Aspects of the Population Dynamics of *Lochmaea suturalis* Thomson., (Coleoptera: Chrysomelidae; Sub-family: Galerucinae), the Heather Beetle: A Combined Laboratory and Modelling Approach

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***Lochmaea suturalis* Thomson, the heather beetle**

(Coleoptera: Chrysomelidae; sub-family: Galerucinae)

Two adult heather beetles on its host plant, *Calluna vulgaris*
***note*: colour variation and two yellow eggs**

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Abstract

This thesis describes a series of laboratory and field experiments that quantify the population dynamics of the heather beetle (*Lochmaea suturalis* Thomson), in relation to temperature and its host plant heather (*Calluna vulgaris* (L.) Hull). The sex ratio, fecundity, egg laying threshold temperature, emergence threshold temperature, life stage development periods, and life stage mortalities were investigated. It was shown that the life stages were significantly dependent on temperature, whilst it was shown that there was no significant relationship between larval growth and *Calluna vulgaris* plants sourced from the study sites.

The results of the population dynamics experiments were incorporated into a temperature driven, cohort based, and daily looped, stochastic population dynamics computer model. The temperature component of the model was derived from temperature data collected from nine moorland sites, at different altitudes, where there was shown to be a significant relationship between temperature and altitude. The population dynamics model was run for a fifty year period with a population of 1 million beetles at seven temperature regimes and five different altitudes. The model predicted that as daily mean temperatures rose, so there was a greater chance of increasing populations and that as altitude increases, so the chance of increasing populations decreases. At a predicted daily mean temperature rise of 2-3°C there was evidence of considerable population increases at lower altitudes, and with a daily mean temperature rise of 4-6°C the beetle population exhibited persistent, large, fluctuating populations in the region of three to sixty fold increases at all modelled altitudes over a number of years.

An uncertainty and sensitivity analysis of the model was undertaken utilising a Latin Hypercube Sampling regime, where it was shown that fecundity, egg mortality and pupal mortality were the most important life history variables in

contributing to the model output imprecision. The thesis discusses these results in the light of predicted climate change and their use as an aid to moorland and heathland managers.

PAGE NUMBERING AS ORIGINAL

Contents

List of Figures

List of Tables

List of Maps

Chapter 1: General introduction

1.1 Introduction

Heather (*Calluna vulgaris* (L.) Hull) occurs in many areas of upland and lowland Great Britain with Bunce (1987) estimating that there were approximately one million hectares of land covered in pure heather in 1987. Those areas where heather is dominant in the uplands are known as heather moorland and, as such, have a high conservation value for a variety of reasons. These include their significance in supporting marginal rural practices; in particular hill sheep farming and grouse moors, their unique habitat sustains rare or vulnerable species of plants, invertebrates and vertebrates (Usher & Thompson 1993), and the considerable amenity value of the landscape (Institute of Terrestrial Ecology 1989; Thompson *et al.* 1995).

Recently public concern has focused on heather dominated upland and lowland land as a result of research that has shown that these areas are in decline. The reasons for this decline are extensive, ranging from unsustainable sheep stocking densities and afforestation (Armstrong 1991) to an increase in soil fertility as a result of aerial nitrogen deposition (Berendse & Aerts 1984; Berendse *et al.* 1987; Breemen 1988; Van der Eerden *et al.* 1991).

This thesis concerns itself with an area of moorland ecology that has been little studied; that of the effects of the heather beetle and in particular its population viability. This may be an important agent in the continuing success of *C.vulgaris* dominated moorlands as several researchers in the Netherlands have implicated *L.suturalis* as a factor in the decline of lowland heaths, (see Figure 1-1, page 3). However, in heather moorland regions of Britain its effects are for the most part only known locally and generally only anecdotally; particularly by game-keepers. It is hoped that this study will throw some light on a field of

moorland ecology that is occasionally a problem and may be, if the threatened climate change in the form of global warming occurs, a greater problem on the heathlands and moorlands of Great Britain.

Figure 1-1: *Lochmaea suturalis* damage on *Calluna vulgaris* dominated moorland; light grey areas are the dead heather

1.2 Research history

The heather beetle, *Lochmaea suturalis* Thomson. (Coleoptera: Chrysomelidae; sub-family: Galerucinae), was initially described by the Swedish entomologist C.G.Thomson in 1869. As early as 1911, P.H.Grimshaw recognised it as a pest of *Calluna vulgaris*, (L.) Hull., (heather), in the British Isles and believed that it was responsible for the occasional damage or death of *C.vulgaris* with consequences for grouse populations and grazing availability for sheep. Since then there has been very little research on *L.suturalis*, apart from a small flurry of activity in the 1980's as a result of concern for the loss of the increasingly rare lowland heaths in Denmark, Germany and the Netherlands.

The majority of this work focused on field-based surveys to investigate the relationship between *L.suturalis* and the transition from *C.vulgaris* dominated heathland to grass dominated heathland (Smidt 1977; Brunsting 1982; Berdowski & Zeilinga 1983; Heil & Diemont 1983; Diemont & Heil 1984; Brunsting & Heil 1985; Berdowski 1987; Berdowski & Siepel 1987; Berdowski & Zeilinga 1987; Heil & Bruggink 1987). Further research investigated the possibility of an historical association between pest outbreaks and climate (Melber & Heimbach 1984; Neilsen 1986), field-based research on the biology of *L.suturalis* (Schrier 1981; Vagn Jensen & Nielsen 1985a, b) and laboratory-based experiments on flight capacity and egg production, (Schaick Zillesen & Brunsting 1983). However in the British Isles research has been very limited, with only Cameron, McHardy & Bennetts' general heather beetle study of 1944 (subsequently revised by Morison in 1963), a study of parasitism of *L.suturalis* on lowland heaths by Waloff in 1987, and the investigation of a local outbreak on a wet heath in north-east Scotland by Scandrett & Gimingham in 1991.

1.3 *Lochmaea suturalis* overview

L.suturalis is a phytophage of *C.vulgaris* and is endemic on the upland and lowland heathlands of Palaearctic NW Europe. There are records for Great Britain, Holland, Germany, Belgium, Sweden, France, Switzerland and Denmark (Brunsting 1982). The adult is c. 5-6 mm in length (Grimshaw 1911; Cameron *et al.* 1944; Smidt 1977; Webb 1989) and ranges in colour from olive green to dark brown/black. Several authors consider it to be monophagous with both larvae and imagoes feeding exclusively on *C.vulgaris* (Smidt 1977; Brunsting 1982; Schaick Zillesen & Brunsting 1983; Brunsting & Heil 1985; Berdowski 1987; Berdowski & Zeilinga 1987; Webb 1989; Scandrett & Gimingham 1991). However, Waloff (1987) reports that "...*Erica cinerea, E.tetralix* and various cultivated species of *Erica* may also serve as food.", whilst Morison (1963) and Cox (1976) also cite the *Erica* genus as a food source. The distribution of *L.suturalis* is closely related to the distribution of *C.vulgaris* in Western Europe (Brunsting 1982). This is because, as Smidt (1977) notes, the optimal requirements for the development of *L.suturalis* are a moist understorey of moss and litter, covered by tall dense stands of *C.vulgaris* and optimal conditions for *L.suturalis* are also optimal for the survival of heather.

1.4 Thesis aims

This thesis has two distinct, but connected goals. The first is to investigate the factors that affect *L.suturalis* abundance and distribution, and the second is to develop a method of predicting using a computer simulation model, with environmental or management changes, a given population's viability. To achieve the former it is necessary to study the ecology of the species in question. The word 'ecology', first coined by Ernst Haeckel in 1869 is, as Burdon-Sanderson in 1893 noted,

> "...the science which concerns itself with the external relations of plants and animals to each other, and to the past and present conditions of their existence."

In 1927, Elton who recognised the importance of animal distribution and abundance studies and argued that ecology should stand-alone wrote,

> "...in solving ecological problems we are concerned with what animals do in their capacity as whole, living animals, not as dead animals or as a series of parts of animals. We have next to study the circumstances under which they do these things, and, most important of all, the limiting factors which prevent them from doing certain other things. By solving these questions it is possible to discover the reasons for the distribution and numbers of animals in nature."

The second goal can be realised by constructing a mathematical model to describe, when the population processes are combined, the dynamics of a population; it was with this in mind that ecological modelling was developed. Ecological modelling, particularly in entomology, gained credence in the 1920's due to economic considerations, in that it offered a tool for use in resource management (Kingsland 1985), and came of age when Vito Volterra and Alfred Lotka used a series of analytical models to investigate fluctuations in populations. With the advent of increased computing power in the 1960's and 1970's population dynamics models were being developed that could predict population changes over a number of generations. Nowadays the prediction of population abundances and distributions of insects using temperature dependent mathematical models is being used extensively (De Loach 1974; Woodson & Edelson 1988; Hayakawa *et al.* 1990).

There are many processes and factors that can influence an invertebrate's population dynamics, in particular, biotic processes (for example, density

dependent processes and predator-prey dynamics) and abiotic factors (for example, the effects of temperature or relative humidity). Across the geographic range of a terrestrial invertebrate the importance of the biotic and abiotic mechanisms that contribute to its population dynamics is likely to vary. For example research in Holland has shown that the high population numbers found on the lowland heaths are greatly influenced by density dependent processes (Smidt 1977; Brunsting 1982); this aspect of the population dynamics of the heather beetle is discussed in more detail in Chapter Three. However as the population numbers of the *L.suturalis* found on the moorlands of the north of England and Scotland, where it is at its most northerly extreme, are relatively low and localised it is likely that abiotic processes, in particular temperature, relative humidity and food quality are the main factors influencing the population dynamics.

Given that *L.suturalis* is monophagous, feeding exclusively on *C.vulgaris* this study investigated its population dynamics focussing on the role of temperature as it is considered by many researchers to have the greatest effect on the development of poikilotherms (Birch 1948; Andrewartha & Birch 1954; Lamb & Gerber 1985; Aldyhim & Khalil 1993; Manel & Debouzie 1995), and its food quality.

Having decided on the area of investigation, the study aimed to answer the following four questions: -

1. Do the host plants growing in different soils and at different altitudes affect the abundance and distribution of *L.suturalis*?
2. Will the predicted increase in mean daily temperatures; as a consequence of global climate change, affect the abundance and distribution of the species?
3. Which, if any, of the beetles' life stages are the most important in controlling its population viability?

4. Finally, if conservation or moorland managers wished to attempt to control population numbers, where in the beetle's life cycle would it be best to concentrate their efforts?

In an attempt to answer these questions, this study aimed to test four hypotheses: -

1. That the life history parameters of *L.suturalis* are dependent on temperature.
2. That *C.vulgaris* sourced from different sites has an effect on *L.suturalis* larval growth.
3. That the altitude and the soil type at which a population exists, will have an effect on *L.suturalis* population viability.
4. That any predicted increases in daily mean temperatures, as a consequence of climate change, would affect the viability of *L.suturalis* populations.

1.5 Thesis structure

Chapter Two investigates *Lochmaea suturalis* population dynamics and begins with a brief introduction to the study of population dynamics and a summary of published research on *L.suturalis* life history. This is followed by the methodology for *L.suturalis* collection and culturing, and a series of laboratory based experiments that quantify the effect of temperature on sex ratio, fecundity, life stage development period, life stage mortality rates and overwintering and emergence temperature thresholds. It concludes with the analysis and discussion of the results in the light of the first hypothesis and established research on *L.suturalis* and related invertebrates.

Chapter Three investigates the relationship between *Lochmaea suturalis* larval growth and *Calluna vulgaris*, sourced from the study sites. It begins with a brief introduction to *C.vulgaris* and insect-plant interactions and a summary of published research on *C.vulgaris* life history and its relationship with *L.suturalis*. It is followed by the methodology for the laboratory analysis of *C.vulgaris* total soluble nitrogen and total soluble tannins. This is followed by the methodology for *C.vulgaris* seedling propagation, and a host plant and *L.suturalis* larval growth experiment. It concludes with the analysis and discussion of the results in the light of the second hypothesis and established research on *C.vulgaris* and *L.suturalis* - *C.vulgaris* interaction.

Chapter Four deals with the construction of the *L.suturalis* computer simulated population dynamics model. It begins with a general introduction to modelling and an overview of the model. The methodology for the construction of the various components of the computer model follows with the analysis and integration into the model of the population parameters, the daily mean temperature generator and the stochasticity element. The analysis of the results of the model population outcomes, over a range of altitudes and temperature

regimes, with particular reference to population viability and the testing of the fourth hypothesis follows. It is completed with a discussion of the results in relation to the third and fourth hypotheses and the use of the model in relation to the prediction of population viabilities in the light of possible global temperature change.

Chapter Five begins with an introduction to the concept of sensitivity and uncertainty analysis and its importance in understanding the behaviour of biological systems models. This is followed by the methodology of various statistical analyses to test the models' sensitivity and output uncertainty using a Latin Hypercube Sampling regime. It concludes with a discussion of the results.

Chapter Six completes the thesis with a general discussion of the study and an assessment of the four hypotheses and an appraisal of the model in terms of its use as a management tool in conservation management scenarios. It concludes with suggestions for further research.

Chapter Seven lists the references cited in the thesis.

Chapter Eight contains two appendices: the program code for the *Lochmaea suturalis* population dynamics model and the study site details and the criteria used for selection of the study sites.

Chapter 2: Quantifying some aspects of the population dynamics of *Lochmaea suturalis*

2.1 Introduction

Population dynamics is how a population changes whilst subject to factors that contribute over a period of time, to the potential for a change of numbers in that population. These factors can be external, i.e. temperature or food quality; internal i.e. density dependent regulation; the result of emigration and immigration or, as is often the case, a combination of all three. In its simplest form this involves an initial state, i.e. population size, under the influence of the various life processes, such as natality and mortality, over a set time period. At the end of this period the population may have remained steady, increased, decreased or become extinct.

This chapter quantifies the life stage parameters of the beetle empirically, with a sequence of controlled laboratory experiments. These experiments were conducted for two reasons. Firstly they fill a gap in scientific knowledge as a literature review of available published research on the heather beetle found that several researchers in the UK and on the continent had investigated various aspects of *L.suturalis*, but the research was generally concentrated on field studies. Secondly, to provide life stage parameters for the population dynamics model, as it is of paramount importance in the construction of a mathematical model that attempts to describe the population dynamics of an invertebrate, that definitive and meaningful life stage parameters are employed. As the following account illustrates these were not available.

L.suturalis exhibits a univoltine life cycle with overwintering immature adults emerging in early March (Cox 1976), March-April (Cameron *et al.* 1944; Waloff 1987; Webb 1989) and April-May to late June-early July (Vagn Jensen & Nielsen 1985b). During the early stages of emergence the adults climb on to

the heather and begin to feed, returning to the overwintering sites if environmental conditions deteriorate (Cameron *et al.* 1944; Waloff 1987).

Once emergence is completed the adults, (see Figure 2-1, page 15) disperse by flight on warm, sunny, windless days; although if these conditions change abruptly, the beetles immediately return to the heath. During this period of dispersal sexual development takes place followed by copulation and oviposition, with Waloff (1987) noting that once maturity is reached flight ability is lost. Oviposition occurs throughout April, May and June (Waloff 1987), between mid-May and late July (Cox 1976), between May and June (Brunsting 1982) and in May (Vagn Jensen & Nielsen 1985b). The eggs are yellow-brown in colour, spherical and c. 1 mm in diameter. They are laid either singly or in groups of two or three (Cox 1976) on the understorey of *C.vulgaris*; in particular, on stem bases and often on *Sphagnum* species (Scandrett & Gimingham 1991), plant debris (Waloff 1987) and stems and leaves (Cox 1976). After copulation and oviposition the adults begin to die, with some surviving until late June (Brunsting 1982; Vagn Jensen & Nielsen 1985b), late July (Cox 1976) or as Waloff (1987) indicates, until August when they overlap with the new generation adults.

Egg hatching occurs between early June to late July with a few specimens in September (Vagn Jensen & Nielsen 1985b), in June (Scandrett & Gimingham 1991), between May and August (Brunsting 1982; Schaick Zillesen & Brunsting 1983), between June and August with peak numbers in July (Cox 1976; Waloff 1987). Larval development takes four to five weeks (Cox 1976). There are three instars, (see Figures 2-1 & 2-2, pages 15 & 16) with the first instar reaching 1.0-2.25 mm in length, the second instar 2.5-3.25 mm and the third instar at maturity 4.5-6.0 mm (Paterson 1931). However Scandrett & Gimingham (1991) give a figure of c. 20 mm in length at maturity, which appears to be spurious. The larvae feed on leaves and the cortex of young shoots (Scandrett & Gimingham 1991), leaves and stem of Ericaceae (Cox 1976), stem apices, leaves and bark of young shoots (Gimingham 1972). Smidt

(1977) noted that the larvae feed at night on shoots and leaves and, as a defence mechanism, drop promptly to the ground at the slightest noise, whilst during the day they remain undercover in humid moss and litter.

L.suturalis pupae, (see Figure 2-1, page 15) are bright yellow in colour, with pupation occurring within earthen cells in the bryophyte layer or below the soil surface between early August and mid-September (Cox 1976). Vagn Jensen & Nielsen (1985b) found pupae in early August in the upper raw humus layer. Eclosion takes three weeks with the new generation adults emerging between late August and late September (Grimshaw 1911), early August (Cox 1976). The new generation adults feed on the foliage and accumulate yellow, flocculent fat, remaining immature during this period. New generation adults overwinter in the litter and upper raw humus layers of the soil; Waloff (1987) includes ground cover bryophytes as an overwintering site with the onset between mid-September and late October; Cox (1976) gives a final date for overwintering of 13th November. The new generation adults remain overwintered until conditions both physiologically and environmentally are right for spring emergence. This completes the life cycle of *L.suturalis*. The life cycle is shown graphically, (see Figure 2-2, page 16).

As can be seen from this account of previous researchers' findings there is considerable variation in the seasonal timings of life stages and there is little or no quantification of the life history parameters or the effect of abiotic influences on the success, or otherwise, of *L.suturalis*' ability to complete its life cycle. This is due to the fact that the majority of the work focussed on field-scale surveys and observations. The knowledge gained from this research is important in its own right but the *scale* and *focus* of the research is inadequate for integration into a mathematical model. As successful population dynamics models require definitive life stage parameters it was necessary to conduct a series of experiments to quantify the major life stage parameters.

For *L.suturalis* these were sex ratio, fecundity, egg, larval, pupal, adult and new generation adult mortalities, egg to larva, larva to pupa and pupa to adult development periods and the emergence and egg-laying temperature threshold temperatures.

Furthermore, population dynamics models require a driving variable that underlies and influences the life stage parameters. It was therefore necessary to investigate the life stages of *L.suturalis* with respect to one or more abiotic influences. As a range of abiotic factors influence all of the life stage parameters of invertebrates, and as a consequence of time constraints, it was necessary to focus on those factors that are the most significant. Andrewartha (1970) considers that there are five components to the environment that influence an invertebrate's chance to survive and reproduce. These are the weather, resources (food), mates, malentities (hazards) and predators, pathogens and aggressors. As weather and food are the only universal components of the animal's environment these were chosen as the influencing factors to study.

As mentioned earlier, this section of the thesis investigates the effect of temperature on the various life stages of *L.suturalis*. As a consequence the experiments have three roles. Firstly they contribute to, and fill gaps in the knowledge about *L.suturalis*, secondly they are analysed to test the hypothesis that temperature has an effect on the life stage parameters, and thirdly the results are incorporated into the temperature driven population dynamics model as the temperature dependent life history parameters.

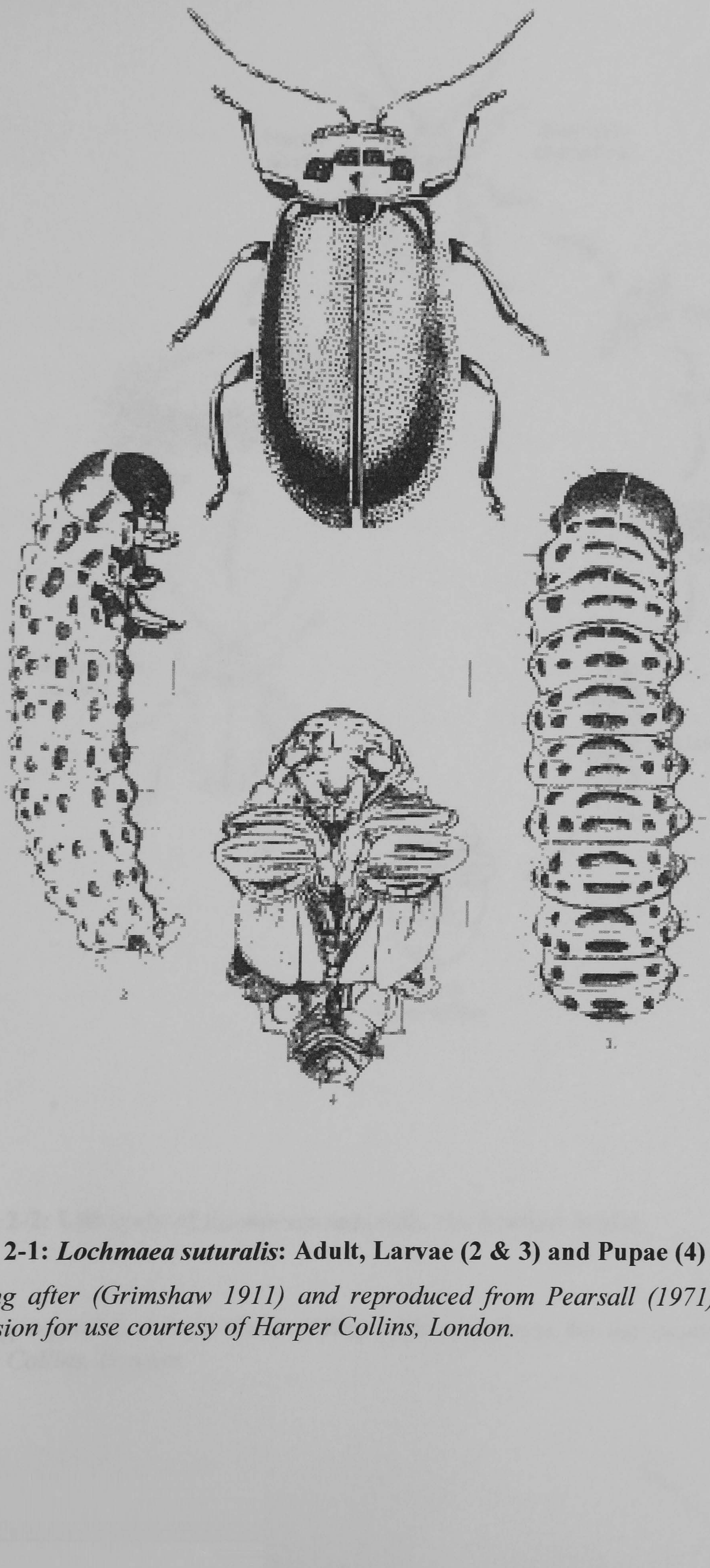


Figure 2-1: *Lochmaea suturalis*: Adult, Larvae (2 & 3) and Pupae (4)

Drawing after (Grimshaw 1911) and reproduced from Pearsall (1971) with permission for use courtesy of Harper Collins, London.

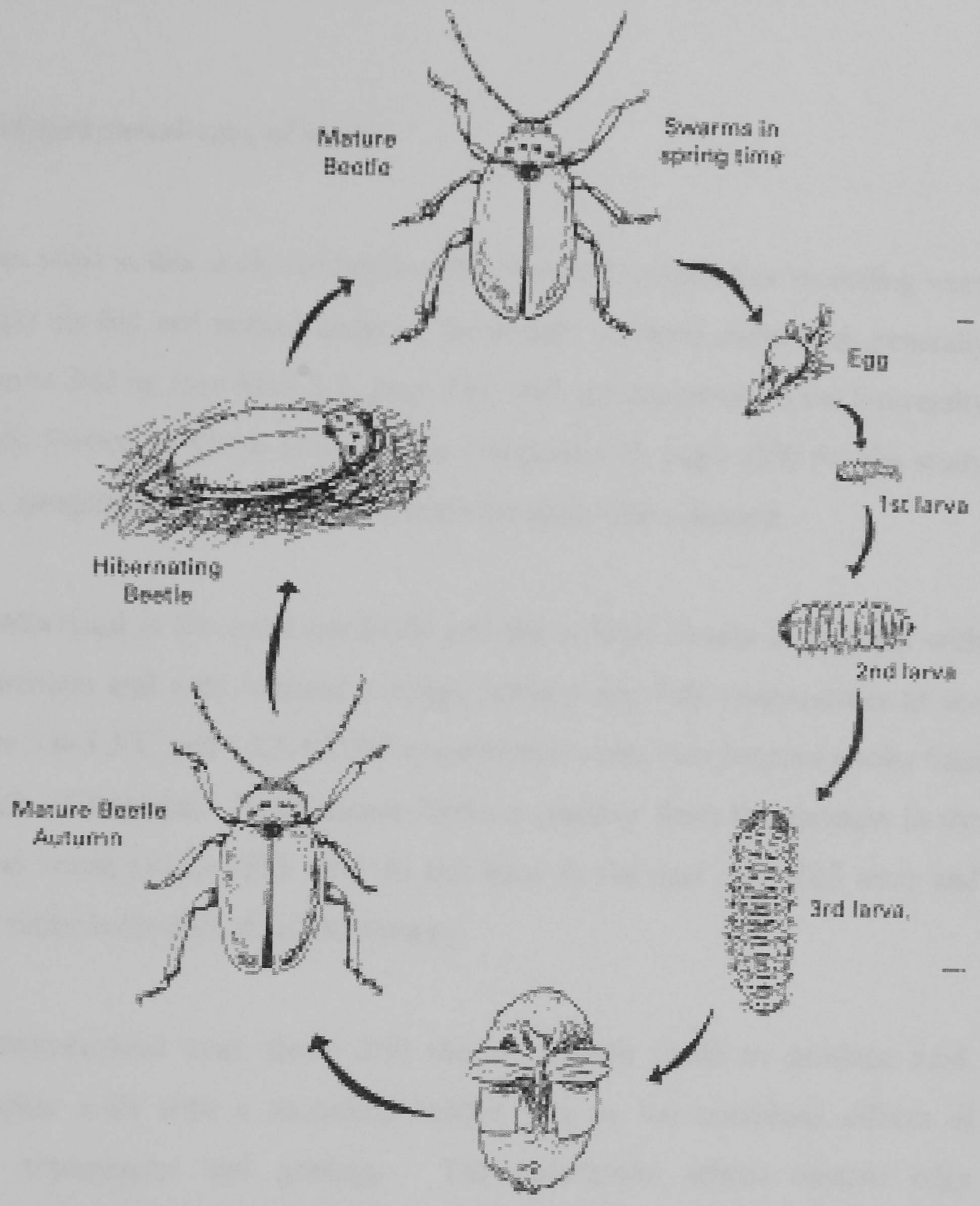


Figure 2-2: Life cycle of *Lochmaea suturalis*, the heather beetle

Drawing reproduced from Webb (1986) with permission for use courtesy of Harper Collins, London.

2.2 Materials and methods

2.2.1 Geographical area of study

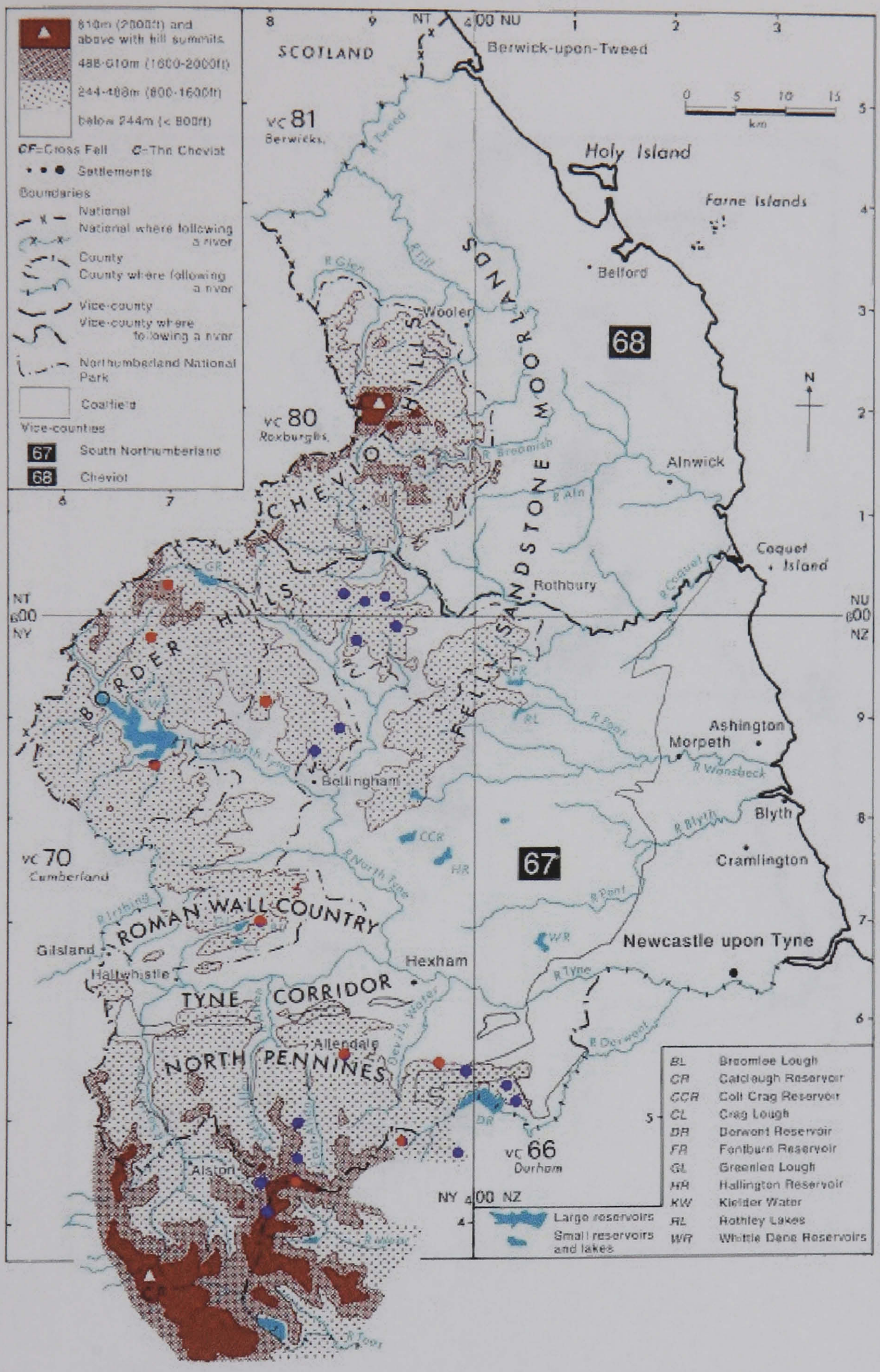
The sites used in this study for beetle collection and temperature recording were all within the hill and upland areas of the county of Northumberland; generally land above 200 m, (see Map 2-1, page 19), with the exception of the University Research Station at Close House. See (Appendix II, page 290) for the study site list, geographical location and criteria for study site selection.

Northumberland is the most northerly and the coldest county in England with cool summers and cold winters; average January and July temperatures at sea level are 3.0-3.5°C and 14.5-15.0°C respectively; some two degrees cooler than the south of England. Precipitation forms a gradient from the greatest in the west and south (1145-1525 mm) to the least in the east (635-825 mm) and broadly reflects the altitudinal differences.

In Northumberland land above 200 metres altitude tends to produce acid, oligotrophic soils with a moorland habitat due to the combined effects of climate, topography and geology. The moorlands, whose eastern edge coincides approximately with the 890 mm isohyet (Swan 1993), can be broadly divided into two *Calluna* vegetation communities. Those that overlay the Carboniferous grits and shales south of the Tyne corridor and the Carboniferous sandstones in the north of the region tend to be *C.vulgaris* dominant communities growing on a variety of thin, acidic podzols, (see Map 2-2, page 20). Whilst those to the west, on the Border hills plateau, under the influence of the greater precipitation and colder temperatures have tended to produce ombrogenous and blanket mires with a co-dominant *Calluna vulgaris* - *Eriophorum vaginatum* community, (see Map 2-3, page 21). These combined

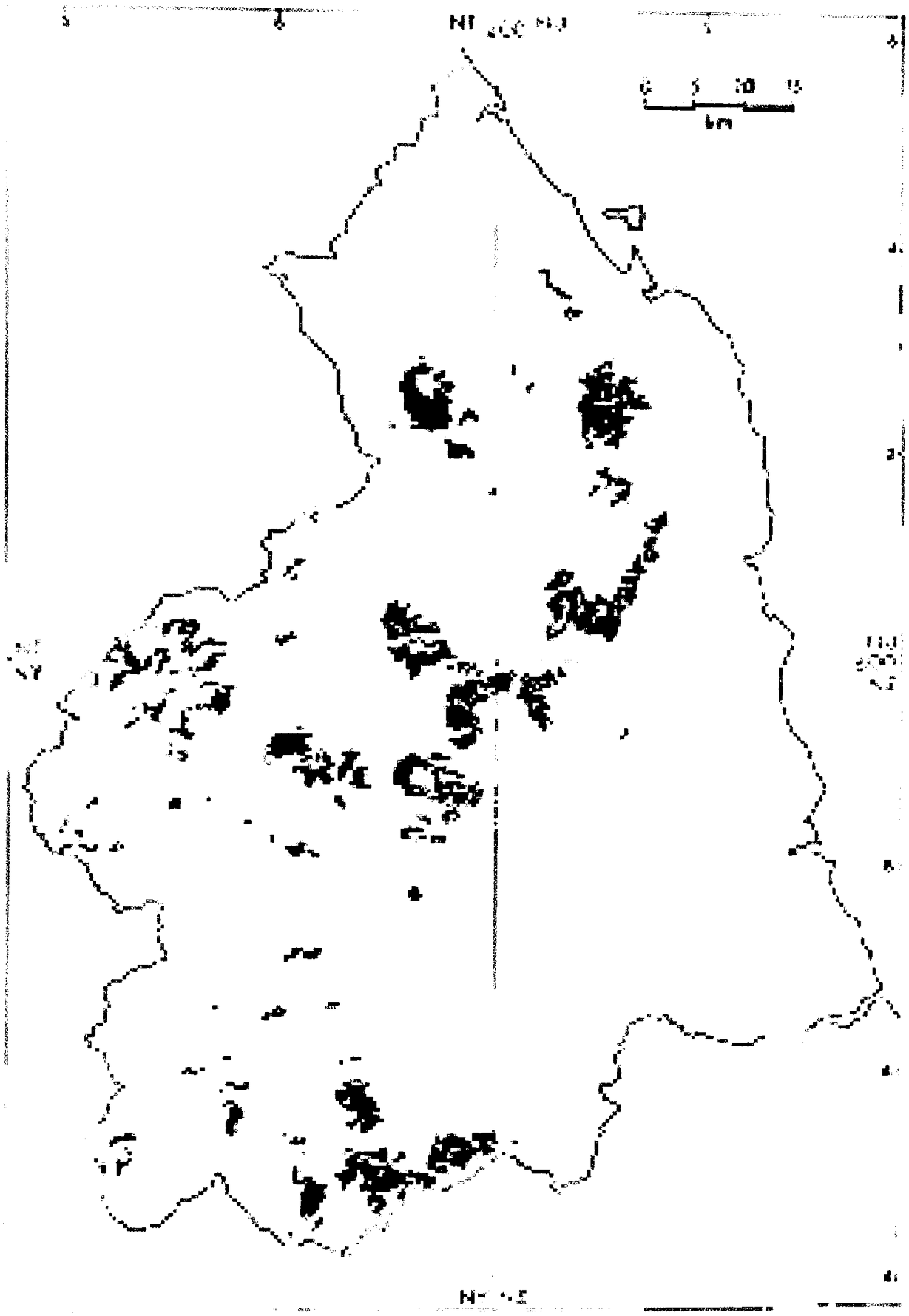
habitats comprise the 'moorlands' and as such account for some 30% of the total 5032 km^2 of the county (Swan 1993). These moorlands are generally managed as extensive hill farms for sheep and cattle or as grouse moors.

Close House field station was used as one of the temperature recording sites and for the laboratory and culture studies both for the beetle and the heather. It is situated approximately 16 km west of Newcastle upon Tyne on the northern bank of the River Tyne at approximately 35 metres OD. It is managed by the Department of Agriculture and Environmental Science at the University of Newcastle upon Tyne and incorporates both animal and plant science facilities.



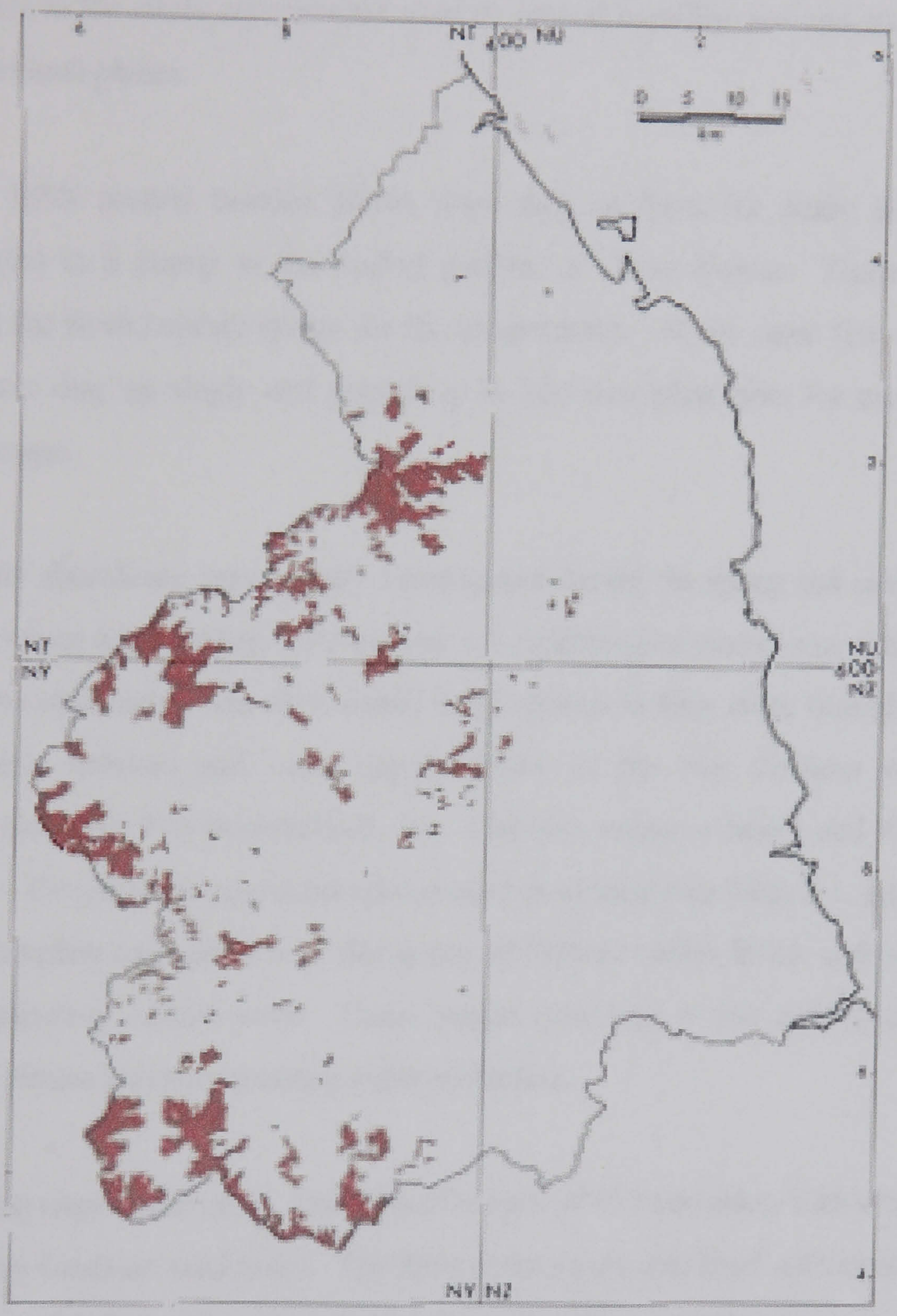
Map 2-1: The River Tyne catchment in the county of Northumberland; blue spots – *Lochmaea suturalis* sampling sites, red spots – study sites

Map reproduced from Swan (1993) with permission for use courtesy of the Natural History Society of Northumbria, Newcastle upon Tyne.



Map 2-2: Distribution of *Calluna vulgaris* heath in Northumberland

Map after (Lunn 1976) and reproduced from Swan (1993) with permission for use courtesy of the Natural History Society of Northumbria, Newcastle upon Tyne.



Map 2-3: Distribution of *Calluna vulgaris – Eriophorum vaginatum* mire in Northumberland

Map after (Lunn 1976) and reproduced from Swan (1993) with permission for use courtesy of the Natural History Society of Northumbria, Newcastle upon Tyne.

2.2.2 *L.suturalis* collection and culturing

All weights in the study experiments were measured in milligrams and recorded to two decimal places.

In early 1995 several heather plants were dug up from the study sites and transplanted in a clump in the walled garden, at Close House. These plants provided the fresh heather sprigs for the experiments. At the same time mature plants were dug up singly and potted up in 200 mm plant pots for use in the holding cages.

L.suturalis abundance was initially investigated during the spring and summer of 1994 by sweep-net sampling (100 sweeps x 3 replicates) at twenty-one sites in the River Tyne catchment. The sites visited were chosen as they were thought to be good beetle habitats and were representative of the two *Calluna vulgaris* habitats found in Northumberland, *viz. Calluna vulgaris* heath and *Calluna vulgaris – Eriophorum vaginatum* dominated moorland (see Map 2-1, page 19). Further sampling took place over the spring of 1995 to collect larvae and/or adults for the laboratory culture work. Those caught were kept in two holding cages at the Close House insectary awaiting experimentation.

The holding cages were cubic, made from Perspex of 400 mm sides, with ventilation provided by mesh-covered holes. The floor of the cages was lined with moist tissue paper, on which there were four plant pots, each with an established heather plant. Periodically they were watered and inspected for dead beetles, which if found, were removed (see Figure 2-3, page 24).

As very low numbers of larvae were found in the field (see section 2.3.1, page 38) and as the prospect of culturing sufficient numbers of larvae from the adults caught was low, additional larvae were sourced. Dr. Sally Power of Silwood Park, Imperial College, University of London, supplied these. They were caught by

sweep netting on the Surrey Heaths. The larvae were kept in holding boxes at the Close House insectary.

The holding boxes were Perspex, 200 mm x 125 mm x 75 mm, with a detachable lid and mesh-covered holes for ventilation. The floor of the boxes was covered with moist tissue paper onto which fresh heather sprigs were laid. Periodically they were inspected and watered, if dead heather sprigs were found they were replaced and dead larvae, if found, were removed (see Figure 2-4, page 25).

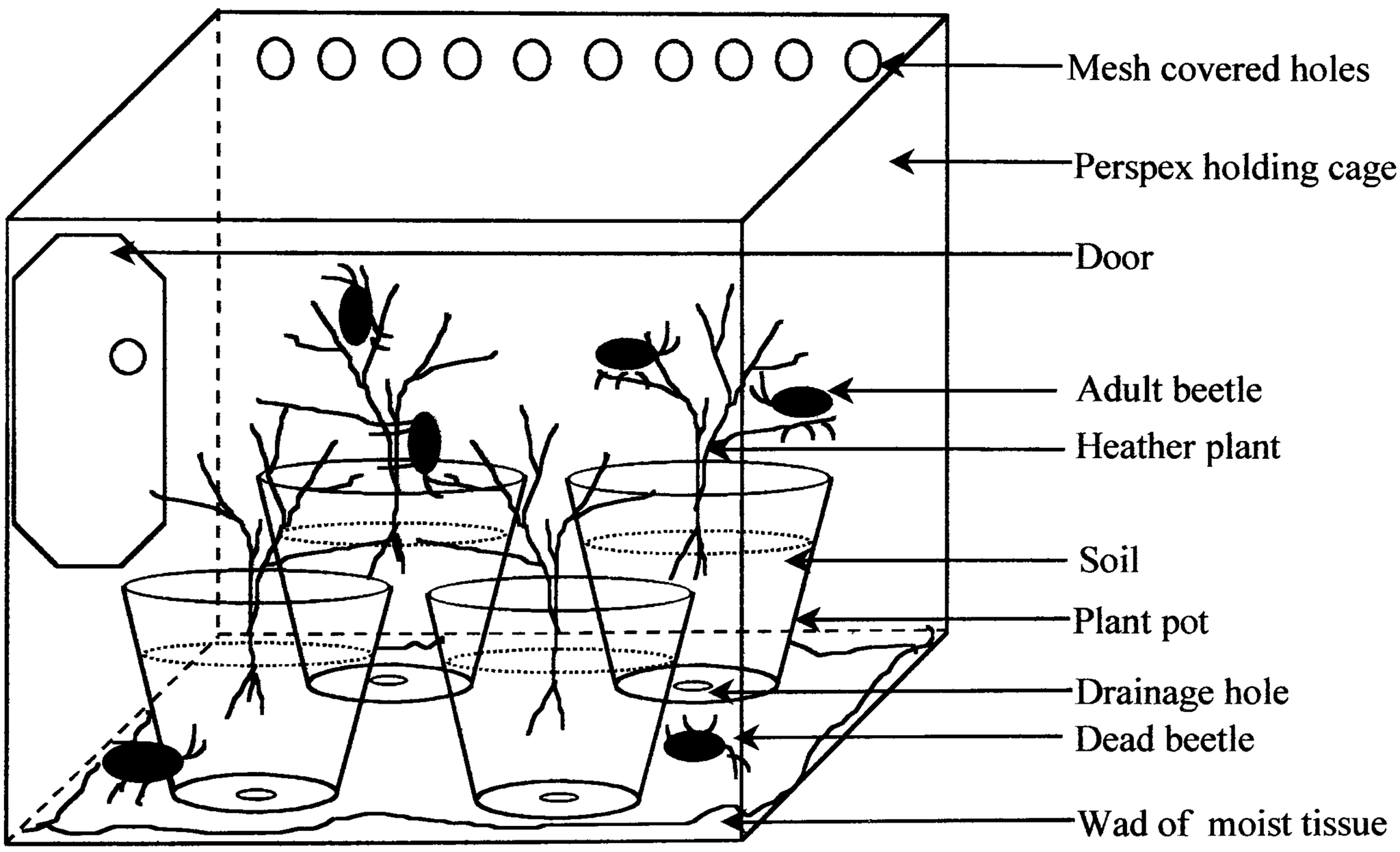


Figure 2-3: Design of the holding cages for *L.suturalis* adults

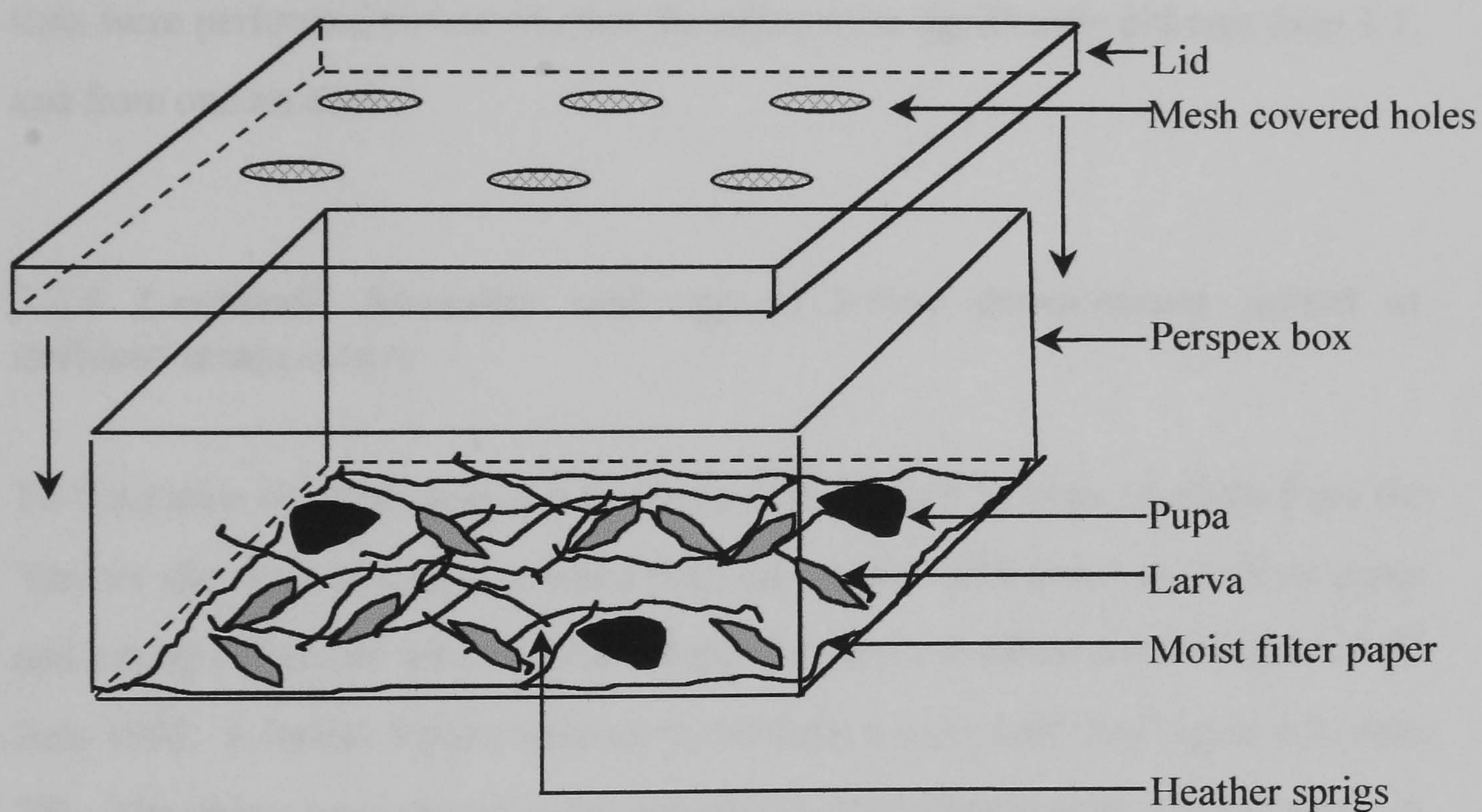


Figure 2-4: Design of the holding boxes for *L.suturalis* larvae

2.2.3 *L.suturalis* sex ratio

The adult sex ratio for both those new generation adults caught in the field by sweep netting at the Yarrow site during the summer of 1995 and the new generation adults cultured at Close House was determined by comparing the third tarsal segment on the hind legs; which is larger in the male (see Figure 2-5, page 27). Chi-squared tests were performed to test whether the ratios were significantly different from 1:1, and from one another.

2.2.4 *L.suturalis* fecundity and egg to larvae development period at ambient temperature

To determine fecundity and egg to larvae development 11 pairs of adults from the Yarrow site were placed in covered petri dishes lined with moist sterile filter paper and a sprig of heather with the stem wrapped in moist sterilised cotton wool on 22nd June 1995. A further 9 pairs were set up similarly a week later (see Figure 2-6, page 28). The dishes were placed in the unheated outdoor insectary at Close House. At intervals of four to five days the dishes were inspected for signs of oviposition, watered and the heather replaced with fresh sprigs. Any eggs that were healthy, i.e. turgid and blemish free were recorded and left. Those appearing to be unhealthy were removed, so as not to increase the chance of infection. As the eggs hatched the larvae were counted and removed to a holding box until needed for further experimentation. Mean numbers of eggs laid per adult pair were calculated.

The egg to larvae development period was determined by calculating the number of days between each of the peaks for each life stage (Southwood 1978). The accumulated day degrees were calculated from the ambient temperature recorded at the Close House weather station, taken as daily means, multiplied by the number of the days of the development period.

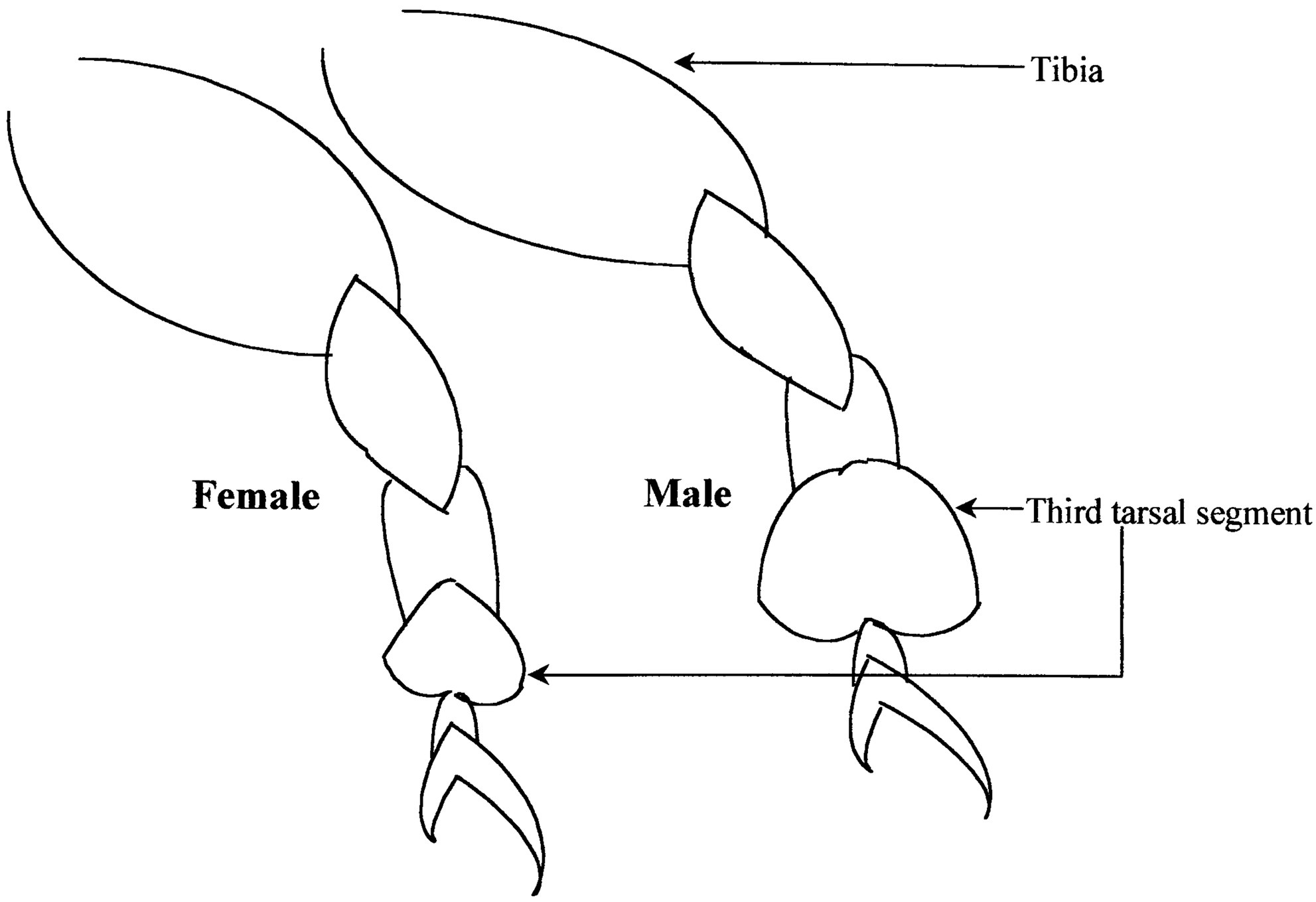


Figure 2-5: Representative drawing of the relative difference in size between sexes of the third tarsal segment of the hind leg of an adult *L.suturalis*

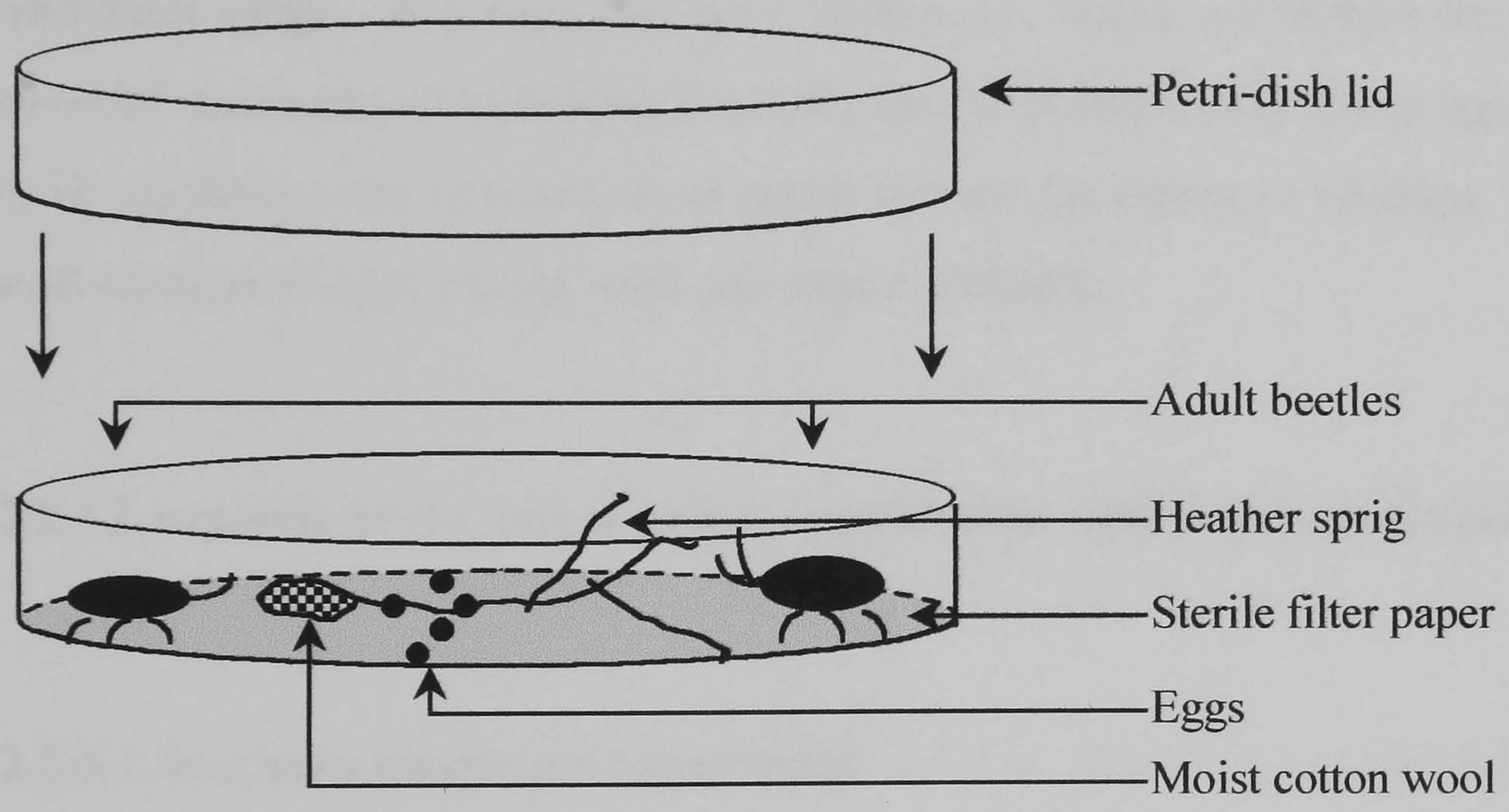


Figure 2-6: Design of the *L.suturalis* sex ratio and fecundity experiment

2.2.5 *L.suturalis* fecundity at controlled temperatures

Fifteen pairs of adults, one male and one female, were placed in covered petri dishes lined with moist sterile filter paper and a sprig of heather on 19th April 1996 (see Figure 2-6, page 28). Five each of the dishes were placed in calibrated incubators at three controlled temperatures (15, 20 and 25°C). At intervals of four to five days the dishes were inspected for signs of oviposition, watered and the heather replaced with fresh sprigs. Any eggs that were healthy, i.e. turgid and blemish free were recorded and removed to holding boxes for later experimentation. Those appearing to be unhealthy were removed, so as not to increase the chance of infection. Mean total numbers of eggs laid per adult pair were calculated.

2.2.6 *L.suturalis* larvae, pupae and new generation adult development periods

2.2.6.1 Southern plastic pot experiment

Larval development and the effects of temperature were evaluated using two sets of larvae. The first set from the Surrey heaths was divided into two groups. The first group of forty larvae were placed singly in a container consisting of two transparent plastic pots (80 mm dia. x 100 mm), inverted one on the other, separated by a plastic lid with a hole large enough for the stem of a sprig of heather to be inserted. The bottom pot was filled with water to the top and the top pot had a 30 mm, mesh-covered hole at the top. A sprig of heather was placed so that the bottom of the stem was immersed in the water and where it passed through the hole of the plastic lid was wrapped in cotton wool so that the larvae could not pass through (see Figure 2-7, page 31). The larvae were placed on the sprig and the forty individual pots were randomly assigned to one of four groups and kept at each of four temperatures (10, 15, 20 and 25°C) in incubators with a photoperiod of 16/8 hours. At intervals of four to six days the larvae were removed and weighed, the heather

sprig was replaced with a fresh one, the water in the bottom container topped up and the incubator checked for temperature control.

2.2.6.2 Southern and northern glass experiments

The second group of forty larvae from Surrey and a group of sixty larvae hatched from eggs laid by adults caught at Yarrow, were placed singly in a 50 x 20 mm cylindrical glass tube, at the bottom of which there was a 5 mm thick, circular piece of floral arrangers water retentive "oasis" into which a sprig of heather was placed. After watering the oasis to saturation, the container was covered with mesh secured by a rubber band (see Figure 2-8, page 32). The forty individual pots and the sixty individual containers were randomly assigned to one of four groups and kept at each of four temperatures (10, 15, 20 and 25°C) in incubators with a photoperiod of 16/8 hours. At intervals of four to five days the larvae were weighed, the oasis watered, the heather sprig replaced and the incubator checked for temperature control.

In all three experiments weighing continued until either, the larvae were dead, they had metamorphosed to the pupal stage, or the number of larvae was less than two, for each temperature. The effect of temperature on life stage development period was derived by recording the number of larvae, pupae and new generation adults progressing through the life stages from the three previous experiments.

Development periods were determined by calculating the number of days between each of the peaks for each of the life stages; larvae to pupae and pupae to new generation adult. The accumulated day degrees were calculated from the relevant temperature regime multiplied by the number of the days of the development period.

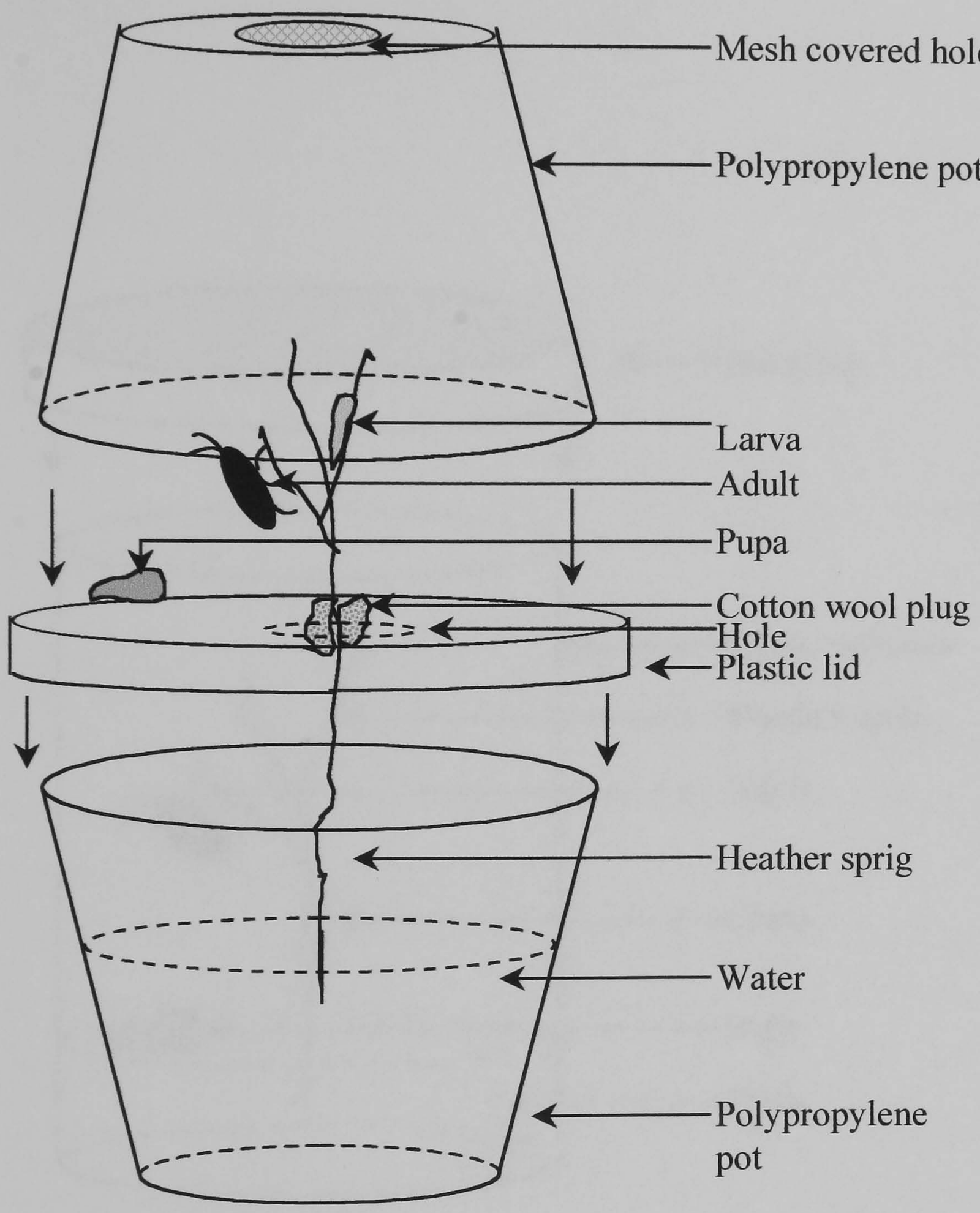


Figure 2-7: Design of the apparatus for the *L.suturalis* larval, pupal and adult development, (plastic pot experiment)

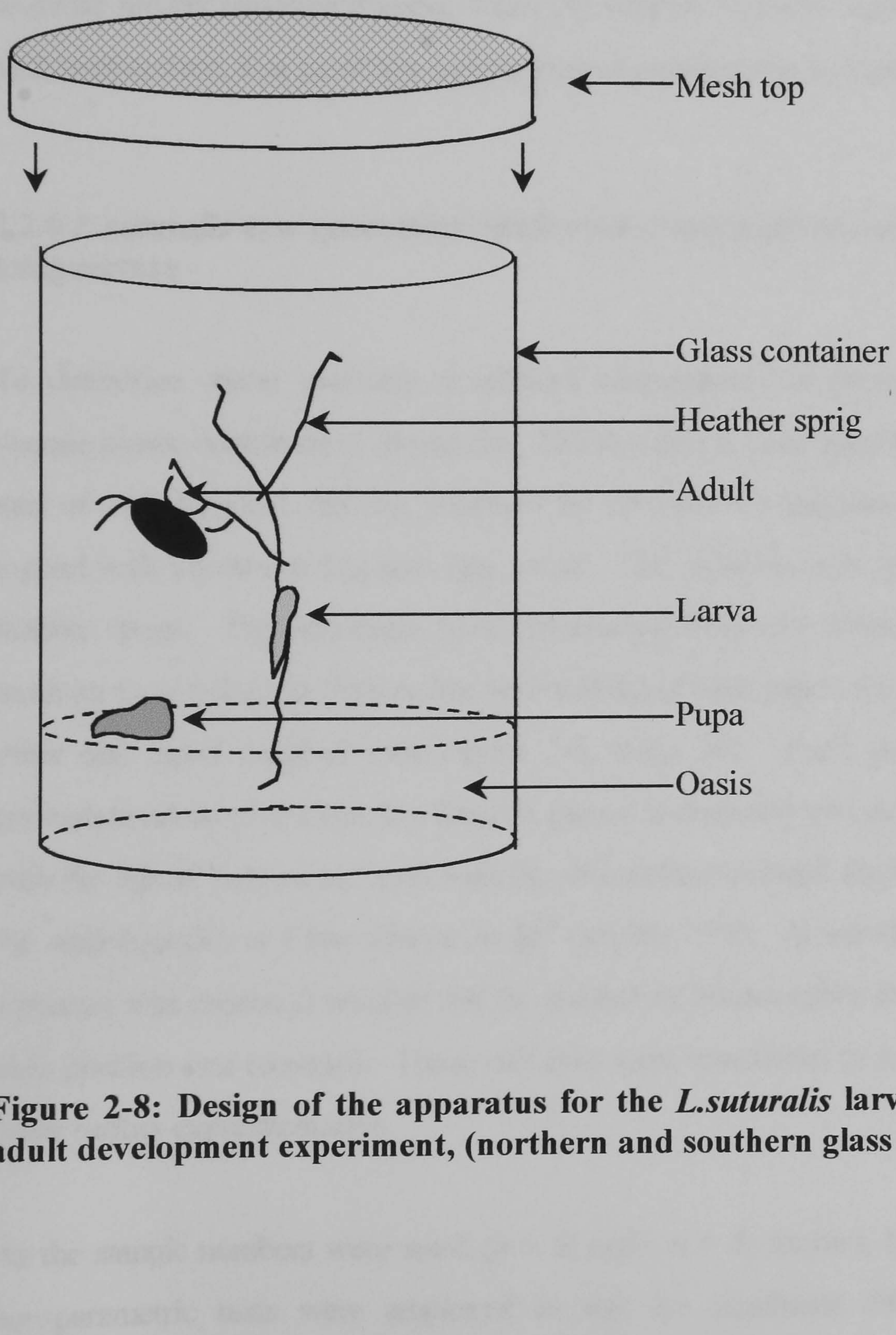


Figure 2-8: Design of the apparatus for the *L.suturalis* larval, pupal and adult development experiment, (northern and southern glass experiments)

2.2.7 *L.suturalis* new generation adult growth

The effect of temperature on new generation adult growth was determined by maintaining the new generation adults in their respective containers (see Figures 2-7 and 2-8, pages 31 and 32). The adults were weighed at weekly intervals for five weeks. At the end of the experiment they were transferred to holding cages to await further experimentation. When the number of adults was less than two for each temperature, that particular temperature experiment was terminated.

2.2.8 *L.suturalis* new generation adult winter mortality at ambient temperature

To determine winter mortality at ambient temperature, six closed, mesh-topped opaque plastic containers (170 mm dia., 120 mm deep), were filled in layers with 60 mm of a peat/podzol mixture, followed by 25 mm of *Sphagnum* spp. moss and topped with 25 mm of *Hypnum* spp. moss. This substrate was 'planted' with 15 heather sprigs. The containers were constructed from two containers, both with mesh covered holes; the bottom one with a lining of filter paper, inverted one on the other and taped together (see Figure 2-9, page 34). Each pot had ten new generation adults (five male, five female), placed in them and was sunk in the ground with the top of bottom pot level with the soil surface amongst the heather plants in the walled garden at Close House on 26th October 1995. At monthly intervals one container was chosen at random and the number of beetles either dead or alive, and their position was recorded. Those still alive were transferred to a holding cage to await further experimentation.

As the sample numbers were small (n = 5; male, n = 5; female), Kruskal – Wallis non-parametric tests were employed to test for significant differences in the mortalities between the sexes and over time.

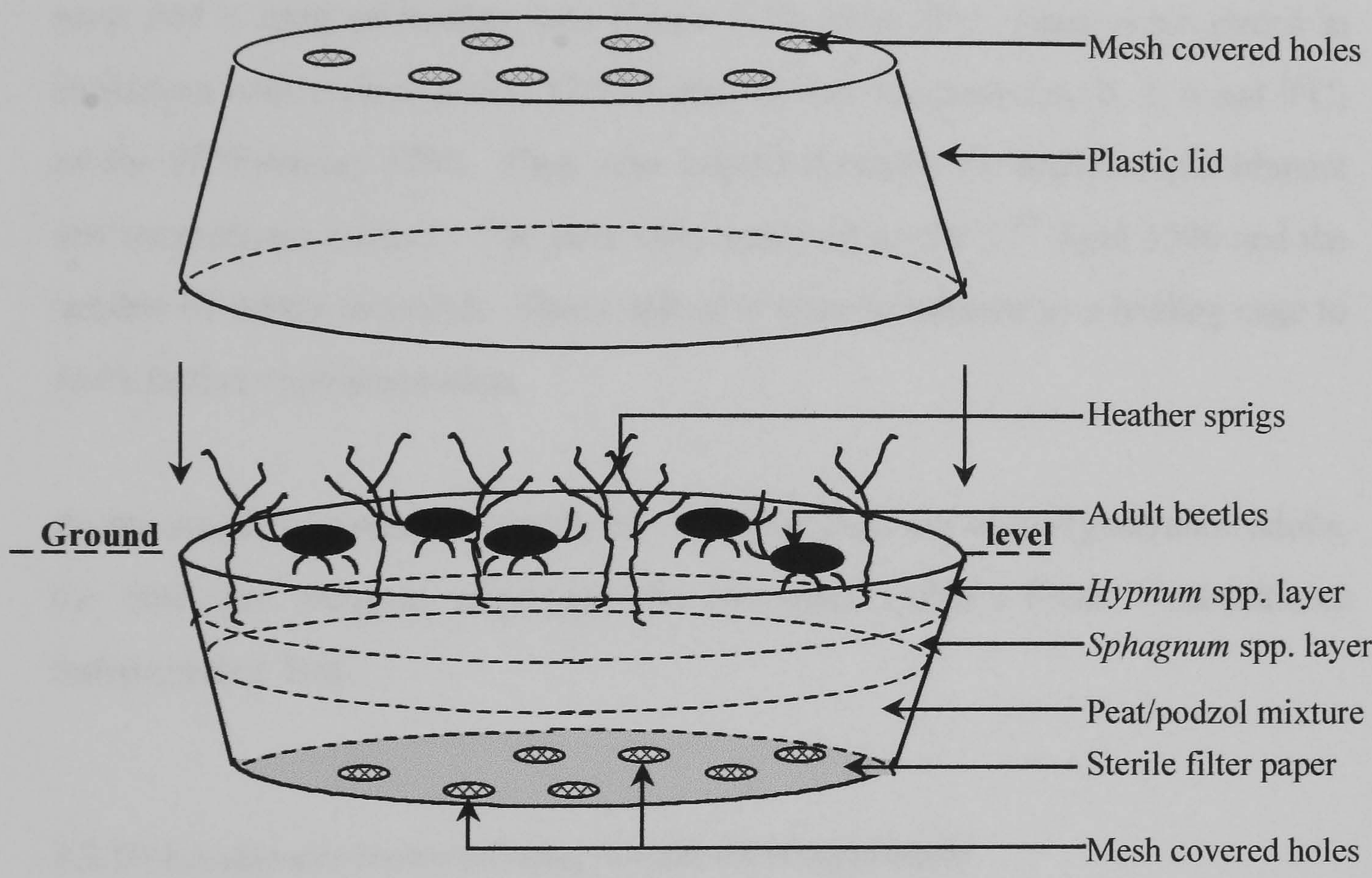


Figure 2-9: Design of the *L.suturalis* overwintering mortality experiment

2.2.9 *L.suturalis* new generation adult winter mortality at controlled temperatures

New generation adult winter mortality at controlled temperatures was evaluated by placing twenty new generation adults, singly, in mesh-topped transparent plastic pots (80 mm dia. x 100 mm), with 40 mm of a 50/50 amorphous peat and A horizon podzol mix topped with a 40 mm 50/50 mix of *Sphagnum* and *Hypnum* spp. of moss and a sprig of heather (see Figure 2-10, page 37). These were placed in incubators with a photoperiod 12/12 hours, at four temperatures (0, 3, 6 and 9°C) on the 19th February 1996. They were inspected weekly for heather replenishment and temperature control. The pots were removed on the 17th April 1996 and the number of deaths recorded. Those still alive were transferred to a holding cage to await further experimentation.

As the sample size was very small, due to limited numbers of new generation adults, the data was analysed employing the two-tailed Fisher's Exact Unconditional Independence Test.

2.2.10 *L.suturalis* overwintering threshold temperature

To determine the overwintering threshold temperature, twenty new generation adults (ten male, ten female), were placed singly in mesh topped transparent plastic pots, (80 mm dia. x 100 mm), with 40 mm of a 50/50 amorphous peat and A horizon podzol mix topped with a 40 mm mix of *Sphagnum* and *Hypnum* spp. moss (see Figure 2-10, page 37). The pots were placed in an incubator with a photoperiod of 12/12 hours, at the beginning of October 1995. Two weeks before the experiment was due to begin four incubators were calibrated for temperature control and at the start date, the temperature was set at 15°C. Every week the pots were inspected to ascertain the position and physiological state of the beetles, and then returned to the incubator and the temperature reduced by 1°C. The

temperature reduction continued until it was decided that all the beetles had entered diapause. This was determined by the observation of the production of a small cell for overwintering in. Beetles from the holding cages replaced any beetles found dead. The depth (in cm) was recorded for any beetles that entered the soil layer and became physiologically inactive.

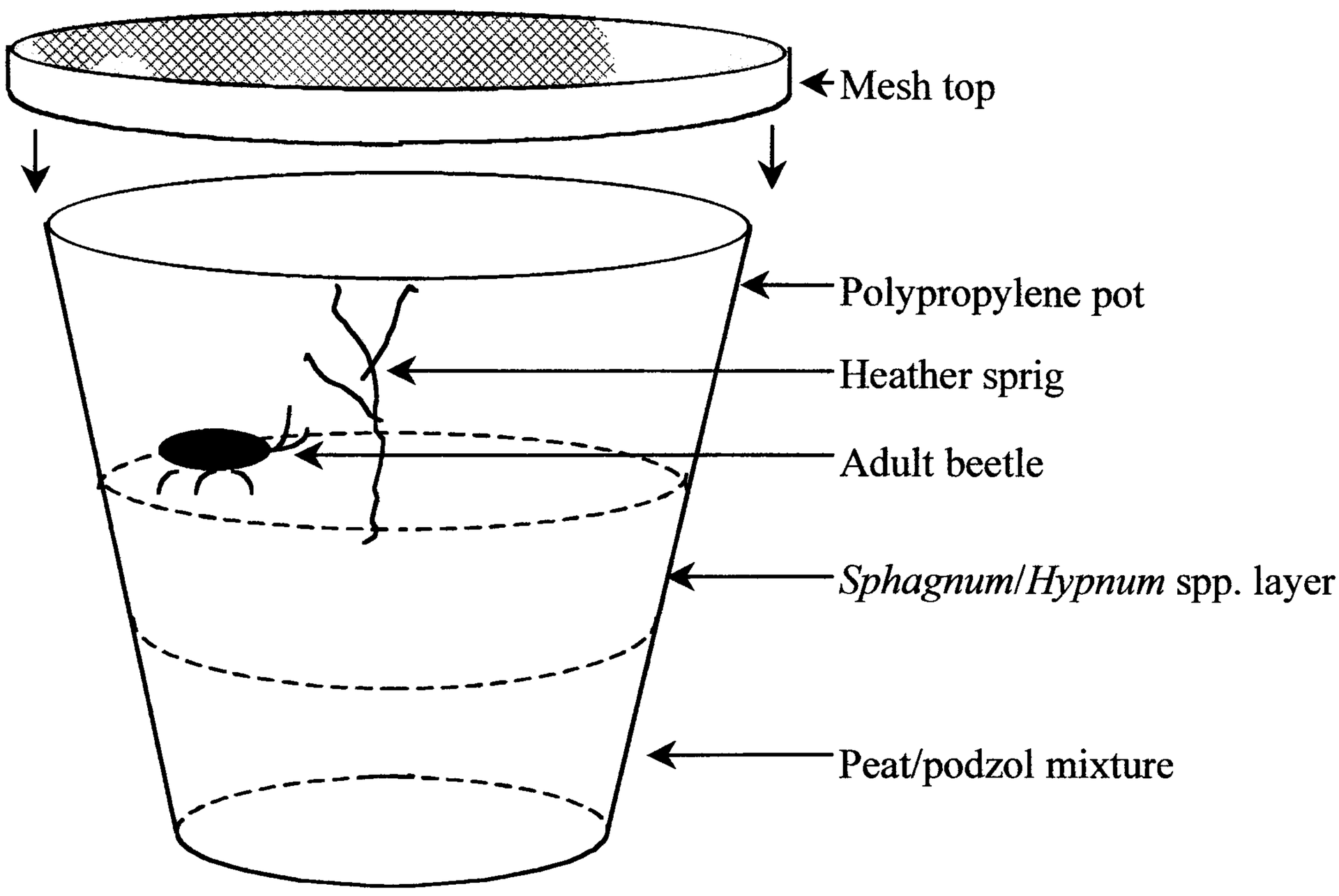


Figure 2-10: Design of the *L.suturalis* overwintering threshold and controlled decreasing temperature mortality experiments

2.3 Results

In all thesis analyses the following statistical significances were used (see Table 2-1) and where appropriate, tests for normality were conducted on the data.

Symbol	Significance	*P* values
NS	not significant at	$P \geq 10\%$
ns	not significant at	$5\% \leq P < 10\%$
*	significant at	$1\% \leq P < 5\%$
**	significant at	$0.1\% \leq P < 1\%$
***	significant at	$P < 0.1\%$

Table 2-1: Statistical significances used in all thesis analyses

2.3.1 *L.suturalis* field sampling and collection

During the spring and summer of 1994 twenty-one sites were visited between three and nine times and sweep-netted for either adult of larval stage *L.suturalis*. Numbers found were very low (see Table 2-2, page 39). The following year in the spring the sites were further visited, but again the numbers caught were very low or non existent, except for the Yarrow (Kielder Water) site where a total of 57 adults were caught between 4.6.95 - 27.6.95.

Site	Grid reference	No. of visits	Mean adults	s.e.	Mean larvae	s.e
Otterburn Ranges	NT890012	3	0.0	-	1.33	0.33
Otterburn Ranges	NT854031	6	0.0	-	7.0	0.73
Otterburn Ranges	NT883014	3	0.0	-	0.33	0.29
Otterburn Ranges	NT934006	3	0.0	-	0.66	0.33
Muggleswick Common	NZ003477	3	0.33	0.29	0.0	-
Edmundbyers Common	NY987446	3	0.0	-	0.0	-
Huntstanworth Moor	NY940466	3	0.0	-	0.0	-
Allendale Common	NY848500	3	0.0	-	1.0	0.58
Thorngrafton Common	NY794662	3	0.0	-	0.0	-
Padon Hill	NY822917	3	1.0	0.58	0.0	-
Kielder Water	NY704869	3	2.66	0.33	0.33	0.29
East Kielder Moor	NY690972	3	13.0	3.51	0.0	-
Ealinghamrigg Common	NY820821	3	0.33	0.29	0.0	-
Corsenside Common	NY873877	3	0.66	0.33	0.0	-
Steng Moss	NY957915	9	0.66	0.38	4.67	0.51
Pithouse Fell	NY984539	3	0.33	0.29	0.0	-
Black Hill	NY795445	3	0.0	-	0.0	-
Swinhope Moor	NY825460	3	0.0	-	0.0	-
Allenheads	NY868455	3	0.0	-	0.0	-
Muggleswick Common	NZ035455	3	0.33	0.29	0.0	-
Muggleswick Park	NZ046490	3	0.0	-	0.0	-

Table 2-2: Mean and standard error of *Lochmaea suturalis* adults caught by sweep netting, (100 sweeps x 3 replicates) over the number of visits at the twenty-one sites in the River Tyne catchment during the spring and summer of 1994

2.3.2 *L.suturalis* sex ratio

The sex ratios (male to female) of the field sampled adults (n = 57), and laboratory cultured new generation adults (n = 122), were 1.00:1.71 and 1.00:1.37 respectively. Chi-squared, 2 x 2 contingency tests were undertaken to test whether the observed sex ratios were different from equal numbers of males and females, and whether they were significantly different from one another. The laboratory cultured adult sex ratio was not significantly different from equal numbers of males and females, however the field-sampled adults were significantly different from equality. A comparison of the two sex ratios shows a highly significant difference in the sex ratios of the field sampled and laboratory cultured adults. The significances are shown below, (see Table 2-3).

Statistical Test	Sex Ratio	X^2	significance	*n*	d.f.
Field sampled versus 1:1	1:1.71	3.94	*	122	1
Laboratory cultured versus 1:1	1:1.37	2.66	NS	57	1
Field versus laboratory	-	55.1	***	179	1

Table 2-3: Chi-squared test for difference of field sampled and laboratory cultured adult sex ratios from 1:1, and from each other

2.3.3 *L.suturalis* fecundity and egg to larvae development at ambient temperature

The first group of 11 pairs of adults had a mean fecundity of 35.09 (s.e. 6.28) and the second group of nine, 37.67 (s.e. 7.96). The mean number of eggs laid per adult

pair and those successfully hatching to the larval stage are shown graphically (see Figures 2-11 and 2-12, pages 42 and 43).

The accumulated day degrees for the egg to larvae development period was derived by taking the mean development period over the two experiments (15 days) and multiplying by the mean daily temperatures over the development period that were collected from the Close House weather station, it was found to be 362°C.

2.3.4 *L.suturalis* fecundity at controlled temperatures

The mean fecundity of the adults at the three temperatures (15, 20 and 25°C) was 7.25 (s.e. 4.31), 39.60 (s.e. 26.60) and 51.4 (s.e. 27.81) respectively (see Figure 2-13, page 44).

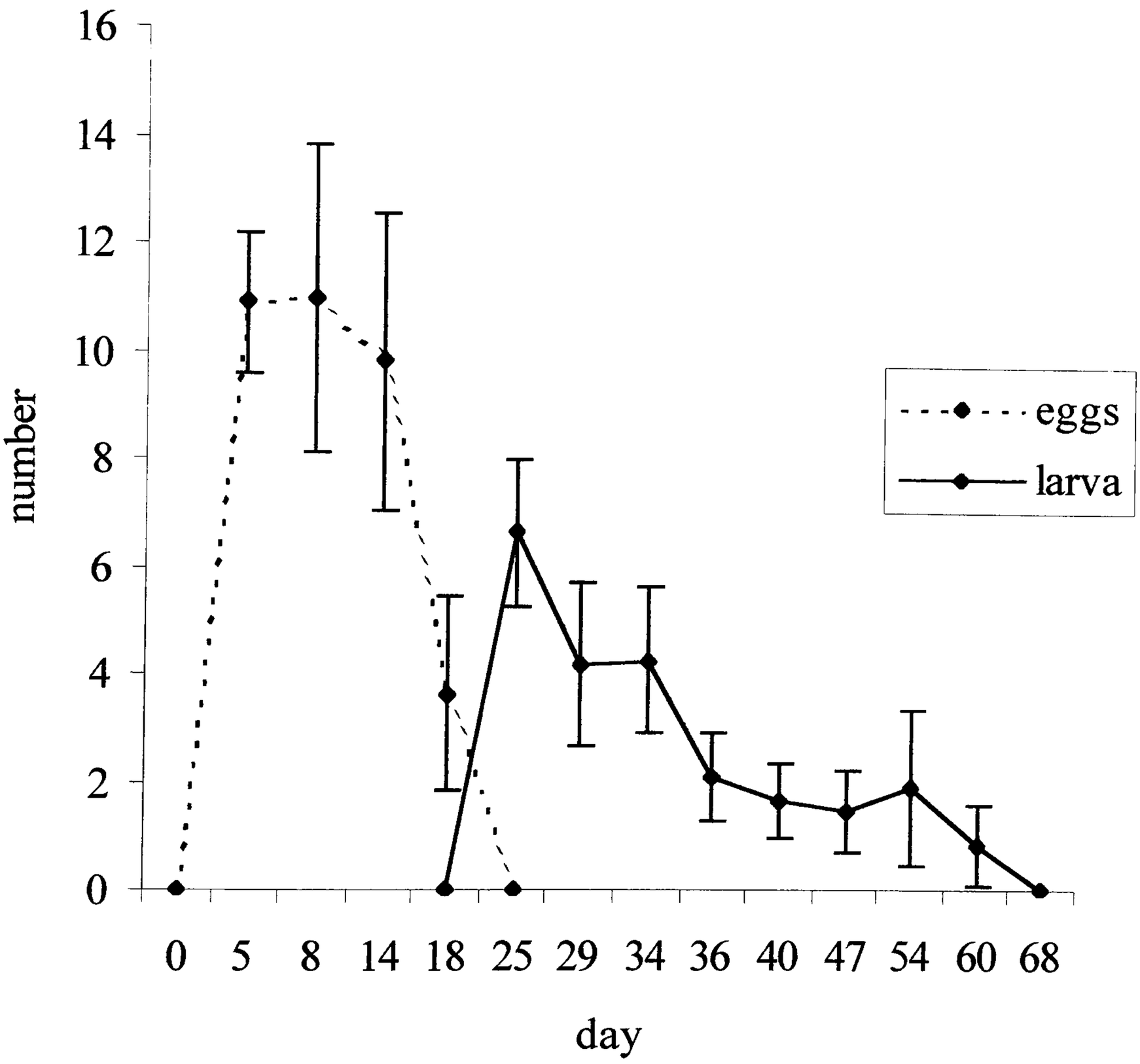


Figure 2-11: Mean and standard error (*n*=11) of the number of eggs laid per adult pair of *L.suturalis* and successful hatching to larval stage, cultured at ambient temperature; first experiment

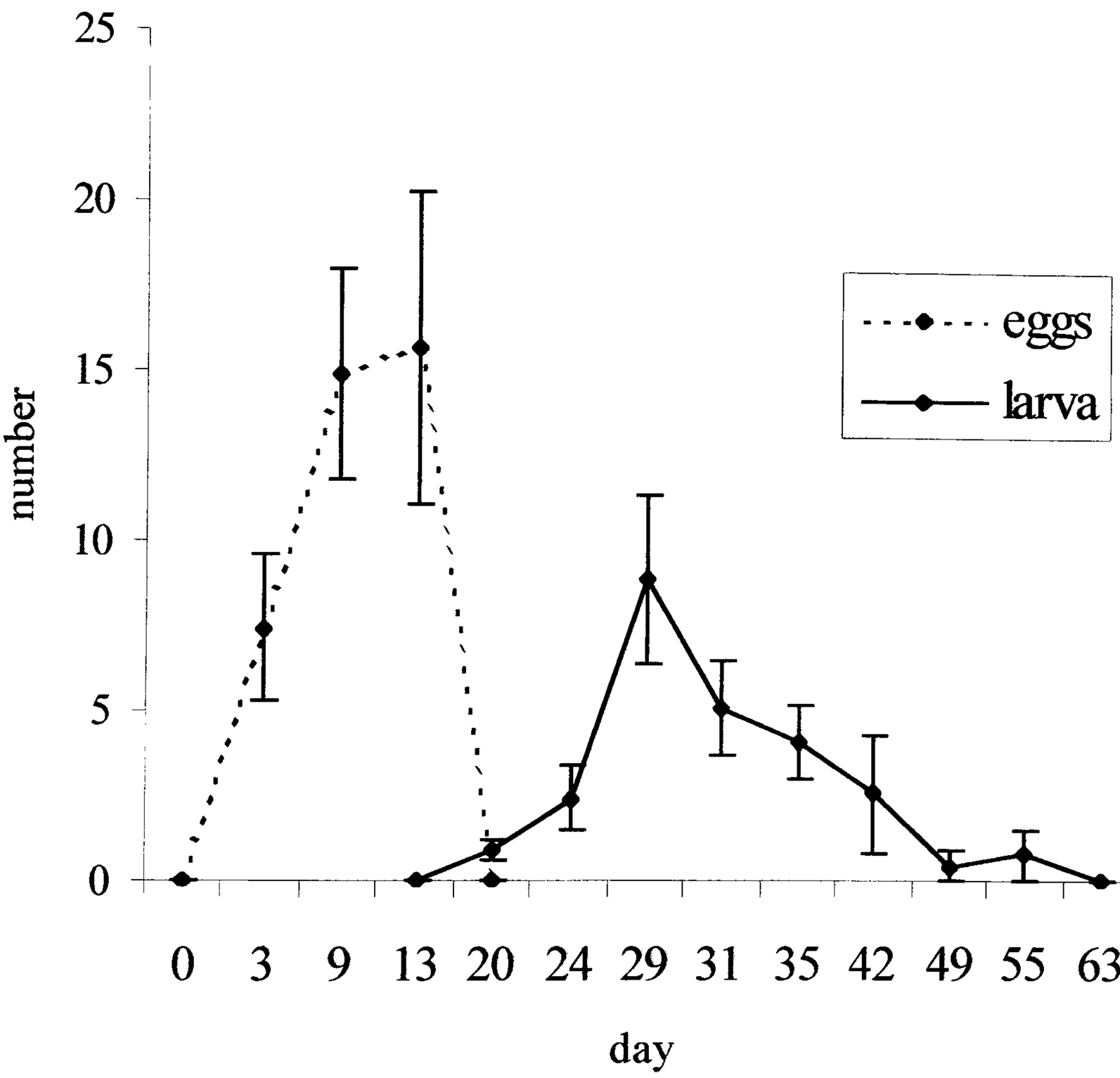


Figure 2-12: Mean and standard error (*n*=9) of the number of eggs laid per adult pair of *L.suturalis* and successful hatching to larval stage, cultured at ambient temperature; second experiment

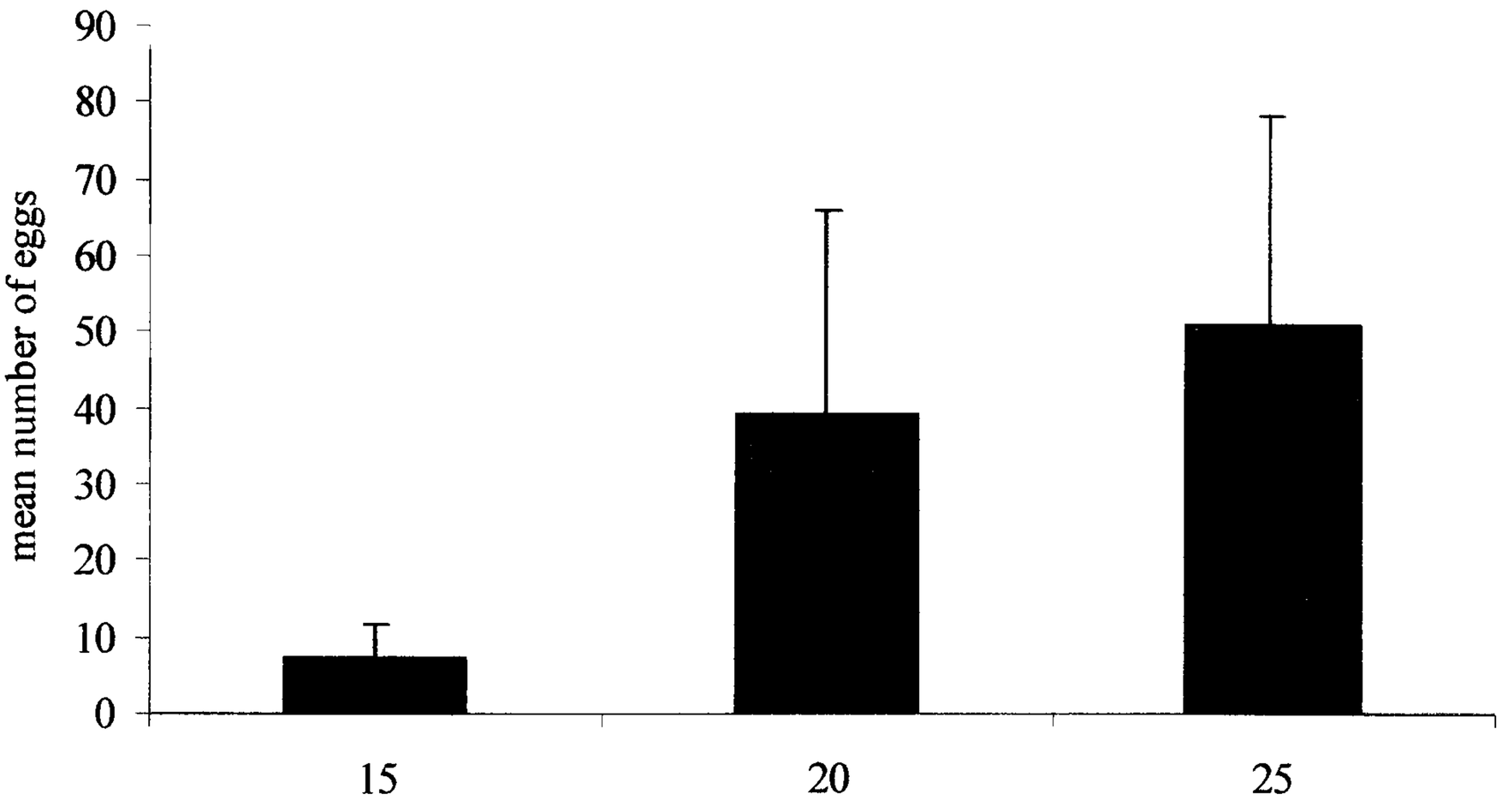


Figure 2-13: Mean (*n*=5) and standard error of the total number of eggs laid per pair of *L.suturalis* adults at 15, 20 and 25°C

2.3.5 *L.suturalis* larval growth and temperature

There was a noticeable effect of temperature on the growth of the larvae with a greater increase in weight per unit time as temperature increased. The larvae in the northern glass experiment at 10°C failed to thrive and all died (see Figures 2-14, 2-15 and 2-16, pages 48, 49 and 50).

A linear regression analysis was undertaken for each of the positive linear phases of each growth curve for the three experiments. The positive linear phase was determined, by inspection, as the initial section of the growth curve that exhibited continuous larval weight gain (see Table 2-4). The coefficients of the slope of the lines, *m* were plotted against the four control temperatures (see Figure 2-17, page 51).

Experiment	**T°C**	***m*** **(slope)**	***significance***	r^2
Southern plastic	10	0.16	***	0.91
	15	0.55	***	0.94
	20	0.79	***	0.95
	25	1.65	*	0.96
Southern glass	10	0.25	***	0.99
	15	0.75	*	0.91
	20	0.77	*	0.95
	25	0.95	*	0.89
Northern glass	10	0.04	**	0.94
	15	0.29	***	0.97
	20	0.45	***	0.96
	25	0.90	*	0.94

Table 2-4: The regression coefficient of the slope, *m*, the significance and r^2 for the three *L.suturalis* larval growth experiments

A further linear regression of these results was undertaken to compare the larval growth weight gains at each of the temperatures (see Table 2-5).

Experiment	***m*** **(slope)**	***significance***	r^2
Southern plastic	0.094	*	0.93
Northern glass	0.057	*	0.96
Southern glass	0.042	ns	0.82

Table 2-5: The regression coefficient, *m*, the *P* value with significance, and r^2 for the three *L.suturalis* larval growth experiments

The results show that larval weight gain increases in a linear relationship with the four control temperatures for the southern plastic and northern glass experiments, $b \neq 0$ at $1\% \leq P < 5\%$, but for the southern glass experiment, $b \neq 0$ at $5\% \leq P < 10\%$.

For the southern plastic and southern glass experiments a linear regression analysis of the negative linear growth phase observed at 10°C was undertaken (see Table 2-6, page 47). The combined results show that at 10°C the larvae gained weight initially, but this was not sustained. At approximately the halfway stage (45 days) of the experiment, they began to lose weight.

Experiment	*m* (slope)	*p value*	*b* (intercept)	*p value*	r^2
Southern plastic	-0.080	**	14.276	***	0.937
Southern glass	-0.058	**	14.891	***	0.973

Table 2-6: The slope, *m* and intercept, *b* of *L.suturalis* larval growth, (latter stage) at 10°C for the southern glass and southern plastic experiments

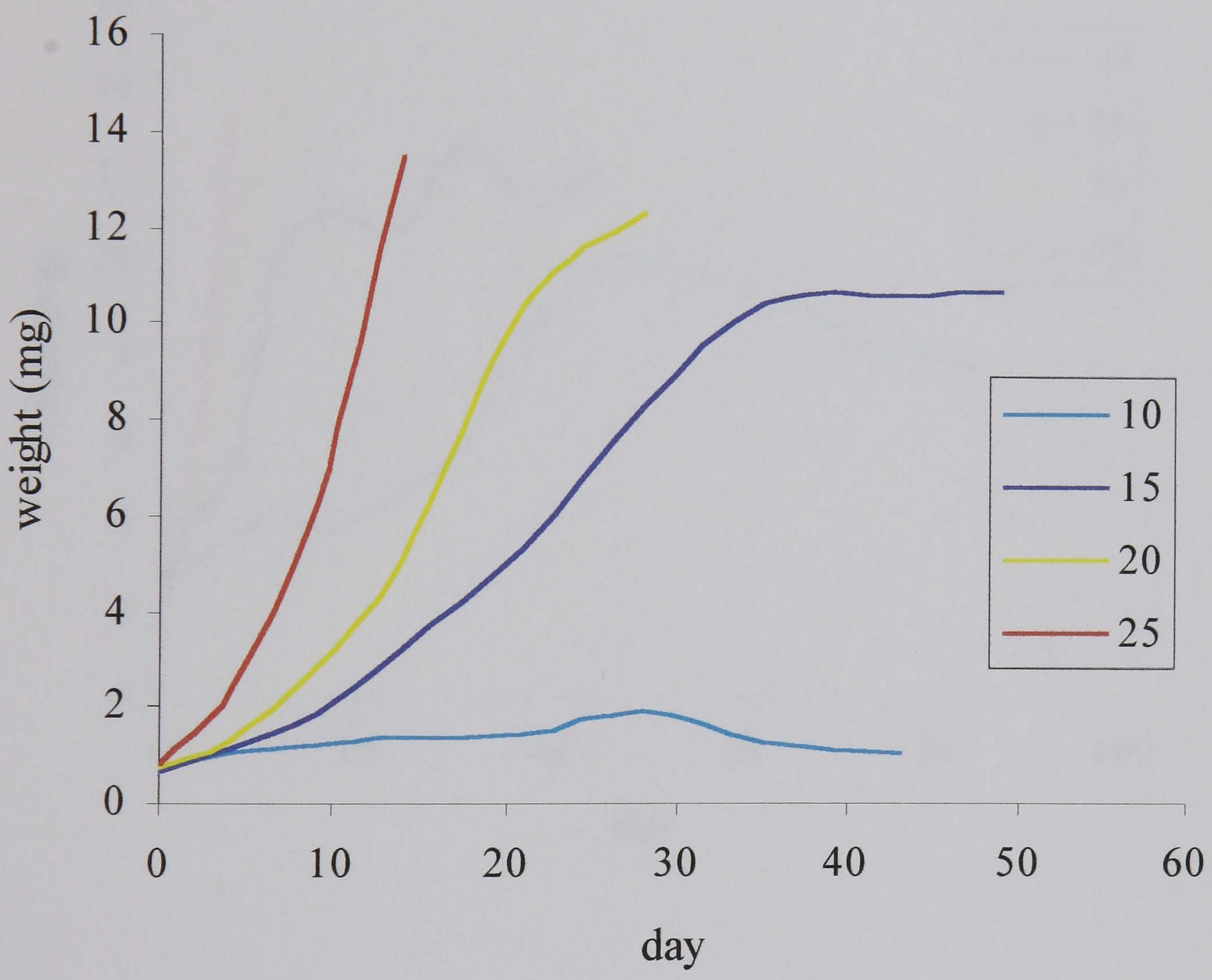


Figure 2-14: Mean (*n*=15) of *L.suturalis* larval growth at 10, 15, 20 and 25°C; northern glass pots, all standard errors are < 1.12

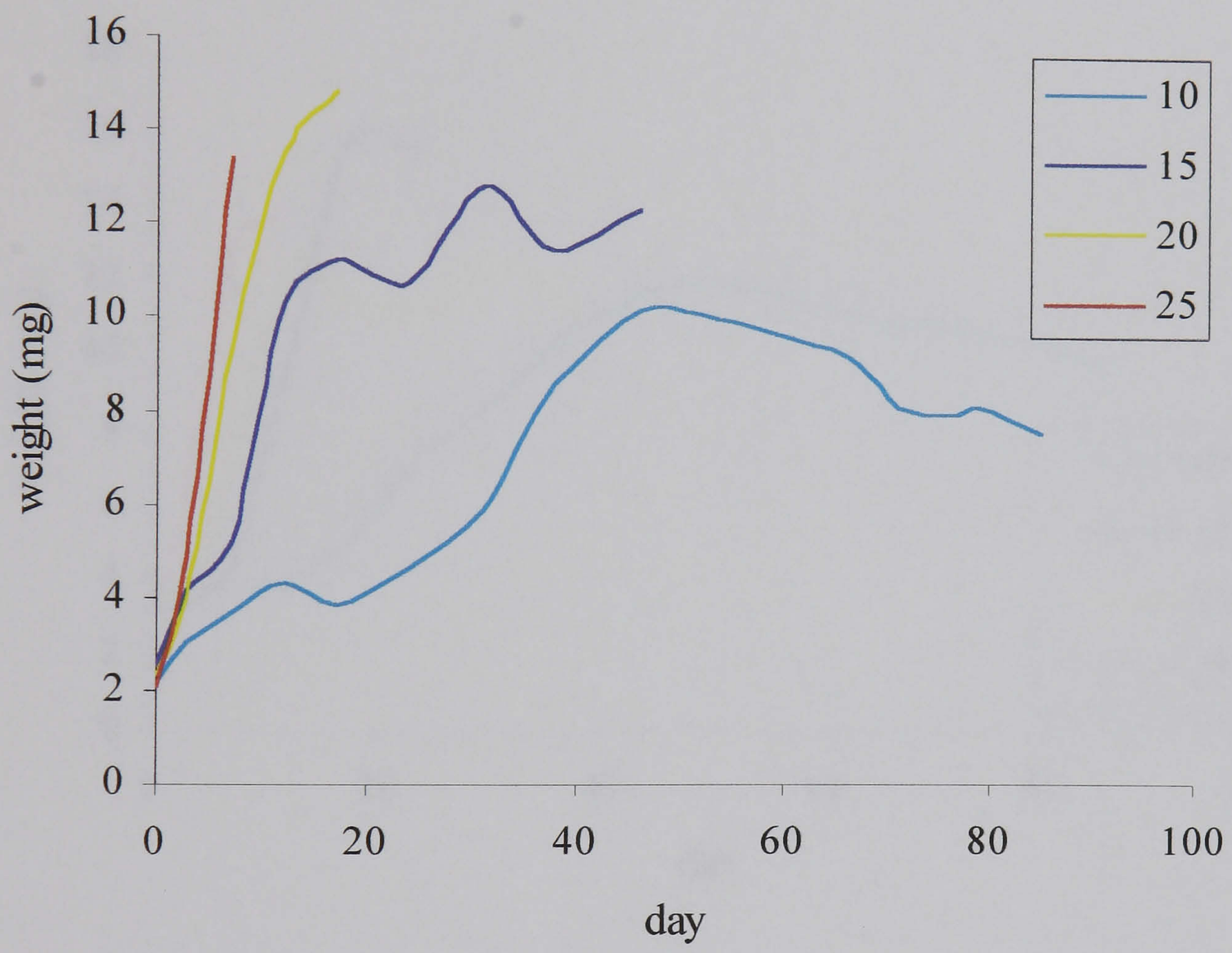


Figure 2-15: Mean (n=10) of *L.suturalis* larval growth at 10, 15, 20 and 25°C; southern plastic pots, all standard errors are < 1.82

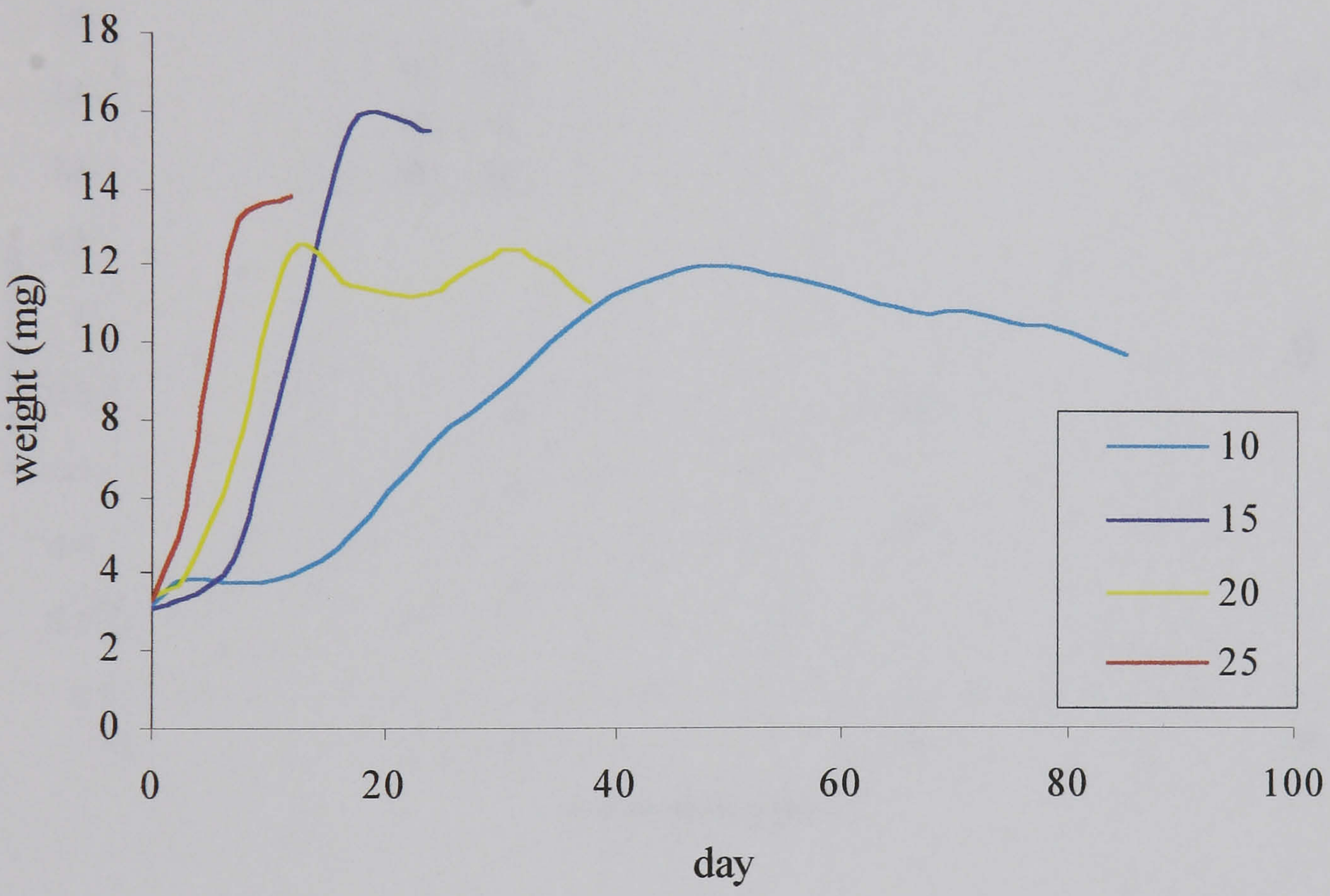


Figure 2-16: Mean (*n*=10) of *L.suturalis* larval growth at 10, 15, 20 and 25°C; southern glass pots, all standard errors are < 1.35

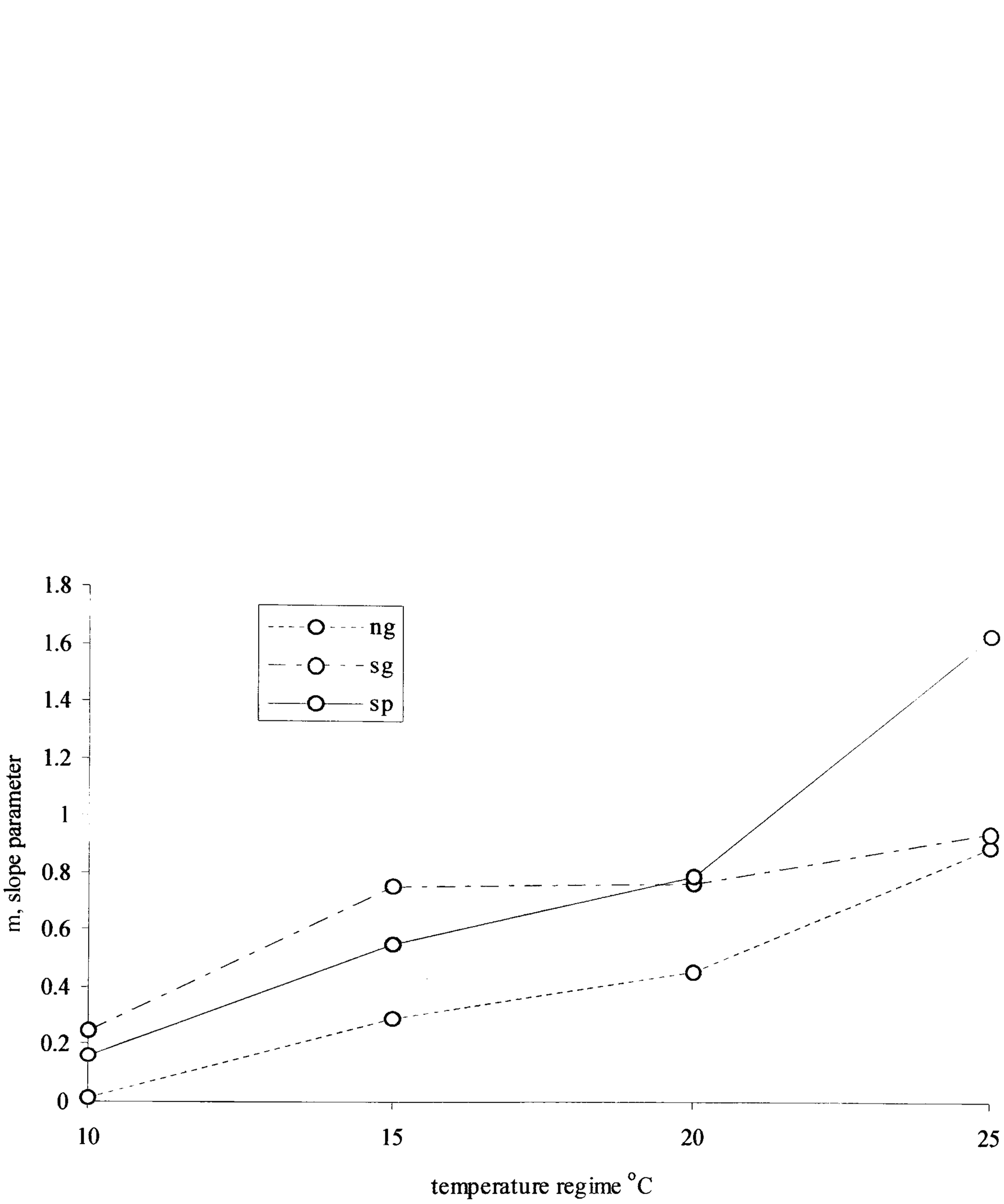


Figure 2-17: The relationship between the regression slope parameter, *m*, and the three control temperatures for the three *L.suturalis* larval growth experiments

(ng = northern glass, sg = southern glass and sp = southern plastic)

2.3.6 *L.suturalis* larvae, pupae and new generation adult development periods

2.3.6.1 Southern plastic pot experiment

At 10°C metamorphosis to the pupal stage did not occur, and at 15, 20 and 25°C all stages were present with low numbers of new generation adults coming through. At these three temperatures the development periods from larvae to pupae and pupae to new generation adults decreased as the temperature increased (see Figure 2-18, page 53).

2.3.6.2 Southern glass pot experiment

At 10°C metamorphosis only occurred to the pupal stage and at 15, 20 and 25°C all stages were present with higher numbers of new generation adults coming through. At these three temperatures the development periods from larvae to pupae and pupae to new generation adults decreased as the temperature increased (see Figure 2-19, page 54).

2.3.6.3 Northern glass pot experiment

At 10°C development to the pupal stage did not occur, and at 15, 20 and 25°C all stages were present with low numbers of new generation adults coming through at 15°C and high numbers at 20 and 25°C. At these three temperatures the development periods from larvae to pupae and pupae to new generation adults decreased as the temperature increased (see Figure 2-20, page 55).

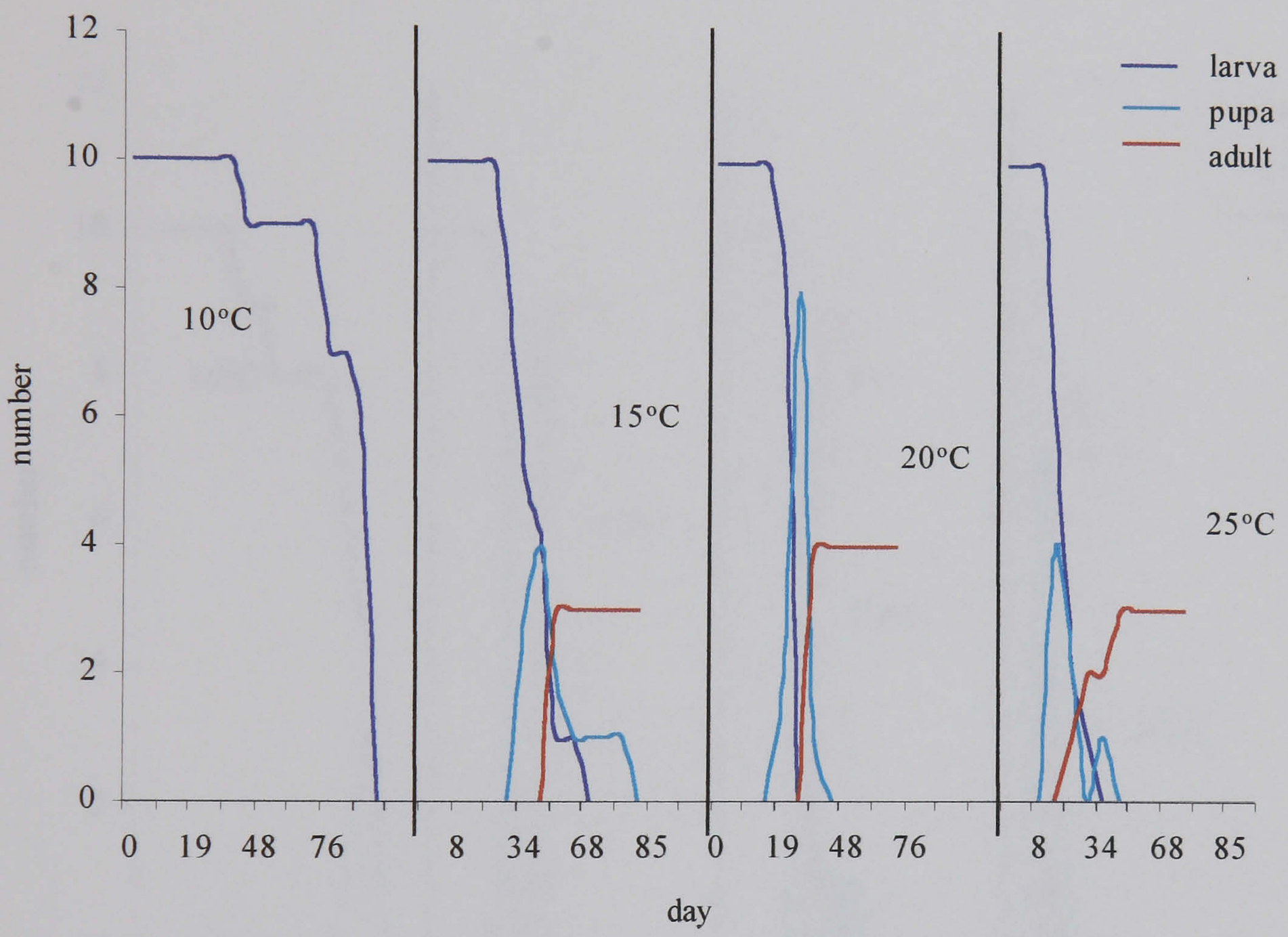


Figure 2-18: Number of *L.suturalis* larvae, pupae and new generation adults at 10, 15, 20 and 25°C; southern plastic pot experiment

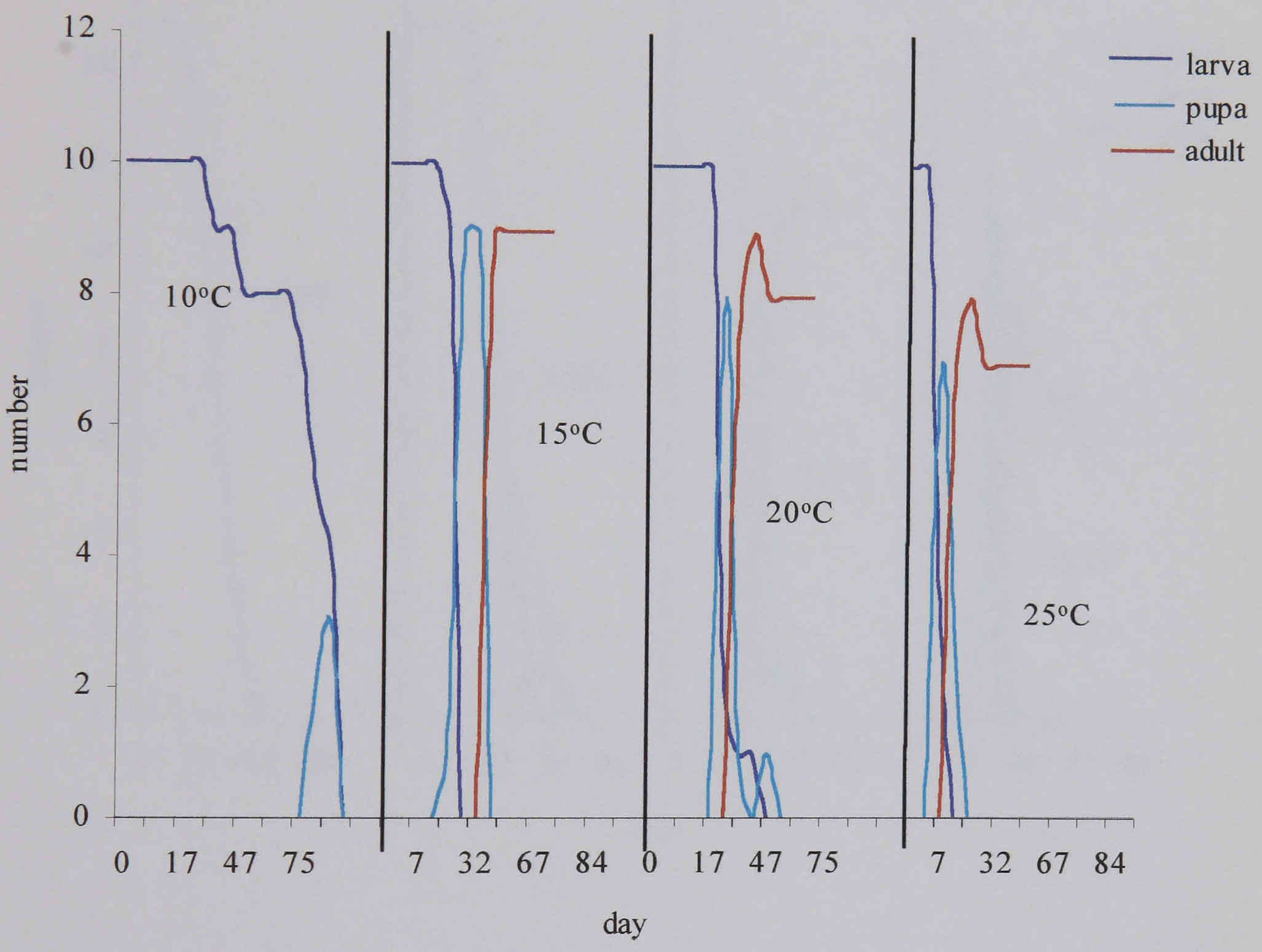


Figure 2-19: Number of *L.suturalis* larvae, pupae and new generation adults at 10, 15, 20 and 25°C; southern glass pot experiment

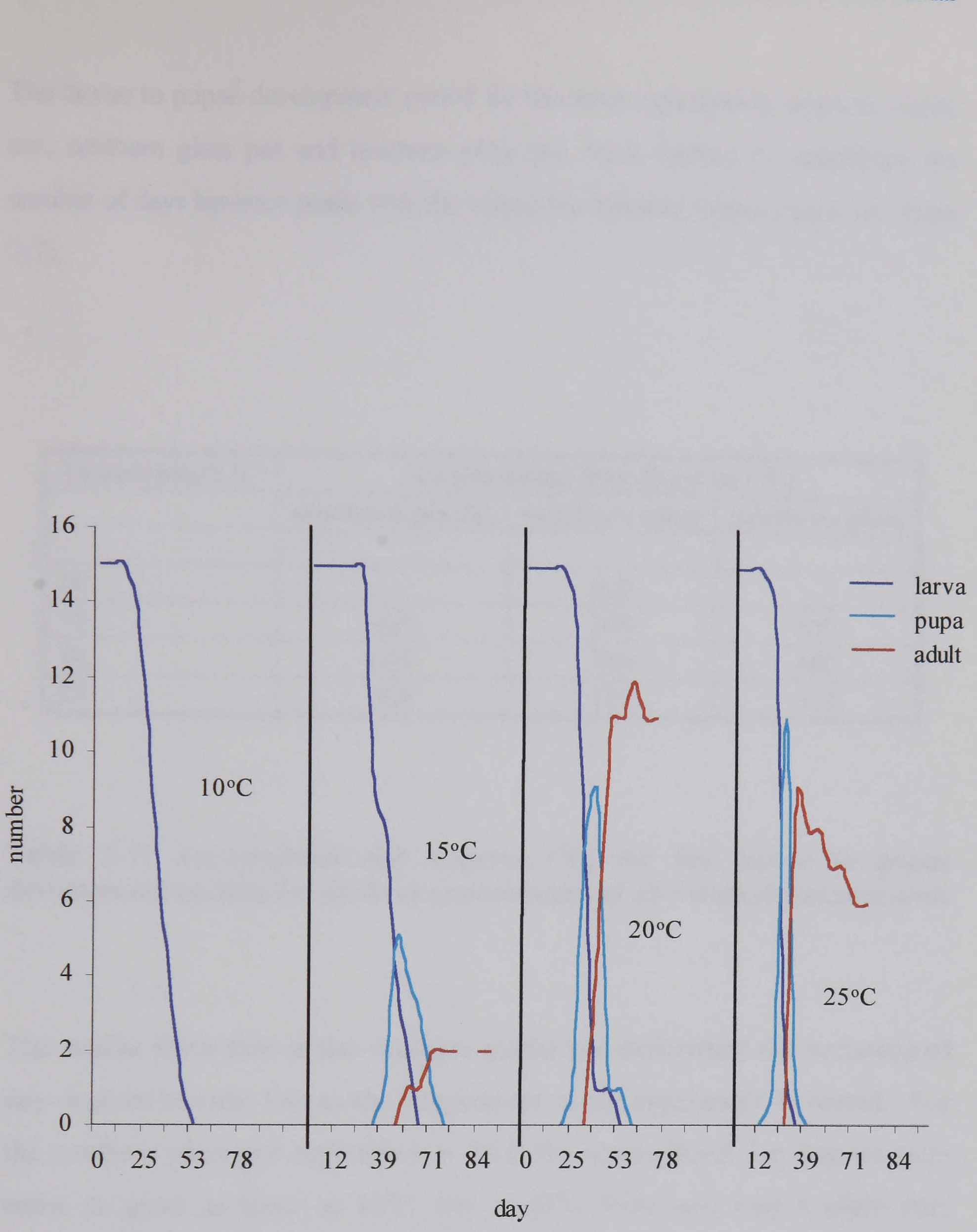


Figure 2-20: Number of *L.suturalis* larvae, pupae and new generation adults at 10, 15, 20 and 25°C; northern glass pot experiment

The larvae to pupae development period for the three experiments; southern plastic pot, northern glass pot and northern glass pot, were derived by multiplying the number of days between peaks with the respective constant temperatures (see Table 2-7).

Temperature °C	Accumulated Day Degrees (°C)		
	southern plastic	southern glass	northern glass
10	-	600	-
15	405	300	450
20	400	380	460
25	300	225	425

Table 2-7: Accumulated day degrees (°C) for the larvae to pupae development period, for all three experiments, at all constant temperatures

The results show that in the southern plastic pot experiment the accumulated day degrees become less as the temperature of the experiment increased. For the southern glass pot experiment at 10°C the accumulated day degrees were twice as great as those at 15°C, but at 20°C there was only a slight rise, followed by the lowest figure at 25°C. For the northern glass pot experiment the 15°C and 20°C experiments produced similar results, with a decrease at 25°C. At 10°C, in the southern plastic pot and northern glass pot experiments, the larvae failed to metamorphose to pupae.

The pupae to new generation adult development period for the three experiments; southern plastic pot, northern glass pot and northern glass pot, were derived by multiplying the number of days between peaks with the respective constant temperatures, (see Table 2-8, page 57).

Temperature °C	Accumulated Day Degrees (°C)		
	southern plastic	southern glass	northern glass
15	150	240	390
20	260	300	500
25	450	250	250

Table 2-8: Accumulated day degrees (°C) for the pupae to new generation adult development period, for all three experiments, at all constant temperatures

The results show that in the plastic pot experiment the accumulated day degrees become greater as the temperature of the experiment increased. For the southern glass pot experiment those at 15°C and 25°C were similar, but at 20°C there was a slight rise. For the northern glass pot experiment at 20°C there was a large accumulated day degree figure, but as the temperature decreased from 15°C to 25°C there was a decrease in accumulated day degrees.

The means of all sets of experiments, at all temperatures, 10, 15, 20 and 25°C were calculated to give an overall mean accumulated day degrees for the larvae to pupae and pupae to new generation adult development periods (see Table 2-9, page 58).

Development Period	Mean Accumulated Day Degrees	Standard error
Larvae to pupae	395°C	34.7
Pupae to adult	310°C	35.8

Table 2-9: Mean accumulated day degrees (°C) and standard error for the larvae to pupae, (*n*=9) and pupae to new generation adult, (*n*=10) development periods

2.3.7 *L.suturalis* new generation adult growth and temperature

The weights of the new generation adults were plotted against time, (see Figure 2-21, page 60). This was followed by a linear regression analysis of each growth curve for the three experiments at the four temperatures (see Table 2-10).

Experiment	T°C	*m* (slope)	*significance*	r^2
Southern plastic	15	0.17	*	0.87
	20	0.11	ns	0.72
	25	0.09	ns (*p*=0.052)	0.65
Southern glass	15	0.16	***	0.99
	20	0.14	**	0.93
Northern glass	20	0.17	***	0.98
	25	0.17	*	0.84

Table 2-10: The regression coefficient, *m*, the significance and r^2 for the *L.suturalis* new generation adult growth experiments

As can be seen, all three experiments showed that the new generation adults continued to feed and put on weight, with the exception of the 20°C southern plastic pot experiment. The adult stage was not reached at 10°C in the southern plastic pot and northern glass experiments and at 10 and 25°C in the southern glass experiment. In the northern glass experiment at 15°C the number of adults was less than two. Adult weight gain was greatest for the 20°C experiments with a 50% gain from initial adult weight, whereas for 15 and 25°C they were 41% and 42% respectively.

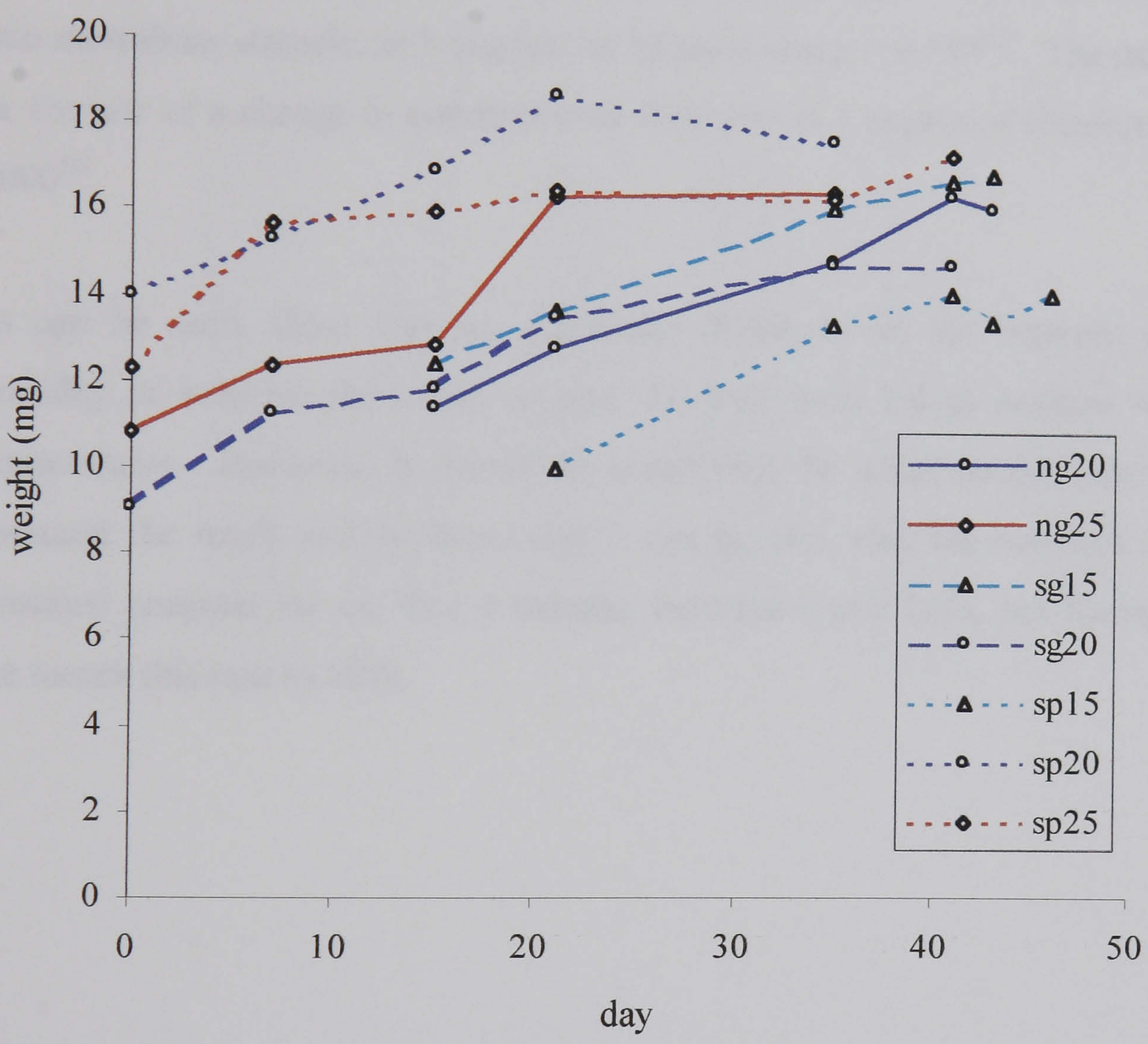


Figure 2-21: Mean new generation adult *L.suturalis* weight gain, all standard errors are < 0.75

(ng = northern glass (*n*=15), sg = southern glass (*n*=10) and sp = southern plastic (*n*=10))

2.3.8 *L.suturalis* new generation adult winter mortality at ambient temperature

The number of male and female *L.suturalis* adults alive at each monitoring period during the winter is shown graphically (see Figure 2-22, page 62).

Non-parametric Kruskal-Wallis statistical significance tests were conducted on the ambient temperature winter mortality experiment data. The between sex ratio mortalities statistic, at 5 degrees of freedom was $p = 0.143^{NS}$. The statistic for the test of a change in numbers over time was at 1 degree of freedom, $p = 1.000^{NS}$.

As can be seen, there was no significant difference in the between sexes mortality or between the length of time the pots were left at ambient winter temperatures. However, it should be noted that the small sample may have obscured the result and by inspection it can be seen that the numbers dying remained constant for the first 4 months, between 0 and 10%, but during the last month this rose to 40%.

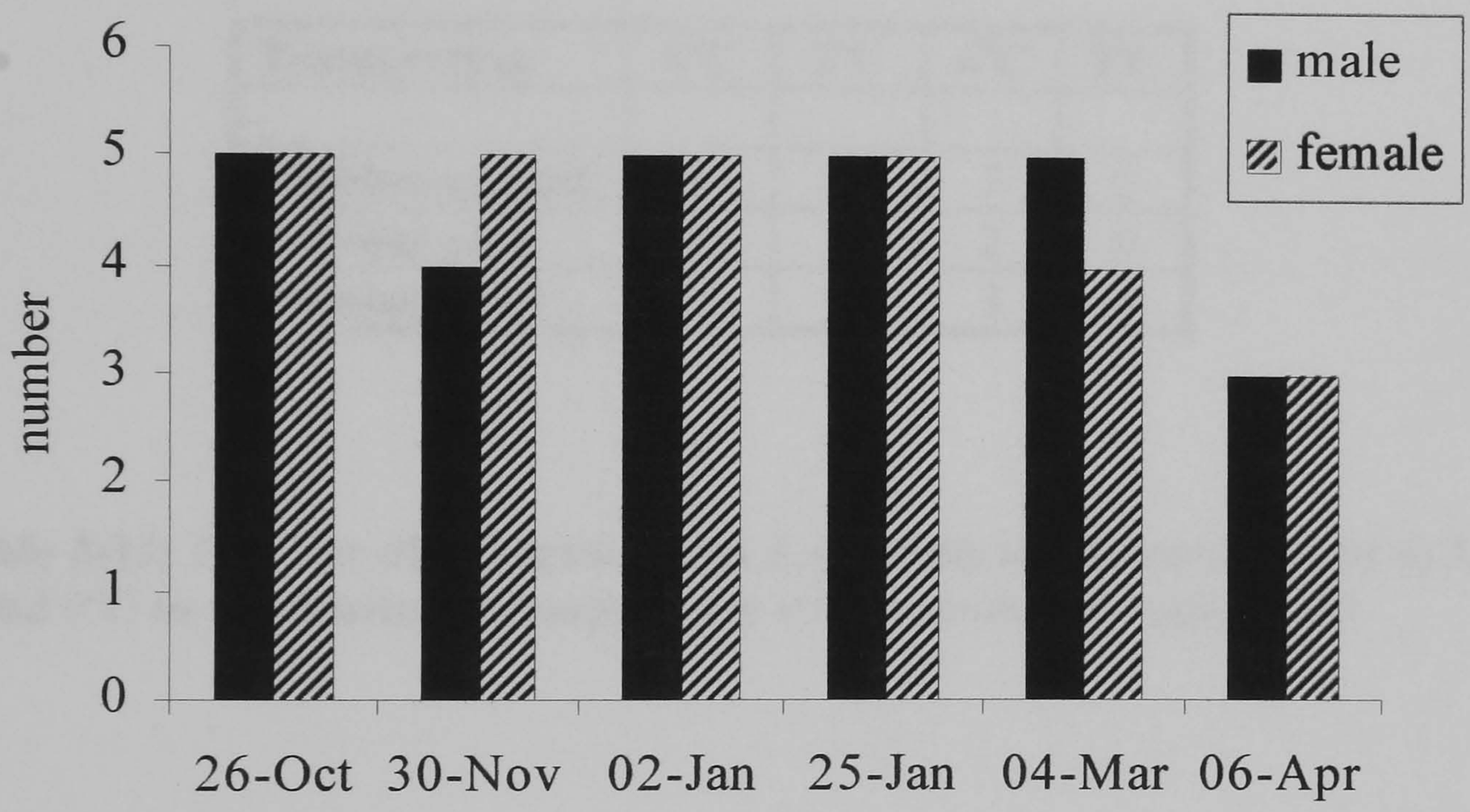


Figure 2-22: Number of male and female adult *L.suturalis* alive at the date each container was opened for the ambient temperature winter mortality experiment

2.3.9 *L.suturalis* new generation adult winter mortality at controlled temperatures

After the period of the experiment, (60 days) the numbers found alive and dead were as follows (see Table 2-11).

Temperature	0°C	3°C	6°C	9°C
Number at start	5	5	5	5
Number alive	2	4	2	0
Number dead	3	1	3	5

Table 2-11: Number of new generation *L.suturalis* adults surviving at 0, 3, 6 and 9°C in the controlled temperature winter mortality experiment

As the dataset from this experiment was a 4 x 2 contingency table with cell values less than five, a Fisher's Exact Test was performed to test the significance of all possible combinations of the pairs of temperatures, (see Table 2-12, page 64).

Control temperature pairings	Fisher's Exact test *p*-value
0°C and 3°C	0.52 ^{NS}
0°C and 6°C	1.00 ^{NS}
0°C and 9°C	0.44 ^{NS}
3°C and 6°C	0.52 ^{NS}
3°C and 9°C	0.05 ^{ns}
6°C and 9°C	0.44 ^{NS}

Table 2-12: The Fisher's Exact test *p* value, with significance, for all pairings of the number of new generation *L.suturalis* adults; alive or dead, in the controlled temperature winter mortalty experiment

There were no differences between mortalities at the different temperature regimes, with all combinations of pairs not significant at $P > 0.01$, with the exception of the combination of 3 and 9°C that was not significant at $P \geq 0.05$.

2.3.10 *L.suturalis* overwintering threshold temperature

The numbers of the new generation adults with their position and physiological state are given below (see Table 2-13) and graphically (see Figure 2-23, page 66).

Temp°C	Position and physiological state in experiment				
	Active in moss	Active in moss/soil	Active in soil	Inactive in soil	Dead
16	20	0	0	0	0
15	9	0	10	0	1
14	13	0	6	0	1
13	7	7	4	0	2
12	7	6	0	6	1
11	6	8	0	6	0
10	3	9	0	8	0
9	5	3	0	11	1
8	5	3	0	11	1
7	3	2	0	14	1
6	2	1	0	17	0
5	0	1	0	19	0

Table 2-13: Numbers of new generation adults, (*n*=20) in each of the position and physiological state categories of the overwintering threshold temperature experiment

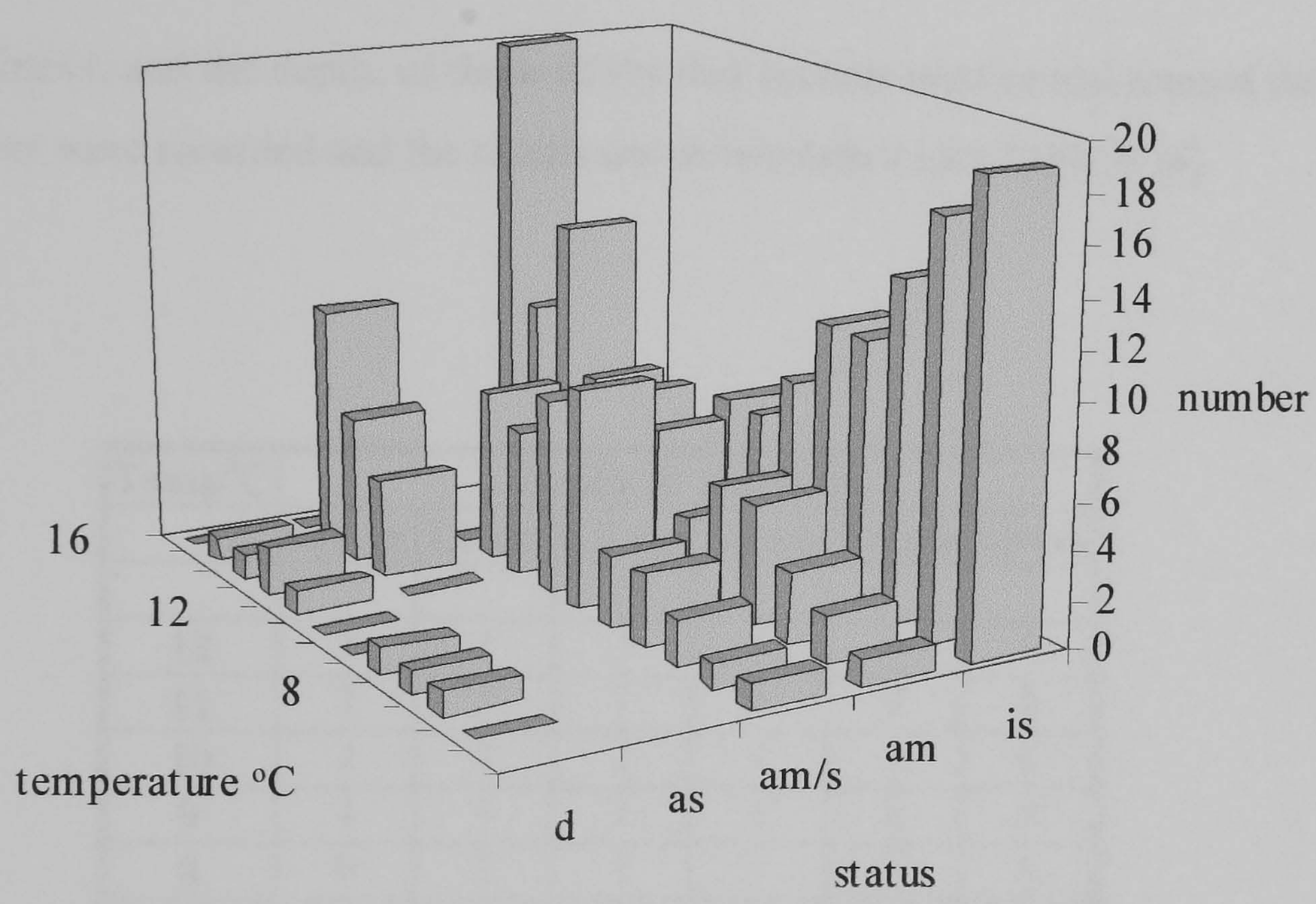


Figure 2-23: Movement and physiological state of new generation *L.suturalis* adults as temperature decreased in overwintering threshold experiment

(d = dead, as = active in soil, am/s = active in soil/moss boundary, am = active in moss, is = inactive in soil)

Initially, whilst the temperature remained between 15°C and 13°C the beetles remained in an active state, with movement between the three substrates. Between 13°C and 10°C approximately one third of the beetles began to become inactive with the remaining two thirds equally split between the moss and the moss/soil layer. Below 10°C the numbers in the top two substrates gradually decreased as all, bar one, of the beetles retreated to the soil substrate and became inactive. The number dying was between 0 and 10% at any given temperature.

The number, and the depth, of those adults that became inactive and entered the soil layer were recorded and the results are shown below (see Table 2-14).

Temp°C	Depth in soil layer					
	0.5 cm	1.0 cm	1.5 cm	2.0 cm	2.5 cm	3.0 cm
12	3	1	1	1	0	0
11	2	2	1	1	0	0
10	2	1	2	2	1	0
9	4	1	1	2	0	0
8	0	2	1	1	0	0
7	4	1	2	5	0	0
6	3	3	2	5	3	0
5	4	3	2	4	2	1

Table 2-14: Number of new generation *L.suturalis* adults and depth within the soil layer, of those that entered the soil (below the moss layer), as temperature decreased in the overwintering threshold temperature experiment

The mean and standard error of the depth was calculated for each temperature and is shown graphically, (see Figure 2-24, page 69).

The general trend is for those overwintering adults to move to increasing depths with a lowering of temperature with the mean depth ranging from 1cm at 12°C to c. 1.5 cm at 5°C. Between 12 and 8°C there was a mean of 39% in the top 0.5 cm, whilst between 7 and 5°C the percentage dropped to a mean of 25. Conversely between 12 and 8°C there was a mean of 24% in the lower (<= 2.0 cm) strata, whilst between 7 and 5°C the mean percentage increased to 42. At 5°C, 6% had reached a depth of 3cm.

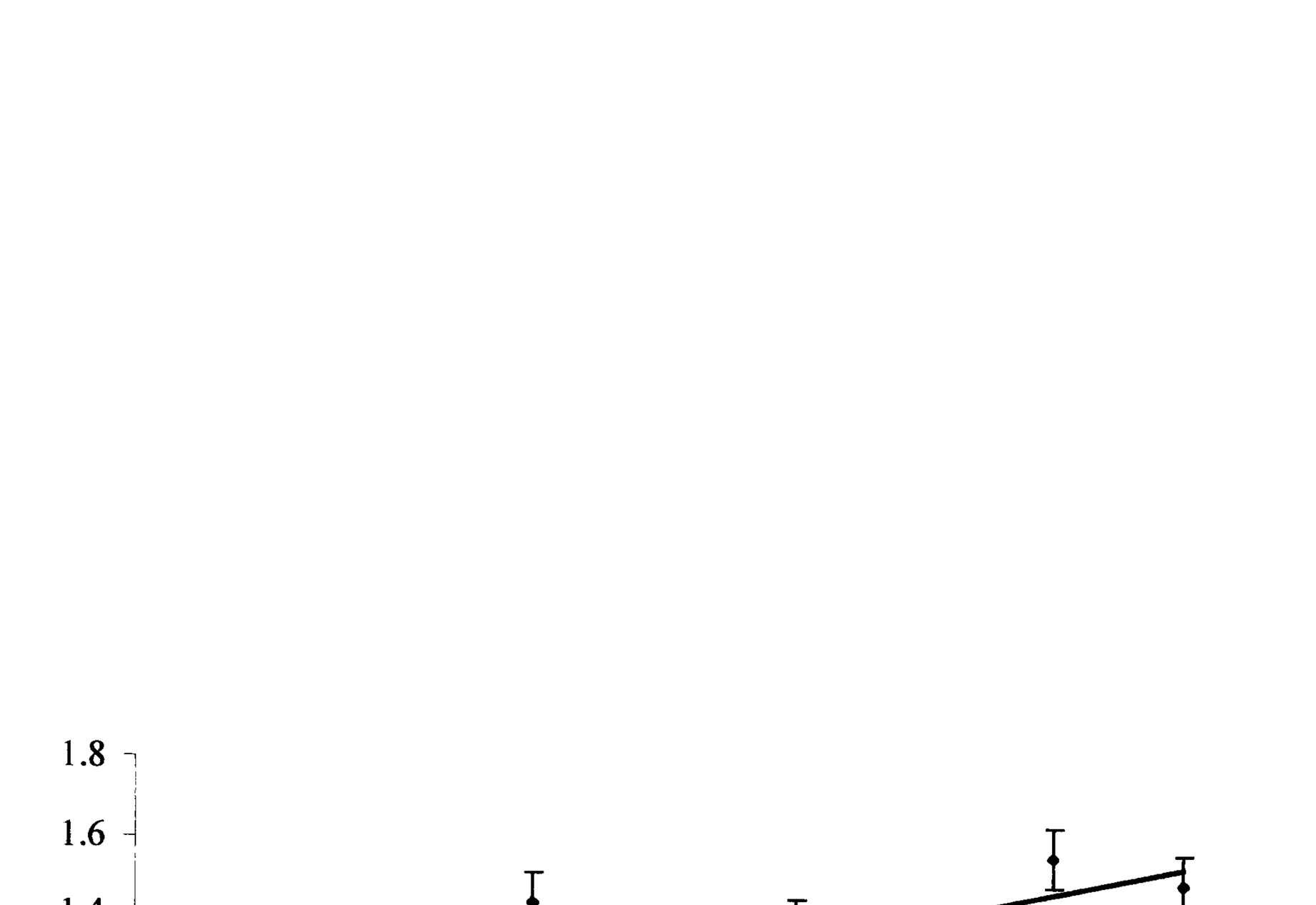


Figure 2-24: Mean and standard error of depth in the soil of those new generation *L.suturalis* adults that entered the soil (below the moss layer), as temperature, (°C) decreased in the overwintering threshold temperature experiment

Regression: $y = -0.07x + 1.89$; $r^2 = 0.63$, the slope $m \neq 0$ at $p = 0.018$ (n=6 at 12 & 11°C, n=8°C at 10 & 9°C, n=4 at 8°C, n=12 at 7°C, n=16 at 6 & 5°C)**

2.4 Discussion

Quantifying the influence of temperature on the developmental rate of invertebrates is fundamental to the understanding of their population dynamics (Birch 1948; Andrewartha & Birch 1954; Honek & Kocourek 1990). This thesis combines the data from the laboratory experiments and fieldwork and integrates them within a computer simulation model. This understanding of the processes of population dynamics is employed to explore *L.suturalis* life stage parameters, seasonal occurrence, and the phenomena of population extinctions or outbreaks.

The male to female sex ratios, both for the field sampled and the ambient temperature cultured adults, were significantly different from one another, 1.00:1.71 and 1.00:1.37 respectively. However within the context of the available published research, they were within the ranges cited; 1.0:1.66 and 1.0:1.38 (Cameron *et al.* 1944), 1.0:1.63, in the overwintering period (Vagn Jensen & Nielsen 1985a) and 1.0:1.61, determined in the summer period (Scandrett & Gillingham 1991). Scandrett & Gillingham (1991) also note that from previous studies in the Netherlands that ratios varied from 1.0:1.3-2.5. The reasons for this difference in the numbers of males and females may be due either to greater numbers of females emerging from the pupal stage (Scandrett & Gillingham 1991), or due to greater male mortality just before overwintering (Vagn Jensen & Nielsen 1985a). Scandrett & Gillingham (1991) add that as there were greater numbers of females, ratios would be expected to vary through the season; this could account for the anomalous figure of 1.0:0.91 in newly emerged adults as cited by Waloff (1987). They also concede that the mechanisms behind the ratio are not understood. Cameron *et al.* (1944) also noted that:

"...the percentage of the sexes varied widely when individual captures were compared; variation occurred not only among collections made within a few days of each other, but also among collections made at different times of the same day in the same locality."

Whilst it is always desirable to include a greater range of control temperatures in invertebrate population dynamics experiments, i.e. 5°C or 30°C, to investigate the effects of unusually low or high seasonal temperatures on the developmental rates of the beetle, it is not always possible. In this case the temperature range was limited by the unexpectedly low numbers of adults and larvae collected in the first 18 months of the study. As a consequence, the temperatures chosen for the fecundity, life stage growth and development period studies were in line with those used for similar experiments on invertebrates occurring in temperate latitudes (De Loach 1974; Wyatt & Brown 1977).

The two experiments to quantify the fecundity of *L.suturalis* at ambient temperature yielded very similar results. As the fecundity of *L.suturalis* had not been established before, it is necessary to compare the results with other species within the Chrysomelidae. However the fecundity of the Chrysomelidae varies greatly. Selman (1994) cites a range from 2804 for *Leptinotarsa decemlineata* (Say), the Colorado potato beetle (Kovton 1966) to 16 for *Promecotheca reichei* Baly (Taylor 1937).

The mean fecundity at ambient temperature of c. 36, and its evaluation in the context of this large range, requires it to be considered with the results from the controlled temperature fecundity experiment. The ambient temperature fecundity experiment was conducted in spring, in the outdoor insectary where, combined with its northern latitude, gave rise to a considerable diurnal temperature fluctuation and cool daily mean temperatures, c. 10°C. It is widely known that controlled temperature development experiments do not mimic the 'real world' and studies have shown that there are considerable differences in

invertebrate development between controlled and fluctuating temperatures (Eubank *et al.* 1973; Behrens *et al.* 1983; Huffaker *et al.* 1984).

However, given this problem, it does seem ill considered to suggest that the range of eggs laid per adult pair for the ambient temperature fecundity experiment *should* fall at the lower end of the range for the 15 and 20°C controlled temperature experiments. The range of the fecundity for both ambient temperature experiments was 0 - 72 and for the controlled temperature experiments 0 - 17, 0 - 139 and 4 - 152 at 15, 20 and 25°C, respectively. Combining the 15 and 20°C figures gives a range of 0 – 139. As the ambient and controlled temperature results are comparable and are within the overall limits of the overall Chrysomelid range, it seems that the experimentally derived fecundities for *L.suturalis* are realistic. They can therefore be confidently employed as parameters within the computer simulation model.

It should be noted that Cameron *et al.* (1944) set up pairs of adults caught in the field and recorded a mean number of eggs laid per adult of 122.25 with a standard error of 19.82, the range was 0 - 289. However the temperature that the adults were maintained at is not recorded, except for the sentence:

> "...the beetles can be induced to breed indoors without interruption provided the temperature remains sufficiently high."

Obviously this research cannot be used in a discussion of experimental fecundity, but is nevertheless included for completeness. Additionally they also noted:

> "...there was a progressive loss of fecundity and vigour in the successive generations of reared beetles."

In fact they record that the fecundity of the beetle dropped from their field sampled adults mean of 122.25 to a mean of 27 for the first cultured generation.

The *L.suturalis* larval growth and controlled temperature experiments showed that temperature influences larval growth. At 15, 20 and 25°C weight gain increased as temperature increased. At 10°C the larvae showed initial growth but as time passed began to lose weight and eventually died. Under constant temperatures rates of development in insects generally assume a sigmoidal curve (Andrewartha 1970; Liu *et al.* 1995). Increasing mortality is observed at either end of the curve, in effect, at the outer limits of the temperature range. The middle, linear section, of the curve defines the optimal temperature for development, and in the case of *L.suturalis* this was shown to be within the range 15 – 25°C. These observations conform to the established research on northern temperate Coleoptera larvae (Crowson 1981).

Establishing an upper lethal temperature was not possible, due to the lack of beetles for a further experiment at 30°C, however in the case of a western Palaearctic Chrysomelid beetle, investigating larval growth at a constant 30°C would be unrealistic, as these temperatures are not likely to occur, continuously in field conditions, particularly in late spring - early summer. The lower lethal temperature can be said to lie below 10°C, as the larvae did not die at this temperature but "failed to thrive". Several studies have shown that larval size is positively correlated to fecundity (Wiklund & Karlsson 1988; McLain *et al.* 1990). Consequently it can be surmised that the low or falling larval weights at 10°C would lead to population extinction and that this temperature is therefore close to the lower lethal temperature for *L.suturalis* larvae.

An accumulated day degree figure (ADD's), for the egg to larvae development period, of 362°C seems plausible, given that Cameron *et al.* (1944) record figures of 324 ADD's (at 18.5 days of 17.5°C), 260 ADD's (at 13 days of 20°C) and 225 ADD's (at 9 days of 25°C). These results were all obtained in constant temperature experiments, whilst the ADD figure for this experiment was

conducted at ambient temperature in a northern clime in mid spring. In fact they are perhaps too similar given the differences in invertebrate development that can occur between controlled and fluctuating temperature experiments as discussed earlier (Eubank *et al.* 1973; Behrens *et al.* 1983; Huffaker *et al.* 1984).

The larvae to pupae development period ADD's, when inspected at the individual result level, gives a range of 300-450 ADD's for 15°C, 380-460 for 20°C and 225-425 for 25°C. These ranges bracket the figures given by Cameron *et al.* (1944) for all larval instars of 372 ADD's (at 24 days for 15.5°C) and 400 ADD's (at 16 days for 25°C), which again were derived from constant temperatures experiments. Therefore the controlled temperature larvae to pupae ADD's also seem plausible.

However, when the pupae to new generation adult development period, ADD's are inspected individually they show ranges of 150-390 for 15°C, 260-500 for 20°C and 250-450 for 25°C. Cameron *et al.* (1944) recorded 416 ADD's (at 26 days for 16°C - at constant temperature), which is just outside the upper end of the range. They also record 150 ADD's (at 6 days for 25°C - at constant temperature), which is considerably below the lower end of the range. This is difficult to explain, but may be due to phenotypic differences between the northern and southern larvae.

As the means of the accumulated development period day degrees are used in the population dynamics model, a comparison between the means of the two controlled temperature development period ADD's and the means of ADD's from the work of Cameron *et al.* (1944) seems worthwhile and gives the following result, (see Table 2-15, page 75).

	Larvae to pupae development period	Pupae to Adult development period
	ADD's °C	ADD's °C
Thesis mean	395	310
Thesis s.e.	104.1	113.1
Cameron *et al.* mean	386	283
Cameron *et al.* s.e.	19.7	188

Table 2-15: Comparison of the mean and standard error of the thesis and Cameron *et al.* (1944)'s accumulated day degrees for the larvae to pupae and pupae to new generation adult development periods

It can be seen that the ADD's are of the same magnitude and therefore the empirically derived results can be confidently used as the day degree development parameters within the computer model.

New generation adult growth at different temperatures showed that the adults continued to feed and put on weight, except for the 20 and 25°C southern plastic pot experiments. However the greatest weight gain over the period of the experiment was for the 20°C experiment with the 15 and 25°C adults putting on the same percentage weight. This suggests that the optimum temperature for new generation adult weight gain lies between 14 and 24°C. Again for a western Palaearctic Chrysomelid with an overwintering adult life stage, this seems an acceptable figure.

It should be noted at this point that the following discussion of the results of the winter mortality and overwintering emergence threshold temperature experiments and the larval growth and the site sourced *Calluna vulgaris* experiment described in the following chapter were all conducted with new generation adults or larvae cultured from a random mix of progeny from beetles either caught in

Northumberland or from larvae sourced from the Surrey Heaths. Organisms from different parts of its range may exhibit slight differences in performance, however without this combining of the differently sourced animals there would not have been sufficient numbers to complete the study experiments and it was felt that it was better to conduct more experiments on the population dynamics of the beetle at the expense of a possible dilution of the results.

The winter mortality experiment at ambient temperature showed no significant difference in mortality between the sexes. If this result is extrapolated to all adults that overwinter, it brings it into conflict with the ratio recorded of males to females, caught on the moorlands at the beginning of the thesis, *viz.* 1:1 against 1:1.37-1.71. All available research points to a greater number of females to males leaving winter diapause. Vagn Jensen & Nielsen (1985a) suggest that a probable reason for this greater number of females may be that some males die before overwintering occurs. This postulation could account for there being no difference in the mortality between the sexes in this experiment, as the males chosen for the experiment were the ones that had already survived this period of pre-diapause death.

At the end of the experiment, mortality increased, and as the only noteworthy mortality occurred after some months it may have been due to the death of small beetles, (elytra < 4 mm), whose resources had become depleted, as suggested by Vagn Jensen & Nielsen (1985a). In an overwintering experiment conducted by Cameron *et al.* (1944) where adults were subjected to a constant temperature of 0°C for periods between one and three months, and where the survivors were returned to ambient outdoor conditions, the adults were found to be still alive after a further six weeks. This gives a maximum winter survival time of seventeen weeks. Similarly, the ambient overwintering mortality experiment that ran for five months only recorded noticeable mortality at around the same, four-month time period.

The winter mortality experiment at controlled temperatures showed that the temperature range between 0 - 9°C had no significant effect on adult mortality.

Indeed a univoltine, Palaearctic Chrysomelid beetle that exhibits an adult overwintering life stage would be expected to survive the range of sub-zero temperatures experienced in *C.vulgaris* habitats; with local populations acclimatised to winter temperatures of their particular habitat. Vagn Jensen & Nielsen (1985a) conducted experiments on cold hardiness and found that *L.suturalis* was resistant to short exposures of temperatures down to c. -10°C. In the winter of 1982-83 they recorded minimum air and soil temperatures of -21.9°C and -6°C respectively. In the overwintering experiment conducted by Cameron *et al.* (1944), where adults were maintained at 0°C continuously for 87 days, it was found that there were no deaths, of either sex at one month, and that at five weeks, a mean of 30% had died, whilst at eleven weeks none had survived. Even though the dataset, (see Table 2-11, page 63) was small and the experiment only lasted for two months the results are similar to those obtained in the Cameron *et al.* (1944) zero degree experiment.

The overwintering threshold temperature experiment produced results that conform to what is known about overwintering *L.suturalis* adults. The results show that below 10°C there was a definite movement to the lower soil substrate, beneath the moss layer, where they became inactive and entered winter diapause. This is indicative of an overwintering strategy as Cameron *et al.* (1944) and Brunsting (1982) both report that new generation adults overwinter in November when temperatures fall below 9°C.

The depth that *L.suturalis* adults chose for their overwintering diapause sites showed a tendency for increased depth up to 3 cm below the soil surface, as the temperature decreased to 5°C. Available research is markedly dissimilar on this subject. Adult beetles have been recorded at less than 1 cm below the soil surface (Vagn Jensen & Nielsen 1985a), although this does not imply that they were not found at a deeper location. Whilst Cameron *et al.* (1944) reported that the adults:

> "...do not burrow deeply in the soil, but lie dormant in the moss and soil only two to three inches below the surface, little protection is secured against the frost, which penetrates quickly to that depth."

Two to three inches is 5 cm to 7.5 cm and none of the experiments' findings recorded such a depth. This may have been because they were found when conditions were well below zero centigrade.

2.5 Conclusions

The experiments described in this chapter to quantify the major life history parameters of *L.suturalis* in relation to the effects of temperature have all yielded results. Results on their own are of little use, as they need to be 'tested' to be able to employ them with confidence. Initially this 'testing' is accomplished by analysis, that attempts to assign a *measure* or *degree* of confidence to the results. Once the robustness of the results has been assessed they are then put up for scrutiny, by comparison to other work in the field or, if this is not available, work on similar species; this is the role of the discussion.

The analysis and discussion in this chapter have shown the results of the experiments to be robust and meaningful in relation to other research on the heather beetle. These are important pre-requisites for their insertion into the population dynamics model described in Chapter Four. Biological modelling of life stages and population dynamics needs a sound framework around which stochastic variation can be incorporated to produce a reasonably realistic model that is able to predict population changes given the vagaries of our environment.

This chapter has also tested the first hypothesis, posed in the introduction: that the life history parameters of *Lochmaea suturalis* are dependent on temperature and found it to be true.

During the spring and summer of 1994 and 1995 collecting beetles for the various experiments proved to be difficult. All types of suitable habitats in varying weather conditions were visited on many occasions to little or no avail. This may have been due to poor luck, unusual and consequently unsuitable climatic conditions, a period of low population numbers or an outbreak of the predators or diseases of *L.suturalis*. Whatever the reason, this paucity of beetles at the beginning of the study limited some of the experiments in terms of

numbers. However it has been shown that the quantification of the various life stages outlined at the beginning of the chapter has been fulfilled. The following chapters in this thesis endeavour to throw some light on the reasons for the presence, absence or fluctuations of the heather beetle, whether temporally or spatially.

Chapter 3: Study site sourced *Calluna vulgaris* and *Lochmaea suturalis* larval growth

3.1 Introduction

Several researchers have shown that *Calluna vulgaris* dominated habitats in Britain and the Netherlands are in decline (Heil & Diemont 1983; Diemont & Heil 1984; Berdowski 1987; Bunce 1989; Armstrong 1991; Bardgett *et al.* 1995; Thompson *et al.* 1995). Reasons for this decline range from increased grazing pressures, through afforestation and changes in agricultural use, (i.e. conversion to improved grasslands) to seral changes as seen in the Netherlands. Research in the Netherlands, where the heathlands comprise small fragmented patches of *Calluna vulgaris* has focussed on the role that *Lochmaea suturalis* plays in this decline, for as Berdowski (1993) notes:

> "...outbreaks of the Chrysomelid heather beetle *Lochmaea suturalis* have become more and more an important cause of *C.vulgaris* mortality." (*sic*)

Infestations of the heather beetle have been observed since the nineteenth century (Cameron *et al.* 1944). Recently however the outbreaks appear to have become more frequent and severe, (*pers obs.)*. Berdowski (1993) postulated that this might be due to an increased concentration of nitrogen in *C.vulgaris* leaves, brought about by an increase in the deposition of atmospheric nitrogen. In the Netherlands the main avenue of research has been to investigate the relationship between the nitrogen content of *C.vulgaris* and the level of infestation by *L.suturalis* (Brunsting 1982; Brunsting & Heil 1985; Berdowski 1987; Berdowski & Zeilinga 1987).

3.1.1 *Calluna vulgaris*

C.vulgaris is widely distributed in the Palaearctic, but only becomes dominant in sub-oceanic and oceanic montane areas. It flourishes on acidic, oligotrophic soils (Armstrong 1991); although Grime *et al.* (1988) note that there are rare records on species-rich calcareous grasslands. It requires open conditions, high relative humidity and soil moisture with an equable temperature regime (Gimingham 1989). Grime *et al.* (1988) place it as a stress-tolerant competitor within the strategy triangle. Associated species of *C. vulgaris* are *Erica cinerea* and *Erica tetralix*, which have similar growth forms and physiology and overlap *C.vulgaris* along a hydrological and edaphic gradient. *E.cinerea* generally grows on drier, freely drained mineral soils and *E.tetralix* on wetter, poorly drained organic soils (Gimingham 1972). *C.vulgaris* is an evergreen, shrubby chamaephyte or phanerophyte flowering from August to September, with seed shed from September onwards (Grime *et al.* 1988). In Scotland two forms are exhibited, the familiar variety and *C.vulgaris* var. *hirsuta* (Gimingham 1960; Scandrett & Gillingham 1991).

Germination of *C.vulgaris* occurs anytime between spring and autumn (Grime *et al.* 1988) and to be effective the soil needs to be at least to field capacity (Bannister 1964a; Gimingham 1972), with a relatively humid climate. Seedling establishment requires a soil at field capacity and a relative humidity of c. 80%; although very wet soils are detrimental and consequently growth is better on mineral soils (Gimingham 1972). Irradiance is required for successful seedling establishment and therefore seedlings are rarely found within dense stands of heather. In upland heathland systems where strong winds are often coupled with peaty soils, low bushes are the favoured growth form. This form of growth is necessary as any long shoots that grow above the general form of the bush may be killed off (Gimingham 1989). The mature plant cannot tolerate persistent drought as it reduces its vigour; nor waterlogging, where a period of

six to eight weeks is sufficient to significantly reduce transpiration rates brought about by the poor aeration of the root system (Bannister 1964b; Gimingham 1972). *C.vulgaris* also requires a period when the soil is not waterlogged (Gimingham 1989).

C.vulgaris growth can be divided into four phases, as described by Gimingham (1972). Initially there is a pioneer phase where the seedling establishes itself and exhibits a monopodial growth form. This period usually lasts three to six years, but can be ten; during this phase the monopodial growth is gradually replaced by sympodial growth. The building phase follows with a period of annual, peripheral extension of the long shoots and a concentration of photosynthesising leaves on the short shoots. The canopy reaches its maximum density and flowering is profuse; this phase lasts until approximately 15 years of age. The mature phase follows with reduced vigour in the long growth shoots and a shortening of the flowering zone. The plant reaches its maximum height and the oldest central branches begin to become procumbent, allowing greater light to reach the understorey. This phase continues until the plant is 20-25 years of age. The degenerate phase is the final phase with senescence of the central frame branches and the outer branches becoming fully procumbent. This produces a central area of open ground that expands as the plant dies back. The old flattened outer stems may produce adventitious roots, delaying degeneration within these branches; although with time the new shoots produced, die along with the rest of the bush.

C.vulgaris is particularly efficient at utilising soil nitrogen; Loach (1968) thought that it was due to its association with the ericoid mycorrhiza *Hymenoscyphus ericae*. More recently it has been found that nitrogen in the form of amino-complexes can be exploited by ericoid mycorrhiza (Bajwa & Read 1986; Gimingham 1989). Nitrogen-amino complexes found in the organic horizon of heathland soils can be utilised by *Hymenoscyphus ericae*. This association allows *C.vulgaris* to grow in oligotrophic habitats, particularly those

that have a low pH and low nitrogen and phosphorous levels (Abuarghub & Read 1988; Gimingham 1989).

3.1.2 *Lochmaea suturalis* and *Calluna vulgaris* damage or death

Infestations of *C.vulgaris* by *L.suturalis* can have a great effect on moorlands and heaths. Between 0.01 and 3 hectares of *C.vulgaris* can be damaged as a result of a single, initial *L.suturalis* infestation. However not all plants are killed and not all parts of the area are infested. From this initial infestation an area of 10-100 hectares may become infested within one to two years (Smidt & Brunsting 1990). However areas greater than 100 m^2 seldom suffer total death (Smidt 1977), as the resultant damage produces a mosaic pattern comprising healthy, debilitated or dead heather with bare ground, bryophyte cover or *Deschampsia* spp. (Berdowski & Zeilinga 1987). After a light infestation the heather will usually survive, but dies after a heavy attack. This death occurs progressively after a six-month time lag (Berdowski & Zeilinga 1983), or within six months, in variable sized patches, if it is a particularly heavy attack (Berdowski & Zeilinga 1987).

The death of the heather is thought to be caused by a combination of factors including a disturbance in the carbohydrate balance brought about by the removal of green leaves or infiltration of air into damaged xylem vessels (Berdowski & Zeilinga 1983). *L.suturalis* attacks *C.vulgaris* at the end of its annual growth cycle, and as such limits the potential for regenerative growth and if there is any regenerative growth after an attack it dies during the following winter (Berdowski & Zeilinga 1987).

Once a patch of heather is suffering from an infestation the effects of days or weeks of feeding by *L.suturalis* becomes visible after a spell of hot weather or dry wind. This is manifest as all or part of the plant suddenly becoming rust coloured, with July colours often surpassing autumn colours. The damage, at

the time, appears to be homogenous, but a mosaic pattern becomes apparent the following year when the dead plants become grey in colour. Plants that manage to regenerate resume their normal green colour (Smidt 1977).

The following account by Brunsting (1982) summarises the course of an outbreak on the development of vegetation patterns on an area of heathland in Holland between 1979 and 1981. Initially an outbreak was signalled by the appearance of areas (> 10 m^2), of rust coloured *C.vulgaris* caused by high densities of larvae (1000 m^{-2}), feeding on the foliage. Once the new generation adults had emerged they migrated in search of food to the edge of the dead patches, where densities of adults reached 2000 m^{-2}. The beetles caused a "front" to be formed that remained throughout the winter as the new generation adults overwintered. The front experienced only intermediate damage, whilst the area outside the front was healthy, with few adults found. During the spring the emergent adults left the front, dispersed and colonised the surrounding area evenly. In the vacated front, adult mortality caused by the fungal parasite *B.bassiana*, was high (285 m^{-2}), and damage to the *C.vulgaris* was sufficiently low to allow it to regenerate successfully. The area outside the initial front however became heavily infested with the subsequent death of *C.vulgaris*. The situation in the autumn of 1981 was therefore an area of dead *C.vulgaris* (the initial outbreak) with an area (boundary strip) that survived the infestation and, beyond this strip, dead *C.vulgaris*. The following year nearly all the adults left the area, a few remained and tried to establish a colony on the old front (surviving heather), but this failed. The research also found that in the area of the initial outbreak there were smaller numbers of eggs produced (1300 m^{-2}), and greater larval mortalities (5000 m^{-2}), than beyond the boundary strip. It was concluded that the mosaic pattern formed as a result of the colonisation of grasses into the areas of dead *C.vulgaris*, was brought about entirely by the *L.suturalis* infestation and that the population dynamics, primarily migration and mortality, of this infestation determined the shape of the pattern.

Smidt (1977) argues that the complicated interactions between *L.suturalis* and *C.vulgaris* can act in a regulatory capacity and gives the following example of negative feedback, where the interaction lessens the effects of an outbreak, because of the effects of a previous outbreak. If lichens and grasses are present and become dominant as the result of an attack, with the subsequent loss of ground cover bryophytes, then within 5-10 years *C.vulgaris* may become dominant again. This succession is initiated by a *L.suturalis* attack that only occurs every 5-10 years. Bearing in mind that the optimal requirements for the development of *L.suturalis* are a moist understorey of moss and litter covered by dense, tall stands of *C.vulgaris* and, if the heather has not recovered sufficiently, then the next attack may not have the optimal conditions for successful development. Consequently after 10-15 years the patches of *C.vulgaris* that have fully recovered may be attacked again, but this time the area is a mosaic pattern of living *C.vulgaris* (some of which may not be sufficiently mature to provide the optimum conditions), dead heather, mosses and grasses.

As many researchers have established that there is a relationship between the nutrient levels in plants and the nutrient availability of the soils that they are growing in (Wong 1975; Chapin 1980; McNeill & Prestidge 1982; Coley *et al.* 1985; Van Breemen & Dijk 1988; Scandrett & Gimingham 1991; Iason & Hester 1993), and as mentioned in Chapter Two, food is one of the five components of an invertebrate's environment that are important in determining its population success or failure (Andrewartha 1970), it was decided to investigate the relationship between *L.suturalis* larval growth and *C.vulgaris* "food quality".

In the case of *L.suturalis*, which is monophagous, the quality of its host plant, *C.vulgaris* may be an important factor in its ability to devastate areas of heather (Van Der Eerden *et al.* 1991; Berdowski 1993). The "food quality" of a plant can be broadly divided into the nutritional factors, i.e. nitrogen content and the secondary plant compounds, i.e. the tannins. Originally there was considerable

argument as to which factor was the most important (Barbosa 1988). However it is now generally considered that they are both important (Reese 1981, 1983; Duffey *et al.* 1986; Barbosa 1988).

The nitrogen content of plants is well known to be an important limiter of herbivorous terrestrial invertebrate growth and reproduction (McNeill & Southwood 1978; Mattson 1980; Scriber 1984; Slansky & Scriber 1985; Zitzman & May 1988). It is also the best understood area of insect-plant interaction (McNeill & Prestidge 1982). The effect of *C.vulgaris* nitrogen content on the growth of *L.suturalis* larvae has been studied before, but this research was based on field studies where different fertiliser rates were applied to experimental plots (Brunsting & Heil 1985).

Anti-herbivore secondary substances within plants, i.e. tannins are synthesised by plants to "resist" pathogens (Van Emden & Way 1972). Stress tolerant plants growing on low nutrient soils, such as *C.vulgaris*; tend to have low levels of nitrogen (McNeill & Prestidge 1982), and often have high levels of anti-herbivore secondary substances (Feeny 1976; Rhoades & Cates 1976), in an attempt to protect the limited nitrogen from phytophages (Feeny 1970; Wint 1982).

This chapter describes and analyses a series of controlled laboratory experiments that attempt to quantify the relationship between *L.suturalis* larval growth and the *C.vulgaris* growing at the study sites, with a view to incorporating this relationship, as the spatial component, in the population dynamics model constructed in Chapter Four. The differences between the study site *C.vulgaris* plants was established by recording the shoot nitrogen and tannin content, the soil type and the altitude that the plant was growing at. The larval stage was chosen as the growth of the heather beetle occurs almost exclusively during this stage (Cameron *et al.* 1944; Berdowski 1993) and consequently the effects of different levels of nutrients may be more prominent (Brunsting & Heil 1985).

3.2 Materials and methods

3.2.1 *Calluna vulgaris* plant propagation

In September 1995, apical shoot cuttings were taken from mature *C.vulgaris* plants from each of the nine study sites (see Map 2-1, page 19). They were potted up in a 50/50 study site soil and perlite mixture in trays. There were 100 cuttings per tray, with two trays per site, giving a total of 1800 young seedlings. They were placed in propagating units in a cold frame at Close House Research Station and watered when needed.

3.2.2 *Calluna vulgaris*: nitrogen and soluble tannins

In May 1996, five apical shoot cuttings were taken from each of the propagated *C.vulgaris* seedlings that were grown at Close House. These were sealed in airtight plastic bags and labelled. The samples were freeze-dried at the earliest opportunity and when ready for analysis, were pounded with a pestle and mortar and then analysed for their nitrogen content with a 'RoboPrep Automatic Nitrogen and Carbon Analyser'. The results of the analysis were given as the percentage of total nitrogen of total sample dry weight. An analysis of variance test was conducted on the total nitrogen levels to test whether there were any inter-site differences.

The soluble tannins were determined using the same batch of samples and by the extraction method given by Allen (1989). The results of the analysis were given as the percentage of soluble tannins of total sample dry weight. An analysis of variance test was conducted on the soluble tannin levels to test whether there were any inter-site differences.

The relationships between the total nitrogen and the soluble tannin levels and study soil type and site altitude were investigated by fitting generalised linear regression models, (GLM's). To facilitate the analysis the study site soils were given categorical values and treated as a factor in the GLM's (see Table 3-1).

Study site	Soil type	Factor	Altitude
East Kielder Moor	Raw oligo-fibrous peat soil	4	450 m
Sandy's Gears	Cambic stagnohumic gley	1	350 m
Yarrow	Ironpan stagnopodzol	2	200 m
Padon Hill	Ironpan stagnopodzol	2	340 m
Thorngrafton Common	Cambic stagnogley	3	200 m
Allenheads	Cambic stagnohumic gley	1	500 m
Slaley	Cambic stagnohumic gley	1	295 m
King's Law	Cambic stagnogley	3	350 m
Huntstanworth Moor	Cambic stagnogley	3	450 m

Table 3-1: Altitudes and category values assigned to the soil types at the study sites for the generalised linear regression models, employed for the testing of the relationships between total nitrogen and soluble tannin levels and study soil type and site altitude, (in metres)

3.2.3 *Calluna vulgaris* and larval growth

On the 24th May 1996, newly hatched larvae were weighed and then placed singly on the *C.vulgaris* seedlings that were growing in the original study site soils. These were then covered by inverting another, slightly larger pot onto this (see Figure 3-1, page 91). As there were insufficient viable seedlings from two of the nine sets of *C.vulgaris* seedlings (Padon Hill and Sandy's Gears), each of the three temperature treatments involved five replicates for each of the seven remaining site's viable seedlings. This gave a total of 35 pots. One set of 35 pots was kept at each of three temperatures (15, 20 and 25°C) in pre-

calibrated incubators with a photoperiod of 16/8 hours. At intervals of five to six days the larvae were weighed, the pots watered if needed and the incubators checked for temperature control. The experiment was continued until all larvae had pupated. Daily percentage growth rates of the larvae were then determined.

The relationship between the percentage growth rates day^{-1} for the *L.suturalis* larvae and the total nitrogen level content and the soluble tannin levels was investigated by fitting generalised linear regression models at each temperature (15, 20 and 25°C).

Finally the relationship between the percentage growth rates day^{-1} for the *L.suturalis* larvae and temperature and soil type was investigated by fitting a generalised linear regression model.

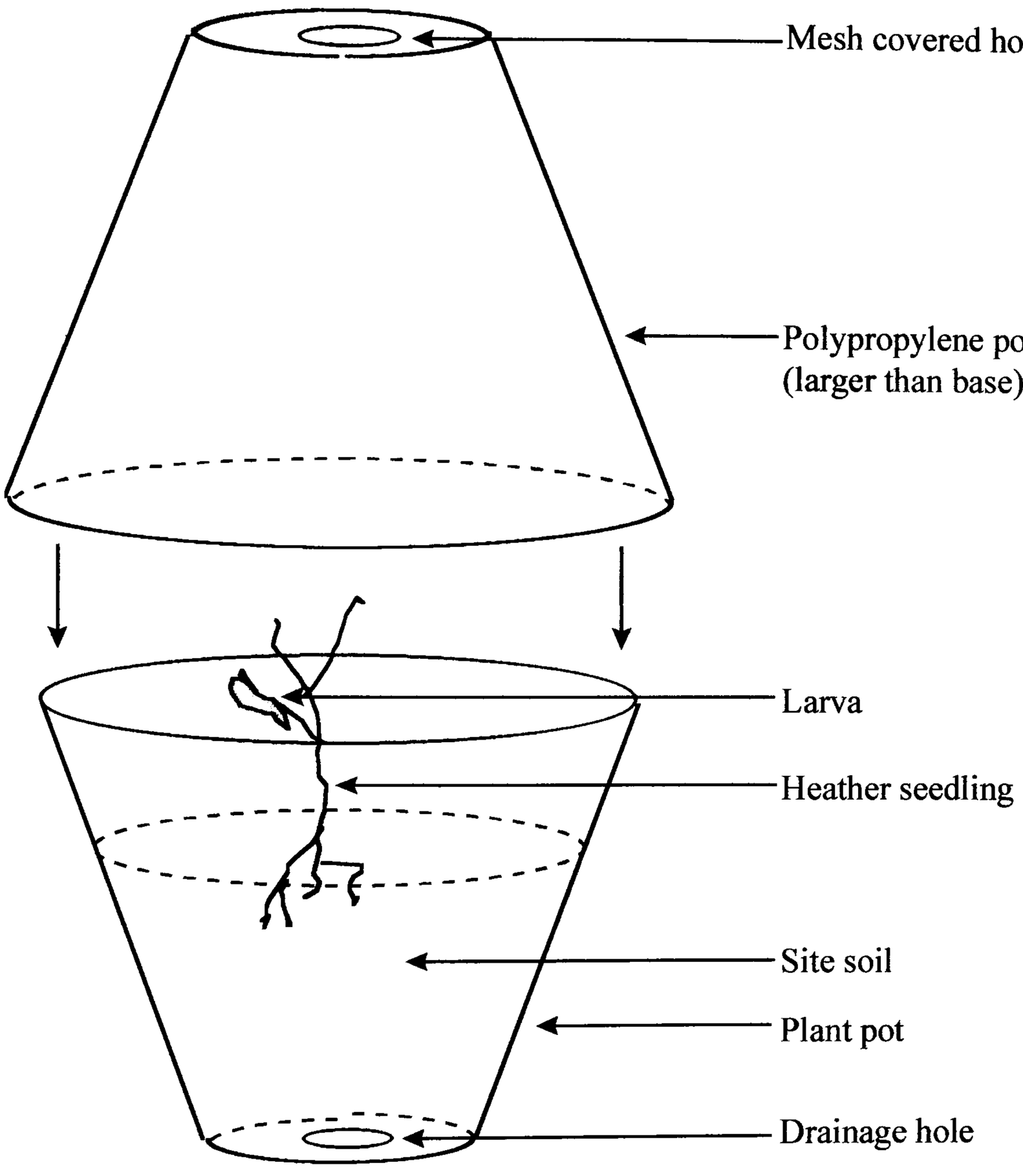


Figure 3-1: Design of the apparatus for the *Calluna vulgaris* and *Lochmaea suturalis* larval growth experiment

3.3 Results

The following abbreviations are used for the study sites: Ekm = East Kielder Moor, Sg = Sandy's Gears, Ya = Yarrow, Ph = Padon Hill, Th = Thorngrafton, All = Allenheads, Sl = Slaley, Kl = Kings Law, Hu = Huntstanworth. Refer to Appendix II, page 290 for the study site details and site selection criteria.

3.3.1 *Calluna vulgaris*: nitrogen and soluble tannins

The results of the percentage total nitrogen of the sample dry weight determinations are presented graphically (see Figure 3-2, page 95).

The results of the analysis of variance test performed on the total nitrogen content data (see Table 3-2), showed that there was a significant difference, (at $P < 0.001$) in the percentage total nitrogen of dry weight found between the study site *C.vulgaris* samples.

Source	d.f.	SS	MS	F-ratio	*P*-value
Factor	8	3.87	0.48	29.65	< 0.001***
Error	36	0.59	0.06		
Total	44	4.45			

Table 3-2: Analysis of variance (*n*=5) for the total nitrogen levels (% of dry weight), of the *Calluna vulgaris* samples from the nine study sites

The results of the percentage soluble tannin content of dry weight of the *C.vulgaris* samples from the nine study sites are presented graphically (see Figure 3-3, page 96).

The results of the analysis of variance test performed on the soluble tannin content data (see Table 3-3), shows that there was no significant difference, (at $P = 0.24^{NS}$) in the percentage soluble tannin of dry weight found between the study site *C.vulgaris* samples.

Source	d.f.	SS	MS	F-ratio	*P*-value
Factor	8	6.14	0.77	1.62	0.24^{NS}
Error	9	4.25	0.47		
Total	17	10.39			

Table 3-3: Analysis of variance (*n*=2) for the soluble tannin content (% of dry weight) of the *Calluna vulgaris* samples from the nine study sites

A Pearson's correlation coefficient was undertaken between the total nitrogen content (% of dry weight) and the soluble tannin content (% of dry weight) of the *C.vulgaris* plants. There was found to be no correlation, with a value of $r = -0.029^{NS}$, at $P = 0.94$.

The results of the generalised linear regression (GLM) to ascertain whether the different nitrogen level values or the soluble tannin levels were related to either the study site soil type or the altitude of the study site, or both, show no significant relationships (see Tables 3-4 & 3-5, page 94).

Source	*n*	d.f.	F-ratio	*P-value*
Study soil type	9	3	0.64	0.63^{NS}
Altitude	9	1	0.01	0.93^{NS}

Table 3-4: Generalised linear model regression results, relating total nitrogen levels (% of dry weight) of the *Calluna vulgaris* samples, (*n*=9), from the study sites to the study soil types and the altitude of the sites

Source	*n*	d.f.	F-ratio	*P*-value
Study soil type	9	3	1.87	0.28^{NS}
Altitude	9	1	0.30	0.61^{NS}

Table 3-5: Generalised linear model regression results, relating total soluble tannin levels (% of dry weight) of the *Calluna vulgaris* samples, (*n*=9), from the study sites to the study soil sites and the altitude of the sites

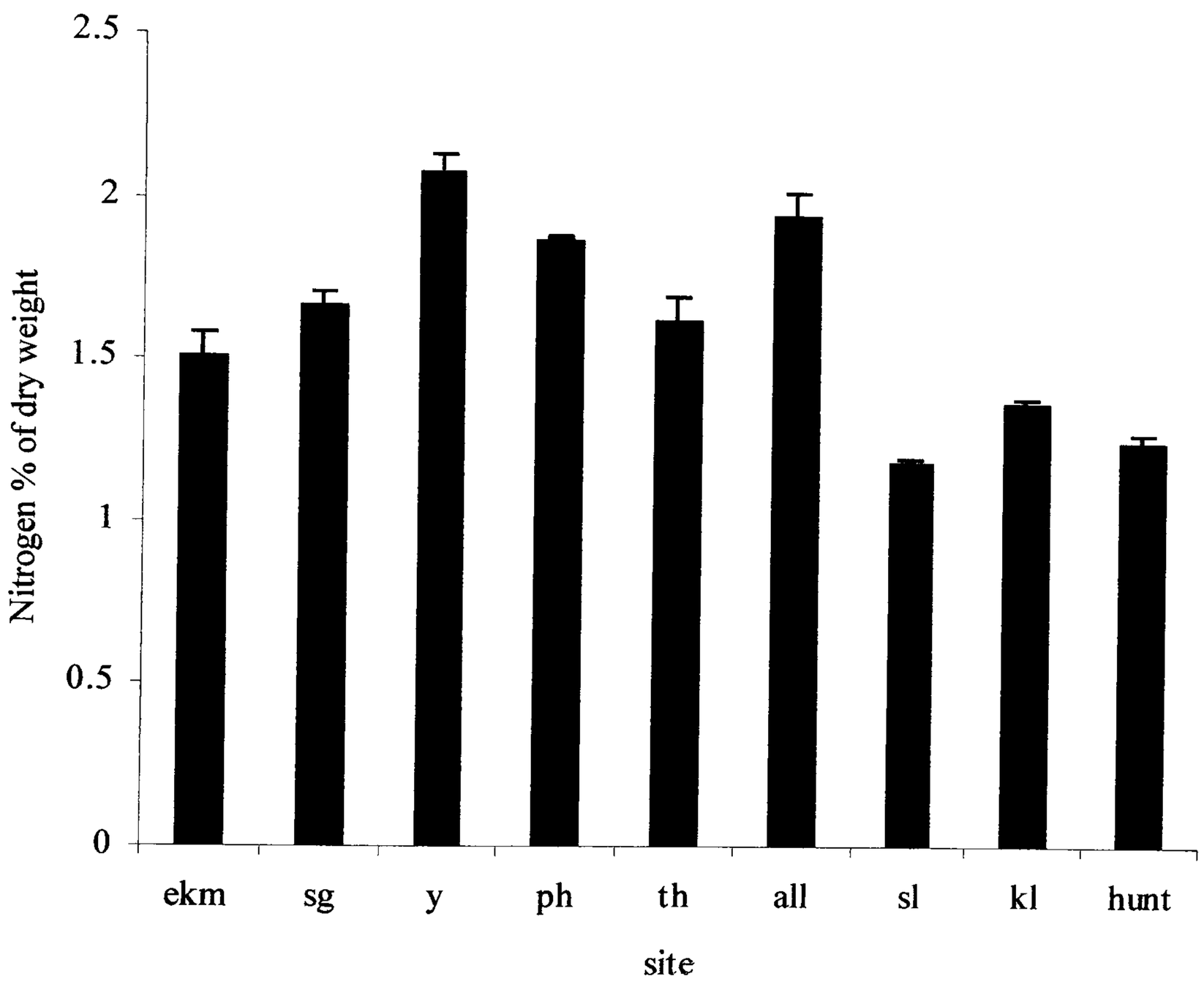


Figure 3-2: Mean and standard error, (*n*=5) of total nitrogen levels (% of dry weight) of the *Calluna vulgaris* samples from the nine study sites

Key: Ekm = East Kielder Moor, Sg = Sandy's Gears, Ya = Yarrow, Ph = Padon Hill, Th = Thorngrafton Common, All = Allenheads, Sl = Slaley, Kl = Kings Law, Hu = Huntstansworth Moor

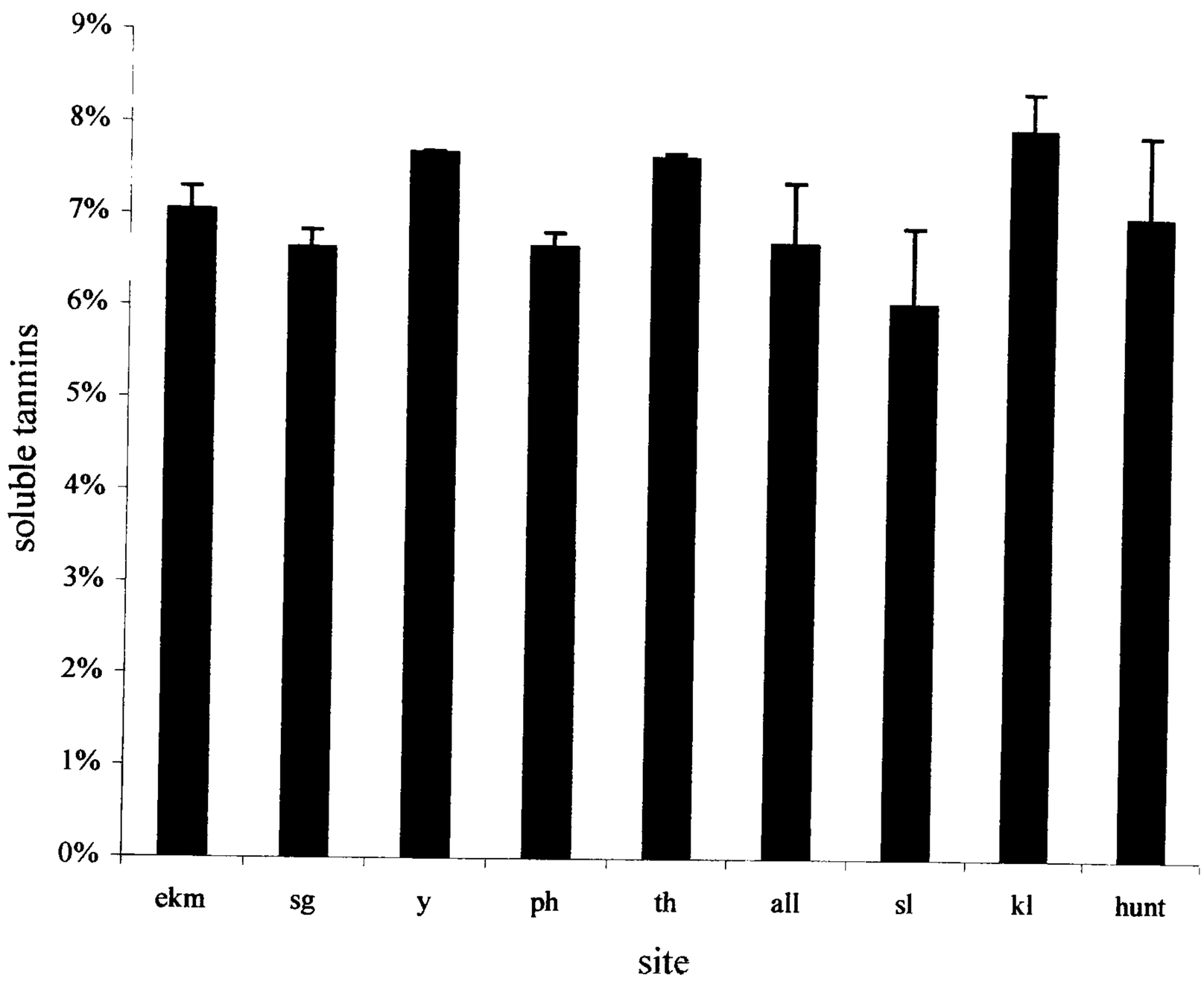


Figure 3-3: Mean and standard error, (*n*=2) of total soluble tannins (% of dry weight) of the *Calluna vulgaris* samples from the nine study sites

Key: Ekm = East Kielder Moor, Sg = Sandy's Gears, Ya = Yarrow, Ph = Padon Hill, Th = Thorngrafton Common, All = Allenheads, Sl = Slaley, Kl = Kings Law, Hu = Huntstansworth Moor

3.3.2 *Calluna vulgaris* and larval growth

The growth rates of the larvae for each of the seven study sites at the three temperatures (15, 20 and 25°C), are shown graphically (see Figure 3-4, page 99). As can be seen, for all seven sites, the growth rates for all larvae, increased as the temperature of the experiment increased.

The results of the generalised linear regressions for the larval growth rates day^{-1} at each temperature, (15, 20 and 25°C) against the total nitrogen content and the soluble tannin levels of the *C.vulgaris* from each study site, show that there was no significant relationship, at $P > 5\%$ (see Table 3-6).

Temperature	Source	*n*	d.f.	F-ratio	*P*-value
15°C	nitrogen content	7	1	1.00	0.37^{NS}
	tannin level	7	1	1.65	0.27^{NS}
20°C	nitrogen content	7	1	0.33	0.60^{NS}
	tannin level	7	1	0.65	0.47^{NS}
25°C	nitrogen content	7	1	3.18	0.15^{NS}
	tannin level	7	1	1.45	0.30^{NS}

Table 3-6: Generalised linear regression results relating *L.suturalis* larval growth rate day^{-1} and *C.vulgaris* total nitrogen and soluble tannin levels, (% of dry weight), at the three temperatures (15, 20 and 25°C)

The mean growth rate for all seven study sites was plotted against the temperature (see Figure 3-5, page 100). A linear regression was conducted and the regression slope, $m \neq 0$ at, $P = 0.22^{NS}$. This shows that growth rate of the larvae increased as temperature increased.

The results of the generalised linear regression to ascertain whether the *L.suturalis* larval growth rate day^{-1} was related to temperature and study soil type shows that the growth rate was significantly related to temperature, at $P < 0.001$, but there was no significant relationship with study soil type (see Table 3-7).

Source	*n*	d.f.	F-ratio	*P*-value
Temperature	3	1	18.34	< 0.001***
Soil type	7	3	1.14	0.37^{NS}

Table 3-7: Generalised linear regression results relating *L.suturalis* larval growth rate day^{-1} to temperature (^{o}C) and study soil type

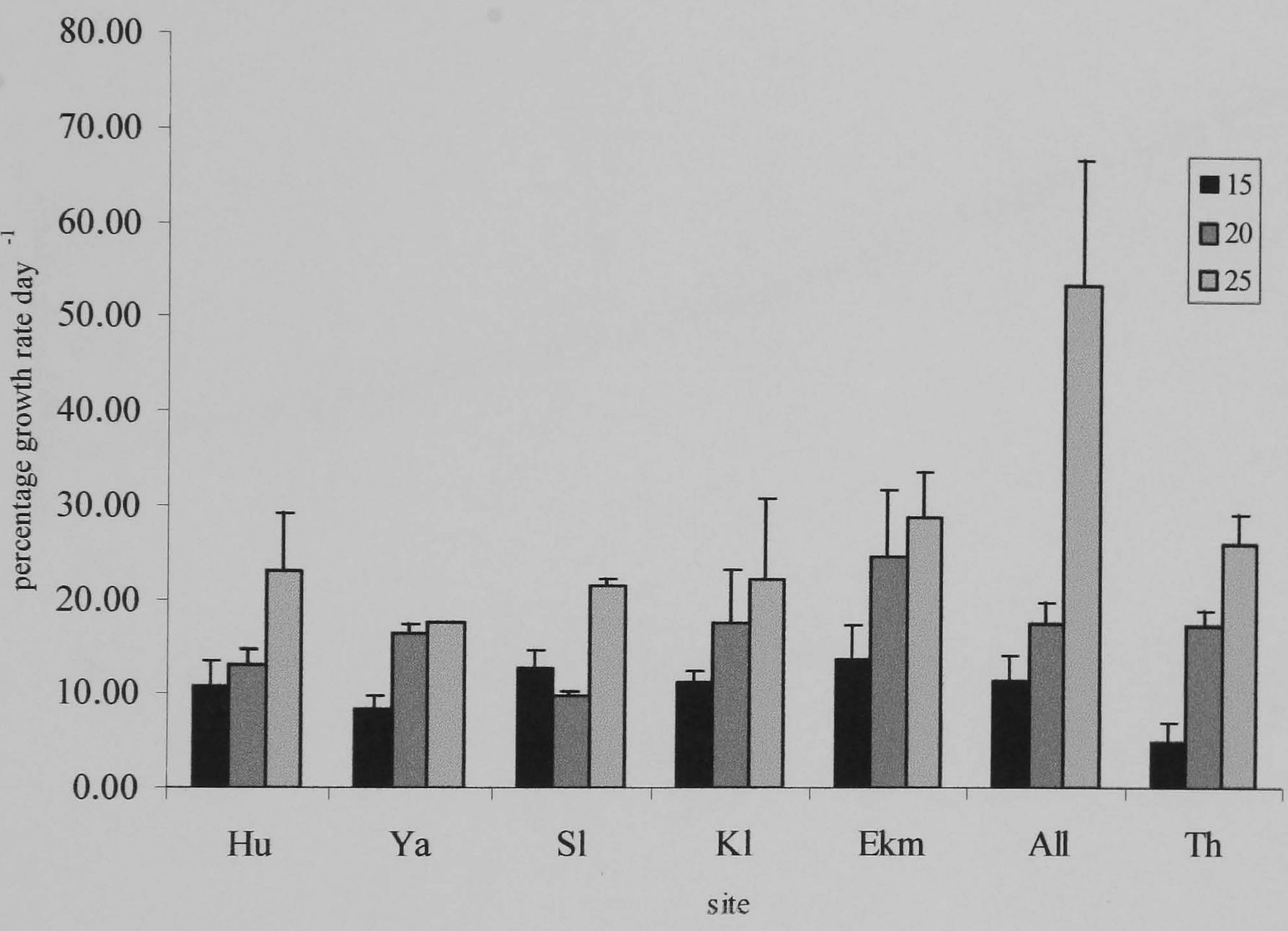


Figure 3-4: Mean and standard error, (n=5) of percentage growth day^{-1} of *L.suturalis* larvae in the *C.vulgaris* and larval growth experiment; for seven of the nine study sites at 15, 20 and 25°C

Key: Hu = Huntstansworth Moor, Ya = Yarrow, Sl = Slaley, Kl = Kings Law, Ekm = East Kielder Moor, All = Allenheads, Th = Thorngrafton Common

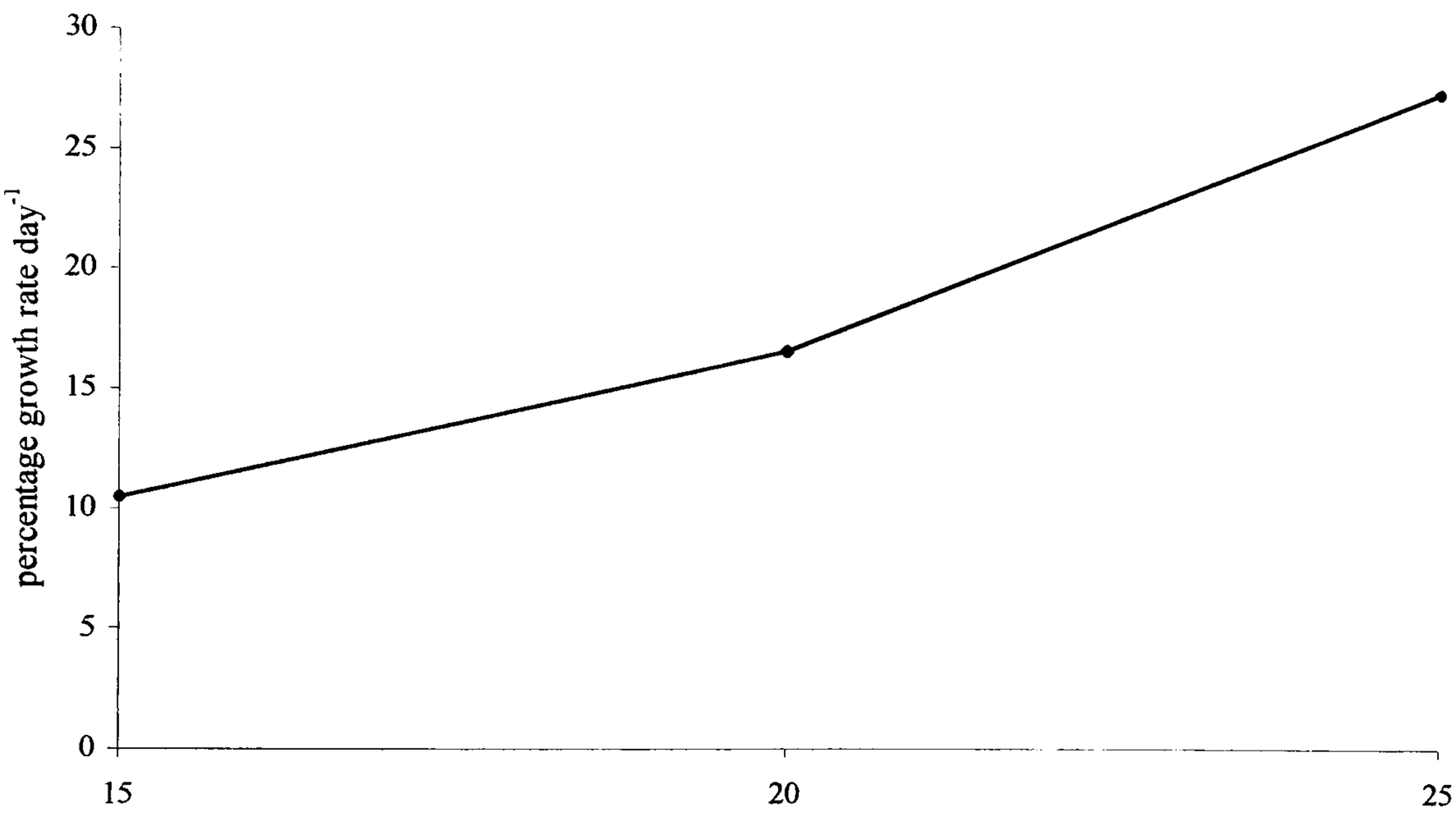


Figure 3-5: Mean of all seven sites, percentage larval growth rates day^{-1} plotted against the three temperatures; all standard errors are < 4.59, the regression slope $m \neq 0$, at $P = 0.22^{NS}$

3.4 Discussion

The results of the investigation into the relationship between the larval growth of *Lochmaea suturalis* and the provenance of the *Calluna vulgaris* can be broadly divided into two groups. The first group investigated if there was a relationship between the "nutrient quality" of the *C.vulgaris* and the study site that the shoot samples were sourced from. The results of these experiments showed that the levels of total nitrogen found in the *C.vulgaris* leaves, sourced from the different study sites were significantly different from one another, with a range of c. 1.25 to 2.2 % of total nitrogen of total dry weight. This range of total nitrogen content is in line with those found in other similar studies of *C.vulgaris* shoot nitrogen content (see Table 3-8).

Source	Range or Mean	Time(s) of analysis and age of plant (in years)
Thesis study	1.25-2.2 %	June (1)
Whitehead *et al.* (1997)	9.3-23.7 mg g^{-1}	October, June (2)
Hartley & Gardner (1995)	1.22 %	August (10-15)
Iason *et al.* (1993)	1.1-1.25 %	May, August, Sept., Nov. (15)
Iason & Hester (1993)	1.15 %	November (20)
Loach (1968)	126-141 mg $10g^{-1}$	September (5)
***note:** 1.0 mg g^{-1} ≈ 0.1 % and 1 mg $10g^{-1}$ ≈ 0.01 % total N of total dry weight		

Table 3-8: Comparison of range or mean of total nitrogen (% of dry weight), found in *Calluna vulgaris* shoots, by different researchers and the thesis study

Although the levels found in the study samples are of the same magnitude, it is difficult to make direct comparisons as the other studies differed in the age and phenological stage of the *C.vulgaris* when the samples were taken. The nearest comparative studies were that of Whitehead *et al.* (1997) and Loach (1968) whose studies of similar aged seedlings, found very similar results. It should be noted however that the Whitehead *et al.* (1997) study used a "richer substrate", a 9:1 Irish moss peat /moorland soil and Loach (1968) conducted the work on a dry lowland heath.

Wong (1975) researched the effects of climate on the seasonal variation of soil and leaf nutrients of *C.vulgaris* on Waldridge Fell, Co.Durham. It was found that there were lower levels of total nitrogen in the *C.vulgaris* plants growing in the waterlogged areas and the total nitrogen content in leaf tissues was highest in the period, late spring to summer. This was attributed to anaerobic conditions that are unfavourable for both decomposition and mineralisation of nitrogen. These findings fit in with the results from the Hartley & Gardner (1995); Iason *et al.* (1993) and Iason & Hester (1993) studies, that reported slightly lower total nitrogen levels overall, with a slight increase over the summer period. They postulated that this may be accounted for by the fact that the studies were on wet, relatively high moorland sites, where nitrogen would be expected to be lower because of the lower nutrient availability (McNeill & Prestidge 1982; Scandrett & Gimingham 1991; Iason & Hester 1993).

However, if the findings from Wong (1975) are applied to the study results it would be expected to find lower levels of nitrogen in the samples from the colder, higher altitude and wetter sites; but by inspection (see Figure 3-2, page 95 and Table 3-1, page 89) it was not the case. Indeed the GLM analysis used to test for a relationship between total shoot nitrogen and the study site and the altitude of the site corroborated this, with a non-significant result.

The lack of a relationship between the total nitrogen content of the seedlings and the study sites may have been due to the nature of the experiment. The

seedlings were propagated in a 50/50 perlite and study site soil mixture to increase the likelihood of successful propagation by a homogenisation of the growth medium. Caporn *et al.* (1995) found that increased shoot growth in *C.vulgaris* was not seen, when additional nitrogen was applied, until the second seasons growth. This finding may account for the lack of a relationship between total nitrogen content and the site that the *C.vulgaris* came from, as the "nitrogen effect" may have been lessened, due the "real" effect of the study site soils being delayed.

The soluble tannin levels of the *C.vulgaris* seedlings from the study sites were not significantly different from one another, ranging from 6.2 to 7.8 % of dry weight. These results are generally in line with similar studies that quantified *C.vulgaris* shoot soluble tannins (see Table 3-9).

Source	Range or Mean	Time of analysis and age of plant (in years)
Thesis study	6.2-7.8 %	June (1)
Hartley & Gardner (1995)	3.58 %	August (10-15)
Iason *et al.* (1993)	9.0, 6.0, 8.0, 5.0 %	May, Aug., Sept., Nov. (15)
Iason & Hester (1993)	6.0 %	November (20)

Table 3-9: Comparison of range or mean of soluble tannins (% of dry weight) found in *Calluna vulgaris* shoots, by different researchers and the thesis study

The values gained from the analysis are as high as would be expected from plants associated with poor nutrient habitats. These plants usually have a higher allocation of defensive compounds such as phenolics and tannins (Coley *et al.* 1985; Hartley & Gardner 1995). In particular *C.vulgaris* is noted for its

richness in phenolic compounds (Jalal *et al.* 1982; Hartley & Amos 1999), and high concentrations of secondary chemicals (Iason *et al.* 1993; Hartley & Amos 1999). McNeill & Prestidge (1982) cite, as comparisons, the following soluble tannin levels for non stress tolerant trees: *Crataegus* 3 % rising to 10%, *Corylus* < 1 % rising to 4 %, *Fagus & Quercus* 1 % rising to 2 %, *Prunus & Malus* < 1 %, (% soluble tannins of total weight).

The high soluble tannins and secondary chemical levels are thought to be because stress tolerating plants in low nutrient habitats generally have low tissue nitrogen levels, and are particularly sensitive to the loss of valuable leaf material to herbivores. They therefore tend to have high anti-herbivore secondary substances (Feeny 1976; Rhoades & Coates 1976; Chapin 1980; McNeill & Prestidge 1982).

Iason *et al.*'s (1993) study showed a decrease in soluble tannins over the summer season and Hartley & Gardner's (1995) study a low figure in August (see Table 3-9, page 103). This seasonal variation could be accounted for by the carbon nutrient balance hypothesis, as proposed by Bryant *et al.* (1983) and reinforced by Waring *et al.* (1985) and Bryant *et al.* (1987). This states that plants in a low nutrient supply situation allocate carbon resources into secondary chemical production. Also research by Palo *et al.* (1985) and Baldwin *et al.* (1987) shows that secondary compound concentrations vary over a growing season. In *C.vulgaris* this variation has been shown to decrease gradually over the summer and increase at the end of the summer (Grace & Woolhouse 1973; Miller 1979; Iason *et al.* (1993).

Given that that there is a relationship between low substrate nutrient availability and low nutrient levels within a plant (McNeill & Prestidge 1982; Scandrett & Gimingham 1991; Iason & Hester 1993), and that the above two hypotheses state that the lower the nutrient levels available to *C.vulgaris*, the greater the levels of phenolic in the plant, it would have been expected to find greater levels of tannins in the samples taken from the colder, wetter, higher altitude sites.

However in this study no such relationship was found; this may have been due to, as previously discussed, that there was not enough time in the experiment for the seedlings to reflect their site-specific plant chemistry.

The second set of experiments, which investigated the relationship between *L.suturalis* larval growth and the *C.vulgaris* plants from different sites at the three controlled temperatures, *viz.*15, 20 and 25°C, all yielded non-significant results. This was as expected, as it had already been found that there was no relationship between the study sites and the plant nutrient levels. *L.suturalis* larval growth was significantly related to temperature; this was expected, given the discussion in the previous chapter, on the mechanisms involving insect growth and temperature.

However, the question remains, would there have been an effect if, as previously postulated, the experiments had been conducted over a longer period. Research on the interaction between phytophagous plants and plant nutrition is complex and has produced conflicting ideas, as the following summary will show. Various researchers have shown that nitrogen content in plants is positively correlated to growth, reproduction and survival of phytophagous insects (McNeill & Southwood 1978; McNeill & Prestidge 1982; Mattson 1980; Scriber 1984). Whilst other research has shown no correlation or a negative correlation between insect performance and host plant nitrogen content (Zitzman & May 1988). Scriber (1984) considers that, as nitrogen is also a component of toxins and antifeedants in the form of non-utilisable nitrates that this could account for the negative or no correlations found. Additionally soil nitrogen is positively related to plant nitrogen content (Tingey & Singh 1980), and in particular, *C.vulgaris* nitrogen content (Wong 1975; Brunsting & Heil 1985; Iason & Hester 1993).

Research on the relationship between *L.suturalis* and *C.vulgaris* has shown that *L.suturalis* larval growth is affected by the nutrient quality of the host plant and that this nutrient quality is in turn a function of the available nutrients in the

growth medium (Brunsting & Heil 1985; Berdowski & Siepel 1987; Berdowski & Zeilinga 1987; Heil & Bruggink 1987). It would seem likely that *L.suturalis* populations on *C.vulgaris* stands with higher nitrogen levels would have more vigour and consequently, the heather would suffer greater heather beetle attacks. Iason & Hester (1993) found that increased nutrient availability lowered the lignin and increased the nitrogen content of the shoots and surmised that increased nutrient availability may predispose heather to greater herbivore attack. Berdowski & Zeilinga (1987) cite unpublished work by Brunsting (1982) who recorded that *L.suturalis* produced greater numbers of eggs and larger larvae when feeding on nutrient-rich plants than on nutrient-poor plants. The increased growth rates and weights led to a shorter larval stage, with the possibility of a lower vulnerability to attack by natural enemies, and a greater adult weight. Berdowski & Zeilinga (1987) suggested that the increased nutrient status of the plants may increase natality and decrease mortality, and that this may increase the frequency and severity of attacks. In contrast Gimingham (1972) found the severest heather beetle attacks on, what would be considered by the Dutch researchers, low nutrient habitats. He noted that young shoot stem apices, bark and leaves are eaten by both adult and larvae causing severe damage to patches or extensive areas of *C.vulgaris*. Adding that individual mature and degenerate phase plants may be killed and concluded that attacks seem to be worst where *C.vulgaris* has low vigour, for example, old stands on flat, wet ground. To add to the conundrum, Morison (1963) found that *C.vulgaris* on dry, freely drained soils was particularly susceptible to damage.

It should also be noted however that the damage to the heather may also be related to the amount of food consumed by the beetle. Insofar that damage to the heather may be as a consequence of a large population of beetles thriving on a high nutrient status stand of heather *or* because of a small beetle population consuming large amounts of low nutrient status heather.

As can be seen the relationship between *L.suturalis* and *C.vulgaris* is not straightforward. It seems that the beetles' relationship with heather may be a combination of two factors. Firstly, as it is a monophage of a stress tolerating plant, it will be as McNeill & Prestidge (1982) concluded, when discussing insect herbivores on stress tolerant plants, a slow growing taxonomic specialist and a nutrient generalist. A nutrient generalist can withstand both seasonally varying plant nutrient levels, and those levels conferred on the host plant by differing site nutrient levels without a profound effect on its population, thus ensuring relative population stability. Secondly, as Berdowski & Zeilinga (1987) postulated, when confronted by an unexpected result in one of their studies, where some low nutrient status sites had suffered heavy damage. That the damage pattern may not have been propagated by certain environmental parameters attached to certain vegetation types, but may have been related to spatial differences in beetle density resulting from its behaviour.

3.5 Conclusions

The experiments described in this chapter have produced individual, significant results that conform to established research on *C.vulgaris* and *L.suturalis*. In particular the total nitrogen and tannin levels found in the *C.vulgaris* samples, and the increase in growth rates of the larvae, in relation to temperature were what would be expected.

However, the aims of this section of the study were to investigate the relationship between *L.suturalis* larval growth and the provenance of the *C.vulgaris* seedlings, quantified as it's nutrient quality, in an attempt to unify "both sides of the equation". This investigation was undertaken with a view to testing the second hypothesis, posed in the introduction: that the nutrient quality, and hence, the site that the *C.vulgaris* was growing on, had an effect on *L.suturalis* larval growth. Unfortunately the results of the larval growth and study site experiment failed to find a significant relationship, although other researchers were able to show a significant relationship, albeit at the "field scale".

At the beginning of the thesis it was envisaged that if a relationship could be found between the *C.vulgaris* plants from different sites and *L.suturalis* larval growth, that the results garnered, would be incorporated, with the population dynamics results from Chapter Two, into a temporally and spatially explicit population dynamics model. Such a model would have been able to predict changes in *L.suturalis* populations over a heathland or moorland landscape, with their inherently different nutrient levels.

In conclusion, I feel that if the *C.vulgaris* seedlings had been established earlier in the study and grown for longer, so they could properly reflect their nutritional differences, before being used in the experiment; coupled with an analysis of the

study site soils, then the possibility of significant results would have been greatly increased. This would have allowed for their incorporation, as a "second layer", into the temporally explicit population dynamics model, whose construction and sensitivity and uncertainty analysis is described in the following two chapters.

Chapter 4: Modelling the population dynamics of *Lochmaea suturalis*

4.1 Introduction

This chapter describes the method by which the empirically derived *Lochmaea suturalis* life history data, evaluated and analysed in Chapter Two, are incorporated into a simulation model to test the third and fourth thesis hypotheses. These were that the altitude and the soil type at which a population exists, will have an effect on *L.suturalis* population viability and that any predicted increases in daily mean temperatures, as a consequence of climate change, would have an affect on the viability of *L.suturalis* populations. As discussed in Chapter Three no significant relationship was found between soil type and *L.suturalis* larval growth, consequently the third hypothesis was revised to whether just altitude had an effect on a population's viability.

A computer simulation "model" was constructed to test these two hypotheses. The term model has many definitions; however the following concise definition sums up the overall philosophy behind the term.

> "...a model is the formal expression of the essential elements of some problem in either physical or mathematical terms." (Jeffers 1978, 1988).

By broadening this definition, modelling can be described as a method of describing the basic elements of a system in a reproducible way, either mathematically or physically to simulate that system and that once the elements have been described, they can be linked together to imitate actual processes and predict an outcome from an initial starting point given a set of criteria.

With this modelling structure, there is, as Killon & Grant (1995) have noted, an important objective; that the simulation of the system should be as accurate as possible whilst constructing the simplest model based on the key processes.

There are also many "types" of models; in Jorgensen's (1994) classification, eighteen are described. However, broadly speaking, models can be divided into two families, dependent on whether they are static or dynamic. Static models are defined as those whose variables are not dependent on time, whilst dynamic models are those whose variables are dependent on time. These two families of models can be further sub-divided into models that are either deterministic or stochastic. Deterministic models are defined as those whose predicted values can be computed exactly, for example, if the variables and starting value of the model remain constant, then over successive runs of the model the answer will always be the same. However, with stochastic models the values of the variables are derived from probability distributions that describe the variables, subsequently each run of the model, assuming the stochastic value is *randomly* drawn from the distribution, will give a different answer each time the model is run. This stochastic variation has been increasingly employed to describe ecological processes as it can exploit, and attempts to mimic, the inherent variability of living organisms (Chalabi 1991; Renshaw 1991).

This chapter describes a dynamic, stochastic model that predicts the change in an initial population of *L.suturalis* adults that utilises a predicted daily mean temperature as its driving variable. It has been developed as an exploratory tool to investigate viabilities of the heather beetle populations over a range of temperature and altitude scenarios.

Temperature was chosen as the life stage variables employed in the model were all derived from temperature dependent experiments and, as Wagner *et al.* (1984) and Tauber *et al.* (1994) noted, temperature driven models can be useful in predicting phenological events, as in many cases thermal accumulations accurately reflect the seasonal progression and dynamics of terrestrial

invertebrates. The stochastic variation of the model processes was realised by first, varying the predicted daily mean temperature and second, by varying the majority of the life stage variables and threshold temperatures. However some of the variables were not subject to variation, the reasons for this are considered in the discussion section at the end of the chapter.

4.1.1 *Lochmaea suturalis* population dynamics model overview

The *Lochmaea suturalis* population model was constructed as a daily looped, individual cohort based model, with each cohort being subject to either constant or stochastic variables that "shape" the annual life cycle of the beetle. It comprised a main module that linked together three sub-modules (see Figure 4-1, page 115).

The main module required, as inputs the following. The initial beetle population, the number of years run, the altitude at which the model was run and the number of replicates required. The main module driving variable was a stochastically derived daily mean temperature drawn from the daily mean temperature sub-module (see Figure 4-2, page 116). The daily mean temperature sub-module required, as inputs, the day of the year, the altitude of the model run and the temperature of the day before. If it was the first year of the model run, then the temperature on the day before was derived from a stochastically varied regression model.

The number of females on day one was derived from the initial population figure subjected to a stochastically varying sex ratio variable. The females were then subjected to a stochastically varying daily winter adult mortality until the temperature on a given day was greater than the emergence threshold temperature; the temperature at which the overwintering adults emerge from their overwintering diapause. The newly emerged females were subjected to a stochastically varying summer adult mortality. Once the daily mean temperature

had risen to an egg-laying temperature threshold the beetles (females) were subjected to a stochastically varying breeding mortality. At the end of the breeding season the females were subjected to a female mortality variable; this was not stochastic and was set to a high level to "kill off" the remaining, old generation adults (females).

Once breeding had begun the egg generation sub-module was called (see 4-3, page 117). This sub-module required as its inputs, the day since breeding began and the temperature on that particular day. The egg generation sub-module returned the stochastically derived number of eggs that each female would lay on that day. The total number of eggs laid on that day by all females, was defined as a cohort and was dealt with, for the rest of the model, as an individual cohort by the cohort sub-module (see Figure 4-4, page 118).

Each cohort, within the cohort sub-module, was assigned an accumulated day degree counter. The counter summed the day degrees for each cohort, beginning at day one of a particular cohort, if that day's temperature was greater than the emergence threshold temperature. The accumulated temperature determined the life stage transitions for each cohort. Each cohort was subjected to life stage specific mortality factors, e.g. the egg, larval, pupal, adult summer and adult winter mortalities, dependent on the life stage that the cohort was in, at any given point in time.

At the end of the year the number of new generation adults in each cohort was totalled to give the year-end total. The total number of new generation adults was carried forward, together with the temperature of last day of the year, as the inputs for the next year. This was continued until that particular model scenario was complete.

4.2 Methods

4.2.1 *Lochmaea suturalis* population dynamics model flow charts

The *Lochmaea suturalis* population dynamics model construction and modularisation are presented as four flow charts. The main module (see Figure 4-1, page 115), controls the main flow of the model and during its execution calls the three sub-modules: the daily mean temperature model (see Figure 4-2, page 116), the egg generator model (see Figure 4-3, page 117), and the cohort sub-module (see Figure 4-4, page 118).

In the *L.suturalis* population dynamics model flow charts the following abbreviations are used.

Initial population: **p (n=1)**

Subsequent year populations: **p (n+1)**

Number of years run: **y (max)**

Number of year: **y (n)**

Daily mean temperature in degrees centigrade: $\mathbf{T^o}$

Day number since egg-laying began: **eggday = c (n)** egg generation model only

Yes: **Y**, No: **N**

Number of individual cohort: **c (n)** for cohort sub-module only

Accumulated day degrees temperature for individual cohort: $\mathbf{accT^o}$ **(n)**

Egg to larvae accumulated day degrees development: **eld**

Larvae to Pupae accumulated day degrees development: **lpd**

Pupae to Adult accumulated day degrees development: **pad**

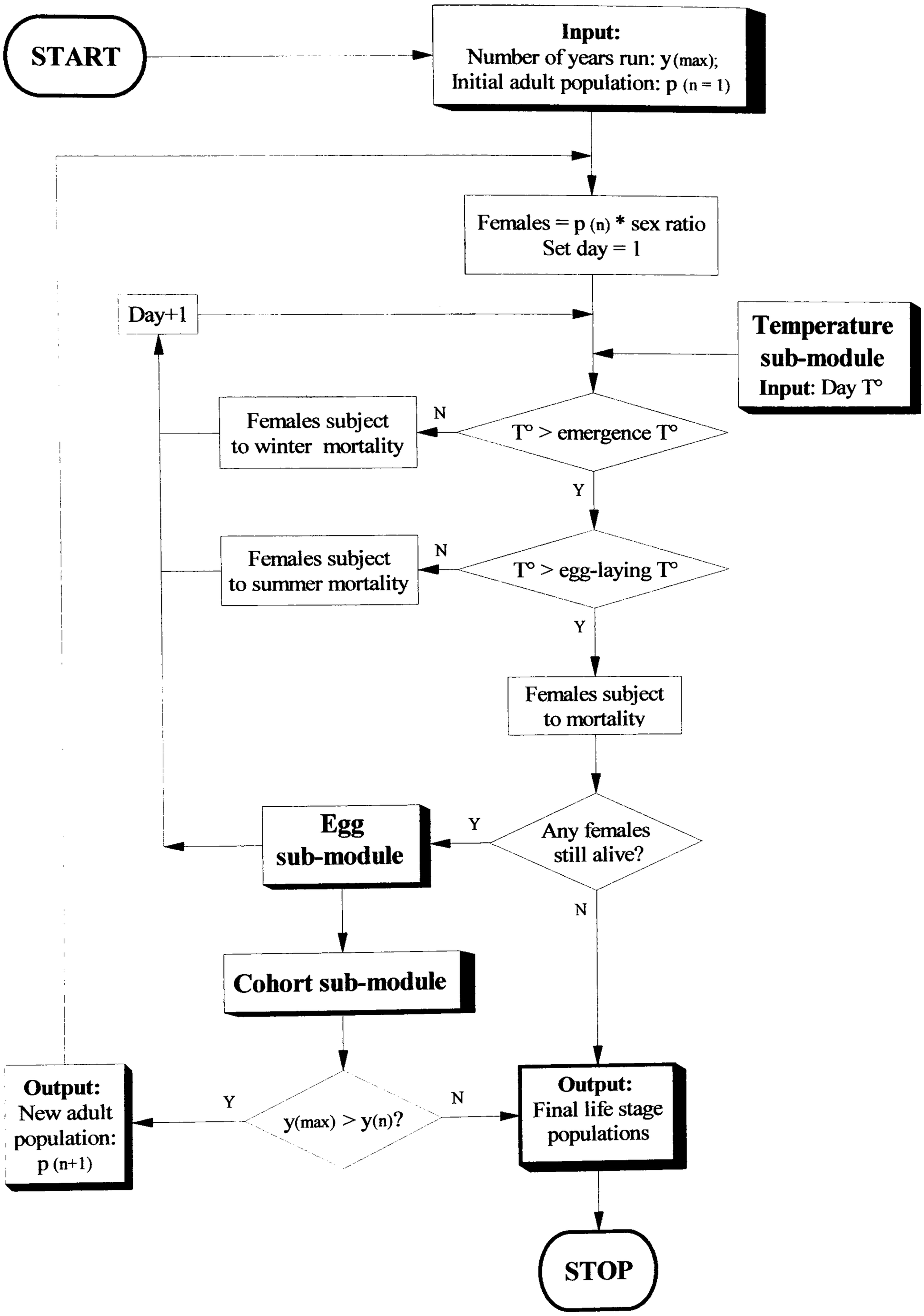


Figure 4-1: Flow chart of the *Lochmaea suturalis* population dynamics model main-module

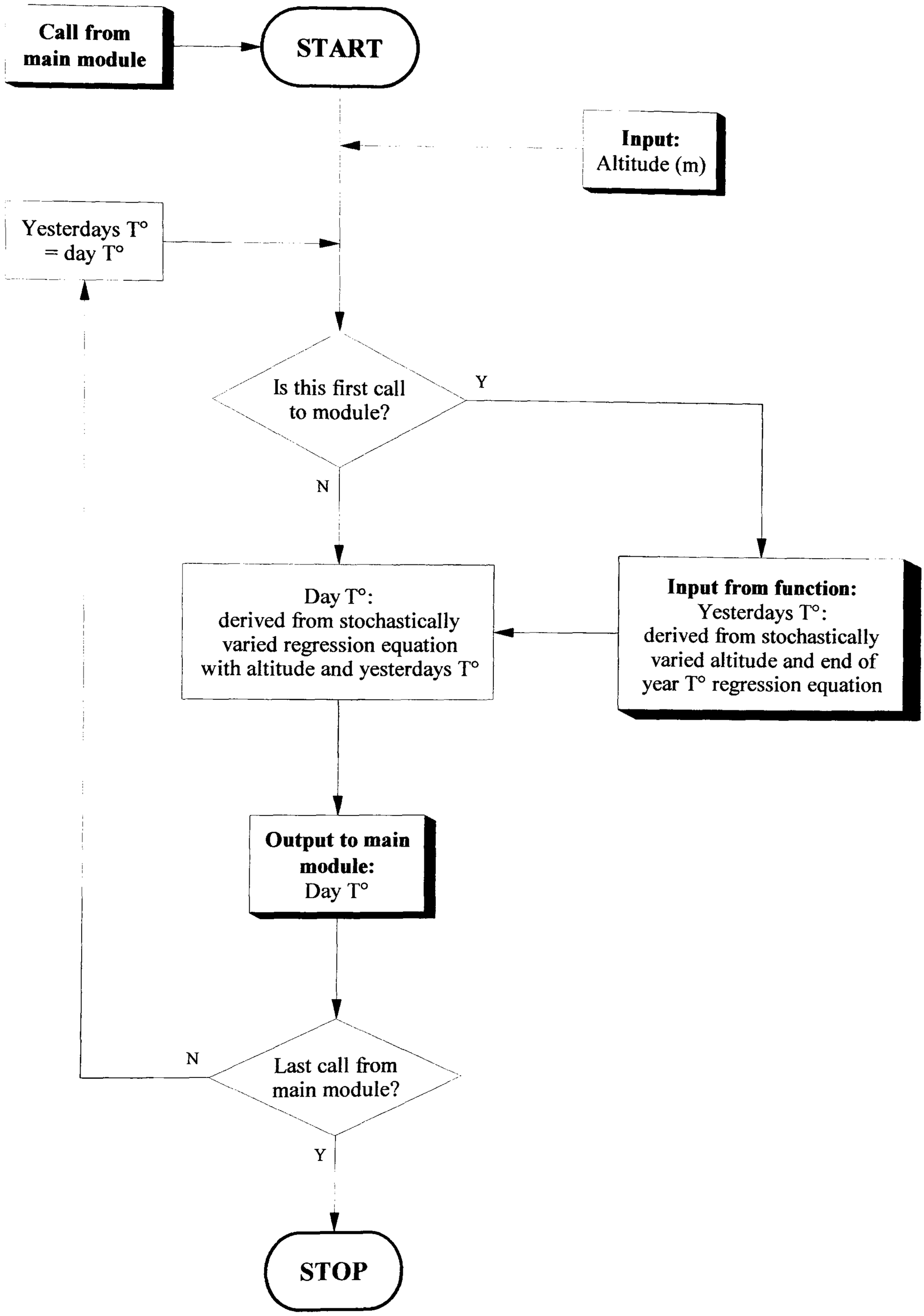


Figure 4-2: Flow chart of the simulated daily mean temperature sub-module; a component of the *Lochmaea suturalis* population dynamics main module

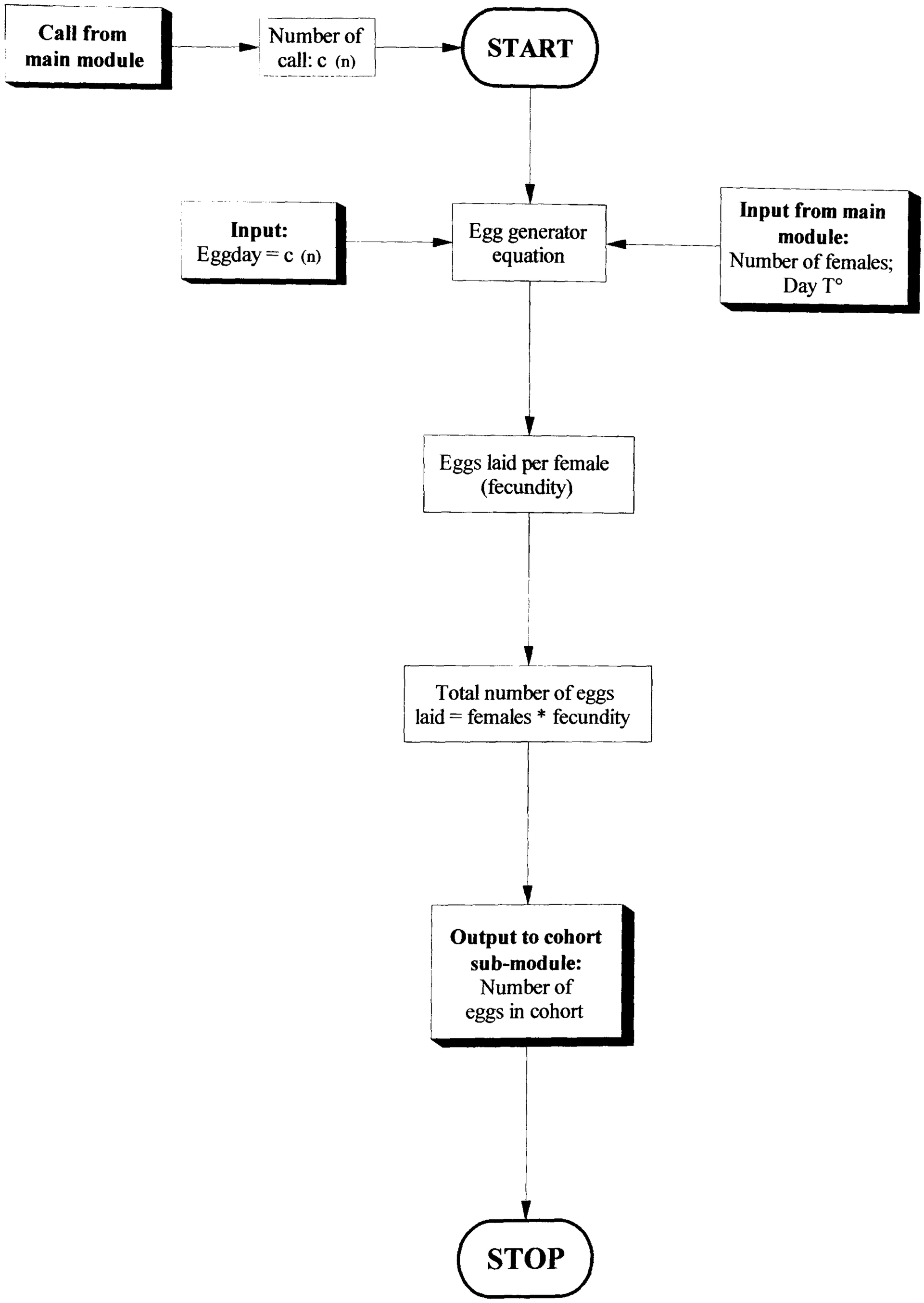


Figure 4-3: Flow chart of the egg generation sub-module; a component of the *Lochmaea suturalis* population dynamics main

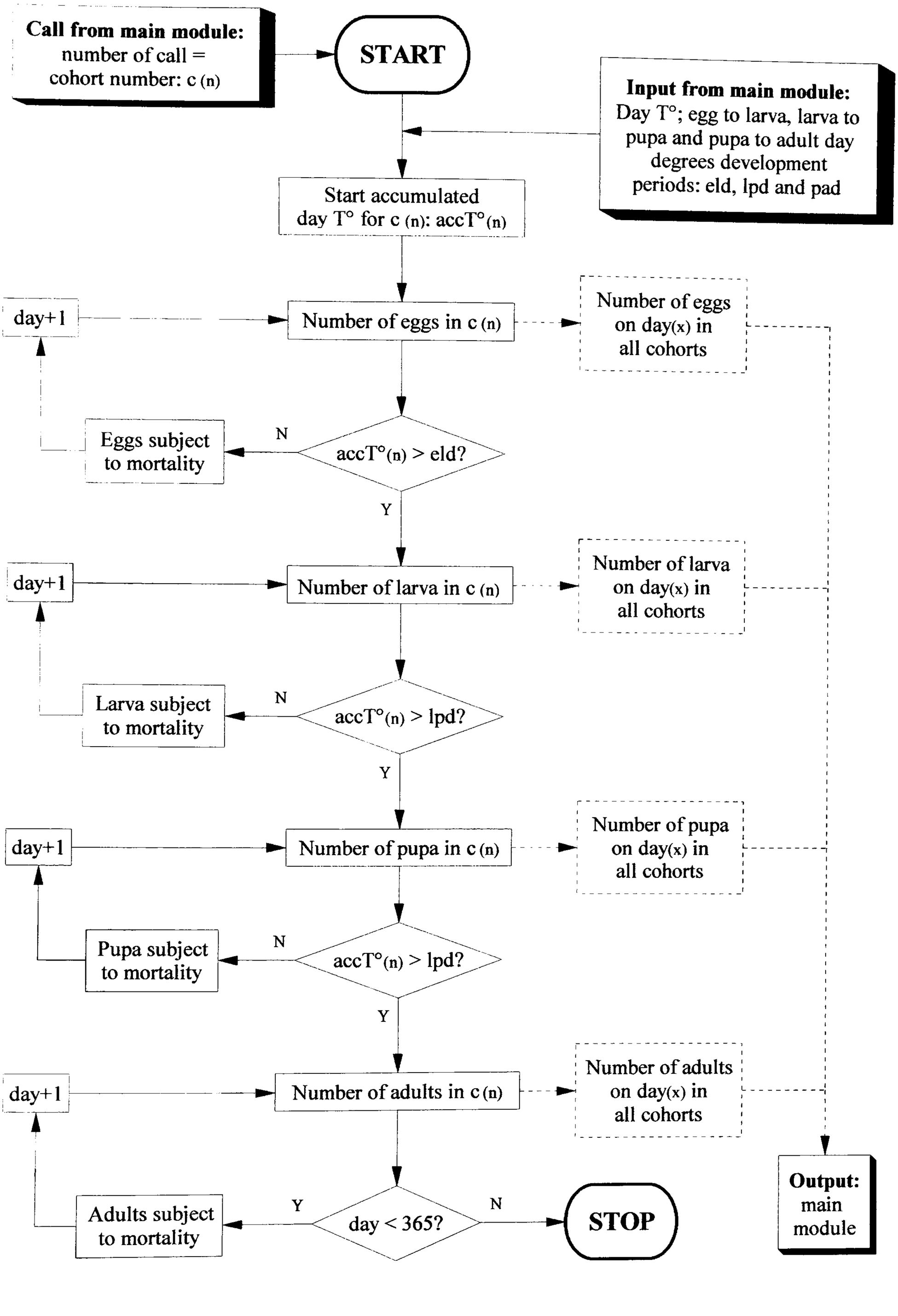


Figure 4-4: Flow chart of the cohort sub-module; a component of the *Lochmaea suturalis* population dynamics main module

4.2.2 Predicting the daily mean temperature

4.2.2.1 Study site temperature recording

At each of the nine study sites, a 'Tinytalk' remote temperature logger, sealed in a plastic bag, was placed on top of the litter layer beneath the heather canopy. The logger was set to record the temperature in Centigrade every 48 minutes for the period, February 1995 to April 1996, and was downloaded every two months onto computer disk for analysis. The temperature data was converted to daily mean temperatures.

Close House daily temperatures were recorded on a 'Squirrel' data logger as part of the field stations' daily weather record. The data was collected for the period, January 1995 to January 1996 and converted to daily mean temperatures.

4.2.2.2 Study site altitude and temperature

The study site temperature data was investigated to test whether there was a relationship between the altitude and the daily mean temperature of the study sites. This was achieved by regressing the daily mean temperatures from the nine study sites and Close House against the altitude of each site.

4.2.2.3 Daily mean temperature model

Initially the simulated daily mean temperature for the model was determined by fitting a sine-sine regression equation (after Johnson & Parsons 1985), relating daily mean temperature to day of the year, to the 1995 daily mean temperature data set collected from the nine study sites (see equation 4-1, page 120).

$$T_t = \alpha + \beta \sin^2 \left\{ \frac{\pi (t \pm l)}{365} \right\} \qquad (4\text{-}1)$$

where, T_t is the predicted daily mean temperature in °C on day t (Jan 1st = t_1), α and β are constants and l is the time lag in days since t_1.

The simulated temperature model was then modified to allow for the colder daily temperatures at the beginning of the year, and the shorter summer period in the Northumberland temperature data. This was accomplished by converting the equation to a sine wave model (see equation 4-2).

$$T_t = \alpha + \beta \sin \left\{ \frac{2\pi (t \pm l)}{365} \right\} \qquad (4\text{-}2)$$

A further parameter, the temperature on the day before a given day, was added to the regression model to achieve a stronger fit to the Northumberland data (see equation 4-3, page 121).

$$T_t = \alpha + \left[\beta \sin \left\{ \frac{2\pi(t \pm l)}{365} \right\} \right] + \delta T_{t-1} \qquad (4\text{-}3)$$

where, δ is a constant and T_{t-1} is the temperature in °C on day, (t-1).

To model the differences in temperature that occur as a result of different altitudes, an altitude variable was added to the multiple regression model (see equation 4-4).

$$T_t = \alpha + \left[\beta \sin \left\{ \frac{2\pi(t \pm l)}{365} \right\} \right] + \delta T_{t-1} + \theta\, alt \qquad (4\text{-}4)$$

where, θ is a constant and *alt* is the altitude in metres (O.D.).

The multiple regression model relating the nine study site temperatures to the explanatory variables (see equation 4-4), was repeatedly fitted to the temperature, data with a different day time lag (l) until the sum of squares error term of the multiple regression model was at its minimum, at this point it was considered to be the best fit for the model.

4.2.2.4 Stochastic variation within the daily mean temperature model

The stochastic variation of the daily mean temperature model was simulated by randomly varying the standard deviations of the coefficients: σ_α, σ_β, σ_δ and σ_θ. This was achieved by drawing a normally distributed deviate with zero mean and unit

variance (z_r), from a function that utilised a random number generator seeded by time, as a source for the uniform deviates. This normal standard deviate was then multiplied by the standard deviation of the coefficients (see equation 4-5).

$$T_t = [\alpha + (z_r \sigma_\alpha)] + \left[(\beta + (z_r \sigma_\beta)) \left\{ \sin\left(\frac{2\pi\ (t \pm l)}{365} \right) \right\} \right] \quad (4\text{-}5)$$
$$+ [(\delta + (z_r \sigma_\delta))\ T_{t-1}] + [(\theta + (z_r \sigma_\theta))\ alt]$$

where, σ_α, σ_β, σ_δ and σ_θ are the standard deviations of the subscript coefficients and z_r is a randomly drawn normal standard deviate.

4.2.2.5 Validation of the daily mean temperature model

The validation and robustness of the predicted daily mean temperature model was evaluated by comparing the actual temperature data, collected over a period of 6 years from the ADAS Experimental Husbandry Farm at Redesdale in Northumberland at an altitude 253 metres, with that simulated by the model. To assess if there was a significant difference between the daily mean Redesdale temperature data and the temperature model output an analysis of variance was undertaken and the Pearson's correlation coefficient calculated. The mean annual temperatures were calculated from the daily mean Redesdale temperature data and the temperature model output. The percentage change between the temperature model annual mean and the Redesdale annual mean temperatures was also calculated.

The six years of Redesdale daily mean temperatures was fitted, year-by-year, to the multiple regression model (see equation 4-4, page 121). The predicted Redesdale daily mean temperatures were compared to those predicted by the

daily mean temperature model, set at 253 metres altitude. To assess if there were significant differences between the predicted Redesdale temperatures and the predicted model temperatures an analysis of variance was performed and the Pearson's correlation coefficient calculated. The mean annual temperatures were calculated from the predicted daily mean Redesdale temperatures and the temperature model output. The percentage change between the temperature model annual mean and the predicted Redesdale annual mean temperatures was also calculated.

The predicted daily mean temperature model was run for a year at zero altitude with the variation in the model to simulate the approximate outer limits of the total stochastic variation of the model. Therefore the coefficients were varied by plus the standard deviation of that coefficient, multiplied by + 2.58, + 3.29, - 2.58 and - 3.29; the 99% and 99.9% values of a standard normal deviate. These temperature values were plotted against the model run at zero altitude with no variation.

4.2.2.6 Altitude and the year start temperature model

The initial temperature on the last day of the year, required as the input of the temperature model on day one, year one was determined by regressing the study sites daily mean temperature at Dec 31st with the altitudes of the study sites (see equation 4-6).

$$T_{(t=365,\, year=0)} = \alpha + (\beta\, alt) \qquad (4\text{-}6)$$

where, $T_{(t=365,\, year=0)}$ is the temperature on the last day of year 0, α is a constant, β is a constant and *alt* is the population dynamics model input altitude variable.

The stochastic variation of the year start temperature model was achieved by using the procedure previously outlined (see section 4.2.2.4, page 121), for the stochastic variation of the simulated temperature model (see equation 4-7).

$$T_{(t=365,\,year=0)} = [\alpha + (z_r\,\sigma_\alpha)] + [(\theta + (z_r\,\sigma_\theta))alt] \qquad (4\text{-}7)$$

where, σ_α and σ_β are the standard deviations of the subscript coefficients and z_r is a randomly drawn normal standard deviate.

4.2.3 Predicting the fecundity of *Lochmaea suturalis*

4.2.3.1 *L.suturalis* egg generation model

The egg generation model was determined using the empirically derived data from the *L.suturalis* fecundity at controlled temperatures experiment (see Chapter Two, section 2.2.5, page 29). A Poisson error, GLIM multiple regression model was fitted, relating the number of eggs laid per adult pair at each temperature (15, 20 and 25°C), to day, day^2 and the three experimental temperatures. The response variable, the fecundity of *L.suturalis* adults was included in the regression model as the number of eggs laid on the mid-interval day at each of the temperatures. For example if 30 eggs were laid in a five day period, then the input for the regression model was six eggs at a mid-interval day of 2.5.

The fit of the regression model was assessed by calculating the percentage scaled deviance, D^2 (see equation 4-8, page 125). Each variable included in the model was tested for significance by calculation of its t statistic; found by dividing the

coefficient of the parameter estimate by its standard error. This value was tested against the *t* distribution statistical tables (after Crawley 1993).

$$D^2\,\% = \left(\frac{NULL\ deviance - FITTED\ deviance}{NULL\ deviance} \right) \times 100 \qquad (4\text{-}8)$$

where, *NULL deviance* is the scaled deviance of the model fitted to the response data only and *FITTED deviance* is the scaled deviance of the model fitted to the response and explanatory variables.

4.2.3.2 *L.suturalis* egg generation model stochastic variation

The stochastic variation of the egg generation model was realised by a two-fold process. First, the returned value from the egg generation model was rounded up or down to the nearest integer. Second, the rounded egg fecundity value was input to a function that returned a random variate from a Poisson distribution with a mean and variance equal to the input value. This new stochastically derived egg value was returned to the main model as the fecundity of *L.suturalis* on that particular egg generation day.

4.2.3.3 Verification of the *L.suturalis* egg generation model

The egg generation multiple regression model was validated by substituting the three temperatures, used in the *L.suturalis* fecundity at controlled temperature experiment, into the egg generation model equation and running it until no more

eggs were produced. The results were compared with the range of eggs laid per adult pair from the empirically derived data.

4.2.4 Population dynamics model life stage variables: selection and parameterisation

To enable the modelling of the population dynamics of *L.suturalis*, thirteen life stage variables were included in the model. Each variable included in the model was evaluated empirically (see Chapter Two, section 2.2, page 17).

Nine of the thirteen life stage variables were varied stochastically using a modification of the method employed for the daily mean temperature simulation model (see 4.2.2.4, page 121). In the case of the life stage variables, the normal standard deviate was reselected until it was within the range –1.96 to +1.96, if the standard normal deviate produced a mortality factor ≥ 1.00, the value was changed to a value of 0.999999 (see equation 4-9).

$$input\ value\ of\ variable\ (x) = \overline{X} + \left(\sigma_x\ z_{r(-1.96,+1.96)}\right) \qquad (4\text{-}9)$$

where, x is the model input variable, $\overline{X}$ is the mean of variable (x), σ_x is the standard deviation of variable (x) and $z_{r\ (-1.96,\ +1.96)}$ is a randomly drawn normal standard deviate, bounded by the range –1.96 to +1.96, only if the positive deviate does not produce a value of $x \geq 1.00$, when it is replaced by a value of 0.999999.

4.2.4.1 Sex ratio variable

The sex ratio variable applied annually, to the starting adult population, to evaluate the number of females at the beginning of each year, was derived by

recoding the two ratios, found in the field and laboratory, to proportions and calculating the mean and standard deviation. The sex ratio variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.2 Emergence threshold temperature

The emergence threshold temperature (°C) variable was set at 5°C. This figure represents the temperature at which 95% of the adult beetles in the emergence threshold temperature experiment became inactive (see Chapter Two, section 2.3.10, page 65). The emergence threshold temperature variable was not varied stochastically.

4.2.4.3 Egg laying temperature

The egg laying temperature (°C) was derived by taking the mean and standard deviation of the range, 10-15°C. The minimum value represents the temperature below which 50% of adults were inactive in the overwintering experiment (see Chapter Two, 2.3.10, page 65). The range of values represents the daily mean temperatures at which dispersal and copulation takes place on the warmest days of late spring and early summer. The egg laying temperature variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.4 Egg mortality variable

The egg mortality variable was derived by calculating, for each replicate, the proportion of eggs still viable at the end of the *L.suturalis* fecundity experiment at ambient temperature (see Chapter Two, section 2.2.4, page 26). The proportions of eggs were converted to a daily survival variable by taking

logarithms, the antilog of x was then used as the mortality rate day^{-1} (see equations 4-10a, b). The mean and standard deviation values employed in the model were calculated from the 20 replicates. The egg mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

$$\log_{(x)} = \frac{\log\left(proportion\ living\ (x)\right)}{number\ of\ days} \qquad (4\text{-}10a)$$

where, x is the proportion of life stage (x) surviving on a given day and *number of days* is the period over which the life stage variable is being calculated.

$$daily\ mortality\ rate\ day^{-1}(x) = \text{antilog}\left[\log_{(x)}\right] \qquad (4\text{-}10b)$$

4.2.4.5 Larval mortality variable

The larval mortality variable was derived by calculating the mean proportion of larvae still viable at the end of each larval growth and temperature experiment (see Chapter Two, section 2.2.6, page 29). The proportions were converted to a daily survival factor by taking logarithms (see equations 4-10a, b). The mean and standard deviation values employed in the model were calculated from 10 of the 12 experiments. The plastic pot and glass pot northern experimental data at 10°C was not included in the calculation, as the larvae were not considered to be viable. The larval mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.6 Pupal mortality variable

The pupal mortality variable was derived by calculating the mean proportion of pupae still viable at the end of each larval growth and temperature experiment (see Chapter Two, section 2.2.6, page 29). The proportions were converted to a daily survival factor by taking logarithms (see equations 4-10a, b, page 128). The mean and standard deviation values employed in the model were calculated from 9 of the 12 experiments. The plastic, glass pot southern and glass pot northern experimental data at 10°C was not included in the calculation as there were either no pupae or very low numbers of pupae. The pupal mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.7 New generation adult mortality variable

The new generation adult mortality variable was derived by calculating the mean proportion of new generation adults still viable at the end of each larval growth and temperature experiment (see Chapter Two, section 2.2.6, page 29). The proportions of new generation adults were converted to a daily survival factor by taking logarithms (see equations 4-10a, b, page 128). The mean and standard deviation values employed in the model were calculated from 9 of the 12 experiments. The plastic, glass pot southern and glass pot northern experimental data at 10°C was not included in the calculation as there were no new generation adults. The new generation adult mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.8 Breeding mortality variable

The breeding mortality variable was derived by calculating the mean proportion of breeding females still viable at the end of each fecundity and controlled temperature experiment (see Chapter Two, section 2.2.5, page 29). The proportions of breeding females were converted to a daily survival factor by taking logarithms (see equations 4-10a, b, page 128). The mean and standard deviation values employed in the model were calculated from the 5 replicates from each experimental temperature. The breeding mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.9 Winter adult mortality variable

The winter adult mortality variable was derived by calculating the mean proportion of adults still alive at the end of each ambient temperature winter mortality experiment (see Chapter Two, section 2.2.8, page 33). The proportions of new generation adults were converted to a daily survival factor by taking logarithms (see equations 4-10a, b, page 128). The mean and standard deviation values employed in the model were calculated from the six experimental time treatments. The winter adult mortality variable was varied stochastically within the model as previously defined (see section 4.2.4, page 126 and equation 4-9, page 126).

4.2.4.10 Female mortality variable

As the females did not contribute to the model population numbers, after breeding was finished, they were subject to instant mortality.

4.2.4.11 Egg to larval development period

The egg to larval accumulated day degrees development period (ADD) was derived by taking the mean of the ADD's from the two fecundity and egg to larvae development period experiments at ambient temperature (see Chapter Two, section 2.3.3, page 40). The egg to larval ADD variable was set to its mean and was not varied stochastically.

4.2.4.12 Larval to pupal development period

The larval to pupal accumulated day degrees development period (ADD) was derived by taking the mean of the ADD's from each of the larval growth and temperature experiments (see Chapter Two, section 2.2.6, page 29 and Table 2-7, page 56). The larval to pupal ADD variable was set at its mean and was not varied stochastically.

4.2.4.13 Pupal to adult development period

The pupal to new generation adult accumulated day degrees development period (ADD) was derived by taking the mean of the ADD's from each of the larval growth and temperature experiments (see Chapter Two, section 2.2.6, page 29 and Table 2-8, page 57). The pupal to new generation adult ADD variable was set at its mean and was not varied stochastically.

4.2.4.14 Summary of life stage model input values

The values of the life stage variables employed in the *L.suturalis* population dynamics model are summarised (see Table 4-1, page 132).

Input variable for model	Mean	s.d.	Stochastic variation and limits of z_r
Sex ratio	0.5985	0.0460	Yes - ± 1.96
Emergence temperature (°C)	5.00	-	No
Egg laying temperature (°C)	12.500	1.8708	Yes - ± 1.96
Egg mortality day^{-1}	0.9789	0.0284	Yes - ± 1.96
Larval mortality day^{-1}	0.9852	0.0147	Yes - ± 1.96
Pupal mortality day^{-1}	0.9670	0.0250	Yes - ± 1.96
New generation adult mortality day^{-1}	0.9965	0.0044	Yes - ± 1.96
Breeding mortality day^{-1}	0.9766	0.0094	Yes - ± 1.96
Winter adult mortality day^{-1}	0.9969	0.0038	Yes - ± 1.96
Egg to larval add's **	362°C	-	No
Larval to pupal add's **	395°C	-	No
Pupal to adult add's **	310 °C	-	No
Female mortality day^{-1} **	0.50	-	No
* Female mortality – a "killing factor" to kill off post-breeding females			
** add's – accumulated day degrees development period			

Table 4-1: *Lochmaea suturalis* life stage model input values; mean, standard deviation and the limits of the random normal standard deviate (z_r), for those variables that were stochastically varied and the mean for those variables not varied, s.d. = standard deviation

4.2.5 *Lochmaea suturalis* population dynamics model runs

The model was initialised with a population of 1 x 10^6 beetles and set to run for 50 years. Thirty-five scenarios were simulated; five altitudes, 0, 50, 100, 300 and 500 metres at seven temperature regimes, base temperature where the predicted temperature was input into the model and +1, +2, +3, +4, +5, +6°C, where this factor was added to all predicted daily temperatures. Each of the 35 scenarios was replicated 100 times.

For each scenario, the population numbers at the end of each year were logged and the mean calculated from the 100 replicates. The mean and standard error of the population numbers at the end of 5, 10, 25 and 50 years was calculated from the 100 replicates. The number of populations that became extinct after the 50 year simulation, for each set of 100 replicates was calculated for each temperature and altitude scenario, to give the percentage extinction of a particular scenario population.

4.3 Results

4.3.1 Predicting the daily mean temperature

4.3.1.1 Study site altitude and temperature

The results of the regression relating the study sites temperature data and the altitude of the study sites showed a significant negative linear relationship, (see Table 4-2). The correlation coefficient (r^2), between the study sites temperatures and the altitude for each site was significant at –0.11***, at $p <$ 0.001. This shows that the ambient temperature of a site decreases as altitude increases.

Variable	Coefficient	*t* value	*p* value
constant	9.235	19.28	< 0.001***
altitude (°C)	-0.0045	-5.44	< 0.001***

Table 4-2: The coefficients with the *t* statistic and *p* value of the regression relating temperature and the altitude of the nine study sites and Close House, (*n*=3650)

4.3.1.2 Predicted daily mean temperature model

The equation employed in the population dynamics model to predict daily mean temperatures as defined in sections 4.2.2.3, page 119 and 4.2.2.4, page 121,

was fitted to the study site temperature data. A best fit was attained when the time-lag factor (l), was set at + 64 days (see equation 4-11).

$$T_t = [1.7209 + (z_r(0.1752))] - \left[(1.611 + (z_r(0.106))\left\{\sin\left(\frac{2\pi(t+64)}{365}\right)\right\}\right]$$
$$+ [(0.7816 + (z_r(0.0126)))T_{t-1}] - [(0.0007 + (z_r(0.0004)))alt] \quad (4\text{-}11)$$

where, T_t is the predicted daily mean temperature in °C on day t (Jan $1^{st} = t_1$), T_{t-1} is the temperature in °C on day (t-1), *alt* is the altitude in metres (O.D.) and z_r is a randomly drawn normal standard deviate.

The coefficients of the daily mean temperature model were found to be significant at $p < 0.001$, except for the altitude variable that was not significant at $p = 0.06$ and r^2 was found to be 89.6%, significant at $p < 0.001$ (see Table 4-3, page 136).

Variable	Coefficient	Standard deviation	*t* value	*p* value
constant	1.7209	0.1752	3.24	$< 0.001^{***}$
sin(2π(*t* + *l*)	-1.611	0.106	-15.2	$< 0.001^{***}$
ytemp (°C)	0.7816	0.0126	62.15	$< 0.001^{***}$
altitude (m)	-0.0007	0.0004	-1.83	0.06^{ns}

Table 4-3: Daily mean temperature model multiple regression coefficients with the standard deviation, *t* statistic and *p* value, (n=3285), $r^2 = 89.6^{***}$, significant at $p < 0.001$; altitude was not significant at $5\% \leq p < 10\%$. Note: *t* = day, *l* = + 64 and ytemp = yesterdays temperature

4.3.1.3 Validation of the daily mean temperature model

The results of the analysis of variance performed on the six years of daily mean temperature data from Redesdale and the predicted daily mean temperature from the model, with the model set at 253 metres, showed that there were significant differences at $0.1\% \leq p < 1\%$ (see Table 4-4).

Source	d.f.	SS	MS	F-ratio	*p* value
Between group	6	444	73.9	3.24	0.0035^{**}
Error	2539	57805	22.8		
Total	2545	58249			

Table 4-4: Results of the ANOVA testing for differences between the six years of raw daily mean temperature data from Redesdale and the model predicted daily mean temperatures, set at 253 metres altitude; the *p* value was significant at $0.1\% \leq p < 1\%$

As there was a significant result in the ANOVA relating the six years daily mean Redesdale temperatures and the predicted model temperature, analyses of variance were conducted on each pairing of the model and year (see Table 4-5).

	Temperature data set					
	1987	**1988**	**1989**	**1990**	**1991**	**1992**
Model	0.33^{NS}	0.25^{NS}	0.03*	0.008**	0.55^{NS}	0.65^{NS}

Table 4-5: The *p* values from the individual ANOVA's testing for significant differences between the predicted daily mean temperature model, set at 253 metres, and the year by year daily mean Redesdale temperatures

The analysis shows that the predicted model temperature was not significantly different from the daily mean Redesdale temperature data from 1987, 1988, 1991 and 1992, at $p \geq 10\%$, but was significantly different from 1989 at $1\% \leq p > 5\%$ and 1990 at $0.1\% \leq p < 1\%$.

The correlation coefficients (r^2), between the predicted daily mean temperatures and the daily mean Redesdale data were all significant, at $p < 0.001$ (see Table 4-6, page 138).

	Redesdale daily mean temperature year					
	1987	**1988**	**1989**	**1990**	**1991**	**1992**
model	0.82***	0.84***	0.82***	0.80***	0.86***	0.81***

Table 4-6: The correlation coefficients (r^2), between the predicted daily mean temperatures from the model, set at 253 metres altitude, and the six years of Redesdale daily mean temperature; all correlations were significant at $p < 0.001$, (n=365)

The percentage change in the mean annual temperature for each year against the predicted mean annual temperature is shown below (see Table 4-7).

	Redesdale mean annual temperature year						
	model	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
Mean	7.00	6.63	7.39	7.77	7.93	7.21	7.15
% change	-	-5.3	5.6	11.0	13.3	3.0	2.1

Table 4-7: Mean annual temperatures (^{o}C) and the percentage change from the six years of Redesdale mean annual temperature and the population dynamics model predicted mean annual temperature

By inspection it can be seen that the greatest percentage change of the Redesdale mean annual temperature from that predicted by the temperature model is for the years 1989 and 1990, with relatively small changes for the other years.

The daily mean temperatures from the Redesdale data over the six years were plotted with the predicted daily mean temperature, with the altitude variable set at 253 metres (see Figure 4-5, page 140).

By inspection it can be seen that the daily mean temperature predicted by the temperature model fits the daily mean temperature from the six years of Redesdale data reasonably well. Although it should be noted that at the beginning of the year, approximately the first 80 days, the model tends to underestimate the daily mean temperature by in the region of minus one to two degrees.

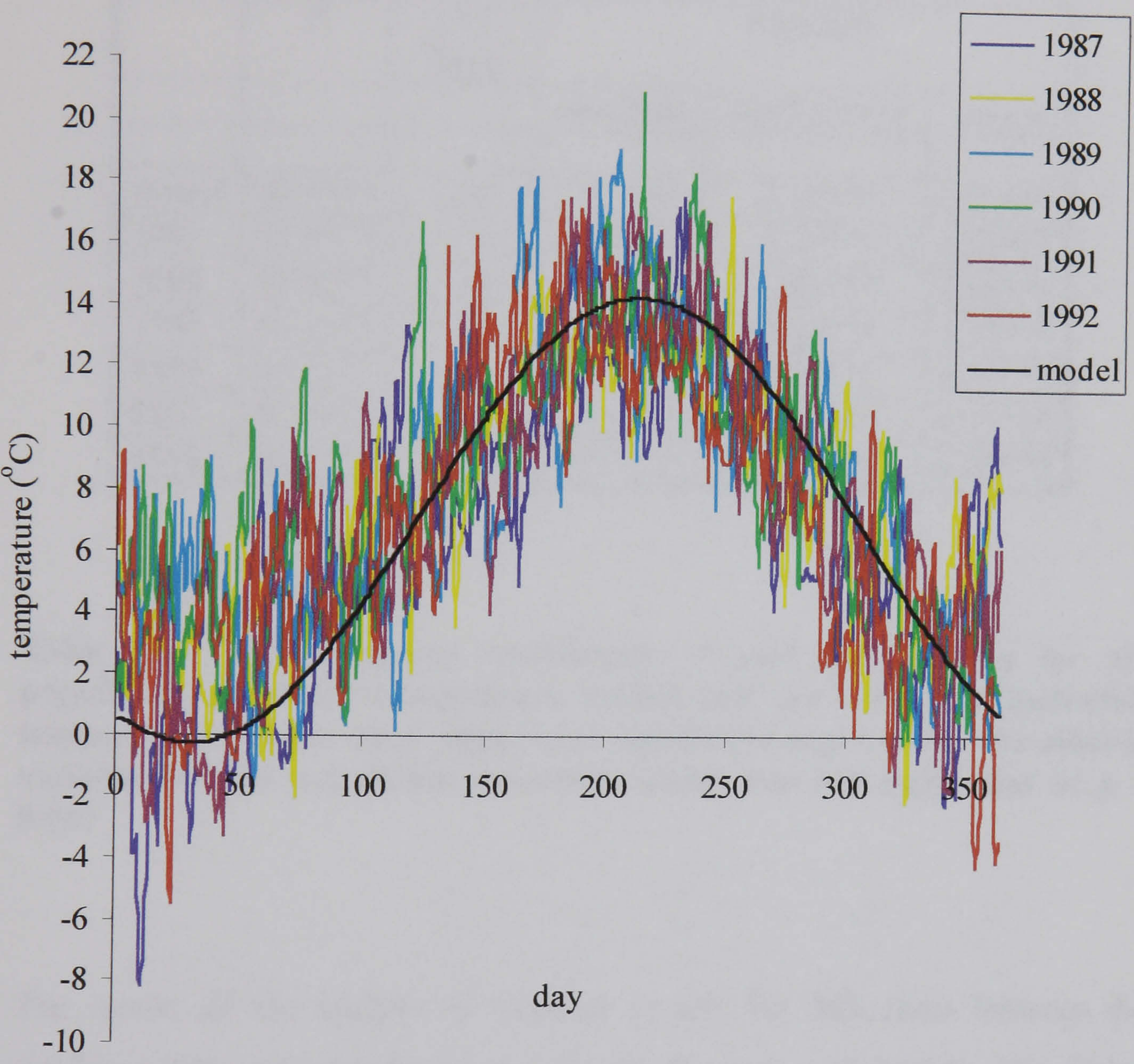


Figure 4-5: Graph of the six years of Redesdale daily mean temperatures a and the predicted daily mean temperatures from the model, with the altitude variable set at 253 metres

The six years of daily mean Redesdale temperature data was fitted to the population dynamics temperature model regression equation (see equation 4-3, page 121). The regression parameters are shown below (see Table 4-8).

	r^2	$t + l$ (lag)	Variable		
			constant	$\sin(2\pi(t + l)$	ytemp
model	89.7***	+ 64	1.72***	-1.61***	0.78***
1987	88.4***	+ 70	1.35***	-1.16***	0.80***
1988	84.9***	+ 68	2.35***	-1.61***	0.68***
1989	84.1***	+ 66	2.18***	-1.55***	0.72***
1990	83.7***	+ 73	2.13***	-1.34***	0.73***
1991	87.8***	+ 70	2.12***	-1.83***	0.71***
1992	85.4***	+ 80	2.17***	-1.80***	0.69***

Table 4-8: The regression coefficients, r^2 and the time-lag for the population dynamics temperature model and the six fitted Redesdale temperature models; all p values were significant at $p < 0.001$, the altitude variable for the population dynamics model was not significant at $p = 0.067$

The results of the analysis of variance to test for differences between the predicted daily mean temperatures from the six years at Redesdale, after fitting the model, and the predicted daily mean temperature from the population dynamics temperature model, set at 253 metres, showed that there were significant differences at $p < 0.001$ (see Table 4-9, page 142).

Source	d.f.	SS	MS	F-ratio	*p* value
Between groups	6	428	71.3	4.2	0.0003***
Error	2541	43174	17.0		
Total	2547	43602			

Table 4-9: Results of the ANOVA testing for differences between the predicted temperatures from the six years of Redesdale temperature data after fitting the model and the predicted daily mean temperatures, with the altitude variable set at 253 metres; the result was significant at $p < 0.001$

As there was a significant result in the ANOVA relating the six years Redesdale predicted temperatures and the predicted model temperature, analyses of variance were conducted on each pairing of the model and year (see Table 4-10)

	Redesdale temperature data year					
	1987	**1988**	**1989**	**1990**	**1991**	**1992**
Model	0.34^{NS}	0.17^{NS}	0.03*	0.004**	0.50^{NS}	0.71^{NS}

Table 4-10: The *p* values from the individual ANOVA results, testing for significant differences between the predicted daily mean temperature model, set at 253 metres, and the year by year model predicted Redesdale temperatures

This analysis shows that the predicted model temperature was not significantly different from the predicted Redesdale temperature data from 1987, 1988, 1991

and 1992, but was significantly different from 1989 at $1\% \leq p > 5\%$ and 1990 at $0.1\% \leq p < 1\%$.

The correlation coefficients (r^2), between the predicted daily mean model temperatures and the predicted Redesdale temperatures after fitting the model were all significant at $p < 0.001$ (see Table 4-11).

	Year of fitted Redesdale data					
	1987	**1988**	**1989**	**1990**	**1991**	**1992**
model	0.995***	0.993***	0.995***	0.998***	0.997***	0.995***

Table 4-11: The correlation coefficients (r^2), between the predicted daily mean temperatures from the model, set at 253 metres altitude, and the six years Redesdale data fitted to the temperature regression model; all correlations were significant at $p < 0.001$, (n=365)

The percentage change in the predicted Redesdale mean annual temperatures for each year against the model predicted mean annual temperature is shown below (see Table 4-12).

	Year of Redesdale temperature model						
	model	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
Mean	7.00	6.68	7.45	7.76	8.00	7.25	7.14
% change	-	-4.6	6.4	10.9	14.3	3.6	2.0

Table 4-12: Mean annual temperatures (°C) and the percentage change from the six years of Redesdale model predicted temperatures and the population dynamics model predicted temperature

By inspection it can be seen that the greatest percentage change of the predicted mean annual temperature from the Redesdale data from that predicted by the temperature model is for the years 1989 and 1990, with relatively small changes for the other years.

The predicted daily mean temperatures for the six years at Redesdale are plotted with the population dynamics temperature model predicted daily mean temperature with the altitude variable set at 253 metres (see Figure 4-6, page 145).

By inspection it can be seen that the daily mean temperature predicted by the model has a slightly narrower summer range than the Redesdale fitted temperatures. Also that the winter and summer temperatures are respectively c. one degree lower and c. one degree higher than the predicted Redesdale temperatures.

The comparison of the temperature model with no variation and the 99% and 99.9% outer limits of its possible stochastic variation at zero altitude is presented graphically (see Figure 4-7, page 146). As can be seen the maximum temperature derived from the model was $\approx 24^{\circ}C$ and the minimum was $\approx -0.5^{\circ}C$.

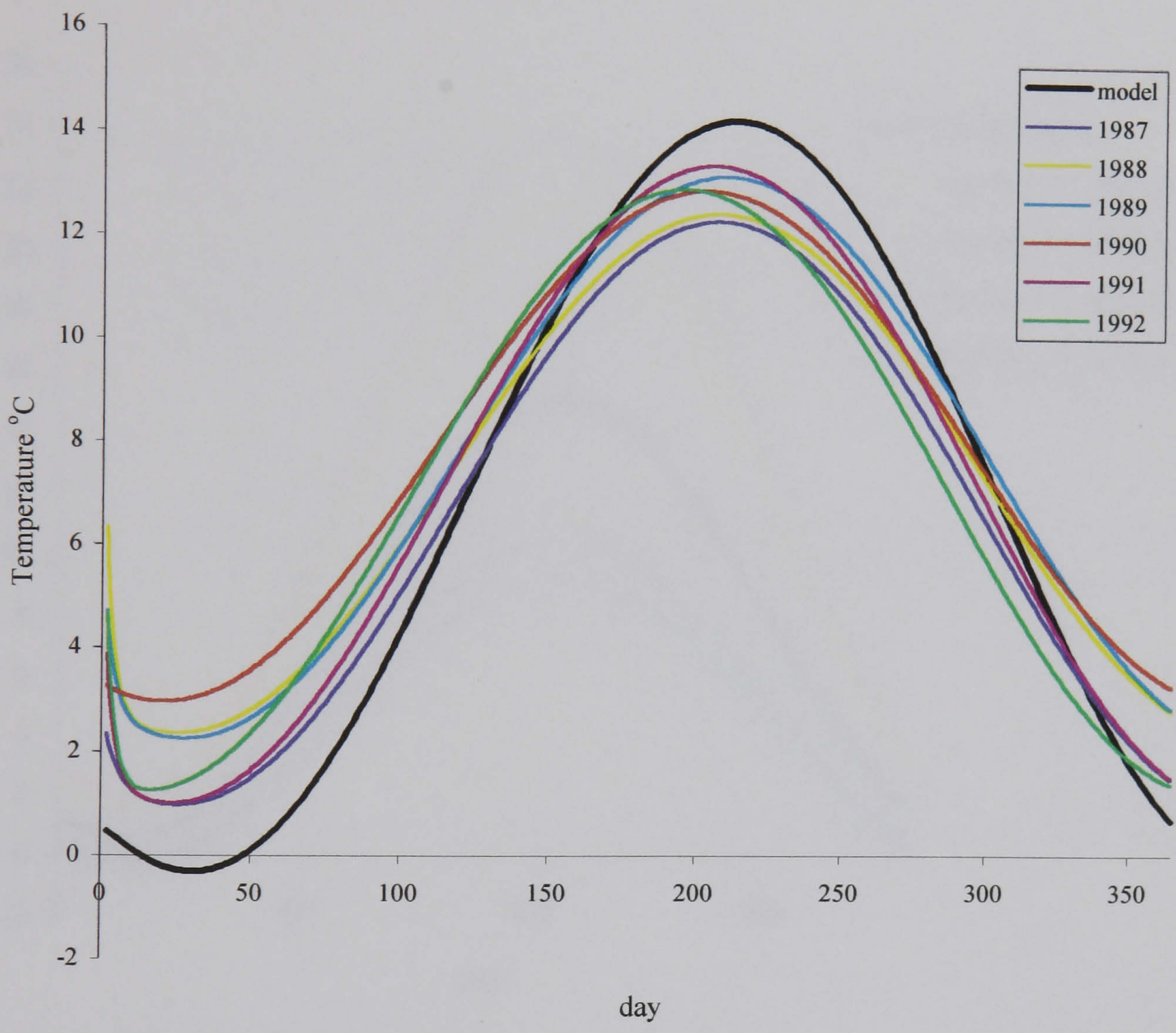


Figure 4-6: Graph of the six years of predicted daily mean Redesdale temperatures data and the model predicted daily mean temperature, with the altitude variable set at 253 metres

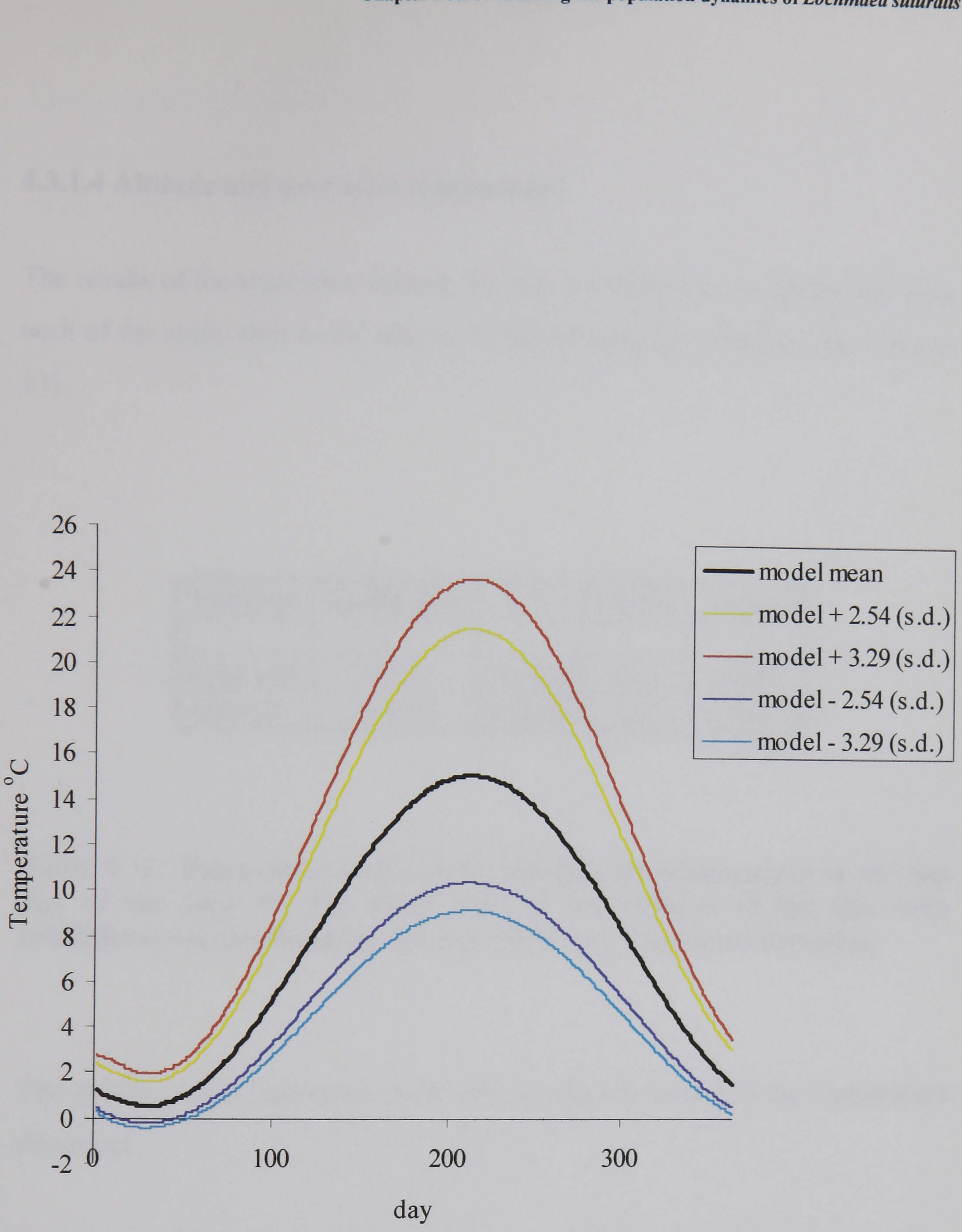


Figure 4-7: Graph of the predicted temperature model output with no variation and the stochastic output determined by varying all coefficients by adding + 2.58, + 3.29, - 2.58 and – 3.29 multiplied by the standard deviation of the coefficient

4.3.1.4 Altitude and year start temperature

The results of the regression relating the last day of the year's temperature from each of the study sites to the altitude of the site are shown below (see Table 4-13).

Variable	Coefficient	s.d.	*t* value	*p* value
constant	1.3675	0.5449	2.51	0.04*
altitude	-0.0037	0.0015	-2.47	0.043*

Table 4-13: Regression results (n=9), relating the temperature on the last day of the year for the study sites to the altitude of the site, both coefficients are significant at 1% ≤ p > 5%; s.d. = standard deviation

The results of the regression show that as altitude increased the temperature decreased.

As both coefficients were found to be significant at $p < 0.05$, they were employed to derive the start temperature input model (see equation 4-12).

$$T_{(t=365,\, year=0)} = 1.3675 - (0.0037\, alt) \qquad (4\text{-}12)$$

where, $T_{(t=365,\, year=0)}$ is the temperature on the last day of year 0 and *alt* is the altitude input variable.

The stochastically varied, start temperature model employed in the population dynamics model as the initial yesterdays temperature input to the predicted daily mean temperature sub-module is shown (see equation 4-13).

$$T_{(t=365,\,year=1)} = [1.3675 + (z_r\,(0.5449))] - [(0.003 + (z_r\,(0.0015)))alt] \quad (4\text{-}13)$$

4.3.2 Predicting the fecundity of *L.suturalis*

The results of the Poisson error structure, GLIM multiple regression relating the number of eggs laid per pair of adults to temperature, day and day^2, showed that the fitted model had a percentage D^2 value of 23.8% and that the coefficients were all significant at $p < 0.001$ (see Table 4-14).

Parameter	Coefficient	s.e.	*t* value
Constant	-4.930	0.7189	6.85***
Temperature	0.1922	0.0282	6.80***
Day	0.2627	0.0424	6.18***
Day^2	-0.0074	0.0015	5.07***

Table 4-14: Coefficients, standard errors (s.e.), and *t* statistic with significance, of the GLIM multiple regression relating the number of eggs laid per adult pair day^{-1} to temperature, day and day^2, (n=64), D^2 = 23.8%

As the coefficients were significant, they were employed in the egg generation model (see equation 4-14).

$$eggs = \exp\left[\begin{array}{l}\left(-0.0074\left(eggday^2\right)\right)+\left(0.2627\left(eggday\right)\right)\\ \\ +\left(0.1922\left(T_t\right)\right)-4.93\end{array}\right] \qquad (4\text{-}14)$$

where, *eggs* is the predicted number of eggs laid per female day^{-1}, *eggday* is the number of the day the eggs are being laid, starting from the first egg laying day, and T_t is the predicted temperature (°C) on a given day.

4.3.2.1 Verification of the *L.suturalis* egg generation model

The number of eggs laid per adult pair when the three temperatures 15, 20 and 25°C were substituted into the egg generation model equation, without the stochastic variation, was compared to those laid over the thirty day period of the *L.suturalis* fecundity at controlled temperatures experiment (see Table 4-15, page 150).

	15°C	20°C	25°C	Ambient T°C
Thesis range	0-17	0-139	4-152	-
Thesis range	-	-	-	0-73
Model output	12	60	170	-

Table 4-15: Range of eggs laid per pair of *L.suturalis* adults in the controlled and ambient fecundity and temperature experiments, and the number laid per adult pair as predicted by the egg generation model, without stochastic variation of temperature or fecundity

The number of egg predicted by the egg temperature model is within the range derived empirically in the controlled and ambient temperature experiments for the 15, 20°C, controlled and ambient temperature experiments, but is slightly greater than the range of the 25°C controlled temperature experiment.

The output of the egg generation model, with the three substituted temperatures, 15, 20 and 25°C, with no stochastic variation of the number of eggs or the temperature is presented graphically (see Figure 4-8, page 151).

As can be seen by inspection the egg generation model produces eggs in a unimodal manner, peaking at the mid period of egg laying.

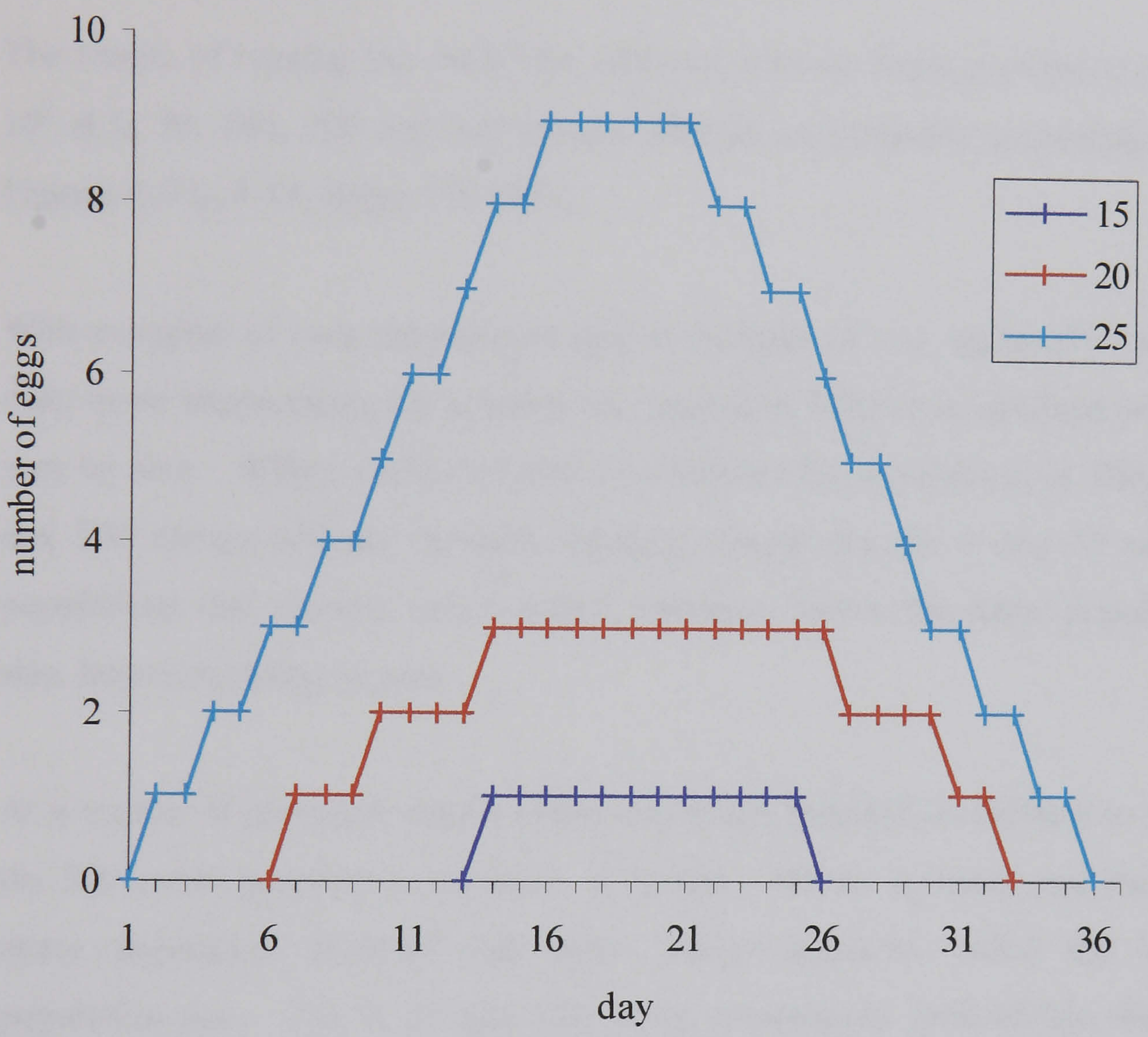


Figure 4-8: Predicted number of eggs laid per pair of *L.suturalis* adults, as derived from the egg generation sub-model run at 15, 20 and 25°C; with no stochastic variation

4.3.3 *Lochmaea suturalis* population dynamics model output

4.3.3.1 *L.suturalis* population numbers over a 50 year simulation at five altitudes and six temperatures

The results of running the model for 100 runs with an initial population of 1 x 10^6 at 0, 50, 100, 300 and 500 metres, altitude are presented graphically (see Figures 4-9 to 4-15, pages 154-160).

With a regime of base temperature and an increase of one degree (°C) to the daily mean temperature, the populations, regardless of altitude, declined year by year to zero. With a regime of plus two degrees the populations at 100, 300 and 500 metres altitude declined similarly, except for the 0 and 50 metres populations that showed minor annual increases, below the initial population size, before declining to zero.

At a regime of plus three degrees only two of the populations declined to zero, the 500 metre populations declined, as before, with no increases and the 300 metre population declined with minor annual increases, below the initial population size. The 0, 50 and 100 metre populations declined but did not decline to zero and for the first time the decline involved an increase in numbers greater than the initial population. In the case of the 50 and 100 metre populations these increases were only small, approximately a 20% increase and only lasted for three and two years respectively. However the zero metre population showed a significant increase in numbers, greater than the start population, for a prolonged twenty-five and a shorter three-year period. During the 25 year increase the population was nearly treble the start population.

With an increase in temperature of four degrees, the populations at 300 and 500 metres declined to virtually zero, but this decline took the 50 years. At 50

metres the population generally showed a stable pattern of numbers around the start population size apart from a four-fold increase for a five-year period mid way through the simulation. The 0 and 100 metre populations exhibited large population increases with the 100 metre population peaking, over a three year period, with an 18 fold increase. The zero metre population peaked with an increase, in the region of 20 times the initial population, for much of the final 20 years of the simulation.

With an increase of plus five degrees, the 500 metre population was relatively stable, with minor fluctuations around the start population. The 50 and 300 metre populations were less stable, with the 50 metre population showing a prolonged increase, approximately three times the start population for a period of 20 years, whilst the 300 metre population had two peaks at 15 and 30 years where the populations showed approximately, 14 and 6 fold increases respectively. Both populations ended the simulation in a stable manner, at the start population figure. The 0 and 100 metre populations both started in a stable manner, fluctuating just above the initial population. However at the 25 year mark the 0 metre population experienced an approximate twenty fold peak, followed by a marked increase, ending the simulation with a 25 fold increase. The 100 metre population steadily increased from the 30 year mark to end the simulation with a 35-40 fold increase.

The plus six degree scenario, showed that the populations at all altitudes experienced large increases in numbers. The 100, 300 and 500 metre populations exhibited 10-20 fold increases for periods of approximately 10 years. Whilst the 0 and 50 metre populations showed, approximately 40-50 fold and 65 fold increases in numbers, respectively, over much of the last 30 years.

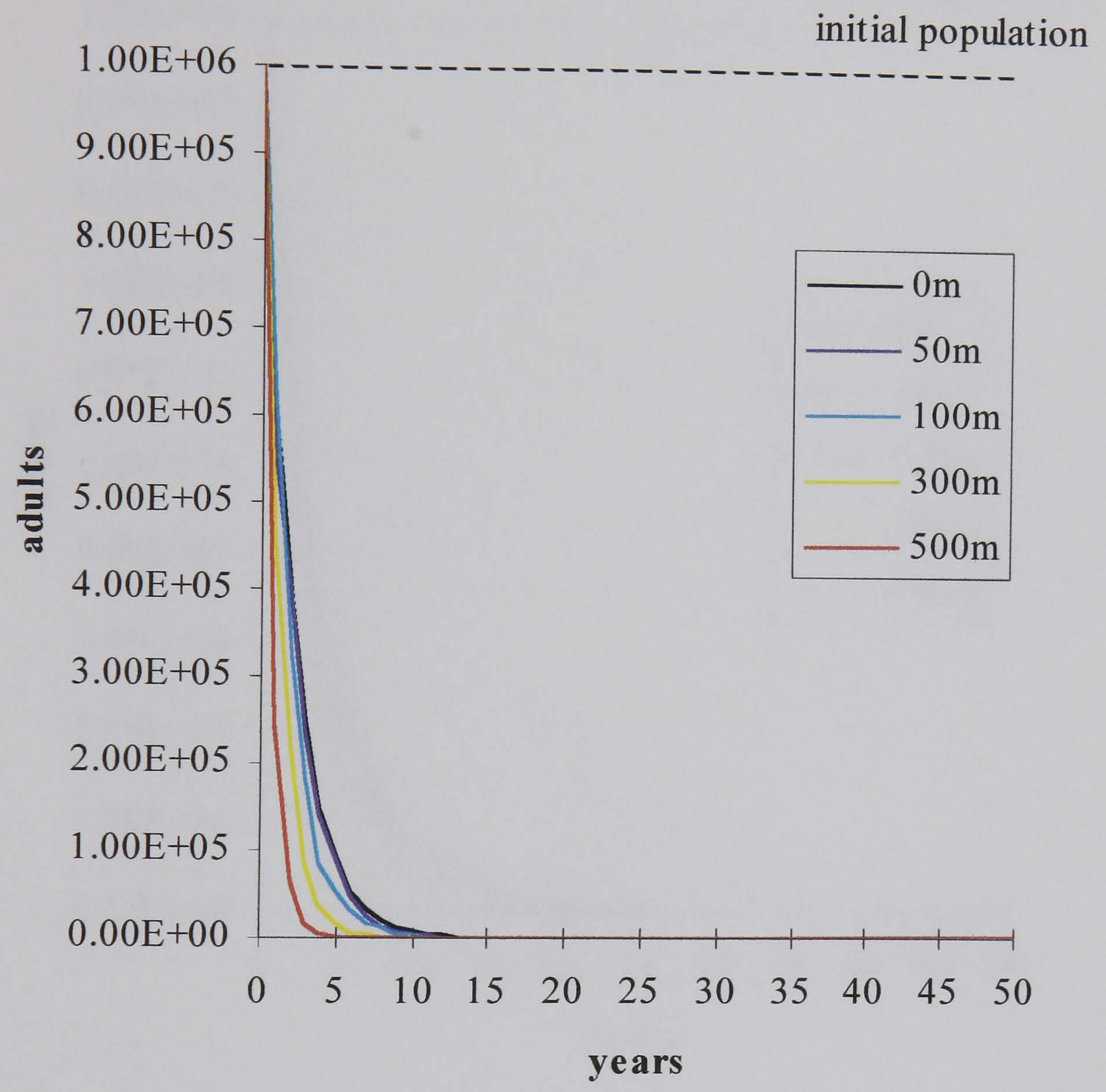


Figure 4-9: Model output of the mean annual population numbers, (*n*=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature, at five altitudes (m). Note *y*-axis scale x 10^5

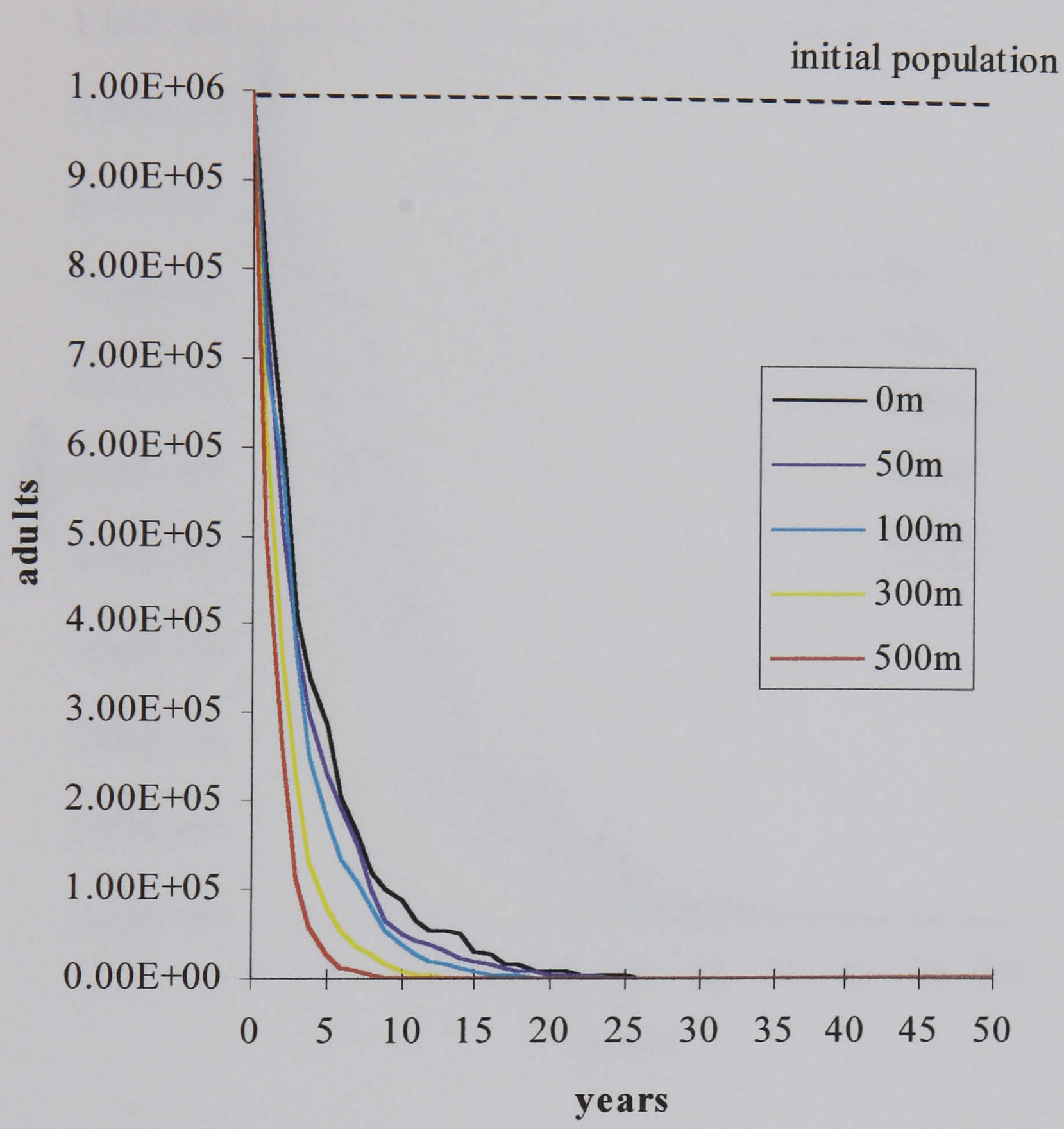


Figure 4-10: Model output of the mean annual population numbers, (n=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +1°C, at five altitudes (m). Note y-axis scale x 10^5

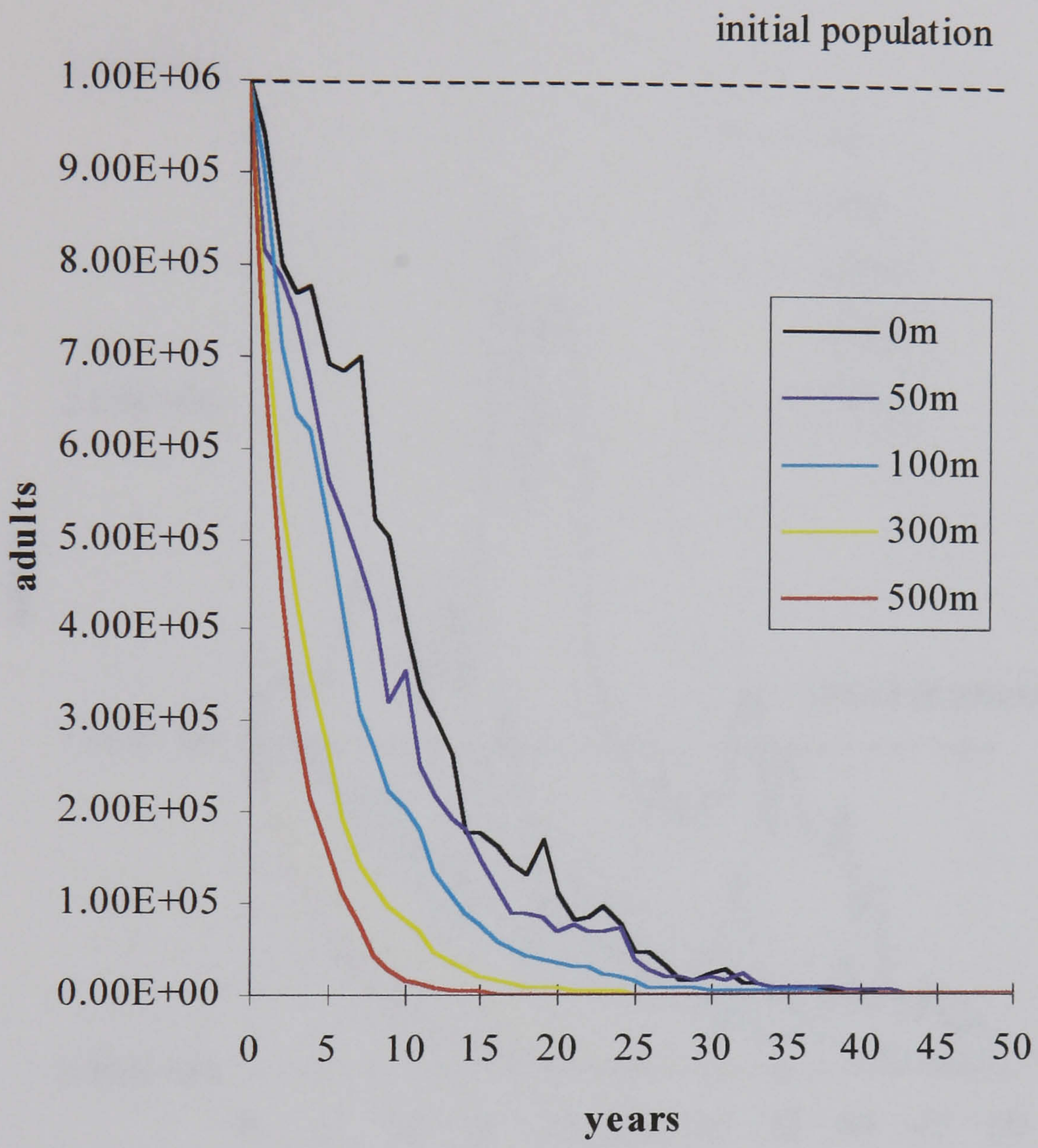


Figure 4-11: Model output of the mean annual population numbers, (*n*=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +2°C, at five altitudes (m). Note *y*-axis scale x 10^5

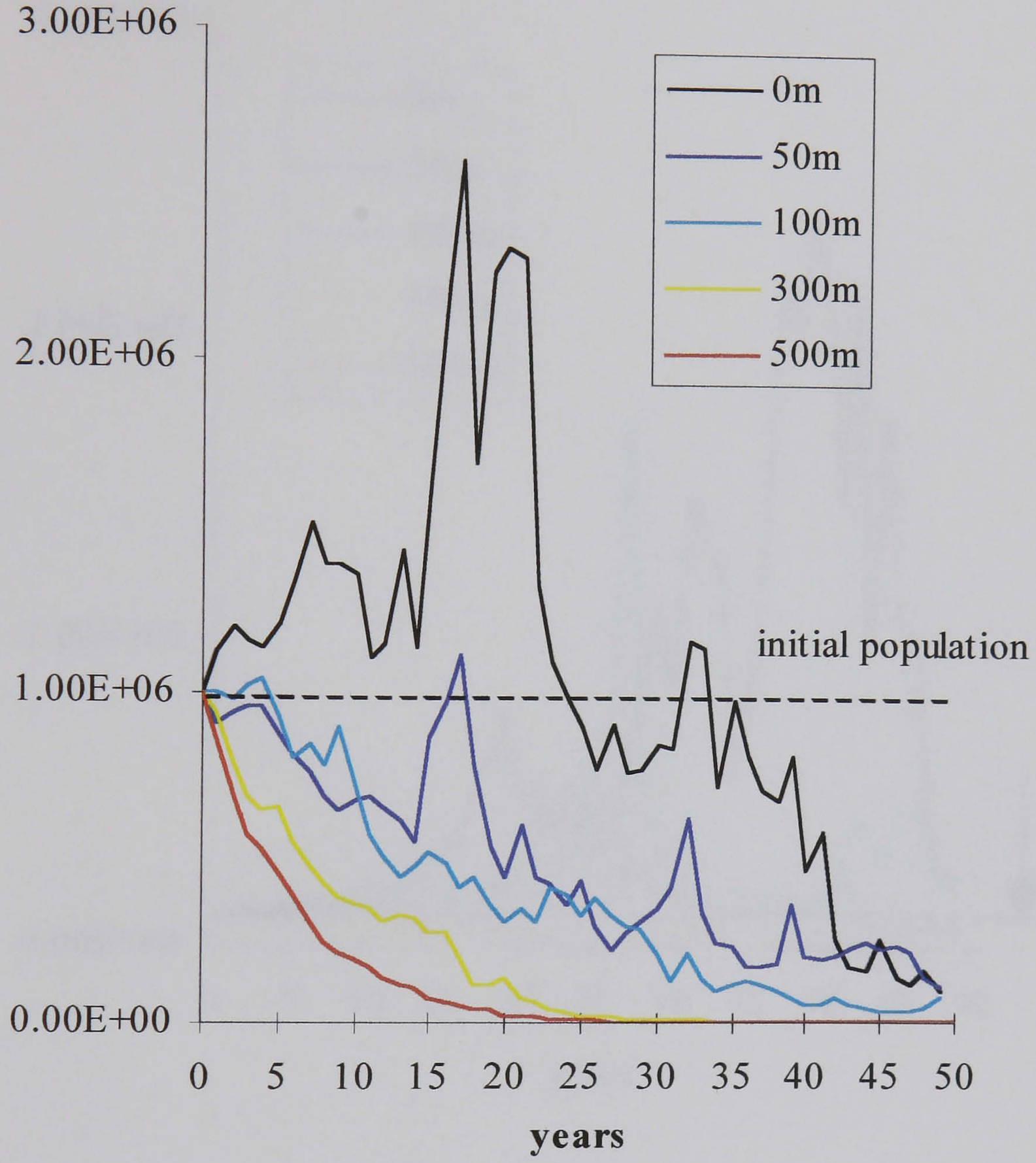


Figure 4-12: Model output of the mean annual population numbers, (n=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +3°C, at five altitudes (m). Note y-axis scale x 10^6

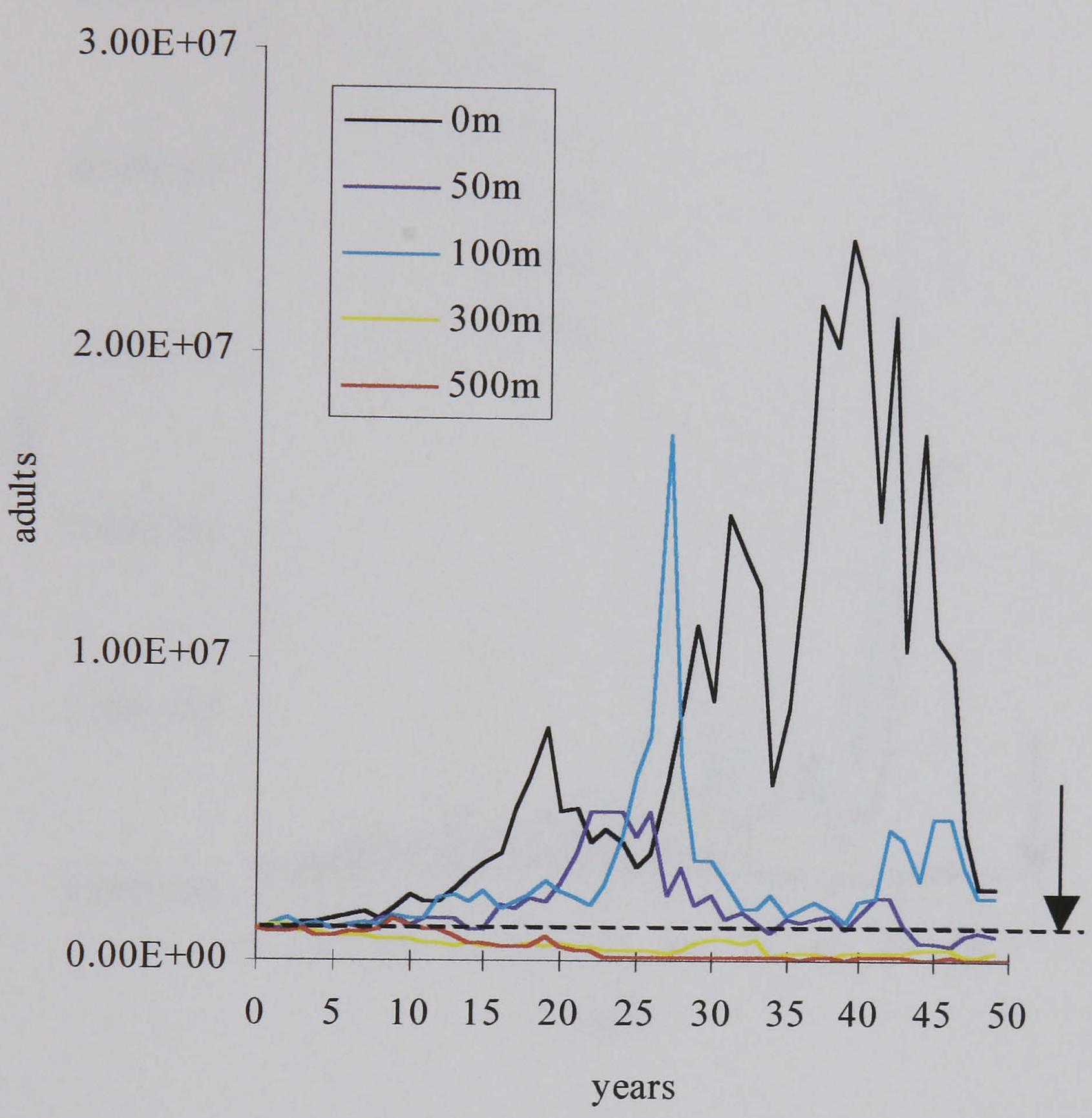


Figure 4-13: Model output of the mean annual population numbers, (*n*=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +4°C, at five altitudes (m). Arrowed, dotted line shows initial population, 1 x 10^6, note *y*-axis scale x 10^7

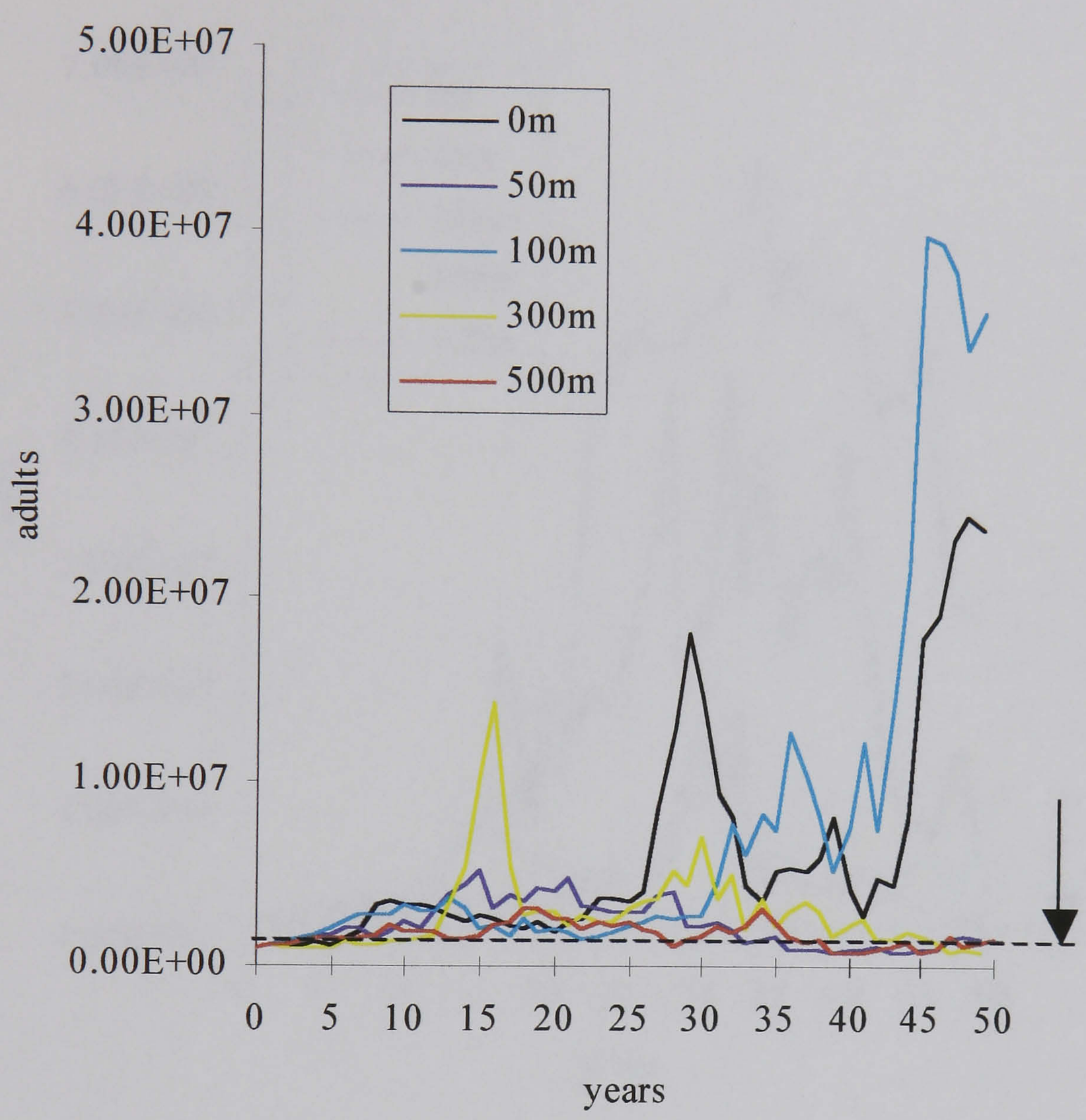


Figure 4-14: Model output of the mean annual population numbers, (n=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +5°C, at five altitudes (m). Arrowed, dotted line shows initial population, 1 x 10^6, note y-axis scale x 10^7

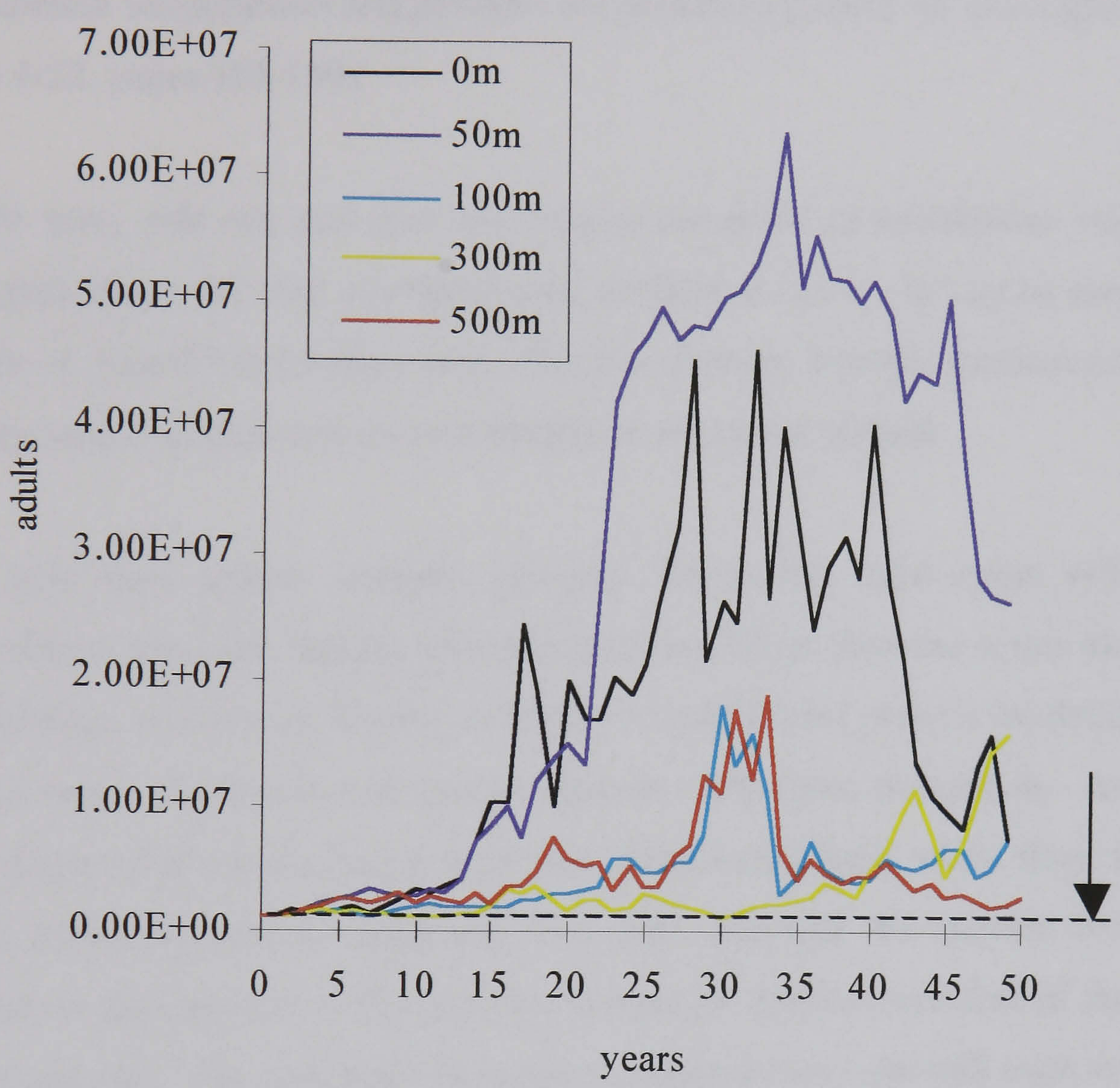


Figure 4-15: Model output of the mean annual population numbers, (n=100) of *Lochmaea suturalis* adults during a 50-year simulation with base temperature +6°C, at five altitudes (m). Arrowed, dotted line shows initial population, 1 x 10^6, note y-axis scale x 10^7

4.3.3.2 *L.suturalis* population numbers over a 50 year simulation after 5, 10, 25 and 50 years at five altitudes and six temperatures

The population numbers at the end of five, ten, twenty-five and fifty years, at the different temperatures and altitudes are presented graphically (see Figures 4-16 to 4-22, pages 163-169).

At the zero, plus one and plus two degree scenarios all populations had not increased above the start population and declined to zero. As can be seen the decline in population numbers was related to altitude, with the quickest decline at the greatest altitude and slowest decline at the lowest altitude.

The plus three degree scenario generally shows the same trend with the populations from the highest altitudes declining faster than the lower altitude populations, however at the end of the 5, 10 and 50 year periods the decline of the 50 metre population was greater than the 100 metre population. At plus four degrees the populations at the higher altitudes declined, whilst those at the lower altitudes generally increased over time, although the increase was not related to their altitude as the greatest increase in numbers occurred at the 100 metre altitude. The zero and 100 metre populations were the only ones to have greater numbers than the start population over the four time periods.

At plus five degrees, for the first 25 years there is a relationship between altitude and population growth, where higher altitude populations increased at a greater rate. However at 50 years, this no longer holds, as population growth became unrelated to altitude, for example the 300 and 500 metre populations had greater numbers than the 50 metre population.

The plus six degree scenario showed that the relationship between altitude and population growth no longer holds at any of the time periods. For example at five years the 500 metre had a greater population than the 100 and 300 metre

populations, and after 50 years the 300 metre population showed the second highest population.

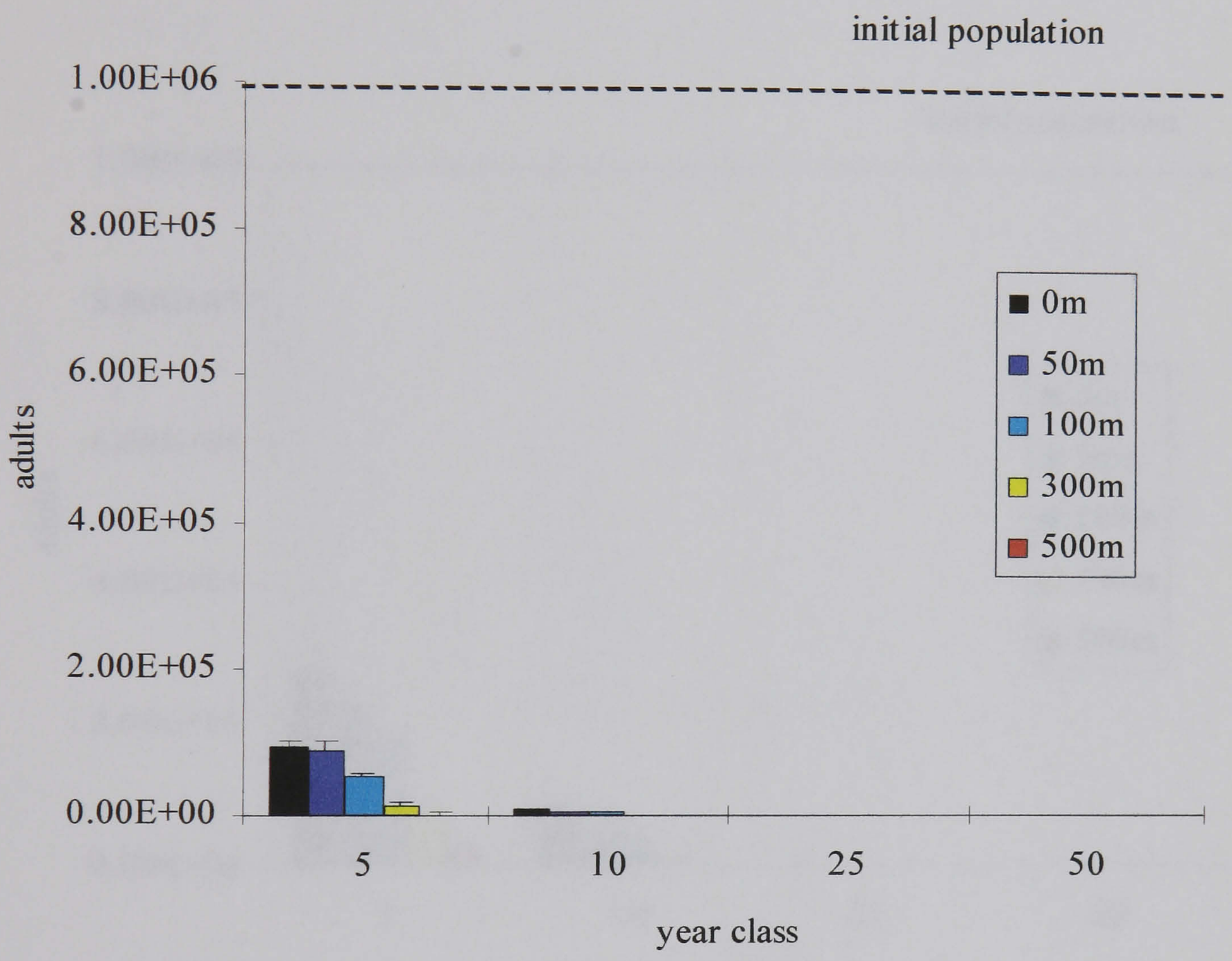


Figure 4-16: Model output of mean and standard error (*n*=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature at five altitudes

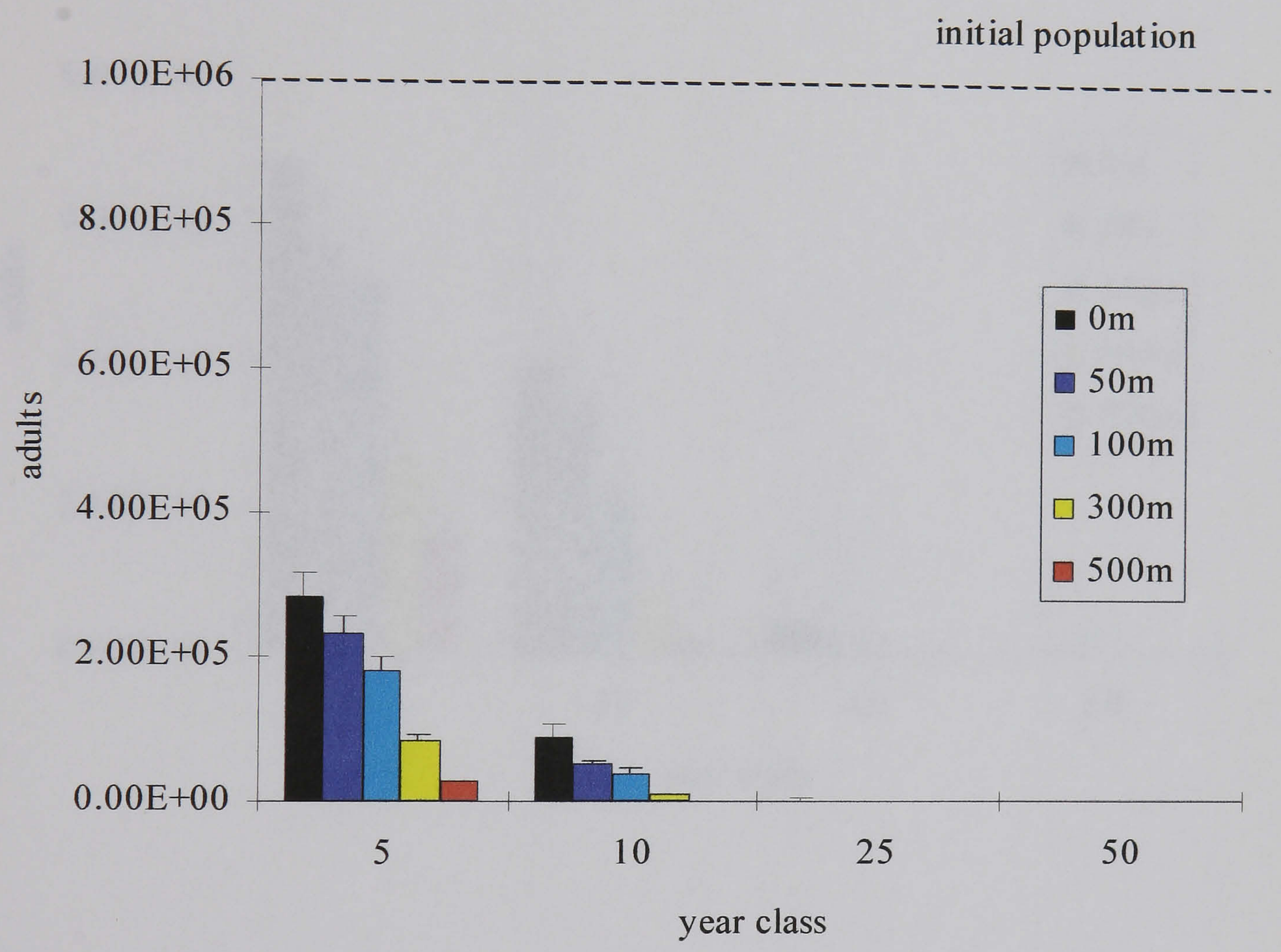


Figure 4-17: Model output of mean and standard error (*n*=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature +1°C at five altitudes

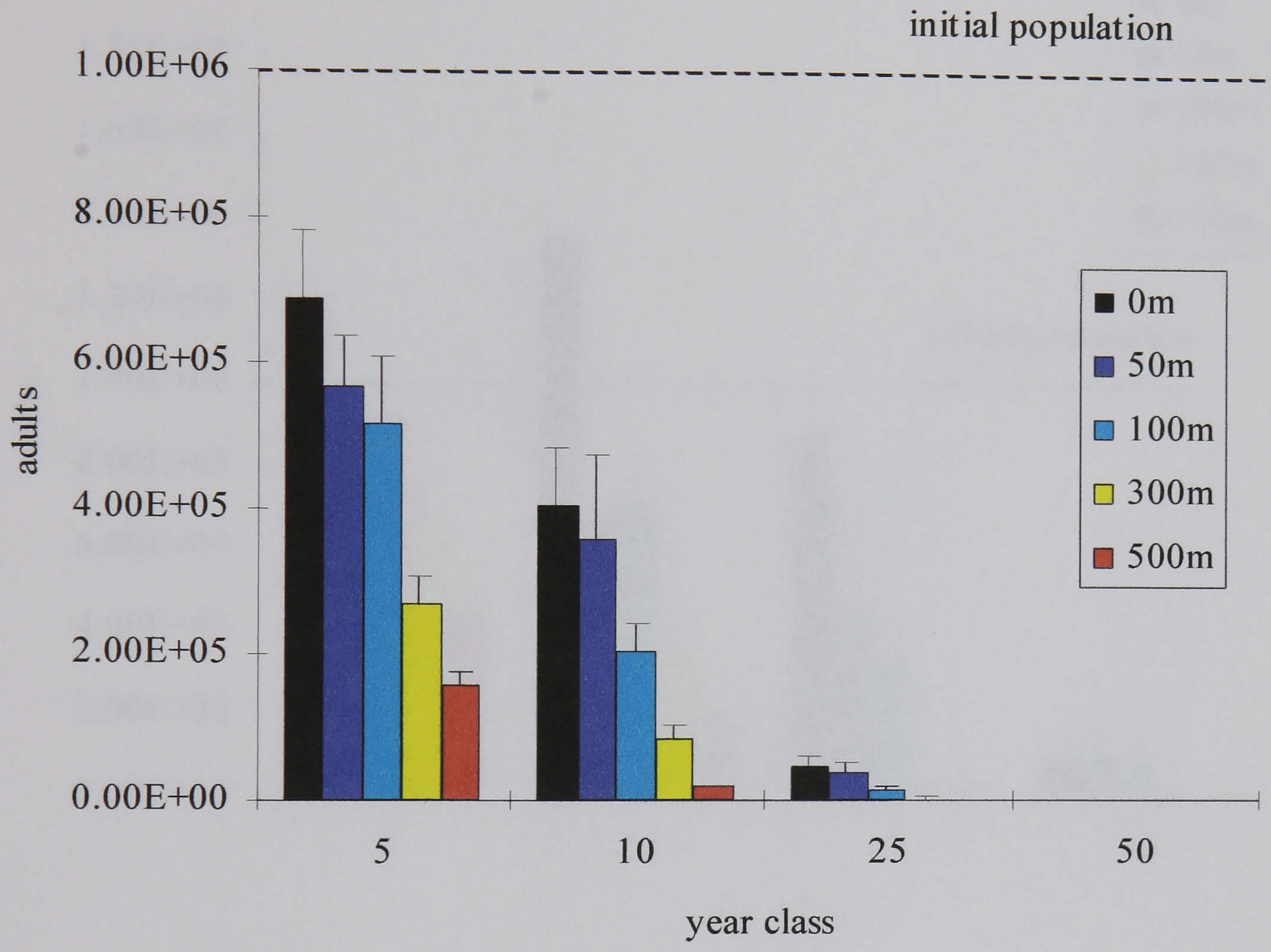


Figure 4-18: Model output of mean and standard error (*n*=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature +2°C at five altitudes

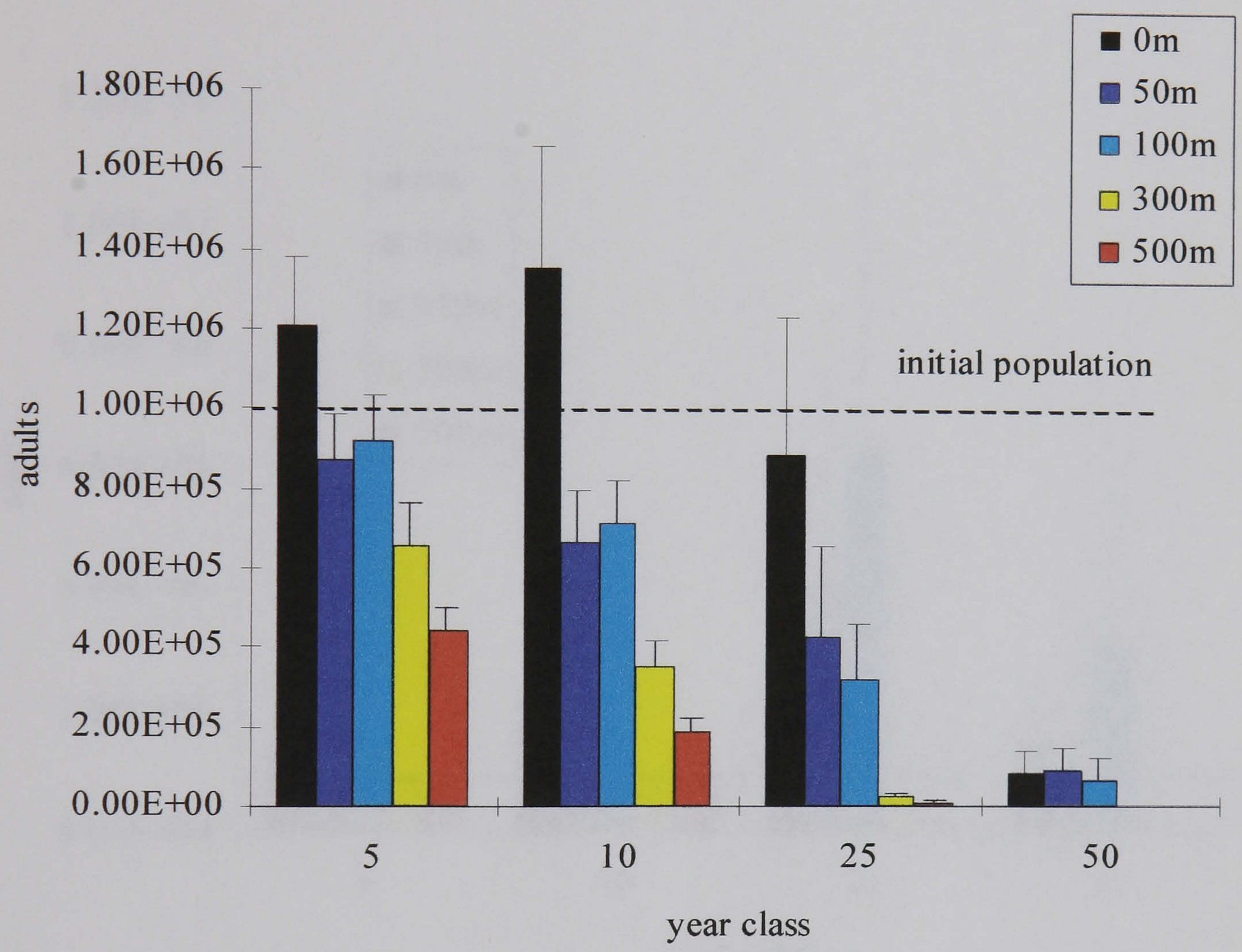


Figure 4-19: Model output of mean and standard error (n=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature +3°C at five altitudes

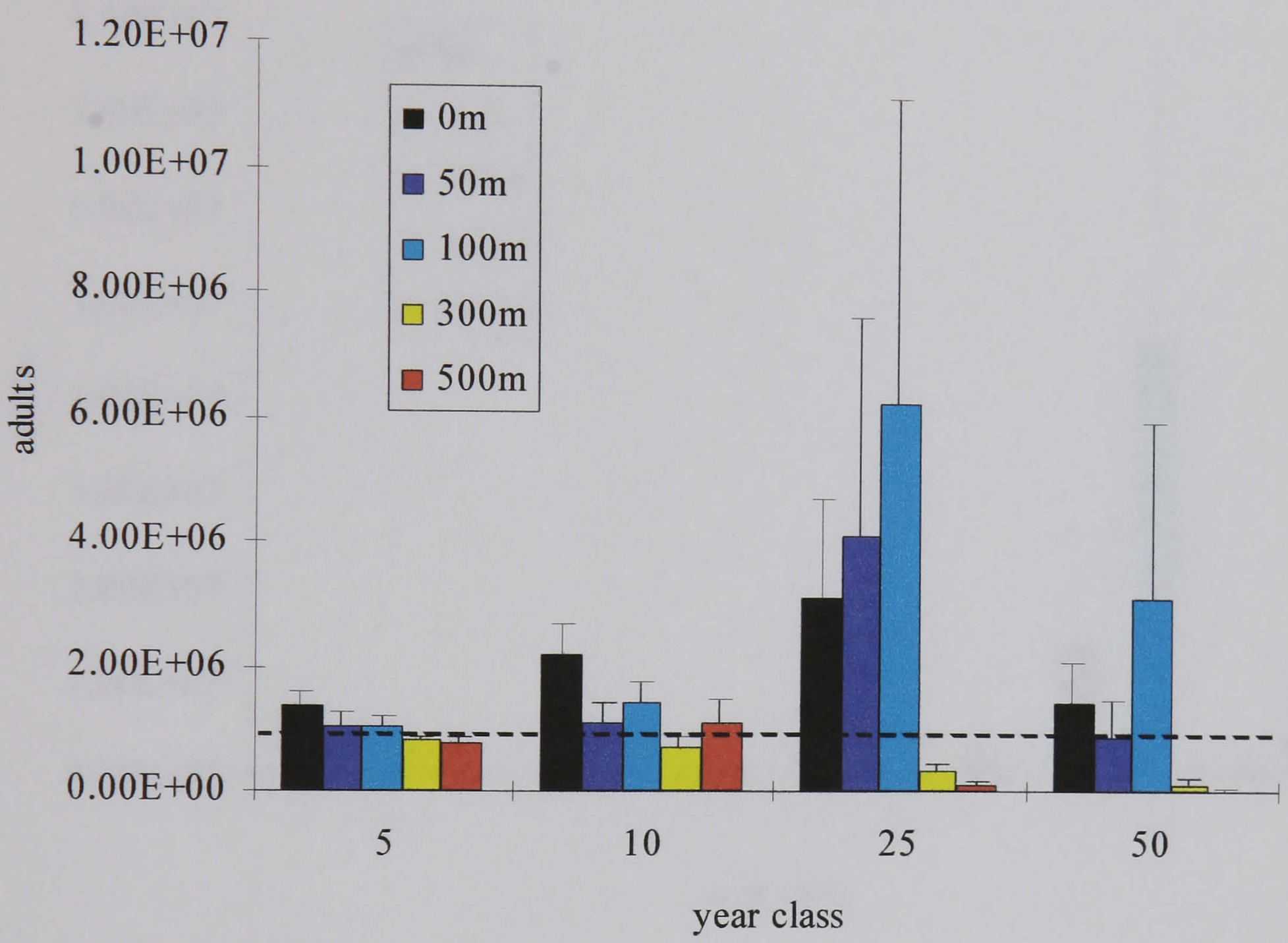


Figure 4-20: Model output of mean and standard error (*n*=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature +4°C at five altitudes, dotted line shows initial population, 1 x 10^6

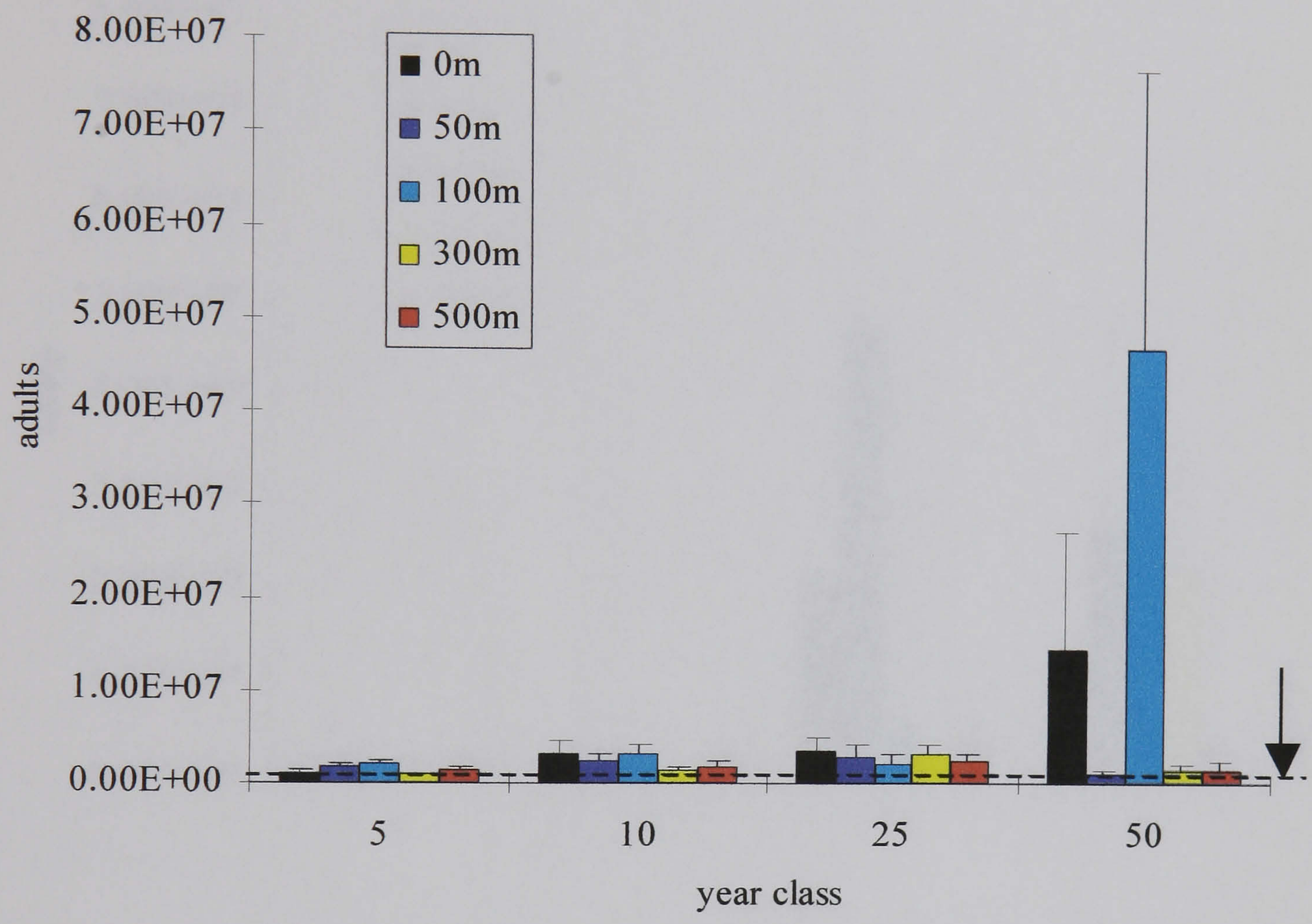


Figure 4-21: Model output of mean (n=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years with base temperature +5°C at five altitudes arrowed, dotted line shows initial population, 1 x 10^6

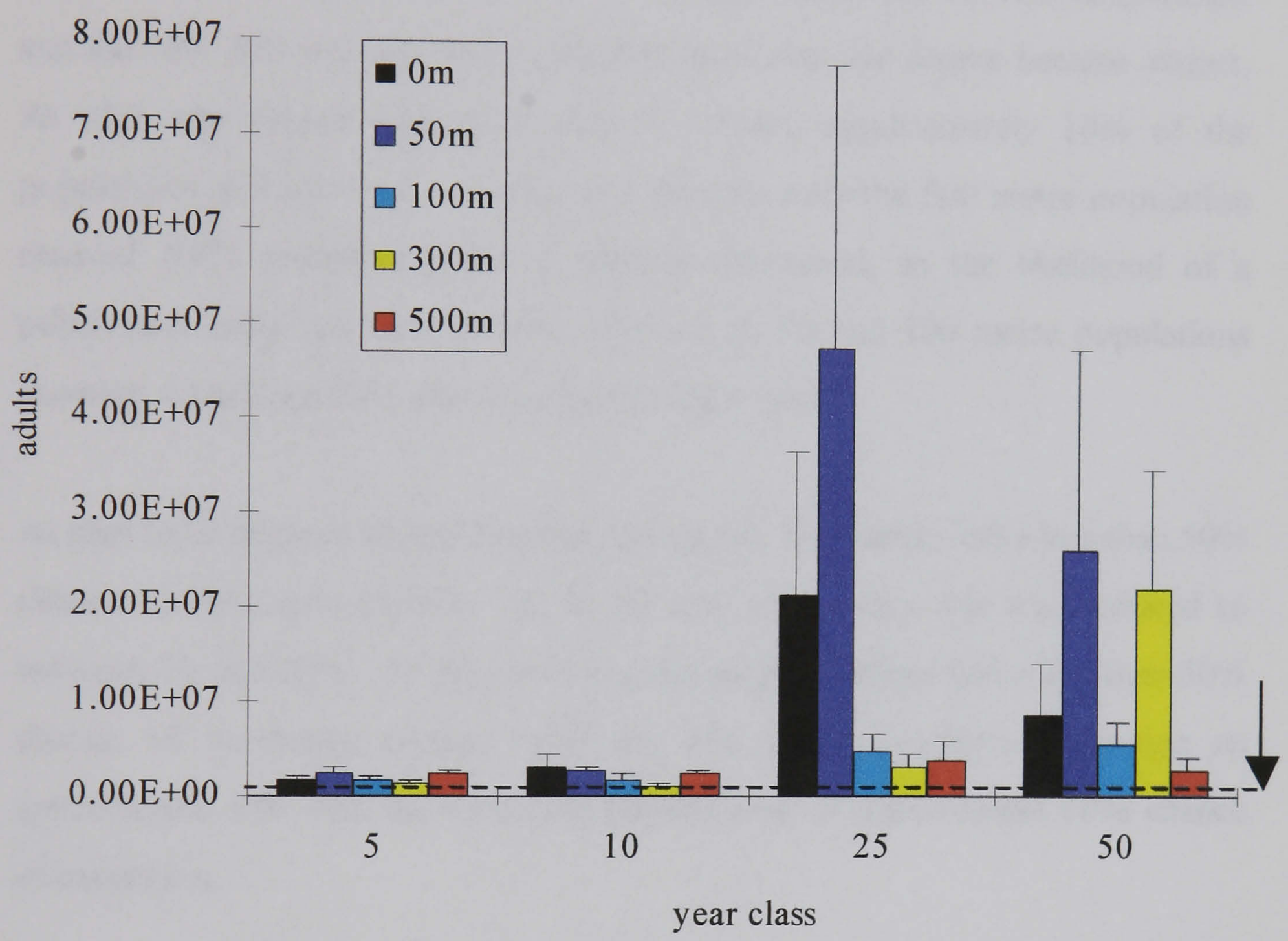


Figure 4-22: Model output of mean and standard error (n=100), of adult *Lochmaea suturalis* population numbers after 5, 10, 25 and 50 years, with base temperature +6°C at five altitudes, arrowed, dotted line shows initial population 1 x 10^6

4.3.3.3 *L.suturalis* population model extinction predictions after a 50 year simulation at five altitudes and six temperatures

The percentage extinctions of each temperature and altitude scenario after a 50 year simulation is shown graphically (see Figure 4-23, page 171).

It can be seen that all of the replicated, 100 populations, at the base temperature and the 100, 300 and 500 metre populations at plus one degree became extinct. At plus one degree and at 0 and 50 metres, approximately 10% of the populations still survived. At plus two degrees only the 500 metre population showed 100% extinction, and as altitude decreased, so the likelihood of a population extinction became less, with the 0, 50 and 100 metre populations showing a less than 50% chance of becoming extinct.

At plus three degrees all populations, except the 500 metre, had a less than 50% chance of becoming extinct. At 0, 50 and 100 metres this was reduced to between 10 and 20%. At plus four degrees all populations had a less than 50% chance of becoming extinct, with the 500 metre population showing an approximate 40% and the remaining populations, an approximate 10% chance of extinction.

The plus five and six degree temperature regimes showed that the probability of becoming extinct for all altitude populations was approximately within the range 2-10%.

By inspection of the graph showing the predicted temperature increase at which 50% of the 100 simulation populations would survive after a 50 year simulation (see Figure 4-24, page 172), it can be seen that for the 0, 50 and 100 metre populations this would occur at approximately a two degree rise and with a rise of three and four degrees for the 300 and 500 metre populations, respectively.

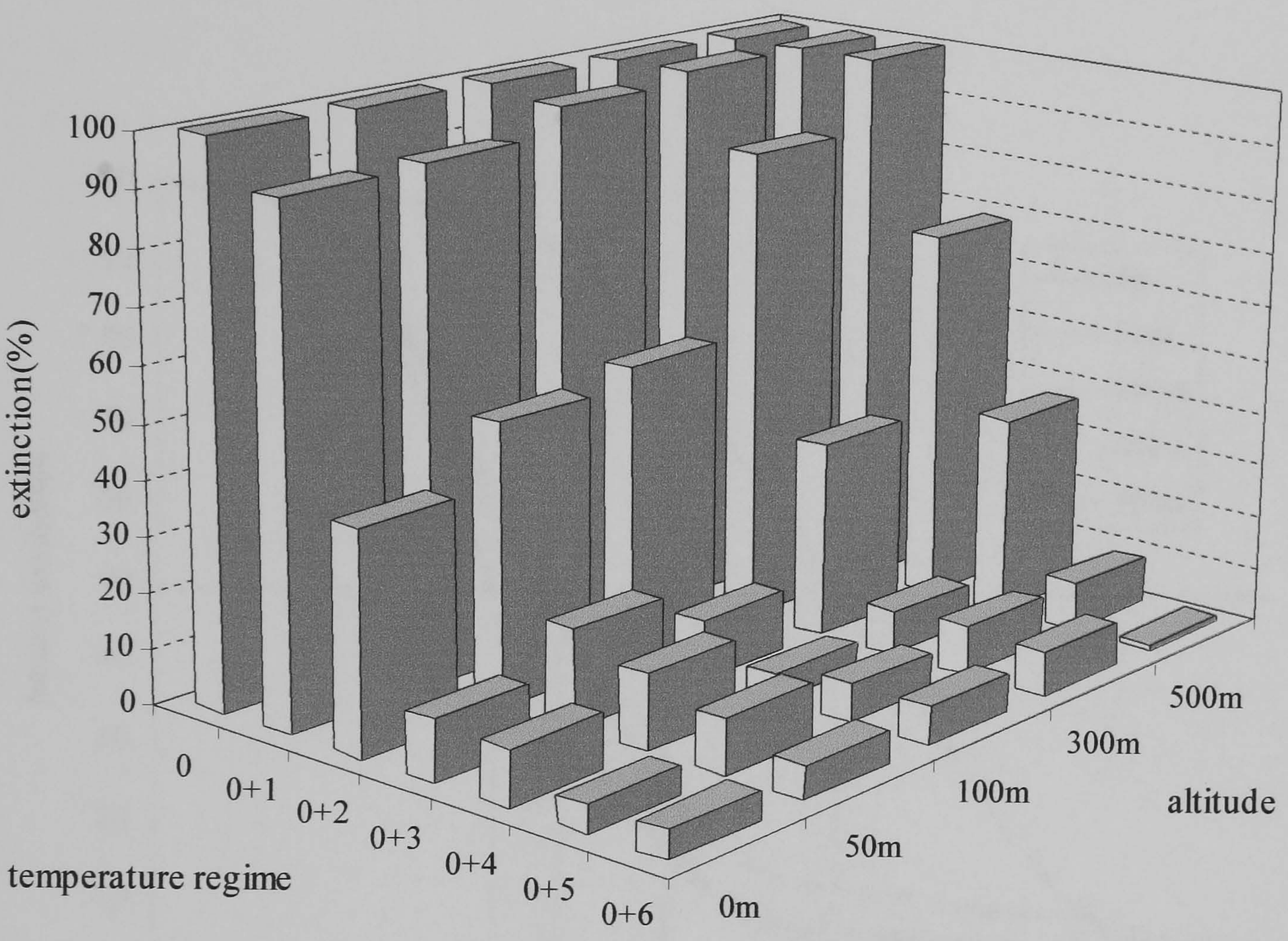


Figure 4-23: Model predictions of percentage extinction of *Lochmaea suturalis* populations after 50 years of a 50-year simulation (n=100), at the five altitudes, with base and alternative temperatures (°C)

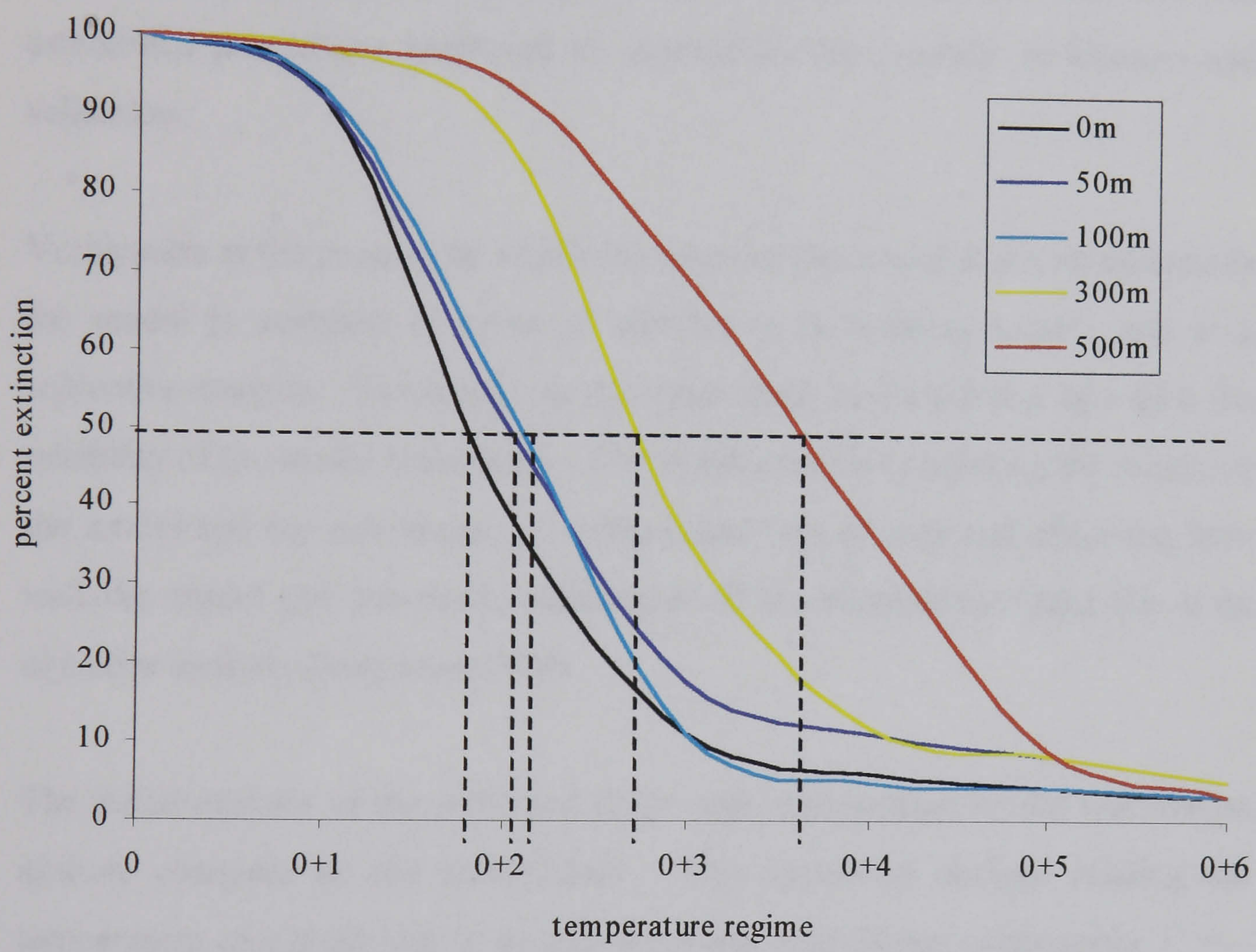


Figure 4-24: Graph showing the predicted extinction curves of the 100 simulated *Lochmaea suturalis* populations after 50 years of a 50-year simulation (*n*=100), at the five altitudes, with base and alternative temperatures (°C); the temperature regimes at which the probability that 50% of the populations (dotted lines) will become extinct can be read off the *x*-axis

4.4 Discussion

As the success of a model depends on the assumptions that underlie the modelling processes and the accuracy of the estimated parameters (North & Jeffers 1991), it is dangerous to give too much credence to the output and start making sweeping statements based on the output (Thomas 1986; Bart 1995), without first *testing* the model. The confidence by which the output of a model can be used to make predictions is assessed by evaluating the robustness of a model. There are two established procedures employed to accomplish this, namely verification and validation.

Verification is the process by which the *logic* of the model is tested; essentially the model is assessed in terms of whether it is "making sense", and is a *subjective* analysis. Validation, on the other hand, is the process by which the reliability of the model is assessed. This is achieved by comparing the output of the model and *key* sub-models to independent sets of data and observing how well the model and sub-model simulations fit the independent data; this is an *objective* analysis (Jorgensen 1994).

The initial premise of the predicted daily mean temperature model was that as altitude changed, so did temperature. The regression analysis relating the temperature of a study site to its altitude found a significant relationship, $r^2 = -0.11$*** and both regression coefficients significant at $p < 0.001$ (see section 4.3.1.1, page 134). The altitude coefficient was –0.0045, this figure shows that for every 100 metres gain in altitude there was a drop in temperature of -0.45°C. The established environmental lapse rate for the decrease in temperature as height is gained is $\approx$ - 0.6°C 100 m^{-1} (Northumbrian River Authority 1973; Smith 1984). Given that the dataset was a small sample and that it was only collected for one year it was accepted as a reasonable reflection of

temperature change with altitude, and as such the altitude variable was included in the temperature modelling process.

However, once the multiple regression equation relating daily mean temperature to day, the temperature on the day before and altitude, was fitted, it was found that the significance of the altitude variable became marginally not significant at $p = 0.06^{ns}$, with a coefficient of 0.0007. This value predicts an environmental lapse rate of 0.07°C 100 m^{-1}, a ten-fold difference in order of magnitude. On inspection of the regression output (see Table 4-3, page 136), it can be seen that the high *t* values for the day and the temperature on the day before may account for this anomaly, as these two variables may have been "swamping" the effect of altitude. Nevertheless altitude was kept in the temperature model as its parameter value would have some effect on the predicted daily mean temperature as altitude was varied.

The predicted daily mean temperature sub-model that acts as the driving variable for the *L.suturalis* population dynamics model, in terms of verification, produced meaningful output. For example, it did not produce warmer temperatures in winter than summer and the greatest temperatures occurred at the height of the summer, whilst those in the depths of winter were the lowest (see section 4.3.1.3, page 136).

The validation of the temperature model involved a comparison of its output with the raw temperature data from Redesdale. The predicted mean temperatures from the temperature model showed good correlations with the six years of Redesdale temperatures ranging from 0.80*** to 0.86***. Also four out of the six percentage differences between the mean annual Redesdale temperatures and the mean annual temperature produced by the model were acceptable, with values of less than 6%, with not significant *p* values in the individual ANOVA's (see Table 4-5, page 137). The other two years' mean annual temperatures were marginally acceptable with percentage changes of 11 and 13.3 %. By inspection of the graph showing the predicted temperature and the raw Redesdale data (see Figure 4-5, page 140), it can be seen that the

differences are due to the greater winter daily mean temperatures recorded at Redesdale in 1989 and 1990.

The correlations between the predicted Redesdale temperatures, derived by fitting the temperature model equation to the Redesdale data and the predicted model temperatures were all found to be significant at $p > 0.993$***. The individual ANOVA's performed on the predicted Redesdale and model temperatures found two significant differences (see Table 4-10, page 142). These were the 1989 and 1990 years, this was as expected, as they were previously found to be significantly different. Similarly the percentage change between the predicted mean annual Redesdale temperature and the mean annual temperature predicted by the model was greatest for these years. By inspection of the graph showing the model predicted temperature and the predicted Redesdale temperatures (see Figure 4-6, page 145), it can be seen that the model predicted temperatures that overestimated the maximum summer temperatures and underestimated the winter values, by approximately +1°C and −1°C, respectively. The other noticeable difference was that the temperature model predicted a slightly narrower range of summer temperatures and a correspondingly slightly wider range of winter temperatures. This difference may have been due to the fact that the temperatures recorded at the study sites were taken from the *C.vulgaris* understory, where the micro-climate may have "buffered" the temperatures. For example, cold night temperatures would have remained colder for longer as the effects of insolation would have been lessened under the heather.

The mean annual temperature predicted by the model was 7.0°C; this predicted temperature was for the altitude of Redesdale (253 m). The Meteorological Office (1984) found a mean annual temperature for the coastal lowland area in the northeast region of the British Isles of 8.5°C. If the mean height of this region were approximately 100 metres, then by using the environmental lapse rate of -0.6°C 100 m^{-1}, a value at Redesdale would be approximately 7.5°C.

This figure is very similar to the predicted mean annual temperature, set at this altitude.

Finally, the temperature model was run at the outer limits of its stochastic variation, to observe if meaningful temperatures were being produced when low probability standard normal deviates were being drawn. The model was shown, at a probability of 1 in a 1000, not to produce a daily mean temperature greater than 25°C. It should be noted that the predicted temperature model relies on the temperature on the day before as one of its parameters and therefore this particular validation procedure effectively, over and underestimated the maximum and minimum temperature values. Nevertheless, the Meteorological Office (1984) give an extreme maxima figure of 28°C, recorded at Durham, with an of altitude 102 metres, showing that the maximum possible temperature predicted by the model to be within acceptable limits.

As a consequence of the validation procedure, which found that the model predicted temperatures within the same magnitude and range of those found at Redesdale and those recorded over a period from 1961-1980 by the Meteorological Office, the predicted temperature model was accepted for use as the driving variable in the population dynamics model.

The egg generating sub-model passes the verification test, in that it produces eggs over a similar time period, and the number of eggs laid varies depending on the temperature of a particular egg laying day. Although it does produce fractions of eggs, which does not "make sense"; a prerequisite for verification. The main model compensates for this failing by the use of function that converts these fractions to integers by rounding up or down.

The validation of the egg model was evaluated by comparing the predicted number of eggs laid, using the three temperatures of the controlled fecundity experiment, with those actually laid in the experiment and in the ambient fecundity experiment (see section 4.3.2.1, page 149). Using 15 and 20°C as

inputs to the egg model produced a total number of eggs laid within the range laid by the adults in the controlled temperature fecundity experiment. The number of eggs was also within the range laid by the adults at ambient temperature. However comparing the number of predicted eggs laid against those at ambient temperature is tenuous, as the development of invertebrates is generally more rapid at mean temperatures several degrees lower than controlled temperature experiments (Worner 1992; Jones & Stephen 1994). Given this fact, the daily mean temperature experienced by the adults in the ambient temperature experiment is likely to be, for June and July, in the region of 12 to 16°C.

A problem with the validation of the egg sub-model arises with an input of 25°C, where the predicted number of eggs laid was greater than those laid by the controlled temperature beetles at the same temperature. Nevertheless, the egg generating model validation was accepted as the number of times that a value of 25°C would be predicted by the temperature model would be very rare (see previous discussion of the temperature model validation), and the egg laying period in the main model was set to begin after the stochastically varied egg laying temperature threshold was reached. In the model this was set at a mean of 12.5°C and varied by multiplying the standard deviation of 1.87 with a randomly drawn standard normal deviate. Thus, there was a 1 in a 100 probability that the egg-laying threshold would be 17°C; showing that eggs would always have begun to be laid before a predicted temperature of 25°C was randomly drawn.

Before discussing the main model output it is necessary to note the model assumptions. First, the females were assumed to be in the position to lay eggs on every day, whether they did or not, was determined by the randomly drawn Poisson deviate. Second, the emergence threshold was set at a constant value 5°C and not varied. Third, the life stage development periods only accumulated when the temperature on a given day was greater than 5°C. Fourth, different aged cohorts would experience the same life stage mortalities on any given day.

Obviously some of these assumptions do not necessarily reflect what would actually happen in the field or indeed the laboratory, for example, Jefree & Jefree (1996) note that it is inappropriate to use constant temperature thresholds when modelling a species in different regions as phenotypic acclimation is likely to alter these thresholds in different regions. However, as with all modelling projects, there is an obligatory trade off between model complexity and trying to include all the modelling possibilities. This trade off is inevitable and has been well documented by many ecological modellers (Jeffers 1978, 1988; Boyce 1992; Jorgensen 1994; Smith 1996). The above assumptions were made to reduce the complexity of the model. For example, to incorporate the reality of different aged cohorts experiencing different mortalities on a given day or that females may not have the possibility of producing eggs on an every egg laying day would have added an additional level of complexity at the expense of parsimony. This greater level of complexity would have made the construction of the model and the interpretation of the model output, particularly the uncertainty and sensitivity analysis, described in the next chapter, a much more difficult task.

The initial population number of 1 million was chosen because it represents an area of heather covered by beetles of between 0.05 and 0.1 hectare. This was based on the densities of beetles found by Smidt (1977) who recorded 1000 adults m^{-2} in high density pest years and Brunsting (1982) who found local adult densities of c.2000 m^{-2}. As Smidt & Brunsting (1990), recorded initial damage to *C.vulgaris* patches in the region of 0.01 to 3.0 hectares, the figure of 1 million adults modelled a "typical" initial level of infestation.

The altitudes chosen for the model runs, 0, 50, 100, 300 and 500 metres, were representative of the range of altitudes that *C.vulgaris* occurs at. Grime (1988), records it occurring up to 1100 metres, however Usher & Thompson (1993) noted that above 500-700 metres, *C.vulgaris* it is no longer the dominant species.

The range of temperatures used for the model simulations (base temperature to + 6°C), were selected as they represented the range of predicted daily mean temperature increases that recent research has suggested will be brought about as a consequence of global climate change. These predictions have ranged from a figure of 4 ± 2°C (Mitchell *et al.* 1990) to 3-5°C (Schneider 1992) and 3°C (Houghton *et al.* 1990).

The verification of the main model output was accepted as the results produced were within the realms of possibility. With the population numbers varying as the altitude and temperature input parameters were varied.

The validation of the model output was more problematical as there was little or no similar data to compare it with, either derived within the thesis study, where very few beetles were found at the study sites, or from other researchers. The overall picture of the model output was that, as either temperature increased or altitude decreased, so the beetle populations increased. For a successful validation the question to be answered was: do the model predictions agree with the known demographics of *L.suturalis*?

The temperature model predicted daily mean temperatures for northern England. The Meteorological Office (1984) found in an analysis of 30 years temperature data, that the differences between mean annual temperatures in the Shetland Isles, in the far north of Scotland, and the extreme southwest of England was in the region of four degrees centigrade, with the north of England about midway on this gradient. For the purposes of this discussion it is assumed that southern England would, on average, be two degrees warmer than northern England; this is confirmed by Swan (1977); and that northern Scotland would be two degrees cooler on average.

The model predicted that outbreaks of the heather beetle would begin to occur with a temperature rise of + 3°C at 0, 50 and 100 m altitudes. The Netherlands is a low-lying country and generally experiences warmer summer temperatures than the

British Isles, due to the effects of continentality. These factors would, as the model confirms, predispose their heaths to prolonged, heavy attacks of the heather beetle and as discussed in Chapters Two and Three the heather beetle is considered a serious pest of their lowlands heaths. In contrast, heather moorlands in Scotland and the north of England, defined as those *C.vulgaris* dominated habitats generally above 300 metres (Farrell 1989), would, because of the lower daily mean temperature, be expected to experience light, sporadic outbreaks; however the model does not predict this, as at base temperature, + 1°C and + 2°C the populations, for the most part, gradually declined to extinction. (see section 4.3.3.3, page 170). However Cameron *et al.* (1944) and Morison (1963), had noted outbreaks had occurred in these colder regions after two or three years of unseasonally dry, warmer weather. They do not give figures, but the Meteorological Office (1984) have shown that mean extremes of temperature in the north of England of temperature can vary by as much as 5-6°C. If it is assumed that there was an increase in temperature in Scotland of 3°C for two or three years, particularly in the spring and early summer, then the model predicts that at lower altitude sites (150m), that there would be evidence of heather beetle outbreaks. Cameron *et al.* (1944) and Morison (1963) also noted that outbreaks were more common in the south and southwest of Scotland, where temperatures were generally warmer than those experienced further north.

One aspect of the model that warrants further discussion was the apparently anomalous output when + 4°C, + 5°C and + 6°C was added to the base temperature model. The model output showed that the populations at 50 and 100 metres were larger than those at 0 metres. Intuitively this appears to be wrong, but it may be "real" in terms of the model as the increase in predicted daily mean temperatures was swamping the effect of the change in temperature due to the increase in altitude where the temperature model was only producing, on average, a 0.07°C decrease in temperature for every 100 metre increase in altitude.

So far the discussion has centred on, in the absence of quantitative empirical data, validating the model predictions by linking possible altitude and temperature scenarios to qualitative data. However, Miller *et al.* (1966) in their study of heather performance and Red Grouse populations recorded the percentage of 1 m^2 quadrats exhibiting damage or death of *C.vulgaris* caused by with heather beetle. This was conducted at 17 moorland sites across an altitudinal gradient from 25 m to 760 m for the years 1959-1961 in northeast Scotland. The data is presented graphically (see Figure 4-25, page 183).

Having arcsin transformed the percentage data; a regression analysis was performed on the data to test if there was a significant relationship between the amount of heather damaged at a site and the altitude of that site (see Table 4-16, page 182).

The regression analysis showed that there was a significant relationship in 1959, $r^2 = 0.58^*$ at $p = 1\% \leq p > 5\%$, showing that as altitude decreased, so the incidence of heather damage caused by the heather beetle increased. There was no relationship found for the years 1960 and 1961. Although the data does not provide convincing evidence of an altitudinal relationship, it was noticeable that for all three years there was no beetle damage found at the five sites above 500 metres.

Year	Coefficient	*t* value	*p value*	r^2	*n*
1959					
Constant	31.2	5.4	0.0001***	0.58*	15
Altitude	-0.05	-4.2	0.001***	-	-
1960					
Constant	4.22	1.15	0.27^{NS}	0.02^{NS}	15
Altitude	-0.005	-0.57	0.58^{NS}	-	-
1961					
Constant	18.64	4.11	0.001***	0.35^{ns}	14
Altitude	-0.03	-2.6	0.025**	-	-

Table 4-16: Results of the regression analysis (*n*=17), testing for a relationship between altitude and the percentage of 1 m^2 quadrats of damaged or killed *Calluna vulgaris* caused by *Lochmaea suturalis* on 17 moorland sites in north-east Scotland between 1959 and 1961 (*after* Miller *et al.* 1966); the data is arcsin transformed

All the researchers who have studied the heather beetle have noted that it is endemic on most *Calluna vulgaris* habitats in all regions and at all altitudes, except the sub-montane moorlands. Indeed Waloff (1986) noted that there had been a population on the back lawn of Silwood Park for over thirty years. It should be noted that the population predictions (see 4-9 to 4-22, pages 154-169) are mean figures calculated from the 100 replicates. As such the extinction predictions of the model (see Figure 4-23, page 171), provide information on whether *any* of the 100 populations was able to survive, given a particular altitude and temperature regime. The extinction predictions predict the endemic populations as at all temperature regimes above + 1°C and at all altitudes, except 500 metres, there was always some percentage of the 100 replicate populations that remained viable after the fifty year run, with the exception of the 500 metre population that only began to show viable populations with a temperature regime of +3°C.

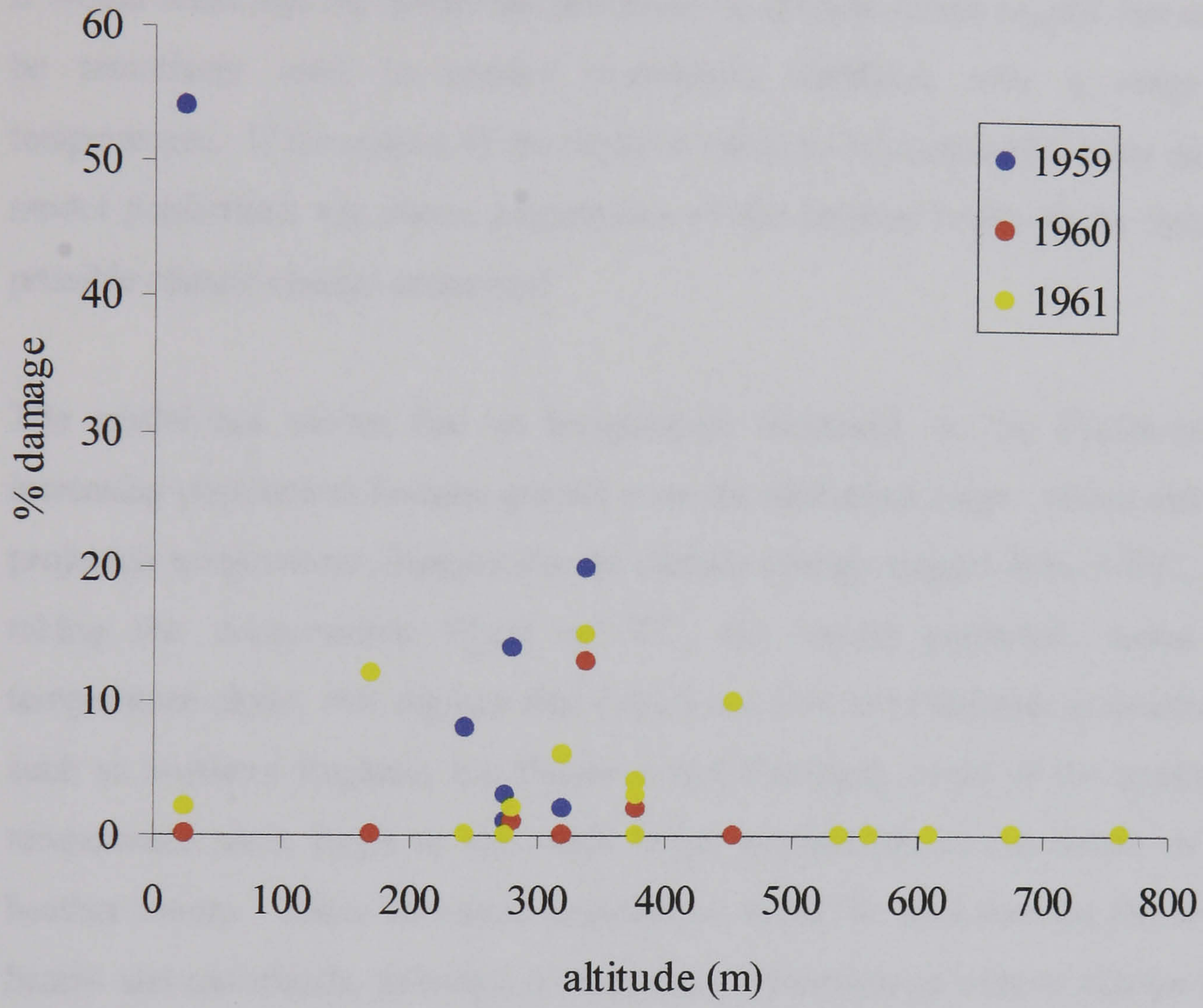


Figure 4-25: Percentage of 1 m^2 quadrats with *Calluna vulgaris* damage or death caused by *Lochmaea suturalis* in 1959, 1960 1961 at 17 moorland sites in north-eastern Scotland, *after* Miller *et al.* (1966)

Given the preceding discussion and bearing in mind the following quote:

> "...all models should be considered with a healthy scepticism, and neither blindly accepted nor dismissed out of hand." (Smith 1996)

It would seem that the model has produced reasonably robust output that could be tentatively used to predict population viabilities over a range of temperatures. If the output of the model is taken to be meaningful, what do the model predictions say about populations of the heather beetle in the light of possible climate change scenarios?

The model has shown that as temperature increased, so the likelihood of increasing populations became greater over the altitudinal range. Given that the projected temperature changes due to climate change ranged from 3-6°C, and taking the conservative figure of 3°C, the model predicted; based on temperature alone, that regions that experience low level endemic populations, such as northern England, the Pennines and Scotland, could as the predicted temperature rises, begin to see much larger populations of the beetle on the heather moors. These increased populations would be first seen on the lower heaths and moorlands, although if daily mean temperatures were to change in a positive direction, then beetle populations would begin to increase on moorlands at the lower limits of the sub-montane zone.

In regions such as western mainland Europe, where temperatures are perhaps 2-3°C higher naturally, and there is already a major heather beetle pest problem on the lowland heaths, a shift of + 1°C or + 2°C in the daily mean temperatures caused by climate change would move the model predictions into the + 4 to + 5°C, with low altitude scenarios. These predictions show dramatic increases in numbers with, in some cases, a forty-fold increase in two or three years. It is also worth noting that the model was run for 100 replicates for each altitude and temperature scenario. As a consequence the model output is the mean of all

possible scenarios; it is therefore important to note that the mean model outputs hide more extreme population outcomes. For example, years with unusually high temperatures may impact on the fecundity of the beetle with a prolonged period of egg laying leading to greater population numbers or conversely a greater mortality of eggs with a subsequent lower population.

4.5 Conclusions

The *Lochmaea suturalis* population dynamics model has been shown to provide a method of predicting the effect of ambient temperature rises on the population viability of the heather beetle. However the use of this model to predict population increases in different regions should be viewed as a purely exploratory exercise, as it may be wrong to assume that a mean annual temperature increase would alter a particular species distribution into areas that it did not exist in before. Jefree & Jefree (1996) point out that by simply adding x degrees to every day's temperature and making a prediction, for example, that a particular species would move its range up 200 metres is an oversimplification, as it may require, in winter, a rise of $+x$ degrees and in summer, a decrease of $-x$ degrees.

Nevertheless, given the assumptions discussed earlier and the fact that the model operates in "one dimension", the model output has been shown to support the revised third, and fourth hypotheses; namely that altitude and predicted temperature increases, as a result of climate change, has been shown to have an effect on population viabilities. Oreskes *et al.* (1994) comment that models can corroborate a hypothesis by offering evidence to strengthen what may be already partly established through others means. This is true for this model, as intuitively it may have been surmised from the previous two chapter's evidence and what is already known about terrestrial invertebrates and temperature, that increases in daily mean temperatures would probably increase the likelihood of greater population numbers.

The final stage of the modelling process is to subject the model to an uncertainty and sensitivity analysis. This procedure statistically assesses the amount of influence that each model variable has on the output. Its value is two-fold, first it can highlight areas of the model that may "weak" and consequently may require further empirical experimentation, and second, it can draw attention to aspects of the life cycle that may be of interest to conservation or moorland mangers.

Chapter 5: Sensitivity and uncertainty analysis of the *Lochmaea suturalis* population dynamics model

5.1 Introduction

An important aspect of the modelling process is the uncertainty and sensitivity analysis of the model (Miller 1974; Jeffers 1978, 1988; Havens & Fontaine 1991; Chang *et al*. 1993; Hamby 1994; Jorgensen 1994; McCarthy *et al*. 1995; Henderson-Sellers & Henderson-Sellers 1996). It is the process by which a modeller learns about the properties of a model. In the *Lochmaea suturalis* population dynamics model the development of the initial population number, year by year, was a function of the model variables, with each variable having an effect on the population. The sensitivity analysis of the model allows the modeller to assess which of the variables are the most *sensitive* in the model. In essence this means which of the model variables had the most or least influence on the model population output. In practice the analysis is carried out by varying a model variable by a known amount and by observing the change in the model output. The variables can then be ranked based on their relative importance. The uncertainty analysis assesses the prediction imprecision (uncertainty) in the model output due to the uncertainty in the estimation of the input variables.

Traditionally, the sensitivity and uncertainty analysis of a model was conducted by varying a model parameter, one at a time, by some, often arbitrarily chosen amount. For example, varying the input parameters by ± one standard deviation or ± 10% of its mean value. The variations in the input value are then compared to the changes in the model output (Henderson-Sellers & Henderson-Sellers 1996). However, three problems with this method have been identified. First, deciding by how much the parameters are varied, as the choice can greatly effect the interpretation of the sensitivity analysis (Swartzman & Kaluzny 1987). Second, limiting the variation of the input variable in this manner fails to sample

the sensitivity of the variable across its full distribution (Hamby 1994), and third, it does not allow for the effects of input variable interactions (Vose 1996).

In order to address the third problem factorial designs have been used to allow for the interaction of the input variables. However, with a large number of variables to sample the number of different simulation runs of the parameter sensitivity analysis can quickly become large; as it requires, for k parameters at m levels of variation, k^m simulations. In the case of the *L.suturalis* population dynamics model with 13 variables, and varying them by four levels, for example, ± 1 and 2 standard deviations would require, 13^4 or 28,561 simulations to investigate the effect on the model output of all possible combinations of the varied input variables. Fractional factorial designs can reduce the number of simulations required, where some of the *higher order* (greater than two-way), combinations of variables are assumed to be accounted for by *lower order* (two-way), combinations. The number of simulations would be k^{m-c}, where c, the fraction, is determined by the modeller. However as Swartzman & Kaluzny (1987) note, this design gives up the ability of testing some higher order combinations.

In an attempt to address the first and second problems and the large number of simulations required in factorial designs a method of conducting a sensitivity and uncertainty analysis has been developed using a random sampling procedure. This method involves varying all the variables simultaneously, as opposed to the above methods, where each variable was assessed one at a time. Also the distribution of each parameter is randomly sampled to produce, for each model run, a different set of input variable values. This method is a useful sensitivity and uncertainty analysis tool as it assesses the model in a *global* sense (Iman & Helton 1988; Chang *et al.* 1993; Hamby 1994), as the large array of randomly selected input parameters values takes into account both the distributions of the parameters *and* the interrelationships between the parameters (Hamby 1994).

However, as random sampling from a distribution other than uniform, will over-represent parameter values around the mean value it was modified by the use of a stratified sampling (Monte Carlo) regime. This generates samples of the parameter values from the variable distributions divided into *n* (the number of simulations required) intervals of *equal distance*, thereby including samples from the tail of a distribution. With this method *equal weight* is given to all of the intervals of the sampling space; there is as great as chance of drawing a very low probability value as there is of a mean value, and is consequently an unrealistic representation of the sampling space.

McKay *et al*. (1979) and Iman and Conover (1980) developed a method where the samples from the variable distribution were drawn from the sampling distribution divided into *n* intervals of equal probability, thus *weighting* the input variables; samples nearer the mean are more likely to be drawn than those at the tail of the distribution, but this likelihood is based on the probability distribution of the variable in question. Additionally this method also addresses the other problem with the stratified sampling regime, in that there can be repeated samples drawn from the same interval. With this improved method the samples are only drawn once from each probability interval, by a non-replacement selection method. This method is known as Latin Hypercube Sampling (LHS) and ensures that the samples drawn, *map* the actual distribution of the variable and are never repeated. One of the drawbacks of this method was that the random pairing of variable sample values, for each simulation, was likely to result in unwanted (high) correlations between the variables. Iman & Conover (1982) further enhanced the LHS procedure by testing the randomly drawn pairings for inter-correlation and reselecting the samples if they were above a predetermined correlation coefficient, this method was known as restricted pairing Latin Hypercube Sampling.

Since a large array of randomly selected input parameter values and calculated output values allows for a suite of techniques to be employed to test the strength of relationships between the model variables and the output (Hamby

1994), it was decided to employ three different measures of variable sensitivity and compare the results.

The first procedure employed to test the statistical relationship between the input variables from the LHS matrix and the model output was the calculation of the partial rank correlation coefficients for each variable, from the non-parametric ranked data, with the full LHS matrix. This statistical measure of correlation was appropriate as the *L.suturalis* model employs variables that are not necessarily linearly correlated with the output, but exhibit a monotonic relationship (Iman & Conover 1982; Iman & Helton 1988). The analysis allows for the independent effects of each variable to be determined while holding all the other variables at their expected value (Blower *et al.* 1991; Blower & Dowlatabadi 1994).

The second procedure estimates the percentage contribution of each variable to the output's uncertainty using mean deviation sensitivity analysis, as proposed by Vose (1996). The LHS matrix is used as before but this time the simulations are run once with all the variables uncertainty intact, and then with each variable, in turn, set to its mean. The absolute mean deviation is calculated for each simulation. Then the reduction in the outputs uncertainty from the full model is calculated where the uncertainty of a variable is removed.

The third procedure employs the cumulative percentile sensitivity analysis proposed by Vose (1996) to illustrate the effect of the individual input variables on the model output uncertainty. The LHS matrix is used as before, but this time the input variables are all set to their mean and each variable in turn is varied by a set number of percentile values to reflect the effect on the output of a range of individual input variable values.

The uncertainty (prediction imprecision), of the model that was due to the input variable estimation uncertainty was investigated by inspection of the output

summary statistics and the cumulative frequency distribution of the model output (Blower & Dowlatabadi 1994).

The final consideration to be addressed when conducting a Latin Hypercube Sampling sensitivity and uncertainty analysis is the number of simulations required, enabling robust statistical analyses to be performed. The number of simulations is a trade off between computing runtime and the number of runs. As the LHS design involves sampling without replacement the number of simulations drawn must be greater than $k + 1$, where k is the number of variables. McKay *et al.* (1979) have empirically established that the number of simulations should satisfy the inequality $n > (4/3)\, k$. The number of simulations must also be appropriate for the desired significance level for the partial rank correlation coefficients.

5.2 Methods

5.2.1 Creating the Latin Hypercube Sampling matrix

5.2.1.1 Parameter input distributions

The distributions of the model variables, for input into the Latin Hypercube Sampling (LHS) matrix generation program were as follows (see Table 5-1).

Variable	Mean	s.d.	Min	Max	Dist^{n}
Sex ratio	-	-	0.566	0.631	U
Emergence T°C	-	-	4.0	9.0	U
Egg laying T°C	-	-	10.0	15.0	U
Egg mortality	0.9789	0.0284	-	-	N
Fecundity	0.0	1.0	-	-	N
Larval mortality	0.9852	0.0147	-	-	N
Pupal mortality	0.9670	0.0250	-	-	N
New gen^{n} adult mortality	0.9965	0.0044	-	-	N
Breeding mortality *	-	-	0.9672	0.9865	U
Winter adult mortaliy	0.9969	0.0038	-	-	N
Egg to larval add's **	-	-	348.0	377.0	U
Larval to pupal add's **	-	-	225.0	600.0	U
Pupal to adult add's **	-	-	150.0	500.0	U
* - female					
** - accumulated day degrees development period					

Table 5-1: Input distributions with the mean, standard deviations (s.d), minimum and maximum values of the *Lochmaea suturalis* population dynamics model variables for the Latin Hypercube Sampling (LHS) matrix generating computer program, where U=uniform and N=normal distributions

The LHS program was set to select samples from 100 intervals from the normal distribution limited by 2.58 standard deviations. As the values from the upper tail of the normal distribution would have returned values greater than one for the mortality values, those values ≥ 1.00, were assigned values of 0.999999. Thus, the values generated for the LHS mortality values were drawn from an upper-tail truncated normal distribution.

Since the egg generation sub-model was based on a Poisson distribution, and the LHS matrix generating program could only return values from normal or uniform distributions, the fecundity variable was input into the LHS matrix generation program as a value drawn from a normal distribution with zero mean and a standard deviation of one. If the values were ≥ 1.96 they were assigned a value of 1.96, and if they were ≤ 1.00 they were assigned a value of 1.0. These new egg generating function values were used to predict the number of eggs for each simulation by varying the egg function constant coefficient by the converted LHS value multiplied by the standard error of the constant coefficient.

The generated LHS matrix of possible parameter values was inputted to the population dynamics model as the variable values for each run of that 100 simulation run. The stochastic element of the main model was removed, so that it would function in a deterministic manner.

5.2.1.2 Latin Hypercube Sampling: number of simulations

As the inequality, $n > 4/3k$ and the Pearson's correlation coefficient r^2 significance level, at $p < 0.001$ and $n = 100$, was 0.32 for the restricted pairing of the variable inputs, the number of simulations for the LHS matrix was set at 100. The correlation coefficient limit was set for the reselection of variables at, $r^2 = 0.40$.

The LHS generation program therefore produced a matrix of 13 variable input values x 100 simulations with correlation coefficients less than 0.40 for all possible pairings of the randomly drawn variable values. The LHS matrix was input into the model, one simulation at a time as the variable parameters. Three replicate sets of 100 simulations were run from three replicate LHS matrices produced with seeds of 2, 4 and 6.

5.2.2 Uncertainty and sensitivity analysis

The uncertainty of the model output was determined employing the full LHS matrices uncertainty, where all the variables were varied. Summary statistics, frequency distributions and cumulative probability distributions were determined for each of the three LHS replicates.

5.2.2.1 Partial rank correlation coefficient sensitivity analysis

To conduct the partial rank correlation coefficient analysis (PRCC), the model was set for one year with all of the variables uncertainty intact and run for 100 iterations. This was repeated for the three replicate LHS matrices.

The calculation of each variables' PRCC was conducted as follows, using the procedures of Blower & Dowlatabadi (1994) and Zar (1996).

Each of the variables (X_1....X_{13}) and the output variable (Y), were replaced by their rank and standardised (see equation 5-1, page 195).

$$\frac{x_i - \overline{X}_1}{sX_1}, \frac{x_i - \overline{X}_2}{sX_2}, \ldots\ldots\ldots\ldots\ldots, \frac{x_i - \overline{X}_k}{sX_k} \qquad (5\text{-}1)$$

where, x_i is the i^{th} observation, $\overline{X}$ is the mean of variable x and s is the standard deviation of the variables $X_1 \ldots X_k$.

The standardised rank regression coefficient, (b_j) and the coefficient of determination R^2_y, was determined by regressing Y on X_1, X_2,....., X_k

This was followed by regressing X_j on Y, X_{j-1}, X_{j+1},....., X_k. and determining the coefficients of determination, R^2_{xj}.

The partial rank correlation coefficient for each input variable was then calculated (see equation 5-2).

$$\Upsilon_{xj.y} = b_j \left(\frac{1 - R^2_{xj}}{1 - R^2_y} \right)^{1/2} \qquad (5\text{-}2)$$

where, $\Upsilon_{xj.y}$ is the partial rank correlation coefficient, (PRCC) for X_j and Y.

To test the significance of a non-zero value of $\Upsilon_{xj.y}$ the t statistic $t_{xj.y}$ for X_j and Y was calculated using N-2 degrees of freedom (see equation 5-3, page 196).

$$t_{xj.y} = \Upsilon_{xj.y}\sqrt{\frac{N-2}{1-\Upsilon_{xj.y}}} \qquad (5\text{-}3)$$

The significance of the t value was then compared to the critical values from a two-tailed student's t distribution table.

5.2.2.2 Mean deviation sensitivity analysis

To conduct the mean deviation analysis (MDA), the model was run for one year with an LHS table of 100 iterations. An initial simulation was run with all thirteen variables uncertainty intact followed by thirteen simulations with each variable in turn replaced by its mean value. This process was repeated three times using the three differently seeded LHS tables.

For each of the fourteen output results (the total number of adults at the years end) the mean deviation was calculated. This is the average of the absolute differences between the data points and the mean (see equation 5-4). This measure of spread was chosen as it is in the same units as the output and gives equal weighting to all data points.

$$\mathrm{MD} = \frac{\sum_{i=1}^{n}[x_i - \bar{x}]}{n-1} \qquad (5\text{-}4)$$

where, MD is the mean deviation, x is the i^{th} variable, $\bar{x}$ is the mean of the variable x and n is the number of iterations.

Once the mean deviations of the model's output for the fourteen simulations were calculated the absolute reduction in uncertainty from the full model was calculated. The value for each variable was then normalised by dividing each by the sum of the total variable reductions in uncertainty. This gave the estimated percentage contribution of each model input variable to the output uncertainty (see equation 5-5).

$$\%\text{contribution}_{(\text{var})} = \left(\frac{\text{MD}_{(\text{full model})} - \text{MD}_{(\text{var})}}{\text{Total } \Delta\text{MD}_{(\text{all vars})}} \right) \text{x } 100 \qquad (5\text{-}5)$$

where, $\text{MD}_{(\text{full model})}$ is the mean deviation of the model output simulation with all variables varied, $\text{MD}_{(\text{var.})}$ is the change in mean deviation of each variable from the full model and Total $\Delta\text{MD}_{(\text{all vars.})}$ is the sum of the variable mean deviations from the full model.

5.2.3.3 Cumulative percentile sensitivity analysis

To conduct the cumulative percentile analysis (CPA), the model was run for one year with an LHS table of 100 iterations. In turn, each variable was varied by their 1st, 5th, 10th, 20th, 50th, 80th, 90th, 95th and 99th cumulative percentile values derived from the LHS matrix values, whilst the remaining variables were set at their mean. The percentage change from the output value with the variable set at the 50th percentile was calculated, for each variable. This process was repeated three times using the three differently seeded LHS tables.

5.2.3.4 Scatter plots of the LHS sensitivity analysis

Scatter plots were plotted for the range of individual Latin Hypercube Sampling derived variable values against the LHS output values.

5.2.3.5 Combining the sensitivity analyses

The variable sensitivity indices derived from each of the three sensitivity analyses were ranked in order of importance in their contribution to the model output imprecision. The mean and standard error was calculated from each set of three replicates. The overall mean and standard error was calculated for the rankings of the variables from all three analyses.

5.3 Results

In this section the following abbreviations for the main model variables are used: sr = sex ratio, eme = emergence threshold temperature °C, eglt = egg laying temperature °C, em = egg mortality, lm = larval mortality, pm = pupal mortality, wm = winter mortality, nadm = new generation adult mortality, bm = breeding mortality, eld = egg to larval accumulated day degrees development, lpd = larval to pupal accumulated day degrees development, pad = pupal to adult accumulated day degrees development, add's = accumulated day degrees development period.

5.3.1 Uncertainty analysis

The results of the uncertainty analysis summary statistics show that the likely range of outcomes of the model output, its prediction imprecision, at the 95% confidence level were, for each of the three differently seeded LHS simulations, 834721 to 1827763, 684478 to 1354336 and 740758 to 1504006. The minimum value predicted was zero and the maximum 17,708,038 (see Table 5-2, page 200).

By inspection it can be seen that the frequency distributions of the three replicate LHS sensitivity analysis outcomes were skewed to the right; this was confirmed with values of 4.4, 4.1 and 4.4 for the 3rd moment of the mean. The right side skewness was accounted for by the small number of model outcomes in the region of a ten to twenty fold increase in population number (see Figure 5-1 page 201). The mean, most frequent class predicted for all three LHS simulations was 500,000 to 1,000,000, with approximately 40 out of the 100 simulations predicting this figure (see Figure 5-2, page 202).

The cumulative probability distributions of the three LHS model outcomes (see Figure 5-3, page 203) show that approximately 70% of the output values predict population numbers between zero and 1 million, (the start population number), with approximately 25% falling within the range 1 million to five million and the remaining 5 % of the model predictions accounting for the greater population predictions.

Statistic	LHS 2	LHS 4	LHS 6
Minimum	0	0	0
Maximum	17708038	11840437	14838301
Mean	1331242	1019407	1122382
Standard deviation	2502353	1687967	1923301
Skewness	4.4	4.1	4.4
Confidence interval (95%)	± 496521	± 334929	± 381624

Table 5-2: Summary statistics of the uncertainty analysis of the model output with three differently seeded Latin Hypercube Sampling matrices of 100 variable combinations with an initial population of 1.0E06

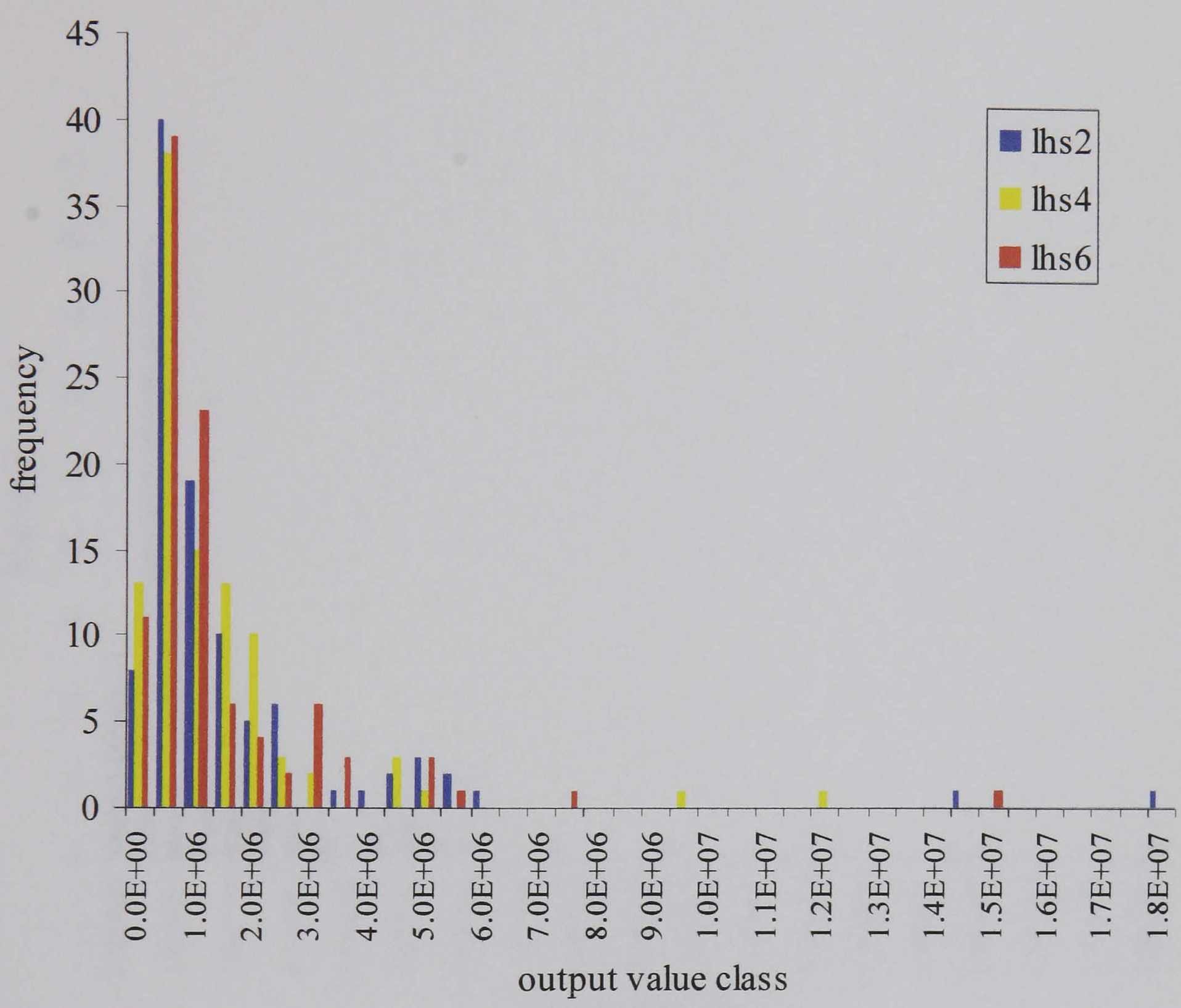


Figure 5-1: Frequency histogram of the model output with the three differently seeded Latin Hypercube Sampling matrices, run for one year with an initial population number of 1.0E +06; classes are 0.0E +00 = 0 to 500,000 and 1.0E +06 = 1 million to 1.5 million etc.

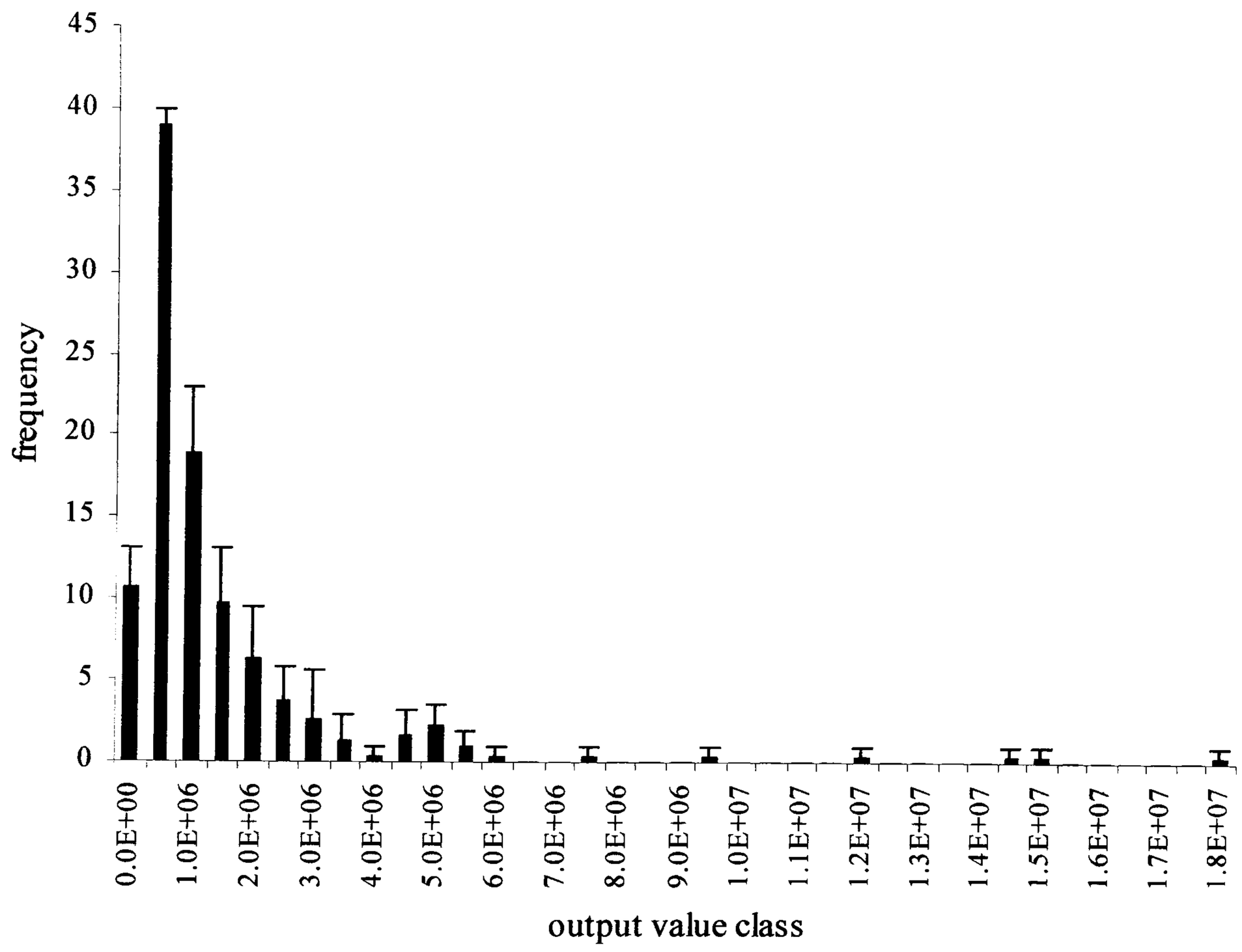


Figure 5-2: Mean and standard deviation of the three differently seeded Latin Hypercube Sampling matrices output frequency histograms; classes are 0.0E +00 = 0 to 500,000 and 1.0E +06 = 1 million to 1.5 million etc.

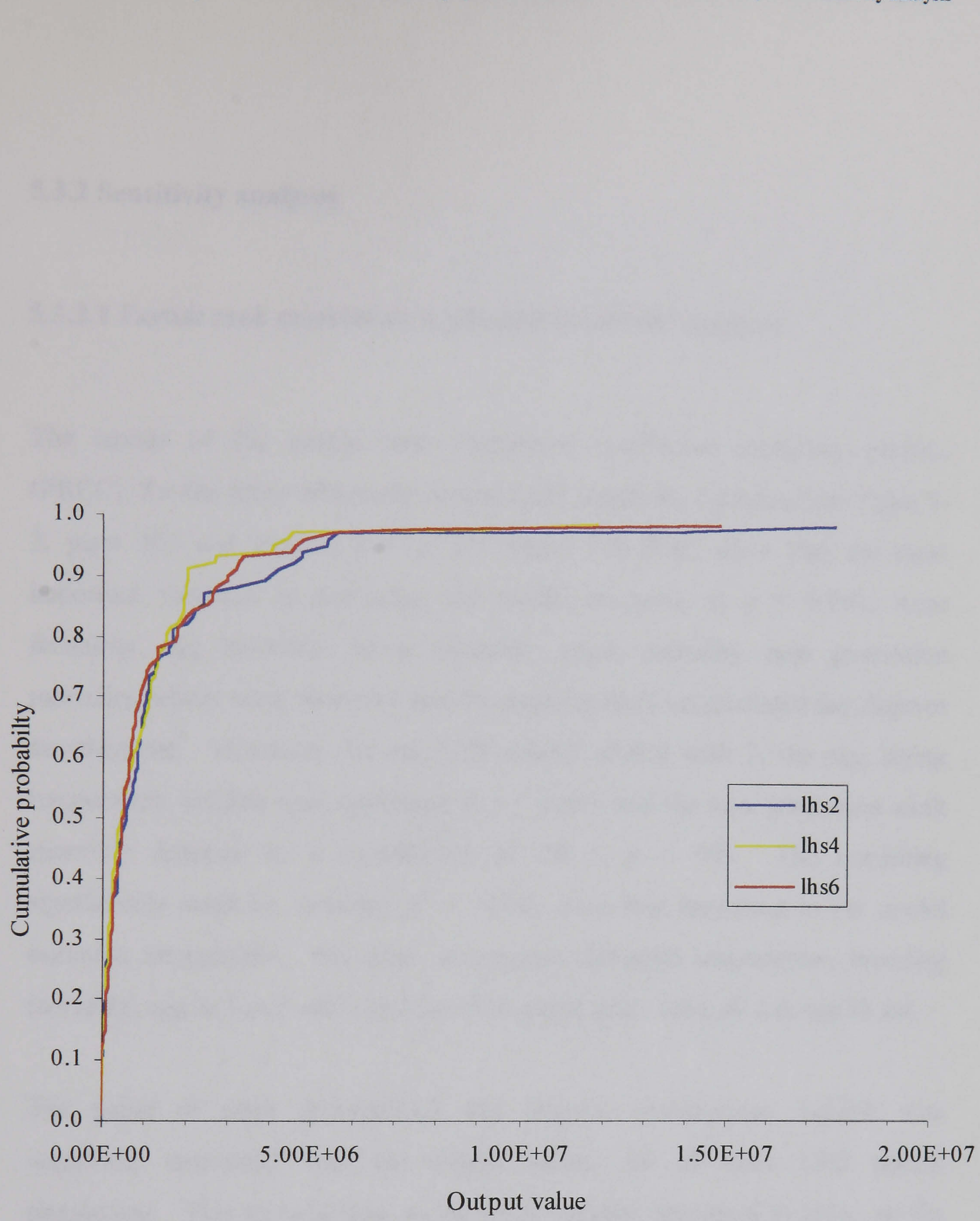


Figure 5-3: The cumulative probabilities of the *L.suturalis* model outputs with the three differently seeded Latin Hypercube Sampling matrices, run for one year with an initial population number of 1.00E +06

5.3.2 Sensitivity analyses

5.3.2.1 Partial rank correlation coefficient sensitivity analysis

The results of the partial rank correlation coefficient sensitivity analysis (PRCC), for the three differently seeded LHS sensitivity analyses (see Table 5-3, page 205 and Figures 5-4 to 5-6, pages 206-208), show that the most important variables in predicting the model outcome, at $p < 0.001$, were fecundity, egg mortality, larval mortality, pupal mortality, new generation mortality, winter adult mortality and the pupal to adult accumulated day degrees development. However, for the LHS matrix seeded with 2, the egg laying temperature variable was significant at $p < 0.001$ and the new generation adult mortality dropped to a significance of $1\% \leq p < 5\%$. The remaining significantly sensitive variables ($r^2 < 0.39$), were less important in the model outcome imprecision. Sex ratio, emergence threshold temperature, breeding mortality, egg to larval add's and larval to pupal add's were all not significant.

The pupal to adult accumulated day degrees development variable was negatively correlated with the output values, for all three LHS matrix simulations. This showed that, as the input variable decreased in value, so the predicted population increased. The remaining variables whose PRCC values were significant all exhibited a positive correlation with the model output, except for the larval to pupal accumulated day degrees development period variable that was negatively correlated at a significance of $1\% \leq p < 5\%$.

Variable	Partial rank correlation coefficient (ϒ)		
	LHS 2	LHS 4	LHS 6
Sex ratio	0.06 (NS)	-0.11 (NS)	-0.04 (NS)
Emergence T°C	0.19 (*)	0.06 (NS)	-0.18 (ns)
Egg laying T°C	0.39 (***)	0.26 (**)	0.19 (*)
Fecundity	0.74 (***)	0.69 (***)	0.63 (***)
Egg mortality	0.52 (***)	0.51 (***)	0.52 (***)
Larval mortality	0.26 (**)	0.39 (***)	0.48 (***)
Pupal mortality	0.56 (***)	0.51 (***)	0.57 (***)
New generation mortality	0.29 (**)	0.40 (***)	0.40 (***)
Breeding mortality *	0.18 (ns)	0.15 (NS)	0.08 (NS)
Winter adult mortality	0.50 (***)	0.43 (***)	0.52 (***)
Egg to larval add's **	-0.11 (NS)	-0.17 (ns)	0.03 (NS)
Larval to pupal add's **	-0.09 (NS)	-0.17 (ns)	-0.19 (*)
Pupal to adult add's **	-0.34 (***)	-0.32 (***)	-0.36 (***)
* - female			
** - accumulated day degrees development			

Table 5-3: Results of the partial rank correlation coefficient sensitivity analysis with the r^2 value and its significance, derived from the three differently seeded Latin Hypercube Sampling matrices input to the *L.suturalis* population dynamics model, run for one year with an initial population number of 1.0E +06

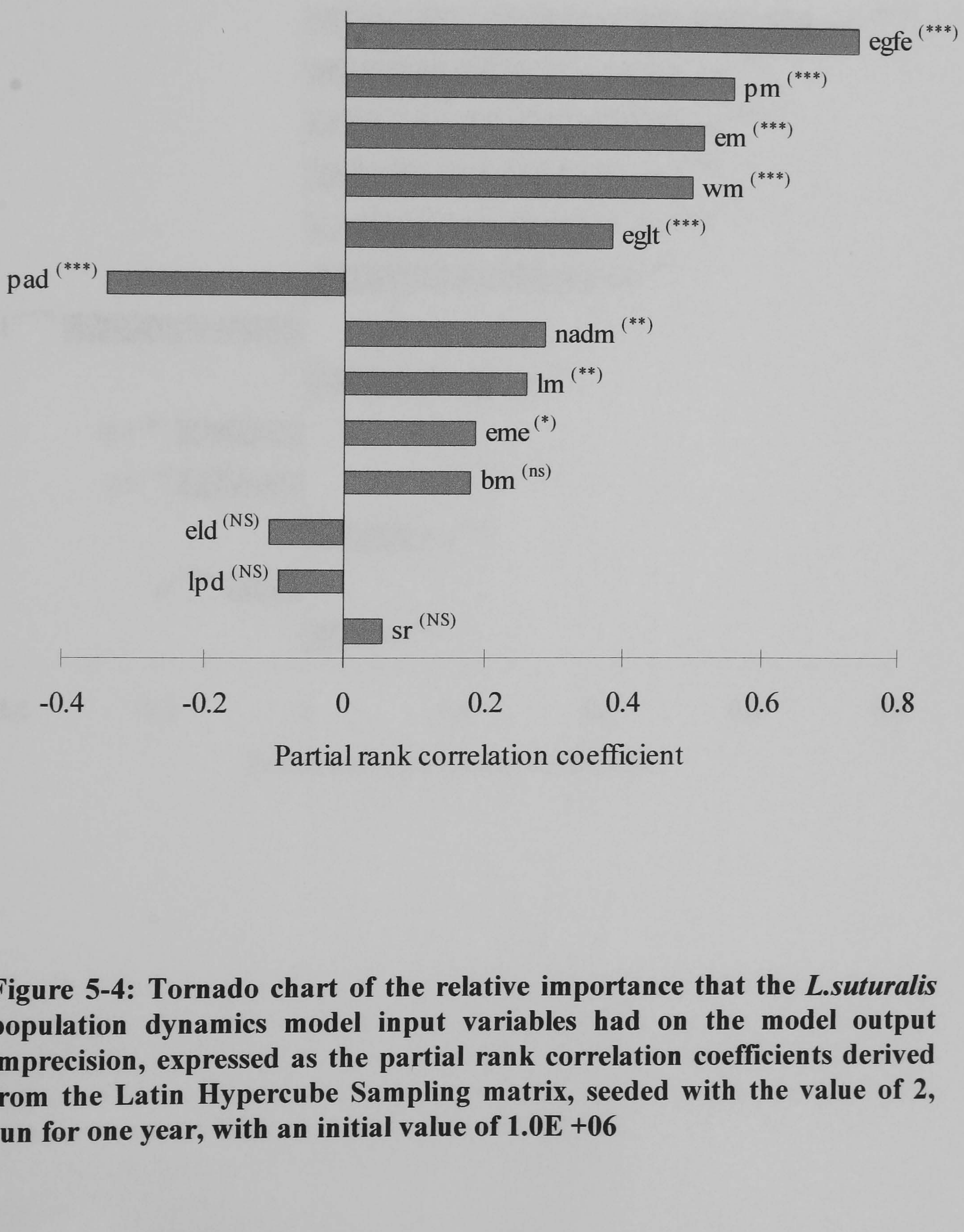


Figure 5-4: Tornado chart of the relative importance that the *L.suturalis* population dynamics model input variables had on the model output imprecision, expressed as the partial rank correlation coefficients derived from the Latin Hypercube Sampling matrix, seeded with the value of 2, run for one year, with an initial value of 1.0E +06

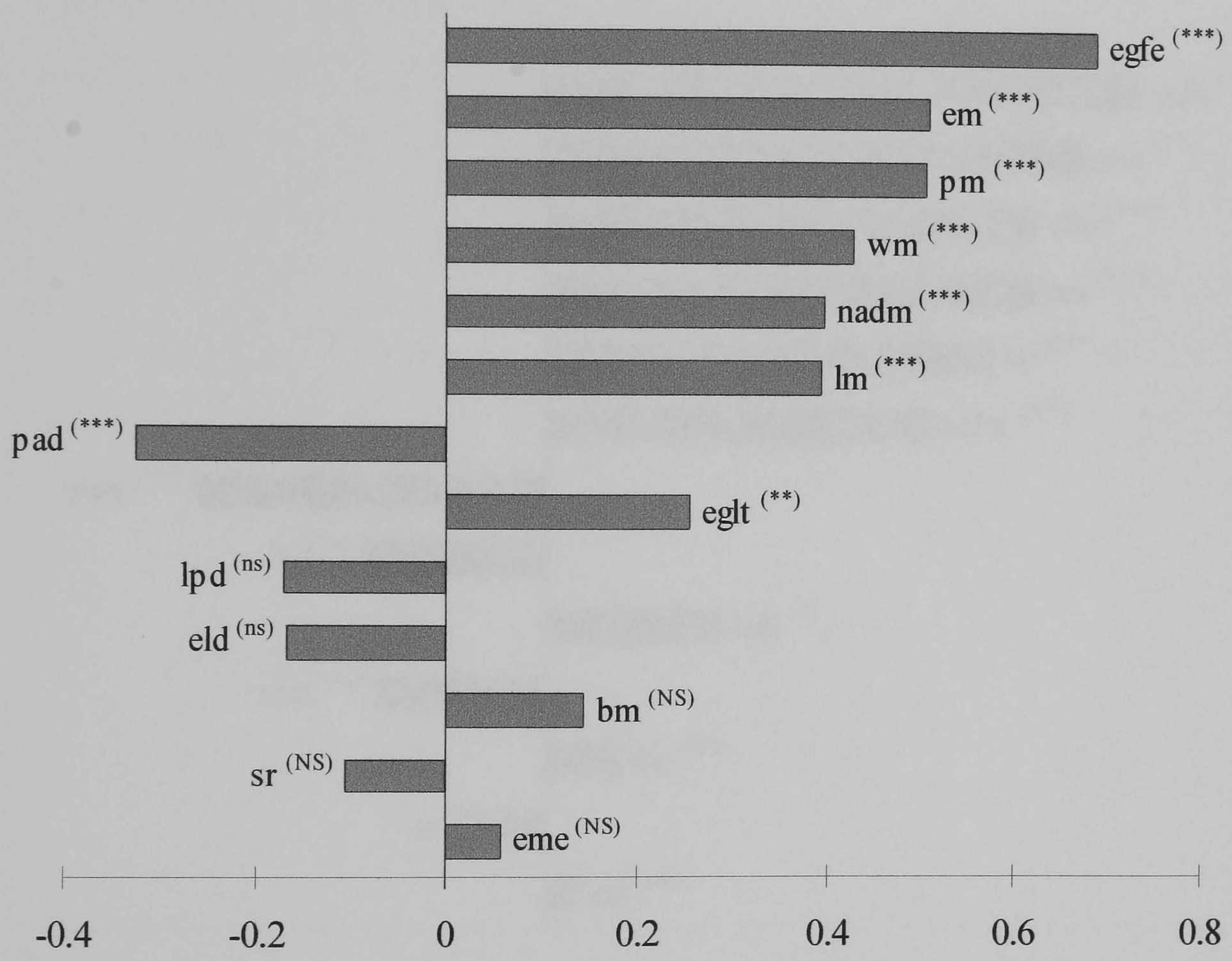


Figure 5-5: Tornado chart of the relative importance that the *L.suturalis* population dynamics model input variables had on the model output imprecision, expressed as the partial rank correlation coefficients derived from the Latin Hypercube Sampling matrix, seeded with the value of 4, run for one year, with an initial value of 1.0E +06

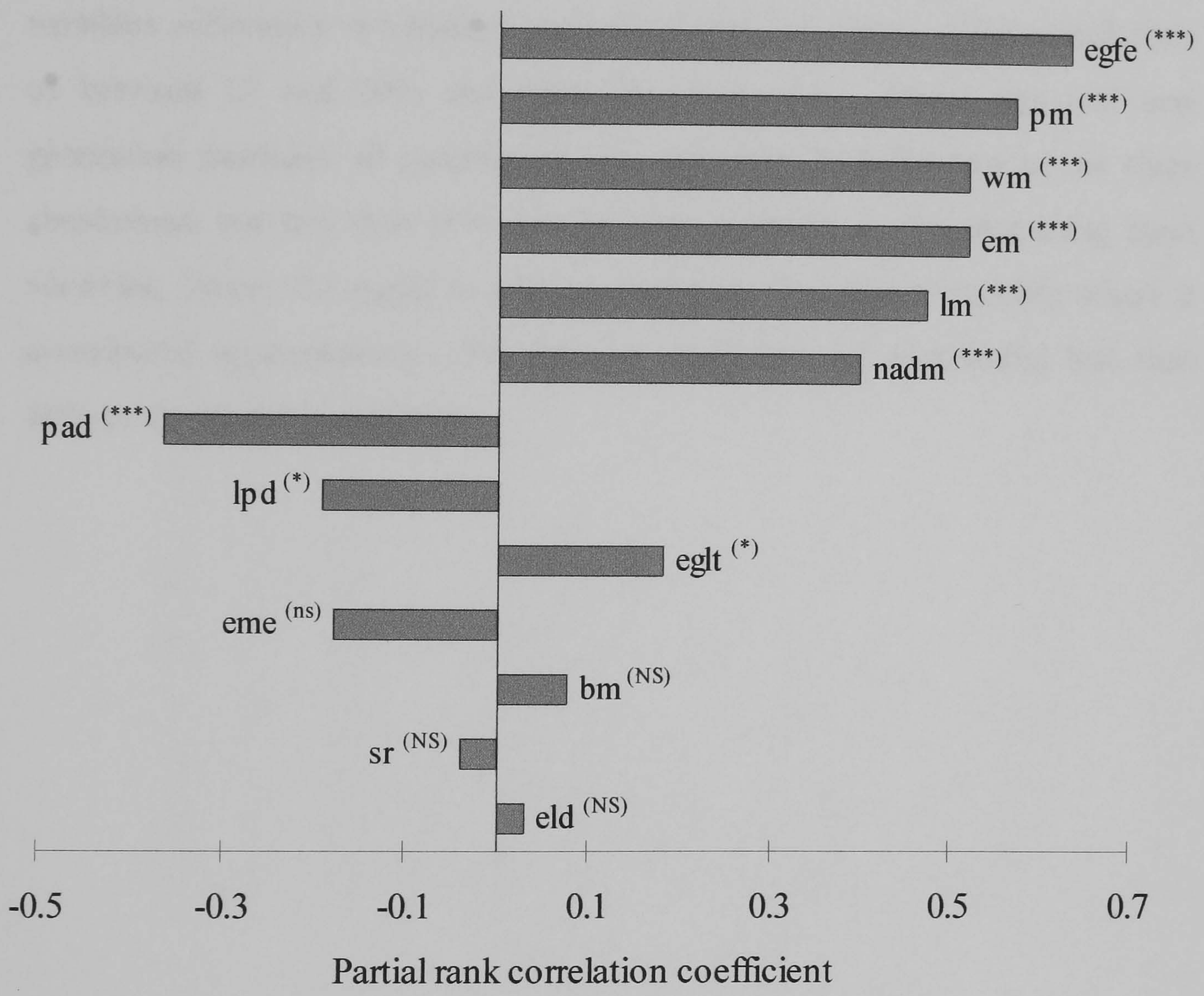


Figure 5-6: Tornado chart of the relative importance that the *L.suturalis* population dynamics model input variables had on the model output imprecision, expressed as the partial rank correlation coefficients derived from the Latin Hypercube Sampling matrix, seeded with the value of 6, run for one year, with an initial value of 1.0E +06

5.3.2.2 Mean deviation sensitivity analysis

The results of the mean deviation sensitivity analysis that was a measure of the relative percentage contribution that each the input variable had on the model output are presented graphically (see Figures 5-7 to 5-9, pages 210 to 212). They showed that for all three LHS matrix input values, the fecundity variable contributed to approximately 35% of the output uncertainty. The remaining variables exhibited a two-banded level of contribution; those with a contribution of between 10 and 20% and those less than 10%. Pupal, egg and new generation mortality all contributed approximately 20% for two of the three simulations, but less than 10% for the other simulation. The remaining input variables, except the pupal to adult accumulated day degree variable where it contributed approximately 15% for one simulation, all contributed less than 10% to the model imprecision.

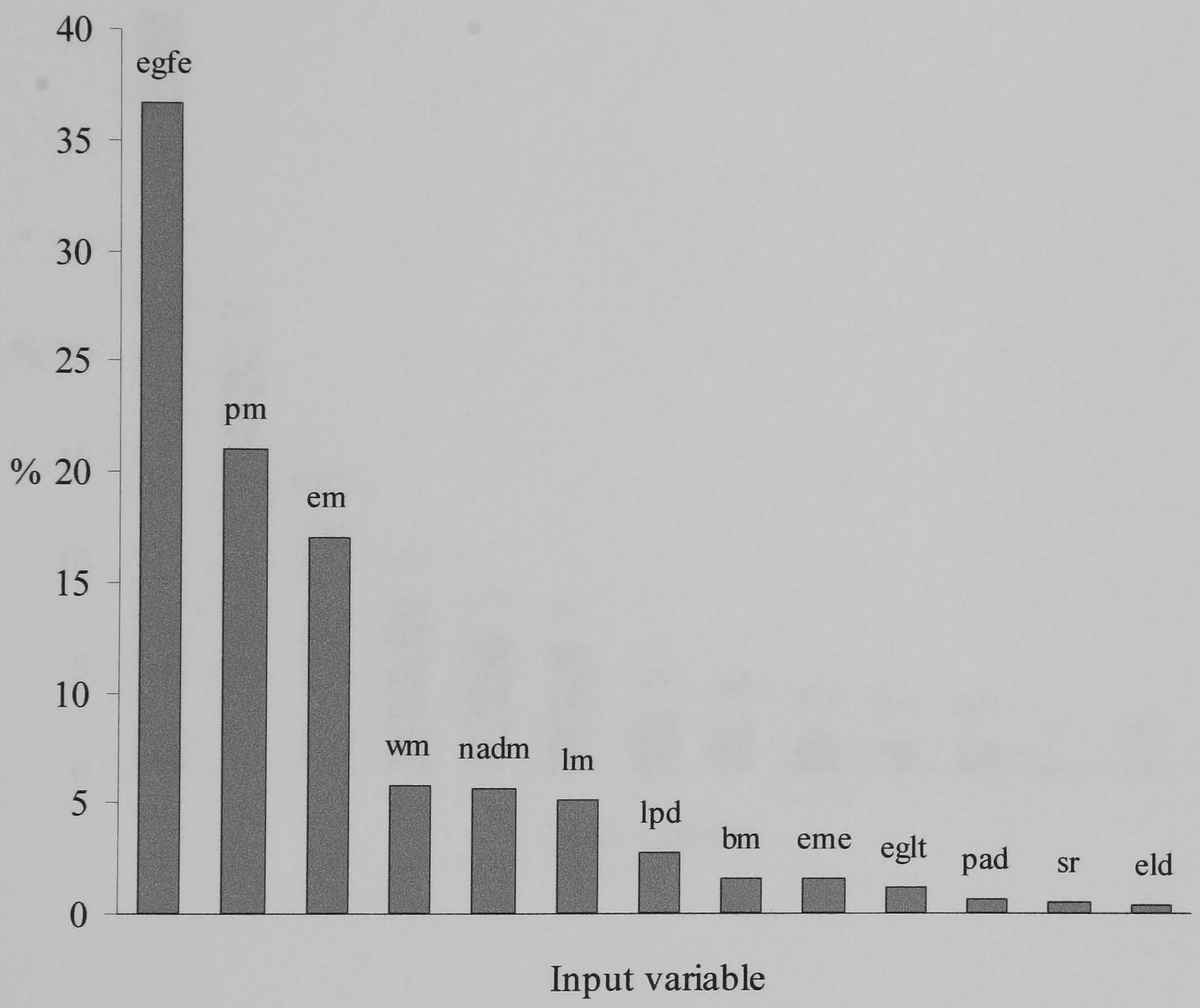


Figure 5-7: Bar chart showing the percentage contribution that each *L.suturalis* population dynamics model variable had on the model outcome, as derived by the mean deviation analysis, using the Latin Hypercube Sampling matrix with a seed of 2, run for one year with an initial population of 1.00E +06

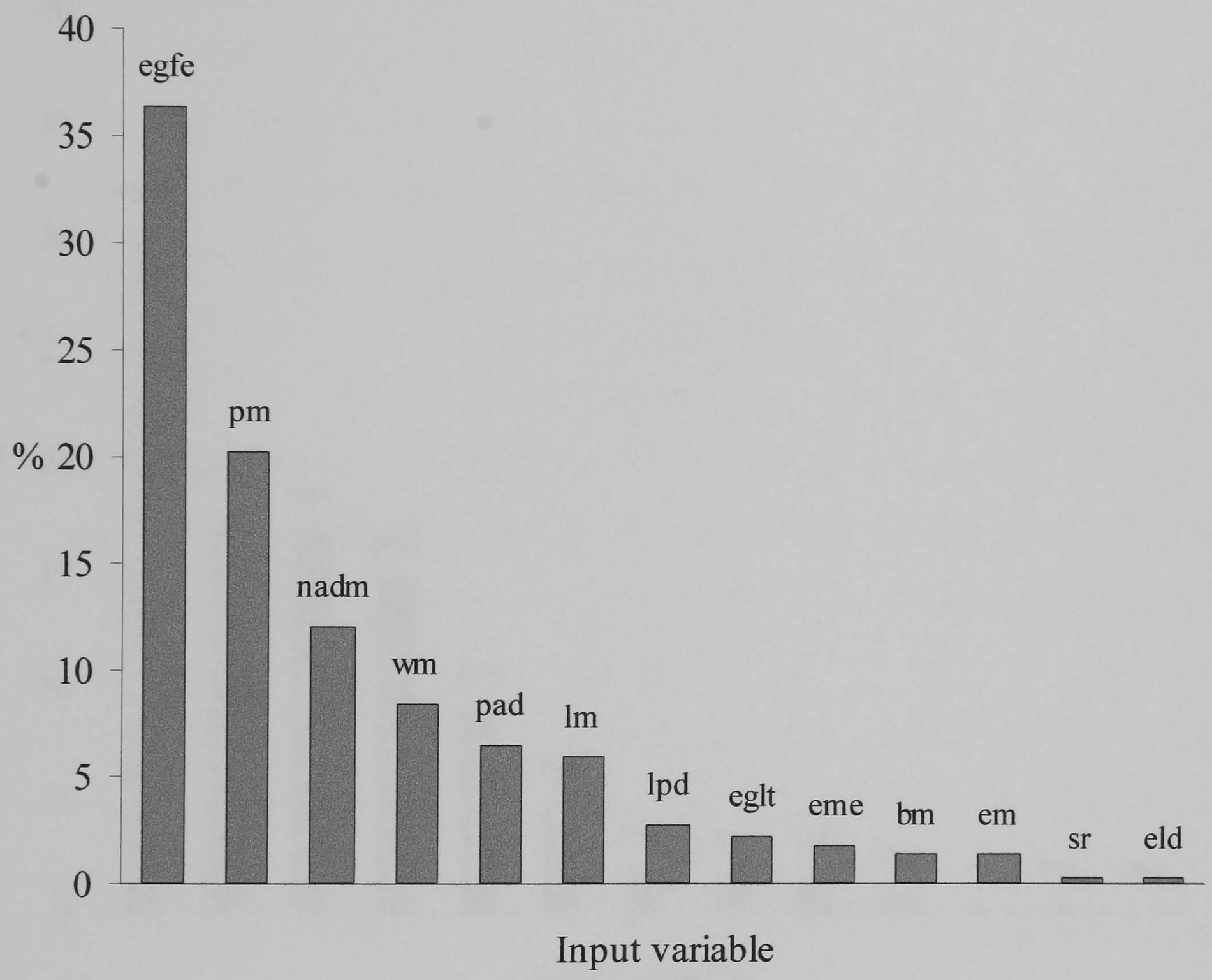


Figure 5-8: Bar chart showing the percentage contribution that each *L.suturalis* population dynamics model variable had on the model outcome, as derived by the mean deviation analysis, using the Latin Hypercube Sampling matrix with a seed of 4, run for one year with an initial population of 1.00E +06

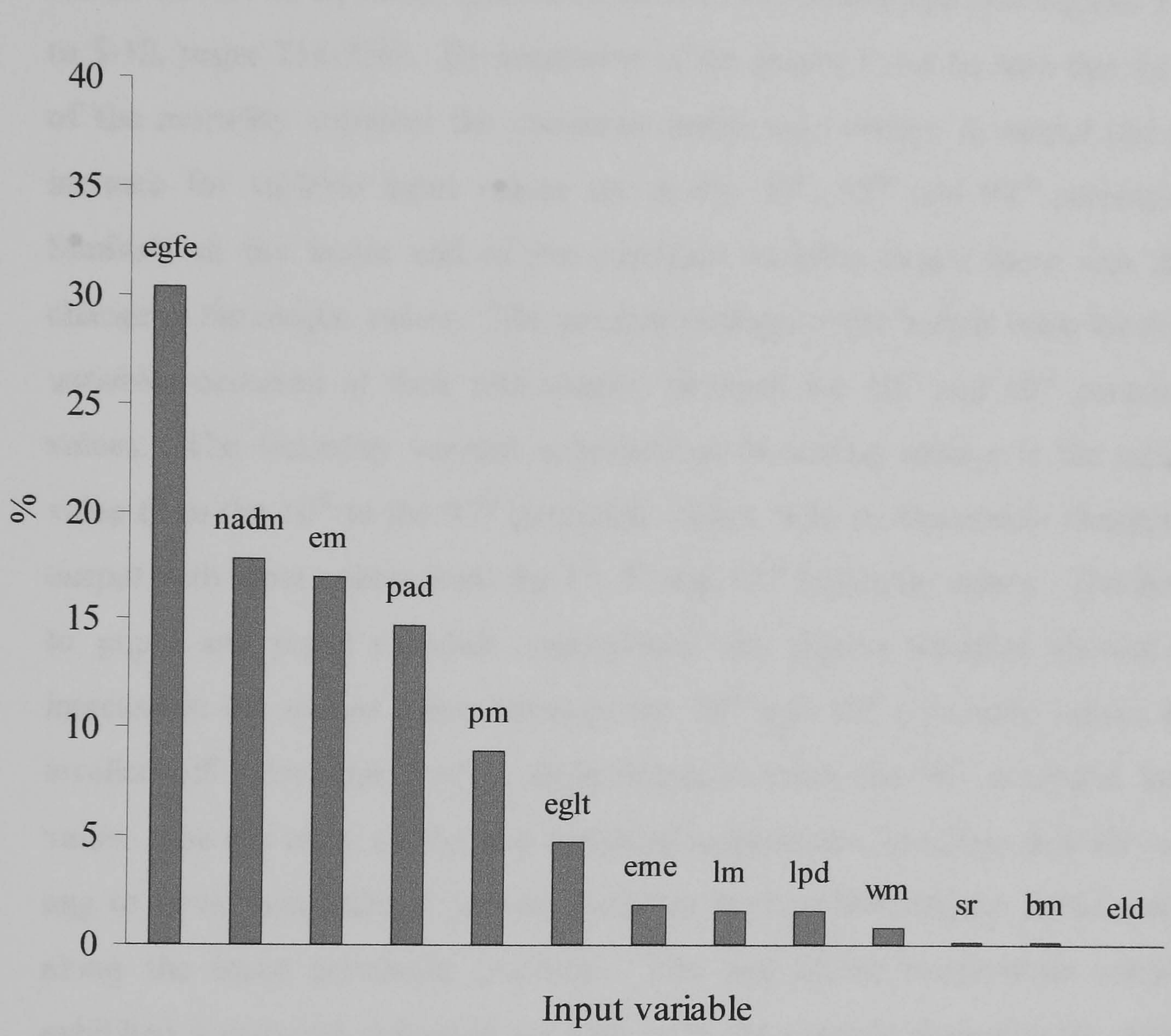


Figure 5-9: Bar chart showing the percentage contribution that each *L.suturalis* population dynamics model variable had on the model outcome, as derived by the mean deviation analysis, using the Latin Hypercube Sampling matrix with a seed of 6, run for one year with an initial population of 1.00E + 06

5.3.2.3 Cumulative percentile sensitivity analysis

The results of the cumulative percentile sensitivity analysis that gave a measure of the effect of the range of the input variable on the output value showed very similar results for all three, differently seeded LHS simulations (see Figures 5-10 to 5-12, pages 214-216). By inspection of the graphs it can be seen that for all of the mortality variables the maximum percentage change in output did not increase for variable input values set at the 90th, 95th and 99th percentiles. Similarly at the lower end of the mortality variable ranges there was little change in the output values. The greatest changes in the output value for these variables occurred at their mid ranges, between the 10th and 90th percentile values. The fecundity variable exhibited an increasing change in the output value from the 10th to the 99th percentile values, with no discernible changes in output with input values from the 1st, 5th and 10th percentile values. The larval to pupal and pupal to adult accumulated day degree variables showed an increase in the output value between the 10th and 50th percentile values, but levelled off below this, with a slight decrease above the 50th percentile input value. The sex ratio, emergence threshold temperature, breeding mortality and egg to larval accumulated degrees variables showed little change in the output along the input percentile gradient. The egg laying temperature variable exhibited a marginal unimodal response with the greatest change in the output value recorded between the 10th and 90th percentiles.

Generally the percentage changes in the output as a result of changing the individual variables by the selected percentiles could be assigned to three groups. The fecundity variable produced the greatest range, - 65 to + 274%, at least twice the highest of the next group, egg, larval, pupal, new generation adult and winter mortality. The remaining variables produced ranges varying between 3 and 73% (see Table 5-4, page 217).

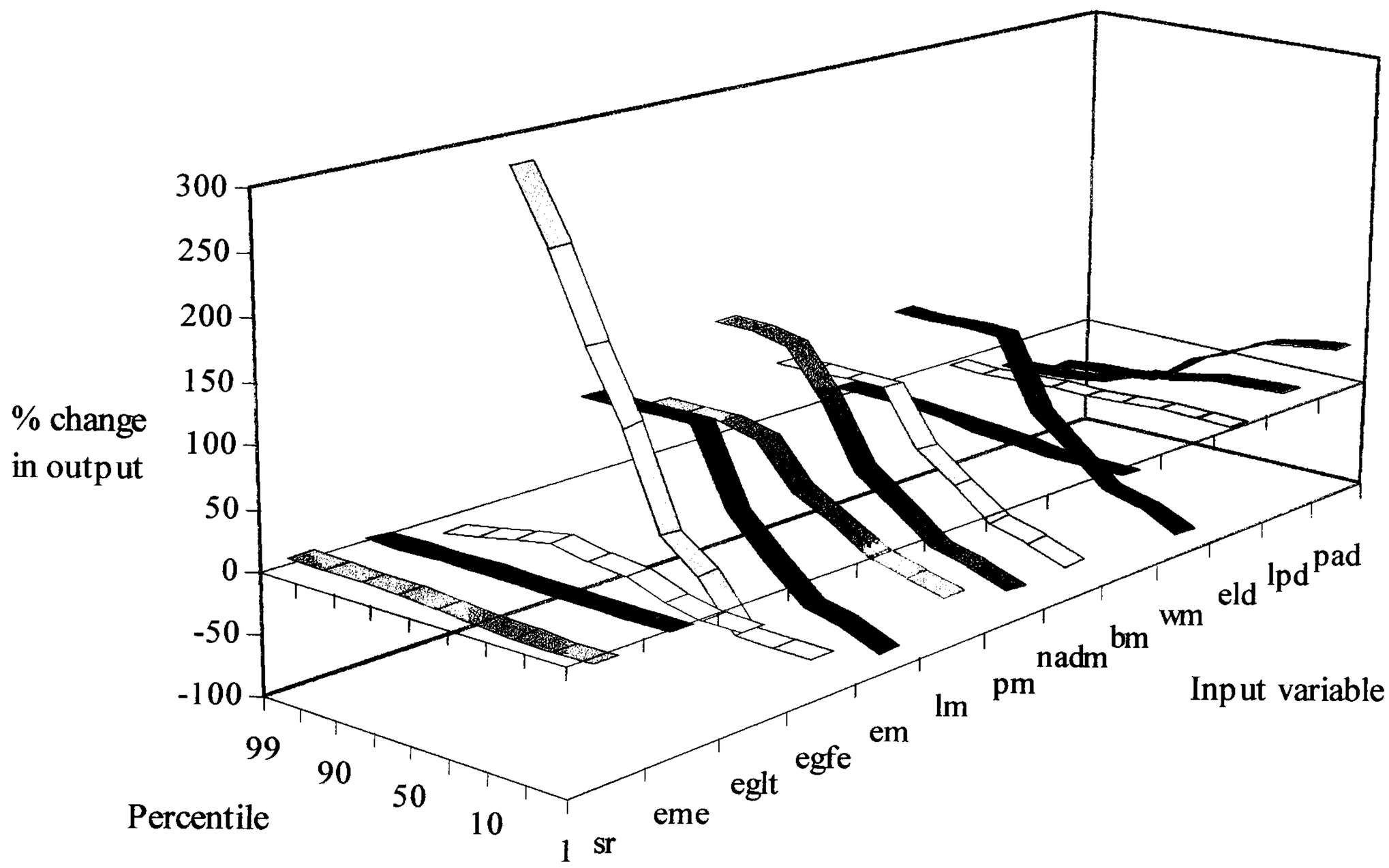


Figure 5-10: Graph showing the percentage change in the output from the 50th percentile of the variable input value, derived from the Latin Hypercube Sampling matrix, seeded with 2, to the 1st, 5th, 10th, 20th, 80th, 90th, 95th and 99th percentile input values for the cumulative percentile sensitivity analysis of the *L.suturalis* population dynamics model

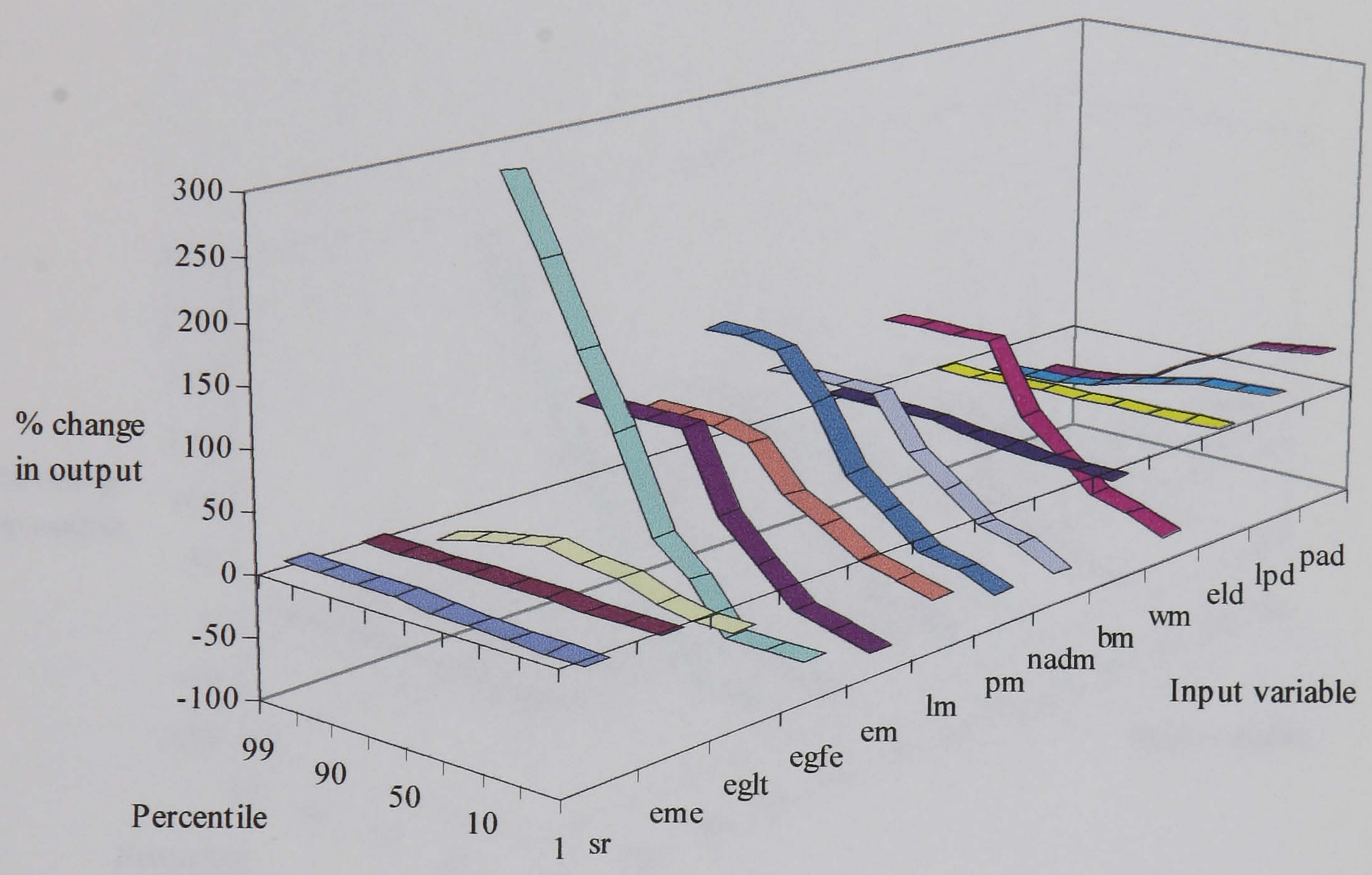


Figure 5-11: Graph showing the percentage change in the output from the 50th percentile of the variable input value, derived from the Latin Hypercube Sampling matrix, seeded with 4, to the 1st, 5th, 10th, 20th, 80th, 90th, 95th and 99th percentile input values for the cumulative percentile sensitivity analysis of the *L.suturalis* population dynamics model

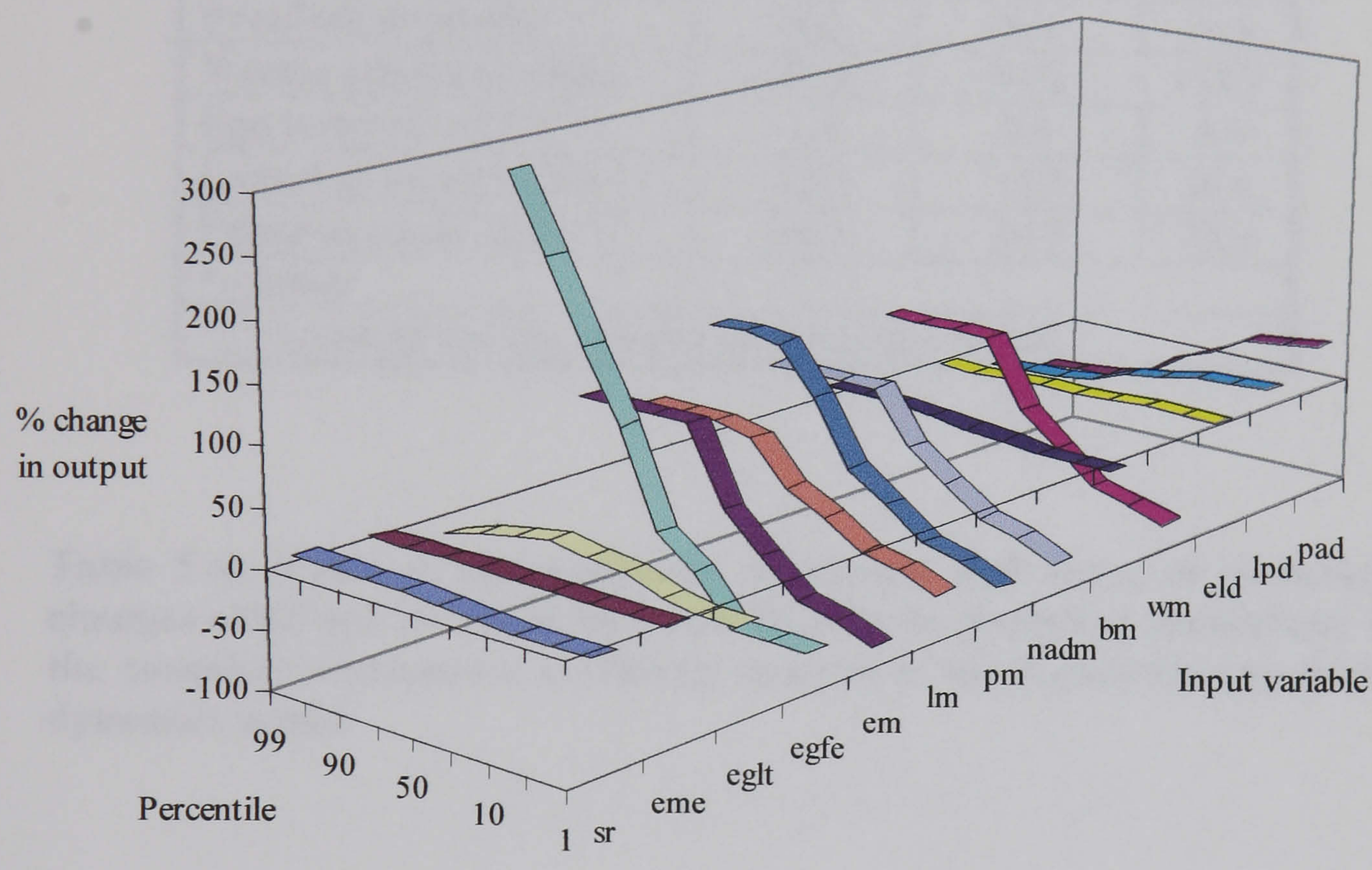


Figure 5-12: Graph showing the percentage change in the output from the 50th percentile of the variable input value, derived from the Latin Hypercube Sampling matrix, seeded with 2, to the 1st, 5th, 10th, 20th, 80th, 90th, 95th and 99th percentile input values for the cumulative percentile sensitivity analysis of the *L.suturalis* population dynamics model

Variable	Minimum	Maximum	Range
Sex ratio	-5.3	5.3	10.5
Emergence T°C	-1.7	1.6	3.2
Egg laying T°C	-21.9	5.0	26.9
Fecundity	-64.9	273.9	338.8
Egg mortality	-81.6	67.2	148.9
Larval mortality	-57.4	44.9	102.3
Pupal mortality	-72.1	99.6	171.7
New generation mortality	-71.4	47.3	118.6
Breeding mortality *	-8.0	8.9	16.9
Winter adult mortality	-77.2	61.8	138.9
Egg to larval add's **	-1.9	2.0	3.9
Larval to pupal add's **	-18.6	16.2	34.8
Pupal to adult add's **	-34.2	39.2	73.4
* - female			
** - accumulated day degrees development period			

Table 5-4: Mean of the minimum, maximum and range of percentage changes exhibited by the three Latin Hypercube Sampling simulations for the cumulative percentile sensitivity analysis of the *L.suturalis* population dynamics model

5.3.2.4 Scatter plots of the LHS sensitivity analysis

By inspection of the individual scatter plots (see Figures 5-13 to 5-17, pages 218-222), of the three combined Latin Hypercube Sampling model simulation outputs and the input variables, it can be seen that all the variable values exhibited a monotonic relationship with the output values. The sex ratio, emergence threshold temperature, breeding mortality, egg to larval and larval to pupal accumulated day degrees variables all showed a reasonably even spread of output values throughout the input variables ranges. In contrast the fecundity, egg and pupal mortality variables showed a strong positive linear trend. The,

larval, new generation adult and winter adult mortality and egg laying temperature variables showed a weaker positive linear trend. The pupal to adult accumulated day degrees variable exhibited a weak negative linear relationship.

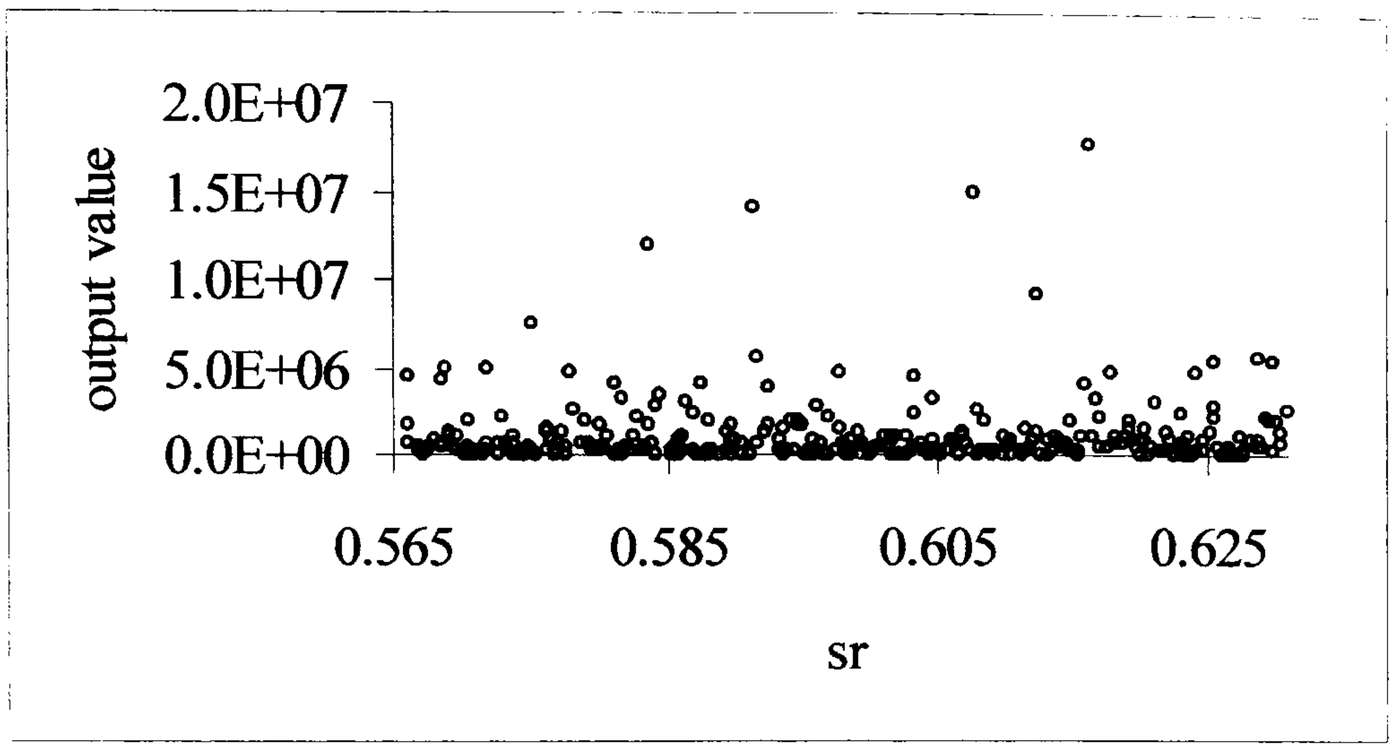


Figure 5-13: Scatter plots of the Latin Hypercube Sampling matrix values for the sex ratio (sr) and emergence threshold temperature (eme) variables against the output from the *L.suturalis* population dynamics model sensitivity analysis, for all three seeded matrices

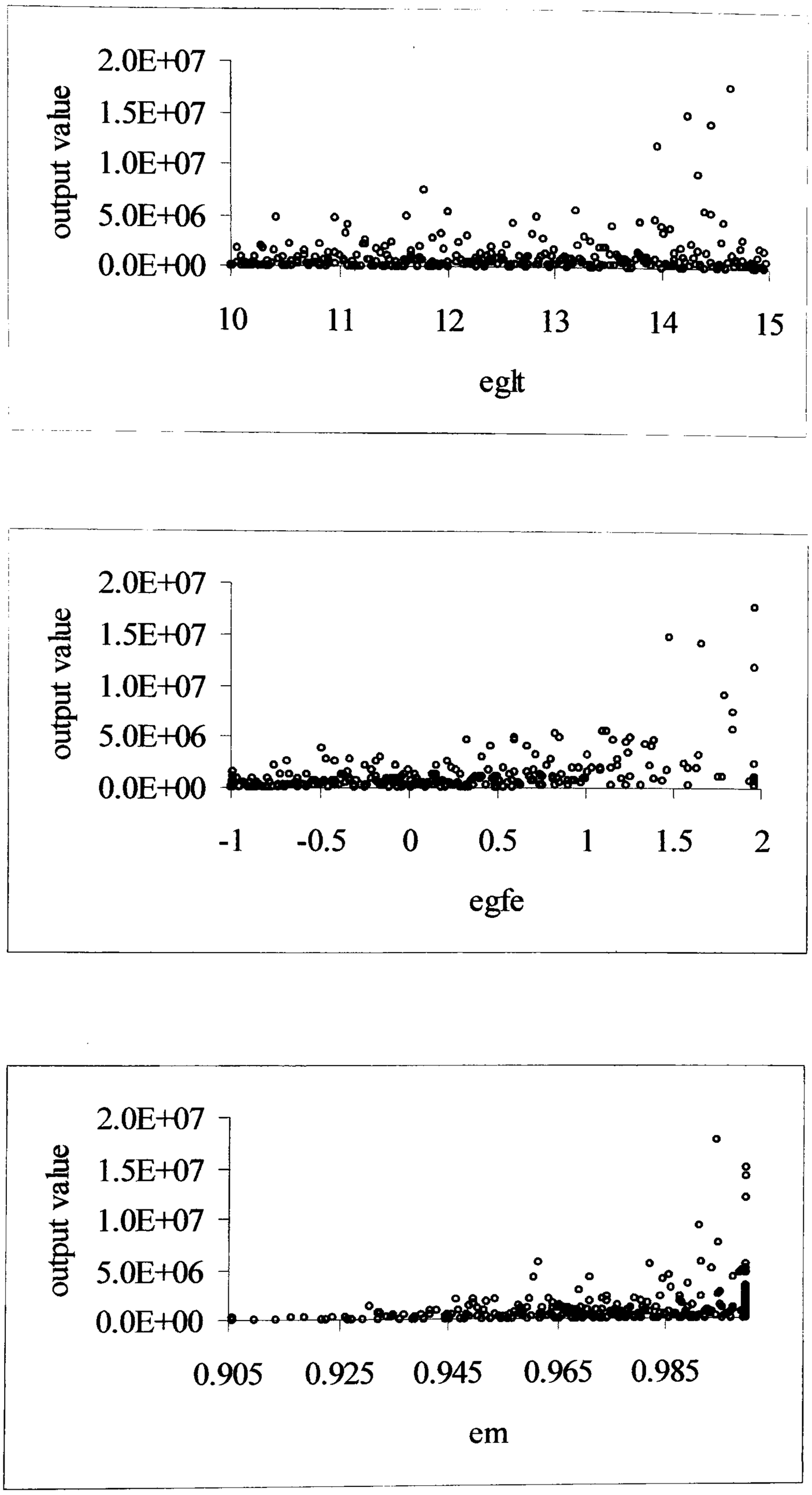
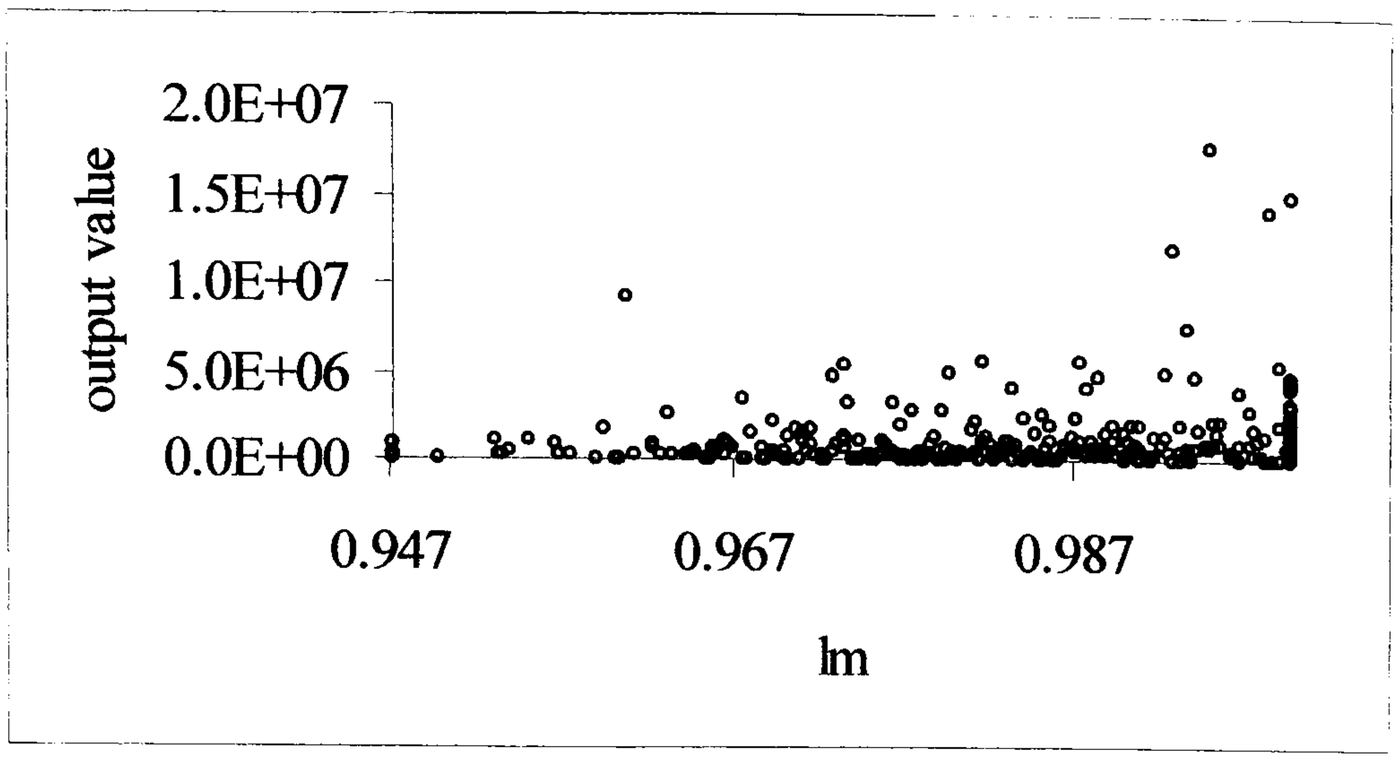
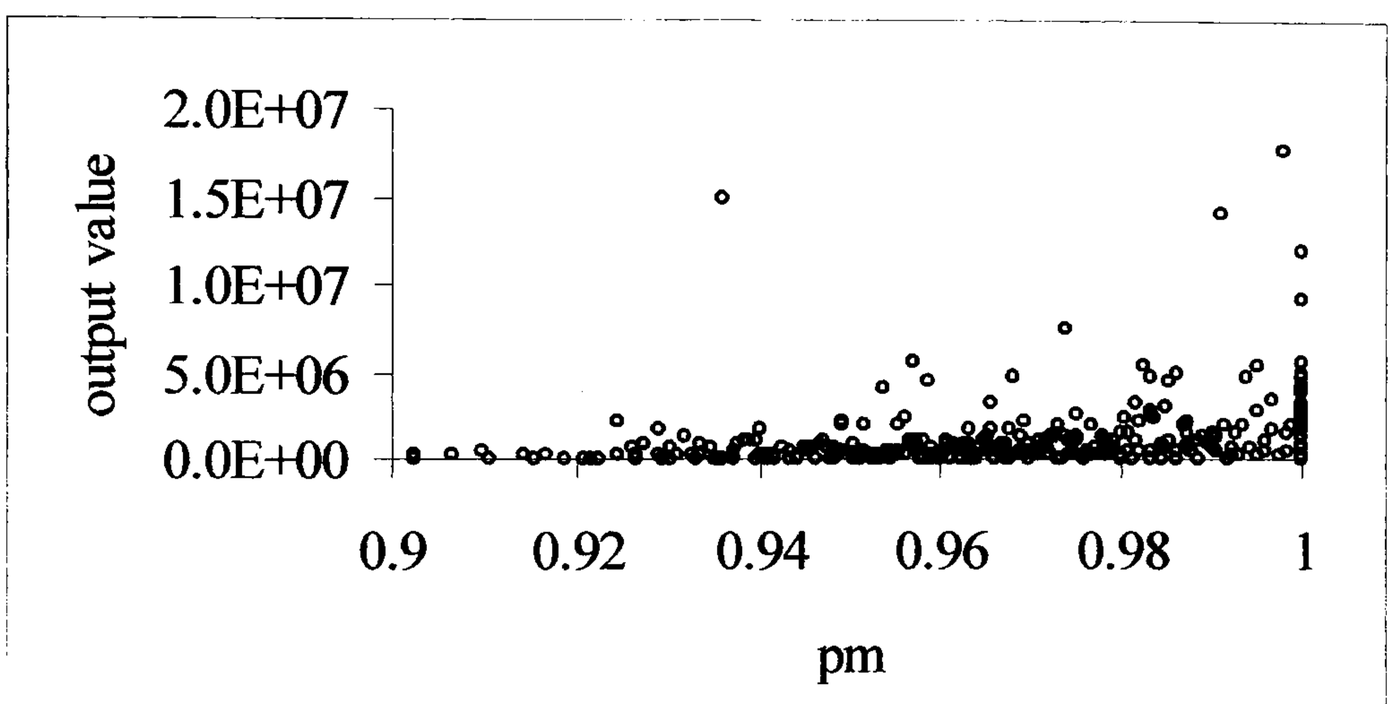


Figure 5-14: Scatter plots of the Latin Hypercube Sampling matrix values for the and egg laying temperature (eglt), fecundity (egfe) and egg mortality (em) variables against the output from the *L.suturalis* population dynamics model sensitivity analysis, for all three seeded matrices





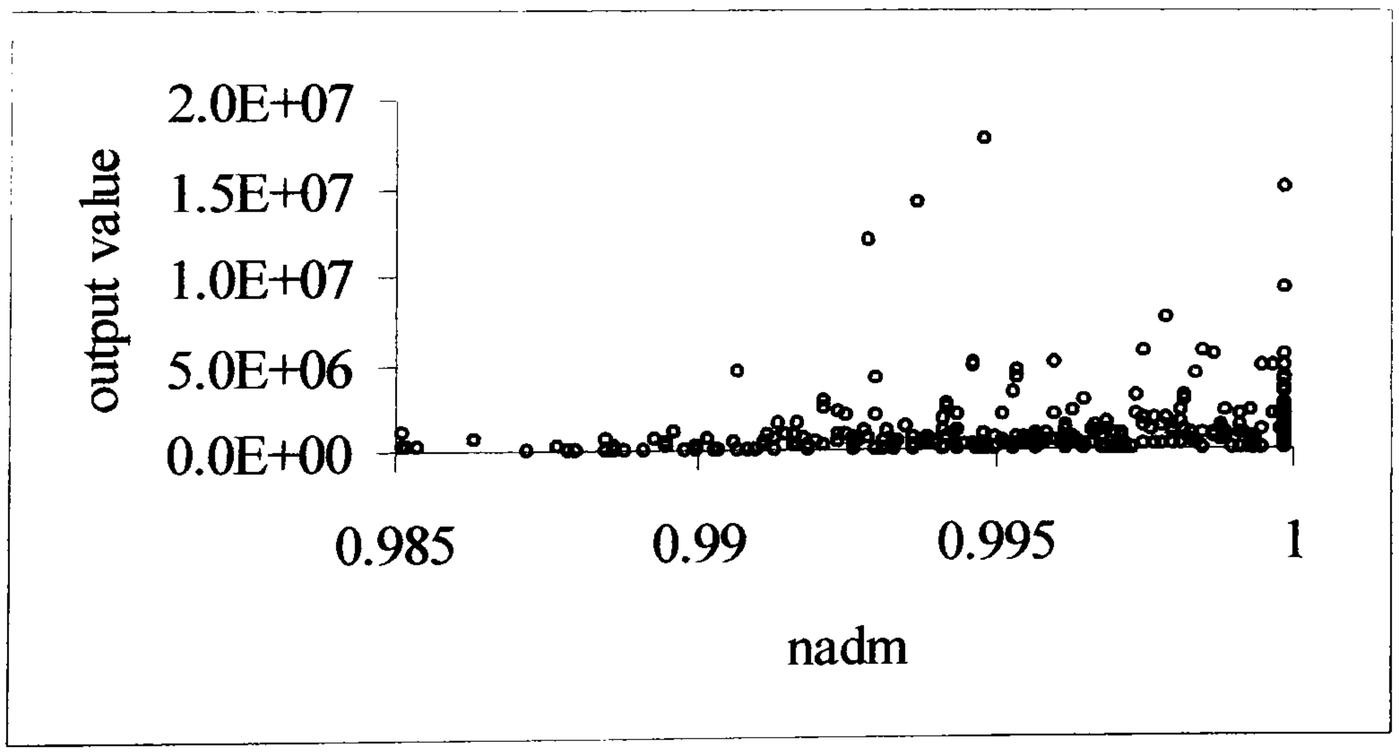
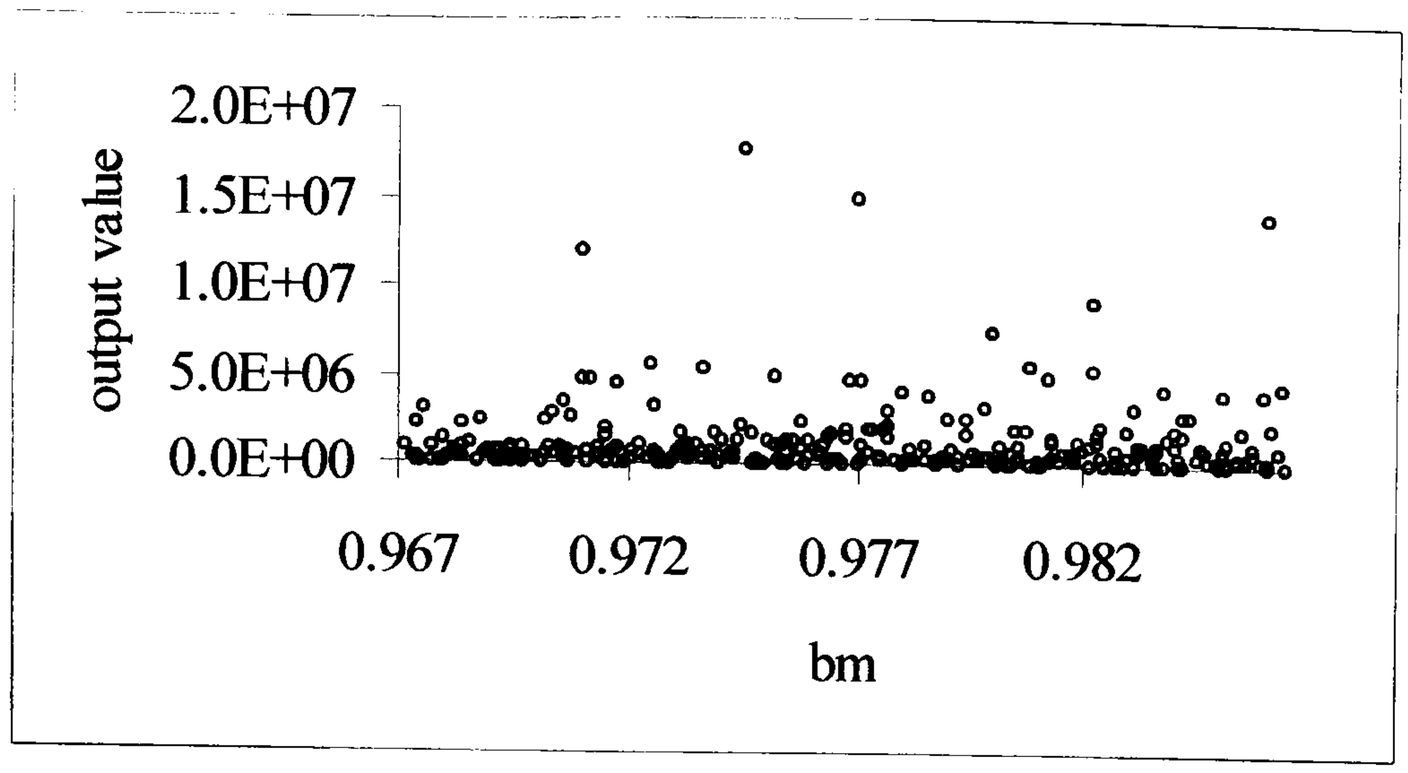


Figure 5-15: Scatter plots of the Latin Hypercube Sampling matrix values for the larval mortality (lm), pupal mortality (pm) and new generation adult mortality (nadm) variables against the output from the *L.suturalis* population dynamics model sensitivity analysis, for all three seeded matrices



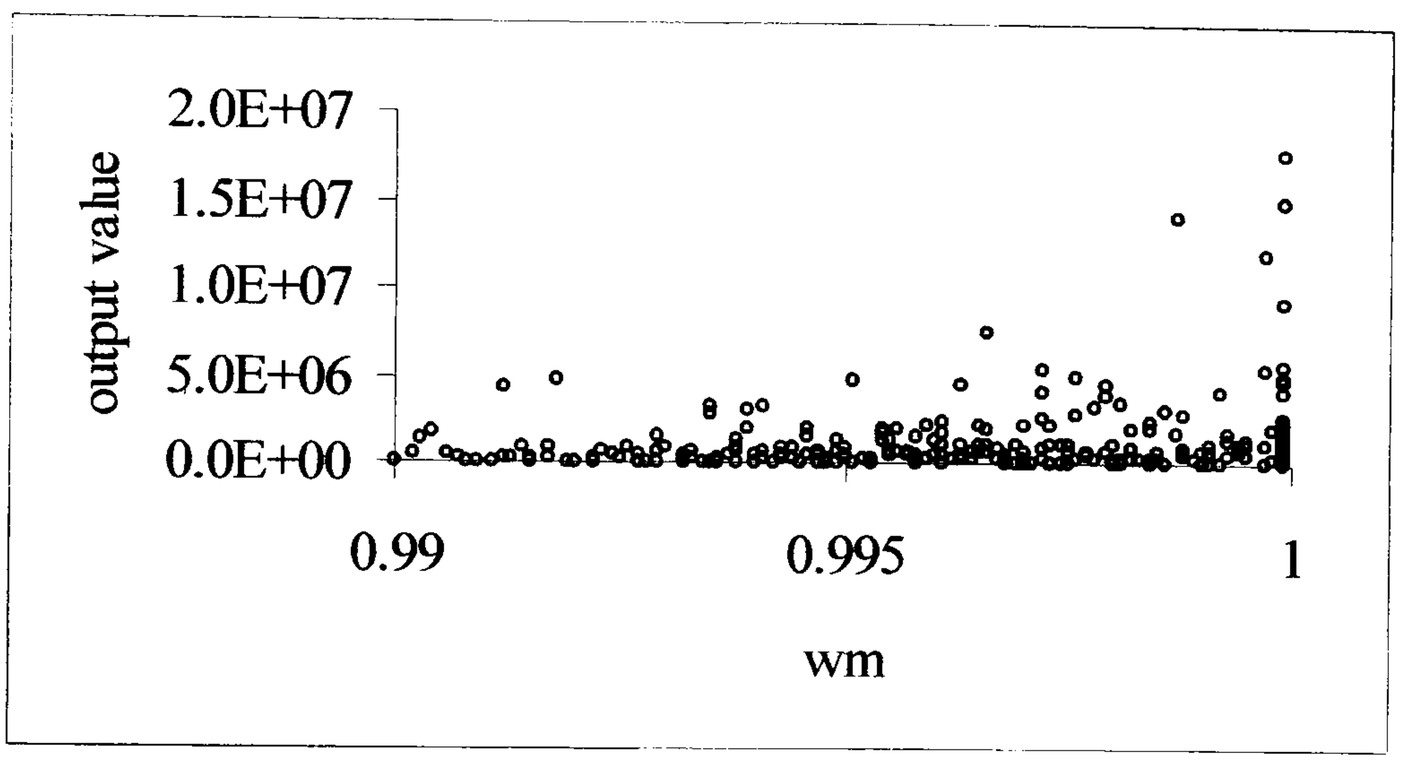


Figure 5-16: Scatter plots of the Latin Hypercube Sampling matrix values for the breeding mortality (bm), winter mortality (wm) and egg to larval accumulated day degrees (eld) variables against the output from the *L.suturalis* population dynamics model sensitivity analysis, for all three seeded matrices

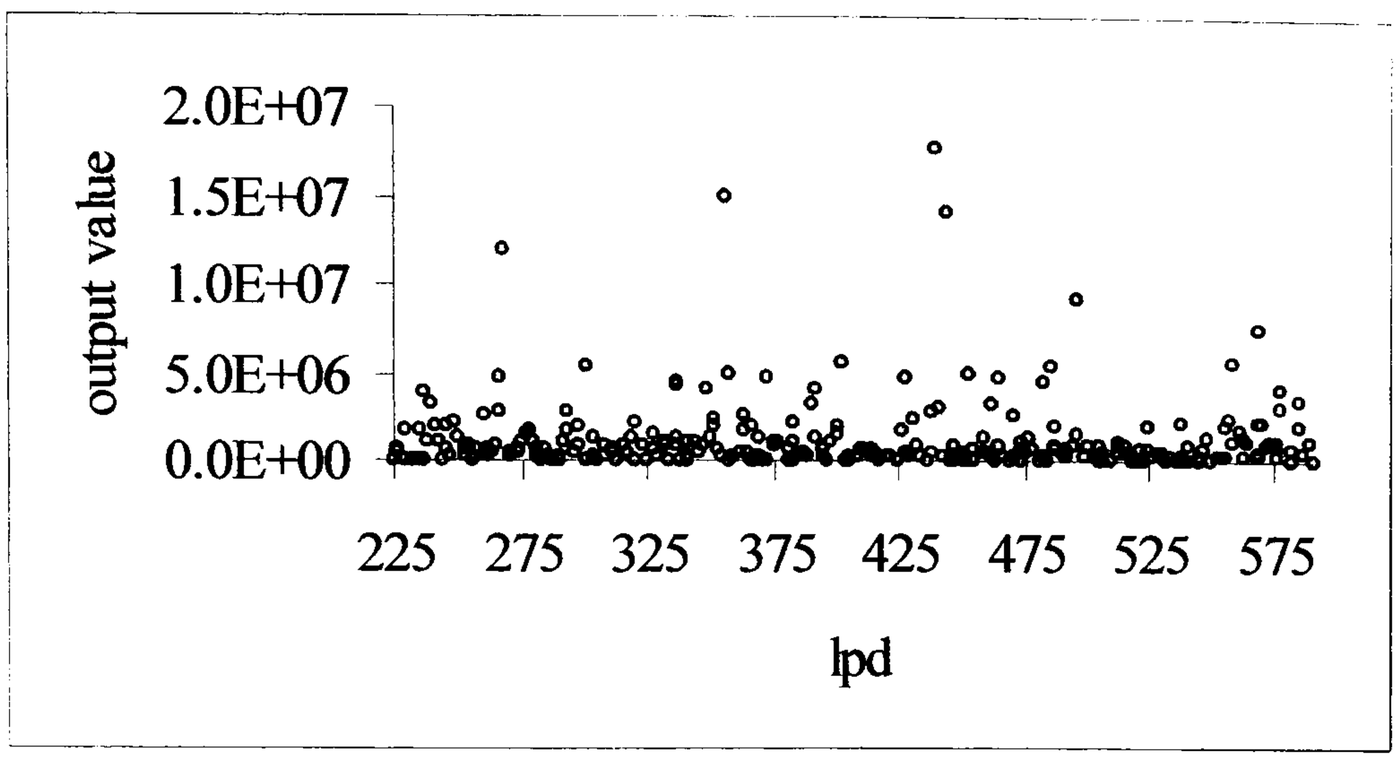


Figure 5-17: Scatter plots of the Latin Hypercube Sampling matrix values for the larval to pupal accumulated day degrees (lpd) and pupal to adult accumulated day degrees (pad) variables against the output from the *L.suturalis* population dynamics model sensitivity analysis; for all three seeded matrices

5.3.2.5 Combining the Latin Hypercube Sampling sensitivity analyses

The results of ranking of the *L.suturalis* input variables in order of importance of their contribution to the imprecision of the output value for each analysis have produced similar results (see Table 5-5, page 224). From the mean of the ranks for each analysis (see Figures 5-18 to 5-20, pages 225-227), it can be seen, by the absence or small standard errors, that the cumulative percentile sensitivity analyses ranked the importance of the variables similarly, except for the egg laying temperature and larval to pupal accumulated day degrees variables. In contrast the mean deviation sensitivity analyses only ranked the fecundity input variable consistently as the most important variable. For all the other variables each mean deviation sensitivity analysis produced a different result. The partial rank correlation coefficient sensitivity analyses found that the fecundity and pupal mortality variables were ranked first and second for all three replications of the analysis. The remaining variables were ranked similarly for the three replication of the analysis, as can be seen by the relatively small standard errors.

The overall mean and standard error of the importance rankings for all three analyses are presented graphically (see Figure 5-21, page 228).

Variable	Analysis								
	PRCC			MDA			CPA		
	2	4	6	2	4	6	2	4	6
Sex ratio	1	2	2	2	2	3	3	3	3
Emergence T°C	5	1	4	5	5	7	1	1	1
Egg laying T°C	9	6	5	4	6	8	5	6	6
Fecundity	13	13	13	13	13	13	13	13	13
Egg mortality	11	12	10	11	3	11	11	11	11
Larval mortality	6	8	9	8	8	6	8	8	8
Pupal mortality	12	11	12	12	12	9	12	12	12
New generation mortality	7	9	8	9	11	12	9	9	9
Breeding mortality *	4	3	3	6	4	2	4	4	4
Winter adult mortality	10	10	11	10	10	4	10	10	10
Egg to larval add's **	3	4	1	1	1	1	2	2	2
Larval to pupal add's **	2	5	6	7	7	5	6	5	5
Pupal to adult add's **	8	7	7	3	9	10	7	7	7
* - females									
** - add's = accumulated day degrees development									

Table 5-5: The rank of the importance of each input variable in contributing to the prediction imprecision of the output of the *L.suturalis* population dynamics model for each of the three different sensitivity analyses used to conduct the Latin Hypercube Sampling sensitivity analysis; 13=most sensitive, 1=least sensitive

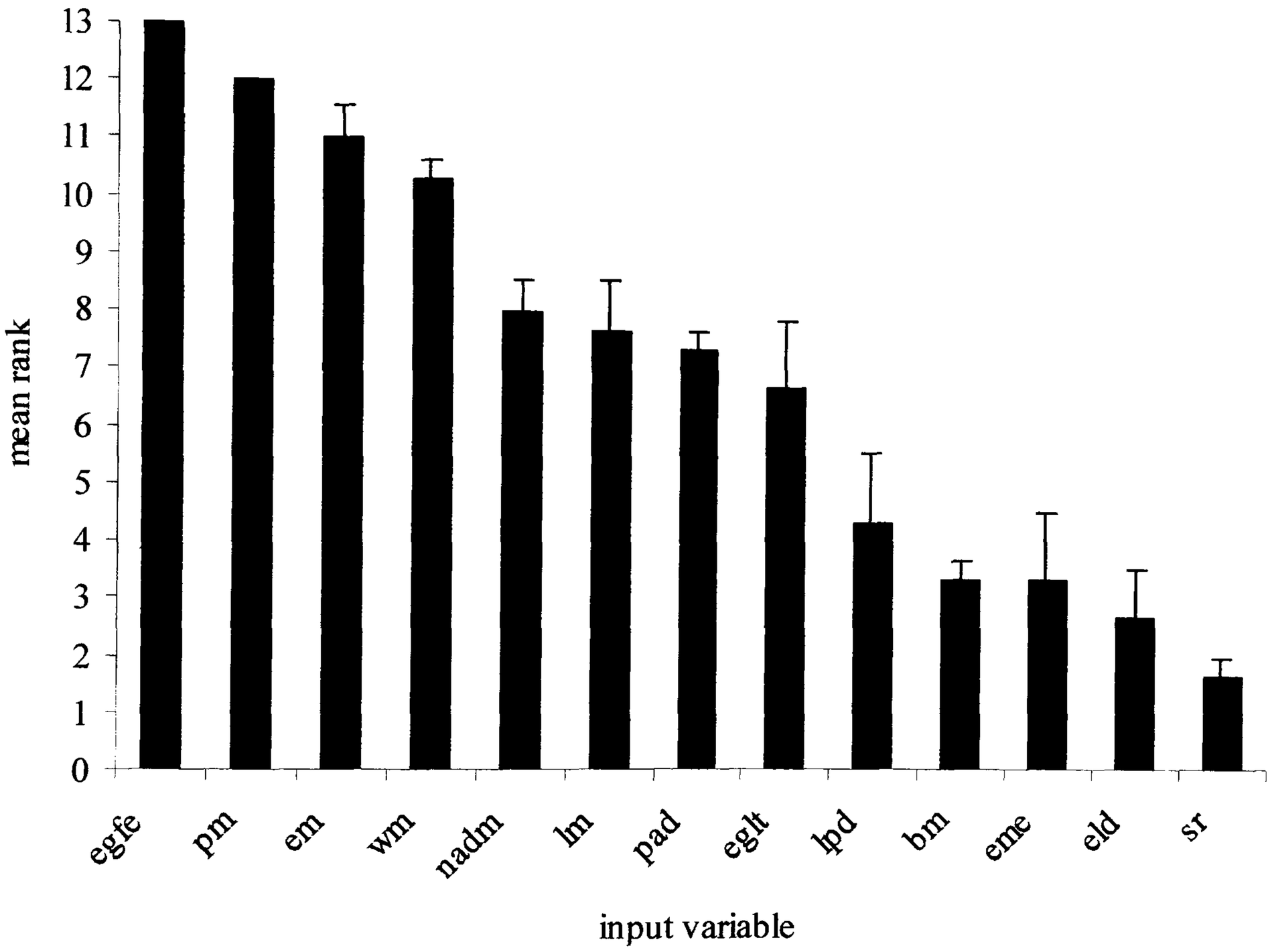


Figure 5-18: Mean and standard error (*n*=3), of the ranks of the input variables of the *L.suturalis* population dynamics model Latin Hypercube Sampling partial rank correlation coefficient sensitivity analysis

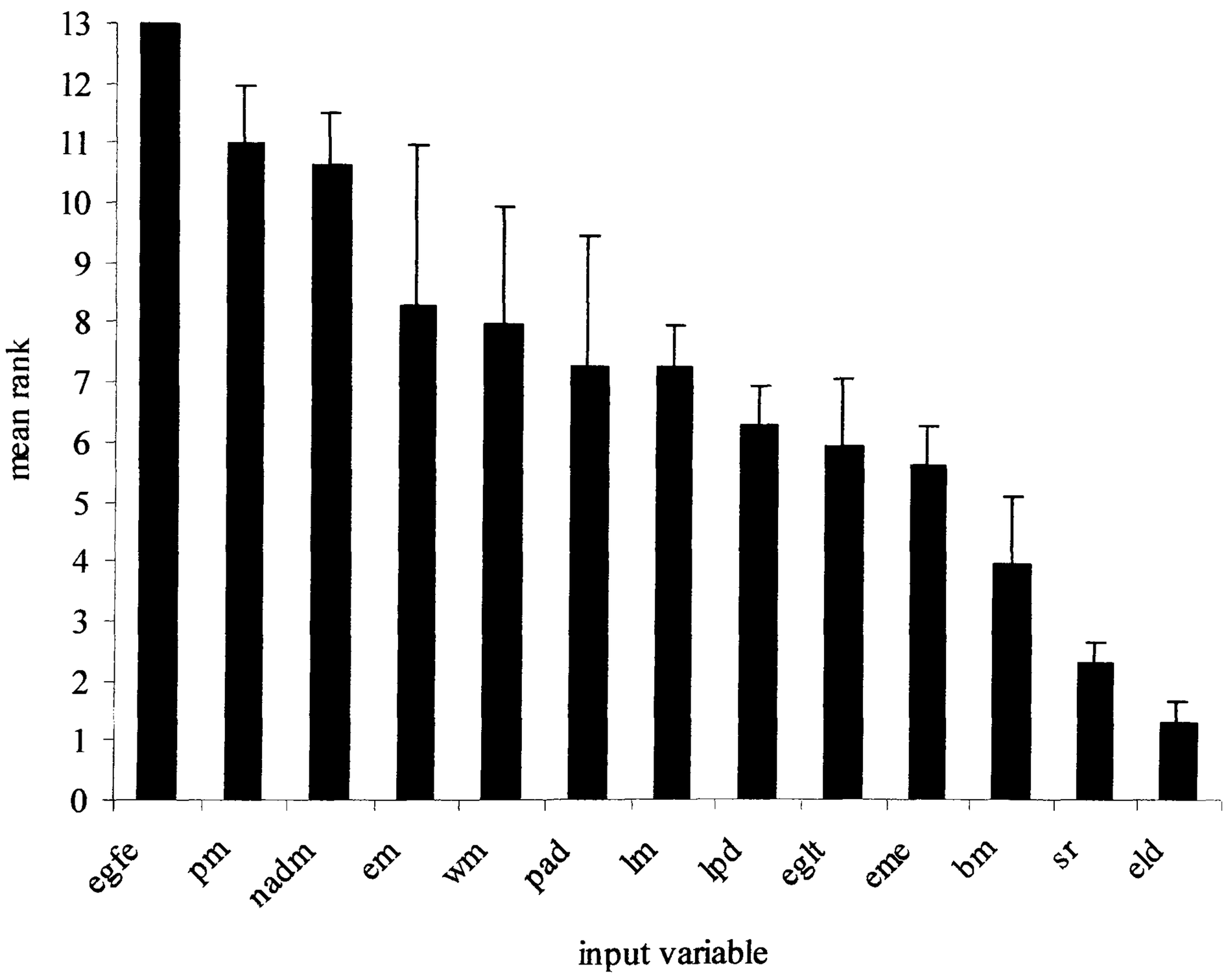


Figure 5-19: Mean and standard error (*n*=3), of the ranks of the input variables of the *L.suturalis* population dynamics model Latin Hypercube Sampling mean deviation sensitivity analysis

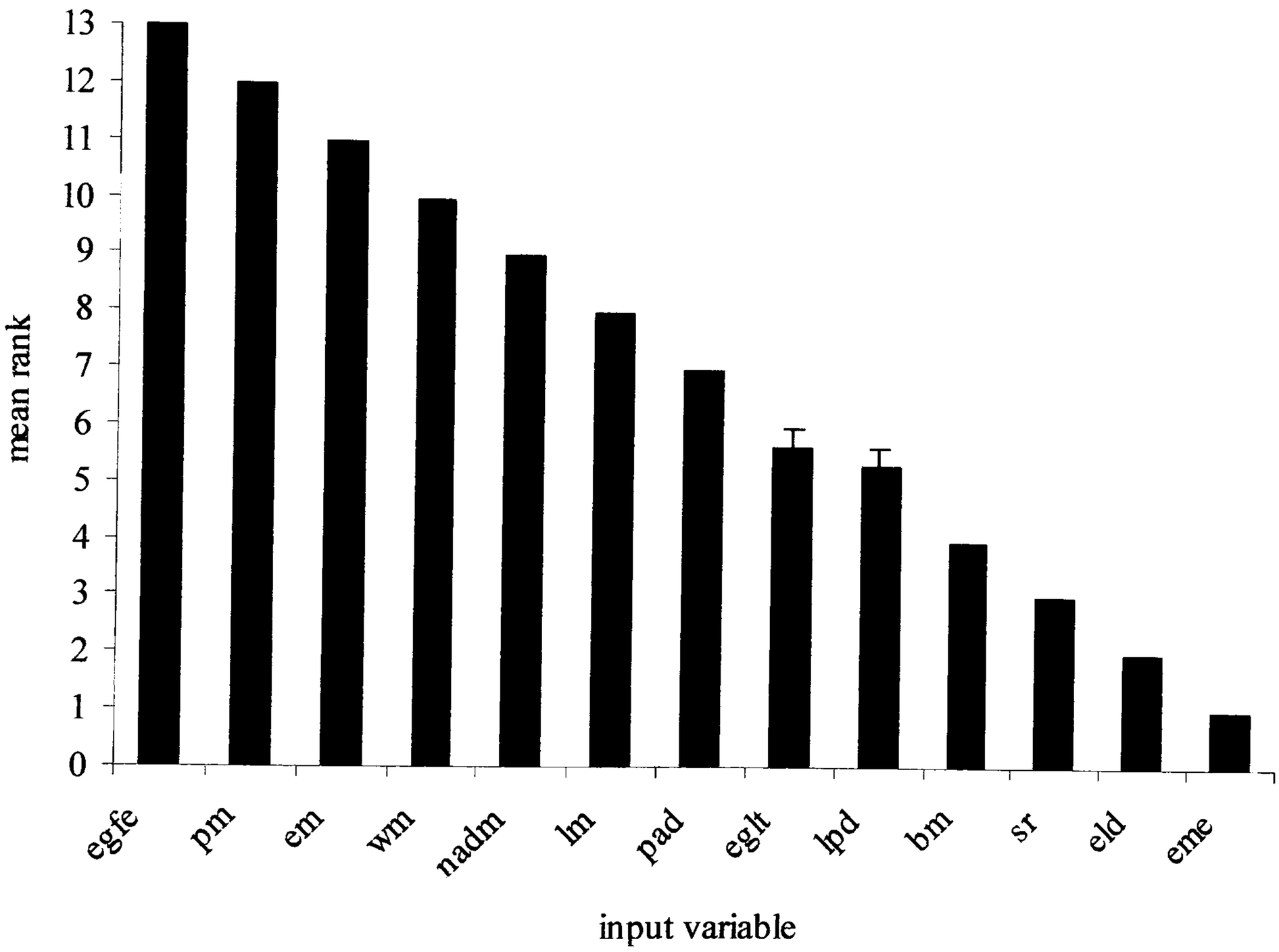


Figure 5-20: Mean and standard error (*n*=3), of the ranks of the input variables of the *L.suturalis* population dynamics model Latin Hypercube Sampling cumulative percentile analysis

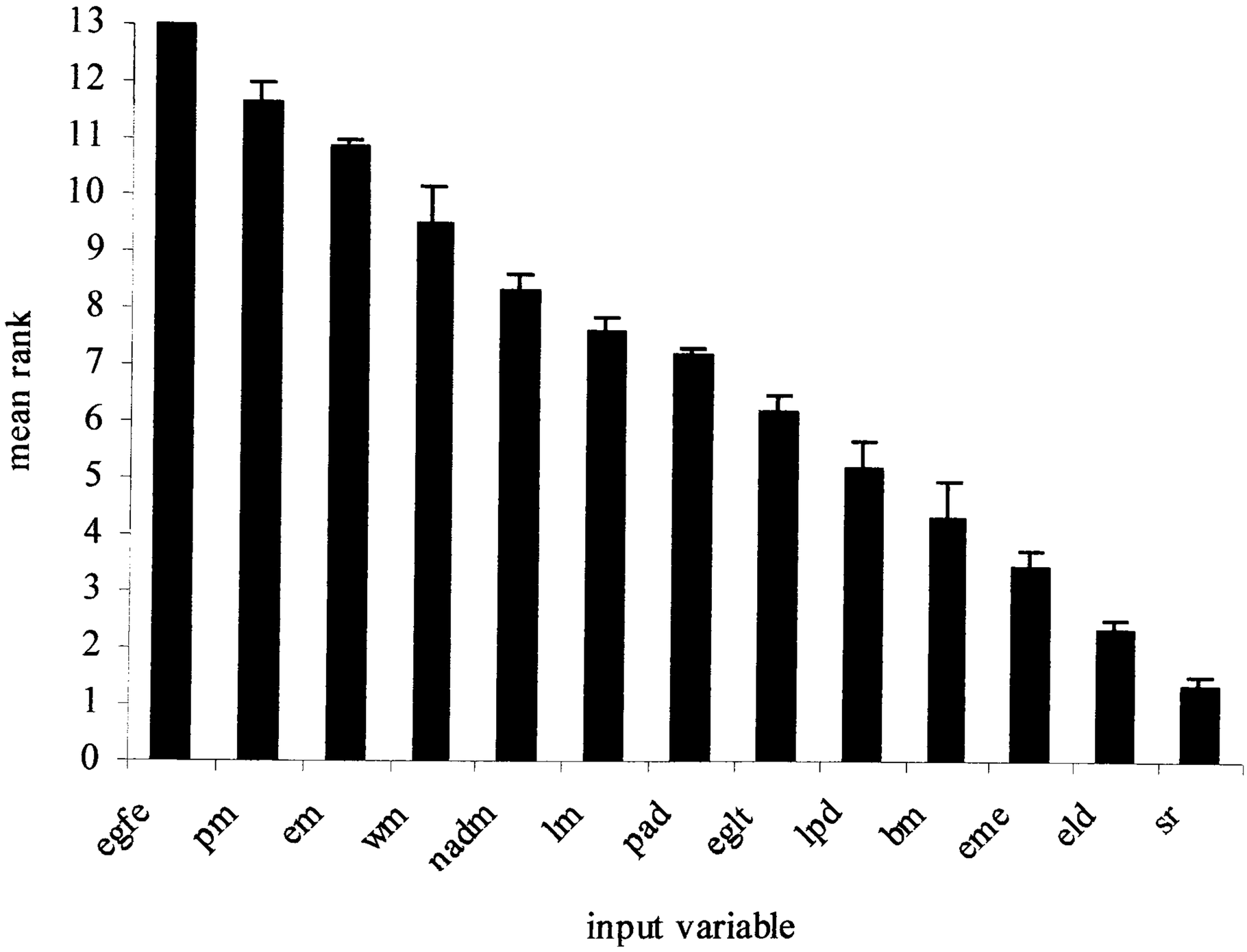


Figure 5-21: Graph showing the overall mean and standard error, (n=3) of mean ranks of all three Latin Hypercube Sampling sensitivity analyses for the *L.*suturalis population dynamics model

5.4 Discussion

The uncertainty and sensitivity analysis conducted on the *Lochmaea suturalis* population dynamics model involved assessing the level of uncertainty associated with estimating each of the input variables. The uncertainty analysis has evaluated the degree of uncertainty of the output values, whilst the sensitivity analysis has evaluated the uncertainty of estimating the model input variables. The parameter space of the model was defined by the thirteen input distributions. An important aspect of a Latin Hypercube Sampling sensitivity analysis is the type of distribution that describes the parameter space of a particular variable because as Vose (1996) advised, it is important that every suite of random variables inputted to the model must be scenario that could physically occur.

Unfortunately the computer program that was employed to generate the Latin Hypercube Sampling matrix was only coded to sample from either a normal or uniform distribution. Consequently it was decided to assign uniform distributions to seven of the thirteen variables. Uniform distributions can be used to describe the parameter space of a variable either if the variable is uniformly distributed or, as the case here, a combination of insufficient data to identify the probability distribution of that variable and low confidence in quoted research figures (Rose *et al.* 1991; Vose 1996). However the uniform distribution is likely to overestimate the likely parameter space of these variables, as values from the extremes are as likely to be selected as those from the mean. However if the bounds of the distribution are selected from empirical data then all the values will reflect the *reality* of the experiments.

The sex ratio, emergence threshold temperature, egg laying temperature and breeding mortality variables were assigned uniform distributions for the above reasons. The sex ratio variable distribution was bounded by the values found

empirically from the three study experiments; and described the lowest value found in the ambient temperature experiment and the highest value found in the field collected samples. The emergence threshold temperature variable was assigned a uniform distribution as the emergence temperatures derived from the study were only based on one experiment and the research literature appeared to be mainly anecdotal. As such, the lower bound of the distribution was set at the level at which all but one of the beetles had entered diapause and the upper bound was set at the temperature at which the beetles began to show evidence of entering diapause. The egg laying temperature was also assigned a uniform distribution for the same reasons as the emergence temperature variable. The upper and lower bounds reflected the likely reality based on the thesis study experiment at ambient temperature and thin research evidence. For example, several researchers had noted that copulation occurred on "warm spring days" (Brunsting 1982; Schaick Zillesen & Brunsting 1983; Brunsting & Heil 1985; Vagn Jensen & Nielsen 1985). The breeding mortality variable was also assigned a uniform distribution as the mortality factor was based on one small experiment (see section 2.2.5, page 29), where assumptions of normality were not as robust, as a consequence the distribution was bounded by its mean value ± one standard deviation.

The three accumulated day degree variables, egg to larval, larval to pupal and pupal to adult, and were all assigned uniform distributions for two reasons. First, to ensure that the parameters space of each variable was explored evenly from the values found in the thesis study. Second, as the thesis study values were markedly different for each temperature regime of the experiment (see section 2.3.6, page 52) then, if a normal distribution had been assigned to the variables, based on the mean and standard deviation of the empirically derived values, then some of the sample input parameters would have been selected from the tails of the distribution and would have been unrealistic. For example, the larval to pupal day degree development variable exhibited a mean of 310°C and standard deviation of 113 as such, values would have been selected equal to

the mean ± 2.58 times the standard deviation, which would have given potential larval to pupal day degrees development values as low as 18°C.

Five of the remaining six variables, egg, larval, pupal, new generation adult and winter mortality were all assigned normal distributions as the values were derived from larger experiments, where assumptions of normality were more robust. However, as described in the methods section, the parameter selections generated by the Latin Hypercube Sampling regime had to be truncated at the upper end of the tail of the distribution, so that values greater than or equal to one were not generated. Vose (1996) remarks that if a distribution has to be truncated then it is the wrong distribution for the data. However in this case, there are two reasons why this truncation was appropriate. First, the number of times that this would occur would be approximately 5% of the simulations for the pupal mortality and approximately 16% for the four other variables. Second, that when a sample was selected greater than or equal to one (where there is no mortality), and inputted to the model as 0.999999 it would be valid as in effect this was *very near* to no mortality.

The fecundity variable was derived from a Poisson distribution and the sub-model equation was of an exponential from, therefore suggesting that an exponential distribution would be required for the generation of LHS values. However this was not available and so the fecundity equation constant was varied by values selected from a normal distribution (see section 5.2.1.1, page 192), with the egg sub-model tested to check that the lower and upper bounds of the distribution samples produced meaningful results. The lower bound of samples that could be drawn from this distribution was set at 1.0, as below this value no eggs at all were produced over the egg laying period and this scenario would therefore have been meaningless. The upper bound was set at 1.96, as above this figure the number of eggs produced daily over the egg laying period would have exceeded the highest number recorded in the fecundity experiments.

The level at which the correlation coefficient was set for the restricted pairings of the LHS matrix generation was set at $r^2 = 0.40$. However, for a sample size of 100 the significance at the 0.1% level was $r^2 = 0.32$. The reason for allowing correlations between the variables greater than the lowest significance was the result of a trade off between computer run time and the acceptance of the nearest possible value. In this case, if the LHS computer program was set to only allow correlations less than 0.32 therefore not allowing for *any significant* correlations between pairs of variables, it could not reach a solution. However, a solution to the matrix of selected values could be attained at the $r^2 = 0.40$ level after some minutes of reselection.

The uncertainty analysis has shown that the model, given the suite of LHS generated variables values, could produce a wide range of estimates of heather beetle population numbers. However the maximum and minimum values of the frequency distributions shown in the summary statistics (see Table 5-2, page 200), only reflect the likely ranges of the output and not the upper and lower bounds of the model, as it is unlikely that the runs of the LHS simulations will have produced a combination of all the extreme variable values. This prediction imprecision was due to the uncertainty in estimating the values of the model variables. As such, the uncertainty analysis does not show which variables are important in determining this uncertainty; that is the role of the sensitivity analysis, whose discussion follows.

The three sensitivity analyses performed on the population dynamics model have all produced similar results, particularly with regard to the fecundity variable. They have all ranked it as the variable that was by far the most important in its contribution to the output uncertainty. In the partial rank correlation coefficient (PRCC) analysis it was highly significant at $p < 0.001$ with PRCC values of between 0.63 and 0.74. Intuitively the fecundity of the heather beetle would be considered to be important as this variable determines the maximum number of adults in the new generation. If, for example there are 500,000 adults on a given day and the fecundity variable on that day is assigned a value of five eggs

laid per adult, then there would be 2.5 million new larvae in that cohort. However, are there any other variables that can be considered important in contributing to some of the unaccounted for model prediction imprecision?

In the partial rank correlation coefficient sensitivity analysis the egg, pupal and winter mortalities and the pupal to adult day degrees development variables were also shown to be key variables, with their PRCC's all significant to the same level as the fecundity variable, for all three replicates. They had values of between 0.51-0.52, 0.51-0.57, 0.43-0.52 and –0.32 to –0.36. These PRCC's beg the question, are they all important or can they be separated out? Blower *et al.* (1991) employed a LHS analysis that produced similar results; the PRCC's for their epidemiological study variables were significant at $p < 0.001$, with the same number of simulations (n=100), with magnitudes of 0.77, 0.77, 0.51 0.36, 0.36 and 0.35. In their discussion they regarded the most important as the 0.77 and 0.51 variables and of a lesser importance, the 0.36 and 0.35 variables. The discussion of their results does not say why or how this dividing line was drawn, and it can only be assumed that it was chosen arbitrarily. If an arbitrary line were drawn for this analysis at the point at which at any of the replicate variables with a significance of $p < 0.001$ and a magnitude of < 0.50 were considered less important, then the most sensitive variables from the PRCC analysis would be the fecundity, egg and pupal mortality variables. This result would seem to be reasonable as the egg mortality variable is likely to work in tandem with the fecundity variable, as it is the first variable in the model that has an effect on the cohorts, and a combination of a high fecundity value and a low egg mortality value would produce larger cohorts, indeed Cameron *et al.* (1944) found the egg stage to be the most critical period of the life cycle of the heather beetle. The pupal mortality is also likely to have had a significant effect on the model output as it has the highest value of the mortality factors with a mean of 0.967 and a relatively high standard deviation of 0.025.

In the PRCC analysis the egg to larval, larval to pupal day degrees, the breeding mortality, sex ratio and emergence threshold temperature variables can be

disregarded, in terms of their contribution to the model output uncertainty, as they were all shown to not have had a significant effect on the output imprecision; this is confirmed by inspection of the scatter plots (see section 5.3.2.4, page 217). Sample sex ratio values drawn by the LHS program would have been from a fairly small range and with a start population of one million beetles, the number of females going forward into the model would vary between 566,000 and 631,000; this variation is unlikely to have had a big impact on overall population numbers.

The emergence threshold temperature variable was shown to have had a negligible effect on the model output, and is confirmed by inspection of the scatter plot (see Figure 5-13, page 218). It shows that relatively high population numbers were produced throughout its range. If it assumed that the fecundity variable plays a large part in determining population numbers, then *when* the beetles emerge from diapause is unlikely to have an effect, unless it was coupled with a low egg laying temperature value, when new populations would be initiated earlier in the year. Also the only difference in the fate of the adult beetles at this stage of the modelling process was whether they were subject to, the very similar, winter and new generation adult mortalities.

The breeding mortality variable was shown to have little effect on the output, and is confirmed by inspection of the scatter plot (see Figure 5-16, page 221). This shows an even spread of output values across the range of values. This variable had a relatively high mortality rate but, as this factor was only applied during the egg laying stage its effects were likely to be swamped by the large effect of the fecundity variable and additionally it was only "killing off" the old generation adults.

The final two non-significant variables were the egg to larval (eld) and larval to pupal (lpd) day degrees development. The eld values were drawn from a small range, and as such, were unlikely to have had a large impact on the output. The lpd had a much larger range of values, and it is difficult to see why this range of

values does not effect the output to a greater extent than was shown. However it may be due to the fact that during this transition period the larvae are subject to a relatively low mortality.

The pupal to adult day degrees variable was the only variable that was significantly important in it contribution to the output uncertainty with a negative PRCC. By inspecting the scatter plot (see Figure 5-17, page 222), it can seen that low values of this variable produced some high output values. This seems reasonable because if a short development period had been selected by the LHS matrix generator for this life stage transition, then the pupae would have been subjected to the high pupal mortality factor for less time.

The cumulative percentile analysis (CPA), produced similar ranking results as the PRCC analysis, with the fecundity and all the mortality variables, except breeding mortality, accounting for the bulk of the variation in the output. This analysis, because of its structure, allows for the inspection of the effect of a variable across its range. The graphs of the percentage change in the output from that obtained with the variable set at its mean (see Figures 5-10 to 5-12, pages 214-216), can be used to judge where, in the range of values of a variable, the greatest effects in determining the output uncertainty are found. For example it can seen that the fecundity variable has little effect at the lower end of its range; between the 1st and 10th percentile values. However the graphs can be misleading as it would seem that the significant mortality variables do not exhibit an effect between their 90th and 99th percentile values, but inspection of the data shows that at these percentiles the input value was the same at 0.999999; consequently each run at these values would produce the same output. This was also seen at the lower end of the fecundity variable range. The graphs do show however, that as the values of the mortality variables drop, thereby increasing mortality, so the effect on the output is less; as is shown by the slope of the line becoming shallower. The CPA has shown that the pupal to adult day degrees development variable had its greatest effect between the 50th and 10th percentile values and that below this the effects were less noticeable.

The analysis has also shown that there is a separation between the other two day degree development variables in that the larval to pupal variable had a stronger effect than the egg to larval development variable.

Consideration of the mean deviation sensitivity analysis (MDA), results was more difficult, as it was essentially a straight forward ranking process with no indication of the model variables level of significance. However as reported in the results section the fecundity variable accounts for the greatest deviation in the output and has generally mirrored the PRCC results for the other variables, when the mean rank of the three replicate simulations are considered. It has shown that the various life stage mortalities, apart from the breeding mortality, are responsible for bulk of the remaining deviation. However it is noticeable that the MDA has not ranked the variables similarly, as the PRCC did, over the three individual replicates, as can be seen by the larger standard errors. There was one anomalous observation; that of the low ranking of the egg mortality variable in the LHS4 replication (see Figure 5-8, page 211). One possible explanation for this is that in this analysis each variable was held at its mean whilst the others had their uncertainty intact. The effect of this structure as Vose (1996) notes is that the interactions between the variables cannot be accounted for, in contrast to the other two analyses. Hence, particular values of this simulation may have confounded the effect of the mean egg mortality value. Nonetheless as Vose (1996) notes it is prudent to run replicates of the simulations to "iron out" any such anomalies. Considering this point, and that overall, this analysis has been shown to be not as robust as the other two analyses, perhaps more replicate simulations would have reduced the standard errors of these results.

The graphs of the MDA have highlighted a potential problem with this Latin Hypercube Sampling analysis of the population dynamics model; that the egg laying temperature variable does not exhibit a monotonic response to the output. The greatest effects on the output uncertainty are seen at the middle of its range. This finding may have implications for the PRCC analysis, as

monotonicity is the main assumption for the calculation of PRCC's (McKay *et al.* 1979; Blower *et al.* 1994). Although LHS sensitivity analyses, if the number of simulations are great enough, have been found to be reasonably robust, even if the monotonicity assumption does not hold (Iman & Helton 1988). In this particular analysis the potential problem can be disregarded for three reasons. First the number of simulations was greater than five times the empirically established level for confidence in the LHS results. Second the low PRCC value for this variable was validated by its low ranking in the two other analyses, and third by inspection of the scatter plot (see Figure 5-14, page 219) it can be seen that the non-monotonic behaviour was marginal.

Having discussed the results of the four analyses there remains the question, what can be deduced from the results? The analyses revealed that the model could produce a considerable range of outcomes across the variable parameter space, and that this prediction imprecision was in large part, due to effects of three variables, fecundity, egg and pupal mortality and to a lesser extent the larval, new generation adult and winter mortalities and the pupal to adult development period. Therefore the results suggest that it important to accurately quantify these variables, as reducing the uncertainty in the estimation of these parameters will greatly reduce the prediction imprecision of the model. Hence, the results of the three analyses can be used to suggest a strategic agenda for further research on the key variables.

Swartzman & Kaluzny (1987) suggest the following three-stage classification of the model input variables for this strategy. First the parameter sensitivity of a variable is assigned a high, medium or low classification. Second the parameter variability and ease of measurement are classified qualitatively as either, high (easily measured and available for the species under consideration), moderate (either more difficult to measure, measured in the laboratory and somewhat variable in the field, or available only for a related species), or low (either not yet measured, extrapolated from a related species, or measured in the laboratory but highly variable in the field). Third priorities for future research are set,

based on both parameter sensitivity and the data availability, with the emphasis placed on those parameters that had a strong influence on the model outcome, but that were not yet measured or were variable in their estimates. Applying this protocol to the *L.suturalis* population dynamics model sensitivity analyses gives the following results (see Table 5-6). The benefits of this analysis, as Swartzman & Kaluzny (1987) note, are that it avoids the inherent problems of interpreting differences between numbers and that the nonquantifiable nature of the categories can be combined, such as the ease of estimation of a parameter and its availability.

Variable	Sensitivity	Availability	Research priority
Sex ratio	L	L	H
Emergence T°C	L	L	M
Egg laying T°C	L	M	M
Fecundity	H	M	H
Egg mortality	H	M	H
Larval mortality	M	M	M
Pupal mortality	H	M	H
New generation mortality	M	M	M
Breeding mortality *	L	L	H
Winter adult mortality	M	M	M
Egg to larval add's **	L	M	M
Larval to pupal add's **	L	M	L
Pupal to adult add's **	M	M	M
* - female			
** - accumulated day degrees development			

Table 5-6: Summary of the three sensitivity analyses of the *L.suturalis* population dynamics model parameters as derived from the Latin Hypercube Sampling regime and implications of the need for further research, for an explanation of the criteria see text

The results of this strategic review show that the variables most in need of further research were the sex ratio, fecundity and egg, breeding and pupal mortalities. The egg and pupal mortality and the fecundity variables require more research as they were consistently ranked as the most important in their contribution to the output uncertainty. The sex ratio variable was included in the high priority category as the research literature suggests high variability in its value from field studies, and as such if it was studied further, a broader LHS distribution may have been assigned to it, which may have led to a different sensitivity analysis importance ranking than was found. The breeding mortality was included in this category as the LHS distribution was necessarily limited due to its small data set. The only low priority research area was considered to be the larval to pupal development variable as the LHS seemed to describe its possible values realistically, and it was found to the of little importance in the sensitivity analysis. The remaining variables have been assigned to the medium category as they deserve further research for the variety of reasons noted in the parameter estimation and sensitivity analysis discussion earlier, but as with most things you cannot do everything at once.

5.5 Conclusions

The strength of the results of a Latin Hypercube Sampling regime sensitivity analysis are intimately linked to the correct choice of input variable distributions and ranges. In this particular analysis the input variables could only be assigned to one of two distributions. This limitation may have weakened the results, particularly with regard to the variables assigned a uniform distribution, as it is unlikely that life history parameters for poikilotherms will not have optimum values. Nevertheless, given this limitation, the sensitivity analysis of the *Lochmaea suturalis* population dynamics model has produced meaningful results that stand up to intuitive and deductive logic.

This initial, exploratory investigation into the behaviour of the model has provided a reasonable indication of the level of importance of the input variables in their contribution to the output uncertainty. It has highlighted two areas for further study. First, the need for a concentration of further research on key variables, in particular the uncertainty in estimating the model input variable values from empirical data. Second the necessary requirement for the employment of a Latin Hypercube Sampling matrix generating program that can sample from a wider range of distributions.

As Chang *et al.* (1993) and McCarthy *et al.* (1995) have noted, uncertainty and sensitivity analyses not only provide valuable insights with regard to model performance but also offer essential information that can help in fine tuning the model design and help in determining effective management strategies in decision making processes. The following, final chapter, as well as discussing the overall thesis study and areas for future research, considers possible management options available to heath and moorland managers with regards to the heather beetle in the light of the results of the population dynamics model simulations and its sensitivity analysis.

Chapter 6: General discussion and conclusions

This thesis has presented the results of first, a series of experiments concerning the relationship between *Lochmaea suturalis* life history stages and the effect of temperature, where it was shown that the various *L.suturalis* life stages were significantly dependent on temperature and that they generally conformed to the established research on *L.suturalis* or to related species. Second, a series of experiments concerning the relationship between *L.suturalis* larval growth and *Calluna vulgaris* plants sourced from differing study sites in Northumberland, where it was shown that there was no significant relationship. Third, an analysis to test the relationship between the daily mean temperature at the nine study sites and the altitude of the site; where a significant relationship was demonstrated.

The significant results from the first and third sets of experiments were utilised to form the basis of a temperature driven, cohort based, *Lochmaea suturalis* population dynamics model, with the model parameters stochastically varied to mimic the inherent environmental and demographic variability of biological systems. The predicted temperature component of the model was shown to have predicted good approximations of daily mean temperatures found in the north of England, when compared to validation data. The population dynamics model was used to predict the changes in a population of one million *L.suturalis* adult beetles over a period of fifty years at different altitude and temperature regimes.

The model, was run at base temperature and six other temperature regimes; chosen to encompass the range of possible temperature rises that may occur as a consequence of predicted climate change caused by global warming. The model showed that as the daily mean temperature rose, so the chances of an increase in population numbers, year by year, increased. When the model was run at different altitudes, for each of the temperature scenarios it generally showed

that the greater the altitude the less chance there was of large population increases; in the case of a daily mean temperature increases of plus three to plus six degrees the population numbers at the lower altitudes exhibited three to sixty fold increases. Further analysis of the model results showed that there was a greater than fifty percent chance that populations would survive over the fifty year period, for the lower altitude populations, with temperature increases in the region of two degrees, and for the higher altitudes in the region of two and half to three and a half degrees.

Validation of the model proved to be problematical as comparative data was not available. However, it was shown that the results, if projected to the known occurrences and levels of infestation of *L.suturalis* populations in Great Britain and the continent, were a reasonable reflection of possible population numbers given the suite of different altitude and temperature scenarios.

The *L.suturalis* population dynamics model was subjected to an uncertainty and sensitivity analysis utilising a Latin Hypercube Sampling regime. The results of this analysis were investigated using partial rank correlation coefficient, mean deviation and cumulative percentile analyses to test the robustness of the model and to rank the life stage variables in order of importance in determining the predicted *L.suturalis* population numbers. The uncertainty analysis showed that the model could produce a considerable range of output values and that this range was due to the estimation of the input variables. The results of the three analyses consistently showed that the uncertainty in the estimation of the fecundity variable was the most important of the life history variables in contributing to the model output imprecision. The egg and pupal mortalities were shown to be the next most important, followed by the larval, new generation adult, and winter mortalities and the pupal to adult development period. The remaining life history variables were all shown to contribute little to the model output uncertainty.

This general discussion considers the overall thesis results in the light of the following four questions.

1. Can the population dynamics experiments be improved, by further research, so that they can be used with more confidence in the population dynamics model?
2. Has the population dynamics model been truly validated?
3. Can the population dynamics model be utilised as a tool to aid management decisions concerning heath and moorland management, and if so, where should management considerations be focussed?
4. Can the population dynamics model be improved so that it provides a truer reflection of *Lochmaea suturalis* ecology?

In considering the first question it should be noted that the experiments conducted to quantify the life history stages of *L.suturalis* were either laboratory based or of a controlled nature. In this study the structure and type of experiments was limited by the low numbers of beetles caught from the study sites during the eighteen months of field investigations; this may been either because of a dip in the cycling populations, the wrong weather or simply bad luck. Several of the experiments would have benefited from a greater number of beetles "to work with", in particular, as highlighted by the sensitivity analysis, the fecundity and the suite of winter mortality experiments.

Perhaps, of more importance, was the lack of empirical field evidence to support the laboratory work, because as Dempster (1975) noted, to fully understand the factors that determine the level of abundance of animals requires intensive study in the field. The absence of the corroborative fieldwork was again due to the lack of beetles found in the field. The life stage evaluations likely to have benefited from field research were the sex ratio, where the research literature suggested a wide range of estimates, and the temperature range at which copulation, in the model the egg laying temperature variable, takes place. In the research literature several authors have observed and

documented this phenomenon, both in Great Britain and the continent, indeed Morison (1963) noted that millions of males and females had covered hundreds of hectares and travelled up to 3 km; but unfortunately I have never witnessed it! Summing up, it seems that future research efforts could be directed towards field-scale evaluations of the life stage parameters. In fact, given the model predictions, personal communications from moorland workers, and the predicted temperature rises as a consequence of climate change, this may be possible in the north of England in the not to distant future.

In considering the second question it is worth summarising the arguments regarding the verification and validation of models put forward by Oreskes *et al.* (1994). They pointed out, that simply because the predicted outcome of a model matches some empirical data it has not been validated, (or verified; they report that the terms are often used interchangeably). Their argument was that by making this claim of validation the modeller was 'committing the fallacy of the consequent'. In as much that, if a model fails to reproduce observed data, then the modeller knows that the model was faulty in some way, but the reverse was never the case. They go on to argue that the best that can be said about a model is that it has been 'confirmed'; where observed data confirms the model output. They add that the confirmation of a model does not demonstrate validation or veracity, it only supports its probability and that the language of verification and validation implies the need for an either-or response. In practice few models are entirely confirmed or refuted by observational data, and they therefore suggest that the problem is rooted in language and degree. They suggest that a neutral language be used to describe the evaluation of model performance, such as excellent, good, fair, poor etc. The heather beetle population numbers that have been predicted as a result of different altitude and temperature regimes described in this thesis, would seem to benefit from this approach to the evaluation of model robustness.

By adopting this approach, it is necessary to rephrase the initial question to: How "good" is the *Lochmaea suturalis* population dynamics model? The

answer to this question should take into account that, as Smith (1996) noted, all models and their results should be viewed with a healthy scepticism, and neither blindly accepted nor dismissed out of hand and as Saarenmaa *et al.* (1988) noted when discussing agricultural insect pest models, that when populations are large enough and the environment is relatively homogenous, population level equations are adequate to describe the populations dynamics with acceptable variance. Given these insights, and as this model represents a first, exploratory step towards a better understanding of *L.suturalis* ecology it would seem that the model, given its limitations, has produced fair to good results. The model has generally reflected previous research on the beetle, and coupled with the uncertainty and sensitivity analysis, has provided some useful insights into aspects of heather beetle life history that could be of use in future research.

The use of models to assist in management decisions concerning biological systems is becoming increasingly common (Bart 1995; Dunning *et al.* 1995). However it is important to realise that with any model there exists the problem that more credence may be given to the model predictions than is warranted (Thomas 1986; Bart 1995). As such, it is vital that models are assessed and evaluated adequately before use to assist in management problems. Bart (1995) provides the following general principle concerning the use of predictive models.

> "Models should not be used to make or defend management decisions until they have been thoroughly evaluated and the results of the evaluation have been subjected to peer review."

Bart (1995) however adds that this does not mean models cannot play a role in management decision-making until they are fully evaluated, as none would ever be used; just that substantial effort at evaluation should be made. Given that the evaluation of the *L.suturalis* population dynamics model, as proposed by Bart (1995), has not been met, the assessment of the third question is considered on a "what if" basis.

Nevertheless, the third question: is the model, as it stands, a useful tool to aid management decisions concerning heath and moorland management?, depends for its answer, on the acceptance of both the answer to question two, and the sensitivity analysis results. In that, *if* the model is regarded as a more than "passable" reflection of likely beetle population scenarios and that the life stages, highlighted as sensitive, are the *L.suturalis* life stages that have the greatest effect on the population numbers, then the model may well be of use.

As discussed earlier in the thesis, the heather beetle is generally considered to be a pest of *C.vulgaris* dominated habitats, particular on lowland heaths. Decision-making in pest management requires the ability to anticipate and evaluate changes in pest populations (Rykiel *et al.* 1984), with a need to predict or anticipate extreme outbreaks. This model predicts that persistent, large, fluctuating populations of the heather beetle may be experienced if there are increases in daily mean temperatures. The predictions may be of interest to the statutory bodies and environmental agencies that are the custodians of *Calluna vulgaris* habitats, insofar that extra resources could be targeted at further research into the interaction between the heather beetle and the heather in the event of confirmed global temperature rises.

The model highlighted the egg and pupal stages of the beetles' life cycle as being sensitive variables; these stages may be of interest when considering the timing of any management prescriptions regarding the rotational burning, flailing or mowing of heather. If outbreaks of the heather beetle become more frequent, and the limitation of beetle numbers becomes an important objective of the management of *C.vulgaris* habitats, then the efforts available for pest management should be focussed either in the spring or autumn, as this is when these life stages occur. For example, traditionally heather burning is undertaken in the late autumn; although this practice is in decline as a management option (Gimingham 1989), and coincides with the pupal development stage. A continuation of this practice, with perhaps greater monitoring of the moorlands and heaths for signs of increasing *L.suturalis* populations, coupled with a more

precise timing of the event, to coincide with notable pupal numbers, may well help to limit the overall beetle population numbers, as the model sensitivity analysis has shown that low numbers of pupae will effectively reduce the number of new generation adults. It is worth adding that both Grimshaw (1911) and Morison (1963), recommended burning during the larval stage (when it is not allowed by law), on the premise that the pupae were "below the surface of the soil" and out of reach of the burn; however in the experiments described in this thesis all the pupae were recorded *on* the surface of the substrate. This observation, coupled with the temperature (400-600 °C), and timing (2 minutes), at which the fire burns near the surface of the substrate (Gimingham 1972), and the fact that pupae are susceptible to low relative humiditities of less than 70%, it does not seem unreasonable to suppose that burning will have a negative effect on pupal survival. Although this method may not be possible on wet bogs because, as Hobbs (1984) notes, there are very few suitable "burning days" under the very wet conditions.

The other life stage shown to be sensitive was the fecundity variable. "Muirburn" is likely to have an effect on the survival of the eggs of the beetle as they are laid on the plant. However it is not likely to be considered as a management option as producing a successful burn is more difficult at this time of year, than in the autumn, due to the "sappy" nature of the heather (Cameron 1944). Burning during the copulation period is also unlikely to be successful as at the first signs of smoke, preceding the fire, the adult beetles take to flight or drop to the ground and burrow beneath the surface, where they experience very low mortalities during a burn (Cameron *et al.* 1944).

In consideration of the fourth question it is worth reiterating that the *L.suturalis* population dynamics model was a first attempt to model *one* aspect of the ecology of the beetle and it *only* produced results in relation to the beetle and temperature. Also that the validity and performance of a model is likely to be improved by incorporating other factors that are suspected to be important in the system under consideration (Killon & Grant 1995). Consequently future

development of the model could include other abiotic factors that are important to terrestrial invertebrates, in particular the relationship between population success and relative humidity; this environmental factor has been shown to be important in the success of *L.suturalis* life stages. Waloff (1986) noted that wet springs favour larvae, Cameron *et al.* (1944) recorded that below a threshold figure of 70% relative humidity, few pupae survive and Melber & Heimbach (1984) noted that aridity was important in terminating outbreaks and that consequently micro-climate moisture was important in the life cycle of *L.suturalis*. The relationship between the life stages of *L.suturalis* and relative humidity could be linked to the differing relative humidities experienced in the canopy of heather found along the gradient from ombrotrophic blanket bogs to dry heaths.

The model could be further developed into a spatial dispersal model, utilising Geographical Information System (GIS) technology, enabling heather beetle populations to be "tracked" across landscapes. The movement of the beetle over the landscape could be incorporated into the spatial model via the study and establishment of the following elements. A sub-module predicting the direction and distance of migration based on the predicted wind speed and direction as Schaick Zillesen & Brunsting (1983) found that the adult beetles only attempted migration on warm, sunny days with no wind or low wind speeds and Morison (1963) noted that millions of males and females had covered hundreds of hectares and travelled up to 3 km.

Once the model had predicted the movement of beetles to a new "patch" of heather, a further sub-module could predict the survival of the population based on the "type" of heather patch that the population had alighted on. Each possible patch could be assigned a suitability class for population survival, defined by a suite of sub-models describing its meso-climate and nutrient quality. The factors defining the meso-climate and nutrient quality could include the type of *C.vulgaris* habitat; whether dry, wet, lowland, upland or sub-montane, and the growth stage of the heather as defined by Gimingham

(1972). Different *C.vulgaris* growth stages have been shown to experience different amounts of irradiation reaching the understorey, with the consequent differences in canopy temperatures and relative humidity (Barclay-Estrup & Gimingham 1969).

Movement to the next patch would be determined by a "food shortage" factor as Schaick Zillesen & Brunsting (1983) found that food shortages prolonged dispersal activity and postponed oviposition, and concluded that this mechanism gave *L.suturalis* a choice, dependent on the environment, as to the location and timing of its breeding activity enabling it to react dynamically to the best chances available in their environment.

So far the possible future development areas of the model have dealt with *L.suturalis* population viability as a single species model with increasing levels of complexity. However to fully develop the model it would be necessary to include a further element; not only the heather beetle density dependent processes, but also the density dependent processes involving fungal parasitism, its endoparasitoids and predators. Adding these factors to the model would entail a major leap in model complexity; the discussion of which is beyond this thesis. However, if a full model were envisaged then quantification of the following relationships would be required. *L.suturalis*'s susceptibility to attack by the entomopathogenic fungus *Beauveria bassiana* (Bals) Vuill. (Scandrett & Gimingham 1991). Attack by its predators, *Coccinella hieroglyphica* L., (Cameron *et al.* 1944; Waloff 1987; Webb 1989) and the pentatomid bug *Rhacognathus punctatus* (L.) (Webb 1989), and attack by the endoparasitoid of the adult, *Degeeria* (=*Medina*) *collaris* Fallen., (Diptera; Tachinadae), (Cameron *et al.* 1944; Waloff 1987; Cox 1994) and the endoparasitoid of the larvae, *Asecodes mento* Walker., (Hymenoptera; Eulophidae) (Golightly 1962; Waloff 1987; Cox 1994).

In conclusion, it should be noted that by expanding the model structure by conducting further empirically based *L.suturalis* population studies would increase

the model complexity and with it the difficulty in analysing, interpreting, verifying, and validating the model. However I feel that the initial experimentation and the model described in this thesis provide a firm foundation with which to further investigate the ecology of *Lochmaea suturalis* through empirical and simulation modelling research.

Chapter 7: List of references

Abuarghub, S.M. & Read, D.J. (1988) The biology of mycorrhiza in the Ericaceae. XI The distribution of nitrogen in soil of a typical upland *Callunetum* with special reference to the "free" amino acids. *New Phytologist,* **108**, 425-431.

Aldyhim, Y.N. & Khalil, A.F. (1993) Influence of temperature and daylength on population development of *Aphis gossypii* on *Cucurbita pepo*. *Entomologica Experimentalis Applicata*, **67**, 167-172.

Allen, S.E. (1989) (Ed.) *Chemical analysis of ecological materials*. Blackwell Scientific Publications, Oxford.

Andrewartha, H.G. (1970) (2nd edn.) *Introduction to the study of animal populations*. Chapman and Hall, London.

Andrewartha, H.G. & Birch, L.C. (1954) *The distribution and abundance of animals.* University of Chicago Press, Chicago.

Armstrong, H. (1991) Britain's declining heather moorlands. *Outlook on Agriculture*, **20**,103-107.

Bach, C.E. (1990) Plant successional stage and insect herbivory: flea beetles on sand dune willow. *Ecology,* **71** (2), 598-609.

Bajwa, R. & Read, D.J. (1986) Utilisation of mineral and amino-nitrogen sources by the ericoid mycorrhizal endophyte *Hymenoscyphus ericae* and by mycorrhizal and non-mycorrhizal seedlings of *Vaccinium*. *Transactions of the British Mycological Society,* **87**, 269-277.

Baldwin, I.T., Schultz, J. & Ward, D. (1987) Patterns and sources of leaf tannin variation in yellow birch (*Betula allegheniensis*) and sugar maple (*Acer saccharum*). *Journal of Chemical Ecology*, **13**, 1069-1078.

Bannister, P. (1964a) Stomatal responses of heath plants to water deficits. *Journal of Ecology,* **52**, 151-158.

Bannister, P. (1964b) The water relations of certain heath plants with reference to their ecological amplitude. III. Experimental studies: General conclusions. *Journal of Ecology,* **52**, 499-509.

Barbosa, P. (1988) Some thoughts on the evolution of host range. *Journal of Ecology*, **69** (4), 912-915.

Barclay-Estrup, P & Gimingham, C.H. (1969) The description and interpretation of cyclical processes in a heath community. I. Vegetational change in relation to the *Calluna* cycle. *Journal of Ecology,* **57**, 737-758.

Bardgett, R.D., Marsden, J.H. & Howard, D.C. (1995) The extent and condition of heather on moorland in the uplands of England and Wales. *Biological Conservation*, **71**, 155-161.

Bart, J. (1995) Acceptance criteria for using individual-based models to make management decisions. *Ecological Applications*, **5** (2), 411-420.

Behrens, W., Hoffmann, K., Kempa, S., Gasler, S. & Merker-Wallner, G. (1983) Effects of diurnal thermoperiods and quickly oscillating temperatures on the development and reproduction of crickets, *Gryllus bimaculatus*. *Œcologica,* **59**, 279-287.

Berdowski, J.J.M. & Zeilinga, R. (1983) The effect of the heather beetle (*Lochmaea suturalis* Thoms.) on heather (*Calluna vulgaris* (L.) Hull) as a cause of mosaic patterns in heathlands. *Acta Botanica Netherlanda,* **32**, 250-251.

Berdowski, J.J.M. (1987) Transition from heathland to grassland initiated by the heather beetle. *Vegetatio,* **72**, 167-173.

Berdowski, J.J.M. & Siepel, H. (1987) Vegetative regeneration of *Calluna vulgaris* at different ages and levels of fertilisation. In: *The catastrophic death of Calluna vulgaris in Dutch heathlands*. (J.J.M. Berdowski), PhD Thesis, University of Utrecht, pp.79-87.

Berdowski, J.J.M. & Zeilinga, R. (1987) Transition from heathland to grassland: damaging effects of the heather beetle. *Journal of Ecology*, **75**, 159-175.

Berdowski, J.J.M. (1993) The effect of external stress and disturbance factors on *Calluna* dominated heathland vegetation. In: *Heathlands: Patterns and Processes in a Changing Environment*. (eds.) Aerts, R. & Heil, G.W. Kluwer Academic Publishers, Dordrecht. pp. 85-124.

Berendse, F. & Aerts, R. (1984) Competition between *Erica tetralix* and *Molinia caerulea* as affected by the availability of nutrients. *Acta Oecologica - Oecologica Planta,* **5**, 3-14.

Berendse, F., Beltman, B., Bobbink, R., Kwant, R. & Schmitz, M. (1987) Primary production and nutrient availability in wet heathland ecosystems. *Acta Oecologica - Oecologica Planta,* **8**, 265-279.

Birch, L.C. (1948) The intrinsic rate of natural increase of an insect population. *Journal of Animal Ecology*, **17**, 15-26.

Blower, S.M, Hartel, D., Dowlatabadi, H., Anderson, R.M. & May, R.M. (1991) Drugs, sex and HIV: a mathematical model for New York City. *Philosophical Transactions of the Royal Society of London B*, **321**, 171-187.

Blower, S.M. & Dowlatabadi, H. (1994) Sensitivity and uncertainty analysis of complex models of disease transmission: an HIV model, as an example. *International Statistical Review*, **62** (2), 229-243.

Boyce, M.S. (1992) Population Viability Analysis. *Annual Review of Ecological Systematics*, **23**, 481-506.

Breemen van, M. (1988) Ecosystem effects of atmospheric deposition of nitrogen in the Netherlands. *Environmental Pollution,* **54**, 249-274.

Brunsting, A.M.H. (1982) The influence of the dynamics of a population of herbivorous beetles on the development of vegetational patterns in a heathland system. In: *Proceedings of the 5th International Symposium on Insect-Plant Relationships*, (1982), pp. 215-223. Pudoc, Wageningen.

Brunsting, A.M.H. & Heil, G.W. (1985) The role of nutrients in the interactions between a herbivorous beetle and some competing plant species in heathlands. *Oikos,* **44**, 23-26.

Bryant, J.P., Chapin, F.S. & Klein, D.R. (1983) Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos*, **40**, 357-368.

Bryant, J.P., Clausen, T.P., Reichardt, P.B., McCarthy, M.C. & Warner, R.A. (1987) Effect of nitrogen fertilization upon the secondary chemistry and nutritional value of quaking aspen (*Populus tremuloides* Michx.) leaves for the large aspen tortrix ((*Choristoneura conflictana*) (Walker)). *Oecologica* (*Berlin*), **73**, 515-517.

Bunce, R.G.H. (1987) The extent of upland areas in Great Britain. In: *Agriculture and conservation in the hills and uplands*. Bell, M. & Bunce, R.G.H. (eds.), pp.19-21. (I.T.E. symposium no. 23.) Grange-over-Sands: Institute of Terrestrial Ecology.

Cameron, A.E., McHardy, J.W. & Bennett, A.H. (1944) The Heather Beetle (*Lochmaea suturalis*) - An enquiry into its biology and control. *British Fields Sports Society*, Petworth, Sussex.

Caporn, S.J.M., Carroll, J., Lei, Y, Song, W., Read, D.J. & Lee, J.A. (1995) Critical loads of nitrogen for upland heather (*Calluna vulgaris*) In: Battarbee, R.W., (ed) *Acid Rain and its Impact: the Critical Loads Debate*. Ensis Ltd, London. pp. 146-151.

Chalabi, Z. (1991) The interface between biologists and mathematicians. In *The art and craft of modelling in applied biology*, pp. 81-88. Association of Applied Biologists, Warwick.

Chang, C.H., Yang, J.C. & Tung, Y.K. (1993) Sensitivity and uncertainty analysis of a sediment transport model: a global approach. *Stochastic Hydrology and Hydraulics*, 7, 299-314.

Coley, P.D., Bryant, J.P. & Chapin, F.S. (1985) Resource availability and plant anti-herbivore defense. *Science*, **230**, 895-899.

Cox, M.L. (1976) *The taxonomy and biology of the British Chrysomelidae*. Ph.D. Thesis, University of Newcastle upon Tyne, (unpublished).

Cox, M.L. (1994) *The Hymenoptera and Diptera parasitoids of Chrysomelidae*. In: *Biology of the Chrysomelidae* (eds. Jolivet, P., Petitpierre, E. & Hsiao, T.H.,) (1988), pp. 419-467. Kluwer Academic Publishers.

Crawley, M.J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.

De Loach, C.L. (1974) Rate of increase of populations of cabbage, green peach and turnip aphids at constant temperatures. *Annals of the Entomological Society of America*, **67**, 332-340.

Dempster, J.P. (1975) *Animal population ecology*. Academic Press, London.

Diemont, W.H. & Heil, G.W. (1984) Some long-term observations on cyclical and seral processes in Dutch heathlands. *Biological Conservation*, **30**, 283-290.

Duffey, S.S., Bloem, K.A. & Campbell, B.C. (1986) Consequences of sequestration of plant natural products in plant-insect interactions. In *Interactions of plant resistance and parasitoids and predators of insects*. (eds. Boethel, D.J. & Eikenbary, R.D.). pp. 31-60. Ellis Horwood, Chichester, England.

Dunning, J.B., Stewart, D.J., Danielson, B.J., Noon, B.R., Root, T.L., Lamberson, R.H. & Stevens, E.E. (1995) Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5** (1), 3-11.

Elton, C. (1927) *Animal Ecology.* Sidgwick and Jackson, London.

Eubank, W.P., Atmar, J.W. & Ellington, J.J. (1973) The significance and thermodynamics of fluctuating versus static thermal environments on *Heliothis zea* eggs development rates. *Environmental Entomology*, **2**, 491-496.

Farrell, L. (1989) The different types and importance of British heaths. *Botanical Journal of the Linnean Society*, **101**, 291-299.

Gimingham, C.H. (1972) *Ecology of Heathlands*. Chapman and Hall, London.

Gimingham, C.H. (1989) Heather and heathlands. *Botanical Journal of the Linnaean Society*, **101**, 263-268.

Golightly, W.H. (1962) Biological control of *Lochmaea suturalis* Thomson (Col., Chrysomelidae). *Entomologists Monthly Magazine*, **98**, 196.

Grace, J. & Woolhouse, H.W. (1973) A physiological and mathematical study of the growth and productivity of a *Calluna* and *Sphagnum* community. 3. Distribution of photosynthate in *Calluna vulgaris*. *Journal of Applied Ecology*, **10**, 77-91.

Grime, J.P., Hodgson, J.G. & Hunt, R. (1988) *Comparative Plant Ecology.* Unwin Hyman, London.

Grimshaw, P.H. (1911) The heather beetle. In: *The Grouse in health and disease*, London, I. pp. 414-429.

Hamby, D.M. (1994) A review of techniques for parameter sensitivity analysis of environmental models. *Environmental Monitoring and Assessment*, **32**, 135-154.

Havens, P.L. & Fontaine, D.D. (1991) An introduction to sensitivity analysis. In: *The art and craft of modelling in applied biology*, pp. 135-149. Association of Applied Biologists, Warwick.

Hayakawa, D.L., Grafius, E. & Stehr, F.W. (1990) Effects of temperature on longevity, reproduction and development of the Asparagus aphid and the parasitoid *Diaeretiella rapae*. *Environmental entomology*, **19**, 890-897.

Heil, G.W. & Diemont, W.H. (1983) Raised nutrient levels change heathlands into grasslands. *Vegetatio*, **53**, 113-120.

Heil, G.W. & Bruggink, M. (1987) Competition for nutrients between *Calluna vulgaris* (L.) Hull and *Molinia caerulea* (L.) Moench. *Oecologia,* **73**, 105-107.

Henderson-Sellers, B. & Henderson-Sellers, A. (1996) Sensitivity evaluation of environmental models using fractional factorial experimentation. *Ecological Modelling*, **86**, 291-295.

Hobbs, R.J. (1984) Length of burning rotation and community composition in high-level *Calluna-Eriophorum* bog in N England. *Vegetatio*, **57**, 129-136.

Honek, A. & Kocourek, F. (1990) Temperature and development time in insects: A general relationship between thermal constants. *Zoological Journal of Systematics*. **117**, 401-439.

Houghton, J.T., Jenkins, G.J. & Ephraums, J.J. (1990) *Climate change. The IPCC scientific assessment.* Cambridge University Press, Cambridge.

Huffaker, R.D., Jones, R.E. & Gutierrez, A.P. (1984) Short term patterns of population change: the life system approach to their study. In Huffaker, R.D. & Rabb, R.L., (eds.) *Ecological Entomology*, pp. 309-351. Wiley, New York.

Iason, G.R. & Hester, A.J. (1993) The response of heather (*Calluna vulgaris*) to shade and nutrients - predictions of the carbon-nutrient balance hypothesis. *Journal of Ecology*, **81**, 75-80.

Iason, G.R., Hartley, S.E. & Duncan, A.J. (1993) Chemical response of *Calluna vulgaris* (Ericaceae): Do responses to fertilizer vary with phenological stage? *Biochemical Systematics and Ecology*, **21** (3), 315-321.

Iman, R.I. & Conover, W.J. (1980) Small sample sensitivity analysis techniques for computer models, with an application to risk assessment *Communications in Statistics-Theory and Methods*, **A9**, 1749-1842.

Iman, R.I. & Conover, W.J. (1982) A distribution-free approach to inducing rank correlation among input variables. *Communications in Statistics-Simulation and Computation*, **11** (3), 311-334.

Iman, R.I. & Helton, J.C. (1988) An investigation of uncertainty and sensitivity analysis techniques for computer models. *Risk Analysis*, **8** (1), 71-90.

Institute of Terrestrial Ecology, (1989) *Heather in England and Wales*. I.T.E. research publication number 3. Natural Environment Research Council, HMSO, London.

Jalal, M.A., Read, D.J. & Haslam, E. (1982) Phenolic composition and its seasonal variation in *Calluna vulgaris*. *Phytochemistry* **21**, 1397-1401.

Jeffers, J.N.R. (ed.) (1978) *An introduction to Systems Analysis: with ecological applications.* Edward Arnold, London.

Jeffers, J.N.R. (1988) *Practitioner's handbook on the modelling of dynamic change in ecosystems.* John Wiley & Sons, Chichester.

Jefree, C.E. & Jefree, E.P. (1996) Redistribution of the potential geographical ranges of Mistletoe and Colorado beetle in Europe in response to the temperature component of climate change. *Functional Ecology*, **10**, 562-577.

Johnson, C.G. (1969) *Dispersal of Insects by flight.* Methuen, London.

Johnson, I.R. & Parsons, A.J. (1985) Use of a model to analyse the effects of continuous grazing managements on seasonal patterns of grass production. *Grass and Forage Science*, **40**, 449-458.

Jones, J.M. & Stephen, F.M. (1994) Effect of temperature on development of hymenopterous parasitioids of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environmental Entomology*, **23** (2), 457-463.

Jorgensen, S.E. (1994) *Fundamentals of Ecological Modelling*: *Developments in Environmental Modelling 19.* (2nd Edn.). Elsevier, Amsterdam.

Killon, M.J. & Grant, W.E. (1995) A colony growth model for the imported fire ant: potential geographic range of an invading species. *Ecological Modelling,* 77, 73-84.

Kingsland, S.E. (1985) *Modelling Nature - Episodes in the History of Population Ecology.* The University of Chicago Press, London.

Lamb, R.J. & Gerber, G.H. (1985) Effects of temperature on the development growth, and survival of larvae and pupae of a north temperature chrysomelid beetle. *Oecologica*, **67**, 8-18.

Liu, S., Zhang, G. & Liu, J. (1995) Influence of temperature variations on rate of development in insects: Analysis of case studies from entomological literature. *Annals of the Entomological Society of America*, **88** (2), 107-119.

Loach, K. (1968) Relations between soil nutrients and vegetation in wet heaths. II. Nutrient uptake by the major species in the field and in controlled conditions. *Journal of Ecology*, **56**, 117-127.

Lunn, A.G. (1976) *The vegetation of Northumberland: map at 1: 200,000.* Department of Geography, University of Newcastle upon Tyne.

Mallik, A.U. & Gimingham, C.H. (1985) Ecological effects of heather burning. *Journal of Ecology*, **73**, 633-644.

Manel, S & Debouzie, D. (1995) Prediction of egg and larval development times in the field under variable temperatures. *Acta Oecologica*, **16** (2), 205-218.

Mattson, W.J. (1980) Herbivory in relation to plant nitrogen content. *Annual Review of Ecology and Systematics,* **11**, 119-161.

Marrs, R.H. (1986) The role of catastrophic death of *Calluna* in heathland dynamics. *Vegetatio*, **66**, 109-116.

McCarthy, M.A., Burgman, M.A. & Ferson, S. (1995) Sensitivity analysis for models of population viability. *Biological Conservation*, **73**, 93-100.

McKay, M.D., Conover, W.J. & Beckman, R.J. (1979) A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics*, **21** (2), 239-245.

McLain, D.K., Lanier, D.L. & Marsh, N.B. (1990) Effects of female size, mate size, and number of copulations on fecundity, fertility, and longevity of *Nezara viridula* (Hemiptera: Pentatomidae). *Annals of the Entomological Society of America*. **83**, 1130-1136.

McNeill, S. & Prestidge, R.A. (1982) Plant nutritional strategies and insect herbivore community dynamics. In: *Proceedings of the 5th International Symposium of Insect-Plant Relationships,* pp 225-235. Wageningen, Pudoc.

McNeill, S. & Southwood, T.R.E. (1978) The role of nitrogen in the development of insect/plant relationships. In *Biochemical aspects of plant and animal co-evolution*, Harborne, J.B. (ed.) Academic, New York.

Melber, A. von & Heimbach, U. (1984) Outbreaks of the heather beetle (*Lochmaea suturalis* Thomson) (Col., Chrysomelidae) in Northwest German *Calluna* heathlands during this century. *Anzeiger-fur-Schadlingskunde, Pflanzenschutz, Unweltschutz,* **57**, 87-89.

Meteorological Office (1984) The climate of Great Britain: north-east England. *Climatological Memorandum 127*. Meteorological Office, London.

Miller, G.R., Jenkins, D. & Watson, A. (1966) Heather performance and Red Grouse populations. *Journal of Applied Ecology,* **3**, 313-326.

Miller, D.R. (1974) Sensitivity analysis and validation of simulation models. *Journal of Theoretical Biology*, **48**, 345-360.

Miller, G.R. (1979) Quantity and quality of the annual production of shoots and flowers by *Calluna vulgaris* in North-East Scotland. *Journal of Ecology*, **67**, 109-129.

Morison, G. (1963) *The Heather Beetle* (*Lochmaea suturalis* Thomson). North of Scotland College of Agriculture, Aberdeen.

Moss, R. (1989) Management of heather for game and livestock. *Botanical Journal of the Linnaean Society*, **101**, 301-306.

Nielsen, Overgaard B. (1986) Outbreaks of the heather beetle (*Lochmaea suturalis* Thoms.) in Danish heathland, 1900-1984. *Entomologiske Meddelelser*, **53**, 99-109.

North, P.M. & Jeffers, J.N.R. (1991) Modelling: management or an illusion. In: Spellerberg, I., Goldsmith, F.G. & Morris, M.G. (Eds.) *The scientific management of temperate communities for conservation*: the 31st Symposium of the British Ecological Society, Southampton, 1989. Blackwell Science Ltd., Oxford.

Northumbrian River Authority (1973) *Report on the survey of Water Resources*, NRA.

Oreskes, N, Shrader-Frechette, K. & Belitz, K. (1994) Verification, validation, and confirmation of numerical models in the earth sciences. *Science*, **263**, 641-646.

Palo, R.T., Sunnerheim, K. & Theander, O. (1985) Seasonal variation of phenols, crude protein and cell wall content of birch (*Betula pendula* Roth) in relation to ruminant *in vitro* digestibility. *Oecologica* (*Berlin*), **65**, 314-318.

Paterson, N.F. (1931) The bionomics and comparative morphology of the early stages of certain Chrysomelidae (Coleoptera: Phytophaga). *Proceedings of the Zoological Society,* (1931), pp. 898-899.

Pearsall, W.H. (1971) *Mountains and Moorlands*. Collins, London.

Phillips, W.M. (1976) Effects of leaf age on feeding preference and egg laying in the chrysomelid beetle, *Haltica lythri. Physiological Entomology*, **1**, 223-226.

Reese, J.C. (1981) Insect dietetics: complexities of plant-insect interactions. In: Bhaskaran *et al.* (eds.) *Current topics in insect endocrinology and nutrition*, pp. 317-335. Plenum, New York.

Reese, J.C. (1983) Nutrient-allelochemical interactions in host plant resistance. In: Hedin, P. (ed.) *Plant resistance to insects*. pp. 231-243. American Chemical Society Symposium Series, 208.

Renshaw, E. (1991) *Modelling Biological Populations in Space and Time*. Cambridge University Press, Cambridge.

Rose, K.A., Smith, E.P, Brenkert, A.L. & Bartell, S.M. (1991) Parameter sensitivities, Monte Carlo filtering, and model forecasting under uncertainty. *Journal of Forecasting*, **10**, 117-133.

Rykiel, E.K. (1984) Computer aided decision-making and information accessing in pest management systems, with emphasis on the Southern Pine Beetle (Coleoptera: Scolytidae). *Journal of Economic Entomology*, **77** (4), 1073-1082.

Saarenmaa, H., Stone, N.D., Folse, L.J., Packard, J.M., Grant, W.E., Makela, M.E. & Coulson, R.N. (1988) An artificial intelligence modelling approach to simulating animal/habitat interactions. *Ecological Modelling*, **44**, 125-141.

Scandrett, E & Gimingham, C.H. (1991) The effect of the heather beetle *Lochmaea suturalis* on vegetation in a wet heath in NE Scotland. *Holarctic Ecology*, **14**, 24-30.

Schaick Zillesen van, P.G. & Brunsting, A.M.H. (1983) Capacity for flight and egg production (Col., Chrysomelidae). *Netherlands Journal of Zoology*, **33**, 266-275.

Schneider, S.H. (1992) The climatic response to greenhouse gases. In Woodward, F.I., (Ed.) *The Ecological Consequences of Global Climate Change*: *Advances in Ecological Research*, **22**. Academic Press, London.

Scriber, J.M. (1984) Host-plant suitability. In *Chemical ecology of insects*, Bell, W.J. & Carde, T. (eds.) Sinauer, USA.

Schrier, A. (1981) The heather beetle *Natura* **78**, 322-325.

Selman, B.J. (1994) Eggs and oviposition in chrysomelid beetles. In: *Novel aspects of the biology of the Chrysomelidae* (eds.) Jolivet, P.H., Cox, M.L. & Petitpierre, E. (1994), pp. 69-74. Kluwer Academic Publishers.

Slansky, F. & Scriber, J.M. (1985) Food consumption and utilization. In: *Comprehensive Insect Physiology, Biochemistry and Pharmacology*, Volume 4, (eds.) Kerkut, G.A. & Gilbert, L.I., pp.87-164. Pergamon, Oxford.

Smidt de, J.T. (1977) Interaction of *Calluna vulgaris* and the heather beetle (*Lochmaea suturalis* Thoms.). In *Vegetation and Fauna* (ed.) Texen, R. (1977), pp. 179-186. J. Cramer, Vaduz.

Smidt de, J.T. & Brunsting, A.M.H. (1990) Prevention of grass dominance after a plague of the Heather beetle *(Lochmaea suturalis*). *De Levende Natuur*, **91**, 60-62.

Smith, G.C. (1996) Population models and their relevance to prediction of trends in naturalised populations and management implications. In: *The introduction and naturalisation of birds*. (eds.) Holmes, J.S. & Simons, J.R., pp. 57-61. HMSO, London.

Smith, L.P. (1984) *The agricultural climate of England and Wales: areal averages 1941-1970*. Ministry of Agriculture, Fisheries and Food: Reference Book 435. London: HMSO.

Southwood, T.R.E. (1978) *Ecological Methods with particular reference to the study of insect populations*. (2nd Edition). Chapman and Hall, London.

Swartzman, G.L. & Kaluzny, S.P. (1987) *An Ecological Simulation Primer*. Macmillan Press.

Swan, G.A. (1993) *Flora of Northumberland*. The Natural History Society of Northumbria, Newcastle upon Tyne, England.

Tauber, M.J., Tauber, C.A. & Nyrop, J.P. (1994) Soil moisture and postdormancy emergence of Colorado Potato Beetles (Coleoptera: Chrysomelidae): Descriptive model and field emergence patterns. *Population Ecology*, **23** (6), 1485-1496.

Tauber, M.J., Tauber, C.A., Obrycki, J.J., Gollands, B. & Wright, R.J. (1988) Geographical variation in responses to photoperiod and temperature by *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) during and after dormancy. *Annals of the Entomological Society of America*, **81**, 764-773.

Taylor, T.H.C. (1937) The biological control of an insect in Fiji. An account of the Coconut Leaf Mining Beetle and its Parasite Complex. *Imperial Institute of Entomology*, London.

Thomas, J.W. (1986) Wildlife habitat modelling - cheers, fears, and introspection. In: Verner, J., Morrison, M.L. & Ralph, C.J. (Eds.) *Wildlife 2000*. University of Wisconsin Press, Madison, Wisconsin, USA.

Thompson, C.G. (1866) *Lochmaea suturalis. Scandinaviens. Coleoptera,* III, 151.

Thompson, D.B.A., McDonald, A.J., Marsden, J.H. & Galbraith, C.H. (1995) Upland heather moorland in Great Britain: A review of international importance, vegetation change and some objectives for nature conservation. *Biological Conservation*, **71**, 163-178.

Tingey, W.M. & Singh, S.R. (1980) Environmental factors influencing the magnitude and expression of resistance. In: *Breeding Plants Resistant to Insects*. (eds.) Maxwell, F.G. & Jennings, P.R., pp. 87-113. John Wiley, New York.

Usher, M.B. & Thompson, D.B.A. (1993) Variation in the upland heathlands of Great Britain: Conservation importance. *Biological Conservation*, **66**, 69-81.

Vagn Jensen, K.M. & Overgaard Nielsen, B. (1985a) Biology of overwintering heather beetles (*Lochmaea suturalis* Thoms.) (Coleoptera: Chrysomelidae). *Flora og Fauna*, **91**, 4-12.

Vagn Jensen, K.M. & Overgaard Nielsen, B. (1985b) The biology of the heather beetle (*Lochmaea suturalis* Thoms.) (Coleoptera: Chrysomelidae) during the summer half. *Flora og Fauna*, **91**, 17-24.

Van Breemen, N. & Van Dijk, H.F.G. (1988) Ecosystem effects of atmospheric deposition of nitrogen in the Netherlands. *Environmental Pollution*, **54**, 249-274.

Van der Eerden, L.J., Dueck, Th.A., Berdowski, J.J.M., Greven, H. & Dobben van, H.F. (1991) Influence of NH_3 and $(NH_4)_2SO_4$ on heathland vegetation. *Acta Botanica Neerlanda,* **40** (4), 281-296.

Van Emden, H.F. & Way, M.J. (1972) Host plants in the population dynamics of insects. In *Insect/Plant Relationships*. Symposia of the Royal Entomological Society, **6**, 181-197. Blackwell Scientific Publications, London.

Vose, D. (1996) *Quantitative risk analysis: a guide to Monte Carlo simulation modelling.* John Wiley, Chichester, England.

Wagner, T.L., Wu, H.I., Sharpe, P.J.H., School-field, R.M. & Coulson, R.N. (1984) Modelling insect development rates: a literature review and application of a biophysical model. *Annals of the Entomological Society of America*, 77, 208-225.

Waloff, N. (1987) Observations on the heather beetle *Lochmaea suturalis* (Thomson) (Coleoptera: Chrysomelidae) and its parasitoids. *Journal of Natural History*, **21**, 545-556.

Waring, R.H., McDonald, A.J.S., Larsson, S., Ericsson, S., Wiren, A., Arwidsson, E., Ericsson, A. & Lohammar, T. (1985) Differences in chemical composition of plants grown under constant relative growth rates with stable mineral nutrition. *Oecologica* (*Berlin*), **66**, 157-160.

Webb, N.R. (1986) *Heathlands*. Collins, London.

Webb, N.R. (1989) The invertebrates of heather and heathland. *Botanical Journal of the Linnaean Society*, **101**, 307-312.

White, T.C.R. (1976) Weather, food and plagues of Locusts. *Oecologica*, **22**, 119-134.

Whitehead, S.J., Caporn, S.J.M. & Press, M.C. (1997) Effects of elevated CO_2, nitrogen and phosphorous on the growth and photosynthesis of two upland perennials: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist*, **135**, 201-211.

Wiklund, C. & Edelson, J.V. (1988) Sexual size dimorphism in relation to fecundity in some Swedish Satyrid butterflies. *American Naturalist*, **131**, 132-138.

Williams, D.W. & Liebhold, A.M. (1995) Herbivorous insects and global change: potential changes in the spatial distribution of forest defoliator outbreaks. *Journal of Biogeography*, **22**, 665-671.

Wong, M.H. (1975) Seasonal fluctuations of nutrients in soil and leaf tissue of heather *(Calluna vulgaris* (Hull. L.)). *International Journal of Ecological and Environmental Science,* **1**, 167-174.

Woodson, W.D. & Edelson, J.V. (1988) Developmental rate as a function of temperature in a carrot weevil, *Listronotus texanus*. *Annals of the Entomological society of America*, **81**, 252-254.

Worner, S.P. (1992) Performance of phenological models under variable temperature regimes: consequences of the Kaufman or rate summation effect. *Environmental Entomology*, **21**, 689-699.

Wyatt, I.J. & Brown, S.J. (1977) The influence of light intensity, daylength and temperature on increase rates of four glasshouse aphids. *Journal of Applied Ecology*. **14**, 391-399.

Zar, J.H. (1996) *Biostatistical Analysis.* (2^{nd} Edn) Prentice Hall Inc., U.S.A.

Zitzman, A. & May, M.L. (1988) Growth, food consumption, and nitrogen and lipid compositions of the Colorado potato beetle, *Leptinotarsa decemlineata*, (Coleoptera: Chrysomelidae), as a function of the nitrogen supply of its host plant. *Journal of Entomological Science,* **24** (1), 62-69.

Chapter 8: Appendix

Appendix I: Program code for the *Lochmaea suturalis* population dynamics model

The *Lochmaea suturalis* population dynamics model was written in the 'C' programming language. The array structures are accessed from a custom-built array library.

The explanation for each line of code (in bold), is bracketed by the symbols /* and */, and is not read by the program.

```
1   /****
2   *Program code for the Lochmaea suturalis population dynamics model
3   ****/
4
5   %W% %G%                                  /*code for version control using SCCS debugger progam*/
6
7   #include <stdio.h>                       /*declare input/output header file*/
8   #include <math.h>                        /*declare maths library file*/
9   #include <string.h>                      /*declare string header file*/
10  #include <stdlib.h>                      /*declare standard library header file*/
11  #include "array.h"                       /*declare customised  array library file*/
12
13  float gaus ARGS((void));                 /*declare normal deviate function*/
14  float ytemppr ARGS((float));             /*declare initial yesterdays temp function*/
15  int roundup ARGS((float));               /*declare roundup eggs function*/
16  int poissdev ARGS((int));                /*declare Poisson egg function*/
17
18  main()                                   /*main program start*/
19  {                                        /*declare float variables*/
20
21  float   daytemp, eggmort, larmort, pupmort, adultmort, startadults, meaneggmort, stdeggmort, varstdeggmort, meanlarmort,
22  stdlarmort, varstdlarmort, meanpupmort, stdpupmort, varstdpupmort, meanadultmort, stdadmort, varstdadmort,
23  meanbreedmort, stdbmort, varstdbmort, meanwmort, stdwmort, varstdwmort, meansexratio, stdsexratio, meanegglayt, stdegglayt,
24  varstdegglayt, varstdsexratio, egglayt, sex_ratio, emerth, nextadults, newadults, females, emergthrestemp, egglaytemp, eggs, larva,
25  pupa, eggtolardev, lartopupdev, puptoadudev, wintadultmort, totnewad, breebmort, femalemort, acctemp, daylar, daypup,
```

```
26  dayadu, ytemp, lastytemp, yestemp, sin2piday, realeggs, alt, deviate, varconstant, varsin2piday, varytemp, varalt, predtemp,
27  tempincr, stdlimit196;
28                                                                          /*declare integer variables*/
29
30  int     altchange, reps, repsmax, day, totday, year, numyears, eggstart, eggday, cohort, cohortnum, integgs, flag, numeggs, yearflag,
31          years_toprint;
32
33  ARR *lifehis;                                                           /*declare arrays*/
34  ARR *liferun;
35
36  char altchangefile_longrun[100];                                        /*set up file name*/
37
38  FILE *out3;                                                             /*declare file pointer*/
39
40  lifehis = arrnew(6,365,D_FLOAT);                                        /*declare array sizes and types*/
41  liferun = arrnew(1,100,D_FLOAT);
42
43  for(altchange = 0; altchange <= 500; altchange += 50)                   /*loop for different altitudes; 50 m increments, up to 500 m*/
44      {
45      sprintf(altchangefile_longrun,"/data/jim/lochsut_data/ycoeyr100-50%dm.dat",altchange);      /*loop through files*/
46
47      out3 = fopen(altchangefile_longrun,"w");                            /*open file to write to*/
48
49      repsmax = 100;                                                      /*set maximum number of replications*/
50
51      for(rep = 1; reps <= repsmax; reps ++)                              /*replication loop*/
52          {
```

```
53  arr_zero(liferun);                                  /*zero array liferun*/
54  numyears = 50;                                      /*number of years run*/
55  years_toprint;                                      /*number of years to print*/
56  tempincr = 0.0;                                     /*temp increase-added to each mean daily temperature above base (i.e. 1.0-6.0)*/
57  srand(time(NULL);                                   /*take random number seed from computer time*/
58  startadults = 1000000.0;                            /*set number of initial adults*/
59  alt = altchange;                                    /*assign altitude of present loop to altitude variable*/
60  nextadults = 0.0;                                   /*initialise nextadults to zero*/
61  day = 0.0;                                          /*initialise day number to zero*/
62  predtemp = 0.0;                                     /*initialise predicted day temperature to zero*/
63  deviate = 0.0;                                      /*initialise normal standard deviate to zero*/
64  sin2piday = 0.0;                                    /*initialise sin2piday to zero*/
65  daytemp = 0.0;                                      /*initialise day temperature to zero*/
66  yearflag = 0;                                       /*initialise year flag to zero*/
67  ytemp = 0.0;                                        /*initialise yesterdays temp to zero*/
68  lastytemp = 0.0;                                    /*initialise last day of years temp to zero*/
69  meansexratio = 0.5985;                              /*initialise mean sex ratio to 0.5985*/
70  stdsexratio = 0.046;                                /*initialise standard deviation of sex ratio to 0.046*/
71  meanegglaytemp = 12.5;                              /*initialise mean egg laying temp to 12.5*/
72  stdegglaytemp = 1.8708;                             /*initialise standard deviation of egg laying temp to 1.8708*/
73  eggmort = 0.0;                                      /*initialise egg mortality to zero*/
74  meaneggmort = 0.9789;                               /*initialise mean egg mortality to 0.9789*/
75  stdeggmort = 0.0284;                                /*initialise standard deviation of egg mortality to 0.0284*/
76  varstdeggmort = 0.0;                                /*initialise variation of s.d. of egg mortality*/
77  larmort = 0.0;                                      /*initialise larval mortality to zero*/
78  meanlarmort = 0.9852;                               /*initialise mean of larval mortality to 0.9852*/
79  stdlarmort = 0.0147;                                /*initialise standard deviation larval mortality to 0.0147*/
```

```
varstdlarmort = 0.0;          /*initialise variation of s.d. of larval mortality to zero*/
pupmort = 0.0;                /*initialise pupal mortality to zero*/
meanpupmort = 0.9670;         /*initialise mean of pupal mortality to 0.9670*/
stdpupmort = 0.025;           /*initialise standard deviation pupal mortality to 0.025*/
varstdlarmort = 0.0;          /*initialise variation of s.d. of pupal mortality to zero*/
adultmort = 0.0;              /*initialise adult mortality to zero*/
meanadultmort = 0.9965;       /*initialise mean of adult mortality to 0.9965*/
stdadultmort = 0.0044;        /*initialise standard deviation adult mortality to 0.0044*/
varstdadultmort = 0.0;        /*initialise variation of s.d. of adult mortality to zero*/
breedmort = 0.0;              /*initialise breeding female mortality to zero*/
meanbreedmort = 0.9766;       /*initialise mean of breeding female mortality to 0.9766*/
stdbmort = 0.0094;            /*initialise s.d. breeding female mortality to 0.0094*/
varstdbmort = 0.0;            /*initialise variation of s.d. of breed. female mort. to zero*/
wintadultmort = 0.0;          /*initialise winter adult mortality to zero*/
meanwmort = 0.9969;           /*initialise mean of winter adult mortality to 0.9969*/
stdwmort = 0.0038;            /*initialise s.d. of winter adult mortality to 0.0038*/
varstdwmort = 0.0;            /*initialise variation of s.d. of winter adult mort. to zero*/
femalemort = 0.50;            /*initialise non-breeding female mortality to 0.50*/
eggtolardev = 362.0;          /*initialise egg to larvae accumulated day degrees to 362.0*/
lartopupdev = 757.0;          /*initialise larva to pupa accumulated day degrees to 757.0*/
puptoadudev = 1067.0;         /*initialise pupa to adult acc. day degrees to 1067.0*/

for(year = 1; year <= numyears; year ++)   /*loop for number of years run in each replication*/
    {
    yearflag ++;              /*increment yearflag*/
    arr_zero(lifehis);        /*zero array lifehis*/
    daytemp = 0.0;            /*initialise day temperature to zero*/
```

```
107     acctemp = 0.0;                  /*initialise accumulated temperature to zero*/
108     varconstant = 0.0;              /*initialise variation of constant to zero*/
109     varsin2piday = 0.0;             /*initialise variation of sin2piday coefficient to zero*/
110     varytemp = 0.0;                 /*initialise variation of yesterdays temp coefficient to zero*/
111     varalt = 0.0;                   /*initialise variation of altitude coefficient to zero*/
112     varstdegglayt = 0.0;            /*initialise variation of s.d. of egg laying temp to zero*/
113     varstdsexratio = 0.0;           /*initialise variation of s.d. of sex ratio to zero*/
114     sex_ratio = 0.0;                /*initialise sex ratio to zero*/
115     egglayt = 0.0;                  /*initialise egg laying temperature to zero*/
116     emerth = 5.0;                   /*initialise emergence threshold temperature to five degrees*/
117     flag = 0.0;                     /*initialise flag to zero*/
118     eggstart = 0.0;                 /*initialise eggstart to zero*/
119     cohort = 0;                     /*initialise cohort number to zero*/
120     cohortnum = 0.0;                /*initialise sub-cohort number to zero*/
121     totday = 0;                     /*initialise day total number to zero*/
122     females = 0.0;                  /*initialise number of females to zero*/
123     eggday = 0.0;                   /*initialise day of egg laying to zero*/
124     eggs = 0.0;                     /*initialise number of eggs to zero*/
125     integgs = 0.0;                  /*initialise integer number of eggs to zero*/
126     numeggs = 0.0;                  /*initialise number of eggs to zero*/
127     larva = 0.0;                    /*initialise number of larva to zero*/
128     pupa = 0.0;                     /*initialise number of pupa to zero*/
129     newadults = 0.0;                /*initialise number of new generation adults to zero*/
130
131     do
132         {
```

```
133         deviate = gaus();                   /*repeatedly draw a standard normal deviate from gaus function until absolute value less than
134                                             1.96*/
135         }
136     while(fabs(deviate) > stdlimit196);
137
138     varstdsexratio = deviate * stdsexratio;     /*variation in s.d. of sex ratio assigned deviate multiplied by s.d. of sex ratio*/
139     sex_ratio = meansexratio + varstdsexratio;  /*sex ratio assigned value of mean sex ratio plus variation in s.d. of sex ratio*/
140
141     do
142         {
143         deviate = gaus();                   /*repeatedly draw a standard normal deviate from gaus function until less than 1.96*/
144         }
145     while(fabs(deviate) > stdlimit196);
146
147     varstdegglayt = deviate * stdegglayt;       /*variation in s.d. of egg laying temp assigned deviate multiplied by s.d. of egg laying temp*/
148     egglayt = meanegglayt + varstdegglayt;      /*egg laying temp assigned value of mean egg laying temp plus variation in s.d. of egg laying
149                                                 temp*/
150
151     if(year == 1)                               /*if it is the first year of model run, number of females is assigned the number of initial adults
152                                                 multiplied by the sex ratio and yesterdays temperature is drawn from the altitude and
153                                                 yesterdays temperature function to initialise day temperature model*/
154         {
155         females = startadults * sex_ratio;
156         ytemp = ytemppr(alt);
157         }
158
```

```
159         else                                    /*if this is not the first year of model run, number of females assigned the number of last years
160                                                 adults at the end of the previous year multiplied by the sex ratio and yesterdays temperature is
161                                                 assigned the temperature on the last day of the previous year for the temperature model*/
162         {
163         females = nextadults * sex_ratio;
164         ytemp = lastytemp;
165         }
166
167       for(day = 1; day <= 365; day ++)          /*loop for each day in a year*/
168         {
169         totnewad = 0.0;                         /*initialise total new generation adults for all cohorts on any given day to 0.0*/
170
171         realeggs = 0.0;                         /*initialise actual number of eggs laid per female to 0.0*/
172
173       sin2piday = sin(((float)(day + 64) * 6.28319 / 365.0);    /*assign the sin2piday coefficient a value fro each day*/
174
175       deviate = gaus();                         /*draw a standard normal deviate from gaus function*/
176       varconstant = deviate * 0.1752;           /*variation in temperature models' constant assigned the deviate multiplied by the s.d. of the
177                                                 temperature models' constant*/
178
179       deviate = gaus();                         /*draw a standard normal deviate from gaus function*/
180       varsin2piday = deviate * 0.1060;          /*variation in temperature models' sin2piday coefficient assigned the deviate multiplied by
181                                                 the s.d. of the temperature models' sin2piday coefficient*/
182
183       deviate = gaus();                         /*draw a standard normal deviate from gaus function*/
184       varytemp = deviate * 0.01258;             /*variation in temperature models' yesterdays temp coefficient assigned the deviate multiplied
185                                                 by the s.d. of the temperature models' yesterdays temp*/
```

```
186
187     deviate = gaus();                          /*draw a standard normal deviate from gaus function*/
188     varalt = deviate * 0.0003918;              /*variation in temperature models' altitude coefficient assigned the deviate multiplied by the
189                                                s.d. of the temperature models' altitude coefficient*/
190                                                /*predicted mean daily temperature model*/
191
192     predtemp = (1.7209 + varconstant) – ((1.611 + varsin2piday) * sin2piday) + ((0.78158 + varytemp) * ytemp) –
193                ((0.0007178 + varalt) * alt);
194
195     ytemp = predtemp;                          /*assign predicted temperature to yesterdays temperature*/
196     daytemp = predtemp + tempincr;             /*assign predicted temperature plus daily temperature increase to day temp*/
197
198     if(daytemp < emerth && eggstart == 0)      /*if the day temperature is less than the emergence threshold temperature and egg laying has
199                                                not started, execute the following block*/
200         {
201     do
202         {
203         deviate = gaus();                      /*repeatedly draw a standard normal deviate from gaus function until absolute value less than
204                                                1.96*/
205         }
206     while(fabs(deviate) > stdlimit196);
207
208     varstdwmort = deviate * stdwmort;          /*variation in s.d. of the winter adult mortality assigned deviate multiplied by the
209                                                s.d. of the winter adult mortality*/
210     wintadultmort = meanwmort + varstdwmort;   /*winter adult mortality assigned mean winter adult mortality
211                                                plus the variation in the s.d. of the winter adult mortality*/
212     wintadultmort = wintadultmort >= 1.0 ? 0.999999 : wintadultmort;   /*if the value of the winter adult mortality is equal to or
213                                                greater than 1.0 then assign it the value of 0.999999*/
```

```
214             females *= wintadultmort;                       /*assign the number of females variable the value of females
215                                                             multiplied by the winter adult mortality variable*/
216             }
217
218     if(daytemp >= emerth && daytemp < egglayt && eggstart == 0)   /*if the day temperature is greater than the emergence threshold
219                                                             temperature and egg laying has not started, execute the
220                                                             following block*/
221         {
222         do
223             {
224             deviate = gaus();                               /*repeatedly draw a standard normal deviate from gaus function
225                                                             until absolute value less than 1.96*/
226             }
227          while(fabs(deviate) > stdlimit196);
228
229             varstdadmort = deviate * stdadmort;             /*variation in s.d. of the adult mortality assigned deviate
230                                                             multiplied by the s.d. of the adult mortality*/
231             adultmort = meanadultmort + varstdadmort;       /*winter adult mortality assigned mean adult mortality plus the
232                                                             variation in the s.d. of the adult mortality*/
233             adultmort = adultmort >= 1.0 ? 0.999999 : adultmort;   /*if the value of the adult mortality is equal to or greater than
234                                                             1.0 then assign it the value of 0.999999*/
235             females *= adultmort;                           /*assign the number of females variable the value of females
236                                                             multiplied by the adult mortality variable*/
237             }
238
239     if(daytemp >= egglayt)                                  /*if the day temperature is greater than the egg laying
240                                                             temperature, execute the following block*/
241         {
```

```
                eggday ++;                                              /*start egg day counter*/
                                                                        /*model to predict the number of eggs laid per female on a given
                                                                        day*/
                eggs = exp((-0.007423 * ((float)eggday * (float)eggday)) + (0.2627 * (float)eggday) + (0.1922 * daytemp) – 4.930);
                integgs = roundup(eggs);                                /*function call to round up or down float value for eggs
variable*/
                if(integgs >= 1)
                    {
                    numeggs = poissdev(integgs);                        /*function call to return an integer Poisson deviate given an
                                                                        integer number of eggs greater than 1*/
                    }
                if(numeggs >= 1)                                        /*if number of eggs laid per female is equal to or greater than 1
                                                                        execute the following block*/
                    {
                    cohort ++;                                          /*start cohort counter*/
                    acctemp = 0.0;                                      /*initialise accumulated temperature to 0.0*/
                    eggstart = 1;                                       /*initialise eggstart to 1*/
                    realeggs = females * (float)numeggs;                /*numbers of eggs laid by females assigned the  value of the
                                                                        number of females multiplied by the predicted number of eggs
                                                                        laid per female*/
                    numeggs = 0;                                        /*initialise number of eggs to 0*/
```

```
269             arr_put(lifehis,1,cohort,realeggs);          /*place into column 1 and row cohort (number) of the array
270                                                          lifehis the number of eggs laid by all females*/
271             arr_put(lifestage,1,day,realeggs);           /*place into column 1 and row day (number) of the array
272                                                          lifestage the number of eggs laid by all females*/
273             arr_put(lifehis,5,cohort,acctemp);           /*place into column 5 and row cohort (number) of the array lifehis
274                                                          the accumulated temperature*/
275             }
276         }
277
278     if(eggstart == 1 && daytemp > emerth)                /*if eggstart is equal to 1 and the days temperature is greater than
279                                                          emergence threshold temperature execute the following block*/
280         {
281         do
282             {
283             deviate = gaus();                            /*repeatedly draw a standard normal deviate from gaus function
284                                                          until absolute value less than 1.96*/
285             }
286         while(fabs(deviate) > stdlimit196);
287
288         varstdbmort = deviate * stdbmort;                /*variation in s.d. of the breeding female mortality assigned deviate
289                                                          multiplied by the s.d. of the breeding female mortality*/
290         breedmort = meanbreedmort + varstdbmort;         /*breeding female mortality assigned mean breeding female plus the
291                                                          variation in the s.d. of the breeding female mortality*/
292         breedmort = breedmort >= 1.0 ? 0.999999 : breedmort;  /*if the value of the adult mortality is equal to or greater than 1.0
293                                                          then assign it the value of 0.999999*/
294         }
295
```

```
296     if(eggstart == 1 && daytemp <= emerth)                  /*if eggstart is equal to 1 and the day s temperature is less than or
297                                                             equal to emergence threshold temperature*/
298         {
299         females *= femalemort;                              /*assign the number of females variable the value of females
300                                                             multiplied by the female mortality variable*/
301         }
302
303     do
304         {
305         deviate = gaus();                                   /*repeatedly draw a standard normal deviate from gaus function
306                                                             until absolute value less than 1.96*/
307         }
308     while(fabs(deviate) > stdlimit196);
309
310     varstdeggmort = deviate * stdeggmort;                   /*variation in s.d. of the egg mortality assigned deviate multiplied by
311                                                             the s.d. of the egg mortality*/
312     eggmort = meaneggmort + varstdeggmort;                  /*egg mortality assigned mean egg mortality plus the variation in the
313                                                             s.d. of the egg mortality*/
314     eggmort = eggmort >=1.0 ? 0.999999 : eggmort;           /*if the value of the egg mortality is equal to or greater than 1.0 then
315                                                             assign it the value of 0.999999*/
316
317     do
318         {
319         deviate = gaus();                                   /*repeatedly draw a standard normal deviate from gaus function
320                                                             until absolute value less than 1.96*/
321         }
322     while(fabs(deviate) > stdlimit196);
```

```
varstdlarmort = deviate * stdlarmort;                  /*variation in s.d. of the larval mortality assigned deviate multiplied
                                                       by the s.d. of the larval mortality*/

larmort = meanlarmort + varstdlarmort;                 /*larval mortality assigned mean larval mortality plus the variation
                                                       in the s.d. of the  female larval mortality*/

larmort = larmort >=1.0 ? 0.999999 : larmort;          /*if the value of the larval mortality is equal to or greater than 1.0
                                                       then assign it the value of 0.999999*/

do
    {
    deviate = gaus();                                  /*repeatedly draw a standard normal deviate from gaus function
                                                       until absolute value less than 1.96*/

    }
while(fabs(deviate) > stdlimit196);
varstdpupmort = deviate * stdpupmort;                  /*variation in s.d. of the pupal mortality assigned deviate multiplied
                                                       by the s.d. of the pupal mortality*/

pupmort = meanpupmort + varstdpupmort;                 /*pupal mortality assigned mean pupal mortality plus the variation
                                                       in the s.d. of the pupal mortality*/

pupmort = pupmort >=1.0 ? 0.999999 : pupmort;          /*if the value of the pupal mortality is equal to or greater than 1.0
                                                       then assign it the value of 0.999999*/

if(cohort > 0)                                         /*if the cohort number is greater than zero then execute the
                                                       following block*/

    {
    for(cohortnum = 1; cohortnum <= cohort; cohortnum ++)   /*loop for each cohort*/
        {
        acctemp = arr_fget(lifehis,5,cohortnum);       /*retrieve from column 5 and row cohortnum  of the array, lifehis
                                                       the accumulated temperature*/

    if(daytemp >= emerth)                              /*if the day temperature is greater than or equal to the emergence
                                                       threshold temperature then execute the following block*/

        {
```

```
351        acctemp += daytemp;                                  /*the accumulated temperature is assigned the the value of daytemp
352                                                             plus the present days temperature
353        }
354
355     arr_put(lifehis,5,cohortnum,acctemp);                   /*place into column 5 and row cohortnum  of the array lifehis the
356                                                             accumulated temperature*/
357     flag = arr_fget(lifehis,6,cohortnum);                   /*retrieve from column 6 and row cohortnum  of the array, lifehis
358                                                             the value of variable flag*/
359     arr_put(lifehis,6,cohortnum,(float)flag);               /*place into column 6 and row cohortnum  of the array lifehis the
360                                                             float value of variable flag*/
361     if(acctemp <= eggtolardev)                              /*if the accumulated temperature for the cohort is <= the
362                                                             accumulated day degrees for that cohort, execute the following
363                                                             block*/
364        {
365        flag = 1;                                            /*assign flag the value of 1*/
366        arr_put(lifehis,6,cohortnum,acctemp);                /*place into column 6 and row cohortnum of the array lifehis the
367                                                             value of the accumulated temperature for that cohort
368
369        arr_put(lifehis,1,cohortnum, (arr_fget(lifehis,1,cohortnum) * eggmort));   /*subject eggs in cohort to egg
370                                                                                    mortality*/
371        }
372
373     If(acctemp > eggtolardev && flag==1)                    /*if the accumulated temperature of the cohort is > the egg to larval
374                                                             development day degrees and the flag is set to 1, execute the
375                                                             following block*/
376        {
377        larva = arr_fget(lifehis,1,cohortnum);               /*eggs in cohort change to larvae*./
```

```
                arr_put(lifehis,2,cohortnum,larva);          /*place number of larvae in array lifehis, column 2, row
cohortnum*/
                arr_put(lifehis,1,cohortnum,0.0);            /*reset cell of array lifehis, column 1, row cohortnum to zero*/
                flag = 2;                                    /*set flag to 2*/
                arr_put(lifehis,6,cohortnum,(float)flag);    /*put float value of flag in array lifehis, column 6, row cohortnum*/
                }

        else if (acctemp > eggtolardev && acctemp < lartopupdev && flag==2)
                                                             if the accumulated temperature of the
                                                             cohort is > the egg to larval development
                                                             day degrees and < the larval to pupal
                                                             development day degrees and the flag is 2,
                                                             execute the following block*/
                {
                larva = arr_fget(lifehis,2,cohortnum) * larmort;   /*subject larvae in cohort to larval mortality*/
                arr_put(lifehis,2,cohortnum,larva);                /*put number of larvae in array lifehis, column 2, row cohortnum*/
                }

        If(acctemp > lartopupdev && flag==2)                 /*if the accumulated temperature of the cohort is > the larval to
                                                             pupal development day degrees and the flag is set to 2, execute the
                                                             following block*/
                {
                pupa = arr_fget(lifehis,2,cohortnum);        /*larvae in cohort change to pupae*./
                arr_put(lifehis,3,cohortnum,pupa);           /*place number of pupae in array lifehis, column 3, row
cohortnum*/
                arr_put(lifehis,2,cohortnum,0.0);            /*reset cell of array lifehis, column 2, row cohortnum to zero*/
                flag = 3;                                    /*set flag to 3*/
                arr_put(lifehis,6,cohortnum,(float)flag);    /*put float value of flag in array lifehis, column 6, row cohortnum*/
                }
```

```
406
407     else if (acctemp > lartopupdev && acctemp < puptoadudev && flag==3)     if the accumulated temperature of the cohort is
408                                                                             > the larval to pupal development day degrees
409                                                                             and < the pupal to adult development day
410                                                                             degrees and the flag is 3, execute the following
411                                                                             block*/
412         {
413         pupa = arr_fget(lifehis,3,cohortnum) * pupmort;          /*subject pupae in cohort to pupal mortality*/
414         arr_put(lifehis,3,cohortnum,pupa);                       /*put number of pupae in array lifehis, column 3, row cohortnum*/
415         }
416
417     If(acctemp > puptoadudev && flag==3)                         /*if the accumulated temperature of the cohort is > the pupal to adult
418                                                                  development day degrees and the flag is set to 3, execute the
419                                                                  following block*/
420         {
421         newadults = arr_fget(lifehis,3,cohortnum);               /*pupae in cohort change to new generation adults*./
422         arr_put(lifehis,4,cohortnum,newadults);                  /*place number of new generation adults in array lifehis, column 4,
423                                                                  row cohortnum*/
424         arr_put(lifehis,3,cohortnum,0.0);                        /*reset cell of array lifehis, column 3, row cohortnum to zero*/
425         flag = 4;                                                /*set flag to 4*/
426         arr_put(lifehis,6,cohortnum,(float)flag);                /*put float value of flag in array lifehis, column 6, row cohortnum*/
427         }
428
429     else if (acctemp > puptoadudev && flag==4 && daytemp > emerth)   /*if the accumulated temperature of the cohort
430                                                                      is > the pupal to adult development day degrees
431                                                                      and the flag is 4 and the temperature is > the
432                                                                      emergence temperature threshold, execute the
433                                                                      following block*/
```

```
434             {
435             newadults = arr_fget(lifehis,4,cohortnum) * adultmort;          /*subject new adults in the cohort to adult
436                                                                             mortality*/
437             arr_put(lifehis,4,cohortnum,newadults);                         /*put number of new generation adults in array
438                                                                             lifehis, column 3, row cohortnum*/
439             }
440
441         else if (acctemp > puptoadudev && flag==4 && daytemp < emerth)      /*if the accumulated temperature of the cohort
442                                                                             is > the pupal to adult development day degrees
443                                                                             and the flag is 4 and the temperature is < the
444                                                                             emergence temperature threshold, execute the
445                                                                             following block*/
446             {
447             newadults = arr_fget(lifehis,4,cohortnum) * wintadultmort;      /*subject new adults in the cohort to winter
448                                                                             adult mortality*/
449                 arr_put(lifehis,4,cohortnum,newadults);                     /*put number of new generation adults in array
450                                                                             lifehis, column 3, row cohortnum*/
451                 }
452
453             }                                                               /*end of individual cohort loop*/
454
455         cohortnum = cohortnum-1;                                            /*adjust cohortnum loop*/
456         }                                                                   /*end of all cohorts loop*/
457
458     for(totday = 1; totday <= cohort; totday ++)                            /*loop through all cohorts*/
459         {
460         totnewad += arr_fget(lifehis,4,totday);                             /*for each day total the new generation adults*/
461         }
```

```
462
463         totday = totday-1;                                          /*adjust total day counter*/
464
465         if(day==365)                                                /*if dayis equal to 365, execute the following block*/
466             {
467             arr_put(liferun,1,year,totnewad);                       /*put into array liferun,column 1, row year the number of new
468                                                                       generation adults at the end of that year*/
469             fprintf(out3,"%d %d %d %-12d\n",altchange,reps,year,(int)arr_fget(liferun,1,year));
470
471                                                                     /*print to file the altitude of the run, the number of the replicate, the
472                                                                       year, and the total number of new generation adults at the end of the
473                                                                       year
474             }
475
476         }                                                           /*end of day loop*/
477
478             nextadults = totnewad;                                  /*the total of new generation adults at the years end is assigned to
479                                                                       the value of the new years adult population*/
480
481             lastytamp = ytemp;                                      /*the temperature on thre last day of the year is assigned to the
482                                                                       yesterdays component of the temperature model*/
483
484             day = day-1;                                            /*adjust daycounter*/
485             }                                                       /*end of year loop*/
486         }                                                           /*end of replicates loop*/
487
488     fclose(out3);                                                   /*close file*/
489     }                                                               /*end of altitude loop*/
```

```
490
491     arr_rel(lifehis);                       /*release array lifehis from memory*/
492     arr_rel(liferun);                       /*release array liferun from memory*/
493     return 0;
494     }                                       /*end of main program*/
495
496
497
498
499     /****
500     *
501     *function to return a random normal standard deviate
502     *
503     ****/
504
505     float gaus()
506         {
507         float iset,r,fac,gasdev,v1,v2;
508
509         int checker;
510
511         iset = 0.0;
512         r = 10.0;
513         v1 = 0.0;
514         v2 = 0.0;
```

```
515         fac = 0.0;
516         gasdev = 0.0;
517
518     while(iset==0.0)
519         {
520         while(r >= 1.0)
521             {
522             v1 = (double) (rand() %100 /100.0;
523             checker = rand() %1000;
524
525             if(checker < 499)
526                 {
527                 v1 = v1 * -1.0;
528                 }
529
530             v2 = (double) (rand() %100 /100.0;
531             checker = rand() %1000;
532
533             if(checker < 499)
534                 {
535                 v2 = v2 * -1.0;
536                 }
537             r = (v1 * v1) + (v2 * v2);
538             }
539
540         fac = sqrt(-2.0 * log ( r ) / r);
541         gasdev = v1 * fac;
```

```
542         iset = 1.0;
543         r = 10.0;
544         }
545
546     return gasdev;
547
548     }
549
550
551
552
553     /****
554     *
555     *function for generating a Poisson deviate from an integer
556     *
557     ****/
558
559
560     int poissdev(num)
561     int num;
562
563         {
564         int n;
565         float p, c, u;
566
```

```
567         p = 1.0;
568         n = 0;
569
570         c = exp(-(double)num);
571
572         while(p > c)
573             {
574             u = (double) rand() %10000000 / 10000000.0;
575             p = p * u;
576             n++;
577             }
578
579          n = n-1;
580
581         return (n);
582         }
583
584
585
586
587
588
589
590
591
592
593
```

```
/****
*
*function for rounding of floating values
*
****/


int roundup(fin)
float fin;

    {
    int iout;
    float lowervalue, mantissanum, abscissanum;

    lowervalue = floor(fin);
    mantissanum = fmod(fin,1.0);
    abscissanum = (mantissanum >= 0.5) ? (1.0) : (0.0);
    iout = (lowervalue + abscissanum);

    return (iout);
    }
```

```
/****
*
*function to predict yesterdays temperature
*
****/


float ytemppr (alt)
float alt;

    {
    float yestemp, deviate1, deviate2, varcoeff1, varcoeff2, stdevcoeff1, stdevcoeff2;
    stdevcoeff1 = 0.5449;
    stdevcoeff2 = 0.001489;
    deviate1 = gaus();
    varcoeff1 = deviate1 * stdevcoeff1;
    deviate2 = gaus();
    varcoeff2 = deviate2 * stdevcoeff2;

    yestemp = (1.3675 + varcoeff1) – ((0,003675 + varcoeff2) * alt);

    return (yestemp);
    }
```

Appendix II: Study site evaluations

During the autumn of 1994, 21 locations within the study region were investigated for their suitability as field sites, (see Map 2-1, page 19). At each site the altitude (taken to the nearest 10 m), the aspect (taken to the nearest 22.5 degrees) and the gradient (estimated by trigonometry) were recorded by reference to the appropriate Ordnance Survey maps at 1:25000 scale. The drift and solid geology were recorded by reference to the appropriate Ordnance Survey map (1:50000). Soil type was recorded by reference to the appropriate Soil Survey of England and Wales soil association map (1:50000).

Meteorological Office records were consulted for the rainfall and temperature. Rainfall (mm) was recorded as the total annual average over the period 1987-1990 at the nearest rainfall recording station to each site. Temperature (°C) was recorded as the annual average over the period 1951-80. The maximum and minimum air and 30 cm soil depth temperatures were recorded from the average over the period 1988-1991. The temperature data was taken from the nearest meteorological station to each site viz. Haydon Bridge (H); Kielder Castle (K); Redesdale (R). Vegetation cover (whether *Calluna* dominant or co-dominant *C.vulgaris* - *E.vaginatum*) and growth phase were recorded by visual estimation. The management of the sites was determined by a combination of information supplied by the landowners and on-site observation.

The following nine study sites were chosen for the *Lochmaea suturalis* population dynamics study. Selection was based on optimising the variation between heather moorlands, encompassing as wide a range of environmental and soil conditions as possible.

NY 822917 Padon Hill, 1.25 km SSE of Padon Hill monument

Geology: Till on Lower Carboniferous; Lower Limestone group

Altitude, aspect and gradient: 340 m, SW, 0-5°

Soil association: Belmont; Ironpan stagnopodzol

Management: hill sheep grazing

Vegetation and *C.vulgaris* growth phase: heather dominant, mature

Rainfall (mm): 934 at NY834955 (235 m)

Temp (R), Max, Min, Soil: 6.8, 25.5, -6.9, 8.4

NY 712982 Oh Me Edge, East Kielder Moor

Geology: Lower Carboniferous; Fell sandstone and Cementstone Group

Altitude, aspect and gradient: 450 m, S, 0-2°

Soil association: Winter Hill, Raw oligo-fibrous peat soil

Management: none (SSSI)

Vegetation and *C.vulgaris* growth phase: heather dominant, mature

Rainfall (mm): 1464 at NY632935 (201 m)

Temp (K), Max, Min, Soil: 7.0, 26.0, -9.8, 9.1

NY 690972 Sandy's Gears, 2.4 km ESE of Kielder Head

Geology: Alluvium on Lower Carboniferous, Scremerston Coal Group

Altitude, aspect and gradient: 350 m, S, 0-2°

Soil association: Wilcocks 1, Cambic stagnohumic gley

Management: none

Vegetation and *C.vulgaris* growth phase: heather dominant, degenerate

Rainfall (mm): 1464 at NY632935 (201 m)

Temp (K), Max, Min, Soil: 7.0, 26.0, -9.8, 9.1

NY 704869 Yarrow, 1 km WSW of Yarrow

Geology: Lower Carboniferous; Upper Border group

Altitude, aspect and gradient: 200 m, NNW, 0-5°

Soil association: Belmont; Ironpan stagnopodzol

Management: none

Vegetation and *C.vulgaris* growth phase: heather dominant, degenerate

Rainfall (mm): 1109.25 at NY707869 (196 m)

Temp (K), Max, Min, Soil: 7.0, 26.0, -9.8, 9.1

NY 794662 Thorngrafton Common, 1 km NE of Thorngrafton

Geology: Lower Carboniferous, Upper Limestone group

Altitude, aspect and gradient: 200 m, SSE, 0-5°

Soil association: Brickfield 3, Cambic stagnogley

Management: hill sheep grazing

Vegetation and *C.vulgaris* growth phase: heather dominant, degenerate

Rainfall (mm): 735.75 at NY839645 (82 m)

Temp (H), Max, Min, Soil: 8.3, 28.3, -7.1, 10.2

NY 868455 Allenheads, 0.8 km E of Allenheads

Geology: Upper Carboniferous; Upper Limestone Group

Altitude, aspect and gradient: 500 m, WSW, 10-15°

Soil association: Wilcocks 1, Cambic stagnohumic gley

Management: hill sheep grazing and grouse

Vegetation and *C.vulgaris* growth phase: heather dominant, mature

Rainfall (mm): 1131 at NY889479 (421 m)

Temp (W), Max, Min, Soil: 6.3, 25.2, -7.9, 7.0

NY 940466 Huntstanworth Moor, 0.75 km WSW of Boltshope

Geology: Upper Carboniferous; Millstone Grit Series

Altitude, aspect and gradient: 450 m, NE, 0-5°

Soil association: Brickfield 3, Cambic stagnogley

Management: hill sheep grazing

Vegetation and *C.vulgaris* growth phase: heather, mature/degenerate

Rainfall (mm): 916 at NY960478 (397 m)

Temp (W), Max, Min, Soil: 6.3, 25.2, -7.9, 7.0

NY 984539 Slaley, 0.8 km ENE of High Actonmill

Geology: Upper Carboniferous; Millstone Grit series - Sandstone

Altitude, aspect and gradient: 295 m, SE, 0-2°

Soil association: Wilcocks 1, Cambic stagnohumic gley

Management: grouse moor

Vegetation and *C.vulgaris* growth phase: heather dominant, mature

Rainfall (mm): 780 at NY979537 (259 m)

Temp (H), Max, Min, Soil: 8.3, 28.3, -7.1, 10.2

NY 901545 Kings Law, Hexhamshire Common

Geology: Upper Carboniferous; Millstone Grit Series

Altitude, aspect and gradient: 350 m, ENE, 0-5°

Soil association: Brickfield 3, Cambic stagnogley

Management: hill sheep grazing and grouse

Vegetation and *C.vulgaris* growth phase: heather dominant, mature

Rainfall (mm): 780 at NY979537 (259 m)

Temp (H), Max, Min, Soil: 8.3, 28.3, -7.1, 10.2