Calluna vulgaris*

5.1. Introduction

Britain has a temperate climate with distinct seasonal changes in variables such as temperature, rainfall and photoperiod. These changes affect herbivorous insects such as Lepidoptera both directly and indirectly through their foodplants. In the severe winter climate, few plants produce new growth and much of the foliage on deciduous trees and herbaceous plants is lost. Evergreen plants, such as *Calluna*, have green foliage throughout the year, although seasonal alterations in the chemical and physical state of the plant cause changes in the quality of the food available for herbivores. It is therefore likely that there will be seasonal changes in the utilisation of plants by herbivorous insects. As most of the feeding in the lepidopteran life-cycle occurs during the larval stage, interest in this study has concentrated on seasonal patterns of larval presence on *Calluna*.

Feeny (1970) studying the Lepidoptera associated with oak (*Quercus robur*) found a peak in the number of species feeding as larvae during May and June with a reduction in July and August followed by a secondary peak in September. Feeny explained the high species richness of Lepidoptera in the spring as a result of selection for larval feeding to coincide with maximum leaf palatability, which is highest during the spring because of maximum protein and minimum tannin levels in the leaves compared to later in the summer. In one of the individual Lepidoptera species, *Operophtera brumata*, the larval and pupal weights obtained were markedly lower on a diet of mature compared to young oak leaves.

Lawton (1978, 1982) found a different seasonal pattern in the species richness of herbivorous insects on bracken compared to oak. From May onwards there is a gradual increase in the number of species with a peak in late July and early August followed by a gradual decrease through to the end of September. Lawton (1978) proposed two hypotheses for this pattern. Initially he thought it was "determined by, and inversely related to, the level and numbers of kinds of defences deployed by the plant". Alternatively, he explained it as an effect of plant architecture, with the growth of the bracken frond through the spring and summer causing an increase in the variety and quantity of resources available for the insects to exploit. Similar seasonal patterns are found on soybeans (Price 1976) and nettle (Davis 1973).

The difference between oak and bracken is therefore determined by the growth structure of the two types of plants (Lawton 1982). The second group of plants as typified by bracken get bigger and more complex through the growing season. In contrast, trees and woody shrubs have most of their structure in place as soon as their leaves open. The seasonal changes in the levels of nitrogen and plant defences then modify this overall pattern. *Calluna* might be expected to fall into the first of these categories although work by Niemela *et al.* (1982) has shown that the species richness of macrolepidopteran larvae on this plant is relatively stable over the spring and summer in Finland.

The seasonal deterioration in food quality for folivorous insects is usually determined by the increased maturity of the leaves available (Rockwood 1974; Feeny 1975; Schwertzer 1979; Scriber and Feeny 1979; Scriber and Slansky 1981). Although examples are known of insects showing preference for mature rather than younger foliage (Bernays and Chapman 1976; Rhoades and Cates 1976; Cates 1980; Damman 1987).

One of the most important determinants of leaf quality is the level of nitrogen (Slansky and Feeny 1977; McNeill and Southwood 1978; Mattson 1980; Strong *et al.* 1984), with levels decreasing with leaf and shoot maturity (van Emden and Bashford 1969; Feeny 1970; Woodwell 1974; Schultz *et al.* 1982; Lawson *et al.* 1984). Animals have higher nitrogen requirements than plants because they use proteins for structural building blocks and excrete nitrogen compounds (Mattson 1980). Although sap feeding insects usually show a correlation between total nitrogen levels and growth (Dixon 1970), there is often no such relationship in folivorous insects (Auerbach & Strong 1981) as a result of plant defences complexing with leaf proteins to reduce their availability (Wint 1983). Therefore a relationship exists between the available nitrogen levels and insect growth and fecundity (House 1965; van Emden and Bashford 1969; Feeny 1970). Phosphorus and potassium show a similar seasonal pattern to nitrogen with other micronutrients such as calcium varying in their seasonal patterns (Mattson and Scriber 1987).

Levels of secondary compounds, such as tannins, are known to increase in mature leaves (Feeny 1970; Dement and Mooney 1974; Schultz *et al.* 1982), although the highest levels of alkaloids are found in new leaves (Robinson 1968). Increased tannin levels have been shown to cause reductions in growth and fecundity of insects (Feeny 1970; Rhoades and Cates 1976) and increased mortality rates (Berenbaum 1983), although in some species high levels of tannins have little effect (Fox and Macauley 1977; Salama and Saleh 1972; Bernays 1981; Rausher 1981; Lawson *et al.* 1984).

The concentration of water in food is important to phytophagous insects (Scriber 1977; Mattson and Scriber 1987) with levels often positively correlated with nitrogen (Scriber and Slansky 1981) and showing a decline with foliage age (Feeny 1970; Woodwell 1974; Scriber 1977; Schultz *et al.* 1982). An increase in the amount of

fibre or toughness of leaves with increasing age is known to adversely affect insects (Feeny 1970; Benz 1974; Hough and Pimentel 1978; Schultz *et al.* 1982), with plants growing on nutrient poor soils often showing high levels of fibres such as cellulose and lignins (Morrow 1983; Mattson and Scriber 1987).

Selection might be expected to synchronise the feeding of the larval stage of Lepidoptera with plant phenology in order to optimise development and survival (Reavey and Lawton 1991). However other constraints may affect the life-cycle timing, for instance, the need to overwinter in a certain life history stage or to synchronise the adult stage with favourable weather or plant flowering times. The overwintering stage is an important consideration when studying the phenology of the larval stage. For example if a species overwinters in the egg stage, the larvae can be present sooner when new plant growth begins in the spring than if the overwintering stage occurs as a pupa. Reavey and Lawton (1991) concluded that the need to overwinter in a resistant stage is not a strong constraint on when larvae feed and allows selection to optimise the timing of larval feeding periods. However, changes in the incidence of overwintering in the different life-cycle phases have been documented with latitude (Mikkola 1980; Hayes 1982), altitude (Coulson and Whittaker 1978), habitat succession (Brown 1986) and food plant architecture (Slansky 1974; Niemela *et al.* 1982; Gaston and Reavey 1989).

As a preliminary to the work done on the phenology of the lepidopteran species associated with *Calluna*, a summary has been compiled of the phenology of the plant itself.

5.2. The phenology of *Calluna vulgaris*

The commencement of spring growth in *Calluna* is determined by photoperiod and temperature, factors which vary annually and with latitude and altitude (Woolhouse and Kwolek 1981). This variation therefore results in growth beginning as late as May or as early as February. As in many woody shrubs, the main period of shoot growth is completed early in the season. In the period preceding and including flowering, new assimilate is almost exclusively directed into wood and with the onset of winter, it is diverted into a sugar pool. The main flowering period of *Calluna* in Britain is the latter half of August and the greater part of September (Gimingham 1960) with the majority of the seed dispersed in October and November. The larval period of Lepidoptera species feeding on the flowers and seeds is therefore determined by these dates. In the northern Pennines *Calluna* has a definite period of winter dormancy characterised by cessation of vegetative growth and flowering, and induction of leaf pigmentation.

The quantity of herbage available through the year varies annually, with the biomass of green material lowest in April and May and rising by about 40% to a broad

maximum through late summer into autumn (Miller 1979). By the end of August, 90% of the annual production of green material has been produced. The current year's shoots only become lignified later in the season.

The concentration of nutrients in the edible green foliage varies in relation to season. Gimingham (1972) states quality to be at a maximum in June and July, thereafter declining to a minimum in winter and with these differences becoming negligible in older heather. Miller (1979) sampled the foliage quality at intervals of three months in March, June, September and December. He found that levels of nitrogen, phosphorus, potassium and soluble carbohydrate were highest in June when growth was most active and then showed little change through the rest of the year. There is no information on how nutrient levels change on a monthly basis so how figures for April, May and July compare to the known levels in March and June are uncertain. In addition the changes in the total nitrogen content as measured by Miller (1979), do not necessarily accord with the amounts of nitrogen available to lepidopteran herbivores because no account was taken of the levels of tannins. As *Calluna* is an evergreen, the foliage in one year consists of the current year's growth along with that of previous years which generally has a lower concentration of nutrients (Miller 1979).

The levels of soluble sugars in the foliage of *Calluna* is highest during the winter months (Grace and Woolhouse 1970). Although soluble sugars are important for the nutrition of insect herbivores they are not known to be essential nutrients (House 1965; Clancy 1992).

Ericaceous plants are known to contain high levels of polyphenols including tannins and anthrocyanins (Brown and Love 1961; Brown *et al.* 1963; Ahtardjieff 1966; Brachet and Paris 1970; Reader 1979; Read and Jalal 1980) with few containing alkaloids (Levins 1976). The general nitrogen deficiency of bog habitats may inhibit protein synthesis resulting in excess carbohydrate being diverted into polyphenol synthesis (Forrest 1971). This is supported by the fact that in many plants, including *Calluna*, the levels of polyphenols are higher in plants growing on mor compared to mull soils (Coulson *et al.* 1960; Davies *et al.* 1964). The latter study also found that *Calluna* had higher levels of leuco-anthocyanin in its leaves compared to a number of deciduous and evergreen trees. The number and quantity of phenolic compounds are higher in the summer months than in the winter, with the highest levels in July and September (Jalal *et al.* 1982).

The thick leaf cuticles of ericaceous plants are said to be the result of adaptations to prevent water loss (Reader 1979) and a characteristic of phosphate deficient habitats (Loveless 1962; Beadle 1966). How the thickness and toughness of *Calluna* leaves vary through the season is not recorded by the literature but it can be assumed that it increases with the maturity of the leaves.

Therefore the *Calluna* plant represents a changing resource for phytophagous insects through the year both in terms of its chemical and physical properties.

5.3. General Methods

The phenology of the macrolepidoptera associated with *Calluna* have been investigated for three groups of species:

Group A. All species stated by the literature to feed as larvae on *Calluna* in Britain.

Group B. All species stated by the literature to feed as larvae on *Calluna* and to have a distribution which includes County Durham.

Group C. All species recorded during the course of this study feeding as larvae on *Calluna* in County Durham. This group incorporates species in Group B which were recorded and also species found feeding on *Calluna* which were not stated to do so by the literature.

The species which comprise the three groups are given in Chapter 4. The only omission is *Scrankia taenialis* from Group A as the life-cycle of this species is uncertain.

As well as analysing the macrolepidoptera species in these three groups collectively for patterns in their life-cycle and phenology, the taxonomic groups of the Geometridae, Noctuidae and 'Others' are investigated for differences in their response. As shown in Chapter 4, the Geometridae and Noctuidae contribute the majority of the species of macrolepidoptera found on *Calluna* and the remaining macrolepidopteran families of the Lycaenidae, Zygaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae have been grouped into a category called 'Others'. The microlepidopteran species have been excluded.

5.4. The overwintering stages of the macrolepidoptera associated with *Calluna vulgaris*

5.4.1. Methods

The stage of the life-cycle in which overwintering occurs for the macrolepidoptera species in Groups A, B and C were determined. Information was obtained from Skinner (1984) for the moth species, and Carter and Hargreaves (1986) for the Lycaenidae. The overwintering phase has also been tabulated separately for Geometridae, Noctuidae and 'Others'.

In Groups A, B and C, χ^2 goodness-of-fit tests have been calculated from the numbers overwintering in the egg, larvae, pupae and adult stage. Additionally a χ^2 contingency test has been used to examine for any significant differences in the proportions overwintering in each stage between Groups A and B, and B and C. Since Group B is a subset of A and C of B it is not appropriate to test them directly against

each other and therefore the figures for Group B have been subtracted from A and those for Group C from B before testing for differences.

5.4.2. Results

The overwintering stages for the entire macrolepidoptera assemblage are given in Table 5.1. For each of the groups of A, B and C, the majority of species overwinter in the larval stage, with smaller proportions overwintering as pupa and eggs. None of the species whose larvae are recorded as feeding on *Calluna* in Britain overwinter in the adult stage.

The proportions of species overwintering as larvae are similar between Groups A and B but are reduced in Group C. In contrast, the proportion of species overwintering in the egg stage increases from Group A to C. There is no clear pattern in the proportions overwintering as pupae with a decrease from Group A to B and an increase from B to C. Despite these patterns there is no statistically significant difference in the incidence of the four stages between Groups A and B and Groups B and C.

The overwintering stages of the three macrolepidopteran taxonomic groups within Groups A, B, and C are given in Table 5.2. An examination of the results for the Geometridae show that from Groups B to C there is a significant decrease in the number of species overwintering as larvae (χ^2=15.3, d.f.=2, P<0.001). Only one species, *Entephria caesiata,* overwinters in the larval stage in Group C. The number of species overwintering in the egg stage remains constant from A to C while those overwintering as pupae decreases. However due to the decrease in the number of larval overwintering species, a large proportion of the species in Group C overwinter as eggs and pupae. Of the geometrids that overwinter as pupae, 80% consist of species which feed as larvae on the flowers of *Calluna* in August and September. Therefore the overwintering phase in these species is perhaps determined by the short amount of time available for advancement of the life-cycle before winter.

The Noctuidae show an inverse pattern compared to the Geometridae. There is an increase in the number of species overwintering as larvae in Group C although these changes are not statistically significant (χ^2=1.9, d.f.=2, P>0.05; χ^2=3.9, d.f.=2, P>0.05). A comparison of Groups A and B show there is no change in the proportion overwintering as larvae. However there is a slight reduction in the proportion overwintering as pupae and a slight increase in the proportions overwintering as eggs. In the change from Group B to C there is an increase in the proportions overwintering in the larval and pupal phases with no species of Noctuidae overwintered as eggs.

In the 'Others' category which constitutes six other families of the Lepidoptera, there were no prominent changes in overwintering stage from A to C (χ^2=3.2, d.f.=2, P>0.05; χ^2=2.9, d.f.=2, P>0.05). From Group A to B there was a reduction in the

Table 5.1. The overwintering stages of the macrolepidopteran species which feed as larvae on *Calluna*. Information on overwintering has been obtained from Skinner (1984) for the moths and Carter and Hargreaves (1986) for the Lycaenidae. The results are shown for three groups: (A) all species stated by the literature to feed as larvae on *Calluna* in Britain (B) all species stated by the literature to feed as larvae on *Calluna* and to exist in County Durham (C) all species recorded feeding on *Calluna* in County Durham during the study. Biennial species have had both overwintering stages included where the overwintering stage in the second year is different compared to that of the first year. The results of χ^2 goodness-of-fit tests for differences in the numbers overwintering in each life-cycle stage in each of the Groups A, B and C are given. A χ^2 contingency test has been used to test for differences between groups. Since Group B is a subset of A and C is a subset of B, a prerequisite of the test is that the figures for B are subtracted from A and those for C from B when the groups are tested against each other. Statistical significance has been taken at the 95% probability level.

Overwintering stage	Lepidoptera Group		
	(A)	(B)	(C)
Eggs	11 16%	9 20%	7 25%
Larvae	36 54%	24 55%	12 43%
Pupae	20 29%	11 25%	9 32%
Adults	0 0%	0 0%	0 0%
χ^2 (d.f.) *P*	38.9 (3) <0.01	26.7 (3) <0.01	11.1 (3) <0.01
χ^2 (d.f.) *P*	2.3 (2) >0.05	1.9 (2) >0.05	
Total number of species	64	42	26
Biennial species	3	2	2

Table 5.2. The overwintering stages of the three taxonomic groups of the macrolepidopteran species which feed as larvae on *Calluna*. The taxonomic groups are the Geometridae, Noctuidae and 'Others' and the information about overwintering has been taken from Skinner (1984) for the moths and Carter and Hargreaves (1986) for the Lycaenidae. The results are shown for three groups: (A) all species stated by the literature to feed as larvae on *Calluna* in Britain (B) all species stated by the literature to feed as larvae on *Calluna* and to be present in County Durham (C) the species recorded feeding on *Calluna* in County Durham during the study. 'Others' comprises the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. Biennial species have had both overwintering phases included where the overwintering stage in the second year is different to that of the first year. χ^2 contingency tests have been used to test for differences between groups. Since Group B is a subset of A and C is a subset of B, a prerequisite of the test is that the figures for B are subtracted from A and those for C from B when the groups are tested against each other. Statistical significance has been taken at the 95% probability level.

Lepidopteran taxonomic group & overwintering stage	**Lepidoptera group**		
	(A)	**(B)**	**(C)**
Geometridae			
Eggs	5 (17%)	5 (28%)	5 (46%)
Larvae	16 (53%)	9 (50%)	1 (9%)
Pupae	9 (30%)	4 (22%)	5 (46%)
χ^2 (d.f.)	4.3 (2)	15.3 (2)	
P	>0.05	<0.001	
Noctuidae			
Eggs	3 (13%)	3 (18%)	0
Larvae	14 (59%)	10 (59%)	5 (71%)
Pupae	7 (29%)	4 (24%)	3(33%)
χ^2 (d.f.)	1.9 (2)	3.9 (2)	
P	>0.05	>0.05	
'Others'			
Eggs	3 (23%)	1 (11%)	2 (20%)
Larvae	7 (54%)	5 (56%)	6 (60%)
Pupae	3 (23%)	3 (33%)	2 (20%)
χ^2 (d.f.)	3.2 (2)	2.9 (2)	
P	>0.05	>0.05	

proportion overwintering as eggs and larvae and an increase in the proportions overwintering as pupae. Between Groups B to C, these changes were reversed.

The patterns observed in Table 5.1 can therefore be ascribed to changes within individual taxonomic groups of the Lepidoptera. The reduction in the proportion of Lepidoptera on *Calluna* overwintering as larvae in Group C can be seen to be mainly due to a reduction in the proportions of Geometridae overwintering as larvae in Group C. This trend compensates for an increase in the proportion of Noctuidae in Group C overwintering as larvae. The increase in the proportion of Lepidoptera overall overwintering as eggs would seem to be due to the Geometridae with there being a complete loss of Noctuidae overwintering as eggs in Group C.

5.5. The phenology of the species richness of macrolepidoptera present as larvae on *Calluna vulgaris*

5.5.1. Methods

The seasonal patterns in the number of macrolepidopteran species present as larvae on *Calluna* can be investigated from two separate sources.

(a) From the literature

Literature sources generally list the duration of the larval stage for individual Lepidoptera. This data can be used to compile a monthly estimate for the species richness of larvae on *Calluna* for Groups A, B and C. The information on larval periods was obtained from Skinner (1984) for the moths and Carter and Hargreaves (1986) for the Lycaenidae. The literature lists the duration of the larval phase but this is not necessarily synonymous with the period of larval feeding. This distinction is most relevant to the winter months when species overwintering as larvae are unlikely to be feeding. It should also be emphasised that the larval duration is the period over which the species and not the individual feeds.

For a few species, the literature specifies the limits of the larval period to a season rather than a particular month. In these circumstances, autumn has been taken to begin in October and spring as ending in May. The literature designates the limit of some larval periods to either 'early' or 'late' in the month but as this only applies to a few species and as there is a lack of information about the precision and origin of the records, the totals have only been calculated using complete months.

(b) From the samples

As an alternative to using the literature information, there is the monthly species richness of larvae recorded on *Calluna* during the progress of this study. This

method involves the Group C species for which there are therefore two estimates of larval species richness through the year. All data collected from 1988-1990 by all sampling methods were utilised.

5.5.2. Results

(a) As evaluated from the literature

The species richness of macrolepidopteran larvae on *Calluna* through the year is shown in lines A to C in Figure 5.1 which correspond with the Groups A, B and C. The literature based estimates of larval species richness show a peak during April and May followed by a large reduction during June and July and a second peak in August and September. The number of species remains relatively constant through from October to March. Groups A to C in Figure 5.1 show a successive dampening of this pattern and in Group B the second peak in September is absent. The transition from Groups A to C illustrates an increasing stability to species richness across the spring and summer, due to a reduction in the decrease of species richness in June and July. The stability of the number of species present as larvae during the winter months represents a suspension of development with no larvae pupating or hatching from eggs.

(b) As evaluated from the samples taken

The results obtained from field samples are shown in line D of Figure 5.1. It can be seen that from September to May line D falls below line C whereas during June, July and August line D species richness is greater than line C. Theoretically, line C should equal line D as they are composed of data for identical species of Lepidoptera. However whereas Group C is the species richness as derived from literature sources, line D is the monthly species richness as recorded from field data. Line D should equal line C if the following conditions are fulfilled:

1. Each of the 26 species found during the study were recorded during each month of their larval phase.
2. The limits of the literature and field larval periods coincide.

The first of these two conditions is likely to have been affected by the intensity of sampling and the abundance of the individual species. The intensity of sampling varied through the year. It was consistent during the main fieldwork season which extended from April to October but was reduced from November to March when many of the species were inactive and difficult to find. An estimate of the efficiency of species recording can be obtained from the proportion of species stated by the literature to feed during each month that were actually found (Figure 5.2). Using the periods stated by Skinner (1984) for the 26 species found during the study

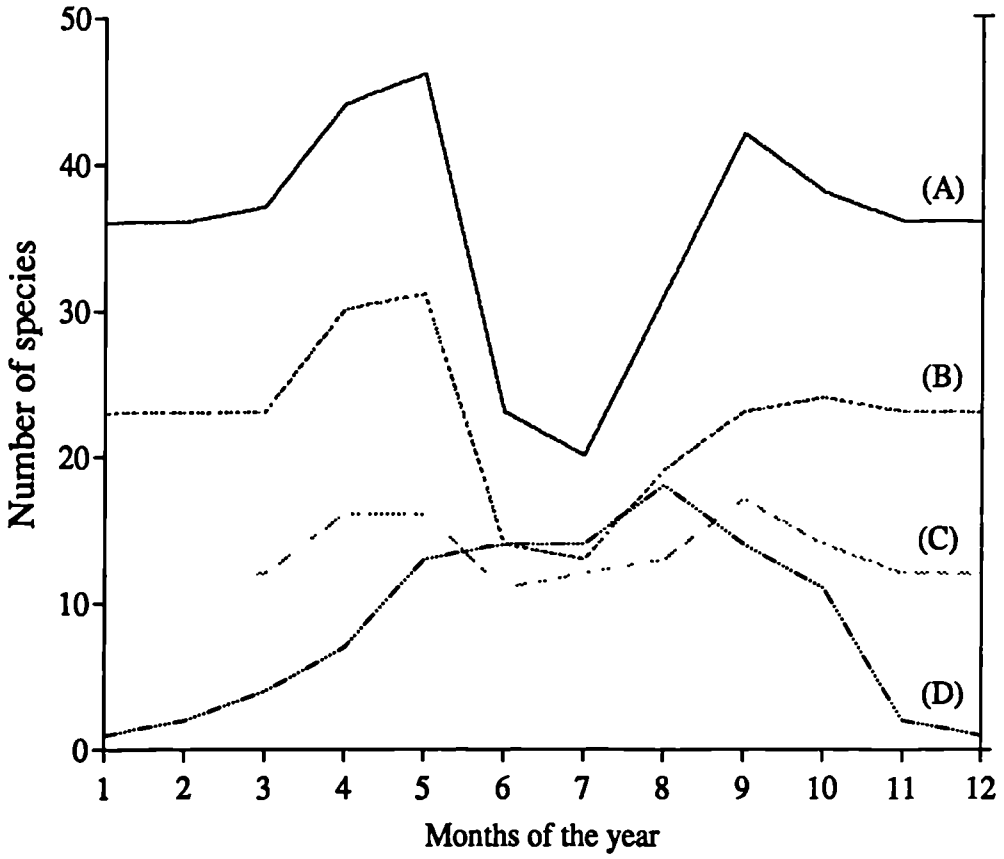

Figure 5.1. The changes through the year in the number of macrolepidopteran species present as larvae on *Calluna*. The changes are shown for four groups of Lepidoptera: (A) All species stated by the literature to feed as larvae on *Calluna* in Britain (B) All species stated by the literature to feed as larvae on *Calluna* and to have a distribution which includes County Durham (C) All species recorded as larvae on *Calluna* during the study (D) All species recorded as larvae on *Calluna* during the study but using field collected data on larval periods. Information about larval periods for Groups A, B and C is taken from Skinner (1984) for the moths and Carter and Hargreaves (1986) for the Lycaenidae. Group D uses field data collected during 1988-1990 in the northern Pennines.

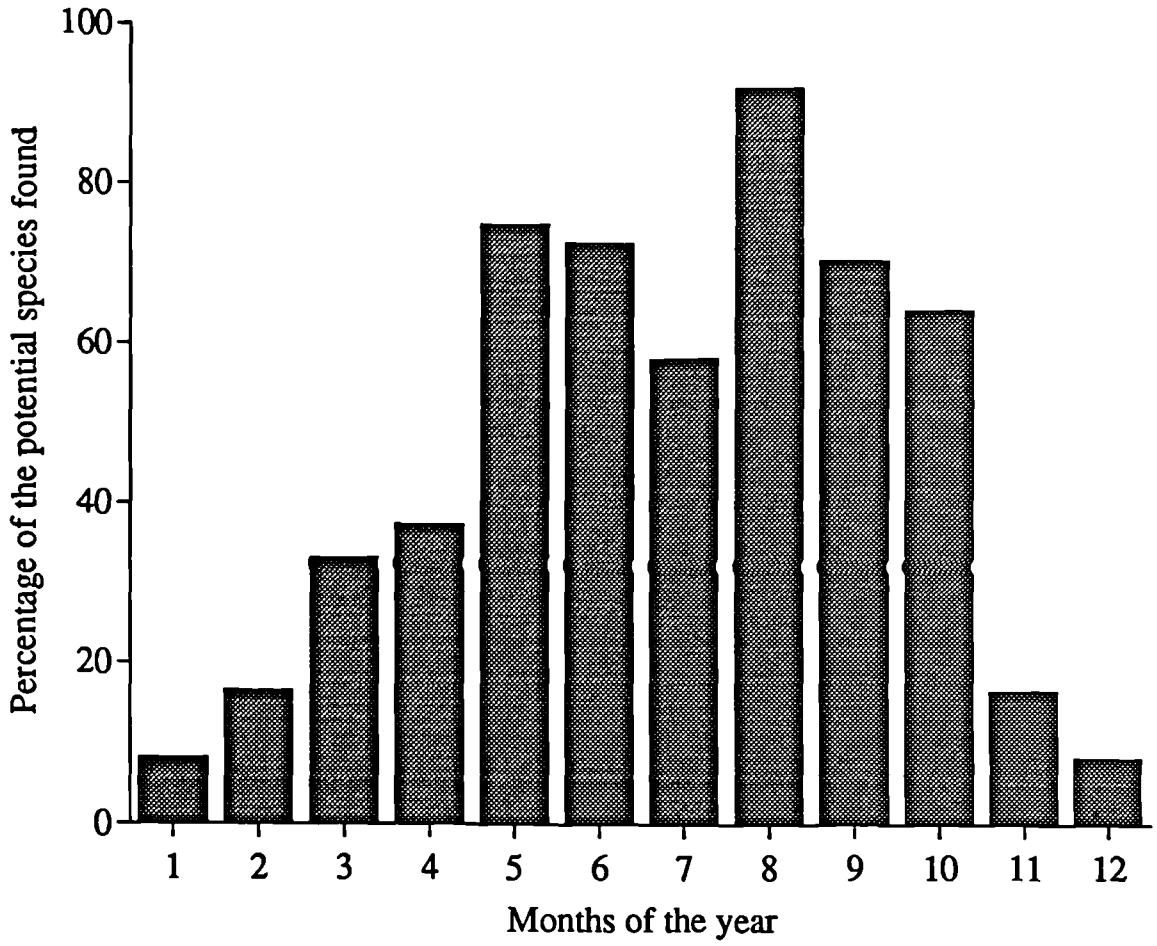

Figure 5.2. The percentage of the macrolepidopteran species stated by the literature to be present as larvae on *Calluna* during each month of the year that were actually recorded during each of these months. A total of 26 species were recorded and information about the larval periods has been obtained from Skinner (1984) for the moths and Carter and Hargreaves (1986) for the Lycaenidae.

shows that between November and April less than 50% of the species thought to be present as larvae were actually found (Figure 5.2).

Rarer species, of which only a few individuals were discovered, are unlikely to have been recorded in each of the months of their designated larval periods. Species are perhaps more likely to have been encountered at the end rather than the beginning of their larval periods because of size differences. It is also possible that misidentification of larvae may have contributed to the asynchrony of the literature and field observed larval periods.

The inequality of lines C and D is also partially due to the larval periods quoted by Skinner (1984) not being adhered to by the Lepidoptera species found during this study. It is to be anticipated that some divergence of expected and observed larval periods should occur. It is often impossible for authors to give more than generalised and approximate information about time schedules of Lepidoptera species when allowance must be made for factors such as latitude and the state of the season (Emmet 1991). Of the 26 macrolepidopteran species found as larvae, 61% were found outside the dates of their larval periods as designated by the literature, with the degree of divergence between the actual and literature larval periods varying between species (Table 5.3). For example, in *Eupithecia nanata* only a few individuals were found outside their 'expected' larval period whereas for *Entephria caesiata* the figure was 42% of larvae. Transgression of literature larval periods occurred both at their beginning and end (Table 5.3). The fact that species do not adhere to their literature larval periods means that estimates of seasonal values of species richness derived from literature sources (*e.g.* Figures 5.3, 5.4 and 5.5) are likely to be inaccurate.

5.6. The larval phenology of the different families of macrolepidoptera associated with *Calluna vulgaris*

5.6.1. Methods

The macrolepidoptera species in Groups A, B and C have been divided taxonomically into Geometridae, Noctuidae and 'Others'. The information given in Skinner (1984) about the duration of the larval period has then been used to determine the number of species in each of the three taxonomic groups that are present as larvae on *Calluna* during each month of the year.

In addition to the species richness, the abundance of larvae in individual taxonomic groups has been calculated for each month of the year. This was taken from field data for all three years of the study combined (1988-1990). The proportions of the three taxonomic groups are likely to be biased by varying capture efficiency by the different sampling techniques. The data has therefore been limited to all larvae captured by the sampling methods of sweep-netting and Berlese funnel

Table 5.3. The sixteen species of macrolepidoptera feeding as larvae on *Calluna* that were recorded outside the limits of the dates of the larval periods as designated by Skinner (1984). The total percentage of larvae outside the limits are sub-divided into whether they were recorded either at the start or end of the larval period. The two *Eulithis* species are given separately with only larvae of the genus which had been positively identified to one of the species included. The total number of larvae found of each species is denoted by *n*. The other ten species of macrolepidoptera found feeding as larvae on *Calluna* during the study were recorded within the literature designated limits of the larval period.

Family & Species	**Percentage of larvae found outside limits of dates of larval period**		
	Total (*n*)	**Start**	**End**
Lasiocampidae			
Macrothylacia rubi	<1% (252)	<1%	
Saturniidae			
Pavonia pavonia	9% (68)		9%
Geometridae			
Entephria caesiata	42% (123)	3%	39%
Eulithis testata	10% (7)		10%
Eulithis populata	10% (5)		10%
Hydriomena furcata	10% (760)	4%	6%
Operophtera brumata	<1% (164)		<1%
Perizoma didymata	29% (34)		29%
Eupithecia nanata	<1% (288)		<1%
Eupithecia goossensiata	23% (13)	23%	
Ematurga atomaria	23% (152)	23%	
Lymantriidae			
Dicallomera fascelina	40% (5)	40%	
Noctuidae			
Noctua comes	100% (1)	100%	
Lycophotia porphyrea	2% (462)	2%	<1%
Diarsia mendica	44% (101)	28%	16%
Aporophyla lueneburgensis	70% (10)	50%	20%

extraction. As the use of these two sampling methods excludes captures of large numbers of larvae of species in the 'Others' taxonomic group only the results for the geometrids and noctuids have been examined. The geometrids have been divided into species that feed mainly on the reproductive parts of the *Calluna* plant (*i.e. Eupithecia nanata, E. goossensiata* and *E. satyrata*) and the remaining species. This was done because the seasonal patterns of the two groups may be determined by different selection pressures.

For the 26 species in Group C the relationship between the month in which the larval phase begins and the total length of time spent as a larvae has been investigated. Information on the two parameters has been taken from Skinner (1984). The two biennial species, *Lasiocampa callunae* and *Trichiura crataegi*, have been excluded because the constraints of completing the life-cycle within a single year are absent.

5.6.2. Results

The numbers and proportions of macrolepidoptera species present on *Calluna* in any month that are composed of the Geometridae, Noctuidae and 'Others' are given in Figures 5.3, 5.4 and 5.5 for Groups A, B and C respectively.

For Group A (Figure 5.3), which includes all the macrolepidoptera on *Calluna* in Britain, it can be seen that the seasonal change in larval species richness as described in Section 5.5 are shown individually by each lepidopteran taxonomic group of Geometridae, Noctuidae and 'Others'. This results in the proportions of species in the three taxonomic groups remaining relatively constant through the year.

In Group B (Figure 5.4), the spring peak in larval species richness is shown in all three taxonomic groups. However none of the groups show a distinct peak in species richness during September although there is a late summer rise in species richness. The proportion of the total species richness in each taxonomic group varies more seasonally than in Group A. The geometrids show a reduction in their contribution in June and July but peak during May and August. The decrease in the proportion of geometrids results in an increased proportion of the larval species richness in June and July being composed of species of the 'Others' taxonomic grouping.

In Group C (Figure 5.5), the effects of the changes in the incidence of the overwintering stages of the three families are evident. The proportion of species which are Geometridae during the spring and summer months are approximately equal to Groups A and B. However during the late autumn to early spring less than 10% of the species existing as larvae on *Calluna* are geometrids. The life-cycle of the majority of noctuid species involves hatching from eggs in late summer and pupating in the late spring of the following year. This accounts for the stability in noctuid species richness

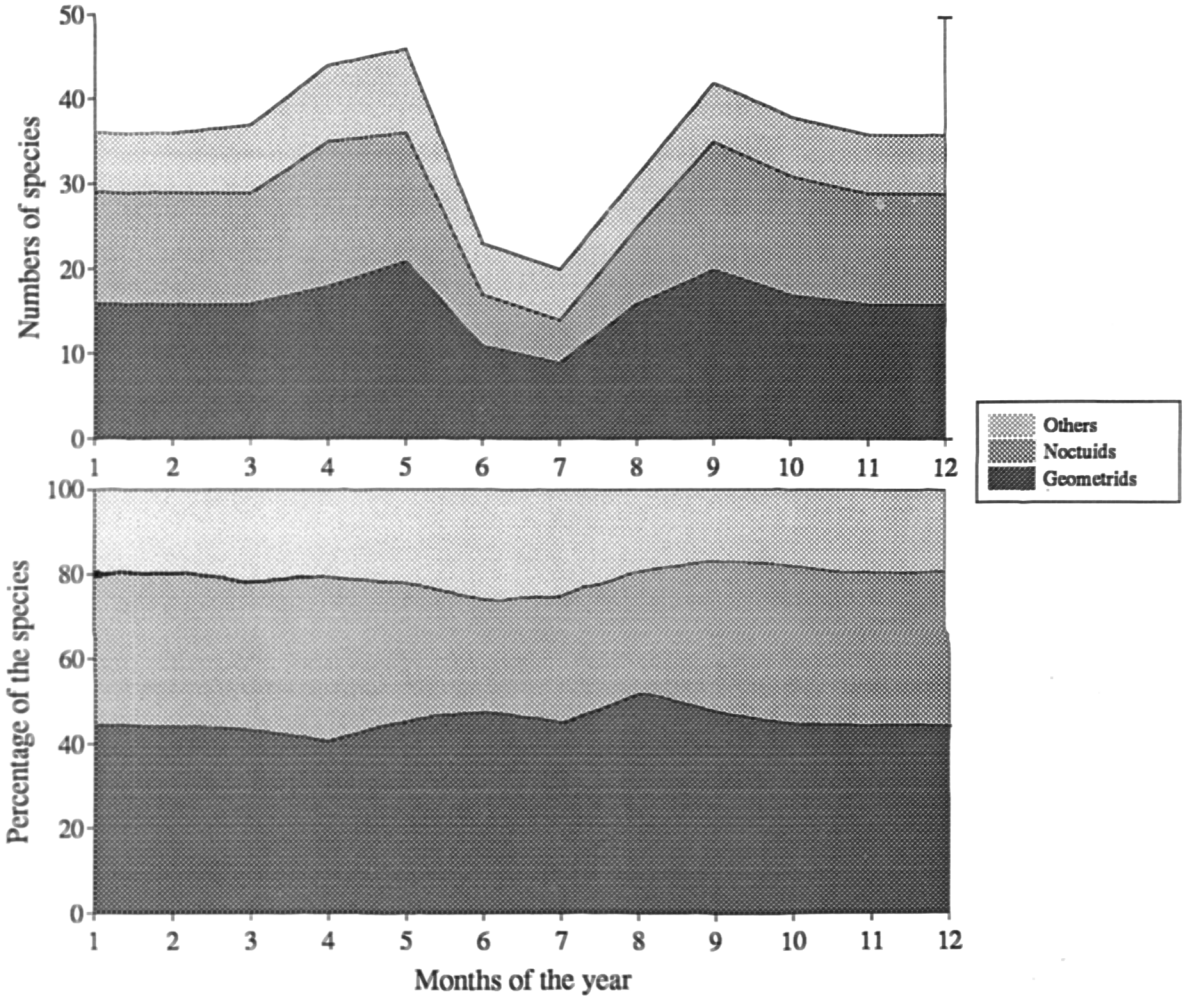

Figure 5.3. The representation of species in the three taxonomic groups of Geometridae, Noctuidae and 'Others' as larvae on *Calluna* during the months of the year for the macrolepidopteran species of Group A. Information on the duration of larval periods has been taken from Skinner (1984). Group A includes all species of macrolepidoptera stated by the literature (see text) to feed as larvae on *Calluna* in Britain. The results are shown both as the number of species and the percentage of the total number of species in each taxonomic group. 'Others' includes the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

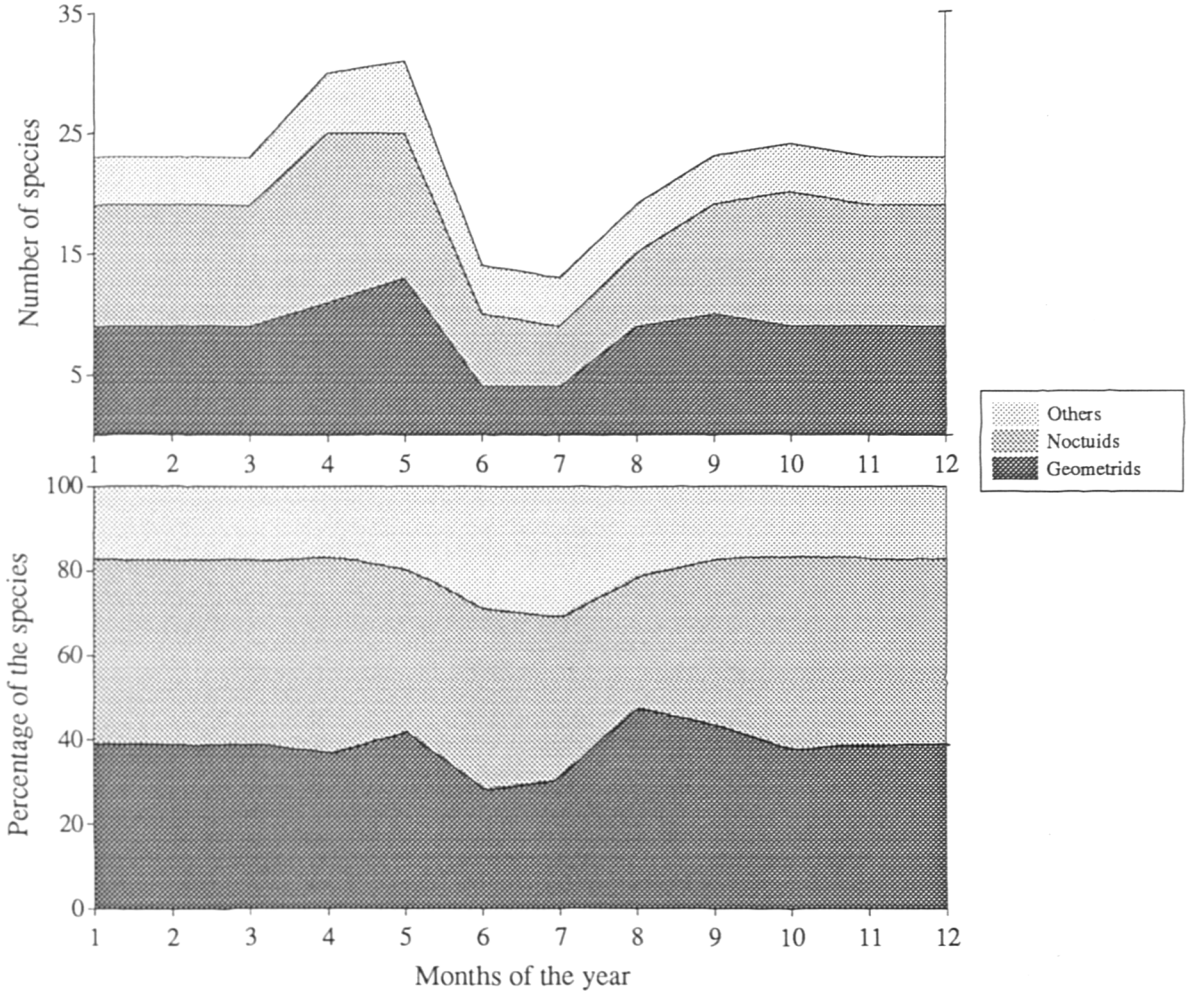

Figure 5.4. The representation of species in the three taxonomic groups of Geometridae, Noctuidae and 'Others' as larvae on *Calluna* during the months of the year for the macrolepidopteran species of Group B. Information on the duration of the larval periods has been obtained from Skinner (1984). Group B includes all species of macrolepidoptera stated by the literature (see text) to feed as larvae on *Calluna* and to have a distribution which includes Co. Durham. The results are shown both as the number of species and the percentage of the total number of species in each taxonomic group. 'Others' includes the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

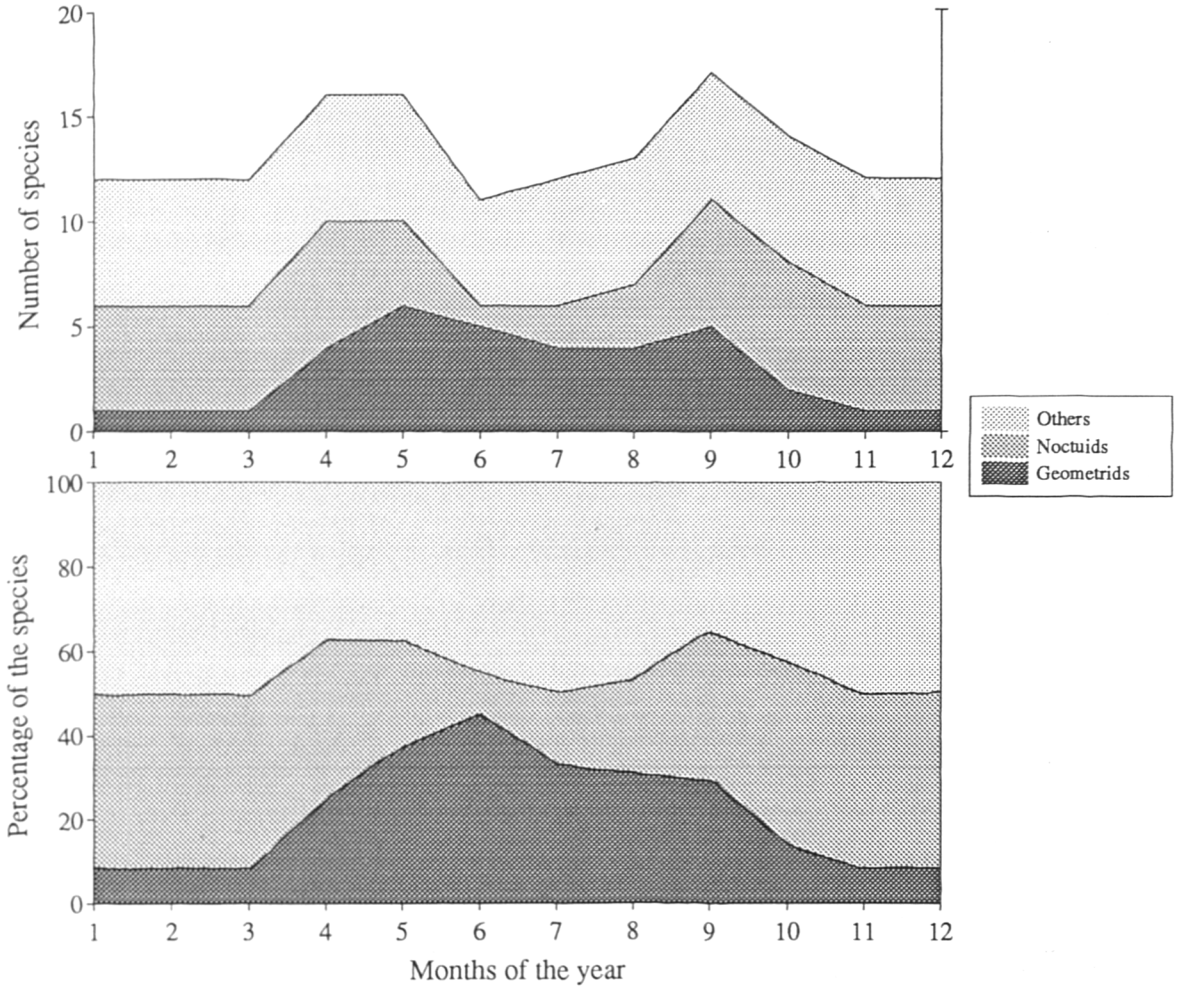

Figure 5.5. The representation of species in the three taxonomic groups of Geometridae, Noctuidae and 'Others' as larvae on *Calluna* during the months of the year for the macrolepidopteran species of Group C. Information on the duration of the larval periods has been obtained from Skinner (1984). Group C includes all species of macrolepidoptera recorded during the progress of this study. The results are shown both as the number of species and the percentage of the total number of species in each taxonomic group. 'Others' includes the families of the Zygaenidae, Lycaenidae, Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

through the year until there is a decrease in summer when the pupal, adult and egg stages are passed through.

The 'Others' taxonomic group comprises a much larger proportion of the species richness of larvae on *Calluna* in Group C than in A or B, representing between 40 and 50% of the species present. The numbers of 'Others' species remains constant at about six species through the year except for a slight decrease in June. This reflects the fact that these species tend to have relatively long larval periods with two of the species being biennial and existing as larvae throughout the year. The high numbers of 'Others' species compared to Geometridae and Noctuidae in Group C represents the high discovery rate of species of the 'Others' group (71%) compared to the Geometridae (44%) and Noctuidae (35%). There was also a high ratio of extra species (*i.e.* species not stated by the literature to feed on *Calluna*) found in this group (0.6) relative to its overall size compared to the geometrids (0.38) and noctuids (0.17) (Table 4.6).

In Group C, the peaks in species richness in September visible in Group A are again present due to an increase in the larval species richness of geometrids and noctuids. The peak in the numbers of geometrids at this time can be attributed to the presence of *Eupithecia* species feeding on the flowers of *Calluna*. The same peak in geometrid species richness is present in Group B but it is obscured by the high number of geometrid species which overwinter as larvae in this group.

The abundance of geometrid and noctuid larvae on *Calluna* through the year is shown in Figure 5.6 demonstrating a pattern which is an exaggeration of the pattern of the species richness as shown in Figure 5.5. This is because the most abundant species on *Calluna*, namely *Lycophotia porphyrea, Diarsia mendica, Hydriomena furcata, Entephria caesiata* and *Eulithis* were those which followed the seasonal pattern typified in Figure 5.5. During the interval from April to July, 80 to 90% of all larvae found were geometrids after which the numbers of foliage feeding geometrids decreases to less than 20%. However from August through to the end of September when *Calluna* flowers and sets seed, about 40% of the larvae are flower feeding geometrid species of the *Eupithecia* genus. From June the proportion of the species which are noctuids becomes increasingly important and in the winter months, from October to the beginning of April, the majority of the larvae are of this taxonomic group.

There is a significant positive correlation between the month in which the larval period begins and the total length of the larval period for the macrolepidoptera species in Group C (Figure 5.7). The hatching of larvae from eggs is limited to the months between April and October. Species that hatch from eggs later in the year, *i.e.* after August, generally have to pass the winter as a larvae.

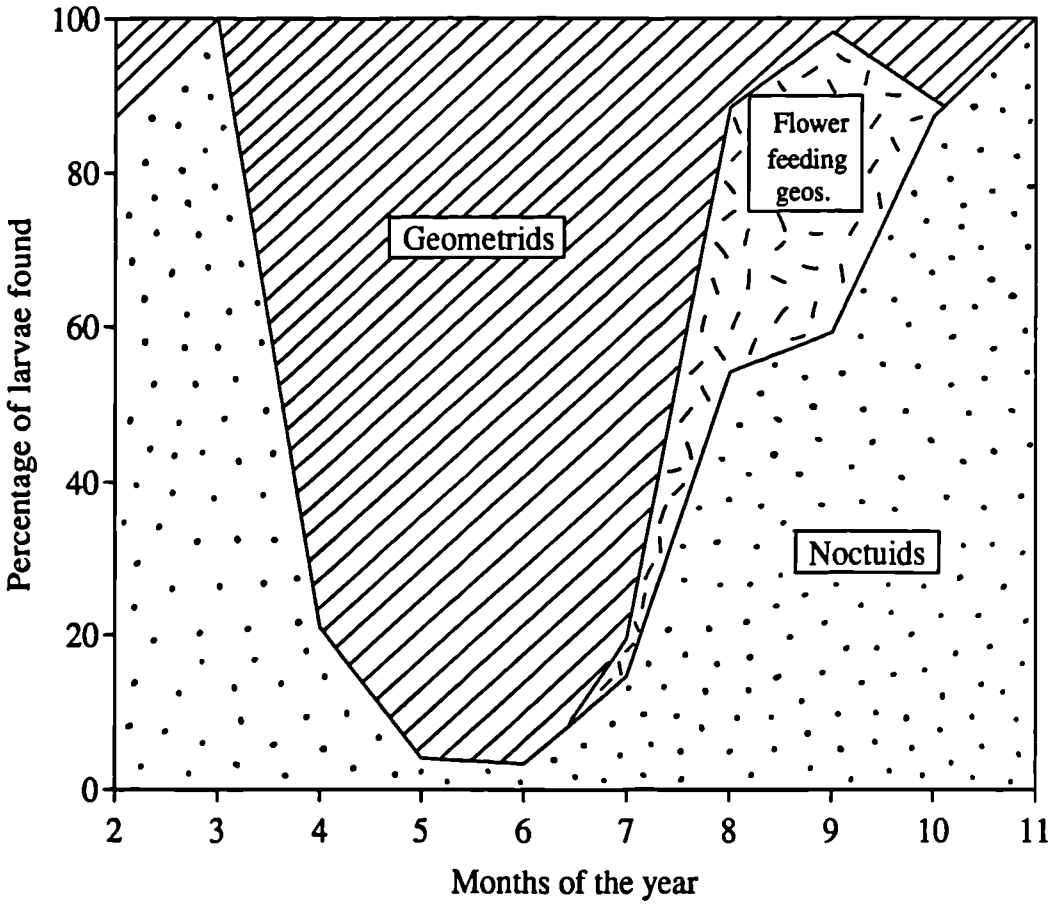

Figure 5.6. The percentages of the macrolepidopteran larvae found on *Calluna* during each month of the year belonging to each of the taxonomic groups of Geometridae and Noctuidae. The Geometridae are further split into those species which feed on Calluna flowers (*i.e. Eupithecia nanata, E. goossensiata and E. satyrata*) and those which do not. The data consists of all larvae found during the years 1988-1990 by the methods of sweep-netting and Berlese funnel extraction.

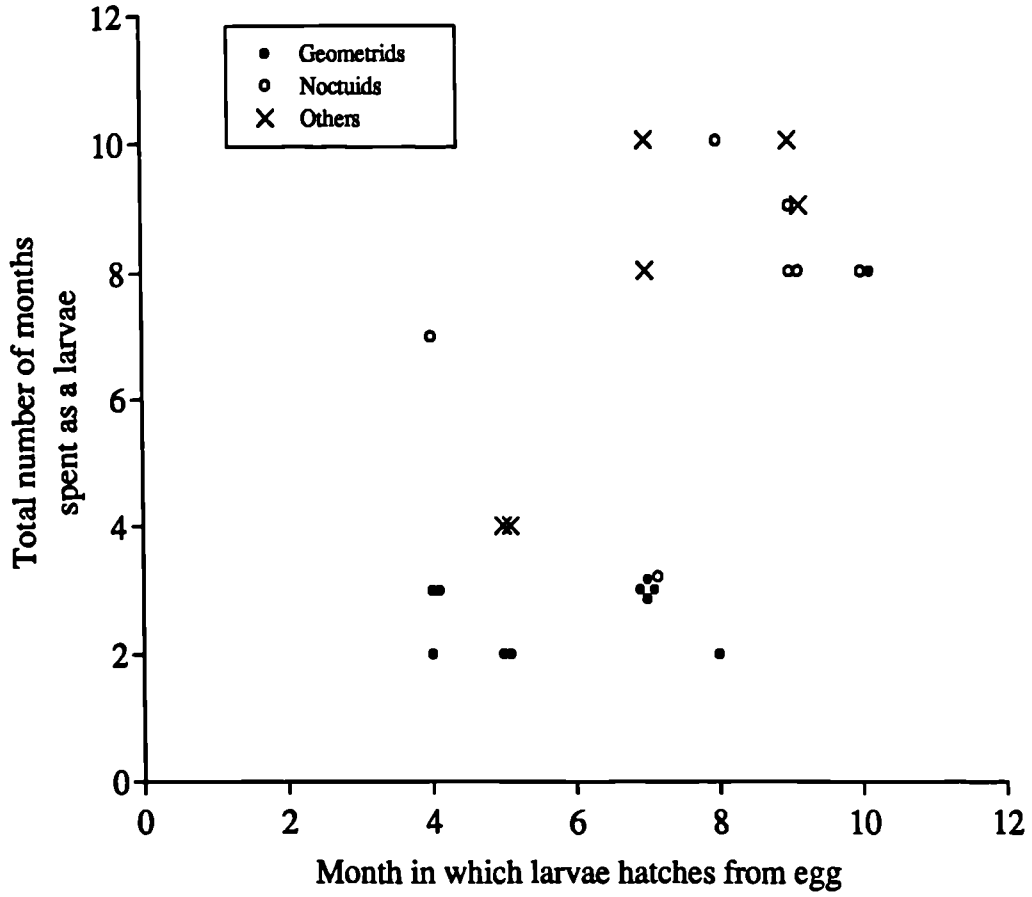

Figure 5.7. The relationship between the month in which the larval phase of the life-cycle begins and the total length of the larval phase in months for the macrolepidoptera species feeding as larvae on *Calluna* (r=0.639, d.f.=22, P<0.01). Information on the larval phase has been obtained from Skinner (1984) and the data are for the 24 species found as larvae on *Calluna* during this study with the exclusion of the two species with a biennial life-cycle (*Trichiura crataegi* and *Lasiocampa q. callunae*). The larval phase is the duration for the population and not the individual with the difference between the two dependent on the synchronisation of development.

5.7. Discussion

Overwintering in insects can occur in any of the stages of the life-cycle although there is rarely intraspecific variation in the stage of diapausing. The different phases are said not to vary in their inherent ability to tolerate the harsh conditions often associated with the diapausing phase (Tauber *et al.* 1986). The same authors consider that the pupal stage is better protected than any other because the animal is contained within a relatively hard cuticle and a tough cocoon. None of the species feeding on *Calluna* overwinter in the adult stage although Lepidoptera do overwinter as adults in Britain. Ford (1945) notes that 11% of the 63 species of butterflies resident in Britain overwinter as adults.

Hayes (1982) found correlations in North American butterfly species between the stage of overwintering and other life history characters. Species that underwent pupal or reproductive diapause showed a preference for warmer habitats, whereas those diapausing as eggs seem primarily to occupy cooler climes. Larval diapausing species also showed a preference for cooler habitats and the most extreme cold tolerance. Gaston and Reavey (1989) consider that such patterns are not apparent in a smaller geographical region such as Britain where there are fewer extremes of climate. Mikkola (1980) quoted in Niemela *et al.* (1982), found proportionally more species of Lepidoptera overwintering as larvae further north in Scandinavia and Danks (1978) notes that overwintering in the larval stage predominates in Arctic habitats. This may be related to the predominance of biennial life-cycles at high latitudes which compels species to spend at least one winter as a larvae. The results of Hayes study are supported by the fact that in general insect eggs have a lower supercooling point than the other life-history stages (Somme 1982). The same author notes that although few pupae have been studied, their ability to supercool appears to be generally poorer than that of most eggs and larvae. In contrast, Danks (1978) considers the larval and pupal stage to be more freezing tolerant than the other life-cycle stages. Therefore there appears to be some confusion as to which if any of the stages are more cold tolerant.

The change from Group A to B represents an adjustment from considering all species in Britain on *Calluna* to only those on *Calluna* in County Durham and hence a change to a more northern and less oceanic type climate. The change from Group B to C represents an alteration from considering lepidopteran species found in all habitats occupied by *Calluna* in County Durham to that of higher altitude moorland and blanket bog habitats. This results in a change to a more harsh climate in terms of temperature as discussed by Hayes (1982) and also in terms of rainfall and exposure. The higher amounts of rainfall associated with increasing altitudes in Britain may hinder overwintering in the pupal stage. The site of lepidopteran pupation is often in the substrate which tends to be waterlogged at higher altitudes. A high moisture level in the soil and litter layer affects the survival of overwintering insects (Danks 1978)

especially pupae (Somme 1982; Leather 1984). It has been suggested that on blanket bog habitats at high altitudes there is a greater tendency than at lowland situations to overwinter in the egg stage (Coulson and Whittaker 1978; but see section 7.7).

The geometrid species found in this study showed a lower incidence of overwintering in the larval stage compared to the lepidopteran species occurring on *Calluna* in County Durham and Britain as a whole. The Noctuidae showed an increased propensity to overwinter as larvae rather than as eggs, although low sample sizes meant that there was no significant effect. These particular life histories may not be a result of constraints on which stage should overwinter but rather a result of interaction to optimise the timing of larval feeding periods.

The seasonal pattern in the number of species present as larvae on *Calluna* is similar to that found by Feeny (1970) on oak. The pattern varies only in that on *Calluna* the spring peak of species richness was slightly earlier, occurring during April and May, and the summer reduction in numbers begins in June. These differences are probably a consequence of *Calluna* beginning its growth earlier in the spring compared to oak and being evergreen rather than deciduous.

Niemela *et al.* (1982) looked at the seasonal patterns of larval macrolepidoptera in Finland on trees and shrubs including *Calluna*. The methods of the Finnish study are comparable with the present one and comparison with Group A is relevant. The shorter length of the growing season at the higher latitudes means the Finnish data consist of species richness during May to September only. In Finland the number of species present as larvae on *Calluna* during June, July and August is comparable with Britain with larvae of 20 to 30 species found. However during the months of May and September species richness is much reduced in Finland compared to Britain. The result is that the species richness of larval macrolepidoptera remains fairly constant through the spring and summer on *Calluna* in Finland. It is difficult to explain this disparity in seasonal changes in Finland and Britain given the lack of data on differences in life-cycles. It is probably related to the much shorter and later growing season at higher latitudes. This restricts the temporal variability of the plant and animal species and possibly the low temperatures of winter alter the direction of selective forces (Niemela *et al.* 1982). However the seasonal pattern of utilisation of oak by macrolepidopterous larvae in Finland was similar to that found by Feeny (1970) in Britain.

Unfortunately there is no information available as to whether new leaves produced later in the season by the *Calluna* plant are as nutritionally 'good' as the growth produced in the spring. In meadowsweet (*Spirea latifolia*), leaves are tougher later in the growth season (mid-June) regardless of whether they are new or old. The water and nitrogen content of leaves of all ages also declines through the season, such that by July, new leaves have no more nitrogen than mature leaves (Stamp and Bowers 1990). As previously noted in the introduction the effect on herbivorous insects of feeding on leaves of lower nutritional quality varies. Some species show a marked

reduction in growth whereas others show no effect. Therefore it is impossible to directly relate the seasonal patterns to host plant nutritional quality without investigating the response of the individual species.

Feeny (1970) notes the difference in the larval periods of late and early feeding species of Lepidoptera on oak. Early feeding species tend to complete their growth rapidly within two to three weeks. In contrast late feeding species grow slowly over several months with some of them overwintering in order to recommence feeding in the spring. Feeny believed this difference was due to the quality of the food that was available to the two groups of species.

Similar patterns seem to be occurring in the Lepidoptera feeding on *Calluna*, with a positive relationship between the timing of the initiation of the larval period and its overall duration. In Group C these differences seem to become related to divergences between the Geometridae and Noctuidae. The majority of geometrid species are spring feeders whereas the noctuids begin their larval growth in the late summer/autumn, overwinter as larvae and then complete their growth in the spring. This difference between noctuids and geometrids does not occur in Groups A and B and it is possible that this pattern is a result of the change to a moorland habitat. Noctuids are generally larger than geometrids but this size difference is not large enough to restrain the noctuids from completing their larval period within a spring and summer season. Other aspects of the geometrid and noctuid life-cycle may be constrained in a moorland habitat, for instance, the timing of the adult flight period and/or the method of overwintering. Coulson and Whittaker (1978) note the relative absence of flowers on high moorland, and if adult Lepidoptera feed, then synchronisation with the flowering of *Erica* and *Calluna* as occurs in the majority of the recorded abundant noctuid species may be necessary. It is possible that the viability of different overwintering stages varies for the geometrids and noctuids.

One possible reason for the disparity in the seasonal patterns of the Geometridae and Noctuidae may be related to their different sizes (Table 6.3). It is thought that larger size in insects confers an advantage to coping with nitrogen poor foliage (Packard 1895; Opler 1978; Uvarov 1977; Niemela *et al.* 1981; Bernays 1986; Nakasuji 1987). Mattson (1980) explains this finding as the result of mechanical advantages in dealing with the usually increased leaf toughness of such material, the lower metabolic rates due to reduced surface to volume ratios and the greater digestive efficiencies of larger sized insects. Mattson (1980) uses the example of the forest feeding Lepidoptera in North America where the smaller microlepidopterous species are predominantly early season feeders compared to the macrolepidoptera. Within the macrolepidoptera the largest species (mature larvae > 40mm) such as the Saturniidae are almost entirely late season consumers, while the early season macrolepidoptera are usually the smaller species (mature larvae 20-40mm). Therefore he expects larger species to feed nearly anytime during the growing season if competition, predation,

allelochemicals and temperature permit. Smaller species, by contrast, ought to be more strictly limited to the most nutrient rich and succulent plant parts, that is the early season tissue and special plant parts in late season. One of the advantages of being small is that there is a relatively short feeding period and hence limited exposure to natural enemies. This may become negligible on poorer diets however because of the reduced relative growth rates of smaller compared to larger species (Mattson 1980). The Geometridae and Noctuidae on *Calluna* accord well with the pattern related by Mattson (1980), with the *Eupithecia* species that feed in August and September on *Calluna* flowers representing the smaller species feeding on special plant parts in late season. An impediment to this idea is that in late summer and autumn, the noctuids are in their younger instars and hence no larger than a geometrid, although for a given instar they have larger heads. There is also the fact that the difference between the geometrids and noctuids is only evident in Group C. This might be due to the fact that the data for Groups A and B has been obtained exclusively from the literature or because of overwintering constraints in the more severe environment in which Group C species exist.

Cates (1980) found that whereas the larvae of monophagous and oligophagous herbivores prefer young leaf tissue, the larvae of polyphagous species prefer the mature leaves of their various host plants. These differences result from younger leaf tissue having higher levels than mature tissue of qualitative toxins to which the more specialised feeders can become immune. In contrast the levels of quantitative plant toxins are higher in mature foliage with nutrient, water and digestibility levels reduced. The polyphagous species unable to cope with the qualitative toxins in younger tissue therefore feed on the older leaves. There is no evidence that the noctuids feeding on *Calluna* are more polyphagous than the geometrids or that the young leaves of *Calluna* contain qualitative defences.

Chapter Six

Aspects of the growth and development of the Lepidoptera associated with *Calluna vulgaris*

6.1. Determination of the instar development

6.1.1. Introduction

In order to study the development and growth of an lepidopteran species it is necessary to allocate individuals of the larval stage into their appropriate instar. For the species recorded during this study there was no available information on instar development and a preliminary study on this aspect was undertaken.

Lepidoptera species have between two and nine larval instars (Richards and Davies 1977) with the number generally constant within a species. The changes in weight and dimension of the soft bodied parts of insects are not appropriate for instar determination because they change greatly within the stadia. However, the hard sclerotised parts of an insect change in dimension only when the insect moults, conforming with empirical rules of allometric growth as formulated by Dyar (1890). He found the head capsules of Lepidoptera to increase in a regular geometrical progression in successive instars by a ratio of approximately 1.4, which allowed him to predict the larval instar from the head capsule width. This relationship has since been found to apply to a wide variety of insects for a range of cuticular body parts although there are some exceptions (Richards and Davies 1977). The empirical relationship discovered by Dyar has been noted for its similarity to the ecological constants in body size between sympatrically occurring conspecific species (Hutchinson 1959; Pianka 1969; Horn and May 1977). Both developmental and ecological constants have been related to competition between different body sizes and age classes, although this is disputed (Horn and May 1977; Lawton and Strong 1981; Roth 1981). Maiorana (1978) suggests it is the result of a constant amount of variability in morphology.

In the Lepidoptera it is the head capsule that has traditionally been used to determine the instar, although Podoler and Klein (1978) consider the measurement of the distance between the frontal setae to be a more accurate and stable parameter for distinguishing larval stadia. The need to measure larvae while alive in addition to limitations imposed by the availability of time and equipment meant that during this study, the width of the head capsule was used.

Since the work of Dyar (1890) the determination of instars by the use of head capsule widths (HCW) has been found to be affected by factors which complicate the

use of this method, either through causing greater variability of head widths within an instar or by altering the number of instars. These factors may influence the ability to determine the number of instars especially if the sample is polymorphous (Schmidt *et al.* 1977). In some species, a dimorphism of head widths occurs in the later instars as a consequence of the sex of the individual (Miles 1931; Drooz 1965; Atchley 1971; Hamon *et al.* 1984) and parasitism (McGugan 1954; Nealis 1987; Strand 1989). This may cause the head widths of larger larvae in one instar to overlap with those of the smaller larvae in the subsequent instar. It has also been noted that the number of moults is affected by the sex of the individual (Wigglesworth 1939), parasitism (Jones *et al.* 1982), host plant nutritive value (Smith 1959; Fogal and Kwain 1972) and temperature (Guppy 1969; Ross and Merritt 1978). Adverse nutritional conditions during larval growth may result in the number of instars increasing to such an extent that there is little resultant increment in head capsule size between instars (Beck 1973). Drooz (1965) found that variation in the number of instars of the elm spanworm (Geometridae) was dependent on the foodplant and concluded that a plant species which resulted in a greater number of instars was deficient in certain nutritional requirements. Within a single instar, factors such as temperature (Guppy 1969) and diet (Bernays 1986) may affect the head capsule width without altering instar number. Eggs which are relatively small may undergo an extra moult in the larval stage to compensate for their smaller size at birth (Albrect 1955 quoted in Wigglesworth 1939).

The number of instars is usually determined by visually inspecting a frequency distribution of the head widths. This simple method is adequate when the instars form discrete non-overlapping distributions but in many cases adjacent distributions overlap and must be separated. Daly (1985) and Beaver and Sanderson (1989) review some of the different methods used to this effect, including probit analysis (Frampton 1986), goodness-of-fit (Caltagirone *et al.* 1983) and probability paper (Harding 1949). As a result of the complicating factors mentioned above, the plotting of frequency distributions does not always give accurate results (Kishi 1971). In these circumstances the only way to determine instars may be to directly observe larvae throughout their growth (Nealis 1987).

6.1.2. Methods

In order to determine the larval instars of the Lepidoptera species in this study, the width of the head capsule was measured at its broadest extent when viewed dorsally. Dimensions were taken from the head capsules of live and dead larvae and these were checked against the sloughed head capsules when available. The measurements were taken to the nearest graticule unit at a magnification of x20 using a binocular microscope fitted with a eyepiece graticule. The larger larvae of two of the largest species, *Lasiocampa callunae* and *Macrothylacia rubi*, had to be measured at a

magnification of x10. Ocular measurements were converted to millimetres at a factor of 0.0494mm per graticule unit. Errors in the estimations of head capsule width (HCW) may have occurred due to the difficulty of holding live larvae stationary and correctly aligning the graticule with the head capsule. Some measurements of head widths were also taken from larvae stored in 70% alcohol for periods of a few months. Britt (1953) has shown with Ephemeroptera samples that although storage in alcohol causes large changes in the dimensions of soft tissues, the size of the chitinous head capsule increased by only 1.5%.

The HCW of larvae was measured immediately after capture in order to allow calculation of the development rate of the larval population in the field. Larvae kept in the laboratory were also routinely measured for HCW. Therefore, HCW data for each species originate from two sources; those representing head measurements attained in a 'field' situation and those attained in the laboratory. The two groups have been differentiated between because factors such as temperature and food availability, which are known to influence head capsule size, differ in the two environments. Field data may be more reliable than laboratory measurements because of the difficulty of supplying adequate amounts of food to the larvae at all times in the laboratory. However Daly (1985) recommends the use of a mixture of field and laboratory measurements. The frequency distributions of HCW were initially plotted exclusively from 'field' data. Laboratory measurements were then included if the pool of 'field' data was too small to construct a frequency distribution and/or if there appeared to be little difference between the two groups. Data for the first larval instar were generally obtained by hatching eggs in the laboratory, since few larvae of this age are collected in the field. This is probably a consequence of the short duration of this instar and possibly of the unsuitability of the sampling techniques.

For each species, the frequency distribution of head measurements was used to determine the instar boundaries. Where the frequency distribution shows discrete non-overlapping distributions, there was little difficulty in determining the individual instars. However where the distribution was unclear, the method of Harding (1949) was used to discriminate between instars. This involves graphically separating the component parts using the inflexion point when the distribution is plotted on probability paper. In species where the number of observations was low, the data have been condensed into fewer frequency classes. Once instars had been determined, a bivariate plot of the $\log_{10}$ of the mean head width in an instar against instar number was plotted. From this a straight line should be obtained; major deviations from this line indicate that an instar has been omitted. The slope of the line indicates the growth ratio of the head capsule between instars (Dyar 1890; Wigglesworth 1939; Daly 1985).

The frequency of larvae in separate instars gives an indication of how many larvae of each stage were caught. This reflects both the instar duration and abundance and its apparency to sampling techniques. The mean and standard deviation of the

HCW for each instar illustrates the variability of the head measurements within the instar.

The relationship between larval and adult size in species has been investigated by correlating the mean HCW in the final larval instar with adult wingspan. The expanse of the adult wingspan is measured as twice the distance from the centre of the thorax to the apex of the forewing. Information on adult wingspan has been obtained from Skinner (1984) with the middle value taken where a wingspan range is listed.

6.1.3. The results of instar development

The frequency distribution of HCW and the log. mean HCW of each instar are shown in Figures 6.1 to 6.15 for fifteen species of macrolepidoptera. These are the species for which adequate data on head capsule width were collected to form a frequency distribution. There were insufficient data for the eleven other species recorded as larvae during the study. The frequency diagram has been drawn from a combination of field and laboratory measurements with the exception of *Lycophotia porphyrea* and *Diarsia mendica*, for which field data only has been utilised. The mean HCW in each of the instars for all species are summarised in Table 6.1 along with the standard deviation and the number of measurements acquired. There is no significant correlation between the number of larval instars and the size of the larvae in the final instar (r=0.495, d.f.=13, P>0.05).

It is obvious from Figures 6.1 to 6.15 that individual species vary widely in the ease of interpretation of the histograms of head capsule width. Species such as *Eupithecia nanata* show relatively little variation in HCW within an instar. In contrast there is less distinction between the later instars of species such as *Lycophotia porphyrea* and *Diarsia mendica* which consist of widespread multimodal distributions. For some of the species a bimodality is apparent within what has been defined as a single instar. For example, instar IV in *Entephria caesiata*, instars III and IV in *Operophtera brumata*, instars IV and V in *Lycophotia porphyrea*, instar V in *Anarta myrtilli* and the last three instars of *Diarsia mendica*. The reasons for this bimodality are difficult to establish, they may be the result of variation between sexes or polymorphism in the instar numbers for individual species. The discreteness between HCW in successive instars seems to be greatest for the geometrid species and least for the noctuid and lasiocampid species. Unfortunately it has not been possible to elucidate the reasons for the bimodality as insufficient numbers were reared through to the adult stage for sexing. Some of the differences in the ease of interpretation of instar characteristics are a result of sample size, *e.g.* the earlier instars of *Macrothylacia rubi*. As a consequence of these limitations, the data given in Table 6.1 must be taken as estimates. Definite information on instar development in some of the species, *e.g. Diarsia mendica*, could only have been obtained by detailed surveillance of their growth and development in a laboratory situation as

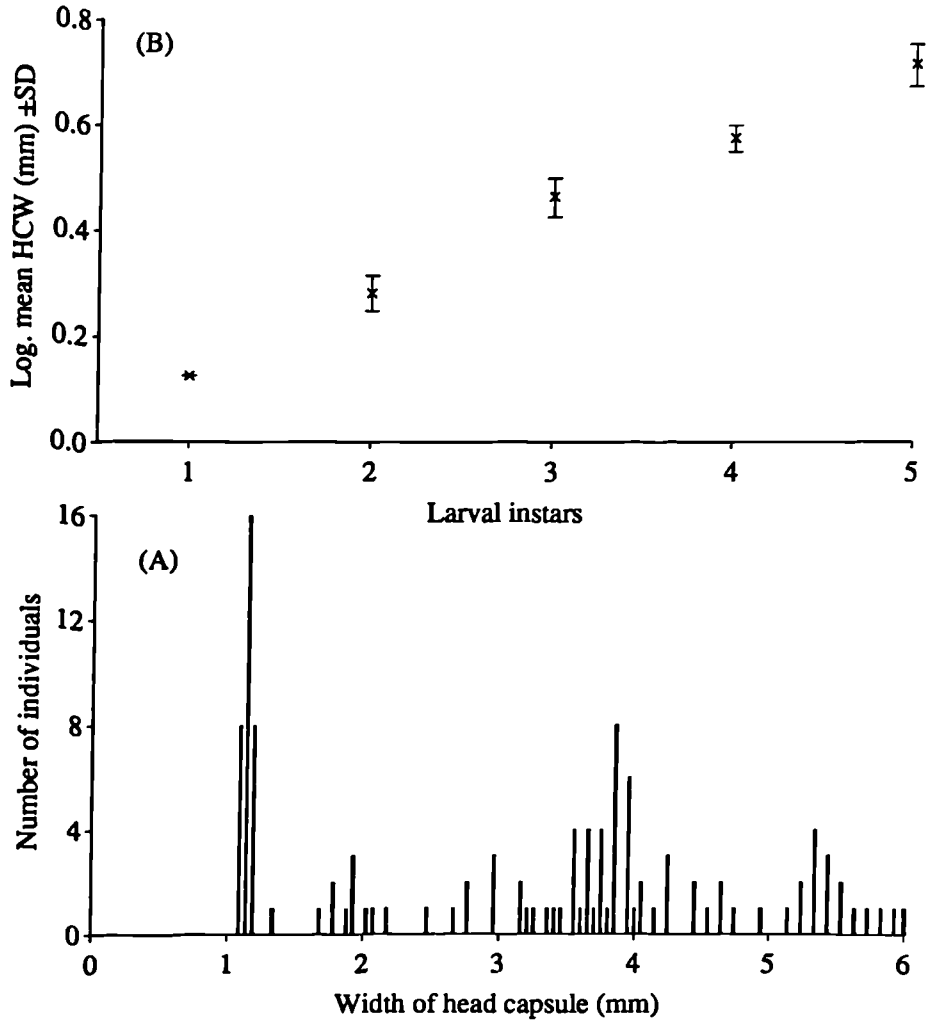

Figure 6.1. The larval instars of *Lasiocampa callunae* (Lasiocampidae). (A) The frequency distributions of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (0.98-1.34mm); Instar II (1.58-2.32mm); Instar III (2.37-3.26mm); Instar IV (3.31-4.40mm); Instar V (4.44-6.00mm). The later instars were measured at a magnification of x10 and then multiplied by two hence the predominance of even measurements at the greater HCW.

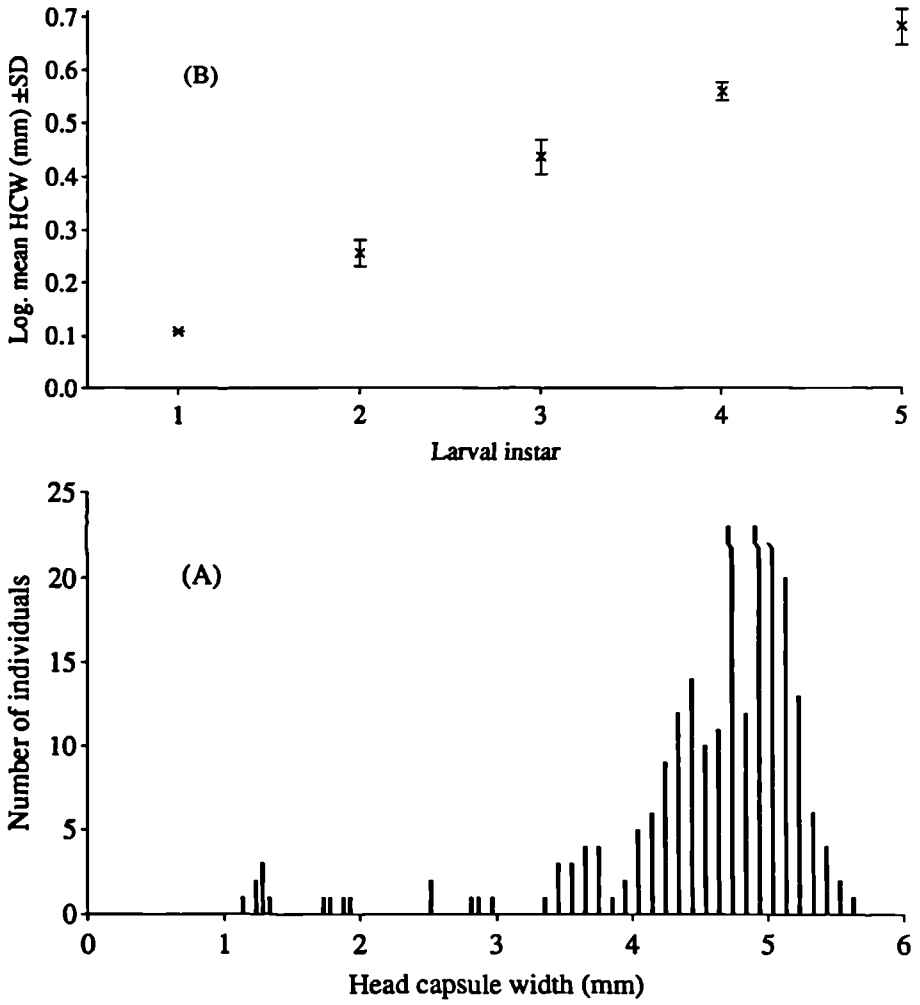

Figure 6.2. The larval instars of *Macrothylacia rubi* (Lasiocampidae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (1.14-1.49mm); Instar II (1.50-1.98mm); Instar III (2.47-3.07mm); Instar IV (3.11-3.86mm); Instar V (3.95-5.63mm). The later instars were measured at a magnification of x10 and then multiplied by two hence the predominance of even measurements at the greater HCW.

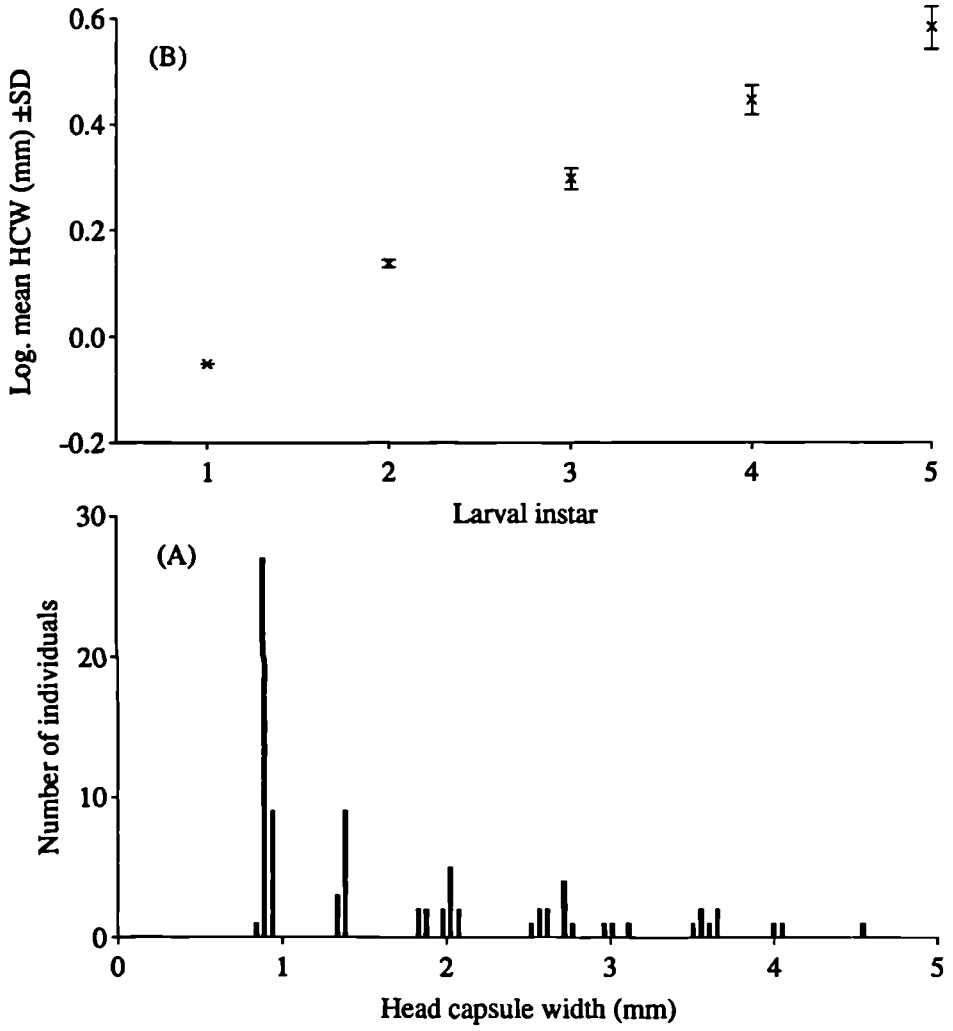

Figure 6.3. The larval instars of *Saturnia pavonia* (Saturniidae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (0.74-0.99mm); Instar II (1.23-1.49mm); Instar III (1.53-2.23mm); Instar IV (2.47-3.21mm); Instar V (3.45-4.55mm).

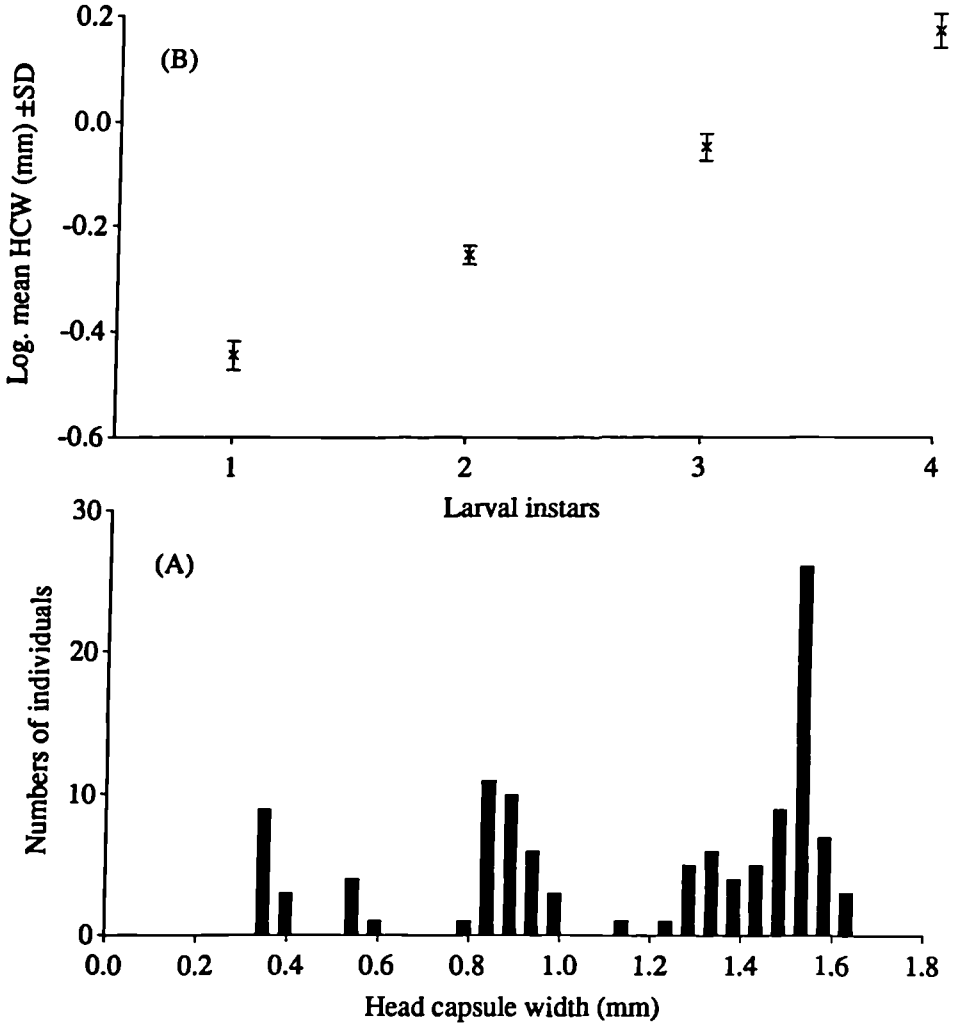

Figure 6.4. The larval instars of *Entephria caesiata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the instar have been taken at: Instar I (0.34-0.40mm); Instar II (0.54-0.60mm); Instar III (0.79-0.99mm); Instar IV (1.13-1.64mm).

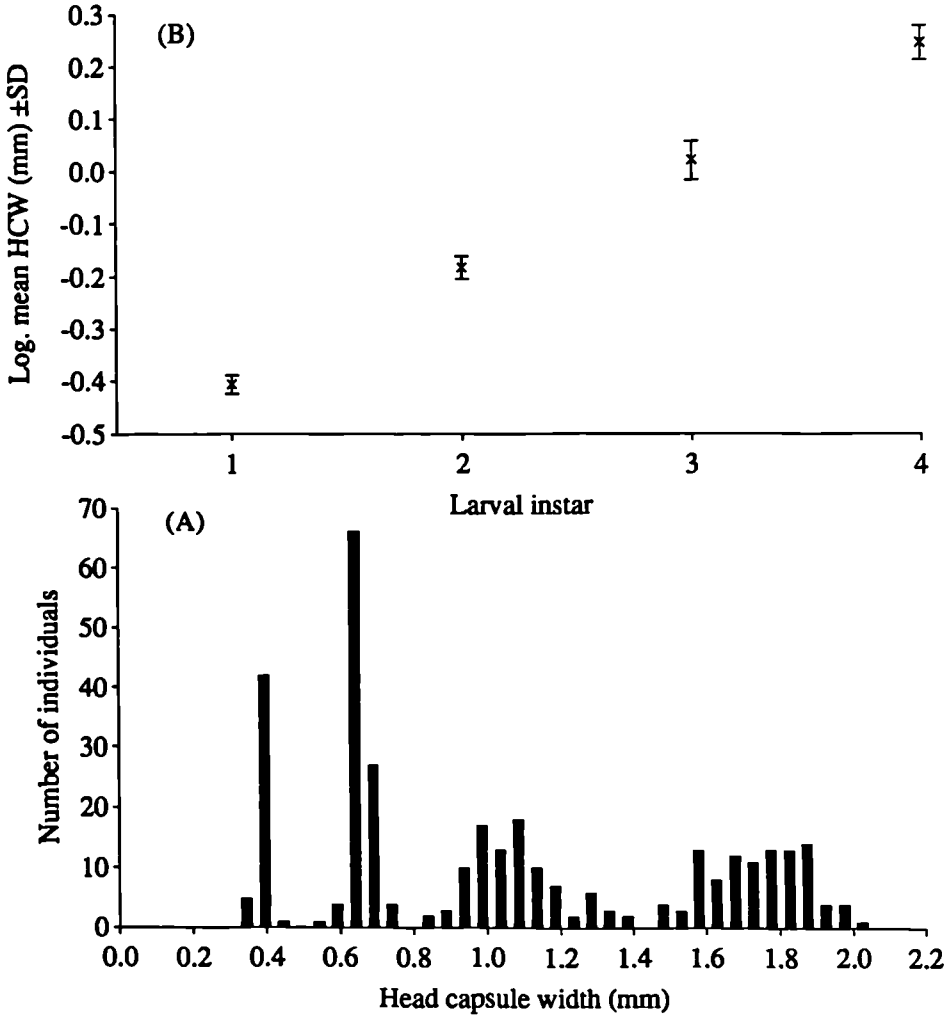

Figure 6.5. The larval instars of *Eulithis* species (Geometridae). Data from *E. populata* and *E. testata* has been pooled because of the difficulties of differentiating between larvae of the two species. (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the larval instars have been taken at: Instar I (0.34-0.45mm); Instar II (0.54-0.75); Instar III (0.84-1.24); Instar IV (1.48-2.08mm). Head capsule widths of 1.28 to 1.40 were not assigned to an instar because of difficulties with determining whether they were of instar IV or V.

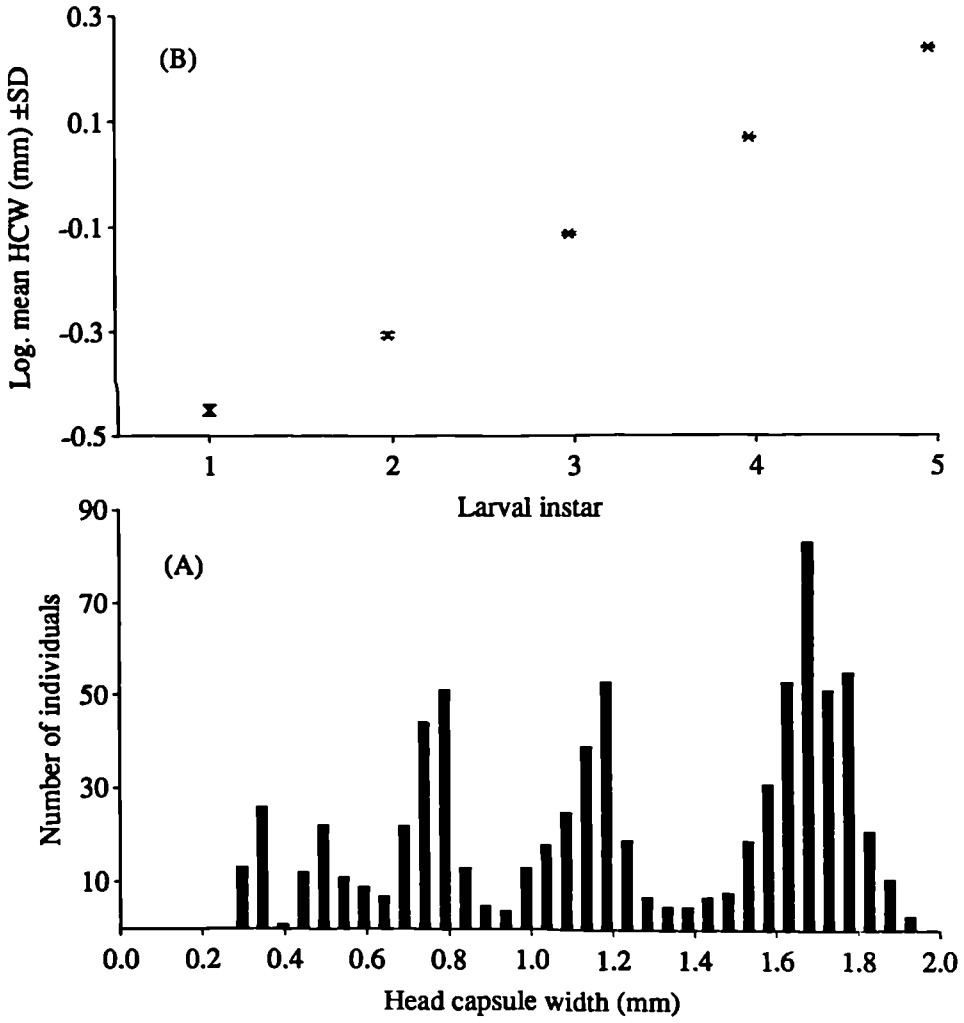

Figure 6.6. The larval instars of *Hydriomena furcata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (0.29-0.39mm); Instar II (0.44-0.54mm); Instar III (0.64-0.90mm); Instar IV (0.98-1.34mm); Instar V (1.43-1.95mm). Head capsule widths of 0.59, 0.94 and 1.38 were not assigned to an instar because of difficulties with determining whether they were of instar II or III, III or IV and IV or V respectively..

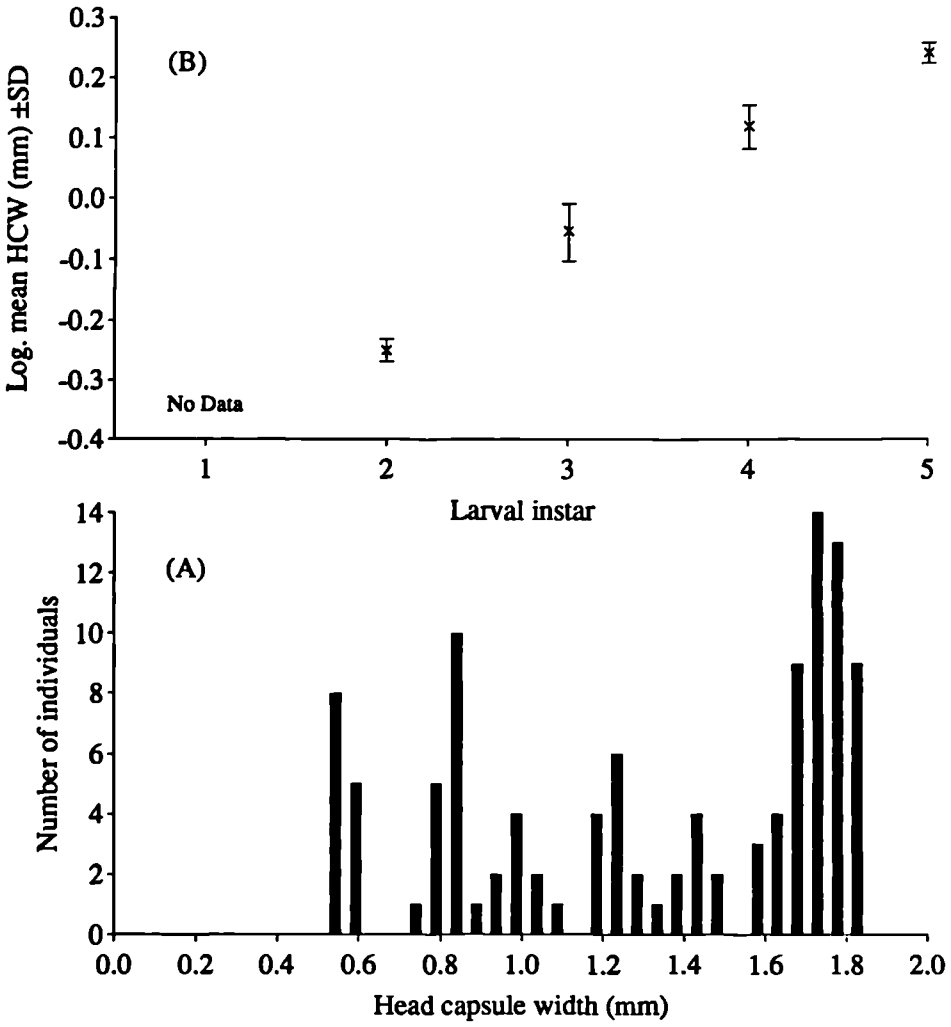

Figure 6.7. The larval instars of *Operophtera brumata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (no data); Instar II (0.54-0.60mm); Instar III (0.74-1.09mm); Instar IV (1.18-1.49mm); Instar V (1.58-1.83mm).

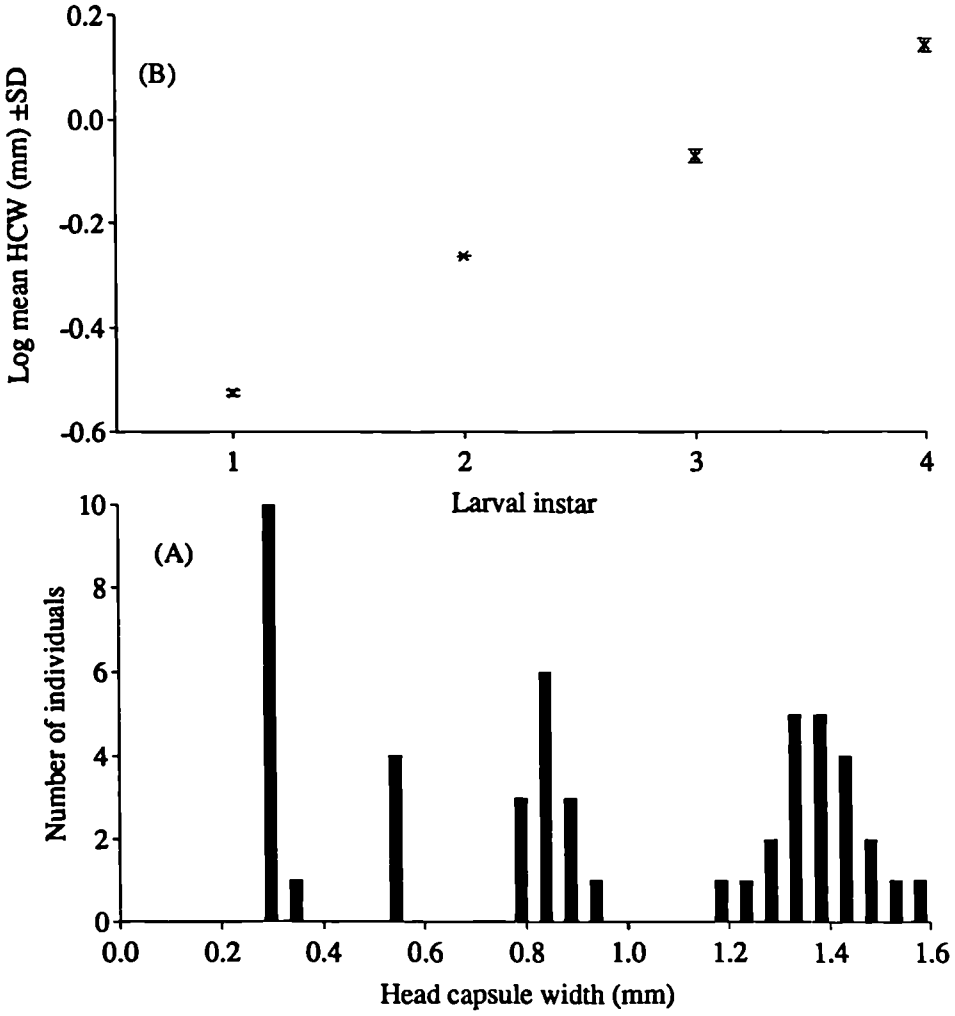

Figure 6.8. The larval instars of *Perizoma didymata* (Geometridae). (A) The frequency distributions of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the larval instars have been taken at: Instar I (0.29-0.35mm); Instar II (0.54-0.55mm); Instar III (0.79-0.94mm); Instar IV (1.18-1.59mm).

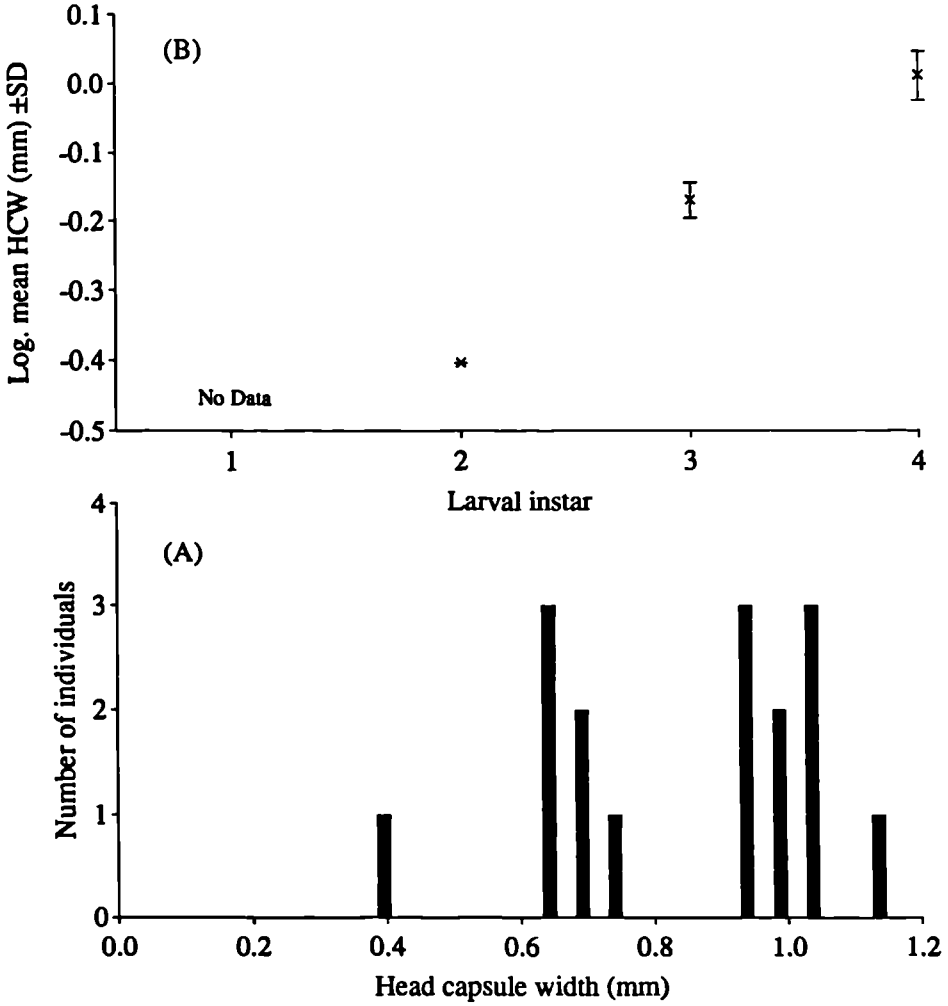

Figure 6.9. The larval instars of *Eupithecia satyrata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the larval instars have been taken at: Instar I (no data); Instar II (0.39-0.40mm); Instar III (0.64-0.75mm); Instar IV (0.93-1.14mm).

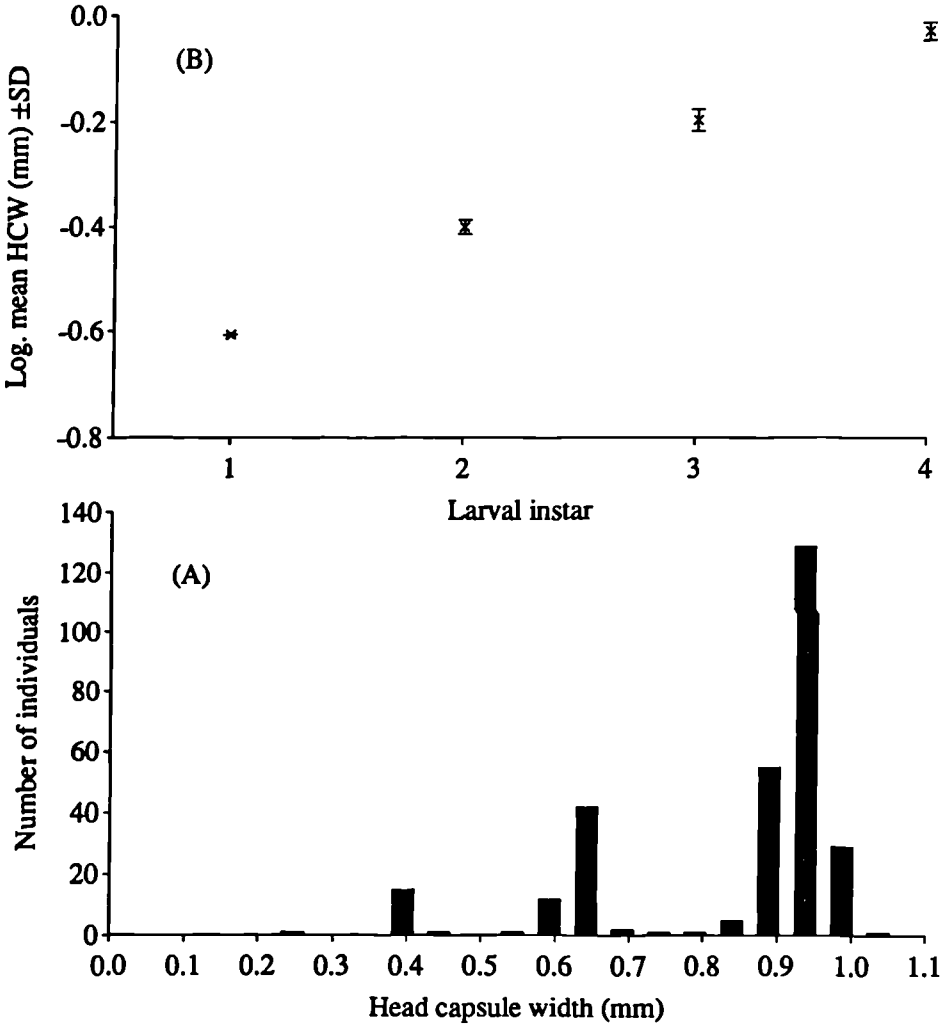

Figure 6.10. The larval instars of *Eupithecia nanata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the larval instars have been taken at: Instar I (0.24-0.25mm); Instar II (0.39-0.45mm); Instar III (0.54-0.75mm); Instar IV (0.79-1.24mm).

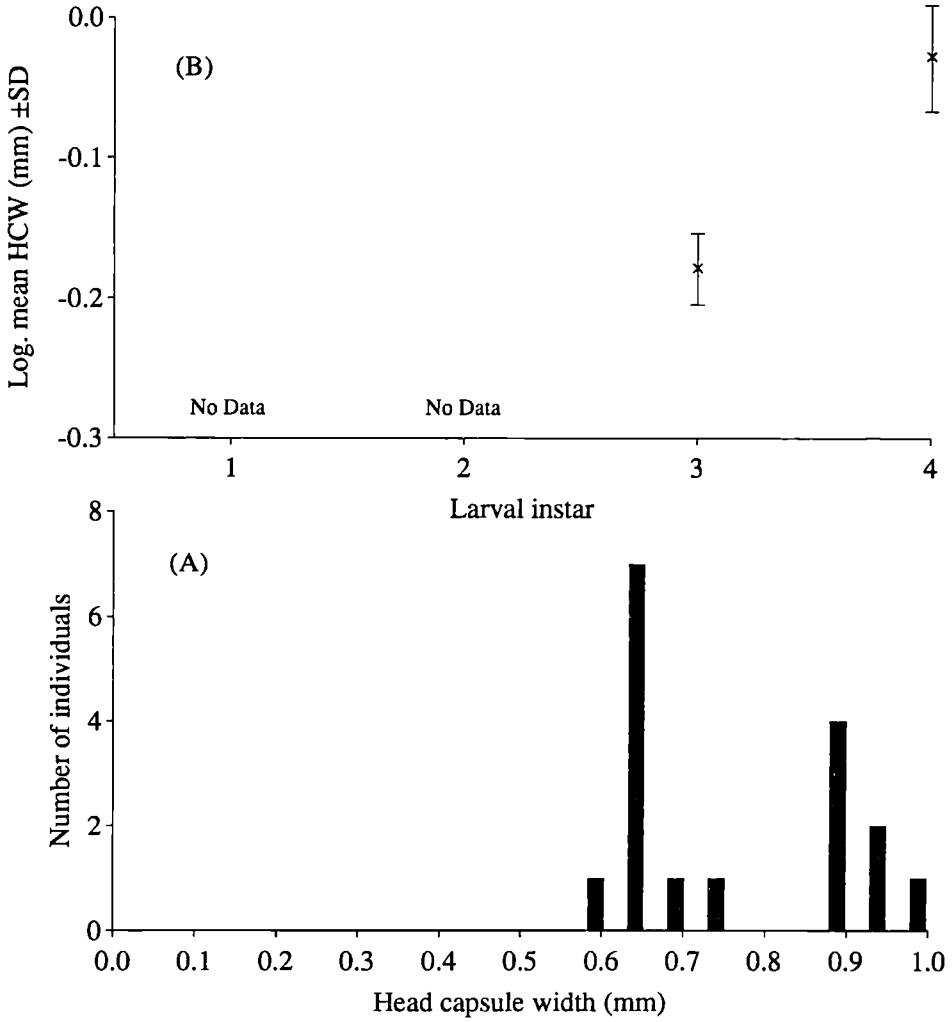

Figure 6.11. The larval instars of *Eupithecia goossensiata* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the four larval instars. The limits of the larval instars have been taken at: Instar I (no data); Instar II (no data); Instar III (0.59-0.75mm); Instar IV (0.88-1.09mm).

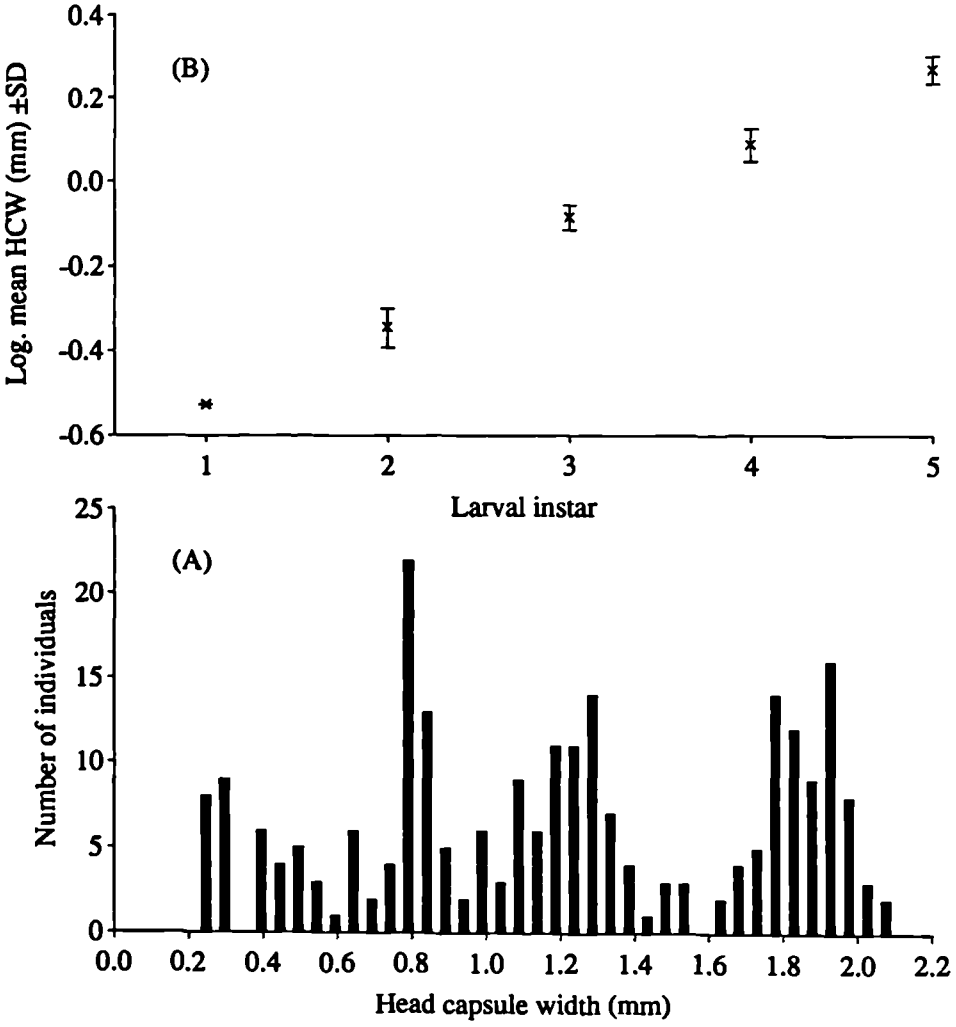

Figure 6.12. The larval instars of *Ematurga atomaria* (Geometridae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (0.24-0.30mm); Instar II (0.39-0.55mm); Instar III (0.69-0.94mm); Instar IV (0.98-1.44mm); Instar V (1.48-2.08mm). Head capsule widths of 0.59-0.64mm were not assigned to an instar because of difficulties with determining whether they were of instar II or instar III.

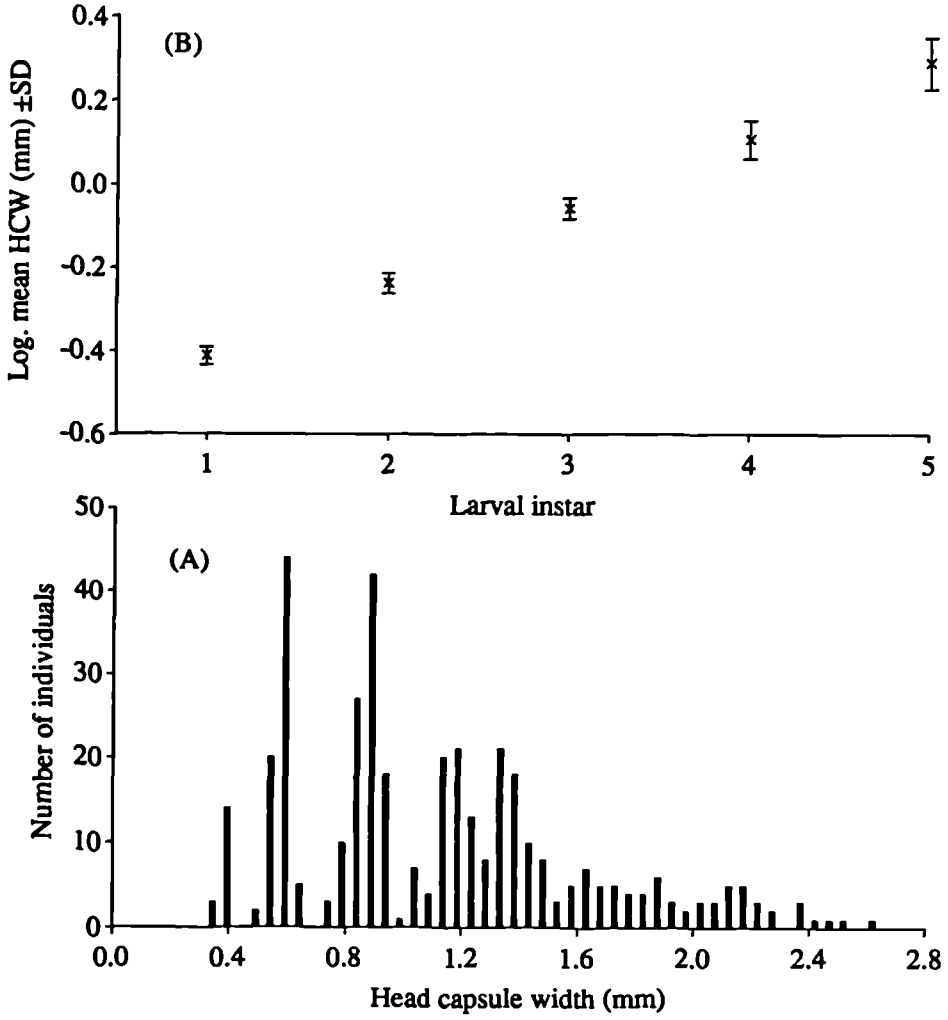

Figure 6.13. The larval instars of *Lycophotia porphyrea* (Noctuidae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (0.34-0.40mm); Instar II (0.49-0.65mm); Instar III (0.74-0.99mm); Instar IV (1.03-1.54mm); Instar V (1.58-2.62mm).

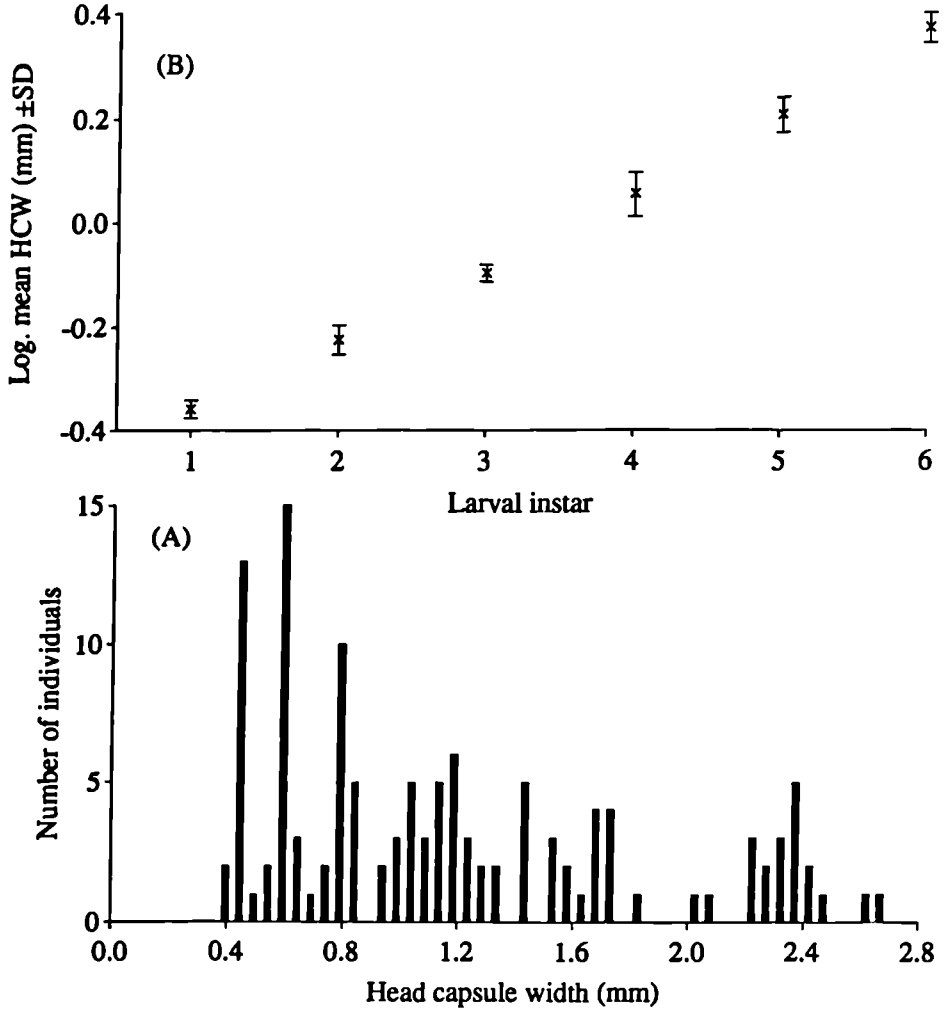

Figure 6.14. The larval instars of *Diarsia mendica* (Noctuidae). (A) The frequency distribution of the head capsule widths (HCW) of the larvae (B) The mean head capsule width in each of the six larval instars. The limits of the larval instars have been taken at: Instar I (0.39-0.49mm); Instar II (0.54-0.70mm); Instar III (0.74-0.84mm); Instar IV (0.93-1.33mm); Instar V (1.43-1.83mm); Instar VI (2.02-2.67mm).

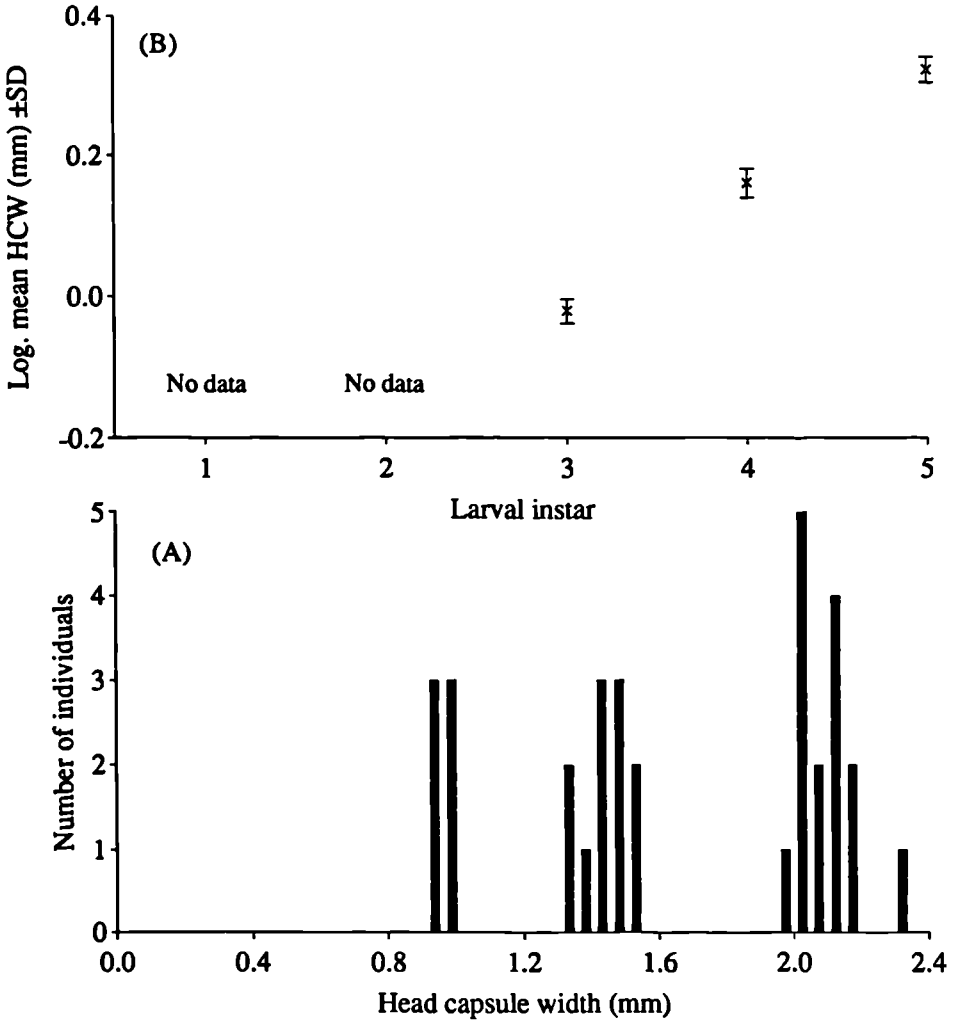

Figure 6.15. The larval instars of *Anarta myrtilli* (Noctuidae). (A) The frequency distribution of the head capsule widths of the larvae (B) The mean head capsule width (HCW) in each of the five larval instars. The limits of the larval instars have been taken at: Instar I (no data); Instar II (no data); Instar III (0.88-0.99mm); Instar IV (1.33-1.54mm); Instar V (1.97-2.33mm).

Table 6.1. The mean head capsule width (HCW) ± SD (mm) of the larval instars for fifteen macrolepidopteran species. Parenthesis denote that there is an absence of data for a particular instar but that an estimation of the HCW has been calculated based on the mean ratio change for the known instars. *Eulithis* species incorporates data for *E. populata* and *E. testata* which are difficult to differentiate between in the larval phase. Dashes indicate that instars do not exist for that species.

Species	Number of instars	Mean HCW ± SD (mm) (*n*)					
		Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI
Lasiocampa callunae	5	1.33 (1)	1.92 ± 0.150 (10)	2.79 ± 0.187 (7)	4.34 ± 0.250 (13)	5.47 ± 0.292 (18)	-
Macrothylacia rubi	5	1.28 ± 0.000 (3)	1.80 ± 0.108 (2)	2.74 ± 0.210 (5)	3.62 ± 0.139 (16)	4.80 ± 0.370 (194)	-
Pavonia pavonia	5	0.89 (1)	1.37 ± 0.020 (12)	1.97 ± 0.089 (13)	2.77 ± 0.176 (11)	3.79 ± 0.342 (9)	-
Entephria caesiata	4	0.36 ± 0.022 (12)	0.55 ± 0.022 (5)	0.89 ± 0.052 (31)	1.47 ± 0.107 (67)	-	-
Eulithis species	4	0.39 ± 0.016 (56)	0.66 ± 0.032 (113)	1.04 ± 0.088 (94)	1.75 ± 0.130 (130)	-	-
Hydriomena furcata	5	0.35 ± 0.020 (6)	0.49 ± 0.035 (46)	0.76 ± 0.056 (149)	1.15 ± 0.082 (202)	1.68 ± 0.099 (400)	-
Perizoma didymata	4	0.30 ± 0.012 (35)	0.54 ± 0.025 (4)	0.85 ± 0.044 (13)	1.38 ± 0.093 (22)	-	-

Table 6.1. (continued).

Species	Number of instars	Mean HCW ± SD (mm) (*n*) Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI
Operophtera brumata	5	(0.38)	0.56 ± 0.025 (14)	0.88 ± 0.094 (26)	1.31 ± 0.107 (21)	1.73 ± 0.069 (52)	-
Eupithecia satyrata	4	(0.25)	0.40 (1)	0.67 ± 0.040 (6)	1.02 ± 0.084 (4)	-	-
E. nanata	4	0.25 (1)	0.40 ± 0.012 (16)	0.64 ± 0.030 (53)	0.93 ± 0.035 (193)	-	-
E. goossensiata	4	(0.32)	(0.46)	0.66 ± 0.039 (7)	0.94 ± 0.083 (6)	-	-
Ematurga atomaria	5	0.30 ± 0.000 (7)	0.45 ± 0.048 (21)	0.82 ± 0.054 (45)	1.21 ± 0.110 (90)	1.83 ± 0.014 (130)	-
Lycophotia porphyrea	5	0.39 ± 0.019 (17)	0.58 ± 0.031 (71)	0.87 ± 0.050 (101)	1.27 ± 0.129 (133)	1.94 ± 0.268 (69)	-
Diarsia mendica	6	0.44 ± 0.017 (15)	0.59 ± 0.039 (22)	0.80 ± 0.031 (17)	1.13 ± 0.110 (31)	1.60 ± 0.126 (20)	2.34 ± 0.152 (20)
Anarta myrtilli	5	(0.43)	(0.64)	0.95 ± 0.037 (7)	1.44 ± 0.690 (11)	2.09 ± 0.087 (15)	-

advocated by Schmidt *et al.* (1977). However time limitations prevented this approach.

An obvious question with regard to these frequency distributions is whether there is a relationship between the size of individual larvae in successive instars. For species where a reasonable number of larvae were followed through at least two instars there was a positive correlation between head capsule width of individual larvae in successive instars (Table 6.2).

The mean ratio of change of HCW in successive instars within species are shown in Table 6.3. They range from 1.26 to 1.82 with a mean of 1.5 (mean=1.50, SD=0.118, n=49). These growth ratio statistics are similar to those discovered by Dyar (1890) for Lepidoptera: he found a range of 1.27 to 1.72, with a mean of 1.5. The relationship between instar progression and the coefficient of HCW increase is illustrated in Figure 6.16, with the ratio of increase of the HCW declining in later ecdyses (P<0.05).

From the measurements on the larval head widths of species given in Table 6.1 it is evident that there is a size progression from the largest species of Lasiocampidae through the Saturniidae and Noctuidae to the smallest Geometridae species. The smallest and largest macrolepidopteran species, *Eupithecia nanata* and *Lasiocampa callunae* respectively, have mean head widths of 0.25mm and 1.33mm in their first larval instar; an approximate five fold difference. The mean head widths for the first and final larval instars for species of the three taxonomic groups of Geometridae, Noctuidae and 'Others' are given in Table 6.4. The 'Others' group, which encompasses the Lasiocampidae and Saturniidae, has a larger mean HCW than the Geometridae and Noctuidae. The ranking of the size of the three groups is the same in the first and final instar. In terms of HCW the 'Others' taxonomic grouping is approximately 3.3 times larger than the Geometridae and 2.5 times larger than the Noctuidae, with the latter group 1.3 times larger than the Geometridae. The mean ratio of HCW increase for the species in the three taxonomic groupings of 'Others', Geometridae and Noctuidae (Table 6.4) is significantly different ($F_{[2,46]}$=10.44, P<0.001). The mean ratio of increase of HCW is inversely related to the mean size of the head capsule of the three taxonomic groups.

The mean weight of larvae in each of the instars for fifteen of the macrolepidopteran species are shown in Table 6.5. Correlation analysis has been carried out for selected species between the head size and weight of larvae within an instar. Larvae with larger heads tend to be heavier larvae (Table 6.6). This relationship might seem obvious since the head capsule is a proportion of the total larval weight. However since the head capsule does not grow within an instar it might be expected that larvae with small heads would gain weight before moulting to the next instar. All the examples shown in Table 6.6, however, are for the final larval instar before pupation so the conclusion is that larvae are pupating at these varying weights.

Table 6.2. The relationship between the head capsule width of individual lepidopteran larvae in successive instars. A correlation has been calculated between the HCW of individual larvae in two contiguous instars. The analysis has only been completed for those six species for which adequate amounts of data on the growth of individual larvae were collected. NS denotes a non-significant correlation, *i.e.* $P>0.05$.

Species	Number of instars	Instars tested	Correlation		
			r	*n*	*P*
E. caesiata	4	III/IV	0.637	8	NS
Eulithis spp.	4	III/IV	0.534	29	P<0.01
H. furcata	5	IV/V	0.411	28	P<0.05
E. nanata	4	III/IV	0.393	10	NS
L. porphyrea	5	IV/V	0.471	27	P<0.05
D. mendica	6	V/VI	0.464	25	P<0.05

Table 6.3. The mean ratio of increase of the larval head capsule width (HCW) between larval instars for 15 species of macrolepidoptera. The ratios have been calculated from the mean HCW listed in Table 6.1. *Eulithis* species incorporates the data for *E. populata* and *E. testata* which are difficult to differentiate between in the larval phase. Dashes indicate that the species does not enter that instar.

Species	Number of instars	Ratio of increase of HCW between instars				
		Ratio from I to II	Ratio from II to III	Ratio from III to IV	Ratio from IV to V	Ratio from V to VI
Lasiocampa callunae	5	1.44	1.45	1.56	1.26	-
Macrothylacia rubi	5	1.41	1.52	1.32	1.33	-
Pavonia pavonia	5	1.54	1.44	1.41	1.37	-
Entephria caesiata	5	1.53	1.62	1.65	-	-
Eulithis species	4	1.67	1.60	1.68	-	-
Hydriomena furcata	5	1.40	1.55	1.51	1.46	-
Perizoma didymata	4	1.80	1.57	1.62	-	-
Operophtera brumata	5	no data	1.57	1.49	1.32	-
Eupithecia satyrata	4	no data	1.68	1.52	-	-
Eupithecia goossensiata	4	no data	no data	1.42	-	-
Eupithecia nanata	4	1.60	1.58	1.48	-	-
Ematurga atomaria	5	1.5	1.82	1.48	1.51	-
Diarsia mendica	6	1.34	1.36	1.41	1.42	1.46
Lycophotia porphyrea	5	1.49	1.50	1.46	1.53	-
Anarta myrtilli	5	no data	no data	1.52	1.45	-

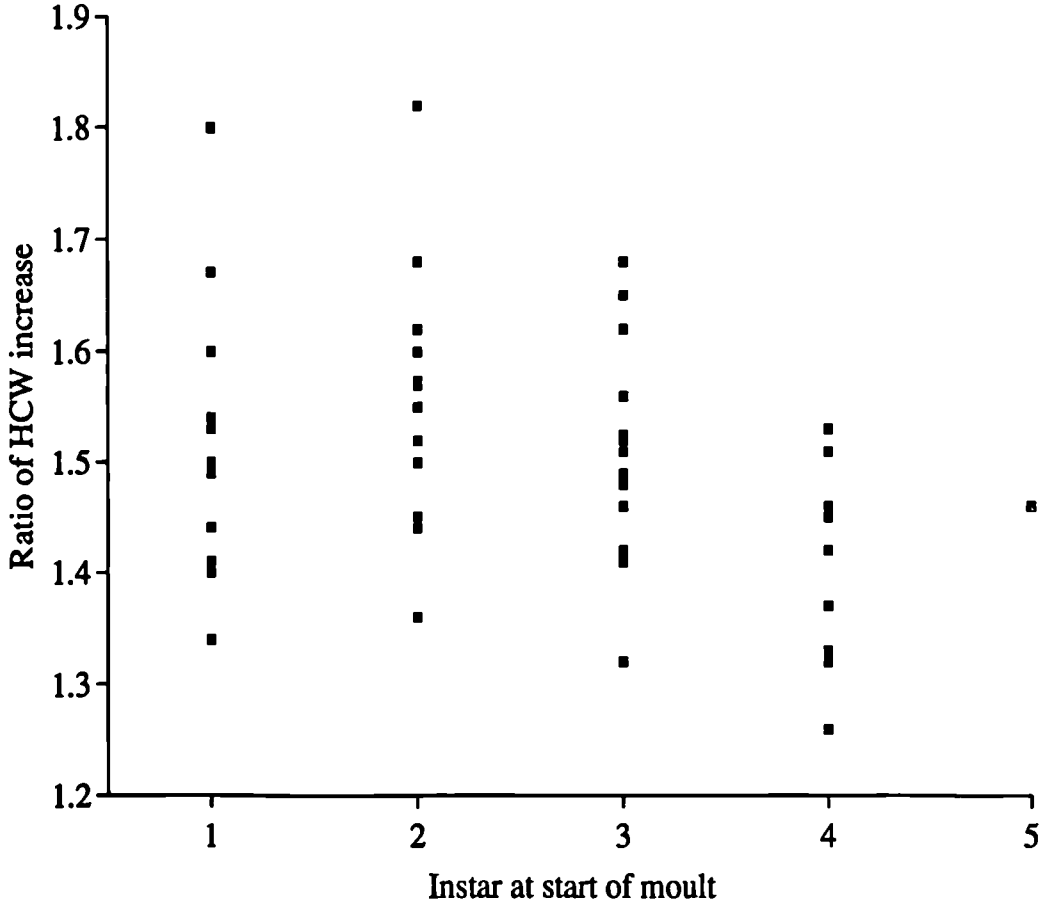

Figure 6.16. The relationship between the instar number and the ratio of increase of the head capsule width (HCW) on moulting to the subsequent instar (r =-0.334, n =49, $P < 0.05$). The data consists of all larval instars for each of the fifteen species listed in Table 6.2.

Table 6.4. The mean width of the head capsules in the first and final larval instars of species in the three macrolepidopteran taxonomic groups of Geometridae, Noctuidae and 'Others'. The results for the 'Others' group are also shown separately for its two constituent families of the Lasiocampidae and Saturniidae. No data for the Lymantriidae and Arctiidae are included as no measurements were taken from species in these families. The data are derived from Table 6.1 and for four of the species there was no information on the first larval instar. Also shown is the mean ratio of HCW increase for the three taxonomic groups calculated from the ratios for the individual species shown in Table 6.3.

Taxonomic group	Mean HCW ± SD (mm) (*n*)		Mean ratio of HCW increase ± SD (*n*)
	First instar	Final instar	
'Others'	1.17 ± 0.241 (3)	4.69 ± 0.846 (3)	1.42 ± 0.091 (12)
Lasiocampidae	1.31 ± 0.035 (2)	5.14 ± 0.474 (2)	-
Saturniidae	0.89 (1)	3.79 (1)	-
Geometridae	0.32 ± 0.051 (6)	1.41 ± 0.367 (9)	1.56 ± 0.114 (26)
Noctuidae	0.42 ± 0.035 (2)	2.12 ± 0.202 (3)	1.45 ± 0.062 (11)

Table 6.5. The mean wet weights (mg) ± SD of the larvae of fifteen macrolepidopteran species in each of their larval instars. Dashes indicate that the species does not enter that instar. *Eulithis* species incorporates data for *E. populata* and *E. testata* which are difficult to differentiate between in the larval stage.

Species	Number of instars	Mean weight (mg) ± SD (*n*)					
		Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI
Lasiocampa callunae	5 (1)	19.3 (9)	289.2 ± 431.9 (7)	335.2 ± 189.8 (33)	1070.5 ± 336.6 (9)	2131.0 ± 938.7	
Macrothylacia rubi	5	8.9 ± 5.7 (43)	24.4 ± 1.6 (2)	198.0 ± 82.1 (3)	1159.4 ± 727.1 (13)	2481.0 ± 846.8 (190)	-
Pavonia pavonia	5	13.9 (1)	35.4 ± 11.0 (12)	373.9 ± 588.6 (11)	444.5 ± 200.4 (9)	1997.8 ± 103.1 (2)	-
Entephria caesiata	4	0.6 ± 0.3 (8)	3.1 ± 1.0 (8)	9.6 ± 5.3 (46)	61.0 ± 35.1 (84)	-	-
Eulithis species	4	0.8 ± 0.3 (4)	3.1 ± 3.0 (110)	10.9 ± 6.8 (86)	54.7 ± 54.6 (114)	-	-
Hydriomena furcata	5	0.1 (1)	0.9 ± 0.4 (39)	3.2 ± 1.8 (121)	11.9 ± 6.8 (166)	46.8 ± 19.1 (349)	-
Operophtera brumata	5	no data	1.6 ± 0.7 (10)	3.6 ± 1.5 (15)	24.6 ± 9.8 (7)	40.0 (1)	-

Table 6.5. (continued)

Species	Number of instars	Mean weight (mg) ± SD (*n*) Instar I	Instar II	Instar III	Instar IV	Instar V	Instar VI
Perizoma didymata	4	no data	2.4 ± 1.0 (4)	9.7 ± 3.7 (14)	28.1 ± 10.7 (28)	-	-
Eupithecia satyrata	4	no data	1.1 (1)	7.0 ± 1.4 (5)	19.4 ± 5.9 (4)	-	-
Eupithecia nanata	4	no data	1.2 ± 0.5 (16)	5.3 ± 2.9 (51)	17.3 ± 6.0 (191)	-	-
Eupithecia goossensiata	4	no data	no data	5.7 ± 1.3 (7)	18.5 ± 4.6 (6)	-	-
Ematurga atomaria	5	0.2 ± 0.1 (7)	1.3 ± 0.7 (19)	5.6 ± 3.5 (44)	17.2 ± 14.0 (87)	51.8 ± 22.3 (127)	-
Lycophotia porphyrea	5	0.9 ± 0.7 (14)	3.4 ± 1.5 (65)	8.9 ± 4.2 (95)	20.5 ± 11.5 (109)	61.2 ± 41.5 (44)	-
Diarsia mendica	6	no data	2.3 (1)	7.2 ± 4.1 (14)	19.1 ± 6.4 (22)	52.0 ± 21.8 (11)	171.1 ± 89.1 (6)
Anarta myrtilli	5	no data	no data	12.9 ± 3.6 (9)	40.1 ± 20.7 (13)	117.7 ± 39.5 (18)	-

Table 6.6. The relationship between the head capsule width and weight of macrolepidoptera larvae within instars.

Species	Instar	Correlation		
		r	d.f.	*P*
Eulithis species	IV	0.336	115	<0.01
H. furcata	V	0.270	343	<0.01
H. furcata	IV	0.335	166	<0.01
E. caesiata	IV	0.390	78	<0.01

The relationship between the size of the larval and adult stages of the life-cycle is shown in Figure 6.17, with larval size estimated as the mean width of the head capsules in the final larval instar. There is a high correlation between the two dimensions (r=0.92, d.f.=16, P<0.0001) with 83% of the variation in larval HCW explained by adult wingspan. Data for the mean HCW in the final larval instar were available for 18 species rather than just the fifteen for which data on all instars has been presented. It is to be expected that species with large larvae develop into large adults, although there is a certain amount of variation which is probably related to factors such as adult weight. For example, four species have adult wingspans between 35 and 40mm, but *Trichiura crataegi* ('Others') and *Ceramica pisi* (Noctuidae), have greater HCW than *Entephria caesiata* (Geometridae) and *Eulithis* (Geometridae) species Gaston and Reavey (1991) considered the same relationship in a much larger sample of the British macrolepidopteran fauna and found certain families to deviate in the same direction from the overall regression line. For example they found most noctuids to have large larvae for their adult wingspan. A similar relationship has been found between adult size and egg size in Lepidoptera (Nakasufi 1987).

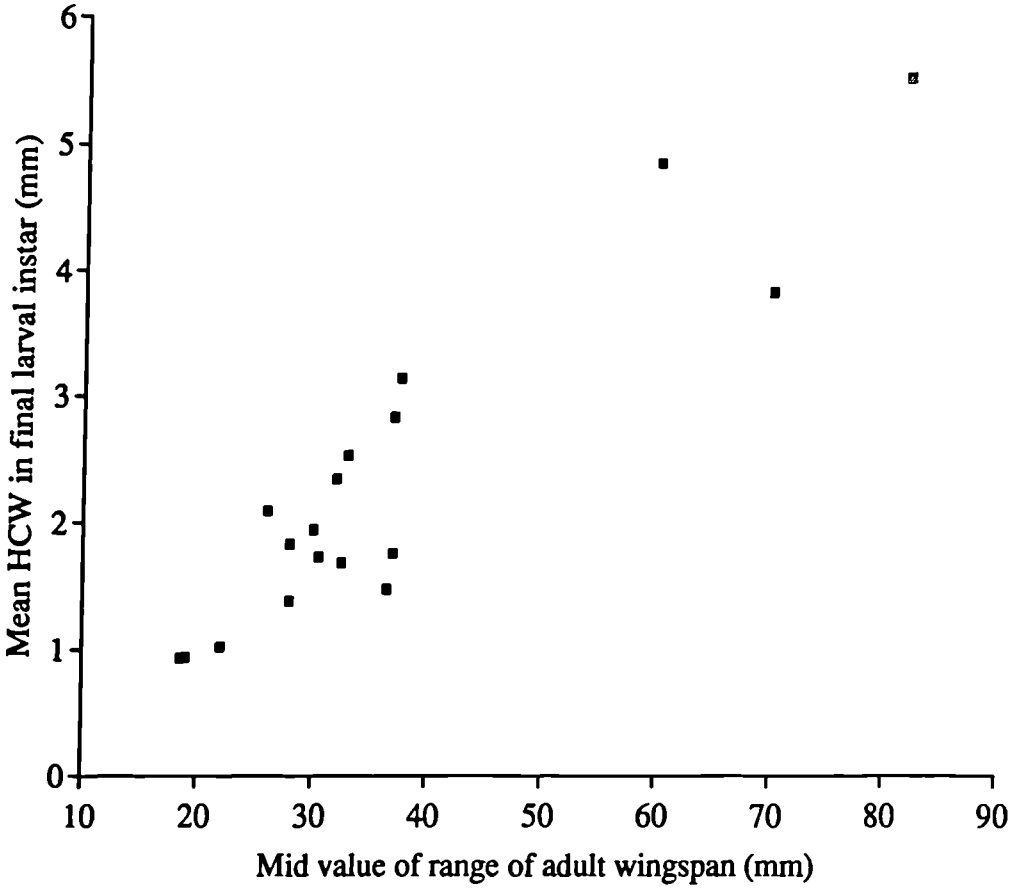

Figure 6.17. The relationship between head capsule width (HCW) in the final instar of the larval stage and the size of the adult (r =0.92, n =18, $P < 0.001$). Data are for the fifteen species listed in Table 6.1 and for the three additional species of *Trichiura crataegi, Phragmatobia fuliginosa* and *Ceramica pisi* for which data was available for the final instar. The size of the adult has been taken as the middle value of the range of wingspan given by Skinner (1984) and the size of the head capsules in the final larval instar are taken from Table 6.1.

Chapter Seven

The effect of altitude on the Lepidoptera associated with *Calluna vulgaris*

7.1. Introduction

Generally the diversity of biological organisms is thought to decline with increasing altitude. However the relationship is often more complex and although such a decline is documented for both vertebrates (Terborgh 1977) and invertebrates (Greenslade 1968; Hagvar 1976; Hebert 1980; Coulson and Butterfield 1986; Wolda 1987; Coulson 1988), other studies have recorded optimum species richness at intermediate altitudes (Turner and Broadhead 1974; Janzen *et al.* 1976; Gilbert 1984; Holloway 1987; McCoy 1990) or have found altitude to have little or no effect on species richness (Claridge and Singhrao 1978; Lawton *et al.* 1987).

The decline in the species richness of insects with altitude has been attributed to a number of factors (Lawton *et al.* 1987): (a) the increasingly unfavourable physical environment at higher altitudes (b) a reduction in the primary production with altitude (c) a reduction in resource diversity with altitude (d) a reduction in the habitat area with altitude. The mid-elevational peaks in species richness found by some studies have been accounted for by two similar processes (McCoy 1990): (a) the upper limits of distribution are set by climate and resource limitation and lower limits by climate and predation (b) the higher net accumulation of photosynthate at mid-elevations allows greater resources for herbivorous insects and hence their insect predators.

It has become apparent that other factors influence the location of optimum species richness on the altitude gradient. Certain aspects of the sampling regime influence the pattern found (Wolda 1987), especially the length of time over which it occurs; with long term sampling giving rise to low elevational peaks whereas short term sampling tends to produce mid-elevational peaks (McCoy 1990). In a survey of recent studies, the elevation at which maximum species richness occurred was found to be negatively related to latitude (McCoy 1990). This finding suggests that in Britain maximum species richness is likely to occur at the lower altitude sites. Discrepancies arise between studies in the location of the highest biological diversity because of: (a) the use of disparate altitudinal ranges (b) human disturbance at lower altitudes (c) differences in the measurement indices, *e.g.* species richness or diversity can be evaluated (d) studies working at different taxonomic levels. For example, Coulson (1988) found that although overall the species richness of invertebrates on peatlands

declined with altitude, the pattern was reversed for a few individual families of invertebrates such as the Tipulidae.

Individual Lepidoptera species are likely to undergo changes in abundance within their altitudinal distribution. Within the geographical range of species, population densities tend to be highest in the centre and decline towards the boundaries (Brown 1984), with a similar pattern often evident within altitudinal ranges (Lawton *et al.* 1987 and references within). Sudden changes in abundance may occur where a single limiting variable alters abruptly (Caughley *et al.* 1988).

Previous studies indicate that Lepidoptera might be susceptible to altitudinal change. A general decline with altitude of the species richness of Lepidoptera associated with moorland habitats has been recorded in Northern England (Coulson 1988). Additionally, the species richness of Lepidoptera has been shown to decline with increasing latitude in Britain (Turner *et al.* 1987). Lawton *et al.* (1987) have shown that an intensive study of the invertebrate fauna associated with a single plant, may show there to be no relationship between altitude and species richness. Previous work therefore imparts a number of conflicting ideas about what would be expected from a study of the effects of altitude on the lepidopteran species associated with *Calluna vulgaris*.

The important changes with altitude that are likely to affect any pattern of change of Lepidoptera on *Calluna* with altitude can be discussed in greater detail:

(a) Climatic change with altitude

Some of the most notable changes in climate with increasing altitude are listed in Table 7.1. Although generally presented as such, these lapse rates are unlikely to be linear across the altitude gradient and they vary with factors such as latitude and aspect (Taylor 1976). The increasing severity of the climate at higher altitudes is not entirely disadvantageous for invertebrates; *e.g.* increased snow cover protects insects from freezing (Gates 1980; Danks 1991). One of the most important climate changes is the decline in temperature which affects the ability of poikilothermic invertebrates to complete their life-cycle. Some species are able to compensate their growth rates at lower temperatures (Butterfield 1976, Coulson *et al.* 1976; Smiley and Rank 1986). Alternatively species may increase the length of their life-cycle, *e.g. Strophingia ericae* (Hodkinson 1973; Parkinson and Whittaker 1975).

Climate also indirectly affects insects with increasing altitude. For example, the increased precipitation and decreased evaporation rates at higher altitudes leads to the formation of blanket bog habitats.

Table 7.1. The lapse rates of selected climatic variables with altitude in Britain. The information has been compiled from Manley (1970), Taylor (1976), White and Smith (1982) and Grace and Unsworth (1988).

Climatic variables	Typical sea level values	Geographical location	Lapse rate (per 100m)
Temperature			
mean	10 °C	Britain	-0.6-0.9 °C
"	"	Northern Pennines	-0.69 °C
maximum	13 °C	"	-0.7-0 9 °C
minimum	7 °C	"	-0.5-0.7 °C
Wind speed	5 m s^{-1}	Britain	0.6-0.7 m s^{-1}
Precipitation	1000 mm	Britain	100-300 mm
"	"	East slope of Pennines	98 mm
Snow cover	10 days	Britain	10-20 days
Sunshine	3.4 h day^{-1}	Britain	-0.13 h day^{-1}
Growth season	-	Britain	-4.3 to 13.1 days

(b) Changes in the *Calluna* plant with altitude

The exact nature of the effect of altitude on the primary production of *Calluna* is uncertain. In one study a 300m increase in altitude, from 200m to 500m, resulted in a 40% decline in productivity (Miller and Watson 1978). Over a similar altitude range Welch (1984) found a 33% decline in production. Other studies, however, have found altitude to have little effect on productivity as a result of plants from higher altitudes showing compensatory adaptation, with higher productivity at lower temperatures than plants from lower altitudes (Summers 1978). The same study did, however, show productivity to be negatively correlated with exposure, with a doubling of exposure levels decreasing productivity by a factor of 0.62. Standing crop has been shown to decline both with exposure and altitude (Summers 1978; Section 2.4). On the blanket bog sites, *Calluna* is co-dominant with *Eriophorum vaginatum* rather than growing in dominant stands as found at lower altitudes. Despite the primary production and standing crop of *Calluna* declining with increasing altitude, it is unlikely that this deleteriously affects the species diversity of herbivorous insects. Folivorous insects are rarely limited by food quantity even if its quality is taken into account (Lawton and Strong 1981).

It is not known if the nutritional quality of *Calluna* declines with altitude The nitrogen concentration in *Vaccinium myrtillus* leaves increases with altitude (Woodward 1986). Upland plants may also have thicker cuticles and leaves at higher altitudes (Woodward 1986; Körner and Diemer 1987).

There is no available information as to whether the initiation of spring growth of *Calluna* is delayed with altitude. If it is, this may retard the development of the herbivorous insects associated with it. Hagvar (1976) noted a delay of four days in the start of birch leaf growth for every 100m rise in altitude, resulting in a retardation of invertebrate development. *Calluna* is evergreen although newly emerging larvae may require the softer, more nutritious young spring growth.

(c) Changes in the habitat and its diversity with altitude

There is a decline in the plant species diversity along the altitude gradient used in this study although its importance when considering the lepidopteran assemblage associated with a single host plant is uncertain. Lawton *et al.* (1987) conclude that investigation of the insect herbivores associated with a single plant species minimises any effects of changes in habitat diversity with altitude. For polyphagous species however, there may be less obvious advantages to having alternative host plant species available (Wint 1983). There is a decline in floral diversity with altitude on moorlands (Coulson and Whittaker 1978; Hewson 1990) which may affect flower feeding adult moths. In the current study, the main decline in vegetation diversity probably occurred between North Plantation (290m) and Waskerley (>360m) as all tree species disappeared. There is probably a decline in the habitat diversity with altitude, although there is little quantitative evidence to support this statement.

(d) Changes in habitat area with altitude

Hebert (1980) partially attributed some of the decline in species richness of moths in tropical rain forest to a decrease in habitat area with altitude. The habitat area of heather moorland probably increased with altitude on a local scale. On a national scale the same is probably true although historically the situation may have been different.

(e) Changes in biotic factors with altitude

The incidence of parasitism has been shown to decline with increasing altitude (Whittaker 1962; Hagvar 1976; Randall 1982a; Smiley and Rank 1986). Although interspecific competition has been shown to be important in some Lepidopteran communities along an altitudinal gradient (Gilbert 1984), it would seem unlikely to be important for the Lepidoptera associated with *Calluna vulgaris* (Lawton and Strong 1981).

7.2. The effect of altitude on macrolepidopteran species richness

7.2.1. Methods

Sample sites of different ages and geographical locations but of equal altitude have been classed together to give a species richness of macrolepidoptera on *Calluna* for each altitude. The relationship between altitude and species richness has been analysed by Model I linear regression. The significance of the regression has been examined by analysis of variance and the level of significance taken at the 95% probability level.

There are a number of different categories of data available for the calculation of the relationship between altitude and macrolepidopteran species richness. Species absent from intermediate altitudes but present at higher and lower altitudes have been assumed to be continuously distributed between the two extremes. In addition, records of *Calluna* feeding species that were only found on *Vaccinium* at certain altitudes have been included. Altitude records involving adult Lepidoptera have been excluded as the mobility of this stage of the life-cycle may result in its emigration to altitudes where the species is unable to complete its life-cycle. The situation is the same for the other life-cycle stages but the probability of it occurring and being recorded is less. The majority of the altitudinal records are based on the discovery of the larvae (>95%) and to a lesser extent the egg and pupal stage.

While the study was in progress it became apparent that the highest species richness of Lepidoptera was to be found at North Plantation which was the lowest altitude study area. An *a priori* assumption was that this study area represents a different habitat compared to the other sites because of its proximity to areas of woodland. A regression analysis was therefore completed with the data for this site

excluded to examine whether the significance of the relationship between altitude and species richness is due entirely to this site. Regression analysis has also been carried out separately for the different taxonomic groups of the macrolepidoptera and the data collected in each of the different years of the study to test for any divergences in response.

7.2.2. Macrolepidoptera species richness

The results of linear regression between the number of macrolepidoptera species and altitude is shown in Table 7.2. Overall the inverse relationship is highly significant ($P<0.001$ Equation 1) with 94% of the variation in species richness being explained by altitude and a loss of approximately three species for every 100m increase in altitude (Figure 7.1). The effects of the non-application of the assumption that species found at high and low altitudes also occur at intermediate altitudes and the absence of the records from *V. myrtillus* are recorded in equation 2. Equations 3 and 4 in Table 7.2. show the regression relationship when adults records are included or larval records only are considered. These various modifications to the dataset have no effect on the significance of the relationship.

The highest species richness of Lepidoptera associated with *Calluna vulgaris* was recorded at 280m (North Plantation). When the data for this site are excluded from the regression analysis (equation 5), the relationship is still significant even though the altitudinal range of the dataset was reduced ($P<0.01$), with a loss of 2.6 species per 100m increase in altitude.

7.2.3. Species richness of the individual taxonomic groups of macrolepidoptera

The results of the change in species richness of Geometridae, Noctuidae and 'Others' in relation to altitude shows that the three taxonomic groups differ in their response (Equations 6-11, Table 7.2; Figures 7.2, 7.3, 7.4). The geometrids and 'Others' both show a significant decline in species richness with altitude ($P<0.001$), although its magnitude differs. The regression predicts a loss of one Geometridae and two 'Others' species for every 100m rise in altitude. The Noctuidae, in contrast to the other two taxonomic groups, experience no change in species richness with altitude ($P>0.05$). The proportion of the macrolepidopteran species found feeding as larvae on *Calluna* at each altitude which belong to each of the three taxonomic groups are shown in Figure 7.5.

Table 7.2. The relationship between the species richness of macrolepidoptera associated with *Calluna vulgaris* and altitude (m) as measured by linear regression. Data consists of eight different altitudes from 290 to 650m. Columns 2-7 refer to which sub-sections of the dataset were used in the linear regression calculation. Taxonomic groups refers to whether all macrolepidoptera were considered or only those in the Geometridae, Noctuidae or 'Others' groups. 'Others' incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. Adult records refers to whether records of this mobile stage of the life-cycle were included or if the data consisted of records of the egg, larval and pupal stages only. *Vaccinium myrtillus* refers to whether *Calluna* feeding species which also feed on *V. myrtillus* have had altitude records on the latter plant included. Intermediate altitudes refers to whether the assumption that species occurring at lower and higher altitudes are also present at intermediate altitudes has been applied. R^2 is the coefficient of determination and F and P refer to the significance of the regression as tested by an ANOVA. NS denotes a non-significant regression, *i.e.* $P>0.05$.

Eq. No.	Altitude	Taxonomic group	Adults records included	*V. myrtillus* records included	Years included	Intermediate altitudes included	$b \pm SE$	constant ± SE	R^2	$F_{[d.f.]}$	P
1	All	All	No	Yes	All	Yes	0.032 ± 0.003	32.8 ± 1.54	94%	$97.9_{[1,6]}$	<0.001
2	All	All	No	No	All	No	0.036 ± 0.004	32.4 ± 2.13	91%	$64.4_{[1,6]}$	<0.001
3	All	All	Yes	No	All	No	0.034 ± 0.005	31.5 ± 2.21	90%	$52.8_{[1,6]}$	<0.001
4	All	All	Larvae	No	All	No	0.036 ± 0.004	32.4 ± 2.13	91%	$64.4_{[1,6]}$	<0.001
5	290m excluded	All	No	Yes	All	No	0.026 ± 0.006	27.8 ± 2.76	82%	$22.1_{[1,5]}$	<0.01

Table 7.2. (continued)

Eq. No.	Altitude	Taxonomic group	Adults records included	*V. myrtillus* records included	Years included	Intermediate altitudes included	$b \pm SE$	constant ± SE	R^2	$F_{[d.f.]}$	P
6	All	Geometrids	No	Yes	All	No	0.009 ± 0.002	13.0 ± 0.87	81%	$26.4_{[1,6]}$	<0.01
7	All	Noctuids	No	Yes	All	No	0.002 ± 0.004	3.8 ± 2.09	3%	$0.2_{[1,6]}$	NS
8	All	'Others'	No	Yes	All	No	0.020 ± 0.004	13.9 ± 1.73	84%	$30.8_{[1,6]}$	<0.01
9	All	Geometrids	No	Yes	All	Yes	0.010 ± 0.001	13.2 ± 0.73	86%	$38.3_{[1,6]}$	<0.001
10	All	Noctuids	No	Yes	All	Yes	0.002 ± 0.001	5.0 ± 0.48	37%	$3.5_{[1,6]}$	NS
11	All	'Others'	No	Yes	All	Yes	0.021 ± 0.004	14.6 ± 1.97	81%	$24.9_{[1,6]}$	<0.01
12	All	All	No	Yes	1988	Yes	0.007 ± 0.004	6.1 ± 2.07	36%	$2.8_{[1,5]}$	NS
13	All	All	No	Yes	1989	Yes	0.017 ± 0.012	13.5 ± 5.86	23%	$1.8_{[1,6]}$	NS
14	All	All	No	Yes	1990	Yes	0.037 ± 0.005	30.7 ± 2.37	90%	$53_{[1,6]}$	<0.001

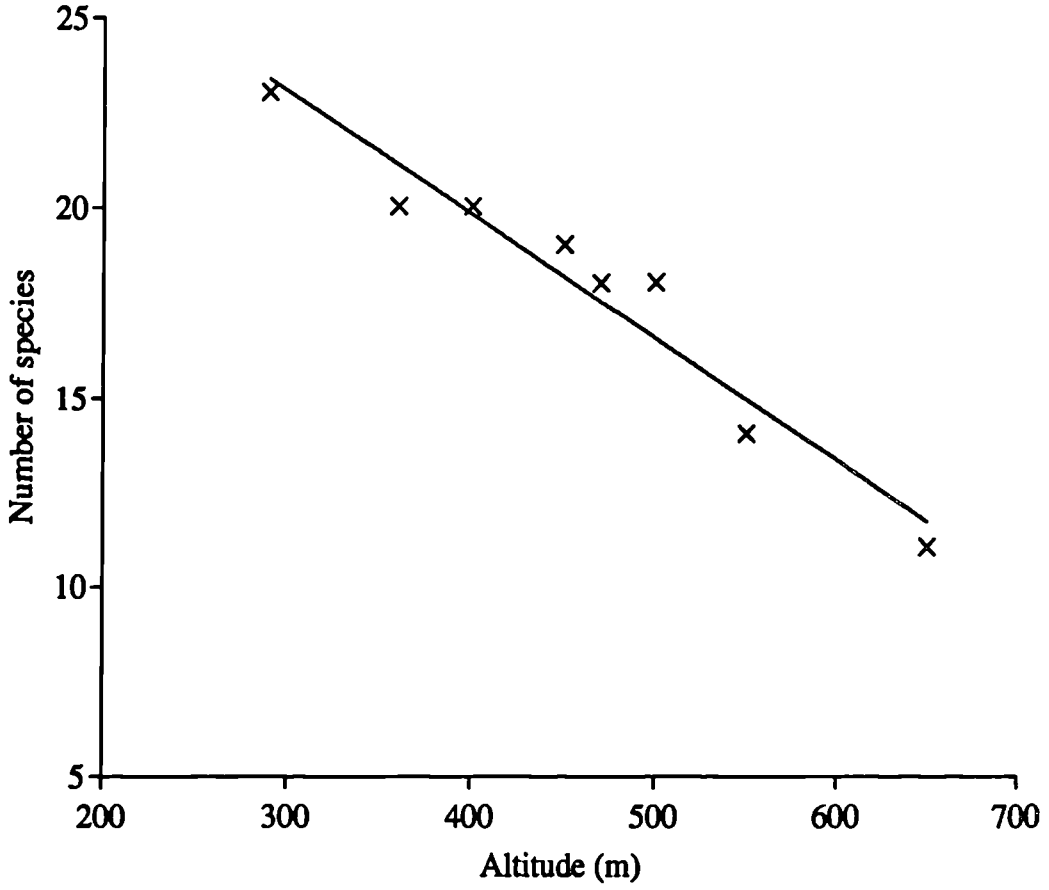

Figure 7.1. The number of macrolepidopteran species found as larvae feeding on *Calluna vulgaris* along an altitudinal transect. The results for all sample sites at each altitude have been combined. It has been assumed that a species occurring at lower and higher altitudes also occurs at intermediate altitudes. Records of the egg, larval and pupal stage but not the adult stage have been included. Species which feed both on *Calluna* and *V. myrtillus* have had altitude records of occurrence on *V. myrtillus* included. The linear regression line is shown: $Y = (-0.032 \pm 0.003)\ X + 32.8$, $R^2=94\%$, $F=97$, $P<0.001$.

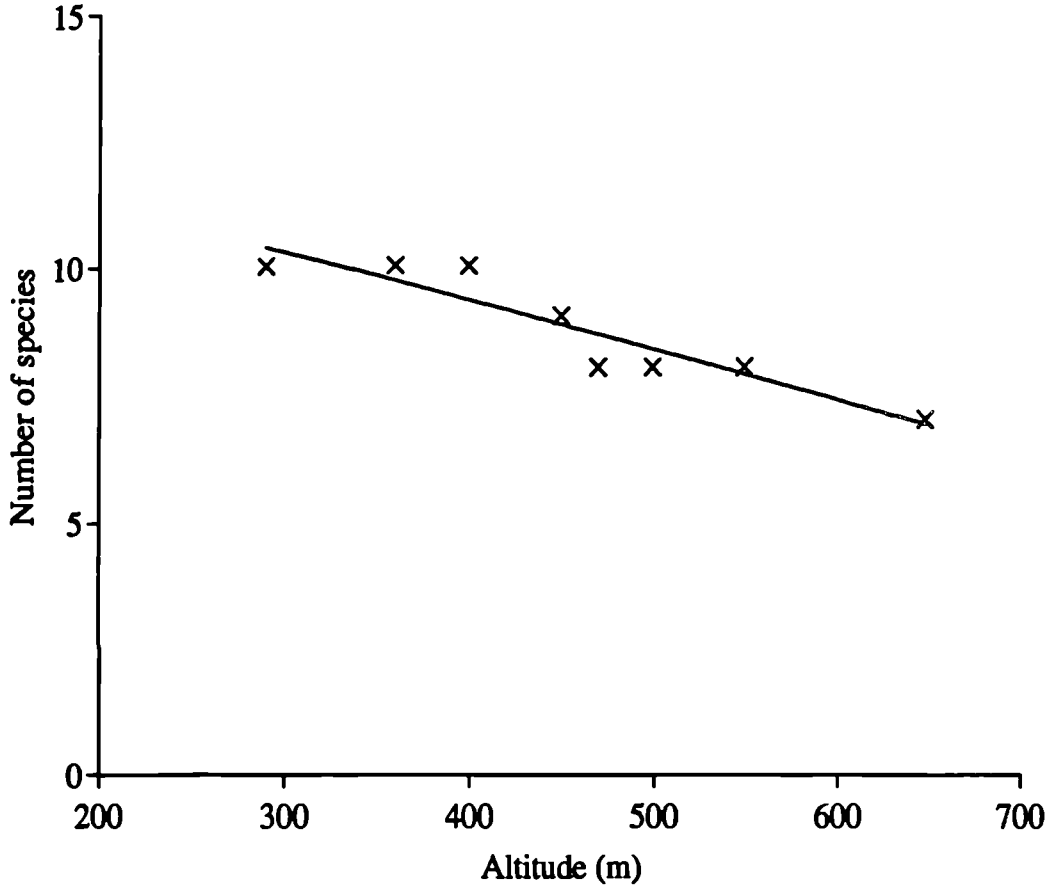

Figure 7.2. The number of macrolepidopteran species of the Geometridae family found as larvae feeding on *Calluna vulgaris* along an altitudinal transect. The results for all sample sites at each altitude have been combined. It has been assumed that a species occurring at lower and higher altitudes also occurs at intermediate altitudes. Records of the egg, larval and pupal stage but not the adult stage have been included. Species which feed both on *Calluna* and *V. myrtillus* have had altitude records of occurrence on *V. myrtillus* included. The linear regression line is shown: $Y = (-0.01 \pm 0.001)\ X + 13.2$, $R^2 = 86\%$, $F = 38$, $P < 0.001$.

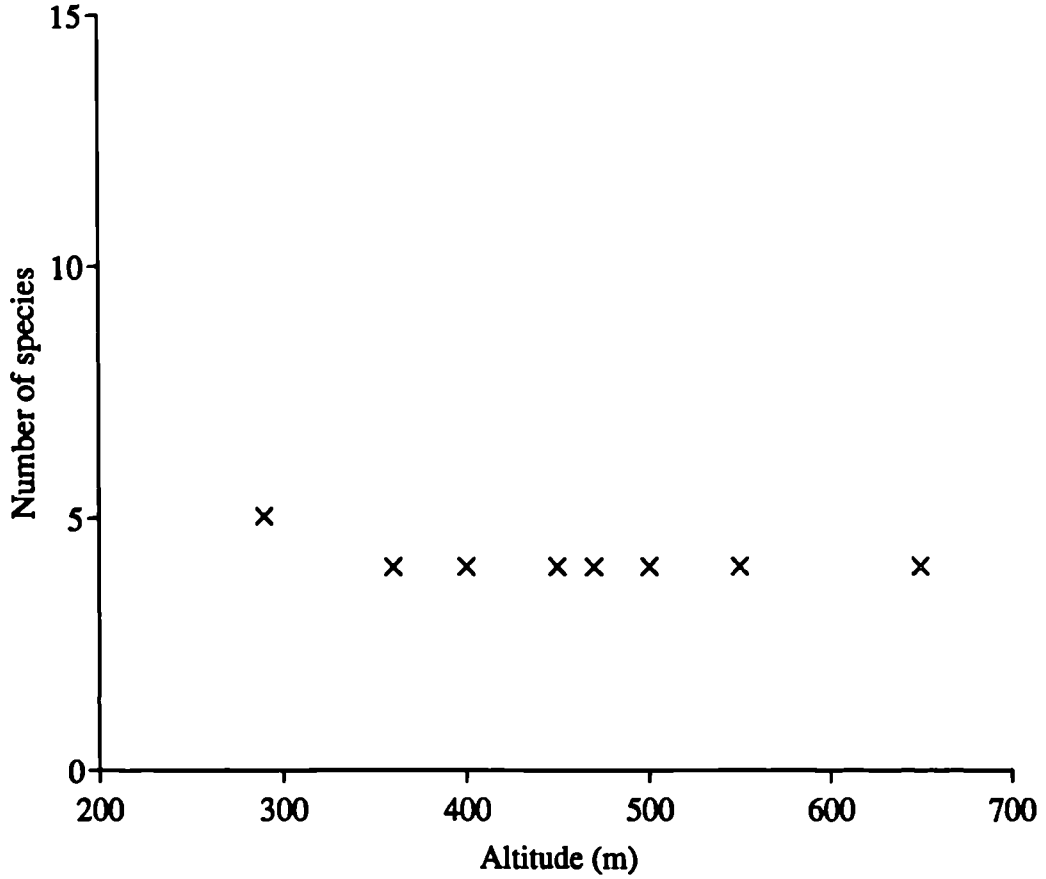

Figure 7.3. The number of macrolepidopteran species of the Noctuidae family found as larvae feeding on *Calluna vulgaris* along an altitudinal transect. The results for all sample sites at each altitude have been combined. It has been assumed that a species occurring at lower and higher altitudes also occurs at intermediate altitudes. Records of the egg, larval and pupal stage but not the adult stage have been included. Species which feed both on *Calluna* and *V. myrtillus* have had altitude records of occurrence on *V. myrtillus* included. The linear regression line is shown: $Y = (-0.002 \pm 0.001)\ X + 5.0$, $R^2=37\%$, $F=3.5$, $P>0.05$.

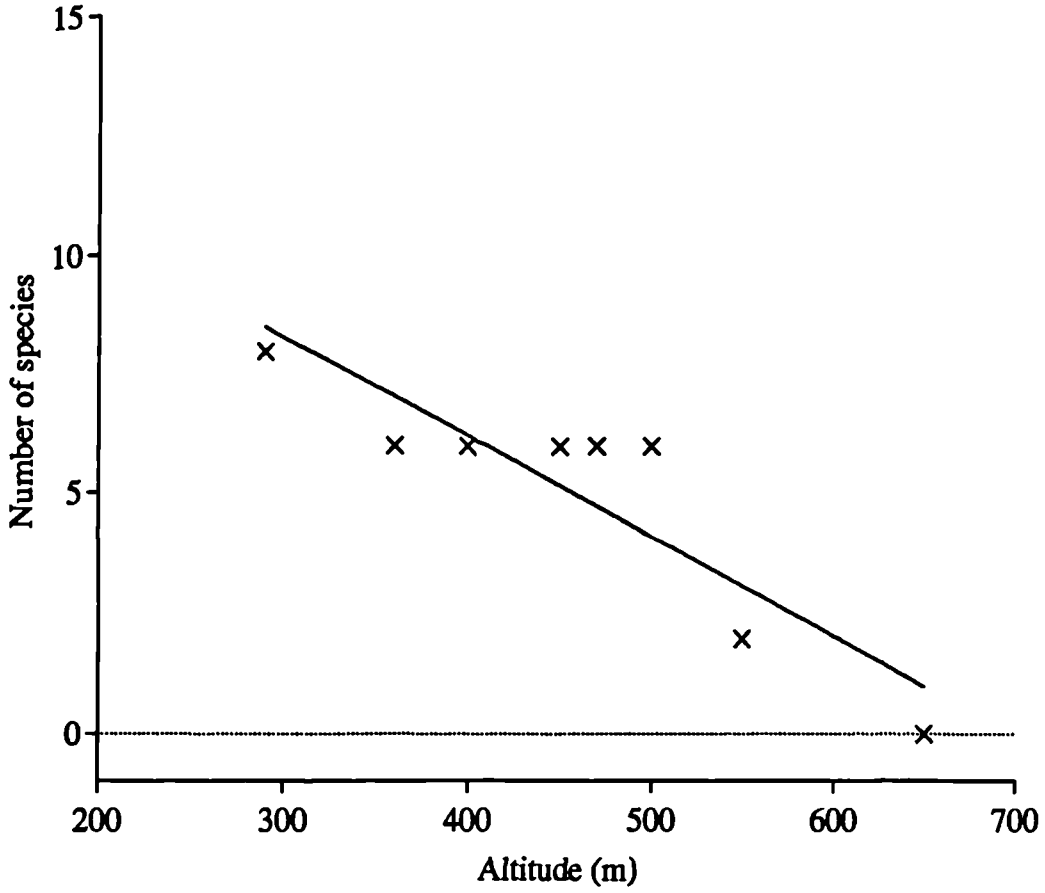

Figure 7.4. The number of macrolepidopteran species of the 'Others' taxonomic group found as larvae feeding on *Calluna vulgaris* along an altitudinal transect. All records for sites at each altitude have been combined. It has been assumed that a species occurring at lower and higher altitudes also occurs at intermediate altitudes. Records of the egg, larval and pupal stage but not the adult stage have been included. Species which feed both on *Calluna* and *V. myrtillus* have had altitude records of occurrence on *V. myrtillus* included. The linear regression line is shown: $Y = (-0.021 \pm 0.004)\ X + 14.6$, $R^2=25\%$, $F=24.9$, $P<0.001$. 'Others' incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae.

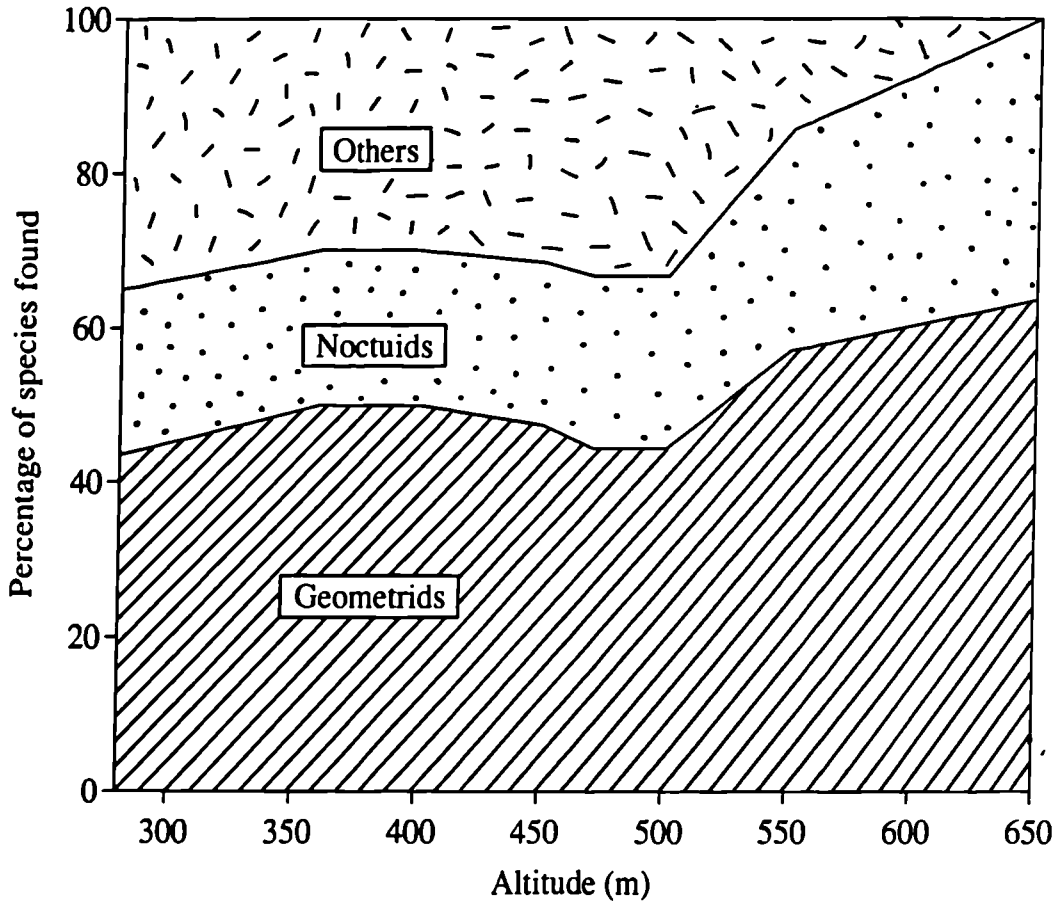

Figure 7.5. The proportions of the macrolepidopteran species found feeding as larvae on *Calluna vulgaris* along an altitudinal transect that were of the three taxonomic groups of the Geometridae, Noctuidae and 'Others'. The latter group incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. The altitudinal transect reached from 290 to 650m.

7.2.4. The species richness of Lepidoptera within each of the separate years of the study

The effects of altitude on the species richness of the macrolepidoptera associated with *Calluna* can be analysed separately for the three component years of the study (Table 7.2 and Figure 7.6). There was no significant effect of altitude on species richness in 1988 ($P>0.05$ Equation 12) and 1989 ($P>0.05$ Equation 13). However there was a significant decline with rising altitude in 1990 ($P<0.001$ Equation 14) with seven species lost for every 200m rise in altitude. The disparity between years in the significance of the relationship is probably the result of variation in the number of species and individual larvae found in the three years (Section 3.4).

7.3. The effect of altitude on the distribution of the macrolepidopteran species

An indication of the distribution of the species over the altitude gradient can be gained from the cumulative curves of the lowest and highest altitude records for the species (Figure 7.7). It can be seen that the majority of the species occurring at the highest altitude are also present at the lowest altitude. The exceptions are *Entephria caesiata* which was not recorded at 290m, and *Noctua comes* which was only encountered on *Calluna* at 650m. The limited distribution of the latter species is probably a sampling artifact rather than the true altitudinal distribution, since large numbers of adults were captured at 290m. Alternatively it may only feed on *Calluna* at the higher altitude sites where other food plants are absent. It also shows that the main loss of species with altitude occurs at the boundaries between the North Plantation (290m) and lowest altitude Waskerley site (350m) and the highest altitude northern heath sites (500m) and the blanket bog sites above 550m.

The altitudinal distributions of 18 of the macrolepidopteran species found during this study (the two *Eulithis* species are considered together) are illustrated in Figure 7.8. The seven excluded species are those of which less than 5 individuals were found and/or that were recorded at a single altitude. The perceived altitudinal distributions of these seven species are likely to be distorted by the low number of individuals found. The altitudinal distributions have been produced from the records of the presence of the egg, larval or pupal stages, with the adult stage excluded because of its high mobility. The inclusion of the egg and pupal records does not alter the distributions, in contrast to exclusive use of the more numerous larval records. The distributions are based on the lowest and highest altitude points at which a species was recorded, therefore species have not necessarily been recorded at all intermediate altitudes.

Of the 18 species there was only one, *Entephria caesiata*, that was not present in the lower part of the altitudinal range. In comparison there were 12 species that were

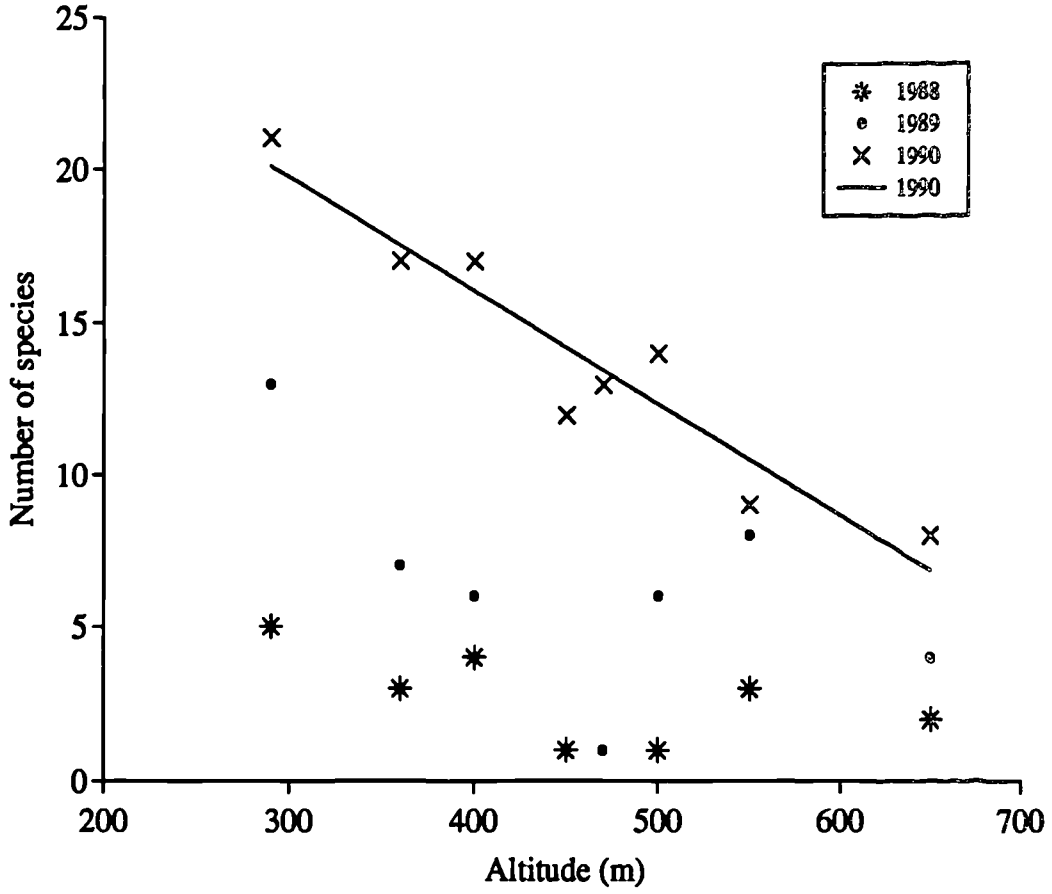

Figure 7.6. The number of macrolepidopteran species found as larvae feeding on *Calluna vulgaris* along an altitudinal transect during each of the three years of the study of 1988-1990. Only in 1990 is there a significant linear regression between altitude and the number of species found. Regression line: $Y = (-0.037 \pm 0.005)\ X + 30.7$, R^2=90%, F=53, P<0.001. It has been assumed that a species occurring at lower and higher altitudes also occurs at intermediate altitudes. Records of the egg, larval and pupal stage but not the adult stage have been included. Species which feed both on *Calluna* and *V. myrtillus* have had altitude records of occurrence on *V. myrtillus* included.

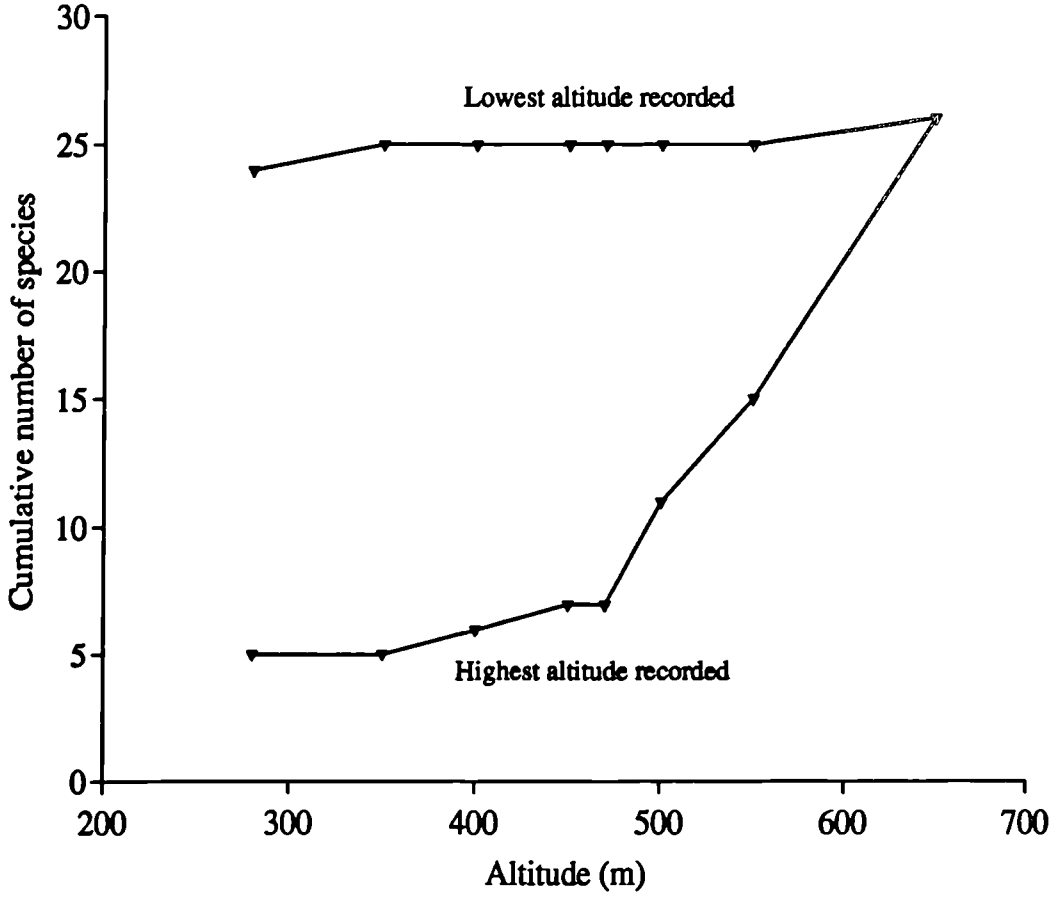

Figure 7.7. The cumulative curves of the lowest and highest altitude records for the macrolepidopteran species feeding as larvae on *Calluna vulgaris*. Data are for the 26 species found as larvae feeding on *Calluna* during this study. The altitude gradient reached from 290 to 650m.

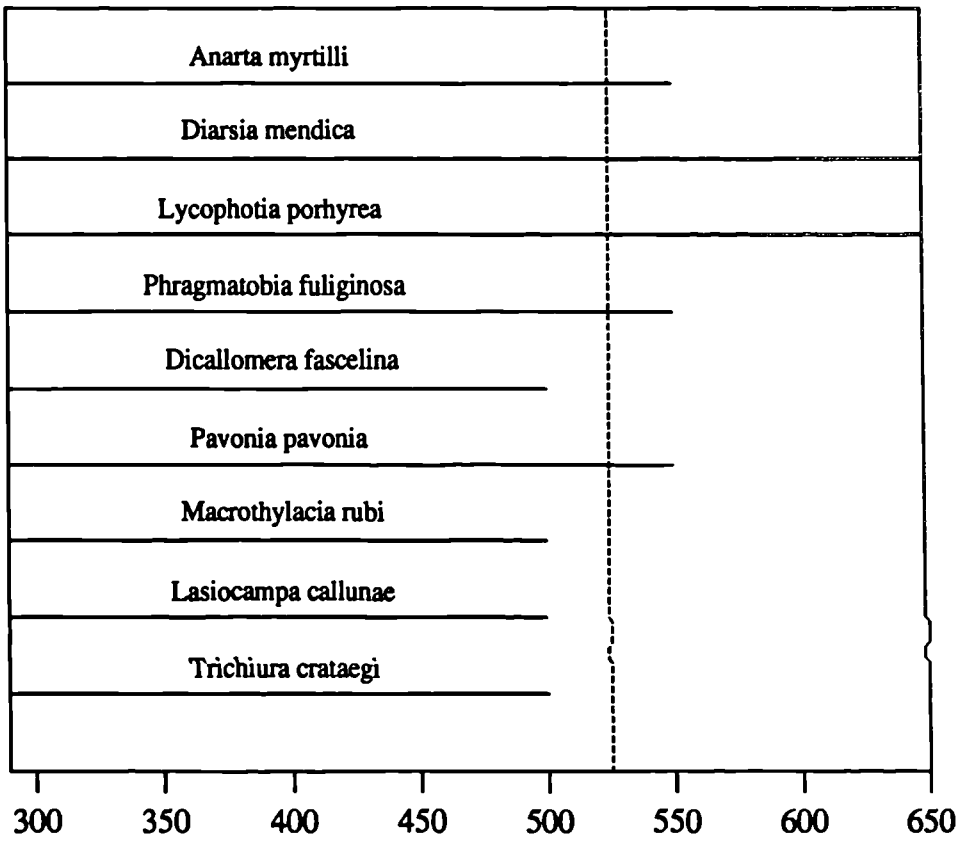

Figure 7.8. The altitudinal distributions of eighteen of the abundant macrolepidopteran species found to feed as larvae on *Calluna vulgaris*. The vertical broken line shows the approximate altitudinal position of the interface between northern heath and blanket bog. The distributions have been taken from the lowest and highest altitude at which a species was recorded and they have not necessarily been recorded at all intermediate altitudes.

Figure 7.8. Continued overleaf.

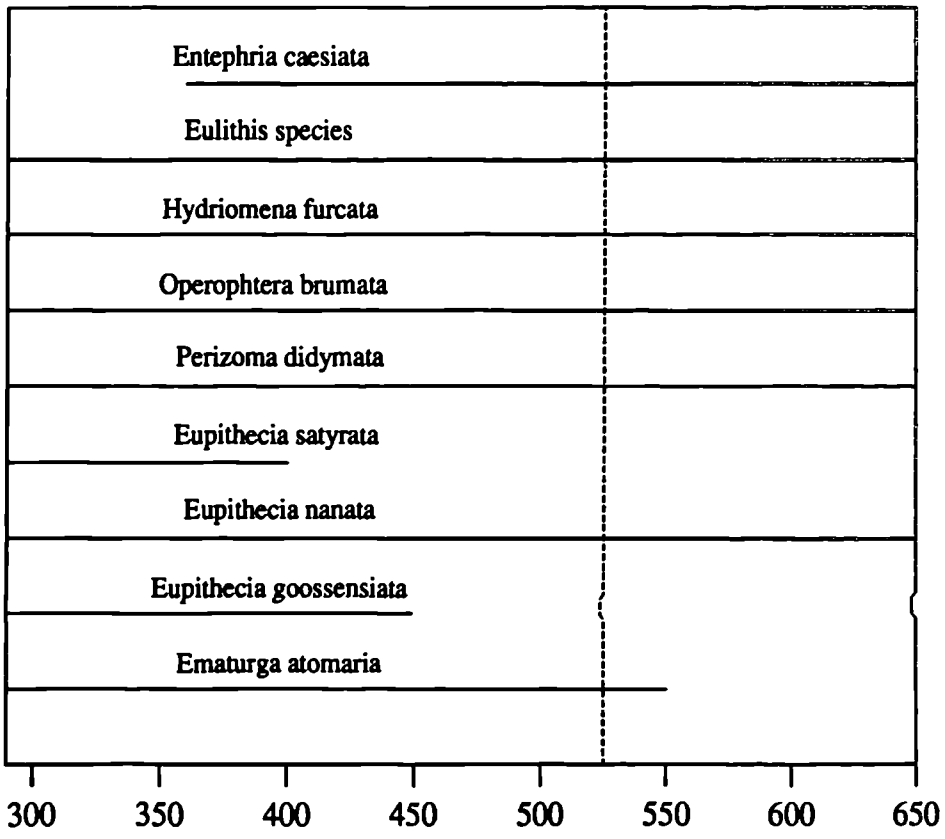

Figure 7.8. (Continued)

absent at the highest altitudes and five species that occurred over the entire altitudinal range. A summary of the altitudinal distributions of the species combined into the three taxonomic groups of Geometridae, Noctuidae and 'Others' is presented in Table 7.3.

The relationship between the altitudinal range and abundance of species is illustrated in Figure 7.9. There is a significant positive correlation between the two (r=0.54, d.f.=23, P<0.01) with an increase in the total altitude range of species that were abundant during the study. However it is likely that the data do not truly represent the relationship between abundance and distribution because more abundant species have a greater probability of being found (Gaston 1991). Therefore a rare but widespread species could have the size of its range underestimated.

It has been suggested that the size of insects is negatively related to their distributional ranges (Gaston and Lawton 1988). In this study, there was no significant relationship between the altitudinal range of a species and its size as measured by either its wingspan (r=-0.006, d.f.=23, P>0.05 Figure 7.10) or head capsule width in the final larval instar (r=-0.296, d.f.=16, P>0.05 Figure 7.10).

7.4. The effect of altitude on the density of the individual macrolepidoptera species

A number of macrolepidopteran species were abundant enough to investigate the effect of altitude on the density of their larvae as estimated by sweep-net, Berlese funnel and quantitative search sampling (Section 3.3).

7.4.1. Methods

The effects of possible predictor variables on the larval density of nine macrolepidopteran species was analysed by stepwise multiple linear regression (Sokal and Rohlf 1981) using SPSS (1990). The dependent variable is the mean number of larvae captured on each sampling occasion. The independent predictor variables offered to the program were:

(a) Days since 1 January was used for those species passing through the entire larval stage within a single calendar year. For the three species that overwintered as larvae, the days were set from 1 July for *Diarsia mendica* and 1 August for *Entephria caesiata* and *Lycophotia porphyrea*.

(b) The altitude of the *Calluna* stand.

(c) The age of the *Calluna* stand.

Other possible predictor variables, such as the height of the *Calluna* and its developmental phase, were strongly correlated with altitude and age and hence excluded because of problems of multicollinearity. It was suspected that the relationship between larval density and the altitude and age of *Calluna* stands might

Table 7.3. The numbers and proportions of macrolepidopteran species in the three taxonomic groups of Geometridae, Noctuidae and 'Others' which were recorded as occurring over the entire altitudinal gradient or only over a lower or upper portion of the gradient. The altitude transect reached from 290m to 650m. The 'Others' group incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. χ^2=6.07, d.f.=4, P>0.05.

Taxonomic group	Altitudinal range		
	Full range	Lower range	Upper range
'Others'	0	6 (100%)	0
Geometridae	3 (33%)	5 (56%)	1 (11%)
Noctuidae	2 (67%)	1 (33%)	0
Total	5 (28%)	12 (67%)	1 (5%)

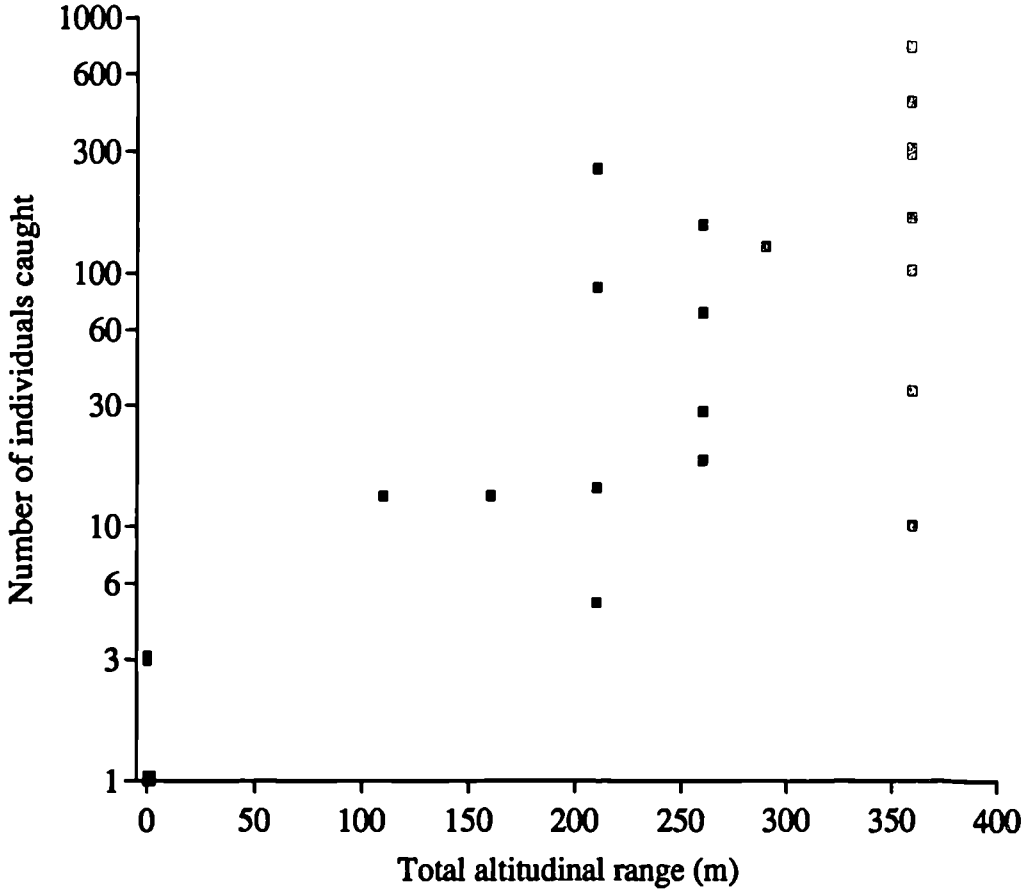

Figure 7.9. The relationship between the altitudinal range and abundance of the macrolepidopteran species found feeding as larvae on *Calluna*. Abundance is the total number of larvae of that species found during the study and altitudinal range is the difference between the lowest and highest altitude at which the species was recorded. Correlation gives r=0.54, d.f.=23, P<0.01. The y-axis is displayed on a $\log_{10}$ scale. Data for the two *Eulithis* species, *E. populata* and *E. testata*, are combined.

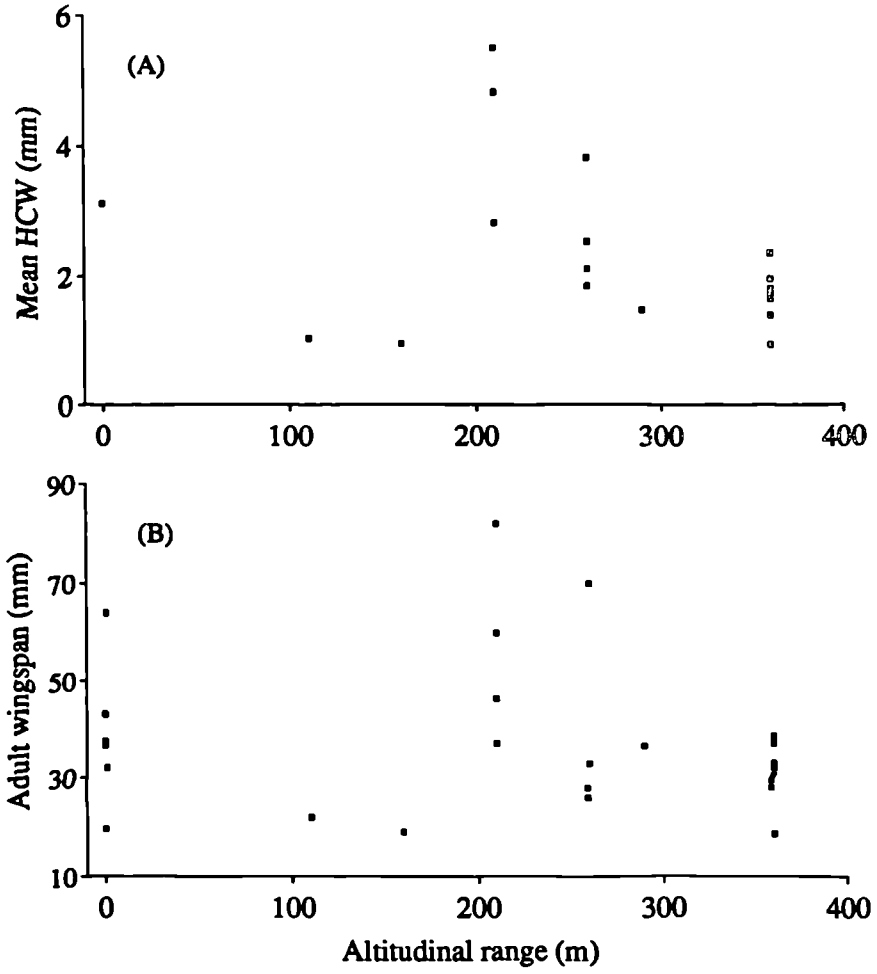

Figure 7.10. The relationship between the altitudinal range and size of the macrolepidopteran species found feeding as larvae on *Calluna* during the course of the study. (A) The size of the species as measured by the width of the head capsule (HCW) in the final larval instar. Data are for the species in Table 6.1 and in addition the species of *Trichiura crataegi*, *Phragmatobia fuliginosa* and *Ceramica pisi*. Correlation: r = -0.296, d.f.=16, P>0.05 (B) The size of the species as measured by the adult wingspan using the middle value of the wingspan range listed by Skinner (1984). The 25 species found during the study are included with the data for the two *Eulithis* species combined. Correlation: r=-0.006, d.f.=23, P>0.05. Altitudinal range is the difference between the lowest and highest altitude at which the species was recorded.

not necessarily be linear. Therefore the square and cube of altitude and age were also 'offered' in the stepwise procedure.

The density estimates for each species were produced by two main sampling techniques, namely Berlese funnel extraction and sweep-net sampling. The exceptions were *Diarsia mendica* and *Eupithecia nanata* which were collected in abundant numbers by one sampling method only, namely Berlese funnel extraction and sweep-net sampling respectively (Table 3.4). There was an additional estimate of density from quantitative search samples for *Hydriomena furcata* and *Macrothylacia rubi*. For the latter species this was the only method of estimating abundance in *Calluna* stands of different ages and altitudes. Sweep-net estimates of density are for a single year (1990) whereas results for Berlese funnel extraction exist for three years (1988-1990). The successive years of the Berlese funnel data have been treated as repeat samples of a single year. Within the entire annual run of samples, a 'window' was set for the samples in which a species could be expected to be caught. The 'windows' were designated by the first and last date on which a species was found by that sampling method with some disparity between the dates for different sampling techniques. Within the 'windows' there were sampling occasions when no larvae of a species were found although known to be available for capture.

During the running of the stepwise multiple regression programme, the probability of *F*-to-enter was set at 0.05 and *F*-to-remove at 0.01. An analysis of variance tested the significance of the Null Hypothesis that there is no linear relationship between the dependent variable and the entire set of independent variables. Individual *t*-tests investigate the significance of the individual independent variables and the significance of their correlation with the dependent variable.

7.4.2. Results

The results of the stepwise multiple linear regressions for each macrolepidoptera species for the relevant sampling methods are given in Table 7.4. It lists those independent variables found to be significant predictors of larval density, the partial regression coefficients (*B*) and their standard errors, the standardised partial regression coefficients (*Beta*), coefficients of determination (R^2), and the results of the *t* and *F* tests described above.

Six of the nine species analysed showed significant changes in density with altitude (Figures 7.11 to 7.17). Two species showed increasing densities at higher altitudes (*Entephria caesiata* and *Diarsia mendica*) and the densities of four species declined with elevated altitude (*Eulithis* species, *Lycophotia porphyrea*, *Macrothylacia rubi* and *Eupithecia nanata*) (Table 7.5). These two groups can be further divided as to whether an altitudinal limit to their distribution was observed within the altitude range. This occurred for one of the increasing species, *E. caesiata*, and one of the

Table 7.4. The results of stepwise multiple linear regressions between the density of the larvae of nine macrolepidoptera species feeding on *Calluna vulgaris* and the altitude(m) and age (years) of the *Calluna* stand and the date of the sampling occasion. Density is measured in terms of numbers of larvae per 10 sweeps for sweep-netting, larvae per 0.25m^2 for Berlese funnel extraction or larvae per five minutes for quantitative searching. Results are shown for all sampling methods by which the density of a species was estimated. *Beta* is the standardised regression coefficient. Values of *t* and *P* give the significance of the individual variables whereas the *F* and *P* values record the significance of the whole equation in explaining R^2 (the coefficient of determination).

Species (sampling method)	Variables & constant	Regression coefficient (*B*)	SE of *B*	*Beta*	R^2	*t*	*P*	*F*	d.f.	*P*
Macrothylacia rubi (search)	1. age^3	3.65×10^{-4}	1.01×10^{-4}	2.065	66%	3.60	0.0013			
	2. altitude	-0.002	0.001	-0.219	72%	-2.31	0.0288			
	3. age^2	-0.007	0.003	-1.303	77%	-2.28	0.0308			
	constant	2.312	0.521			4.43	0.0001	29.79	3, 27	<0.0001
Entephria caesiata (sweep)	1. altitude	2.33×10^{-4}	7.82×10^{-5}	0.364	11%	2.98	0.0042			
	2. days	1.62×10^{-4}	6.56×10^{-5}	0.300	19%	2.47	0.0168			
	constant	0.609	0.039			15.73	<0.0001	6.7	2, 55	0.0025
(Berlese)	1. altitude^2	3.318×10^{-7}	1.11×10^{-7}	0.49	24%	3.00	0.0056			
	constant	0.698	0.029			23.75	<0.0001	9.0	1, 28	0.0056
Hydriomena furcata (search)	1.age	2.280	0.755	8.890	13%	3.02	0.0037			
	2.age^2	-0.108	0.044	-14.997	36%	-2.45	0.0171			
	3.age^3	0.002	7.99×10^{-4}	6.594	40%	2.01	0.0491			
	constant	-12.47	4.01			-3.11	0.0028	13.9	3, 63	<0.0001

Table 7.4. continued.

Species (sampling method)	Variables & constant	Regression coefficient (*B*)	SE of *B*	*Beta*	R^2	*t*	*P*	*F*	d.f.	*P*
Hydriomena furcata (sweep)	1. age	0.025	0.009	0.429	18%	2.64	0.0128			
	constant	0.490	0.158			3.10	0.0041	7.0	1, 31	0.0128
(Berlese)	none									
Eupithecia nanata (sweep)	1. days	0.002	3.29×10^{-4}	0.358	13%	5.52	<0.0001			
	2. altitude	-4.477×10^{-4}	8.56×10^{-5}	-0.344	23%	-5.23	<0.0001			
	3. age^3	-3.071×10^{-6}	1.04×10^{-6}	-0.19	26%	-2.94	0.0037			
	constant	0.543	0.087			6.24	<0.0001	20.9	3, 175	<0.0001
Eulithis spp. (sweep)	1. days	-0.0012	2.241×10^{-4}	-0.506	24%	-5.20	<0.0001			
	2. altitude^2	-3.42×10^{-7}	1.179×10^{-7}	-0.282	32%	-2.90	0.0049			
	constant	1.011	0.047			21.70	<0.0001	17.0	2, 72	<0.0001
(Berlese)	none									
Ematurga atomaria (sweep)	1. days	-0.0013	2.298×10^{-4}	-0.417	17%	-5.84	<0.0001			
	constant	1.035	0.052			19.89	<0.0001	34.1	1, 162	<0.0001

Table 7.4. Continued.

Species (sampling method)	Variables & constant	Regression coefficient (*B*)	SE of *B*	*Beta*	R^2	*t*	*P*	*F*	d.f.	*P*
Ematurga atomaria (Berlese)	none									
Operophtera brumata (sweep & Berlese)	none									
Lycophotia porphyrea (sweep)	1. days	0.00242	3.893×10^{-4}	0.406	13%	6.23	<0.0001			
	2. altitude^3	-7.145×10^{-10}	1.741×10^{-10}	-0.270	18%	-4.10	0.0001			
	3. age^3	-4.172×10^{-6}	1.34×10^{-6}		22%	-3.11	0.0022			
	constant	0.291	0.092			3.17	0.0018	18.1	3, 189	<0.0001
(Berlese)	1. days	(-5.42×10^{-4})	(1.47×10^{-4})	-0.411	17%	-3.67	0.0005			
	constant	0.9099	0.031			29.49	<0.0001	13.5	1, 66	0.0005
Diarsia mendica (sweep)	1. altitude^3	6.885×10^{-10}	1.874×10^{-10}	0.412	17%	3.67	0.0005			
	constant	0.7228	0.033			22.19	<0 0001	13.5	1, 66	0.0005
(Berlese)	none									

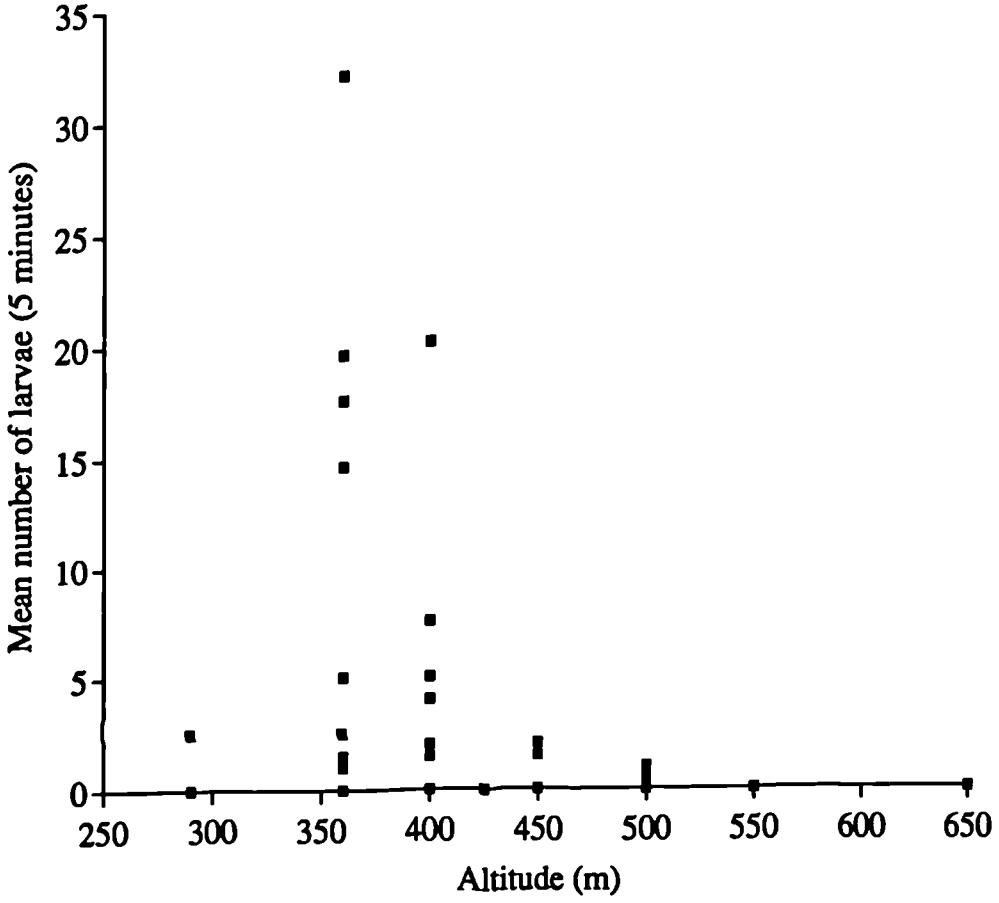

Figure 7.11. The density of the larvae of *Macrothylacia rubi* on *Calluna vulgaris* along an altitude transect from 290 to 650m. The density is the mean number of larvae found on each sampling occasion with two five minute samples taken by quantitative searching. Data are for a total of 38 sampling occasions. As a result of the large number of superimposed points, the graph illustrates only the range of densities found with altitude rather than the complete dataset. Only samples taken within the period from 2 to 13 October when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *M. rubi* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

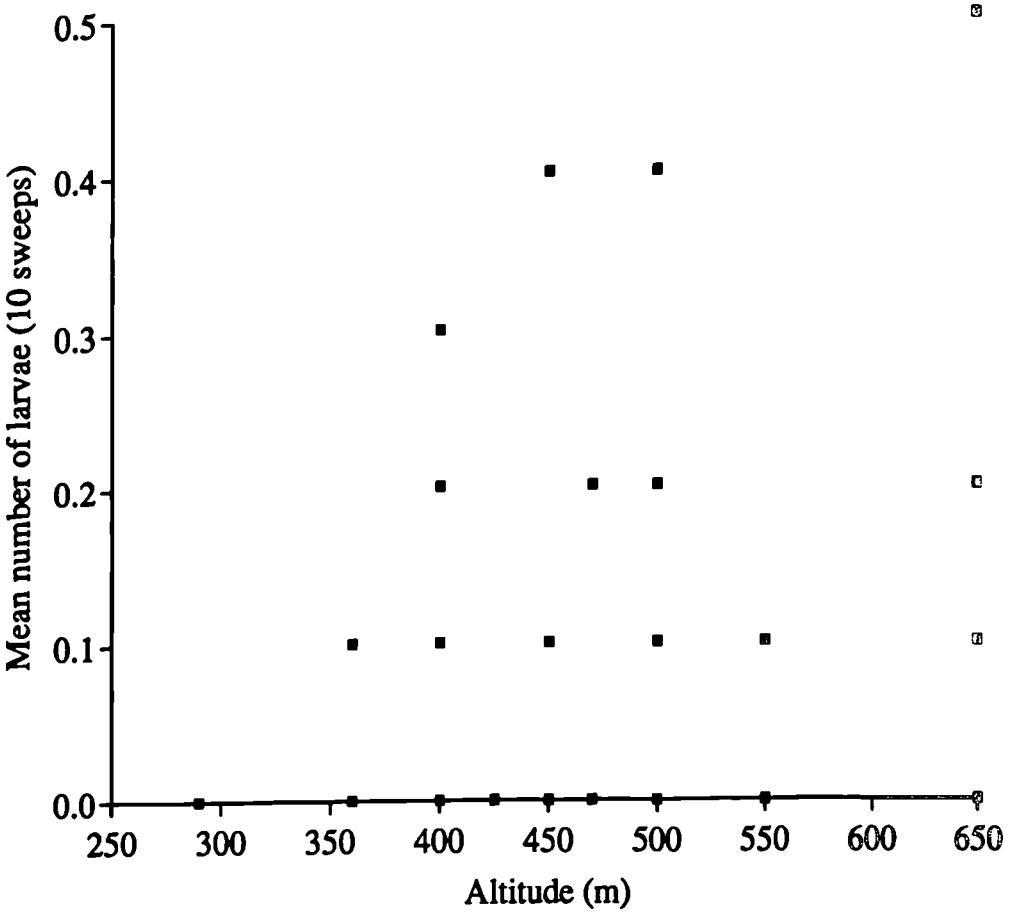

Figure 7.12. The density of the larvae of *Entephria caesiata* on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae found on each sampling occasion with ten samples of ten sweeps of the vegetation taken. Data are for a total of 61 sampling occasions. As a result of the large number of superimposed points, the graph illustrates only the range of densities found with altitude rather than the complete dataset. Only samples taken between 3 May to 14 June and 27 September to 9 October when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *E. caesiata* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

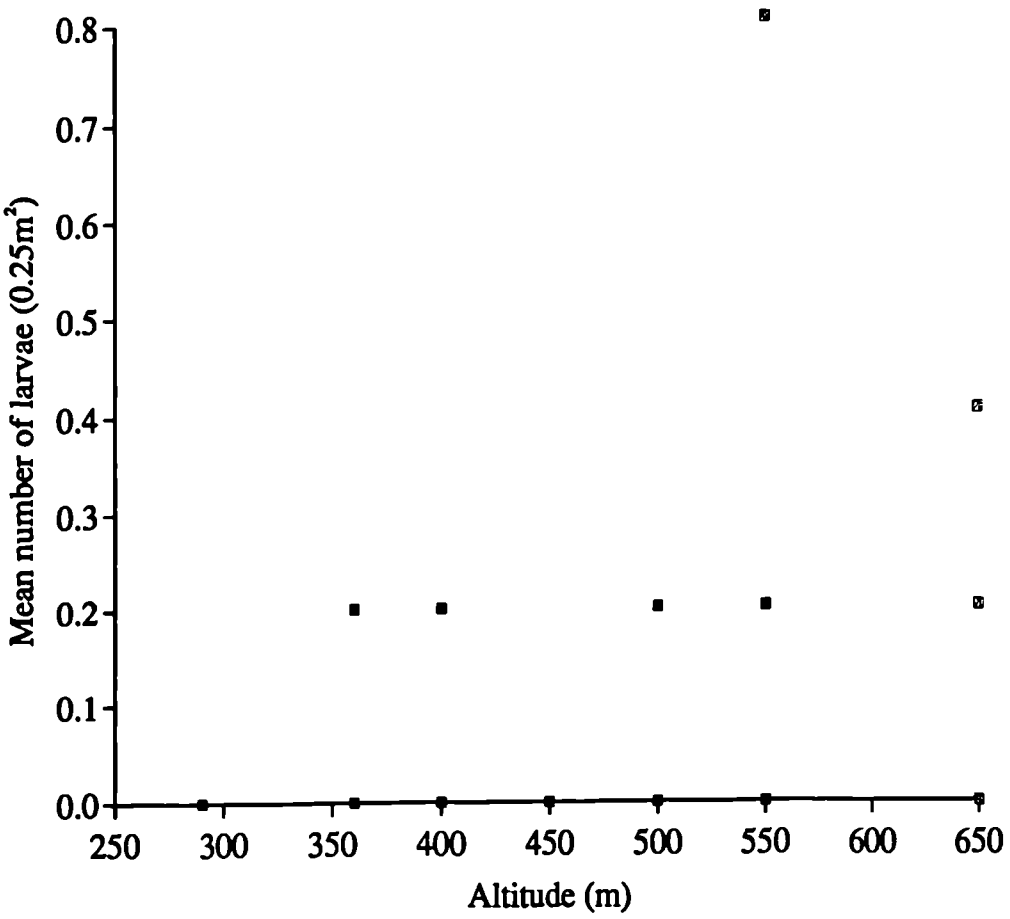

Figure 7.13. The density of the larvae of *Entephria caesiata* on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae on each sampling occasion with five samples of 0.25m^2 area of vegetation taken by Berlese funnel extraction. Data are for a total of 30 sampling occasions. As a result of the large number of superimposed points, the graph illustrates only the range of densities found with altitude rather than the complete dataset. Only samples taken between 20 February to 4 July and on 28 August when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *E. caesiata* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

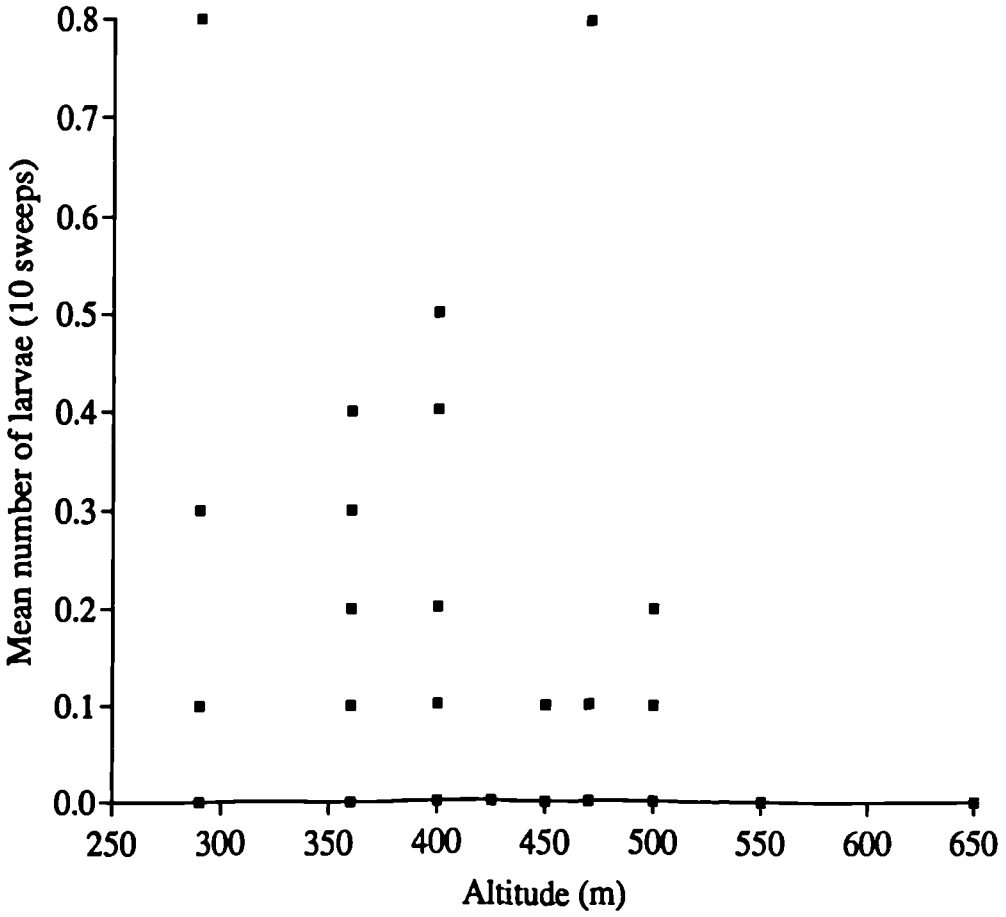

Figure 7.14. The density of the larvae of *Eulithis* species on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae found on each sampling occasion with ten samples of ten sweeps of the vegetation. Data are for a total of 78 sampling occasions. As a result of the large number of superimposed points, the graph only illustrates the range of densities found with altitude rather than the complete dataset. Only samples taken within the period 3 May to 27 July when larvae of this species are available are included. Data for the two *Eulithis* species of *E. populata* and *E. testata* are combined. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *Eulithis* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

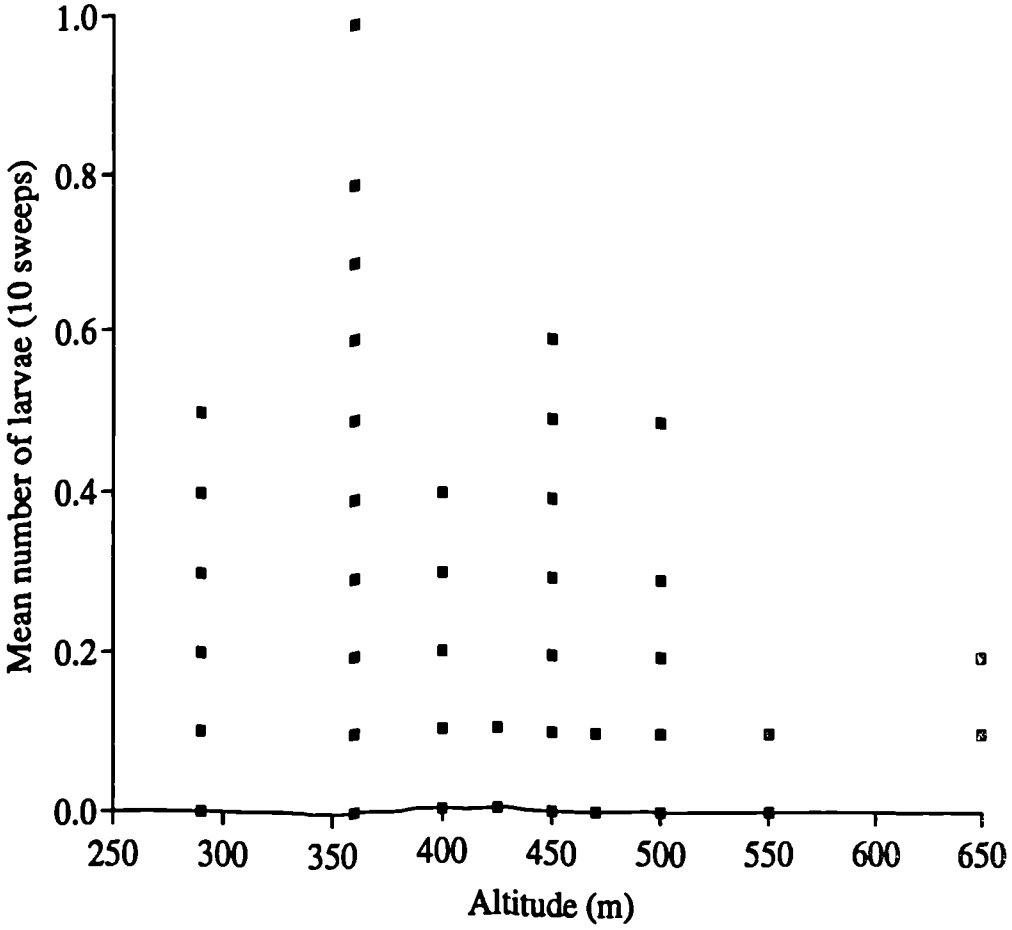

Figure 7.15. The density of the larvae of *Eupithecia nanata* on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae found on each sampling occasion with ten samples of ten sweeps of the vegetation taken. Data are for a total of 179 sampling occasions. As a result of the large number of superimposed points, the graph only illustrates the range of densities found with altitude rather than the complete dataset. Only samples taken within the period 26 July to 6 October when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *E. nanata* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

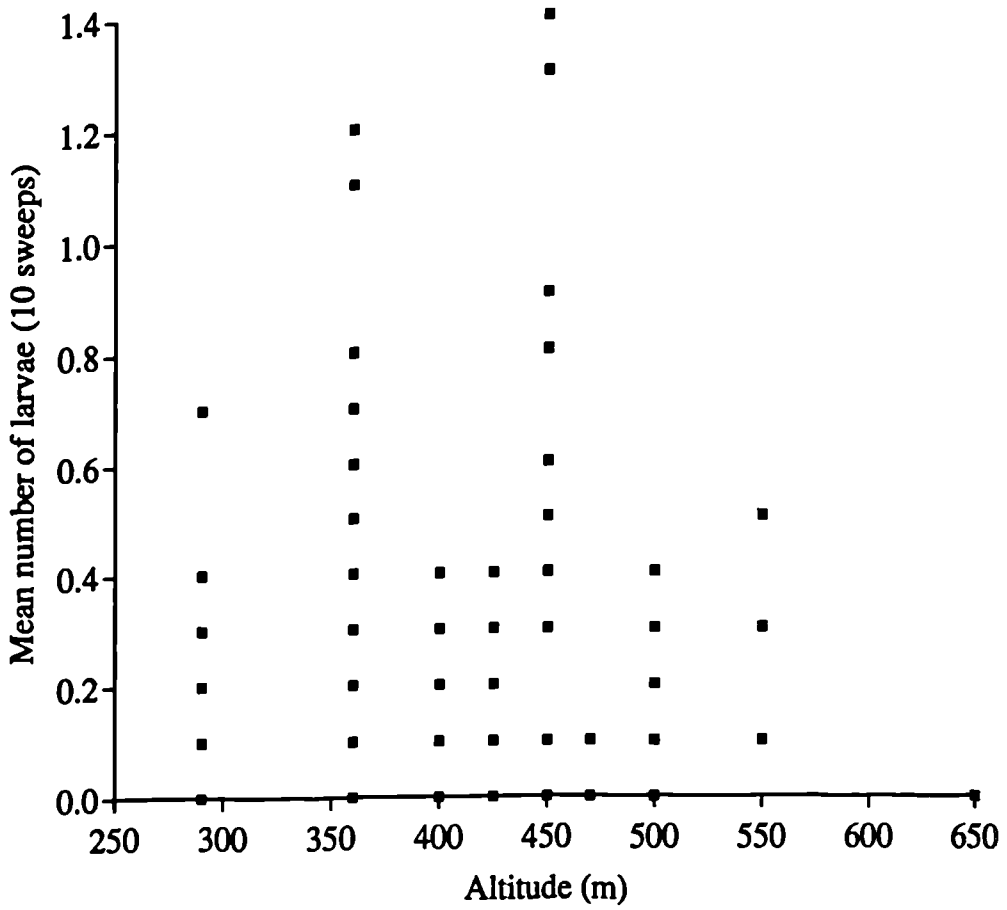

Figure 7.16. The density of the larvae of *Lycophotia porphyrea* on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae found on each sampling occasion with ten samples of ten sweeps of the vegetation. Data are for a total of 193 sampling occasions. As a result of the large number of superimposed points, the graph only illustrates the range of densities found with altitude rather than the complete dataset. Only samples taken within the period 25 July to 9 October when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *L. porphyrea* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

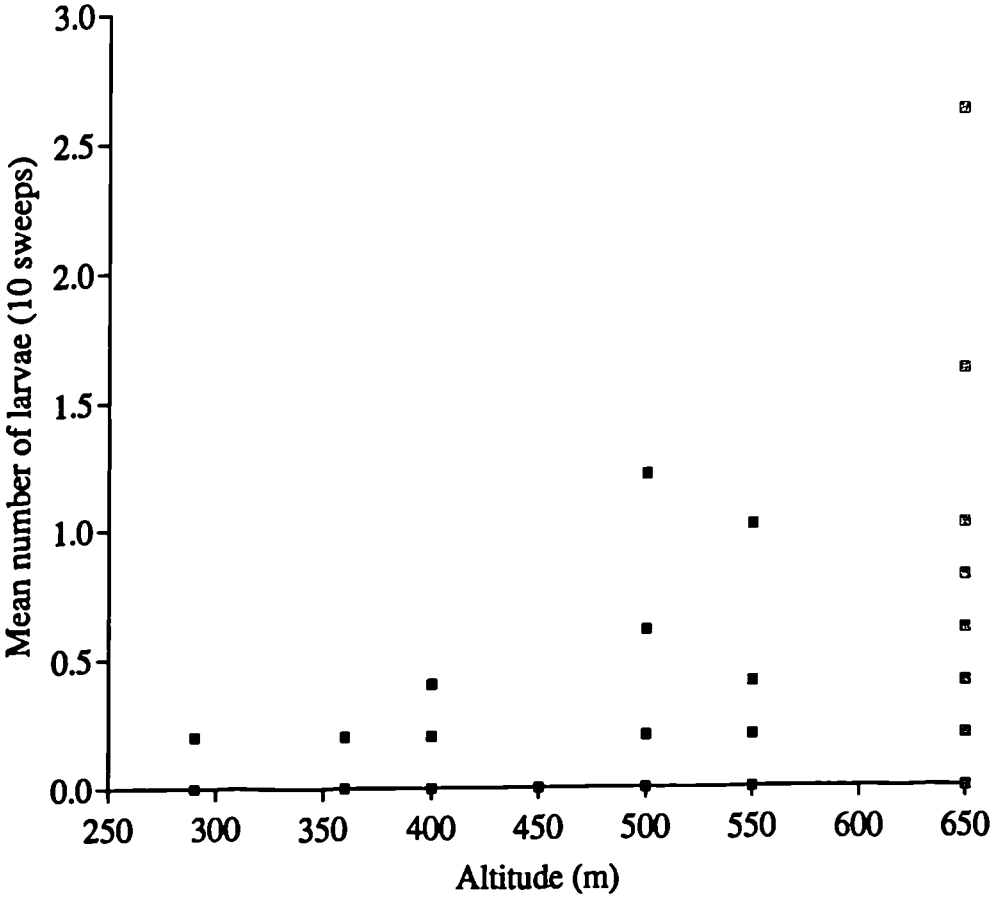

Figure 7.17. The density of the larvae of *Diarsia mendica* on *Calluna vulgaris* along an altitude transect from 290 to 650m. Density is the mean number of larvae found on each sampling occasion with ten samples of ten sweeps of the vegetation. Data are for a total of 68 sampling occasions. As a result of the large number of superimposed points, the graph only illustrates the range of densities found with altitude rather than the complete dataset. Only samples taken within the period 7 February to 28 June and 1 August to 16 November when larvae of this species are available are included. The age of the *Calluna* stands sampled ranged from 8 to 28 years. The multilinear regression equation relating the density of *D. mendica* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

Table 7.5. Summary of the effects of altitude on the macrolepidopteran species feeding as larvae on *Calluna*. Only those six species that showed a significant change in density with altitude are included. The observed altitude range of the species is given and this has been marked with an asterisk where a distinct altitudinal limit to distribution was observed within the altitudinal transect of 290 to 650m. The percentage density change has been calculated using the multiple linear regression equations given in Table 7.4 The altitude at which density reaches zero are the *x*-axis intercepts of these regression lines. Densities have been estimated by three different sampling methods: sweep-netting, Berlese funnel extraction and quantitative searching.

Species & Sampling method	Altitudinal range	Percentage density change per 100m altitude	Altitude at which density equals zero
M. rubi			
search	290-500*	-15%	1037m
E. caesiata			
sweep	360-650*	3%	below sea level
Berlese	360-650*	4%	
Eulithis spp.			
sweep	290-650	-4%	1530m
E. nanata			
sweep	290-650	-6%	2156m
L. porphyrea			
sweep	290-650	-7%	997m
D. mendica			
Berlese	290-650	5%	below sea level

decreasing species, *M. rubi*. The magnitude of the change in density with altitude has been used to calculate the hypothetical altitude limits at which density equals zero if the change is linear across all altitudes (Table 7.5). Of the six species for which altitude had a significant effect on density, three had their densities estimated by two different sampling methods. Of these three species there is only one, *Entephria caesiata*, for which there was a significant effect by both sampling methods. In *Eulithis* and *L. porphyrea* the effect of altitude on density was only significant for density estimated by sweep-netting and not by Berlese funnel extraction. The effect of *Calluna* stand age on macrolepidopteran density is discussed in Chapter 8.

7.5. The effects of altitude on the parasitism of the macrolepidoptera associated with *Calluna vulgaris*

7.5.1. Methods

The level of parasitism was measured as the number of Lepidoptera from which parasites emerged when larvae were reared through the life-cycle in the laboratory. This is likely to lead to an underestimation because of larval and parasitoid mortality before the presence of parasitism is evident. Rather than examine parasitism levels at individual altitudes it has been compared for the lower altitude northern heath habitat ($\lceil$500m) and the higher altitude blanket bog habitat (>500m). The differences between the two habitats have been compared using χ^2 contingency tests.

7.5.2. Results

The overall incidence of parasitism in the macrolepidopteran larval population was 14 ± 1% (Table 7.6). Both for macrolepidoptera overall and for each of the three taxonomic groups of Geometridae, Noctuidae and 'Others' there was no significant difference in parasitism levels on northern heath and blanket bog (Table 7.6).

For the individual macrolepidoptera species there was only two where parasitism levels differed on northern heath and blanket bog (Table 7.7). In *Entephria caesiata* the number of larvae parasitised was significantly higher on northern heath with none of the larvae from the blanket bog habitat parasitised (Figure 7.18). By contrast *Lycophotia porphyrea* showed much higher parasitisation on the blanket bog with 78% of the larvae infested compared to only 18% on the northern heath. In both of these species however sample sizes were low for the number of larvae collected from blanket bog and reared through the life-cycle in the laboratory.

Table 7.6. The parasitism rates of the macrolepidopteran species in the three taxonomic groups of Geometridae, Noctuidae and 'Others' on the two habitats of northern heath (⌠500m) and blanket bog (>500m). Data are for the 26 species found feeding as larvae on *Calluna* during the study. Figures are for parasites emerging during the larval and pupal phase. The figure given for sample size (*n*) is the number of larvae kept in the laboratory under observation for parasitism. The binomial standard errors are given. NS denotes that $P>0.05$.

Taxonomic group	Percentage of larvae parasitised ± SE (*n*)	Percentage of larvae parasitised on habitat ± SE (*n*)		χ^2	*P*
		Northern heath	Blanket bog		
Geometridae	13 ± 1.3 (675)	13 ± 1.3 (648)	4 ± 3.6 (27)	2.3	NS
Noctuidae	16 ± 2.4 (240)	17 ± 2.8 (179)	16 ± 4.7 (61)	0.004	NS
'Others'	20 ± 5.4 (52)	19 ± 5.8 (47)	20 ± 17.9 (5)	0.002	NS
All macro-lepidoptera	14 ± 1.1 (967)	14 ± 1.2 (874)	14 ± 3.6 (93)	0.003	NS

Table 7.7. The percentage of macrolepidopteran species parasitised on the two habitats of northern heath (⌈500m) and blanket bog (>500m). Data are for fourteen of the most abundant macrolepidopteran species found during the study. The figures given are for those parasite species emerging from the host during the larval and pupal stages of the lepidopteran life-cycle. The figure given for sample size (*n*) is the number of larvae kept in the laboratory under observation for parasitism. The binomial standard errors are given. NS denotes that $P>0.05$. Dashes indicate an absence of data either because larvae did not occur on a habitat or because no parasitised larvae were found.

Macrolepidoptera species	Percentage of larvae parasitised ± SE (*n*)	Percentage of larvae parasitised on: Northern heath	Blanket bog	χ^2	*P*
Lasiocampa callunae	0 (10)	-	-	-	-
Macrothylacia rubi	26 ± 10.1 (19)	26 ± 10.1 (19)	-	-	-
Pavonia pavonia	30 ± 10.2 (20)	27 ± 11.5 (15)	20 ± 17.9 (5)	0.09	NS
Entephria caesiata	45 ± 6.7 (55)	49 ± 7.1 (49)	0 (6)	5.21	<0.05
Eulithis species	14 ± 3.3 (110)	15 ± 3.5 (102)	13 ± 11.9 (8)	0.86	NS
Hydriomena furcata	6 ± 1.7 (201)	6 ± 1.7 (192)	0 (9)	0.60	NS
Operophtera brumata	0 (12)	-	-	-	-
Perizoma didymata	23 ± 9.0 (22)	25 ± 9.6 (20)	0 (2)	0.65	NS
Eupithecia satyrata	10 ± 9.5 (10)	10 ± 9.5 (10)	-	-	-
Eupithecia nanata	8 ± 2.2 (146)	8 ± 2.2 (145)	0 (1)	-	-
Eupithecia goossensiata	17 ± 15.3 (6)	17 ± 15.3 (6)	-	-	-
Ematurga atomaria	17 ± 3.8 (98)	17 ± 3.8 (98)	-	-	-
Lycophotia porphyrea	22 ± 3.4 (150)	18 ± 3.2 (141)	78 ± 13 8 (9)	17.3	<0.001
Diarsia mendica	7 ± 3.4 (56)	9 ± 8.6 (11)	7 ± 3.8 (45)	0.08	NS

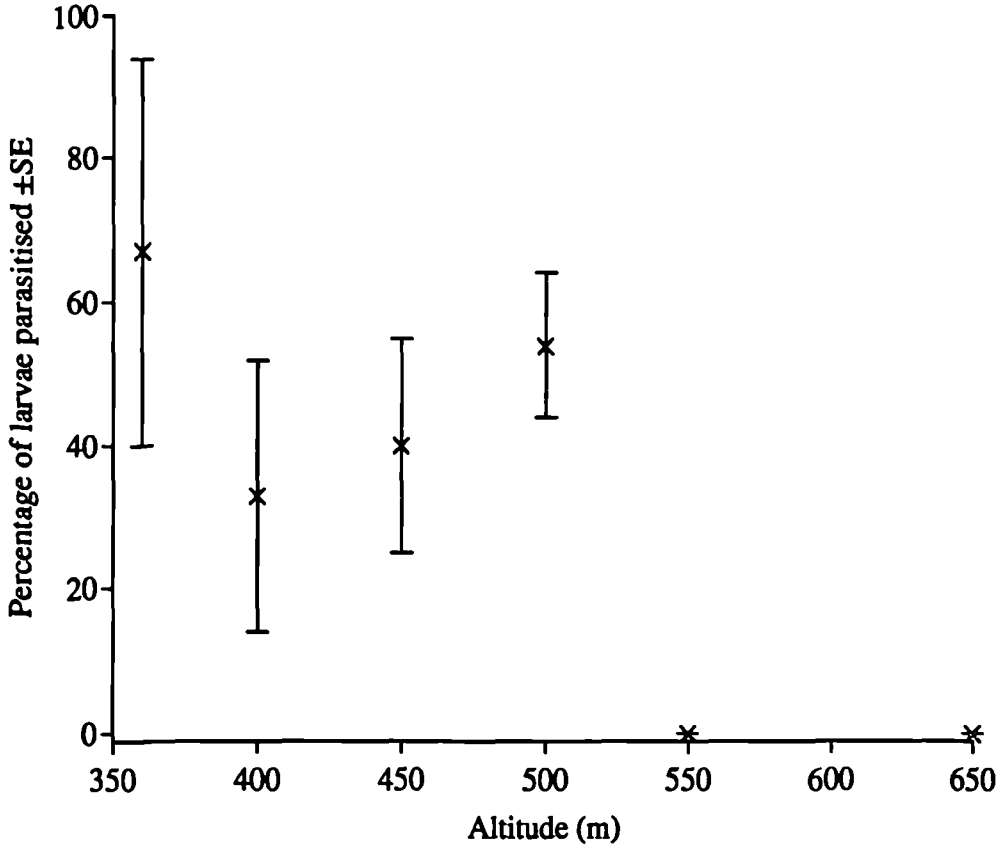

Figure 7.18. The incidence of parasitism of *Entephria caesiata* larvae along an altitudinal transect. Parasitism has been measured as the percentage of larvae from each altitude which were kept in the laboratory that were positively identified as being parasitised. No larvae of this macrolepidopteran species were found at altitudes below 350m.

7.6. Other aspects of the effects of altitude on the macrolepidoptera associated with *Calluna vulgaris*

7.6.1. Introduction and Methods

The feeding specialisations of insect species have been observed as becoming more specialised at higher altitude (Mani 1968). The macrolepidopteran species found in this study have been defined as polyphagous if they feed on families other than the Ericacea, oligophagous if they feed only on species within the Ericacea family and monophagous if they feed on *Erica* and *Calluna*. Information on feeding specialisation of the individual species was collected from the literature search discussed in Chapter Four.

It might be expected that species which pupate in the litter and soil layer would be susceptible to waterlogging on the blanket bog sites, especially during the autumn and winter. This might be especially true when pupation occurs in the ground rather than on the plant. To try and illustrate this effect species have been divided into those that pupate in the ground or aerially on the plant. Information on the overwintering stage and its positioning have been taken from Emmet (1991).

Rather than the effects of altitude on feeding specialisation and overwintering stage being investigated for individual altitudes, they have been compared for the habitats of northern heath and blanket bog. Sample sites of 500m and below are classified as northern heath and above this altitude as blanket bog. Differences between the two habitats have been examined by χ^2 contingency tests.

7.6.2. Results

Of the 26 macrolepidopteran species recorded feeding as larvae on *Calluna* during this study 85% were polyphagous, 15% were monophagous and none were oligophagous. There was no significant difference in the proportions of these three feeding specialisations on the higher altitude blanket bog and lower altitude northern heath habitats (χ^2=0.104, d.f.=1, P>0.05; Table 7.8).

Table 7.9 gives the numbers of species overwintering in each of the three life-cycle stages of eggs, larvae and pupae; with no species overwintering as adults. In the change of habitat from northern heath to higher altitude blanket bog there is an increase in the proportion of species overwintering in the egg stage at the expense of the numbers overwintering as pupae on blanket bog but this difference is not significant (χ^2=0.33, d.f.=2, P>0.05 Table 7.9). There is no significant difference in the incidence of the positioning of pupation depending on whether the species occur on northern heath and blanket bog (χ^2=0.41, d.f.=1, P>0.05 Table 7.10).

Table 7.8. The feeding specialisations of the macrolepidopteran species feeding as larvae on *Calluna vulgaris* on the habitats of northern heath and blanket bog. The numbers and percentages are given for the species that are defined as polyphagous (*i.e.* feeding on families other than the Ericacea) and monophagous (*i.e.* feeding on *Calluna* and *Erica* species only). No species were found that had oligophagous feeding habits (*i.e.* species feeding exclusively on plants within the Ericacea family). Sample sites of 500m and below are classified as northern heath and above this altitude as blanket bog. Information on the feeding specialisation of species has been obtained from the data collected during the literature search discussed in Chapter 4. χ^2=0.10, d.f.=1, P>0.05.

Feeding specialisation	**Habitat**	
	Northern heath	**Blanket bog**
Polyphagous	21 (84%)	12 (80%)
Monophagous	4 (16%)	3 (20%)
Total number of species	25	15

Table 7.9. The numbers and percentages of the macrolepidopteran species found feeding as larvae on *Calluna vulgaris* during this study that overwinter in the egg, larval and pupal stages of the life-cycle. None of the recorded species overwinter as adults. The two biennial species have had both overwintering stages included; *Lasiocampa callunae* overwinters as a egg and larva and *Trichiura crataegi* as a larva and pupa. The information is given for the macrolepidopteran species that were recorded on the two habitats of northern heath and blanket bog. Sample sites of 500m and below are classified as northern heath and above this altitude as blanket bog. Information on the overwintering stage has been obtained from Emmet (1991). χ^2=0.32, d.f.=2, P>0.05.

Overwintering stage	Habitat	
	Northern heath	Blanket bog
Egg	7 (26%)	5 (33%)
Larvae	11 (41%)	6 (40%)
Pupae	9 (33%)	4 (27%)
Number of biennial species	2	0
Total number of species	25	15

Table 7.10. The macrolepidopteran species that were found feeding as larvae on *Calluna vulgaris* and which overwinter in the pupal stage of the life-cycle. Species are divided into those that pupate within the ground and those that position themselves aerially on the plant. Information on the pupation site obtained from Emmet (1991). χ^2=0.41, d.f.=1, P>0.05

Pupation site	Habitat	
	Northern heath	Blanket bog
Aerially	1 (11%)	1 (25%)
Ground	8 (89%)	3 (75%)
Total number of species overwintering as pupae	9	4

7.7. Discussion

The species richness of macrolepidoptera associated with *Calluna* on moorlands declines with altitude to the extent of a loss of three species for every 100m rise in altitude. The result is in consensus with Coulson (1988) who found a significant correlation between altitude and the number of Lepidoptera species found on lowland mires, northern heath and blanket bog (r=-0.49, P<0.05). The strength of the decline in species richness with altitude may be surprising considering the relatively small altitudinal gradient over which this study took place. The altitude range was 300m which compares to the approximate 1000m transects used in some studies (Hagvar 1976; Otto and Svensson 1982), although it is similar in scale to other studies done in Britain (Lawton *et al.* 1987). The optimum species richness was at the lowest altitude on the transect at 290m and how this pattern develops at lower altitudes is open to conjecture. Species richness may continue to increase with the maximum species richness being found at sea level or alternatively it may decrease. In Britain it would have been difficult to increase the altitude range used, both because *Calluna* has a natural upper altitudinal limit and because *Calluna* dominated habitats at lower altitudes in northern England have been seriously disturbed by man. It would have been interesting with hindsight to have included *Calluna* growing in wet peat on oligotrophic mires at sea-level. This would have separated the effects of the severer climate at higher altitudes from the change to the wetter peat habitats of blanket bog.

The findings of Lawton *et al.* (1987) led them to conclude that results based on a single altitudinal transect are likely to be misleading. In their investigation of the species richness of herbivorous insects associated with bracken, all effects of altitude became negligible when a large number of sites in a variety of geographically locations were examined, as opposed to the initial more localised study. In an ideal situation the results presented in this study would have been replicated in other parts of Britain and the changes in the rate of loss of species could then have been compared with geographical location in Britain.

The decline of moth species richness along an altitude gradient can be compared to a similar decline with latitude in Britain (Turner *et al.* 1987). In order to try and compare the rates of change of species richness with altitude and latitude, a conversion factor can be used of a 305m increase in altitude being equal to 4° latitude (Fernandes and Price 1988) or 1° latitude being equal to a 122m altitude rise (Hopkins 1938 quoted by Danks 1978). Turner *et al.*'s decline of -0.385 species per 10km north in Britain translates to a loss of 5.6 or 3.5 species (depending on the conversion used) per 100m rise in altitude as compared to the 3.2 species loss per 100m in this study. The decline in the species richness of Lepidoptera with latitude in Britain has been linked with climatic variables such as the decline in the hours of sunshine. The similarity in the rates of decline of lepidopteran species richness with altitude and latitude suggest

that climatic changes with altitude may be the most important determinant of species richness decline with altitude.

The altitudinal and latitudinal ranges of species are generally correlated (Hagvar 1976; Walker and Matthews 1989). Unfortunately, it has not been possible to discuss this aspect as there was little available information on the latitudinal distributions of the individual macrolepidopteran species.

An interesting discovery was the different reactions to altitude exhibited by the separate taxonomic groups of the Lepidoptera. There was no significant change in the number of Noctuidae species found with varying altitude whereas the other two taxonomic groups displayed significant declines, although at different rates with one Geometridae and two 'Others' family species lost for every 100m rise in altitude. The reasons for this divergence can only be tentative since there is little information about the ecological differences that exist between different moth families. It has been shown in Chapter 5 that the families vary in some of their life history characteristics, such as their overwintering phase. The Geometridae and Noctuidae vary in their size (Table 6.4) and robustness, with noctuids being larger species with a tendency to be nocturnal. From this it might be possible to hypothesize that noctuid adults are better able to cope with the strong winds and heavy rainfall associated with higher altitudes. It is difficult to defend this reasoning however, since the 'Others' taxonomic group that consists of larger species showed a larger decline with altitude. There may be differences in the thermoregulatory abilities of the three taxonomic groups. There is some evidence that noctuids (and other families such as arctiids) are better able to keep body temperature independent of ambient temperature compared to the geometrids (Bartholomew and Heinrich 1973). There may be other physiological reasons for the ability of individual taxonomic groups and species to be better adapted to different altitudes.

Only 28% of the 18 species that were recorded at more than one altitude, occurred over the entire altitude gradient. The majority of species had a distribution restricted at the higher altitudes and a single species had a distribution limited to higher altitudes. Of the seven species recorded at a single altitude, six were found at the lowest altitude site at 290m and one at 650m. There was an absence of endemic high altitude species although two species showed higher densities at elevated altitudes. The distribution of *Xestia alpicola* is restricted to high altitude sites in northern England and Scotland including Moor House (Withers 1974). It may possibly feed on *Calluna* but it was not recorded during this study. The general absence of species restricted to high altitudes has been noted in previous studies of invertebrates along altitude gradients (Greenslade 1968; Otto and Svensson 1982; Ichijo *et al.* 1982; Coulson and Butterfield 1986). For the Lepidoptera recorded in this study, the changes in abundance and distributions would suggest that the majority are lowland in origin with only the two species which showed higher densities at high altitudes, being montane. Of the two species exhibiting higher densities at higher altitudes, one

Entephria caesiata, feeds only on *Calluna* and *Erica* species. By contrast the other species, *Diarsia mendica*, is widely polyphagous. It is possible therefore that the higher densities of this species at higher altitudes results from the absence of alternative host plant species that are utilised in preference to *Calluna* at the lower altitude sites. This suggestion is supported by the fact that abundant numbers of adults of this species were captured in the light trap at 290m. There is little corroborative evidence from the literature of an altitude effect on this species. Dunn and Parrack (1987) record it as occurring on open moorland and ranging down to coastal sand-dunes. The higher altitude distribution of *Entephria caesiata* accords with the generalised descriptions of its habitats in the literature; described as "distributed on the higher bogs and moors" (Fowles 1988) and "common on the higher moorlands" (Dunn and Parrack 1987). The multiple regression equation for this species, suggests that the species would only disappear from the altitude gradient well below sea-level. However the actual absence/presence data for this species during the study suggests that the lower altitude limit is reached somewhat sooner at about 200-300m. Two species, *Hydriomena furcata* and *Ematurga atomaria*, showed no significant effect of altitude on density as analysed by multiple linear regression yet they were absent or very scarce on blanket bog habitats.

The distributions of insect species along altitude gradients tend to be temporally labile (Whittaker 1965; Randall 1982b). There is circumstantial evidence that this occurs for some of the species recorded in this study. For example, *Lasiocampa callunae* was not recorded at Moor House during this study but was previously recorded in large numbers at this location during 1965-1975 (J. C. Coulson pers. comm.). The mobility of the lepidopteran adult phase means that immigration, establishment and extinction at different altitudes could occur on relatively short time scales. There was a significant positive correlation between the abundance of species during the study and their perceived altitudinal distributions. This is consistent with the fact that the geographical distributions of related species are generally known to be positively correlated with average abundance (Hanski 1982; Brown 1984). This has been explained in terms of generalist species being able to use a wide variety of resources and spatial sites and having populations which are more dense locally and more widely distributed geographically than those of related species with narrower requirements (Brown 1984).

There were no macrolepidopteran species for which both upper and lower altitudinal limits occurred within the altitudinal gradient. Where an altitudinal limit did occur, densities generally declined towards this boundary, *e.g. Entephria caesiata*.

There is evidence that insect species find a refuge from parasitism at higher altitudes (Whittaker 1965,71; Hagvar 1976; Randall 1982a). This is thought to be due to a number of reasons (Randall 1982a). The searching and oviposition rates of parasitic Hymenoptera are reduced by low temperatures and other climatic variables, there are

problems with synchronising parasitoid development with that of the host and the diversity of possible hosts for polyphagous species decreases at higher altitudes. With the exception of two individual species there appeared to be no difference in parasitism rates of macrolepidoptera on northern heath and blanket bog. Sample sizes were small for individual species but for macrolepidoptera overall, samples sizes seem adequate to illustrate any disparities that might exist between habitats. Parasitism levels are possibly underestimated because of the method by which larvae were kept in the laboratory, however there no evident reasons as to why this should differential affect larvae collected from one or other of the two habitats.

Coulson and Whittaker (1978) suggest that insects at higher altitudes show an increased tendency to overwinter in the egg stage. Of the macrolepidopteran fauna associated with *Calluna*, no significant change was found in the phase of overwintering on northern heath and blanket bog. The egg and larval stage are thought to be more resistant to severe climates than the pupal phase (Section 5.7). It is difficult to envisage species of Lepidoptera overwintering in the extremely waterlogged ground of blanket bog, and high humidity levels are known to cause high mortality in subterranean pupae (Leather 1984) and reduce the ability of species to supercool (Somme 1982). Despite this, there was no significant change in the incidence of species pupating aerially on the plant or in the ground, between northern heath and blanket bog. It is possible that to find differences in overwintering phase with altitude a larger set of species need to be investigated and greater contrasts need to be found than between northern heath and blanket bog. The information as to whether species pupate in the ground or aerially on the plant has mainly been based on reports from the literature. The possibility remains therefore that the populations on blanket bog behave differently to the more widespread and reported populations of the species.

Chapter Eight

The effects of *Calluna* stand age on the macrolepidopteran herbivores associated with the plant

8.1. Introduction

As plants mature they undergo alterations in their structure and composition that affect the insect herbivores associated with them. These transformations incorporate both modifications to the individual plants such as their architectural diversity and nutritional quality, and to the surrounding habitat, for example the floristic diversity, habitat succession, and plant density. *Calluna* is a woody evergreen perennial with individual plants living up to an age of 40 years. The following discussion is therefore written from the perspective of such a plant life history rather than that of annual plants.

Architectural diversity (Lawton and Schröder 1977, 1978) comprises changes in both the size and variety of plant structures (Southwood *et al.* 1979; Lawton 1983). There are many studies that have related the species richness of insects associated with different species of plants, to the architectural diversity of the plants (*e.g.* Lawton and Schröder 1977, 1978; Moran 1980; Neuvonen and Niemela 1981). Fewer studies however, have documented the changes in architectural diversity of a single plant species as it grows and associated it with changes in its insect fauna (ref. in Lawton 1983). In a similar way, although many studies have investigated the effect of leaf maturity and seasonal variations in leaf quality on insect herbivores (*e.g.* Raupp and Denno 1983; Meyer and Montgomery 1987; Stamp and Bowers 1990), there are few studies relating any changes to the leaf quality of different aged plants. There may also be variations in the production and standing crop of maturing plants that alter the quantity of food available for herbivores.

The modifications that occur in the habitat around a plant as it matures are likely to be as important to any insect herbivores as the changes to the individual plant, although they are perhaps less easy to predict. As a plant matures there are likely to be changes in its density and the overall floristic diversity of the habitat. How this affects the insect herbivores is likely to be partially dependent on how specialised they are in their feeding habits (Kareiva 1982; Jones 1991). There may be changes in the natural enemy fauna which are themselves likely to be affected by the habitat.

Plants of different ages are therefore likely to be of varying quality for herbivores. Insects are able to distinguish between plants of varying levels of quality (Rausher 1983; Jones 1991), although this does not mean that female oviposition behaviour is always optimal for larval fitness and survival (Singer 1984). For Lepidoptera species that have immature stages that do not disperse, it is the egg laying behaviour of the adult females which will primarily determine the patterns of host plant use (Rausher 1979; Stanton and Cook 1984; Thompson 1988).

The age progression of *Calluna vulgaris* and the changes associated with it are relatively well studied (Barclay-Estrup and Gimingham 1969; Barclay-Estrup 1970, 1971). Differences in the morphology and behaviour of maturing *Calluna* plants have been used to divide the age gradient into the pioneer, building, mature and degenerate phases (Watt 1955). The fact that many areas dominated by this plant are managed by burning means that this age classification can be applied to whole stands as well as individual plants. Some of the changes that are likely to be important for insect herbivores as the *Calluna* stands pass through the age gradient are summarised in Table 8.1. The overall pattern is of increased *Calluna* plant dominance up to the mature phase followed by decline in the degenerate phase. One of the most important alterations is in the nutritional quality of the *Calluna* plants. This determines its quality as food for red grouse and sheep, which form the main vertebrate herbivores of *Calluna* in the moorlands of the northern Pennines. The fact that the heather is most nutritious for these herbivores in the pioneer and early building phases (Miller and Miles 1969; Miller 1979) primarily dicates the burning cycle of 10-12 years that maximises the extent of these areas.

Miller (1974) recorded a greater diversity of invertebrates in pioneer and degenerate stands of *Calluna* compared to those of building and mature age. This finding was attributed to the greater homogeneity and lesser floristic diversity associated with the building and mature phases. However those invertebrates families, such as the Lepidoptera, that feed on unlignified green shoots and sap tended to be best represented in the building and mature aged stands where there was the greatest biomass of green foliage (Gimingham 1985). Barclay-Estrup (1974) studied the invertebrate fauna associated with individual plants of the different phases rather than complete stands. Again the greatest numerical abundance of invertebrates were recorded on plants of pioneer and degenerate age although there were exceptions for some invertebrate groups such as the millipedes. The species richness on different aged plants was only investigated for the spiders. Of these, there was a greater species richness in the pioneer and degenerate phases presumably as a consequence of prey availability and a preferred microenvironment. As a result of previous work it might therefore be anticipated that the Lepidoptera are likely to be most diverse in the pioneer and degenerate aged stands but perhaps most abundant in those of building and mature age.

Table 8.1. Typical changes of variables likely to affect lepidopteran herbivores in *Calluna vulgaris* stands as the plants progress through the four age life-history phases. Information has been compiled from Barclay-Estrup and Gimingham (1969), Barclay-Estrup (1970, 1971) and Gimingham (1972).

Feature	*Calluna* life-history phase			
	Pioneer	Building	Mature	Degenerate
Age (years)	3-6	6-15	15-20/25	20/25+
Cover (percentage)	10	90	75	40
Mean height (cm)	24	52	63	55
Net production of shoots (g m^{-2}/yr)	148	442	364	141
Biomass (g m^{-2})	287	1508	1924	1043
Plant diversity *e.g.* Shannon's H	3.4	3.0	2.6	3.5
Temperature	→	less subject to extremes	→	as pioneer
Illumination (percentage)	75	2	17-20	75
Nitrogen and phosphorus levels in current year's shoots (mg per 100g dry matter)	conc. decline by 45% in the first 4 years. N (yr 1) =1.8 P (yr 1) =20	→	relatively constant	→

8.2. General methods

None of the sample sites present on blanket bog habitats were included in the investigation of *Calluna* stand age on lepidopteran herbivores. The absence of burning on this habitat means that in contrast to the stands on northern heath, the patches of the plant tend not to be even aged (Section 2.1).

The differences in the macrolepidopteran herbivores have generally been compared and contrasted between *Calluna* stands of different phases rather than ages. This is a consequence of the number of stands of a particular age being low and of phase rather than age being more descriptive of *Calluna* stands. This is because the growth form of the *Calluna* stand is dependent to some extent not just on age but also on the environmental conditions. Of the four life-history phases of *Calluna* only three, the building, mature and degenerate have been sampled thoroughly. An examination of the pioneer phase was omitted from the study as a result of difficulties with adequately sampling it with the chosen sampling techniques.

8.3. The species richness of macrolepidoptera in *Calluna vulgaris* stands of the different life-history phases

The number of species found in each of the three *Calluna* life-history phases has been determined. The full complement of 25 species that were recorded on the northern heath habitat were not present in any of the three developmental phases. Overall 24, 20 and 20 species were recorded respectively in stands of building, mature and degenerate phases (Table 8.2) with these differences not being statistically significant (χ^2=0.40, d.f.=2, P>0.05). Of the 25 species recorded on northern heath, 18 were found in each of the three phases, one species (*Aporophyla lueneburgensis*) was found in the pioneer and mature phase but not the degenerate, and five species were confined to a single developmental phase. Of the five species unique to an individual phase, four were found in the building phase (*Arctia caja, Ceramica pisi, Orgyia antiqua* and *Eupithecia assimilata*) and one in the degenerate phase (*Xestia agathina*) with no species exclusive to the mature phase (χ^2=4.0, d.f.=2, P>0.05).

There was no significant difference in the mean number of species recorded in stands of the three developmental phases ($F_{[2,17]}$=0.55, P>0.05). A lower mean number of species was recorded in the building phase (7.6 ± 2.1) compared to the mature (10.3 ± 1.7) and degenerate (10.7 ± 3.2) phases (Table 8.2). The higher total number of species found in building phased stands is probably due to the fact that 10 stands of the building phase were sampled as opposed to seven mature aged and three degenerate aged stands.

Of the five species unique to a single developmental phase, four were represented by only one individual and none by more than five individuals. All of

Table 8.2. The number of species of macrolepidoptera recorded in *Calluna vulgaris* stands of the building, mature and degenerate phases of the life-history. There is a total of 25 species since one species, *Noctua comes*, was only recorded on blanket bog habitats. In addition to the total number of species found, the mean number of species found in stands of each phase are given.

	Phase of *Calluna* life-history		
	Building	**Mature**	**Degenerate**
Total number of species found in phase	24	20	20
As a percentage of 25 species found overall	96%	80%	80%
Total number of species found in all three phases	19	19	19
Total number of species found in this and one other phase	1	1	0
Total number of species unique to that phase	4	0	1
Mean number of species found ± SE (*n*)	7.6 ± 2.15 (10)	10.3 ± 1.75 (7)	10.7 ± 3.18 (3)

these five species were recorded at the single study area of North Plantation, which was the lowest altitude site at 290m. Figure 8.1 illustrates the relationship between the frequency with which a species was captured and the number of developmental phases in which it was recorded. It indicates that the confinement of certain species to single phases is probably a consequence of their rarity and/or insufficient sampling.

8.4. The abundance of macrolepidoptera in different ages and phases of *Calluna vulgaris* stands

8.4.1. Methods

Multiple linear regression was used to relate the mean larval densities of individual macrolepidoptera species on each sampling occasion to the altitude and age of the *Calluna* stand and the date of the sampling occasion. The specific methodology for this analysis is discussed in section 7.2. Additional analysis was applied to the densities of *Hydriomena furcata* larvae as estimated by quantitative search sampling. Non-linear regression was applied using SPSS (1990) as multiple linear regression gave a poor fit to the data.

A comparison of the mean larval densities in *Calluna* stands of the different developmental phases rather than ages was also undertaken. These data were highly skewed due to the large number of samples in which no larvae were present. The frequency distributions of the data conform to Poisson and negative binomial series and it is not possible to normalise the data by transformation. For this reason analysis of variance could not be used to test for differences in density between *Calluna* phases, and hence a non-parametric approach using Kruskal-Wallis tests has been utilised.

8.4.2. The abundance of macrolepidoptera and the individual taxonomic groups in *Calluna vulgaris* stands of the different life-history phases

There is a significant difference in the densities of macrolepidopteran larvae in the three *Calluna* phases as measured by sweep-net sampling (Table 8.3 and 8.4). The densities were significantly higher in mature aged stands compared to those of degenerate age. There were no significant differences in macrolepidopteran larval density between stands of the various *Calluna* life history phases when density was estimated by Berlese funnel extraction.

At the level of the individual taxonomic groups of the macrolepidoptera, the Noctuidae show an overall significant difference in larval density between the building/mature and degenerate phases. There are no significant differences in larval density of Geometridae and 'Others' in different phased stands (Table 8.3 and 8.4).

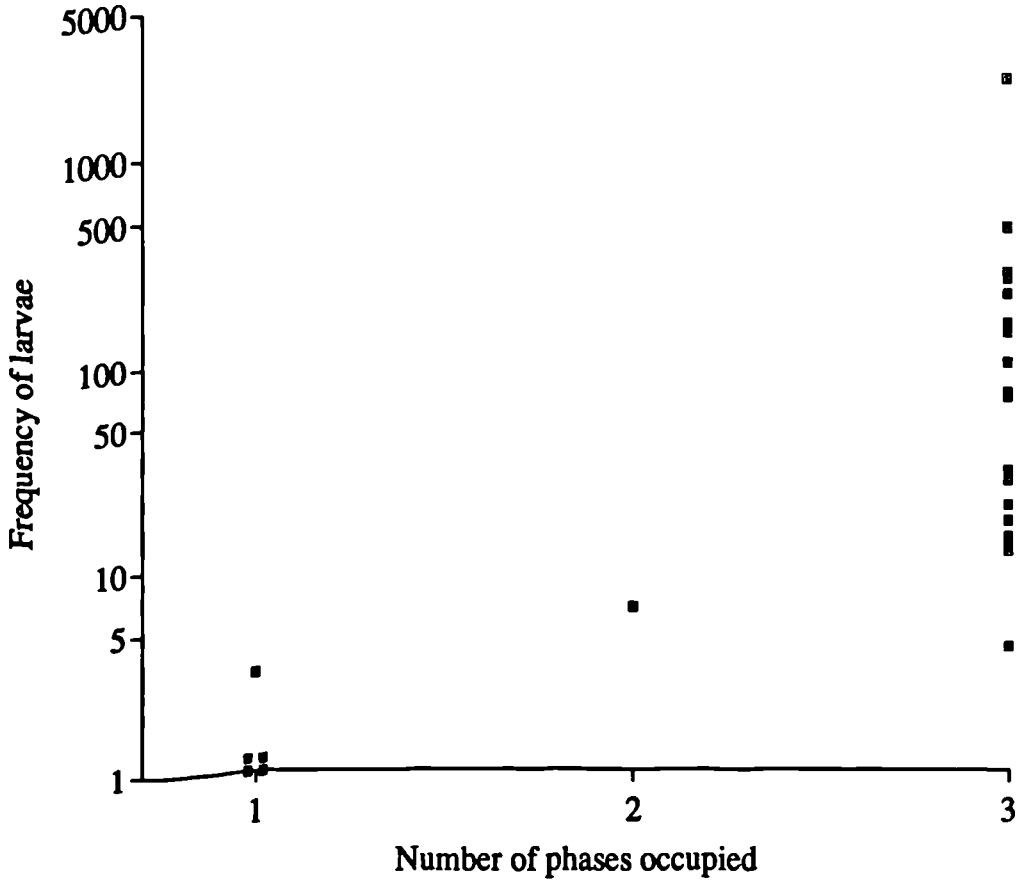

Figure 8.1. The relationship between the abundance of the macrolepidopteran species and the number of the stages of the *Calluna* life-history in which the larvae were recorded. The three phases of the *Calluna* life-history are the building, mature and degenerate as defined by Watt (1955). Abundance has been measured as the total number of larvae of that species found during the three years of the study. Data are for 24 species of macrolepidoptera as one species (*N. comes*) was not found as a larvae on *Calluna* on northern heath habitats and information for the two *Eulithis* species, *E. testata* and *E. populata* has been combined. The *y*-axis is shown on a $\log_{10}$ scale. Correlation gives: r=0.208, d.f.=22, P>0.05.

Table 8.3. The abundances of macrolepidopteran larvae of the three taxonomic groups of Geometridae, Noctuidae and 'Others' and all groups combined, in *Calluna* stands of three different life-history phases. The *Calluna* life-history phases are the building, mature and degenerate as defined by Watt (1955). The density of the larvae have been estimated by the two different sampling techniques of sweep-netting and Berlese funnel extraction. Density is therefore either the mean number of larvae ± SE per 10 sweeps (sweep-net) or per 0.25m^2 area of vegetation sampled (Berlese funnel). The 'Others' taxonomic group comprises the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. An asterisk denotes a significant difference in density compared to the phase succeeding it (Table 8.4). An asterisk after the density in the degenerate phase indicates a significant difference compared to the density in the building phase.

Taxonomic group	Sampling method	Mean larval density ± SE (*n*) Building	Mature	Degenerate
All				
	sweep	0.46 ± 0.026 (1060)	0.64 ± 0.050 * (960)	0.36 ± 0.039 (340)
	Berlese	0.16 ± 0.031 (225)	0.11 ± 0.025 (310)	0.19 ± 0.037 (230)
Geometridae				
	sweep	0.25 ± 0.0.019 (1060)	0.44 ± 0.048 (960)	0.29 ± 0.037 (330)
	Berlese	0.25 ± 0.082 (215)	0.69 ± 0.172 (325)	0.15 ± 0.040 (205)
Noctuidae				
	sweep	0.17 ± 0.015 (1060)	0.16 ± 0.015 * (960)	0.05 ± 0.012 * (330)
	Berlese	0.16 ± 0.031 (225)	0.11 ± 0.025 * (310)	0.20 ± 0.0.038 (230)
'Others'				
	sweep	0.011 ± 0.005 (1060)	0.013 ± 0.004 (960)	0.015 ± 0.006 (340)

Table 8.4. The significance of the differences in the mean larval densities in the three taxonomic groups of Geometridae, Noctuidae and 'Others' and for all groups combined, in the different stages of the *Calluna* life-history as given in Table 8.3. The significance of the differences have been examined by Kruskal Wallis ANOVA tests. The 'Others' taxonomic group comprises the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. NS denotes a non significant result, *i.e.* $P>0.05$.

Taxonomic group	Sampling method	*Calluna* life history phases for which densities compared							
		All phases		Building/ mature		Mature/ degenerate		Building/ degenerate	
		χ^2	*P*	χ^2	*P*	χ^2	*P*	χ^2	*P*
All macro-lepidoptera	sweep	6.83	<0.05	1.30	NS	6.69	<0.01	3.52	NS
	Berlese	0.53	NS	0.30	NS	0.04	NS	0.45	NS
Geometridae	sweep	2.49	NS	1.57	NS	0.16	NS	1.82	NS
	Berlese	2.46	NS	0.40	NS	2.42	NS	0.85	NS
Noctuidae	sweep	20.55	<0.001	0.59	NS	16.50	<0.001	20.73	<0.001
	Berlese	4.62	NS	2.65	NS	4.21	<0.05	0.17	NS
'Others'	sweep	1.23	NS	0.78	NS	0.09	NS	1.00	NS

8.4.3. The abundance of the individual macrolepidopteran species in *Calluna vulgaris* stands of different ages and life-history phases

Multiple linear regression (MLR) analysis (Section 7.2) showed age to have a significant effect on the densities of four species, namely *M. rubi, H. furcata, E. nanata* and *L. porphyrea* (Table 7.4). The changes in the mean larval density of these species in relation to age are illustrated in Figures 8.2 to 8.5. It can be seen that the effect of age on larval density is more distinct in *M. rubi* and *H. furcata,* with other factors such as altitude obviously having an important effect on the densities of the other two species. This impression is confirmed by the results of the multiple regression analysis (Table 7.4) where age or it's powers are the most important determinants of density for *M. rubi* and *H. furcata.* In contrast for both *E. nanata* and *L. porphyrea,* the time of sampling and altitude explain a greater amount of the variation in density than stand age. The results for *Macrothylacia rubi* indicate that the highest densities occur in the very oldest aged *Calluna* stands of 20 years or more in age. The highest densities of *Hydriomena furcata* larvae are in slighly younger stands of 14 to 22 years of age. Although the pattern is less easy to interpret for the other two species, the highest densities of both *Eupithecia nanata* and *Lycophotia porphyrea* larvae occur in stands at the younger end of the scale below 20 years of age.

The results of the application of non-linear regression to the equation derived by multilinear regression for the larval density of *H. furcata* in relation to *Calluna* stand age are given in Table 8.5. The non-linear regression line has been plotted to the data exhibited in Figure 8.3.

The effects of plant developmental phase on macrolepidopteran density are in broad agreement with the results of the MLR analysis that examined individual stand age rather than developmental phase. The density of the same four species, *M. rubi, H. furcata, E. nanata* and *L. porphyrea* were shown to be significantly affected. In addition, the larvae of *E. atomaria* were significantly affected by stand phase. Therefore five of the eight species tested showed significant differences in their densities between plant phases as measured by at least one of the sampling methods (Tables 8.6, 8.7). The three species that showed no significant changes were *Entephria caesiata, Diarsia mendica* and the *Eulithis* species. Of the five species showing significant effects, two had their densities estimated by one sampling method only, namely *Macrothylacia rubi* and *Eupithecia nanata.* Of the remaining three species, *L. porphyrea* and *E. atomaria* showed significant differences in their densities as estimated by sweep-netting but not by Berlese funnel sampling. The remaining species, *H. furcata,* showed significant effects of age on larval density as estimated by all three sampling methods. The highest densities of *Macrothylacia rubi* larvae are in degenerate aged stands (mean of 20-35 larvae found per 5 minutes) whereas those of *Hydriomena furcata* are in mature phase stands. *Eupithecia nanata* larvae show significantly higher densities in the building aged

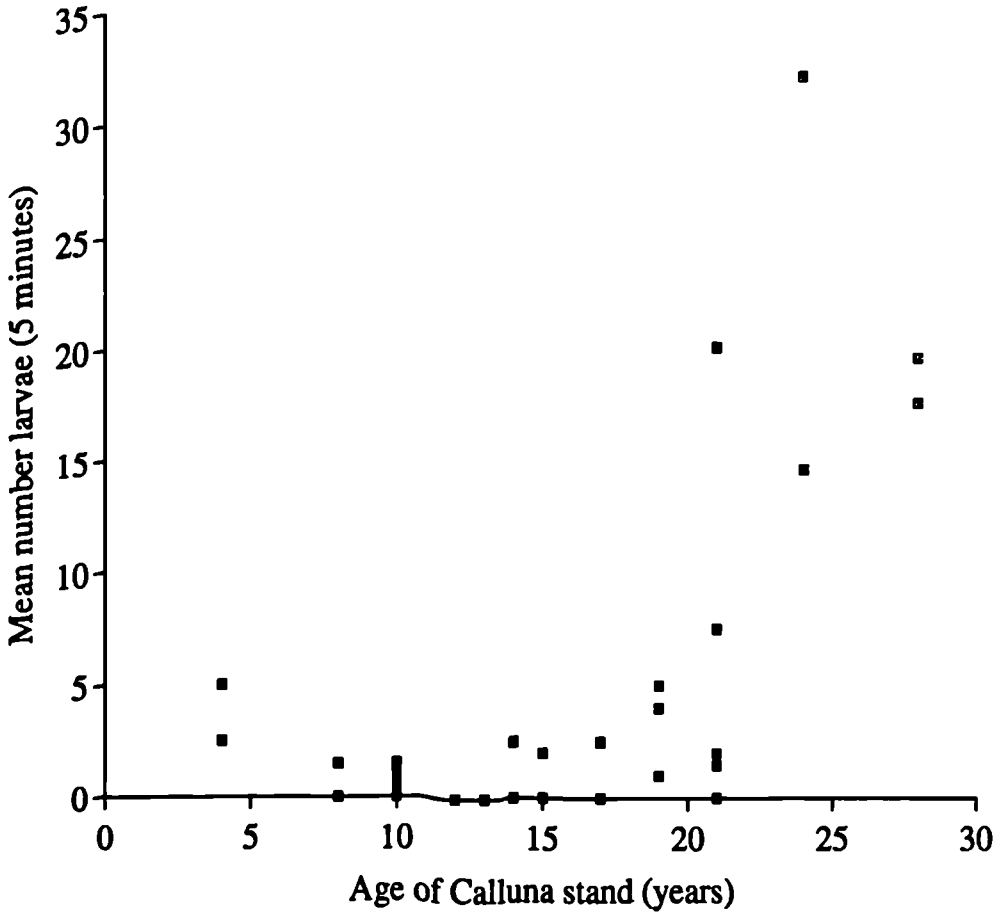

Figure 8.2. The density of the larvae of *Macrothylacia rubi* in *Calluna vulgaris* stands of different ages. Density was measured by quantitative search sampling and is the mean number of larvae found on each sampling occasion with two five minute samples taken. Data are for a total of 38 sampling occasions. As a result of the large number of superimposed points , the graph illustrates the range of densities found at varying ages rather than the complete dataset. Data includes samples taken at a range of altitudes (290-650m) and at dates through from 2 to 13 October when larvae of this species were available. The multiple linear regression equation relating density of *M. rubi* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

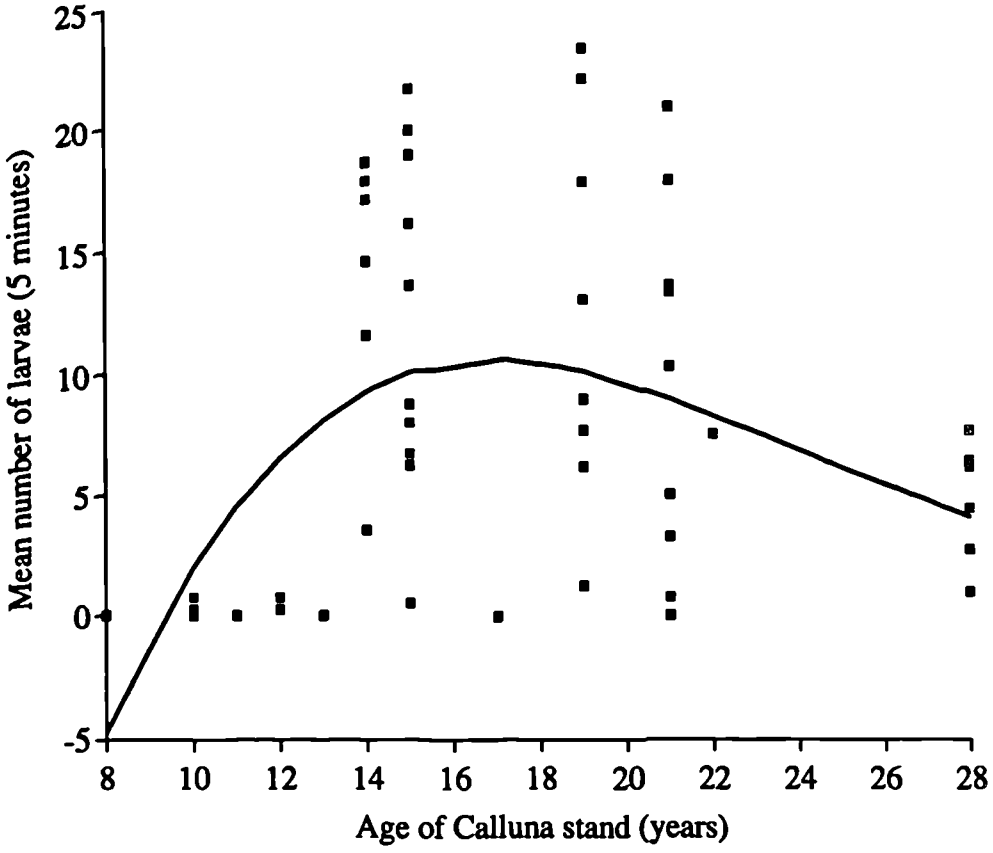

Figure 8.3. The relationship between the density of the larvae of *Hydriomena furcata* and the age of the *Calluna* stand. The curvilinear regression line shows the equation: density = 10.253 age + (-0.475) age^2 + 0.0068 age^3 + (-59.85). The density of the larvae was estimated by the quantitative search sampling method and the density is the mean number of larvae found on each sampling occasion with four five minute samples taken. Data are for a total of 67 sampling occasions. As a result of the large number of superimposed points, the graph illustrates the range of densities found at varying ages rather than the complete dataset. Data includes samples taken at a range of altitudes (290-650m) and at dates through from 30 April to 12 July when larvae of this species were available. The multiple linear regression equation relating density of *H. furcata* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

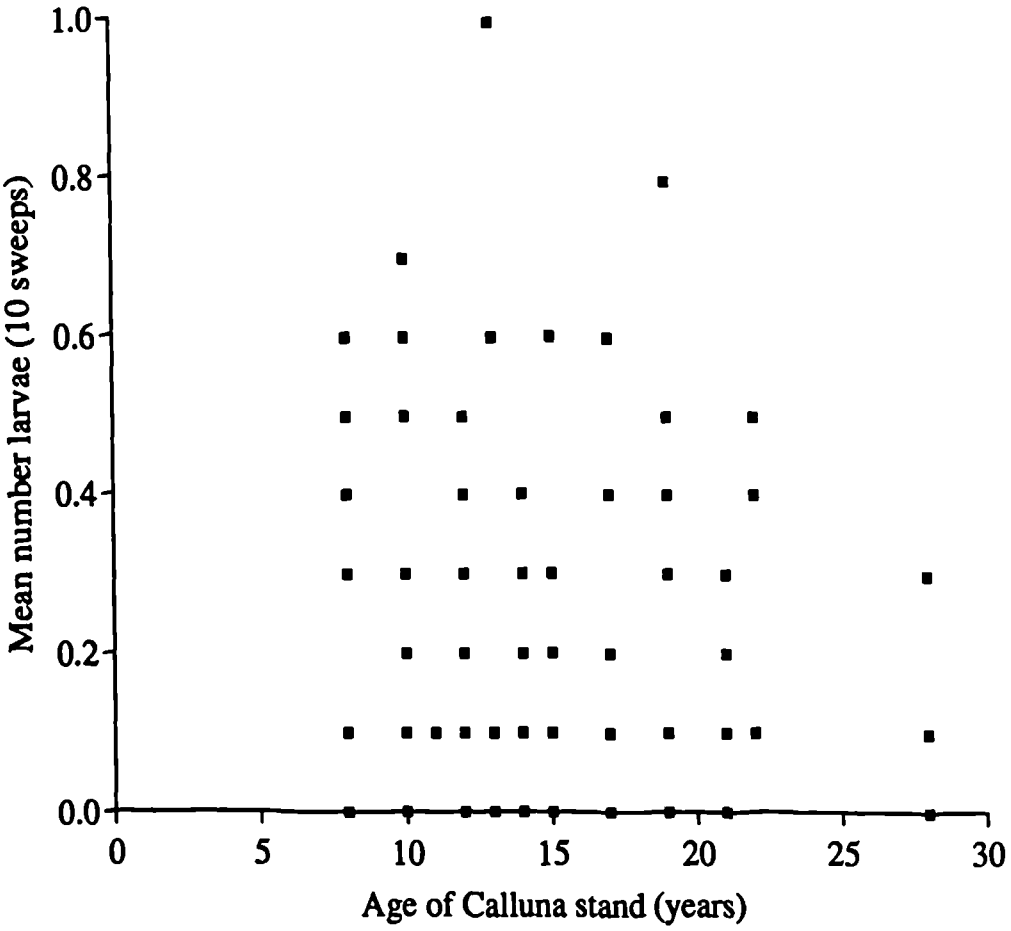

Figure 8.4. The density of the larvae of *Eupithecia nanata* in *Calluna* stands of different ages. Density was measured by sweep-netting and is the mean number of larvae recorded on each sampling occasion with 10 samples of 10 sweeps of the vegetation collected. Data are for a total of 179 sampling occasions. As a result of the large number of superimposed points , the graph illustrates the range of densities found at varying ages rather than the complete dataset. Data includes samples taken at a range of altitudes (290-650m) and at dates through from 26 July to 6 October when larvae of this species were available. The multiple linear regression equation relating density of *E. nanata* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

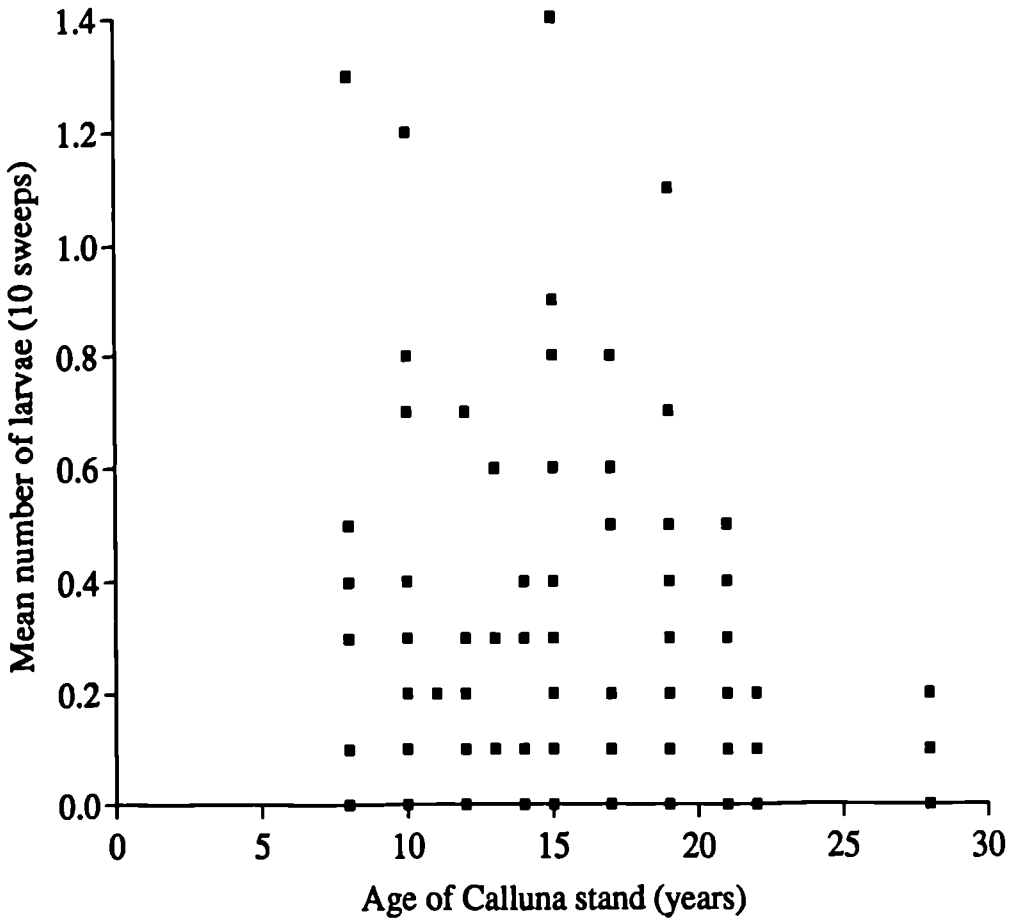

Figure 8.5. The density of larvae of *Lycophotia porphyrea* in *Calluna* stands of different ages. Density was measured by sweep-netting and is the mean number of larvae recorded on each sampling occasion with 10 samples of 10 sweeps of the vegetation collected. Data are for a total of 193 sampling occasions. As a result of the large number of superimposed points , the graph illustrates the range of densities found at varying ages rather than the complete dataset. Data includes samples taken at a range of altitudes (290-650m) and at dates through from 25 July to 9 October when larvae of this species were available. The multiple linear regression equation relating density of *L. porphyrea* larvae to the altitude and age of the *Calluna* stand and the date of the sampling occasion is given in Table 7.4.

Table 8.5. The non-linear multiple regression analysis of the density of *Hydriomena furcata* larvae in *Calluna* stands of varying ages. The initial values assigned to parameters for the initiation of non-linear regression were set to the linear regression values.

	Linear	Non-linear
Age	2.28 ± 0.755	10.25 ± 4.02
Age^2	-0.108 ± 0.044	-0.475 ± 0.234
Age^3	0.002 ± 7.99×10^{-4}	0.007 ± 0.004
Constant	-12.47 ± 4.01	-59.85 ± 21.36

Table 8.6. The mean abundance of larvae of individual macrolepidopteran species in *Calluna* stands of different life-history stages. The three *Calluna* life-history phases are the building, mature and degenerate as described by Watt (1955). The density of larvae as measured by the three different sampling methods are not comparable. The density of larvae is for the number of larvae per 5 minutes (quantitative searching), per 10 sweeps (sweep-netting) and per 0.25m^2 (Berlese funnel). An asterisk indicates a significant difference (*i.e.* $P<0.05$) in density compared to the developmental phase succeeding it (see Table 8.7). An asterisk after the density in the degenerate phase indicates a significant difference compared to the density in the building phase.

Lepidoptera species	Sampling method	Mean density of larvae ± SE (*n*) Building	Mature	Degenerate
M. rubi				
	search	0.54 ± 0.186 * (26)	2.08 ± 0.457 * (24)	13.88 ± 2.915 * (16)
E. caesiata				
	sweep	0.07 ± 0.011 (580)	0.05 ± 0.015 (220)	0.08 ± 0.020 (200)
	Berlese	0.07 ± 0.043 (40)	0.09 ± 0.047 (35)	0.04 ± 0.04 (25)
Eulithis spp.				
	sweep	0.08 ± 0.018 (320)	0.07 ± 0.019 (310)	0.07 ± 0.029 (100)
	Berlese	0.17 ± 0.056 (65)	0.23 ± 0.068 * (65)	0.05 ± 0.028 (65)
H. furcata				
	search	3.17 ± 0.618 * (108)	10.43 ± 0.846 (88)	8.05 ± 0.798 * (60)
	sweep	0.13 ± 0.040* (130)	0.71 ± 0.327* (30)	0.76 ± 0.126* (50)

Table 8.6. Continued

Lepidoptera species	Sampling method	Mean density of larvae ± SE (*n*) Building	Mature	Degenerate
H. furcata (cont.)	Berlese	0.36 ± 0.177* (70)	0.79 ± 0.752* (70)	0.32 ± 0.119 (50)
E. nanata	sweep	0.18 ± 0.017* (790)	0.11 ± 0.013 (710)	0.09 ± 0.018* (250)
E. atomaria	sweep	0.03 ± 0.007* (720)	0.08 ± 0.015 (670)	0.05 ± 0.014 (230)
	Berlese	0.07 ± 0.040 (60)	0.09 ± 0.033 (70)	0.13 ± 0.044 (55)
L. porphyrea	sweep	0.19 ± 0.018 (830)	0.20 ± 0.019 * (750)	0.05 ± 0.014 * (260)
	Berlese	0.19 ± 0.057 (80)	0.32 ± 0.080 (85)	0.34 ± 0.074 (95)
D. mendica	Berlese	0.17±0.061 (65)	0.07±0.035 (55)	0.07±0.043 (55)

Table 8.7. The results of Kruskal-Wallis tests of the difference in the mean abundance of larvae of various macrolepidopteran species in the different phases of the *Calluna* life-history. The abundance is given as the number of larvae per five minutes (search), ten sweeps (sweep-net) and 0.25m^2 (Berlese funnel). The life-history phases are the building, mature and degenerate as defined by Watt (1955). NS denotes non significance, *i.e.* $P>0.05$.

Lepidoptera species	Sampling method	*Calluna* life-history phases for which larval densities compared							
		All phases		Building/ mature		Mature/ degenerate		Building/ degenerate	
		χ^2	*P*	χ^2	P	χ^2	*P*	χ^2	*P*
M. rubi	search	16.65	<0.001	8.59	<0.001	6.70	0.01	11.41	<0.001
E. caesiata	sweep	2.47	NS	1.15	NS	1.90	NS	0.57	NS
	Berlese	0.49	NS	0.03	NS	0.48	NS	0.32	NS
Eulithis spp.	sweep	0.16	NS	0.15	NS	0.005	NS	0.04	NS
	Berlese	4.60	NS	0.48	NS	4.68	<0.05	2.40	NS
H. furcata	search	68.68	<0.001	54.53	<0.001	2.69	NS	45.20	<0.001
	sweep	35.91	<0.001	11.01	<0.001	9.18	<0.01	39.12	<0.001
	Berlese	18.09	<0.001	14.18	<0.001	9.48	<0.01	0.17	NS
E. nanata	sweep	11.49	<0.01	8.60	<0.01	0.17	NS	5.78	<0.05
E. atomaria	sweep	11.92	<0.01	11.98	<0.001	0.73	NS	3.03	NS
	Berlese	2.05	NS	0.58	NS	0.57	NS	2.02	NS
L. porphyrea	sweep	20.12	<0.001	0.002	NS	18.56	<0.001	19.23	<0.001
	Berlese	1.91	NS	1.20	NS	0.05	NS	1.79	NS
D. mendica	Berlese	2.03	NS	0.95	NS	0.13	NS	1.68	NS

stands compared to those of mature and degenerate age whereas *Lycophotia porphyrea* has higher densities in building and mature aged stands compared to those of degenerate age. *E. atomaria* larvae are more abundant in mature stands compared to those of the building phase.

The five species of macrolepidoptera for which significant changes in density were observed with *Calluna* stand age are among the most abundant of the species found in this study. This suggests that other species may also change in density in different aged *Calluna* stands but insufficient larvae were collected to allow appropriate statistical analysis.

8.5. The distribution of *Hydriomena furcata* larvae within *Calluna vulgaris* stands of mature age

In *Calluna* stands of late mature age where the density of *Hydriomena furcata* larvae was high, the micro-distribution of the larvae was examined.

8.5.1. Methods

Investigations took place during the first two weeks of July 1991 at the three sample sites of WK17 (400m), WK23 (500m) and WK26 (500m), which were of late mature age (Table 2.2). During this time the majority of *H. furcata* larvae were in the final (*i.e.* fifth) instar (mean=4.9, SD=0.27, n=40). Within each *Calluna* stand, a ring of 10cm diameter was used to randomly select stems by being thrown blind. The stem of *Calluna* selected by the ring was (a) measured for its height above the ground (b) examined for the number of larvae and empty larval cocoons of *H. furcata* present. Late instar larvae of *H. furcata* construct shelters by tying current year's shoots of *Calluna* together with silk and these cocoons are easily identifiable as belonging to this species. The presence of *H. furcata* on a stem was therefore presumed by the existence of larvae and/or empty cocoons. A subgroup of approximately 15-20 stems from each site had the length measured of the ten longest shoots of the current year's foliage growth. Therefore the presence/absence and number of larvae of *H. furcata* has been related to the height of the stem and the amount of current year's growth present. Stems heights have been categorized into 5cm classes, beginning at 20-24cm, rather than parameters being related to the heights of individual stems. Differences in the proportions of stems infested in the different height classes have been examined using a χ^2 contingency test.

8.5.2. Results

The frequency distribution of *Calluna* stem heights for all sites combined (Figure 8.6) and for each of the individual sites of WK17 (Figure 8.6), WK26 (Figure 8.7)

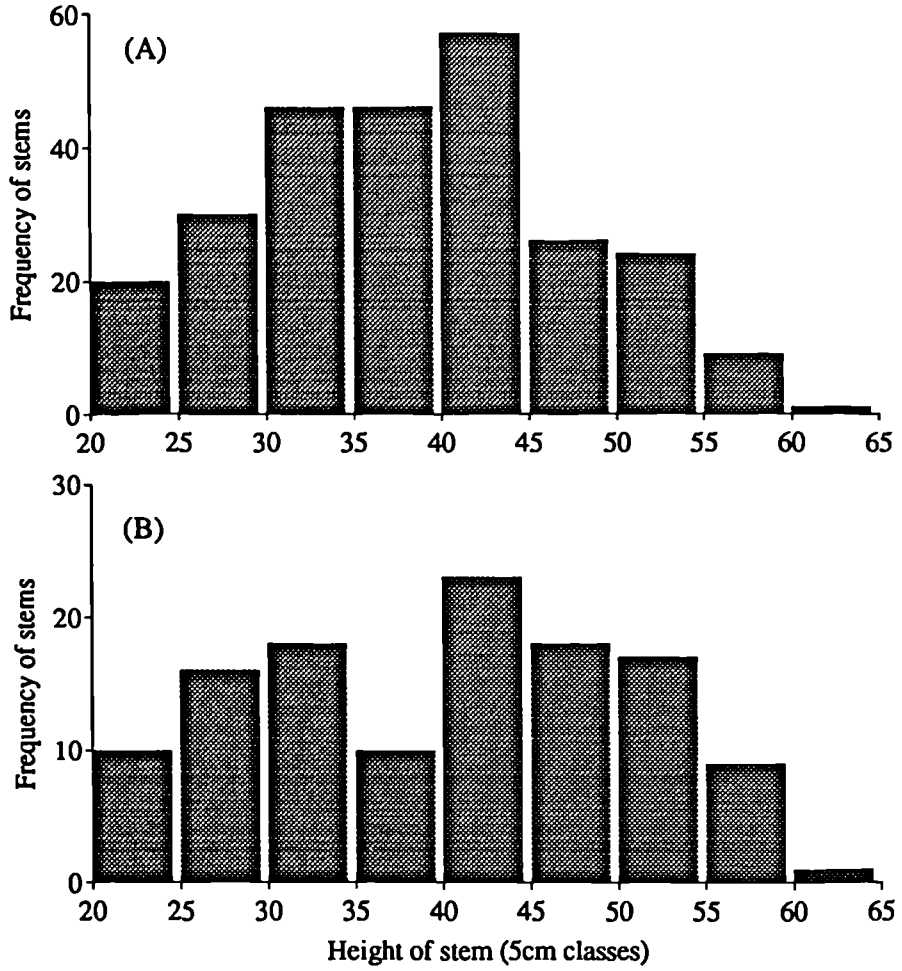

Figure 8.6. The heights of the plant stems in stands of *Calluna vulgaris* in which the distribution of *Hydriomena furcata* larvae were investigated. (A) The frequency of stem heights for all three sample sites combined (sites WK 17, 26 and 23). (B) The frequency of stem heights at site WK17 at 400m. The heights of the stems were measured to the nearest cm and are shown as 5cm classes.

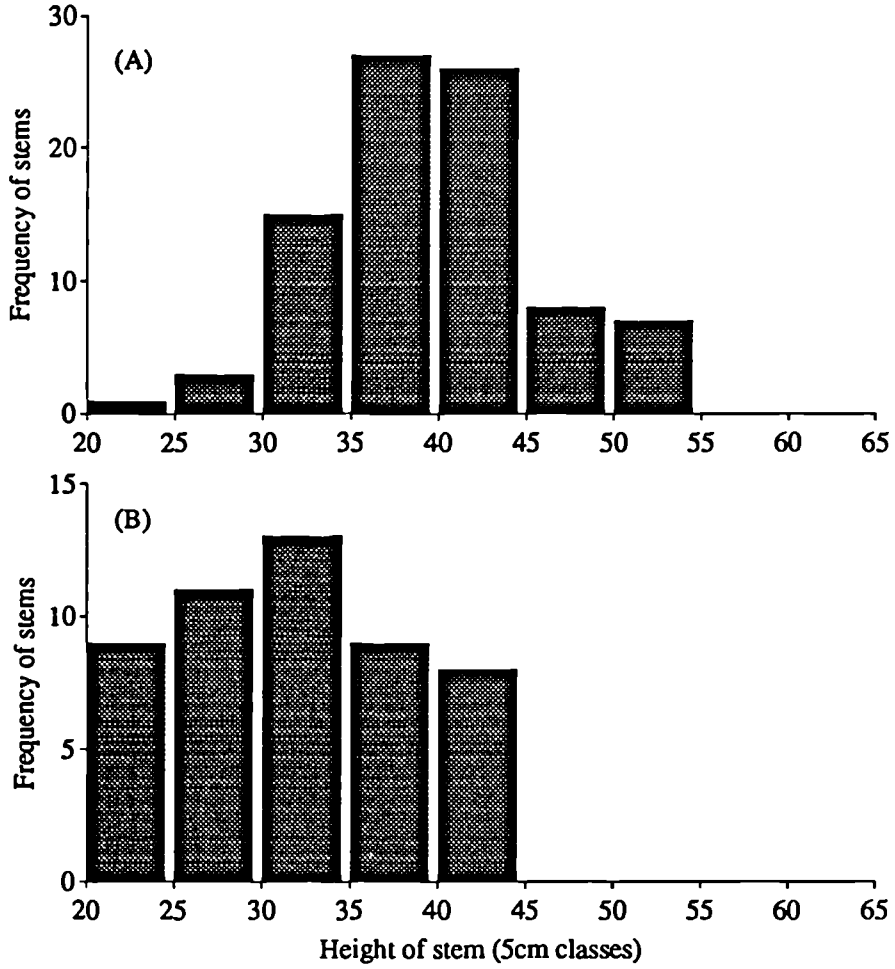

Figure 8.7. The heights of the plant stems in stands of *Calluna vulgaris* in which the distribution of *Hydriomena furcata* larvae were investigated. (A) The frequency of stem heights at site WK26 at 500m (B) The frequency of stem heights at site WK23 at 500m. The heights of the stems were measured to the nearest cm and are shown for 5cm classes.

and WK23 (Figure 8.7) show the overall height range of stems to be between 20cm and 64cm. The range of stem heights varied within the three stands, from 20-64cm at WK17 (Figure 8.6), 24-54cm at WK26 (Figure 8.7) and 20-44 at WK23 (Figure 8.7).

The proportion of *Calluna* stems infested with *H. furcata* larvae increases with enhanced stem height, both at sites WK17 (Figure 8.8) and WK26 (Figure 8.9) and for all sites combined (Figure 8.8). The relationship was not significant at site WK23 (Figure 8.9) where the range of stem heights was reduced.

At site WK23, the maximum height of the stems was lower (40-44cm) compared to the other two sites of WK17 (60-64cm) and WK26 (50-54cm). This allows comparison of the proportion of stems infested at similar heights in different stands where the maximum stem height in one stand is equal to more intermediate stem heights in another. From this an indication can be gained of whether it is absolute or relative height that is important. At WK23 the infestation rate of stems in the 40-44cm height class is 50% (n=8), which compares favourably with 54% (n=14) and 48% (n=23) in the same height class at the other two sample sites (χ^2=1.55, d.f.=2, P>0.05). However in the height class below this, at 35-39cm, there is an infestation rate of 56% at WK23 (n=9) compared to 30% and 10% at WK26 (n=27) and WK17 (n=10), although this difference is not significant (χ^2=2.99, d.f.=2, P>0.05). Therefore at site WK23 where the maximum height of the stems was less than at sites WK26 and WK17, the percentage of stems infested at stem heights present in all three sites is similar. This suggests that it is the absolute height of the stem that is important rather than the its height relative to the surrounding stems. If relative height was important then higher infestation levels would be expected in some of the lower height classes at WK23 compared to WK26 and WK17.

The larvae and their cocoons were generally positioned near the apex of the *Calluna* stems (Figure 8.10). Although for the data displayed in Figure 8.10 there appears to be a relationship between the height of the stem and the distance of the larvae from the top of the stem, this is not significant ($F_{[1,22]}$=4.01, P>0.05, R^2=15%).

There is a significant regression between the number of larvae, number of empty cocoons and total number of larvae and empty cocoons found on a stem and its height (Table 8.8). Therefore as well as a taller stem having a greater probability of being infested, there is likely to be a greater density of larvae and cocoons present on taller stems (Figure 8.11). The mean number of empty cocoons is higher than the mean number of larvae probably because each larva creates more than one cocoon as it grows. The results indicate that on stems of medium height (35-44cm) there are empty cocoons present but few larvae. This may be due to a number of reasons such as the larvae lower down on the stems having already pupated, larvae moving higher as the stem grows or higher mortality of larvae at the lower heights.

On stems where larvae are absent, there is no correlation between the height of the stem and the length of the current year's shoots (Table 8.9). However if the data on

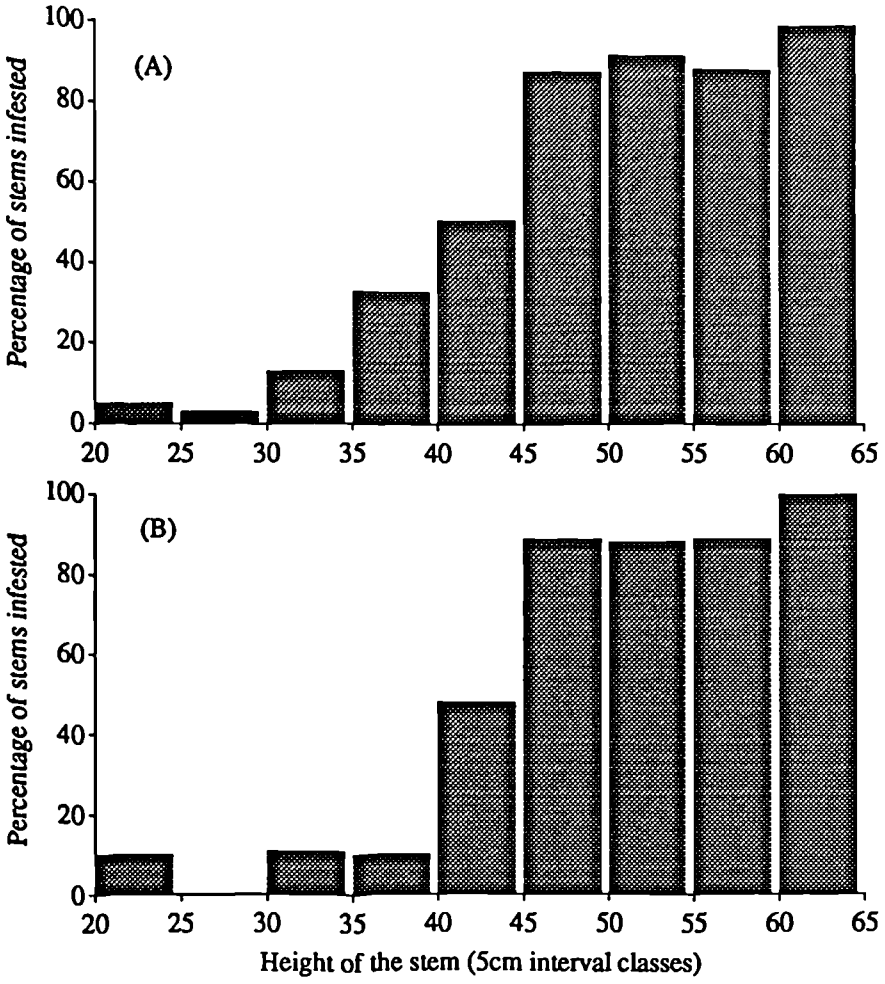

Figure 8.8. The percentage of *Calluna* stems in varying stem height classes infested by *Hydriomena furcata* larvae. (A) There is a significant difference in the percentage of stems of varying heights that are infested when data for all three sites (sites WK17, 26 and 23) are combined (χ^2=79.2, d.f.=8, P<0.001). A total of 259 stems were examined. (B) There is a significant difference in the percentage of stems of varying heights that are infested at site WK17 at 400m. (χ^2=52.65, d.f.=8, P<0.001). The infestation rate was 0% in the 25-29cm height class at this site. A total of 122 stems were examined.

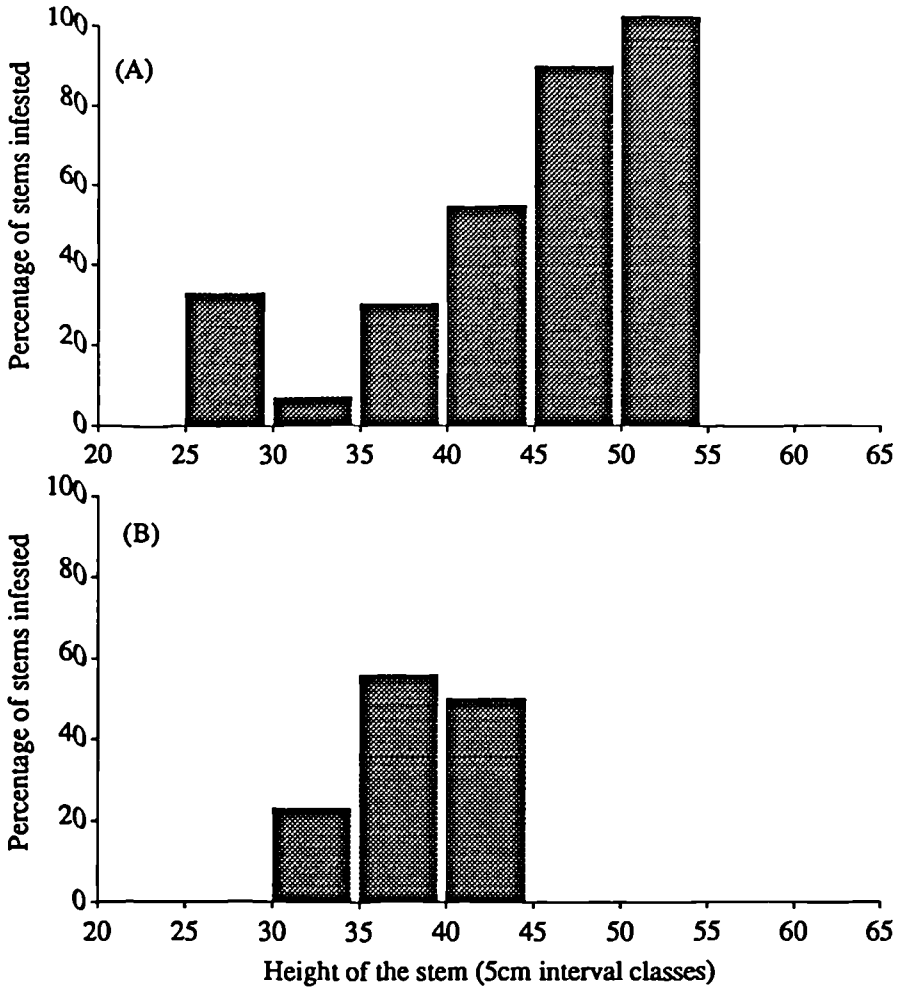

Figure 8.9. The percentage of *Calluna* stems in varying stem height classes infested by *Hydriomena furcata* larvae. (A) There is a significant difference in the percentage of stems of varying heights that are infested at site WK26 at 500m (χ^2=28.3, d.f.=6, P<0.001). The infestation rate was zero in the 20-24cm class. No stems were recorded above a 54cm height. A total of 87 stems were examined. (B) There is no significant difference in the percentage of stems of varying heights that are infested at site WK23 at 500m. (χ^2=8.84, d.f.=4, P>0.05). The infestation rate was 0% in the 20-24cm and 25-29cm height classes at this site. No stems were recorded above 44cm height. A total of 50 stems were examined.

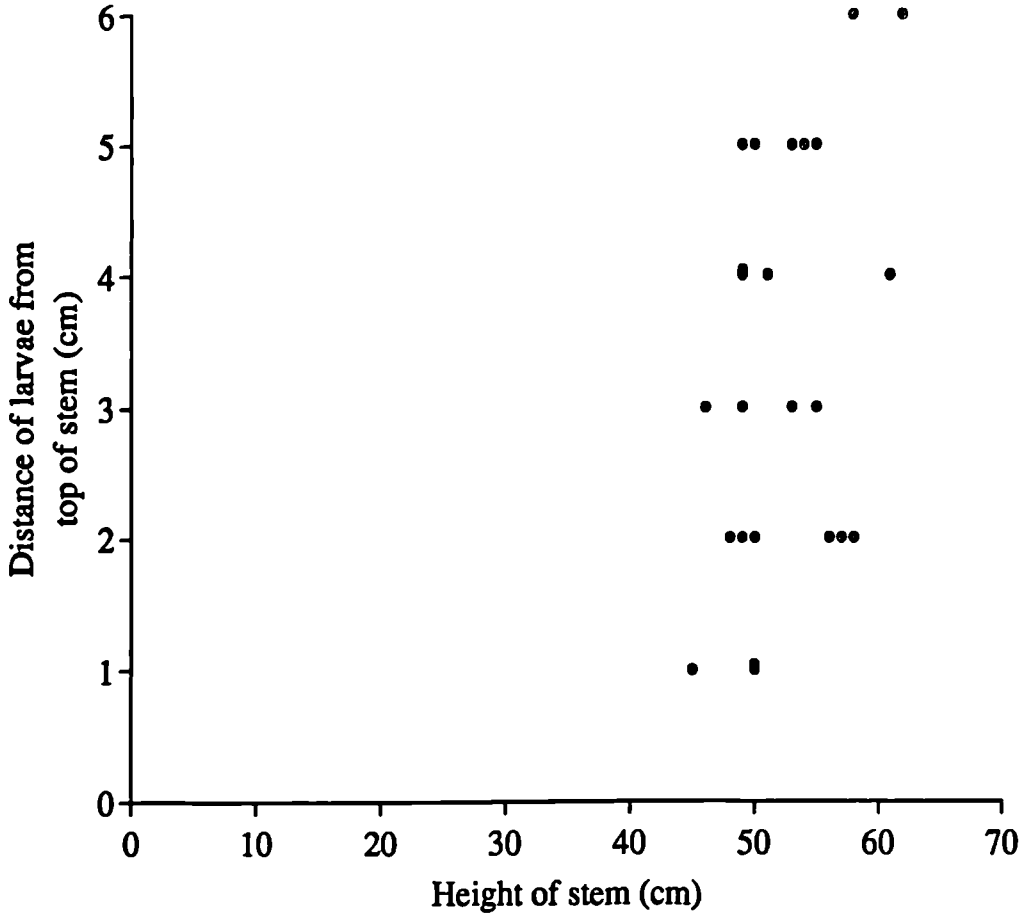

Figure 8.10. The relationship between the distance of *Hydriomena furcata* larvae from the top of the *Calluna* stem and the height of the stem. Regression analysis gives: $Y = (0.136 \pm 0.070)\ X + (-3.794 \pm 3.571)$, $F_{[1,22]}=4.01$, $P>0.05$.

Table 8.8. The results of linear regression analysis between the height of a *Calluna* stem and the number of larvae, empty larval cocoons and total number of larvae and empty cocoons of *Hydriomena furcata* on the stem. Larval cocoons are the shelters formed by the larvae by tying foliage together with silk. Data are a combination for all three sample sites of WK16 (400m), WK27 (500m) and WK23 (500m). The significance of the regression has been taken at the 95% probability level.

Y-axis	$B \pm SE$	Constant ± SE	R^2	$F_{[1,257]}$	P
Larvae	0.026 ± 0.004	-0.80 ± 0.141	17%	50.9	<0.001
Empty cocoons	0.056 ± 0.006	-1.48 ± 0.230	26%	88.3	<0.001
Larvae & empty cocoons	0.082 ± 0.007	-2.28 ± 0.275	35%	136.5	<0.001

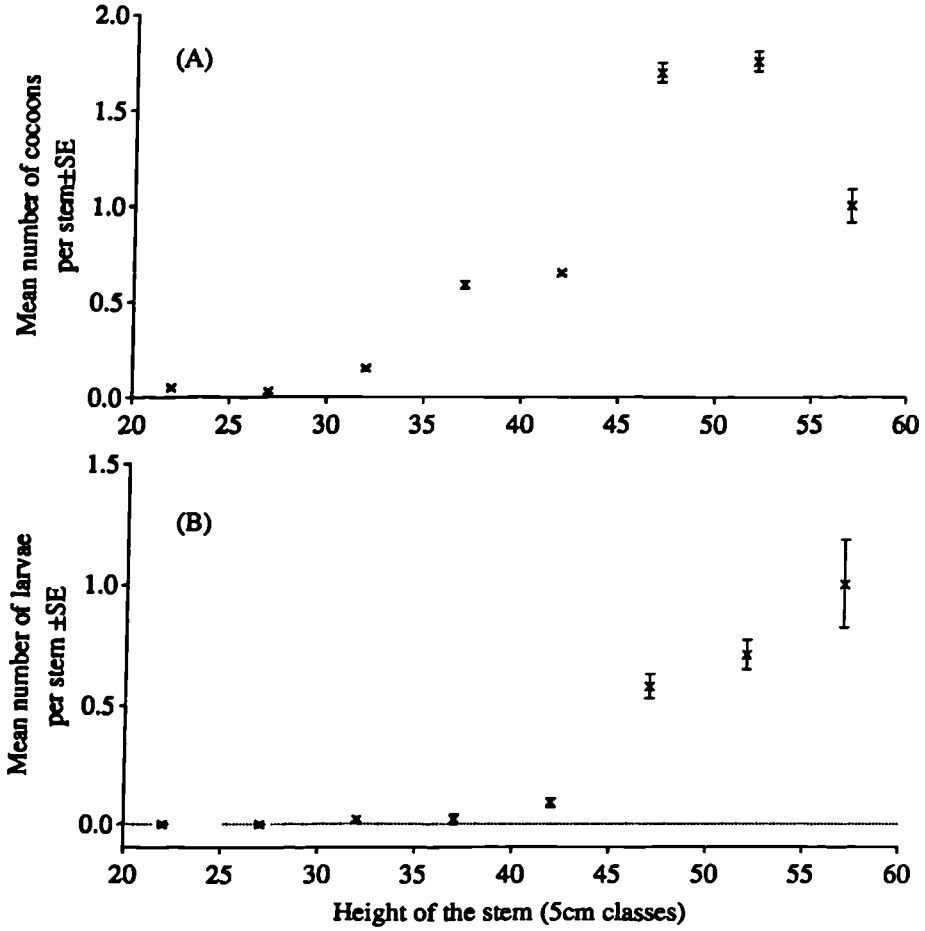

Figure 8.11. The abundance of *Hydriomena furcata* larvae on *Calluna vulgaris* stems of varying heights. (A) The abundance as measured as the mean number of empty cocoons found per stem. Cocoons are the shelters formed by the larvae by drawing together *Calluna* shoots with silk. (B) The abundance as measured by the mean numbers of larvae found on stems. The mean number of larvae/empty cocoons have been calculated for stems within 5cm height classes beginning at 20cm.

Table 8.9. The regression analysis between the height of *Calluna vulgaris* stems and the mean length of the ten longest current year's shoots on the stems. The regression analysis has been done for (a) all stems checked *i.e.* with and without larvae present (b) stems on which *Hydriomena furcata* larvae and cocoons were not present. The analysis has been done separately for each of the three sample sites where data were collected and for all three sites combined. NS denotes that $P>0.05$.

Sample site & infestation group	Regression equation	R^2	$F_{[d.f.]}$	P
All sites combined				
(a) all stems	$Y = (-1.01 \pm 0.21) X + 73.03$	31%	$23.79_{[1,52]}$	<0.001
(b) larvae absent	$Y = (-0.33 \pm 0.25) X + 55.38$	6%	$1.78_{[1,28]}$	NS
Sample site WK17				
(a) all stems	$Y = (-1.26 \pm 0.18) X + 76.00$	77%	$47.67_{[1,14]}$	<0.001
(b) larvae absent	$Y = (-0.91 \pm 0.42) X + 67.33$	49%	$4.77_{[1,5]}$	NS
Sample site WK26				
(a) all stems	$Y = (-1.17 \pm 0.41) X + 76.14$	29%	$7.93_{[1,19]}$	<0.05
(b) larvae absent	$Y = (-1.32 \pm 1.12) X + 87.61$	15%	$1.39_{[1,8]}$	NS
Sample site WK23				
(a) all stems	$Y = (-0.85 \pm 0.33) X + 77.52$	30%	$6.56_{[1,15]}$	<0.05
(b) larvae absent	$Y = (-0.51 \pm 0.29) X + 68.24$	22%	$3.08_{[1,11]}$	NS

the length of the current year's shoots on larval infested stems are included, there is a significant regression between stem height and the length of the longest shoots of the current year's growth (Table 8.9). This relationship is shown graphically for all three sites combined (Figure 8.12) and for each individual sample site (Figures 8.13 to 8.15). It can be seen that generally larvae are present on the highest stems and that on these stems the length of the current year's shoots are significantly reduced. There is a lack of data for the length of the current year's shoots on tall stems with no larvae present because in these stands it was difficult to find a tall stem not infested by larvae.

Analysis of variance reveals there to be a significant difference in the length of the current year's shoots on *Calluna* stems dependent on whether the larvae are absent or present (Table 8.10). The mean length of the shoots on stems where larvae and their cocoons were present were reduced by approximately 58% compared to uninfested stems.

8.6. Discussion

There was little variation in the species richness of macrolepidoptera in *Calluna* stands of the different life-history phases. Certain species of Lepidoptera of which only a few individuals were captured were confined to a single developmental phase. However this specificity is likely to be a consequence of the sampling process and the rarity of the species. It is perhaps surprising that no differences were found considering the described nutritional, structural and environmental changes that occur during the *Calluna* life-history. The pioneer life history phase that occurs directly after burning was not sampled. It is possible that its inclusion would have created greater distinction between phases in the species richness of Lepidoptera.

The density of macrolepidoptera larvae as estimated by sweep-net sampling was significantly higher in the building and mature phases compared to the degenerate. This finding agrees with the observations of Gimingham (1985) who also recorded the highest densities of Lepidoptera in stands of building and mature age. At the level of the individual lepidopteran families, the Noctuidae show significantly higher abundances in the building and mature stands. This difference is mainly the effect of the higher abundances of the noctuid species, *Lycophotia porphyrea*, in the earlier phases. Geometrid species also show significant changes in abundance between *Calluna* phases but individual species prefer different phases so any significant effects at the level of the family are cancelled out.

A number of individual species showed considerable variations in abundance with *Calluna* life history phase, with preference varying between species. *Macrothylacia rubi* occurred at much higher densities in stands of degenerate age. This is possibly a result of its food preferences; it is polyphagous with its alternative foodplants including the grass species which are co-dominant with *Calluna* in the degenerate

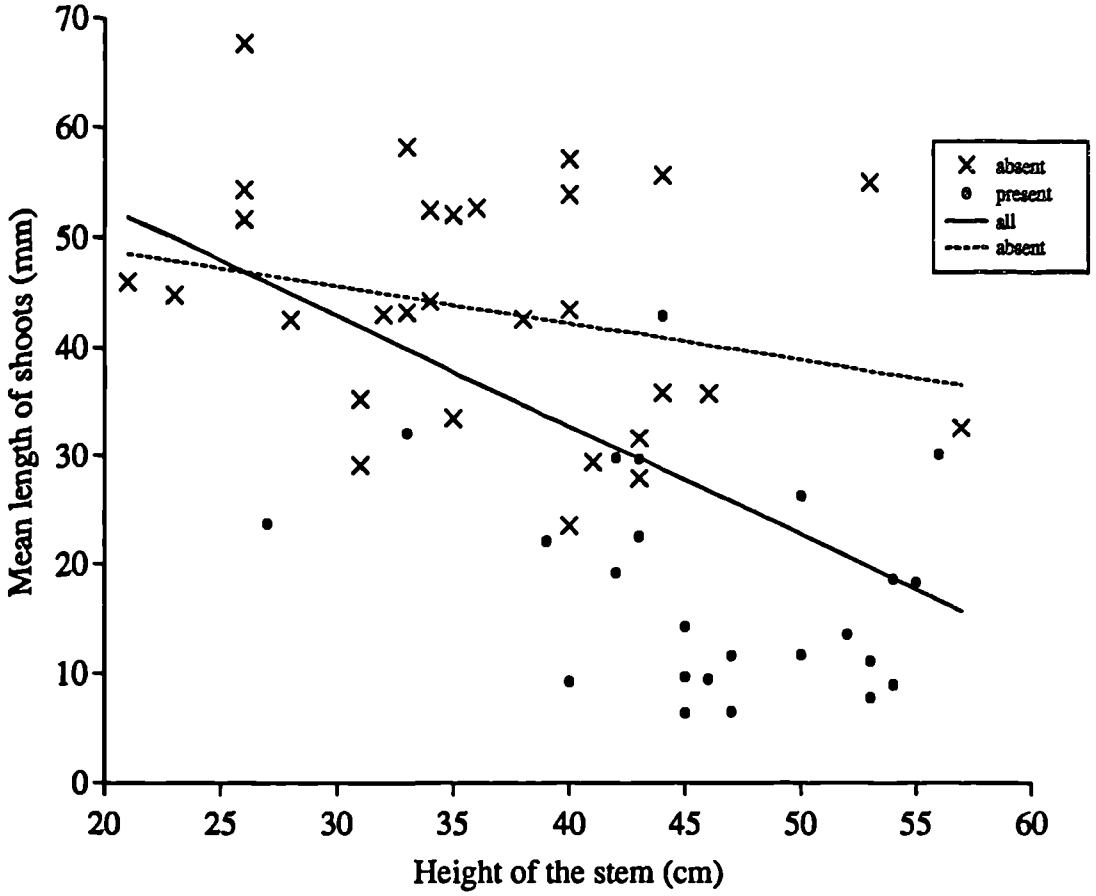

Figure 8.12. The length of the current year's shoots on *Calluna vulgaris* stems of varying heights and the effect of the presence of *Hydriomena furcata* larvae. Data on the length of the shoots at different stem heights are differentiated between where larvae are present (•) or absent (X). The bold line shows the significant regression between the height of the stem and the length of the current year's shoots ($P<0.001$ Table 8.9) and the broken line that of the non-significant regression between the height of the stem and the length of the shoots when only those stems not infested by larvae are included ($P>0.05$ Table 8.9). The shoot length is the mean length of the ten longest current year's shoots on the stem. Data for all of the three sites (WK 17, 26 and 23) have been amalgamated.

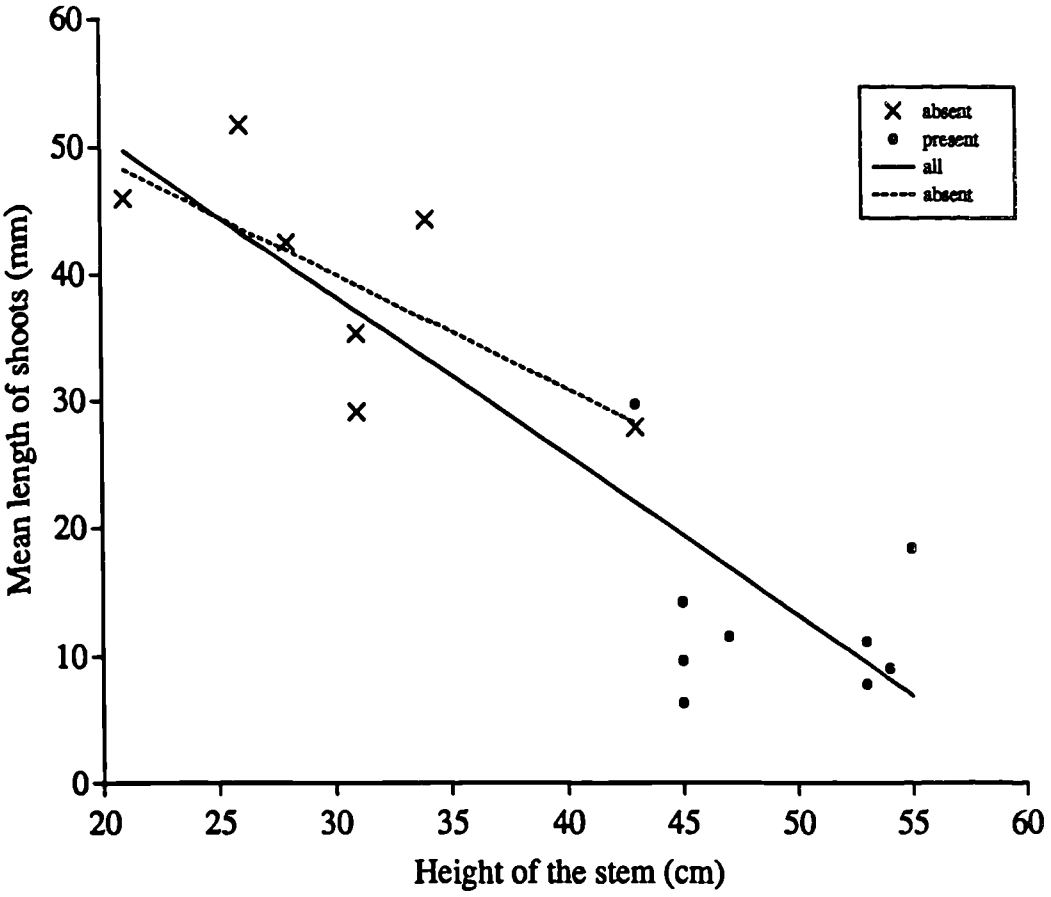

Figure 8.13. The length of the current year's shoots on *Calluna vulgaris* stems of varying heights at sample site WK17 (400m) and the effect of the presence of *Hydriomena furcata* larvae. Data on the length of the shoots at different stem heights are differentiated between where larvae are present (•) or absent (X). The bold line shows the significant regression between the height of the stem and the length of the current year's shoots ($P<0.001$ Table 8.9) and the broken line that of the non-significant regression between the height of the stem and the length of the shoots when only those stems not infested by larvae are included ($P>0.05$ Table 8.9). The shoot length is the mean length of the ten longest current year's shoots on the stem.

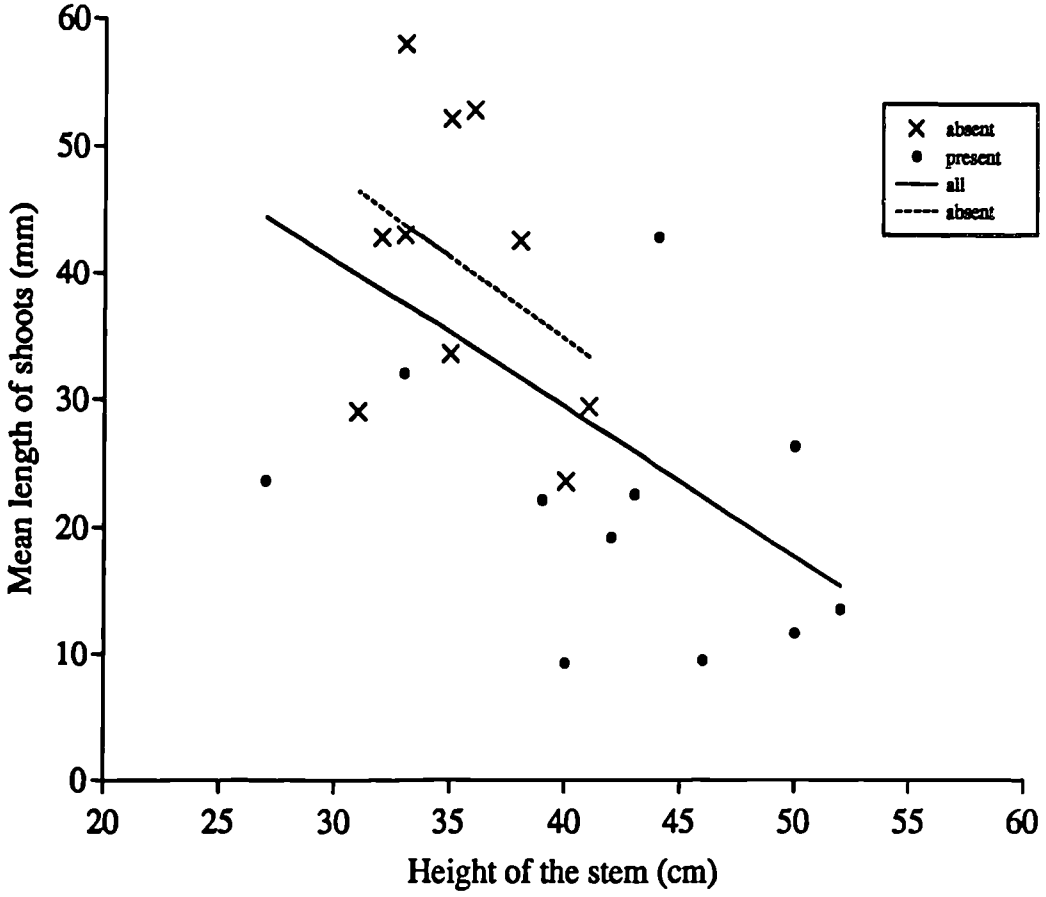

Figure 8.14. The length of the current year's shoots on *Calluna vulgaris* stems of varying heights at sample site WK26 (500m) and the effect of the presence of *Hydriomena furcata* larvae. Data on the length of the shoots at different stem heights are differentiated between where larvae are present (•) or absent (X). The bold line shows the significant regression between the height of the stem and the length of the current year's shoots ($P<0.05$ Table 8.9) and the broken line that of the non-significant regression between the height of the stem and the length of the shoots when only those stems not infested by larvae are included ($P>0.05$ Table 8.9). The shoot length is the mean length of the ten longest current year's shoots on the stem.

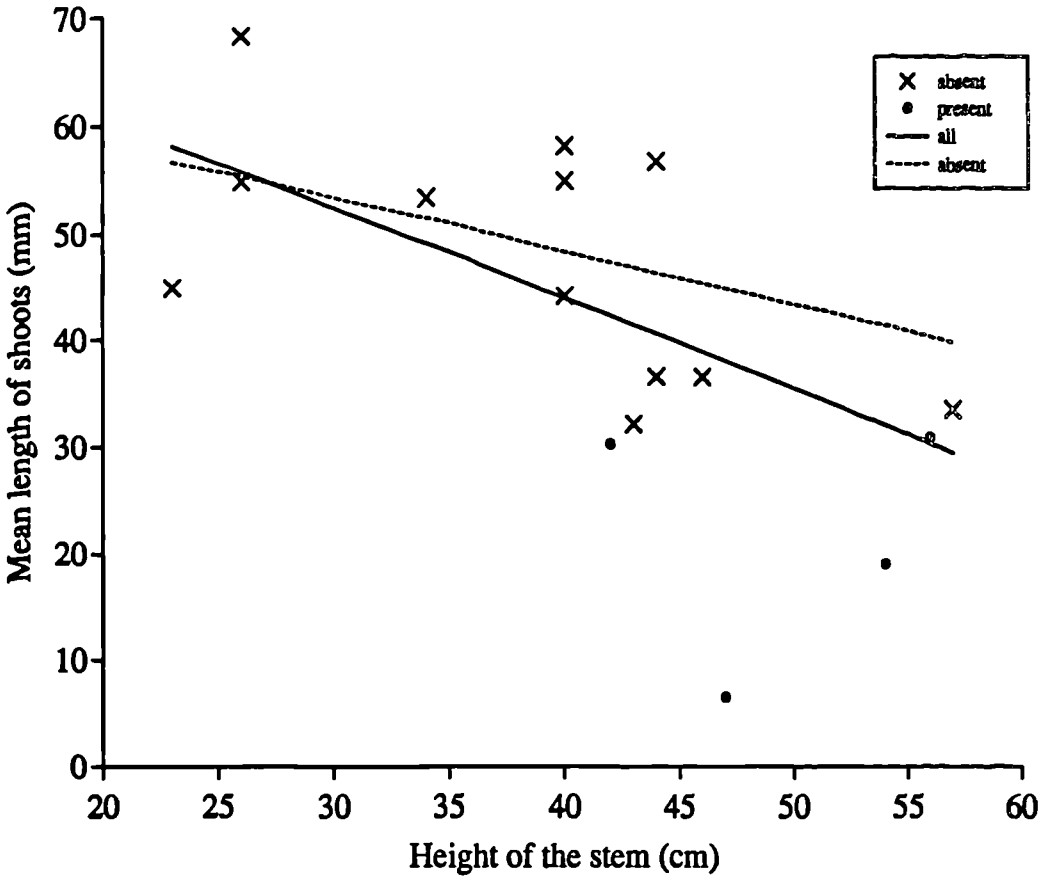

Figure 8.15. The length of the current year's shoots on *Calluna vulgaris* stems of varying heights at sample site WK23 (500m) and the effect of the presence of *Hydriomena furcata* larvae. Data on the length of the shoots at different stem heights are differentiated between where larvae are present (•) or absent (X). The bold line shows the significant regression between the height of the stem and the length of the current year's shoots ($P<0.05$ Table 8.9) and the broken line that of the non-significant regression between the height of the stem and the length of the shoots when only those stems not infested by larvae are included ($P>0.05$ Table 8.9). The shoot length is the mean length of the ten longest current year's shoots on the stem.

Table 8.10. The difference in length of the ten longest current year's shoots on *Calluna* stems with and without the larvae and cocoons of *Hydriomena furcata* present. The difference in shoot length on stems with and without *H. furcata* larvae present has been tested using analysis of variance. The results consist of data for all three individual sample sites and for all sites combined. The reduction in the mean shoot length is the percentage difference in mean shoot length on stems where larvae are absent and present. The mean length of the shoots is calculated from the mean length of the ten longest shoots of the current year's growth. The number of stems examined is denoted by *n*.

Sample site	Mean length of shoots ± SE (*n*) Absent	Present	Percentage reduction in shoot length	*F*	d.f.	*P*
All	43.56 ± 11.18 (30)	18.20 ± 9.84 (24)	58%	76.25	1, 52	<0.001
WK17	39.54 ± 8.98 (7)	13.11 ± 7.18 (9)	67%	42.97	1, 14	<0.001
WK26	40.80 ± 11.57 (10)	21.21 ± 10.29 (11)	48%	16.86	1, 19	<0.001
WK23	47.85 ± 11.21 (13)	21.35 ± 11.26 (4)	55%	17.06	1, 15	<0.001

phase but which are absent in the earlier developmental phases. Another possible explanation that could be investigated is whether the larvae require the copious moss layer of the degenerate phase for overwintering within. The higher abundances of *Eupithecia nanata* larvae in stands of building age are most probably a consequence of the higher densities in this phase of the *Calluna* flowers upon which they feed. For *Lycophotia porphyrea* and *Ematurga atomaria* it is difficult to suggest reasons for their patterns of abundance and further work is needed to investigate the observed patterns. It may possibly be related to the greater biomass of *Calluna* foliage in building and mature phases.

The larvae of *Hydriomena furcata* occurred in each of the three *Calluna* phases sampled but densities were considerably higher in stands of mature age. Within these mature stands, the highest densities of larvae occurred on the tallest stems. The higher abundances in this phase would therefore appear to be a result of maximum *Calluna* stem height occurring in the mature phase with the stems becoming decumbent in the degenerate phase (Table 8.1). This preference for tall *Calluna* stems could be the result of a number of different mechanisms. Firstly it is possible that the preference arises because of the oviposition behaviour of the adult females. It is less likely that any active selection is shown by larvae, as unlike other Lepidoptera species *e.g. Operophtera brumata*, there is no evidence of active dispersion after egg hatching. Alternatively the oviposition rate may not vary between stands but there may be differential survival in the different phases and stem heights during the egg and early larval stages. Although ovipositing lepidopterans are capable of distinguishing vegetation of higher nutritional value, they often fail to select the optimum hosts for their larvae (Singer 1984).

There are a number of possible costs and benefits for *H. furcata* larvae in the different phases of *Calluna*. The optimal nutritional levels for the larvae occur in pioneer and early building aged stands (Miller and Miles 1969; Gimingham 1972; Miller 1979). Phytophagous insects generally show a preference for plant parts of higher nutritional value and growth is often faster on such material. For example, the Silver-spotted Blue butterfly (*Plebejus argus*) feeds exclusively on pioneer aged *Calluna* stands because of their higher nutritional quality (Thomas 1985a, b), although evidence for this is circumstantial. Additionally, survival may be greater if growth is faster since if the length of the larval stage is shortened, the risk of attack by natural enemies is reduced (Cheng 1970; Feeny 1976; Pollard 1979; Price *et al.* 1980). However, other factors may supersede the importance for faster growth, and survivorship may be higher on nutritionally poorer foods (Myers 1981; Raupp and Denno 1983; Stamp and Bowers 1988). For instance the larvae of the pyralid moth have higher survivorship on the older stems of pawpaw because of the suitability of these leaves for the construction of cocoons that act as refuges against predators and parasitoids (Damman 1987). Since *H. furcata* larvae build cocoons, it is possible that the nutritionally poorer food is being compensated for by the greater suitability of these stems for the

construction of shelters that offer protection from natural enemies. Predation rates of larvae by both vertebrate and invertebrates may vary on stems of different heights. The tall stems with their bare woody bases may act to reduce predation by ground dwelling invertebrate predators and vertebrate predators. In addition, some vertebrate predators such as the red grouse are known to avoid taller *Calluna* stands (Savoury 1986). The microclimatic conditions on the taller stems may be more favourable for the eggs or larvae with adult female Lepidoptera able to use microclimate as a distinguishing feature for the oviposition of eggs (Rausher 1979; Forsberg 1987).

The predominance of larvae on taller stems may be related to the conspicuousness of taller stems to adult females. Female *Cactoblastis cactorum* lay more egg batches on taller and more conspicuous *Opuntia* plants as they represent a large target and are hence more easily located by female moths (Robertson 1987). The swallowtail butterfly approaches individuals of the host plant to which they have free access by flight and they consequently never lay eggs on plants growing in dense vegetation (Wiklund 1974). A similar situation does not seem to be occurring for *Hydriomena furcata* as it appeared to be absolute rather than relative height of the stem that was important.

It is not surprising that the larvae are present at the stem apex since this is where the growth of new foliage is concentrated. A consequence of this arrangement is that by mid-July the growth on the upper portion of these stems was visibly reduced, and this suggests the possibility of there being intraspecific competition for food on these stems. The vegetation on these stems is also greatly damaged, a situation which often reduces the food quality of the foliage and impairs phytophagous insect performance (Reavey and Lawton 1991).

Therefore adult oviposition behaviour and/or differential survival of the egg of early larval stages are creating a higher abundance of *H. furcata* larvae on taller *Calluna* stems. Although these stems are likely to be of lower nutritional value they would seem to offer advantages in terms of more favourable microclimate or protection from natural enemies, however further work is needed to fully elucidate this relationship.

Chapter Nine

A comparison between the Lepidoptera associated with *Calluna vulgaris* and *Vaccinium myrtillus*

9.1. Introduction

Calluna vulgaris and *Vaccinium myrtillus* grow in close proximity on moorland and heathland habitats throughout Britain. Both plants are dwarf shrubs of the family Ericacea and have a similar growth structure. The plants differ in that *V. myrtillus*, unlike *Calluna*, is deciduous, initiates growth earlier in the spring (Woolhouse and Kwloek 1981) and has a distribution which extends to higher altitudes (Gimingham 1972).

Less is known of the invertebrate fauna associated with *V. myrtillus* compared to *Calluna*. Previous work has concentrated on the importance of its lepidopteran fauna as a food resource of certain avian predators (Atlegrim 1989, 1992; Baines and Sage 1991). From these studies it is known that sawfly and lepidopteran caterpillars constitute 68% by number and 86% by mass of the invertebrates on bilberry during spring and early summer in a Scottish pinewood (Baines and Sage 1991).

Vaccinium myrtillus may be more palatable for folivorous insects compared to *Calluna*. It has a higher nitrogen and phosphorus content (Pearsall 1950; Moss 1968) with the nitrogen constituent increasing with altitude (Woodward 1986). Its leaf structure is of a ovate flat type compared to the microphyllous leaf structure of *Calluna*. Broad leaved plants generally have a higher species richness of insects associated with them compared to those with finely divided leaves (Lawton and Price 1979). The deciduous nature of bilberry may affect its ability to support insect herbivores that overwinter as larvae and feed during late autumn and early spring. This, together with the earlier availability of spring growth on bilberry, prompts questions about the comparative phenology of insect herbivores common to both plants.

Both with regard to conservation and game interests, it would be useful to elucidate any possible benefits of the presence of bilberry within moorland habitats, in comparison to complete monocultures of *Calluna*. The addition of extra plant species is likely to increase the insect species richness but bilberry areas may also act as reservoirs of high insect abundance for feeding by birds.

Sage (1991) found a ten fold decrease in the number of lepidopteran and sawfly larvae on bilberry along a transect from east to west in Scotland. This was attributed to

the more oceanic conditions in the west being detrimental to Lepidoptera species. Atlegrim (1989) found that exclosure of vertebrate predators from bilberry stands caused an average 63% increase in the density of lepidopteran and sawfly larvae.

9.2. General methods

Vaccinium myrtillus grows in association with *Calluna vulgaris* at the three study areas of North Plantation (290m), Middle End (470m) and Chapel Fell (650m). In each of these areas the cover of *V. myrtillus* was not as extensive as that of *Calluna*. The majority of the comparisons involve work carried out in 1990 although some material from 1988 and 1989 has also been utilised. The stands of *V. myrtillus* and *Calluna* at each study area were chosen to be of approximately the same age and height. Sampling at a particular study area was generally paired on the same day for *Calluna* and *V. myrtillus* therefore the seasonal spread of sampling was equal on the two plant species. The year was divided from 1 January into fortnightly intervals which have been numerically identified, with the sampling season beginning in mid-April (interval 9) and ending in late September (interval 19).

9.3. The species richness of Lepidoptera on *Calluna vulgaris* and *Vaccinium myrtillus*

9.3.1. As assessed from the literature

This aspect has been discussed in Chapter 4 with the conclusion that there are approximately equal numbers of lepidopteran species that feed as larvae on the two plants. The actual numbers are 65 and 57 macrolepidoptera and 21 and 23 microlepidoptera species associated with *Calluna vulgaris* and *Vaccinium myrtillus* respectively. Of these, 24 macrolepidoptera and 3 microlepidoptera species are common to both plants. From the information contained in Appendix B it can be seen that the incidence of species in certain families do show some differences between the two plants. For instance, species of the Tortricidae family seem especially prevalent on bilberry.

9.3.2. As assessed from samples taken in the field

There was a total of 26 macrolepidopteran species whose larvae were found on *Calluna* during this study, of which 15 (56%) were also recorded on *V. myrtillus*. During 1990, when sampling effort by Berlese funnel extraction was equal on the two plant species, no macrolepidopteran species were recorded on *V. myrtillus* that were not also found on *Calluna*.

The larvae of the majority of the microlepidopteran species proved difficult to identify to species level. As a result of this it is impossible to discuss how the species richness of microlepidoptera varies between the two plants, however it is likely that there were species found that feed exclusively on bilberry.

9.4. The relative importance of the various taxonomic groups of Lepidoptera on *Calluna vulgaris* and *Vaccinium myrtillus*

9.4.1. Methods

The Lepidoptera were divided into four taxonomic groupings. These consist of the two most abundant macrolepidopteran families, the Geometridae and Noctuidae, and all the other macrolepidopteran species grouped as 'Others'. In addition, the microlepidopteran species are classed together as 'Micros'. All Lepidoptera larvae caught by Berlese funnel extraction during 1990 at the three study areas on *Calluna* and *V. myrtillus* were allocated to one of the four taxonomic groupings and the differences analysed by χ^2 tests. The relative importance of the four groups may have been affected by the groups differing in their capture efficiency rates for Berlese funnel sampling (Chapter Three). However there should be no differences in efficiency of capture of taxonomic groups between the two plant species.

The representation of the four taxonomic groupings on the two plants have been compared for each fortnightly interval in which the two plants were sampled.

9.4.2. Results

The relative importance of the various taxonomic groupings in terms of larval abundance on the two host plants of *Calluna vulgaris* and *Vaccinium myrtillus* are shown in Table 9.1. The microlepidoptera comprise 60% of the larvae on *V. myrtillus* but only 6% on *Calluna* when the results for all three sites are combined. Therefore the other three taxonomic groups are proportionally more important in terms of abundance on *Calluna* compared to *V. myrtillus*. The importance of the microlepidoptera changes with the altitude of the study areas. The microlepidoptera are a significantly higher proportion of the total number of larvae on *V. myrtillus* compared to *Calluna* at the two lower altitudes of 290m and 470m but not at 650m where few larvae were found on either plant species.

Amongst the macrolepidoptera there is no significant difference in the proportional abundance of the three taxonomic groups on the two plants (Table 9.2). There is no evidence for the suggestion that the incidence of noctuid species, which tend to overwinter as larvae (Chapter 5), may be lower on bilberry because of its deciduous nature.

Table 9.1. The proportions of the total number of lepidopteran larvae on the two plant species of *Calluna vulgaris* and *Vaccinium myrtillus* which were represented by the four taxonomic groupings of Geometridae, Noctuidae, 'Others' and Micros. Data are for all larvae collected by Berlese funnel extraction during 1990. The results are shown for all three altitudes combined and for each of the separate altitudes at which sampling occurred. The 'Others' group incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. A χ^2 statistic has been calculated using the actual numbers in each group. NS denotes a non-significant result, *i.e.* $P>0.05$ and n is the total number of larvae.

Altitude	Plant species	n	Lepidoptera taxonomic group (%)				χ^2 (d.f.)	P
			'Others'	Geometrids	Noctuids	Micros		
All								
	Calluna	80	4	72	18	6	69.3 (3)	<0.001
	V. myrtillus	178	1	36	3	60		
290m								
	Calluna	58	3	76	19	2	65.3 (3)	<0.001
	V. myrtillus	123	1	30	4	65		
470m								
	Calluna	18	6	72	11	11	14.4 (3)	<0.01
	V. myrtillus	46	0	48	0	52		
650m								
	Calluna	4	0	25	25	50	1.9 (2)	NS
	V. myrtillus	9	0	68	11	22		

Table 9.2. The proportions of the total number of macrolepidopteran larvae found on the two plants of *Calluna vulgaris* and *Vaccinium myrtillus* which were represented by the three macrolepidopteran taxonomic groupings of 'Others', Geometridae and Noctuidae. Data are for all larvae collected by Berlese funnel extraction during 1990. The results are shown for all three altitudes combined and for each of the separate altitudes at which sampling occurred. The 'Others' groups incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. A χ^2 statistic has been calculated using the actual numbers in each group. The total number of larvae is denoted by *n* and NS denotes non significance, *i.e.* $P>0.05$.

Altitude	Plant species	*n*	Macrolepidoptera taxonomic group (%) 'Others'	Geometrids	Noctuids	χ^2 (d.f.)	*P*
All							
	Calluna	75	4	77	19	4.54 (2)	NS
	V. myrtillus	72	1	90	8		
290m							
	Calluna	57	4	77	19	1.25 (2)	NS
	V. myrtillus	43	2	86	12		
470m							
	Calluna	16	6	81	13	4.47 (2)	NS
	V. myrtillus	22	0	100	0		
650m							
	Calluna	2	0	50	50	1.15 (1)	NS
	V. myrtillus	7	0	86	14		

The difference in the incidence of different taxonomic groups on the two plant species only occurred during the first three fortnightly intervals corresponding to late April to mid June (Table 9.3). After this period the high proportion of microlepidopteran larvae on bilberry disappears.

9.5. The density of Lepidoptera larvae on *Calluna vulgaris* and *Vaccinium myrtillus*

9.5.1. Methods

The density of lepidopteran larvae on each of the plants was calculated for each fortnightly interval. In order to more easily examine the seasonal patterns the intervals have been combined into early (April to mid June, *i.e.* intervals 9, 10, 11 and 12) and late (late June to September, *i.e.* intervals 13, 14, 15, 16, 17, 18 and 19) season for some aspects of the analysis. Data were kept separately for the three individual altitudes. The density estimates have been calculated by Berlese funnel sampling during 1990 and are the number of larvae per $0.25m^2$ area of vegetation. As the density data was skewed and could not be normalised by transformation, a non-parametric approach has been utilised and Kruskal-Wallis ANOVA tests have been used to examine for differences between the densities of larvae on the two plants.

9.5.2. Results

The densities of lepidopteran larvae on each plant during each fortnightly interval at the three altitudes are given in Table 9.4. The results of the Kruskal-Wallis tests for the significance of the difference in density on the two plants at any altitude during each time interval are given in Table 9.5. For ease of identification, densities which are significantly different are marked with an asterisk in Table 9.4. The general pattern is of higher densities on *V. myrtillus* during the spring and early summer (April to June) whereas after June densities are either higher on *Calluna* or not significantly different on the two plants.

The small number of samples and the extreme clumping of larvae in some of the samples has caused high standard errors. This has meant that in some intervals there is no significant difference even when mean densities on the two plants appear relatively different. To overcome this problem, the densities of larvae on each plant have been calculated for early and late in the season (Table 9.6). For all altitudes combined there was significantly higher densities of larvae on *V. myrtillus* (mean ± SE = 3.02 ± 0.917/$0.25m^2$) compared to *Calluna* (mean ± SE = 0.71 ± 0.304 /$0.25m^2$) early in the season, *i.e.* from late April to mid June. Later in the year after mid June there was no significant difference in the density of larvae on the two plants. The individual results for the three separate altitudes are less conclusive. The results for 470m agree

Table 9.3. The proportions of the total number of lepidopteran larvae found on *Calluna vulgaris* and *Vaccinium myrtillus* which were represented by the four taxonomic groupings of Geometridae, Noctuidae, 'Others' and Micros during each fortnightly time interval. Data are for all larvae collected by Berlese funnel extraction during 1990. The data are a combination of the results for each of the sample sites at 290, 470 and 650m. The 'Others' taxonomic group incorporates the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. A χ^2 statistic has been calculated using the actual numbers in each group. NS denotes that the result of the χ^2 test is not significant, *i.e.* $P>0.05$ and n is the total number of larvae. During intervals 10 and 15 sampling was carried out at Chapel Fell (650m) but no larvae were found. There was no sampling during interval 18.

Time interval (two weeks)	Plant species	*n*	Lepidoptera taxonomic group (%)				χ^2	*P*
			'Others'	Geometrids	Noctuids	Micros		
9 (April/ May)	*Calluna*	1	0	0	100	0	8.0 (2)	<0.05
	V. myrtillus	7	0	86	0	14		
11 (May/ June)	*Calluna*	14	0	93	0	7	16.7 (2)	<0.001
	V. myrtillus	130	0	36	2	62		
12 (June)	*Calluna*	26	4	92	4	0	31.8 (3)	<0.0001
	V. myrtillus	25	0	24	0	76		
13 (June)	*Calluna*	6	0	67	0	33	1.3 (1)	NS
	V. myrtillus	6	0	33	0	67		

Table 9.3. Continued.

Time interval (two weeks)	Plant species	*n*	Lepidopteran taxonomic group (%)				χ^2 (d.f.)	*P*
			'Others'	Geometrids	Noctuids	Micros		
14 (July)	*Calluna*	12	8	75	8	8	1.2 (3)	NS
	V. myrtillus	5	0	80	0	20		
16 (August)	*Calluna*	6	0	83	17	0	2.9 (1)	NS
	V. myrtillus	1	0	0	100	0		
17 (August)	*Calluna*	7	0	43	43	14	1.1 (2)	NS
	V. myrtillus	1	0	0	100	0		
19 (Sept.)	*Calluna*	7	14	0	86	0	0.48 (1)	NS
	V. myrtillus	3	33	0	67	0		

Table 9.4. The densities of larval Lepidoptera on the two plant species of *Calluna vulgaris* and *Vaccinium myrtillus* through the spring and summer of 1990 at each of the three study areas at 290, 470 and 650m. An asterisk denotes that the densities are significantly different ($P<0.05$) on the two plants as tested by Kruskal-Wallis ANOVA (Table 9.5). The density is the mean number of larvae per $0.25m^2$ quadrat as sampled by Berlese funnel extraction. Dashes indicate that no data were collected at that study area during that fortnightly period. There was no sampling during interval 18.

Time interval (two weeks)	Mean density of larvae ± SE ($0.25m^2$) (*n*)									
	290m			470m			650m			
	Calluna		*V. myrtillus*	*Calluna*		*V. myrtillus*	*Calluna*		*V. myrtillus*	
9 (April/May)	0.20 ± 0.199 (5)		1.60 ± 0.678 (5)	-		-	-		-	
10 (May)	-		-	-		-	0.00 (5)		0.00 (5)	
11 (May/June)	0.87 ± 0.291 (5)	*	7.47 ± 2.860 (5)	0.00 (5)		3.60 ± 3.360 (5)	0.20 ± 0.199 (5)		0.20 ± 0.199 (5)	
12 (June)	3.80 ± 3.072 (5)		0.40 ± 0.245 (5)	1.00 ± 0.548 (5)	*	4.20 ± 1.356 (5)	0.00 (5)		0.80 ± 0.374 (5)	
13 (June)	-		-	-		-	0.20 ± 0.199 (5)		0.40 ± 0.245 (5)	

Table 9.4. (continued)

Time interval (two weeks)	Mean density of larvae ± SE (0.25m²) (*n*)					
	290m		470m		650m	
	Calluna	*V. myrtillus*	*Calluna*	*V. myrtillus*	*Calluna*	*V. myrtillus*
14 (July)	0.80 ± 0.327 (10) *	0.07 ± 0.067 (15)	0.80 ± 0.583 (5)	0.40 ± 0.245 (5)	0.00 (5) *	0.60 ± 0.245 (5)
15 (July)	-	-	-	-	0.00 (5)	0.00 (5)
16 (August)	0.10 ± 0.099 (10)	0.20 ± 0.199 (5)	-	-	0.20 ± 0.199 (5)	0.00 (5)
17 (August)	-	-	-	-	0.20 ± 0.199 (5)	0.10 ± 0.099 (5)
19 (Sept.)	0.60 ± 0.399 (10)	0.30 ± 0.213 (10)	0.20 ± 0.199 (5)	0.00 (5)	-	-

Table 9.5. The results of the Kruskal-Wallis ANOVA tests of the differences in the density of larval Lepidoptera on the two plants of *Vaccinium myrtillus* and *Calluna vulgaris* in the fortnightly intervals through the spring and summer (Table 9.4). Significance has been taken at the 95% probability level and NS denotes that $P>0.05$. No samples were taken during interval 18.

Time interval (two weeks)	Results of Kruskal-Wallis test 290m χ^2	290m P	470m χ^2	470m P	650m χ^2	650m P
9 (April/May)	2.36	NS	-	-	-	-
10 (May)	-	-	-	-	0.00	NS
11 (May/June)	4.18	<0.05	2.22	NS	0.00	NS
12 (June)	1.03	NS	4.09	<0.05	3.75	NS
13 (June)	-	-	0.00	NS	0.429	NS
14 (July)	6.19	<0.05	0.057	NS	3.85	<0.05
15 (July)	-	-	-	-	0.00	NS
16 (August)	0.27	NS	-	-	1.00	NS
17 (August)	-	-	-	-	1.00	NS
19 (Sept.)	0.248	NS	1.00	NS	0.269	NS

Table 9.6. The mean densities of lepidopteran larvae on *Calluna vulgaris* and *Vaccinium myrtillus* during the early and late part of the sampling season at each of the three study areas at 290, 470 and 650m. Early season lasts from intervals 9 to 12 (April to mid June) and late from intervals 13 to 19 (mid June to September). The density of larvae was estimated by Berlese funnel sampling during 1990. The differences in the densities on the two plants have been tested for significance by Kruskal-Wallis ANOVA tests. Significance has been taken at the 95% probability level and NS denotes $P>0.05$.

Altitude	Time interval	Mean density of larvae ± SE (*n*) (larvae/0.25m^2) *Calluna*	*V. myrtillus*	Kruskal-Wallis ANOVA χ^2	*P*
All	early	0.71 ± 0.304 (55)	3.02 ± 0.917 (55)	6.34	<0.05
	late	0.36 ± 0.083 (85)	0.24 ± 0.059 (75)	0.62	NS
290m	early	1.32 ± 0.642 (25)	4.88 ± 1.818 (25)	3.08	NS
	late	0.43 ± 0.155 (35)	0.17 ± 0.084 (30)	1.62	NS
470m	early	0.33 ± 0.816 (15)	3.90 ± 1.709 (10)	7.28	<0.01
	late	0.52 ± 0.823 (25)	0.467 ± 0.743 (15)	0.02	NS
650m	early	0.07 ± 0.067 (15)	0.25 ± 0.123 (20)	1.26	NS
	late	0.12 ± 0.067 (25)	0.20 ± 0.074 (30)	0.63	<0.05

with those for all altitudes combined. At 290m the density on the two plant species is not significantly different either early or late in the year. At the Chapel Fell study area (650m), the densities were significantly different later rather than earlier in the year, even though the mean densities are more similar later rather than earlier in the year on the two plant species.

9.6. Aspects of the development of individual Lepidoptera species on two different host plants

9.6.1. Methods

Considerable numbers of larvae of *Hydriomena furcata* and *Eulithis* species (*E. populata* and *E. testata*) were found on both *Calluna* and *Vaccinium myrtillus*. These species overwinter as eggs and hatch as larvae in spring to feed on the new growth of the plants.

As a preliminary observation on the phenology of the two lepidopteran species, the first and final dates that larvae were recorded on each of the two plant species were examined. This is an unsophisticated form of comparison but it provides some idea of any temporal differences in development on the two plants.

The regression of head capsule width of individual larvae against day in the year was carried out separately for the larvae on *Calluna* and *V. myrtillus*. Only larvae captured at North Plantation (290m) were used because altitude affected the rate of growth. The results are a combination of data for the three years of the study from 1988 to 1990. The year of capture has no significant effect on the state of development (see results 9.6.2.) which justifies the use of a combination of data from 1989 and 1990. Head capsule width rather than weight is used as a indicator of development since it is less susceptible to variation caused by factors such as starvation.

Analysis of covariance was used to test for differences in the regression of larval size against time on the two plant species. As an initial assumption of the analysis, the slopes of the regression lines of development on *Calluna* and *V. myrtillus* were tested for homogeneity using SPSS (1990). The relationship between head capsule width and day was linear in *H. furcata* and for *Eulithis* larvae on *V. myrtillus*. For the *Eulithis* larvae present on *Calluna*, development was only linear up to week 24. After this time, the mean head capsule width showed little subsequent increase as the majority of the larvae were in the final (fifth) instar. Therefore the analysis for *Eulithis* larvae only included larvae found before week 25.

To calculate the time lapse in development between the larvae on *Calluna* and *V. myrtillus*, the day on which the mean head capsule width for the first instar of each lepidopteran species intersects the regression line of each of the plants is noted. The

95% confidence limits for these intersects were calculated according to the method given in Sokal and Rohlf (1981).

In order to illustrate the general patterns of development on the two plant species, the mean head capsule width of larvae during weekly intervals has been plotted. Samples of less than three larvae were combined with adjacent weeks and plotted at the mid-date mark.

9.6.2. Results

The first and last dates on which larvae of *Hydriomena furcata* and *Eulithis* species were recorded on the two plants are given in Table 9.7. They indicate that larvae of both species appear earlier on *V. myrtillus* but whereas *Eulithis* larvae disappear earlier on *V. myrtillus*, the larvae of *H. furcata* were recorded at a later date on this plant.

The mean head capsule width of larvae in individual weeks for each lepidopteran species are shown in Figures 9.1 and 9.2. The figures illustrate that in each week that larvae were found on both plant species the mean size of the larvae was always greater on *V. myrtillus* compared to *Calluna*. The results of linear regression of head capsule width of individual larvae against day in the year are given in Table 9.8. The importance of the calculation is that the slopes of the regression lines give an estimate of the growth rate of larvae on the two different plant species. For *H. furcata* larvae, there is no significant difference between the slope for the larvae on *Calluna* ($b \pm SE = 0.0219 \pm 0.0019$) compared to *V. myrtillus* ($b \pm SE = 0.0188 \pm 0.0017$) (Table 9.9). In *Eulithis* the slopes of head capsule width on day was significantly different between *Calluna* ($b \pm SE = 0.0125 \pm 0.0016$) and *V. myrtillus* ($b \pm SE = 0.0331 \pm 0.0052$).

Analysis of covariance indicated the regression lines of head capsule width against day in *H. furcata* to be significantly different on the two plants (Table 9.9). By inference, the *y*-axis intercepts of these two regression lines are also significantly different. For *Eulithis* the results of the analysis of covariance are given but the assumption of homogeneity of the slopes of the lines is not fulfilled, therefore the assumptions necessary for the application of analysis of covariance are not met. For both species, there is no information about the relationship between head capsule width and day at a earlier stage in the larval development. For both of the Lepidoptera species, the year of capture has no significant effect on the state of development (Table 9.9).

The estimations of the time lapse in development on the two different hostplants are shown in Table 9.10. These is a difference of approximately 20 days in *H. furcata* larvae on *V. myrtillus* compared to *Calluna* but a difference of only two days for the *Eulithis* larvae.

Table 9.7. The first and final dates that individual larvae of *Hydriomena furcata* and *Eulithis* species were found on *Calluna* and *V. myrtillus* at North Plantation (290m) during 1990. Days are counted from January 1. *Eulithis* species is a combination of data for *E. testata* and *E. populata*.

Lepidoptera species & plant species	First day recorded	Last day recorded	Total number of days recorded as larvae
H. furcata			
Calluna	124 (4 May)	178 (27 June)	54
V. myrtillus	112 (22 April)	183 (2 July)	71
Eulithis			
Calluna	123 (3 May)	208 (27 July)	85
V. myrtillus	112 (22 April)	146 (26 May)	34

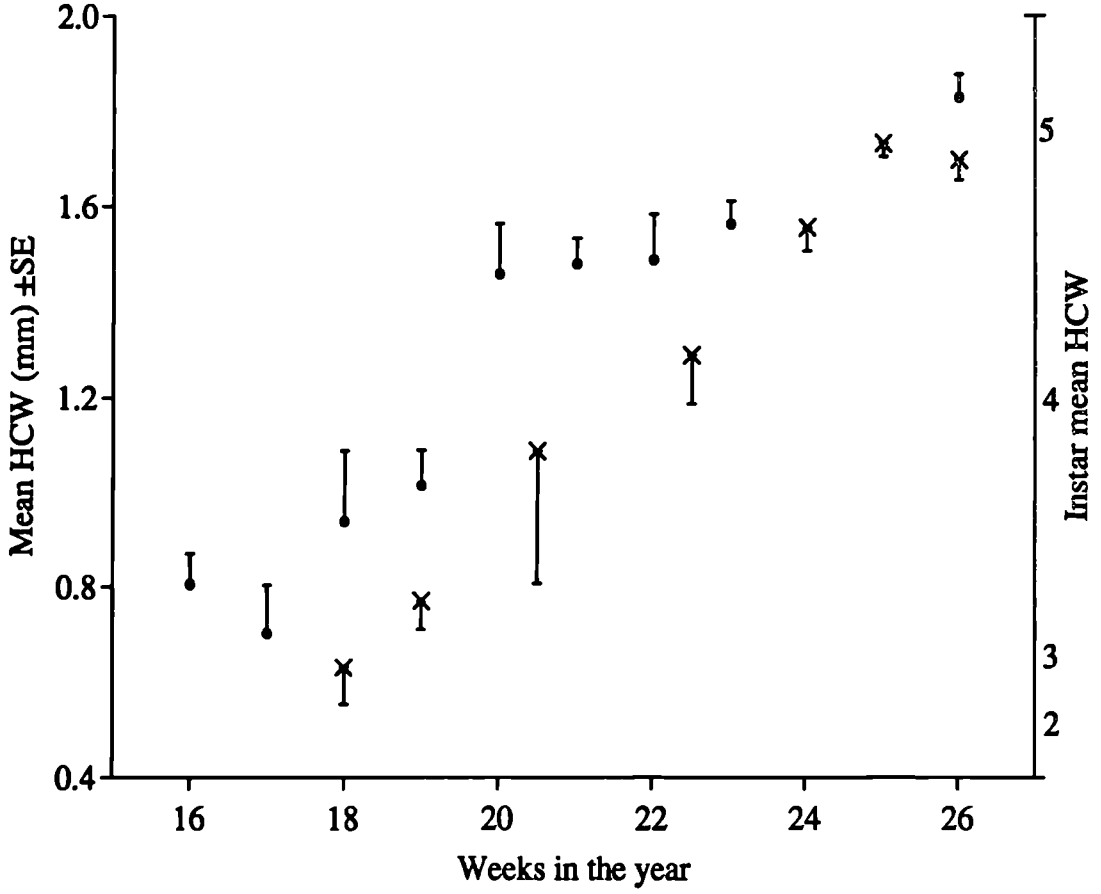

Figure 9.1. The larval development of *Hydriomena furcata* on the two plant species of *Calluna* (x) and *Vaccinium myrtillus* (•). Development is measured as the change in the mean head capsule width (HCW) of the larvae during weekly intervals of the larval period. Weeks are taken as seven day periods from the first of January. Data are for larvae collected at the single study area of North Plantation at 290m altitude during all three years of the study. The right *y*-axis displays the approximate mean head capsule widths of four of the five larval instars and can be used as an indication of the progression of larval development. Precise details of the mean HCW of the larvae in each instar are given in Table 6.1. The vertical bars indicate standard errors.

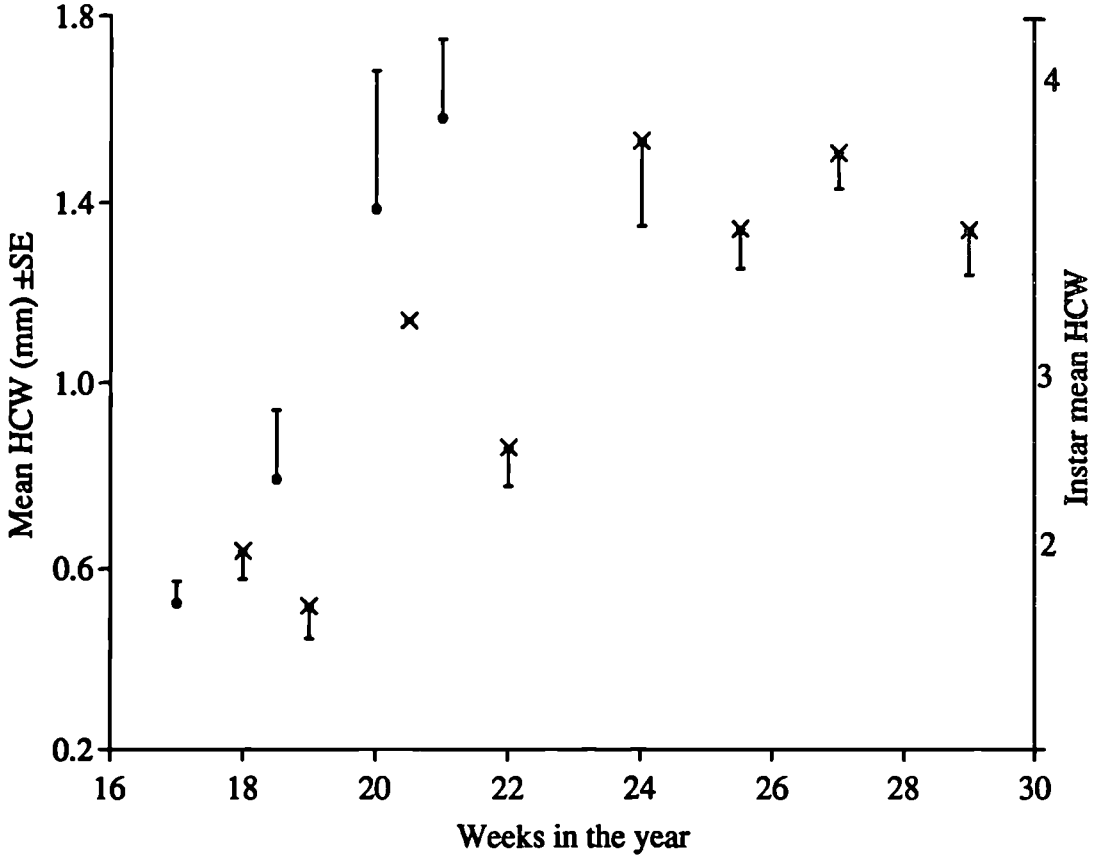

Figure 9.2. The larval development of *Eulithis* species on the two plant species of *Calluna* (x) and *Vaccinium myrtillus* (•). Data are a combination of results for *E. populata* and *E.testata*. Development is measured as the change in the mean head capsule width (HCW) of the larvae during weekly intervals of the larval period. Weeks are taken as seven day periods from the first of January. Data are for larvae collected at the single study area of North Plantation at 290m altitude during all three years of the study. The right *y*-axis displays the approximate mean head capsule widths of the larval instars and can be used as an indication of the progression of larval development. Precise details of the mean HCW of the larvae in each instar are given in Table 6.1. The vertical bars indicate standard errors.

Table 9.8. The development of the larvae of *Hydriomena furcata* and *Eulithis* species at 290m during 1990 on *Calluna vulgaris* and *Vaccinium myrtillus*. The results are shown as the linear regression of head capsule width of individual larvae (*y*-axis) against day in the year (*x*-axis). *b* is the regression coefficient and R^2 the coefficient of determination. The data for the *Eulithis* regression only includes larvae found before week 25, that is the linear part of the growth curve. *Eulithis* species is an amalgamation of data for *E. testata* and *E. populata* because of the difficulty of differentiating between the two species in the larval stage.

Lepidoptera species	Plant species	$b \pm SE$	constant ± SE	R^2	$F_{[d.f.]}$	P
H. furcata	*Calluna*	0.0219 ± 0.0019	-2.052 ± 0.287	74%	$137_{[1,49]}$	<0.0001
	V. myrtillus	0.0188 ± 0.0017	-1.334 ± 0.239	59%	$122_{[1,86]}$	<0.0001
Eulithis	*Calluna*	0.0207 ± 0.0034	-1.971 ± 0.460	54%	$38_{[1,32]}$	<0.0001
	V. myrtillus	0.0331 ± 0.0052	-3.297 ± 0.654	64%	$41_{[1,23]}$	<0.0001

Table 9.9. The analysis of covariance results for the regression lines of growth of *H. furcata* and *Eulithis* larvae on the two different plant species of *Calluna vulgaris* and *Vaccinium myrtillus*. Growth is measured as the head capsule width of individual larvae against day in year from 1 January. The factors are the plant species on which the larvae were found (either *Calluna* or *V. myrtillus*) and the year of capture (1989 or 1990). The analysis for *Eulithis* is a combination of data for *E. testata* and *E. populata* and only includes the larvae found before week 25, *i.e.* on the linear part of the growth curve. The slope column indicates whether the slope of the regression lines of head capsule width against day were significantly different for the different co-variables. Statistical significance has been accepted at the 95% probability level and NS denotes non-significance, *i.e.* $P>0.05$.

Species	Statistical values	Day	Plant	Year	Plant by year	Slope
H. furcata						
	F	138.57	24.45	0.82	0.11	1.44
	P	<0.0001	<0.0001	NS	NS	NS
Eulithis						
	F	67.97	10.32	0.40	-	17.28
	P	<0.0001	<0.01	NS	-	<0.0001

Table 9.10. The estimations of the time lapse in the development of the larvae of two lepidopteran species, *Hydriomena furcata* and *Eulithis* species, on *Calluna* and *Vaccinium myrtillus* at 290m. The intercept is the *x*-axis (days) value where the mean head capsule width for the first larval instar (0.354mm for *H. furcata* and 0.392mm for the *Eulithis* species) intersects the regression line. The difference is the divergence between the values for the two host plant species. The 95% confidence limits (cl) have been calculated according to the method of Sokal and Rohlf (1981). The data for *Eulithis* only includes larvae found before week 25, *i.e.* in the linear part of the growth curve. *Eulithis* species incorporates data for *E. testata* and *E. populata* because of the difficulty of differentiating between their larvae.

Lepidoptera species	Plant species	Intercept	95% cl lower	95% cl upper	Difference (days)
H. furcata					
	Calluna	110	86	131	20
	V. myrtillus	90	59	117	
Eulithis					
	Calluna	114	79	144	2
	V. myrtillus	112	87	132	

9.7. Discussion

The results of the literature review discussed in Chapter 4 indicate that approximately equal numbers of Lepidoptera species are associated with *Calluna* and *V. myrtillus*, although the incidence of species in some taxonomic families differs. During this study, the lepidopteran species richness was lower on bilberry compared to *Calluna* and in contrast to expectations gained from the literature, no species were found on bilberry which were not also found on *Calluna*. This discrepancy is probably the result of a number of factors. The sampling effort applied to bilberry over the three years of the study was much lower compared to *Calluna*. There was also probably an area effect as the general abundance of bilberry within the study areas was much lower in contrast to the extensice cover of *Calluna*. An additional reason is that there was a greater heterogeneity of *Calluna* growth form and habitats sampled compared to *V. myrtillus*.

The microlepidopteran species were more numerically abundant on *V. myrtillus* compared to *Calluna*, although this pattern disappears both on high altitude, blanket bog sites and later in the season. Microlepidopteran species have been recorded as numerically abundant on bilberry in other studies (Atlegrim 1989). The green colouring and shelter construction of the tortricid and pyralid species (*i.e.* micros) on bilberry has been shown to protect them from predation in comparison to the exposed positioning and dark colours of geometrids (Atlegrim 1991). The question arises as to why the microlepidopteran species should be more abundant on bilberry compared to *Calluna*. It is possible that these species may be less able to cope physiologically with the poorer nutritional quality of *Calluna* or be anatomically limited by factors such as bite size to cope with its differently structured leaves. Many microlepidopterans construct shelters from leaves, especially by rolling individual leaves around their body. This behaviour may present difficulties on *Calluna* compared to bilberry because of its growth form. The darker pigmentation of *Calluna* may remove the cryptic advantage of the bright green colouration of the microlepidopteran larvae. The larval periods of these microlepidopteran species that were abundant on bilberry were mainly limited to spring and early summer. This corresponds with the time when the bilberry leaves are at their most green and tender and presumably most nutritious. By mid summer the leaves become a darker green and orange, and have a much tougher texture. Mattson (1980) notes the confinement of the larval feeding of microlepidopteran species to the spring. He accounts for this in terms of their small size restricting their period of feeding to when the plant foliage is at its youngest and less tough (section 5.7).

There was no observable difference in the incidence of noctuid larvae on the two plants. Since these species tend to overwinter as larvae (Chapter 5), with feeding occurring until late in the autumn and beginning early in the spring, it was thought that they might be restricted by the deciduous nature of the plant. Atlegrim (1989)

makes no mention of them being abundant on bilberry although he only sampled from early June to mid August when noctuid species tend not to be in the larval stage. Another aspect is that the different timing of the flowering period in *V. myrtillus* means that there is no peak in flower feeding *Eupithecia* larvae in August and September as on *Calluna*.

The densities of lepidopteran larvae are higher on *V. myrtillus* earlier in the year in spring and early summer but are comparable or lower than those on *Calluna* later in the year after mid June. This would appear to be related to the presence of high numbers of micros on bilberry at the lower altitudes early in the year. Densities of lepidopteran larvae were only compared on the two plants from April to September. The situation in the other six months of the year is uncertain. However, variability in larval numbers are likely to be less during this half of the year as lepidopteran species remain in a single overwintering phase.

Atlegrim (1989) recorded the highest densities of larvae on bilberry during late June and early July although he did not present figures for the individual lepidopteran taxonomic groups. The later peak in densities in his samples are likely to be an effect of the shorter and later growing season in Sweden compared to northern England. Sage (1991) recorded the highest biomass of lepidopteran larvae during the first week of June on *V. myrtillus* in Scotland, although he only sampled during May and June. This finding is in consensus with the results of the present study even though the latitude and habitat differ.

Many of the game bird species such as capercaillie (*Tetrao urogallus*), black grouse (*Tetrao tetrix*) and red grouse (*Lagopus l. scoticus*), that are associated with the habitats of *Calluna* and *V. myrtillus* are generally only insectivorous as chicks. Caterpillars on *V. myrtillus* have been noted as an important food resource for capercaillie (Cramp and Simmons 1980) and black grouse (Picozzi 1986, Baines 1991). The peak in the density of lepidopteran larvae on *V. myrtillus* coincides with the early growth periods of the chicks of these avian species. At this time the densities of lepidopteran larvae are lower on *Calluna*, although the biomass may not necessarily be as proportionally low since microlepidopteran larvae are of smaller body weight compared to the other families. The importance of this difference between the two plant species may be of less consequence on moorlands where red grouse are the predominant game species. It is uncertain how the predation rates of the larvae in the study areas compare to those found by Atlegrim (1989) of about 63% in a Swedish woodland habitat. In contrast to the present study, the Swedish study investigated *V. myrtillus* growing as an forest understorey.

The evidence from *H. furcata* and *Eulithis* suggests that larval growth is initiated earlier on bilberry. There was no difference in the development rate of *H. furcata* larvae on the two plants but there was a significant difference in the time lapse of development on the two plants. In *Eulithis* the development rate was faster on bilberry

and as a result of this difference it was not possible to satisfy the necessary assumptions for the application of analysis of covariance. It is not known if the time lapse in development of larvae on the two plant species is maintained through to other parts of the life-cycle. It is possible that development on the two plant species becomes synchronised during the pupal phase. The results for *Eulithis* are complicated by the fact that it is an combination of data for two species that differ by a month in their larval periods. Therefore less emphasis should be put on these results compared to those for *H. furcata,* as the difference for development on the two plants may represent a difference in the proportions of the two *Eulithis* species feeding on *Calluna* and *V. myrtillus.*

It is not possible to say from this evidence that the individuals on the plants represent different host races (Diehl and Bush 1984) as it is unlikely that the two groups are reproductively isolated. Both of the Lepidoptera species have separate races which feed on *Salix* and birch species. In *H. furcata* this race is reported to be of a larger size (Skinner 1984) and to have an adult emergence that is a month earlier than the *Calluna* feeding race (Beirne 1947). Although it was once thought that female insects preferred to oviposit on the same plant species that they themselves fed on as larvae (Thorpe 1930) there is little evidence to support this theory (Wiklund 1975; Claridge and Wilson 1978b). In lepidopteran larvae there does tend to be habituation to the first plant species on which larvae feed (Jermy 1987). This knowledge together with the fact that *Calluna* and *V. myrtillus* tended to grow in relatively pure stands on the study areas make it unlikely that lepidopteran species were feeding simultaneously on both plant species.

It is only possible to speculate about the cause of the earlier initiation of larval development on *V. myrtillus.* The termination of egg diapause in the spring is likely to be photoperiodically controlled although temperature may also have some modifying effect (Tauber *et al.* 1986). It is possible that as a result of microclimate, the eggs on bilberry experience higher temperatures in early spring causing earlier hatching. An alternative explanation is that the eggs hatch simultaneously on the two plants but the earlier bud burst of bilberry allows the larvae on this plant to gain a lead over those on *Calluna* which are either feeding little or feeding on older less nutritious growth. It is also possible that egg hatch in these species is temporally diffuse and that early hatching eggs on *Calluna* may suffer high mortality. A similar situation has been described for the synchronisation of the growth of the sycamore aphid with bud burst of its host species. There is wide intraspecific variation in the time of bud-burst of sycamore but by having a egg hatch over a long period of time the synchronisation of some eggs is guaranteed (Dixon 1976). The fall cankerworm (*Alsophila pometaria* Lep.) feeds on several species of trees in North America that vary in their timing of bud burst. This species achieves host synchrony by having parthenogenetic host specific

clones that are synchronised with the phenology of their specific hosts (Mitter *et al.* 1979).

The conclusion of this comparison of *Vaccinium myrtillus* and *Calluna* is that the first plant has higher densities of lepidopteran larvae in early spring and summer, with the majority of this peak in numbers consisting of individuals of the microlepidopteran species. The densities equalise on the two plants by mid June which is largely a result of the completion of the larval periods of the microlepidopteran species. The timing of these high abundances on bilberry are such that they coincide with the breeding period of certain avian species. There was no evidence that the species richness of Lepidoptera was higher on bilberry, although this needs more detailed investigation. In two species of Lepidoptera studied there was evidence of earlier initiation of development on bilberry compared to *Calluna* although the mechanisms which allow this need elucidation.

Chapter Ten

General discussion

A survey of the literature revealed that at least 87 species of Lepidoptera are quoted feeding as larvae on *Calluna* in Britain. This figure is higher than any previous estimate of the number of Lepidoptera and insects said to feed on the plant. This total can be compared with oak (*Quercus robur*) which has 200 species of Lepidoptera (Feeny 1970) and over 300 species of herbivorous insects (Claridge and Wilson 1978a) associated with it. The estimate prompts questions about how the species richness of insects associated with *Calluna* varies locally within Britain and within the geographic range of the plant. *Calluna* can be found from northern Scandinavia and Iceland to the Mediterranean and Atlantic seaboard and to the Urals (Beijerinck 1940; Gimingham 1972). However, it is not a vegetational community dominant over the entire range. Lawton (1978) quoting evidence from Southwood (1960, 1961) suggested that plant species have more insect species associated with them near the centre of their geographical range. Britain is within the ecologically optimal part of the range of *Calluna*. Therefore the species richness of insects on *Calluna* in Britain maybe at the maximum within the plant's range, although insufficient data exists from other regions to test this.

Usher and Gardner (1988) comment on the lack of information as to how the presence of *Vaccinium myrtillus* and *Erica* species influence the nature of the invertebrate faunal community on *Calluna* moorlands. The results of the literature search, discussed in Chapter Four, suggest that although the species richness of the lepidopteran fauna is roughly equal for *V. myrtillus* and *Calluna*, it is reduced on *Erica*. An important aspect is the percentage of the fauna that is shared by plant species. For the lepidopteran species on *Erica*, 81% also occur on *Calluna* whereas the figure is only 34% between *V. myrtillus* and *Calluna*. Therefore the presence of *Vaccinium myrtillus* on moorlands is more liable to increase the species richness of Lepidoptera compared to the addition of *Erica* to monocultures of *Calluna*. It is possible however, that this relationship would not be the same if tested in a field situation. The results of Chapter Nine supplement this information in suggesting that the lepidopteran species prominent on *V. myrtillus* show an earlier spring peak in abundance in addition to a higher density of caterpillars. Whether these differences between the two plant species are duplicated in other insect groups requires investigation.

The insects of high altitude blanket bog are known to vary in their seasonal phenology in contrast to mineral grasslands and northern heath (Coulson and

Whittaker 1978; Coulson 1988). On blanket bog there is a very marked spring abundance of invertebrates whereas on the grasslands and dry heath areas, the peak of abundance is in July and August. The Lepidoptera recorded in this study were predominantly of northern heath habitats. With hindsight, the seasonal patterns discussed in Chapter 5 should have been investigated separately for northern heath and blanket bog. The spring peak in abundance of macrolepidoptera on *Calluna* mainly consisted of Geometridae species which illustrated a decline in species richness with altitude. By contrast those Noctuidae species constituting the autumn peak in larval abundance showed no decline in species richness with elevation. This suggests that there is some divergence in the seasonal phenology of the larval utilisation of *Calluna* on the two habitats.

It is obvious that the Lepidoptera compose a significant proportion of the insect fauna associated with *Calluna*, although it would seem that their importance declines with altitude. Coulson and Whittaker (1978) note the greater species richness of lepidopteran herbivores on *Calluna* on southern heathlands compared to blanket bog. This also appears to be true of the invertebrate fauna as a whole (Chapman and Webb 1978; Gimingham *et al.* 1979). On moorlands, the Lepidoptera would seem to be of lesser importance as vertebrate prey compared to other groups such as the Tipulidae, although this may be different in other habitats where capercaillie and black grouse are present (Baines 1991). Merlins *Falco columbarius* are recorded as feeding on adult emperor moths *Pavonia pavonia*, but they form only a small percentage of their diet (Watson 1979; Newton *et al.* 1984; Bibby 1987; Meek 1988). Atlegrim (1989), using exclosures, found avian predators reduced the number of caterpillars on bilberry by 63%. Information on the vertebrate and invertebrate predators of the Lepidoptera in this study is lacking.

The densities of lepidopteran larvae on *Calluna* were generally low and appeared to be well below that of the carrying capacity of the environment. This situation is habitual for folivorous insects with the exception of occasional outbreak species and tends to suggest that much potential niche space is not being utilised (Lawton 1982). Competition tends not to be important for folivorous insects (Hairston *et al.* 1960; Lawton and Strong 1981) with the trophic levels above and below an insect herbivore, in addition to weather, tending to be more important (Lawton and McNeill 1979; Price *et al.* 1980; Strong *et al.* 1984). It is possible although unlikely that much of the *Calluna* foliage is nutritionally inadequate or resistant to attack. Alternatively competition could occur in more subtle ways as suggested by Mason (1987); for example, adult lepidopteran defence of territory could result in exclusion and emigration of another species. McNeill and Prestidge (1982) compared the herbivore community on *Erica* and *Calluna* with that on the grass *Holcus*. They found a typical sample of 100 sweeps in June in the *Holcus* community to produce 1500 to 2000 insects

belonging to 15-20 species while the same sampling effort in an *Erica* community produced only 150-270 insects belonging to 6 species.

With the exception of *Hydriomena furcata* on mature aged stems of *Calluna*, no evidence was seen during the study of significant defoliation of the plant by Lepidoptera. Generally, natural plant communities are rarely seen to suffer from insect damage (Hairston *et al.* 1960) with folivorous insects collectively removing less than 10% of the primary production in most forests (Wiegert and Owen 1971; Mattson and Addy 1975). Despite this, insect species can have significant effects on plant populations (Brown 1982). The removal of invertebrate herbivores from broom (*Cytisus scoparius*) causes changes in the growth rate, mortality, natality and growth form of the plant as a result of reductions in loss of photosynthetic parts, seed predation, disease transmission and disruption of the plants nutrient and hormonal balance (Waloff and Richards 1977). Some of the Lepidoptera species that feed on *Calluna* are recorded as occasionally reaching outbreak proportions. For example, the vapourer (*Orgyia antiqua*) (Cameron *et al.* 1944) and the winter moth (*Operophtera brumata*) (Picozzi 1981). The temporal changes in abundance of Lepidoptera species means that a longer term study might have recorded alternative species as important consumers of heather. An insect species which is more frequently reported as reaching outbreak numbers and defoliating *Callluna* is the heather beetle *Lochmaea suturalis* which may reach larval densities of 1000 m^2 (Brunsting 1982). This species may cause the death of *Calluna* with older plants especially being effected (Morison 1963; Marrs 1986). Although the total intake of the beetles in outbreak areas is calculated to be greater than that of sheep at average stocking densities (0.8 per ha), their total food intake is still less than the potential amount of food available to them (Brunsting 1982). Within areas of heather beetle outbreaks the contemporary lepidopteran fauna is undoubtedly affected by the defoliation, however the restriction of the altitudinal distribution of the beetle to less than about 400m limits the amount of interaction. McNeill and Prestidge (1982) note that generally the insect communities on *Calluna* and *Erica* are stable over time with an order of relative abundance that does not change much between seasons. One of the most abundant invertebrate consumers of *Calluna* on blanket bog habitats is the psyllid *Strophingia ericae* with densities reaching 2,000m^2 (Hodkinson 1973). He estimated, however, that they have little observable effect on the host plant with the shoot production reduced by only 0.1 to 1%. Red grouse, which are one of the main vertebrate herbivores of heather, are recorded as taking less than 5% of the annual *Calluna* production (Hobbs and Gimingham 1987; Lawton 1990). It would therefore appear that *Calluna* foliage represents a super abundant food resource.

The larvae of *Hydriomena furcata* were calculated to take up to 50% of the current year's growth of foliage on tall stems of *Calluna* in mature aged stands. An unknown aspect is how the plants react after the larvae of *H. furcata* pupate. The stems may show compensatory growth and it is uncertain how the flowering and seed

production of the plants in August and September are affected by the defoliation that occurs earlier in spring and early summer. Experiments with vertebrate grazers of *Calluna* have discovered that a 40% utilisation of shoots over a five year period led to a reduction in the current season's production of shoots and a decline in cover from 98 to 71% (Grant *et al.* 1978, 1982). The stands in which the *H. furcata* larvae reach their highest densities are not those commonly utilised by red grouse, as the birds do not venture into taller *Calluna* stands (Savoury 1986). The proportion of stands of this age on a well managed moor are also quite small. It is not known if the high abundance of *H. furcata* on the moors sampled during this study are duplicated in other areas of Britain. Affirmative evidence is provided by Sage (1991) who found it to represent the dominant species on *Vaccinium myrtillus* in Scottish pinewoods. Despite the evidence that invertebrates may have a significant effect on plant growth and survival, they are rarely taken into consideration when the grazing of *Calluna* moorlands is discussed (*e.g.* Mowforth and Sydes 1989).

The conservation of *Calluna* dominated habitats has recently become prominent (Coulson *et al.* 1992), with Lepidoptera an important constituent of the fauna of such habitats. The loss of *Calluna* heathlands and moorlands is likely to be more pronounced at lower altitudes because of disturbance by man. The results of this study suggest that a proportionally greater loss of *Calluna* habitats at lower altitudes may lead to the loss of some Lepidoptera species because of the absence of many species at higher altitudes. However it must be remembered that this study did not investigate sites below an altitude of 290m. The species at the higher altitudes tend to be those also present at lower altitudes, although montane Lepidoptera species do occur in Britain (Beirne 1943). The results of Chapter 8 also illustrate the importance of the presence of *Calluna* stands of a wide range of ages. Good moorland management aims to burn on 12-15 year cycle which reduces the extent of *Calluna* stands of the mature and degenerate developmental phases. The recommendation of producing an increased representation of older *Calluna* stands on moorlands has previously been suggested as important for nature conservation purposes (Gimingham 1981; Coulson *et al.* 1992). Although generally Lepidoptera were recorded in all of the three developmental phases sampled their preferences were apparent in terms of their densities. The actual mechanisms for these preferences need to be further investigated, they may be related to the structure of the stands or the presence of alternative host species in the degenerate phase.

Distinctions were discovered during the study between the two largest macrolepidopteran families, the Geometridae and Noctuidae. Attempts to explain these disparities has highlighted the lack of information about the ecological differences between families and species of moths in contrast to the often more available information about the butterfly species.

The development of most arthropods is retarded at higher elevations, resulting in prolonged life-cycles in some cases, *e.g. Carabus problematicus* (Butterfield 1986).

While most univoltine species overwinter in one particular stage, two or more stages must be sufficiently cold hardy to survive in species that overwinter two or three times. The problems of evolution of multi stage cold hardiness may be one of the barriers that prevent many lowland species from invading high altitudes (Somme 1989). The number of generations that insect species pass through within a year tends to decline with altitude and latitude. *Entephria flavicinctata* is the single British macrolepidopteran species to be single brooded in the south and double brooded in the north, while the reverse is recorded in 33 species (Reavey and Lawton 1991). Few species that could be described as upland specialists were recorded in this study, although 31 macrolepidopteran species in the British fauna are said to be restricted to localities in the mountains of Scotland and North England (Beirne 1943). Scrutiny of these species reveals them to feed on plant species that have a distribution that reaches to higher altitudes than *Calluna*. For example, *Zygaena exulans* feeds on *Empetrum nigrum*, and *Anarta melanopa* on the same species plus *Arctostaphylous uva-ursi*.

The loss of three macrolepidopteran species with altitude on moorlands can be added to other known declines, *e.g.* one Linyphiid species is lost for every 43m rise in altitude (Coulson and Butterfield 1986). This decline in species richness of Lepidoptera may only ultimately be explained by careful investigation of the individual species. As noted by Danks (1978) the understanding of such phenomena is often hindered by the disjunction between biochemistry/physiology and ecology so that species are rarely simultaneously studied from both viewpoints.

Summary

1. Aspects of the ecology of the Lepidoptera associated with *Calluna vulgaris* and *Vaccinium myrtillus* were investigated in the north of England during 1988-1990.
2. Within the six study areas, 25 *Calluna* stands and five *V. myrtillus* stands were chosen as sample sites. The 30 sample sites represented a range of altitudes from 290 to 650m and the two different habitats of northern heath (<500) and blanket bog (>500m). The age of the plant stands varied between 8 and 28 years.
3. Investigations showed a significant decline in the aerial standing crop and height of the *Calluna* with increasing altitude. The height of the *Calluna* stands increased with age.
4. Sampling of the Lepidoptera concentrated on the collection and evaluation of the larval stage of the life-cycle.
5. The sampling techniques included Berlese funnel extraction, sweep-netting, timed searching and light trapping. The efficiency of these methods varied for individual taxonomic groups and species.
6. Within the three years of the study there was a considerable increase from year to year in the number of Lepidoptera species and individuals recorded.
7. A literature search revealed the number of Lepidoptera species recorded as feeding as larvae on *Calluna*, *V. myrtillus* and *Erica* species to be 86, 76 and 47 respectively. This contrasts with previous estimates of 40 species on *Calluna*.
8. The microlepidopteran species have been excluded from much of the analysis because of difficulties with identifying them.
9. The two macrolepidopteran families best represented by those species that feed as larvae on *Calluna* are the Geometridae and Noctuidae.
10. Twenty-six macrolepidopteran species were found to feed on *Calluna* during this study. Seven of these species are not specifically listed as feeding on this food plant by the literature.
11. Possible reasons are discussed as to why less than 50% of the species recorded by the literature as feeding on *Calluna* as larvae and having a distribution which includes Co. Durham, were recorded during the study.

12. The percentage of available species that were recorded differed for the three designated taxonomic groups of the Geometridae, Noctuidae and 'Others'. Species in the 'Others' taxonomic group were most likely to be recorded and those of the Noctuidae least likely.

13. The lepidopteran fauna of *Calluna* showed a greater similarity to that of the genus *Erica* compared to that of *V. myrtillus*.

14. The implications of the literature search are discussed with regard to the use of the literature for the compilation of faunal lists for plant species.

15. From considering all Lepidoptera species associated with *Calluna* in Britain to those found in this study there was a significant decrease in the number of Geometridae species overwintering as larvae ($P<0.001$). For the other taxonomic groups and overwintering stages there were no significant changes ($P>0.05$).

16. An investigation of the phenology of the macrolepidopteran larval utilisation of the *Calluna* plant indicated a peak during early spring followed by a second smaller peak in August and September. During June and July the species richness of larval macrolepidoptera was much reduced.

17. Of the 26 species found as larvae feeding on *Calluna* 61% were found outside the dates of the larval period as designated by the literature.

18. For the macrolepidopteran species found feeding as larvae on *Calluna* during this study some differences in phenology were evident between individual taxonomic groups. Geometridae species tended to overwinter as eggs and pupae and have a larval period in spring. In comparison Noctuidae species tended to hatch from eggs during late summer with the larval stage initiated in autumn and completed in early spring of the following year.

19. The pattern of macrolepidopteran larval abundance on *Calluna* is an exaggeration of that shown for species richness. Between April and July >80% of all larvae on the plant are Geometridae. From August through to April of the following year an increasing proportion of larvae are of the Noctuidae. During August and September the majority of geometrid larvae present are feeding on the flowers and seeds of *Calluna*.

20. There is a positive correlation between the month in which the larval period begins and its total length for the 26 macrolepidopteran species feeding as larvae on *Calluna*.

21. The larval instars for fifteen of the macrolepidopteran species were determined by the use of frequency distributions of larval head capsule widths.

22. No correlation was found between the number of larval instars and the size of the larvae in the final instar, *i.e.* larger species do not have a greater number of instars.

23. For the macrolepidopteran species investigated there was a positive correlation between the size of individual larvae in successive instars. That is, the larger larvae in one instar comprise the larger larvae in the following instar.

24. The mean ratio of increase of HCW between instars was 1.5.

25. There was a positive correlation between larval and adult size of macrolepidopteran species.

26. On an altitudinal gradient from 290-650m there was a loss of approximately three macrolepidopteran species for every 100m rise in altitude.

27. Of the three species lost for every 100m altitude increase, one species was of the Geometridae family and two were from the Others family grouping which incorporated the families of the Lasiocampidae, Saturniidae, Lymantriidae and Arctiidae. There was no significant effect of altitude on the species richness of Noctuidae.

28. The significant decline in macrolepidopteran species richness with altitude was only evident for the data collected in the final year of the study in 1990. Many fewer species and individuals of Lepidoptera were found during 1989 and 1990.

29. There were only two macrolepidopteran species of the 26 recorded that occurred at the highest altitude (650m) and which were not also present at the lowest altitude (290m).

30. There was a significant positive correlation between the altitudinal range and abundance of the 26 macrolepidopteran species recorded feeding as larvae on *Calluna*.

31. The densities of four macrolepidopteran species, *Lycophotia porphyrea*, *Macrothylacia rubi*, *Eupithecia nanata* and *Eulithis* were found to decline with elevated altitudes. In contrast the densities of two species, *Entephria caesiata* and *Diarsia mendica* were found to increase at higher altitudes.

32. Of the six species for which altitude had a significant effect on density, only two, *E. caesiata* and *M. rubi*, exhibited an altitudinal limit to distribution within the sampled altitude range of 290 to 650m.

33. No difference was observed in the levels of parasitism of macrolepidopteran larvae on the two habitats of northern heath and blanket bog. The percentage of all macrolepidopteran larvae parasitised was 14%.

34. There was no difference in the incidence of feeding specialisations and overwintering stages of macrolepidopteran species on northern heath and blanket bog.

35. There was a lower mean number of macrolepidoptera species recorded in *Calluna* stands of the building phase (7.6 species) of the plant life-history compared to those of the mature (10.3 species) and degenerate (10.7 species) phases.

36. Overall 24, 20 and 20 species were recorded in *Calluna* stands of the building, mature and degenerate phases.

37. Five macrolepidopteran species were confined to a single *Calluna* developmental stage, with four species found only in the building phase and one species in the degenerate. All five of these species were represented by less than five individuals.

38. A significantly higher density of macrolepidopteran larvae was recorded in *Calluna* stands of mature (0.64 larvae/0.25m^2) as opposed to degenerate phase (0.36 larvae/0.25m^2). More specifically this distinction was due to dissimilarities in the densities of Noctuidae species.

39. The densities of four species was found to alter significantly with age of the *Calluna* stand. The highest densities of *Macrothylacia rubi* larvae were found in degenerate stands of at least twenty years of age. Optimum densities of *Hydriomena furcata* larvae were recorded in mature phased stands of 14-21 years of age. The larval densities of *Eupithecia nanata* and *Lycophotia porphyrea* were found to be greatest in younger aged stands.

40. The micro-distribution of the larvae of *Hydriomena furcata* was investigated in mature aged *Calluna* stands where they occurred at high densities.

41. Within mature aged stands the chance of a *Calluna* stem being infested by *H. furcata* larvae increased with enhanced stem height. Taller stems also had a greater density of larvae upon them.

42. The larvae reduced the length of the current year's foliage growth of *Calluna* by 58% on the stems where they were present compared to non-infested stems.

43. The Lepidoptera associated with *Calluna* and *Vaccinium myrtillus* were compared and contrasted.

44. No macrolepidopteran species were recorded on *V. myrtillus* that were not also found on *Calluna*. In contrast only 15 of the 26 macrolepidopteran species recorded on *Calluna* were also found on *V. myrtillus*.

45. There were significantly higher densities of lepidopteran larvae on *V. myrtillus* (3 larvae/0.25m^2) compared to *Calluna* (0.7 larvae/0.25m^2) in

the spring and early summer. After this date there was no significant difference in larval densities on the two plant species. The high densities on *V. myrtillus* were attributable to the microlepidopteran species.

46. The larval growth of *Hydriomena furcata* and the genus *Eulithis* were compared for larvae feeding on *Calluna* and *V. myrtillus*.

47. For *H. furcata* larvae there was no difference in the rate of larval development on the two different plant species. However, larval growth appeared to be initiated earlier in the spring on *V. myrtillus* compared to *Calluna*, with an approximate 20 day lapse in development.

48. For *Eulithis*, the rate of larval development was faster for those larvae feeding on *V. myrtillus* compared to *Calluna*.

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Appendix A

The mean, standard deviation and maximum age of the *Calluna* stems at each sample site. Information was derived by counting the growth rings through cross sections of the plant stems as described in Chapter 2. The number of stems sampled is denoted as *n*.

Sample site	Mean age	Standard deviation	Maximum age	*n*
W1	18.00	6.03	26	6
NP2	10.40	1.67	12	5
NP3	11.00	2.24	14	5
NP4	17.80	3.19	22	5
WK10	23.33	3.14	28	6
WK11	8.60	1.34	10	5
WK12	15.80	2.17	19	5
WK13	9.00	1.00	10	5
WK14	11.40	1.34	13	5
WK15	13.20	3.11	17	5
WK16	16.67	2.34	19	6
WK17	13.60	2.07	15	5
WK18	16.80	3.83	21	5
WK19	6.80	0.84	8	5
WK20	10.63	2.39	15	8
WK21	8.50	1.41	10	8
WK22	16.20	3.11	21	5
WK23	9.40	1.95	12	5
WK24	12.80	1.92	15	5
WK26	11.80	2.28	14	5
WK27	8.80	1.30	11	5
ME29	14.60	2.30	17	5
MH32	18.00	3.32	21	5
MH33	14.60	2.61	17	5
CF37	10.40	1.82	13	5

Appendix B

Dates of Berlese funnel sampling

Sample site	Day and month during 1988														
	18/5	19/5	26/5	2/6	7/6	8/6	14/6	22/6	23/6	30/6	6/7	7/7	11/7	18/7	20/7
W1	X				X						X				X
NP2		X				X	X					X			
WK10				X					X				X		
WK16				X					X				X		
WK20				X					X				X		
WK21				X					X				X		
MH32			X								X			X	
MH33			X								X			X	

Sample site	Day and year during 1988														
	21/7	27/7	28/7	2/8	4/8	8/8	10/8	18/8	23/8	26/8	28/8	7/9	31/9	10/10	15/11
W1															
NP2	X				X				X						
WK10		X					X			X					
WK16		X					X			X					
WK20		X					X			X					
WK21			X				X			X					
MH32						X					X	X		X	X
MH33						X					X	X		X	X

Sample site	Day and month during 1989														
	7/2	17/2	14/3	3/4	18/4	19/4	20/4	26/4	27/4	3/5	4/5	9/5	10/5	16/5	17/5
NP1					X					X				X	
NP2		X	X	X		X									X
NP6															
WK10															
WK16							X				X				
WK20								X				X			
MH32	X								X				X		
MH33									X				X		

Sample site	Day and month during 1989														
	18/5	24/5	25/5	30/5	31/5	1/6	5/6	6/6	7/6	13/6	14/6	15/6	20/6	21/6	26/6
NP1				X						X					X
NP2					X						X				
NP6					X		X								
WK10							X								
WK16	X					X						X			
WK20		X						X					X		
MH32			X						X					X	
MH33		X							X					X	

Sample site	Day and month during 1989														
	27/6	28/6	4/7	5/7	10/7	11/7	13/7	19/7	20/7	26/7	27/7	1/8	2/8	7/8	8/8
NP1					X					X				X	
NP2	X					X				X					X
NP6							X					X			
WK10						X					X				
WK16		X				X					X				
WK20			X						X			X			
MH32				X				X					X		
MH33				X				X					X		

Sample site	Day and year in 1989														
	9/8	16/8	17/8	22/8	23/8	24/8	29/8	30/8	5/9	6/9	7/9	10/9	13/9	14/9	21/9
NP1					X				X						
NP2				X						X					X
NP6															
WK10					X							X			
WK16	X					X					X				
WK20		X					X						X		
MH32			X					X						X	
MH33			X					X						X	

Sample site	Day and year in 1989							
	27/9	3/10	4/10	5/10	10/10	12/10	23/10	25/10
NP1		X						
NP2			X					
NP6								
WK10							X	
WK16				X				
WK20	X				X			
MH32						X		
MH33						X		X

Sample site	Day and month during 1990											
	20/2	10/3	28/3	24/4	25/4	2/5	8/5	14/5	15/5	26/5	29/5	11/6
NP2			X									
NP6				X						X		
NP7										X		
WK10		X										
WK11												
WK16		X			X		X					
ME29									X		X	X
ME30											X	X
MH32	X				X				X			
MH33	X				X				X			
CF36								X			X	
CF37						X		X			X	X

Sample site	Day and month during 1990											
	13/6	24/6	26/6	4/7	10/7	23/7	2/8	6/8	9/8	21/8	28/8	18/9
NP2			X									
NP6				X								X
NP7				X								X
WK10											X	
WK11											X	
WK16	X						X					
ME29		X			X				X	X		
ME30		X			X							
MH32											X	
MH33											X	
CF36						X		X		X		
CF37						X		X		X		

Appendix C

Dates of sweep-net sampling

Sample site	Day and month during 1990						
	3/5	4/5	9/5	11/5	14/5	15/5	16/5
NP2		X		X			
NP3							
NP4							
NP5							
NP6							
NP7							
NP9		X					
WK10	X						X
WK11							
WK12							
WK13							
WK14							
WK15							
WK16	X						X
WK17							
WK18							
WK19							
WK20	X						X
WK21	X						X
WK22	X						
WK23							
WK24							
WK26							
WK27							
WK28							
ME29			X		X		
ME30							
MH32						X	
MH33						X	

Sample site	Day and month during 1990						
	20/5	22/5	23/5	24/5	28/5	31/5	6/6
NP2			X		X		
NP3							
NP4							
NP5	X						
NP6							
NP7							X
NP9	X						
WK10	X				X		
WK11	X				X		
WK12							
WK13							
WK14							
WK15							
WK16			X				
WK17							
WK18							
WK19	X						
WK20				X			
WK21		X		X	X		
WK22							
WK23							
WK24						X	
WK26							
WK27							
WK28							
ME29					X		
ME30							
MH32							
MH33							

Sample site	Day and month during 1990						
	13/6	14/6	9/7	13/7	16/7	19/7	20/7
NP2			X		X		
NP3							
NP4							
NP5							
NP6							
NP7						X	
NP9							
WK10						X	X
WK11							X
WK12							
WK13							
WK14							
WK15							
WK16		X	X	X		X	X
WK17							
WK18							
WK19							
WK20		X		X		X	
WK21		X	X	X			X
WK22							
WK23							
WK24							X
WK26					X	X	X
WK27							X
WK28						X	
ME29	X				X		
ME30							
MH32							
MH33							

Sample site	Day and month during 1990						
	25/7	26/7	27/7	30/7	31/7	2/8	6/8
NP2			X	X			
NP3							
NP4				X			
NP5			X	X			
NP6				X			
NP7				X			
NP9							
WK10	X	X					X
WK11	X	X					X
WK12							
WK13							
WK14							
WK15							
WK16	X		X				X
WK17	X		X				
WK18		X	X				
WK19	X		X				X
WK20	X		X				X
WK21	X					X	X
WK22			X				X
WK23			X				
WK24	X		X			X	X
WK26	X		X				
WK27							
WK28							
ME29					X		
ME30					X		
MH32							
MH33							

Sample site	Day and month during 1990						
	7/8	9/8	10/8	14/8	15/8	16/8	17/8
NP2	X	X		X	X		X
NP3							
NP4							
NP5							
NP6							
NP7							X
NP9							
WK10	X				X	X	X
WK11	X					X	X
WK12							
WK13							
WK14							
WK15							
WK16	X			X	X	X	X
WK17	X						X
WK18	X						X
WK19	X						X
WK20	X						X
WK21	X					X	X
WK22	X						
WK23							
WK24	X						X
WK26	X						
WK27							
WK28							
ME29		X	X				
ME30							
MH32							
MH33							

Sample site	Day and month during 1990						
	18/8	21/8	23/8	24/8	26/8	27/8	30/8
NP2	X		X				
NP3						X	X
NP4							X
NP5							
NP6							
NP7	X						
NP9							
WK10	X		X			X	
WK11	X		X			X	X
WK12							
WK13							
WK14							
WK15							
WK16	X		X			X	
WK17	X		X				X
WK18	X		X				X
WK19	X		X			X	
WK20	X		X	X		X	
WK21	X		X	X		X	
WK22			X				
WK23				X			
WK24	X		X			X	
WK26						X	
WK27							
WK28							
ME29		X					
ME30							
MH32					X	X	
MH33						X	

Sample site	Day and month during 1990						
	3/9	5/9	6/9	7/9	11/9	13/9	27/9
NP2				X	X		X
NP3				X			X
NP4				X			
NP5							
NP6							
NP7				X			
NP9							
WK10	X		X	X	X	X	X
WK11	X		X	X	X	X	X
WK12			X	X	X	X	X
WK13			X	X	X	X	X
WK14			X	X	X	X	X
WK15				X	X	X	X
WK16	X	X			X		X
WK17	X				X		X
WK18	X				X		X
WK19	X	X	X		X		X
WK20	X	X	X		X		X
WK21	X	X			X		X
WK22	X				X		X
WK23	X				X		X
WK24	X		X				X
WK26	X				X	X	X
WK27	X						
WK28							
ME29					X		
ME30					X		
MH32							
MH33							

Sample site	Day and month in 1990			
	6/10	7/10	8/10	9/10
NP2				
NP3				
NP4				
NP5				
NP6				
NP7				
NP9				
WK10				
WK11				
WK12				
WK13				
WK14				
WK15				
WK16				
WK17				
WK18				
WK19				
WK20				
WK21				
WK22				
WK23				
WK24				
WK26				
WK27				
WK28				
ME29				
ME30	X		X	X
MH32	X	X	X	X
MH33	X	X	X	

Appendix D

Dates of search sampling (4 samples of 5 minutes)

Sample site	14/6/90	18/6/90	19/6/90	20/6/90	21/6/90	27/6/90	28/6/90	2/7/90	5/7/90	9/7/90
NP2		X								
NP5		X								
WK10	X	X	X	X		X	X			
WK11	X	X	X	X		X	X			
WK16	X	X	X	X		X	X	X		X
WK17				X	X	X	X	X		
WK18				X		X	X			
WK19	X		X			X	X			
WK20	X			X						
WK21	X		X	X		X	X			X
WK22				X	X	X	X	X	X	X
WK24			X	X		X	X			
WK25	X									
WK26						X	X			X
WK27			X	X						

Appendix E

Dates of search sampling (2 samples of 5 minutes)

Sample site	2/10/90	10/10/90	13/10/90
NP2	X		
NP3		X	
NP5			X
WK10	X	X	
WK11	X	X	
WK12		X	
WK13		X	
WK14		X	
WK15		X	
WK16	X	X	
WK17	X	X	
WK18	X	X	
WK19	X	X	
WK20	X	X	
WK21	X	X	
WK22	X		
WK23	X	X	
WK24		X	
WK26		X	
WK32			X
WK33			X

Appendix F.

Lepidoptera stated by the literature (Stokoe and Stovin 1948; Allan 1949; Bradley *et al.* 1973, 1979; Skinner 1984; Carter and Hargreaves 1986; Goater 1986; Emmet 1991) as feeding on *Calluna vulgaris, Vaccinium myrtillus* and *Erica* species (*i.e. Erica tetralix* and/or *Erica cinerea*) within Britain. Information on distribution of macrolepidopteran species has been taken from Skinner (1984) and Dunn and Parrack (1986) and microlepidoptera species from Emmet (1991). X indicates that the Lepidoptera species is mentioned by one of the seven texts as feeding on that foodplant. Nomenclature is taken from Emmet (1991). The subspecific names are given where appropriate. A single quoted sub-species indicates that the other subspecies do not feed on these foodplants. Whereas more than one sub-species indicates that they have the same foodplant preferences.

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
NEPTICULIDAE				
Stigmella myrtillella (Stt.)		X		X
ZYGAENIDAE				
Zygaena exulans (Hohen.)	X	X		
PSYCHIDAE				
Pachythelia villosella (Ochs.)	X		X	
Sterropterix fusca (Haw.)	X			X
COLEOPHORIDAE				
Coleophora juncicolella Stt.	X		X	X
C. pyrrhulipennella Zell.	X		X	X
OECOPHORIDAE				
Pleurota bicostella (Cl.)			X	X
Amphisbatis incongruella (Stt.)	X			X
Diurnea phryganella (Hb.)		X		X

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
GELECHIIDAE				
Aristotelia ericinella (Zell.)	X			X
Xenolechia aethiops (Humph. & Westw.)			X	X
Lita sexpunctella (Fabr.)	X			X
Neofaculta ericetella (Geyer)	X		X	X
SCYTHRIDIDAE				
Scythris empetrella Karsh. & Niel.	X		X	
TORTRICIDAE				
Eupoecilia angustana fasciella (Don.)	X			X
Argyrotaenia ljungiana (Thunb.)	X		X	X
Aphelia viburnana ([D. & S.])		X	X	X
Clepsis senecionana (Hb.)		X		X
Lozotaenia forsterana (Fabr.)		X		X
Epagoge grotiana (Fabr.)		X		X
Philedonides lunana (Thunb.)	X		X	X
Eulia ministrana (Linn.)		X		X
Exapate congelatella (Cl.)	X		X	X
Spatalistis bifasciana (Hb.)		X		
Acleris caledoniana (Steph.)		X		X
Acleris hyemana (Haw.)	X		X	X
A. lipsiana ([D. & S.])		X		X
A. maccana (Treit.)		X		
Celypha cespitana (Hb.)	X			X
Oleuthreutes metallicana (Hb.)		X		
O. schulziana (Fabr.)	X			X
Apotomis sauciana (Frol.)		X		X
Ancylis unguicella (Linn.)	X		X	X
A. uncella ([D. & S.])			X	X

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
A. myrtillana (Treit.)		X		X
Epinotia mercuriana (Frol.)	X	X		X
Rhopobota ustomaculana (Curt.)		X		X
R. naevana (Hb.)		X		X
R. myrtillana (Humph. & Westw.)		X		X
PYRALIDAE				
Selagia argyrella ([D. & S.])	X			
Pyla fusca (Haw.)		X	X	X
Pempelia palumbella ([D. & S.])	X		X	X
LYCAENIDAE				
Callophyrs rubi (Linn.)	X	X	X	X
Plebejus argus (Linn.)	X		X	
LASIOCAMPIDAE				
Trichiura crataegi (Linn.)	X	X	X	X
Lasiocampa trifolii ([D. & S.])	X			
Lasiocampa quercus callunae Palmer	X	X		X
Macrothylacia rubi (Linn.)	X	X	X	X
Phyllodesma ilicifolia (Linn.)		X	X	
SATURNIIDAE				
Pavonia pavonia (Linn.)	X	X	X	X
GEOMETRIDAE				
Clorissa viridata (Linn.)	X		X	
Jodis lactearia (Linn.)		X		X
Scopula ternata (Schr.)	X	X		X
Idaea straminata (Borkh.)	X	X		X
Idaea contiguaria britanniae (Mull.)	X		X	
Scotopteryx mucronata (Scop.)	X			X

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
Entephria caesiata ([D. & S.])	X	X	X	X
Eulithis testata (Linn.)	X		X	X
Eulithis populata (Linn.)		X		X
Chloroclysta citrata (Linn.)	X	X		X
Chloroclysta concinnata (Steph.)	X			
C. truncata (Hufn.)	X	X		X
Hydriomena furcata (Thunb.)	X	X		X
Hydriomena ruberata (Freyer)	X			X
Rheumaptera hastata hastata (Linn.) *nigrescens* (Prout)		X		X
Rheumaptera undulata (Linn.)		X		X
Epirrita dilutata ([D. & S.])		X		X
Epirrita autumnata (Borkh.)		X		X
E. filigrammaria (H. -S.)	X	X		X
Operophtera brumata (Linn.)	X			X
Perizoma didymata didymata (Linn.)		X		X
Eupithecia satyrata satyrata (Hb.) *callunaria* Doubl. *curzoni* Gregs.	X			X
Eupithecia absinthiata goossensiata Mab.	X		X	X
Eupithecis vulgata vulgata (Haw.)		X		X
Eupithecia nanata angusta Prout	X			X
Chloroclystis debiliata (Hb.)		X		
Gymnoscelis rufifasciata (Haw.)	X			
Carsia sororiata (Hb.)		X		X
Abraxas grossulariata (Linn.)	X			X
Semiothisa brunneata (Thunb.)	X	X		X
Cepphis advenaria (Hb.)		X		
Pachycnemia hippocastanaria (Hb.)	X			

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
Odontopera bidentata (Cl.)		X		X
Angerona prunaria (Linn.)	X			
Lycia lapponaria scotica (Harr.)	X		X	
Selidosema brunnearia scandinaviaria Stdgr.	X		X	
Cleora cinctaria cinctaria ([D. & S.])		X	X	
Alcis repandata repandata (Linn.) *murana* Curt. *sodorensium* (Weir.)	X	X		X
Ematurga atomaria atomaria (Linn.) *minuta* Heydemann	X		X	X
Theria primaria (Haw.)		X		X
Gnophos obfuscata ([D. & S.])	X		X	X
Gnophos obscurata ([D. & S.])	X			
Dyscia fagaria (Thunb.)	X		X	X
Perconia strigillaria (Hb.)	X		X	X
LYMANTRIIDAE				
Dicallomera fascelina (Linn.)	X			X
ARCTIIDAE				
Spiris striata (Linn.)	X			
Coscinia cribraria bivattata (South)	X	X	X	
Diacrisia sannio (Linn.)	X		X	X
NOCTUIDAE				
Noctua comes Hb.	X			X
Paradiarsia sobrina (Dup.)	X	X	X	

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
Paradiarsia glareosa glareosa (Esp.)	X		X	X
Lycophotia porphyrea ([D. & S.])	X		X	X
Diarsia mendica mendica (Fabr.)	X	X		X
Diarsia dahlii (Hb.)		X		X
Diarsia brunnea ([D. & S.])		X		X
Xestia alpicola alpina (Humph. & Westw.)	X	X		X
Xestia c-nigrum (Linn.)		X		X
Xestia ashworthii (Doubl.)	X		X	
Xestia baja ([D. & S.])		X		X
Xestia castanea (Esp.)	X		X	X
Xestia agathina agathina (Dup.) *hebridicola* (Stdgr.)	X		X	X
Eurois occulata (Linn.)	X	X		Emigrants
Anaplectoides prasina ([D. & S.])		X		X
Cerastis rubricosa ([D. & S.])		X		X
Cerastis leucographa ([D. & S.])		X		Extinct in Co.D
Anarta myrtilli (Linn.)	X		X	X
A. cordigera (Thunb.)		X		
A. melanopa (Thunb.)		X		
Polia bombycina (Hufn.)		X		X
Polia trimaculosa (Esp.)		X		
Lacanobia contigua ([D. & S.])	X			Single record
Orthosia gothica (Linn.)		X		X
Papestra biren (Goeze)	X	X	X	X
Aporophyla lutulenta lueneburgensis (Freyer)	X			X
Aporophyla nigra (Haw.)	X			X
Lithomoia solidaginis (Hb.)	X	X		X

	Larvae feed on:			Present
	Calluna vulgaris	*Vaccinium myrtillus*	*Erica* species	in Co. Durham
Lithophane lamda (Fabr.)		X		
Agrochola macilenta (Hb.)	X			X
Agrochola helvola (Linn.)	X	X		X
Acronicta menyanthidis	X	X		X
menyanthidis (Esp.)				
scotica Tutt				
Acronicta auricoma ([D. & S.])		X		
Acronicta euphorbiae ([D. & S.])	X			
Acronicta rumicis (Linn.)	X			X
Hyppa rectilina (Esp.)		X		X
Heliothis maritima	X		X	
warnecki Bours.				
Autographa pulchrina (Haw.)		X		X
Syngrapha interrogationis	X	X		X
(Linn.)				
Hypena crassilis (Fabr.)		X	X	
Schrankia taenialis (Hb.)	X			
Hypenodes humidalis Doubl.			X	
Total numbers feeding on the plant species	**86**	**76**	**47**	