Population Ecology of *Pleuroptya ruralis* (Scopoli) (Pyralidae:Pyraustinae)

by

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ABSTRACT

Population Ecology of *Pleuroptya ruralis*
(Lepidoptera:Pyralidae)

A natural population of *Pleuroptya ruralis* has been studied for three years with the following aims: (1) to elucidate its life history; (2) to study the variations in the larval and adult densities; (3) to identify the mortality factors acting upon them; (4) to investigate possible relationships between the intensity of the mortality factors and the spatial distribution (horizontal and vertical) of *P. ruralis* ;(5) to describe the role of the major mortality factors in determining the size of the population studied; (6) to assess the potential of the system for further studies about the mechanism of population regulation.

P. ruralis caterpillars were individually labelled and followed throughout their development on a natural growth of their food plant, *Urtica dioica* (the nettle), near Leeds, Yorkshire, United Kingdom. Parasitism and predation as well as the distribution and movements of the larvae on the host plant were assessed.

Caterpillars were also collected and reared in the laboratory for identification of the parasitoid species and to provide support for the field results.

Adults were studied in the field by the mark-release-recapture method. Potential female fertility was investigated in the laboratory.

The population suffered a dramatic decline in numbers during the period of this study. The main factors determining the observed population levels were the interactions between the weather, time spent in development, deviations in the sex ratio, bird predation towards the completion of pre-adult development and parasitization by a braconid (*Macrocentrus grandii*). Other parasitoids also had some effect, notably *Diadegma* sp. Predation also had a strong impact on the population of *M. grandii*. Birds appear to concentrate their attack in the part of the plant in which they are more likely to find the prey.

Weather also influenced adult activity and availability of nectar sources in the field, and starvation of females reduced fecundity in the laboratory. Thus, egg shortfall may also have been important in the decrease of population size.

The field method used with the caterpillars provided detailed and valuable information about individual and spatial variation and it is suggested that the system 'nettles / *P. ruralis* / natural enemies' can be a powerfull tool for studies on the mechanisms of population regulation.

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SUMMARY OF NOTATION

F - female; relative to/of females

M - male; relative to/of males

SE - standard error

^ - denotes estimated value for the parameter

i - day of sampling, number of days elapsed since the first sampling occasion

n - total number of individuals caught (marked and unmarked); captures

m - number of marked individuals caught; recaptures

mov - movement of individuals recorded between the nettle clumps; number of individuals recaptured in a clump of nettles other than the one they were last captured

movrate - number of individuals recorded moving between nettle clumps as a proportion of recaptures

N - population size

M - number of marks at risk; marks/marked individuals available to capture in the population

SI - sampling intensity

ø - daily survival rate; proportion of the population/ chances of an individual surviving until the next day

B - number of individuals added to the population (birth + immigration) between two consecutive days.

mml - mean minimum longevity

mam - mean age of marks recaptured on the subsequent sampling occasion

MRR - mark-release-recapture

E_o - life expectancy at birth

FY - fed young virgin females

FV - fed virgin females

SV - starved virgin females

FSV - fed suspected virgin females

SSV - starved suspected virgin females

FM - fed mated females

SM - starved mated females

k - dispersion parameter; $k = \bar{x}^2 - (s^2/n) \; / \; s^2 - \bar{x}$

CHAPTER 1 GENERAL INTRODUCTION

Explaining the distribution of organisms in space and the variation of their numbers in time is the basic aim of population ecology. While insect population extinctions and recolonization events are not infrequent in nature, many populations remain extant for long periods and show no signs of becoming extinct. This 'persistence' suggests the existence of demographic mechanisms that are 'density dependent', i.e. that inflict higher mortality (or a drop in production) at high than at low densities. These mechanisms would promote a tendency in populations to return to an 'equilibrium' level after perturbations, and thus 'regulate' population numbers. Factors that cause population change but do not show any relation to population size, though important in determining this equilibrium point, simply 'limit' the size of the population, but do not promote 'stability' in population levels (Sinclair, 1989).

Density dependence has long been believed to be a major aspect in the ecology of populations (e.g. Nicholson, 1933; Nicholson & Bailey, 1935; Solomon, 1949; Milne, 1957; Holling, 1959a & b), and the view that natural enemies can act in a density dependent way is widely held (e.g. Hassell, 1985; Hassell & Waage, 1984; Heads & Lawton, 1983; Huffaker, 1958; Southwood & Commins, 1976; Strong, Lawton & Southwood, 1984).

Certain features of natural enemies are believed to enhance their ability to cause density dependent mortality: (i) prey/host specificity; (ii) synchronization with the prey/host; (iii) potential to increase in density when the prey/host does; (iv) consumption requirement of few (or only one) prey/host items to complete its development (so that its population could persist even when the prey/host density is low); (v) high searching ability (Murdoch, Chesson & Chesson, 1985). These features are more typical of parasitoids than predators. Parasitoids have indeed been shown to have the potential to act in a density dependent way (e.g. Hassell, 1982).

Empirical support for this view comes from the biological control programmes successfully carried out by the introduction and establishment of one or more natural enemies (in many cases parasitoids), which were able to decrease drastically the pest density and keep it at a low equilibrium level (see De Bach, 1974; Hill, 1983 and Hassell & Waage, 1984 for lists of examples).

However, population regulation through density dependence is still a very controversial subject (Murdoch & Walde, 1989) and has generated more debate than almost any other topic in ecology (Hassell, 1987). On the one hand, there are studies (and literature reviews) that conclude that there is not enough evidence for density dependence/natural enemies commonly playing a major role (or being at all necessary) for population regulation and persistence (e.g. Den Boer, 1968; Dempster, 1983; Dempster & Pollard, 1981; Stiling, 1987 & 1988). On the other hand, there are those

works that support, either theoretically and/or with experimental evidence (or literature reviews) that some kind of density dependent process acting as a negative feedback at least some of the time on at least part of the population must be involved in the dynamics of populations (e.g. Hassell, 1985 & 1987; Hassell, Latto & May, 1989; Southwood & Reader, 1987; Heads & Lawton, 1983; Murdoch & Reeves, 1987).

It is argued that, if there is not more published field evidence of the importance of density dependent processes, it is because its detection presents major difficulties. It depends on accurate field measurements of the right parameters, on the right spatial scale over a large number of generations. Which are the 'right' parameters and the 'right' scale cannot be known without a proper understanding of the biology of the species. Moreover, the methods available for the analysis of this type of data seem far from adequate (e.g. Hassell, 1985, 1987 & 1989; Murdoch & Walde, 1989). For instance, within generation individual variability and spatial heterogeneity have been shown to be crucial stabilizing mechanisms, but are generally hidden under averages per generation both in the collection and in the analysis of the data (Hassell, 1987; Heads & Lawton, 1983; Southwood & Reader, 1986).

These ideas seem well grounded now but there is still only little field evidence published because, given the complexities of nature, it is not an easy task to record all the necessary temporal and spatial variation and cover the whole life cycle of the species studied. The first step is finding a natural system where it is possible to investigate thoroughly the ecology of the target population.

The Lepidoptera have proved to be useful tools in the study of natural populations and more is known about the dynamics of their populations than about any other comparable group of invertebrates (Ehrlich, 1984). Natural enemies take a heavy toll on their populations (Dempster, 1984) and parasitoids, in particular, may attack all stages except the adult (Shaw & Askew, 1976). Age classes can be identified based on the succession of stages, and the adults can be studied by methods such as mark-release-recapture. Mortality factors can thus be assessed throughout the different developmental phases.

Some studies (mainly long term ones) were able to identify density dependent processes acting on lepidopteran populations, others were not (see Hassell, Latto & May (1989) for a comprehensive list). However, the knowledge accumulated so far has led to surprisingly few generalities about this group, let alone about herbivores in general (Ehrlich, 1984).

P. ruralis (Lepidoptera: Pyralidae) caterpillars feed on nettles, a plant with a simple structure where spatial parameters can be measured. The behaviour of the larva is such that individuals can be identified in the field according to their location on the plant. As with other Lepidoptera it suffers from the action of a complex of natural enemies, including parasitoids. In other words, the 'nettles / *P. ruralis* / natural enemies' system looked to be very promissing for an investigation of the problems

discussed above.

The Pyralidae family comprises a large number of species, distributed from tropical to temperate regions, many of which are agricultural or stored products pests. Apart from the pest species, very little is known about the ecology of natural populations of pyralids (Beirne, 1954; Goater, 1987; Hill, 1983).

The primary aim of this study was to elucidate the biological intricacies of *P. ruralis* and investigate the potential of the system for longer term and more directed studies on population regulation. Thus, individuals were followed throughout their development, natural enemies identified (as far as possible) and the spatial and temporal variation investigated.

Chapter 2 describes the system studied and the study site in some detail. Chapter 3 deals with the adult population and is divided into two main sections: (3.1) presents a mark-release-recapture study of the adult population; (3.2) investigates the reproductive potential of females reared under different conditions in the laboratory. Chapter 4 forms the bulk of this thesis and reports the laboratory and field results on the development, parasitization, predation and distribution of the immature stages. Variations in the phenology and survival for individuals suffering different fates are analysed and discussed. In both Chapters 3 and 4, the advantages and limitations of methods for the collection and analysis of the data are examined. Finally, Chapter 5 brings together the information from the previous chapters and presents life tables for both *P. ruralis* and its main parasitoid. Some general conclusions are reached and suggestions for further work are given.

CHAPTER 2 THE SYSTEM STUDIED

A moth population, its natural enemies and its host plant (the nettle) were found to be a natural system very well suited to investigate the ideas outlined in the introduction. The nettle-arthropod community has recently been described elsewhere (Davis, 1983); however, very little is known about the population ecology of the species here dealt with.

Based on the findings of this study and as an introduction, a brief description is given below of aspects of the system most relevant to the biology of the moth and a summary diagram of its life cycle is presented in figure 2.1.

2.1 NETTLES

Urtica dioica Linnaeus (Urticaceae), the 'stinging nettle' (fig 2.2) is common and grows in many situations: open fields, semi-shaded areas or woodland; in clay, sandy or peat soils; over a range of altitudes; in large or small clumps; growing in pure stands or mixed with other plants (Greig-Smith, 1948). It is a vigorous perennial with underground rhizomes. Leaves and stems start to be produced very early in spring and die back with air frosts in winter. Thus it is available for the duration of the active part of most insects life histories.

Its most notable feature, for the purpose of this study, is its relatively simple and highly predictable structure: straight upright stalks with fairly regular spacing of the leaves (fig 2.3). This facilitates detailed data on insect distribution to be recorded.

2.2 *Pleuroptya ruralis*

Pleuroptya ruralis (Scopoli) (Pyralidae: Pyraustinae), the mother-of-pearl moth, is widespread over the palaearctic region (Novak, 1980) and very common in Yorkshire, northern England (Sutton & Beaumont, 1989). The ecology of this species - as for the majority of other members of the family Pyralidae - has hardly been studied up to now (Beirne, 1957; Goater, 1984).

The adults are about 25 to 40 mm in size, pearly-cream coloured with beige mottling. Females (fig. 2.4) have their abdomens slightly shorter and broader than males (fig 2.5). They feed on nectar and fly at night from the beginning of July to mid-September. By day they hide amongst the nettles.

Eggs are laid singly, generally on the underside of the nettle leaves. They are small and flattened, light creamy at first (fig 2.6), turning to bright yellow as development proceeds. As they develop, the growing embryos start being visible through the egg shell (fig 2.7). The timing of hatching may vary much depending on the summer temperatures, but is generally about August/September.

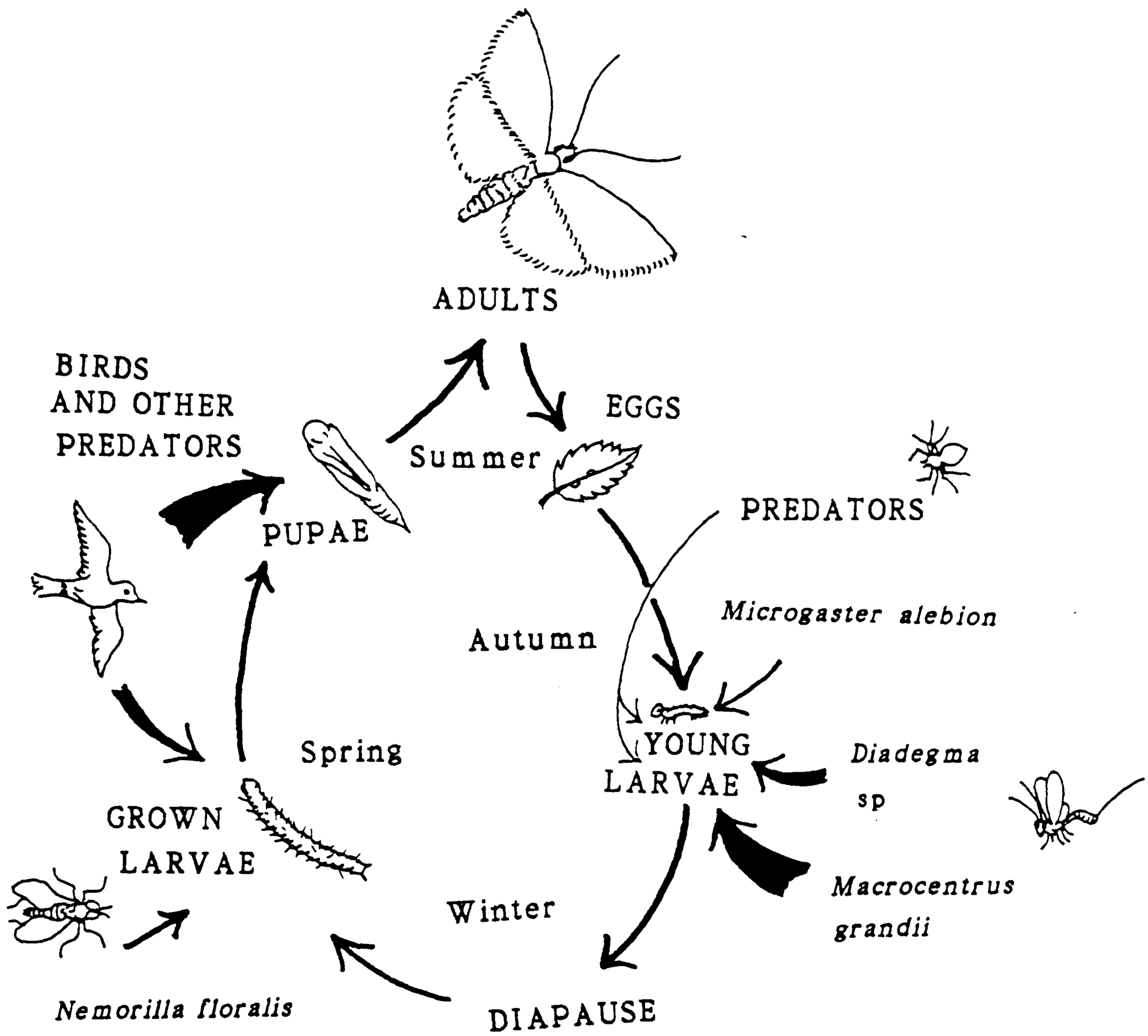


Figure 2.1 *Pleuroptya ruralis* : life cycle

Figure 2.2 *Urtica dioica*

Figure 2.3 *U. dioica* structure

Figure 2.4 Adult female

Figure 2.5 Adult male

Figure 2.6 Newly laid eggs on the underside of a nettle leaf

Figure 2.7 Ten-day old egg with developing embryo visible inside

Pleuroptya ruralis

The first instar larvae is greenish yellow, very small and delicate (fig 2.8); as the caterpillar grows it turns greener with dark spots along the body (fig 2.9). It lives and feeds on the leaves of nettles, which it rolls up as a shelter with strands of strong silk: at first, only the edge of the leaf (fig 2.10), but from about its third instar it starts rolling up a whole leaf (fig 2.11). After having consumed the inner layers of the tube, the larva moves (mostly) up and rolls another leaf. In this way, as it develops, it produces a trail of rolled leaves on the plant stem (fig 2.12).

The mother-of-pearl overwinters as a medium-sized larva (generally fourth instar) probably in the debris or earth at the base of the plant. In April (or May) it reapppears on the leaves. Growth is then faster and last instar larvae are fairly large (about 50 mm long). There are normally six larval instars. Caterpillars are not easily disturbed away from their rolled leaves and move little; thus it is possible to follow individuals through development.

By early summer, the larval development is completed and it pupates (fig 2.13). In about three weeks the moth emerges, males slightly earlier in the season than females. The pupal exuviae remains attached to the leaf after emergence.

2.3 PARASITOIDS OF *Pleuroptya ruralis*

No prior information was available on *P. ruralis* parasitoids, apart from a list of possible species (M. Shaw, pers. comm.). Three species of Hymenoptera and one of Diptera were found to be the main parasitoids attacking the mother-of-pearl on the sites studied.

Macrocentrus grandii Goidanich (Braconidae: Macrocentrinae) (fig 2.14) is gregarious, more than 60 individuals sometimes emerging from a single caterpillar (30 on average). *P. ruralis* larvae parasitized by this braconid tend to grow bigger and stay for a longer time in the sixth instar than do healthy caterpillars. At this stage the parasitoid larval growth is marked and visible (fig 2.15). The larvae of *M. grandii* emerge from the sixth instar caterpillar (fig 2.16) and pupate in a large (up to 40 mm long) brownish communal cocoon in the leaf rolled by the host (fig 2.17).

Diadegma nr sp *fabricianae* Horstmann & Shaw (1984) (Ichneumonidae: Campopleginae) (fig 2.18) is solitary and emerges from the fifth instar caterpillar. It spins a brown capsular cocoon, with a clearer central line, in the rolled leaf. Because of difficulties on the taxonomy of this species, this parasitoid is referred to as *Diadegma* sp throughout this work. Evidences for its identification are given in Chapter 4 (for discussion, see section 4.4.2).

Microgaster alebion var A Nixon (Braconidae: Microgasterinae) is also a solitary parasitoid and seems to attack very early in *P. ruralis* development. Its larva emerges from the last instar caterpillar and pupates in its rolled leaf in a white silk cocoon.

Nemorilla floralis (*Fallen*) (Tachinidae: Goniinae) is a generalist dipteran parasitoid and 1 to 5 flies were recorded emerging from individual *P. ruralis*

Figure 2.8 First instar larvae

Figure 2.9 Fourth instar larva

Figure 2.10 Edge of nettle leaf rolled by a second instar larva

Figure 2.11 Typical look of a whole nettleleaf rolled by a post-diapause larva

Pleuroptya ruralis

Figure 2.12 Sequence of rolled leaves on a nettle stem produced by a larva as it develops

Figure 2.13 A rolled leaf opened to show a pupa inside

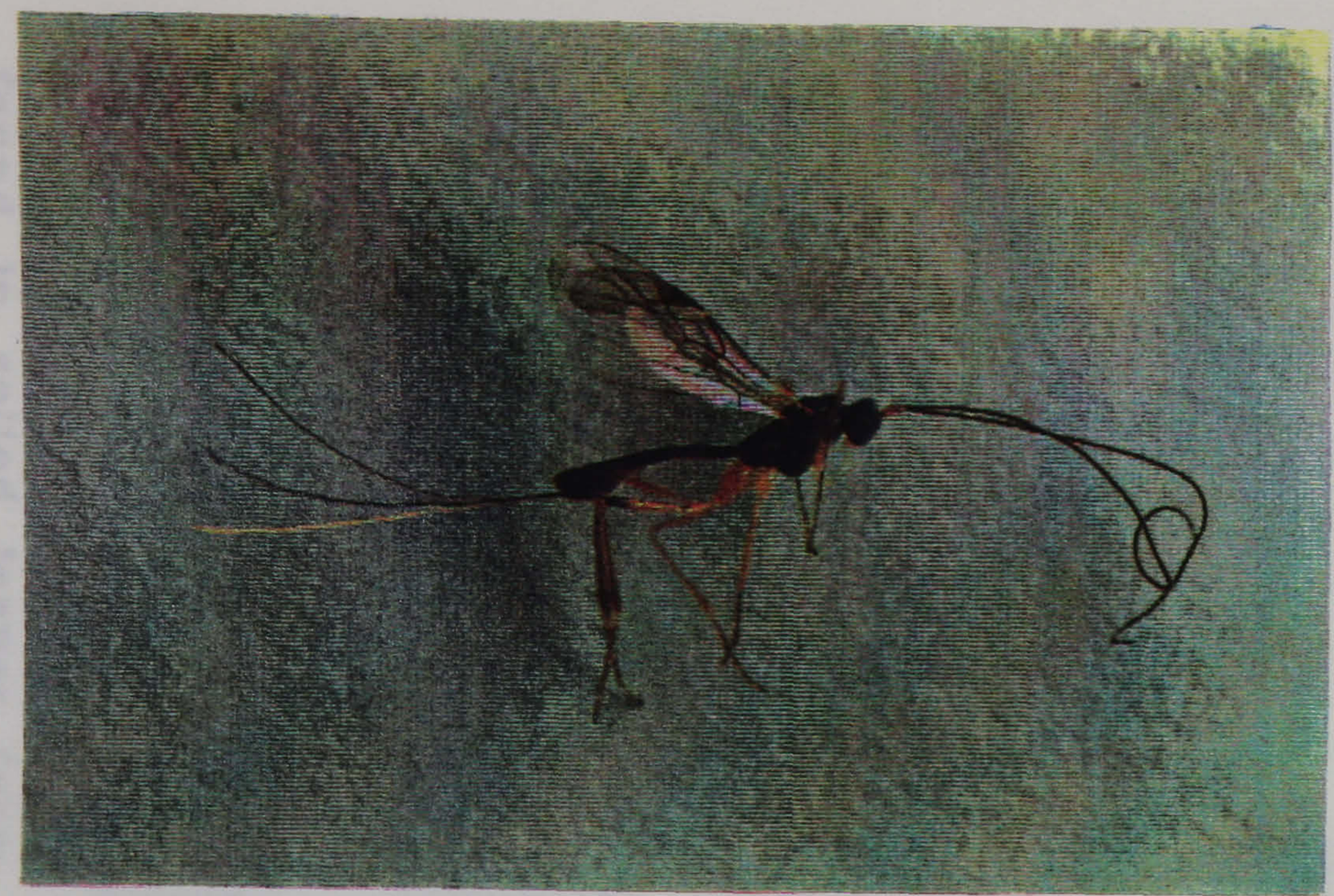


Figure 2.14 *Macrocentrus grandii* adult female

Figure 2.15 Sixth instar *P.ruralis* caterpillar parasitized by *M. grandii* (note difference of appearance from a healthy caterpillar, cf Fig. 2.9)

Figure 2.16 *P. ruralis* rolled leaf open to show *M. grandii* larvae spinning their coccon (note remains of the sixth instar caterpillar exuviae at the top)

Figure 2.17 *P. ruralis* rolled leaf open to show *M. grandii* pupal mass (note the remains of the exuviae of the caterpillar attached to the coccon)

Figure 2.18 *Diadegma* sp

Figure 2.19 Typical look of holes, attributed to birds, that were found in rolled leaves from which larva/pupa of *P. ruralis* had disappeared

caterpillars. The larvae of this fly emerge from the pupa and build their dark brown, rounded puparia near the remainings of the host. This fly parasitizes hosts when these are full-grown larvae.

2.4 OTHER RELEVANT MEMBERS OF THE NETTLE COMMUNITY

Many other Lepidoptera use the same host plant. *Anthophila fabriciana* (Linnaeus) (Choreutidae), the 'nettle tap'; *Eurrhypara hortulata* (Linnaeus) (Pyralidae), the 'small magpie'; *Clepsis spectrana* (Treitschke) (Tortricidae), the 'cyclamen tortrix'; *Orthosia gothica* (Hufnagel) (Noctuidae), the 'hebrew character'; *Aglais urticae* (Linnaeus) (Nymphalidae), the 'small tortoiseshell'; *Polygonia c-album* (Linnaeus) (Nymphalidae), the 'comma'; *Inachis io* (Linnaeus) (Nymphalidae), the 'peacock', and other less common species were also recorded on the nettles.

They were observed mainly in order to check if they shared parasitoids with *P. ruralis* and if their densities at any stage could be so large as to pose competition pression on the latter. Some parasitoids attacking the mother-of-pearl have been reported for some of the lepidopterans observed (M. Shaw, pers. comm.). However, their numbers were generally low and only from *A. fabriciana* were any of the parasitoids shared with *P.ruralis* reared (namely *D. fabricianae* and *M. alebion*). *A. fabriciana* was also of special interest for it too builds a shelter associated with the nettle leaves. However, its density at the study site was low during most of this study, and the numbers obtained were not enough for comparative analyses.

Other members of the arthropod community living on the nettles are also important as potential predators on *P. ruralis.* Spiders (various species) and earwigs (*Forficula auricularia*) are fairly numerous on nettles, and earwigs were seen feeding on a pupa. Beetles - mainly soldier beetles (*Rhagonycha fulva*) and rover beetles (*Tachyporus* sp) - and bugs (e.g. *Phytocoris ulmi* and *Anthocoris nemorum*) were also recorded, but their population levels were generally very low.

Birds - mainly robins and wrens - were seen more than once flying and walking into the nettle stands and searching the leaves for food, particularly in early summer. A hole of a size and shape commensurate with beak damage was a very frequent finding in rolled leaves instead of the grown larvae or pupae previously found there (fig 2.19).

It could be argued that apparent beak marks on empty rolled leaves and observations of birds in a nettle clump do not constitute adequate evidence of predation. However, grown *P. ruralis* larvae (and pupae) generally lie, upside down, on the dorsal part of the rolled leaf and occupy a central position. This is exactly where the beak marks were found. Also, when a moth emerges, the empty pupal case remains attached to the leaf; none was found when these holes were observed in the leaves.

2.5 THE STUDY SITE

Field work was carried out in natural stands of nettles at two different sites, Bond Ing and Spen Farm, both close to Leeds, West Yorkshire, northern England.

The climate in Yorkshire is moist and temperate as in the rest of Britain. West Yorkshire has a very varied relief and it is not possible to produce typical climatological data for the whole area. The region shows a decrease in precipitation from west to east, and the average annual precipitation in Leeds is about 700 mm. The prevailing winds are westerly. The influence of the relief on the weather varies with the cloud cover. Under cloudy cyclonic conditions, temperature falls with increasing altitude. The reverse happens at night under clear skies and anticyclonic conditions, when cold air drains into the valleys leaving the lowlands cooler (Lockwood, 1967). Appendix 2 describes the weather conditions observed during the period of this study.

Bond Ing (SE (44)/344394) is a field on the edge of the village of Shadwell (fig 2.20), about 6 km northeast of Leeds. Shadwell is at the interface between town and country and lies on a ridge forming the watershed between Wharfedale and Airedale. Most of the fields in the region are bounded by hedges in various states of degradation, and with occasional trees which are generally close to houses. The site is about one hectare in extent, on a gentle south facing slope (fig 2.21). It is bounded by good hedges with many well-grown trees. In the south-east corner are two small interconnected ponds. The more westerly of these is drained by an underground brook which surfaces towards the south-west corner of the field. The field has been managed as an unimproved hay meadow for the last 20 years; before that it was a pasture. In the distant past it was ploughed, there being evidence of medieval ridge and furrow. It is a neutral, species-rich grassland with numerous flower species on fertile brown earth soils overlying clay. Common species are hawkweeds (*Hieracium* spp), pignut (*Conopodium majus*), sorrel (*Rumex acetosa*), and meadow pea (*Lathyrus pratensis*). Dominant grasses are red fescue (*Festuca rubra*) and cocksfoot (*Dactylis glomerata*). Scattered in the field, there are islands of shrubs (mainly hawthorn - *Crataegus monogyna* - and bramble - *Rubus fruticosus*). Often, growing close to these or by the hedges, there are clusters of creeping thistles (*Cirsium arvense*) and rosebay willowherb (*Epilobium angustifolium*).

On the west side of the field, there is a house at the top of the slope and, below it, separated from the field by a hedge, there is a large garden, full of good nectar sources - e.g., honeysuckle (*Lonicera periclymenum*) and valerian (*Valeriana officinalis*). The diversity and abundance of flowers and shelter places attract a large number of insects and birds; in particular, it is a very suitable habitat for many species of Lepidoptera.

There are about a dozen nettle clumps of various sizes spread over the field, generally close to shrubs or hedges (fig 2.21). Nettle is by far the most common plant in these clumps, although in most of them there are also other herbs in varying

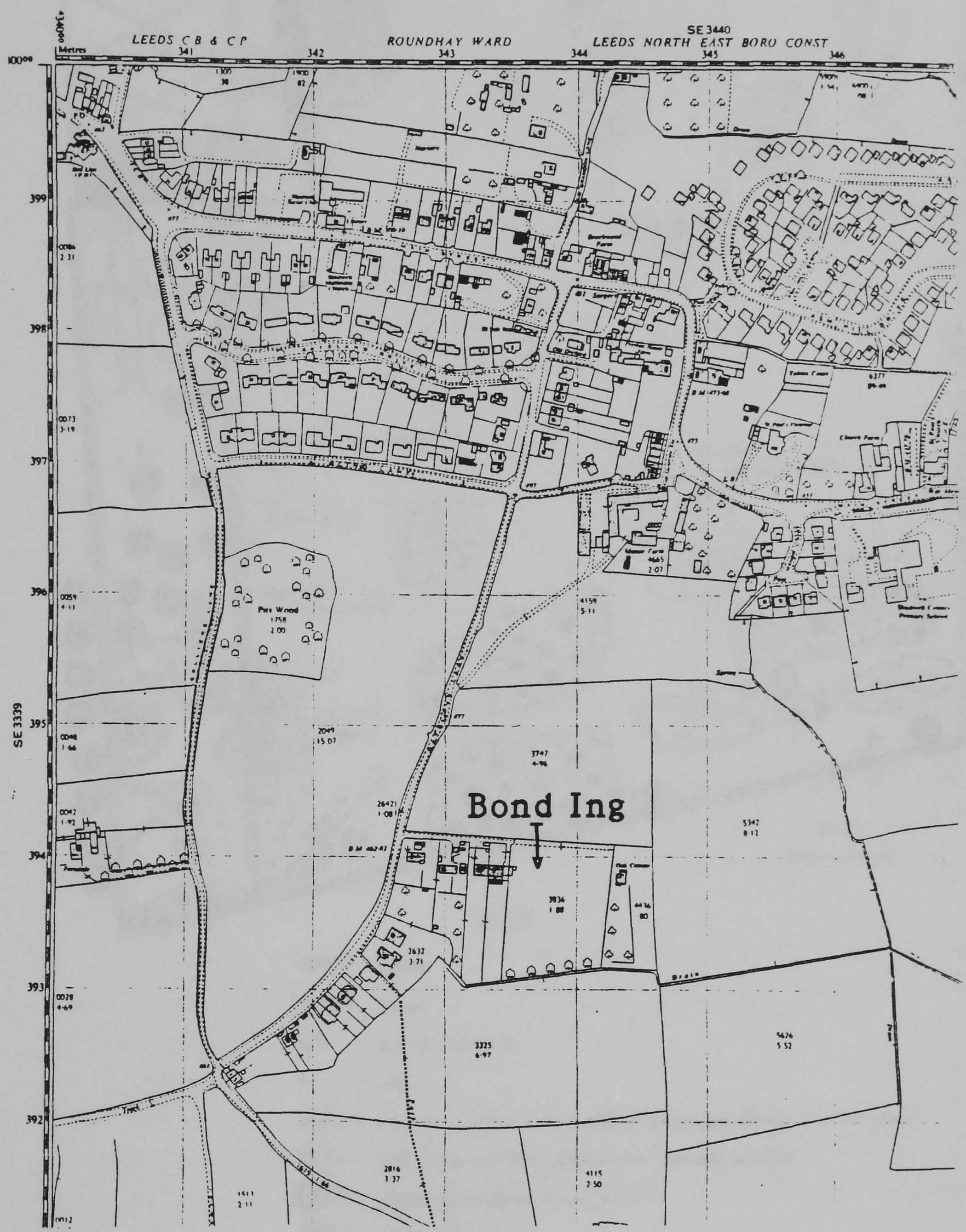
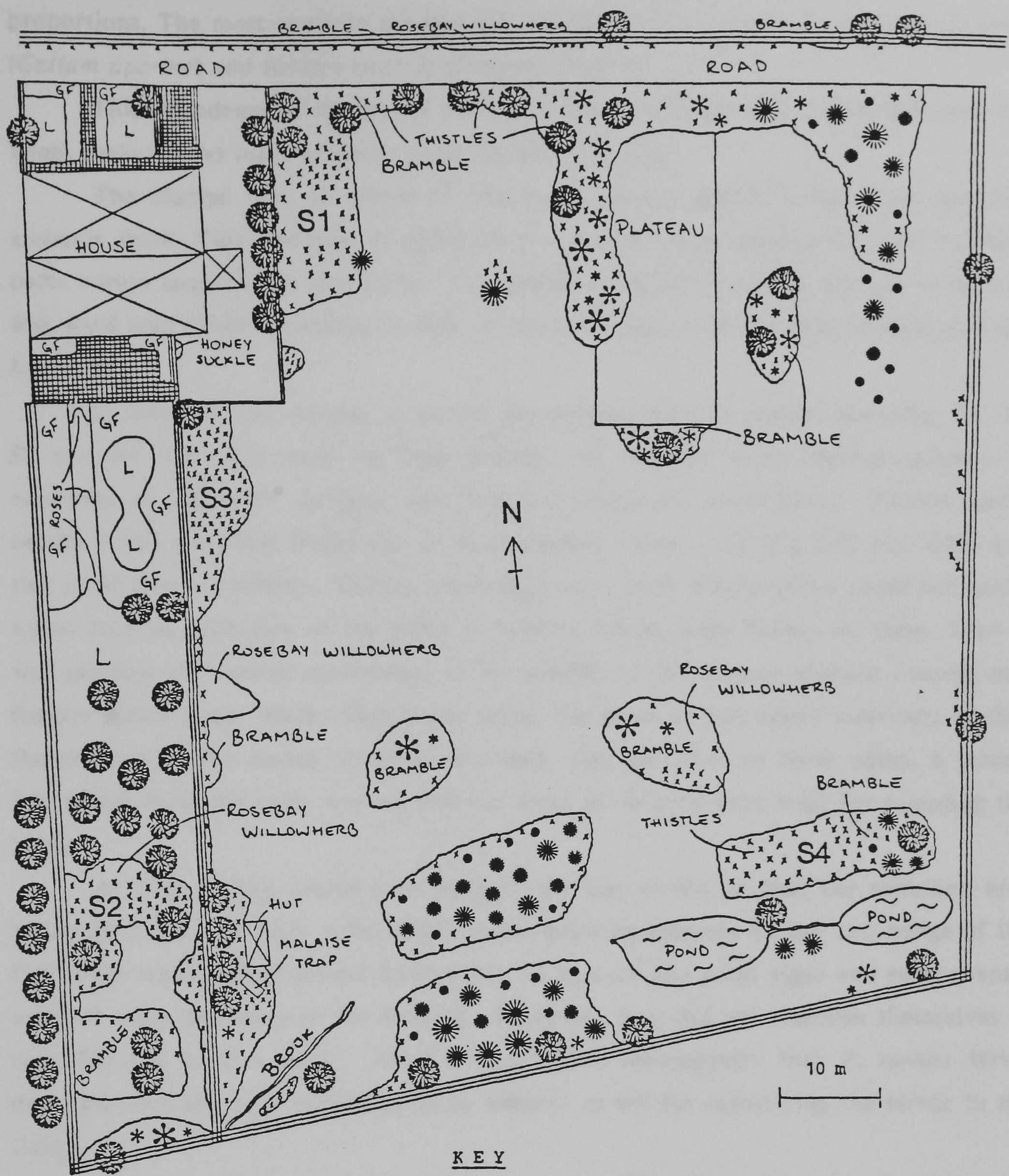


Figure 2.20 Position of the study site at Bond Ing, in the village of Shadwell (SE (44)/344394), Leeds, Yorkshire, England



KEY

hedge

fence

GF garden flowers

L lawn

nettles (density of symbols indicates density of nettles)

bushes of various sizes/ages (mainly thorns)

trees of various sizes/ages

paved area

Additional plants are indicated on the figure

Figure 2.21 Bond Ing study site (SE (44)/344394), altitude 130m. Ground cover= meadow, unless otherwise indicated

proportions. The most common are cow parsley (*Anthriscus sylvestris*), common cleavers (*Galium aparine*) and thistles (mainly *Cirsium arvense*).

This abundance of nettles, in addition to the nectar sources and shelter from the wind, makes Bond Ing a specially good site for *P. ruralis*.

The clumps vary in terms of density of nettles and of other herbs growing amongst them. This variation is observed not only between clumps but also between parts within each clump (fig 2.21). The degree of exposure of the clumps to the sun and wind also varies according to their location in relation to the trees, hedges and the house.

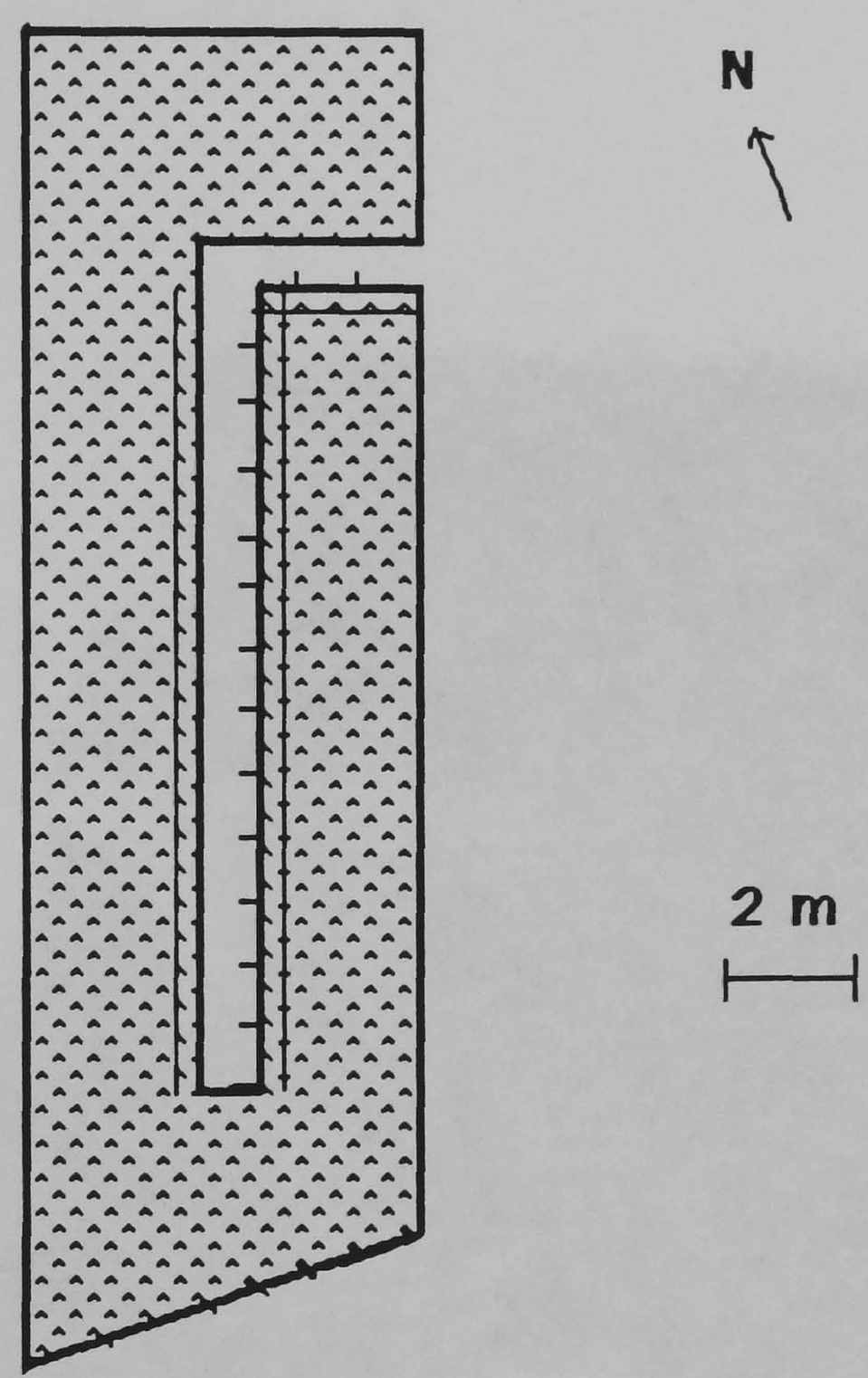
In terms of size, density of nettles and practicability of regular sampling, S1, S2, S3 and S4 (fig 2.21) were the best clumps. S1 and S4 were selected initially as examples of relatively sheltered and exposed situations, respectively. Narrow paths (width 0.7m) were laid lengthwise in these clumps - one in S1 (fig 2.22 and 2.23) and two in S4 (but see below). Fences 1.5 m high were built with bamboo canes and green nylon cord on each side of the paths to prevent nettles from falling on them. Thus it was possible to monitor caterpillars in the middle of the clumps without causing any further disturbance. Marks were made along the paths at one metre intervals, so that the position in the clump could be recorded. On each side of these paths, a second line 0.35m from the path, was set and the areas so defined were used for sampling the larvae.

At first, it was planned to increase the size of S4, so that the sampling area would be larger. In early April 1984, nettles growing sparsely by the east hedge of the field were transplanted around S4 in a bed of manure and pond algae and subsequently watered every two days in the evening. However, they did not establish themselves in time for use in this work. Also, it was found subsequently that *P. ruralis* larval densities were not high enough in S4 to warrant its use for monitoring the larvae in the field.

There are strips of nettles by the narrow roads close to Bond Ing but these are under severe stress due to road traffic and regular cutting. The closest large clump of nettles known is some 600 m northwest of Bond Ing.

The other study site, Spen Farm (SE(43)/264087), is part of the University Field Station, some 15 km northeast of Leeds (fig 2.24). It lies on a magnesium limestone plateau and the fields in the region are mainly arable. Hedges are minimal and field sizes are large, making the site considerably more exposed and windy than Bond Ing. The altitude is 65m and the main crops close by are grass, cereals, potato and sugar beet.

Two big clumps of nettles were selected, one in field 463 (F1), the other in the middle of field 464 (F2). Both were dense and well grown. F1 (fig 2.25) is in a sunny position, partially protected from the wind by buildings some 20m northwest. On the southeast border, there is a narrow footpath (NE-SW) and a grazed field (sheep and/or



Nettles

Path

Markings at 1m intervals

Line delimitating sampling area

Figure 2.22: Diagram of the S1 nettle clump at Bond Ing

Figure 2.23 A view (from the North end) of the central path in the S1 nettle clump at Bond Ing in summer 1984.

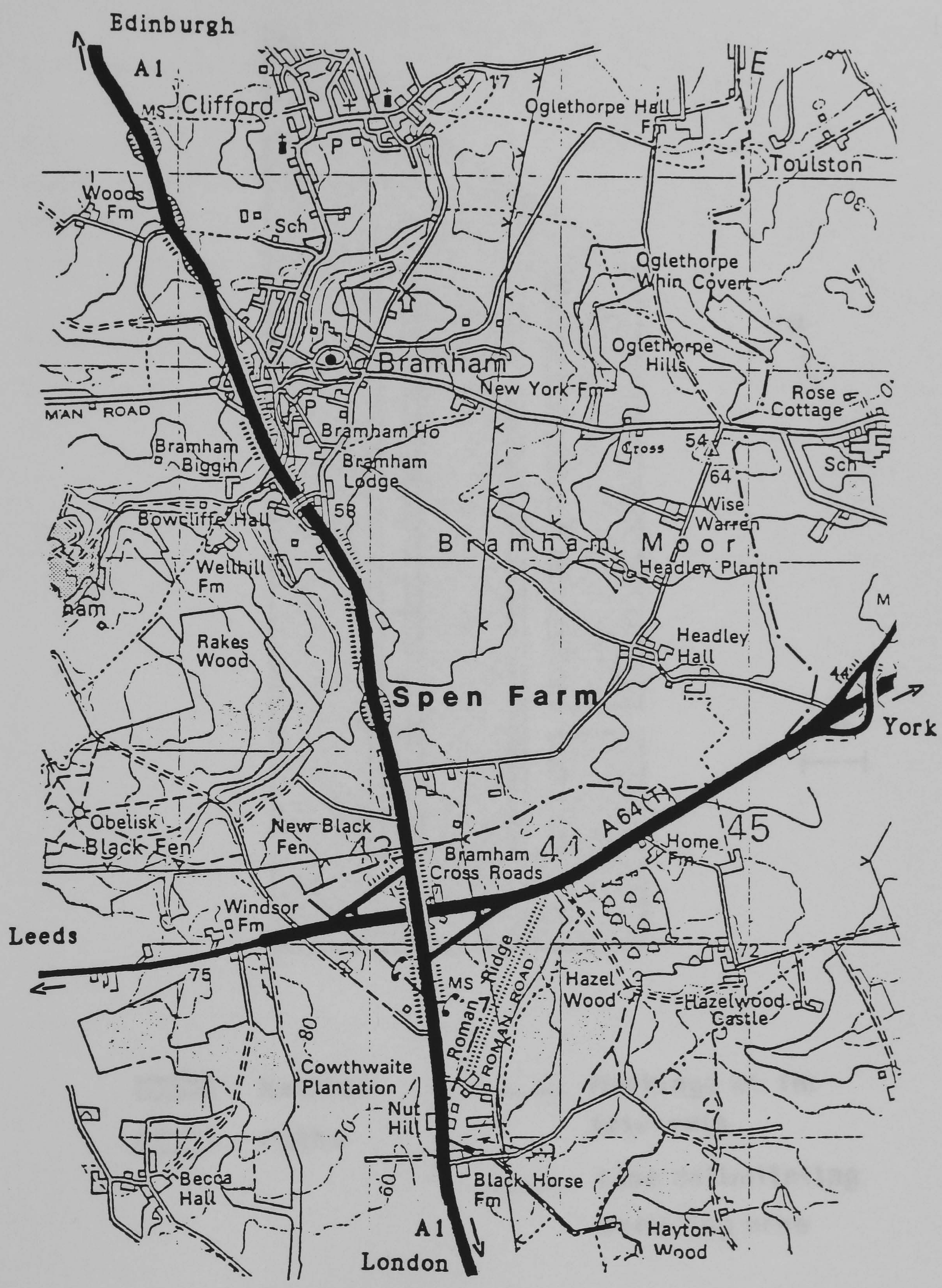


Figure 2.24 Position of the study site at Spen Farm (the University Field Station) (SE (43)/264087), Yorkshire, England

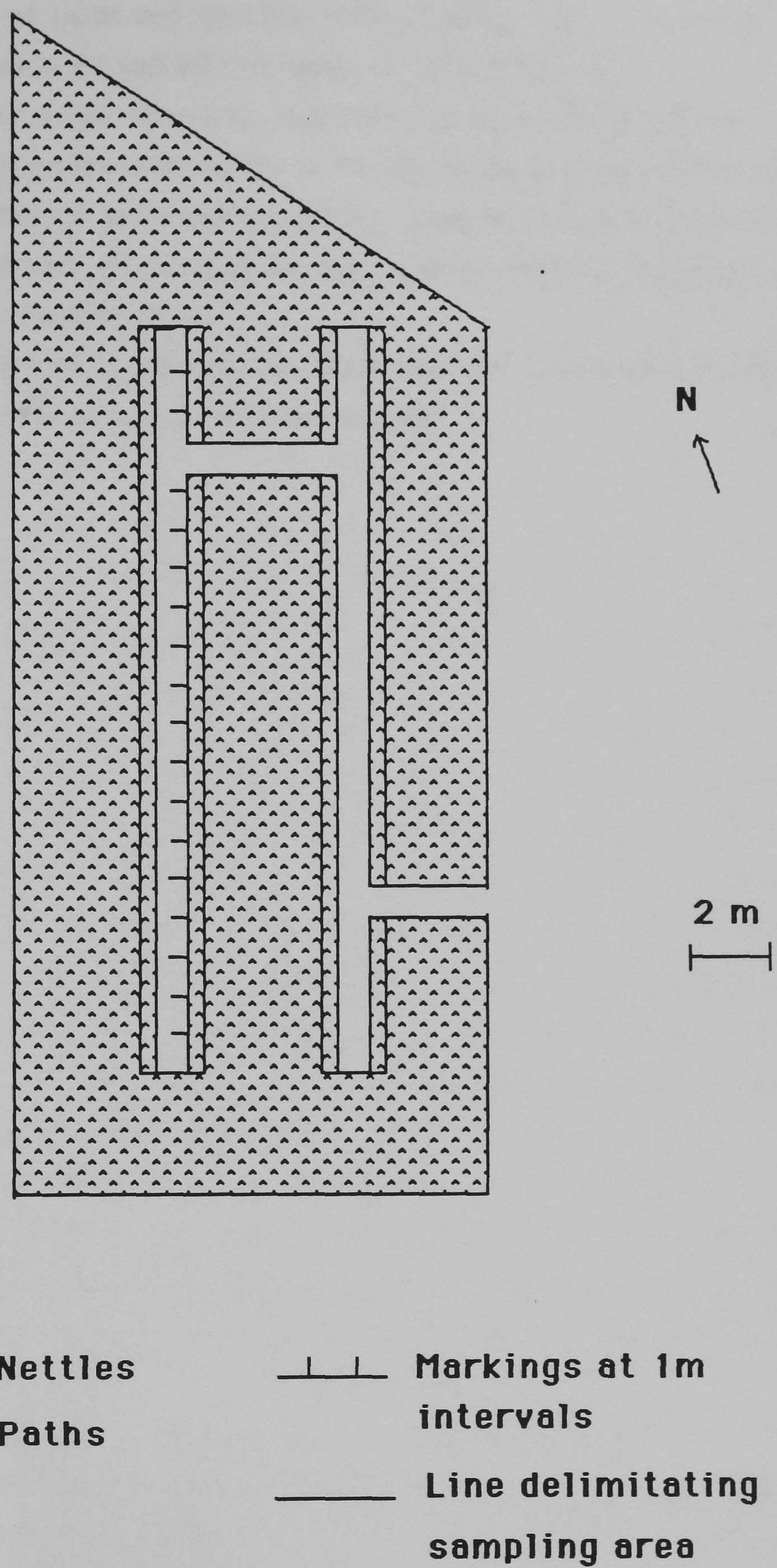


Figure 2.25: Diagram of sampling site F1 at Spen Farm

cattle). A wire fence separates F1 from this field and the nettles spread along this fence, from F1 to some 50m southwest. F2 is about 30m x 20m, under big old beech trees, in a very shady situation, surrounded by an arable field.

The same kind of paths and sampling areas as described for the clumps S1 and S4 in Bond Ing were set in F1 and F2 (two paths in each of them).

There were only a few flowering plants near to these nettle clumps: an elder shrub (*Sambucus nigra*) on the west corner of F1, the herbs growing amidst the nettles (mainly cow parsley, thistles and common cleaver, as at Bond Ing) and a few poppies (*Papaver rhoeas*), dandelions (*Taraxacum* sp) and ragwort (*Senecio jacobeaea*) growing by the borders of the cultivated fields.

Work on F2 was soon abandoned, because hardly any insects were found in it. It is suspected that the fields around it had been sprayed.

CHAPTER 3 THE ADULTS

3.1 POPULATION STRUCTURE

3.1.1 Introduction

To understand the processes shaping a population, it is necessary to investigate its size, seasonal and yearly variations, and the movements and survival rates of its members.

Models for estimating these parameters vary to suit the different animal and habitats under study. Direct counting of all individuals in a population is seldom feasible. When the species is relatively immobile, a representative known fraction of the habitat can be sampled and, from the number of individuals found in it, population size is inferred. However, this procedure does not work for populations of mobile, non-cooperative animals like adult Lepidoptera. Individuals tend to enter or leave the sampling area and some may be counted more than once or not counted at all.

Marking the animals, while sampling over the habitat, allows them to be identified, but the sample is still an unknown proportion of the population. By taking a later sample, it is possible to compute the ratio of marked to unmarked individuals in the population and, therefore, its size. This simple argument is the basis of all models of mark, release and recapture (MRR) and was first used to estimate population sizes by Lincoln (1930). He used the formula $\hat{N} = n_i.n_{i+1} / m_{i+1}$, where ^ denotes estimation, N is population size, n the sample size, m the number of recaptures and i the sampling occasion. This is often called the Lincoln Index.

This index, nevertheless, is of restricted use. It involves only two samples, between which there should be no ingress (birth + immigration) or egress (death + emigration) of individuals in the population, and just one estimate is produced. Also, both samples need to be large, because the precision of the estimate depends on the number of recaptures.

These constraints were overcome by the use of more than two sampling occasions and sequential marking and/or recapturing. Hence the number of marks and/or recaptures can gradually accumulate and more than a single population estimate may be generated; rates of ingress and egress can be computed based on the different recapture histories. A number of MRR models have since been developed. As they generally use more than one marking occasion, they substitute n_i (size of the first sample) by M_i (marks at risk, i.e. the number of marks available to capture in the population) in the Lincoln Index. The way the models calculate M_i is the main difference between them, and this determines the biological and experimental

conditions in which they can be used, as well as the number, type, precision and accuracy of the estimates which they generate. Reviews of the statistics and applicability of these models are presented by Cormack (1968), Southwood (1978), Begon (1979), Blower et al. (1981) and Seber (1982; 1986).

All models for analysis of MRR data are based on the assumptions that marks are permanent, marked and unmarked individuals are otherwise indistinguishable, sampling is random and instantaneous, and individuals mix randomly in the population after release. Particular models may have additional assumptions about the population studied and the sampling process. In general, the more theoretically refined a model is, the less assumptions it makes and, thus, the more realistic biologically. However, progressively more extensive data is required for producing reliable results, since the estimates are based on successively smaller sub-sets of data. On the other hand, the less sophisticated models tend to be fairly robust even with scarce data, as long as their underlying assumptions are not severely violated.

It is crucial to examine the adequacy of the models for the data available, since population estimates obtained by biologically or statistically inappropriate models are totally invalid. First, the biological and experimental aspects need to be considered. Then it is necessary to assess the assumptions on which the models are based. No actual study can completely satisfy all assumptions. Nevertheless, the interpretation and reliability of the estimates the models yield depend on the extent that these assumptions hold true for the data gathered. Finally, the robustness of each model should be examined in the light of the data gathered and the purposes of the study.

Of the models available, Fisher-Ford (Dowdeswell et al., 1940; Fisher & Ford, 1947), Jolly-Seber (Jolly, 1965; Seber, 1965) and Manly-Parr (1968) are the best suited for studies of population dynamics. They require sequential sampling, allow for ingress and egress in the population during sampling intervals and generate series of estimates that express these changes. They all have the same implicit assumptions except for the way they treat the survival rate (ϕ).

Fisher-Ford is a deterministic model and takes survival as a fixed rate, constant on a day-to-day basis and independent of the age of individuals. Jolly-Seber is stochastic and considers each individual as having a probability of survival that can vary daily, but is not dependent of age. Manly-Parr is still more realistic in that it allows for both daily and age related variations in survival.

Biologically it would seem sensible to favour the Manly-Parr model. However, for the estimates calculated by this model to be reliable, data with numerous ($\geq$ 10) multiple recaptures (i.e. more than two captures of the same individual) are necessary. This is rarely possible to achieve in natural populations. The Jolly-Seber model is intermediate between Manly-Parr and Fisher-Ford in the extent of the data needed to produce estimates that can be relied upon, but still requires the number of recaptures per sampling occasion to be fairly large (>10 and preferably >20). One disadvantage of

this model is that was assumed that samples were "large" when the formulae were derived. Because of this, when the number of recaptures is low, relatively small chance variations in the composition of the daily samples are reflected in large fluctuations in the population estimates. Low recapture numbers can arise from "low" sampling intensity (SI=m/M < 0.12), "small" population size (N < 500) and/or "low" daily survival rate (ϕ < 0.5). The Fisher-Ford model, although theoretically simpler, performs better under these circumstances. Also, when ϕ is approximately constant, the Fisher-Ford single estimate of it is more accurate than the average of the $\hat{\phi}_i$'s calculated by the Jolly-Seber model (Manly, 1970; Bishop & Sheppard, 1973). Moreover, the Fisher-Ford model is sensitive to differences of 0.1 in ϕ; Jolly-Seber intersampling values are not unless m>20 (Blower et al., 1981).

Lately, aiming to bring together the advantages of stochastic approach and improved precision, there has been a vigorous interest in models with constant parameters, e.g. Jolly (1982), Crosbie & Manly (1985), Brownie et al. (1986), etc. Of these, Jolly's models are considered to be the more fully developed, though still leaving room for further elaboration (Brownie et al, 1986). Based on propositions similar to the ones of the Jolly-Seber model, Jolly (1982) used a Poisson formulation to derive a model - called Method B - for situations where the probability of survival can be assumed constant. There is little information about its performance in the literature (White, 1985). Up to July 1988, only 8 references of experimental studies using Method B were found through the Science Citation Index - all works on vertebrates, where sampling intensities tend to be higher than with insects. Rosewell & Shorrocks (1987), working with *Drosophila* , reported no significant difference between estimates of survival rates calculated by Fisher-Ford and Jolly's Method B. Furthermore, there is controversy over Method B and its many modifications (c.f. Nichols et al, 1987 and Gill, 1987; Brownie, 1987 and Clobert & Lebreton, 1987). Hence, it was not used in the present work and the choice was limited to the models of Fisher-Ford, Jolly-Seber and Manly-Parr.

Often a decision cannot be made about which of two models is best suited for the analysis of a particular MRR set of data. Begon (1979) advises on how to choose a model when the distinction is not clear or, alternatively, on how to reconcile any discrepancies between the estimates generated by the different models. First, the level of accuracy needed for the purposes of the study should be defined, and then the accuracy that can be achieved by each of the models with the specific data available checked.

The reliability of estimates is generally measured by their precision, as calculated by the standard errors (SE's) and 95% confidence limits. Confidence limits which are too big make an estimate meaningless.

Robson & Regier (1964) recommended a level of accuracy of 0.10 (i.e. 95% confidence limits in the range of 0.9N - 1.1N) for careful research into population

dynamics. This guideline is also endorsed by Begon (1979, 1983), Cormack (1968) and Roff (1973a).

Assessing the reliability of the estimates obtained, however, is not a straightforward process. The accuracy of a MRR population estimate involves more than the precision quantifiable by its SE. Even after the use of a model is validated by testing its assumptions, there still remain important aspects to be dealt with.

First, bias may arise from the mathematical formulation of the models. Bailey (1951, 1952) demonstrated that the Lincoln Index had a positive bias of about 1/m, and that adding 1 to capture (n) and recapture (m) figures counteracted this tendency. MRR models, as derived from this Index, behave in a similar way and their performances also improve in consistency when this correction is used (Blower et al., 1981).

Second, there are difficulties concerning the computation of the SE's and the assessment of their meaning. Fisher-Ford provided no formulae for this purpose. The only measure of the precision of the estimates generated by their model is an estimator of the SE of ϕ, which was derived by Leslie & Chitty (1951). Still, this SE gives an indication of the error involved in the estimation of N, since in the Fisher-Ford model all estimates are based on the determination of the survival rate. For the Manly-Parr model, SE's formulae were developed for N (Manly, 1969). With the Jolly-Seber model it is possible to compute SE's for all estimates. Nevertheless, the effectiveness of the formulae available has been questioned: (a) assuming that samples were "large", Jolly omitted terms that could be important components of the variance, and (b) SE's were shown to be highly correlated to the estimates to which they are attached (Manly, 1971; Roff, 1973a).

The underlying reason for the problem with the SE's in MRR is that they have been derived from the maximum likelihood theory. This theory assumes that the probability distribution of estimators is normal, in which case, confidence limits are symmetrical. The distribution of MRR estimates, however, is strongly skewed to the right. From $\hat{N}_i=\hat{M}_i.n_i/m_i$, whatever the values are for M_i and n_i, as m_i varies, there will always be a lower but never an upper limit for N_i. The mathematical requirements for lower and upper confidence limits are thus very different (Roff, 1973a). Also, in all cases, the formulae for the SE's include terms estimated from the data and, therefore, estimates and their associated SE's cannot be independent (Manly, 1971).

Recently, Seber & Manly (1985) studied ways of estimating approximately unbiased variance for the Jolly-Seber model. However, the correlation between estimates and SE's could not be overcome.

Yet, keeping in mind these limitations, SE's still convey relevant information on the reliability of the estimates (Begon, 1983) and can be specially useful when comparing different results (Blower et al., 1981). Precision levels of about 0.10 are very unlikely to be achieved when there is significant error in the estimates (Roff,

1973a).

Allied with the imperfect information that the SE's can provide, there is always some uncertainty inherent in the models. A criterion by which the estimates can be judged is their internal consistency: wild fluctuations are unlikely to reflect the true biological situation (White, 1985). The degree of precision attainable depends on the relationship between n and N (Robson & Regier, 1964) and increases with the number of sampling occasions (Leslie & Chitty, 1951). There are theoretical and empirical studies reporting on the levels of precision associated with estimates of populations of known parameters under different sampling intensities (Leslie & Chitty, 1951; Robson & Regier, 1964; Cook et al., 1967; Manly, 1970; Manly, 1971; Roff, 1973a; Bishop & Sheppard, 1973; Blower et al., 1981). These can be referred to, and the ones that deal with comparable sets of data should be used as further guidance to the degree of reliability of the estimates obtained with the particular experimental values, in addition to the calculated SE's.

Sadly, MRR studies have often been carried out with little care for the choice of the model for analysis, validation of its assumptions and interpretation of results. This seriously undermines the conclusions reached (Begon, 1983) and has led to the utility of MRR methods being disputed. Arguments are that often the implicit assumptions - and sometimes even the most basic one of random sampling - cannot be met (Singer & Wedlake, 1981; Morton, 1984), and that the tests used to assess these assumptions are insufficient and insensitive (Roff, 1973b). Hence simpler but less informative techniques (e.g. Pollard, 1977) would be more reliable than MRR (Morton, 1984) or, worse still, that there would be no method available that would be worth using (Roff, 1973b). Furthermore, it has been suggested that the estimates which MRR models produce are too inaccurate to be of any use (Roff, 1973a).

Yet, in spite of all this controversy, the MRR technique is still the most instructive method available for estimating parameters of populations of mobile species. No population size can be determined exactly, but this is not needed for answering most ecological questions. A note of optimism can be gained from the field evidence supporting the robustness of the Fisher-Ford model, presented by Cook *et al.* (1967). The model was used to analyse rather scarce data from a population of known size, and good agreement was found between estimates and actual values. In addition, new stochastic models with constant parameters are being developed which try to overcome the limitations of the large data sets required by the Jolly-Seber and, in particular, Manly-Parr models. However, there is not yet much evidence about their performance in field studies.

In conclusion, by being aware of the limitations of MRR techniques so as to avoid unnecessary violations of the assumptions on sampling, and by supporting decisions and conclusions on well formed biological insight, extremely valuable information on population dynamics can be derived from MRR studies.

3.1.2 Methods

In the summers of 1984 and 1985, a MRR programme was carried out at Bond Ing. From the date when the first *Pleuroptya ruralis* adults started to emerge up to the time the adult population died off, adults were searched for, weather permitting, every second evening. Sampling was carried out during their flight period, which was found to be concentrated approximately between 20:30 and 22:30 h.

Initially a mercury vapour lamp was used to attract the moths, but the results were very disappointing. Very few *P. ruralis* individuals were attracted and it was also very difficult to follow and catch them amidst all the other species of moths that came to the light. After that, the moths were captured with butterfly nets, and a head torch was used to help see them in the dark. They were not attracted by this light.

P. ruralis was never found flying over the clumps of nettles exposed to the wind, and efforts were centred around sheltered clumps (S1, S2, S3) and their vicinities. About 40 minutes were spent for each clump. The order in which the clumps were sampled was changed on each occasion to avoid bias.

It was found that *P. ruralis* tends to fly low in the middle of the nettles and this makes the capture process rather difficult. To make them fly out above the plants, the nettle stems were gently moved with a long bamboo cane when sampling.

After capture each moth was put into a separate plastic pot. They were left still in the dark until the following morning. They were then marked with dots on the ventral side of the wing, according to the 'Ehrlich & Davidson 1-2-4-7 system' (Southwood, 1978). This system allows the moths to be marked individually and so it was not necessary to add marks on every recapture occasion. Fordigraph permanent ink markers were used with a different colour for each of the three clumps.

The scales on the wings can be a nuisance in marking lepidopterans, since if the ink is applied to them, when they fall the marks go as well. Care was thus taken to mark the wing itself. As the moths age, damage can occur to the borders of the wings due to predator attacks, bruising on vegetation, etc. To avoid loss of marks, the dots were made away from the tips of the wings. Also, only dark colours were used to minimize the chances of marks fading.

For each individual, in addition to the details of date and site of capture, notes were taken on the sex, 'approximate age' and general condition. Sex was determined by differences in the shape of the abdomen and genital structure. Age was ranked as 'young', 'middle' or 'old', based on the degree of scale loss from the wings (Gilbert & Ehrlich, 1973).

After marking, the moths were released, one by one, low amidst the nettles, in the same clump of nettles where they were caught.

Observations on the effects of marking were made on individuals reared in the laboratory as described in section 3.2.2 and also on moths reared outdoors. These were kept in a 1000 x 750 x 750 mm wooden frame cage, covered with white nylon gauze

and protected from the wind and direct sunshine. The insects within were provided with nettles and fed on 20% honey-water solution in the same way as for the mating experiment (section 3.2.2).

A detailed study was carried out to choose and justify the model of analysis and the following points were considered: (1) adequacy of the model to the experimental design, (2) validation of its implicit assumptions, (3) consistency and precision of estimates obtained and (4) comparison of results with empirical and theoretical studies on the performance of the models with comparable data sets. The data were then analysed by both the models of Fisher-Ford (Dowdeswell et al., 1940; Fisher & Ford, 1947) and Jolly-Seber (Jolly, 1965; Seber, 1965) by means of a computer programme developed by Dr. J. P. Rosewell in this Department. Bailey's correction (1951, 1952) was adopted. Biologically impossible results were dealt with by common sense; i.e. the "best" estimate for ϕ when $\hat{\phi}>1$ was considered to be 1 and, likewise, the rate of ingress was considered nil when $\hat{B}_i$ was negative. Estimates are for the whole population, unless indicated otherwise, and presented with $\pm$ SE's when these could be calculated.

Details about weather data and sources used are given in Appendix 2.

3.1.3 Results

3.1.3.1 Description of the Sample

A summary of the data obtained with the MRR programme is shown on table 3.1.

Table 3.1 Summary of mark-recapture data.

Year	Sex	No. marked	No. recaptured	No. captured	Recaptured as a proportion of captured
1984	F	511	85	596	0.14
	M	536	80	616	0.13
	F+M	1047	165	1212	0.14
1985	F	205	32	237	0.14
	M	480	90	570	0.16
	F+M	685	122	807	0.15

In 1984, spring and summer were warm with little rain, and *P. ruralis* was on the wing from mid-July to the end of August. Over a thousand individuals were marked at Bond Ing of which 25% were from clump S1, 28% from S2 and 47% from S3, in a total of 1212 capture events over 16 sampling occasions.

In 1985, the season was late, windy, rainy and cold. The adults started emerging later, by the end of July, and lived until about the end of September. Fewer than 700 moths were marked, but the proportion captured in each clump was roughly the same

as in the previous year (24% from S1, 32% from S2 and 44% from S3). In total, just over 800 capture events were recorded during the 18 sampling evenings.

The percentage of recaptures was 14% in 1984 and 15% in 1985 (table 3.1) and did not differ significantly between sexes ($F = 0.10$, $P = 0.753$) or years ($F = 0.52$, $P = 0.472$). Males started emerging about a week ahead of females, but no differences in behaviour were observed. The ratio of males to females, as observed by the number of individuals marked, was 1.05:1 in 1984 ($P >> 0.1$) and 2.34:1 in 1985 ($P << 0.001$). This is discussed in section 3.1.4.

Figure 3.1 shows the recorded dispersion of *P. ruralis* at Bond Ing as expressed by their movement between the nettle clumps. In 1984, about half of all recaptures were made in clumps other than the ones where the moths were originally marked. Female and male moths moved about the same. In 1985, there was less movement and only about a third of individuals recaptured changed clump. Compared with 1984, females moved less than males.

Tables A1.1 to A1.4 of appendix 1 detail these results per clump, for each sex and year. (Rates of recovery of marks are also given for comparison with the rates of movement between clumps.) No specific trend in terms of direction of movement could be identified. In both years and for both sexes, transit between S1 and S2 (the farthest apart clumps - Fig 2.1) was less marked than between S1 and S3 or S2 and S3 (Fig 3.1). Transit on both these shorter routes were of similar intensity. There was no indication of whether *P. ruralis* took a step through S3 to move between S1 and S2.

The mobility observed for each sex and year seemed to be linked to n_i, m_i and - intuitively it would appear - to N_i. Section 3.1.3.3 presents the daily population estimates, and further results about *P. ruralis* movements between the nettle clumps are examined in connection with these.

Marks had a higher chance of being recaptured in their clump of origin (Appendix 1, tables A1.1 to A1.4). This suggests that individuals tend to stay within a range smaller than the study site. However, the proportion of moths that moved between the sub-areas was high, and hence the *P. ruralis* at Bond Ing is considered to form a single population. Estimates were thus calculated with the data of all nettle clumps pooled.

3.1.3.2 The Choice of MRR Model

During the present work, marking and recapturing was carried out on several occasions as the population under study was changing. The use of the models of Fisher-Ford, Jolly-Seber and Manly-Parr was investigated. The assumptions underlying these models, together with the results of the statistical procedures available to test them, are listed below.

- ASSUMPTION 1: Marks are permanent and easily recorded on capture

The marking procedure used ensures very persistent and easily identifiable

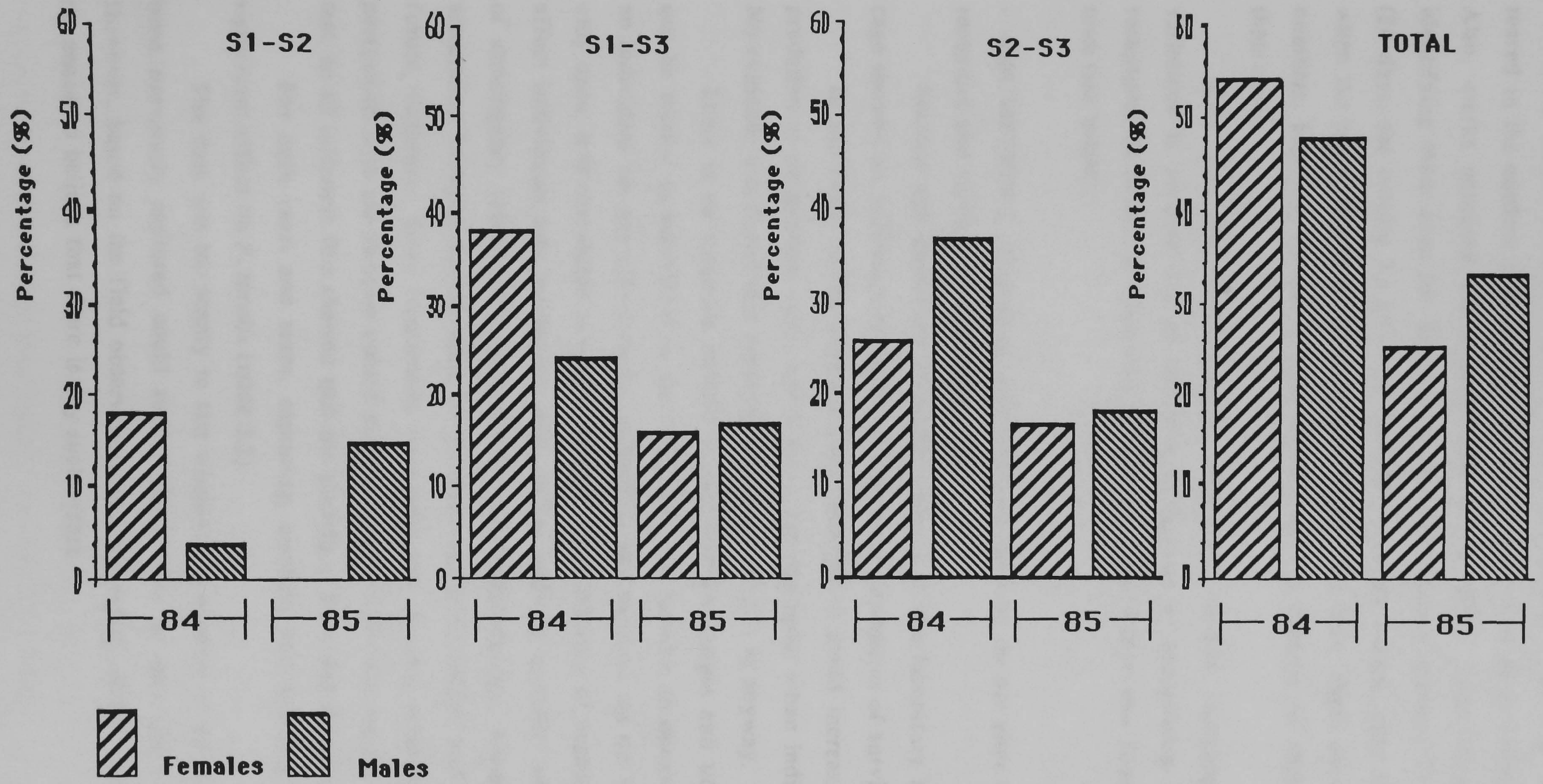


Figure 3.1. Number of individuals moving between the nettle clumps as a percentage of recapture per groups of clumps

marks (Araujo, pers. comm. ; Cook et al., 1976; Jones, 1988; Romanowski et al., 1985), and, indeed, this was also observed in the present study. Marks were perfectly recognizable during the whole life span of more than 60 individuals reared in the laboratory (mean lifespan = 24.8 $\pm$ 3.66 days, longest lived = 44 days) and 25 moths reared in the outdoor cage (mean lifespan = 15.5 $\pm$ 2.56 days, longest lived = 21 days). Also, marks persisted for a long time in the field, there being no difficulty in identifying them even for the longest recorded periods between first and last capture (24 days, see section 3.1.3.5). Of the 287 recapture events, only three times (1.04%), when the moths had their wings severely torn, was there slight doubt about individual numbers. Even so, it was possible to sort out the identity of these insects based on their sexes.

The tests for initial marking mortality, random sampling and age related variations in survival are all sensitive to failures in recognizing marks on multiple recaptures (Rosewell & Shorrocks, 1987). No significance was found in any of these tests (see below).

- ASSUMPTION 2: Capturing, handling and marking do not alter the probabilities of recapture and survival of individuals

Marked and unmarked individuals reared in the laboratory and in the outdoor cage showed no indication of different behaviour or chances of survival.

In the field, moths were carefully released to avoid increasing the chances of predation or emigration. Also, marks are not conspicuous when individuals fly or rest. No evidence was found that marking affected *P. ruralis* in anyway.

There is no available method to test whether caught and uncaught individuals can be treated as equivalent in the field, but it is possible to determine if recapturing an individual has any effect on its catchability and survival. As the moths were marked only once, it is reasonable to suppose that the first instance of capture is more likely to affect individuals than subsequent ones. Initial marking mortality was tested by means of contingency tables that checked, for each sampling day, whether there was any association between having been or not been captured before and the probability of future recapture. Since frequencies were very low in some samples, analysis was also performed with the samples pooled and compared with daily results by a heterogeneity test. In all instances this showed that the pooling of data was justified.

For both years and sexes, capturing, marking and handling did not show any significant effect on *P. ruralis* (table 3.2).

The data was too scanty to test whether the number of times an individual had been previously captured could render them more or less likely to be recaptured. However, based on the field observations and the results of the previous test, there is no reason to believe that there is any such effect.

Table 3.2 Effects of capturing, marking and handling - initial marking mortality. Results shown are for the pooled data.

Year	Sex	df	x^2	P
1984	F	1	0.227	>0.1
	M	1	0.008	>0.9
	F+M	1	0.184	>0.5
1985	F	1	0.002	>0.9
	M	1	0.246	>0.5
	F+M	1	0.154	>0.9

- ASSUMPTION 3: Sampling is random

Random sampling is a basic assumption of all MRR models. It is crucial that there should be no inherent difference in the probabilities of individuals being captured. Although there may be differences between the level of catch on different days, the assumption is not violated if no correlation between individual catchabilities on the different days exists.

Leslie (1958) developed a test for assessing random sampling. The test concerns only marked individuals and requires that at least 20 individuals are known to be alive for a minimum of five sampling occasions. The number of multiple recaptures of *P. ruralis* was too low, even pooling the data, to allow the use of this test. Randomness of captures can also be tested by goodness of fit to a zero-truncated Poisson distribution (Blower et al., 1981). This test was applied and the results for all cases support the hypothesis of random sampling (table 3.3).

Table 3.3 Random sampling - goodness of fit to a zero-truncated Poisson distribution.

Year	Sex	df	x^2	P
1984	F	510	88.191	>0.5
	M	535	83.584	>0.5
	F+M	1046	171.906	>0.5
1985	F	204	30.279	>0.9
	M	479	85.158	>0.5
	F+M	684	115.670	>0.5

Roff (1973b) strongly criticizes these tests, because frequently there are distinct sub-groups in the population (ages, sexes, morphs, etc.) that differ in catchability. If, within each sub-group, catchability is constant, the tests are unable to detect that these are sub-groups. In the case of the test for randomness of sampling based on the Poisson distribution, this is because the sum of two Poisson distributed variables follows a compound Poisson distribution. On the other hand, no evidence is provided

against the effectiveness of these tests for detecting individual differences in catchabilities. No evidence that the *P. ruralis* population should be divided in sub-groups was found. Laboratory observations, the test of independence of age on survival rate (see assumption 7) and the lack of association between age and the rate of movement (see section 3.1.3.5) support this view. Whenever possible, it is advisable to analyse the data for each sex separately, but this division of the data reduces sample size and consequently the accuracy of the population estimates. The differences in the number of captures and recaptures between male and female data were analysed by means of contingency tables. Again, on some sampling occasions expected frequencies were too low: a heterogeneity test was applied and the results supported the pooling of data for the analysis. No significant difference was found and females and males are considered to be equally catchable under the conditions of this study (table 3.4).

Table 3.4 Random sampling - differences between sexes. Results shown are for the pooled data.

Year	df	x^2	P
1984	1	0.626	>0.1
1985	1	0.645	>0.1

- ASSUMPTION 4: Sampling is instantaneous

In practice sampling can never be instantaneous, but should be short in relation to total time. In this work, sampling took only 40 minutes per clump and the MRR programmes had durations of more than 40 days in both years. However, it was only possible to capture *P. ruralis* in numbers that would warrant the use of MRR methods during their short period of activity (roughly between 20:30 and 22:30 h). It was not feasible to mark and release the moths immediately after capture, and they were kept in individual pots overnight. Nevertheless, field observations support the view that the time they were kept away from the population was a period that they would be inactive and not exposed to high rates of predation anyway. In addition, sampling was not daily and this spreading of the sampling occasions is believed to lessen the minor effects that the length of the sampling period could have on the estimation of population parameters (Blower et al., 1981).

- ASSUMPTION 5: Marked and unmarked individuals mix at random in the population

Sufficient movement has to occur to allow this to happen. There were always one, and generally two, evenings between sampling occasions, so there was time for the moths to reassemble naturally in the population. More than 40% of all recaptures were in clumps other than the one where the moths were originally marked (section 3.1.3.1). Also, there was no evidence of association between time elapsed between successive

captures of the same moth and the distance covered by it. This supports the view that the moths were able to fly throughout the sampling area during the intervals between sampling.

- ASSUMPTION 6: Losses are permanent.

If some individuals are temporarily unavailable for capture, population sizes are overestimated. No known feature of the biology of *P. ruralis* suggests this to be the case in the present study. Bond Ing was quite isolated from any other population of this moth and surrounded by habitats rather unsuitable for *P. ruralis* (see description of the study site, section 2.5) making reimmigration an extremely unlikely event. Reimmigration can also happen as an artefact of the sampling procedure, when just part of the population range is sampled. The boundaries of the population studied were well defined and all the area was covered when sampling.

- ASSUMPTION 7: Survival rate is constant

This assumption can be split into two: (1) that survival is not related to age and (2) that the daily survival rate is constant over the period of study.

Age-related differences were examined by comparison of observed and expected numbers of recaptures of each age of marks (Fisher & Ford, 1947). Day-to-day differences on survival were tested by comparing observed and expected total days survived by marks recaptured on each day. Table 3.5 presents the results of these tests.

Table 3.5 Test for constant survival.

		Age-related differences			Daily differences		
Year	Sex	df	x^2	P	df	x^2	P
1984	F	9	11.472	>0.1	11	9.488	>0.5
	M	9	10.294	>0.1	12	19.964	>0.05
	F+M	11	11.413	>0.1	12	18.034	>0.1
1985	F	4	2.828	>0.5	11	18.188	>0.05
	M	8	4.271	>0.5	9	21.039	>0.01[a]
	F+M	8	2.498	>0.9	11	24.289	>0.01[a]

(a) One male first marked on day 2, was recaptured on day 25.
Excluding it from the analysis:

1985	M		12.839	>0.1
	F+M		17.120	>0.1

No influence of age on survival was detected. Records of *P. ruralis* reared in the laboratory also support these results. They did become senescent but only when older than 35 to 40 days, ages never recorded in the field. Based on their life expectancy at birth (section 3.1.3.5), this ageing effect is not considered to influence their dynamics in the field.

Survival was constant on a daily basis in 1984. In 1985, however, there were significant differences in the day-to-day rates in the data for males and females+males ($0.05 > P > 0.01$). However, it was evident that this significance was due to a single recaptured male, whose mark was older than expected, on one specific day. Thus, this deviation is not regarded as a severe violation of the assumption of daily constant survival. Of the models considered, this assumption is implicit only to the Fisher-Ford model, but even this model performs robustly unless the daily variation is quite large (Manly, 1970; Bishop & Sheppard, 1973; Begon, 1979).

The present data are considered to conform satisfactorily to all the above assumptions. Consequently, any of the models - Fisher-Ford, Jolly-Seber or Manly-Parr - could be used. However, multiple recaptures were too scarce to enable use of the Manly-Parr model. The number of recaptures was generally not high, but seemed just enough to make an analysis by the Jolly-Seber model feasible. Both the Jolly-Seber and the Fisher-Ford models offered advantages and disadvantages for the analysis of the *P. ruralis* population. If the data were too scanty for the Jolly-Seber model, this would be reflected by erratic variations in the daily estimates.

More details that could help in the choice of model - as an idea of N, ϕ, SI's and the accuracy each model could reach with this data - could only be derived from a tentative analysis of the data. The best data set - 1984, females + males - was selected for comparing the performances of the models. If the results from Jolly-Seber were not good enough with these data, they certainly would not be with the other less extensive sets and sub-sets.

The models use the recapture data in different ways. Fisher-Ford considers recaptures of marks: in each sampling day, individuals count one recapture for every occasion they were captured before. In the Jolly-Seber model the information is organized in terms of the number of individuals recaptured: no matter how many times each individual has been captured, it counts only one recapture, corresponding to the last time it was caught. Thus the 'recapture' numbers used by the two models are not necessarily identical. Also, the SI's are higher when computed by the Fisher-Ford model than when Jolly-Seber m_i are used.

Table 3.6 shows the results of the analysis of the 1984 data by both models. Apart from the first five and the last two sampling days, m_i's exceed 10 by both models (see section 3.1.1, p 24-5 and section 3.1.2, p 29). However, as population sizes were fairly large, SI's were not high: using Fisher-Ford it was higher than 0.20 only twice, using Jolly-Seber it never passed this level.

Population size estimates were similar with both models, starting at about 30, reaching a peak of about 1600 after two weeks, staying over 500 for most of the time, and then declining towards the end of the season. The Jolly-Seber SE N_i's were high, generally about 0.40 $\hat{N}$.

Survival rates were quite distinct for the two models. The Fisher-Ford single

Table 3.6 Population estimates by the methods of Fisher & Ford and Jolly-Seber. Data for 1984. Day 1 = 13 July; Day 54 = 4 September. For summary of notation, see p vii.

		Fisher & Ford			Jolly-Seber					
i	n_i	m_i	SI	$\hat{N}_i$	m_i	SI	$\hat{N}_i$	$SE\hat{N}_i$	$\hat{\phi}_i$	$SE\hat{\phi}_i$
1	13	-	-	-	-	-	-	-	0.615	-
4	3	0	-	31	0	-	32	-	0.506	-
5	38	0	-	357	0	-	217	-	1.000	0.776
7	50	6	0.179	245	6	0.084	521	307	0.597	0.266
11	160	6	0.141	979	6	0.087	1590	806	0.818	0.307
14	176	20	0.164	1030	19	0.104	1610	667	0.260	0.090
18	130	11	0.072	1660	11	0.124	965	378	0.435	0.110
22	89	12	0.084	993	12	0.133	625	207	0.946	0.261
26	110	26	0.220	484	23	0.146	728	219	0.634	0.201
28	118	29	0.179	645	22	0.142	802	261	0.483	0.176
32	116	29	0.203	557	24	0.198	568	204	0.382	0.153
35	89	16	0.103	819	14	0.173	484	202	0.493	0.224
39	57	12	0.097	551	11	0.144	369	177	0.548	0.577
42	37	20	0.183	197	13	0.194	182	188	0.045	-
47	26	5	0.081	278	4	1.000	22	-	-	-
54	0	0	-	25	0	-	-	-	-	-

Fisher & Ford: ϕ= 0.845; SEϕ= 0.0132

estimate was 0.845 $\pm$ 0.0132, while the Jolly-Seber estimates averaged about 0.55 and varied inconsistently over a wide range (table 3.6).

The SE's calculated for the Jolly-Seber estimates (about 0.40) were far too high for the degree of precision required, whereas the Fisher-Ford SE$\hat{\phi}$ was well under the 0.10 level of accuracy recommended for population dynamics studies.

Bishop & Sheppard (1973) described a simulation study comparing the Fisher-Ford and Jolly-Seber models. Under conditions slightly more favourable to the Jolly-Seber model (ϕ= 0.9; N= 1000, SI= 0.12) than the ones presented here, Fisher-Ford performed somewhat better in the estimation of N and much better in the estimation of ϕ. In simulations under higher SI's, but with other parameters still relatively similar to the present estimates, Manly (1970) too reported a more consistent performance by Fisher-Ford than by Jolly-Seber.

Other simulation and analytical investigations (Robson & Regier, 1964; Roff, 1973a; Blower et al., 1981), although not so directly comparable, also indicate that Fisher-Ford estimates are more reliable, when SI's are similar to the ones found here.

Fisher-Ford was thus chosen in preference to Jolly-Seber and used for all of the analysis presented below.

3.1.3.3 Population Estimates

Figures 3.2 and 3.3 show the estimates of population size and numbers of captures and recaptures for 1984 and 1985 respectively. (Details are given in appendix 1, tables A1.5 to A1.10.)

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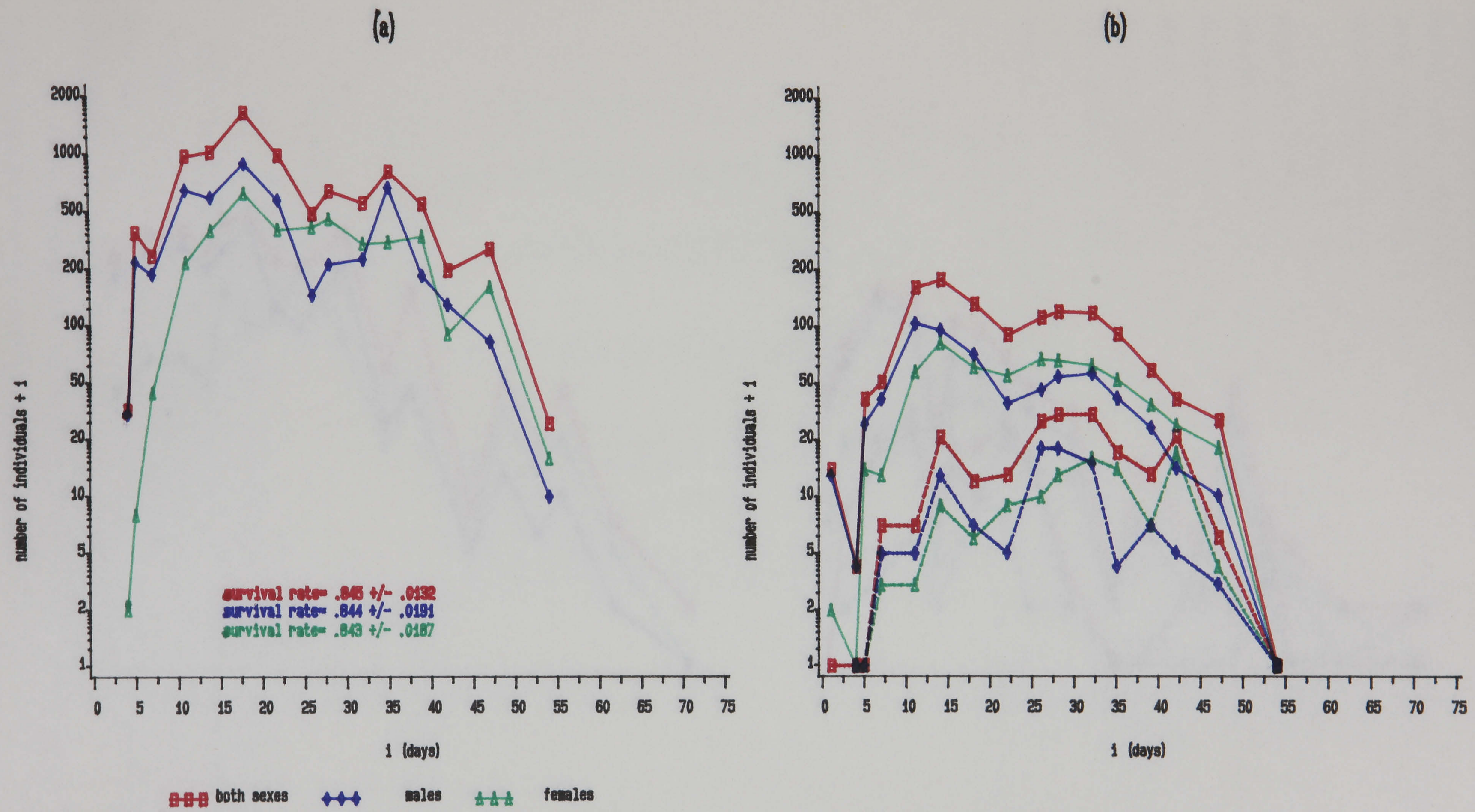

Figure 3.2 (a) Population size estimates by the Fisher-Ford method and (b) number of captures (continuous lines) and recaptures (dotted lines). Data for 1984, Day 1 = 13 July; Day 54 = 4 September.

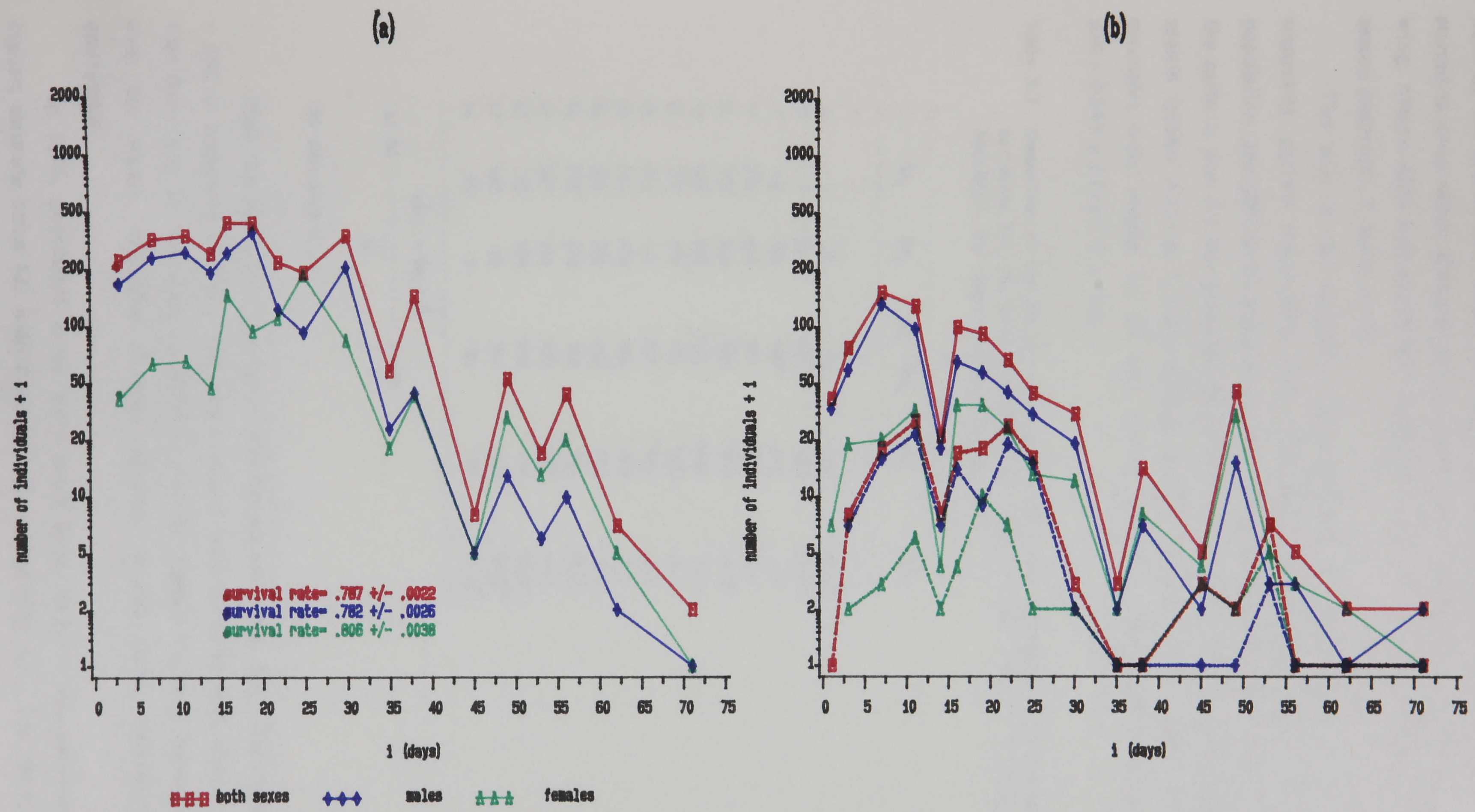

Figure 3.3 (a) Population size estimates by the Fisher-Ford method and (b) number of captures (continuous lines) and recaptures (dotted lines). Data for 1985, Day 1 = 23 July; Day 71 = 1 October.

In the summer of 1984, population size increased quickly, reaching a peak of 1660 by the end of July (Fig. 3.2). Density stayed over 500 for a further month, then started to drop rather abruptly and by September *P. ruralis* was no longer seen on the wing. Almost 4250 individuals were estimated to have emerged at Bond Ing during this season (appendix 1, table A1.5).

The sum of the population size estimates for females and males calculated separately agreed remarkably well with the estimates calculated for the whole population, the difference being lower than 10% for most days when $m \geq 2$ (table 3.7); the same is true for the estimates of the total number of individuals emerging in the season (tables A3.6 & 7, $\Sigma\hat{B}F_i + \Sigma\hat{B}M_i = 4391$; % difference = 3.4). Survival rate estimates were similar for all data sets ($\phi = 0.845 \pm 0.0132$; $\phi F = 0.844 \pm 0.0191$; $\phi M = 0.843 \pm 0.0187$; $P > 0.9$).

Table 3.7 Comparison of the sum of the population estimates for females ($\hat{N}F$) and males ($\hat{N}M$) and estimates for the whole population ($\hat{N}$). Data for 1984. Day 1 = 13 July; Day 54 = 4 September. For summary of notation, see p vii.

i	$\hat{N}F_i$	$\hat{N}M_i$	$\hat{N}F_i + \hat{N}M_i$	$\hat{N}_i$	%d[a]
1	-	-	-	-	-
4	1	29	30	31	-3.2[b]
5	7	223	230	357	-35.6[b]
7	42	186	228	245	-6.9
11	212	649	861	979	-12.1
14	372	593	965	1030	-6.3
18	628	898	1526	1660	-8.1
22	377	576	953	993	-4.0
26	393	144	537	484	11.0
28	450	216	666	645	3.3
32	302	236	538	557	-3.4
35	310	678	988	819	20.6
39	341	184	525	551	-4.7
42	90	129	219	197	11.2
47	162	82	244	278	-12.2[b]
54	15	9	24	25	-4.0[b]

(a) $\%d = \dfrac{(\hat{N}F_i + \hat{N}M_i) - \hat{N}_i}{\hat{N}_i} \times 100$

(b) days when $m_i \leq 2$

Male estimates increased faster than female ones (Fig. 3.2). They peaked higher - 898 as compared to 628 - and had a second peak (678) in mid August, suggesting that there may be two main recruitment periods. Female numbers stayed more stable over the season, indicating a more constant, though slowly decreasing, rate of emergence.

In 1985, population levels were much lower than in the previous year, the highest estimate being 421 individuals in mid-August (Fig. 3.3). For the first 30 days,

estimates fluctuated around 300. In the second half of the season, the weather was particularly windy and rainy. Samples were then so irregular and with so few recaptures, that the estimates they generated are too erratic to be of much use.

The total number of individuals emerging in this season was estimated to be 1602 (table A1.8), but due to the paucity of data in the second half of the season this estimate is unreliable. However, summing the estimates for females (table A1.9) and males (table A1.10) a similar figure is obtained ($\Sigma\hat{B}F_i + \Sigma\hat{B}M_i = 1566$; % difference = -2.2). Furthermore, for days when $m_i \geqslant 2$ (first part of the season), the sum of the estimated numbers of females and males was within 10% of the size estimated for the whole population (table 3.8).

Table 3.8 Comparison of the sum of the population estimates for females ($\hat{N}F$) and males ($\hat{N}M$) and estimates for the whole population ($\hat{N}$). Data for 1985. Day 1 = 23 July; Day 71 = 1 October. For summary of notation, see p vii.

i	$\hat{N}F_i$	$\hat{N}M_i$	$\hat{N}F_i + \hat{N}M_i$	$\hat{N}_i$	%d[a]
1	-	-	-	-	-
3	37	165	202	226	-10.6[b]
7	62	239	301	320	-5.9
11	64	262	326	340	-4.1
14	45	191	236	254	-7.1
16	145	259	404	421	-4.0
19	93	362	455	419	8.6
22	109	122	231	222	4.1
25	186	92	278	191	45.5[b]
30	83	208	291	343	-15.2[b]
35	17	23	40	57	-29.8[b]
38	40	42	82	144	-43.1[b]
45	4	4	8	7	14.3[b]
49	28	12	40	52	-23.1[b]
53	12	5	17	16	6.3[b]
56	19	9	28	41	-31.7[b]
62	4	1	5	6	-16.7[b]
71	0	0	0	1	-100.0[b]

(a) $\%d = \dfrac{(\hat{N}F_i + \hat{N}M_i) - \hat{N}_i}{\hat{N}_i} \times 100$

(b) days when $m \leqslant 2$

As in 1984, male estimates peaked sooner and higher than female ones (Fig. 3.3). Since the estimates were rather erratic in the second half of the season, it was uncertain whether there was again a second peak. Confirming what was previously indicated by the numbers marked of each sex (table 3.1), when data was sufficient to produce reliable estimates, female estimate levels were generally about half of the male figures.

There were small and insignificant ($P > 0.5$) differences between the survival rates estimated for each data set ($\phi = 0.787 \pm 0.0215$; $\phi F = 0.806 \pm 0.0377$;

$\phi M = 0.782 \pm 0.0260$). Survival rates in 1985 were significantly different from those observed in 1984 ($0.05 > P > 0.01$).

It can be seen from Figures 3.2 and 3.3 that variation in $\hat{N}_i$ is directly related to fluctuations in n_i and m_i, and marked peaks or drops in the former correspond to sudden changes in the ratio between the latter two. These changes could have arisen because of day-to-day variations in the activity (and thus availability for capture) of the moths, differences in the daily emergence rates over the season, chance fluctuations in the samples composition, etc, and most probably by a combination of these factors, interacting with the weather conditions.

3.1.3.4 Movement between the Nettle Clumps

The movements of the moths over the field are a good measure of variations in their levels of activity. Figure 3.4 shows the transit of *P. ruralis* between the nettle clumps (mov) through the seasons, together with n_i , m_i and $\hat{N}_i$. Comparing the day-to-day variation observed in each variable, it can be seen that the number of moths recorded moving on each sampling occasion depends on the number of recaptures made. Indeed, variation in m_i explained about 70% of the variation observed in mov_i in both years (1984: $b = 0.357$, $P = 0.0001$; 1985: $b = 0.276$, $P = 0.0001$). Numbers moving is also associated with numbers captured, but since m_i depend on and are limited by n_i, adding n_i to the regression equation only explains about a further 4% of the variation in mov_i, and this contribution is not statistically significant (1984: $P = 0.0852$; 1985: $P = 0.1695$). Roughly, for each recording of individual movement between the nettle clumps, 2.8 recaptures were required in 1984, and 3.6 recaptures in 1985.

To try and explain the observed variation in the activity of the moths, it is therefore necessary to consider the changes in the relationship between the amount of movement recorded and the maximum that it was possible to record, i.e., mov_i / m_i, rather than the fluctuations in the net number of recaptured individuals that moved from one clump of nettles to another. Figure 3.4 suggests that the rate of movement thus defined (movrate) was different for each year. Indeed, the between year variation observed in movrate was very significant ($t = 2.87$; $P = 0.009$). Thus the lower mobility of *P. ruralis* observed in 1985 can be partly explained by the smaller sample sizes - and thus lower probability of recording movement - obtained this year, but also reflects real differences in the activity of the moths between the two seasons.

Daily variations in the rate of movement bore no association with $\hat{N}_i$'s (1984: $r = 0.394$, $P = 0.2051$; 1985: $r = 0.422$, $P = 0.1960$).

3.1.3.5 Age Structure and Longevity

The pattern of recruitment of adults through time can be inferred from changes in the age structure of the population. In 1984 the percentage of young moths in the population stayed near 90% for about three weeks and then decreased gradually to zero

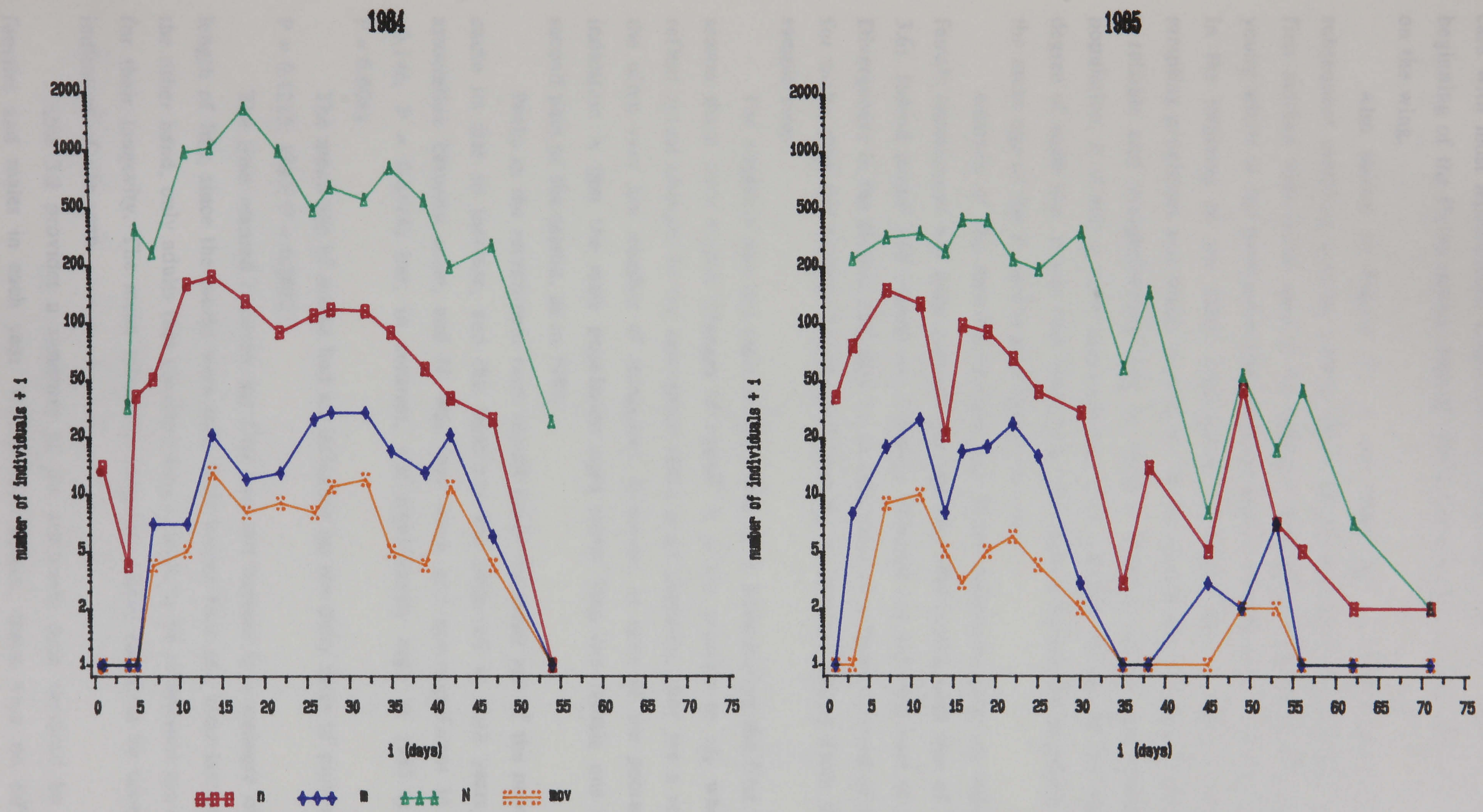

Figure 3.4 Number of moths recorded moving between the nettle clumps (mov), number of captures (n), number of recaptures (m) and population size estimates (N) for each sampling occasion. 1984 - Day 1 = 13 July; Day 54 = 4 September. 1985 - Day 1 = 23 July; Day 71 = 1 October.

by the end of the season (Fig. 3.5). This indicates that *P. ruralis* emergence - as is the case with most lepidopteran species of the temperate regions - is concentrated at the beginning of the flying season, staying fairly constant for the first weeks the adults are on the wing.

Also shown in Figure 3.5 is the mean age of marks recaptured on the subsequent sampling evening (mam). Since all moths are equally catchable, and since first marked individuals tend to be younger than recaptured ones, the proportion of young adults in the population and mam are highly correlated ($r = -0.898$; $P < 0.0001$). In the beginning of the MRR programme, all marks are, of course, new. As the sampling progresses and marks accumulate in the population, the age of marks becomes a reliable and straightforward way to monitor changes in the age structure of the population; it is also a more exact measure than ranking the age of the moths by the degree of scale loss. It was thus selected as the main criterion for assessing changes in the mean age of the *P. ruralis* population over time.

Analysis of the data for females and males separately gives no indication that female recruitment was more constant through the 1984 season than that of males (Fig. 3.6). Indeed mamF and mamM are virtually identical for the first part of the season. Divergences in the second half may be an indication of a shorter period of recruitment for males than for females but it could also be an artefact arising from the reduced sample sizes.

The situation was less clear in 1985 (Fig. 3.7). Even during the first half of the season there were erratic changes in mamF. It is not possible to say whether these reflect actual changes in the emergence rates; more probably, they are a reflection of the often very low number of recaptures. However, in spite of the poorer data, the indication is that the male population aged faster than the female one during the second part of the season, as in 1984.

Peaks in the recruitment rates should lower the mean age of the population and cause its size to increase, and this tendency was observed in both years. However, association between mam_i and N_i was very weak and non-significant in 1984 ($r = -0.146$; $P = 0.6514$) but, in contrast, was significantly high in 1985 ($r = -0.773$; $P = 0.009$).

The mean age of marks had no influence on the daily rates of movement (1984: $P = 0.1215$; 1985: $P = 0.2682$).

The time elapsed between the first and last capture is a measure of minimum length of life, since the moths were alive both before first and after last captures. On the other hand, only adults that survived long enough to be recaptured can be assessed for their longevity. The mean minimum longevity (mml) can thus be taken as a fair indication of life span.

Table 3.9 provides a summary of the minimum days survived by recaptured females and males in each year. Within each season, there were no differences in

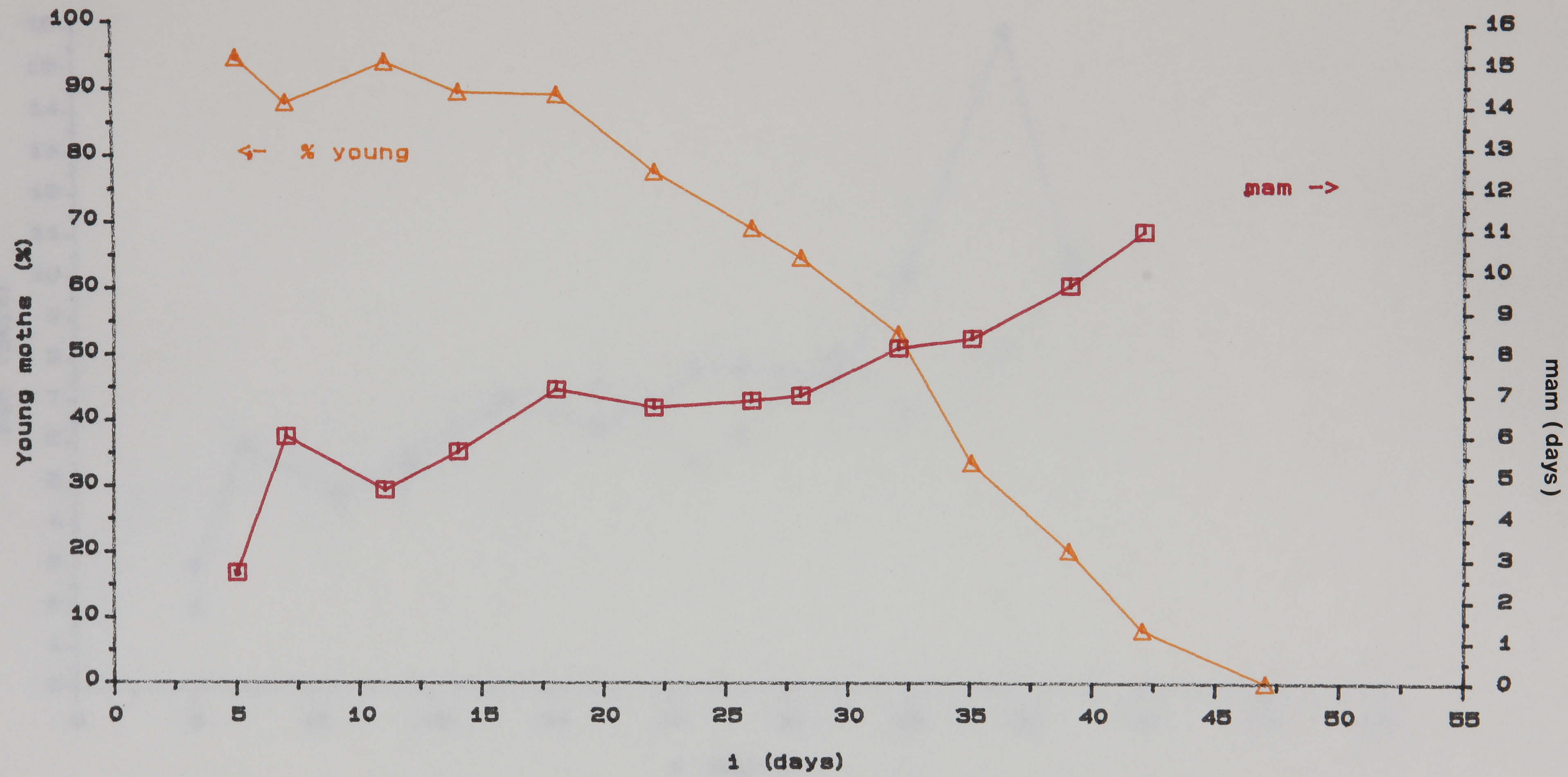

Figure 3.5 Percentage of young moths in the population and mean age of marks recaptured on subsequent sample (mam) through the 1984 season. Day 1 = 13 July; Day 47 = 28 August.

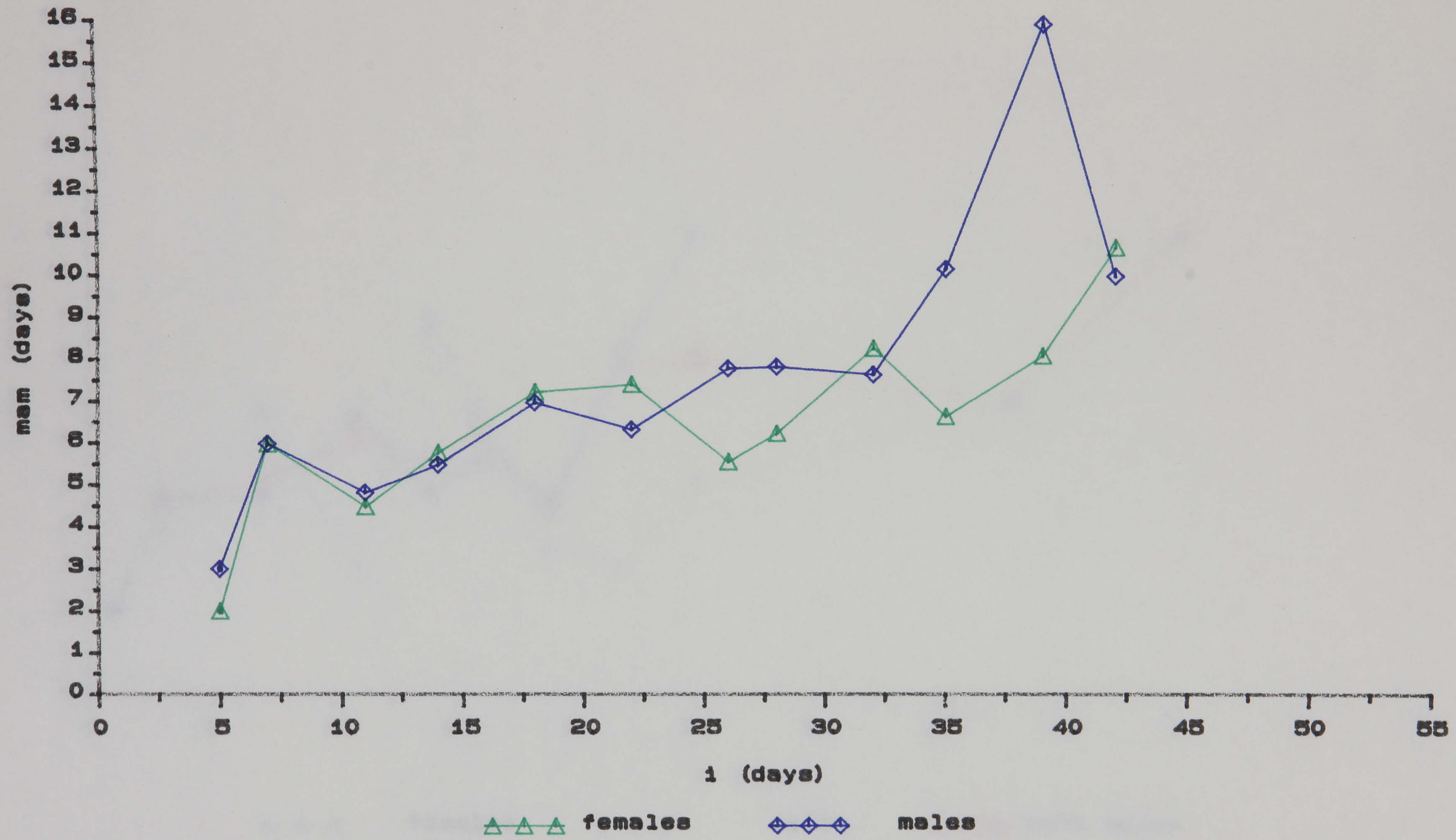

Figure 3.6 Mean age of marks recaptured on subsequent sample (mam) through the 1984 season. Day 1 = 13 July; Day 42 = 23 August.

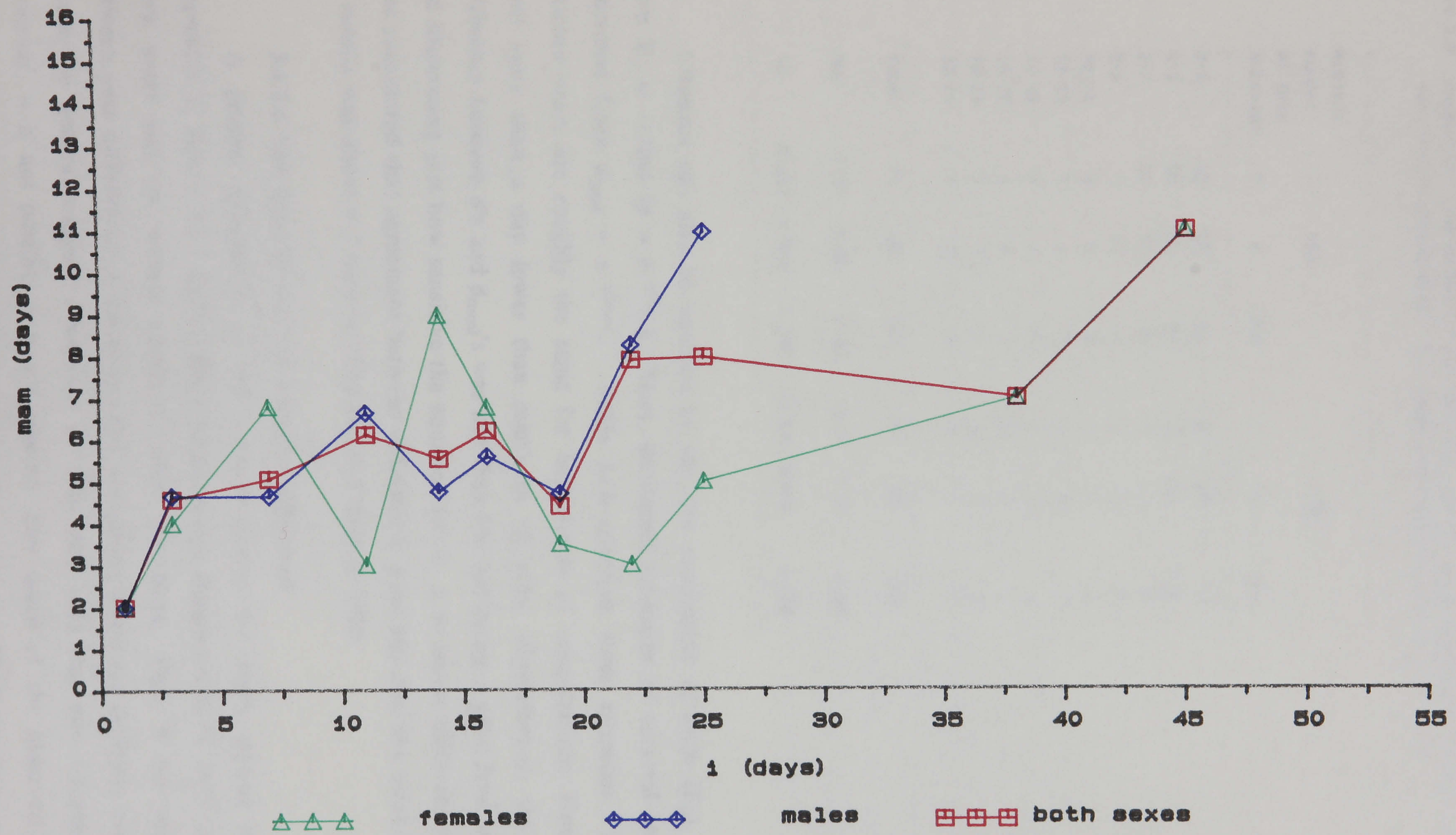

Figure 3.7 Mean age of marks recaptured on subsequent sample (mam) through the 1985 season. Day 1 = 23 July; Day 45 = 5 September.

minimum longevity between the sexes (1984: P > 0.50; 1985: P > 0.35). In 1984, mml was 7.34; in 1985, it was significantly lower - 5.46 days (0.02 > P > 0.01). The maximum minimum longevity in 1984 was 24 days for both females and males. In 1985 the longest lived recaptured moths were a 22 day-old male and a 16 day-old female.

Table 3.9 Longevity: time between first and last capture as a measure of minimum number of days survived by marked moths. For summary of notation, see p vii.

Minimum number of days survived	1984 F	1984 M	1984 F+M	1985 F	1985 M	1985 F+M
2-3	18	15	33	8	26	34
4-5	20	14	34	8	26	34
6-7	14	11	25	3	12	15
8-9	5	11	16	4	6	10
10-11	3	5	8	3	3	6
12-13	1	2	3	1	2	3
14-15	5	5	10	0	2	2
16-18	3	1	4	1	0	1
19-21	3	3	6	0	0	0
22-24	1	2	3	0	1	1
total	73	69	142	28	78	106
mml	7.01	7.68	7.34	6.07	5.24	5.46
SE	0.072	0.079	0.037	0.125	0.045	0.033

Lifespan can also be assessed by the life expectancy at birth (E_o), calculated from $E_o = -1/\ln\phi$ ($\phi = e^{-1/E_o}$). Thus, additional estimates of survival rates can be generated from $\phi_{mml} = e^{-1/mml}$. Table 3.10 contrasts these estimates. The trends between years are roughly the same for both forms of computations. However, E_o's were more than a day lower than mml's in all cases. Nevertheless, the maximum difference between ϕ's and ϕ_{mml}'s was less than 6%, indicating a good level of precision and illustrating just how sensitive the equation for E_o is to minor differences in ϕ. It is thus considered that agreement between estimates is good and that the mean lifespan of *P. ruralis* was about 6-7 days in 1984 and 4-5 days in 1985.

3.1.3.6 The Weather and the Variation Observed

A general description of the weather during the study period is given in Appendix 2; figure A2.1 shows the monthly mean temperatures in each of the field work years and the normal values for West Yorkshire. Part, if not most, of the between year differences observed in adult population levels are certainly related to the distinctive general weather conditions of 1984 and 1985 (see also Chapters 4 & 5). However, it is not possible to assess directly how much of the observed changes in population size can be attributed to the weather; only its effects on daily variations of

Table 3.10 Comparison between life expectancy (E_o) and mean minimum longevity (mml) and survival rates (ø) calculated in different ways (see text for explanation). For summary of notation, see p vii.

	1984			1985		
	F	M	F+M	F	M	F+M
ø	0.844	0.843	0.845	0.806	0.782	0.787
E_o	5.90	5.86	5.94	4.64	4.07	4.17
mml	7.01	7.68	7.34	6.07	5.24	5.46
$ø_{mml}$[a]	0.867	0.878	0.873	0.848	0.826	0.833

(a) $ø_{mml} = e^{-1/mml}$

specific demographic features can be tested.

To check whether temperature had any direct relationship with the observed day-to-day fluctuations in samples composition and parameters estimates, data on the daily weather prevailing during sampling times was used (appendix 2, section 2). Table 3.11 summarizes the mean temperatures between 20:00 and 23:00 h recorded during the flying seasons in 1984 and 1985. These temperatures followed the same pattern observed from the general monthly means: evenings were warmer in 1984 than in 1985 (except for the last fortnight in September), and these differences were highly significant in August.

Table 3.11 Mean temperature between 20:00 and 23:00 h. Data from Leeming RAF Meteorological Station (for details see Appendix 2).

Month	Days	1984 (°C)	1985 (°C)	t	P
Jul	1-15	15.4	15.2	0.292	0.773
	16-31	15.7	14.5	2.034	0.051
Aug	1-15	14.9	13.1	3.391	0.002 **
	16-31	17.0	13.8	5.013	0.000 ***
Sep	1-15	12.9	12.3	0.725	0.475
	16-30	11.2	14.3	3.400	0.002 **

Correlation analysis was carried out to study any association between daily evening temperatures (mean (TMEAN) and minimum (TMIN)), and the mean of the minima over the last three (TMIN3) and five evenings (TMIN5), and n_i , m_i, $movrate_i$, N_i and mam_i. TMEAN's and TMIN's were very highly correlated with each other in both years (1984: $r = 0.933$, $P < 0.0001$; 1985: $r = 0.972$, $P < 0.0001$), and so their degree of association with any of the variables was similar.

No significant direct influence of any of the four measures of temperature on n_i, m_i, $movrate_i$ and N_i was found in either year (table 3.12). On the other hand, variations in the mam_i were related to changes in temperature (table 3.12). Thus, in 1984, there was significant positive association with TMIN3 and TMIN5; whereas, in 1985, there was a stronger, significant negative relationship with TMEAN and TMIN.

Table 3.12 Test for association between temperatures, samples composition and population estimates. Values in each cell of the table, from top to bottom, are the following: Pearson correlation coefficient (r), probability under the null hypothesis and number of observations.

Year	Variable	TMEAN	TMIN	TMIN3	TMIN5
1984	n_i	-0.187	-0.521	-0.507	-0.466
		0.540	0.068	0.077	0.109
		13	13	13	13
	m_i	-0.167	-0.287	-0.307	-0.293
		0.587	0.342	0.308	0.332
		13	13	13	13
	$movrate_i$	0.036	0.065	0.017	0.062
		0.913	0.842	0.959	0.848
		12	12	12	12
	N_i	0.075	-0.145	0.048	0.068
		0.809	0.636	0.875	0.825
		13	13	13	13
	mam_i	0.222	0.243	0.618	0.632
		0.487	0.446	0.032	0.028
		12	12	12	12
1985	n_i	0.254	0.257	0.263	0.438
		0.343	0.336	0.326	0.089
		16	16	16	16
	m_i	0.007	0.006	-0.089	0.084
		0.978	0.983	0.744	0.757
		16	16	16	16
	$movrate_i$	0.175	0.204	0.010	0.254
		0.607	0.547	0.976	0.451
		11	11	11	11
	N_i	0.308	0.294	0.254	0.350
		0.284	0.307	0.380	0.219
		14	14	14	14
	mam_i	-0.802	-0.806	-0.550	-0.546
		0.003	0.003	0.080	0.083
		11	11	11	11

The influence of the weather on the age structure of the population may come about through its effect on development/recruitment rates and/or on survival rates.

Survival rates have already been shown to be independent of age and constant on a day-to-day basis (section 3.1.3.2, assumption 7), although in 1985 the daily differences were almost significant (table 3.5). In this year, the weather in the second half of the season was markedly worse than in the first with the TMEAN's more than one degree centigrade lower on average and this difference was significant (table 3.13). Also, winds and rain were more frequent and stronger. If daily weather had indeed a direct effect on survival rate, this could have been the cause of the differences found on testing for constancy of survival rate in 1985, and thus these differences could be of significance. However, comparison of survival rates calculated with the complete 1985 data and with data only from the first 30 days (the part of the season with the more favourable weather) contradicts this conjecture. Differences between the two figures were minor and statistically not significant (table 3.14). Thus, the hypothesis of constant survival rate throughout the season is supported and it is suggested that the main influence of the weather is on recruitment rates. Analysis of larval development supports this view (Chapter 4).

Table 3.13 Comparison of the evening mean temperatures (TMEAN) of the first (days 1 to 30) and second (days 31 to 62) halves of the 1985 flying season.

Days	TMEAN (°C)	SE	t	P
1-30	14.07	0.082		
			2.528	< 0.02
31-62	12.85	0.151		

Table 3.14 Comparison of survival rates calculated with data for the whole 1985 season (total) and with data only for the first 30 days (1-30).

Data	n	ø	SE	t	P
Total	807	0.787	0.0215		
				1.068	> 0.5
1-30	734	0.798	0.0233		

3.1.4 Discussion

The analysis of the data with the Fisher-Ford model yielded very rich information on the population dynamics of *P. ruralis*. It illustrates the usefulness and robustness of the MRR models, in general, and Fisher-Ford, in particular, when used legitimately.

In many lepidopteran species, females have patterns of behaviour which are distinct from those of males. Even when differences are not striking, females tend to spend more time close to the food plant, searching for oviposition sites (Romanowski,

1982). It is suggested that, if there were any such differences between females and males in *P. ruralis*, the method of capture employed here (among the nettles, gently moving the stems) prevented these from being reflected in different probabilities of capture. Thus, the pooling of data for both sexes is justified (section 3.1.3.2, assumptions 2 and 3).

According to the recommendations of Robson & Regier (1964), the sampling intensities attained in the present work were low, although by the criteria of Bishop & Sheppard (1973) SI's were satisfactory. A way of increasing SI - and consequently, the accuracy of the estimates - is by diminishing the sampling intervals. This, however, could result in an intersampling period too short for the captured moths to thoroughly remix with the population, causing assumption 5 to be violated and invalidating the use of MRR methods. Moreover, sampling intervals were longer when weather conditions were poor and, under these circumstances, decreasing the sample intervals would probably not improve SI's a lot, for only few moths were captured during bad weather.

Still, in spite of the moderate values of SI's, the estimates obtained were consistent (except for the second part of the 85 season) and the target level of accuracy was reached. Also the calculated precision of estimates for the whole population was further corroborated in both years by the sum of the separate estimates for females and males, and by the simmilarity observed between E_o and mml.

The value of the demographic parameters estimated and the magnitude of the fluctuations observed for *P. ruralis* are well within the usual range for lepidopterans of temperate regions (e.g. Courtney & Duggan, 1983; Crawley & Gillman, 1989; Dempster, 1982; Ehrlich, 1984; Scott, 1973; White, 1975). The most relevant results for this study concern the life expectancy, the decline in population numbers, the delayed emergence of females as compared to males and the deviation from 1:1 in the sex ratios, because these have direct effect on the population size in the next generation.

The short life span, may result in the females being time constrained for egg laying (Courtney & Duggan, 1983; Crawley & Gillman, 1989; Ehrlich, 1984). This aspect is considered in the light of the results of the laboratory experiments on fecundity in section 3.3.

The delay in the emergence of females as compared to males increases their chances of early mating and thus may minimize the pre-reproductive energy use and risk of predation of adult females (Ehrlich, 1984; Scott, 1973). However, it may also increase the chances of pre-adult mortality, and the highly male biased sex ratio observed in 1985 may be related to this fact.

These topics are further discussed in Chapter 5 in connection to the results obtained for the immatures.

3.2 REPRODUCTIVE POTENTIAL

3.2.1 Introduction

Fecundity and fertility are critical features in the ecology of any organism. Fecundity is considered here as a measure of the total number of egg cells produced within the ovaries of the female (Norris, 1933), and fertility as the production of viable eggs (Norris, 1932). Variations in these are often the essence of the regulatory mechanism of a population (Southwood, 1978). Dempster (1983), reviewing studies on 14 species of lepidopterans, found that in half of the cases the failure of females to lay their full complement of eggs was the main factor in determining fluctuations in numbers from one generation to the next.

The conditions under which the immature stages develop are decisive for the potential fecundity of adult insects (Engelmann, 1970). In some species, the materials utilized for egg synthesis are all accumulated during larval stages and no adult feeding is required; in other cases the synthesis of the eggs depends upon food intake by the adult (Johansson, 1964). Therefore, realized fecundity depends not only upon potential fecundity, but on various ecological factors, particularly those related to nutrition (Chew and Robbins, 1984).

In this context, various questions arise in relation to the reproductive biology of *Pleuroptya ruralis*. Is the number of eggs fixed at emergence or does egg production continue throughout female life? How important is adult feeding for egg development? Even if feeding is not important for egg production, it can affect fecundity indirectly by affecting lifespan and so the realization of potential fecundity (Johansson, 1964; Southwood, 1978). What would be the effects of adult starvation? Ability to resorb eggs during unfavourable periods can guarantee female survival until better conditions take place and consequently improve reproductive success (Hinton, 1981). Starvation is known to be a major cause of oosorption and lack of mating can enhance its effects (Bell and Bohm, 1975). Do either of these effects occur and does starvation affect fertility?

It is also necessary to consider that mating can stimulate the maturation of the oocytes, ovulation and/or oviposition (Hinton, 1981; Sehnal, 1985). In many species of insects, moreover, the amount of material transferred by the male to the female during copulation is sizeable and may be used as a source of food (Leopold, 1976; Thornhill, 1976). This is known to occur in many lepidopterans (Khalifa, 1950; Thornhill, 1976; Boggs and Gilbert, 1979; Boggs and Watt, 1981).

Individual fecundity is also affected by external factors. The weather can affect availability of food and oviposition sites, speed of sexual maturation and gamete production (Eidmann, 1931). In addition, it can also restrict the time available for adults to fly and, therefore, mate, feed and oviposit (Courtney and Duggan, 1983; Dempster, 1983; Chew and Robbins, 1984; Springer and Boggs, 1986).

It is far beyond the scope of this thesis to embrace the whole of this topic, but a general idea of the reproductive potential of *P. ruralis* is important on considering the significance of adult population levels in the dynamics of *P. ruralis* populations.

3.2.2 Methods

Newly emerged *Pleuroptya ruralis* (Scopoli) adults were obtained from larvae collected at Bond Ing and reared in the laboratory as described in Chapter 4.

A laboratory experiment was designed to find out (a) the mating behaviour of the moths, (b) how many eggs females bear on emergence and whether they are already ripe or not, (c) what the influences of feeding and mating are on egg production and oosorption and (d) the effect of starvation on the fertility of eggs.

In order to observe *P. ruralis* mating behaviour, a 400 x 330 x 200 mm wooden frame cage, covered with white nylon gauze, was used. The bottom of the cage was a plastic tray (340 x 210 x 40 mm) lined with paper tissue. A 20% honey-water solution was used as food and presented in a small plastic pot (25 mm in diameter and 25 mm in height) containing a piece of foam impregnated with the solution. Water was given in the same way. Both food and water were changed daily. In addition, fresh *Urtica dioica* (nettles) and flowers of *Lonicera periclymenum* (honeysuckle) were provided in jars with water. The tops of these jars were sealed with a plastic bag around the plant stem to avoid the moths getting trapped in the water.

In July 1986, pairs of moths were observed under red light, on eight different evenings, from 20:00 to 24:00 h. The following kinds of pairs were used: (a) freshly emerged males and females; (b) two-day old males and freshly emerged females; (c) seven-day old males and freshly emerged females; (d) seven-day old males and three-day old females. All individuals were virgins. For each combination, two pairs (of the same type) were observed together on the first evening, but only one pair on the subsequent evening, because it was realized that the presence of two males could influence the outcome.

For the fecundity and fertility experiments, glass jars (120 mm in diameter and 100 mm in height) lined with paper tissue and covered with fine white gauze were used for rearing the moths. In the early experiments a nettle stem with some leaves was provided as a perch but, as they did not use it, it was no longer supplied.

Soon after emergence, males were kept in these rearing jars in groups of three or four, provided with water and fed with a 20% honey-water solution for at least three days before being allocated a mate.

Females were either fed (with 20% honey-water solution) or starved and either kept as virgins or reared with a male. There were five different categories of females used: FY - fed young virgins (mostly less than three days but up to a week old), FV - fed virgins (older than a week), SV - starved virgins, FM - fed mated and SM - starved mated. All experimental categories were provided with water. Each mated pair was reared in a separate jar; the virgins were kept in groups of two or three.

At first, nettle leaves were provided as oviposition sites, but the moths laid their eggs equally anywhere. As the eggs were more efficiently counted and reared on the paper tissue (since it does not get mouldy as easily as the leaves) and seemed to hatch equally well on it, nettle leaves were no longer given.

The jars were inspected every two days for eggs laid. Eggs found were taken with their substrate and placed in plastic pots (250 x 100 x 100 mm) lined with paper tissue. These pots were kept in the shade in a cold, ventilated green-house. Three times a week they were checked for hatching and larval survival up to the second instar, and fresh nettle leaves were given.

When the moths were unable to stand, it was assumed that they were in the last or penultimate day of their life (this was based on previous experience). They were either dissected immediately or frozen for future dissection.

Six females on each of the above rearing categories were dissected in saline. The amount of fat body present in the abdomen was ranked from 1 (none left) to 5 (abdomen filled with fat body). The reproductive organs were removed, spread, fixed in Bouins fixative for 30 minutes and then transferred to 75% alcohol. The length of the ovarioles and the diameter of the corpus of the bursa copulatrix were measured. The egg cells in the ovarioles and in the oviducts (if any) were counted and the length and width of the larger ones measured. As they are approximately cylindrical their volume was calculated using the formulae $V = h.\pi(d^2/4)$. All values are expressed $\pm$ SE.

3.2.3 Results

Individuals accepted well the rearing conditions and were frequently seen drinking and feeding. Comparison of observed longevity of females in the field and laboratory supports this view: mean longevity in the laboratory was 24.8 $\pm$ 3.66 days, which is similar to the maximum minimum longevity observed in the field (section 3.1.3.5).

During the day, the moths rested horizontally on the gauze at the top of the cage or jars, in a posture similar to that observed in the field, where they generally rest on the underside of the nettle leaves.

3.2.3.1 Courtship Behaviour

In all the evening observations "calling" behaviour was observed. As soon as dusk arrived the moths became active and the female would settle on the walls of the cage, facing up. The abdomen would be bent dorsally, thus exposing the hairy end-plates of the ovipositor and the copulatory opening (ostium bursae). She would also rotate her antennae and intermittently flutter her wings. All females in all observations performed in this way, irrespective of their age or whether there were one or two couples in the cage.

All males answered to this display. The male would first fly around the female

and after a while settle near her. Soon he would also start to rotate his antennae and flutter his wings. Some couples would behave like this, without stopping, during the whole observation period; most of them would pause briefly every 20-30 minutes and then resume courting. In spite of the observed displays, no obvious attempts to mate were ever observed.

When two couples were present in the cage, the males would spend most of the time chasing each other, "answering" the females only during short intervals, even if they were each paying attention to a different female (as they generally seemed to do).

This "calling and answering" pattern was also seen in those couples reared in the jars and, just the same, it was difficult to get individuals (both fed and starved) to mate. As judged from the production of fertile eggs, of the 14 fed and 15 starved pairs reared, only three in each condition did mate successfully.

When the male died before the female or had been with her in the glass jar for ten days or more and no egg was laid, a new mate was allocated to the female. Each of these situations happened three times with fed couples and another three times with starved ones. In none of the cases did successful matings occur after a new male was presented to the female.

This difficulty in mating in captivity, meant that the size of the samples available for the analyses were very low for the categories of mated females (FM & SM) and highly unbalanced in relation to the virgins. This impeded the use of multivariate analysis of variance on the analysis presented below.

3.2.3.2 Oviposition Patterns and Fertility

The six females that did mate took quite different periods of time from the day each of them were put together with the male until they started ovipositing (Figure 3.8 - unfortunately, records on the daily oviposition of one of the starved females were not taken; she laid a total of only 80 eggs). Considering the apparent difficulty of *P. ruralis* to mate in captivity, it seems likely that different delays were mostly due to different lengths of time elapsing before the couples actually mated, rather than by variation in the time necessary for them to start ovipositing after having mated.

Females laid more eggs per day at the beginning of the oviposition period (Figure 3.8). Feeding had a striking effect on the life span of the moths (see table 3.17 below), the oviposition period and, therefore, the number of eggs laid. Thus fed females (FM) lived for a longer period (mean lifespan = 37.0 $\pm$ 4.75 days) and laid more eggs (mean number of eggs = 891 $\pm$ 48.1) than did starved ones (SM) (mean lifespan = 19.3 $\pm$ 3.60 days; mean number of eggs = 284 $\pm$ 110.6): a difference of 68% in fecundity. Fertility, however, was not affected by starvation, there being no significant difference in the survival of offspring up to the second instar (FM = 0.65 $\pm$ 0.0085, SM = 0.78 $\pm$ 0.0001; $P > 0.20$).

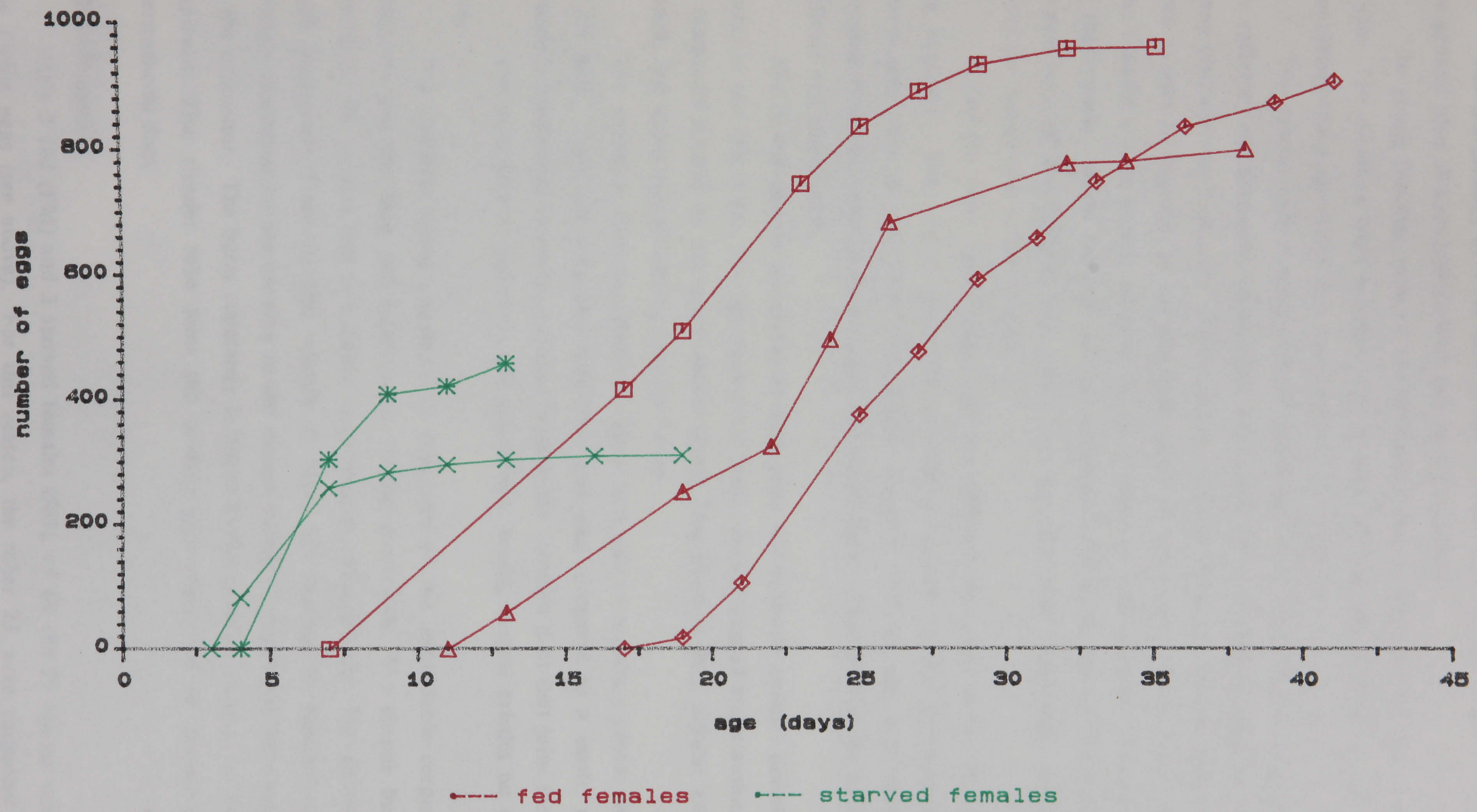

Figure 3.8 Cumulative number of eggs laid per female during lifespan. Each line represents one individual and ends on the day of her death.

3.2.3.3 General Morphology of *P.ruralis* Female Internal Reproductive Organs

The morphology of *P. ruralis* female reproductive organs (Figure 3.9a) follows the general plan of Lepidoptera with two genital openings.

In young females, most of the abdomen space is taken up by the reproductive organs. The digestive tract occupies only a small portion and the rest of the space is completely filled up with a very large amount of fat body.

The ovaries each consists of four (sometimes five) very slender ovarioles. These are reflected on themselves about eight times and tightly packed as rounded masses by many tracheoles and fat body. There are no terminal filaments and the anterior tips of both ovaries lie together in the abdomen dorsal to the corpus of the bursa copulatrix. The follicles can be seen as an array of beads gradually getting larger towards the base of the ovarioles. Nurse and egg cells are distinguishable in the top and bottom regions, respectively, of the follicles (fig 3.9b). The egg cell takes increasingly more follicle space the nearer it is to the oviduct.

In females older than 5 days, ripe egg cells can be found in the distal part of the ovarioles. They differ from the developing follicles in that nutritive cells are absent and they do not stain with Bouins fixative. As the egg cells ripen, some accumulate in the oviducts until oviposition takes place. When empty, the oviducts are delicate and transparent.

The coiled slender spermathecal duct joins the common oviduct dorsally at its posterior end (fig 3.9a). The spermatheca is small, kidney-shaped and translucent, and is continued distally by the spermathecal gland. This gland is thin, tubular and blind-ended, and sometimes bifurcates towards its tip.

The vagina is short and bulbous. There is a pair of accessory glands that opens at its base. They are long and tube-like, and each broadens to a small, perfectly rounded, transparent reservoir, before fusing in the common duct that joins the vagina.

The ovipositor is yellowish and sclerotized, having several bristles on the end-plate.

The chitinous bursa copulatrix is composed of the expandable corpus bursae anteriorly and the long and wide ductus bursae posteriorly. The corpus bursae lies ventral to the ovaries and is a fairly large whitish, rounded sac. The ductus bursae leads posteriorly from it, also whitish at first, but turning to brown-yellow and strongly chitinized before opening in the ostium bursae (= copulatory opening) ventral to the ovipositor. The bursa copulatrix is linked to the common oviduct by the ductus seminalis. This slender tube joins the oviduct near the point of insertion of the spermathecal duct.

3.2.3.4 Fecundity

Only 3 fed (FM) and 3 starved females (SM), of all the 29 reared with males, laid fertile eggs (see above). For this reason, the other 23 were suspected to have remained virgins. The size of the corpus bursae is a very helpful character in

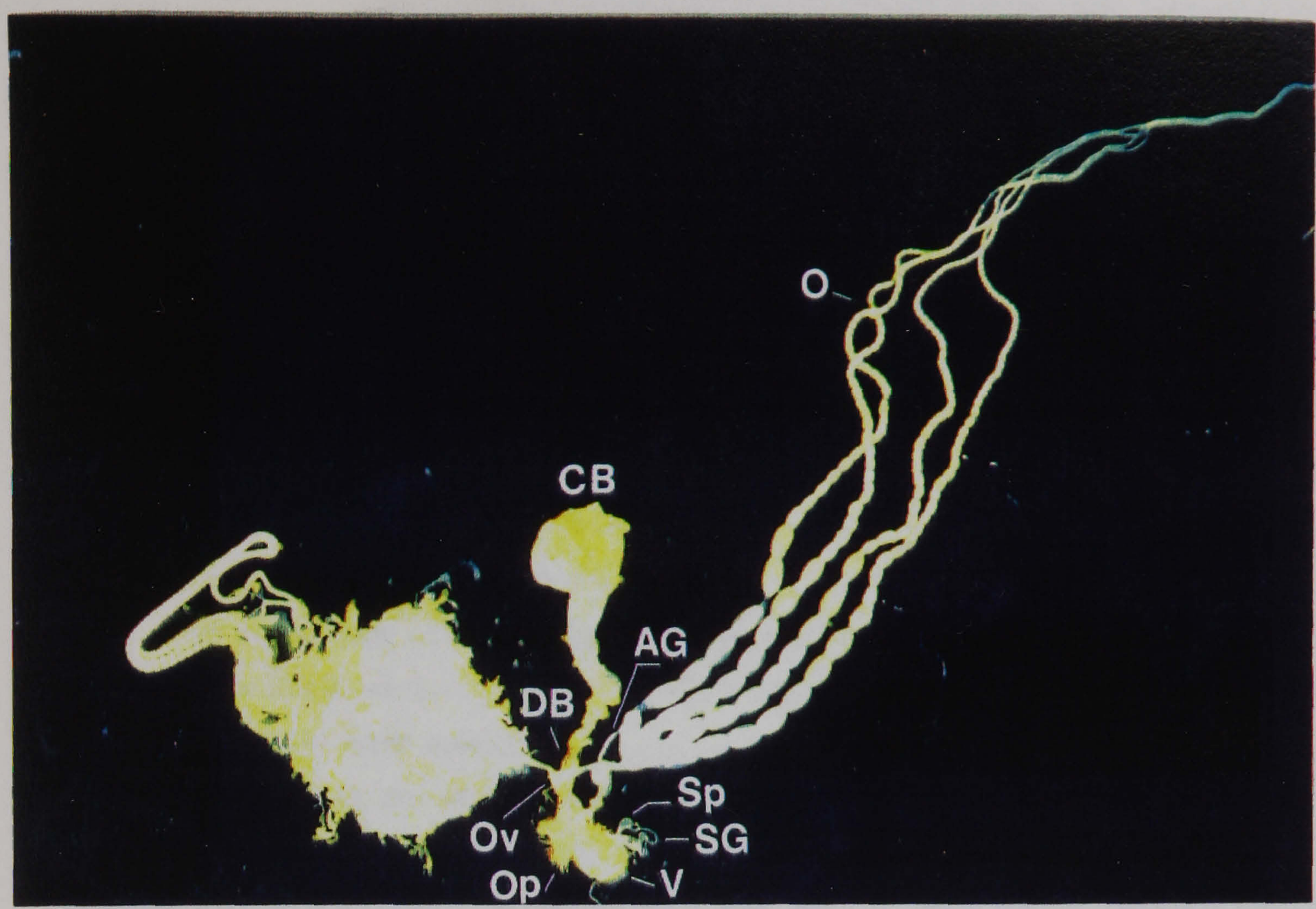

Figure 3.9 (a) Young female internal reproductive organs

O=ovary (note the other ovary, which was not spread out, how it is reflected on itself and surrounded by fat body); Ov=oviduct; Sp=spermatheca; SG=spermathecal gland; V=vagina; AG=accessory gland; Op=ovipositor; CB=corpus bursae; DB=ductus bursae;

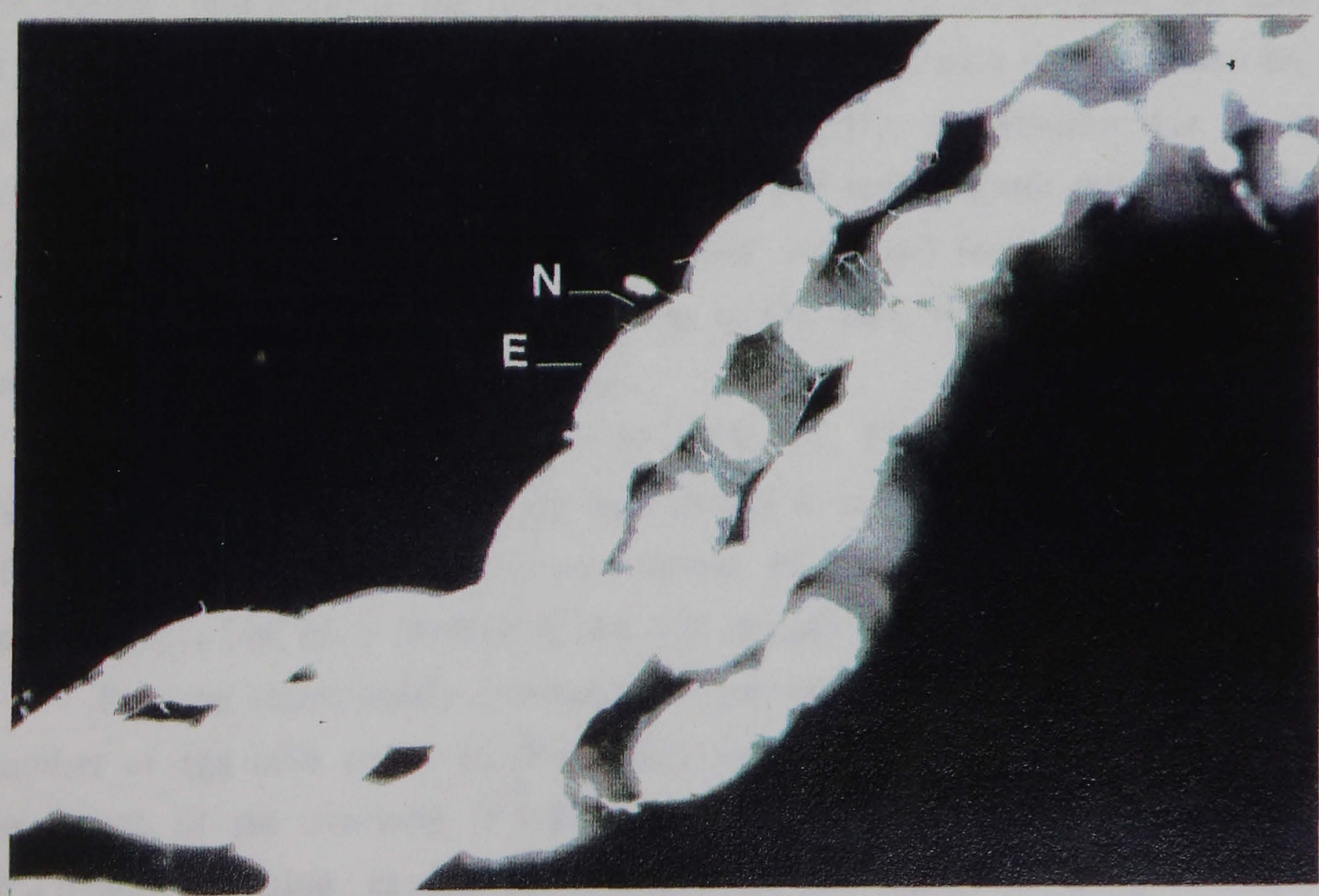

Figure 3.9(b) Detail of the ovarioles, showing the follicles with the nurse (N) and egg cells (E).

distinguishing whether a female has mated or not, since it becomes expanded when a spermatophore is present within it (Norris, 1932; Khalifa, 1950).

Females (both starved and fed) that laid fertile eggs had a corpus bursae much larger than that of the females that did not; this difference was very significant in both cases ($P < 0.005$). Furthermore, FMs that produced offspring and the fed suspected virgins also differed significantly both in the number of egg cells produced and in the length of the ovarioles. The starved individuals also showed significantly greater fat body depletion (table 3.15). In both the fed and the starved groups there is no significant difference between the suspected virgins and the known virgins (table 3.15). Thus they are all considered to be virgins.

The counts and measurements obtained from the dissections are summarized in Appendix 3. Figures 3.10, 3.11, 3.12, and 3.13 illustrate the general appearance of the female reproductive organs for each of the rearing conditions.

No correlation was found between the number of egg cells produced and the age of the individuals, no matter whether the data for all females ($P > 0.21$) or the separate groups ($P > 0.72$) were considered.

Also, ageing per se does not cause degeneration of the reproductive organs. FV (aged up to 41 days - Figure 3.10) differed from the FY females (aged up to 7 days - Figure 3.9) only by the presence of ripe egg cells in their ovaries and oviducts. No significant difference was found in the corpus bursae size, total number of egg cells, egg cell size, fat body depletion or length of ovarioles between these two groups (table 3.16).

Feeding and mating, on the other hand, have been shown to influence strongly the changes that occur in the reproductive organs during the female's life; deterioration is caused both by starvation and/or "use". Short ovaries with reduced numbers of small egg cells were observed in the SVs (Figure 3.11), presumably due to oosorption triggered by starvation. FMs, after producing and laying many eggs during their lives, had still shorter ovaries, with loose "wrinkled" walls and few egg cells in them (Figure 3.12). This picture was still more striking in the SMs, where the effects of starvation and "use" were combined (Figure 3.13).

The observed differences between FV, SV, FM and SM females are supported by the results of the statistical analyses shown in tables 3.17 (survival), 3.18 (diameter of the corpus bursae), 3.19 (total number of egg cells produced), 3.20 (egg cell volume), 3.21 (fat body depletion) and 3.22 (length of the ovarioles).

Feeding significantly increased the survival of the moths ($P < 0.005$), the total number of egg cells produced ($P < 0.002$), egg cell volume ($P < 0.001$) and, in virgins, the length of the ovarioles ($P < 0.01$), and reduced the degree of fat body depletion ($P < 0.005$). Mating caused an increase in the diameter of the corpus bursae ($P < 0.001$), the total number of egg cells ($P < 0.02$) and fat body depletion ($P < 0.001$), but caused the length of the ovarioles to decrease ($P < 0.001$). A slight interaction

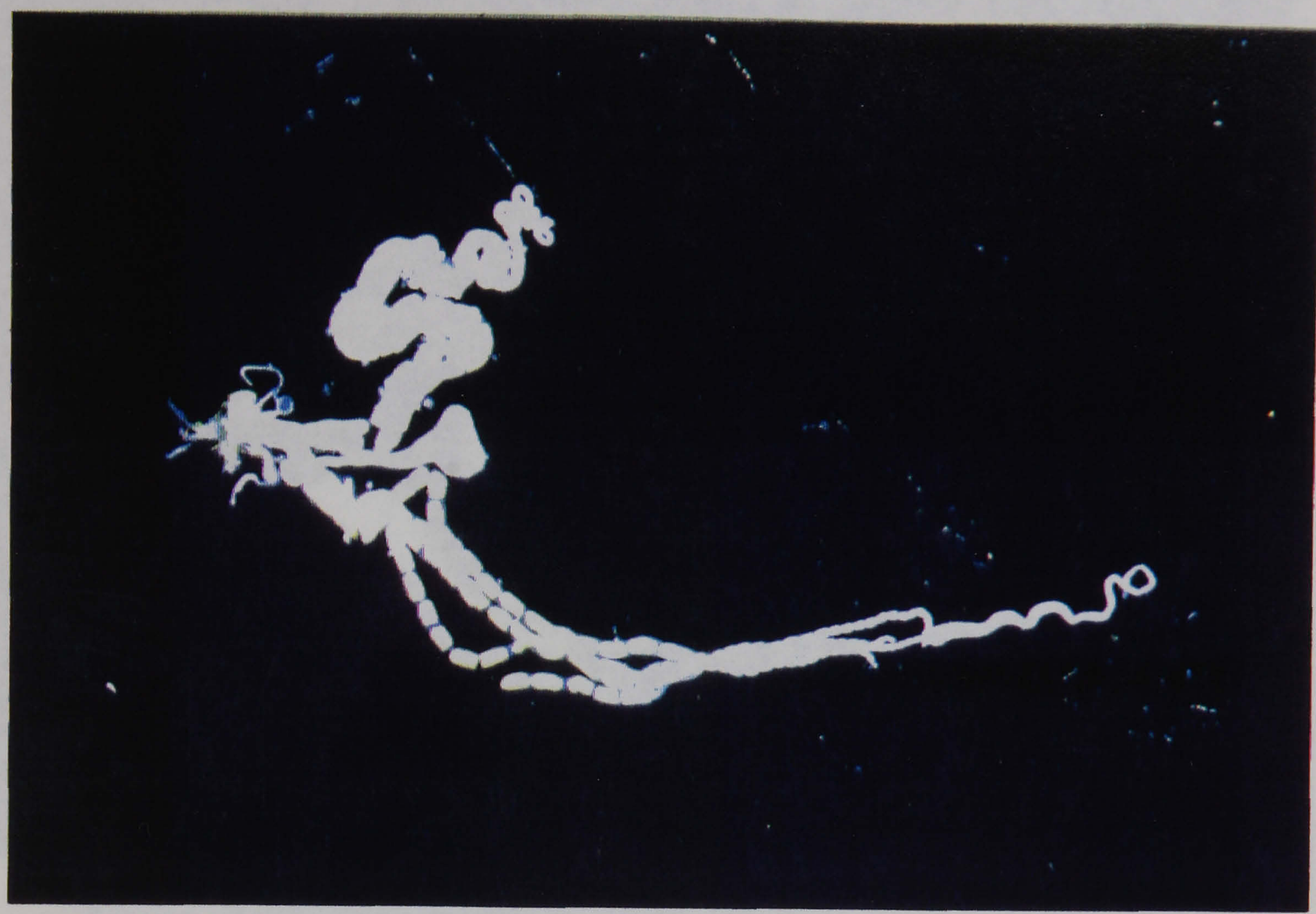

Figure 3.10 Fed virgin internal reproductive organs

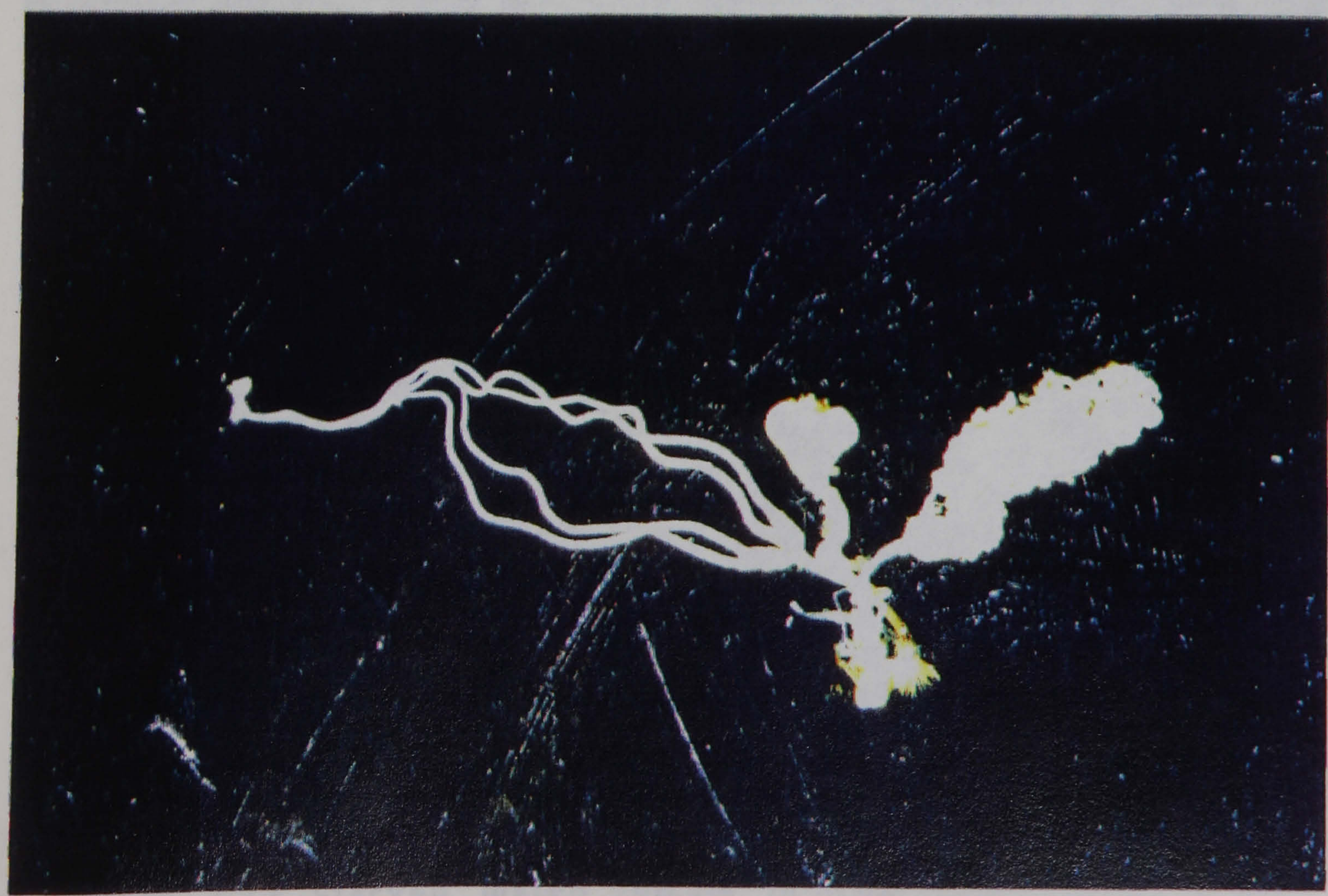

Figure 3.11 Starved virgin internal reproductive organs

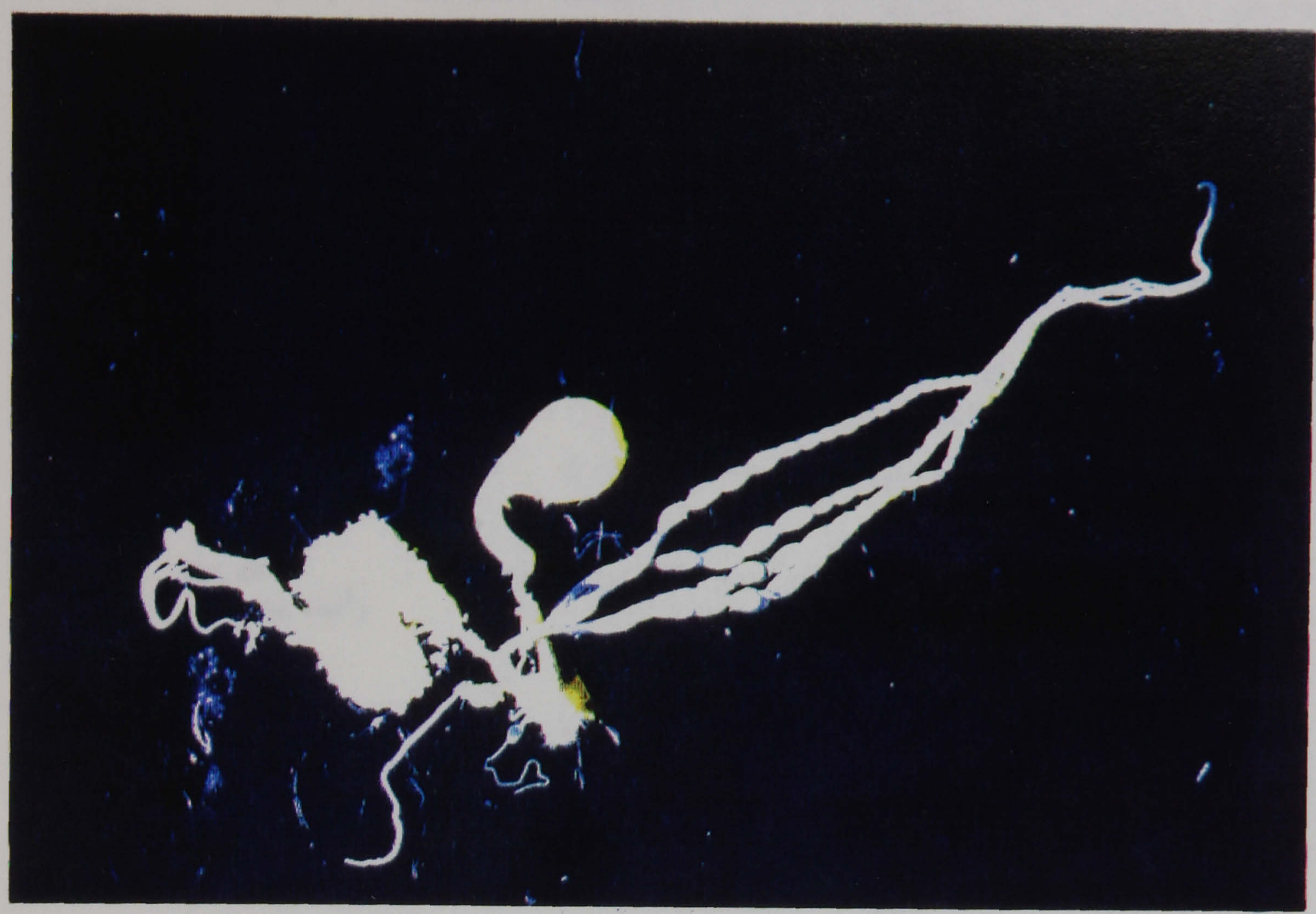

Figure 3.12 Fed mated female internal reproductive organs

Figure 3.13 Starved mated female internal reproductive organs

Table 3.15 Comparison between females reared with males that laid no fertile egg (i.e, suspected virgins, FSV and SSV), females reared with males that laid fertile eggs (FM and SM) and virgin females (FV and SV). F indicates fed, S indicates starved; P indicates the level of statistical significance of the differences between two adjacent groups.

a)Fed females

	FM	P	FSV	P	FV
Corpus bursae diameter (mm)	2.97	<0.005	1.70	0.31	1.77
Total number of egg cells produced	1402.7	0.01	843.0	0.62	1007.7
Egg cell volume (mm^3)	0.120	0.21	0.057	0.94	0.058
Remaining fat body*	1.67	0.08	3.33	0.10	4.83
Ovarioles length(mm)	10.0	0.002	19.0	0.67	19.8

b)Starved females

	SM	P	SSV	P	SV
Corpus bursae diameter (mm)	2.60	0.001	1.83	0.62	1.72
Total number of egg cells produced	855.3	0.28	747.3	0.65	700.7
Egg cell volume (mm^3)	0.003	>0.05	0.028	0.60	0.018
Remaining fat body*	1.00	0.0004	2.00	>0.05	3.00
Ovarioles length(mm)	11.17	0.07	13.67	0.59	15.08

* ranked from 1 (none left) to 5 (abdomen filled with fat body).

effect between feeding and mating was detected in the egg cell volume ($P < 0.02$) and the length of the ovarioles ($P < 0.05$). Table 3.23 summarizes these results.

Table 3.16 Comparison between fed virgins (FV) and young females (FY).

Parameter	FV	FY	P
Corpus bursae diameter (mm)	1.77	1.80	>>0.05
Total number of egg cells produced	1007.7	995.7	>>0.05
Egg cell volume (mm^3)	0.058	0.071	>>0.05
Remaining fat body*	4.83	5.00	>>0.05
Ovarioles length(mm)	19.8	21.4	>>0.05

* ranked from 1 (none left) to 5 (abdomen filled with fat body).

Table 3.17 Influence of feeding and mating on survival.

	FV	SV	FM	SM
Mean age (days) at death	25.7	18.8	37.0	19.3
(n)	(9)	(9)	(3)	(3)
± SE	23.67	11.51	4.75	3.60

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	285.91	<0.02
Mating	1	165.05	ns
Feeding	1	550.97	<0.005
Interaction	1	141.72	ns
Residual	20	51.01	

Table 3.18 Influence of feeding and mating on the diameter of the corpus bursae.

	FV	SV	FM	SM
Mean (mm)	1.77	1.75	2.97	2.60
(n)	(9)	(9)	(3)	(3)
± SE	0.028	0.015	0.082	0.027

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	1.67	<<0.001
Mating	1	4.81	<<0.001
Feeding	1	0.03	ns
Interaction	1	0.17	ns
Residual	20	0.03	

Table 3.19 Influence of feeding and mating on total number of egg cells produced per female.

	FV	SV	FM	SM
Mean*	924	700	1398	823
(n)	(9)	(9)	(3)	(3)
95% confidence				
upper limit	845	612	1101	384
lower limit	1152	800	1776	1941

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	0.0070	ns
Mating	1	0.0686	<0.02
Feeding	1	0.1259	<0.002
Interaction	1	0.0144	ns
Residual	20	0.0144	

* calculated from the log transformed data.

Table 3.20 Influence of feeding and mating on egg cell volume.

	FV	SV	FM	SM
Mean* (mm^3)	0.049	0.012	0.103	0.003
(n)	(9)	(9)	(3)	(3)
95% confidence				
upper limit*	0.029	0.005	0.016	0.001
lower limit*	0.085	0.029	0.665	0.006

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	1.8227	<0.001
Mating	1	0.1121	ns
Feeding	1	4.3328	<<0.001
Interaction	1	1.0232	<0.02
Residual	20	0.1550	

* calculated from the log transformed data.

Table 3.21 Influence of feeding and mating on the amount of fat body remaining in the abdomen. Fat body ranked from 1 (none left) to 5 (abdomen filled with fat body).

	FV	SV	FM	SM
Mean*	4.16	2.45	1.59	1.00
(n)	(9)	(9)	(3)	(3)
95% confidence				
upper limit*	5.35	3.34	4.29	1.28
lower limit*	3.24	1.79	0.59	0.78

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	0.3455	<0.001
Mating	1	0.7373	<<0.001
Feeding	1	0.2982	<0.005
Interaction	1	0.0009	ns
Residual	20	0.0235	

* calculated from the log transformed data.

Table 3.22 Influence of feeding and mating on length of the ovarioles.

	FV	SV	FM	SM
Mean (mm)	19.56	14.72	10.00	11.17
(n)	(9)	(9)	(3)	(3)
± SE	0.79	1.08	0.82	0.83

Two way ANOVA table

Source of variation	df	MS	P
Subgroups	3	100.19	<0.001
Mating	1	193.39	<<0.001
Feeding	1	66.67	<0.01
Interaction	1	40.50	<0.05
Residual	20	7.87	

Table 3.23 Summary of the results on the effects of mating and feeding on the parameters measured. Title table

Parameter	Mating	Feeding	Interaction
Survival	ns	<0.005	ns
Corpus bursae diameter	<<0.001	ns	ns
Total number of egg cells produced	<0.02	<0.002	ns
Egg cell volume	ns	<<0.001	<0.02
Remaining fat body	<<0.001	<0.005	ns
Ovarioles length	<<0.001	<0.01	<0.05

3.2.4 Discussion and Conclusion

The results above should be looked with caution given the small size of the samples of the mated females. However, given the consistency of the results, the levels of significance obtained and the directly observed differences in the different categories of females (figs 3.9 to 3.13), some conclusions can be drawn.

3.2.4.1 Courtship Behaviour and Morphology

The morphology of the female internal reproductive organs and the courtship behaviour of *P. ruralis* are similar to those of other pyralid moths (Norris, 1932; Khalifa, 1950; Krasnoff, 1983) and indeed to those of lepidopterans in general (Eidmann, 1929; Stern and Smith, 1960; Richards and Davies, 1977). Even the difficulty in getting pairs to mate in the laboratory is not unusual. Norris (1933) reported that in *Ephestia kuhniella*, although most individuals would mate during their lifespan under normal laboratory conditions, failure of the male to pair on any given day was not at all uncommon. Stern and Smith (1960) also encountered difficulties in getting the pierid *Colias philodice eurytheme* to mate in the laboratory.

The causes for this difficulty remain obscure. However, it is noteworthy that during the whole three years of diurnal and nocturnal field work, on no occasion were *P. ruralis* seen mating.

3.2.4.2 The Influence of Feeding on Fecundity and Fertility

Most adult Lepidoptera seemed to have lost the need for nitrogenous foodstuff, owing to a series of modifications by which their requirements have come to be met by the reserves contained in the fat body (Norris, 1934). Contrasting levels of dependence on adult resources can be found in this group of insects (Murphy, Launer and Ehrlich, 1983): many do not feed at all when adults, while *Heliconius* butterflies, at the other extreme, are able to collect pollen and produce a rich amino acid solution that can support life and egg laying for several months (Gilbert, 1972). The varied importance of adult feeding is also expressed by the fact that some species emerge with up to 40% of the eggs ripe (Norris, 1934), while others have no eggs yolked at all (Eidmann, 1931). Boggs (1981 and 1986) emphasized that fecundity patterns in the Lepidoptera must be considered in the context of resource allocation, particularly in relation to the differences in the importance of adult nutrition on egg production. She proposed that lepidopteran species can be classified along a spectrum of relative potential importance of adult nutrient intake to egg production, based on normal feeding habits and timing of egg maturation. As adult feeding becomes more important for egg production, age-specific fecundity becomes more constant.

Pyralid moths are known to use proteins obtained from larval feeding for egg development (Engelmann, 1970). Based on the present results, it is suggested that in *P. ruralis* most nutrients for egg development are acquired during the larval stages.

However, the sugars obtained by adult feeding proved to be very important for individual maintenance (table 3.17) and, possibly, contribute to egg production. If no food is available for the adult moth, the nitrogenous compounds of the fat body might have to be spent (table 3.21) for the sake of its survival. Egg production then suffers a severe reduction (Figure 3.8 and table 3.19).

P. ruralis, which feeds on nectar - a relatively poor nutrient source - and emerges with no ripe eggs, is near the middle of the spectrum suggested by Boggs (1986), similarly to *Colias philodice eurytheme* Boisduval (Pieridae) (Stern and Smith, 1960), *Lasiommata megera* L. (Satyridae) (Wiklund and Karlsson, 1984) and *Speyeria mormonia* Edwards (Nymphalidae) (Boggs, 1986). Also, the pattern of oviposition of *P. ruralis* (Figure 3.8) is similar to that in *S. mormonia* (Boggs, 1986): most of the eggs are laid at the beginning of adult life and fecundity gradually decreases with age.

The variability due to larval intake of nutrients was kept to a minimum, since all individuals used in the experiments were reared in the laboratory with fresh food ad lib.. All young females dissected had their abdomens completely filled with fat body (table 3.16); thus it is assumed that all adults emerged with their full potential nutritive reserves. Benson (1973) described a positive correlation between female size at emergence and fecundity in species of lepidopterans that do not feed as adults. However, studies on species that depend on nectar feeding for egg production have failed to find any such correlation (Karlsson and Wiklund, 1984; Wiklund and Karlsson, 1984; Boggs, 1986; Springer and Boggs, 1986). Benson (1973) also noted that female size is affected by the density at which the larvae are reared and by the quality and quantity of food they are given. Considering the methods used here for rearing the larvae and the fact that *P. ruralis* feeds when adult, variations in female size were minor, and there were no indications that size had a significant role in determining potential fecundity under the experimental conditions of this work.

The amount of fat body is an indication of the nitrogenous resources available for the individual. Fat body is the site of synthesis of insect vitellogenin - the yolk protein (Kunkel and Nordin, 1983) and also a major site of glycogen deposition in the insect body. The lepidopterans that do not feed as adults use it as a major source of energy for flight (Bailey, 1975). In species in which individuals feed as adults, carbohydrates are used as fuel instead. However, if deprived of sugary foods, they can still use the energy stored in the fat body for general purposes in addition to egg production. The nectar on which the female may eventually feed, on the other hand, cannot replace the protein of the fat body used up (Norris, 1933).

The dimensions of eggs laid tend to be fairly constant within a species (Johansson, 1964). Therefore, the size of the egg cells in the ovarioles is primarily a clue to its developmental stage. The smaller egg cells observed in the ovarioles of the starved females (table 3.20) can be taken as an indication that they have exhausted the

nitrogenous reserves for purposes other than yolking their eggs. This, added to the increased (or total, in some cases) depletion of fat body (table 3.21), the reduction in the total number of egg cells (table 3.19) and in the length of the ovarioles (table 3.22), as compared to what was observed in the young females (table 3.16), provides good evidence that oosorption takes place under starvation.

It is still possible that starved females could lay smaller and/or lighter eggs. Eggs were not weighed, but no difference in fertility was found between eggs laid by fed or starved females. This corroborates Johansson (1964) in that a reduction on food which can lower fecundity usually has little effect on the fertility of the female. Karlsson and Wiklund (1984 and 1985) and Wiklund and Karlsson (1984) tested egg fertility and fitness of larvae emerging from light and heavy eggs in four species of satyrids and failed to find any significant difference, even in situations of extreme stress.

The levels of egg fertility observed for *P. ruralis* (65-78%) are similar to the records available for other pyralids (Norris, 1933; Benson, 1973).

3.2.4.3 The Influence of Mating on Fecundity

The increase in the number of egg cells produced (table 3.19) by mated females could be due to nutritional provision by the males. However, mated females showed a significantly greater depletion of fat body (table 3.21) and it could be that mating serves as trigger to convert the fat body reserves. The smaller corpus bursae of the SMs (table 3.18) may indicate that starved males produce smaller spermatophores and/or that females absorb them to a greater degree or more quickly. It could also be that starved couples mate less. The literature very seldom deals with the possible relationship between sexual behaviour and nutritional condition in insects (Johansson, 1964).

3.3 POPULATION DYNAMICS AND REPRODUCTIVE POTENTIAL

The laboratory findings on egg production are considered to represent the maximum potential fecundity, but given the life expectancy estimated from the MRR data, the levels of fecundity attainable in the field are probably much lower. In this way, the effect that the changes in the weather observed during field work may have had upon fecundity and, consequently, population levels can be only speculated. There may be a relationship between the observed 60% reduction in the numbers of eggs laid in the laboratory, as a result of starvation, and the decline in the larval population observed in the field (Chapter 4). However, it seems that females, on average, do not live long enough to have their fecundity affected by starvation to such extent in the field. On the other hand, they certainly spend much more energy in flight in the field than they do in the laboratory, and the energy from nectar feeding may be important for survival as well as egg production.

Given their life span, the time they take in the field from emergence until they start to oviposit is of crucial importance. Stern & Smith (1960) report this time lag for mating and egg maturation to be increased by low temperatures and/or lack of carbohydrates in the diet. The delayed emergence of females in the field may increase their chances to mate promptly.

In addition, the influence of mating on egg production seems to be more than just triggering the process of egg yolking. Thus we need to know much more about the factors affecting fecundity, especially the role of male nutrient contribution for reproduction and how these mechanisms operate in the field. Although documented for some species of lepidopterans (Khalifa, 1950; Boggs and Gilbert, 1979; Boggs, 1981; Boggs and Watt, 1981), the latter remains virtually unknown for most. If the male provides nitrogenous compounds for the female via the spermatophore, the influence that the lack of food and/or chances to feed may have on realized fecundity can be either eased (if he can compensate for the female nutritional deficit) or worsened (if he habitually provides her with nutrients and, under starvation, produces smaller, less nutritious spermatophores). More data on this subject should help to provide a better understanding of observed fluctuations of lepidopteran population levels in the field.

CHAPTER 4 THE IMMATURE STAGES

4.1 INTRODUCTION

The various age classes or developmental phases of a species may (and most often do) differ in distribution, behaviour, nutritional and habitat requirements, etc, and are vulnerable to different patterns of mortality. It is the interactions of these factors which shapes the levels of variation in density within and between generations.

Information on the biology of the immature stages of a population is fundamental for an understanding of any species; particularly so for those, like *P. ruralis*, in which the adult phase is such a brief period in the life of individuals and it is at the larval phase that most reserves for reproduction are obtained.

Predation and parasitization are marked in the immature stages of Lepidoptera. The potential of the various types of mortality for regulating population size and the importance of spatial heterogeneity have already been described in chapter 1. However, problems of quantifying them and some other biological aspects, which are relevant to the results presented in this chapter, are dealt with below.

4.1.1 Stage Frequency Data

The life cycle of insects, with its succession of stages, makes it relatively easy to identify the 'age' of individuals. The set of counts or estimates of the numbers of individuals in different developmental stages in a population at a series of points in time is called 'stage frequency data' (Manly, 1990). This data provides for the calculation of stage-specific population parameters such as (i) recruitment, i.e numbers entering each stage; (ii) length of development, in terms of duration of stages; (iii) timing of entry to stages; (iv) survival rates; (v) population sizes (for a recent review, see Manly, 1989).

However, given the complexity of stage frequency data sets, even sophisticated models designed for cases similar to the *P. ruralis* population studied here (e.g. the models of Kiritani-Nakasuji-Manly, Kempton or Bellows & Birley (Manly, 1989)), require some previous knowledge of the species' biology. In addition, they also are based on assumptions that are difficult to meet in practice. In spite of this, checking their very assumptions (such as knowledge of numbers entering the first stage, constant duration of stages, constant survival through stages, etc) *per se* provides valuable biological insight into the population being investigated.

4.1.2 Parasitization

Parasitization is a major aspect of host mortality due to parasitoids and provides a very important component of life tables in population dynamics investigations. However, the total impact of parasitoids on a host population is more than mortality due to parasitoid reproduction (i.e. parasitization): parasitoid induced mortality also includes deaths caused by adult parasitoids feeding on hosts, trauma from oviposition or attempted oviposition, host niche breadth reduction due to parasitoid activity and changes in host behaviour leading to increased exposure to predators and/or environmental factors (Askew, 1971; Shaw & Askew, 1976; Van Driesche, 1983). Most of these aspects are not measurable in 'normal' field work and are beyond the scope of this study.

Internal parasitoids of lepidopteran larvae commonly oviposit in the young host stages and emerge from the caterpillar later on in its development (Askew & Shaw, 1986). They are thus affected by those factors that influence host survival during this period. Therefore, assessing actual parasitization rates is not straight forward.

It is essential to define what is meant by 'percentage parasitization' since, depending on how it is estimated, it may or may not mirror actual parasitization levels. If it is meant to be an assessment of the total host mortality per generation caused by a parasitoid species as a result of its reproduction, all hosts on which successful oviposition occurred need to be considered, whether or not the parasitoid(s) manages to complete development.

The ratio of parasitized individuals to the total number of hosts in a given sample collected from the field provides only a partial picture of the parasitoid fauna attacking that species at a certain site at a given time. Much more detail is needed to assess the role of specific parasitoids in the population dynamics of a host (Van Driesche, 1983).

Not all stages of the host are equally susceptible to parasitoid oviposition. Indeed, most parasitoid species tend to concentrate the period of attack on a limited stage of the host development, although not necessarily one single instar (Askew & Shaw, 1976; Beckage, 1985; Vinson & Iwantsch, 1980). Thus, hosts at different ages or sizes have distinct 'values' in terms of suitability for each parasitoid species. Host reduced quality often causes a decline in parasitoid survival or adult fecundity, longevity or mobility. For instance, egg survival is generally lower in older hosts (Waage, 1986), and hosts which are too small may provide insufficient nutrition for the parasitoid, resulting in decreased adult fitness (Waage, 1986; Strand, 1986). Although host suitability to parasitoids has been broadly studied and reviewed (e.g. Shaw & Askew, 1976; Strand, 1986; Van Alphen & Vet, 1986; Vinson, 1980; Vinson & Iwatsch, 1980), it is often omitted in population dynamics studies.

Determining the host target stage for parasitoid attack and the period of

oviposition is crucial, because being parasitized may alter the development and the mortality and/or dispersion and/or collection chances of the host. Furthermore, if this is not taken into account when calculating parasitization percentages, estimates are distorted. Thus, if levels are calculated from samples taken before parasitoid oviposition is completed, parasitization is underestimated for the generation.

If at a certain time of the generation, the period of oviposition is complete and all hosts are at this target phase, or just past it (e.g. Varley, Gradwell & Hassell, 1973), estimation of parasitization levels can be straight forward. However, many insect life histories are such that stages overlap, and at no time are all members of the population at the susceptible phase. In such cases, samples of healthy and parasitized hosts, taken without regard of time in the season or stages sampled, do not estimate accurately the generational mortality due to parasitization (Van Driesche, 1983).

Rates of development may differ between healthy and parasitized hosts (Beckage, 1985; Shaw & Askew, 1976; Vinson, 1985). One category may then 'accumulate' in the population (and be available during a longer period for collection), causing levels calculated at this phase to be affected: percentages are overestimates if parasitization delays development and underestimates if it is accelerated. Thus it is important to obtain an assessment based on numbers recruited to the susceptible stage only and not one based on overall densities at any time of the season.

Mortality or dispersal may be more intense in parasitized hosts (Beckage, 1985; Vinson,1985) and thus percentages calculated taking into account individuals developed further than the susceptible stage will underestimate parasitization (and vice-versa). An indication of this effect is given by decreasing parasitization levels on consecutive stages of the host.

Accurate estimates of parasitization are necessary for assessing the impact of the parasitoid species on the host as well as for building life tables for the parasitoid, since fecundity, fertility and mortality are miscalculated if rates are over or underestimated.

'Density is a complex parameter reflecting the balance of recruitment, mortality due to various factors and advancement to subsequent stages, the separate effects of which cannot be distinguished' (Van Driesche & Bellows, 1988). Numbers recruited to the susceptible stage, in contrast, do not contain these internal counteracting processes.

Where exact timing and numbers of hosts and parasitoids recruited are not available, knowledge of the biology of both species is necessary and should be used in connection with the information gathered on parasitization from collections.

There are a number of commonly used methods which purport to estimate the total percentage of a generation attacked by a parasitoid, e.g. overall percentages for samples summing up all host stages, peak percentages for the season, mean of the percentages for the generation, percentages based on isolated samples at certain times of the season. However, Van Driesche (1983) has demonstrated theoretically and provided field evidence that none of these provide actual levels of parasitization on any

one generation. He concluded that a more meaningful and satisfactory way was to pool samples of hosts recruited to the susceptible stage and, from these, assess the proportion bearing parasitoids. In addition, if parasitization rates in all host stages are monitored, this procedure allows life tables for both the host and parasitoid to be constructed (Bellows, Van Driesche & Elkington, 1989).

Other aspects that can mask actual levels of attack by a parasitoid species (as well as parasitoid mortality) is multi-, super- and hyperparasitism. However, estimation of parasitization rates at the target instars lessens the errors on the estimates that may arise for these reasons. Furthermore, only one hyperparasitoid individual was recorded during the whole investigation (*Encrateola laevigata* (Ratzeburg) (Ichneumonidae:Phygadevontinae)).

4.1.3 Predation

All stages of the lepidopteran life cycle are subject to predation (Dempster, 1984). The egg and early larval stages are reported to be preyed upon mainly by arthropods (e.g. spiders, earwigs, beetles, bugs), losses between hatching and the second instar being particularly high (e.g. Courtney & Duggan, 1983; Dempster, 1971 & 1982; Dempster, King & Lakhani, 1971; Pollard, 1979; Subinprasert & Svensson, 1988)). This group of predators tends to favour tall dense ground vegetation, such as nettles provide (Davis, 1983), and higher mortality rates were recorded amidst this structure of habitat than others (Dempster, 1983).

Older larval stages and pupae are less susceptible to arthropod attack, but vertebrate (birds, in particular) predation tends to be an important mortality factor (Dempster, 1984; Feichtinger & Reavey, 1989; Pollard, 1979; Varley & Gradwell, 1968).

Identification of predators and quantification of their effect poses formidable difficulties, since most of the times no clues are left behind, and direct observation is difficult. Also, most predators are polyphagous, each individual consuming many and varied prey items through its life, and attack depends on the densities of alternative prey present, so that there is no direct relationship between numbers in the populations of the predator and prey species. However, this may render them likely to act in a density dependent way, at least over a range of densities (Hassell, 1986).

Arthropod predators are often nocturnal (Davis, 1983; Dempster, 1984), thus diminishing the chances of predation being observed and causing their densities and impact often to be underrated. Methods exist for evaluating the impact of predators on insects in the field (for a review, see Luck, Shepard & Kenmore, 1988), albeit complex, imperfect or applicable only under certain situations. In the few studies on lepidopterans where more detailed investigations were carried out (Demspter,1967; Jones *et al.*, 1987; Pollard, 1979; Subinprasert & Svensson, 1988), there was good agreement between numbers of individuals recorded 'missing' and evidence of predation. Also, potential predators did prove to be preying upon the studied prey.

Therefore, observations on the guild of predators of a community can give some indication of the mortality agents.

4.1.4 Other Mortality

Starvation due to complete defoliation of the food plant has been recorded as the key factor for some Lepidoptera (e.g. the cinnabar moth: Crawley & Gillmann, 1989; Dempster, 1971 & 1982, forest pests: Varley, Gradwell & Hassell, 1973). Nevertheless, most natural populations of insect herbivores - the nettle community included - tend to (or at least appear to) stay at levels well below the point of depletion of food resources (Strong, Lawton & Southwood, 1984).

Fungi, protozoa, viruses and bacteria also attack caterpillars (for a review, see Rivers, 1976), although there is little evidence of their role in the field. Densities and weather are important factors for spreading disease and so is stress (such as laboratory rearing, from where most of the data on lepidopteran diseases comes - Dempster, 1984). Courtney & Duggan (1983) associated bacterial disease with suboptimal field conditions in a study of *Anthocharis cardamines*.

Weather is often mentioned as a major factor in population changes (Courtney & Duggan, 1983; Dempster, 1983; Gilbert & Singer, 1975; Varley, Gradwell & Hassell, 1973). Its effect is fundamentally indirect, but can influence a whole range of aspects of the life history: temperature delayed development can cause longer exposure to predation, lower chances of survival through diapause, desynchronization with resources, limited flying season and oviposition period and thus lowered fecundity, etc; not forgetting its effect on the host plant (abundance and quality) and on the spread of disease.

4.1.5 Heterogeneity

Sampling errors and random variation may cause 'noise' in the data and interfere with the correct assessment of population parameters (Hassell, 1987; Manly, 1990). This stresses the importance of identifying and quantifying rigorously the biologically meaningful heterogeneity, i.e. individual, spatial and temporal variation, that may promote stability (see chapter 1).

4.1.6 This Chapter

Details of the development and survival of *P. ruralis* were investigated in the light of the points raised in chapter 1 and above and both laboratory and field data are presented. The laboratory data are not expected to mirror field populations, since exposure to weather variations and mortality factors are obviously distinct. However, they provide background evidence which can be helpful in interpreting the field data.

4.2 MATERIALS & METHODS

4.2.1 Laboratory

From spring 1984 to the end of summer 1986, larvae and pupae of *P. ruralis* were collected at Bond Ing (from nettles in the sampling area at the western side of the path in S1 (fig 2.22) and also from S2, S3 and S4) and Spen Farm (from F1)(see section 2.5). The sampling time used was three hours for each site, with intervals of two to three weeks between two successive collections in the same place. The sampling programme was initiated early in the spring, so that the date the first caterpillars appeared in the stems could be determined, and was terminated in the autumn on the second consecutive occasion that no larvae were found. For every two individuals found, only one was taken to the laboratory and the other was left undisturbed in the field. Notes were made on the date, site and instar at collection. For the sake of conciseness, only those dates when any individuals were sampled are shown in the results. Other lepidopteran species were also looked for on the nettles for identification, to assess roughly competition and to check whether *P. ruralis* parasitoids also attacked other species.

Eggs were extremely difficult to detect in the field and indeed were found only once in July 1984 in S1. Also, as *P. ruralis* numbers in the field in the generation 85/6 were very low, only few individuals could be collected. Thus, the data used for estimating the duration of stages and diapause in generation 85/6 were supplemented with that from eggs laid and closely monitored in the laboratory during the fecundity and fertility experiment (section 3.2.2).

The caterpillars were reared individually in small plastic pots (50 x 50 mm) lined with tissue paper, and were fed with nettle leaves previously washed. The pots were kept in the shade, in a cool, ventilated green-house and, every second or third day, they were cleaned and fresh food provided. Records were made of the development and fate of the caterpillars and of the sex of any resulting adults. (Sex was determined by the differences in the shape of the abdomen and genital structure, as for the MRR study.)

In the first winter of this investigation, it was feared that keeping the diapausing caterpillars in their plastic pots could affect adversely their chances of survival through the period. There could be condensation in the pots and this could, e.g., be propitious to fungus growth. Thus, half of the caterpillars were put in small individual gauze sachets on a tray with soil. The other half was kept in their original pots. As there was no difference in survival, in the next winter, all were left in their pots.

Development was noted in terms of the instar number so that numbers alive (or dying) at any given stage could be known. For accuracy, in the calculation of the

duration of each stage, only those cases were used where recent moulting, at the start and end of the instar, could be confirmed by the present of the exuviae. The resulting sample sizes for stage duration are thus reduced, as compared to total sample sizes, and unequal between the various instars. For this reason, some statistical tests could only be performed for some instars, but the above criteria aimed to minimize any 'error' arising due to the length of the intervals between two successive checkings of the pots.

Fates were classified as follows: (i) if the caterpillars metamorphosed successfully into adults, they were considered 'healthy'; (ii) if the *P. ruralis* larva/pupa died of a cause not known, it was simply classified as 'dead'; (iii) if parasitoids emerged from them and these, in their turn, managed to reach the adult stage, they were called 'healthy parasitoids' or (iv), if not, 'dead parasitoids'.

In the winter, diapause was only considered confirmed after two weeks of immobility and cessation of food consumption. The date of onset was considered to be that when inactivity was first recorded.

Parasitoids that emerged were sexed, counted and identified. A type collection of the pupal cases of the species was arranged, so that identification in the field could be made as soon as the parasitoids had emerged from the caterpillars and pupated. The following references were found to be the most helpful in the taxonomic work for the present study: Van Achterberg (1975 & 1976), Van Achterberg & Haeselbarth (1983), Askew (1971), Horstmann (1969 & 1979), Horstmann & Shaw (1984), Nixon (1968), Oldroyd (1970), Richards (1956) and Townes (1969-74). The identification of all the hymenopteran species was checked by Dr. M. Fitton in the British Museum (Natural History) and the dipterans were also examined by Mrs. E. Broadhead in this Department, since misidentification is a common and very misleading occurrence in the literature (Shaw,1981).

There were thus two aspects to the data gathered from the laboratory monitoring: (i) the stage frequencies in the field through time were obtained from the periodic collections and (ii) the details of development were obtained from rearing the caterpillars.

To find out about *P. ruralis* overwinter sites, samples of debris and soil from various depths from the nettle clump in the University Farm were brought to the laboratory during the winter. Part was sieved and searched for caterpillars and part was left under a hot light to see whether any caterpillars would emerge. Only one *P. ruralis* was found.

Attempts were also made to study overwinter mortality outdoors. Nettles were grown in normal plant pots and also in larger trays and were left in the open with known numbers of caterpillars before winter. However, there was often flooding of the soil and, even when this did not occur, no larvae were found again in the next spring.

For checking the mobility of the caterpillars on the nettle stems, ten *P. ruralis* larvae were reared individually on potted nettles. They were isolated from invasion by

other insects by acetate sheet cylinders (0.15 m diameter x 0.6 m high) covered with nylon gauze. The larvae were observed from the third/fourth instar until they had pupated. Younger caterpillars were not used because it had been observed in the laboratory and in the field that they move very little prior to diapause (see section 4.3.3.1).

4.2.2 Field

During the same period - i.e., spring 1984 to summer 1986 - larvae and pupae were also looked for and followed in the field. The sampling area on the eastern side of S1 at Bond Ing (fig 2.22) was selected for this purpose. In addition, from September 1984, the first three metres on the west of the path in the the same nettle clump were used to increase sample sizes.

At approximately weekly intervals the nettle stems in the sampling area were inspected one by one. No time limit was imposed: sampling was only finished when all the area was covered. When a *P. ruralis* larva or pupa was found, an individual number was assigned to it and a plastic lock-on label attached to the stem just below its rolled leaf (fig 4.1). Individuals could then be identified and followed throughout their development. On each sampling occasion, records were made of the following aspects for each caterpillar/pupa: (i) stage of development, (ii) the leaf on which it was found (node counting from the top), (iii) the height of this leaf from the ground, (iv) whether it had moved to another leaf since it was last seen, (v) the position in the nettle clump (metres along and distance from the path), (vi) presence and taxa of other arthropods (with special attention to potential predators) on the same nettle stem or close to it and, when the nettle was flowering, (vii) the sex of the plant.

In the field it was not possible to be as strict about recording duration of instars as in the laboratory. First, because while inspecting the caterpillars, observations were carried out with none or a minimum of manipulation (just enough to see the larva inside the rolled leaf) to avoid disturbance. Second, because the intervals between inspections were longer in the field than in the laboratory, again to avoid unnecessary disturbance but also because of the highly time consuming nature of the field work. Hence, instars durations were calculated simply based on the time elapsed between any two observations for the same individual, when successive instars were recorded. The same type of criteria were used when considering recruitment.

When the larva or pupa could not be found on the subsequent sampling occasion, its fate was assessed according to the evidence left in the rolled leaf. Emergence of a 'healthy' adult was indicated by the state of the exuviae of the pupa. Predation could only be established in those cases where clear signs of it were left, e.g. the remains of the caterpillar or pupa, or the characteristic marks of birds beaks on the rolled leaves. If no clues were found, the larva was considered 'missing'. If a parasitoid had emerged from the caterpillar or pupa, the species was identified by its

Figure 4.1 A lock-on label attached to the nettle stem indicating the location of a *P. ruralis* larva in the rolled leaf above.

pupa(e) - based on the laboratory study (see above) - and left in place to develop. Finally, some individuals were found dead or failed to metamorphose for no known reason and were then simply considered 'dead'. The fate of the parasitoids was assessed in the same way as for *P. ruralis*.

Records were also made of other lepidopteran larvae. However, they were not labelled because most species are easily disturbed and hence tend to change their location.

Observations were made on the numbers of empty rolled leaves attributable to *P. ruralis* and on those of other shelters built with nettle leaves by other species. General notes were also taken about the condition, height and inclination of the nettle stems.

In early summer 1986, a pilot study was carried out to ascertain which species of birds were preying upon *P. ruralis*, how they detected and removed individuals from the rolled leaves and how effective they were. On five occasions, with a day or two between them, observations of S1 were made in the early morning (4:30 to 7:30h), from sheltered points around the site, with the help of binoculars. Various birds - mainly robins and wrens - did come to the nettles and walked around and seemed to be looking for prey. But only once was it possible to distinguish a robin in the act of pecking a rolled leaf. On the other occasions, it was most of the times impossible to determine what the birds were doing amidst the nettles or they would just fly away. It was therefore considered that the effort necessary for getting any reasonable data project was too great in the face of the priorities of this work.

Individual larval movement was also monitored in the field. A small clump of nettles (1 m^2), close to S3, was fenced and the nettles were cut in a belt of 0.5 m width around the fence to isolate the clump. This clump was searched and cleared of all larvae except for one *P. ruralis*. The position of this larva was monitored weekly. This procedure was replicated three times with different individuals.

4.2.3 Analysis

Since *P. ruralis* was followed individually throughout development in both the laboratory and the field, the length of the instars, recruitment numbers and intensity of the mortality factors could be estimated directly from the data using standard statistical methods (Sokal & Rohlf, 1981; Manly, 1986), without the need to use more specific models of analysis for stage frequency data.

The susceptible stages of *P. ruralis* for each parasitoid species were defined by examining percentages of parasitized hosts per instar at collection (see introduction). Levels of parasitization per generation were estimated based on these target instars. Mortality of parasitized hosts at different instars was inferred by assessing changes in parasitization percentages as development advanced.

The SAS package was used for processing the data. Values shown are $\pm$ SE

whenever these could be calculated. Figures in parentheses after the statistics are the degrees of freedom associated with them.

It should be noted that often there are missing values for one or more variables for each individual studied - both in the laboratory and in the field - so totals between tables for analysis of different variables are not always the same. This was because for all variables investigated (numerical and categorical) precise notes could only be taken when there was enough evidence to confirm their value, and frequently this was not the case (for instance, see above note on calculations of stage duration in the laboratory). Thus, multivariate analysis could not be used in some cases where it would be recommended.

4.3 RESULTS

4.3.1. Description of the Sample

From April 1984 to July 1986, a total of 1559 *P. ruralis* larvae and pupae were collected and reared in the laboratory and 461 monitored in the field. These comprised the post-diapause phase of the 83/4 generation plus the two complete generations of 84/5 and 85/6. (It is important to have clear this distinction between calendar years and generations.) Total sample sizes varied between seasons throughout this period, and this variation was in the same direction for all data: from the sites where larvae were collected for the laboratory study and where they were left undisturbed in the field (table 4.1). From spring 1984 numbers increased until the cold summer of 1985 and then fell sharply. Larval density rose again in the spring of 1986, but by the end of the sampling programme, levels were still less than a third of those observed in the first half of 1984.

Table 4.1 Total number of individuals monitored per generation and year.

Generation	Year	Period	Laboratory	Field	Total
83/4	1984	pos-diapause	333	132	465
		pre-diapause	500	142	642
84/5	1985	pos-diapause	527	145	672
		pre-diapause	97	12	109
85/6	1986	pos-diapause	102	30	132
Total			1559	461	2020

Unfortunately, these smaller samples somewhat restrained the analysis for some

of the aspects of *P. ruralis* life history and dynamics.

In addition to these changes in abundance, variations in the fates of the caterpillars were observed between generations, in both the laboratory and the field samples (tables 4.2 and 4.3).

Of the larvae reared in the laboratory, 34.6% turned into healthy moths, 39.8% died from unknown causes, 17.9% produced healthy parasitoid adults and 7.7% contained parasitoids that either had not metamorphosed or emerged successfully (i.e., 25.6% were parasitized) (table 4.2).

Table 4.2 Fate of P. ruralis reared in the laboratory by place of collection: BI = Bond Ing, UF = University Farm.

Generation	Place of Collection	Fate: Healthy	Fate: Dead	Fate: Parasitoids Healthy	Fate: Parasitoids Dead	TOTAL
83/4	BI	74	14	24	14	126
	UF	62	6	33	7	108
	BI+UF	136	20	57	21	234
	(%)*	(58.1)	(8.5)	(24.4)	(9.0)	
84/5	BI	247	321	106	58	732
	UF	69	108	49	16	242
	BI+UF	316	429	155	74	974
	(%)	(32.4)	(44.1)	(15.9)	(7.6)	
85/6	BI	3	17	4	1	25
	UF	11	70	25	8	114
	BI+UF	14	87	29	9	139
	(%)	(10.1)	(62.6)	(20.8)	(6.5)	
Pooled	BI	324	352	134	73	883
	UF	142	184	107	31	464
	BI+UF	466	536	241	104	1347
	(%)	(34.6)	(39.8)	(17.9)	(7.7)	

* The percentages shown are row percentages.

The differences in the proportion of individuals suffering each fate were statistically significant between generations (G=114.18 (6), P=0.0001) but not, within generations, between data originating from the two collection sites - Bond Ing and the

University Farm (G=5.61 (3), P=0.1322). A log-linear model fitted to the data showed that generation accounted for most of the variation observed (G=13.23 (9), P=0.1526). Based on this result the laboratory data from the two sites were pooled for the rest of the analysis.

There were more possibilities as to what could happen to *P. ruralis* in the field. To start with, samples needed to be divided in two major groups, according to whether they were pre- or post-diapause, because during winter the larvae disappeared in the debris or soil (section 2.2) and could not be followed throughout this phase. Table 4.3a shows the numbers of the caterpillars that were monitored up to diapause and of those that went missing or died before this. The term 'missing', for this period, embraces those that actually moved away from their leaves and could not be found again (which was not totally unlikely to happen as the young larvae are very minute, but does not seem very probable, as they move very little in their initial stages - see section 4.3.3 below) plus those that were preyed upon and completely consumed or removed by their predators (this seems very likely, considering the numbers of potential predators observed on and about the nettles during autumn - see section 4.3.2.3 below).

Unfortunately, there were no pre-diapause samples in the 83/4 generation (the study had not yet started) and population levels were very low in the autumn of 1985. It is thus not possible to say much about between generation variation in the destiny of the caterpillars prior to diapause (table 4.3a).

Table 4.3 Fates of P. ruralis monitored in the field.

(a) Pre-diapause samples

Fate	Generation 84/5	Generation 85/6	Total (%)
Diapause (%)*	81 (57.0)	5 (41.6)	86 (55.8)
Missing (%)	61 (43.0)	6 (50.0)	67 (43.5)
Death (%)	0	1 (8.3)	1 (0.6)
Total	142	12	154

* The percentages shown are column percentages.

Of the individuals observed post-diapause, 18.2% developed into adults, 2.2% died from unidentifiable causes, 48.5% went missing, 19.2% were recognizably predated, and from 11.7% of them parasitoid larvae emerged. In the last two groups, further classification could be made according to the type of predator and the fate of

the parasitoids (table4.3b).

Table 4.3 (cont.)

(b) Post-diapause samples.

Fate	Generation 83/4	84/5	85/6	Total (%)
Healthy	33	22	1	56
(%)*	(25.0)	(15.2)	(3.3)	(18.2)
Dead	2	4	1	7
(%)	(1.5)	(2.7)	(3.3)	(2.2)
Missing	50	84	15	149
(%)	(37.9)	(57.9)	(50.0)	(48.5)
Predated:				
Birds	20	23	13	56
Others	2	1	0	3
Total Pred.	22	24	13	59
(%)	(16.7)	(16.6)	(43.3)	(19.2)
Parasitoids:				
Healthy	17	2	0	19
Dead	0	1	0	1
Missing	7	5	0	12
Predated:birds	0	3	0	3
others	1	0	0	1
Total Parasit.	25	11	0	36
(%)	(18.9)	(7.6)	(0.0)	(11.7)
Grand Total	132	145	30	307

* The percentages shown are column percentages.

Because there were many potential fates and some with low frequencies, it was necessary to pool some of the categories for testing the significance of these differences observed between generations. Thus, all the predated individuals - whether by birds or other agents - were considered a single class and the parasitized ones were only subdivided on whether the emerging parasitoids managed to reach the adult stage or not. Also, the 85/6 generation could not be included in the analysis due to the very reduced sample sizes found in spring 1986. The log likelihood ratio test performed on this data gave significant results for the between generation differences ($G = 24.71$ (5), $P < 0.01$).

It is not possible to compare the differences between laboratory and field data

in the proportions of individuals suffering each fate, because in the field *P. ruralis* was exposed for longer and to additional mortality factors (tables 4.2 and 4.3). Furthermore, if the observations of the caterpillars that were predated or went missing are excluded in order to try a rough comparison, the field sample sizes become too small to justify any statistical analysis.

4.3.2 Life History and Mortality Factors

4.3.2.1 Healthy Individuals

LABORATORY

- Length of Development

The mean time individuals spent in each instar is shown in table 4.4 for the three generations studied. (This is maturation time, for diapause see below.)

Table 4.4 Mean time (days) spent in each stage and sample sizes (n) for each generation and overall means. Healthy P. ruralis, laboratory data.

Stage	Generation 83/4±SE (n)	84/5±SE (n)	85/6±SE (n)	Overall Mean±SE (n)
Egg	·	·	13.6 ± 0.04 (2121)	13.6 ± 0.04 (2121)
1	·	·	7.1 ± 0.09 (15)	7.1 ± 0.09 (15)
2	·	5.0 ± 0.41 (4)	·	5.0 ± 0.41 (4)
3	·	8.4 ± 0.87 (25)	·	8.4 ± 0.87 (25)
4	8.3 ± 0.88 (3)	8.9 ± 0.52 (31)	10.2 ± 1.56 (6)	9.0 ± 0.47 (40)
5	8.5 ± 0.96 (4)	20.1 ± 2.51 (14)	10.1 ± 0.51 (58)	11.8 ± 0.75 (76)
6	6.4 ± 0.25 (5)	13.8 ± 0.63 (51)	8.7 ± 0.86 (20)	12.0 ± 0.57 (76)
Pupa	15.1 ± 0.29 (112)	24.0 ± 0.47 (290)	17.6 ± 0.61 (76)	20.9 ± 0.36 (478)

Sample sizes were variable over the three years, sometimes very small (mainly in the first year and for the younger instars), and data for stages egg to 3 were available only for one generation each. Where enough data were available, much variation could

be seen in stage durations between generations. This seems to reflect the average temperatures prevailing in the periods when individuals were in each particular stage (see App. 2 and recruitment, below). In 1984, spring temperatures were close to normal, and this was the season when the shorter durations for instars 4 and 5 were recorded. June and July 1984 were the warmest of the three summers, and instar 6 and pupal development were markedly rapid. In 1985, late spring and early summer were very cold as compared to normal, and stages 5 (particularly), 6 and pupa took very much longer then in 1984. In 1986, early spring was very cold, and this was when the longest duration for stage 4 was recorded; temperatures kept below normal for the rest of spring and early summer, but were not as cold as in 1985, and stage durations for instars 5, 6 and pupa were intermediate between those for 1984 and 1985.

The distribution of the time spent in each instar was significantly different from the Normal (Shapiro-Wilk and Kolmogorov-Smirnov tests, $P < 0.01$ for all stages, except for 2, where the sample size was four and $P = 0.573$) and strongly skewed to the right as it would be expected for insects developing under variable temperatures (Manly, 1990). Even transforming the data did not normalize the distribution. Hence the differences between generations were tested using Kruskal-Wallis test and the results were significant for all stages where there were sufficient data for analysis ($P < 0.01$).

In spite of these differences, and considering that the three years of study had differing weather conditions (App. 2, fig A2.1), it makes sense to compute the mean duration of stages through the whole study to build a general picture of development time for *P. ruralis* (table 4.4). Thus, the markedly shorter mean obtained for instar 2 (5 days) seems more likely to be due to the combined effects of (i) chance on a small sample, (ii) a warmer than usual September in 1985 and (iii) unavoidable 'error' due to the intervals between two successive inspections of the caterpillars (2-3 days, see methods above), than to any biological reason for faster development in this stage.

In summary, it takes about two weeks for eggs to hatch, and the young larval stages (1 to 4) each last about 7-9 days. Instars 5 and 6 take a little longer, with a mean of almost twelve days each. This is when the caterpillars grow the most and fastest and, presumably, accumulate reserves for reproduction and maintenance in adult life. The pupal stage is about three weeks long.

Correlation analysis between the duration of successive stages in the same individuals was carried out where possible - instars 5 to pupa - and was statistically significant ($P < 0.01$), although the association was not very marked (Spearman coefficients of rank correlation: between instars 5 and 6, $r_s = 0.577$; 5 and pupa, $r_s = 0.392$; 6 and pupa, $r_s = 0.383$). It thus appears that there are slow and fast developing individuals, but other factors such as temperature may, to some extent, mask these differences.

There was no statistical significance between the values obtained for length of

development for the two sampling sites (P > 0.05 for all instars except 6, where P = 0.04).

- Diapause

In the laboratory, healthy individuals diapaused in their fifth, fourth or (in a very few cases) third instar. Proportions diapausing in each instar varied markedly between years (table 4.5). For the 84/5 generation, the summer was hot and autumn temperatures were slightly above normal (App. 2), and all caterpillars had passed their third instar, most being already in their fifth instar, by the onset of diapause. In the 85/6 generation, after a cold and late summer, 82.0% of the diapausing *P. ruralis* were in their fourth instar and none had yet reached the fifth.

Table 4.5 Frequencies of diapause in different instars as observed in the laboratory for each generation. Healthy P. ruralis.

Instar of Diapause	Generation 84/5 (%)*	Generation 85/6 (%)	Total (%)
3	0	8 (16.0)	8 (5.8)
4	25 (28.1)	41 (82.0)	66 (47.5)
5	64 (71.9)	1 (2.0)	65 (46.8)
Total	89	50	139

* The percentages shown are column percentages.
Test for association between generation and instar of diapause:
G = 83.69 (2) P < 0.001

The mean period of dormancy (table 4.6) varied significantly according to the instar in which the individuals diapaused (F = 5.8 (1), P < 0.05) and also differed between the two winters of study (F=58.11 (1), P < 0.001).

In 84/5, diapause lasted 178.0 ± 1.43 days for larvae in the fourth instar and 184.3 ± 1.36 for the ones in the fifth instar. In 85/6, diapause took longer: 197.2 ± 1.92 days for instar 4 (data available, unfortunately, were not enough for calculating duration for instar 3).

Also shown in table 4.6 is the mean full duration of the instars in which the caterpillars diapaused, i.e., period of dormancy + maturation time. As expected, from the results above and the knowledge of the duration of instars (table 4.4), there were significant differences between instars (F = 21.54 (2), P < 0.001) and between generations (F = 49.90 (1), P < 0.001). Also, the development time, as distinct from the

Table 4.6 Mean duration (days) of diapause and total length of the diapausing instar observed in the laboratory by generation. Healthy P. ruralis.

Generat.	Instar of Diapause	Mean Duration (days) Diapause±SE (n)	Mean Duration (days) Instar±SE (n)	Development time *
84/5	4	178.0 ± 1.43 (25)	206.6 ± 4.25 (7)	28.6
	5	184.3 ± 1.36 (59)	230.4 ± 1.71 (37)	46.1
Differences between instars		F= 5.8;P=0.01	F=21.5;P<0.001	
85/6	4	197.2 ± 1.92 (46)	233.6 ± 1.14 (29)	36.4
Differences between generats.		F=50.1;P<0.001	F=49.9;P<0.001	

* Development time = total duration instar of diapause - duration of diapause (see text for explanation).

dormancy period, is greatly increased as compared with the non-diapausing corresponding stage durations: it was about 28 days for instar 4 and 46 days for instar 5 in 84/5; in 85/6, it was more then 36 days for instar 4. Part of this development time was before and part after dormancy. In general, most of the caterpillars had moulted within seven to ten days of breaking diapause - some immediately after. It is only logical (and well documented) that physiological time - i.e. development - is slower during the period of lowest temperatures in the year and in the colder years, but it is a point that should not be overlooked and left unquantified in the analysis of the population dynamics.

The timing of diapause in the laboratory is shown in tables 4.7a & b. Onset of diapause was very synchronized both in 1984 and 1985 and, by the third/fourth week of October, all *P. ruralis* had built their diapause cell, halted feeding and were dormant.

Breaking of dormancy though was much more spread in time. In both years, the first larvae to resume activity did so in the beginning of April. However, the similarities between the two generations stop here.

In 1985 (generation 84/5 - table 4.7a), caterpillars that overwintered in the fourth instar and had shorter dormancy periods (see table 4.6), broke diapause over about three and a half weeks; more than 90% of them had resumed development by 23

Table 4.7 Frequencies by dates of onset and breaking of diapause observed in the laboratory for each generation. Healthy P. ruralis.

(a) Generation 84/5

	Instar 4			Instar 5			Total		
	n	%	Cum%	n	%	Cum%	n	%	Cum%
Onset (1984)									
Oct 15	6	24.0	24.0	8	13.6	13.6	14	16.7	16.7
18	1	4.0	28.0	0	0	13.6	1	1.2	17.9
19	4	16.0	34.0	39	66.1	79.7	43	51.2	69.0
24	14	56.0	100.0	12	20.3	100.0	26	31.0	100.0
Breaking (1985)									
Apr 10				1	1.7	1.7	1	1.2	1.2
11	3	12.0	12.0	2	3.4	5.1	5	6.0	7.1
12	6	24.0	36.0	8	13.6	18.6	14	16.6	23.8
17	11	44.0	80.0	28	47.5	66.1	39	46.4	70.2
18	1	4.0	84.0			66.1	1	1.2	71.4
23	2	8.0	92.0	5	8.5	74.6	7	8.3	79.8
29	1	4.0	96.0	4	6.8	81.4	5	6.0	85.7
May 1			96.0	1	1.7	83.1	1	1.2	86.9
5	1	4.0	100.0			83.1	1	1.2	88.1
10				4	6.8	89.8	4	4.8	92.8
11				3	5.1	94.9	3	3.6	96.4
12				1	1.7	96.6	1	1.2	97.6
16				1	1.7	98.3	1	1.2	98.8
17				1	1.7	100.0	1	1.2	100.0
Total	25			59			84		

of April and all were active by 5 May. A similar percentage (90%) was only reached more than two weeks later for the larvae that diapaused in the fifth instar. Taking both instars together, the peak frequency was observed in mid April, about 86% of the individuals had broken diapause by the end of April and all were active by 17 May.

In 1986 (generation 85/6 - table 4.7b), although no diapausing individuals had reached the fifth instar before winter, the period of breaking diapause lasted until 30 May. There was no defined peak and by 1 May 50% of the caterpillars were still dormant.

- Recruitment

The composition of samples collected for the laboratory study provides a picture of recruitment to successive stages in the field (table 4.8).

It is not very exact, for sampling intervals were a little irregular and too spaced apart as compared to instar durations. However, it provides a further basis against which to assess if individuals suffering different fates have distinct developmental rates and timings. Also, it allows between generation comparisons as regards the peaks and ranges of the periods when the successive stages were present (table 4.8). Furthermore,

Table 4.7 (cont.) Frequencies by dates of onset and breaking of diapause observed in the laboratory for each generation. Healthy P. ruralis.

(b) Generation 85/6

	Instar 4 (=total)		
	n	%	Cum%
Onset (1985)			
Oct 16	10	20.0	20.0
18	16	32.0	52.0
20	24	48.0	100.0
Breaking (1986)			
Apr 6	1	2.0	2.0
9	3	6.0	8.0
10	2	4.0	12.0
16	1	2.0	14.0
21	1	2.0	16.0
30	10	20.0	36.0
May 1	7	14.0	50.0
7	1	2.0	52.0
8	7	14.0	66.0
9	2	4.0	70.0
14	13	26.0	96.0
21	1	2.0	98.0
30	1	2.0	100.0
Total	50		

it provides supportive evidence to the more detailed but not as large data set from the field monitoring programme (see below).

Development is not very synchronized, with almost half of the samples containing three or four different instars (table 4.8). In spring 1984, *P. ruralis* immatures were found in the nettles from late May to early July. Although sampling was started by mid April, the first caterpillars were not found until 23 of May, and the samples comprised individuals from the third to the fifth instars, the majority being in instar 5. This, considered in conjunction with the knowledge of stage durations and the usual diapausing stages and timing, indicates that the larvae may well had started coming out of dormancy about a week (or two) before. By 7 June most caterpillars were already in their sixth instar and, on the 20, 59.3% of the sample were pupae. By mid July, most *P. ruralis* had emerged, and no more immature stages were found for collection.

The next generation young larvae were first seen on the nettles on 21 August. In the first week of September, 221 individuals, mainly in the first, second and third, but also some in the fourth, instars were collected. The last time caterpillars were seen prior to diapause was 17 October and these were all in instars 3 or 4.

In 1985, *P. ruralis* took longer in the post-diapause development than in the former year and were found in the nettles from mid April to the beginning of August.

Table 4.8 Stage frequency composition of samples collected for laboratory rearing. Non-parasitized *P. ruralis*.

Year	Generat	Date	Day(std)	Stage at Collection 1	2	3	4	5	6	Pupa	Total
1984	83/4	May23	1 (44)			4	3	9			16
		Jun 7	16 (59)				1	18	33		52
		20	29 (72)					6	18	35	59
		Jul 3	42 (85)						2	27	29
		17	56 (99)								0
	84/5	Aug21	1(133)		1						1
		Sep 6	17(149)	72	84	55	10				221
		26	37(169)		11	35	9				55
		Oct17	58(190)			32	31				63
1985		Apr15	1 (6)			36	15				51
		May 6	22 (27)			30	16	2			48
		23	39 (44)			28	28	18			74
		Jun12	58 (64)				10	30	73		113
		Jul 8	84 (90)						5	55	60
		Aug 3	110(116)							3	3
		13	120(126)								0
	85/6	Sep23	1(167)	1	1						2
		Oct 3	11(177)	8	23	37	9				77
		23	31(197)			3					3
1986		Apr16	1 (7)			1	2				3
		27	12 (18)				1				1
		May15	30 (36)			1	18	3			22
		Jun 3	49 (55)				2	6			8
		18	64 (70)					1	3		4
		Jul 7	83 (89)						2	10	12
		19	95(101)								0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

Initially they were in the third and fourth instars, adding evidence that these were the instars they diapaused in the field in that winter. The first caterpillars in stage 5 were collected on 6 May, in stage 6 on 12 June and as pupae on 8 July.

In autumn 1985, *P. ruralis* seems to have started hatching from egg about a month later as compared with the 84/5 generation. Only on three sampling occasions were caterpillars found. The first date was 23 September and the only good sized sample was obtained on 3 October. Individuals were then mostly in the second and third instars, but there were also some in the first and fourth. No more larvae were detected on the nettles after the 23 of that month, when the few collected were in instar 4.

In 1986, *P. ruralis* started to reappear on the plants by mid April (as in the

former year) but only small numbers were recorded until mid May. Individuals breaking diapause were in the third and fourth instars and the first caterpillars in the fifth instar were seen by mid May, and in the sixth by mid June. Pupae were only found in the first week of July and, in contrast to 1985, development was complete by mid July (as had been observed back in 1984).

Table 4.9 presents the periods of recruitment to the adult stage for *P. ruralis* reared in the laboratory, for the 83/4, 84/5 and 85/6 generations and by sex. These again are in close agreement with the above results. In 1984, most moths (92.8%) had emerged by mid July.

Table 4.9 Recruitment to adult stage of individuals reared in the laboratory by generation and by sex. Healthy P. ruralis.

Year	Month	Quarter	Females			Males			Total		
			n	%	Cum%	n	%	Cum%	n	%	Cum%
1984	Jul	1	31	43.7	43.7	27	50.0	50.0	58	46.4	46.4
		2	32	45.1	88.7	26	48.1	98.1	58	46.4	92.8
		3									
		4	7	9.9	98.6	1	1.9	100.0	8	6.4	99.2
	Aug	1									
		2									
		3	1	1.4	100.0				1	0.8	100.0
	Total		71			54			125		
1985	Jul	1	21	12.7	12.7	36	23.7	23.7	57	17.9	17.9
		2	91	54.8	67.5	81	53.3	77.0	172	54.1	72.0
		3									
		4	11	6.6	74.1	9	5.9	82.9	20	6.3	78.3
	Aug	1									
		2	4	2.4	76.5	1	0.7	83.6	5	1.6	79.9
		3	38	22.9	99.4	24	15.8	99.3	62	19.5	99.4
		4	1	0.6	100.0	1	0.7	100.0	2	0.6	100.0
	Total		166			152			318		
1986	Jul	4				2	33.3	33.3	2	18.2	18.2
	Aug	1									
		2				4	66.7	100.0	4	36.4	54.5
		3									
		4	5	100.0	100.0				5	45.5	100.0
	Total		5			6			11		

Factorial analysis by year:
influence of sex on timing of emergence, P = 0.143.

In 1985 the emergence period was more protracted and a similar level was only reached about a month later. There was an emergence peak in the second week of July but there was another lower one in the third week of August. Numbers for 1986 were too small for detailed comment.

- Sex ratio & developmental differences between sexes

The cumulative percentage of emergence for males was about 10% higher than that of females for most of the recruitment period. This was not statistically significant (G = 9.59 (6), P = 0.143), although this pattern was present in all years, and indications of delayed emergence of females in relation to males was also obtained in the MRR programme (see section 3.1.3.3, fig 3.2).

Sex ratios did not depart significantly from 1:1 in any generation (G = 2.20 (2), P > 0.33). Sex did not affected duration of instars (Kruskal-Wallis test, P > 0.2 for all instars), duration of diapause (F = 0.31 (1), P > 0.5) or the overwintering stages (G = 2.66 (2), P > 0.2).

FIELD

- Length of development

The duration of instars recorded in the field is presented in table 4.10. It was not possible to gather data on instars 1 and 2 in the field: the few caterpillars that were monitored in these early stages either went missing or were predated before entry to the subsequent stage could be noted. As with the laboratory programme, sample sizes varied much between generations.

Table 4.10 Mean time (days) spent in each stage and sample sizes (n) for each generation and overall means. Healthy P. ruralis, field data.

Stage	Generation 83/4±SE (n)	84/5±SE (n)	85/6±SE (n)	Overall Mean±SE (n)
3	-	16.1 ± 2.82 (17)	9.0 ± 0.00 (4)	14.7 ± 2.35 (21)
4	7.0 ± - (1)	12.1 ± 1.19 (17)	17.0 ± - (1)	12.1 ± 1.13 (19)
5	9.3 ± 1.25 (4)	14.0 ± 0.78 (41)	18.0 ± 0.00 (9)	14.3 ±0.66 (54)
6	11.7 ± 1.97 (11)	19.7 ± 1.44 (34)	19.0 ± 8.00 (2)	17.8 ± 1.25 (47)
Pupa	21.7 ± 0.93 (28)	31.4 ± 1.84 (22)	16.0 ± - (1)	25.3 ± 1.13 (51)

Development was generally shorter in the warmer 1984 than in the other years (Kruskal-Wallis test, P < 0.05 for instars where numbers warranted testing: 5, 6 and pupa), but sample sizes were too reduced in 1986 to allow comparisons. Overall, stages

took longer in the field than in the laboratory (cf table 4.4 above). This was expected, since the larvae were exposed to harsher weather conditions. This effect is perhaps compounded by the larger intervals between inspections in the field, as expressed in the larger SEs obtained (table 4.10).

Instar 3 lasted almost 15 days, instar 4 about 12, instar 5 about 14, instar 6 about 18 and the pupal stage about 25 days. It is possible that there is a further 'noise' component in the estimates for the stages when diapause may take place - in particular instar 4 (see diapause below). This is because in early spring, when 'new' individuals were found, it was only possible to assign to each individual the instar it was, without being certain whether it had moulted recently or had diapaused in that instar. This may be the reason why instar 4, which is passed through during the period of lowest temperatures outdoors, had the shortest estimate in the field, while in the laboratory its duration was about a day longer than for instar 3 (cf table 4.4). Based on this and on the estimates for the duration of instars 3 and 5 outdoors, it is suggested that in the field instar 4 may take on average a couple of days more than the figures shown in table 4.10.

The distributions of stage durations was also significantly different from the Normal (Kolmogorov-Smirnov and Shapiro-Wilk tests, $P < 0.01$ for all stages except the pupa, where $P < 0.02$), and skewed to the right. Data transformations did not correct for normality.

The duration of instars 5 and 6, and 6 and pupa was correlated ($P < 0.01$), although the association was again not very marked and was negative between instars 5 and 6 (Spearman coefficients of rank correlation: between instars 5 and 6, $r_s=-0.565$; 6 and pupa, $r_s=0.575$).

- Diapause

P. ruralis diapaused mostly in instar 4 in the field, but also in instars 2, 3 and 5. Table 4.11a presents the stages larvae were in when last seen in the study site in late autumn. These match with the instars caterpillars were in when first found again in the following spring, but for a slight shift towards more developed stages (table 4.11b). It is not clear whether those individuals detected in instar 5 had actually managed to reach this stage before diapause in 1984 or whether they had just moulted when sampled in 1985 after overwintering in stage 4.

However, since no caterpillars were found in instar 5 prior to diapause, and considering the cooler conditions in the field than in the laboratory, it appears that diapause in instar 5 is not a common event in the field.

In spite of the reduced samples in the 85/6 generation, there is still an indication that caterpillars were on average younger during the diapause period in this season.

Timings of onset and breaking of diapause in the field were slightly later than in the laboratory (table 4.12a & b). In 1984, the first larvae to enter diapause did so by

Table 4.11 Frequencies of diapause in different instars as observed in the field for each generation. Healthy *P. ruralis*.

(a) Instar on onset of diapause

Instar	Generation 84/5 (%)*	Generation 85/6 (%)	Total (%)
2	3 (3.7)	0	3 (3.5)
3	26 (32.1)	0	26 (30.2)
4	52 (64.2)	5 (100.0)	57 (66.3)
Total	81	5	86

(b) Instar on breaking of diapause

Instar	Generation 84/5 (%)*	Generation 85/6 (%)	Total (%)
2	1 (0.9)	0	1 (0.8)
3	38 (35.9)	9 (56.3)	47 (38.5)
4	53 (50.0)	7 (43.8)	60 (49.2)
5	14 (13.2)	0	14 (11.5)
Total	106	16	122

* The percentages shown are column percentages.

early October. By 25 of this month, over 70% had already left the nettles, but it was not until mid November that all *P. ruralis* had ceased activity. The caterpillars reappeared on the plants from mid April till late May.

There is no obvious distinctions in timings for individuals diapausing in different instars, apart from the fact that the individuals first found in spring in instar 5 were met much later than the younger ones. On the one hand, diapause in instar 5

Table 4.12 Table 4.12 Frequencies by dates of onset and breaking of diapause observed in the field for each generation. Healthy *P. ruralis*.

(a) Generation 84/5

	Instar 2			Instar 3			Instar 4			Instar 5			Total		
	n	%	Cum%	n	%	Cum%	n	%	Cum%	n	%	Cum%	n	%	Cum%
Onset (1984)															
Oct 2							1	1.9	1.9				1	1.2	1.2
12							2	3.9	5.8				2	2.5	3.7
17	1	33.3	33.3	6	23.1	23.1	2	3.9	9.6				9	11.1	14.8
25	2	66.7	100.0	16	61.5	84.6	27	51.9	61.5				45	55.6	70.4
Nov 15				4	15.4	100.0	20	38.5	100.0				24	29.6	100.0
Total	3			26			52						81		
Breaking (1985)															
Apr 15							1	1.9	1.9				1	0.9	0.9
24				9	23.7	23.7	4	7.6	9.4				13	12.3	13.2
May 6	1	100.0	100.0	9	23.7	47.4	8	15.1	24.5				18	17.0	30.2
13				13	34.2	81.6	19	35.9	60.4				32	30.2	60.4
22				7	18.4	100.0	14	26.4	86.8	1	7.1	7.1	22	20.8	81.1
30							7	13.2	100.0	13	92.9	100.0	20	18.9	100.0
Total	1			38			53			14			106		

(b) Generation 85/6

	Instar 3			Instar 4			Total		
	n	%	Cum%	n	%	Cum%	n	%	Cum%
Onset (1985)									
Nov 13				3	60.0	60.0	3	60.0	60.0
22				2	40.0	100.0	2	40.0	100.0
Total				5			5		
Breaking (1986)									
Apr 22				1	14.3	14.3	1	6.3	6.3
May 7	4	44.4	44.4			14.3	4	25.0	31.3
23	5	55.6	100.0	6	85.7	100.0	11	68.8	100.0
Total	9			7			16		

also took longer than in younger stages in the laboratory. Conversely, it may be an indication that at least some did not overwinter in this stage, but moulted just after breaking diapause in instar 4.

Onset and breaking of diapause started a little later in the cooler season of generation 85/6, but differences are not as marked as to rule out the possibility of this

being simply a chance effect due to small sample sizes in this generation.

It was not possible to measure duration of dormancy directly in the field, but based on the average times of onset and breaking, an idea of the period length can be drawn. Thus, it took about 196 days in the 84/5 generation and 181 in the 85/6. These figures are very close to those recorded in the laboratory, although - surprisingly - slightly lower for the last generation studied. This, again, may be due to the small sample sizes in this season.

- Recruitment

Recruitment in the field up to adult stage is shown in table 4.13. These figures are the numbers entering successive stages.

Table 4.13 Recruitment. Healthy *P. ruralis*, field data.

Year	Generat	Date	Day(std)	Stage at Inspection 1	2	3	4	5	6	Pupa	Adult	Total
1984	83/4	Jun 5	1 (56)			3	12	19	21			55
		11	7 (62)				3	7	26			36
		19	15 (70)				2	15	30	14		61
		26	22 (77)					1	2	15	3	21
		Jul 2	28 (83)					2	5	19	2	28
		9	35 (90)						3	8	5	16
		19	45(100)								25	25
		23	49(104)								9	9
		Ago 2	59(114)								2	2
		8	65(120)								3	3
		17	74(129)									0
		24	81(136)								1	1
		30	87(142)									0
	84/5	Aug 8	1(120)	1								1
		17	10(129)									0
		24	17(136)	4	2							6
		30	23(142)	7	9							16
		Sep 5	29(148)	1	1							2
		13	37(156)	1	5	5						11
		21	45(164)	24	25	14						63
		28	52(171)	13	44	9						66
		Oct 2	56(175)		2	21						23
		12	66(185)			8						8
		17	71(190)	3	9	8						20
		25	79(198)		1	11						12
		Nov15	100(219)			1						1

(continued)

Numbers per sample are in most cases smaller than for the laboratory results. This is because the intersampling intervals were shorter and the sampling area more restricted than for the laboratory collections. For these same reasons they provide a more detailed and representative picture of what happens in nature. Recruitment can be seen as more realistically spread in time. Still, the same trends observed with the

Table 4.13 (cont.)

Year	Generat	Date	Day(std)	Stage at Inspection 1	2	3	4	5	6	Pupa	Adult	Total
1985	84/5	Apr15	1 (6)				1					1
		24	10 (15)			9	4					13
		May 6	22 (27)		1	9	12					22
		13	29 (34)			14	26					40
		22	38 (43)			7	26	5				38
		30	46 (51)				14	56	2			72
		Jun10	57 (62)					12	55			67
		22	69 (74)						22	1		23
		Jul 1	78 (83)					1	16	24		41
		8	85 (90)						5	29		34
		18	95(100)						1	12		13
		25	102(107)							2	5	7
		Aug 6	114(119)								16	16
		15	123(128)								3	3
		22	130(135)									0
	85/6	Oct 3	1(176)	1								1
		17	15(190)		5	6						11
		23	21(196)		1	5	1					7
		Nov 1	30(205)				6					6
1986		Apr22	1 (13)				1					1
		May 7	16 (28)			4						4
		23	32 (44)			5	7					12
		Jun 9	49 (61)				1	21				22
		27	67 (79)						18			18
		Jul 8	78 (90)							4		4
		24	94(106)							1	1	2
		Aug 4	105(117)									0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

laboratory data show here.

The very young stages are poorly represented again (mainly in the first year), stressing the difficulties involved in finding and following them, even when sampling exhaustively nettle stem by nettle stem.

In 1984, the first larvae were only located in the sampling site in early June. *P. ruralis* had clearly broken diapause for some time by then, for while some were in instars 3, 4 and 5, a large proportion was already in the 6th instar. The 19 June was the peak for recruitment to this instar and when the first pupae were seen. Before the end of this month the moths started to emerge. From mid July no more larval or pupal recruitment occurred. More than 80% of the moths emerged during this month but the emergence period finished in late August.

In the autumn, young caterpillars were detected from the first week of August

till mid November. Individuals in the first instar were never spotted in the sampling area in this year. Judging from the pattern of recruitment to the 2nd instar, hatching may well have started in late July and extended for more than a month. Recruitment was slow during August. The first larvae in stage 3 were recorded on 24 August, and in stage 4 on 13 September. Towards the end of September there was a peak for instars 2, 3 and 4. Most individuals had passed instar 2 during this month. Numbers moulting to instar 3 were lower in October, while development to the 4th instar kept more or less steady till November when eventually all *P. ruralis* underwent diapause.

Breaking of dormancy in spring 1985 started in mid April and recruitment to stages 3 and 4 was recorded until 22 and 30 May respectively. The first entries to stage 5 were observed on the 22 of this month and showed a peak on 30 May, when a few caterpillars were already beginning their 6th instar. The peak for instar 6 followed 11 days later. Most pupal recruitment took place in early July and the few adults registered in this cool season emerged between 18 July and 15 August.

The next generation started to appear almost two months later than in the previous year and peaked about a month later. The only caterpillar in instar 1 was found in S1. Density was low. In the second half of October individuals were moulting to 2nd and 3rd stages and, by early November, the last recordings of recruitment for the season - instar 4 - were made.

Not surprisingly, sample sizes were very small again next spring and hence it is difficult to draw comparisons with the spring of 1985. However, the time span of recruitment was very similar, although peak recruitment to instars 5 and 6, at least, occurred somewhat later in 1986. As for the laboratory collections, larval and pupal recruitment was recorded from the second half of April to mid July. The only moth emerging from the sampling area did so on 24 July.

4.3.2.2. Parasitization

LABORATORY

- Main parasitoid species attacking P. ruralis and overall parasitization rates

The overall numbers of parasitoids per species for all pooled laboratory collections are given in table 4.14.

These data, as discussed in the introduction, provide an incomplete picture of parasitoid impact on the host generations, but do indicate the main species attacking *P. ruralis*.

Overall, 42.5% of the caterpillars that survived up to pupation were parasitized but this percentage varied over the years.

Four species of parasitoids attacked *P. ruralis* in at least two of the three generations studied: *Macrocentrus grandii*, *Diadegma* sp, *Microgaster alebion* Nixon var A and *Nemorilla floralis*. Numbers of the last two were very low. More than 30% of all caterpillars were parasitized by *M. grandii* and about 6% by *Diadegma* sp. Data on these two species are dealt with in detail below.

Table 4.14 Parasitoid numbers and percentages per species for all individuals collected that reached pupal stage in the laboratory.

Generation	Parasitoid species*					Total No. Parasitoid Pupae	Total
	Mg	Ds	Ma	Nf	Other		
83/4	61	5	3	3	6	78	214
(%)	(28.5)	(2.3)	(1.4)	(1.4)	(2.8)	(36.4)	
84/5	164	41	13	2	9	229	545
(%)	(30.1)	(7.5)	(2.4)	(0.4)	(1.7)	(42.0)	
85/6	34	0	3	0	1	38	52
(%)	(65.4)		(5.8)		(1.9)	(73.1)	
Pooled	259	46	19	5	16	345	811
(%)	(31.9)	(5.7)	(2.3)	(0.6)	(2.0)	(42.5)	

* Parasitoid species: Mg = Macrocentrus grandii
Ds = Diadegma sp
Ma = Microgaster alebion var A
Nf = Nemorilla floralis

- Length of development

For *M. grandii* the same between generations trends observed for the healthy individuals occurred (table 4.15a, cp table 4.4). Thus, development was faster in the warmer spring of 1984, slower in the colder 1985 and intermediate in 1986. These differences are significant for stages 5, 6 and pupae (Kruskal-Wallis test, $P < 0.004$).

Frequency distributions were also significantly different from the Normal (Shapiro-Wilk and Kolmogorov-Smirnov tests, $P < 0.01$ for all cases) and skewed to the right.

Instars 3 and 4 lasted about nine days, instar 5 ten days, instar 6 about 16 days and the pupal stage about three weeks. Again, no difference in stage durations was detected between the two sites of collection ($P > 0.05$). As compared to length of development for healthy *P. ruralis* these values are generally slightly higher, except for instar 5 which was slightly lower. However, the only marked and statistically significant difference was in instar 6, which was more than four days longer in individuals parasitized by *M. grandii* than in healthy ones (Kruskal-Wallis test, $H = 13.80$ (1), $P = 0.0002$). This is not surprising, since these caterpillars grow larger than healthy ones and at this instar the parasitoid larval growth is marked and visible (fig 2.15, section 2.3).

Data on development for caterpillars parasitized by *Diadegma* sp are very scanty (table 4.15b), but the available evidence points to the same between generation trends observed in healthy and *M. grandii* parasitized *P. ruralis*. The overall mean for instar

Table 4.15 Mean time (days) spent in each stage and sample sizes (n) for each generation, and overall means. Parasitized host larvae and parasitoid pupae (laboratory data).

(a) Macrocentrus grandii

Stage	Generation 83/4±SE (n)	84/5±SE (n)	85/6±SE (n)	Overall Mean±SE (n)
3	-	9.3 ± 1.48 (6)	-	9.3 ± 1.48 (6)
4	8.8 ± 0.80 (5)	9.4 ± 0.73 (13)	-	9.2 ± 0.56 (18)
5	7.7 ± 0.30 (11)	13.7 ± 0.67 (6)	10.5 ± 1.71 (6)	10.0 ± 0.70 (23)
6	7.8 ± 0.35 (29)	19.3 ± 0.70 (90)	11.3 ± 1.48 (6)	16.2 ± 0.68 ** (125)
Pupa	15.3 ± 0.48 (42)	23.6 ± 0.68 (95)	22.7 ± 1.29 (17)	21.2 ± 0.54 (154)

** Difference between healthy and M. grandii parasitized individuals H = 13.80 (1), P < 0.0002

(b) Diadegma sp

Stage	Generation 83/4±SE (n)	84/5±SE (n)	85/6±SE (n)	Overall Mean±SE (n)
4	-	7.0 ± - (1)	-	7.0 ± - (1)
5	7.0 ± - (1)	17.6 ± 3.56 (5)	6.0 ± - (1)	14.4 ± 3.20 (7)
Pupa	10.9 ± 1.44 (7)	16.0 ± 1.06 (31)	12.7 ± 1.28 (6)	14.7 ± 0.85 (44)

5 duration (14.4 days) is higher than for healthy individuals, but this difference was not significant (H = 0.30 (1), P = 0.587). Pupal development (about two weeks) was faster than for *P. ruralis* or *M. grandii*. Total development time is shorter, as *Diadegma* sp causes the sixth instar usually to be missed: of the 46 *P. ruralis* from which this parasitoid emerged, for only three was this stage recorded.

- Diapause

Diapause for individuals parasitized by *M. grandii* was spent in instars 3, 4 or 5 (table 4.16).

Table 4.16 Frequencies of diapause in different instars as observed in the laboratory for each generation. Caterpillars parasitized by M. grandii.

Instar of Diapause	Generation 84/5 (%)*	Generation 85/6 (%)*	Total (%)*
3	0	1 (50.0)	1 (2.3)
4	8 (19.0)	1 (50.0)	9 (20.5)
5	34 (81.0)	0	34 (77.3)
Total	42	2	44

* The percentages shown are column percentages.

Test for association between generation and instar of diapause:
G = 9.99 (2), P < 0.007, but sample sizes too low on 1985.

In the 84/5 generation dormancy was mostly (80.95%) in the fifth instar as for the healthy caterpillars (cp table 4.5). The little data there are for the 85/6 generation (two individuals, one in instar 3 and one in instar 4) also points to a smaller degree of development achieved before diapause as compared to the previous year. Information available for duration of dormancy is consequently limited to the 84/5 generation (table 4.17) and is remarkably similar to what was recorded for healthy individuals (cp table 4.6) and also varied with the stage the larvae overwintered ($F = 7.9$ (40), $P < 0.01$): instar 4 caterpillars were inactive for 179 days, instar 5 in excess of 190. Data are scarcer still for the full length of the instar of diapause, but again values are very close to those of normal larvae (table 4.6).

The timing of diapause observed in the laboratory for individuals parasitized by *M. grandii* (table 4.18) did not differ much from the healthy ones (cp table 4.7a). For the 84/5 generation, onset was rather synchronized (third week of October) and breaking more spread in time (10 April to 16 May), with larvae in the fourth instar resuming activity much earlier than the ones in the fifth.

Peak frequencies were observed on 17 April, as for healthy caterpillars. However, the cumulative percentage of *M. grandii* parasitized individuals that were active till that date was only 43.9% as compared to 70.2% of the healthy caterpillars.

Table 4.17 Mean duration (days) of diapause and total length of the diapausing instar observed in the laboratory by generation. Caterpillars parasitized by M. grandii.

Generat.	Instar of Diapause	Mean Duration (days) Diapause±SE (n)	Mean Duration (days) Instar±SE (n)	Development time *
84/5	4	179.0 ± 2.17 (8)	216.5 ± 11.50 (2)	37.5
	5	190.5 ± 1.75 (34)	229.6 ± 2.67 (19)	39.1
Differences between instars		F= 7.9;P<0.01	F= 2.7;P=0.157	

* Development time = total duration instar of diapause - duration of diapause (see text for explanation).

Table 4.18 Frequencies by dates of onset and breaking of diapause observed in the laboratory for caterpillars parasitized by M. grandii, generation 84/5.

	Instar 4			Instar 5			Total		
	n	%	Cum%	n	%	Cum%	n	%	Cum%
Onset (1984)									
Oct 15	2	25.0	25.0	6	17.6	17.6	8	19.0	19.0
19	4	50.0	75.0	26	76.5	94.1	30	71.4	90.5
24	2	25.0	100.0	2	5.9	100.0	4	9.5	100.0
Breaking (1985)									
Apr 10	1	14.3	14.3				1	2.4	2.4
12	1	14.3	28.6	2	5.9	5.9	3	7.3	9.7
17	4	57.1	85.7	10	29.4	35.3	14	34.1	43.9
23			85.7	6	17.6	52.9	6	14.6	58.5
24	1	14.3	100.0			52.9	1	2.4	61.0
29				3	8.8	61.8	3	7.3	68.3
30				2	5.9	67.6	2	4.9	73.2
May 1				2	5.9	73.5	2	4.9	78.0
10				4	11.8	85.3	4	9.8	87.8
11				4	11.8	97.1	4	9.8	97.6
16				1	2.9	100.0	1	2.4	100.0
Total	7			34			41		

This difference gradually diminishes, but by the end of April was still evident (73.2% and 85.7%, respectively). The two caterpillars of the 85/6 for which data on diapause are available, broke diapause on the 10 May 1986 (values for onset are missing).

Data on diapause in *Diadegma* sp parasitized *P. ruralis* are limited to five

individuals from the 84/5 generation. Two of these overwintered in instar 4 and three in instar 5, and the average duration of dormancy was 175 and 183 days respectively. Onset was from 15 to 24 October and breaking took place between 12 and 23 April.

- Recruitment

Table 4.19a presents the composition of the laboratory samples per instar of collection for the *M. grandii* parasitized individuals.

Table 4.19 Stage frequency composition of samples collected for laboratory rearing.

(a) Individuals parasitized by M. grandii.

Year	Generat	Date	Day(std)	Stage at Collection 1	2	3	4	5	6	Pupa	Total
1984	83/4	May23	1 (44)		2	3	2				7
		Jun 7	16 (59)				2	10	3		15
		20	29 (72)					7	15	1	23
		Jul 3	42 (85)					1	14	1	16
		17	56 (99)								0
	84/5	Aug21	1(133)								
		Sep 6	17(149)		6	11	7				24
		26	37(169)			3	9				12
		Oct17	58(190)			2	4				6
1985		Apr15	1 (6)			14	6				20
		May 6	22 (27)			10	5	2			17
		23	39 (44)			10	7	8			25
		Jun12	58 (64)				6	11	13		30
		Jul 8	84 (90)						26	2	28
		Aug 3	110(116)							2	2
		13	120(126)								0
	85/6	Sep23	1(167)								0
		Oct 3	11(177)		2						2
		23	31(197)								0
1986		Apr16	1 (7)								0
		27	12 (18)			1	1				2
		May15	30 (36)			1	1				2
		Jun 3	49 (55)					1			1
		18	64 (70)						1		1
		Jul 7	83 (89)						16	5	21
		19	95(101)							5	5

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

Again the pattern is similar to that for healthy individuals and corroborates the results above on the duration of instars. In all seasons, except when sample sizes were very small (cp table 4.8: 21 August 1984, n=1; 23 September 1985, n=2; 16 April 1986, n=3), as soon as *P. ruralis* caterpillars were available in the field, a proportion of them was parasitized by *M. grandii*. There is a very slight shift towards less developed

Table 4.19 (cont.)

(b) Individuals parasitized by Diadegma sp

Year	Generat	Date	Day(std)	Stage at Collection 1	2	3	4	5	6	Pupa	Total
1984	83/4	May23	1 (44)			1	1	1			3
		Jun 7	16 (59)				1	1			2
		20	29 (72)								0
		Jul 3	42 (85)								0
		17	56 (99)								0
	84/5	Aug21	1(133)								
		Sep 6	17(149)			7					7
		26	37(169)			3					3
		Oct17	58(190)			1					1
1985		Apr15	1 (6)			4	4				8
		May 6	22 (27)			1	2	2			5
		23	39 (44)			2	2	4			8
		Jun12	58 (64)				2	2	1		5
		Jul 8	84 (90)							4	4
		Aug 3	110(116)								0
		13	120(126)								0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

instars in general and, more pronounced, a tendency for delay in the recruitment to pupae, consequent from the longer permanency in stage 6.

Hence, in 1984, on 20 June, 15 (65.2%) of the individuals parasitized by *M. grandii* were still in instar 6 and only one pupal mass (4.3%) was found, as opposed to 18 (30.5%) and 35 (59.3%) in instar 6 and the pupal stage, respectively, for the non-parasitized. On the next sampling occasion (3 July) 93.1% (27) of the sample of healthy *P. ruralis* were pupae, but still only one (6.3%) *M. grandii* cocoon was collected. Similarly, in the summer of 1985, on 8 July 92.9% (26) of the *M. grandii* parasitized caterpillars were in stage 6, whereas 91.7% (55) of the healthy *P. ruralis* were already pupae. Again, on 7 July 1986, instar 6 and pupae comprised respectively 76.2% (16) and 23.8% (5) of the *M. grandii* sample, as compared to 16.7% (2) and 83.3% (10) for healthy *P. ruralis*.

Data for *Diadegma* sp (table 4.19b), notwithstanding the low frequencies, seem to indicate a reduction in the proportion of caterpillars carrying this parasitoid towards the end of the season. *Diadegma* sp pupae were only found in 1985. In the two summers, the last dates *Diadegma* sp parasitized individuals were gathered were about 20-25 days before *P. ruralis* was last found. This may, at least partly, result from earlier completion of development, as suggested by the above results on stage durations (table 4.15).

The period of recruitment of *M. grandii* to the adult stage in the laboratory is presented in table 4.20a by generation and by sex of broods. Emergence of this parasitoid happens slightly later than for the moth (cf table 4.9), a consequence of their prolonged development (table 4.15a). In 1984, by mid July, while more than 90% of the moths had already completed metamorphosis, only about half of the *M. grandii* broods had emerged. In the cooler summer of 1985, about 80% of the moths had reached adult stage by mid August, compared to only about 60% of *M. grandii* broods, and in this year their period of emergence was extended well into September. In 1986, with smaller samples this trend is not evident.

Table 4.20 Recruitment to adult stage of individuals reared in the laboratory by generation and by sex.

(a) M. grandii

Year	Month	Quarter	Female Broods			Male Broods			Mixed Broods			Total		
			n	%	Cum%	n	%	Cum%	n	%	Cum%	n	%	Cum%
1984	Jul	1	2	10.0	10.0	4	33.3	33.3	2	20.0	20.0	8	18.2	18.2
		2	6	30.0	40.0	5	41.7	75.0	5	50.0	70.0	16	36.4	54.5
		3												
		4	5	25.0	65.0	3	25.0	100.0	2	20.0	90.0	10	22.7	77.3
	Aug	1												
		2												
		3	7	35.0	100.0				1	10.0	100.0	10*	22.7	100.0
	Total		20			12			10			44*		
1985	Jul	1	1	2.0	2.0	1	2.6	2.6				2	1.9	1.9
		2	10	20.4	22.4	18	47.4	50.0	4	23.5	23.5	32	30.8	32.7
		3												
		4	4	8.2	30.6	7	18.4	68.4	6	35.3	58.8	17	16.3	49.0
	Aug	1												
		2	10	20.4	51.0	2	5.3	73.7	3	17.6	76.5	15	14.4	63.5
		3	22	44.9	95.9	6	15.8	89.5	3	17.6	94.1	31	29.8	93.3
		4	1	2.0	98.0	3	7.9	97.4				4	3.8	97.1
	Sep	1				1	2.6	100.0				1	1.0	98.1
		2												
		3	1	2.0	100.0				1	5.9	100.0	2	0.9	100.0
	Total		49			38			17			104		
1986	Jul	2							1	11.1	11.1	1	4.8	4.8
		3	1	11.1	11.1				2	22.2	33.3	3	14.3	19.0
		4												
	Aug	1	4	44.4	55.6	1	33.3	33.3	6	66.7	100.0	11	52.4	71.4
		2	2	22.2	77.8							2	9.5	81.0
		3	1	11.1	88.9	2	66.7	100.0				3	14.3	95.2
		4	1	11.1	100.0							1	4.8	100.0
	Total		9			3			9			21		

* totals higher than sums because of missing values for sex in two observations.
Factorial analysis by year: influence of sex on timing of emergence, P = 0.019.

Table 4.20 (cont.)

(b) Diadegma sp

Year	Month	Quarter	Females n	Females %	Females Cum%	Males n	Males %	Males Cum%	Total n	Total %	Total Cum%
1984	Jun	2	1	50.0	50.0	1	33.3	33.3	2	40.0	40.0
		3									
		4				1	33.3	66.7	1	20.0	60.0
	Jul	1				1	33.3	100.0	1	20.0	80.0
		2									
		3	1	50.0	100.0				1	20.0	100.0
	Total		2			3			5		
	Oct	1	3	50.0	50.0	1	50.0	50.0	4	50.0	50.0
		2	2	33.3	83.3	1	50.0	100.0	3	37.5	87.5
		3									
		4	1	16.7	100.0				1	12.5	100.0
	Total		6			2			8		
1985	Apr	4	1	7.1	7.1				1	3.8	3.8
	Jun	1				1	9.1	9.1	1	3.8	7.7
		2									
		3				1	9.1	18.2	1	3.8	11.5
		4	3	21.4	28.6	4	36.4	54.5	7	26.9	38.5
	Jul	1	3	21.4	50.0	4	36.4	90.9	7	26.9	65.4
		2	3	21.4	71.4	1	9.1	100.0	4	15.4	80.8
		3	4	28.6	100.0				5*	19.2	100.0
	Total		14			11			26*		

* totals higher than sums because of missing value for sex in one observation.

In contrast, *Diadegma* sp, with its faster development, emerged much earlier (table 4.20b). In 1984, the first adults appeared by mid June, and before the end of July, all pupae had emerged in the laboratory. Eight individuals of the following generation (84/5) that were brought to the laboratory early in the Autumn emerged before winter (October) and thus did not undergo diapause. In 1985, one wasp emerged in late April, and again before the end of July they were all adults.

- Sex ratio and developmental differences between sexes

For both species of parasitoids there is some evidence that males start emerging before females. Differences between sexes in timing of recruitment were significant for broods of *M. grandii* (G = 26.89 (14), P = 0.019), but not for those of *Diadegma* sp (G = 2.78 (5), P = 0.733).

The proportion of female, male and mixed broods of *M. grandii* varied over the

three generations, but this difference was not significant (G = 6.57 (4), P = 0.160). In all years there were more female broods (n=78, 46.15%) than male (n=53, 31.36%) or mixed ones (n=36, 21.30%) (G = 16.04 (2), P < 0.001) .

Sex influenced the size of broods (F = 6.47 (2), P = 0.002). Thus female broods had a mean of 25.59 ± 1.623 individuals, male broods 32.26 ± 2.532 and mixed broods 38.58 ± 2.526. The number of wasps per brood did not differ significantly between generations (F = 0.27 (2), P = 0.767) or site of collection (F = 0.14 (1), P = 0.680). Within mixed broods there was on average more females (22.95 ± 2.007) than males (15.63 ± 2.025) and this difference was significant (F = 6.59 (1), P < 0.01).

For *Diadegma* sp the sex ratio did not differ overall from 1:1 (G = 0.947 (1), P > 0.1).

- Target instars and generational parasitization levels

The percentage of parasitization per instar at collection is given in table 4.21 for the pooled data for all the four main species, and also by generation for *M. grandii* and *Diadegma* sp.

Percentages varied over the years and instars. No data are available for instar 1. Frequencies are low for the younger stages in the 83/4 generation (this work only started in spring 1984, after this generation had undergone diapause) and for all instars in generation 85/6.

For *M. grandii*, percentages at instar 2 varied considerably (20 to 100%) between generations, probably because of the small sample sizes in 83/4 and 85/6. In 83/4 and 84/5, the levels remained fairly steady throughout instars 3, 4, 5 and 6 (i.e. between 27 and 41%) and then fell markedly in the pupal stage.

In 85/6, the sample sizes were very small for instars 2-5 but, where they were of reasonable size, as for instar 6 and the pupal stage, levels differed from the ones found in the two previous generations, with a 100% parasitization of instar 6 and 43.5% in the pupal stage. This is unrealistic (there cannot be 100% parasitization in an instar and then healthy individuals found later in development) but the differences from the two former generations seem considerable and thus this generation is treated separately from 83/4 and 84/5.

The above data indicate that parasitization starts early in the season (at or before instar 2), as already evidenced by results on recruitment (table 4.19a above). The percentage level effectively reaches its peak in instar 3, indicating that at this stage *M. grandii* oviposition is completed. Instar 3 is thus considered the target instar for the purpose of estimation of parasitization levels by this wasp. (It is possible that levels calculated at this stage may still be a slight underestimate of actual parasitization, as some samples containing this stage could have been taken a little before all oviposition was finished.)

Speculation as to why these levels varied in the more developed stages can be made based on the knowledge on development (see above, table 4.15a) and mortality

Table 4.21 Percentage of parasitization per parasitoid species and generation, according to the instar P. ruralis were when collected (see text for explanation).

Generat	Sp[a]	Stage at Collection 2	3	4	5	6	pupa	Total
G83/4								
	Mg	2	3	4	18	32	2	61
	(%)[b]	(100.0)	(37.5)	(36.4)	(36.7)	(37.2)	(3.4)	(28.5)
	Ds	0	1	2	2	0	0	5
	(%)		(12.5)	(18.2)	(4.1)			(2.3)
Total Collected[c]		2	8	11	49	86	58	214
G84/5								
	Mg	6	50	44	21	39	4	164
	(%)	(20.0)	(34.5)	(33.1)	(26.9)	(41.1)	(5.9)	(30.1)
	Ds	0	18	10	8	1	4	41
	(%)		(12.8)	(7.5)	(10.3)	(1.1)	(5.9)	(7.5)
Total Collected		30	141	133	78	95	68	545
G85/6								
	Mg	2	2	2	1	17	10	34
	(%)	(50.0)	(100.0)	(100.0)	(25.0)	(100.0)	(43.5)	(65.4)
	Ds	0	0	0	0	0	0	0
Total Collected		4	2	2	4	17	23	52

(continued)

a) Parasitoid species: Mg = M. grandii; Ds = Diadegma sp;
Ma = M. alebion var A; Nf = Nemorilla floralis.

b) The percentages given are per column total per generation.

c) Total = total numbers of individuals collected that reached the pupal stage.

(see below section 4.3.2.3). The rate of development of the younger stages of *P. ruralis* did not appear to be altered significantly in *M. grandii* parasitized caterpillars. Pooling the data for 83/4 and 84/5 indicates a slight reduction in the level of parasitization in stage 4 and again in stage 5 (table 4.21, generations 83/4 and 84/5 pooled).

This suggests a slight increase in mortality in the field of parasitized caterpillars as compared to healthy ones during these stages. The corresponding increase observed in instar 6 may be explained in terms of the delay in development and consequent 'accumulation' of parasitized larvae at this stage in the population. Furthermore, the low levels in the pupal stage may be an indirect effect of this developmental rate

Table 4.21 (cont.)

Generat Sp[a]	Stage at Collection 2	3	4	5	6	pupa	Total
G83/4 & G84/5 Pooled							
Mg	6	53	48	39	71	6	225
(%)[b]	(18.8)	(35.6)	(33.3)	(30.7)	(39.2)	(4.8)	(29.6)
Ds	0	19	12	10	1	4	46
(%)		(12.8)	(8.3)	(7.9)	(0.6)	(3.2)	(6.1)
Total Collected[c]	32	149	144	127	181	126	759
All Pooled							
Mg	10	55	50	40	88	16	259
(%)	(27.8)	(36.4)	(34.3)	(30.5)	(44.4)	(10.7)	(31.9)
Ds	0	19	12	10	1	4	46
(%)		(12.6)	(8.2)	(7.6)	(0.5)	(2.7)	(5.7)
Ma	6	5	1	5	0	2	19
(%)	(16.7)	(3.3)	(0.7)	(3.8)		(1.3)	(2.3)
Nf	0	0	0	0	2	3	5
(%)					(1.0)	(2.0)	(0.6)
Other spp	0	0	6	3	3	4	16
(%)			(4.1)	(2.3)	(1.5)	(2.7)	(2.0)
Total parasit.	16	79	69	58	94	29	345
(%)	(44.4)	(52.3)	(47.3)	(44.3)	(47.5)	(19.5)	(42.5)
Total Collected	36	151	146	131	198	149	811

a) Parasitoid species: Mg = M. grandii; Ds = Diadegma sp;
Ma = M. alebion var A; Nf = Nemorilla floralis.
b) The percentages given are per column total per generation.
c) Total = total numbers of individuals collected that reached the pupal stage.

difference (i.e. *M. grandii* pupae did not become available for collection until later in the season), and/or perhaps a consequence of a longer/later exposure to predation as compared to *P. ruralis* pupae.

The percentages calculated for the different instars and in the two ways (i.e. all stages pooled vs target instar) were significantly different ($G = 48.08$ (5), $P < 0.0001$) and in the same direction for all generations ($G = 7.58$ (10), $P = 0.6695$). The process uncovers various aspects of the biology of these populations, the counteracting effects

of which caused percentages at target stage and pooled data to be similar. It also illustrates all the aspects that can distance estimated from actual parasitization levels raised in the introduction of this chapter. It is easy to see how biased results can be if calculated from samples taken at certain points of the generation (say, at instars 5, 6 or pupa). Moreover, in spite of the sometimes small sample sizes, results are very consistent between generations and with the results on recruitment and development. Also, as can be seen below, this similarity between estimates based on target instar and on the summing of all stages is by no means usual for most parasitoid species.

Diadegma sp target instar is not so easy to define due to the much lower levels of parasitization found. Only 5 caterpillars of the 83/4 generation bore this parasitoid and none was detected in the 85/6 generation. Based on the 84/5 data, when reasonable frequencies of this wasp were obtained, instar 3 seems very likely to be the *P. ruralis* susceptible stage.

No parasitization by this species was observed for larvae collected in the second stage. Percentages detected in instar 3 were about 12.5% for generations 83/4 and 84/5 and for the pooled data. Instar 4 had a higher level in 83/4 (18.2%), but this estimate is based on only two individuals out of a total of eleven collected. In the next generation, when sample sizes were considerably larger, the level in instar 4 was just above half of that for instar 3. Percentages for instar 5 were low in 83/4 (4.1%), but higher than for instar 4 in 84/5 (10.3%). Only one 6th instar larvae bearing *Diadegma* sp was collected. This is not surprising, since this parasitoid tends to suppress this instar (see section on length of development above). Pupae of this species were also scarce, perhaps due to faster development and/or higher mortality.

Percentages estimated using all stages were much lower (2.3 to 7.5%) than the levels observed for instar 3.

Little can be said about the two other species. *M. alebion* oviposits very early in the season and levels for instar 2 were about 17%. *N. floralis* parasitized between 1 and 2% of the full grown *P. ruralis* caterpillars. In both cases, pooled instars percentages are probably grossly distorted estimates of parasitoid impact, due to the low level parasitization and the impossibility of identifying the target instar.

FIELD

- Main parasitoid species and parasitization rates

Total numbers of parasitoid pupae, per species, originating from the caterpillars monitored in the field are given in table 4.22.

Thirty six parasitoid pupae were traced in the field monitoring study site. Numbers are low because, in addition to the limited area sampled (due to the extremely time consuming nature of the field work), only post-diapause individuals of *P. ruralis* that managed to survive up to pupation can be included. This is because parasitization of the field monitored caterpillars was only detectable after winter, at pupation. The

Table 4.22

(a) Parasitoid numbers and percentages per species for all individuals monitored in the field that reached pupal stage.

Generation	Parasitoid species*					Total No. Parasitoid Pupae	Total
	Mg	Ds	Ma	Nf	Other		
83/4	4	12	8	0	1	25	75
(%)	(5.3)	(16.0)	(10.7)		(1.3)	(33.3)	
84/5	9	1	0	1	0	11	64
(%)	(14.1)	(1.6)		(1.6)		(17.2)	
Pooled	13	13	8	1	1	36	139
(%)	(9.3)	(9.3)	(5.7)	(0.7)	(0.7)	(25.9)	

(b) Percentage of parasitization per parasitoid species in collected pupae of
P. ruralis
(pooled data for 83/4 and 84/5 generations only).

	Parasitoid species*					Total No. Parasitoid Pupae	Total
	Mg	Ds	Ma	Nf	Other		
Numbers	6	4	2	3	4	19	126
(%)	(4.8)	(3.2)	(1.6)	(2.4)	(3.2)	(15.1)	

* Parasitoid species: Mg = M. grandii; Ds = Diadegma sp;
Ma = M. alebion var A; Nf = N. floralis.

85/6 generation is not included in the table because only 5 individuals survived until pupation and none of them was parasitized.

The overall parasitization rate observed in the field was 25.9%. The main species of parasitoids were the same as observed in the laboratory: *M. grandii* (9.3%, n=13), *Diadegma* sp (9.3%, n=13), *M. alebion* (5.7%, n=8), *N. floralis* (0.7%, n=1) (and also one unidentified species). *M. grandii* and *Diadegma* sp again showed the two highest levels of parasitization.

That the overall percentage observed in the field are so much lower than that recorded in the laboratory (table 4.14) is a consequence of the different nature of the two sets of data and points to the importance of accounting for the stage(s) sampled when computing levels of parasitization. Figures shown in table 4.14 are derived from individuals that were removed from the field (and thus from factors such as mortality,

dispersion and collection) at various stages of development (instar 2 to pupa); in contrast, only individuals that reached pupal stage in the field (and so could be classified as parasitized or not parasitized) could be included in table 4.22a. Therefore, figures in table 4.22a are actually percentage parasitization for pupae, of the same type as shown in the 'pupa' column of table 4.21 for the laboratory data.

When viewed in this light, the magnitude of the differences between field and laboratory results is much smaller than it seemed at first. Comparing results for the pooled generations from tables 4.21 ('pupa' column) and 4.22a, it should be noted that, in the field results, generation 85/6 is not included. Totals for the laboratory pupae data subtracting this generation are given for comparison in table 4.22b. Thus, levels of parasitization recorded for individuals monitored in the field were actually higher for the first three species than for pupae collected for laboratory rearing.

As with the laboratory data, rates for *M. grandii* were lower in the 84/5 generation (5.3%) than in the 83/4 (14.1%). For *Diadegma* sp, however, these trends are reversed: rates were higher in 83/4 (16.0%) than in 84/5 (1.6%).

Development and recruitment of *P. ruralis* parasitized by *M. grandii* and *Diadegma* sp monitored in the field are described below.

- Length of development

Stage durations recorded in the field are shown in table 4.23a for individuals parasitized by *M. grandii* and of parasitoid pupae.

There is considerable variation between generations but the samples sizes are very small and the SE's are large. Pooling the data gives a value of 9.5 days for instar 4, 17.2 for instar 5, 23.3 for instar 6 and 23.6 for pupae. These figures are higher than the laboratory ones (cf table 4.15a) - particularly for instars 5 and 6, which were each about a week longer in the field. Compared to healthy *P. ruralis* in the field (cf table 4.10), there were differences, but trends are not so clear. As observed in the laboratory, when contrasting *M. grandii* bearing and healthy individuals, the most marked difference was the delayed development in the last larval stage. Instar 6 was 5.5 days longer in parasitized than in healthy *P. ruralis* monitored in the field.

The data available for *Diadegma* sp (table 4.23b) are very sparse, but tends to support the evidence from the previous sections: *Diadegma* sp in the field seems to develop slower than in the laboratory (cf table 4.15b), but faster than healthy individuals (cf table 4.10; pupal stage is about a week faster).

- Recruitment

Recruitment to the larval stages of parasitized *P. ruralis* is presented in table 4.24 (remember that data are restricted to the post-diapause period - see above). Given the low numbers recorded it is difficult to identify in the *M. grandii* recruitment field data (table 4.24a) any differences from either *M. grandii* laboratory data (cp table 4.19a) or healthy *P. ruralis* field data (cp table 4.13).

Regarding recruitment to adult stage, in each generation, 83/4 and 84/5, only

Table 4.23 Mean time (days) spent in each stage and sample sizes (n) for each generation and overall means. Parasitized host larvae and parasitoid pupae, field data.

(a) Macrocentrus grandii

Stage	Generation 83/4±SE (n)	Generation 84/5±SE (n)	Overall Mean±SE (n)
4	-	9.5 ± 1.50 (2)	9.5 ±1.50 (2)
5	13.0 ± - (1)	18.0 ± 4.14 (5)	17.2 ± 3.48 (6)
6	7.0 ± 0.00 (2)	28.0 ± 3.43 (7)	23.3 ± 4.05 (9)
Pupa	26.7 ± 3.33 (3)	19.0 ± 0.00 (2)	23.6 ± 2.62 (5)

(b) Diadegma sp

Stage	Generation 83/4±SE (n)	Generation 84/5±SE (n)	Overall Mean±SE (n)
4	13.0 ± - (1)	-	13.0 ± - (1)
Pupa	18.3 ± 2.19 (3)	-	18.3 ± 2.19 (3)

two *M. grandii* pupal masses survived up to eclosion and in both years adults emerged in early August (table 4.24a). Compared to parasitoids reared in the laboratory (cf table 4.20) this time was later than most in 1984, but about average in 1985.

For *Diadegma* sp, the data are just as sparse, and mostly concentrated in 1984. (N.B. the complete absence of records for instar 6 in both years.) In the 83/4 generation, pupae were detected as early as 5 June, but none of the *Diadegma* sp parasitized individuals collected for laboratory rearing were found at pupal stage (cf table 4.19b). Thus, no parallel can be detected here, but the beginning of June is certainly early for the pupal stage for *P. ruralis* in the field (cf table 4.13), and this reiterates the faster development caused by *Diadegma* sp. In contrast, emergence of the six wasps in 1984 occurred through an extended period - early July to late August - and later than observed in the laboratory (cf table 4.20b), but similar to *P. ruralis* in

Table 4.24 Recruitment of parasitized *P. ruralis*, field data.

(a) *M. grandii*

Year	Generat	Date	Day(std)	Stage at Inspection 1	2	3	4	5	6	Pupa	Adult	Total
1984	83/4	Jun 5	1 (56)					1				1
		11	7 (62)									0
		19	15 (70)						1			1
		26	22 (77)							1		1
		Jul 2	28 (83)						1			1
		9	35 (90)						1	1		2
		19	45(100)							1		1
		23	49(104)									0
		Ago 2	59(114)									0
		8	65(120)								2	2
		17	74(129)									0
		24	81(136)									0
		30	87(142)									0
1985	84/5	Apr15	1 (6)									0
		24	10 (15)									0
		May 6	22 (27)		1							1
		13	29 (34)			2						2
		22	38 (43)		2	1						3
		30	46 (51)			3	4					7
		Jun10	57 (62)				2	3				5
		22	69 (74)					4				4
		Jul 1	78 (83)					1				1
		8	85 (90)					1	2			3
		18	95(100)						5			5
		25	102(107)						2			2
		Aug 6	114(119)								2	2
		15	123(128)									0
		22	130(135)									0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

the field (cp table 4.13).

4.3.2.3 Other Mortality

LABORATORY

- Survival per stage (excluding overwinter mortality)

Table 4.25 shows numbers of deaths and survivals per developmental stage. Larval mortality comprises both non-parasitized and parasitized caterpillars; thus all larvae collected, for which records on instar at death are available, are included in table 4.25a. Towards the end of stage 6, a prepupal phase can be distinguished (separation of head capsule). This phase lasts about one or two days, but on the analysis of the data it was evident that most mortality in instar 6 occurred at this phase and thus it was decided to treat it as distinct phase. Also, from such prepupal

Table 4.24 (cont.)

(b) Diadegma sp

Year	Generat	Date	Day(std)	Stage at Inspection 1	2	3	4	5	6	Pupa	Adult	Total
1984	83/4	Jun 5	1 (56)				4	1		2		7
		11	7 (62)					1		4		5
		19	15 (70)							4		4
		26	22 (77)									0
		Jul 2	28 (83)								2	2
		9	35 (90)								2	2
		19	45(100)									0
		23	49(104)									0
		Ago 2	59(114)								1	1
		8	65(120)						1			1
		17	74(129)									0
		24	81(136)								1	1
		30	87(142)									0
1985	84/5	Apr15	1 (6)									0
		24	10 (15)									0
		May 6	22 (27)									0
		13	29 (34)			1						1
		22	38 (43)									0
		30	46 (51)					1				1
		Jun10	57 (62)						1			1
		22	69 (74)									0
		Jul 1	78 (83)									0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

caterpillars, it is possible to assess separately mortality on *P. ruralis* (table 4.25b) and on the main parasitoids (tables 4.25c & d).

The data were derived from individuals collected at all stages, so that, in many cases, numbers increase through successive stages (as opposed to what would happened if single, fixed number, cohorts were followed per generation).

Each individual counted one survival for each stage, from collection until death or successful emergence (except for the instar of diapause). In table 4.25b-d, the total number of deaths for each row can be obtained by summing those occurring at each phase. However, the total of survivals is that at emergence. Note that the total numbers of deaths are lower than shown in table 4.2, because overwinter mortality is dealt with separately (see below), and parasitoid mortality here concerns only *M. grandii* and *Diadegma* sp.

There was significant variation between stages (G = 69.65 (5), P = 0.0001) and between generations (G = 20.06 (2), P = 0.0001), but between larval instars the pattern did not significantly differ between generations (G = 15.80 (8), P = 0.069). There were also differences in mortality rates at pupation, during the pupal stage and at emergence

Table 4.25 Survival per stage. Laboratory data, non-diapausing stages.

(a) Larval survival per instar.

	STAGE					
	1 (%)*	2 (%)	3 (%)	4 (%)	5 (%)	6 (%)
- Generat. 83/4						
No. Died	-	0	1 (7.7)	0	2 (2.6)	1 (0.6)
No. Survived	-	4 (100.0)	12 (92.3)	24 (100.0)	76 (97.4)	163 (99.4)
Total	-	4	13	24	78	164
- Generat. 84/5						
No. Died	-	15 (16.7)	27 (8.2)	19 (4.0)	20 (5.6)	67 (10.9)
No. Survived	-	75 (83.3)	304 (91.8)	459 (96.0)	335 (94.4)	547 (89.1)
Total	-	90	331	478	355	614
- Generat. 85/6						
No. Died	7 (77.8)	2 (50.0)	4 (40.0)	2 (15.4)	0	3 (8.6)
No. Survived	2 (22.2)	2 (50.0)	6 (60.0)	11 (84.6)	16 (100.0)	32 (91.4)
Total	9	4	10	13	16	35
- Pooled Generats.						
No. Died	7 (77.8)	17 (17.4)	32 (9.0)	21 (4.1)	22 (4.9)	71 (8.7)
No. Survived	2 (22.2)	81 (82.6)	322 (91.0)	494 (95.9)	427 (95.1)	742 (91.3)
Total	9	98	354	515	449	813

* column percentages, per instar, per generation.

Factorial analysis:

generation effect - G = 20.06 (2), P =0.0001;

instar effect - G = 69.65 (5), P = 0.0001.

Table 4.25 (cont.) stages.

(b) Survival from pupation, P. ruralis.

	PHASE			Total
	prepupa[a] (%)[b]	pupa (%)	emergence (%)	(%)
- Generat. 83/4				
No. Died	3 (3.4)	7 (4.7)	6 (4.2)	16 (10.5)
No. Survived	84 (96.6)	142 (95.3)	136 (95.8)	136 (89.5)
Total	87	149	142	152
- Generat. 84/5				
No. Died	29 (8.7)	44 (12.0)	5 (1.6)	78 (19.8)
No. Survived	303 (91.3)	321 (88.0)	316 (98.4)	316 (80.2)
Total	332	365	321	394
- Generat. 85/6				
No. Died	1 (20.0)	3 (17.6)	0	4 (22.2)
No. Survived	4 (80.0)	14 (82.4)	14 (100.0)	14 (77.8)
Total	5	17	14	18
- Pooled Generats.				
No. Died	33 (7.8)	54 (10.2)	11 (2.3)	98 (17.4)
No. Survived	391 (92.2)	477 (89.8)	466 (97.7)	466 (82.6)
Total	424	531	477	564

a) see text for explanation.

b) column percentages, per stage, per generation.

Table 4.25 (cont.)

(c) Survival from pupation, *M. grandii*.

	PHASE			Total
	prepupa[a] (%)[b]	pupa (%)	emergence (%)	(%)
- Generat. 83/4				
No. Died	2 (3.4)	15 (25.4)	0	17 (27.9)
No. Survived	57 (96.6)	44 (74.6)	44 (100.0)	44 (72.1)
Total	59	59	44	61
- Generat. 84/5				
No. Died	10 (6.3)	53 (34.4)	1 (1.0)	64 (39.0)
No. Survived	149 (93.7)	101 (65.6)	100 (99.0)	100 (61.0)
Total	159	154	101	164
- Generat. 85/6				
No. Died	1 (4.2)	8 (24.2)	0	9 (26.5)
No. Survived	23 (95.8)	25 (75.8)	25 (100.0)	25 (73.5)
Total	24	33	25	34
- Pooled Generats.				
No. Died	13 (5.4)	76 (30.9)	1 (0.6)	90 (34.7)
No. Survived	229 (94.6)	170 (69.1)	169 (99.4)	169 (65.3)
Total	242	246	170	259

a) see text for explanation.

b) column percentages, per stage, per generation.

Table 4.25 (cont.)

(d) Survival from pupation, Diadegma sp.

	PHASE			Total
	prepupa[a] (%)[b]	pupa (%)	emergence (%)	(%)
- Generat. 83/4				
No. Died	0	0	0	0
No. Survived	5 (100.0)	5 (100.0)	5 (100.0)	5 (100.0)
Total	5	5	5	5
- Generat. 84/5				
No. Died	0	7 (17.1)	0	7 (17.1)
No. Survived	37 (100.0)	34 (82.9)	34 (100.0)	34 (82.9)
Total	37	41	34	41
- Pooled Generats.				
No. Died	0	7 (15.2)	0	7 (15.2)
No. Survived	42 (100.0)	39 (84.8)	39 (100.0)	39 (84.8)
Total	42	46	39	46

a) see text for explanation.

b) column percentages, per stage, per generation.

between *P. ruralis*, *M. grandii* and *Diadegma* sp (G = 138.98 (2), P = 0.0001). For the sake of clarity, results for larvae (table 4.25a) and for *P. ruralis* pupal survival (table 4.25b) will be described first; then survival of parasitoids (tables 4.25c & d) will be presented comparatively to those.

Early instars are misrepresented in the 83/4 generation (table 4.25a), as there was no pre-diapause sampling in 1983. Survival was generally high in this generation; death at emergence (4.2%), however, was at its highest (table 4.25b).

In the 84/5 generation, larval mortality ranged from 4.0 to almost 17% (table 4.25a). Instar 2 had a low survival rate (83.3%); intermediate instars survived better (91.8 to 96.0%), but levels dropped a little in instar 6 (89.1%). *P. ruralis* prepupal and

pupal survival was near 90% and the rate of success at emergence was 98.4% (table 4.25b).

In the last generation studied (85/6) the numbers collected were smaller and yielded mostly lower survival rates but the trends are not dissimilar to those of the previous year.

Pooling the generations indicates lower survival at younger stages (22.2% at instar 1, but sample size is only 9; 82.6% at instar 2), followed by levels in excess of 90% for the remaining instars. There is a slight increase between stages 3 and 4 and a decrease of similar magnitude between stages 5 and 6. A similar level of survival to that in instar 6 (i.e. about 90%) was also observed both at the prepupal phase and during the pupal stage. Considering the short duration of the prepupal phase (one or two days as compared to about two weeks for instar 6 and three for the pupa), it can be considered a relatively vulnerable phase. Emergence was mostly successful (97.7%).

Larval mortality of the parasitoids cannot be separated directly from *P. ruralis* larval mortality: externally caterpillars bear no obvious signs of parasitization and, unfortunately, there was no time available - or indeed, for some instars and in some generations, enough individuals - to allow for dissections of larvae at each instar. Therefore, the above larval survival rates in the laboratory embrace both *P. ruralis* and parasitoids.

However, concerning prepupal, pupal and emergence survival, in the data available the variation between generations for *M. grandii* (table 4.25c) and *Diadegma sp* (table 4.25d) does not differ much from what was recorded for *P. ruralis* (table 4.25b).

The pooled prepupae survival for *M. grandii* was slightly higher (94.6) than that for *P. ruralis* (92.2%) although in the 83/4 generation levels were identical. Pupal survival, however, was much lower (65.6 to 75.8% (pooled = 69.1%) as compared to 82.4 to 95.3% (pooled = 89.8%)). The *M. grandii* rate of success at emergence (99 to 100%) was probably lower than recorded: ideally, the cocoons should have been examined after emergence to check whether all pupae within had completed development but this was not feasible due to time constraints. Thus it is possible that, within broods, mortality at this phase was higher.

The numbers of *Diadegma* sp were rather low but the available data indicates survival levels higher than those of *P. ruralis* for pupation and emergence but lower for the pupal phase.

In terms of the level of survival from the start of the prepupal phase through to the adult stage *P. ruralis* (82.6%) and *Diadegma* sp (84.8%) were similar and considerably higher than *M. grandii* (65.3%).

- Overwinter mortality

Survival per instar during diapause is given in table 4.26. Caterpillars survived much better over winter in generation 84/5 (57.7%) than in the following one (29.5%)(G = 15.25 (1); P = 0.0001).

In generation 84/5, the larvae overwintered mainly in the fourth (21.1%) and fifth instars (78.3%), and survival was slightly better in the former (60.3%) than in the latter (56.7%).

In generation 85/6, individuals had not reached the same level of development by winter: 25 were still in instar 2, most diapaused in instars 3 (25.7%) and 4 (62.5%) and only one had reached instar 5. Survival was noticeably lower the younger the individuals were: 0% at instar 2, 16.4% at instar 3, 34.5% at instar 4.

Differences in overwinter survival according to instar at diapause were significant (G = 15.25 (1), P = 0.014), but data were slightly heterogeneous between generations (G = 6.19 (2), P = 0.045). Pooling the generations showed instar 5 to have the best survival rate. However, this is strongly influenced by the generally higher survival rates in the 84/5 generation and the respective sample sizes in the two generations. By looking at the data within generations, it seems reasonable to suggest that diapause at instar 4 actually promotes the highest chances of survival.

As explained above, these results for larval survival include both non-parasitized and parasitized *P. ruralis*.

- Length of development

Caterpillars that died before the adult stage developed mostly slower than did healthy *P. ruralis* (table 4.27, cf table 4.4), particularly in instar 6 which was on average six days longer.

These differences were significant for the last three larval stages. No data were compiled for pupal development, because pupae could only be considered dead after too long a period had elapsed and no emergence occurred. Otherwise, between generation trends were not different from healthy (cp table 4.4) or parasitized caterpillars (cp table 4.15).

Durations of diapause and instar of diapause (table 4.28), and timing of diapause onset and breaking (table 4.29) were remarkably similar to what was observed for healthy *P. ruralis* (cp tables 4.6 & 4.7), with corresponding differences between instars and generations.

FIELD

- Survival per stage (excluding overwinter mortality)

Survival rates in the field are given in table 4.30. Efforts were made to identify the factors responsible for mortality (section 4.2.2).

However, more often than not, direct evidence was not available and individuals were simply considered 'missing' (but see discussion below on timing, potential

Table 4.26 Frequencies of diapause in different instars and survival over winter and up to the adult stage, by generation. Laboratory data, healthy and parasitized *P. ruralis*.

	STAGE				Total
	2 (%)*	3 (%)	4 (%)	5 (%)	(%)
- Generat. 84/5					
No. Died Overwinter	-	0	31 (39.7)	125 (43.3)	156 (42.3)
No. Survived Diapause	-	2 (100.0)	47 (60.3)	164 (56.7)	213 (57.7)
Total	-	2	78	289	369
No. Died Later	-	1 (50.0)	15 (19.2)	64 (22.1)	
- Generat. 85/6					
No. Died Overwinter	25 (100.0)	51 (83.6)	97 (65.5)	0	148 (70.5)
No. Survived Diapause	0	10 (16.4)	51 (34.5)	1 (100.0)	62 (29.5)
Total	25	61	148	1	210
No. Died Later	0	2 (3.3)	10 (6.8)	0	
- Pooled Generat.					
No. Died Overwinter	25 (100.0)	51 (81.0)	128 (56.6)	125 (43.1)	304 (52.5)
No. Survived Diapause	0	12 (19.0)	98 (43.4)	165 (56.9)	275 (47.5)
Total	25	63	226	290	579
No. Died Later	0	3 (4.8)	25 (11.1)	64 (22.1)	

* column percentages, per instar, by generation.

Table 4.27 Mean time (days) spent in each stage and sample sizes (n) for each generation and overall means. Laboratory data, non-diapausing stages.

Stage	Generation 83/4±SE (n)	84/5±SE (n)	85/6±SE (n)	Overall Mean±SE (n)
1	-	10.0 ± 0.00 (8)	6.7 ± 0.25 (66)	7.1 ± 0.25 (74)
2	-	7.2 ± 0.86 (15)	12.9 ± 0.87 (28)	10.9 ± 0.76 (43)
3	-	9.1 ± 0.71 (43)	-	9.1 ± 0.71 (43)
4	-	10.6 ± 0.42 (94)	-	10.6 ± 0.42 * (94)
5	-	17.0 ± 2.21 (13)	11.2 ± 1.45 (15)	13.9 ± 1.38 * (28)
6	6.00± - (1)	19.2 ± 1.52 (46)	14.5 ± 3.14 (12)	18.0 ± 1.37 * (59)

* Caterpillars that did not survive to adult stage had significantly longer instars than healthy ones, (c. f. table 4.4).

Kruskal-Wallis test:

instar 4 - 1.6 days longer : H = 7.94 (1), P = 0.005

instar 5 - 2.1 days longer : H = 3.52 (1), P = 0.05

instar 6 - 6.0 days longer : H = 4.67 (1), P = 0.02

Table 4.28 Mean duration of diapause (days) and total length of the diapausing instar observed in the laboratory for P. ruralis that died, by generation.

Generat.	Instar of Diapause	Mean Duration (days) Diapause±SE (n)	Mean Duration (days) Instar±SE (n)	Development time *
84/5	4	177.1 ± 1.80 (12)	201.5 ± 7.24 (4)	34.4
	5	188.6 ± 1.87 (43)	231.6 ± 2.08 (35)	43.0
Differences between instars		F = 9.8; P < 0.01	F = 5.0; P = 0.08	
85/6	4	-	229.1 ± 2.58 (9)	-
Differences between generats.		-	F = 9.4; P = 0.003	

* Development time = total duration instar of diapause - duration of diapause.

Table 4.29 Frequencies by dates of onset and breaking of diapause observed in the laboratory for each generation for *P. ruralis* that died.

(a) Generation 84/5

	Instar 4			Instar 5			Total		
	n	%	Cum%	n	%	Cum%	n	%	Cum%
Onset (1984)									
Oct 15	3	23.1	23.1	8	16.7	16.7	11	18.0	18.0
19	3	23.1	46.2	38	79.2	95.8	41	67.2	85.2
24	7	53.8	100.0	2	4.2	100.0	9	14.8	100.0
Breaking (1985)									
Apr 10	1	8.3	8.3	1	2.3	2.3	2	3.6	3.6
11				1	2.3	4.5	1	1.8	5.4
12	3	25.0	33.3	6	13.6	18.2	9	16.1	21.4
17	7	58.3	91.7	17	38.6	56.8	24	42.9	64.3
23	1	8.3	100.0	2	4.5	61.4	3	5.4	69.6
29				1	2.3	63.6	1	1.8	71.4
30				2	4.5	68.2	2	3.6	75.0
May 1				2	4.5	72.7	2	3.6	78.6
10				6	13.6	86.4	6	10.7	89.3
11				3	6.8	93.2	3	5.4	94.6
16				2	4.5	97.7	2	3.6	98.2
24				1	2.3	100.0	1	1.8	100.0
Total	12			44			56		

(b) Generation 85/6 (no data is available for dates of onset)

	Instar 4 (=total)		
	n	%	Cum%
Breaking (1986)			
Apr 9	1	9.1	9.1
16	1	9.1	18.2
30	3	27.3	45.5
May 1	1	9.1	54.5
8	2	18.2	72.7
14	1	9.1	81.8
30	2	18.2	100.0
Total	11		

Table 4.30 Survival per stage and mortality by type of record. Field data.
(a) Pre-diapause larval survival.

	STAGE 1 (%)*	2 (%)	3 (%)	4 (%)
- Generat. 84/5				
No. Died (Unknown causes)	-	0	0	0
No. Missing	-	18 (54.6)	19 (31.2)	24 (31.6)
Total Died	-	18 (54.6)	19 (31.2)	24 (31.6)
No. Survived	-	15 (45.4)	42 (68.8)	52 (68.4)
Total		33	61	76
- Generat. 85/6				
No. Died (Unknown causes)	0	0	0	1 (14.3)
No. Missing	0	1 (33.3)	4 (66.7)	1 (14.3)
Total Died	0	1 (33.3)	4 (66.7)	2 (28.6)
No. Survived	1 (100.0)	2 (66.7)	2 (33.3)	5 (71.4)
Total	1	3	6	7
- Pooled Generats.				
No. Died (Unknown causes)	0	0	0	1 (1.2)
No. Missing	0	19 (52.8)	23 (34.3)	25 (30.1)
Total Died	0	19 (52.8)	23 (34.3)	26 (31.3)
No. Survived	1 (100.0)	17 (47.2)	44 (65.7)	57 (68.7)
Total	1	36	67	83

(continued)

* column percentages, per instar, per generation.

Factorial analysis G = 3.94 (4), P = 0.4147

stage effect - G = 5.36 (6), P = 0.4981

generation effect - G = 0.09 (2), P = 0.9560.

Table 4.30 (cont.)

(b) Post-diapause larval survival.

		STAGE				
		2 (%)*	3 (%)	4 (%)	5 (%)	6 (%)
- Generat. 83/4						
No. Died (Unknown causes)	-		0	0	2 (3.9)	0
No. Missing	-		1 (33.3)	1 (5.9)	8 (15.7)	30 (29.7)
No. Predated (Birds)	-		0	0	2 (3.9)	13 (12.9)
Total Died	-		1 (33.3)	1 (5.9)	12 (23.5)	43 (42.6)
No. Survived	-		2 (66.7)	16 (94.1)	39 (76.5)	58 (57.4)
Total	-		3	17	51	101
- Generat. 84/5						
No. Died (Unknown causes)		0	0	1 (1.2)	0	2 (5.8)
No. Missing		0	5 (12.8)	20 (23.0)	14 (17.3)	33 (32.0)
No. Predated (Birds)		0	0	0	0	6 (5.8)
Total Died		0	5 (12.8)	21 (24.1)	14 (17.3)	41 (39.8)
No. Survived		1 (100.0)	34 (87.2)	66 (75.9)	67 (82.7)	62 (60.2)
Total		1	39	87	81	103

(continued)

Table 4.30b (cont.)

	STAGE				
	2 (%)*	3 (%)	4 (%)	5 (%)	6 (%)
- Generat. 85/6					
No. Died (Unknown causes) -	1 (11.1)	0	0	0	
No. Missing -	1 (11.1)	3 (20.0)	3 (14.3)	5 (25.0)	
No. Predated (Birds) -	0	0	1 (4.8)	11 (55.0)	
Total Died	2 (22.2)	3 (20.0)	4 (19.1)	16 (80.0)	
No. Survived -	7 (77.8)	12 (80.0)	17 (80.9)	4 (20.0)	
Total -	9	15	21	20	
- Pooled Generats.					
No. Died (Unknown causes)	0	1 (2.0)	1 (0.8)	2 (1.3)	2 (0.9)
No. Missing	0	7 (13.7)	24 (20.2)	25 (16.3)	68 (30.4)
No. Predated (Birds)	0	0	0	3 (2.0)	30 (13.4)
Total Died	0	8 (15.7)	25 (21.0)	30 (19.6)	100 (44.6)
No. Survived	1 (100.0)	43 (84.3)	94 (79.0)	123 (80.4)	124 (55.4)
Total	1	51	119	153	224

(continued)

* column percentages, per instar, per generation.

Factorial analysis: G = 19.56 (18), P = 0.3579,
stage effect - G = 33.93 (12), P = 0.0007,
generation effect - G = 26.60 (6), P = 0.0002.

Table 4.30 (cont.)

(c) Pupal survival: *P. ruralis*, *M. grandii* and *Diadegma* sp

	SPECIES		
	P. ruralis (%)*	*M. grandii* (%)	*Diadegma* sp (%)
- Generat. 83/4			
No. Died (Unknown causes)	0	0	0
No. Missing	10 (20.0)	1 (25.0)	4 (33.3)
No. Predated (Birds)	5 (10.0)	0	0
No. Predated (Other)	2 (4.0)	0	1 (8.3)
Total Died	17 (34.0)	1 (25.0)	5 (41.7)
No. Survived	33 (66.0)	3 (75.0)	7 (58.3)
Total	50	4	12
- Generat. 84/5			
No. Died (Unknown causes)	1 (1.9)	1 (11.1)	0
No. Missing	12 (22.6)	4 (44.4)	1 (100.0)
No. Predated (Birds)	17 (32.1)	2 (22.2)	0
No. Predated (Other)	1 (1.9)	0	0
Total Died	31 (58.5)	7 (77.8)	1 (100.0)
No. Survived	22 (41.5)	2 (22.2)	0
Total	53	9	1

(continued)

* column percentages, per instar, per generation.

Table 4.30c (cont.)

	SPECIES		
	P. ruralis (%)*	*M. grandii* (%)	*Diadegma* sp (%)
- Generat. 85/6			
No. Died (Unknown causes)	0	-	-
No. Missing	3 (60.0)	-	-
No. Predated (Birds)	1 (20.0)	-	-
No. Predated (Other)	0	-	-
Total Died	4 (80.0)	-	-
No. Survived	1 (20.0)	-	-
Total	5	-	-
- Pooled Generats.			
No. Died (Unknown causes)	1 (0.9)	1 (7.7)	0
No. Missing	25 (23.2)	5 (38.5)	5 (38.5)
No. Predated (Birds)	23 (21.3)	2 (15.4)	0
No. Predated (Other)	3 (2.8)	0	1 (7.7)
Total Died	52 (48.2)	8 (61.5)	6 (46.2)
No. Survived	56 (51.8)	5 (38.5)	7 (53.8)
Total	108	13	13

* column percentages, per instar, per generation.

Factorial analysis - G = 1.63 (2), P = 0.4424,

species effect - G = 1.06 (2), P = 0.5897,

generation effect - G = 10.92 (2), P = 0.0043.

predators and 'missing' individuals). Only very seldom were individuals found dead in their rolled leaves.

As for the laboratory data, the results are shown separately for larval survival (embracing *P. ruralis* and parasitoids together - tables 4.30a & b) and pupal survival (for which species can be discriminated - table 4.30c). In addition, larval survival is further divided into pre- (table 4.30a) and post-diapause period (table 4.30b).

Since there are many more factors acting upon individuals in the field, mortality levels were much higher than in the laboratory (as one might expect); also, sample sizes were inevitably smaller. Consequently, patterns in the variations between stages and between generations are not so clear. Nonetheless, in terms of larval survival per instar, the same general trends observed in the laboratory seem to have occurred in the field: lower survival in younger stages (particularly pre-diapause - table 4.30a) than in intermediate ones, but increased mortality in the last larval instar (table 4.30b).

Survival in the pre-diapause samples (table 4.30a) ranged between about 45 and 69% in generation 84/5. The range was wider in generation 85/6, but the samples for this generation were all small. Differences in levels per year and per instar were not significant ($P > 0.4$). A mean survival rate of 63.6% is obtained by pooling the numbers of survivals at each stage (119) and dividing by the total sample size (187). This is considered the best estimate for survival at each pre-diapause stage.

In the post-diapause phase (table 4.30b), survival differences between instars and between generations were significant ($G = 33.93$ (12), $P = 0.0007$ and $G = 26.60$ (6), $P = 0.0002$, respectively). On closer examination, however, it can be seen that these differences are primarily due to survival levels in instar 6 that were much lower than in the other instars, ranging from about 60 to 20%. Survival was generally similar in stages 3 to 5, especially in the 84/5 and 85/6 generations. Calculating the mean survival rates for these three stages in the same way as for the pre-diapause samples (above) gives values of 80.3, 80.7 and 80.0% for 83/4, 84/5 and 85/6 generations, respectively.

For instar 6, in the 85/6 generation the survival level was only about a third of the rates in the former two years, but this rate was based on only 20 caterpillars.

Higher mortality at the sixth instar as compared to the fourth and fifth was also recorded in the laboratory (table 4.25a). However, there is a further aspect to note about mortality at instar 6 (and also pupae (see below) and, to a minor extent, instar 5): it is at this time of the season that bird predation was seen to be concentrated (see also table 4.34 below). Often evidence of this was left behind: marks of beaks on the empty rolled leaves where the caterpillars were last seen. Sometimes the leaves also disappeared.

Robins and wrens were seen very frequently amidst the nettles searching on the leaves. They were certainly not searching exclusively for *P. ruralis*, but it is suggested that at least some of the 'missing' individuals were actually preyed upon by birds and

the whole rolled leaves taken or had fallen from the nettle stem because of the pecking. Thus, probably more than the 30% of all mortality recorded for instar 6 (table 4.30b - pooled generations) may have been caused by bird predation.

P. ruralis pupal survival was 66.0, 41.5 and 20.0% for generations 83/4, 84/5 and 85/6 respectively (table 4.30c). These differences were significant (G = 10.92 (2), P = 0.004), but the sample size was very small in the last generation. Evidence of bird predation was found on 10.0, 32.1 and 20.0% of all pupae monitored in the three generations respectively (44% of all mortality for the pooled data)

The low numbers of parasitoid pupae do not allow much analysis (table 4.30c). Keeping this in mind, statistical results do not point to significant differences in survival between *P. ruralis*, *M. grandii* and *Diadegma* sp (G = 1.06 (2), P = 0.5897), in spite of the almost 14% lower survival rate obtained for *M. grandii*, when pooling the generations.

Table 4.31 summarizes the above results on survival. It must be stressed that the survival values shown for instars 2 to 4 (pre-diapause) and 3 to 5 (post-diapause) are for each of the instars within these phases and not a rate for the whole of each of these periods of development.

- Adjusted survival rates for parasitized and healthy larvae

The different levels of parasitization obtained from caterpillars collected from the field at different instars (section 4.3.2.2 - table 4.21) indicate that survival rates per stage are not the same for parasitized and non-parasitized *P. ruralis* (see section 4.1.2).

Table 4.32 illustrates how, by combining these parasitization levels per stage with the 'non-specific' survival rates from table 4.31, it is possible to distinguish survival rates for *P. ruralis* from parasitoids.

As in former sections, only data for *M. grandii* and *Diadegma* sp will be dealt with here, because, although desirable, numbers are far too low for the other parasitoids to be included.

Thus, for example (table 4.32), if there were 100 caterpillars in instar 4 in the field in generation 83/4, it is known from the individuals that were brought to the laboratory (table 4.21) that 33.3% of them would be parasitized by *M. grandii* and 8.3% by *Diadegma* sp ; the remaining 58.3% would be healthy. About 80.5% of all caterpillars monitored in the field survived instar 4 and reached instar 5 (table 4.31). From the laboratory records, only about 30.7% of the caterpillars in instar 5 bore *M. grandii* larvae and 7.9% *Diadegma* sp. Thus number of each species in instar 5 can be estimated. The ratios between numbers in instar 5 and those in instar 4 are the specific survival rates for *P. ruralis*, *M. grandii* and *Diadegma* sp (shown in the last column of table 4.32).

It is striking how a relatively minor difference in parasitization rates may be the result of a much larger distinction in survival rates, with its direct and indirect consequences for host and parasitoids dynamics.

Table 4.31 Summary of results on survival per stage through larval instars and pupal stage. Cases marked with an '*' indicate that the pooled generations rate is considered the best estimate due to lack of significant differences between years and/or small sample sizes per generation.

	Percentage Survival per Stage			
	83/4 (n)	84/5 (n)	85/6 (n)	Pooled Generations (n)
Larvae				
instars 2 to 4 * (pre-diapause)	-	64.1 (170)	41.2 (17)	63.6 * (187)
instars 3 to 5 * (post-diapause)	80.3 (71)	80.7 (207)	80.0 (45)	80.5 * (323)
instar 6	57.4 (101)	60.2 (103)	20.0 (20)	55.4 (224)
Pupae				
P. ruralis	66.0 (50)	41.5 (53)	20.0 (5)	51.8 (108)
M. grandii *	75.0 (4)	22.2 (9)	-	38.5 * (13)
Diadegma sp *	58.3 (12)	0.0 (1)	-	53.8 * (13)

Table 4.32 Worked example of the calculation of the differential survival rates. Rates shown below are for generation 83/4: percentages of parasitization from table 4.21, percentage of survival from table 4.31.

Species	Numbers Alive		Survival (%) at
	Instar 4	Instar 5	Instar 4
P. ruralis	58.3	49.4	84.8
M. grandii (%)	33.3 (33.3)	24.7 (30.7)	74.2
Diadegma sp (%)	8.3 (8.3)	6.3 (7.9)	76.1
Total	100.0	80.5	80.5

Differences in the duration of stages may also influence parasitization levels (see section 4.1.2). Therefore, these need to be considered when trying to translate the distinct rates of parasitization through stages into differential mortality.

A significant difference was observed in the field in the duration of instar 6, which was 23.3 days for *M. grandii* parasitized caterpillars (table 4.23) as compared to 17.8 for non-parasitized ones (table 4.10). This is about 1.3 times longer. Assuming that this increase in development time raises the chances of collection proportionally, the rate can be 'corrected', i.e. a value closer to the actual proportion of numbers recruited to instar 6 that bore *M. grandii* larvae can be obtained. For instance, when allowing for this difference in development, the level for generations 83/4 and 84/5 can be 'adjusted' from 39.2% (table 4.21) to 30.0% (within rounding error, 39.226 / 1.309 = 29.966).

Instar 6 for *M. grandii* was the only case where significant differences in development were found. For all other stages, percentages of parasitization per stage used to estimate differences in mortality are the ones shown in table 4.21.

Table 4.33 presents the adjusted survival rates per species per stage.

Levels for instar 4 in the generation 84/5 were calculated (based on the evidence presented in the former sections) considering that in this generation the population studied spent on average half of instar 4 before diapause (and thus half suffered pre-diapause survival levels) and half after (and then post-diapause rates apply). Generation 85/6 could not be analysed as sample sizes were far too small to yield reliable estimates (tables 4.21 and 4.31).

For all instars and in both generations, levels of survival for *P. ruralis* were higher than the 'non-specific' rates from table 4.31, and higher still than the parasitoids levels (table 4.33). Up to instar 5, survival for *M. grandii* and *Diadegma* sp was very similar. For both species of parasitoid survival was markedly lower in the last stage before pupation, which for *Diadegma* sp is instar 5 and for *M. grandii* is instar 6.

The notedly lower rate of survival of *M. grandii* parasitized caterpillars accounted for most of the decrease in survival in instar 6 observed in the 'non-specific' rates (table 4.31).

- Timing, potential predators and 'missing' individuals

Table 4.34 shows the field records of individuals 'missing', predated and dead by sampling occasion. There does not seem to be any particular peak in numbers missing that are not reasonably proportional to variations in the density of *P. ruralis* during the season (cp tables 4.13 and 4.24a & b).

Bird predation was concentrated around July, but the timing varied according to the late spring / early summer temperatures (fig A2.1, appendix 2). As stated in the section on field survival per stage, it is believed that bird predation was more intense than indicated by the direct evidence left behind.

Due to the combined effects of the time of the season when bird predation is

Table 4.33 Adjusted survival rates per instar for P. ruralis, M. grandii and D. fabricicanae.

	Percentage Survival	
	83/4	84/5
Instar 3		
P. ruralis	-	67.3
M. grandii	-	59.6
Diadegma sp	-	59.9
Instar 4		
P. ruralis	84.8	75.7
M. grandii	74.2	66.2
Diadegma sp	76.1	67.9
Instar 5		
P. ruralis	87.6	87.6
M. grandii	78.6	78.6
Diadegma sp	32.6	32.6
Instar 6		
P. ruralis	73.5	81.9
M. grandii	9.1	9.6

concentrated and the alterations in the development of the caterpillars caused by *M. grandii* (i.e. longer length of and later recruitment to instar 6), the impact of bird predation is probably much stronger on this parasitoid than on the host.

To some extent this may explain the low numbers of *M. grandii* pupae found in the field (tables 4.21 and 4.30c) and the very high mortality rates estimated for *M. grandii* parasitized 6th instar larvae (table 4.33). Also it may be the reason why no *M. grandii* pupae were found in the field monitoring site in generation 85/6 (table 4.30c), while in the collections taken to the laboratory the highest overall rate of parasitization by this wasp was obtained in this generation (table 4.21). Conceivably, parasitization rates were also very high in the field for this generation, but were obscured by very intense mortality.

Apart from birds, little other direct evidence of predators was found (table 4.34), but data on *P. ruralis* mobility (section 4.3.3.1) support the view that a

Table 4.34 Numbers of individuals dying, by type of record and by sampling occasion. Field data.

Year	Generat	Date	Day(std)	Mortality Record: Missing	Death	Pred-Gen.	Pred-Bird	Total
1984	83/4	Jun 5	1 (56)					
		11	7 (62)	3				3
		19	15 (70)	8	1	1		10
		26	22 (77)	15			11	26
		Jul 2	28 (83)	12	1	1	8	22
		9	35 (90)	5			1	6
		19	45(100)	5				5
		23	49(104)	4				4
		Ago 2	59(114)	4		1		5
		8	65(120)	1				1
		17	74(129)					
		24	81(136)					
		30	87(142)					
	84/5	Aug 8	1(120)					
		17	10(129)	1				1
		24	17(136)					
		30	23(142)	1				1
		Sep 5	29(148)	9				9
		13	37(156)	3				3
		21	45(164)	2				2
		28	52(171)	5				5
		Oct 2	56(175)	5				5
		12	66(185)	13				13
		17	71(190)	17				17
		25	79(198)	5				5
		Nov15	100(219)					

(continued)

Table 4.34 (cont.)

Year	Generat	Date	Day(std)	Mortality Record: Missing	Death	Pred-Gen.	Pred-Bird	Total
1985	84/5	Apr15	1 (6)					
		24	10 (15)					
		May 6	22 (27)					
		13	29 (34)	5	1			6
		22	38 (43)	11				11
		30	46 (51)	4				4
		Jun10	57 (62)	12				12
		22	69 (74)	13				13
		Jul 1	78 (83)	4				4
		8	85 (90)	10	1		1	12
		18	95(100)	11	1		13	25
		25	102(107)	9	1		7	17
		Aug 6	114(119)	10			5	15
		15	123(128)		1	1		2
		22	130(135)					0
	85/6	Oct 3	1(176)					
		17	15(190)					
		23	21(196)	2				2
		Nov 1	30(205)	4	1			5
1986		Apr22	1 (13)					
		May 7	16 (28)	2				2
		23	32 (44)		1			1
		Jun 9	49 (61)	2				2
		27	67 (79)	4				4
		Jul 8	78 (90)	4			12	16
		24	94(106)	3			1	4
		Aug 4	105(117)					0

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

considerable proportion of 'missing' individuals would have been the result of predation.

A thorough analysis of predation is far beyond the scope of this work. However, observations were made on the presence and numbers of 'potential' predators during field work (table 4.35) to support the interpretation of survival data.

The only group of possible predators of *P. ruralis* for which the numbers recorded were more or less constant and not too low were spiders.

In 1984 there was a marked similarity through the season between numbers of larvae and pupae 'missing' and numbers of spiders (fig 4.2a). In 1985, however, the pattern was not repeated (fig. 4.2b). Unfortunately, there was no time available in the field to identify the species of spiders, which may have produced clearer patterns. Spiders were frequently seen close to and, sometimes even inside, rolled leaves from where P. ruralis had disappeared. It is not possible to infer much from this limited evidence (it could be that they were simply opportunistic in using the shelter available) but it is suggested that spiders may be responsible for at least some of the caterpillars that went missing.

- A note on overwinter mortality

No data are available on mortality during diapause in the field, since this study did not manage to elucidate accurately *P. ruralis* overwinter sites and habits. The little evidence there is (one caterpillar, see section 4.2.1) supports the view that they diapause in the debris and soil under the nettles.

Numbers found pre- and post-diapause in the field monitoring site (table 4.1) indicate almost no mortality over winter. In the laboratory, however, overall mortality in this period was higher than 50% (table 4.25). It could be that the conditions provided for them in the cold green house during winter were inappropriate due to ignorance of their natural site, and this may have handicapped their chances of survival. However, the laboratory results may provide at least an idea of the comparative chances of survival according to instar at diapause.

4.3.3 Behaviour, Spatial Distribution and Variation in Mortality Rates

4.3.3.1 Movement and Vertical Distribution

P. ruralis moves little on the nettles and when it does it is mostly to leaves at nodes upwards on the nettle stem (table 4.36).

Movement is coupled with food consumption. Unless the larva is severely disturbed, only when most (or all) of the inner layers of the rolled leaf have been eaten, does it move to and rolls up a new leaf. Thus, younger caterpillars (pre-diapause), that consume leaves at a slower pace, were recorded moving less frequently than post-diapause ones ($G = 138.08$ (3), $P = 0.0001$). Additional observations made in

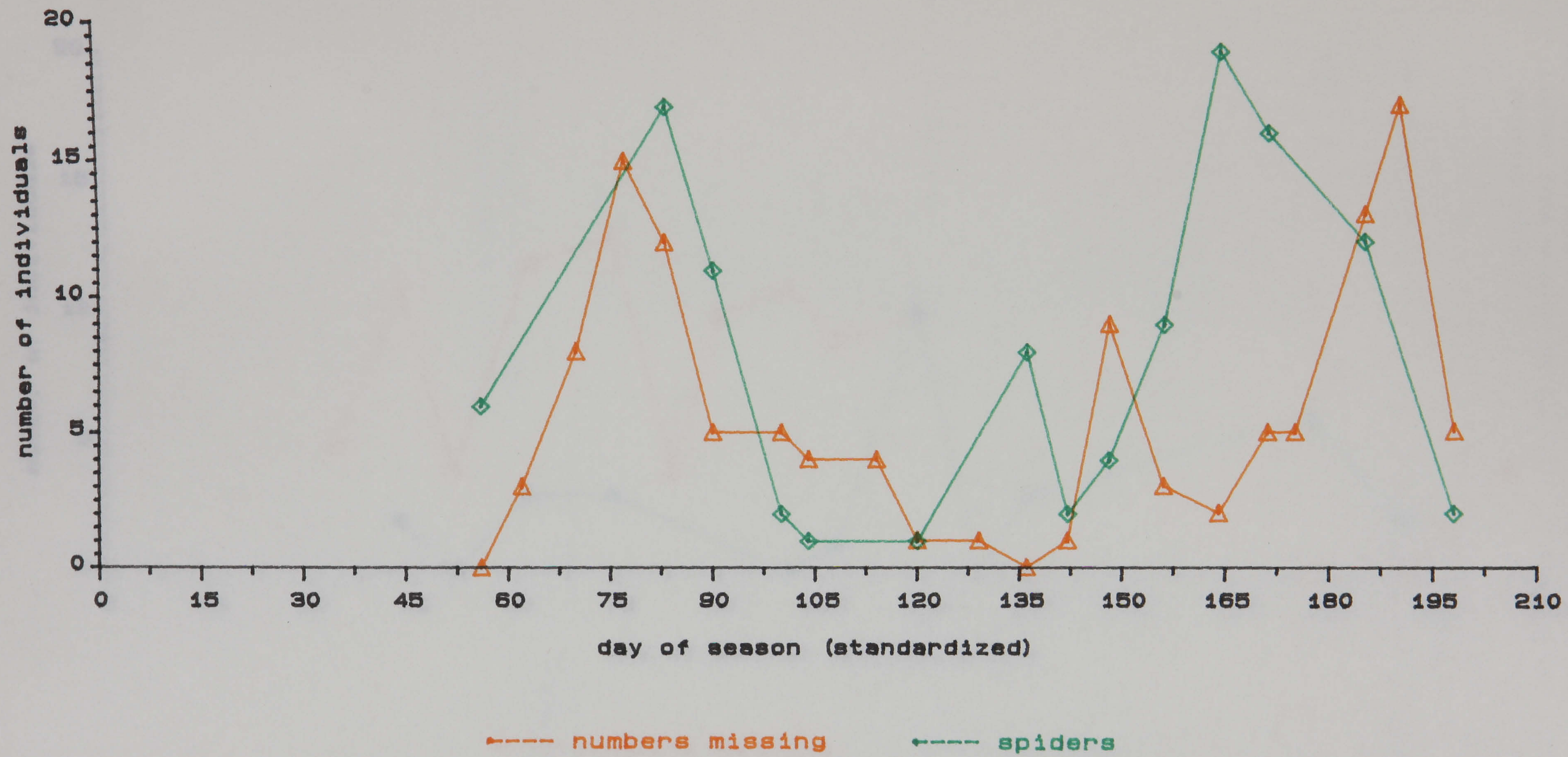

Figure 4.2a Numbers of field monitored individuals recorded "missing" and of spiders observed close to (or inside) the empty rolled leaves by sampling occasion. (Day of season standardized as for recruitment and frequency tables: day 1 = 10 April, day 100 = 19 July, day 200 = 27 October.) Data for 1984.

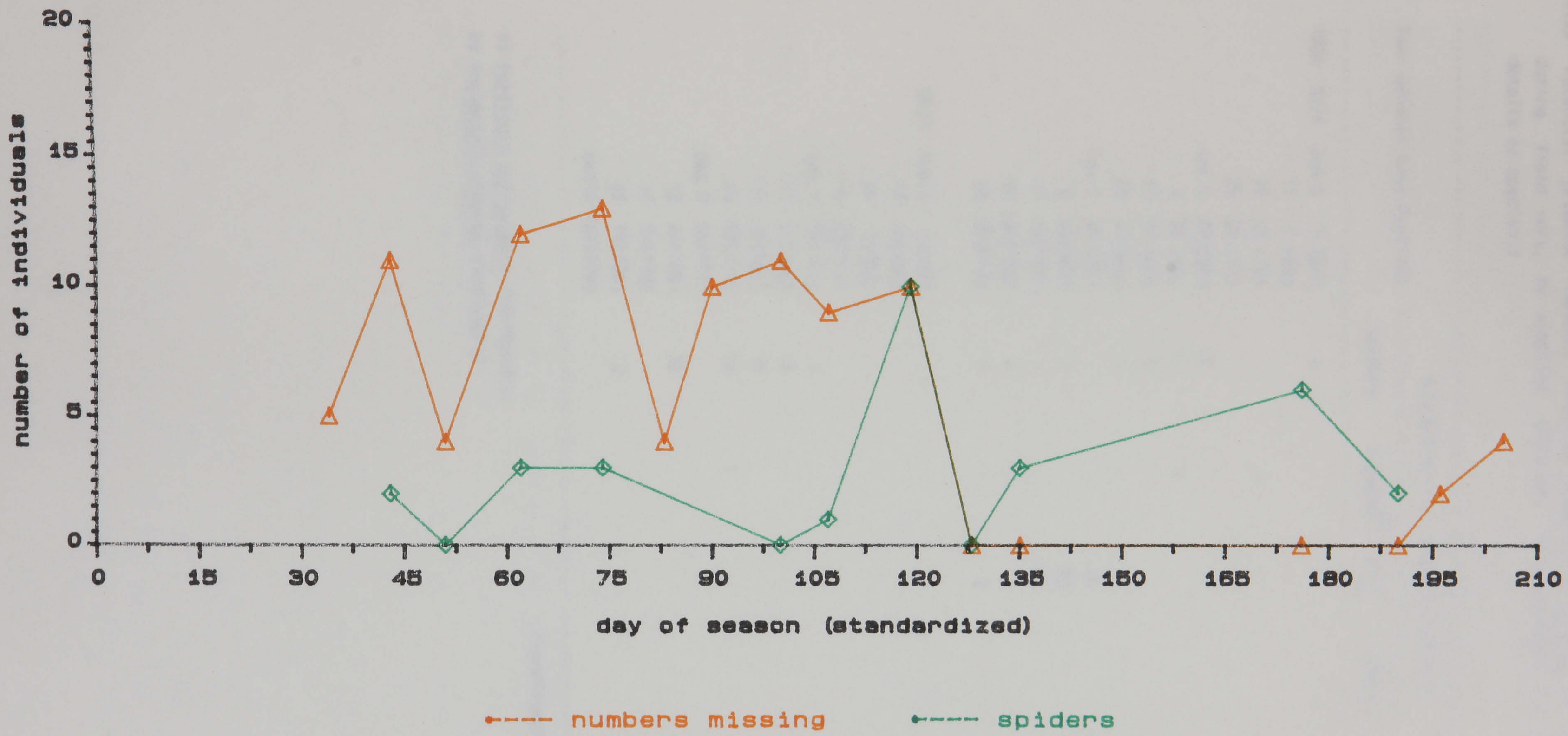

Figure 4.2b Numbers of field monitored individuals recorded "missing" and of spiders observed close to (or inside) the empty rolled leaves by sampling occasion. (Day of season standardized as for recruitment and frequency tables: day 1 = 10 April, day 100 = 19 July, day 200 = 27 October.) Data for 1985.

Table 4.35 'Potential' predator numbers recorded close to *P. ruralis* or their rolled leaves during field work, by sampling occasion. (See sections 2.4 & 2.5 for further details of species.)

Year	Generat	Date	Day(std)	Numbers Recorded: Spiders	Earwigs[a]	A.n.[b]	Others
1984	83/4	Jun 5	1 (56)	6			
		11	7 (62)				
		19	15 (70)		1		
		26	22 (77)				
		Jul 2	28 (83)	17			
		9	35 (90)	11	1		
		19	45(100)	2			
		23	49(104)	1			
		Ago 2	59(114)			20	
		8	65(120)	1		80	
		17	74(129)			90	
		24	81(136)	8			
		30	87(142)	2		2	
	84/5	Aug 8	1(120)				
		17	10(129)				
		24	17(136)				
		30	23(142)				
		Sep 5	29(148)	4			
		13	37(156)	9			
		21	45(164)	19			
		28	52(171)	16	1		
		Oct 2	56(175)				
		12	66(185)	12			
		17	71(190)				
		25	79(198)	2			
		Nov15	100(219)				

(continued)

a) *Forficula auricularia* (Dermaptera)

b) *Anthocoris nemorum* (Hemiptera)

Table 4.35 (cont.)

Table 4.35 (cont.)

Year	Generat	Date	Day(std)	Numbers Recorded: Spiders	Earwigs[a]	A.n.[b]	Others
1985	84/5	Apr15	1 (6)				
		24	10 (15)				
		May 6	22 (27)				
		13	29 (34)				
		22	38 (43)	2			
		30	46 (51)			1	
		Jun10	57 (62)	3	1	3	
		22	69 (74)	3	1		
		Jul 1	78 (83)	21			
		8	85 (90)	21			
		18	95(100)		3		
		25	102(107)	1	1		
		Aug 6	114(119)	10	10		
		15	123(128)		30		
		22	130(135)	3	1		5
85/6		Oct 3	1(176)	6	1		10
		17	15(190)	2	2		1
		23	21(196)				
		Nov 1	30(205)				
1986		Apr22	1 (13)				
		May 7	16 (28)				
		23	32 (44)	2			
		Jun 9	49 (61)				
		27	67 (79)				
		Jul 8	78 (90)				
		24	94(106)				
		Aug 4	105(117)				

std = day of sampling standardized for comparison between years, where Day 1 = April 10.

a) *Forficula auricularia* (Dermaptera)

b) *Anthocoris nemorum* (Hemiptera)

Table 4.36 Number of records of movement and direction (in relation to previous position in the nettle stem). Field data for pre- and post-diapause caterpillars.

	Period	
	Pre-diapause (%)*	Post-diapause (%)
Movement:		
Up	21 (4.8)	248 (32.1)
Lateral	10 (2.3)	75 (9.7)
Down	0	5 (0.7)
Total Movement	31 (7.0)	328 (42.5)
None	410 (93.0)	444 (57.5)
Total Observations	441	772

* column percentages

the field on three isolated caterpillars, monitored in a small nettle clump, and in the laboratory on ten individuals reared on potted nettles corroborate these findings.

Taking the total length of period (days) that each individual was monitored and the number of times it was recorded moving to new leaves, a rate of movement per day can be calculated. Values obtained were very low: 0.0058 $\pm$ 0.00120 translocations/day (n = 153) in the pre-diapause period and 0.0294 $\pm$ 0.00179 translocations/day (n = 353) post-diapause (F = 33.27 (1), P = 0.0001). This allows comparisons between the mobility on different fates. In the pre-diapause phase, the rate of movement was not significantly different for individuals that survived up to diapause and those that died (or 'disappeared') before this (F = 0.10 (2), P = 0.907). After overwintering, however, there were significant differences (F = 9.58 (2), P = 0.0001): caterpillars that were predated by birds had a markedly higher rate of movement (0.0362 $\pm$ 0.00433, n = 59) than larvae that went missing (0.0300 $\pm$ 0.00260, n = 223) or developed into healthy adults (0.0208 $\pm$ 0.00246, n = 75). That birds prey more intensely on individuals that move more, is probably due to the vertical distribution resulting from this higher rate of movement (see below), rather than to the movement per se. During the three years of this investigation, no *P. ruralis*

was ever seen in the field away from its shelter in daylight.

Individuals from which *M. grandii* cocoons originated also had a higher rate of movement (0.0414 $\pm$ 0.00645, n = 13) as compared to those from which *Diadegma* sp (0.0111 $\pm$ 0.00386, n = 13) or healthy moths emerged (0.0230 $\pm$ 0.00270, n = 56)(F = 3.34 (2), P = 0.04). This may be explained by the total length of development the caterpillars have up to pupation in each case (cf tables 4.23 & 4.10): if they grow larger, as they do in the case of *M. grandii* parasitized individuals, they need to eat more and therefore roll up more leaves.

The vertical distribution of *P. ruralis* on the nettles ranged from the top to the bottom leaves, but was mainly concentrated between the second and fifth nodes (counting from the top of the stems)(table 4.37). This was true for both pre- and post-diapause samples, but older caterpillars had a significantly more stratified distribution than the younger ones (G = 214.78 (13), P = 0.0001). The former had a marked preference for leaves of the third and fourth nodes, about 55% of the caterpillars being found in these. In the pre-diapause period, distribution was more even between the second to eighth nodes. This extension of the range to lower leaves was simply because the nettles were taller in late summer / early autumn and therefore had more nodes / stem.

As noted above, the young larvae moved less frequently than the older ones to new leaves. Thus their vertical distribution may be determined, initially, by where the eggs they hatched from were laid, and so the spreading also may arise because the nettles develop new top leaves at a faster rate than they develop and move during this phase.

From the series of observations of the positions the larvae and pupae were throughout their development, individual means for vertical distribution were calculated. These were in accord with the results for rates of movement. There were no differences between individuals suffering different fates in the pre-diapause period (F = 0.17 (2), P = 0.8412). Post-diapause means varied, but overall differences were not quite significant (F = 2.75 (2), P = 0.0654). However, the average vertical distribution of individuals that were predated by birds (3.9 $\pm$ 0.15, n = 59) was significantly lower (at the 0.05 level) than of the ones that survived up to adulthood (4.7 $\pm$ 0.22, n = 74). This is in accordance with the remark made above that a more intense predation by birds on more mobile individuals was probably related to their resulting position in the nettle stem. Individuals that went 'missing' had a 'mean leaf' value intermediate between healthy and bird attacked (4.4 $\pm$ 0.13, n = 227).

For caterpillars that completed larval development, there was no significant difference in the vertical distribution between healthy *P. ruralis* and individuals parasitized by *M. grandii* or *Diadegma* sp (F = 1.25 (2), P = 0.297).

Table 4.37 Vertical distribution of P. ruralis caterpillars. Frequency of observations of individuals per node (counting from the top) on the nettle stem. Field data for pre- and postdiapause caterpillars.

Leaf node	Pre-diapause n	%	cum%	Post-diapause n	%	cum%	Total n	%	cum%
1	6	1.4	1.4	25	2.4	2.4	31	2.1	2.1
2	71	16.1	17.5	97	9.4	11.8	168	11.4	13.5
3	68	15.4	32.9	316	30.6	42.5	384	26.1	39.6
4	78	17.7	50.6	250	24.2	66.7	328	22.3	61.9
5	46	10.4	61.0	187	18.1	84.9	233	15.8	77.7
6	34	7.7	68.7	93	9.0	93.9	127	8.6	86.3
7	38	8.6	77.3	32	3.1	97.0	70	4.8	91.1
8	35	7.9	85.3	16	1.6	98.5	51	3.5	94.6
9	24	5.4	90.7	10	1.0	99.5	34	2.3	96.9
10	19	4.3	95.0	5	0.5	100.0	24	1.6	98.5
11	8	1.8	96.8				8	0.5	99.0
12	9	2.0	98.9				9	0.6	99.7
13	3	0.7	99.5				3	0.2	99.9
14	2	0.5	100.0				2	0.1	100.0
Total	441			1031			1472		

4.3.3.2 Horizontal Distribution and Mortality Rates

P. ruralis horizontal distribution in the field monitoring site is given in table 4.38. Numbers of individuals/metre varied considerably. For all periods, the means were much smaller than the variances, pointing to a high level of aggregation (Elliot, 1977). Indeed, in all periods, there was a highly significant departure from a random distribution ($P < 0.01$).

The level of clumping (k) was not the same for all seasons (table 4.38), probably as a combined result of sample sizes and the variation between seasons of nettles quality, location of high and low density patches and overall densities (Hassell, 1987; Southwood, 1978).

From the field observations and the densities per metre section recorded, no

Table 4.38 Horizontal Distribution. Total number of individuals per metre along the path in the field monitoring site (E = east, W = west, see figure 2.22; k = parameter of dispersion, P = probability level, assuming random distribution).

Metre	Gen.83/4	Generation 84/5		Generation 85/6	
	Post-diap	Pre-diap	Post-diap	Pre-diap	Post-diap
1E	9	4	-	-	-
2E	20	3	-	-	-
3E	13	7	6	0	0
3W	-	48	23	1	2
4E	13	4	4	0	1
4W	-	22	27	1	2
5E	7	1	3	0	1
5W	-	33	21	1	3
6E	10	2	7	1	0
7E	6	1	9	0	3
8E	4	2	4	0	1
9E	4	2	7	0	0
10E	5	2	5	0	1
11E	9	4	7	0	1
12E	10	1	6	0	0
13E	5	3	5	1	1
14E	5	0	1	1	3
15E	9	0	5	1	3
16E	3	3	5	5	8
Total	132	142	145	12	30
Mean ± SE	8.3 ± 1.11	7.5 ± 2.94	8.5 ± 1.82	0.7 ± 0.29	1.8 ± 0.47
k	5.92	0.30	0.11	0.81	0.75
P	0.005	0.0001	0.0001	0.005	0.005

particular part of the nettle clump seems to be 'constantly better' for *P. ruralis*. However, densities for each metre section were somewhat similar between the pre- and post-diapause periods of the same generation, which indicates that overwinter dispersal may be low.

To test if there were differences in the fates of the caterpillars in relation to the density of the patches within the nettle clump in which they lived, metre sections were classified by season according to the numbers of individuals found on them. Those with up to two individuals were considered 'very low' density metre sections; with between three and five 'low' density; five and ten 'medium'; ten and twenty 'high'; more than twenty 'very high'. Factorial analyses were then carried out for the pre- and post-diapause periods. For both phases, results were on the border line of statistical significance (P = 0.03 and P = 0.04, respectively), and the differences were

mainly due to one generation (84/5). Also, no pattern could be detected between observed and expected numbers (e.g., lower/higher chances of survival, the higher/lower the densities). Nevertheless, since the 84/5 generation was also the generation which had the highest population levels, it is possible that there were actual differences in the proportions in each fate depending on the density per metre section (which would be more detectable when total sample size was larger). However, given the limited time of this study and the limited number of sub-areas (metre sections) delimited, it was not possible to identify them clearly.

Concerning parasitization, conclusions are harder still. If parasitoid attack is linked to larval densities, it would be to the distribution of the target instars (pre-diapause). As stated above, with the methods used in this study, parasitization was only detectable when individuals reached pupal stage (post-diapause). Accepting that the distribution of the older individuals is similar to that of the younger ones (see above), some indication could still be gathered from the analysis of their distributions. However, evidence would be diluted by any minimal dispersion plus the effects of differential mortality. In addition, numbers reaching the pupal stage were not high. Not surprisingly, no significant relationship between parasitization rates and densities were found (P = 0.3180).

A rough estimate of the total number of caterpillars recruited per season on the whole nettle clump (Nt), can be calculated based on the total number of individuals (n) monitored in the field (table 4.1) and the area sampled each season (a = number of metre sections (table 4.38) x width of sampling area (0.35 m)) and the total area of the nettle clump (At = 116.77 m2). Thus, Nt = n x At /a. Values obtained are given in table 4.39.

Table 4.39 Estimates of total numbers of larvae recruited per season (Nt) on the whole nettle clump (see text for explanation). a = area sampled.

Generation	Year	Period	a (m^2)	Nt
83/4	1984	pos-diapause	5.60	2752.4
		pre-diapause	6.65	2493.4
84/5	1985	pos-diapause	5.95	2845.7
		pre-diapause	5.95	235.5
85/6	1986	pos-diapause	5.95	588.8

Increases in numbers from the pre- to the post-diapause phases of the same generation are a biological impossibility for *P. ruralis* (eggs are only laid in late

summer) and indicate that the efficiency in sampling was not as good with the small larvae as it was with the more developed ones. (This may have contributed to some extent to the lack of evidence about overwinter mortality.) Thus, taking the post-diapause figures as the best estimates for each generation, about 2800 *P. ruralis* lived in the nettle clump in the 83/4 and 84/5 generations, followed by a drastic decrease of about 80% in the 85/6 generation.

These estimates are minimum values (since it is evident that, at least in the pre-diapause phase, not all individuals were recorded) and its accuracy is also uncertain considering the contagious distribution of *P. ruralis*, the heterogeneity of the nettles in the clump (density and quality), and the possible (not assessed) differences between the middle and the borders of the clump. However, the sampling area is considered representative of the whole clump (it crossed right through it (fig 2.23) and embraced areas of varying conditions and densities of both *P. ruralis* and nettles), and such estimates provide an idea of the size of the larval population that such a clump can support and its variations in time.

More complex still would be to estimate total larval densities in the whole field (Bond Ing). No doubt numbers were high, judging from the above estimates and on the estimates of total numbers of adults emerging (4250 in 1984 and 1620 in 1985) and fecundity (chapter 3), and also on the numbers of caterpillars collected for laboratory rearing (remember that only one of each two *P. ruralis* found was collected; see methods). However, from observations made during collections, it seems that there is at least as much, and probably more, variation in numbers between nettle clumps as there is within a clump.

4.4 DISCUSSION

4.4.1 Methods for Data Gathering

A frequent problem with methods in ecology is reaching a satisfactory compromise between biological realism, practicalities and suitability for analysis when collecting data. Given the aims of this work (see Chapter 1), one of the main requirements for the sampling programme was the ability to detect variation within and between generations in the population studied.

It is believed that a reasonable balance was obtained in this investigation. The field methodology (following the individual caterpillars throughout their development) enabled the recording of important factors and interactions that would otherwise have been overlooked. There was the obvious drawback, stated throughout this Chapter, of the small sample sizes. However, the ability of obtaining parameters from actual individual observations, instead of calculating them based on population size estimates

(with their unavoidable errors and possible bias), compensates for this to a considerable extent. Also, the larger data sets collected for the laboratory study further supported the field observations.

Even so (as is often the case when dealing with so many variables), in many instances important estimates were based on small numbers and/or had fairly large SE's, and some analysis had to be performed with data sets that contained zero observations in one or more cells. Nevertheless, biological consistency can be observed between the results for the various tests performed, supporting the view that the overall methods and results are sound.

More limiting was the inability to sample thoroughly the very young stages in the field and, consequently, to estimate accurately their survival rates and to generate reliable estimates of total larval population sizes. In spite of this, the (minimum) estimates of numbers of larvae recruited (Nt) in the post-diapause period (section 4.3.3.2) were consistent with the decline in population level recorded during the course of this study. Also, differences in development, distribution and survival for individuals suffering different fates were detected. These often cannot be recorded, and therefore have to be disregarded in population studies, but may prove important in understanding their dynamics.

4.4.2 Development

No obvious effect of rainfall (fig A2.2) could be seen on length of development, but the effect of temperature was evident between generations, as well as during the course of each instar, by their skewed distributions. This unsurprising result has cumulative consequences. Weather is a very important factor in small ectothermic animals (Dobkin, Olivieri & Ehrlich, 1987). Lower ambient temperatures mean longer development time and development time is not independent of time of entry to the stage. In the pre-diapause phase, the slower the caterpillars develop, the lower the temperatures they will face in successive stages before diapause and thus the younger the stage they will pass in diapause (tables 4.5). This may possibly reduce their chances of survival (table 4.26, but see below). Even if it does not, there is still a higher proportion of development to be achieved after winter. The development of the caterpillars is also a result of the quality of the nettles (Pullin, 1986), which may also vary depending on the weather.

The chances of survival decrease with time spent in development (Braner & Hairstone, 1984; Pollard, 1979; Price et al., 1980) since time of exposure to mortality factors increases. It was not possible to quantify this for the younger stages, but judging from their survival rates, this seems to hold (table 4.31). The effect was certainly marked in the later stages of development when spring was cool (tables 4.30 & 4.31).

Additional evidence for this is the fact that the duration of instars was

correlated and that those individuals that died (table 4.27) were slower developers than healthy ones.

Another very important point about development concerned the differences recorded between parasitized and non-parasitized individuals, *M. grandii* delaying development and *Diadegma* sp accelerating it. This is not by any means unusual. It has important consequences for the system and its analysis (see section 4.1.2 and also 4.4.3 & 4.4.4 below) but, even when recognized (e.g., Dempster, 1984), it is generally unaccounted for in field population studies (for the few exceptions, see Van Driesche & Bellows (1988) and references therein).

4.4.3 Parasitization

The two main species of parasitoids attacking *P. ruralis* are reported also to parasitize other species of Lepidoptera. *M. grandii* seems to be specific to the nettles, but attacks a range of host species which feed on the plant (Shaw & Askew, 1976). In the present study, it was never reared from a host other than *P. ruralis* from a total of 1135 nettle feeding caterpillars of other species collected from Bond Ing. It appears that *P. ruralis* is its main host in the study site, more than a third of instar 3 caterpillars bearing this parasitoid in the 83/4 and 84/5 generations (table 4.21).

The species of *Diadegma* attacking *P. ruralis* could be *D. fabricianae* or *D. chrysostictos*. *D. fabricianae* has only recently been separated from the other very similar species, *D. chrysostictos* (Horstmann & Shaw, 1984). This was partly based on its hosts selectivity towards *Anthophila fabriciana* as compared to other usual hosts of *D. chrysostictos*. The authors suggest that this may be related to synchronization of the diapausing stage between host and parasitoid, since both diapause as early or middle grown larva. *P. ruralis* also overwinters as a middle grown larva, and thus this requirement is also met with this host. M. Shaw (pers. comm.) suggested that *P. ruralis* could well be a host to *D. fabricianae* sp.

Davis (1987), in a study of host finding behaviour of the parasitoids of lepidopteran larvae feeding on nettles, refers to *D. fabricianae* as being specific to *A. fabriciana*. In his experiments of parasitoid responses to silk of *P. ruralis*, *D. fabricianae* showed no response, but neither did *D. chrysostictos*, which is reported as an usual parasitoid of *P. ruralis*.

The taxonomy of this sub-family (Campopleginae) is particularly difficult (Shaw & Askew, 1976) and specimens reared from *P. ruralis* and *A. fabriciana* during the present study were carefully compared following Horstmann & Shaw's criteria (1984): no difference was found between the specimens from the two hosts. They were then sent to K. Horstmann for checking the identification but they never reached their destination. Despite this setback, based on the evidence above, the species of *Diadegma* found in this study is considered almost certain to be *D fabricianae*.

Overall levels of parasitism by this wasp were 12.8% in the 83/4 and 84/5

generations (table 4.21) for *P ruralis* and 6.4% over the whole period of this study for *A. fabriciana* The latter agrees with the results of Shaw & Askew (1984) who recorded a level of 4-12%.

The calculation of the parasitization rates based on the susceptible stage of *P. ruralis* yielded much information about the phenology, development and survival of the moth and its parasitoids (sections 4.3.2.2 & 4.3.2.3). This calculation is based on the simple idea that 'if a larva is already parasitized and host and parasitoid are alive, the host is counted as certain to die' (Varley, Gradwell & Hassell,1973).

In spite of the importance and correctness of the above concept, it is seldom adopted. Parasitization is most often analysed as a mortality factor acting upon the stage of the host from which the parasitoid emerges (e.g. Dempster, 1971 & 1982; Courtney & Duggan,1983; Crawley & Gillman,1989), even when it is suggested that mortality is higher on parasitized caterpillars (Dempster, 1982). At the stage of emergence from the host, differential mortality could already have caused a distortion in the proportion of hosts that were parasitized. This misevaluation underrates parasitoid impact and obscures possible evidence of density dependence on parasitoid attack.

Results from this study (section 4.3.2.2) showed that mortality is higher for parasitized caterpillars. Estimates of parasitization based on stages other than the target stage of the host, in most cases did not reflect accurately the actual level of attack by each parasitoid. For *M. grandii* this effect on estimated rates was further complicated by the longer development time.

4.4.4 Predation & Other Mortality

The pattern of survival through development observed for *P. ruralis* in the field (section 4.3.2.3, tables 4.31, 4.32 & 4.33) is common in the Lepidoptera (Dempster, 1984). Also, most of the species recorded as potential predators in the present work have been shown to prey upon eggs and caterpillars. Thus, eggs are reported to be taken by *Forficula auricularia* and *Anthocoris nemorum* (Dempster, 1971 & 1982; Subinprasert & Svensson,1988). There are no data for the egg stage in the field for *P. ruralis*, but both predator species are common on the nettles during the summer.

Predation of young larvae has been attributed to *F. auricularia* (Dempster,1971; Crawley & Gillman,1989), *A. nemorum* (Dempster,1971; Pollard,1979), *Tachyporus* sp and *Rhagonycha fulva* (Dempster,1971), which were all common in the study site. Spiders, in particular, are often referred to as causing high losses in young stages (Dempster, 1984 and references therein) and some species that are common amidst the nettles (Davis, 1983) have been shown to prey upon young lepidopteran larvae (*Xisticus cristalus*, *Theridium ovatum* and *Meta* sp (Dempster, 1971 & 1976), and *Enoplagnata ovata* and *Lyniphia* sp (Pollard, 1979)). These references add support to the view that a high percentage of the mortality in the young stages may have been

due to arthropod predation. The fact that these arthropods are mostly nocturnal in habits may have contributed to the lack of an obvious relationship between numbers missing and potential predators (table 4.35 & fig 4.2).

Arthropod predation may also have been responsible to some extent for the mortality of older larvae (e.g. Dempster (1971) and Jones *et al.* (1987) report spiders preying upon third to fifth instar caterpillars of,respectively, *Tyria jacobaeae* and *Pieris rapae*). However, birds are generally believed to be major predators of full-grown larvae and pupae in early summer. Pollard (1979) obtained significantly different levels of survival for caterpillars caged against birds as compared to exposed ones, and concluded that bird predation was the key factor for *Ladoga camilla*. In the population here studied, levels of bird predation also seem to be very high.

It is not possible to evaluate the accuracy of the 'specific' survival rates for *P. ruralis* and its parasitoids (table 4.33), since they were estimated from estimates of length of development, 'non-specific' survival rates and percentage parasitization based on samples which were not always large. The information they provide, however, shows a more complete picture than the 'non-specific' rates. Even if the magnitude of the differences are exaggerated due to accumulated errors in the calculations, they do point to a considerable higher mortality in parasitized caterpillars as compared to healthy ones. If this difference in survival had been ignored, the interpretation of the dynamics of the *P. ruralis* population would have been misleading.

Lower survival of parasitized hosts are recorded in a few studies on population dynamics. Higher predation rates on parasitized caterpillars was the reason for a strong inverse correlation between estimated percentage of parasitization by *Cotesia glomerata* and other mortality factors acting upon *Pieris rapae* (Jones *et al.*, 1987). Van Driesche & Bellows (1988) demonstrated how a decline in parasitization rates estimated for successive stages of the same butterfly species by *Cotesia glomerata* originated from higher mortality rates of parasitized hosts.

There was no evidence of disease being an important mortality factor in the field during the generations studied. However, disease could have contributed to the high overwinter mortality in the laboratory, since its incidence may increase under stress (Rivers, 1976).

4.4.5 Distribution

From the similarity of the horizontal distribution of pre- and post-diapause caterpillars, and the low mobility of the larvae (section 4.3.3.2, table 4.38), the distribution of *P. ruralis* on the nettles would seem depend primarily on the sites where the females lay their eggs; this therefore being the origin of the aggregation. Thus those factors acting in late summer, during the oviposition period, which render the nettles more attractive to the adult females, are of paramount importance in determining distribution. This view is often held for other species (Dempster, 1984).

However, since the very young stages are so under-represented in the data here presented, the distribution recorded for the youngest instars that were observed could have resulted just as well from the patterns of mortality on the very young instars (Jones *et al.*, 1987; White, 1985). A pattern of larvae moving upwards on the plant, as found here for the mother of pearl caterpillars, is also recorded for other lepidopterans (e.g. *Tyria jacobeaceae* (Dempster,1982) and *Achlya flavicornis* (Feichtinger & Reavey,1989)), and so is the ability of vertebrate predators to concentrate attack where prey densities are higher (see section 4.1.3).

Bird predation on *P. ruralis* is concentrated on individuals which had a mean node vertical distribution of a value (3.9 + 0.15) between the node numbers where the highest frequencies of individuals were found (nodes 3 and 4, table 4.37).

No spatial pattern was detected for the distribution of parasitization. However, the analysis carried out was quite unsophisticated and deserves to be expanded in future work. Spatial variation of mortality factors should be tested in relation to the stage they act upon (in the case of parasitization this was not possible in the present work), across larger numbers and different sizes of units in space (Heads & Lawton, 1983), and with larger sample sizes. This is not an easy task, but the 'nettle / *P. ruralis* / natural enemies' system shows great potential for this sort of investigation.

CHAPTER 5 LIFE TABLES & FINAL DISCUSSION

5.1 LIFE TABLES

Life tables were compiled for *Pleuroptya ruralis* and *Macrocentrus grandii*, following the procedure recommended by Varley, Gradwell & Hassell (1973), in order to summarize the results presented in Chapters 3 and 4. The origin of the various estimates used are given below.

- *P. ruralis* (table 5.1)

Numbers of females at the start of the generation are based in the number of pupae which successfully completed development in the field monitoring site (table 4.30c), the sex ratio observed during the MRR investigation (section 3.1.3.1) and the area sampled each season (table 4.39). Table 5.2 presents these values.

The potential number of eggs per unit area was computed based on the study on reproductive potential (section 3.2) and the moths' life expectancy estimated during the MRR programme (section3.1.3.5). The data on fed mated females is taken as a measure of *P. ruralis* full reproductive potential. These females laid 891 ($\bar{x}$) eggs during an average life span of 37.0 days (section 3.2.3.2). The life expectancy in the field is much lower than this (table 3.10), so an estimate of daily egg laying was necessary. There was no obvious difference in the inclination of the curves of cumulative number of eggs laid (figure 3.8) and no significant influence of age on egg cell production was detected (section 3.2.3.4). Thus a rough estimate of number of eggs laid per day can be gained by dividing the mean number of eggs laid by the average life span of the experimental females (891/37 = 24.08)(table 5.2). Laboratory conditions were admittedly different from the field and the sample size was small, but this is the only indication of fecundity available.

In the laboratory it took some time before females started laying (figure 3.8), but this was possibly due to delays in mating under the experimental conditions (section 3.2.3.2). However, young virgin females had no ripe egg cells in their ovaries. Thus a period of maturation should be allowed for estimating the potential number of eggs during a female life span. Unfortunately no data are available on this aspect. However, in many lepidopteran species, mating is known to occur soon after or on female emergence from the pupa (e.g. Bopre, 1984; Dempster,1982; Ehrlich, 1984; Stern & Smith, 1960). Thus it is conceivable that, in the field, *P. ruralis* should mate more promptly. In addition, mating was shown to stimulate egg production (table 3.19) and yolking (egg cell volume, table 4.20). How soon this is effected is not possible to say from the data available. In the absence of evidence in the contrary, and given the short life expectancy observed in the field, an arbitrary period of one day is taken as

Table 5.1 Life tables for *Pleuroptya ruralis*

(a) generation 83/4

Age class	Proportion killed	Number killed per m^2	Number surviving per m^2	log number alive	k value
			50.0	1.699	
Instar 3					
parasitization					
M. grandii **	0.356	17.8	32.2	1.508	$0.191=k_4$
Diadegma sp.**	0.128	6.4	43.6	1.640	$0.059=k_5$
			25.8	1.412	
other mortality (arthropod predation)	0.333	8.6	17.2	1.236	$0.176=k_6$
Instar 4					
miscellaneous parasitoids	0.041	0.7	16.5	1.218	$0.018=k_7$
other mortality (arthropod predation)	0.152	2.5	14.0	1.146	$0.072=k_8$
Instar 5					
mortality (arthropod and vertebrate predation)	0.124	1.7	12.3	1.089	$0.058=k_9$
Instar 6					
parasit. *N. floralis*	0.010	0.1	12.2	1.085	$0.004=k_{10}$
other mortality (mainly bird predation)	0.265	3.2	8.9	0.951	$0.134=k_{11}$
Pupa					
mortality (mainly bird predation)	0.340	3.0	5.9	0.770	$0.181=k_{12}$
Adult					
females emerging (sex ratio 1:1)			2.9		

( ) Probable main cause of mortality
****M. grandii** and *Diadegma* sp are considered to occur simultaneously

Table 5.1(cont.) Life tables for *Pleuroptya ruralis*

(b) generation 84/5

Age class	Proportion killed	Number killed per m^2	Number surviving per m^2	log number alive	k value
Adult					
females			2.9		
Eggs					
number expected			347.7	2.541	
fertility	0.300	104.3	243.4	2.386	
early life mortality	0.614	149.4	93.9	1.973	$0.414=k_1$
Instar 2					
parasit. *M. alebion*	0.167	15.7	78.2	1.893	$0.079=k_2$
other mortality (arthropod predation)	0.364	28.5	49.8	1.697	$0.197=k_3$
Instar 3					
parasitization					
M. grandii **	0.356	17.7	32.0	1.506	$0.191=k_4$
Diadegma sp. **	0.128	6.4	43.4	1.637	$0.060=k_5$
			25.7	1.410	
other mortality (arthropod predation)	0.327	8.4	17.3	1.238	$0.172=k_6$
Instar 4					
miscellaneous parasitoids	0.041	0.7	16.6	1.219	$0.018=k_7$
other mortality (arthropod predation)	0.243	4.0	12.5	1.098	$0.121=k_8$
Instar 5					
mortality (arthropod and vertebrate predation)	0.124	1.6	11.0	1.041	$0.056=k_9$
Instar 6					
parasit. *N. floralis*	0.010	0.1	10.9	1.037	$0.004=k_{10}$
other mortality (mainly bird predation)	0.181	2.0	8.9	0.950	$0.087=k_{11}$
Pupa					
mortality (mainly bird predation)	0.585	5.2	3.7	0.568	$0.382=k_{12}$
Adult					
females emerging (sex ratio 1:1)			1.1		

( ) Probable main cause of mortality
* this includes any egg shortfall from the expected number laid in addition to egg and instar 1 mortality
***M. grandii* and *Diadegma* sp are considered to occur simultaneously

Table 5.1(cont.) Life tables for *Pleuroptya ruralis*

(c) generation 85/6

Age class	Proportion killed	Number killed per m^2	Number surviving per m^2	log number alive	k value
Adult					
females			1.1		
Eggs					
number expected			97.0	1.987	
fertility	0.300	29.1	67.9	1.832	
early life mortality	0.409	27.8	40.1	1.604	$0.228=k_1$
Instar 2					
parasit. *M. alebion*	0.167	6.7	33.4	1.524	$0.079=k_2$
other mortality (arthropod predation)	0.364	12.2	21.3	1.328	$0.197=k_3$
Instar 3					
parasit. *M. grandii*	0.500	10.6	10.6	1.027	$0.301=k_4$
other mortality (arthropod predation)	0.364	3.9	6.8	0.830	$0.197=k_6$
Instar 4					
miscellaneous parasitoids	0.041	0.3	6.5	0.812	$0.018=k_7$
other mortality (arthropod predation)	0.195	1.3	5.2	0.718	$0.094=k_8$
Instar 5					
mortality (arthropod and vertebrate predation)	0.195	1.0	4.2	0.623	$0.094=k_9$
Instar 6					
mortality (mainly bird predation)	0.800	3.4	0.8	-0.076	$0.699=k_{11}$
Pupa					
mortality (mainly bird predation)	0.800	0.7	0.2	-0.775	$0.699=k_{12}$

( ) Probable main cause of mortality
* this includes any egg shortfall from the expected number laid in addition to egg and instar 1 mortality

Table 5.2 Summary of the values used for calculating the numbers of P. ruralis females and the expected numbers of eggs per m^2. E_o = Life expectancy; see text for explanation of numbers of eggs.

	1984	1985	1986
No. adults emerging	33	22	1
No. / m^2	5.9	3.7	0.2
sex ratio (M:F)	1:1	2.34:1	-
No. females / m^2	2.9	1.1	-
E_o females	5.9	4.6	-
Potential No. eggs / day	24.1	24.1	-
Potential No. eggs/ female expected life span	118.0	87.7	-
Total potential No. eggs / m^2	347.7	97. 0	-

necessary maturation time before females can start laying. Therefore, subtracting this day from the females expectancy of life for each year, and multiplying this quantity by the estimated daily number of eggs, the potential number of eggs per female expected life span can be computed. The potential number of eggs laid per m^2 is then obtained from this value together with the estimated number of females per unit area (table 5.2).

There was no statistically significant difference in fertility between eggs laid by fed or starved females (section 3.2.3.2); thus their data was pooled and the resulting value of 0.700 fertile eggs was used in table 5.1.

Rates of survival per stage used in the life tables were the best estimates presented in Chapter 4, which are the following: instar 2 in the 84/5 generation., all larval instars in the 85/6 generation and pupal stage for all generations, table 4.31; instar 3 in the 83/4 generation, table 4.30b; instars 4 to 6 in the 83/4 generation and 3 to 6 in the 84/5 generation, table 4.33.

For each generation, parasitization by all species of parasitoids which were present, at least in the laboratory samples (table 4.14), was included in the life tables. Presence in these samples was considered evidence of presence in the 'system'.

Percentages of parasitization given in the life tables are those from table 4.21.

For *Microgaster alebion*, *Nemorilla floralis* and the other miscellaneous species, which were present only in low numbers, the rates (in the target instar) from the pooled generations were selected for table 5.1.

Macrocentrus grandii and *Diadegma* sp were present in higher numbers, so that more detailed estimates could be used. The rates of parasitization shown in table 5.1a & b are both taken from the pooled 83/4 and 84/5 generations from table 4.21.

In the 85/6 generation, *Diadegma* sp was not found in the field monitoring area (table 4.22) nor in the samples brought to the laboratory (table 4.14). Thus this wasp was not included in table 5.1c.

It is believed that the percentages estimated for *M. grandii* in the 85/6 generation are not accurate (table 4.21), due to the small-sized samples. However, it does seem that the levels of parasitization by this wasp were markedly higher than in the former two generations. A value intermediate between that used for the 83/4 and 84/5 generations (35.6%) and the overall rate calculated for the 85/6 generation (65.4%) was used for table 5.1c. This value should thus be taken with caution.

Finally, the factor called 'early life mortality' in table 5.1 includes not only egg and instar 1 mortality but also the shortfall in egg expected production. This phase of *P. ruralis* could not be monitored adequately in the field, so the proportion killed is calculated based on the difference between numbers alive in the previous and subsequent age classes.

Each k value is a measure of the intensity of the mortality factor and is computed from the difference between the logarithm of the numbers alive in the previous stage and the logarithm of the numbers alive after the mortality factor has acted (Varley, Gradwell & Hassell, 1973).

The oviposition periods for *M. grandii* and *Diadegma* sp are regarded as being 'simultaneous', because instar 3 was considered the host susceptible stage for both species. Thus the k value for both is calculated in relation to numbers alive in instar 2. All other mortality factors are assumed to occur sequentially. The k values are numbered and numbers of individuals are given per unit area to facilitate comparisons between generations.

- *M. grandii* (table 5.3)

The life tables for *M. grandii* had to be calculated from the bottom upwards, because there was no information on the number of adults at the start of the study, nor of potential fecundity or fertility.

The number of cocoons from which adults emerged successfully were derived from table 4.30c. The mean number of adults per brood and the overall sex ratio were obtained from the pooled laboratory data. Based on this information, the expected number of wasps emerging per unit area was calculated (table 5.4).

The rates of mortality within *P. ruralis* larvae at each stage were taken from

Table 5.3 Life tables for *M. grandii*

(a) generation 83/4

	Proportion killed	Number killed per m^2	Number surviving per m^2	log number alive	k value
P. ruralis stage bearing *M. grandii*					
Instar 3			34.5	1.538	
Instar 4	0.248	8.6	25.9	1.414	$0.124=k_8$
Instar 5	0.214	5.6	20.4	1.309	$0.105=k_9$
Instar 6	0.909	18.5	1.9	0.268	$1.041=k_{11}$
Coccons	0.615	1.1	0.7	-0.146	$0.414=k_{12}$
Adults					
total			21.8		
females			12.1		

(b) generation 84/5

	Proportion killed	Number killed per m^2	Number surviving per m^2	log number alive	k value
Adult females			12.1	1.082	
Caterpillars successfully parasitized (expected number)			132.0	2.121	
P. ruralis stage bearing *M. grandii*					
Instar 3	0.404	53.3	78.7	1.896	$0.225=k_6$
Instar 4	0.338	26.6	52.1	1.717	$0.179=k_8$
Instar 5	0.214	11.1	40.9	1.612	$0.105=k_9$
Instar 6	0.904	37.0	3.9	0.594	$1.018=k_{11}$
Coccons	0.615	2.4	1.5	0.180	$0.414=k_{12}$
Adults					
total			46.2		
females			25.6		

from table 4.33 and pupal (cocoon) mortality from table 4.31. The k values for *M. grandii* are numbered according to the ones shown for *P. ruralis* in order to relate the factors acting on host and parasitoid.

Table 5.4 Summary of values used for estimating numbers of M. grandii females.

Mean No. wasps/ brood	30.5
Sex ratio (M:F)	0.81:1
Mean No. females/ brood	16.9

	1984	1985
No. broods emerging	4	9
No. broods / m^2	0.7	1.5
No. females / m^2	12.1	25.6

5.2 RESULTS & DISCUSSION

The various mortality factors acting on each stage of *P. ruralis* have already been discussed in detail and related to work on other lepidopterans in the previous chapters. The life tables presented here provide a measure of the relative importance of each factor through development and in determining population numbers for both host and parasitoid.

During the period covered by this study, the moth population suffered a marked decline, as already indicated by the partial data sets on adults (Chapter 3) and immature stages (Chapter 4). The temporal variation in the relative importance of each mortality factor needs to be interpreted with caution, since too few generations were followed and some estimates had to be made with data pooled across the generations due to the small-sized samples. Indeed, population levels were so low in the 85/6 generation that the meaning of table 5.1c is questionable. Nevertheless, in the three tables for *P. ruralis*, two main periods of mortality can be identified. These are 'early life mortality' (k_1, which was the highest k value) and mortality towards the completion of development (i.e. instar 6 (k_{11}) and pupa (k_{12})). The latter is believed to be due to bird predation (section 4.4.4) and affects both host and parasitoid.

In the 83/4 generation (table 5.1a), birds appear to have been responsible for the

losses of 26.5% of the instar 6 caterpillars (k_{11} = 0.134) and 34.0% of the pupae (k_{12} = 0.180). An average of 5.9 adults/m^2 emerged from the nettle clump and sex ratios were 1:1 (table 5.2).

In the following generation, 'early life mortality' was high (k_1 = 0.414). Mortality at this phase embraces a series of aspects, as mentioned above. Egg shortfall is not believed to have been unusually high since, during the summer of 1984, the weather was favourable to moth activity, with many flowers for the adults to feed on and the survival rates were high (ø = 0.845, Chapter 3). Moths should have had plenty of opportunities to fly, mate, feed and oviposit and indeed the numbers of young caterpillars was high (table 4.39). However, there was also large numbers of arthropod predators (fig 4.2) which may well have been very active during the hot late summer/early autumn. Thus predation should have been heavy on eggs and young caterpillars, as indeed is indicated by the level of mortality in instar 2. If predation upon eggs and first instar larvae are each of the same intensity as observed in instar 2 (k_2 = 0.197), this would account for most of the estimated early life mortality.

Parasitization by *M. grandii* is important as a mortality factor (k_4 = 0.191) and affected about a third of the instar 3 caterpillars. From this point in development up to instar 6, various other mortality factors act upon *P. ruralis* but, as in the former year, no individual k was markedly high. Perhaps worthy of note is that the summed impact of arthropod predation in the pre-diapause stages (part of k_1, k_3 and k_6), is quite high.

The number of individuals at the beginning of the post-diapause phase (instar 4) was very similar in the 83/4 (table 5.1a) and 84/5 generations (table 5.1b). This is partly because some parameters for these two generations were calculated from their pooled data. However, data were pooled where there was statistical support for it. In addition, the same level of similarity was observed between the estimated number of larvae recruited for the post-diapause period of the two generations (table 4.39). It is thus suggested that the population level was stable during this period.

Bird predation on instar 6 caterpillars in generation 84/5 (table 5.1b, k_{11} = 0.087) was lower than in 83/4. However, for the pupal stage (k_{12} = 0.382) its impact was more than twice as high as that observed in the former year. Birds have no way of knowing before attack, what is inside a rolled leaf; it might be a caterpillar or a *P. ruralis* pupa or a *M. grandii* cocoon. These differences seem to be related to the very low June temperatures in this year (fig A2.1). Most bird attack occurred later in the season than in the former year (table 4.34) and the duration of the pupal stage of *P. ruralis* was about ten days longer ($P < 0.05$, table 4.10). This much increased the time they were exposed to predation. Also cold weather can increase the nutritional requirements of small vertebrate predators like birds.

Therefore, only 3.7 moths / m^2 (table 5.2) survived the pupal stage, a reduction of about 37% on what was observed in the 83/4 generation. If pupal predation had been of a level similar to the former year (34%, table 5.1a), expected numbers

surviving the pupal stage would have been virtually equal (5.9 moths /m^2). Thus, increased mortality at this phase (bird predation) was the main cause for the observed reduction in the adult population.

More serious still for the dynamics of the *P. ruralis* population, was the highly significant departure from 1:1 observed in the adult sex ratio ($P < 0.001$) in 1985. Less than a third of the adults were females and the reduction in their numbers as compared to the previous generation was 62 %. This can be explained in terms of differential mortality between the sexes. Females took longer to emerge from the pupae than the males in the laboratory, and though this was not statistically significant, it was observed in all generations studied (section 4.3.2.1 - table 4.9). In addition, estimates of population sizes for each sex showed that female numbers peaked later than male numbers in both years of the MRR study (section 3.3.1.3, figs 3.2 & 3.3). This supports the longer length of development for females. Thus the impact of predation by birds upon pupae should have been much stronger on females than males and the effect on population size in the next generation was escalated.

The weather in the summer of 1985 was cold and rainy (figs A2.1 & A2.2), and the survival rates of adults were lower ($\phi = 0.787$, section 3.1.3.3) and the moths less active than in 1984 (section 3.1.3.4). It is possible that the moths may have experienced more difficulties in mating, feeding and ovipositing.

In the 85/6 generation (table 5.1c) *P. ruralis* numbers were very low. Mortality rates had to be estimated based on small samples and may be inaccurate. The k value for 'early life mortality' ($k_1 = 0.228$) was lower than in the previous year, which is surprising because, given the above facts about the adult population, one would expect egg shortfall to be higher than in the 84/5 generation.

Three factors (not necessarily mutually exclusive) could be the reason for the low estimated value of 'early life mortality'. First, it could have been a consequence of an overestimation of *M. grandii* parasitization rates. However, recalculating the table using the same rates of parasitization as in the 83/4 and 84/5 generations, still gives a value of k_1 (0.388) lower than observed in the previous years. In addition, the life tables for the parasitoid support the adoption of a parasitization level higher than in the previous years.

Second, it may be that location of mates and oviposition sites do not present major difficulties for *P. ruralis*, even under adverse weather conditions, since the adults live amidst the larval food plant. In the light of the discussion in Chapter 3 (studies on other lepidopterans and the results of the MRR and fecundity investigations), this possibility does not look very likely.

Third, the same weather conditions that influenced the decline in *P. ruralis* numbers, may also have had adverse effects on, and/or reduced the activity level of, the predator community on the nettles. This seems more likely than either of the above two.

Estimated bird predation in the 85/6 generation was again high, both in full grown larvae and pupae, but note that for this generation 'specific' survival rates could not be calculated, due to the paucity of data. Thus, these estimates include both moth and parasitoid mortality.

Total bird impact in this generation ($k_{11} + k_{12} = 1.398$) can be compared with the impact observed in the 83/4 and 84/5 generations by summing up the estimates for *P. ruralis* and *M. grandii* predation on instar 6 and the pupal stage (i.e *P. ruralis* ($k_{11} + k_{12}$) + *M. grandii* ($k_{11} + k_{12}$) = 1.769 (83/4) and 1.902 (84/5)). Thus, bird attack was actually less intense in the 85/6 generation than in the two previous ones. This would be expected if birds are indeed able to select prey according to their densities.

The impact of bird predation was more intense upon *M. grandii* (table 5.3) than upon *P. ruralis*, both in the 83/4 and 84/5 generations, particularly in instar 6. Again, the interaction between the weather, timing of bird attack, longer duration of instar 6 and late pupal recruitment provide the explanation for the chain of events: longer development, longer exposure, higher mortality.

Values of k_{12} (predation of pupae) for *M. grandii* did not differ between the 83/4 and 84/5 generations because samples were very small and had to be pooled for the estimation of pupal mortality. Pupal survival recorded in the field was actually better in the 83/4 generation than in the 84/5. Based on this and on the results above on *P. ruralis*, it is suggested that bird attack on *M. grandii* cocoons was higher than the estimate shown in table 4.3b. However, based on the evidence available, it is not possible to say if the increase was proportional to that recorded for *P. ruralis*

Caution should be exercised when examining the present *M. grandii* life tables. As observed in section 4.4.3, parasitoid sample sizes were small and their survival rates were estimated from estimates, so that error may have accumulated. However, keeping this in mind, bird predation seems to have a less negative effect on the *P. ruralis* population when the effect of the mortality factor upon the parasitoid is taken into account, because it limits the number of adult parasitoids attacking the next generation. At least, this is the case when the interaction with weather conditions are not such as to distort seriously the sex ratios as observed in the summer of 1985. If parasitization had not been calculated based on the target instar or if developmental differences had not been considered, the 'specific' survival rates could not have been calculated, and this major aspect (weather/development/predation/sex ratio/parasitization) in the dynamics of both *P. ruralis* and *M. grandii* could not have been detected.

Still, very much information is lacking about *M. grandii*, such as adult habits, sex ratios in the field, potential fecundity, all crucial aspects for its population dynamics. However, if the same relationship between the estimated number of females emerging in the 83/4 generation and the numbers of instar 3 caterpillars parasitized in the 84/5 generation was maintained in the following year, a rate of parasitization higher than in the previous years would indeed be expected in the 85/6 generation.

This was observed in the laboratory but predation may have obscured it in the field monitoring site. It may be that *M. grandii* parasitization is density dependent in a delayed way.

5.3 CONCLUSIONS & SUGGESTIONS FOR FURTHER WORK

This study aimed to describe *P. ruralis* ecology, trying to identify the important factors which determined the observed population levels, with the emphasis on those aspects where variability could promote stability. Although set against a theoretical background, the intention was to provide the biological basis necessary to assess the potential of the system 'nettles / *P. ruralis* / natural enemies' and thereby add evidence for the debate on the role of density processes in population change. This aim was fulfilled and it is suggested that the system offers many possibilities.

Concerning *P. ruralis*, perhaps the most important point was the evidence of how interactions between various factors (rather then the individual factors) are fundamental in the dynamics of the population studied, and how these interactions can be obscured if the assessment of each factor is not rigorous. This statement is made with the awareness that there are many factors that remain unidentified and that probably many connections between the factors studied were not realized. As it is often the cases, more questions were raised than answered.

Predation (most probably by birds) in instar 6 and the pupal stage was the direct cause of mortality that led numbers to fall drastically from the 84/5 to the 85/6 generations. However, its impact was higher than in the previous year due to delays in development caused by temperatures lower than usual in early summer. The effect on the next generation was more intense still due to the higher mortality of the slower developing females in comparison to males.

Birds were shown to concentrate their attack spatially on those leaves that had the highest chance of being inhabited by *P. ruralis*, i.e. about the mode value of the vertical distribution of the prey. This aspect is lost in the life table analysis, but may be important in interpreting the patterns of bird predation.

Predation of parasitized caterpillars and cocoons appears to have a marked effect on the numbers of *M. grandii*. As for the above mentioned differential mortality between the sexes, the stronger impact on the parasitoid seems to be linked to longer development time.

This phase of the *P. ruralis* life cycle certainly deserves to be studied further. Experiments excluding the predator or assessing the percentage of mortality at experimentally controlled densities and vertical distributions would be most informative, about the host as well as the parasitoid. An interesting question is whether parasitization rates would be higher if birds are experimentally excluded or in areas where bird population levels are low.

The other phase of development where mortality was high was in 'early life'. Unfortunately, it remains unclear in the present study what exactly this means. It was demonstrated in the laboratory that reduced fecundity can result from starvation of adults. However, considering the life expectancy of moths in the field, is hard to speculate how important adult starvation can be in the dynamics of this population. It is questionable whether it would have any effect on egg production in less than a week. On the other hand, the higher activity of moths in the field as compared to the laboratory conditions could translate into faster depletion of reserves.

Mating was also demonstrated in the laboratory to have an effect on egg production, and it appears not to be acting simply as a trigger to yolking. The time females take to mate in the field may be another important variable. In addition, the absence of mature eggs in young females raises the question of the length of time they take until eggs are ready to be laid. These aspects are all the more crucial given the short life span of moths in the field (Scott, 1973) and suggest that egg 'shortfall' may be an important factor.

Studies of fecundity (from mating behaviour to maturation time and egg production) in the field (e.g. dissections of marked females of reasonably known age or of a series of females as the flying season progresses) would be valuable.

The interaction weather/realized fecundity is often quoted as the major cause of population changes (Courtney & Duggan,1983; Pollard, 1979; Dempster, 1983, and references therein).

'Early life mortality' also comprises egg and first instar larva mortality. Given the difficulty of finding these stages in the field during this study and the impossibility of separating them from egg shortfall, it can only be speculated that mortality can be high, as is indicated for so many lepidopterans (Dempster, 1984). Also it may be density dependent since arthropod predators, the main suspected cause, are able to concentrate attack on areas of high prey density (e.g. Jones *at al.*, 1990). This also applies to other stages where some of mortality is suspected to be due to arthropods.

Parasitization affected a large proportion of individuals, the overall percentage being higher than 40%, with *M. grandii* alone killing more than a third of the caterpillars. Little can be said about the other parasitoid species due to the low numbers found attacking *P. ruralis*.

Unfortunately, no data about the parasitoid adult population in the field could be gathered (in spite of tentative sampling with suction traps). This, added to the few generations studied, makes it difficult to interpret the between generation variation in the parasitization levels. It would be most informative to collect longer term data to check the very weak indication obtained that *M. grandii* parasitization may have a component of delayed density dependence, and also gauge more accurately the impact of bird predation on the population of this wasp.

The data collected using the method of identifying the target instar produced important information on the high level of mortality of *M. grandii* ; this would have been missed, had the levels been calculated based on the host instar from which the parasitoids emerge.

Investigations of parasitization rates at the target instar, taking into account both patch densities and the vertical distribution, could produce much needed information on the importance of spatial heterogeneity on parasitoid attack in the field and also on their searching strategies.

Given the lack of previous knowledge about *P. ruralis* ecology, little data could be collected on the pattern of distribution in each phase of development. However, this brings us to one of the main potentials for research on the system studied. It offers the possibility of investigating the relationships between mortality factors and spatial distribution in a way similar to that suggested by Heads & Lawton (1983): not only different patches within one nettle clump can be studied, but also variations in distribution, densities and mortality rates could be examined on smaller (within stem vertical distribution) and larger (other nettle clumps in the field) scales. Ideas like the concept of a 'viscous' environment (i.e. the tendency of natural enemies to remain in the area of the environment which they were born (Walde & Murdoch, 1988)) could be tested.

In conclusion, the main aspects determining the observed levels in the population studied were the interactions between weather, development, predation (bird) towards completion of development and *M. grandii* parasitization. Predation also had a strong impact on the parasitoid population. Starvation of females reduced fecundity in the laboratory and egg shortfall may also have been important in the field. The field method of following individuals had the advantage of making it possible to record parameters rather than estimate them from samples. In spite of the sometimes small samples, the consistency of the results obtained highly recommends the method, supported (as was the case in this study) by laboratory evidence. Finally, it is suggested that the system 'nettles / *P. ruralis* / natural enemies' offers great possibilities to provide evidence for the debate on population regulation.

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APPENDIX 1

Mark-Release-Recapture Data

Table A1.1 Movement between the three clumps of nettles. Individuals were marked according to site of first capture. Origin of mark was noted on recapture. Numbers in brackets indicate proportion of total number recaptured in each site. Data for 1984, females (section 3.1.3.1).

Site of recapture	Recaptures site of first capture S1	S2	S3	Total between clump mov.	Total number recapt.	Overall recapt. rate
S1	10 (0.42)	5 (0.21)	9 (0.38)	14 (0.58)	24	0.16
S2	5 (0.16)	17 (0.53)	10 (0.31)	15 (0.47)	32	0.19
S3	11 (0.38)	6 (0.21)	12 (0.41)	17 (0.59)	29	0.10
Total movement recorded	16 (0.19)	11 (0.13)	19 (0.22)	46 (0.54)	85	0.14
				Total		
Total number marked	127	135	249	511		
Number of marks recovered	26	28	31	85		
Rate of recovery	0.17	0.17	0.11	0.14		

Table A1.2 Movement between the three clumps of nettles. Individuals were marked according to site of first capture. Origin of mark was noted on recapture. Numbers in brackets indicate proportion of total number recaptured in each site. Data for 1984, males (section 3.1.3.1).

Site of recapture	Recaptures site of first capture S1	S2	S3	Total between clump mov.	Total number recapt.	Overall recapt. rate
S1	9 (0.60)	1 (0.07)	5 (0.33)	6 (0.40)	15	0.10
S2	1 (0.03)	20 (0.65)	10 (0.32)	11 (0.35)	31	0.16
S3	7 (0.21)	14 (0.41)	13 (0.38)	21 (0.62)	34	0.12
Total movement recorded	8 (0.10)	15 (0.19)	15 (0.19)	38 (0.48)	80	0.13
				Total		
Total number marked	134	162	240	536		
Number of marks recovered	17	35	28	80		
Rate of recovery	0.11	0.18	0.10	0.13		

Table A1.3 Movement between the three clumps of nettles. Individuals were marked according to site of first capture. Origin of mark was noted on recapture. Numbers in brackets indicate proportion of total number recaptured in each site. Data for 1985, females (section 3.1.3.1).

Site of recapture	Recaptures site of first capture S1	S2	S3	Total between clump mov.	Total number recapt.	Overall recapt. rate
S1	6 (0.67)	0 (0.00)	3 (0.33)	3 (0.33)	9	0.14
S2	0 (0.00)	4 (0.57)	3 (0.43)	3 (0.43)	7	0.13
S3	1 (0.06)	1 (0.06)	14 (0.88)	2 (0.12)	16	0.13
Total movement recorded	1 (0.03)	1 (0.03)	6 (0.19)	8 (0.25)	32	0.14
				Total		
Total number marked	49	46	110	205		
Number of marks recovered	7	5	20	32		
Rate of recovery	0.13	0.10	0.15	0.14		

Table A1.4 Movement between the three clumps of nettles. Individuals were marked according to site of first capture. Origin of mark was noted on recapture. Numbers in brackets indicate proportion of total number recaptured in each site. Data for 1984, males (section 3.1.3.1).

Site of recapture	Recaptures site of first capture S1	S2	S3	Total between clump mov.	Total number recapt.	Overall recapt. rate
S1	20 (0.71)	2 (0.07)	6 (0.21)	8 (0.29)	28	0.20
S2	6 (0.21)	16 (0.59)	5 (0.19)	11 (0.41)	27	0.13
S3	5 (0.14)	6 (0.17)	24 (0.69)	11 (0.31)	35	0.15
Total movement recorded	11 (0.12)	8 (0.09)	11 (0.12)	30 (0.33)	90	0.16
				Total		
Total number marked	112	174	194	480		
Number of marks recovered	31	24	35	90		
Rate of recovery	0.22	0.12	0.15	0.16		

Table A1.5 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data F + M, 1984. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
13 Jul	1	13	-	-	-	-	-
	4	3	0	7.8	-	31	330
	5	38	0	9.2	-	357	0
	7	50	6	33.6	0.179	245	854
	11	160	6	42.6	0.141	979	439
	14	176	20	122.0	0.164	1030	1130
	18	130	11	152.0	0.074	1660	150
3 Aug	22	89	12	143.0	0.084	993	0
	26	110	26	118.0	0.220	484	299
	28	118	29	162.0	0.172	645	229
	32	116	29	143.0	0.203	557	484
	35	89	16	155.0	0.103	819	134
	39	57	12	124.0	0.097	551	0
	42	37	20	109.0	0.183	197	194
	47	26	5	61.8	0.081	278	0
4 Sep	54	0	0	24.8	-	25	-

Total Gains = 4246

$\phi = 0.845 \pm 0.0132$

$E_o = 5.94$ days

Table A1.6 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data F, 1984. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
13 Jul	1	1	-	-	-	-	-
	4	0	0	0.6	-	1	7
	5	13	0	0.5	-	7	37
	7	12	2	9.6	0.208	42	191
	11	57	2	11.0	0.182	212	245
	14	81	8	40.8	0.196	372	439
	18	60	5	61.7	0.081	628	59
3 Aug	22	54	8	61.7	0.130	377	202
	26	66	9	58.6	0.154	393	171
	28	65	12	88.7	0.135	450	74
	32	61	15	77.9	0.193	302	129
	35	51	13	83.4	0.156	310	184
	39	34	6	68.1	0.088	341	0
	42	24	16	61.3	0.261	90	124
	47	17	3	36.1	0.083	162	0
4 Sep	54	0	0	15.2	-	15	-

Total Gains = 1860

ϕ = 0.844 ± 0.0191

E_o= 5.90 days

Table A1.7 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data M, 1984. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
13 Jul	1	12	-	-	-	-	-
	4	3	0	7.2	-	29	199
	5	25	0	8.6	-	223	28
	7	38	4	23.9	0.167	186	555
	11	103	4	31.2	0.128	649	205
	14	95	12	80.4	0.149	593	598
	18	70	6	88.5	0.068	898	123
3 Aug	22	35	4	80.0	0.050	576	0
	26	44	17	57.5	0.296	144	114
	28	53	17	72.1	0.236	216	127
	32	55	14	63.2	0.222	236	537
	35	38	3	69.6	0.043	678	0
	39	23	6	53.8	0.112	184	18
	42	13	4	46.0	0.087	129	27
	47	9	2	24.7	0.081	82	0
4 Sep	54	0	0	9.0	-	9	-

Total Gains = 2531

$\phi = 0.843 \pm 0.0187$

$E_o = 5.86$ days

Table A1.8 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data F + M, 1985. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
23 Jul	1	38	-	-	-	-	-
	3	76	7	23.5	0.298	226	233
	7	150	17	38.1	0.446	320	217
2 Aug	11	127	26	71.7	0.366	340	89
	14	20	7	96.8	0.072	254	264
	16	98	16	72.3	0.221	421	214
	19	90	17	82.9	0.205	419	18
	22	65	24	84.2	0.285	222	83
	25	41	15	72.7	0.206	191	285
	30	29	2	34.3	0.058	343	0
	35	2	0	19.1	-	57	116
	38	13	0	10.3	-	144	0
5 Sep	45	4	2	4.3	0.461	7	50
	49	42	1	2.4	0.412	52	0
	53	6	6	15.9	0.377	16	33
	56	4	0	8.2	-	41	0
	62	1	0	2.9	-	6	0
1 Oct	71	1	0	0.5	-	1	-

Total Gains = 1602

$\phi = 0.787 \pm 0.0215$

$E_o = 4.17$ days

Table A1.9 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data F, 1985. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
23 Jul	1	6	-	-	-	-	-
	3	18	1	3.9	0.256	37	46
	7	19	2	9.3	0.216	62	38
2 Aug	11	31	5	11.9	0.420	64	12
	14	3	1	22.5	0.044	45	116
	16	34	3	16.6	0.181	145	17
	19	34	9	26.5	0.340	93	60
	22	23	6	31.7	0.189	109	129
	25	12	1	28.6	0.035	186	20
	30	11	1	13.8	0.072	83	0
	35	1	0	8.5	-	17	31
	38	7	0	5.0	-	40	0
5 Sep	45	3	2	2.6	0.758	4	27
	49	28	1	2.0	0.510	28	0
	53	4	4	11.8	0.339	12	12
	56	2	0	6.2	-	19	0
	62	1	0	2.2	-	4	0
1 Oct	71	0	0	0.5	-	0	-

Total Gains = 507

ϕ = 0.806 ± 0.0377

E_o = 4.64 days

Table A3.10 Number of captures and recaptures and population estimates by the Fisher & Ford method. Data M, 1985. (section 3.1.3.3) For summary of notation, see p vii.

Date	i	n_i	m_i	$\hat{M}_i$	SI	$\hat{N}_i$	$\hat{B}_i$
23 Jul	1	32	-	-	-	-	-
	3	58	6	19.6	0.306	165	177
	7	131	15	29.0	0.517	239	172
2 Aug	11	96	21	59.3	0.354	262	66
	14	17	6	74.2	0.081	191	142
	16	64	13	55.7	0.233	259	239
	19	56	8	57.2	0.140	362	0
	22	42	18	54.1	0.333	122	33
	25	29	14	45.9	0.305	92	181
	30	18	1	21.8	0.046	208	0
	35	1	0	11.6	-	23	31
	38	6	0	6.0	-	42	0
5 Sep	45	1	0	2.1	-	4	10
	49	14	0	0.8	-	12	1
	53	2	2	5.2	0.388	5	6
	56	2	0	2.9	-	9	0
	62	0	0	1.1	-	1	0
1 Oct	71	1	0	0.1	-	0	-

Total Gains = 1059

$\phi = 0.782 \pm 0.0260$

$E_o = 4.07$ days

APPENDIX 2

Weather Data

APPENDIX 2

Weather Data

1 Description of the weather over the study period

Generalized weather data were obtained from Bramham Meteorological Station (National Grid Reference SE 441442, altitude 54 m), 15 km NE of Leeds City Centre, 10 km NE of Bond Ing and 2.5 km NW of the University Farm. Figures A2.1 and A2.2 present the monthly mean temperatures and the monthly rainfall, respectively, recorded for 1984-6. Also shown in figure A2.1 are the normal monthly mean temperatures for West Yorkshire (Lockwood, 1967). Field observations coupled with these weather data were the basis for the general description presented below.

The weather in 1984 was very favourable to *P. ruralis*. The winter was cold, but spring was sunny and dry although sometimes windy. June, specially, was very warm and sunny. Summer was hot: July and particularly August were dry and very sunny; September, however, was very wet with winds often strong. Weather conditions in autumn were fairly close to the normal for the time of the year, but for the very high levels of precipitation in November.

Winter 1985 was very cold indeed. Spring temperatures rose slowly, and June, in particular, was much cooler than normal. Summer was also unusual: August was very cold and, specially from the second fortnight, very windy and rainy; September, however, although pretty windy, was warmer than normal, dry and had a fair amount of sunshine. Autumn too presented a mixed picture: October was very windy, November very cold but very sunny and December weather was pretty typical of the time of the year.

In 1986, the winter was cold and snowy but fairly sunny. April was still cold, temperatures only rising to Spring levels from May. Summer started warm and dry, but from August it got very cold and wet, with September a little drier. Autumn was sunny throughout, in spite of the generally low November temperatures.

2 Summer evening temperatures

Detailed data on summer evening temperatures (daily means and minima from 20:00 to 23:00 h) were needed for the mark-recapture study (section 3.1.3.6). These were not available from Bramham Meteorological Station. The nearest hourly reporting station that could supply this information was the RAF-Leeming Meteorological Station (National Grid Reference SE 430489, altitude 32 m), some 50 km N of Bond Ing and about 56 km N of Leeds City Centre.

Ideally the weather data would have been collected on the study site. However, the cost and effort necessary to get this information locally were high, and only during part of the Summer 1985 it was possible to carry this out. Temperatures were slightly lower in Bond Ing than in Leeming, but the figures from the two sites were very

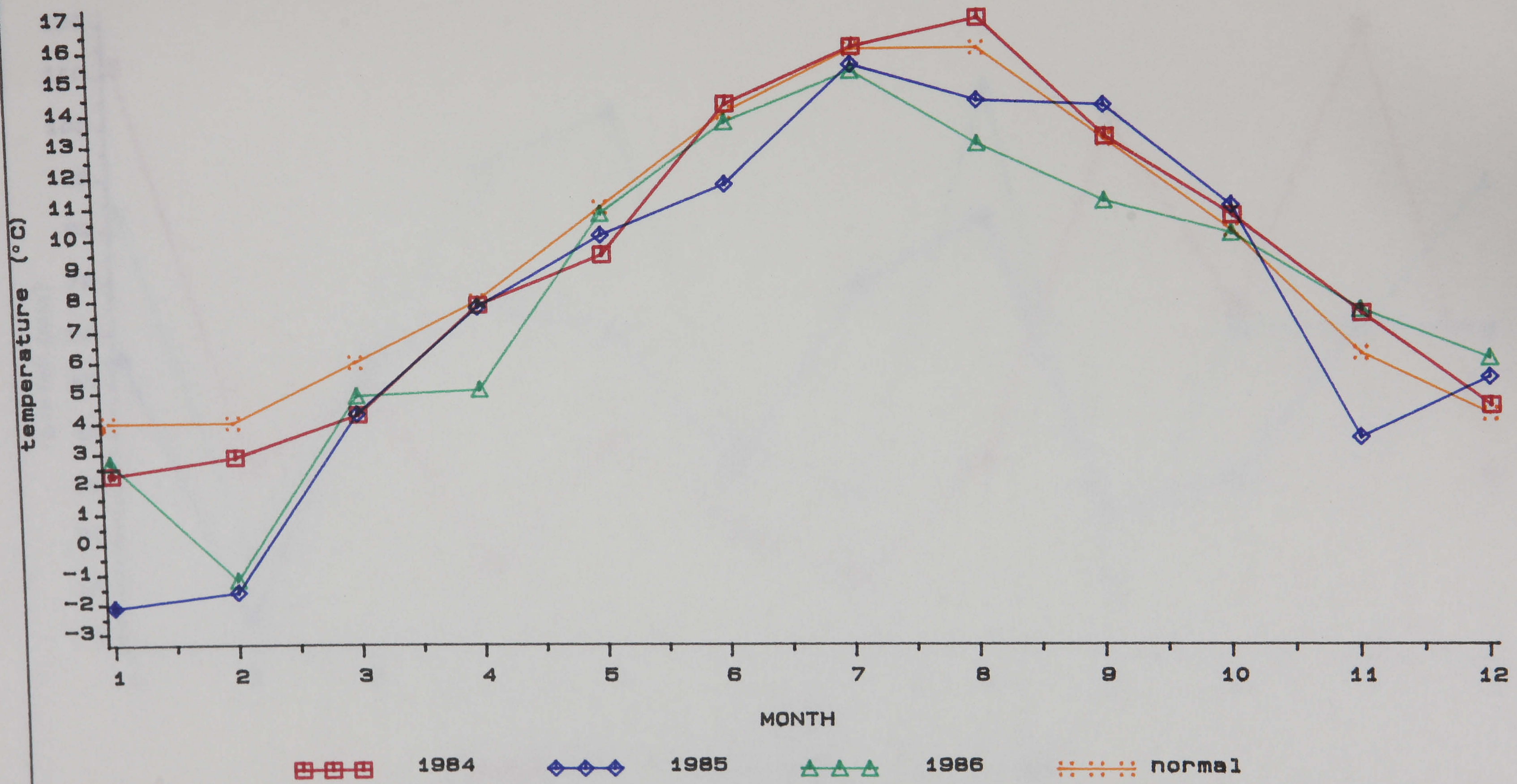

Figure A2.1 Normal monthly mean temperatures for Yorkshire and means recorded in 1984-86. Bramham Meteorological Station.

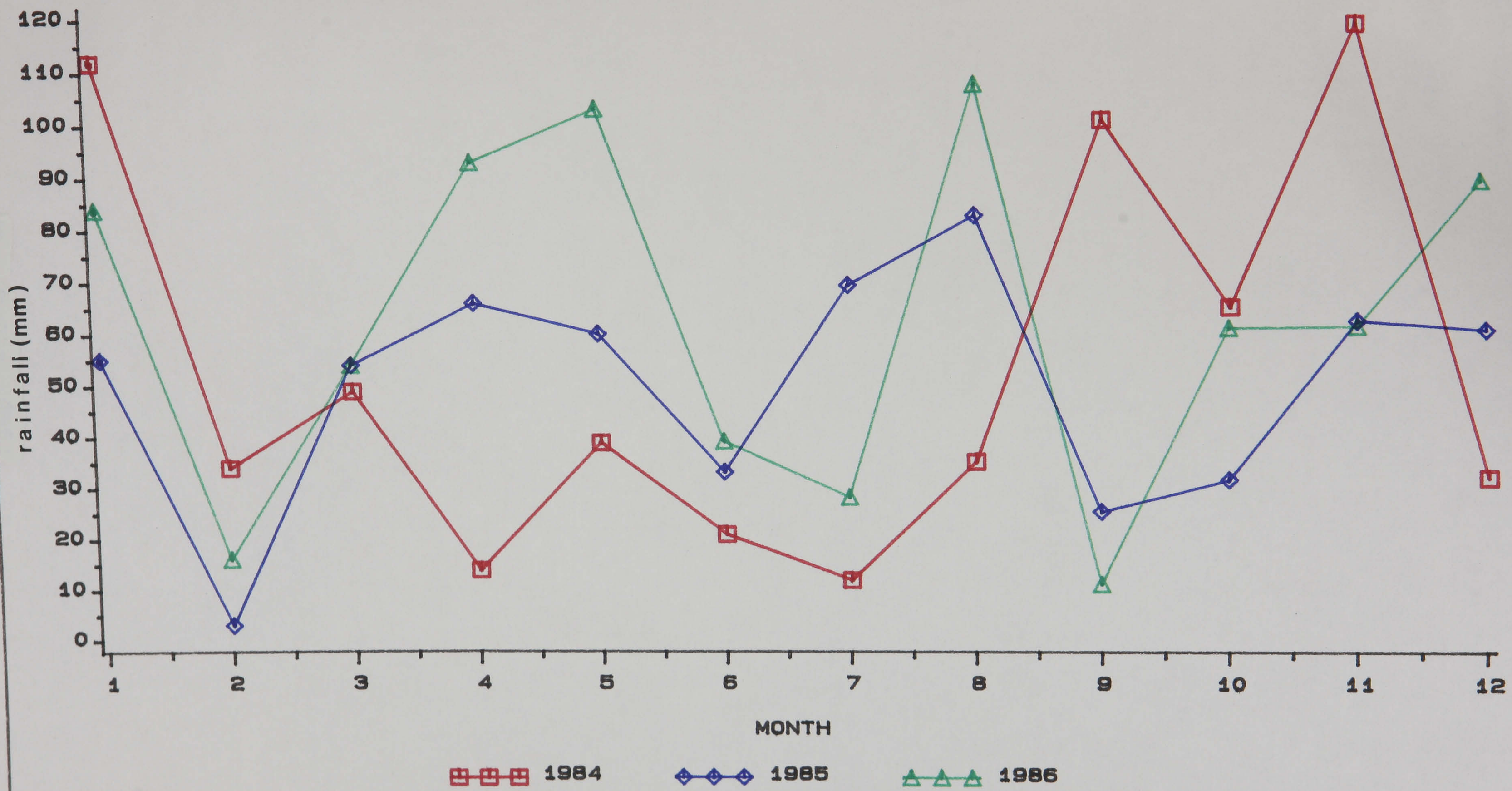

Figure A2.2 Monthly rainfall recorded for Yorkshire Bramham Meteorological Station.

highly correlated (table A2.1). Thus the data from Leeming was considered suitable for investigating general trends and possible associations between temperatures and the observed variation in the samples and population estimates.

Table A2.1 Summer 1985 evening temperatures(°C). Correlation analysis between figures from Bond Ing and RAF-Leeming Meteorological Station.

Source of data	n	mean (°C)	r	P
Bond Ing	16	13.97		
			0.860	0.0001
Leeming	16	14.62		

APPENDIX 3

Summary of Counts and Measurements Recorded on the Dissections of the Female Internal Organs

Table A3.1. Summary of the counts and measurements recorded from the dissections of the females internal reproductive organs. Female codes: F=fed; S=starved; Y=young (generally three days, but up to a week old); V=virgin; V'=virgin reared with male; M=mated; ¯ denotes mean for the group, e.g. $\overline{FY}$= mean for the young fed females. Females marked with an asterisk had 9 ovarioles; all others had 8. Fat body ranked from 1 (none left) to 5 (abdomen filled with it). Within each group animals are ranked according to their longevity (age). Standards errors are given in tables 3.2.1 to 3.2.8. For more details, see Section 3.2.

Female code	Age (days)	Eggs laid	Fat body	Corpus Bursae (mm)	Egg cells in oviducts	Egg cells in ovaries		Egg cell size (mm^3)	Ovarioles lenght (mm)	Total number egg cells produced
						Ripe	Unripe			
FY1	1	0	5	1.8	0	0	804	0.017	15.0	804
FY2	2	0	5	1.8	0	0	1104	0.060	30.0	1104
FY3	3	0	5	1.6	0	0	971	0.156	23.0	971
FY4	5	0	5	1.9	0	46	1080	0.095	24.0	1126
FY5*	6	0	5	1.9	11	44	1062	0.097	22.0	1117
FY6*	7	0	5	1.8	0	0	852	0.003	14.5	852
$\overline{FY}$	4	0	5	1.8	(1.8)	993.8		0.071	21.4	995.7
FV'5*	15	0	3	1.8	41	180	830	0.036	20.0	1051
FV4	16	0	4	1.8	12	32	566	0.080	17.0	610
FV2	18	0	5	1.8	38	97	1122	0.062	21.0	1257
FV3	20	0	5	1.8	18	46	1170	0.063	24.0	1234
FV'9	24	20	5	1.6	19	59	521	0.090	17.0	619
FV1	30	0	5	1.6	29	260	706	0.040	20.0	995
FV'10	31	14	2	1.7	19	347	479	0.045	20.0	859
FV6	36	0	5	1.8	10	0	813	0.010	16.0	823
FV5	41	0	5	1.8	28	136	963	0.096	21.0	1127
$\overline{FV}$	25.6	(3.7)	(4.3)	1.8	23.8	925.23		0.058	19.6	952.8

(continued)

Table A3.1.(cont.)

Female code	Age (days)	Eggs laid	Fat body	Corpus Bursae (mm)	Egg cells in oviducts	Egg cells in ovaries		Egg cell size (mm^3)	Ovarioles lenght (mm)	Total number egg cells produced
						Ripe	Unripe			
SV'18	11	0	2	2.0	17	41	620	0.057	12.0	678
SV1	14	0	5	1.5	26	0	596	0.064	23.0	622
SV'13	15	0	2	1.8	0	0	645	0.023	14.5	645
SV2	18	0	5	1.8	0	0	948	0.020	13.5	948
SV4	18	0	2	1.6	0	0	625	0.012	16.0	625
SV3	20	0	2	2.0	0	0	755	0.003	12.0	755
SV6	20	0	2	1.6	0	0	670	0.004	14.0	670
SV'2	22	0	2	1.7	26	0	893	0.004	15.5	919
SV5	32	0	2	1.8	0	0	584	0.008	12.0	584
$\overline{SV}$	18.9	0	2.7	1.8	(5.4)	708.5		0.022	14.7	716
FM12	33	964	2	2.6	1	45	521	0.172	9.0	1531
FM3	37	800	1	3.0	0	64	400	0.043	9.0	1264
FM8	41	908	2	3.3	5	5	495	0.146	12.0	1413
$\overline{FM}$	37.0	891	1.7	3.0	(2.3)	510		0.120	10.0	1402.7
SM20	16	460	1	2.6	0	0	533	0.004	9.5	993
SM17	20	312	1	2.4	0	0	707	0.003	13.0	1019
SM12	22	80	1	2.8	2	0	472	0.003	11.0	554
$\overline{SM}$	19.3	284	1	2.6	0.7	570.7		0.003	11.2	855.3