

Thesis  
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# **INSECTS ON FARMLAND AND THEIR IMPORTANCE TO GRANIVOROUS BIRDS**

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## **Abstract**

Many species of farmland birds have shown huge declines in numbers and range since the 1970s due to agricultural intensification, and these declines have been worst amongst granivorous species. Recent studies have suggested that low abundance of invertebrate chick food may have been important in driving the declines of a number of granivorous species, however causation has still only been proved for the Grey Partridge, whose decline has been attributed to low chick survival due to the indirect effects of herbicides reducing invertebrate abundance.

We investigated invertebrate declines and how they may have affected farmland bird populations in a number of ways. There is little long-term data on abundance of farmland invertebrates. Thus we first looked at how representative data from a long-running suction trap was of invertebrate abundance on local farmland. Suction trap catches reflected abundance of aerial invertebrates on local farmland, and also to abundance of epigeal invertebrates in many cases, particularly abundances in predominant crop types. Secondly, we looked at spatial and temporal distribution of invertebrates on farmland in order to make recommendations about how to increase invertebrate availability to farmland bird populations. Field margins were by far the most invertebrate rich habitats sampled. Most differences in invertebrate abundance between different crop types were found early in the season, at this time spring barley and spring oilseed rape had very low abundances. Winter wheat had relatively high invertebrate abundance compared to spring barley at this time. Winter oilseed rape and set-aside had relatively high abundances of the crop types sampled.

We investigated how low invertebrate abundance may have affected populations of granivorous passerines by looking for evidence of reproductive trade-offs in a population

of Tree Sparrows, and by supplementary feeding experiments with Tree Sparrow and Yellowhammer chicks. There was no evidence for reproductive trade-offs within years, conversely an effect of individual quality was found. There was some evidence of reproductive trade-offs between years. Supplementary feeding increased the mass of Tree Sparrow first broods early in May but not later in May, and also of chicks with yearling parents, who had a lower provisioning rate. Chicks fledged early in May had a lower survival rate to the following year than chicks fledged later, supplementary feeding and parental age had no effect on chick survival. Supplementary feeding a parent's first brood had no effect on their later reproductive output that season, or on their survival to the next breeding season. Supplementary feeding Yellowhammer chicks early season increased their mass, but had no effect later in the season. This complies with results from a previous study of Yellowhammers in southern England, which showed that a higher proportion of chicks fledge late in the season. Further analysis of this data showed that this was because chicks were more likely to starve early in the season, and also that chick mass was lower early season, even when just looking at chicks which went on to fledge.

Thus, it would appear that low invertebrate abundance was affecting the granivorous passerines looked at most in the early season, and through chick mass and survival.

Measures to increase invertebrate abundance at this time would be beneficial to populations of granivorous passerines.

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<b>Contents</b>	<b>Page</b>
<b>Chapter 1</b> General Introduction	<b>1</b>
<b>Chapter 2</b> Relationships between invertebrates sampled at different spatial scales	<b>16</b>
<b>Chapter 3</b> Spatial and temporal trends of invertebrates on farmland	<b>70</b>
<b>Chapter 4</b> Effects of previous reproductive effort on parents and chicks in a population of Tree sparrows, <i>Passer montanus</i>	<b>132</b>
<b>Chapter 5</b> The effect of supplementary chick-food on a population of Tree Sparrows, <i>Passer montanus</i>	<b>168</b>
<b>Chapter 6</b> The effect of supplementary chick-food on a population of Yellowhammers, <i>Emberiza citrinella</i>	<b>215</b>
<b>Chapter 7</b> General Discussion	<b>246</b>

## Declaration

This thesis is a result of my own research, and no part of this thesis has been submitted in application for a higher degree at this or any other institution. All collaborative involvement has been duly acknowledged.

Signed: J.A. Bala

Date: 5/09/05

# Chapter 1:

## General Introduction

### *Farmland bird declines*

It has been well publicised that many species of farmland birds have shown alarming decreases in range and/or numbers over the past three decades (Baillie *et al.*, 1997, Fuller *et al.*, 1995, Marchant & Gregory, 1994, Siriwardena *et al.*, 1998). These declines have not been paralleled by bird populations in other habitats (Gregory *et al.*, 2000, Fuller *et al.*, 1995), and have been attributed to changes in farming practice (Chamberlain *et al.*, 2000). Intensification of farming methods has been particularly rapid since 1973, when the UK joined the EC. The resulting increase in subsidies reduced market pressures on farmers, which allowed them more freedom to become more mechanised and increased access to new agricultural technology (Donald *et al.*, 2002). Agricultural intensification has led to many practices which have a detrimental effect on farmland wildlife, including birds. These include the loss of mixed farming, the switch from spring to autumn sowing of cereals and associated loss of over-winter stubbles, the switch from hay to silage, increased agrochemical input, and loss of unfarmed structures such as ponds and hedgerows (Evans *et al.*, 1995, O'Connor & Shrub, 1986).

### *Background*

Farmland represents the predominant land use throughout much of western Europe (Robinson & Sutherland, 2002) accounting for 75% of the UK land mass (Evans *et al.*, 2002). Whilst many bird species show no preference for farmland, often preferring other habitats, its predominance in the British landscape means it supports the majority of

populations of many species (Baillie *et al.*, 1997). Prior to the 1990s, conservation effort focused mainly on threatened semi-natural habitats such as heathland, woodland and lowland wet grassland (Evans *et al.*, 2002), and it is relatively recently that the decline of farmland bird populations has been recognised as one of the most pressing bird conservation issues in Europe (Pain & Pienkowski, 1997, Tucker & Dixon, 1997, Newton, 1998).

Annual monitoring of widespread and common bird species began in the 1960s with the Common Bird Census (CBC), run by the British Trust for Ornithology (BTO). Although in retrospect it is clear that the declines of many farmland bird populations began in the mid to late 1970s (Fuller *et al.*, 1995, Siriwardena *et al.*, 1998), the severity of the situation was not realised until much later than this. One of the first indications of the threat posed to farmland wildlife by agricultural intensification came from the Game Conservancy Trust's long-running study of the Grey Partridge, which concluded that declines were due to low chick survival caused by the indirect effect of herbicides in reducing invertebrate chick food (Potts, 1986).

There are several examples where highly targeted conservation action, directing resources to particular aspects of species management, have been very successful at conserving rare or localised species/populations (Aebischer *et al.*, 2000). In the late 1980s, the RSPB began research on three species on the brink of extinction in the UK; the Corncrake, the Stone Curlew and the Cirl Bunting, and this research has formed the basis of management practices which have resulted in population increases (Aebischer *et al.*, 2000).

In the last decade, however, conservation priorities in the UK have switched as huge declines in the populations of widespread and common species associated with farmland have become more apparent (Evans *et al.*, 2002). In 1990, the BTO and Nature Conservancy Council published *Population Trends in British Breeding Birds* (Marchant *et*



*al.*, 1990), which, for the first time, described 25-year trends in the abundance of breeding species as measured by the CBC. In 1995 a number of non-governmental wildlife organisations reviewed trends in abundance in order to revise priorities for bird conservation in the UK (Gibbons *et al.*, 1996). Birds were assigned to the 'Red List' if they had undergone population declines over 50% in the last 25 years, or had undergone a historical decline between 1800 and 1995. Fourteen of the thirty six species were farmland bird species, and ten of these had been previously common and widespread. The Government's Biodiversity Action Plan (Anon., 1995) recognised the severity of the problem, and action plans were published for all 14 red list species of farmland birds (Swash *et al.*, 2000). The Government also recognised the importance of farmland bird conservation by including an index of farmland bird numbers as one of its fourteen 'quality of life' headline indicators of sustainability (DETR, 1999), and later adopting a public service agreement (PSA) to reverse the long-term declines in farmland bird populations by 2020.

### *Seed-eating farmland passerines*

Amongst farmland bird species, granivorous passerines have shown the worst declines (Fuller *et al.*, 1995). Demographic causes of population declines affecting farmland bird populations are productivity and survival, as immigration and emigration are unlikely to be important at the national scale (Paradis *et al.*, 1998), and these are usually broken down as follows;

1. Breeding performance per attempt,
2. Number of breeding attempts per year,
3. Annual survival,
4. Post-fledging survival.

Siriwardena *et al.*, 2000, looked at breeding performance of 12 granivorous species, and found that, with the exception of the linnet, which has little dependence on invertebrates (Wilson *et al.*, 1999), their population declines could not be attributed to decreased breeding performance per attempt. In fact, for five of the species, including Skylarks, Yellowhammers, Tree Sparrows, and Corn Buntings, breeding performance per attempt was higher whilst populations were in decline. However, variation in annual survival and fledgling production per breeding attempt alone could not explain changes in abundance for at least seven species, suggesting that changes in post-fledging survival rates and/or number of breeding attempts per year could have been important.

Reduced survival has also been suggested as contributing to the decline of House Sparrows, Corn Buntings and Cirl Buntings (Baillie *et al.*, 1997). Reduced survival of first-year adult Reed Buntings fully explains their declines (Peach *et al.*, 1999), whilst for the Skylark, declines have been attributed to a combination of reduced over-winter survival and a decline in the number of breeding attempts (Siriwardena *et al.*, 2000, Wilson *et al.*, 1997).

Thus, for granivorous passerines in general, adult survival, in combination with post-fledging survival, and possibly number of breeding attempts per year, seems to be the most likely cause of declines (table 1). This has generally been referred to as 'over-winter survival', however this is an assumption as the survival rates come from Common Birds Census data which just gives annual survival rates.

**Table 1. Suggested demographic mechanisms for declines of some granivorous farmland passerines, shown alongside habitat and food requirements**

Species	Main Habitat	Foraging Habitat	Summer Diet	Winter Diet	Suggested Demographic Mechanism
House Sparrow	Urban	Ground	Seeds & Invert.	Seeds	Adult over-winter survival (Siriwardena <i>et al.</i> , 1998)
Tree Sparrow	Farmland	Ground	Seeds & Invert.	Seeds	? Nesting success increasing during period of decline, points to over-winter survival (Peach <i>et al.</i> , 1999)
Linnet	Farmland	Margins & Ground	Seeds	Seeds	Reduced breeding success (Wilson <i>et al.</i> , 1999)
Bullfinch	Farmland	Hedgerows	Plants & Insects	Plants	Survival alongside other factors (Siriwardena <i>et al.</i> , 1998)
Yellowhammer	Farmland	Ground & Margins	Invert. & Seeds	Seeds	Productivity and Survival (Bradbury <i>et al.</i> , 2000)
Cirl Bunting	Farmland	Ground & Margins	Invert. & Seeds	Seeds	Adult over-winter survival (Evans <i>et al.</i> , 1997)
Reed Bunting	Farmland	Margins & Ground	Invert. & Seeds	Seeds	Adult & First year over-winter survival (Peach <i>et al.</i> , 1999)
Corn Bunting	Farmland	Ground	Invert. & Seeds	Seeds	Adult over-winter survival (Crick, 1997, Donald, 1997)
Skylark	Farmland	Ground	Invert.	Plants & Seeds	No. of breeding attempts per season, possibly alongside reduced survival (Siriwardena <i>et al.</i> , 2000, Wilson <i>et al.</i> , 1997)

It has often been suggested that population declines amongst granivorous species are caused by decreased over-winter survival due to lack of seed food during the winter (Peach *et al.*, 1999, Robinson & Sutherland, 1999, Donald, 1997). Increased herbicide use, increased efficiency of harvesting methods, and loss of winter stubbles have all caused a decrease in the availability of weed and crop seeds for birds to eat in the winter.

However, most of these 'granivorous' passerines are partially insectivorous, at least during the breeding season, when they also rely on invertebrates as a source of high-protein chick food (Baillie *et al.*, 1997). There is evidence that among these declining granivorous passerines those that are more dependent on insects have shown significantly worse declines (Wilson *et al.*, 1999). Invertebrate numbers have been declining in recent decades (Aebischer, 1990, Benton *et al.*, 2002), and relationships have been found between insect abundance and farmland bird population sizes the following year (Benton *et al.*, 2002).

## *Invertebrate Declines*

Changes in agricultural practices in Britain have also affected farmland invertebrates.

Many farmland invertebrate populations have decreased since the introduction of herbicides in the late 1950s, and continued to do so since the 1970s, due to factors such as the huge increase in insecticides, the introduction of foliar fungicides, increased specialisation of farming, loss of uncultivated field margins, ploughing and landscape simplification (Aebischer, 1990, Wilson *et al.*, 1999). Pesticides are usually cited as the primary cause of declines (Aebischer, 1990, Wilson *et al.*, 1999). Pesticides can affect invertebrate populations, both via direct effects through mortality of non-target invertebrates (Moreby *et al.*, 1997, Aebischer, 1990), as well as by indirect effects, for example herbicide use causing loss of weed food, as well as loss of prey and refuges, and changes in microclimate (Moreby & Southway, 1999).

A long-term study of invertebrates on 100 fields in Sussex showed that, when Collembola were excluded from counts, the total number of invertebrates per sample had almost halved between 1979 and 1989 (Aebischer, 1990). However, there is less good long-term data on farmland invertebrate declines, with what data there is often being localised. A good source of long-term invertebrate data comes from the Rothamsted Suction Traps. The first trap was set up in 1963, with the aim of making pesticide applications more effective, and soon there were a network of 16 across Britain. The Stirling suction trap has been collecting invertebrates daily since 1972. However, the suction traps are located in a range of habitats, and so it is not clear how well they relate to abundance of chick food invertebrates available to farmland birds.



## *Trade-offs*

Parents have to make a trade-off as to how much of the available resources they invest in current reproduction at a cost to their future reproduction or 'residual reproductive value' (Trivers, 1972). The outcome of this trade-off will depend on a number of things, including the costs of care and the benefits to the fitness of the offspring (Williams, 1966, Trivers, 1972). Life-history theory predicts that in long-lived species the trade-off will favour the parents, as they will have a higher average residual reproductive value than parents in short-lived species, whilst in short-lived species it will favour the offspring (Linden & Moller, 1989). Previous supplementary feeding experiments on birds have supported this theory (Wernham & Bryant, 1998, Mauck & Grubb, 1995).

In the case of granivorous farmland passerines, a decrease in invertebrate food during the breeding season could have impacted on parents (and/) or chicks. As most granivorous passerines are fairly short-lived, life-history theory would predict that parents would want to maximise their current productivity, and will sacrifice their own condition to maintain that of their chicks. Thus we would predict that as farmland invertebrate numbers have decreased in recent decades, parents will have compensated by working harder at chick-feeding, at a possible cost to their own future survival and reproduction. This could cause parents to be in poor condition at the end of the breeding season, which could lead to low over-winter survival. It is important to investigate this in order to know how to divide conservation action between the seasons.

It is interesting to note here that the Grey Partridge is the only UK farmland bird whose decline is known to have been driven primarily by a reduction in invertebrate chick-food, due to the indirect effects of herbicides (Potts, 1986). This is intriguing as Grey Partridges, unlike passerine species, have precocial young. Thus, given that the above theory was

correct, Grey Partridges, unlike passerines, could not compensate for the reduction in chick food.

### *Aims and Thesis Outline*

This thesis aims to look at farmland invertebrate abundance and distribution, and how these may be affecting granivorous farmland passerine populations. Chapter 2 looks at whether invertebrate data from a long-running Rothamsted-type suction trap relates to invertebrates on local farmland so that conclusions can be made about invertebrate abundance on farmland. Chapter 3 looks at how invertebrates are distributed temporally and spatially on farmland, both between different crop types, and different areas within fields, so that recommendations can be made about how to increase invertebrate food abundance for farmland birds. Chapter 4 looks at how current reproductive effort affects future survival and/or reproduction in a population of Tree Sparrows. In Chapter 5 the response to providing Tree Sparrow chicks from the same population with supplementary food is investigated. Chapter 6 discusses the results of a similar experiment with Yellowhammers in Stirlingshire.

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## **Chapter 2:**

# **Relationships between invertebrates sampled at different spatial scales**

### **Abstract**

Agriculture has become increasingly intensive in the UK in recent decades, and this has resulted in huge declines in the numbers of many species of farmland birds. Changes in agricultural practice have also had a detrimental effect on other farmland biodiversity, such as plants and invertebrates. Recent studies have highlighted the possible importance of low invertebrate abundance in driving declines of farmland bird species. Despite their conservation importance, there is little long-term data on farmland invertebrates. The Stirling suction trap has been collecting aerial invertebrates daily since 1972, and there is a network of 23 suction traps across the UK. These suction traps are in a variety habitats. This study aimed to look at whether invertebrates caught in such suction traps were representative of invertebrate abundance to farmland bird species; first to aerial feeders, and also to ground feeders.

Positive relationships were found between total numbers of invertebrates caught in the Stirling suction trap, and the number caught in a portable suction trap on local farmland. There were significant relationships between numbers of Coleoptera and non-nematoceran Diptera caught in the portable suction trap and the Stirling suction trap, but not between numbers of Nematocera. There were also positive relationships between numbers of invertebrates caught in the Stirling suction trap and epigeal invertebrates caught by the G-vac in the centres of spring barley and pasture fields, which were the most predominant crop types in the surrounding area. In some cases there were also positive relationships between the numbers in the Stirling suction trap and G-vac samples in margins of fields.

## 2.1 Introduction

Agriculture has become increasingly intensive since the Second World War in the UK (Evans *et al.*, 1995, O'Connor & Shrub, 1986), and much of Europe (Pain & Pienkowski, 1997). This intensification has taken form as a suite of changes in farming practice, such as increased agrochemical input, the switch from spring to autumn sowing of cereal crops and subsequent loss of over-winter stubbles, the switch from hay to silage, and the loss of mixed farming and unfarmed structures such as hedgerows and ponds (O'Connor & Shrub, 1986), which have resulted in a reduction in landscape diversity. The resulting declines in farmland bird populations have been well documented (Baillie *et al.*, 1997, Fuller *et al.*, 1995, Marchant & Gregory, 1994, Siriwardena *et al.*, 1998), but the changes have also affected other farmland wildlife, such as plants and invertebrates (Campbell *et al.*, 1997, Sotherton & Self, 2000, Robinson & Sutherland, 2002).

A review of data on farmland invertebrate abundance concluded that many species of invertebrates have been declining on farmland, with the exception of most aphid species (Sotherton & Self, 2000). A long-term study of invertebrate abundance on over 100 cereal fields on the Sussex Downs found that although different invertebrate groups have shown varying trends in recent decades, overall numbers of invertebrates, excluding Collembola, declined by about 50% between 1970 and 1990, and it is predicted that there has probably been a roughly 75% decline in invertebrate abundance in cereal fields since the introduction of herbicides in the 1950s (Aebischer, 1991). Although data from the Rothamsted insect survey, from a network of suction traps in a range of habitats, show that aphid populations have shown little marked change since the 1960s, with a few species having increased (Woiwod, 1991), the Sussex Downs study, which was specific to arable fields, found that aphid numbers had decreased dramatically since the 1970s (Aebischer & Potts, 1990). Data from a network of light traps have shown that macro Lepidoptera have

decreased in numbers on farmland between the periods 1933-1950, and 1960-1989, with no similar decrease being found for woodland traps (Woiwod & Thomas, 1993). A study of ground beetle (Carabidae) diversity in a weedy arable plot in the Tyne Valley has also found a decreasing trend in species of ground beetles since 1981 (Luff, 1990), and similar carabid declines have been shown across Europe (Luff & Woiwod, 1995, Kromp, 1999). Both common and localised butterfly species have decreased in frequency in pastoral north Wales between 1901 and 1997 (Cowley *et al.*, 1999). Declines in butterfly populations have been reported elsewhere in Europe, although they seem less severe in southern Europe, which generally has a less intensively managed landscape (Van Swaay, 1990, Pavlicek-van Beek, Ova & van der Made, 1992). There have also been declines in many bumblebee *Bombus* species in Britain, particularly eastern and central England (Williams, 1986), and throughout Europe (Corbet *et al.*, 1991).

These declines are generally accepted to have been predominantly driven by increased pesticide use; by insecticides killing non-target invertebrates, and by increased herbicide use causing a reduction in plant food and refuges for invertebrates (Aebischer & Potts, 1990, Moreby & Southway, 1999, Sotherton & Self, 2000, Wilson *et al.*, 1997). Other possible factors contributing to invertebrate declines are increased specialisation of farming, decreased undersowing, timing and depth of ploughing, and a reduction in the number of uncultivated field margins (Sotherton & Self, 2000, Wilson *et al.*, 1999).

As well as their own conservation importance, invertebrates are an important food source for farmland birds (Baillie *et al.*, 1997, Wilson *et al.*, 1999). Many farmland bird populations have shown huge decreases in range and abundance over the past three decades, with granivorous species showing the worst declines (Fuller *et al.*, 1995).



However, many of these 'granivorous' species rely on invertebrates as a source of high-protein chick food during the breeding season (Baillie *et al.*, 1997, Wilson *et al.*, 1999) The decline of the Grey Partridge has been attributed to the indirect effect of herbicides leading to lack of invertebrate chick food (Potts, 1986), and lack of invertebrate chick food is also likely to have contributed to the declines of at least three farmland passerine species in the UK (Skylark: Poulsen *et al.*, 1998; Cirl Bunting: Evans *et al.*, 1997; Corn Bunting: Brickle *et al.*, 2000). Amongst declining granivorous species, those which are more dependent upon invertebrate food have shown the worst declines (Wilson *et al.*, 1999)

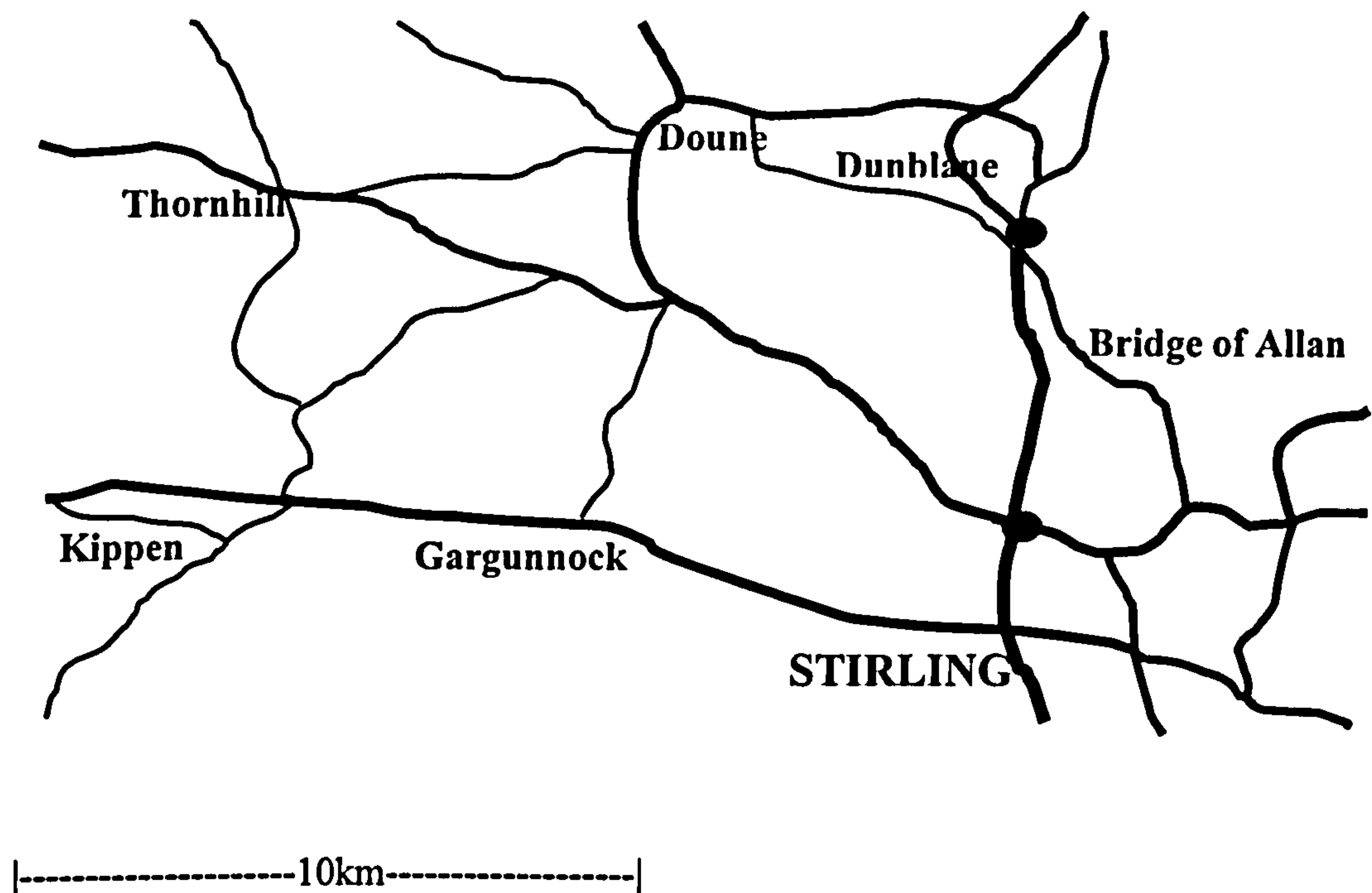
Despite the conservation importance of farmland invertebrates, and the recognised importance of long-term monitoring schemes, there is relatively little long-term national data on invertebrate abundance on farmland (see Sotherton & Self, 2000 for review), with there being little long-term data generally, and much of this being restricted to one location. Long-term monitoring schemes for insects include one for butterflies (Pollard *et al.*, 1995), moths and aphids (Woiwod & Harrington, 1994). The latter of these, the Rothamsted Insect Survey, consists of the suction trap network, and also a network of light traps on the ground which collect Lepidoptera. The Suction Trap Survey was introduced in 1964 in order to make predictions about pest populations and their movements so that insecticides could be applied more efficiently (Taylor, 1973). The first trap was set up in Rothamsted, and there is now a network of 23 suction traps across the UK (Sotherton & Self, 2000). Traps are 12.2m high and collect aerial invertebrates. For most suction traps the main group to be looked at are aphids (Hemiptera: Aphididae). Overall aphid abundances in the suction traps have shown no long-term change, although two species have shown increases (Woiwod & Harrington, 1994).

The Stirling suction trap has operated on the Stirling University campus (grid reference NS812967, 56°08'54'' latitude, -3°54'45'' longitude), Stirling, Scotland since 1972. Invertebrates are trapped in alcohol, and removed daily at 0900h between April and October (Benton *et al.*, 2002). Analysis of a subset of eight sample days per month has shown relationships between insect abundance and farmland bird population sizes the following year (Benton *et al.*, 2002). Suction trap catches have been related to timing of breeding, feeding rates, clutch size, chick growth rates and weights in a number of hirundines (Bryant, 1973, Bryant, 1975, Turner, 1980, Johnston 1990). However, whilst the suction trap is accepted as being suitable for estimating the diet of insectivorous aerial-feeding birds, such as House Martins and Swallows (Bryant, 1973), as traps are 12.2.m high, it is not clear how suitable they are for estimating invertebrate availability for ground-feeding farmland bird species, for example the Yellowhammer and Tree Sparrow. This chapter aims to look for relationships between Stirling suction trap catches and invertebrates sampled on farmland within a 20-mile radius to Stirling University by two different methods, in order to investigate the suitability of suction trap data in predicting availability of invertebrate food for farmland bird species with differing foraging habits.

## 2.2 Methods

### Study Area

The study area was a lowland mixed farming landscape lying largely to the west of Stirling, Scotland (figure 1).



**Figure 1. Map of study area**

Invertebrates were sampled from May to August 2001, and April to August 2002 in 150 fields on 29 farms within a 20 mile radius of Stirling University. Farms were selected pseudorandomly, on the basis of being within the study area and permission for access being granted.

Seven different crop types were sampled, these were: winter wheat; spring barley; winter oilseed rape; spring oilseed rape; silage; pasture and set-aside. The breakdown of these crop types across the study farms is shown in Table 1. The crop types studied accounted for 75% of the fields on study farms, with the rest being largely winter oats. Replicates of

each crop type were sampled on a monthly basis, with different fields being used each month (except for oilseed rape fields which sometimes had to be sampled for several months due to their limited numbers). Different fields were used in order to try to prevent effects of specific farm management from having undue influence on results.

**Table 1. Breakdown of crop and land use types across the 29 farms studied**

<b>Crop Type</b>	<b>% of total no. of fields in study area</b>
Winter Wheat	3
Spring Barley	34
Winter Oilseed Rape	1
Spring Oilseed Rape	1
Set-aside	8
Silage	6
Pasture	22

### **Sampling Methods**

Two different sampling methods were used; these were the portable suction trap and the G-vac. These two different methods were used as they sample different strata in the field, reflecting invertebrates which may be available to birds with different foraging habitats.

The portable suction trap is 2m high and so samples aerial invertebrates and the G-vac was used to sample invertebrates on vegetation, in litter and on the ground.



### ***Portable suction trap***

A Johnson-Taylor insect suction trap was used to sample aerial invertebrates. The trap runs off a generator and consists of a 9-inch diameter fan, with the mouth horizontal, which sucks air through a gauze funnel into a cylindrical collecting magazine. Insecticide-coated discs drop into the collecting cylinder magazine hourly.

The portable suction trap was placed in the 'centre' (at least 50m from the edge) of fields, from 0900 to 1700, when the sample was collected and preserved in 70% ethanol before sorting. Samples were taken on 65 days, 42 of these were between May and September in 2001, and 23 between April and September in 2002, with each crop type being sampled an average of once per month per year.

### ***G-Vac***

The G-Vac was a leaf vacuum which was converted for insect sampling by placing a fine-mesh nylon netting collecting bag over the nozzle (after Stewart & Wright, 1995). A mean of three fields of each of the seven crop types were sampled each month. Three zones of the field were sampled: the uncropped margin (i.e. fence, hedgerow, grassy margin); the cropped edge (4m into the field); and the centre (at least 50m into the field). In each of these three areas a 100m transect was walked, stopping every 10m to take a sub-sample, which was done by running the vacuum down over the vegetation and onto the ground, where it was left for 10s. Invertebrates were collected from the net of the G-vac at the end of the 10s using a pooter. At the end of the transect, the insects collected from the ten points were transferred from the pooter into a polythene bag containing 70% ethanol.

### **Invertebrate Identification**

All invertebrates were counted, and identified to at least order level.

## **2.3 Data Analysis**

Two different types of model were used in the analysis: generalised linear models (GLMs) in S-PLUS and generalised linear mixed models (GLMMs) in GENSTAT. GLMs allow the analysis of non-normal error distributions through the use of linearising transformations specified by link functions. GLMMs, being mixed models, allow the inclusion of random effects, such as blocking factors, to account for non-independence of data points (e.g. when comparing several measurements of invertebrates taken on the same day to a single daily measure). GLMMs also allow analysis of non-normal error distributions by use of linearising link functions.

Unless stated otherwise, minimal models were found by step-wise deletion from a maximal model. Model residuals were checked for normality.

### **Portable suction trap**

GLMs with poisson error and log link were conducted in S-PLUS with total number of invertebrates caught by the Stirling Suction Trap in a day as the dependent variable. The number of invertebrates caught by the portable suction trap on the same day was included as a variable in the model. Other terms included in the model were crop type that the portable suction was sampling in and year, which were included as factors, and day (where April 1<sup>st</sup> = 1), day<sup>2</sup>, temperature (9am temperature at Stirling meteorological station), and wind speed (wind speed at Stirling meteorological station on the Beaufort scale), which were included as variables. Interaction terms included in the model were portable suction trap catch x crop type and wind speed x temperature.

Models were then repeated to look at samples collected in July only (as this was the month with most samples corresponding to it), in order to remove large scale seasonal effects.

Models were also repeated replacing 'total number of invertebrates' with any order which constituted a mean of over 10% of each portable suction trap sample.

## **G-Vac**

As G-vac samples were taken from several different fields on the same day, Generalised Linear Mixed Models (GLMMs) with poisson error and log link were used with 'day' as a random factor. Models were conducted for samples from the three different areas of the field (uncropped margin, cropped edge and centre) separately. Total number of invertebrates in the suction trap was the response variable. Total number of invertebrates caught by the G-vac was a variable. Other terms included in the model were year and crop type the G-vac sample came from, which were included as factors, and temperature, day and day<sup>2</sup> which were included as variables. Interaction terms included in the model were G-vac catch x crop type, G-vac catch x day, G-vac catch x temperature, G-vac catch x year and day x crop type

The total number of invertebrates in the G-vac samples excluded counts of collembola, due to their tiny size and relatively huge numbers.

Models were then repeated for any order or sub-order which made up an average of ten percent or more of G-vac samples.

## 2.4 Results

### Aerial Invertebrates: portable suction trap samples

#### *Total number of invertebrates*

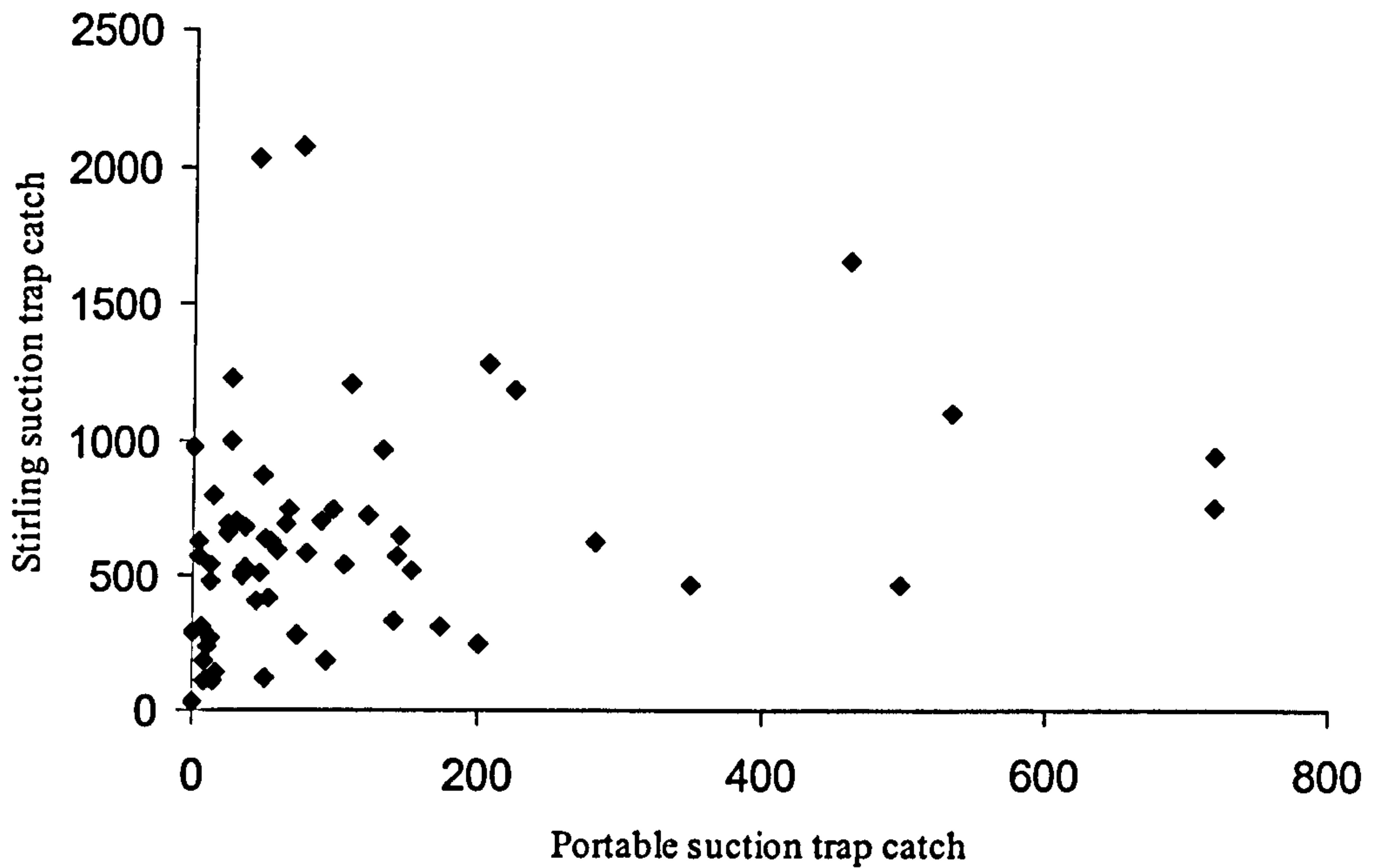
The number of invertebrates caught by the Stirling suction trap was significantly related to the number caught by the portable suction trap on the same day on local farmland (table 2, figure 2). The crop type which the portable suction trap was in was also significant (table 1). Temperature also affected the suction trap catch, with more invertebrates being caught by the Stirling suction trap in warmer weather (table 1). More invertebrates were caught in 2002 than in 2001 (table 1).

**Table 2. GLM relating total number of invertebrates caught in the Stirling suction trap to number caught in the portable suction trap on the same day.**

Significant terms are in bold

Term	d.f.	deviance	p-value
Null model:	60	29.79	
Minimal adequate model:			
<b>Portable suction trap catch</b>	<b>1</b>	<b>1.36</b>	<b>0.035</b>
<b>Crop Type</b>	<b>4</b>	<b>4.53</b>	<b>0.008</b>
<b>Temperature</b>	<b>1</b>	<b>4.16</b>	<b>0.0004</b>
<b>Year</b>	<b>1</b>	<b>6.35</b>	<b>0.00002</b>
Excluded terms:			
Day	1	0.12	0.435
Wind speed	1	0.30	0.313





**Figure 2. Number of invertebrates caught by the portable suction trap and number of invertebrates caught by the Stirling suction trap on the same day**

*Total number of invertebrates: July only*

When analysis was repeated to just look at samples taken in July, in attempt to decrease the influence of large-scale seasonal effects on the results, there was no significant relationship between number of invertebrates caught by the Stirling suction trap and number caught by the portable suction trap (table 3), although the sample size was low (n = 15).

**Table 3. GLM relating total number of invertebrates caught in the Stirling suction trap to number caught in the portable suction trap on the same day for July only.**

Significant terms are in bold

Term	d.f.	deviance	p-value
Null model:	14	10.02	
Excluded terms:			
Wind speed	1	4.38	0.095
Portable suction trap catch	4	2.99	0.111
Crop type	1	0.36	0.302
Temperature	1	0.19	0.427
Year	1	0.43	0.235
Day	1	0.06	0.659

*Analysis by order*

The mean composition of portable suction trap samples, and Stirling suction trap samples for days on which the portable suction trap was used, are given in table 4 (n = 65). The main taxa found in portable suction trap samples were Nematocera (which on average made up 65% of portable suction trap, and 79% of suction trap samples), non-nematoceran Diptera (which make up 15% of portable suction trap samples, but only 3% of suction trap samples on average), and Coleoptera (31% of portable suction trap samples, 5% of suction trap samples).

**Table 4. Main invertebrate taxa found in Stirling suction trap and portable suction trap samples**

	Stirling Suction Trap			Portable Suction trap		
	Mean no. /sample	S. E.	Mean % of sample	Mean no. /sample	S. E.	Mean % of sample
<b>Total</b>	662	20	100	135	15	100
<b>Nematocera</b>	524	11	79	65	17	48
<b>Other Diptera</b>	21	5	3	20	4	15
<b>Hemiptera</b>	60	2	9	1	11	1
<b>Coleoptera</b>	31	12	5	42	7	31
<b>Hymenoptera</b>	15	3	2	5	4	4
<b>Arachnida</b>	7	1	1	0	3	0

Analysis was repeated to look at the relationship between the numbers of these taxa caught in the portable suction trap and those caught in the suction trap separately.

#### *Nematocera*

The number of Nematocera caught by the Stirling suction trap was not related to the number caught by the portable suction trap (table 5). Terms in the model which affected Stirling suction trap catch were year, with more being caught in 2002 than 2001, and temperature, with more being caught in warm weather. The crop type that the portable suction trap sample was from also had a significant effect on the Stirling suction trap catch, but this must have been an artefact of the small sample size.

**Table 5. GLM relating total number of Nematocera caught in the Stirling suction trap to number caught in the portable suction trap on the same day.**

Significant terms are in bold

Term	d.f.	deviance	p-value
Null model:	59	30.99	
Minimal adequate model:			
<b>Year</b>	<b>1</b>	<b>4.72</b>	<b>0.0001</b>
<b>Temperature</b>	<b>1</b>	<b>2.03</b>	<b>0.010</b>
<b>Crop Type</b>	<b>4</b>	<b>3.29</b>	<b>0.032</b>
Excluded terms:			
Wind speed	1	0.20	0.425
Portable suction trap catch	1	0.25	0.368
Day	1	0.11	0.53
Day <sup>2</sup>	1	0.28	0.331

*Non-nematoceran Diptera*

The number of non-nematoceran Diptera caught by the Stirling suction trap was significantly related to the number caught in the portable suction trap on the same day (table 6). There was also a significant effect of crop type which the portable suction trap was in (table 6). Date also affected the number of non-nematoceran Diptera caught in the Stirling suction trap (table 6).



**Table 6. GLM relating total number of non-nematoceran Diptera caught in the Stirling suction trap to number caught in the portable suction trap on the same day.**

Significant terms are in bold

Term	d.f.	deviance	p-value
Null model:	59	76.20	
Minimal adequate model:			
<b>Portable suction trap catch</b>	<b>1</b>	<b>5.13</b>	<b>0.011</b>
<b>Crop type</b>	<b>4</b>	<b>16.10</b>	<b>0.0009</b>
<b>Day</b>	<b>1</b>	<b>12.72</b>	<b>0.0001</b>
Excluded terms:			
Wind speed	1	0.03	0.864
Year	1	1.05	0.265
Temperature	1	1.50	0.185
Day <sup>2</sup>	1	0.23	0.60

### *Coleoptera*

The number of Coleoptera caught by the Stirling suction trap significantly related to the number caught by the portable suction trap, with this effect differing depending upon crop type that the portable suction trap was taken from (table 7). Terms which also affected the number of Coleoptera caught by the Stirling suction trap were year, date and wind speed. (table 7).

**Table 7. GLM relating total number of Coleoptera caught in the Stirling suction trap to number caught in the portable suction trap on the same day.**

Significant terms are in bold

Term	d.f.	deviance	p-value
Null model:	58	137.79	
Minimal adequate model:			
<b>Portable suction trap catch x crop type</b>	<b>4</b>	<b>18.98</b>	<b>0.008</b>
<b>Portable suction trap catch</b>	<b>1</b>	<b>8.60</b>	<b>0.010</b>
<b>Crop type</b>	<b>4</b>	<b>10.50</b>	<b>0.087</b>
<b>Year</b>	<b>1</b>	<b>15.40</b>	<b>0.0008</b>
<b>Wind speed</b>	<b>1</b>	<b>11.00</b>	<b>0.004</b>
<b>Day</b>	<b>1</b>	<b>10.90</b>	<b>0.004</b>
Excluded terms:			
Temperature	1	2.79	0.130
Day <sup>2</sup>	1	0.28	0.637

### **Epigeal invertebrates: G-vac samples**

#### *Total number of invertebrates*

#### *Uncropped margin*

Number of invertebrates caught by the Stirling suction trap was related to numbers caught by the G-vac in the uncropped margin, and this relationship differed depending on which crop type the G-vac sample was taken from (table 8, figure 3), and also upon year (table 8, figure 4). There were positive relationships between the number of invertebrates caught in the Stirling suction trap and number of invertebrates caught by the G-vac in the margins of

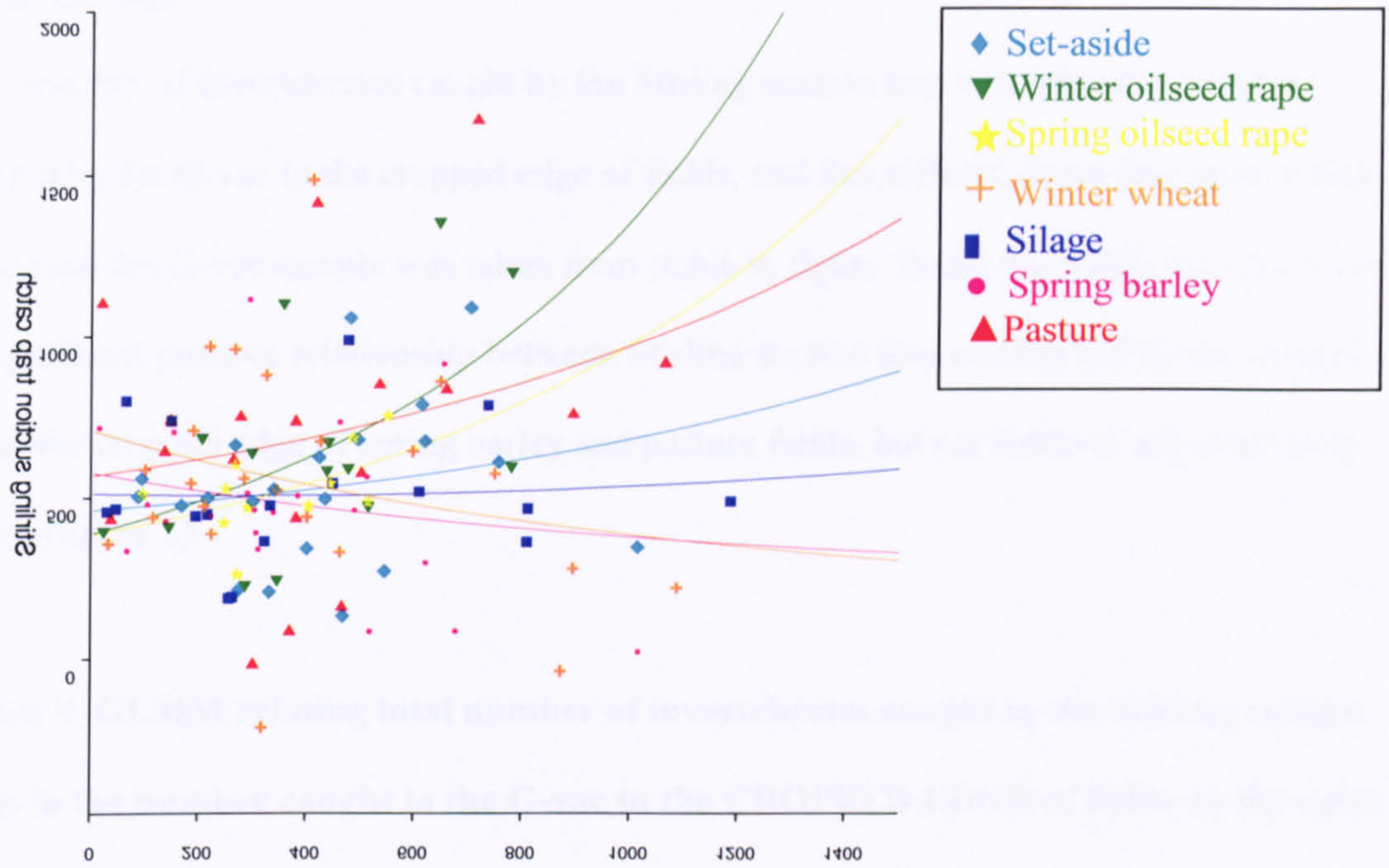
pasture, set-aside, winter oilseed rape, and spring oilseed rape fields, but not numbers caught in the margins of spring barley, winter wheat or silage (figure 3). Overall there was a significant positive relationship between Stirling suction trap catches and G-vac catches in 2002, but not in 2001.

**Table 8. GLMM relating total number of invertebrates caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

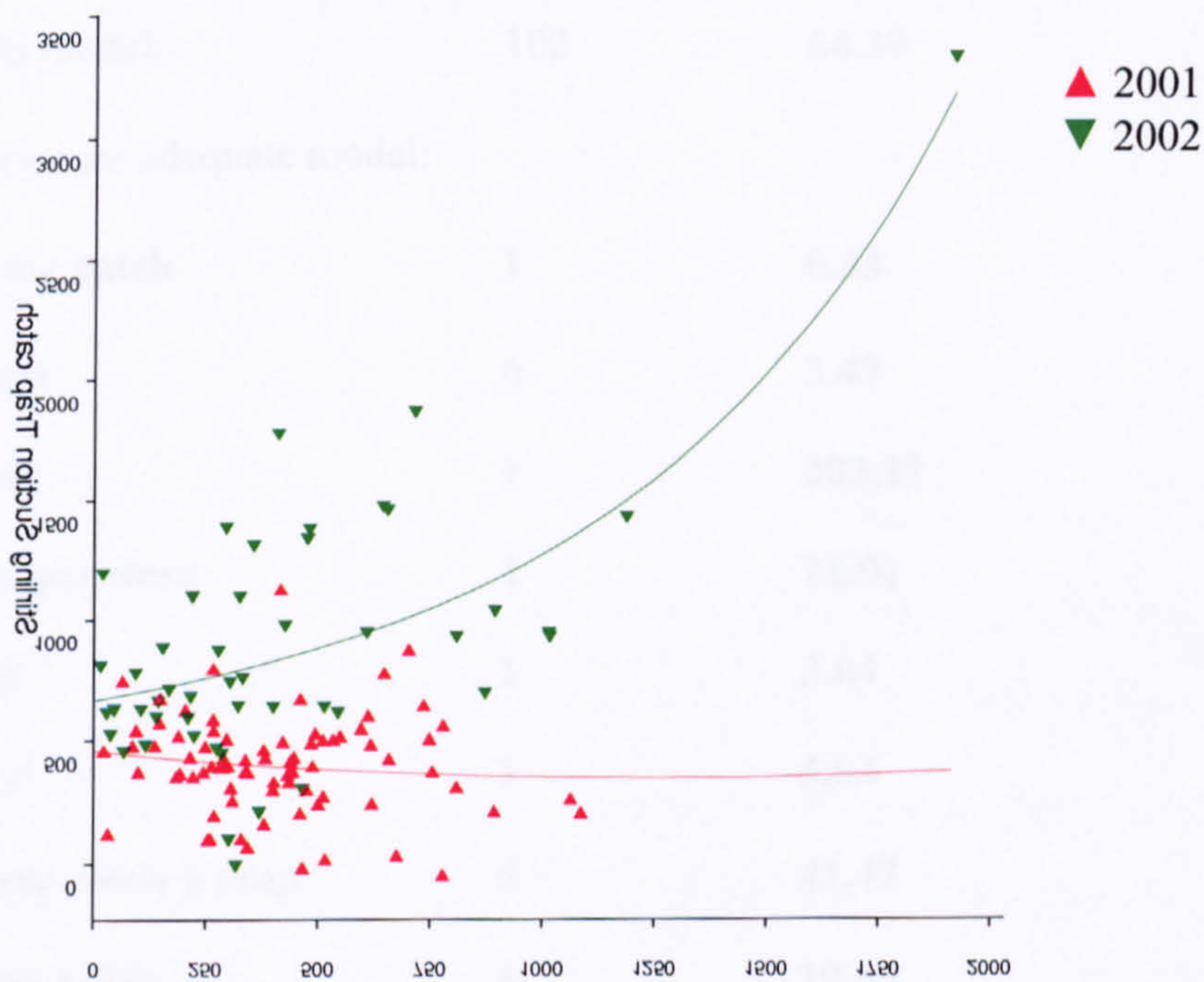
Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	197	189.17	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>6.47</b>	<b>0.001</b>
<b>Crop</b>	<b>6</b>	<b>9.24</b>	<b>0.161</b>
<b>Year</b>	<b>1</b>	<b>382.32</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>91.91</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>1.70</b>	<b>0.192</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>11.28</b>	<b>&lt;0.001</b>
<b>G-vac catch x crop</b>	<b>6</b>	<b>48.09</b>	<b>&lt;0.001</b>
<b>G-vac catch x temp</b>	<b>1</b>	<b>59.58</b>	<b>&lt;0.001</b>
<b>G-vac catch x year</b>	<b>1</b>	<b>44.11</b>	<b>&lt;0.001</b>
<b>Crop x day</b>	<b>6</b>	<b>33.90</b>	<b>&lt;0.001</b>





**Figure 3. Predicted relationship between total number of invertebrates caught in Stirling suction trap and number caught by the G-vac in the UNCROPPED MARGIN of different crop types on the same day.**



**Figure 4. Predicted relationship between total number of invertebrates caught in Stirling suction trap and number caught by the G-vac in the UNCROPPED MARGIN in different years.**



### *Cropped Edge*

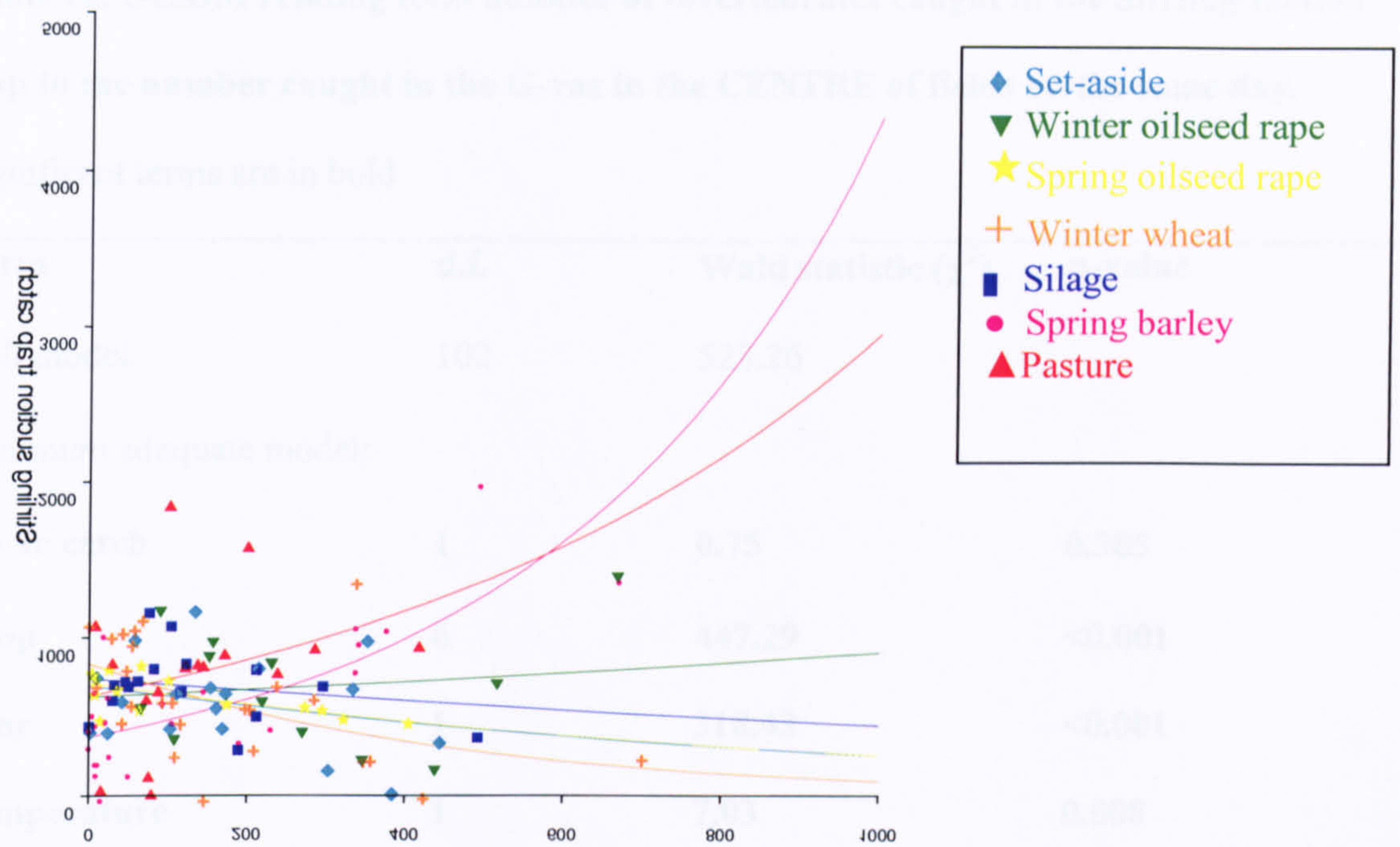
The number of invertebrates caught by the Stirling suction trap was related to numbers caught by the G-vac in the cropped edge of fields, and this differed depending upon which crop type the G-vac sample was taken from (table 9, figure 5) and day (table 9). There was a significant positive relationship between Stirling suction trap catches and G-vac catches from the cropped edge of spring barley and pasture fields, but not fields of any other crop types (figure 5).

**Table 9. GLMM relating total number of invertebrates caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	102	64.39	
Minimum adequate model:	>		
<b>G-vac catch</b>	<b>1</b>	<b>0.33</b>	<b>0.568</b>
<b>Crop</b>	<b>6</b>	<b>3.47</b>	<b>0.002</b>
<b>Year</b>	<b>1</b>	<b>202.23</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>21.92</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>3.64</b>	<b>0.063</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>5.84</b>	<b>0.016</b>
<b>G-vac catch x crop</b>	<b>6</b>	<b>41.47</b>	<b>&lt;0.001</b>
<b>Crop x day</b>	<b>6</b>	<b>19.40</b>	<b>0.004</b>





**Figure 5. Predicted relationship between total number of invertebrates caught in Stirling suction trap and number caught by the G-vac in the CROPPED EDGE of different crop types on the same day.**

### *Centre*

The number of invertebrates caught by the Stirling suction trap was related to numbers caught by the G-vac in the centre of fields, with the relationship differing depending on which crop type the G-vac sample was taken from (table 10, figure 6) and day (table 10). There was a significant positive relationship between Stirling suction trap catches and G-vac catches taken from the centre of spring barley, pasture and spring oilseed rape fields, a mildly positive relationship with those from winter wheat fields, and no relationship with those from silage or set-aside fields.

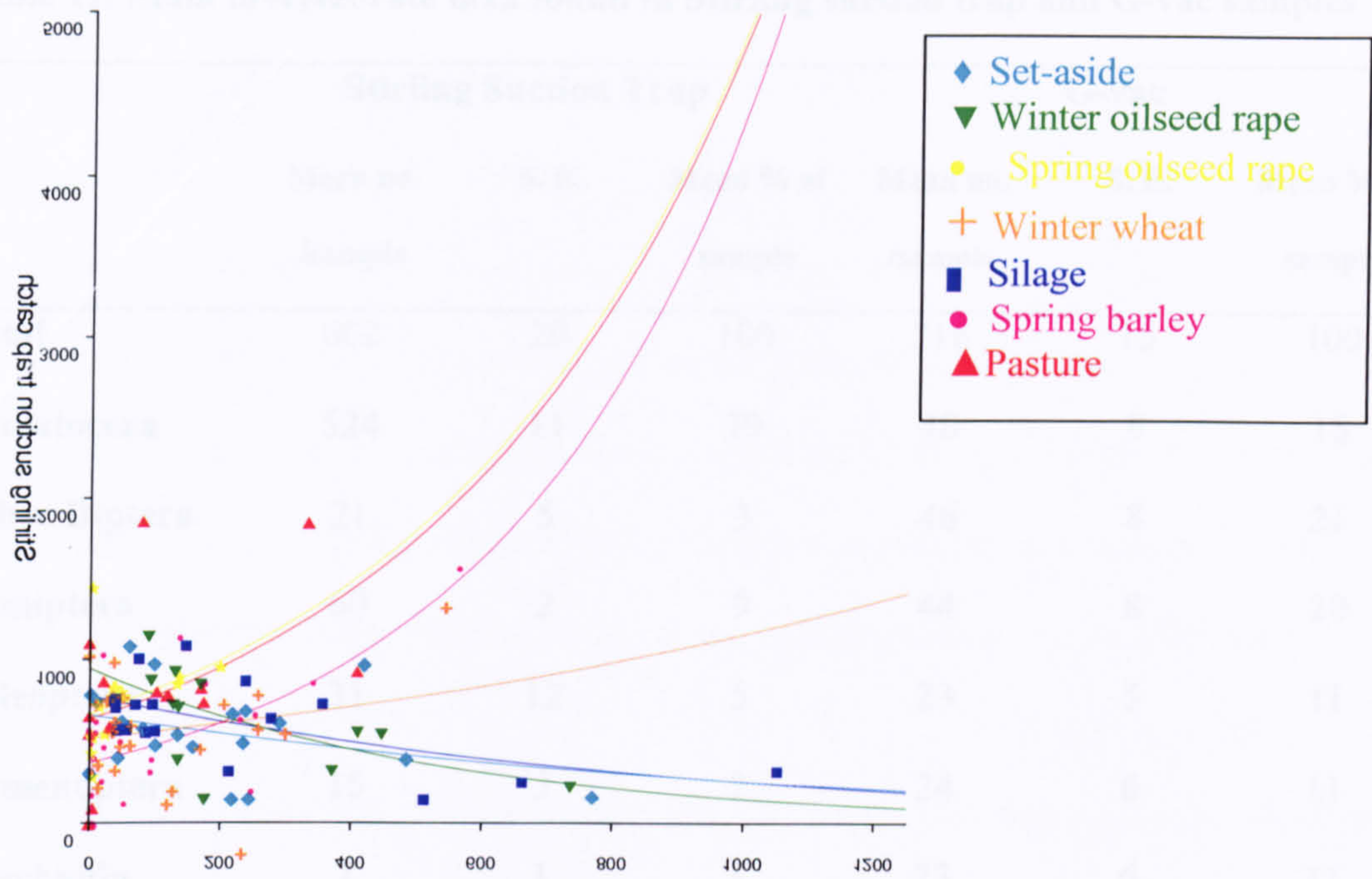


**Table 10. GLMM relating total number of invertebrates caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	102	523.26	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>0.75</b>	<b>0.385</b>
<b>Crop</b>	<b>6</b>	<b>447.29</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>318.43</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>7.03</b>	<b>0.008</b>
<b>Day</b>	<b>1</b>	<b>0.80</b>	<b>0.371</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>10.95</b>	<b>&lt;0.001</b>
<b>G-vac catch x crop</b>	<b>6</b>	<b>73.40</b>	<b>&lt;0.001</b>
<b>G-vac catch x temp</b>	<b>1</b>	<b>4.39</b>	<b>0.036</b>
<b>G-vac catch x day</b>	<b>1</b>	<b>62.79</b>	<b>&lt;0.001</b>
<b>Crop x day</b>	<b>6</b>	<b>239.84</b>	<b>&lt;0.001</b>





**Figure 6. Predicted relationship between total number of invertebrates caught in Stirling suction trap and number caught by the G-vac in the CENTRE of different crop types on the same day.**

#### *Analysis by order*

The mean composition of G-vac samples is given in table 11. The main taxa found in G-vac samples were Nematocera, non-nematoceran Diptera and Hemiptera, which make up a mean of approximately 20% each of a sample, with Coleoptera and Hymenoptera and Arachnida making up about 10% each of samples. Analyses were therefore repeated looking just at numbers of these orders / sub-orders.



**Table 11. Main invertebrate taxa found in Stirling suction trap and G-vac samples**

	Stirling Suction Trap			G-vac		
	Mean no. /sample	S. E.	Mean % of sample	Mean no. /sample	S. E.	Mean % of sample
<b>Total</b>	662	20	100	218	15	100
<b>Nematocera</b>	524	11	79	40	9	18
<b>Other Diptera</b>	21	5	3	46	8	21
<b>Hemiptera</b>	60	2	9	44	8	20
<b>Coleoptera</b>	31	12	5	23	5	11
<b>Hymenoptera</b>	15	3	2	24	6	11
<b>Arachnida</b>	7	1	1	23	6	11

*Uncropped Margin*

There was a significant effect of the G-vac catch x year interaction term for all taxa looked at (Appendix: tables 12-17). The nature of these relationships varied, but they were mainly just involved different gradients of positive relationships between the G-vac catches and the suction trap catches, except for Hymenoptera for which there was no relationship in 2002 between numbers caught in the Stirling suction trap and the G-vac.

There was also a significant effect of the G-vac catch x crop type interaction term for all of the taxa except for Arachnida (Appendix: tables 12-17). The strongest positive relationships between G-vac catches and Stirling suction trap catches were found for G-vac catches in silage (Nematocera, Coleoptera, Hemiptera), spring barley (Hymenoptera), winter oilseed rape (Hemiptera) and spring oilseed rape (non-nematoceran Diptera). Positive relationships between number of Arachnida caught by the G-vac and number caught in the Stirling suction trap were found in all crop types.

### *Cropped Edge*

There was a significant effect of the G-vac catch x year interaction term for four of the six taxa looked at (Appendix: tables 18-23). For Nematocera and Coleoptera there were positive relationships between the number caught in the Stirling suction trap and the G-vac in both years, with the relationship having a higher gradient in 2002 than in 2001. The number of Hymenoptera caught by the G-vac related positively to the number caught in the Stirling suction trap in 2001 but not in 2002. There was a positive relationship between number of non-nematoceran Diptera caught in the Stirling suction trap in 2001, but a negative relationship in 2002.

There was a significant effect of the G-vac catch x crop type interaction term for all of the taxa except Arachnida (Appendix: tables 18-23). For Hemiptera, there was either no relationship or a mildly negative relationship between numbers caught in the G-vac and numbers caught in the Stirling suction trap in all crop types. For Diptera, there was a positive relationship in set-aside, silage, and spring barley, but a negative relationship in other crop types. For Hymenoptera, there was a positive relationship for silage, spring barley and pasture, but no relationship for other crop types. For Coleoptera and Nematocera, there was a positive relationship for spring barley, but no relationship for other crop types. The number of Arachnida caught by the G-vac related positively to number caught in the Stirling suction trap in all crop types.

### *Centre*

There was a significant effect of the G-vac catch x year interaction term for all taxa except Arachnida (Appendix: tables 24-29). There was a positive relationship between G-vac catches and Stirling suction trap catches for Nematocera, non-nematoceran Diptera,



Hemiptera and Hymenoptera in 2002 but not in 2001. For Coleoptera there were negative relationships in both years.

There was a significant effect of the G-vac catch x crop type interaction term for all of the six taxa (Appendix: tables 24-29). There was a positive relationship between number of Coleoptera and number of Hemiptera caught in the G-vac in winter oilseed rape and number caught in the Stirling suction trap, with there being a mild negative (Coleoptera) or no (Hemiptera) relationship in other crop types. There were positive relationships between numbers of Hymenoptera caught in winter oilseed rape, set-aside and spring oilseed rape and number caught in the Stirling suction trap, but no relationship with numbers caught in other crop types. There was a positive relationship between numbers of Arachnida and Nematocera in spring barley and pasture and also set-aside for Nematocera, and numbers in the Stirling suction trap, but no relationship for other crop types. There was a relationship between numbers of Diptera caught in the Stirling suction trap and those caught by the G-vac in spring oilseed rape, but not in other crop types.

## **2.5 Discussion**

Data presented in this chapter show that significant relationships were found between Stirling suction trap catches and number of aerial invertebrates caught by the portable suction trap on nearby farmland, when factors such as weather, time of day and season were controlled for. There were also relationships between the Stirling suction trap catches and epigeal invertebrates caught by the G-vac on local farmland, although these relationships depended on crop type. For the centre of the field, there were relationships between suction trap catches and invertebrates caught in the two most predominant crop types in the local farmland; spring barley and pasture. For the uncropped margins of fields,

there were relationships between suction trap catches and catches in most crop types. This is the first time such relationships have been shown.

Statistical power to detect relationships between suction trap catches and catches on local farmland could have been increased by reducing variation in the samples collected on local farmland by, for example, just sampling one crop type. However, it would then have not been clear whether relationships applied to all farmland or just that crop type. Similarly, just one area of the field (for example the centre) could have been sampled by the G-vac. More particularly, variation caused by external factors could have been reduced by sampling the same group of fields each month. The reason for deciding not to do this was so that effects of particular management regimes were decreased for the study looking at abundances of invertebrates in different crop types, presented in the following chapter.

The portable suction trap was chosen in order to look for relationships between suction trap catches and aerial invertebrates on local farmland. The G-vac was also chosen in order to look for relationships between suction trap catches and invertebrates available to ground-feeding farmland bird species. However, invertebrates caught by the G-vac differed more from those caught by the suction trap in terms of size and taxa of invertebrates caught, and perhaps it would also have been useful to have used a method such as sweep-net sampling to sample invertebrates in the crop.

The Stirling suction trap is situated on the University of Stirling campus, and thus the area in the immediate vicinity of the trap does not include a large area of farmland. Within a 1km radius of the trap is a mixed woodland, parkland, lochs and buildings. Farmland constitutes just approximately 10% of the area. However, agriculture is the dominant land

use in the wider countryside surrounding the trap. Numbers of invertebrates caught by paired suction traps on a given day have been shown to be highly correlated (Taylor, 1973). For example, Benton *et al.* (2002) looked at Taylor's data and found that for aphids in traps 1.4km apart,  $r = 0.921$ , for aphids in traps 81km apart,  $r = 0.821$  and with traps 389km apart,  $r = 0.531$ . Similar patterns were found for single species and whole orders. Thus a single suction trap is representative of a large geographical area (Taylor, 1973), with a 100km radius being considered reasonable for aphid predictions (Woiwod, pers. comm. in Benton *et al.*, 2002). Fifty two percent of Scotland's arable land and 64% of its livestock falls within 100km of Stirling. Thus, catches from the Stirling suction trap are likely to correlate with the catch of any suction trap placed in agricultural central Scotland.

#### **Aerial invertebrates: portable suction trap samples**

The total number of invertebrates caught by the Stirling suction trap was positively related to the total number of aerial invertebrates caught on local farmland. This is not surprising, as suction trap catches have been found to be related to a number of breeding factors in hirundines (Bryant, 1973, Bryant, 1975, Turner, 1980, Johnston 1990). When different orders were looked at separately, there was a significant relationship between number of non-nematoceran Diptera and Coleoptera caught in the Stirling suction trap and the portable suction trap. Number of Nematocera caught in the Stirling suction trap showed no significant relationship with numbers caught in the portable suction trap. This is probably as number of Nematocera is highly influenced by proximity of water features.

## **Epigeal invertebrates: G-vac samples**

### *Uncropped margin*

The number of invertebrates caught in the Stirling suction trap related to the number caught in the uncropped margins of all crop types except spring barley, winter wheat and silage. It is not clear why there should be no relationship for these crop types.

Overall there was a positive relationship between number of invertebrates caught in the Stirling suction trap and those caught by the G-vac in field margins in 2002, but not in 2001. This could be due to the fact that catches in 2002 were higher on average than those in 2001, and also more variable.

### *Cropped edge and centre*

There were positive relationships between the numbers of invertebrates caught in the Stirling suction trap and those caught in the edge or centre of spring barley and pasture fields. This is probably as of the crop types sampled they were the two most common crop types in the study area. Spring barley fields accounted for 34% of fields on study farms, and pasture 22%. This is in contrast to the other crop types, which each accounted for less than 10% each (set aside: 8%; silage: 6%; winter wheat: 3%; winter oilseed rape: 1%; spring oilseed rape: 1%). Thus, it is not surprising that the numbers of invertebrates in these two crop types should have the greatest impact on the number caught in the suction trap. The size of Stirling suction trap catches also related to the size of G-vac catches from the centre of spring oilseed rape fields, however, and slightly to the numbers caught in winter wheat fields, it is not clear why this is the case.



## Conclusions

Suction traps were designed to sample airborne insects, predominantly aphids. Thus whilst it is intuitive that numbers of aphids caught in the suction trap will relate to those in the air on local farmland, this is not necessarily the case for other orders, with different flight patterns, size etc. However, it was shown here that total number of aerial invertebrates, as well as aerial Coleoptera and Diptera caught on local farmland also related to suction trap catches. There were also relationships between suction trap catches and numbers of epigeal invertebrates caught by the G-vac, in certain areas of certain crop types. For the cropped areas of the fields, there were positive relationships between numbers of invertebrates caught in spring barley and pasture, and this is presumably because they were the most predominant local crop types.

Suction traps are a suitable measure of aerial invertebrate abundance for aerial feeding bird species. There were also several positive relationships between numbers of epigeal invertebrates and suction trap catches, particularly epigeal invertebrates from the two most predominant crop types, spring barley and pasture, which together accounted for 56% of fields on study farms. Thus it would appear that suction trap catches are responsive to changes in abundance of farmland invertebrates, overall, and are a suitable measure of abundance of invertebrates on farmland. This is likely to be particularly true when considering long-term trends, as the variation in farmland invertebrate abundances will be greater than those between days sampled in this study, and thus more likely to affect suction trap catches.



## Appendix

**Table 12. GLMM relating total number of Nematocera caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	10031.41	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>5261.61</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>1673.88</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>1947.96</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>130.56</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>1109.08</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>259.07</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>2031.37</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>678.05</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>53.57</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>239.38</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>1816.51</b>	<b>&lt;0.001</b>

**Table 13. GLMM relating total number of non-nematoceran Diptera caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	1198.93	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>21.96</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>55.99</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>60.04</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>50.59</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>2.95</b>	<b>0.086</b>
<b>Crop type x day</b>	<b>6</b>	<b>14.94</b>	<b>0.021</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>166.72</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>27.67</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>50.68</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>89.95</b>	<b>&lt;0.001</b>

**Table 14. GLMM relating total number of Coleoptera caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	2466.04	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>35.66</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>159.21</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>86.70</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>4.99</b>	<b>0.025</b>
<b>Day</b>	<b>1</b>	<b>501.82</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>102.19</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>73.66</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>146.32</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>10.23</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>26.71</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>27.99</b>	<b>&lt;0.001</b>

**Table 15. GLMM relating total number of Hemiptera caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	6888.92	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>498.29</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>76.63</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>1431.67</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>13.64</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>318.82</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>247.97</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>234.53</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>506.27</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>58.84</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>5.11</b>	<b>0.024</b>
<b>Day x G-vac catch</b>	<b>1</b>		<b>&lt;0.001</b>

**Table 16. GLMM relating total number of Hymenoptera caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	579.12	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>36.60</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>45.38</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>45.93</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>20.13</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>1.11</b>	<b>0.291</b>
<b>Crop type x day</b>	<b>6</b>	<b>32.11</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>27.28</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>74.32</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>19.80</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>93.53</b>	<b>&lt;0.001</b>



**Table 17. GLMM relating total number of Arachnida caught in the Stirling suction trap to the number caught in the G-vac in the UNCROPPED MARGIN of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	166.92	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>0.92</b>	<b>0.337</b>
<b>Crop type</b>	<b>6</b>	<b>25.56</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>48.90</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>55.13</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>10.32</b>	<b>&lt;0.001</b>

**Table 18. GLMM relating total number of Nematocera caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	11013.24	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>1135.42</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>382.60</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>1669.99</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>59.42</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>2021.54</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>625.20</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>1793.20</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>7.06</b>	<b>0.008</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>75.34</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>1031.36</b>	<b>&lt;0.001</b>

**Table 19. GLMM relating total number of non-nematoceran Diptera caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	89	1016.59	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>11.15</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>47.63</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>80.16</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>142.18</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>16.39</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>47.13</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>45.26</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>30.29</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>43.50</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>8.38</b>	<b>0.004</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>4.52</b>	<b>0.034</b>

**Table 20. GLMM relating total number of Coleoptera caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	1455.34	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>39.68</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>84.08</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>18.43</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>188.68</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>470.71</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>46.11</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>84.88</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>147.27</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>27.23</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>61.73</b>	<b>&lt;0.001</b>



**Table 21. GLMM relating total number of Hemiptera caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	6807.64	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>95.28</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>272.95</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>2055.27</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>0.17</b>	<b>0.679</b>
<b>Day</b>	<b>1</b>	<b>2083.86</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>80.72</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>158.32</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>162.16</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>3.85</b>	<b>0.050</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>95.17</b>	<b>&lt;0.001</b>

**Table 22. GLMM relating total number of Hymenoptera caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	530.20	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>0.15</b>	<b>0.698</b>
<b>Crop type</b>	<b>6</b>	<b>20.30</b>	<b>0.002</b>
<b>Year</b>	<b>1</b>	<b>79.97</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>172.81</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>0.01</b>	<b>0.925</b>
<b>Crop type x day</b>	<b>6</b>	<b>15.39</b>	<b>0.017</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>58.57</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>47.64</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>75.90</b>	<b>0.050</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>29.41</b>	<b>&lt;0.001</b>

**Table 23. GLMM relating total number of Arachnida caught in the Stirling suction trap to the number caught in the G-vac in the CROPPED EDGE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	105	145.32	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>9.67</b>	<b>0.002</b>
<b>Crop type</b>	<b>6</b>	<b>20.64</b>	<b>0.002</b>
<b>Year</b>	<b>1</b>	<b>7.13</b>	<b>0.008</b>
<b>Day</b>	<b>1</b>	<b>43.12</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>51.41</b>	<b>&lt;0.001</b>

**Table 24. GLMM relating total number of Nematocera caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	11567.42	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>28.34</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>1392.91</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>995.15</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>444.17</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>1104.33</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>469.70</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>1579.28</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>880.27</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>850.46</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>613.30</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>759.28</b>	<b>&lt;0.001</b>



**Table 25. GLMM relating total number of non-nematoceran Diptera caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	642.07	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>48.70</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>51.08</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>3.25</b>	<b>0.071</b>
<b>Temperature</b>	<b>1</b>	<b>32.84</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>4.60</b>	<b>0.032</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>131.22</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>30.10</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>97.52</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>72.35</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>50.53</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>33.43</b>	<b>&lt;0.001</b>

**Table 26. GLMM relating total number of Coleoptera caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	90	3248.33	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>1.34</b>	<b>0.247</b>
<b>Crop type</b>	<b>6</b>	<b>421.18</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>60.67</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>34.01</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>29.39</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>1332.14</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>377.39</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>22.88</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>265.68</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>12.49</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>10.14</b>	<b>&lt;0.001</b>

**Table 27. GLMM relating total number of Hemiptera caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	92	619.34	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>270.92</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>67.14</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>473.87</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>106.76</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>170.63</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>112.81</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>8.48</b>	<b>0.004</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>78.90</b>	<b>&lt;0.001</b>
<b>Day x G-vac catch</b>	<b>1</b>	<b>23.27</b>	<b>&lt;0.001</b>

**Table 28. GLMM relating total number of Hymenoptera caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	647.99	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>101.17</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>43.00</b>	<b>&lt;0.001</b>
<b>Year</b>	<b>1</b>	<b>31.49</b>	<b>&lt;0.001</b>
<b>Temperature</b>	<b>1</b>	<b>20.71</b>	<b>&lt;0.001</b>
<b>Day</b>	<b>1</b>	<b>27.06</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>171.91</b>	<b>&lt;0.001</b>
<b>Crop type x day</b>	<b>6</b>	<b>42.42</b>	<b>&lt;0.001</b>
<b>Year x G-vac catch</b>	<b>1</b>	<b>51.06</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>44.83</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>23.99</b>	<b>&lt;0.001</b>



**Table 29. GLMM relating total number of Arachnida caught in the Stirling suction trap to the number caught in the G-vac in the CENTRE of fields on the same day.**

Significant terms are in bold

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	98	190.73	
Minimum adequate model:			
<b>G-vac catch</b>	<b>1</b>	<b>15.65</b>	<b>&lt;0.001</b>
<b>Crop type</b>	<b>6</b>	<b>18.96</b>	<b>0.004</b>
<b>Year</b>	<b>1</b>	<b>3.70</b>	<b>0.054</b>
<b>Temperature</b>	<b>1</b>	<b>0.05</b>	<b>0.818</b>
<b>Day</b>	<b>1</b>	<b>39.54</b>	<b>&lt;0.001</b>
<b>Day<sup>2</sup></b>	<b>1</b>	<b>36.32</b>	<b>&lt;0.001</b>
<b>Crop type x G-vac catch</b>	<b>6</b>	<b>24.09</b>	<b>&lt;0.001</b>
<b>Temperature x G-vac catch</b>	<b>1</b>	<b>4.21</b>	<b>0.040</b>

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## **Chapter 3:**

### **Spatial and temporal trends of invertebrates on farmland**

#### **Abstract**

Invertebrates were sampled during the summers of 2001 and 2002 from farmland around Stirling, Scotland. Three different sampling techniques were used; a portable suction trap, a converted leaf vacuum (G-vac), and pitfall traps. Seven different crop types were sampled, from three different zones within the field (the uncropped margin; 4m into the field; 50m into the field).

More aerial invertebrates were caught over winter oilseed rape, set-aside and winter wheat than silage or spring barley, and these differences occurred mainly early in the season in April and May.

Field margins were found to have higher invertebrate abundances than cropped areas using the G-vac. There were no differences between the margin and cropped regions of the field for winter oilseed rape and silage, except for Hemiptera, which were found in higher densities in all margins. The magnitude of the differences in invertebrate abundances in the field margins and cropped regions decreased through the season. This was probably due to increased dispersal into the field as vegetation height of the crop increased, and there was some evidence for this. Higher numbers of some orders were also caught 4m into the field than in the 'centre' (at least 50m in). Pitfall traps in the margins and cropped edges of fields caught higher numbers of Hymenoptera, but no other order, than those in the centres of fields.

G-vac catches showed that winter oilseed rape was a relatively valuable crop for invertebrates, as was set-aside, with spring oilseed rape and spring barley being invertebrate-poor habitats. These differences mainly occurred in May and June, with there



being fewer differences in invertebrate abundance between different crop types later in the season. Pitfall trap catches also showed some signs that winter oilseed rape and set-aside were good invertebrate habitats, especially in May and June, as well as silage, however the crop type differences were different, with spring oilseed rape also having high catches early in the season, probably as pitfall traps are affected by vegetation density and spring oilseed rape would have a low stem density at this time.

### **3.1 Introduction**

Farming practices have changed dramatically in the last few decades as a result of agricultural intensification, and the detrimental effects on farmland bird populations have been well publicised (Baillie *et al.*, 1997, Fuller *et al.*, 1995, Marchant & Gregory, 1994, Siriwardena *et al.*, 1998). This has led to the government listing many farmland birds as Birds of Conservation Concern (Gibbons *et al.*, 1996), and developing biodiversity action plans for many of them (Anon., 1995). However, the changes have also affected other wildlife, for example many species of plants and invertebrates (Campbell *et al.*, 1997, Sotherton & Self, 2000, Robinson & Sutherland, 2002).

A review of data on farmland invertebrate abundance concluded that many species of invertebrates have been declining on farmland, with the exception of most aphid species (Sotherton & Self, 2000). A long-term study of invertebrate abundance on over 100 cereal fields on the Sussex Downs found that although different invertebrate groups have shown varying trends in recent decades, overall numbers of invertebrates, excluding Collembola, declined by about 50% between 1970 and 1990, and it is predicted that there has probably been a roughly 75% decline in invertebrate abundance in cereal fields since the introduction of herbicides in the 1950s (Aebischer & Potts, 1990). Data from a network of light traps have shown that macro Lepidoptera have decreased in numbers on farmland

between the periods 1933-1950, and 1960 to 1989, with no similar decrease being found for woodland traps (Woiwod & Thomas, 1993). A study of ground beetle (Carabidae) diversity in a weedy arable plot in the Tyne Valley has also found a decreasing trend in species of ground beetles since 1981 (Luff, 1990).

These declines are generally accepted to have been predominantly driven by increased pesticide use; by insecticides killing non-target invertebrates, and by increased herbicide use causing a reduction in plant food and refuges for invertebrates (Aebischer & Potts 1990, Moreby & Southway, 1999, Sotherton & Self, 2000, Wilson *et al.*, 1997). The area of cereals sprayed with insecticides per year in Britain increased 55-fold between 1974 and 1996 to 2.7 million hectares (due to repeat sprayings) (Pesticide Usage Survey Reports). Other possible factors contributing to invertebrate declines are increased specialisation of farming, decreased undersowing, timing and depth of ploughing, and a reduction in the number of uncultivated field margins (Sotherton & Self, 2000, Wilson *et al.*, 1999).

Farmland invertebrate declines are a matter of concern, not just for their own conservation importance, but also because they are an important source of food for farmland birds.

Declines amongst farmland bird populations have been worst amongst granivorous species (Fuller *et al.*, 1995), however many of these 'granivorous' species are partially insectivorous, and also rely on invertebrates for chick food (Baillie *et al.*, 1997, Wilson *et al.*, 1997). The decline of the Grey Partridge has been attributed to the indirect effect of herbicides leading to lack of invertebrate chick food (Potts, 1986), and lack of invertebrate chick food is also likely to have contributed to the declines of at least three farmland passerine species in the UK (Skylark: Poulsen *et al.*, 1998; Cirl Bunting: Evans *et al.*, 1997; Corn Bunting: Brickle *et al.*, 2000). A recent study found that farmland bird densities significantly relate to numbers of invertebrates caught in a suction trap (Benton *et*

*al.*, 2002), and amongst declining granivorous species, those which are more dependent upon invertebrate food have shown the worst declines (Wilson *et al.*, 1999). This study aims to look at the spatial and temporal distribution of invertebrates on farmland with the aim of identifying particularly important areas of farmland in providing chick food for different granivorous farmland bird populations. Invertebrates were sampled between May and August, in different crop types, and from different areas within the field.

## **3.2 Methods**

### **Study Area**

The study area was a lowland mixed farming landscape in Stirling, Scotland (see chapter 2, figure 1). Invertebrate sampling was conducted from May to September 2001 and April to September 2002, from 150 fields on 29 farms within a 20 mile radius of the University of Stirling.

Fields of seven different crop types were sampled, these were: winter wheat; spring barley; winter oilseed rape; spring oilseed rape; silage; pasture and set-aside. Replications of each crop type were sampled on a monthly basis, with different fields being used each month (except for oilseed rape fields which sometimes had to be sampled for several months due to their limited numbers). Different fields were used in order to try to prevent effects of specific farm management from having undue influence on results. Three different sampling methods were used; these were the portable suction trap, the G-vac, and pitfall traps. These three different methods were used so that comparisons between the three methods could be made, and to allow comparison with other studies using different sampling techniques, and also as they all sample different strata in the field, reflecting invertebrates which may be available to birds with different foraging habitats. The portable

suction trap is 2m high and so samples aerial invertebrates, the G-vac was used to sample invertebrates on vegetation, in litter and on the ground, and pitfall traps sampled soil surface invertebrates.

### **Portable suction trap**

A Johnson-Taylor insect suction trap was used to sample aerial invertebrates. The trap runs off a generator and consists of a 9-inch diameter fan, with the mouth horizontal, which sucks air through a gauze funnel into a cylindrical collecting magazine. Insecticide-coated discs drop into the collecting cylinder magazine hourly.

The portable suction trap was placed in the 'centre' (at least 50m from the edge) of fields, from 0900 to 1700, when the sample was collected and preserved in 70% ethanol before sorting. Samples were taken on 65 days, 42 of these were between May and September in 2001, and 23 between April and September in 2002, with each crop type being sampled an average of once per month per year. Pasture fields were not sampled using the portable suction trap due to the problems of placing a generator in a field of livestock.

### **G-vac**

The G-Vac was a leaf vacuum which was converted for insect sampling by placing a fine-mesh nylon netting collecting bag over the nozzle (after Stewart & Wright, 1995). A mean of three fields of each of the seven crop types were sampled each month. Three zones of the field were sampled: the uncropped margin (i.e. fence, hedgerow, grassy margin); the cropped edge (4m into the field); and the centre (at least 50m into the field). In each of these three areas a 100m transect was walked, stopping every 10m to take a sub-sample, which was done by running the vacuum down over the vegetation and onto the ground, where it was left for 10s. Invertebrates were collected from the net of the G-vac at the end



of the 10s using a pooter. At the end of the transect, the insects collected from the ten points were transferred from the pooter into a polythene bag containing 70% ethanol.

### **Pitfall Traps**

Pitfall traps were only used in 2001. A mean of three fields of the seven different crop types were sampled each month. Three zones of the field were sampled, as for the G-vac. In each of these zones a row of five polystyrene cups were placed each 2m apart, three quarters filled with water plus a small amount of washing up liquid to weaken the surface tension. Cups were collected after a week, and their contents filtered through fine nylon mesh, before being stored (each sample consisting of the five sub-samples from the area) in 70% ethanol.

### **Invertebrate identification**

All invertebrates were counted, and identified to at least order level.

### **3.3 Data Analysis**

Data were analysed using generalised linear models (GLMs) in S-PLUS. GLMs allow the analysis of non-normal error distributions through the use of linearising transformations specified by link functions. Minimal models were found by step-wise deletion from a maximal model. Model residuals were checked for normality. Where a significant factor remained in the model, multiple comparisons were conducted to see which factor levels were significantly different. Data presented in this chapter are observed means.

### **Portable Suction Trap**

GLMs were conducted in S-PLUS with total number of invertebrates caught in the portable suction trap in a day as the dependent variable. Terms included in the model were crop

type, month and year, which were included as factors, and temperature (0900 temperature taken at the site) and wind speed (estimated at the site on the Beaufort scale) which were included as variables. Interaction terms included were crop x month, crop x temperature, crop x wind, and wind x temperature. Due to overdispersion, the models used quasi-likelihood errors, log link and variance =  $\mu^2$ .

### **G-vac**

GLMs were conducted in S-PLUS with total number of invertebrates, excluding Collembola, caught in the G-vac as the dependent variable. Collembola were excluded from the analysis due to their relatively tiny size and large numbers. Terms included in the model were crop type, year, month, and zone of the field sampled (uncropped margin, cropped edge, or centre) which were included as factors, and time and temperature (taken on site prior to sampling) which were included as variables. Interaction terms included were crop x month, crop x area and area x month. Due to overdispersion, the models used quasi-likelihood errors, log link and variance =  $\mu^2$ .

### **Pitfall traps**

GLMs were conducted in S-PLUS with total number of invertebrates, excluding Collembola, caught in the pitfall traps as the dependent variable. Collembola were excluded from the analysis due to their relatively tiny size and large numbers. Terms included in the model were crop type, month, and zone of the field sampled (uncropped margin, cropped edge, or centre) which were all factors. All two-way interaction terms were included. Due to overdispersion, the models used quasi-likelihood errors, log link and variance =  $\mu^2$ .

Models for all sampling methods were then run replacing 'total number of invertebrates' as the dependent variable with any order which constituted a mean of over 10% of each sample.

### **3.4 Results**

Many of the results presented are in terms of total numbers of invertebrates caught.

Collembola are excluded from these counts as their relatively tiny size and large numbers mean that they would make 'total number of invertebrates' a poor index of chick food abundance. In order to look at how 'total number of invertebrates' relates to invertebrate chick food, it is necessary to look at how numbers of invertebrates in a sample relate to its volume, and also whether the invertebrate taxa caught by the different methods are representative of those used as chick food by granivorous passerines.

#### **Comparison of total number of invertebrates and sample volume**

Linear regressions of sample volumes on total number of invertebrates in the samples were conducted for the different sampling methods.

Total number of invertebrates explained 83% of variation in portable suction trap sample volume and 69% of the variation of G-vac sample volume. Volume of pitfall trap samples was not measured.

#### **Invertebrate taxa caught by different sampling methods**

Invertebrate taxa collected by different sampling methods are presented in table 1. Orders marked as 'important chick food groups' are those which were found to make up over 5% of the diet of over 50% of the declining granivorous species looked at in Wilson *et al.*'s review (1999).

### *Portable suction trap*

Portable suction trap samples were made up predominantly of Nematocera (48%), with other Diptera (15%) and Coleoptera (31%) making up most of the rest of the sample.

Nematocera is a sub-order of Diptera, and includes the crane-flies (Tipulidae), the family of Diptera most often recorded in the diet of granivorous farmland birds (Wilson *et al.*, 1999). Coleoptera caught by the portable suction trap were predominantly (75%) pollen beetles, of the family Nitulidae, with rove beetles (Staphylinidae: 9%) and weevils (Curculionidae: 7%) accounting for most of the remaining beetles.

### *G-vac*

G-vac samples were more diverse; Nematocera, other Diptera and Hemiptera all made up about 20% each of the sample, with Coleoptera, Hymenoptera and Arachnida making up about 10% each. About 36% of Hemiptera caught by the G-vac were aphids. Coleoptera caught by the G-vac were Staphylinidae (rove beetles: 35%), Carabidae (ground beetles: 13%) and Curculionidae (weevils: 4%). Hymenoptera caught were predominantly ants (59%).

### *Pitfall traps*

Pitfall traps caught predominantly Coleoptera (27%, predominantly Carabidae), 31% Diptera (9% Nematocera, 22% non-nematoceran Diptera), 18% Arachnida, 12% Hymenoptera and 7% larvae (mainly Coleoptera, also Lepidoptera, Symphata, and Diptera).

The main taxa to be collected by the three sampling methods (Diptera, Coleoptera, Hemiptera, Hymenoptera and Arachnida) are five of the seven groups found to account for almost all the important chick food invertebrates in the diets of the 15 species of declining granivorous farmland birds reviewed by Wilson *et al.* (1999).



**Table 1. Main invertebrate taxa in portable suction trap, G-vac and pitfall trap samples.**

	Portable Suction Trap			G-vac			Pitfall traps			Important chick food group?
	Mean no. /sample	S. E.	Mean % of sample	Mean no. /sample	S. E.	Mean % of sample	Mean no. /sample	S. E.	Mean % of sample	
<b>Total</b>	135	15	100	218	15	100	38	8	100	
<b>Nematocera</b>	65	11	48	40	9	18	4	6	9	*
<b>Other Diptera</b>	20	5	15	46	8	21	8	5	22	*
<b>Hemiptera</b>	1	2	1	44	8	20	1	1	2	*
<b>Coleoptera</b>	42	12	31	23	5	11	10	4	27	*
<b>Hymenoptera</b>	5	3	4	24	6	11	4	3	12	*
<b>Arachnida</b>	0	1	0	23	6	11	7	4	18	*
<b>Isopoda</b>	0	0	0	5	4	2	0	0	0	
<b>Larvae</b>	0	0	0	0	0	0	3	1	7	*
<b>Mollusca</b>	0	0	0	0	0	0	1	2	2	*
<b>Other</b>	2	2	1	14	4	6	1	0	1	

### **Aerial Invertebrates: portable suction trap samples**

The crop type in which the portable suction trap was placed had a significant effect on the total number of invertebrates caught (table 2, figure 1). Multiple comparisons showed that winter oilseed rape had significantly higher invertebrate abundance than silage or spring barley. From figure 1, it appears that winter oilseed rape, winter wheat and set-aside had higher invertebrate catches than silage or spring barley, but other differences were not statistically significant, perhaps due to lack of statistical power.

When broken down by order (figure 2), to look at numbers of Diptera and Coleoptera (which together account for a mean of 94% of samples) caught in different crop types, it

can be seen that the pattern shown by total number of invertebrates also seemed to be followed by Nematocera and other Diptera, which constitute 63% of samples on average.

### *Nematocera*

Despite the trend for numbers of Nematocera to follow the same pattern as for 'total number of invertebrates' with respect to distribution between different crop types (figure 2), there was no significant effect of crop type on number of Nematocera caught (Appendix: table 1). The only factor to significantly affect number of Nematocera caught was year, with more being caught in 2002 than 2001

### *Non-nematoceran Diptera*

The number of other Diptera caught was significantly affected by crop type, and this effect differed depending on month (Appendix: table 2). In April more Diptera were caught above winter oilseed rape, winter wheat and set-aside than silage or spring barley. In May catches were higher over winter oilseed rape than all crop types except for winter wheat, and silage had the lowest catches of Diptera. There were no significant differences between numbers of Diptera in different crop types in June, July and August. In September catches of Diptera were lower in silage than in than any other crop type, and higher in winter oilseed rape than winter wheat. Thus, winter oilseed rape was the most valuable crop type for Diptera early and late season, and silage was a poor habitat for Diptera early and late season.

### *Coleoptera*

The number of Coleoptera per sample was affected by crop type, and this effect differed depending on month (Appendix: table 3). Set-aside had higher catches of Coleoptera in April, and in May there were significantly more Coleoptera in winter wheat than spring barley. Despite the high mean catch of Coleoptera in winter oilseed rape fields (figure 2), there were no significant differences between numbers caught in winter oilseed rape and

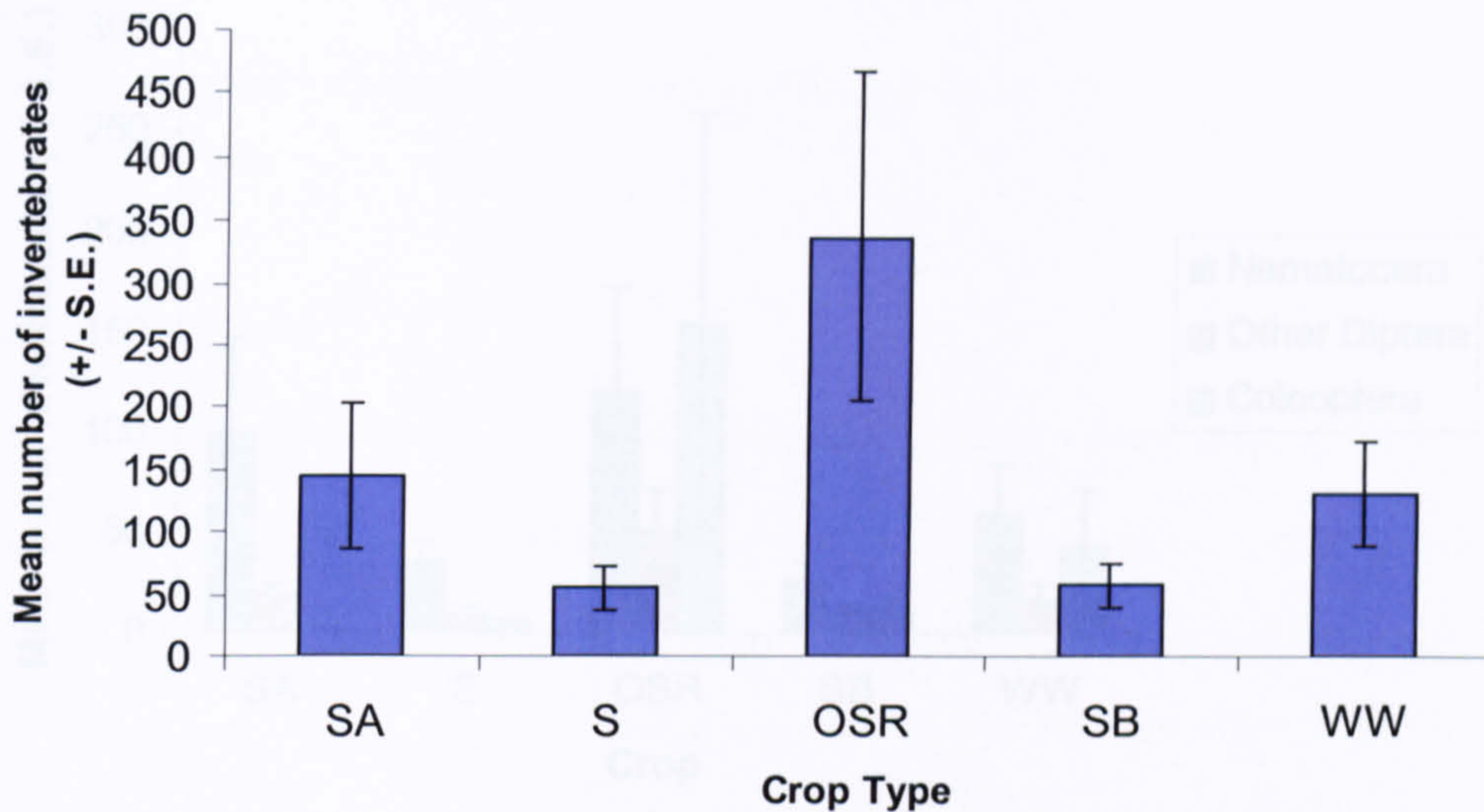
any other crop type, as the catch was very variable, the mean being so high due to outbreaks of oilseed rape pollen beetles (family Nitulidae, genus *Meligethes*) in July, when winter oilseed rape was flowering, when the monthly mean went from below 30 for all other months to 779 +/- 341.

**Table 2. GLM to investigate factors affecting the number of invertebrates caught by the portable suction trap.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	59	99.43	
Minimum adequate model:			
<b>Crop Type</b>	<b>4</b>	<b>17.97</b>	<b>0.013</b>
Excluded terms:			
Wind Speed	1	3.23	0.135
Temperature	1	1.24	0.360
Month	5	9.24	0.142
Year	1	0.02	0.900





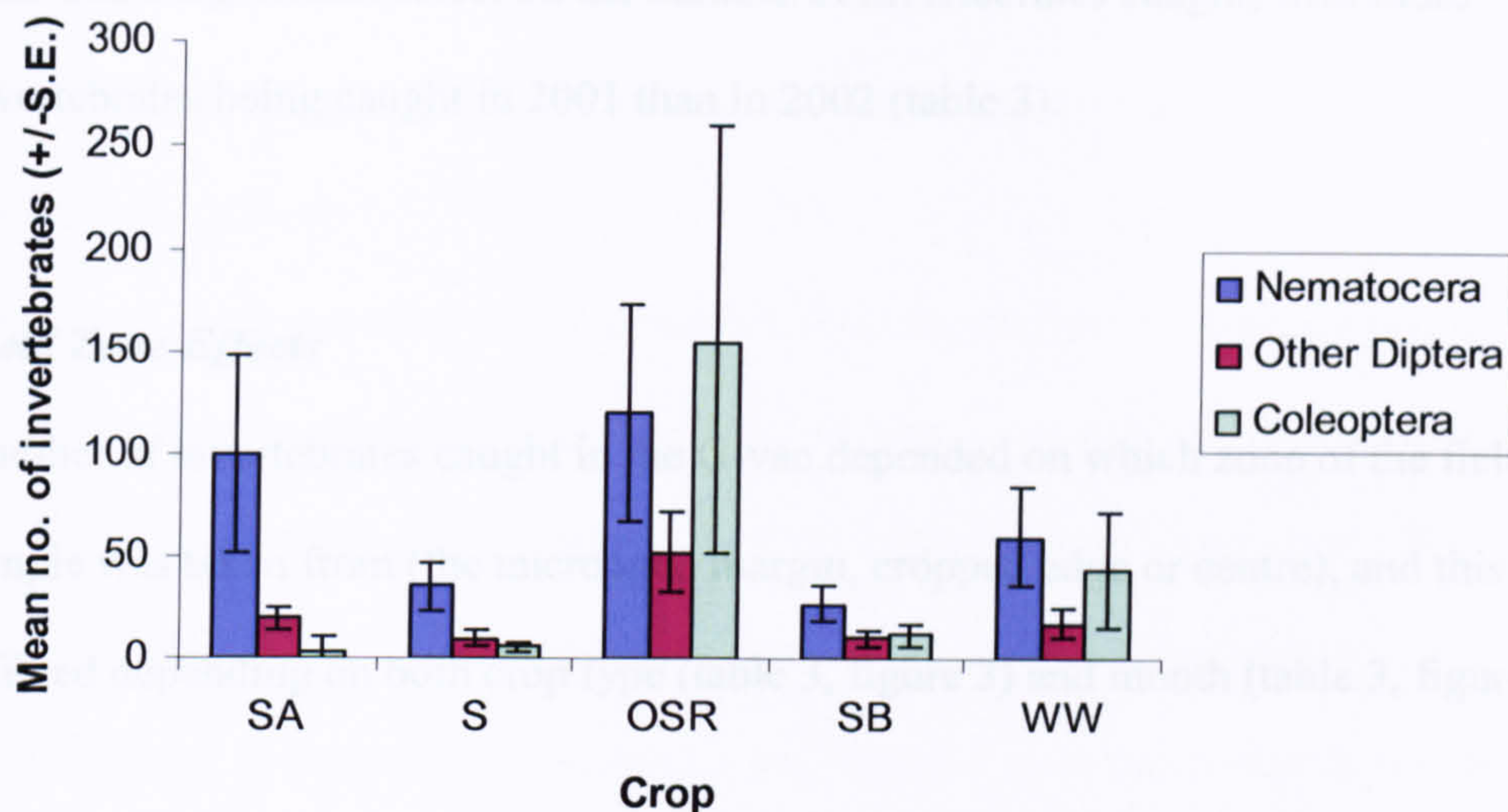
**Figure 1. Mean number of invertebrates caught in the portable suction trap in different crop types**

(SA = set-aside, S = silage, OSR = winter oilseed rape, SB = spring barley, WW = winter wheat).

#### Epigeal Invertebrates: G-vac samples

There were significant effects of year, crop type, month, zone of the field sampled, and the crop x month, crop x zone and zone x month interaction terms on the total number of invertebrates caught by the G-vac (table 3). Models were reported for each of the six major orders or sub-orders caught by the G-vac; Neuroptera, other Diptera, Hemiptera, Hymenoptera, Coleoptera and Arachnida. The maximum adequate models were the same for each group as when 'total number of invertebrates' was used as the dependent variable, except there was no effect of year on catches of Hemiptera, Hymenoptera and Arachnida, and there was no effect of the crop type x zone interaction term on numbers of Hemiptera caught (Appendix tables 4-9).





**Figure 2. Mean number of invertebrates caught in the portable suction trap in different crop types by order / sub-order**

(SA = set-aside, S = silage, OSR = winter oilseed rape, SB = spring barley, WW = winter wheat).

### **Epigeal Invertebrates: G-vac samples**

There were significant effects of year, crop type, month, zone of the field sampled, and the crop x month, crop x zone and zone x month interaction terms on the total number of invertebrates caught by the G-vac (table 3). Models were repeated for each of the six main orders or sub-orders caught by the G-vac; Nematocera, other Diptera, Hemiptera, Hymenoptera, Coleoptera and Arachnida. The minimum adequate models were the same for each order as when ‘total number of invertebrates’ was used as the dependent variable, except there was no effect of year on catches of Hemiptera, Hymenoptera and Arachnida, and there was no effect of the crop type x zone interaction term on numbers of Hemiptera caught (Appendix: tables 4-9).



Year had a significant effect on the number of invertebrates caught, with more invertebrates being caught in 2001 than in 2002 (table 3).

### ***Field Zone Effects***

Number of invertebrates caught in the G-vac depended on which zone of the field the sample was taken from (the uncropped margin, cropped edge or centre), and this effect differed depending on both crop type (table 3, figure 3) and month (table 3, figures 4, 5 and 6).

### ***Field Zone x Crop Type effects***

Multiple comparisons revealed that overall numbers of invertebrates in the uncropped margin were significantly higher than either 4m into the field ('cropped edge') or 50m in ('centre') for all of the crop types except silage and winter oilseed rape. There was no overall difference between number of invertebrates caught 4m into the field ('cropped edge') and 50m in ('centre') for any crop type or month. Overall, the uncropped margins contained an average of 62% more invertebrates than the centres of fields.

When broken down by order the patterns shown were similar, with there being no differences between numbers of any orders caught in the different zones of winter oilseed rape and silage fields, with the exception of Hemiptera which were more common in the margins than in the cropped region of the field in all crop types. Catches of some orders were higher 4m into the field than 50m in; this was significant for Nematocera, other Diptera and Hymenoptera in spring oilseed rape fields, and for Coleoptera in winter wheat fields. There were also several cases where catches of an order were higher in the uncropped margin of the field than the centre, but there was no difference between catches in the cropped edge (4m in) and either the margin or the centre of the field (Nematocera, other Diptera and Hymenoptera in pasture fields; Nematocera and Hymenoptera in set-

aside fields, Arachnida in winter oilseed rape fields). This would imply a non-significant trend for there to be higher abundance in the cropped edge than the centre in these cases.

#### *Field Zone x Month*

The overall difference between the number of invertebrates in the uncropped margin and the cropped area of the field was significant in May, June and July, but the difference steadily decreased through the season, such that there was no significant difference between invertebrate abundance in different zones of the field in August.

When looking at each order separately, it was true for most orders that the differences between the catches in the margins and the cropped region of the field decreased through the season, except for spiders, which were significantly more common in the margins throughout the season. Some of the seasonal patterns shown suggest dispersal into the field, as differences between catches in the cropped edge and uncropped margin initially decreased and those between the cropped edge and centre increased through the season for some orders (Hymenoptera, Coleoptera, non-nematoceran Diptera).

#### *Crop Type Effects*

##### *Crop Type x Month*

There was a significant effect of the crop type x month interaction term on the total number of invertebrates caught (table 3, figures 4, 5, 6). Invertebrate abundance differed most between crop types in May, when more invertebrates were caught in pasture, winter oilseed rape, silage, and set-aside than in spring barley or spring oilseed rape. More invertebrates were caught in winter oilseed rape than in winter wheat, and more in winter wheat than in spring oilseed rape. In June there were fewer differences between crop types; more invertebrates were caught in silage and set-aside than in spring barley, spring oilseed rape, or pasture, and more in winter oilseed rape than spring oilseed rape. In July and August there were no overall differences in invertebrate abundance between the crop types.

When models were repeated for the six main orders separately, these patterns applied fairly well to most orders, with spring oilseed rape and spring barley having relatively low catches of most orders in May and June (Nematocera, other Diptera, Hymenoptera, Arachnida in June). Winter oilseed rape had relatively high abundances of most orders in May and June (Nematocera, other Diptera, Hymenoptera, Arachnida, Coleoptera). Pasture was a valuable habitat for most orders in May, but relatively poor in June (Nematocera, other Diptera, Arachnida, Hemiptera). Set-aside had high invertebrate abundance for some orders in May (Nematocera, other Diptera, Arachnida) and of all orders in June (Nematocera, other Diptera, Hymenoptera, Coleoptera, Arachnida, Hemiptera). Silage had high invertebrate abundance for most orders in May (Nematocera, other Diptera, Hymenoptera, Arachnida) and June (Nematocera, other Diptera, Hymenoptera, Hemiptera). Winter wheat was a good habitat for Nematocera in May and June, but relatively poor for most other orders in May (other Diptera, Hymenoptera, Arachnida, Hemiptera), and for spiders in June.

There were few differences between abundances of any order in different crop types in July and August.

There were no overall significant differences in total number of invertebrates caught in different months or crop types in the uncropped margin, with all margins being relatively invertebrate rich.

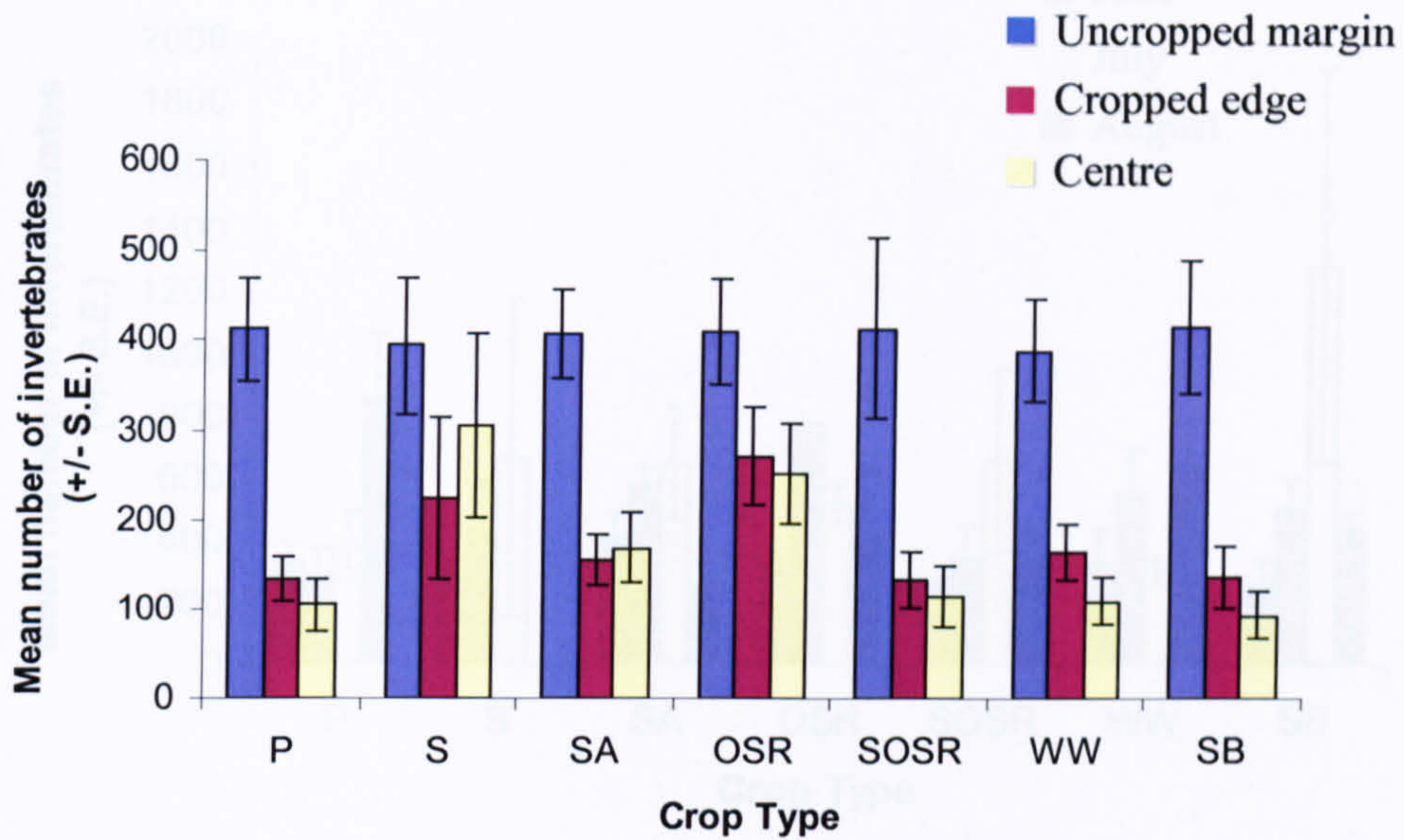
However, a seasonal pattern was shown in the cropped area of the field, with invertebrate numbers being significantly lower in May than in later months.



**Table 3. GLM to investigate factors affecting the number of invertebrates caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	433	683.10	
Minimum adequate model:			
<b>Crop Type</b>	<b>6</b>	<b>48.39</b>	<b>0.000000</b>
<b>Year</b>	<b>1</b>	<b>8.27</b>	<b>0.00025</b>
<b>Month</b>	<b>5</b>	<b>152.96</b>	<b>0.000000</b>
<b>Zone</b>	<b>2</b>	<b>153.13</b>	<b>0.000000</b>
<b>Crop Type x Month</b>	<b>26</b>	<b>67.06</b>	<b>0.0000000001</b>
<b>Crop Type x zone</b>	<b>12</b>	<b>27.84</b>	<b>0.000016</b>
<b>Zone x Month</b>	<b>10</b>	<b>25.80</b>	<b>0.000013</b>
Excluded terms:			
Time	1	0.06	0.741
Temperature	1	0.43	0.393

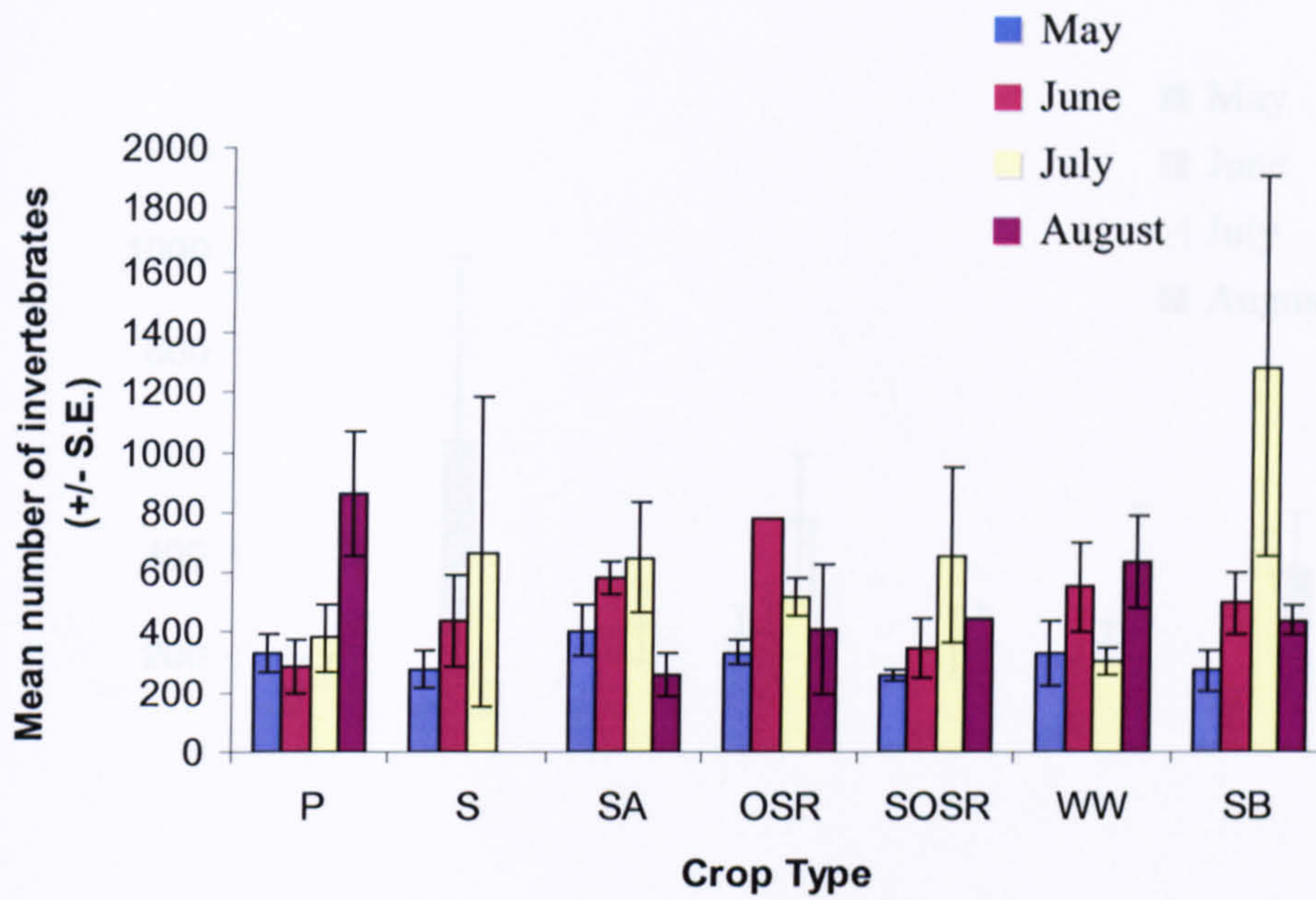


**Figure 3. Mean number of invertebrates caught in the G-vac in different zones of the field in different crop types.**

(P = pasture, S = silage, SA = set-aside, OSR = winter oilseed rape, SOSR = spring oilseed rape, WW = winter wheat, SB = spring barley).

Samples from April to August were combined for this graph.

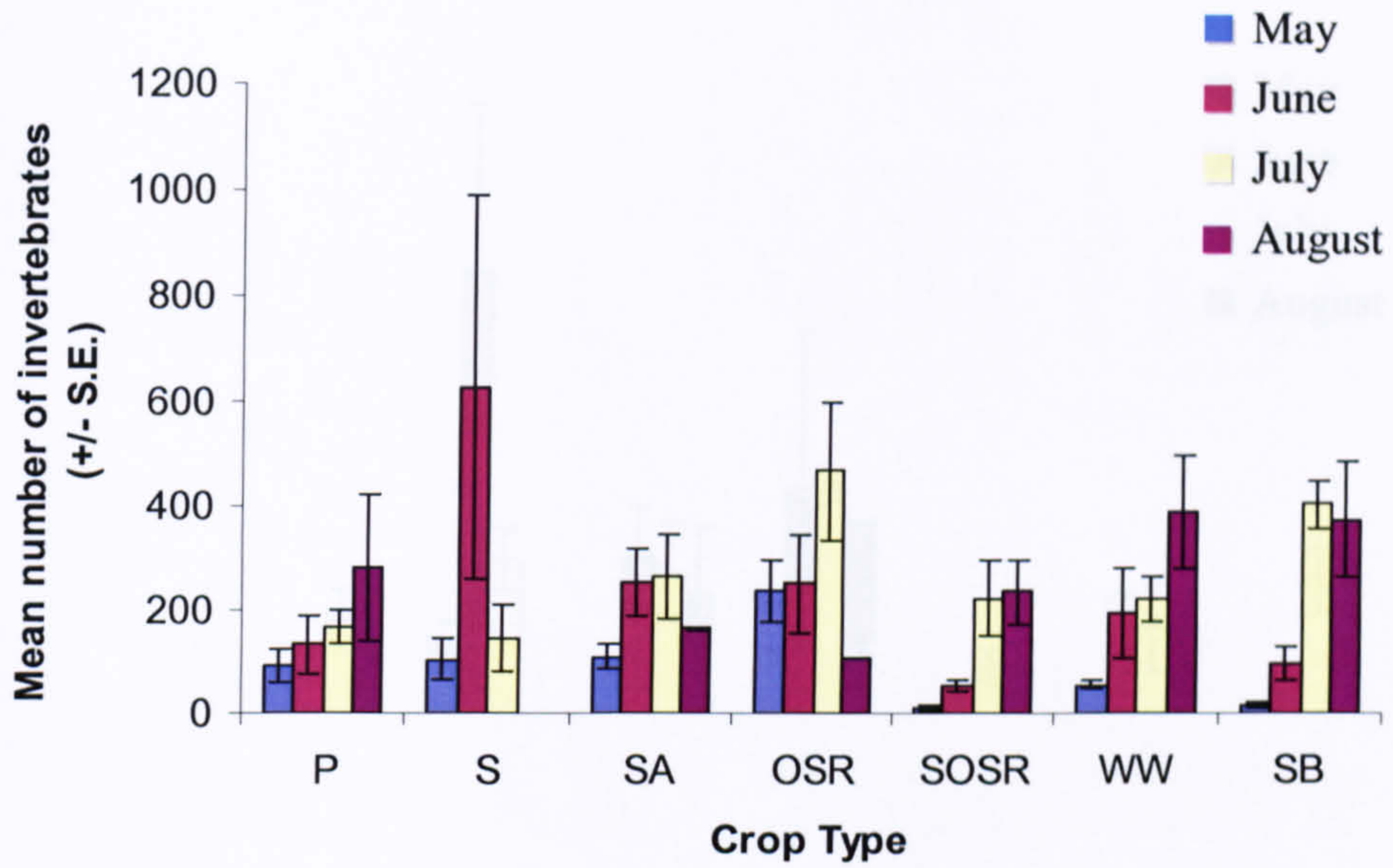




**Figure 4. Mean number of invertebrates caught by the G-vac in the UNCROPPED MARGIN of different crop types for the months May to August.**

(P = pasture, S = silage, SA = set-aside, OSR = winter oilseed rape, SOSR = spring oilseed rape, WW = winter wheat, SB = spring barley).

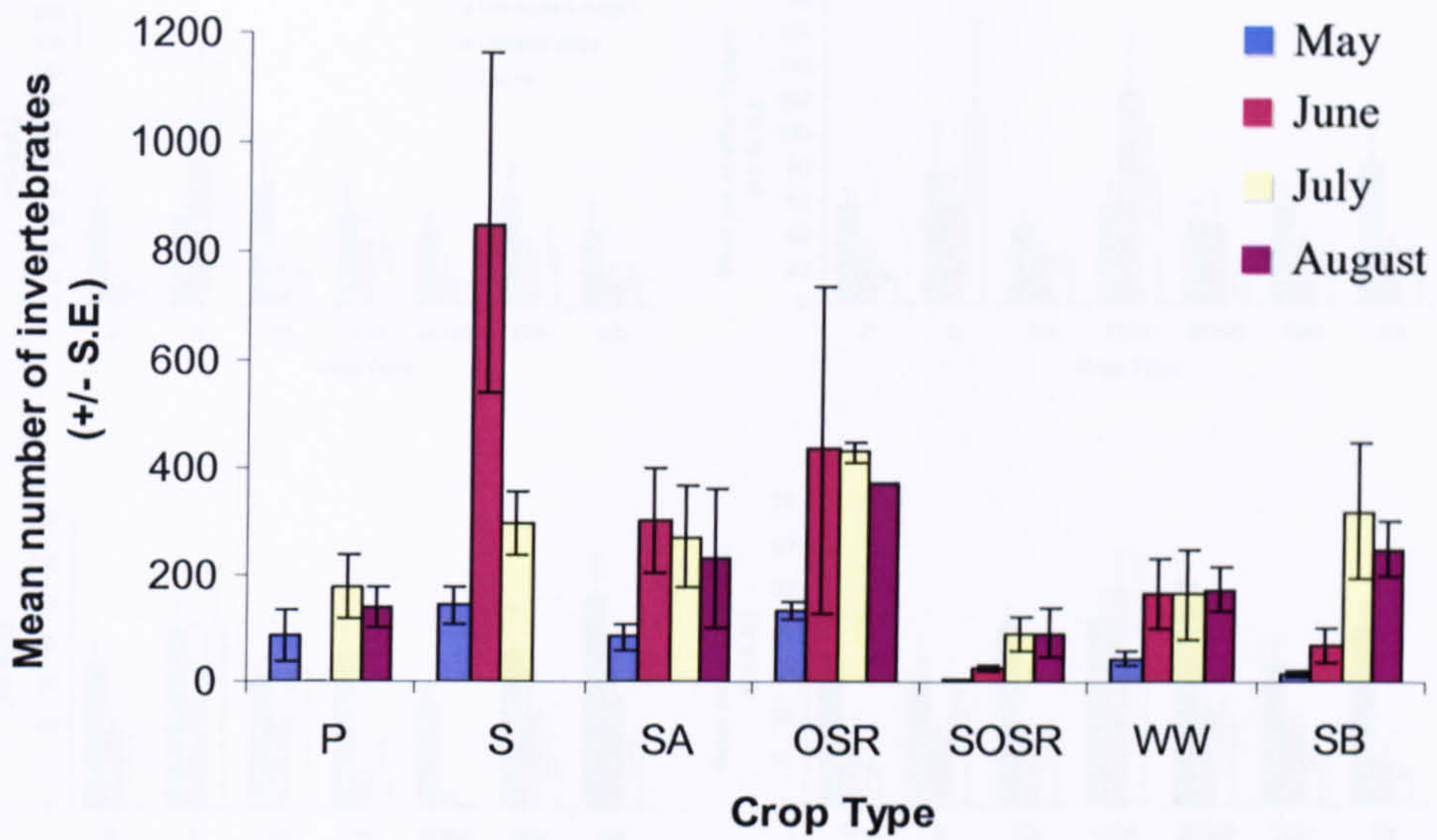




**Figure 5. Mean number of invertebrates caught by the G-vac in the CROPPED EDGE of different crop types for the months May to August.**

(P = pasture, S = silage, SA = set-aside, OSR = winter oilseed rape, SOSR = spring oilseed rape, WW = winter wheat, SB = spring barley).





**Figure 6. Mean number of invertebrates caught by the G-vac in the CENTRE of different crop types for the months May to August.**

(P = pasture, S = silage, SA = set-aside, OSR = winter oilseed rape, SOSR = spring oilseed rape, WW = winter wheat, SB = spring barley).

**Figure 7. Mean number of different orders/sub-orders caught by the G-vac in different zones of the field in different crop types (means shown for the months May to August).**



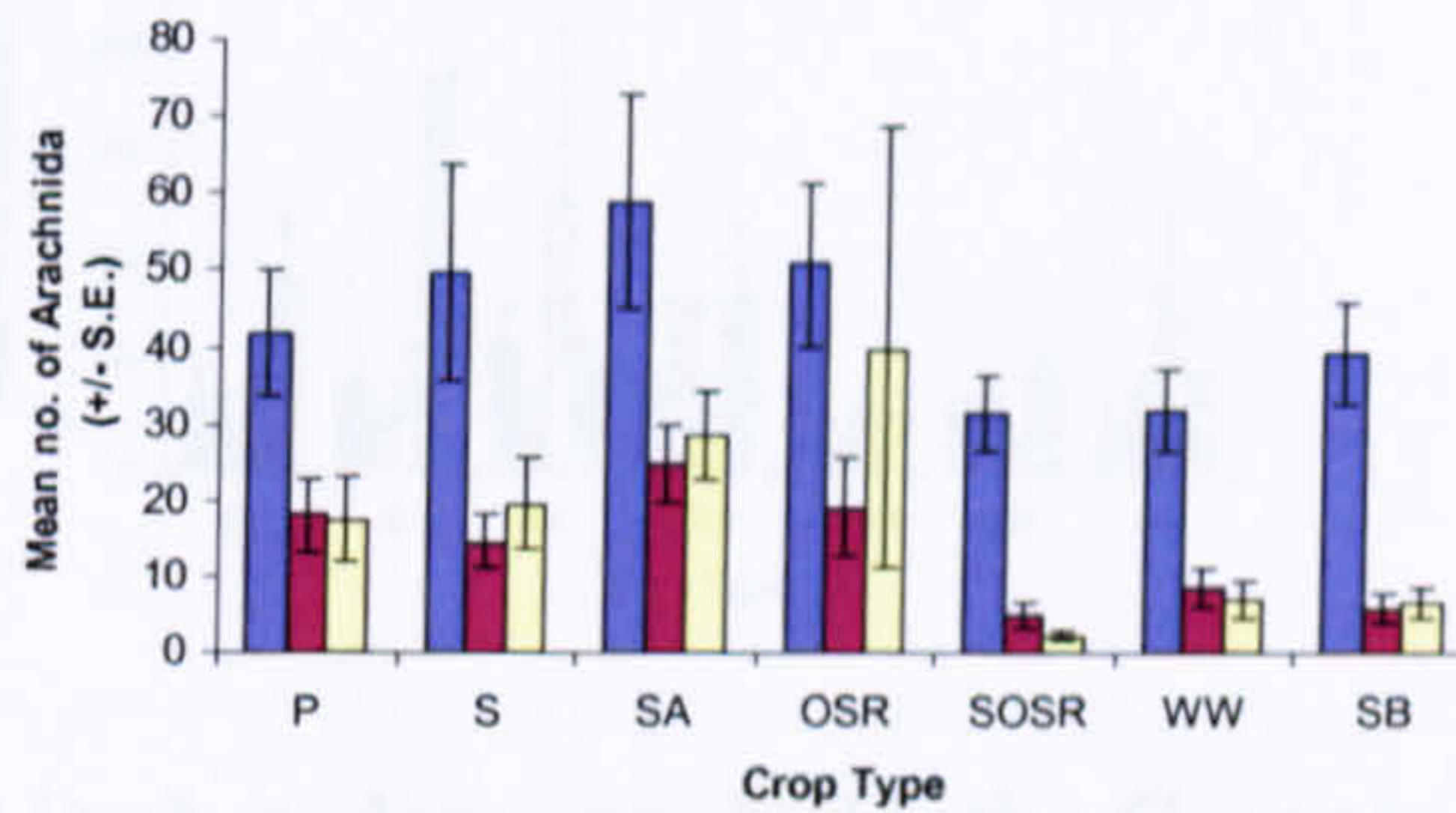
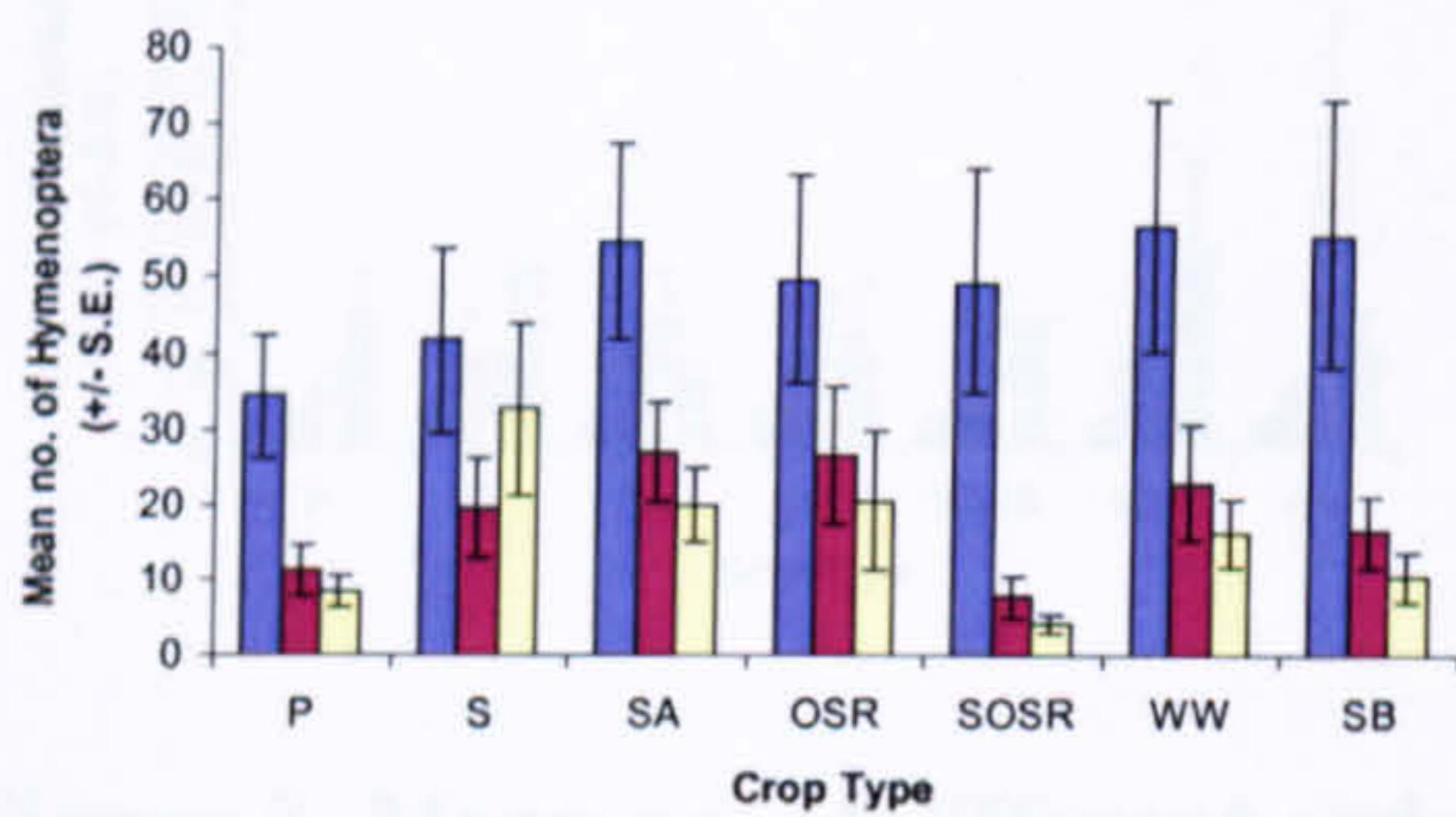
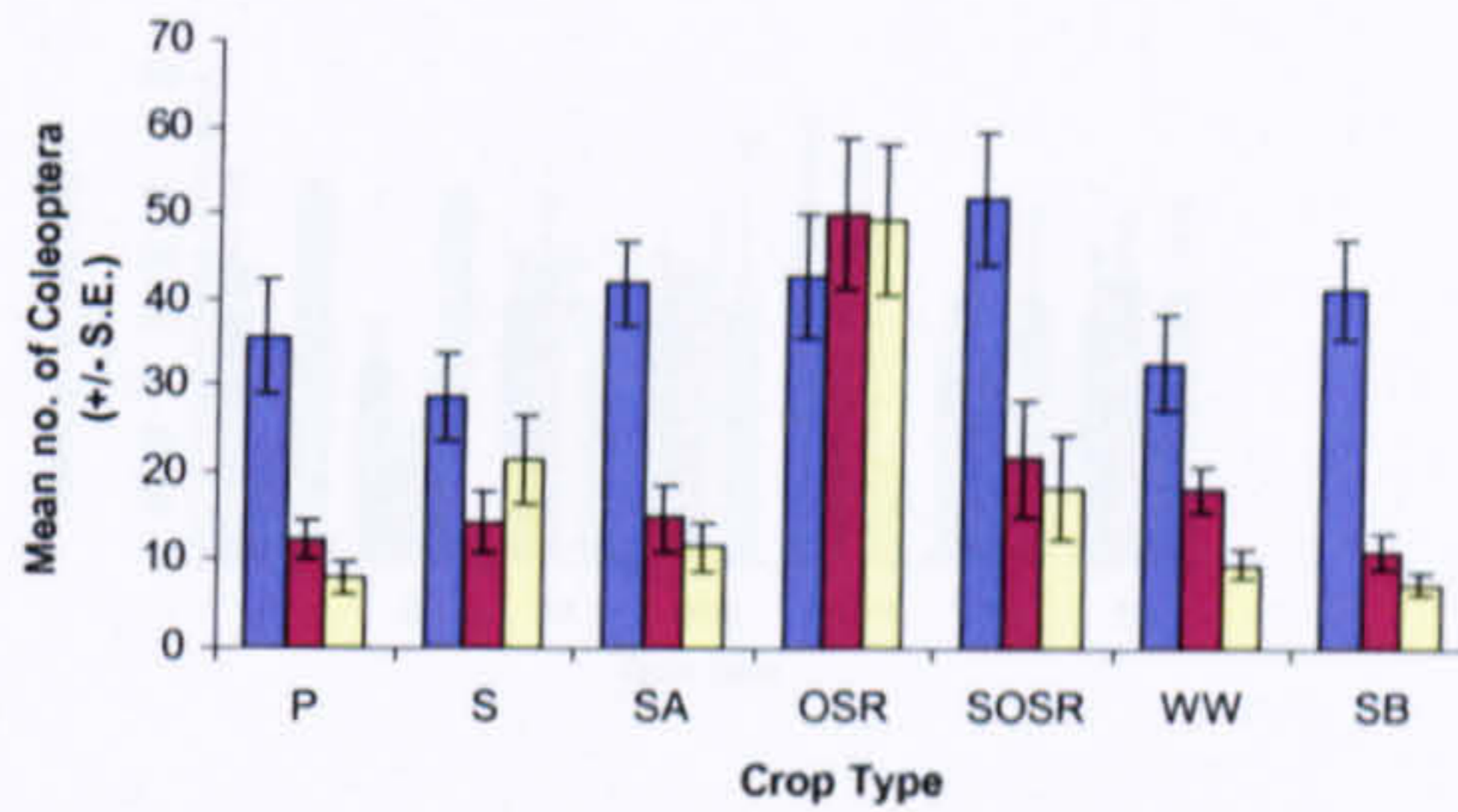
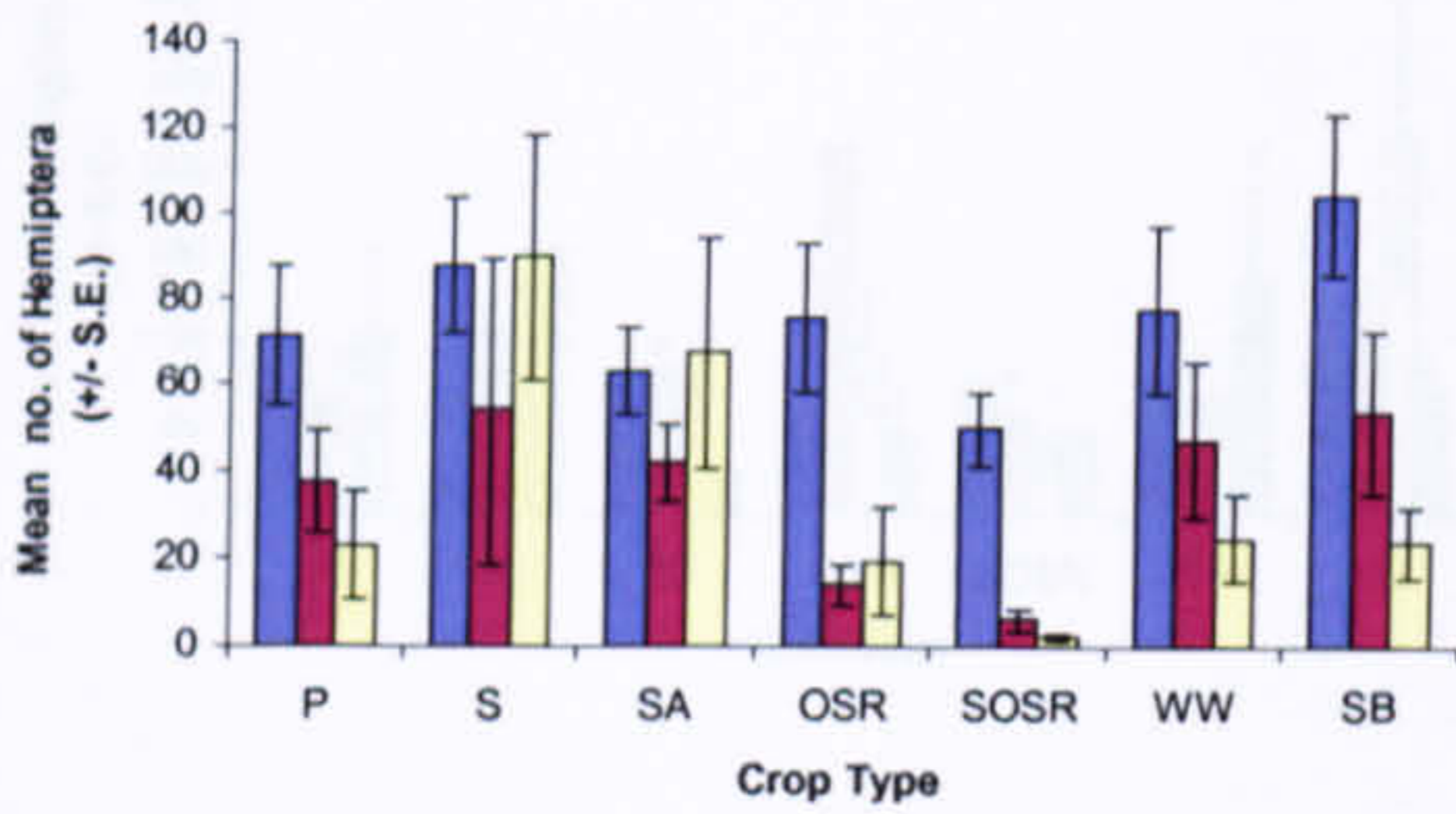
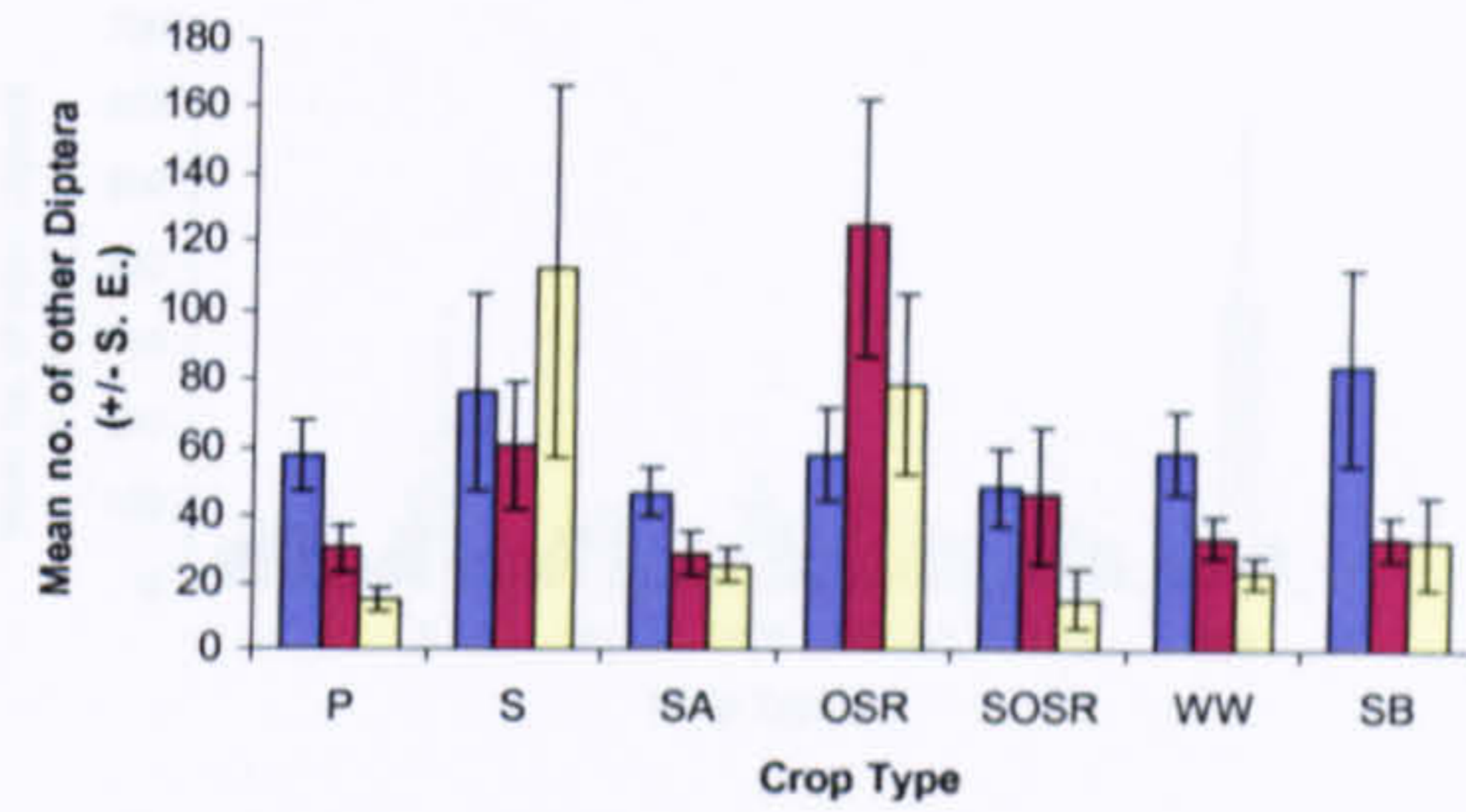
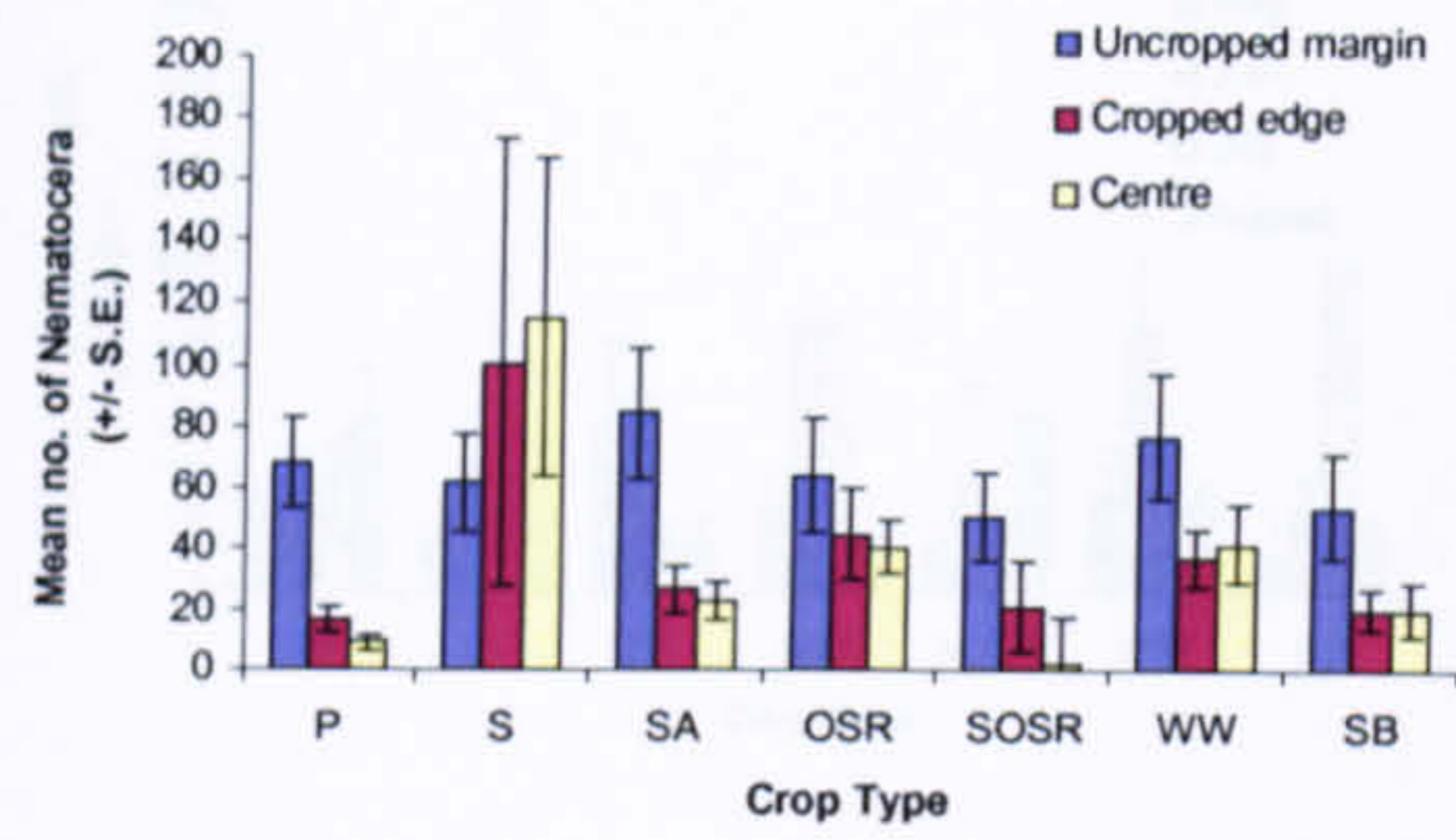
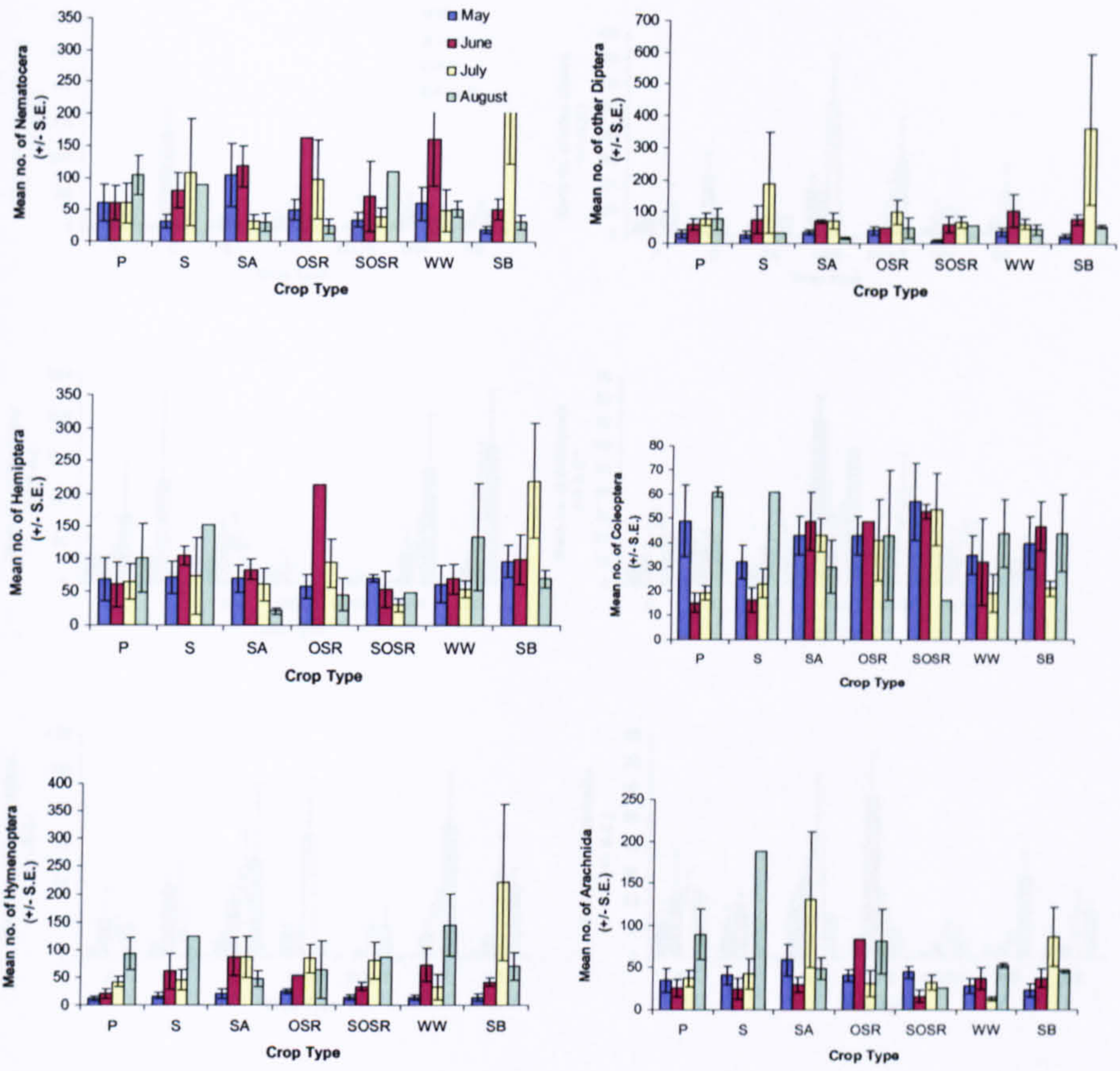


Figure 7. Mean number of different orders/ sub-orders caught by the G-vac in different zones of the field in different crop types (means shown for the months May to August).

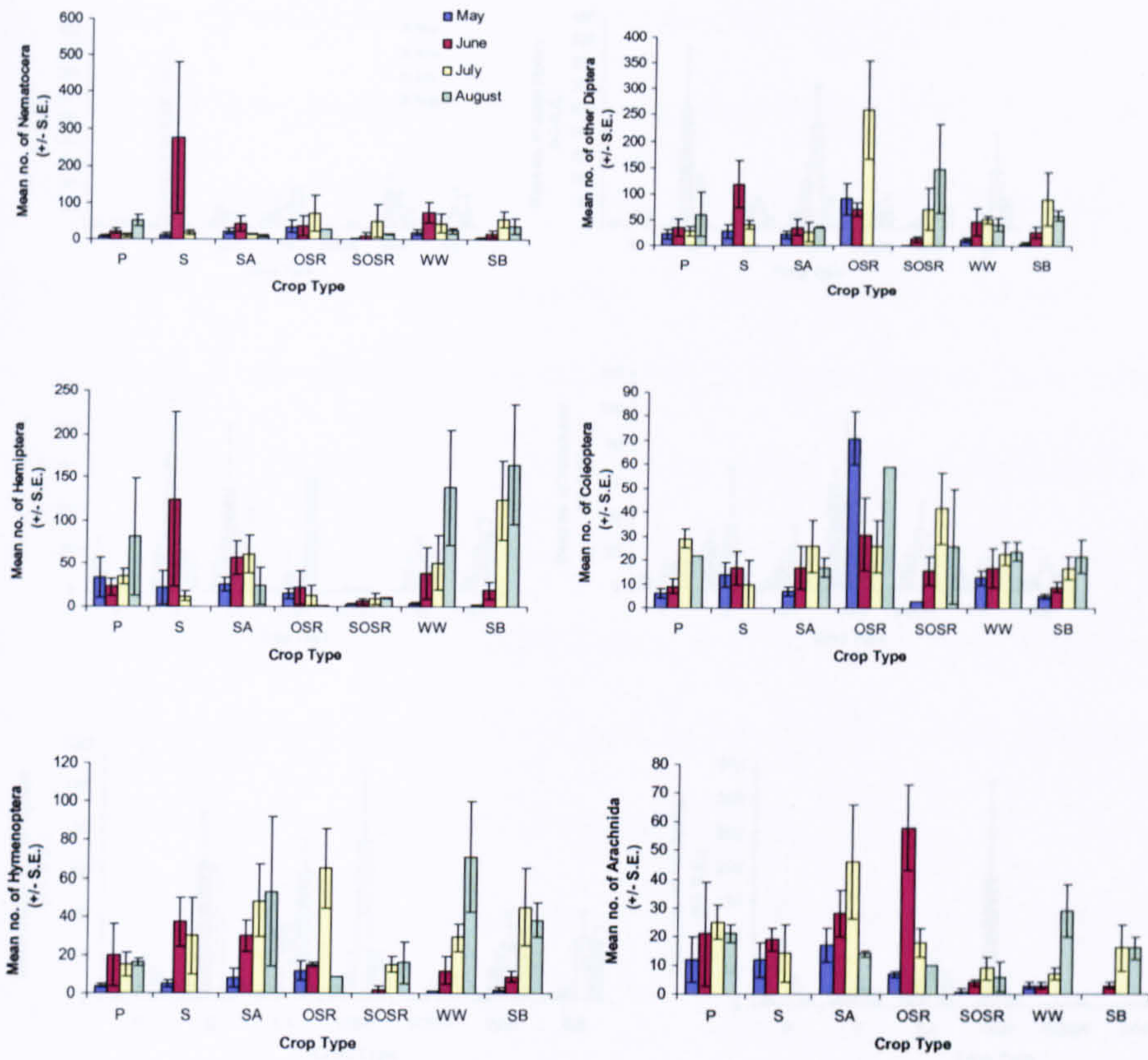
**Figure 7. Mean number of different orders/ sub-orders caught by the G-vac in different zones of the field in different crop types (means shown for the months May to August).**





**Figure 8. Mean no. of different orders / sub-orders caught by the G-vac in different crop types in the UNCROPPED MARGIN by month**



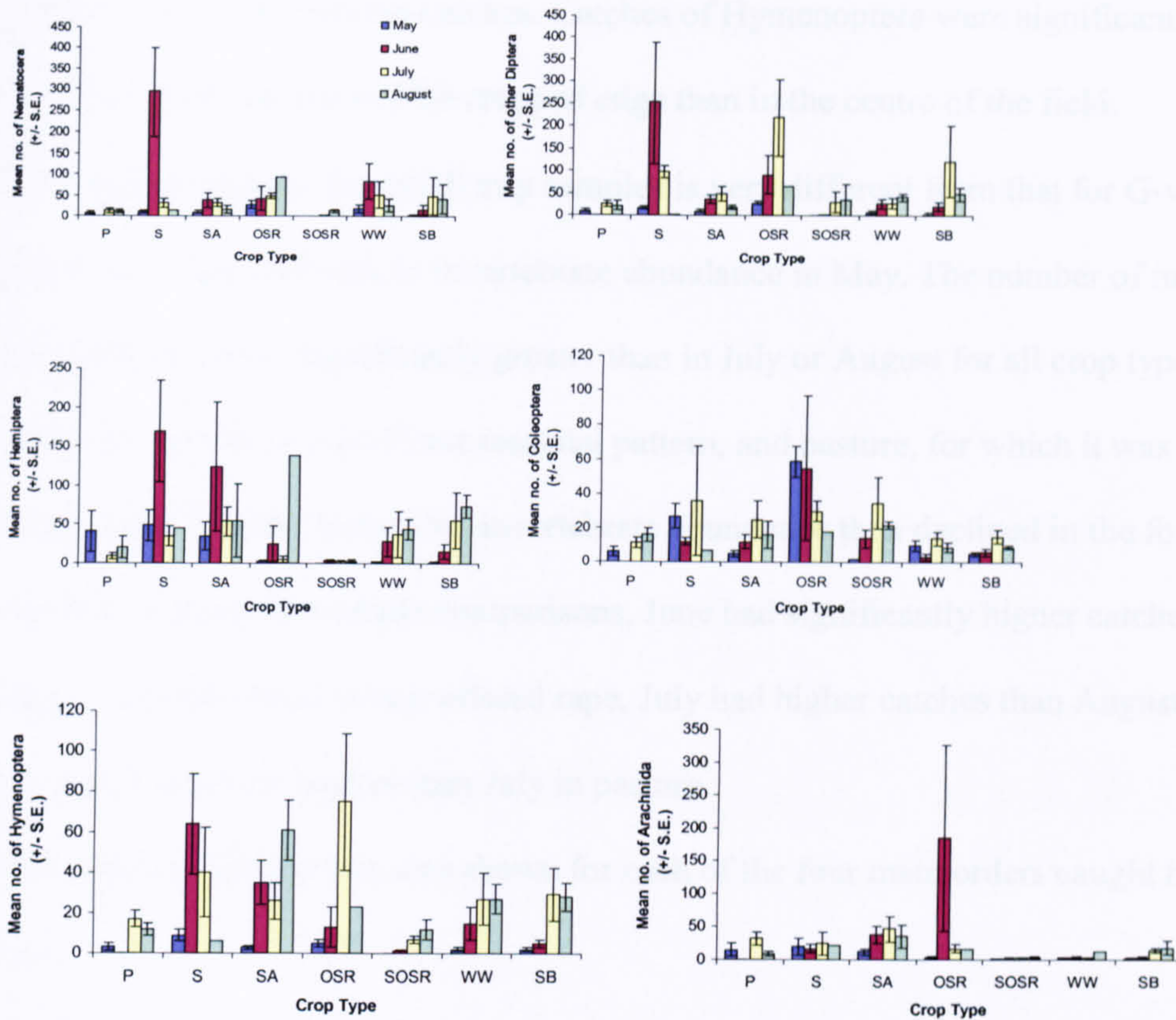


**Figure 9. Mean no. of different orders / sub-orders caught by the G-vac in different crop types in the CROPPED EDGE by month**

Soil surface layer: bristles; pitfall trap samples

Crop type had a significant effect on total number of invertebrates caught by pitfall traps, and this effect differed depending on month (table 4, figure 11). The zone of the field (the sample came from: uncropped margin, cropped edge or center) had no effect on the total number of invertebrates caught by pitfall traps (table 4). Models were rejected for the first main orders caught in pitfall traps: Coleoptera, non-annulose Diptera, Hymenoptera and Arachnida (Appendix tables 10-13). Minimal adequate models were the same as for 'total number of invertebrates', except that there was a significant effect of field zone





**Figure 10. Mean no. of different orders / sub-orders caught by the G-vac in different crop types in the CENTRE by month**

### Soil surface invertebrates: pitfall trap samples

Crop type had a significant effect on total number of invertebrates caught by pitfall traps, and this effect differed depending on month (table 4, figure 11). The zone of the field the sample came from (uncropped margin, cropped edge or centre) had no effect on the total number of invertebrates caught by pitfall traps (table 4). Models were repeated for the four main orders caught in pitfall traps; Coleoptera, non-nematoceran Diptera, Hymenoptera and Arachnida (Appendix: tables 10-13). Minimal adequate models were the same as for ‘total number of invertebrates’, except that there was a significant effect of field zone



sampled on Hymenopteran catches. Catches of Hymenoptera were significantly greater in the uncropped margin and the cropped edge than in the centre of the field.

The seasonal pattern for pitfall trap samples is very different from that for G-vac samples.

There was a general peak in invertebrate abundance in May. The number of invertebrates caught in May was significantly greater than in July or August for all crop types except set-aside, which had no significant seasonal pattern, and pasture, for which it was higher than July but not August. Generally, invertebrate abundance then declined in the following months. Looking at multiple comparisons, June had significantly higher catches than August for spring and winter oilseed rape, July had higher catches than August for silage, but June had lower catches than July in pasture.

This seasonal decline was also shown for each of the four main orders caught by pitfall traps.

In May, the abundance of invertebrates in winter wheat was significantly lower than in winter and spring oilseed rape and silage. Invertebrate abundance also appears to be lower in winter wheat than in spring barley, but this was not significant. Looking at the four orders separately, there were few differences in the abundance of each order between different crop types in May.

In June pasture, silage, winter wheat, and spring barley all had very low pitfall catches, whilst set aside and oilseed rape (spring and winter) had relatively high catches. The only significant difference here is that pasture had fewer ground invertebrates than winter or spring oilseed rape, set-aside, spring barley or winter wheat. Likewise, the main effect looking at the four orders separately is due to pasture being a seemingly poor habitat for Hemiptera, non-nematoceran Diptera and Arachnida (there were no significant differences in numbers of Coleoptera caught in different crop types in June).

Catches in July and August were generally low, with the highest abundances being in pasture. In July, pasture had more invertebrates than spring barley. Catches of Hymenoptera and Arachnida were high in pasture in July. In August there were few significant differences, with spring oilseed rape having low catches of Diptera, and pasture having relatively high and spring oilseed rape and spring barley relatively low catches of Hymenoptera.

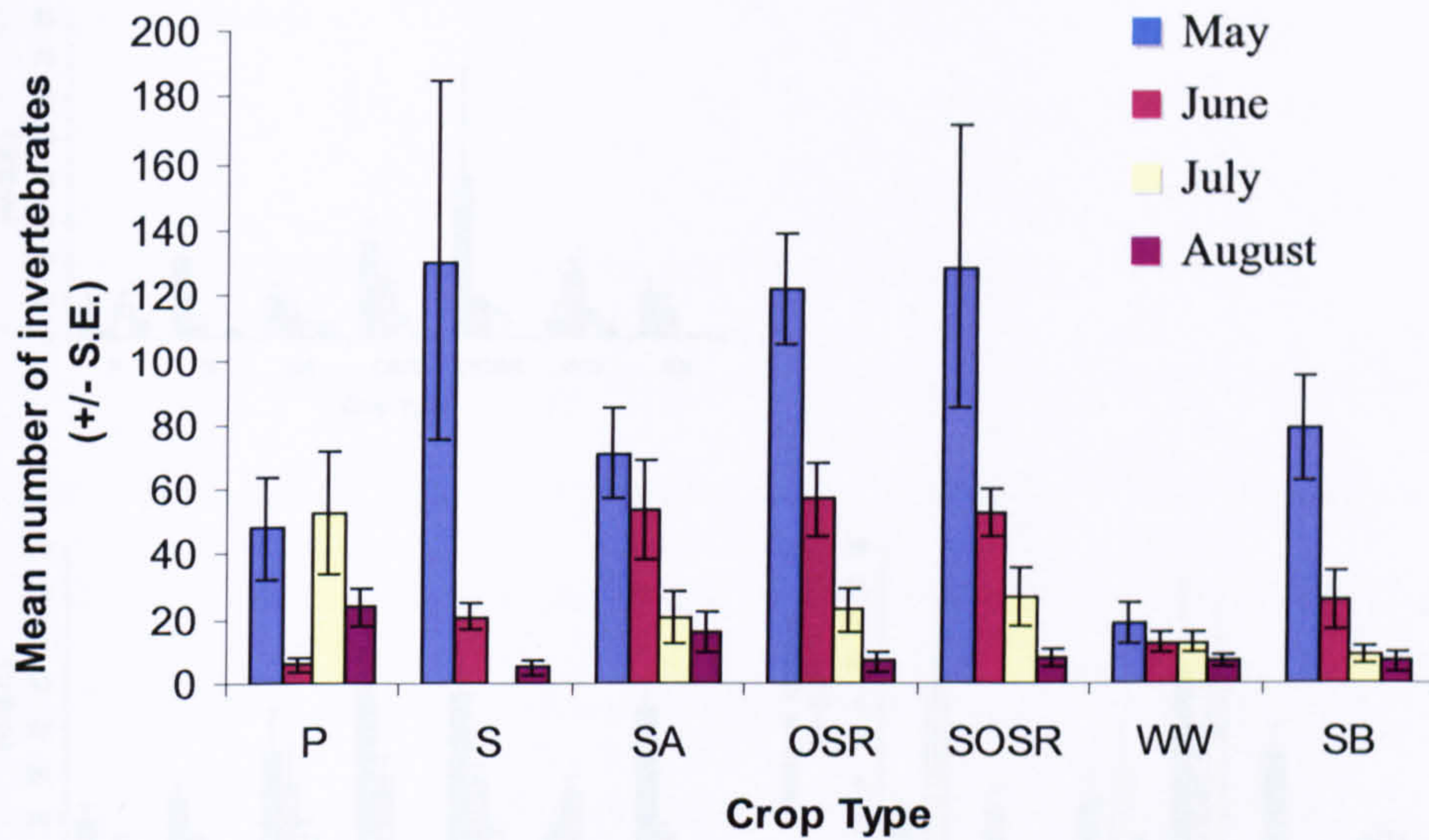
Catches in August were the lowest, and although the highest numbers of invertebrates were caught in pasture and set-aside there were no significant differences between crop types.

**Table 4. GLM to investigate factors affecting total number of invertebrates caught by pitfall traps.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	401	765.54	
Minimum adequate model:			
<b>Crop Type</b>	<b>7</b>	<b>29.63</b>	<b>0.0013</b>
<b>Month</b>	<b>4</b>	<b>178.52</b>	<b>0.0000000000</b>
<b>Crop Type x Month</b>	<b>23</b>	<b>116.63</b>	<b>0.0000000018</b>
Excluded terms:			
Field zone	2	1.73	0.49

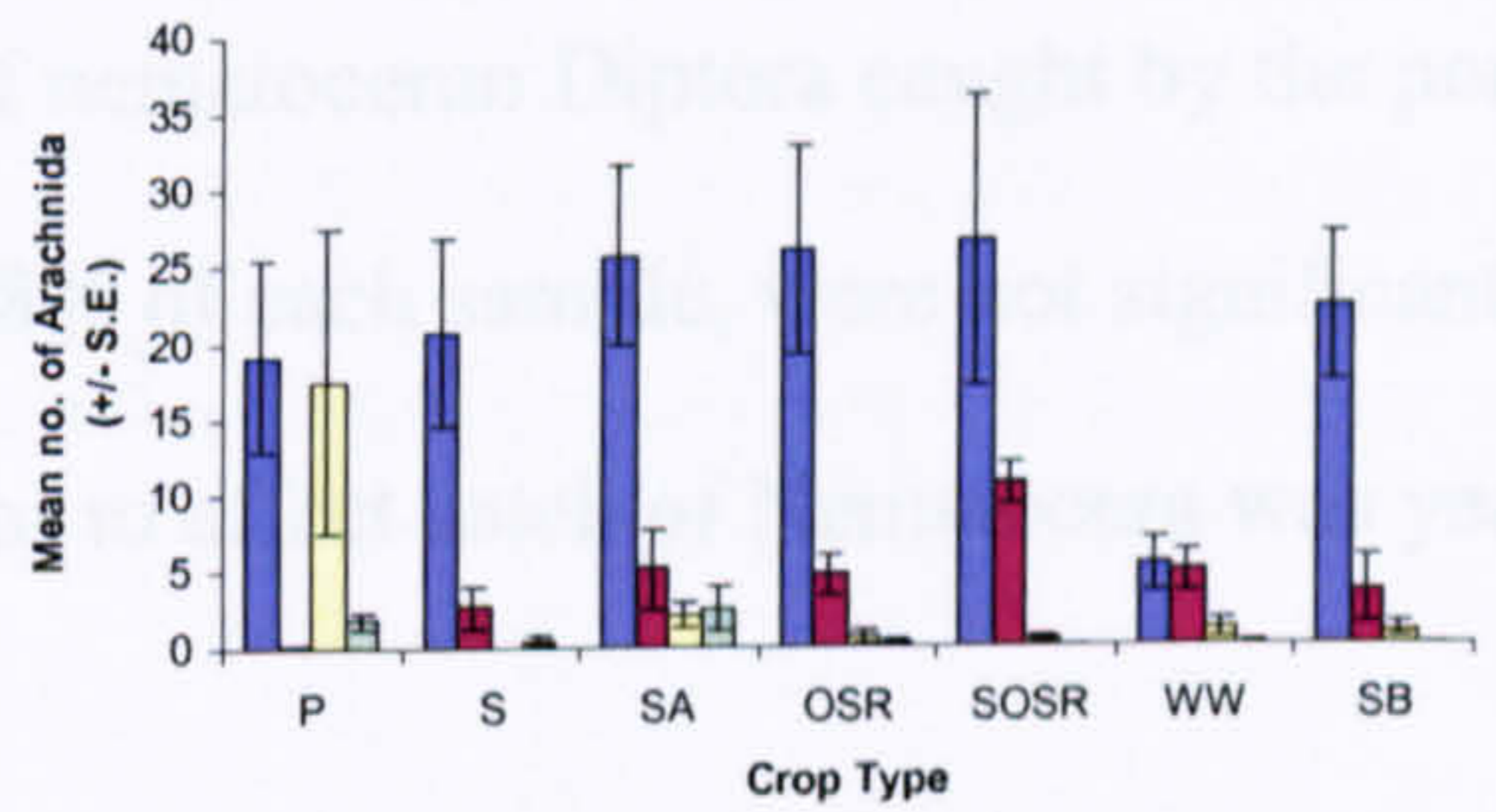
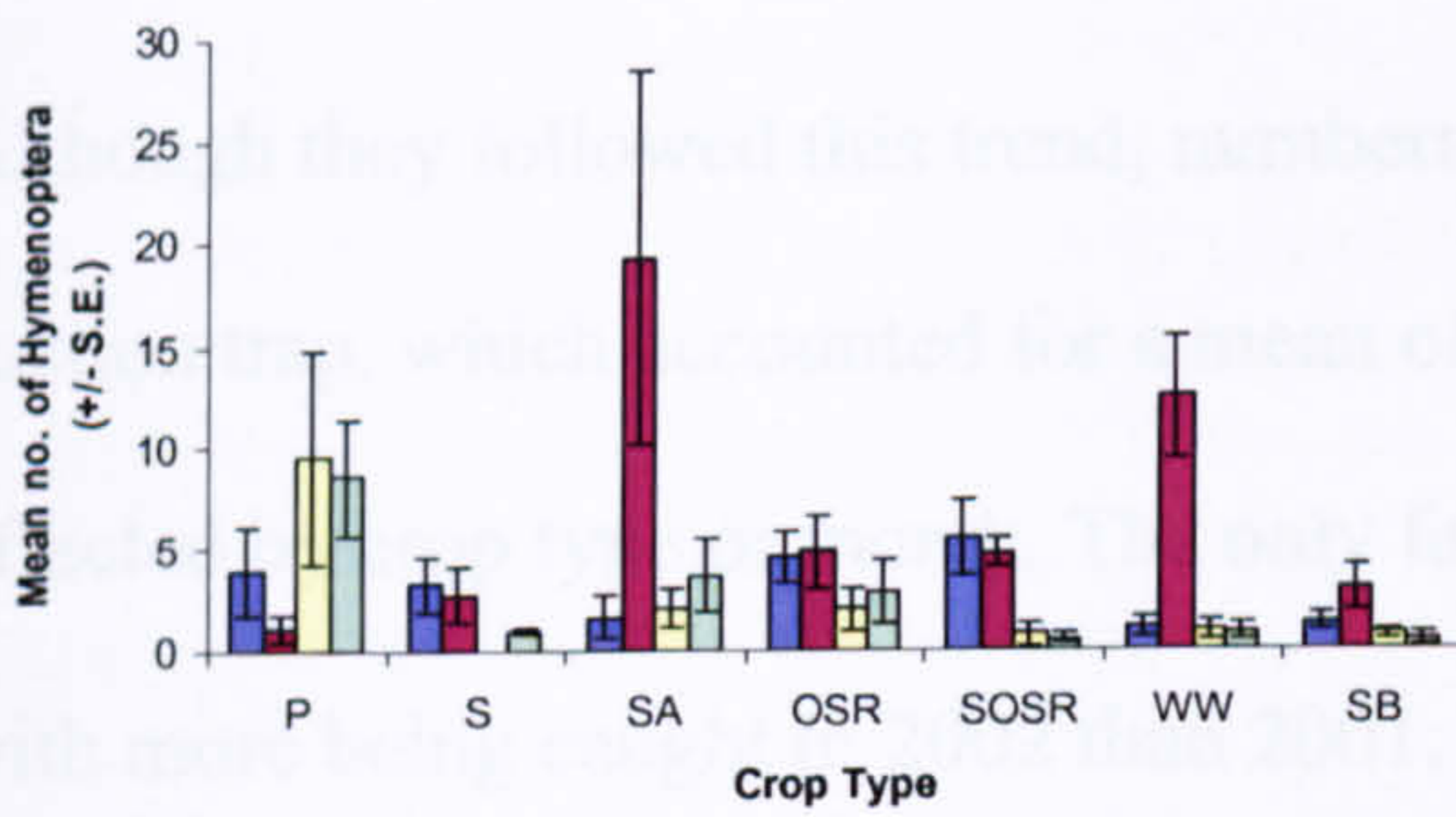
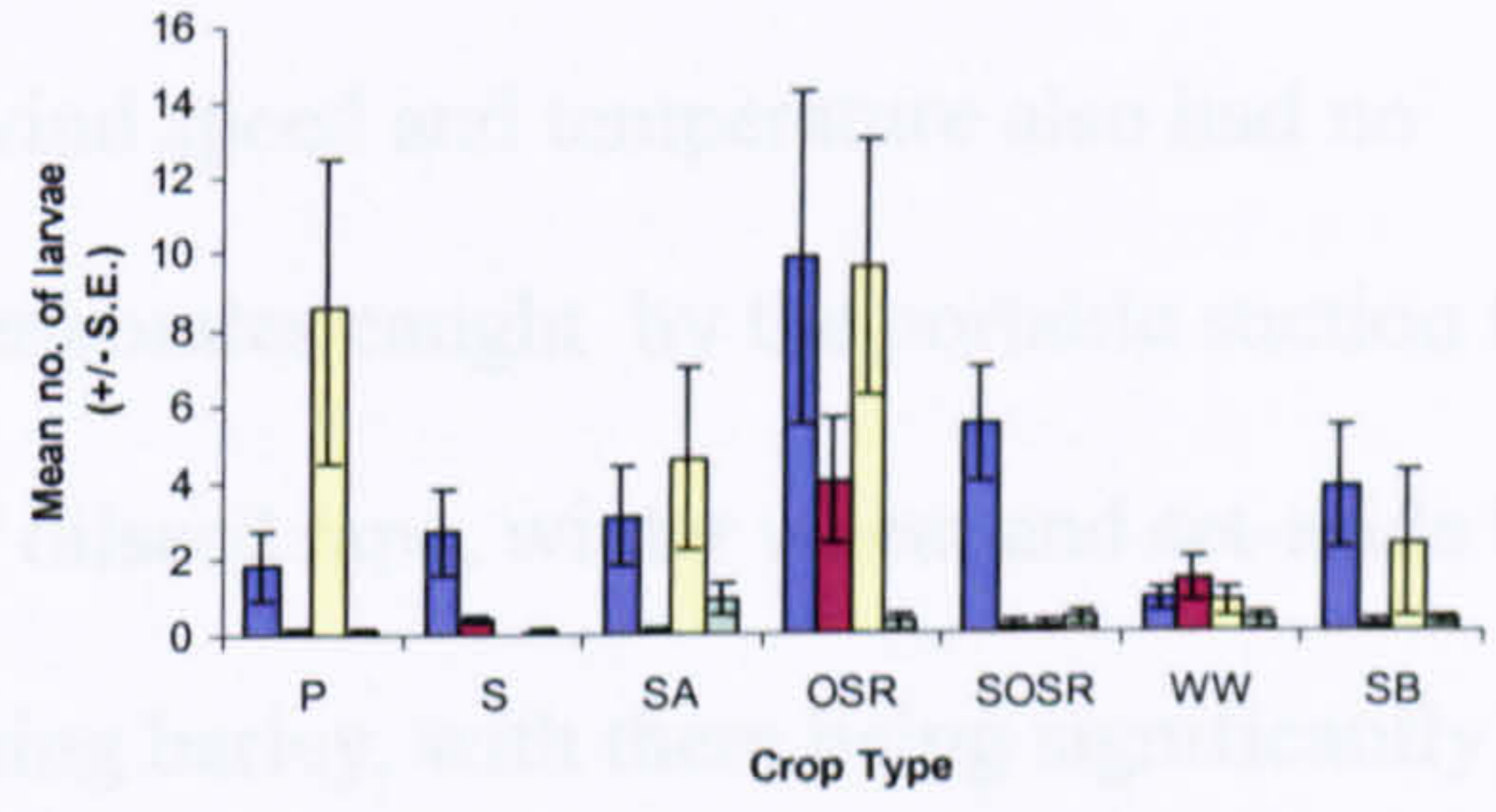
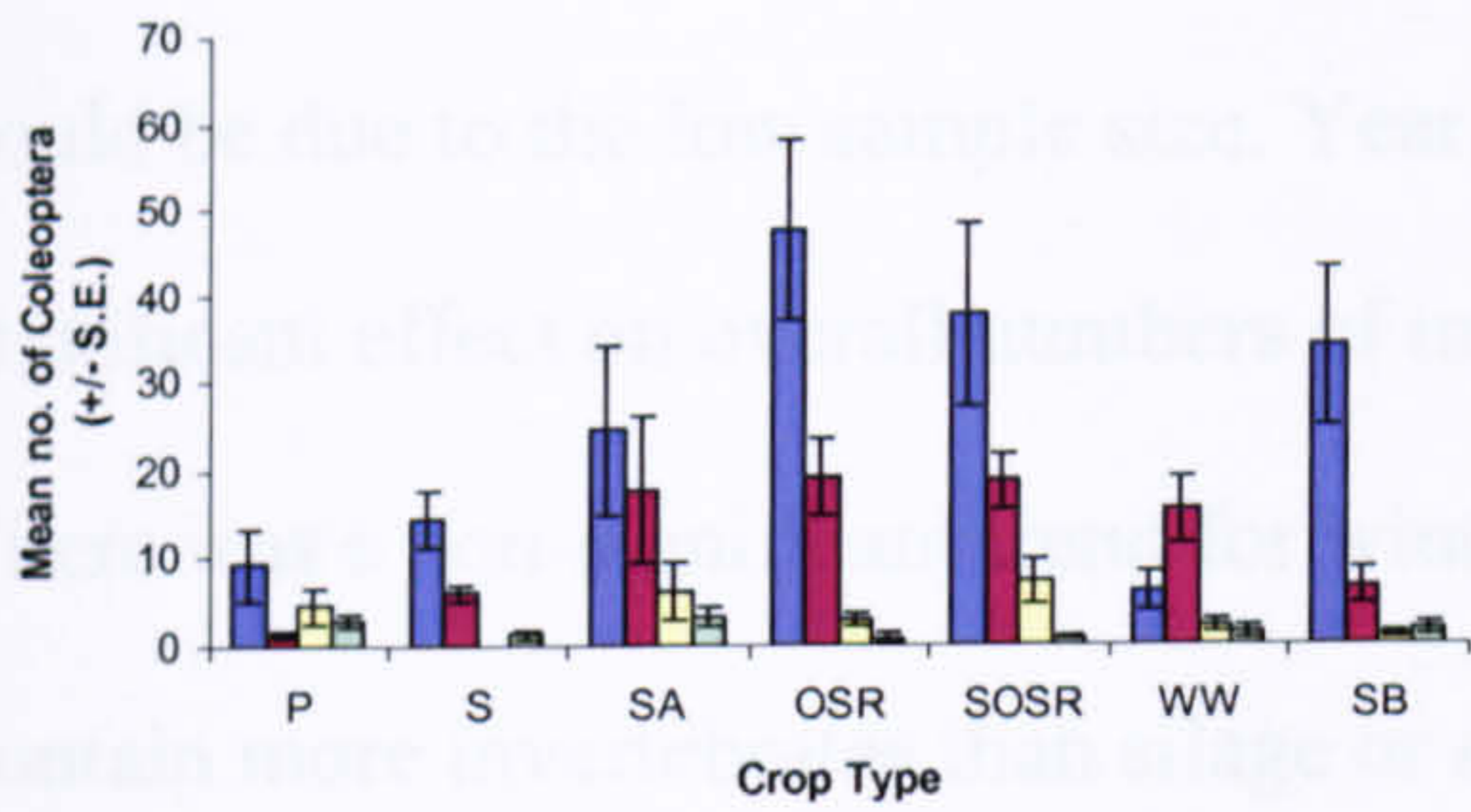
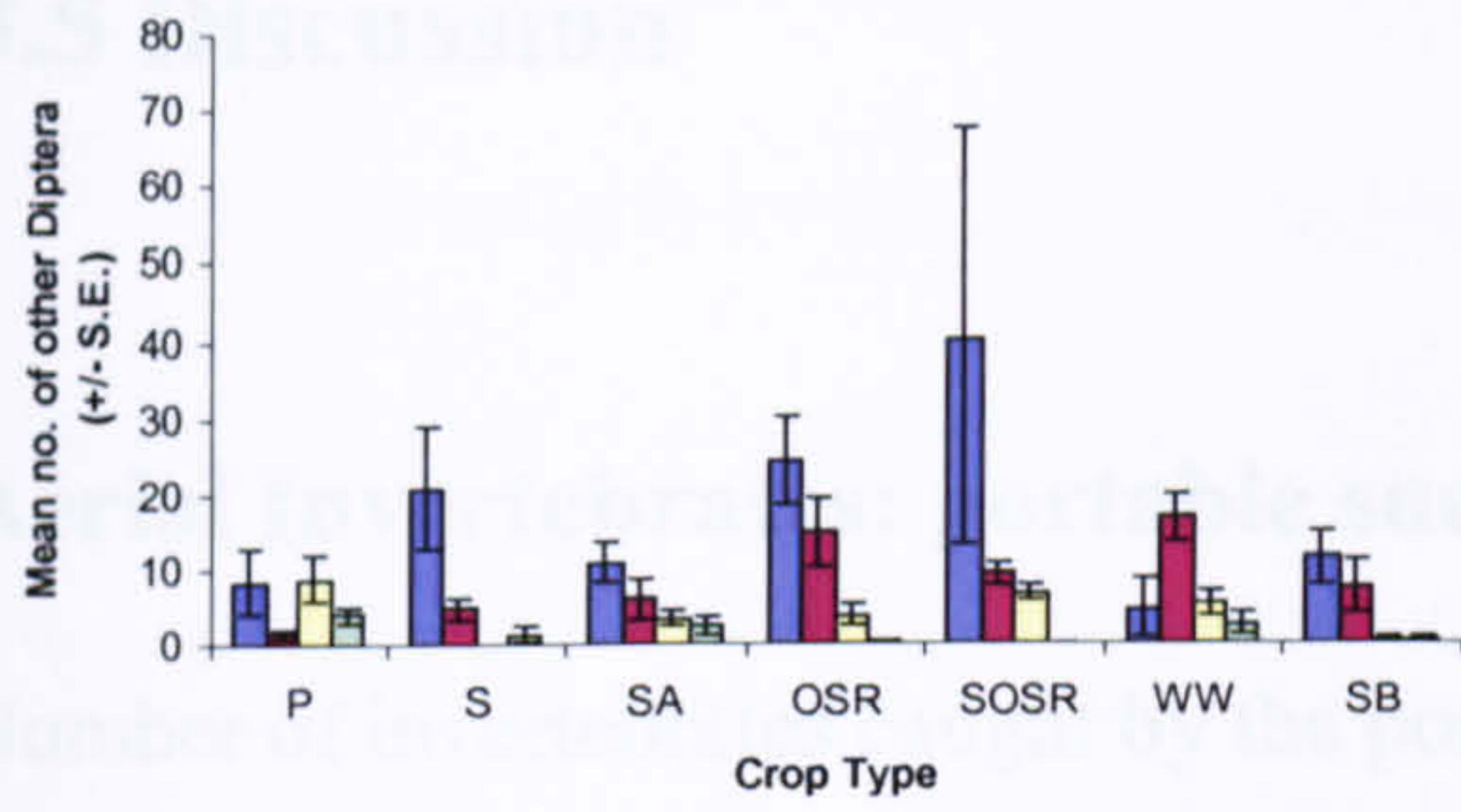




**Figure 11. Mean number of invertebrates caught by the pitfall traps in different crop types for the months May to August.**

(P = pasture, S = silage, SA = set-aside, OSR = winter oilseed rape, SOSR = spring oilseed rape, WW = winter wheat, SB = spring barley).





**Figure 12. Mean no. of invertebrates caught by pitfall traps in different crop types by month and taxa**



### **3.5 Discussion**

#### **Aerial Invertebrates: portable suction trap samples**

Number of invertebrates caught by the portable suction trap (which samples invertebrates from the air at a height of 2m) was unaffected by month. This is a little surprising, and could be due to the low sample size. Year, wind speed and temperature also had no significant effect on overall numbers of invertebrates caught by the portable suction trap.

There was a non-significant trend for winter oilseed rape, winter wheat and set-aside to contain more invertebrates than silage or spring barley, with there being significantly more invertebrates in winter oilseed rape than in silage or spring barley.

Although they followed this trend, numbers of nematoceran Diptera caught by the portable suction trap, which accounted for a mean of 48% of each sample, were not significantly affected by crop type or month. The only factor to affect catch of Nematocera was year, with more being caught in 2002 than 2001.

Numbers of other Diptera caught (mean = 15% of each sample), however, were affected by crop type, with this effect differing depending on month. Winter oilseed rape was the most valuable crop type for aerial Diptera early and late in the season, in April, May and September, when silage was the poorest crop type. Winter wheat and set-aside also had relatively high catches in April, and May for winter wheat, with spring barley having relatively low catches in April. Number of Diptera was also affected by wind, with fewer being caught at high wind speeds, and by year, with more being caught in 2001 than in 2002.

Numbers of Coleoptera caught were affected by crop type, with this effect differing depending on month. Set-aside had higher catches of Coleoptera in April, and in May winter wheat had higher catches than spring barley.



Thus, whilst there are no significant crop type or seasonal effects on number of Nematocera caught, looking at the number of other Diptera and Coleoptera caught would suggest that winter oilseed rape, set-aside, and winter wheat were important crop types for aerial feeding species in April and May, and that silage, and to some extent spring barley, were relatively poor foraging habitats in these months. There were no differences between different crop types in June, July or August for any of the orders looked at.

The height sampled by the portable suction trap is within the foraging range of the Swallow (Bryant & Turner, 1982). A study of foraging preferences of Swallows found they selected hedgerows over the centres of fields, and that they selected pasture over other crop types, with aerial invertebrate abundance and species richness being higher in these selected regions (Evans, 2001). The effect of field zone on aerial invertebrate abundance was not investigated here, due to the limitations of only having one portable suction trap. Pasture was also not sampled in this study, due to problems of leaving the generator-run portable suction trap in a field of livestock.

The fact that swallow foraging habitat selection has been found to relate to the total number of aerial invertebrates caught by sweep net sampling (Evans *et al.*, 2003), however mean that the results of this study would suggest that winter oilseed rape, winter wheat and set-aside may be good foraging habitats for aerial feeding farmland birds, particularly early in the season (April and May).

## **Epigeal and Ground Invertebrates: G-vac and pitfall trap samples**

### ***Field Zones***

#### ***Field Margins***

##### ***G-vac***

Significantly more invertebrates were caught by the G-vac in the uncropped margin than the cropped region of the field for all crop types except silage and winter oilseed rape. For the latter two crop types there was still a non-significant trend for invertebrate abundances to be higher in the uncropped margin but this was not significant, presumably due to the higher numbers of invertebrates within the field in these crop types. This relationship was the same for all orders except for Hemiptera, which were caught in higher numbers in uncropped margins than cropped regions in all crop types.

The magnitude of the difference between invertebrate abundance in the margin and the cropped area of the field decreased through the season, and by August was not significant. This was the case for most of the six main orders to make up G-vac catches also, and was probably due to invertebrates dispersing into the field due to increased sward height of the crop. The fact that for some orders differences in abundance between the cropped edge of the field and the uncropped margin initially decreased through the season supports the hypothesis that invertebrates were dispersing into the field through the season.

The numbers of invertebrates caught in the uncropped margin were unaffected by month or crop type, being relatively high throughout the season, and adjacent to all crop types.

Samples from the uncropped margin were relatively diverse in terms of the orders caught.

### *Pitfall traps*

There was no difference between total number of invertebrates caught by pitfall traps in different zones of the field. When analysis was conducted for the four main orders which made up pitfall trap samples separately, however, it was found that more Hymenoptera were caught in the uncropped margins than the centre of all fields. Although often used to measure invertebrate densities, pitfall traps are very prone to being affected by a number of factors, including vegetation density, as they measure the 'activity-density' of invertebrates, catching the more surface active invertebrates. The fact that soil-surface activity is impeded by dense vegetation could explain the lack of more differences between pitfall trap catches within the field and the often denser vegetation of the uncropped margin. Pitfall traps also sample the more surface active invertebrates, such as ground beetles, whose activity-densities are perhaps more likely to even out across the field due to their high mobility.

Holland *et al.* (2000) found that there were more ground-active invertebrates within 60m of a field's edge, especially carabid beetles. The differences between these results and what was found here could be due to the fact that the 'centre' was defined here as 'at least 50m into the field' and perhaps was not far enough from the edge to make a difference. Thomas & Marshall (1999) found marked differences between field margins and cropped areas using a suction sampler, but not using pitfall traps.

Other studies using suction sampling have also found field margins to have a higher abundance of invertebrates than within fields (Holland *et al.*, 2002, Meek *et al.*, 2002, review in Vickey *et al.*, 2002), and uncropped field margins are the preferred summer foraging habitat of a number of granivorous passerines, such as the Yellowhammer (Perkins, *et al.*, 2002), Corn Bunting (Brickle *et al.*, 2000) and Reed Bunting (Fuller *et al.*,



1995). An agri-environment scheme which included a prescription for provision of grass margins led to a huge increase in Cirl Bunting numbers on project land (83%) compared to non-project land (2%) in their restricted range in the south west of England (Peach *et al.*, 2001).

As a result of this, forms of field margin management have been included within most recent agri-environment schemes in the UK (e.g. countryside stewardship, (MAFF, 1999); arable stewardship (MAFF, 1998); ESAs (MAFF, 1994; Dwyer, 1994)). Common Agricultural Policy reform will make it necessary for farmers to have an uncropped 1m strip either side of all ditches and hedgerows in order to receive subsidies, which will potentially benefit farmland birds and invertebrates, although how margins are managed is also important in determining their value as foraging habitats for farmland bird species, with several studies of this aimed at forming management recommendations (reviewed in Vickery *et al.*, 2002).

### ***Outer field***

#### ***G-vac***

There was no difference between total number of invertebrates caught by the G-vac 4m into the field and the centre (at least 50m in) of the field. However, when analysis was done separately for the six main orders to make up G-vac catches, there were more Nematocera, other Diptera, and Hymenoptera in the cropped edge of spring oilseed rape fields than in the centre, and more Coleoptera in the edge than the centre of winter wheat fields. There were also several cases where catches of an order were higher in the uncropped margin of the field than in the centre, but there was no difference between catches in the cropped edge (4m in) and either the margin or the centre of the field, which implies that there was a non-significant trend in these cases for abundances in the cropped edges to be higher than in the centre of the fields.

### *Pitfall traps*

Catches of Hymenoptera in pitfall traps were higher in the uncropped margin and the cropped edge than in the centre of fields, with there being no difference between numbers of Hymenoptera caught in the margin and the cropped edge. There were no other differences in pitfall trap catches between different zones of the field.

Thus there is some evidence for cropped edges of fields supporting higher numbers of invertebrates than the centres of fields. This suggests that Conservation Headlands (where the outermost 6m of the field receives reduced pesticide inputs) could be of importance in increasing the value of these invertebrate rich areas to farmland birds. Indeed, a policy of reducing agrochemical inputs to the field edge has been considered one of the most effective ways of enhancing invertebrate food for Grey Partridge, and leads to increased chick survival (Sotherton, 1991, 1998). Similar results have been found for wild pheasant chicks (Sotherton *et al.*, 1993). However, other studies have been less conclusive in terms of the value Conservation Headlands. One study looking at abundances of passerines in hedgerows found that 14 of the 18 species surveyed actually had lower incidences in hedgerows adjacent to winter-sown cereals with Conservation Headlands than those without, with the opposite being true of hedgerows next to spring-sown cereals (Green *et al.*, 1994). Cracknell (1994) found no preference for unsprayed headlands by the three species studied which foraged predominantly in cereal fields (Blackbirds, Dunnocks and Yellowhammers). Both of these studies suggest lack of accessibility to be the reason for the limited evidence of benefits of Conservation Headlands to farmland birds, this explains why Conservation Headlands may be of benefit next to spring sown cereals, but not next to winter sown cereals, where weeds have had longer to establish.

### ***Crop types and seasonal trends***

#### ***G-vac***

G-vac catches were generally lowest in May and increased through the season, with this being more pronounced in the cropped region of the field. This is presumably due to a general increase in sward height through the season. Structural diversity increases with increasing vegetation height (Brown, 1991). Taking spiders as an example, increased structural diversity has been related to increased opportunities for web-site selection and prey capture (Wise, 1993, Samu *et al.*, 1996). Vegetation structure has been shown to determine Aranae community structure (Bell *et al.*, 2001), and decreasing vegetation height has been shown to decrease the abundance of a linyphiid spider (Haughton *et al.*, 2001).

There was a significant effect of crop type on number of invertebrates caught by the G-vac, and this effect differed depending on month. Invertebrate abundances differed most between different crop types in May, and the number and degree of differences in abundances between crop types decreased through the season. The trends shown by total invertebrate catches were similar when the six main orders caught by the G-vac were looked at separately. Spring barley and spring oilseed rape had relatively low invertebrate abundances in May and June. Winter oilseed rape, set-aside and silage had relatively high invertebrate abundances of most orders in this period, and winter wheat varied in abundances of different orders, but showed a general trend for catches to be higher than in spring barley.

#### ***Pitfall traps***

Trends shown by pitfall trap catches differed to those for G-vac catches. Catches were highest in May, and decreased through the season. This is presumably due to the adverse effect of vegetation density on the size of pitfall trap catches, as increasing vegetation



density through the season would impede movement of invertebrates within fields. There were some signs from pitfall trap catches that winter oilseed rape, set-aside and silage had high invertebrate abundances, especially in May and June, however, unlike for G-vac catches spring oilseed rape also had high catches early in the season, perhaps due to its low stem density at this time

#### *Winter versus spring sown cereals*

There have been several papers drawing attention to the adverse effects that the switch from spring sowing to autumn sowing of cereals may have had on farmland bird populations, primarily because of the associated loss of seed rich over-winter stubbles, a preferred winter foraging habitat for many species (Cirl bunting: Evans & Smith, 1994, Corn bunting: Donald & Evans, 1994, and others Wilson *et al.*, 1996). The reduction in spring sown cereals may also have had adverse effects on farmland bird populations as some species feed directly on spring sown grain, and thus benefit directly from spring cereals in late winter/ early spring when other food is scarce (Green, 1978), and other species prey on the invertebrates which are disturbed and exposed during spring cultivation. Spring barley is also a preferred nesting habitat for Skylarks and Lapwings (Chamberlain, 2000) due to its sparser vegetation structure. Spring barley is a preferred summer foraging habitat of Corn Buntings, with winter wheat being avoided (Brickle *et al.*, 2000).

However, the results presented in this chapter seem to show that winter wheat could be a relatively good source of invertebrate food early in the season (May and June) compared to spring barley. This is likely to be due to the greater vegetation height, which may support more invertebrates, as well as providing cover for foraging farmland birds. Surveys of passerine abundances within hedgerows during May and June support this finding, with

most species occurring more frequently next to autumn than spring sown cereals (Green *et al.*, 1994).

### *Winter oilseed rape*

Similarly, winter oilseed rape generally had high invertebrate abundances in G-vac and pitfall traps whereas spring oilseed rape had poor G-vac catches early in the season. This is probably due to the lower vegetation height and later flowering of spring oilseed rape.

Thus winter oilseed rape would appear to be a valuable foraging habitat in terms of invertebrate abundance in May and June, the nesting period of many species. Winter oilseed rape would also provide good cover for farmland birds, and has less dense vegetation close to the ground than cereals, improving accessibility of invertebrates. The fact that winter oilseed rape may be a good invertebrate source for farmland birds is supported by other studies; Holland *et al.* (2002) also found invertebrate abundances to be relatively high in break crops such as oilseed rape. Surveys of passerine abundance in hedgerows next to different crop types found winter oilseed rape to be a preferred crop overall (Green *et al.*, 1994), and Lack (1992) found that records of total numbers of hedgerow passerines, as well as Blackbirds and Reed Buntings observed in fields during Common Birds Census fieldwork indicated preference for oilseed rape over all other arable crops. Winter oilseed rape is also selected over other arable crops as a nesting habitat for Reed Buntings, with a study showing that whilst Reed Buntings would nest in oilseed rape fields up to 500m away from wet features, they would only nest in other arable fields which were adjacent to wet features (Gruar *et al.*, in press).

### *Set-aside*

Set-aside also appears to have held high abundances of invertebrates, particularly early season. Set-aside was introduced as a compulsory measure under the Common Agricultural Policy in 1992 to try to prevent over-production. This resulted in over 600 000 ha of land

being taken out of arable production in 1992 (Buckingham *et al.*, 1999). Although not designed to benefit wildlife, set-aside has been shown to be a preferred foraging habitat for a number of declining farmland bird species both in winter (Buckingham *et al.*, 1999) and during the summer (Henderson *et al.*, 2000).

### *Silage*

The results presented here also show that silage has high invertebrate catches early in the season. This could be due to the high level of nitrogen fertiliser input, as increased nitrogen input has been shown to increase invertebrate abundance on grassland, whilst decreasing species richness (Haddad *et al.*, 2000). The replacement of hay with silage has had detrimental impacts on farmland bird populations, in some cases directly, due to nest destruction by earlier mowing (Corncrake: Stowe *et al.*, 1993, Green & Stowe, 1993, Stone Curlew: Green, 1988, Green & Griffiths, 1994), however this study would suggest that silage may provide high invertebrate abundance for foraging farmland birds (whilst not being good in terms of invertebrate diversity).

### **Recommendations**

Based on the results of this study, the main recommendation to increase invertebrate chick food abundance for farmland bird species would be an increase in field margin habitat. Uncropped margins were found to contain on average 62% more invertebrates than the centres of fields. Margins next to all crop types contained about the same numbers of invertebrates. Margins also appeared to act as a source of invertebrates for the cropped area of the field later in the season, making them valuable to farmland birds which prefer to forage within fields, as well as those which forage mainly in the margins. There are proposals under current reform of the Common Agricultural Policy for farmers to be required to leave an uncropped 1m strip either side of any hedgerows or ditches in order to



receive subsidies. This could be of great benefit to farmland bird populations. There is the problem though that many hedgerows and other aspects of field margins are poorly managed for wildlife due to lack of manpower or incentive. Although type of field margin has not been looked at here, there are several studies aiming to provide management recommendations on the subject (Arnold, 1983, Osborne, 1984, Parish *et al.*, 1994, 1995, Green *et al.*, 1994, Macdonald & Johnson, 1995).

Although some evidence was found for cropped edge habitats supporting higher numbers of invertebrates than the centres of fields, recommendation of Conservation Headlands would be dependent on further research into their benefits in different crop types, with current research suggesting that they are of value to farmland birds in spring sown cereals, but that they may actually be selected against in winter sown cereals, perhaps due to lack of accessibility (Green *et al.*, 1994).

Invertebrate accessibility or availability has not been discussed a great deal in this study, with the focus being on abundance, as time constraints did not allow for measurements of vegetation structure. However, the crop types and field zones which were found to support high numbers of invertebrates in this study have often been in accordance with results of studies of habitat selection in farmland bird species. However, it should be noted that a study looking at patch selection by Yellowhammers in cereal fields found that foraging locations had sparser and shorter vegetation than random locations within the same fields, highlighting the importance of measures to promote invertebrate accessibility in the field in cereal crops, such as wider drill row spacing, reduced fertiliser inputs, and the provision of bare patches created by momentarily turning off seed drills (Morris *et al.*, 2002).

Most differences in invertebrate abundances between crop types were found early in the season, when chick-rearing conditions appear to be harsher for many species of granivorous passerines (Evans *et al.*, 1997, this thesis: chapter 6). During the early season, particularly May, spring oilseed rape and spring barley have very low invertebrate abundances, as at this time their vegetation height is very short. Winter oilseed rape is an invertebrate rich habitat throughout the season, but may prove particularly important early in the season. Thus, subsidies to maintain winter oilseed rape, as oppose to spring oilseed rape, would be beneficial to farmland birds. Winter wheat is also a good source of aerial invertebrates, and relatively rich in epigeal invertebrates early in the season compared to spring barley (although both cereals contained low numbers compared to other crop types). As mentioned, spring barley had low invertebrate abundances in May and June, and avoidance of spring cereals by farmland passerine species is also shown by some studies. However, spring barley does provide benefits to farmland birds in terms of providing over-winter stubbles in winter, and nesting habitat for skylarks and lapwings in spring. Thus it would be beneficial to farmland birds with a long breeding season to have a mixture of spring and winter sown cereal in the landscape in close proximity, to provide invertebrate food throughout the breeding season.

The importance of maintaining set-aside in the landscape is shown by this study, as it also provided a good habitat for aerial and epigeal invertebrates. Measures to allow the required area of set-aside to be split could be beneficial, as they would presumably result in it being available within the foraging ranges of more farmland birds.

In conclusion, winter oilseed rape and set-aside would seem to be beneficial crop types for farmland birds, aswell as a mixture of spring and autumn sown cereals and wide margin habitats.

## Appendix

**Table 1. GLM to investigate factors affecting the number of Nematocera caught by the portable suction trap.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	63	125.24	
Minimum adequate model:			
<b>Year</b>	<b>1</b>	<b>14.06</b>	<b>0.008</b>
Excluded terms:			
Crop Type	4	11.37	0.129
Wind Speed	1	2.09	0.133
Temperature	1	0.05	0.808
Month	5	6.19	0.472



**Table 2. GLM to investigate factors affecting the number of non-nematoceran Diptera caught by the portable suction trap.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	59	124.51	
Minimum adequate model:			
<b>Crop Type x month</b>	<b>17</b>	<b>256.29</b>	<b>0.000</b>
<b>Crop Type</b>	<b>4</b>	<b>22.08</b>	<b>0.005</b>
<b>Month</b>	<b>5</b>	<b>5.20</b>	<b>0.507</b>
<b>Wind speed</b>	<b>1</b>	<b>8.75</b>	<b>0.011</b>
<b>Year</b>	<b>1</b>	<b>10.51</b>	<b>0.006</b>
Excluded terms:			
Temperature	1	0.29	0.621

**Table 3. GLM to investigate factors affecting the number of Coleoptera caught by the portable suction trap.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	58	199.75	
Minimum adequate model:			
<b>Crop Type x month</b>	<b>17</b>	<b>418.00</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>4</b>	<b>28.63</b>	<b>0.0039</b>
<b>Month</b>	<b>5</b>	<b>35.61</b>	<b>0.0024</b>
Excluded terms:			
Wind speed	1	4.00	0.104

**Table 4. GLM to investigate factors affecting the number of Nematocera caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	351	778.12	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>109.72</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>59.51</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>76.48</b>	<b>0.0000</b>
<b>Year</b>	<b>1</b>	<b>48.33</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>126.20</b>	<b>0.0000</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>91.23</b>	<b>0.0000</b>
<b>Zone x Month</b>	<b>6</b>	<b>28.17</b>	<b>0.006</b>

**Table 5. GLM to investigate factors affecting the number of non-nematoceran Diptera caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	352	626.25	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>4.79</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>67.11</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>132.02</b>	<b>0.0000</b>
<b>Year</b>	<b>1</b>	<b>28.67</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>73.70</b>	<b>0.0000</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>36.68</b>	<b>0.0007</b>
<b>Zone x Month</b>	<b>6</b>	<b>14.12</b>	<b>0.038</b>



**Table 6. GLM to investigate factors affecting the number of Coleoptera caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	352	409.17	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>89.87</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>58.88</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>9.53</b>	<b>0.001</b>
<b>Year</b>	<b>1</b>	<b>3.02</b>	<b>0.024</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>28.79</b>	<b>0.0002</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>23.62</b>	<b>0.0001</b>
<b>Zone x Month</b>	<b>6</b>	<b>21.10</b>	<b>0.000006</b>

**Table 7. GLM to investigate factors affecting the number of Hemiptera caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	352	833.54	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>102.34</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>81.12</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>24.65</b>	<b>0.007</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>82.81</b>	<b>0.0028</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>12.71</b>	<b>0.001</b>
<b>Zone x Month</b>	<b>6</b>	<b>38.11</b>	<b>0.016</b>
Excluded terms:			
Year	1	0.02	0.931

**Table 8. GLM to investigate factors affecting the number of Hymenoptera caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	352	704.02	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>162.26</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>72.40</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>256.82</b>	<b>0.0000</b>
<b>Year</b>	<b>1</b>	<b>0.95</b>	<b>0.376</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>50.36</b>	<b>0.002</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>50.18</b>	<b>0.00009</b>
<b>Zone x Month</b>	<b>6</b>	<b>17.94</b>	<b>0.0006</b>



**Table 9. GLM to investigate factors affecting the number of Arachnida caught by the G-vac.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	352	620.65	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>159.02</b>	<b>0.0000</b>
<b>Crop Type</b>	<b>6</b>	<b>110.82</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>52.90</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>67.30</b>	<b>0.0000</b>
<b>Crop Type x Zone</b>	<b>12</b>	<b>42.02</b>	<b>0.0001</b>
<b>Zone x Month</b>	<b>6</b>	<b>17.68</b>	<b>0.010</b>

**Table 10. GLM to investigate factors affecting the number of non-nematoceran Diptera caught by pitfall traps.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	337	623.24	
Minimum adequate model:			
<b>Crop Type</b>	<b>6</b>	<b>20.18</b>	<b>0.223</b>
<b>Month</b>	<b>3</b>	<b>183.96</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>156.09</b>	<b>0.0000</b>
Excluded terms:			
Field zone	2	2.09	0.655

**Table 11. GLM to investigate factors affecting the number of Coleoptera caught by pitfall traps.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	337	649.81	
Minimum adequate model:			
<b>Crop Type</b>	<b>6</b>	<b>32.28</b>	<b>0.003</b>
<b>Month</b>	<b>3</b>	<b>256.41</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>106.06</b>	<b>0.0000</b>
Excluded terms:			
Field zone	2	4.96	0.213

**Table 12. GLM to investigate factors affecting the number of Arachnida caught by pitfall traps.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	337	6925.73	
Minimum adequate model:			
<b>Crop Type</b>	<b>6</b>	<b>201.23</b>	<b>0.021</b>
<b>Month</b>	<b>3</b>	<b>2495.01</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>855.14</b>	<b>0.0000</b>
Excluded terms:			
Field zone	2	64.27	0.080

**Table 13. GLM to investigate factors affecting the number of Hymenoptera caught by pitfall traps.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	337	402.28	
Minimum adequate model:			
<b>Field zone</b>	<b>2</b>	<b>33.92</b>	<b>0.002</b>
<b>Crop Type</b>	<b>6</b>	<b>122.87</b>	<b>0.0000</b>
<b>Month</b>	<b>3</b>	<b>105.36</b>	<b>0.0000</b>
<b>Crop Type x Month</b>	<b>18</b>	<b>166.23</b>	<b>0.0000</b>



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## **Chapter 4:**

### **Effects of previous reproductive effort on parents and chicks in a population of Tree sparrows, *Passer montanus***

#### **Abstract**

The Tree Sparrow, *Passer montanus*, has shown one of the greatest population declines amongst farmland bird species in the UK, however, little is known about the causes of this decline. Here, evidence of reproductive trade-offs in a population of Tree Sparrows, both within one breeding season, and also between years was looked for. If found, such trade-offs could be evidence of invertebrate chick food limitation, particularly as the study population has year round access to supplementary seed food.

Within years, there was no evidence of a reproductive trade-off, conversely an effect of individual quality was found, with parents that fledged more chicks in the first brood also fledging more chicks later in the season. Between years there was some evidence of a reproductive trade-off, with birds that invested more in reproduction one year having a lower reproductive output the following year. Males also had a higher survival rate than females, and it is suggested that this is due to their lesser reproductive investment.

## 4.1 Introduction

Many farmland bird species in the UK have shown huge declines in abundance and range since the 1970s (Fuller *et al.*, 1995) due to agricultural intensification (Chamberlain *et al.*, 2000). The Tree Sparrow has shown one of the largest declines in abundance amongst these species, having decreased by 95% between 1970 and 1998 (Gregory *et al.*, 2001). The population has also undergone a range contraction of about 20% between 1970 and 1990 (Fuller *et al.*, 1995). The magnitude of this decline has been reflected in the Tree Sparrow's conservation status; the Tree Sparrow is on the 'Birds of Conservation Concern' red list (Gregory *et al.*, 2002), and has a UK Biodiversity Action Plan to aid its recovery. Declines have also been mirrored in other European countries (Wesolowski, 1991, Winkel, 1994, Summers-Smith, 1995).

The exact demographic and ecological mechanisms behind the Tree Sparrow's decline are unknown. In terms of the ecological mechanism, a reduction of either summer and/or winter food caused by agricultural changes is the most common suggestion (Campbell *et al.*, 1997, Gregory *et al.*, 2000, Sotherton & Self, 2000, Summers-Smith, 1995). Loss of nest sites through hedgerow loss and Dutch elm disease has also been suggested (Gregory *et al.*, 2000), although Dutch elm disease is unlikely to have been a major contributing factor, as elms only provided about 6% of the sites used by Tree Sparrows in Britain prior to the outbreak of the disease (Summers-Smith, 1995). The fact that nesting success per attempt has increased during the period of population decline (Siriwardena *et al.*, 2000), has led to suggestions that poor winter survival due to lack of seed food could be to blame for the declines (Peach *et al.*, 1999).

Granivorous passerines have shown the largest declines of the UK's farmland bird species (Fuller *et al.*, 1995), and this has often been linked to decreased seed food over winter (Peach *et al.*, 1999, Robinson & Sutherland, 1999). However, most of these 'granivorous'



passerines are partially insectivorous, at least during the breeding season, when they also rely on invertebrates as a source of high-protein chick food (Baillie *et al.*, 1997, Wilson *et al.*, 1999). Amongst these declining granivorous passerines those that are more dependent on insects have shown significantly worse declines (Wilson *et al.*, 1999).

Invertebrate abundance has been declining in recent decades (Aebischer, 1990, Benton *et al.*, 2002), and broad scale relationships have been found between insect abundance and farmland bird population sizes the following year (Benton *et al.*, 2002), suggesting that insect availability influences breeding and post-breeding demographic factors.

A lack of available chick food could have affected the Tree Sparrow population in a number of ways;

1. It could have affected annual productivity by reducing the proportion of chicks that fledge per nesting attempt, or by reducing the number of nesting attempts made;
2. Chicks may be in poorer condition at fledging, and thus have a lower first year survival, leading to a lower recruitment rate;
3. Adults may compensate for reduced food availability by expending more energy feeding their chicks, and themselves suffering higher annual mortality rates, or reduced future fecundity.

As mentioned, nesting success per attempt has been increasing in recent decades (Siriwardena *et al.*, 2000). Thus, a decrease in annual productivity is unlikely to have driven the decline, unless through a decrease in number of nesting attempts per year for which there is no data. Chapter 5 looks for evidence of an effect of low invertebrate abundance on number of breeding attempts made per year.

It is generally thought that survival, either first-year or adult, is likely to be the principal demographic factor driving Tree Sparrow declines, although ring-recovery analyses have

failed to provide firm evidence for this, although this could be due to small sample sizes (Siriwardena *et al.*, 1998, 2000).

Life history theory is based on the assumption that there are trade-offs between different life history traits (Stearns, 1992). Lack (1947) was among the first to point out the existence of negative relationships among life history variables by showing that an increased investment in one component may result in decreased investment in another. More specifically, the 'reproductive cost' hypothesis states that investment in current reproduction by iteroparous species is made at a cost to future reproductive success and survival (Williams, 1966, Charnov & Krebs, 1974, Stearns, 1976, Ricklefs, 1981). This can result in conflicting interests between what is optimal for parents to invest in current reproduction, and the level of investment which is optimal to offspring, as parents must trade-off the benefits of investment in current offspring with the potential costs to their own future reproduction and survival. The outcome of this trade-off will depend on a number of factors, including average life span of the species in question. In a short-lived species, such as the Tree Sparrow, life-history theory predicts that this trade-off will favour the current offspring (Linden & Moller, 1989). Thus, we predict that as invertebrate abundance has decreased in recent decades, parents will have had to increase their effort (in the form of their provisioning rate) as much as possible, in order to maintain chick condition and that this may be at a cost to their own future survival and reproduction. The aim of this chapter is to look for evidence of intra- and inter-year reproductive trade-offs in a population of Tree Sparrows, *Passer montanus*, nesting in boxes at Rutland Water Nature Reserve. Firstly, by investigating whether the condition or number of chicks fledged decreases as a function of the number of chicks fledged previously that year, and

secondly by looking at whether high reproductive effort one year affects an adult's chances of survival to, or reproductive output during, the next breeding season.

## **4.2 Methods**

### **Study Site**

The study was conducted on a population of Tree Sparrows breeding in nest boxes on and adjacent to Rutland Water Nature Reserve, Rutland, UK. Tree Sparrows have been present at Rutland Water since the late 1970s when the reservoir was constructed and the nature reserve established. Birds at the reserve have year round access to supplementary seed food, provided at a main feeding station.

### **Colour-ringing**

Unique colour combination ringing began at Rutland Water in 2000 when adults were mist-netted and rung at feeding sites prior to the breeding season. Some of these adults had been ringed or cohort colour-ringed in previous years, so were of known age when rung in 2000. Since then approximately 10 mist-netting and ringing sessions have been conducted per year to ring adults, and all chicks in the nest boxes on the reserve have been rung.

### **Nest records**

Nest boxes were checked weekly for eggs from late March to mid-August, 2000 to 2003. Following 11 days incubation, Tree Sparrow clutches were checked every other day to determine hatch date. On day 9 chicks were rung and their mass taken using an electronic balance. Nests were checked for fledging at day 20; any chicks found on day 9, and then



not found at day 20, were assumed to have fledged (fledging typically occurs at around 15 days).

## **Resighting**

Birds were resighted weekly, year-round, by an observer with a telescope noting the unique colour-ring combinations of birds visiting the seed feeding station for a three hour period.

## **4.3 Data Analysis**

Two different types of model were used in the analysis: generalised linear models (GLMs) in S-PLUS and generalised linear mixed models (GLMMs) in GENSTAT. GLMs allow the analysis of non-normal error distributions through the use of linearising transformations specified by link functions. GLMMs, being mixed models, allow the inclusion of random effects, such as blocking factors, to account for non-independence of data points (e.g. for repeat measurements, or measures of chicks from the same brood). GLMMs also allow analysis of non-normal error distributions by use of linearising link functions.

Unless otherwise mentioned, models were conducted by step-wise deletion from a maximal model. Model residuals were checked for normality. Predicted means or fits were used to display results while controlling for other terms in the minimum adequate model.

### **4.3.1 Does producing a high number of chicks have an effect on the number or condition of chicks produced later that season?**

#### **Number of chicks fledged**

Models were run to look at whether the number of chicks fledged in previous broods affected the number of chicks fledged in broods 2 and 3. GLMs were run in S-PLUS, with poisson errors and log link. Three sets of models were run, with the following dependent variables:

1. Number of chicks fledged in brood 2;
2. Number of chicks fledged in brood 3;
3. Number of chicks fledged in brood 2 plus number fledged in brood 3.

For the model looking at number of chicks fledged in brood 3, a quasi-likelihood model with log link and variance =  $\mu^2$  was used in order to correct for overdispersion.

The number of chicks fledged previously that season was included in the analysis as a variable (i.e. number fledged in brood 1 for models 1 and 3, and number of chicks fledged in broods 1 plus 2 for model 2). The models were only run for chicks which had two identified parents, and the 'number of chicks fledged previously' was the sum of chicks fledged by both parents; that is, if the parents had nested separately before, then the chicks fledged from the separate nests were added together, if the parents had bred together before, then the number of chicks fledged from that nest was multiplied by two. Other terms included in the models were year, parental age (a three-level factor; 1 = both first-year, 2 = mixed, 3 = both second year), and location (the birds were from four different colonies), which were all included as factors. Two-way interaction terms including the 'chicks fledged previously' term were also included.

These models were repeated using 'chick provisioning days' and not chicks fledged as the measure of reproductive effort, as this also includes effort invested in chicks which died before fledging ('chick provisioning days' was the sum of the number of chicks in the nest on each day a parent was provisioning).

Reproductive trade-offs may be masked by effects of individual quality. Therefore, the analysis was repeated on a sub-sample of half of the dataset, having removed the parents which fledged the highest numbers of chicks in broods 2 or 3, so that the analysis was just looking at parents which were presumed to be of 'poorer quality', so that the effect of individual quality on the results was minimised.

## **Chick Condition**

The relationship between the number of chicks fledged prior to the brood in question, and the condition of chicks in broods 2 and 3, was investigated. GLMs with normal errors were run in S-PLUS. All chicks from 2000 to 2003 with two identified parents were looked at. Mean brood mass on day 9 was used as the dependent variable. Models were first run looking at broods 2 and 3 separately, in case brood number explained too much variance for other relationships to be picked up on, and then for both second and third broods together. Year, location, and parental age (1 = both first-year, 2 = mixed, 3 = both second year) were included as factors in the model, and number of chicks that both parents had fledged previously, brood size, and date (date on day 9 of this brood, where June 1<sup>st</sup> = 1), were included as variables. Two-way interaction terms involving the 'chick provisioning days' term were included. These were added two at a time to the brood 3 models (as oppose to all at once followed by stepwise deletion) due to the smaller sample size. These models were repeated using 'chick provisioning days' and not chicks fledged as the measure of reproductive effort, as this also includes effort invested in chicks which died



before fledging ('chick provisioning days' was the sum of the number of chicks in the nest on each day a parent was provisioning).

Reproductive trade-offs may be masked by effects of individual quality. Therefore, the analysis was repeated on a sub-sample of half of the dataset, having removed the parents which fledged chicks of highest condition in broods 2 or 3, so that the analysis was just looking at parents which were presumed to be of 'poorer quality'.

### **4.3.2 Is there an effect of reproductive effort one year on future survival and reproductive output?**

#### **Survival**

Models were run to investigate whether an individual's reproductive effort one year affected its likelihood of surviving to the following breeding season. This was investigated using nest record data from 2000, 2001 and 2002, and ring-resighting data from 2001, 2002 and 2003.

In order to avoid pseudoreplication due to some parents being in the data set over a number of years, GLMMs were conducted in GENSTAT with 'parent' as a random factor.

Binomial analysis was conducted with whether a parent survived to the following breeding season (1) or not (0) as the dependent variable (this was defined by whether or not a bird was resighted after April 1<sup>st</sup> the following year). Three sets of models were run, using different measures of reproductive effort. These were:

1. Number of broods produced;
2. Total number of 'chick provisioning days' (the sum of the numbers of chicks present on each day an adult was provisioning them in the nest);
3. Number of chicks fledged.

These were all per-year measures, and were included as variables. These measures were chosen as they all relate to chick provisioning effort; and to involve measures of both number of broods produced and brood size. Both number of chicks fledged and number of 'chick provisioning days' were used, as the first may be a measure of the quality, not just the quantity, of provisioning, whereas the number of 'chick provisioning days' is in other ways a more complete measure of provisioning effort, as it includes effort invested in chicks which died before fledging. Also included in the models were year, parental age (first-year or older), and parental sex, which were factors. For the models on 'number of chicks fledged', mean chick mass on day 9 (over the whole year) was included as a variable. All two-way interaction terms were included in the model.

Inclusion of parental sex in the models reduced the dataset by about half, as sex was not known for all parents. Therefore, models were also run on the full data set, in order to increase the power of the analysis.

## **Reproductive output**

The next question to be investigated was whether an individual's reproductive effort one year affected its reproductive output the following year. This was investigated using nest record data from 2000, 2001, 2002, and 2003. GLMMs were conducted in GENSTAT with poisson errors and log link, with 'parent' as a random factor (for the same reason as for the 'survival' models). Three sets of models were run, with different measures of reproductive effort as the dependent variable. These were:

1. Number of broods produced;
2. Total number of 'chick provisioning days';
3. Number of chicks fledged.

Prior to analysis, any individuals which did not have nest records the next year were removed from the dataset, (i.e. those individuals which did not survive, or which survived but nested in natural sites). Number of 'chick provisioning days' in the previous year was included in the models as a variable (this was thought to be the most complete measure of provisioning effort), with year, parental age (first-year or older), and parental sex included as factors. Two-way interaction terms were added one at a time, due to the low sample size.

Inclusion of parental sex in the models reduced the dataset by about half, as sex was not known for all parents. Therefore, models were also run on the full data set, in order to increase the power of the analysis.

## **4.4 Results**

### **4.4.1 Does producing a high number of chicks have an effect on the number or condition of chicks produced later that season?**

#### **Number of chicks fledged**

There was a non-significant trend for parents that fledged more chicks in brood 1 to also fledge more in brood 2 (table 1). When this model was repeated, looking at the number of chicks fledged in second broods in relation to the number of 'chick provisioning days' invested in the first brood, rather than number of chicks fledged, the trend became closer to significant (deviance = 3.68, d.f. = 1,  $p = 0.055$ ).



**Table 1. GLM relating number of chicks fledged in second broods to number fledged in first broods.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	48	39.15	
Excluded terms:			
Chicks fledged previously	1	3.19	0.074
Parental age	2	4.23	0.121
Location	3	1.60	0.659
Year	3	1.56	0669

Number of chicks fledged previously had no effect on the number of chicks fledged in brood 3 (table 2).

**Table 2. GLM relating number of chicks fledged in third broods to number fledged in first broods plus number fledged in second broods.**

Significant terms are in bold.

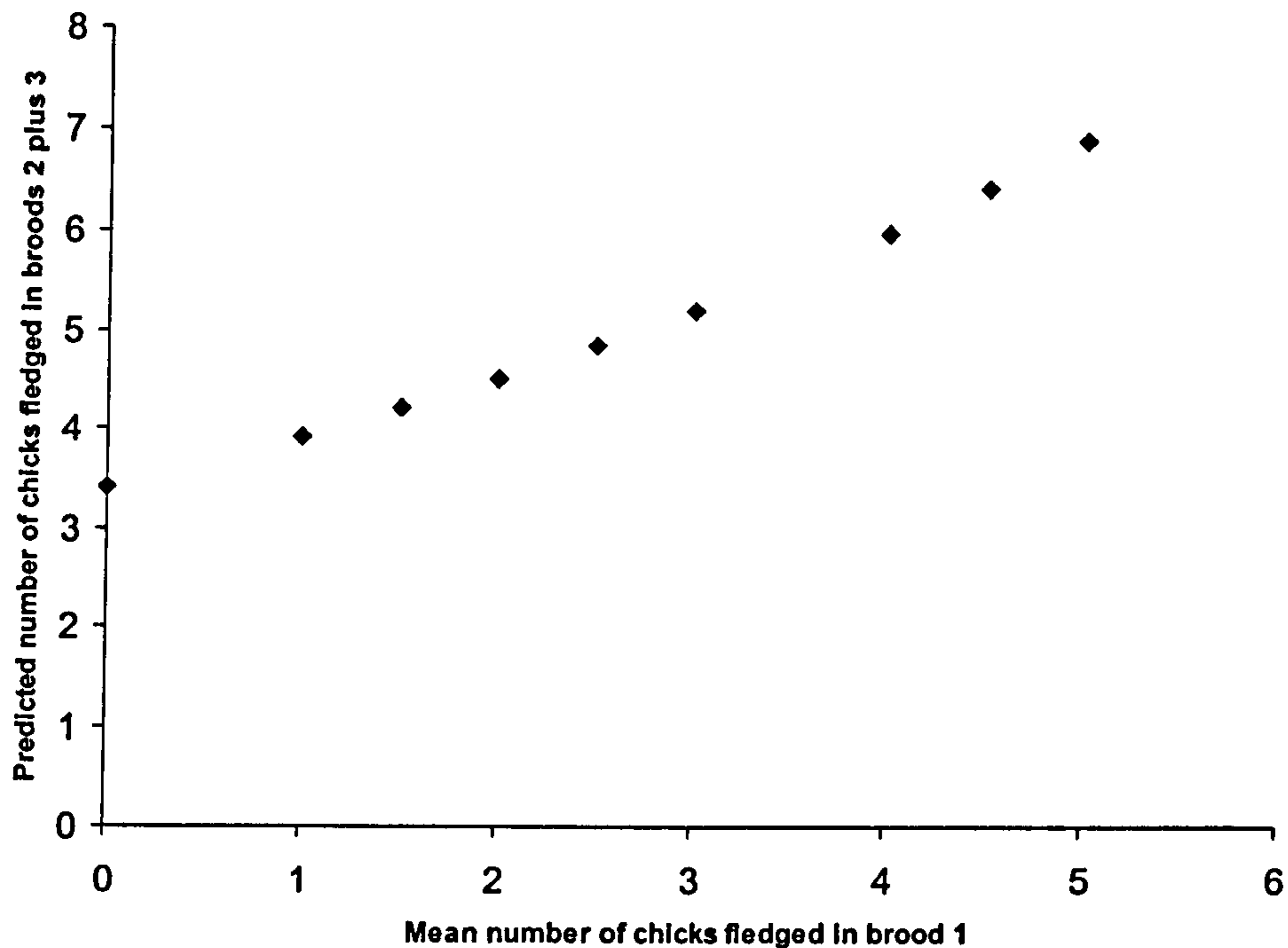
Term	d.f.	deviance	p-value
Null model:	23	12.62	
Excluded terms:			
Chicks fledged previously	1	0.00	0.950
Parental age	2	0.32	0.852
Location	3	0.30	0.863
Year	3	0.50	0.918

Parents which fledged more chicks in the first brood went on to fledge more chicks in the second plus third broods (table 3, figure 1).

**Table 3. GLM relating number of chicks fledged in the second plus third broods to number fledged in the first brood.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	49	16.53	
Minimum adequate model:			
<b>Chicks fledged previously</b>	<b>1</b>	<b>2.37</b>	<b>0.002</b>
Excluded terms:			
Parental age	2	0.31	0.537
Location	3	0.90	0.269
Year	3	0.38	0.728



**Figure 1. Predicted number of chicks fledged in broods 2 plus 3 in relation to mean number fledged in brood 1**

These models were repeated to look at parents which fledged the lowest number of chicks in broods 2, 3, and 2 plus 3. Models were run looking at a sub sample of half the data set, in order to see if there was evidence for a trade-off when just looking at these, presumably poorer ‘quality’ birds. When these models were run, there was no evidence of a trade-off, nor of a quality effect.

### **Chick condition**

The number of chicks a parent fledged in its first brood had no effect on the mass of its second brood (table 4).



**Table 4. GLM relating mean d9 mass of second broods to number of chicks fledged by parents in their first broods**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	40	97.15	
Excluded terms:			
Chicks fledged	1	0.00	0.980
Parental age	2	2.34	0.440
Location	3	5.47	0.544
Year	3	4.70	0.618
Date	1	1.08	0.512
Brood size	1	0.01	0.924

The number of chicks fledged by parents earlier in the season had no effect on the mass of their third brood (table 5).

Year had an effect on mass of third broods, with mean chick mass on day 9 being lower in 2000 than in 2001, 2002 or 2003 (table 5).

**Table 5. GLM relating mean d9 mass of third broods to number of chicks fledged by their parents in previous broods**

Significant terms are in bold.

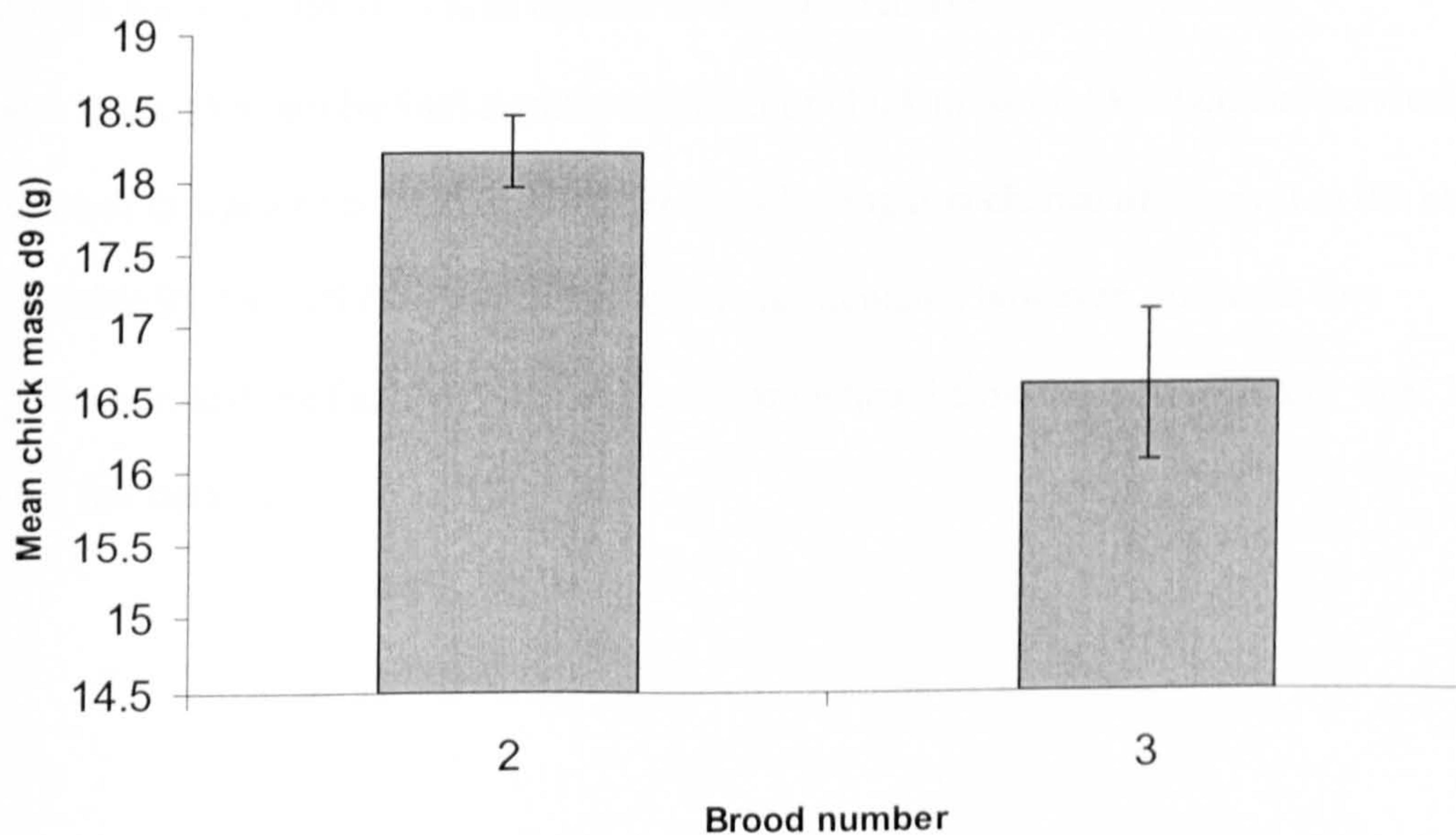
Term	d.f.	deviance	p-value
Null model:	25	175.61	
Minimum adequate model:			
<b>Year</b>	<b>3</b>	<b>52.80</b>	<b>0.045</b>
Excluded terms:			
Chicks fledged	1	2.95	0.480
Parental age	2	0.95	0.942
Location	3	18.39	0.380
Date	1	1.59	0.618
Brood size	1	0.27	0.841

Year also affected mean day 9 brood mass when the data for second and third broods was analysed together (table 6). Mean brood mass decreased with date (table 6). As date did not affect mean brood masses within second and third broods, this relationship has been shown by plotting mean brood mass for second and third broods, rather than as a linear relationship with date (figure 2).

**Table 6. GLM relating mean d9 mass of second and third broods to number of chicks fledged by their parents in previous broods**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	64	310.55	
Minimum adequate model:			
<b>Year</b>	<b>3</b>	<b>51.20</b>	<b>0.006</b>
<b>Date</b>	<b>1</b>	<b>42.88</b>	<b>0.001</b>
Excluded terms:			
Chicks fledged	1	8.61	0.133
Parental age	2	1.61	0.783
Location	3	15.15	0.255
Brood size	1	0.91	0.622



**Figure 2. Mean day 9 chick mass for second and third broods.**



All chick condition models were repeated just looking at parents of chicks with the lowest masses, by dividing the sample in half, in order to see if there was evidence of a trade-off for these 'poorer quality' parents. However, there was no effect of number of chicks fledged previously on later chick mass for these parents either.

#### **4.4.2 Is there an effect of reproductive effort one year on future survival and reproductive output?**

##### **Survival**

Survival to the following breeding season was not related to the number of broods produced, number of 'chick provisioning days' invested, or the number of chicks fledged (tables 7, 8, 9) A bird's sex affected its likelihood of survival to the next breeding season (tables 7, 8, 9) Males had significantly greater chance of survival than females, males having a survival rate of 72% as oppose to 51% for females (figure 3).

There was also a (borderline) significant effect of chick mass on likelihood of survival, with birds that produced chicks of higher mass having less chance of survival to the next year (table 9). The reliability of this result is questionable, however, due to its low significance, and the fact that it is not significant when the model is run without 'sex' in it, on the full data set.

**Table 7. GLMM relating the likelihood of survival to the next breeding season to number of broods produced that year.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	95	244.94	
Minimum adequate model:			
<b>Parental sex</b>	<b>1</b>	<b>4.63</b>	<b>0.031</b>
Excluded terms:			
Number of broods	1	3.48	0.572
Parental age	1	0.55	0.458
Year	2	1.87	0.392

**Table 8. GLMM relating the likelihood of survival to the next breeding season to number of 'chick provisioning days' invested that year.**

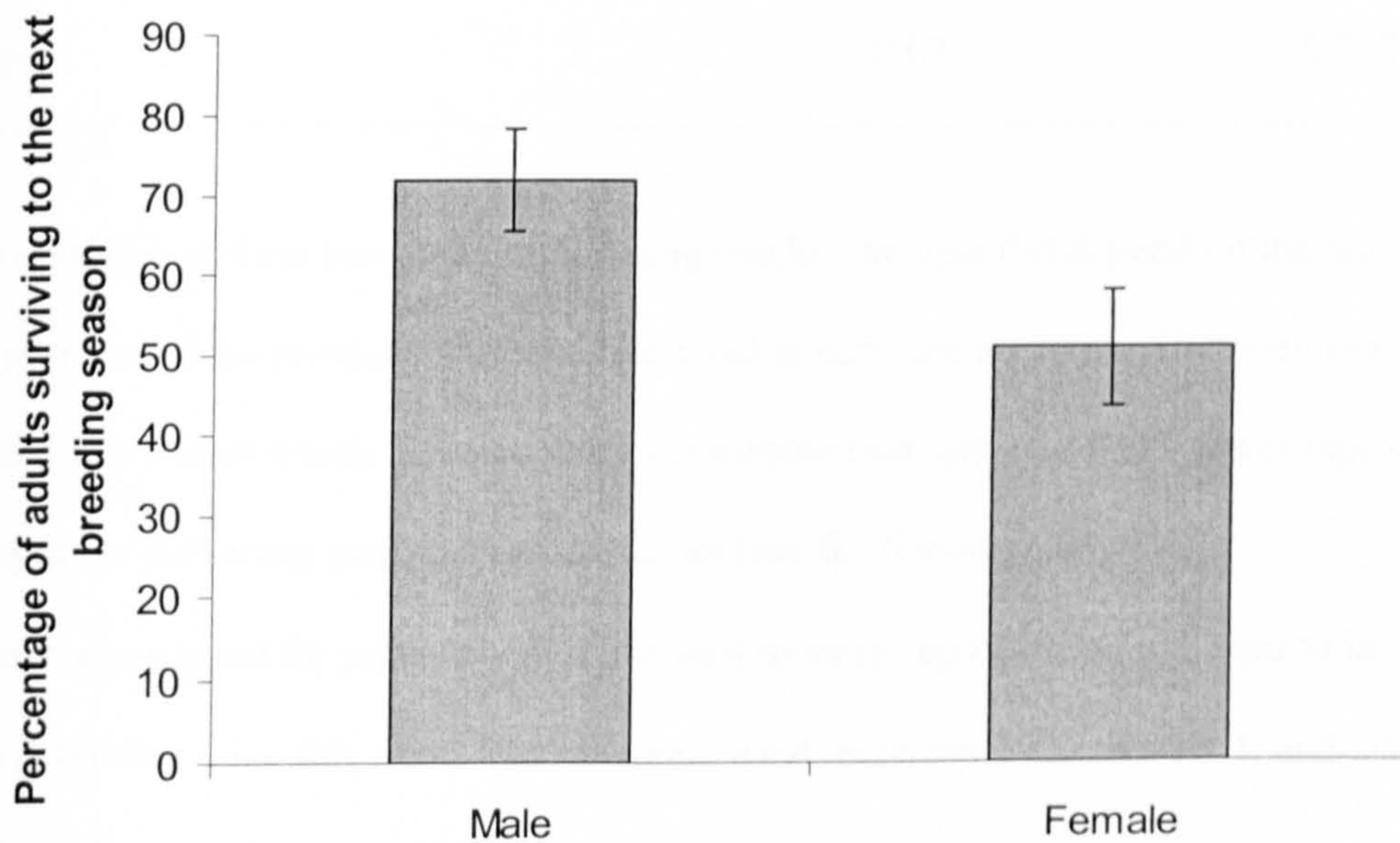
Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	95	244.94	
Minimum adequate model:			
<b>Parental sex</b>	<b>1</b>	<b>4.63</b>	<b>0.031</b>
Excluded terms:			
Chick provisioning days	1	0.37	0.540
Parental age	1	0.55	0.458
Year	2	1.87	0.392

**Table 9. GLMM relating the likelihood of survival to the next breeding season to number of chicks fledged that year.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	169	428.75	
Minimum adequate model:			
<b>Mean chick mass</b>	<b>1</b>	<b>4.02</b>	<b>0.045</b>
Excluded terms:			
Parental sex	1	2.27	0.132
Number of chicks fledged	1	0.14	0.713
Parental age	1	0.41	0.522
Year	2	1.85	0.396



**Figure 3. Percentage of male and female adults surviving to the next breeding season**



## Reproductive output

There was no effect of the number of 'chick provisioning days' invested one year on the number of broods a parent produced the next year (table 10).

**Table 10. GLMM relating number of broods produced to investment in reproduction the previous year.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	28	-2.19	
Excluded terms:			
Chick provisioning days	1	0.85	0.357
Sex	1	0.00	0.949
Year	2	5.78	0.056
Age	1	0.07	0.797

The number of days invested provisioning chicks one year did depend on the number of days invested the previous year, the relationship between the two varied with sex and year (table 11). Males which invested more in reproduction one year had a lower reproductive output the following year; the same was not true for females (figure 4).

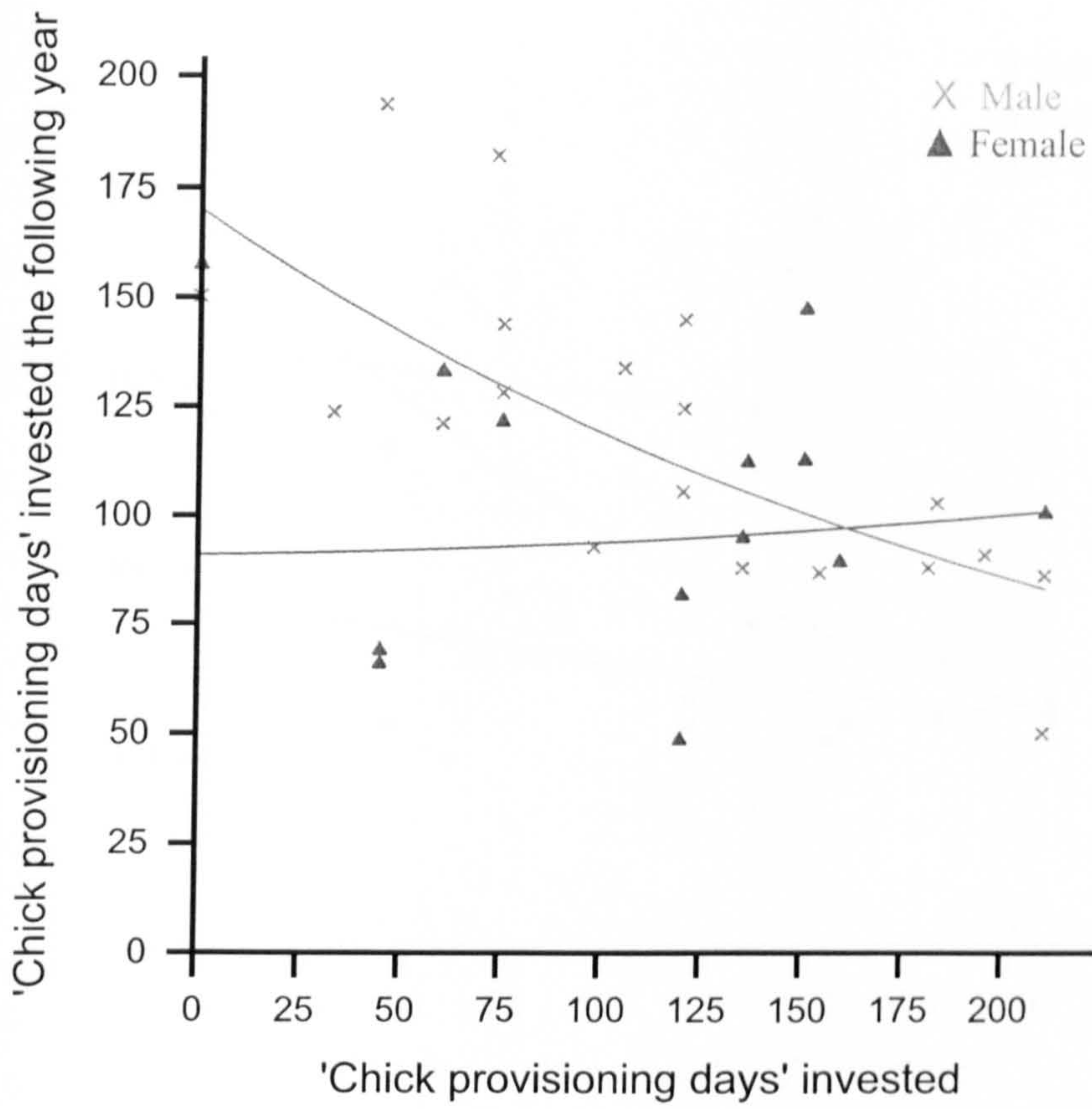
There was a trend for parents which invested more in reproduction one year to invest less the following year, this trend was relatively weak between 2000 and 2001, and 2001 and 2002, but strong between 2002 and 2003 (figure 5).

There was also a significant effect of the age x sex interaction on the number of ‘chick provisioning days’ invested by a parent, with females investing more in their second year, and then less in following years, but males investing about the same in their second year as in later years (figure 6).

**Table 11. GLMM relating number of ‘chick provisioning days’ invested to investment in reproduction the previous year.**

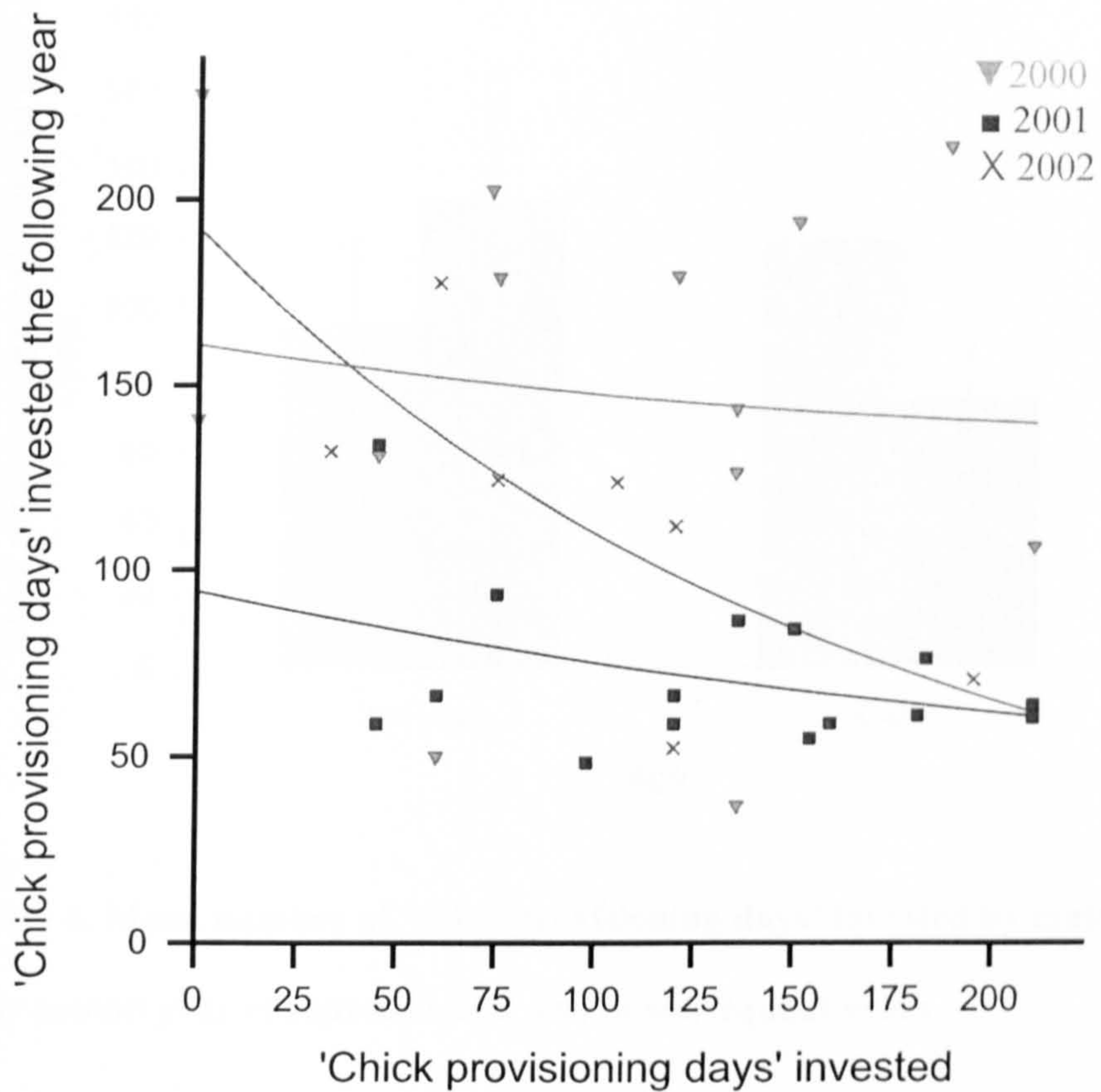
Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	23	61.89	
Minimum adequate model:			
<b>Chick provisioning days</b>	<b>1</b>	<b>111.10</b>	<b>&lt;0.001</b>
<b>Sex</b>	<b>1</b>	<b>4.12</b>	<b>0.042</b>
<b>Year</b>	<b>2</b>	<b>33.26</b>	<b>&lt;0.001</b>
<b>Age</b>	<b>1</b>	<b>11.36</b>	<b>&lt;0.001</b>
<b>Chick days x sex</b>	<b>1</b>	<b>15.49</b>	<b>&lt;0.001</b>
<b>Chick days x year</b>	<b>2</b>	<b>64.97</b>	<b>&lt;0.001</b>
<b>Age x sex</b>	<b>1</b>	<b>7.50</b>	<b>0.006</b>

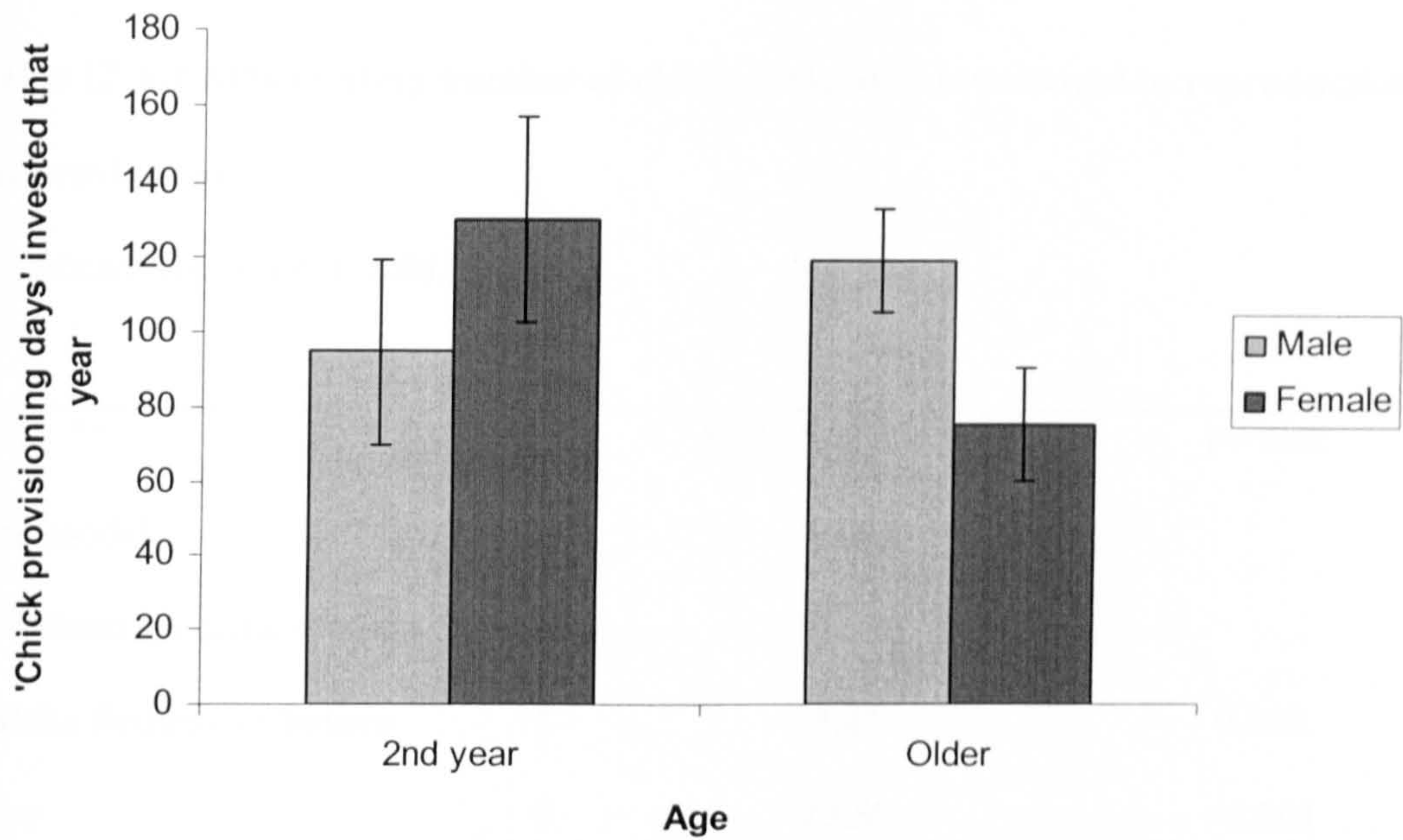


**Figure 4. Investment in reproduction by males and females in relation to investment the previous year.**





**Figure 5. Investment in reproduction in relation to investment the previous year for different years.**



**Figure 6. Mean number of ‘chick provisioning days’ invested by males and females in their second year of reproduction, and in subsequent years**

There was a non-significant trend for parents which fledged more chicks one year to fledge fewer chicks the following year (table 12).

There was also a significant effect of year on the number of chicks fledged.

**Table 12. GLMM relating number of chicks fledged to investment in reproduction the previous year.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	27	17.05	
Minimum adequate model:			
<b>Chicks fledged yr before</b>	<b>1</b>	<b>3.41</b>	<b>0.065</b>
<b>Year</b>	<b>2</b>	<b>23.59</b>	<b>&lt;0.001</b>
Excluded terms:			
Sex	1	0.30	0.581
Age	1	0.00	1.00



## **4.5 Discussion**

### **4.5.1 Does producing a high number of chicks have an effect on the number or condition of chicks produced later that season?**

#### **Number of chicks fledged**

Parents which produced a higher number of fledglings in their first brood went on to fledge significantly more chicks in their second plus third broods. This is probably mainly due to the fact that parents which fledged a higher number of chicks in their first brood were more likely to produce a third brood, but there was also a non-significant trend for parents which fledged a higher number of chicks in their first brood to also fledge more in their second brood. This is contrary to the trade-off found by Sasvari & Hegyi (1993), who found that in a population of Tree Sparrows in Hungary adults which produced fewer than the average number of fledglings in previous broods produced more than average in broods 2 and 3. Reproductive costs and trade-offs may be masked by variation in individual quality, such as those which have presumably led to the results here. The analysis was therefore repeated on just half the data set, for the parents which produced the chicks of lowest masses in broods 2 and 3. However, there was still no evidence for a trade-off, but nor was there evidence of a parental quality effect when looking at this sub-sample, presumably due to the reduction in sample size.

#### **Chick condition**

There was no effect of number of chicks fledged earlier that season on mass of chicks in second and third broods. This result was unchanged when just the 'poorer quality' individuals were looked at.

Third broods had a lower mean chick mass than second broods. Parents rearing later broods often have a lower reproductive success in avian populations, and particularly passerines (Nilsson & Svensson, 1996, Nilsson, 1989, Norris, 1993), and this is commonly attributed to environmental conditions such as poorer resources.

#### **4.5.2 Is there an effect of reproductive effort one year on future survival and reproductive output?**

##### **Survival**

The term 'survival' here is used for birds that were re-sighted at the reserve. This does not take account of the fact that birds may have dispersed between years. However, the fact that the birds in question were adults which were already breeding on the reserve makes this extremely unlikely.

There was no effect of the number of broods a parent produced, or the number of 'chick provisioning days' it invested, on its likelihood of surviving to the following breeding season. There was some evidence of a trade-off between the condition of chicks a parent produced one year, and the chances of it surviving to the next breeding season, although the low significance of this result, and the fact that it did not occur when the analysis was conducted on the full data set, means it should be treated with caution.

Males had a higher survival rate than females. Differential mortality between the sexes is not uncommon amongst avian populations, and there are a number of species for which female mortality has been found to be higher than that of males (Great Tits: Perrins & Mcleery, 1985; Black-capped Chickadees: Smith, 1995). This is probably due to the fact that for most species females invest more energy in reproduction. This is supported by the

fact that a study of Merlins, where, as with most raptors, males appear to invest substantially more in reproduction than females, males have a higher mortality than females (Espie *et al.*, 2000).

## **Reproduction**

There was no relationship between the investment in reproduction one year and the number of broods produced the following year.

When looking at the number of 'chick provisioning days' (the sum of the numbers of chicks in the nest on each day an adult was provisioning) for males there was evidence of a reproductive trade-off, with males that invested more days one year investing less (i.e. having a lower reproductive output) the following year. There was no such evidence of a trade-off for females. There was also evidence of this same trade-off between 2001 and 2002, and 2002 and 2003, but not between 2000 and 2001. This could be because conditions were harsher in these years, perhaps the trade-off was masked by good environmental conditions in the 2000-2001 period.

There was a significant effect of the age x sex interaction term on number of 'chick provisioning days' invested the following year. The number of days invested was higher for 2<sup>nd</sup> year females than older females, but there was no such difference for males. This could be due to higher breeding season mortality for older females, or because they are actually reproducing less as they get older, which again could be due to their higher reproductive investment.

There was a non-significant trend for birds which fledged a higher number of chicks one year to fledge a lower number in the following year.



All of these trade-offs could be due to birds actually reproducing less in the subsequent year, or because of mortality during the breeding season.

## Summary

The aim of this chapter was to look for evidence of reproductive trade-offs in a population of Tree Sparrows, both within years and between years, with the idea that these could be caused by low invertebrate chick food abundance.

Unlike Sasvari & Hegyi (1993) we found no evidence of reproductive trade-offs within years. Conversely, an effect of parental quality was found, with parents which fledged more chicks in brood 1 also fledging more later in the season.

Females had a higher mortality rate than males. This is not uncommon amongst the majority of avian species, where females invest more in reproduction than males.

Females also appear to have a reproductive senescence after their 2<sup>nd</sup> year, which could be due to genuinely lower reproductive output in a breeding season, or to higher breeding season mortality.

There is some evidence for reproductive trade-offs between years; particularly for males.

This could be because the female mortality rate is higher, and there may be differential mortality of poor quality females, leading to the trade-off being masked by individual quality effects in females. There was also evidence for reproductive trade-offs between certain years, but not others. It is odd that these trade-offs did not show up in the analysis looking at over-winter survival in relation to reproductive effort the previous season, as if adult condition is affected by reproductive effort the previous year enough to cause an inter-year reproductive trade-off, we would expect this to also affect over-winter survival.

There are two possible explanations; the first is that there is a peak in mortality during the breeding season, which leads to the observed reproductive trade-offs. This could be the

case, as looking at nest record data for 2000, 19.7% of clutches fledged no chicks, and 54.9% of clutches fledged fewer chicks than the clutch size; it is possible that the parents of some of the whole nest losses died, and perhaps that in some cases one parent died, leaving the other to provision the brood alone (which could make partial brood losses more likely). The second explanation is just that survival is too crude a measure for the relationship to show up, and perhaps if we could have measured adult condition during the winter a relationship would have been evident.

Costs of reproduction and reproductive trade-offs may be masked by individual quality or by good environmental conditions. There is evidence for within year parental quality effects in this population, and the population also has relatively good conditions, in that the birds have year round access to supplementary seed food. The fact that there is still some evidence of a reproductive trade-off between years in this population suggests that stronger effects may well be observed in other populations. If, as hypothesised, these trade-offs are due to lack of invertebrate chick food, there are implications for Tree Sparrows in the wider countryside.

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## **Chapter 5:**

# **The effect of supplementary chick-food on a population of Tree Sparrows, *Passer montanus***

## **Abstract**

The Tree Sparrow, *Passer montanus*, has shown one of the most dramatic population declines amongst farmland bird species in the UK, having decreased by 95% between 1970 and 1998. Although the demographic causes of the decline are unknown, an increase in breeding success per attempt during this period suggests that either reduced survival and/or number of breeding attempts per season was responsible. Few studies have looked at possible ecological causes, but lack of winter seed food leading to decreased over-winter survival has been suggested. However, recent studies have pointed to the importance of invertebrate food in driving farmland bird declines, including those of granivorous species. In this study, the importance of invertebrate food abundance to a Tree Sparrow population is investigated by supplementary feeding of nestlings. Lack of chick-food could affect survival and growth in the nest, first-year survival (through reduced chick condition at fledging), adult survival (through increased parental effort leading to poor post breeding-season condition), or the number of breeding attempts made per year.

Supplementary feeding a brood had no effect on its parent's provisioning rate, reproductive output later that season, or survival to the next breeding season. Pairs where one or both parents were in their first-year had a lower provisioning rate than older pairs.

Supplementary feeding increased the mass of chicks with first-year parents, and also early in May when conditions were less favourable. Chicks of first-year pairs were also lighter than those of older birds in early May. Supplementary feeding had no effect on a chick's

chances of survival to the following breeding season. Chicks from early first-broods had a significantly lower chance of surviving to the next breeding season than those from later first-broods.

## **Introduction**

Many species of farmland birds have shown huge decreases in numbers and range since the 1970s (Fuller *et al.*, 1995) due to agricultural intensification (Chamberlain *et al.*, 2000). Declines have been most pronounced amongst granivorous species (Fuller *et al.*, 1995). Declines of many granivorous passerines have been linked to decreased survival, and so lack of seed food during winter is often suggested as having caused the declines (Peach *et al.*, 1999, Robinson & Sutherland, 1999). However, most of these granivorous passerines use invertebrates as a source of high-protein food for their chicks (Baillie *et al.*, 1997), and recent studies have shown links between invertebrate food abundance and farmland bird populations on a broad scale (Benton *et al.*, 2002). Farmland invertebrate numbers have been decreasing in recent decades (Aebischer & Potts, 1990). However, whilst the link between invertebrate availability and population size is well established for the Grey Partridge (Potts, 1986), there is little evidence as to how reduction in invertebrate availability has affected the demography of granivorous farmland passerines.

The Tree Sparrow, *Passer montanus*, has shown one of the most dramatic population declines amongst farmland bird species in the UK, having decreased by 95% between 1970 and 1998 (Gregory *et al.*, 2000). The population also underwent a range contraction of around 20% between 1970 and 1990 (Fuller *et al.*, 1995). The decline of the UK Tree Sparrow population has resulted in it being a 'Birds of conservation concern' red-list



species (Gregory *et al.*, 2002), and having a UK Biodiversity Action Plan to aid its recovery. The decline in the UK has been mirrored in other European countries (Weslowski, 1991, Winkel, 1994, Summers-Smith, 1995).

Despite the magnitude of this decline, little is known about its causes. A lack of either summer and/or winter food supply due to changes in agricultural practice has been suggested (Campbell *et al.*, 1997, Gregory *et al.*, 2000). As nesting success per attempt has increased during the period of population decline (Siriwardena *et al.*, 2000), it has been proposed that reduced over-winter survival due to lack of seed food during winter may be the cause (Peach *et al.*, 1999). However, it is also possible that lack of invertebrate food for chicks could be causing the declines.

Although adult Tree Sparrows are predominantly granivorous, chicks are fed a high proportion of invertebrate food (usually about 98%, Orszaghova *et al.*, 2002). Lack of invertebrate chick-food could have affected Tree Sparrow populations through a number of mechanisms:

1. It could have reduced chick growth and survival in the nest (although as mentioned, Tree Sparrows have shown an increase in nesting success per attempt);
2. Chick condition at fledging may have been reduced, leading to poor first-year survival;
3. Number of breeding attempts made per year may have decreased;
4. Parental effort during the breeding season could be higher, leading to poor post-breeding season condition, and thus reduced adult survival.

The 'reproductive cost' hypothesis states that investment in current reproduction by iteroparous species is made at a cost to future reproductive success and survival (Williams, 1966, Charnov & Krebs, 1974, Stearns, 1976, Ricklefs, 1981). This results in conflicting

interests between what is optimal for parents to invest in current reproduction, and the level of investment which is optimal to offspring, as parents must trade-off the benefits of investment in current offspring with the potential costs to their own future reproduction and survival. The outcome of this trade-off will depend on a number of factors, including average life span of the species in question. In a short-lived species, such as the Tree Sparrow, life-history theory predicts that this trade-off will favour the current offspring (Linden & Moller, 1989). Thus, we predict that as invertebrate abundance has decreased, parents will have increased their effort (in the form of their provisioning rate) as much as possible, in order to maintain chick condition. We therefore hypothesised that providing first-brood chicks with supplementary food would decrease parental energy expenditure, by reducing provisioning rate, and that this would lead to parents of 'fed' chicks being in better condition at the end of the first brood. This may lead to adults having higher reproductive output later that season, and/or increased chances of survival and increased investment in future reproduction.

This was investigated by providing first-broods at Rutland Water Nature Reserve with supplementary food, and comparing chick condition, growth rate, and survival to the next breeding season, and parental effort, subsequent reproductive output that season and survival to the next breeding season, with that of chicks in and parents of control broods in order to test our predictions. High-protein hand rearing food was used in place of invertebrates.

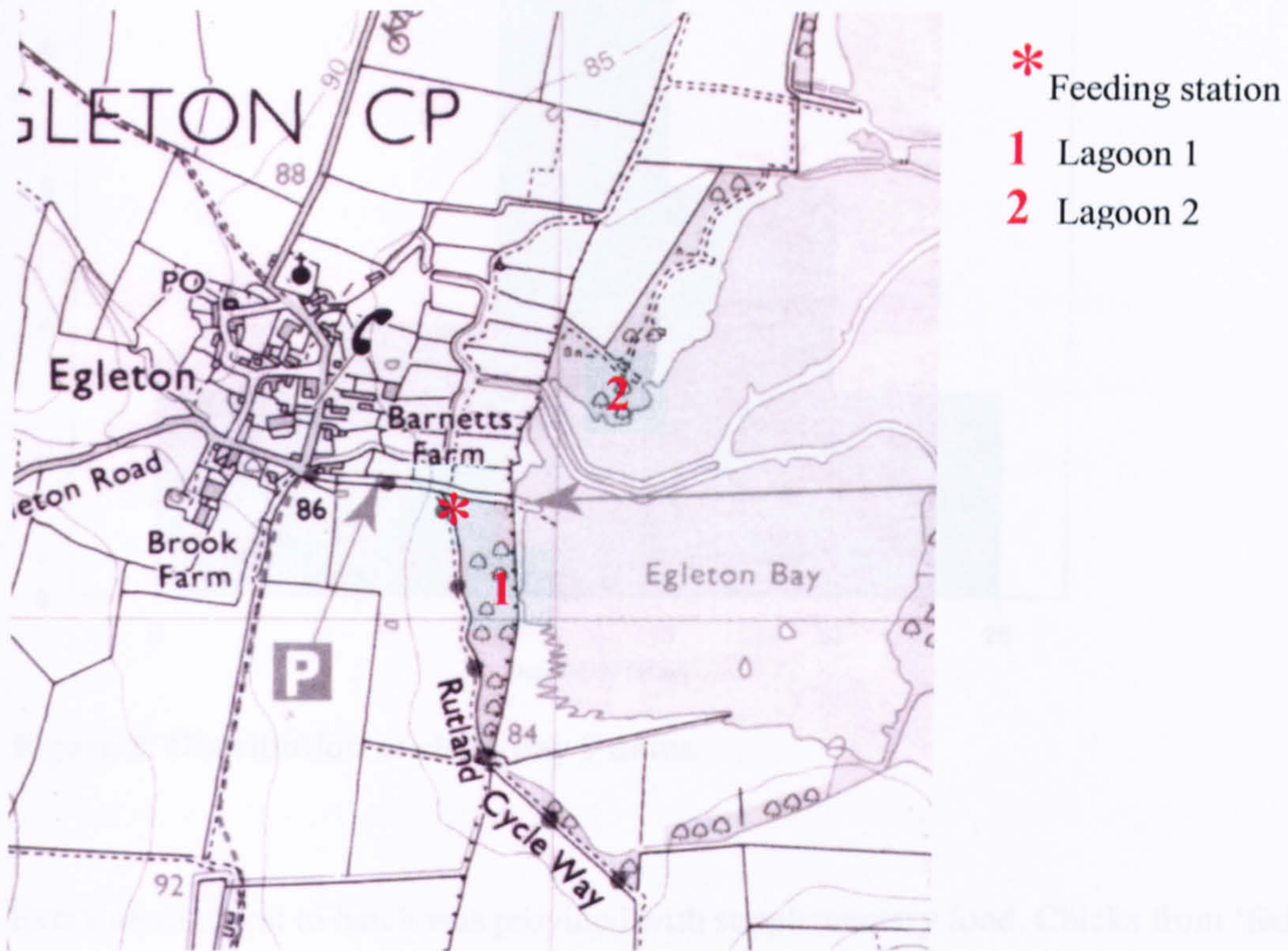
# **Methods**

## **Study area**

Fieldwork was carried out during May 2003, with Tree Sparrows breeding in nest boxes at Rutland Water Nature Reserve, Rutland, UK. Tree Sparrows have been present at Rutland Water since the late 1970s when the reservoir was constructed and the nature reserve established.

Twenty-seven first-brood nests from the 'lagoon 1' and 'lagoon 2' colonies were included in the experiment. The areas known as 'lagoon 1' and 'lagoon 2' are mixed ash/oak plantations, with a dense field layer and moderate shrub layer, on the perimeter of the reservoir. Birds at the reserve have year round access to supplementary seed food, which is provided at a singular seed feeding station situated near to the lagoon 1 colony (figure 1).



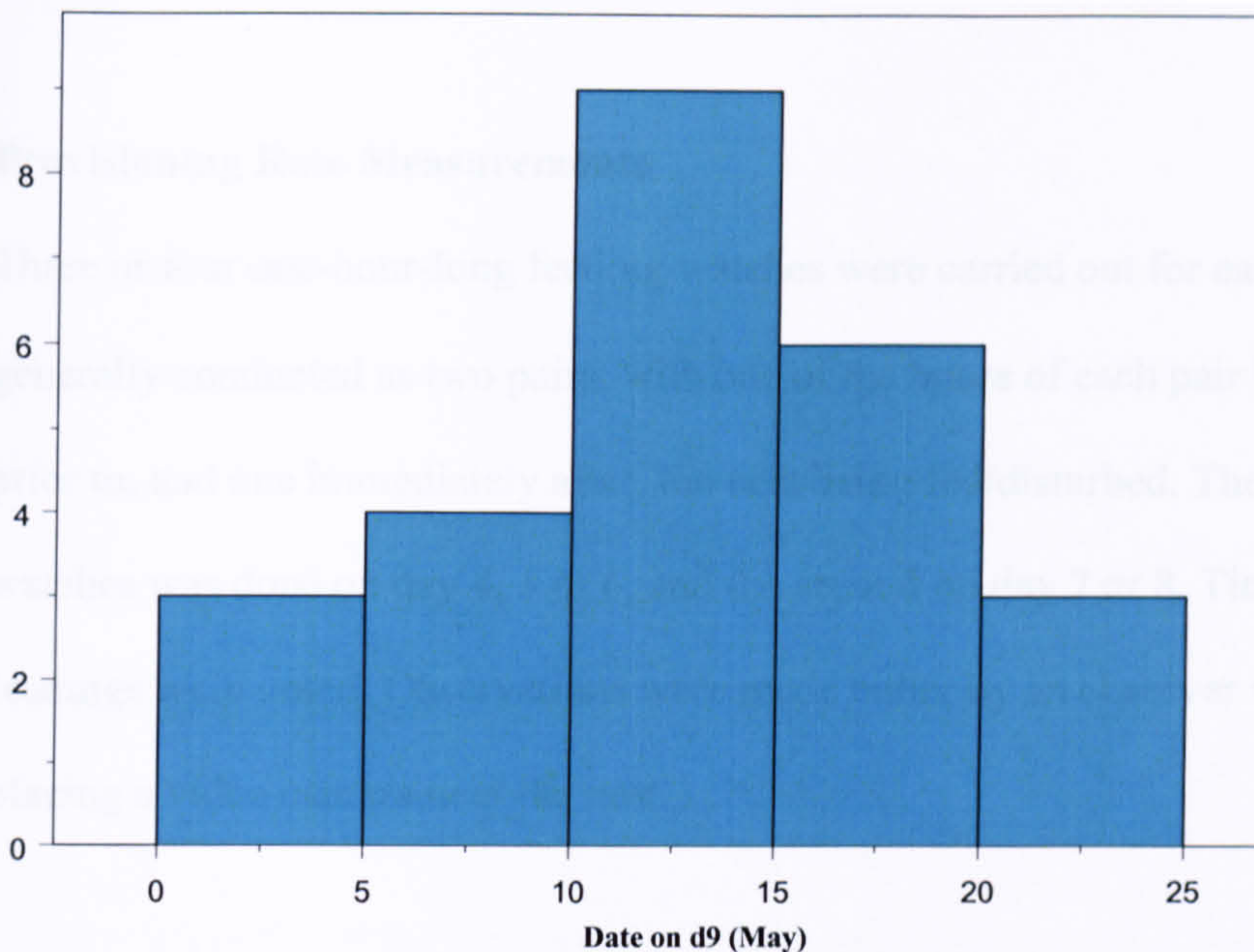


**Figure 1. Map of lagoon 1 and 2 colonies to show situation of seed feeding station.**

## Feeding

All nest boxes in the colonies were checked weekly for eggs, and once a clutch was found it was checked every other day to determine hatch date. Tree Sparrows tend to hatch synchronously, and in this study hatch dates ranged from April 25<sup>th</sup> to May 14<sup>th</sup>. The distribution of chick day 9 dates is shown in figure 2 (we have shown day 9 rather than hatch dates, as this was a term used in later statistical analysis).





**Figure 2. Distribution of chick day 9 dates.**

Every second nest to hatch was provided with supplementary food. Chicks from ‘fed’ nests were given high-protein hand-rearing food (Low energy Gold Label Hand Rearing Food from the Birdcare Company) using a 1mm plastic syringe. Feeding was done four times a day, leaving at least 2 hours between consecutive feeds, from age 4 to 8 d inclusive. Chicks were fed in the nest until they stopped begging. Chicks from control nests were disturbed at the same frequency, and for the same duration, as ‘fed’ nests, in order to control for any effects of nest-visiting.

The daily amount ingested by chicks increased from an average of 1.0 cm<sup>3</sup> per chick on day 4, to 2.4 cm<sup>3</sup> per chick on day 8. The mean amount taken over the feeding period, 1.7 cm<sup>3</sup>, equated to 5.05 KJ per chick per day. This is about 23% of a chick’s average daily metabolised energy (ADME) on day 6, which is 21.84 KJ (this was calculated using the ADME of 1.79 KJ per g per day (Myrcha *et al.*, 1973) and the mean chick mass of 12.2g on d6 (Field, pers. comm.), the mid-point of feeding).



### **Provisioning Rate Measurements**

Three or four one-hour-long feeding watches were carried out for each nest. Watches were generally conducted as two pairs, with one of the hours of each pair being immediately prior to, and one immediately after, the nest being fed/disturbed. The first pair of feeding watches was done on day 4, 5 or 6, and the second on day 7 or 8. Time and weather readings were noted. Observations were made either by an observer with a telescope or by placing a video camera near the nest.

### **Chick Measurements**

Chicks were weighed using an electronic balance before feeding/disturbing on the mornings of days 5 and 9.

### **Subsequent Reproductive Output**

All of the parents from experimental nests had unique colour-ring combinations, which were noted during feeding watches so that their later breeding attempts could be monitored.

Following the experiment, all nest boxes on the reserve were checked weekly for eggs, and Tree Sparrow clutches were then checked every other day, to determine hatch date. After hatching, nests were visited twice more; to ring the chicks at day 9, and to check for fledging at day 20. Any chicks found alive at day 9 but not found at day 20 were assumed to have fledged (fledging typically occurs at around 15 days).



## **Resighting**

Birds were resighted weekly after April the 1<sup>st</sup> 2004 by an observer with a telescope noting the unique colour-ring combinations of birds visiting the seed feeding station for a 3 hour period.

## **Data Analysis**

Effects of supplementary feeding were examined using three types of model; generalised linear models (GLMs) in S-PLUS; and residual maximum likelihood models (REMLs) and generalised linear mixed models (GLMMs) in GENSTAT. GLMs allow the analysis of non-normal error distributions through the use of linearising transformations specified by link functions. REMLs and GLMMs are both forms of mixed model, so allow the inclusion of random effects, such as blocking factors, to account for non-independence of data points (e.g. for repeat measurements, or measures of chicks from the same brood). REMLs only allow for normal error distributions, whereas GLMMs allow analysis of non-normal error distributions, again by use of linearising link functions.

Minimum adequate models were found by a stepwise deletion process from the maximal model. Model residuals were checked for normality. Predicted means or fits were used to display results while controlling for other terms in the minimum adequate model.

## **Provisioning Rate**

Analysis was conducted to see whether supplementary feeding affected provisioning rate. Provisioning rates were measured by conducting hour-long watches, with 3 or 4 watches being done for each nest. Mixed Models were run, with provisioning rate as the dependent variable, and 'nest' as a random factor, in order to avoid pseudoreplication. Mixed models

were used, rather than just analysing mean provisioning rate for each nest using GLMs, so that variables which were specific to a particular watch could be included in the analysis (i.e. time and weather variables). It was not possible to identify individual parents consistently, so rates are just a 'per nest' rate.

GLMMs with poisson errors and log link were run in GENSTAT. Factors in the model were supplementary food, site (lagoon 1 or 2), parental age, and rain (0 or 1), with brood size, chick age, time, and cloud cover (0 to 8 ocktas) being included as covariates.

'Parental age' was a 3-level factor, as the data only allowed the distinction between first-years and older birds. Thus, the three parental age classes were; '1'; both first-year birds, '2' where one parent was first-year and the other not, and '3' where both parents were older than first-year. Two-way interactions were included, except for those involving the time and weather terms.

### **Chick Condition**

Condition of chicks in 'fed' and control broods was compared, using mass on day 9 as the response variable. REMLs were conducted in GENSTAT. Whether a chick had been given supplementary food or not, and site (lagoon 1 or 2) were factors in the model, with brood size, and date (date on day 9, where May 1<sup>st</sup> = 1) included as covariates, along with all 2-way interactions terms. 'Nest' was included as a random effect (i.e. blocking factor) in order to account for non-independence of chicks from the same brood.

### **Growth Rates**

Growth rates of 'fed' and control broods were compared by having mean brood mass on day 9 as the dependent variable, and including mean brood mass on day 5 as a covariate. Mean brood masses were used because chicks were not identified individually.

GLMs were run in S-PLUS with normal errors and identity link. Mean brood mass on day 9 was used as the dependent variable, with mean brood mass on day 5 as a covariate. Whether the brood was given supplementary food or not, and site (lagoon 1 or 2), were included as factors, and brood size and date (date on day 9, where May 1<sup>st</sup> = 1), as covariates in the model. All two-way interaction terms were included. Parental age and associated interaction terms were then added to the model using a step-up, step-down method, as its inclusion reduced the sample size such that all two-way interactions could not be incorporated at the same time.

Any broods that underwent brood reduction prior to the second measurement were excluded from the analysis.

### **Prevalence of ‘runts’**

Parents or offspring may increase their fitness by allowing some individuals to monopolise resources leading to selective mortality of smaller juveniles, or ‘runts’, and this should be most prevalent during periods of food scarcity (Magrath, 1989). Prevalence of runts between ‘fed’ and control broods was compared. Analysis was conducted for both day 5 and day 9 chicks, in case chicks had not been ‘runted’ by day 5, or runts had died by day 9, respectively. Models were run with mass of the lightest chick in each brood (on day 5 or 9) as the dependent variable, controlling for mass of the heaviest chick (on day 5 or 9) by including it as a covariate in the model. Broods that had suffered partial brood losses between day 5 and day 9 were excluded from the day 9 analysis.

GLMs were conducted in S-PLUS with normal errors and identity link. Terms included in the model were supplementary feeding, site (lagoon 1 or 2), and parental age (a 3-level factor; 1=both first year, 2=mix, 3=both older birds), which were included as factors, and



date (date on day 9, where May 1<sup>st</sup> = 1) and brood size, which were covariates. All two-way interaction terms containing the 'supplementary feeding' term were included.

### **Brood survival**

To see if partial or whole brood losses were more common amongst control broods, the numbers of 'fed' and control nests which underwent either a whole or partial brood loss were compared using a Chi-Squared test. Whole brood losses were only included in the analysis if all chicks were found dead in the nest, otherwise it was assumed that the nest had been predated.

### **Subsequent Reproductive Output**

We investigated whether feeding chicks affected their parent's reproductive output later in the season. Four analyses were conducted. These investigated whether supplementary feeding a parent's first-brood affected;

1. Its likelihood of re-nesting that season.
2. The interval between that brood fledging and the hatching of the second brood.
3. Number of eggs it produced later that season.
4. Number of chicks it fledged later that season.

The first analysis, looking at whether birds re-nested, was done prior to more detailed analyses to address the problem of data with multiple zeros.

Thus, the latter three parts of the analysis were *only conducted on parents that had subsequent clutches*.

These measures aimed to look at whether chick food availability limits breeding productivity. Both clutch size and number of fledglings were modelled because sample sizes were larger for the former but number of fledglings is a more complete measure of

parental effort, and is also the important measure in terms of looking at whether low chick food abundance is affecting within-year reproductive output.

The analysis looking at likelihood of re-nesting was done by conducting binomial GLMs in S-PLUS, with whether or not the bird had any further clutches (0/1) as the dependent variable. Factors in the model were supplementary feeding, site (lagoon 1 or 2), and parental age, which was a two-level factor, whether a bird was first-year or not. How many chicks the parent had fledged in the first brood was included as a covariate to investigate whether previous reproductive effort affected likelihood of re-nesting. All two-way interaction terms were included.

The latter three analyses were conducted using GLMs with poisson errors and log link in S-PLUS. Due to the small sample size (only 14 birds went on to have more clutches, and just 4 of these were parents of control broods), a step-up procedure from the null model was used, using the same terms as above.

### **Survival of parents**

We investigated whether survival of parents of 'fed' chicks to the next breeding season differed from that of parents of control chicks. Binomial GLMMs with logit link were conducted in GENSTAT, with survival (0/1) as the dependent variable. Terms in the model were whether the parent's brood had been fed, parental age (1 = first-year, 2 = older birds), and site (lagoon 1 or 2), which were all factors. 'Nest' was included as a random factor. All two-way interactions including the 'supplementary feeding' term were included in the model.

## **Chick survival**

We investigated whether survival of 'fed' chicks to the next breeding season differed from that of control chicks. Only chicks which fledged were included in the analysis. Binomial GLMMs with logit link were conducted in GENSTAT, with survival (0/1) as the dependent variable. Terms in the model were supplementary feeding, parental age (a 3-level factor; 1=both first year, 2=mix, 3=both older birds), site (lagoon 1 or 2), which were all factors, and date (day on d9 where May 1<sup>st</sup>= '1'), and brood size which were variables. 'Nest' was included as a random factor. All two-way interactions including the 'supplementary feeding' term were included in the model, as was the parental age x date interaction.

## **Results**

### **Provisioning Rate**

Supplementary feeding had no effect on provisioning rate (table 1). Parental age had a significant effect on provisioning rate (table 1), with pairs where one or both birds were in their first-year having a lower provisioning rate than non-first-year pairs (figure 3).



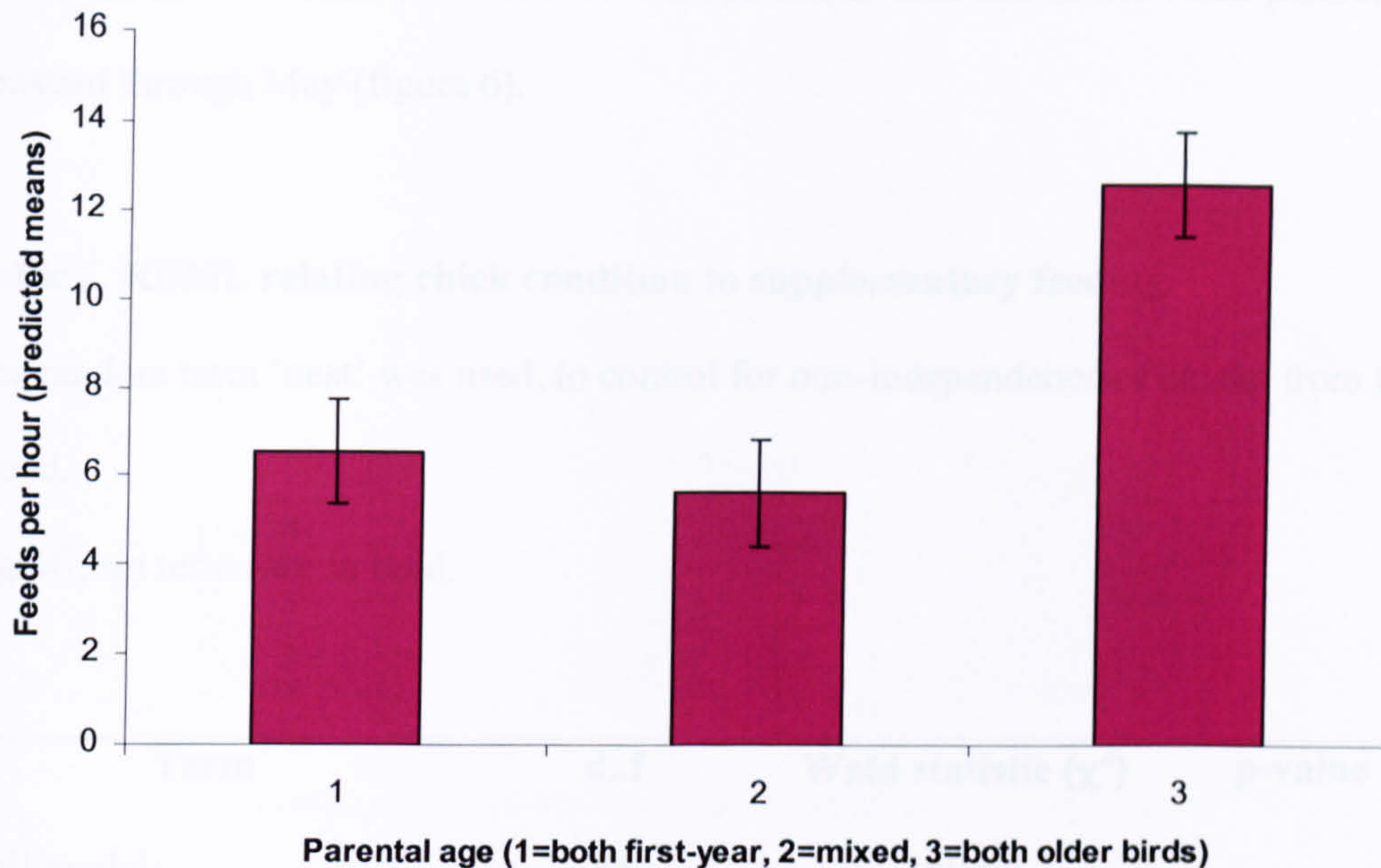
**Table 1. GLMM relating provisioning rate to supplementary feeding.**

The random term 'nest' was used as multiple watches were done for each nest.

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	55	-10.21	
Minimum adequate model:			
<b>Parental age</b>	<b>1</b>	<b>6.17</b>	<b>0.002</b>
Excluded terms:			
Supplementary food	1	0.41	0.516
Brood size	1	2.52	0.113
Chick age	1	2.75	0.097
Site	1	0.14	0.704
Time	1	0.05	0.828
Cloud	1	0.12	0.730
Rain	1	0.09	0.760





**Figure 3. Predicted mean provisioning rate (+/- standard errors) versus parental age.**

### **Chick condition**

There was a significant effect of the interaction between parental age and supplementary feeding on chick mass on day 9 (table 2). Where both parents were first-years, chicks given supplementary food were significantly heavier than control chicks. There was no difference for chicks of older pairs, and fed chicks of mixed age pairs have on average a higher but very variable chick mass than those of control pairs (figure 4).

There was also a significant effect of the interaction between date and supplementary feeding on chick condition (table 2). Chicks given supplementary food had a higher mass than those from control broods in early May, whereas by late May there was no difference in the mass of 'fed' and control chicks (figure 5).

The interaction between date and parental age significantly affected chick condition (table 2). In early May, chicks with two first-year parents were in lower condition than chicks of



older birds. Their condition increased throughout May, and by late May was the same as that of chicks with older parents. Condition of chicks with one or two older parents was constant through May (figure 6).

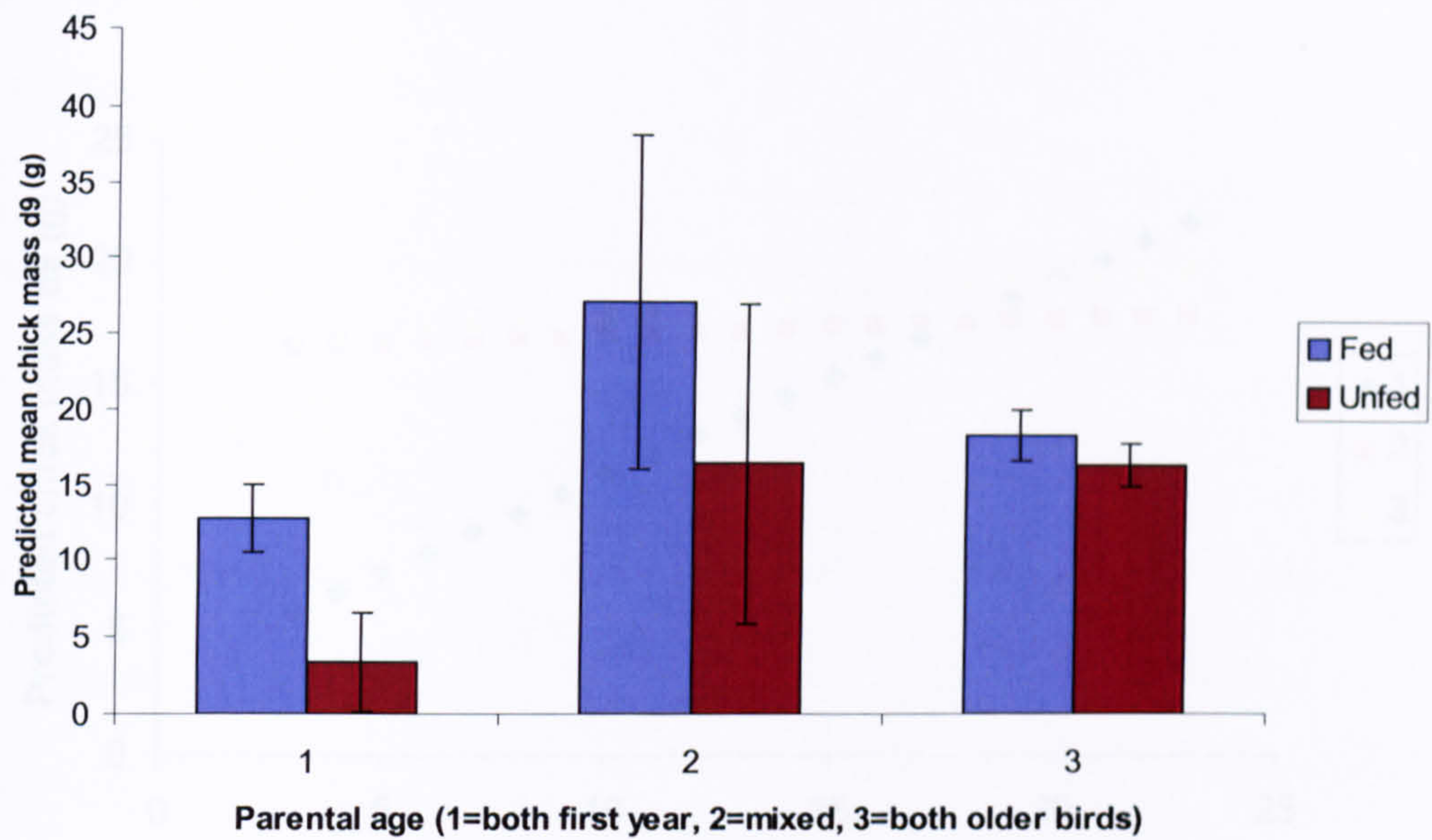
**Table 2. REML relating chick condition to supplementary feeding.**

The random term 'nest' was used, to control for non-independence of chicks from the same brood.

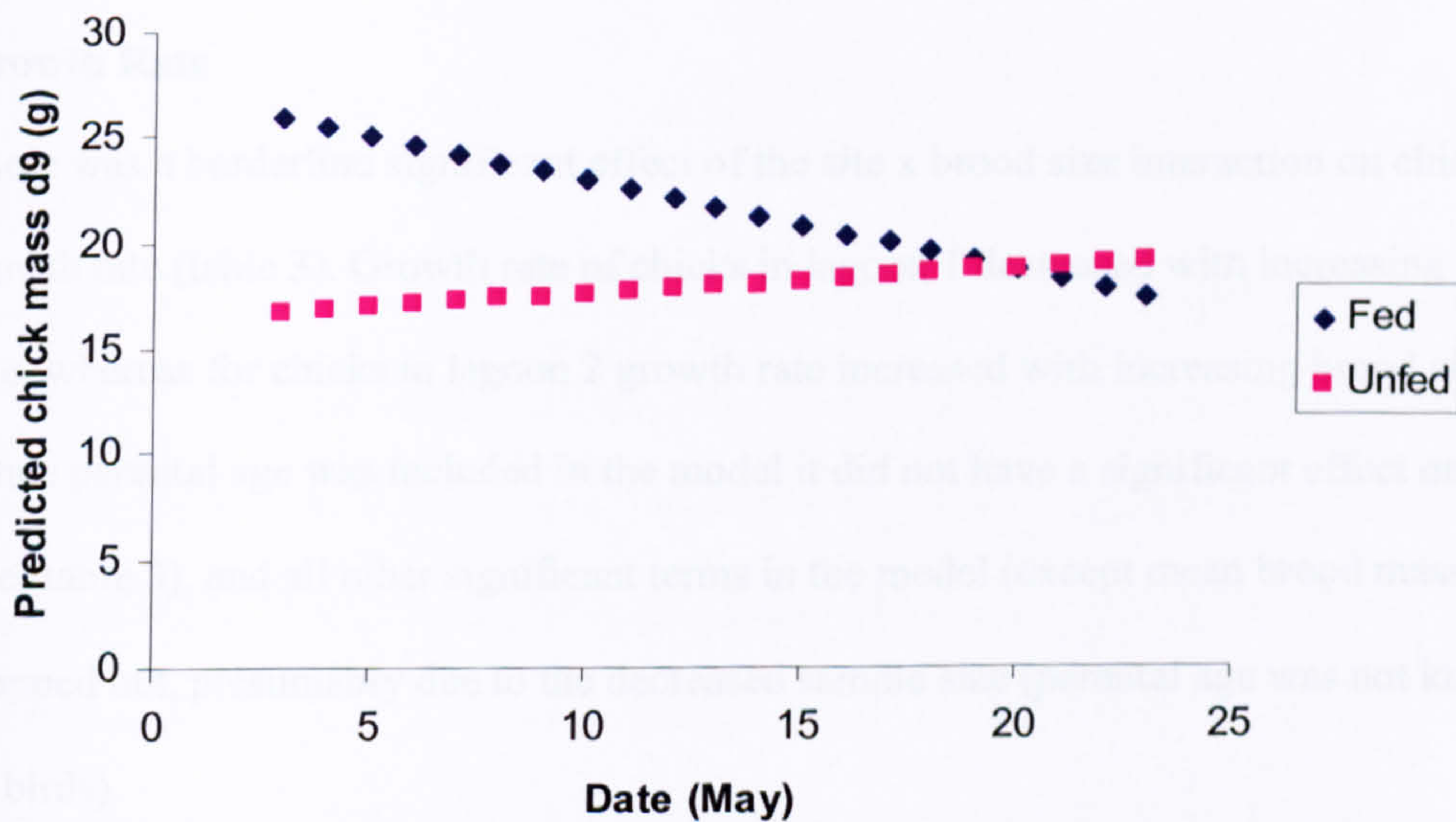
Significant terms are in bold.

<b>Term</b>	<b>d..f</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	65	160.64	
Minimum adequate model:			
<b>Supplementary feeding</b>	<b>1</b>	<b>3.61</b>	<b>0.058</b>
<b>Date</b>	<b>1</b>	<b>1.00</b>	<b>0.317</b>
<b>Parental age</b>	<b>2</b>	<b>1.80</b>	<b>0.407</b>
<b>Feeding*date</b>	<b>1</b>	<b>9.15</b>	<b>0.002</b>
<b>Feeding*parental age</b>	<b>2</b>	<b>22.20</b>	<b>&lt;0.001</b>
<b>Date*parental age</b>	<b>2</b>	<b>11.08</b>	<b>0.004</b>
Excluded terms:			
Site	1	3.73	0.054
Brood size	1	0.00	0.963



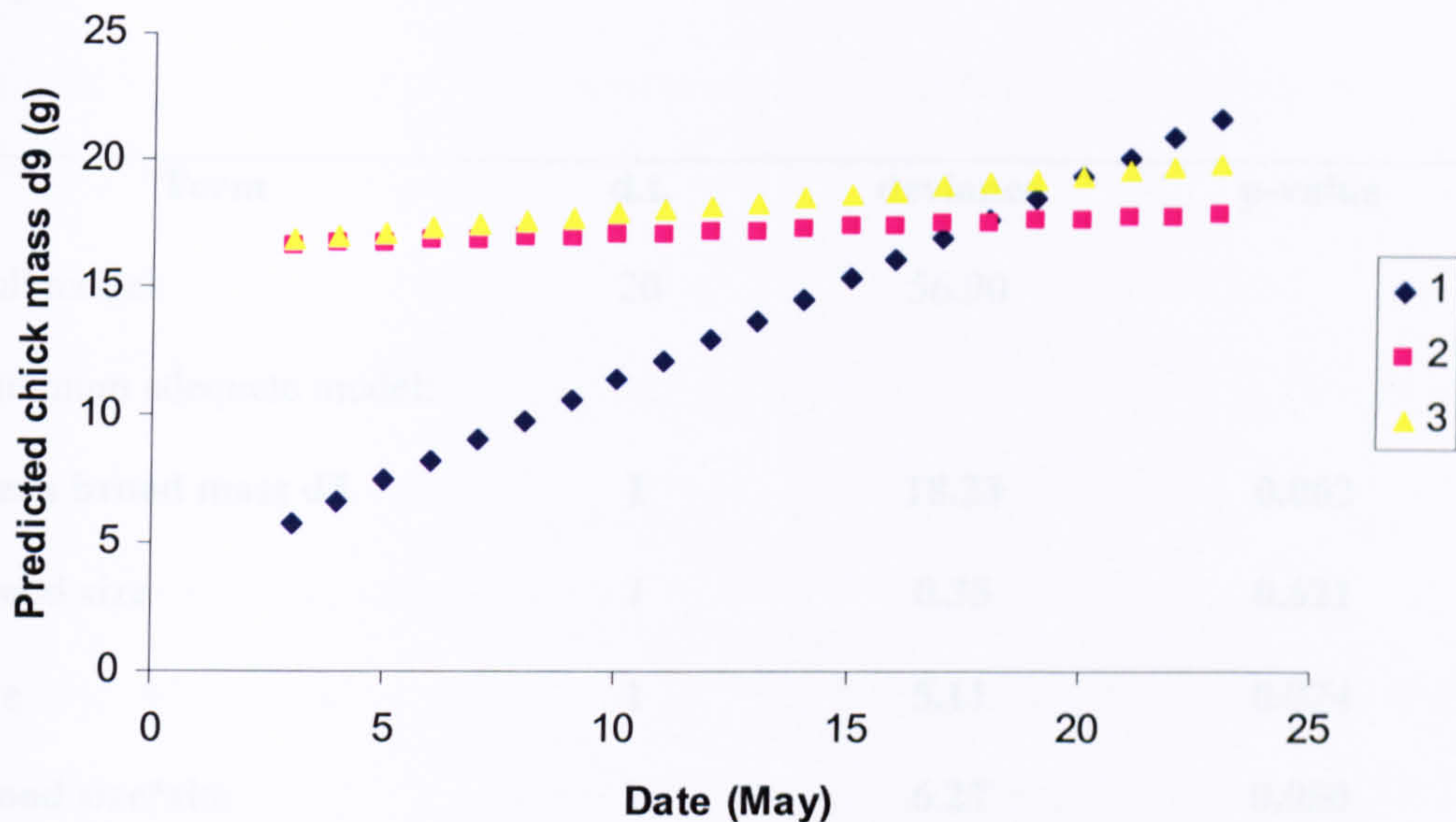


**Figure 4. Predicted mean chick masses on day 9 (+/- standard errors), in relation to parental age and supplementary feeding.**



**Figure 5. Predicted fits for chick mass on day 9 in relation to supplementary feeding and date.**





**Figure 6. Predicted fits for chick mass on day 9 in relation to parental age and date.**

Parental age classes: 1 = both first-year, 2 = mixed, 3 = both older birds.

### Growth Rate

There was a borderline significant effect of the site x brood size interaction on chick growth rate (table 3). Growth rate of chicks in lagoon 1 decreased with increasing brood size, whereas for chicks in lagoon 2 growth rate increased with increasing brood size.

When parental age was included in the model it did not have a significant effect on growth rate (table 3), and all other significant terms in the model (except mean brood mass day 5) dropped out, presumably due to the decreased sample size (parental age was not known for all birds).



**Table 3. GLM relating mean brood mass day 9 to supplementary feeding, controlling for mean brood mass day 5.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	20	56.90	
Minimum adequate model:			
<b>Mean brood mass d5</b>	<b>1</b>	<b>18.23</b>	<b>0.002</b>
<b>Brood size</b>	<b>1</b>	<b>0.35</b>	<b>0.621</b>
<b>Site</b>	<b>1</b>	<b>5.11</b>	<b>0.074</b>
<b>Brood size*site</b>	<b>1</b>	<b>6.27</b>	<b>0.050</b>
Excluded terms:			
Supplementary feeding	1	0.72	0.427
Date	1	0.04	0.858

### Prevalence of runts

#### Day 5 broods

There was a significant effect of the interaction between date and supplementary feeding on mass of the lightest chick, controlling for the mass of the heaviest, on day 5 (table 4, figure 7). Mass of the lightest chick, controlling for the heaviest, was fairly constant through May for 'fed' broods. For control broods, the mass of the lightest chick, controlling for that of the heaviest, was lighter than for 'fed' broods in early May, but increased such that by late May it was about the same as for 'fed' broods. Thus, in early May, supplementary feeding reduced the variability of chick mass within broods.

Parental age had a significant effect on prevalence of runts (table 4). For pairs where one



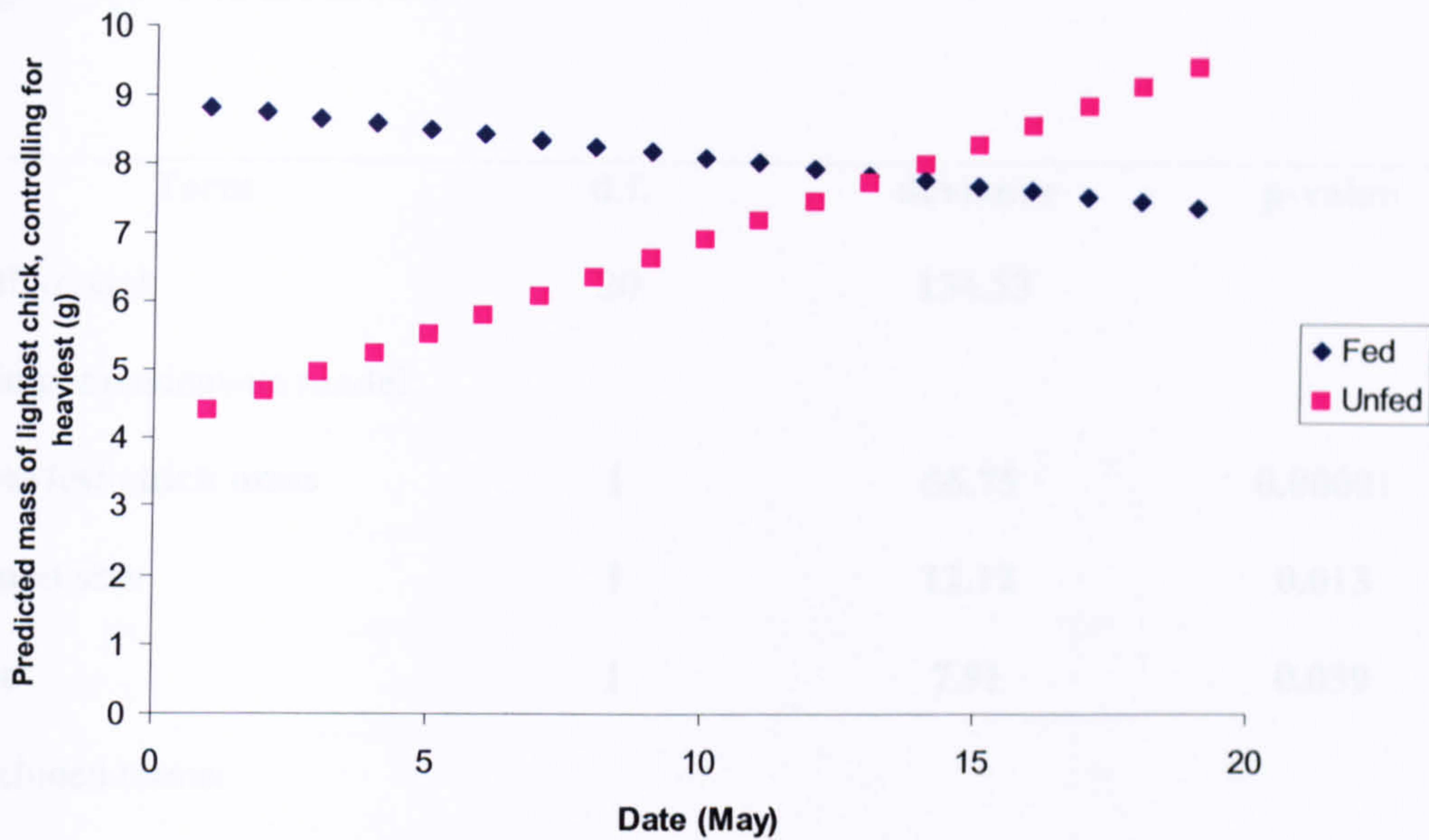
or both parents were first-year, the mass of the lightest chick, controlling for mass of the heaviest chick, was larger than for pairs of older birds.

**Table 4. GLM relating mass of lightest chick on day 5 to supplementary feeding.**

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>deviance</b>	<b>p-value</b>
Null model:	21	188.28	
Minimum adequate model			
<b>Heaviest chick mass</b>	<b>1</b>	<b>108.07</b>	<b>0.0000001</b>
<b>Parental age</b>	<b>1</b>	<b>14.294</b>	<b>0.014</b>
<b>Supplementary feeding</b>	<b>1</b>	<b>1.55</b>	<b>0.283</b>
<b>Date</b>	<b>1</b>	<b>1.02</b>	<b>0.381</b>
<b>Feeding x date</b>	<b>1</b>	<b>19.95</b>	<b>0.001</b>
Excluded terms			
Brood size	1	1.77	0.206
Site	1	2.52	0.135





**Figure 7. Predicted lightest d5 chick masses in relation to supplementary feeding and date.**

### Day 9 broods

There was no effect of supplementary food on prevalence of runts at day 9 (table 5).

There was a significant effect of site on mass of the lightest chick at day 9, controlling for mass of the heaviest ( $p = 0.039$ ), with mass of the lightest chick, controlling for the heaviest, being lighter in lagoon 1. Mass of lightest chick, controlling for the heaviest decreased with increasing brood size, but this is as expected as it is just a function of variance (between the lightest and heaviest chick) increasing with sample (i.e. brood) size.



**Table 5. GLM relating mass of lightest chick on day 9 to supplementary feeding.**

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>deviance</b>	<b>p-value</b>
Null model:	20	134.53	
Minimum adequate model:			
<b>Heaviest chick mass</b>	<b>1</b>	<b>56.75</b>	<b>0.00001</b>
<b>Brood size</b>	<b>1</b>	<b>12.12</b>	<b>0.013</b>
<b>Site</b>	<b>1</b>	<b>7.91</b>	<b>0.039</b>
Excluded terms:			
Supplementary feeding	1	2.51	0.200
Date	1	0.02	0.918
Parental age	2	0.33	0.901

### **Brood success**

Of twenty-seven nests, only two were lost to predation (fed: 1, unfed: 1). There were two other whole nest failures (fed: 1, unfed: 1, table 6), and three partial brood losses (fed: 1, unfed: 2, table 6). This left twenty nests of the original twenty-seven (74%) that fledged a full quota of chicks.

Incidence of whole or partial brood losses did not differ between fed and unfed broods ( $\chi^2$ -statistic = 0.013, d.f. = 1, p = 0.909).



**Table 6. Reproductive Output of parents of 'fed' and 'unfed' nests.**

		Fed		Unfed
		Both fed	Mixed	
Brood 1	Total Nests	14		13
	No. of experimental parents	28		26
	Whole nest losses (not due to predation)	1		1
	Partial nest losses	1		2
	Fledging success (chicks fledged/chicks hatched)	0.82		0.68
	Chicks fledged/nest	3.5		2.9
Brood 2	Total nests	2	4	3
	No. of experimental parents	4	4	4
	Days between brood 1 fledging and brood 2 hatching	27	23.3	27.8
	Mean no. eggs	4	4	4.7
	Mean no. chicks fledged	3	3	1.5
Brood 3	Total nests	0	4	3
	No. of experimental parents	0	4	4
	Mean no. eggs		5.3	4.3
	Mean no. chicks fledged		4	3.3

The 'mixed' column refers to a pair where a parent of a 'fed' brood has re-paired with a non-experimental bird. Where parents of 'unfed' broods re-paired with non-experimental birds, they were included in the table in the 'unfed' column, as although the non-experimental birds were not strictly controls, they would not have had supplementary food.

## **Subsequent Reproductive Output**

Overall, 22% of experimental birds went on to have a second brood, and 15% to have a third brood.

### **1. Did supplementary feeding a parent's first brood affect its likelihood of re-nesting that year?**

There was no effect of supplementary feeding a parent's first brood on that parent's likelihood of re-nesting that year.

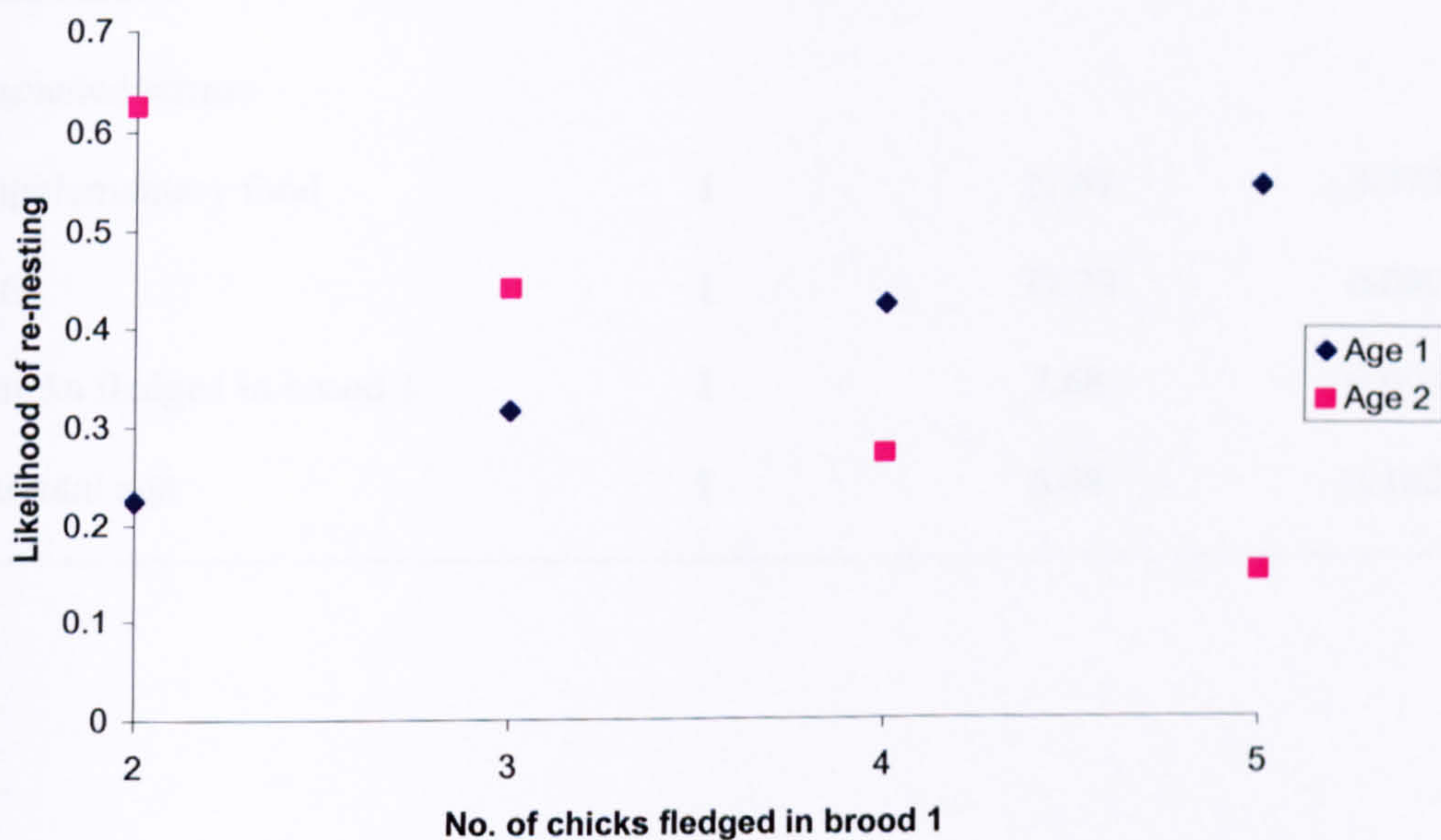
There was a significant effect of the interaction term (parental age) x (number of chicks fledged in brood 1) on a parent's likelihood of having further clutches (table 7). For first-year parents, the more chicks they fledged in brood 1, the more likely they were to have further clutches, whereas for older birds, the relationship was reversed (figure 8).



**Table 7. GLM relating likelihood of re-nesting to supplementary feeding.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	48	60.36	
Minimum adequate model:			
<b>Fledged</b>	<b>1</b>	<b>0.67</b>	<b>0.414</b>
<b>Parental age</b>	<b>1</b>	<b>0.10</b>	<b>0.751</b>
<b>Fledged*Parental age</b>	<b>1</b>	<b>7.45</b>	<b>0.006</b>
Excluded terms:			
Supplementary food	1	0.24	0.627
Site	1	0.03	0.860



**Figure 8. Predicted fits for likelihood of re-nesting, in relation to number of chicks fledged in brood 1, for parents of different ages (age 1 = first-year, age 2 = older).**



**2. Did supplementary feeding a parent's first brood affect the interval between that brood fledging and the hatching of its second brood?**

Supplementary feeding a parent's first brood had no effect on the interval between that brood fledging and the second brood hatching (table 8).

**Table 8. GLM relating interval between first brood fledging and second brood hatching to supplementary feeding.**

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>deviance</b>	<b>p-value</b>
Null model:			
Excluded terms:			
Supplementary food	1	21.61	0.379
Site	1	77.79	0.080
Chicks fledged in brood 1	1	7.68	0.604
Parental age	1	6.08	0.162

**3. Did supplementary feeding a parent's first brood affect the number of eggs it produced later that season?**

Supplementary feeding a parent's first brood did not affect the number of eggs it produced later that season (table 9).

**Table 9. GLM of number of eggs produced in second and third broods, in relation to supplementary feeding.**

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>deviance</b>	<b>p-value</b>
Null model:			
Excluded terms:			
Supplementary food	1	0.007	0.970
Site	1	8.64	0.174
Chicks fledged in brood 1	1	2.75	0.456
Parental age	1	2.08	0.520

**4. Did supplementary feeding a parent's first brood affect the number of chicks it fledged later that season?**

Supplementary feeding a parent's first brood had no effect on the number of chicks it fledged later that season (table 10).

**Table 10. GLM relating number of chicks fledged in second and third broods to supplementary feeding.**

Significant terms are in bold.

<b>Term</b>	<b>d.f.</b>	<b>deviance</b>	<b>p-value</b>
Null model:			
Excluded terms:			
Supplementary food	1	0.53	0.467
Site	1	0.08	0.852
Chicks fledged in brood 1	1	1.91	0.366
Parental age	1	3.81	0.205

**Survival of parents**

Supplementary feeding a parent's first brood had no effect on the parent's chances of survival to the following breeding season (table 11). Parental survival was not affected by any of the terms in the model (table 11).



**Table 11. GLMM relating parental survival to the next breeding season to whether or not its first brood had been provided with supplementary food**

Significant terms are in bold.

<b>Term</b>	<b>d..f</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	49	135.91	
Excluded terms:			
Supplementary feeding	1	0.00	0.967
Parental age	1	0.23	0.629
Site	1	1.61	0.205

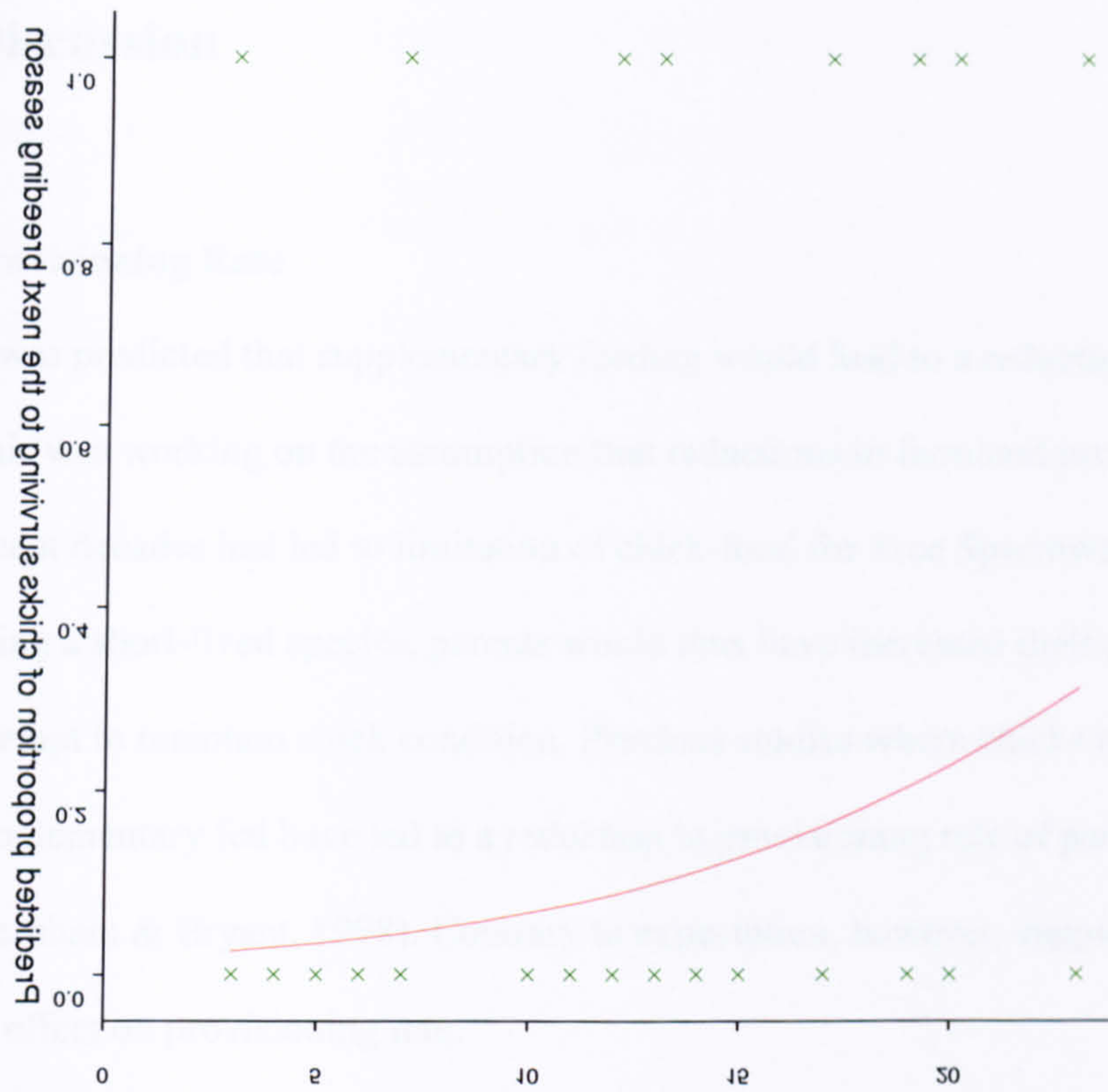
### **Survival of chicks**

Supplementary feeding had no effect on a chick's chances of surviving to the following breeding season (table 12). There was a significant effect of day on a chick's chances of survival, with chicks which were from early first-broods being significantly less likely to survive to the following breeding season than chicks from later first-broods (table 12, figure 9).

**Table 12. GLMM relating chick survival to the next breeding season to supplementary feeding**

Significant terms are in bold.

<b>Term</b>	<b>d..f</b>	<b>Wald statistic (<math>\chi^2</math>)</b>	<b>p-value</b>
Null model:	91	259.29	
Minimum adequate model:			
<b>Day</b>	<b>1</b>	<b>5.09</b>	<b>0.024</b>
Excluded terms:			
Supplementary feeding	1	0.81	0.367
Parental age	2	2.50	0.287
Brood size	1	0.60	0.437
Site	1	1.36	0.244



**Figure 9. Predicted proportion of chicks surviving to the next breeding season depending upon when in May they were 9 days old**



## **Discussion**

### **Provisioning Rate**

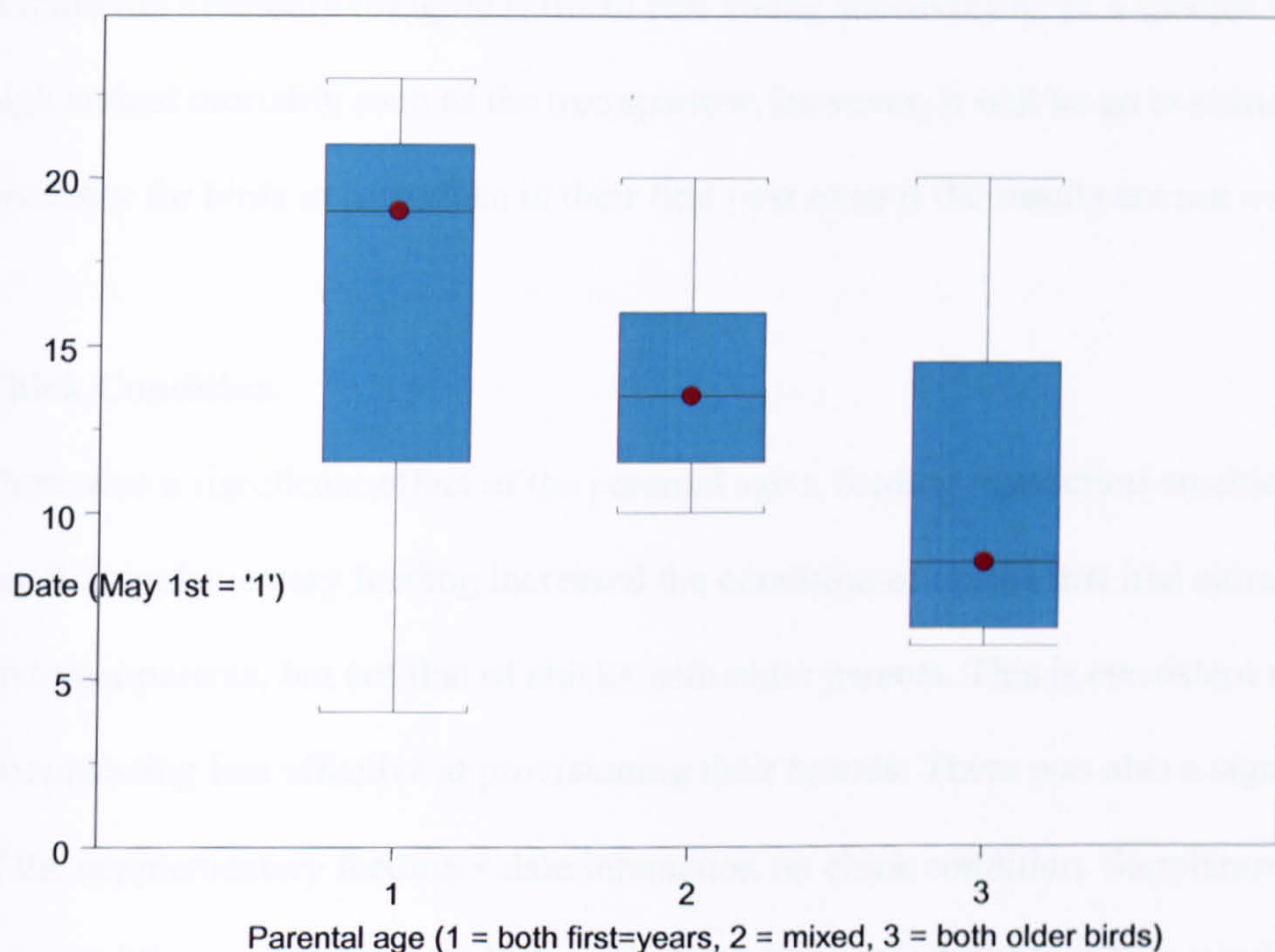
It was predicted that supplementary feeding would lead to a reduction in provisioning rate. This was working on the assumption that reductions in farmland invertebrate abundance in recent decades had led to limitation of chick-food for Tree Sparrows. We expected that being a short-lived species, parents would thus have increased their provisioning rate in an attempt to maintain chick condition. Previous studies where chicks have been supplementary fed have led to a reduction in provisioning rate of parents (Johnston, 1993, Wernham & Bryant, 1998). Contrary to expectation, however, supplementary feeding had no effect on provisioning rate.

Pairs where one or both parents were in their first-year had a significantly lower foray rate than older pairs. Many bird species show an improvement in breeding performance with age (Fowler, 1995, Martin, 1995). Possible explanations for this are that there is an increase in reproductive performance with age and/or experience (Curio, 1983, Forslund & Part, 1995), or to differential mortality of poor quality birds (Forslund & Part, 1995). The lack of variation in provisioning rate amongst first-year pairs in this study would suggest that the former was the case here.

Age-related improvements in foraging ability are often suggested as a potential cause of differences in various aspects of breeding performance (Daunt *et al.*, 1999, Perrins & McCleery, 1985, de Forest & Gaston, 1996, Ainley & Schlatter, 1972, Espie *et al.*, 2000). Some studies have indirectly demonstrated this, for example Källander (1974) provided Great Tits with supplementary food and found that this advanced the laying date of



yearlings more than that of older birds (yearlings usually lay later, and are thus presumably constrained by poor foraging ability). First-year parents also laid later in May than older parents on average in this study (figure 10), although this difference was not significant, and it is possible that this too is due to the constraint of poor foraging ability.



**Figure 10. Mean day 9 date of broods laid by parents of different ages.**

Few studies have directly shown differences in provisioning rate of birds of different ages. It has been shown that juvenile Little Blue Herons (Recher & Recher, 1969) and Brown Pelicans (Orians 1969) miss prey more frequently than do older birds. Likewise, first-winter Sandwich Terns dive at the same rate as older birds, but have a lower success rate at catching fish, resulting in a mean 10 fish per hour being caught as oppose to 14 per hour for older birds (Dunn, 1972). Under conditions when fish were super-abundant (on beaches when seine-netting was taking place) the success rate of first-winter and older terns was the



same (Dunn, 1972). Catry & Furness (1999) found that Great Skua pairs containing young males spent more time away from the nest (presumably foraging) than pairs with older males. They found no resulting increase in chick body condition, so concluded that young males are less efficient foragers. Lack (1968) even suggested that the occurrence of delayed breeding in some long-lived species was to allow sufficient time for individuals to acquire the necessary foraging skills to rear young successfully. In a species with relatively high annual mortality such as the tree sparrow, however, it will be an evolutionary necessity for birds to reproduce in their first year even if the results are not so good.

### **Chick Condition**

There was a significant effect of the parental age x feeding interaction on chick mass on day 9. Supplementary feeding increased the condition of chicks that had either one or two first-year parents, but not that of chicks with older parents. This is consistent with first-year parents being less effective at provisioning their broods. There was also a significant effect of the supplementary feeding x date interaction on chick condition. Supplementary feeding increased the condition of chicks in early May, but not in late May. This would suggest that conditions were harsher in early May, due to perhaps poor weather or lower invertebrate abundance causing chick food to be limiting at this time.

There was also a significant effect of the interaction between date and parental age on the condition of chicks. In early May chicks with two first-year parents (which have a lower provisioning rate) were in lower condition than chicks of older birds. Their condition increased throughout May, and by late May was the same as that of chicks with older parents. Condition of chicks with one or two non-first-year parent was fairly constant through May. Thus it would seem that having young parents is only detrimental to chick mass when conditions are less favourable.



Thus, low food availability appears to limiting nestling mass when conditions are less favourable, that is in early May, and when parents are in their first-year (and have a lower provisioning rate). There is no evidence that chick food is a limiting factor on chick condition at Rutland Water when parents are older than first-year, and in late May when food is likely to be more abundant.

As the experiment was only conducted on first broods, it is not possible to tell what effect supplementary chick food would have had at other points in the season. For example, supplementary feeding may have had a bigger effect on chick condition in third broods, which are of worse condition than second broods (see chapter 4).

### **Growth Rate**

Supplementary feeding chicks had no effect on their growth rate.

There was a significant effect of the site x brood size interaction on chick growth rate.

Growth rate of chicks in lagoon 1 decreased with increasing brood size, whereas for chicks in lagoon 2, growth rate increased with increasing brood size.

This result is hard to interpret, and was only borderline significant ( $p=0.05$ ), so could just be an artefact of the low sample size.

### **Prevalence of runts**

#### **Day 5 broods**

The interaction between supplementary feeding and date had a significant effect on the mass of the lightest chick, controlling for the mass of the heaviest, on day 5. Mass of the lightest chick, controlling for the heaviest, was fairly constant through May for 'fed' broods. For control broods, the mass of the lightest chick, controlling for that of the heaviest was lighter than for 'fed' broods in early May, but increased such that by late May

it was about the same as for 'fed' broods. This is consistent with supplementary food reducing the prevalence of runts within broods early in May, when it appears that conditions were less favourable.

Parental age had a significant effect mass of the lightest chick, controlling for that of the heaviest. For pairs where one or both parents were first-year, the mass of the lightest chick, controlling for mass of the heaviest chick, was larger than for pairs of older birds. Thus, chick mass was more variable in broods which had older parents. This is hard to interpret, as there was no evidence of older birds laying larger clutches.

### **Day 9**

There was no effect of supplementary food on prevalence of runts at day 9.

There was a significant effect of site on mass of the lightest chick at day 9, controlling for mass of the heaviest, with mass of the lightest chick, controlling for the heaviest, being lighter in lagoon 1. Mass of lightest chick, controlling for the heaviest decreased with increasing brood size. This is as expected, as we are looking at effectively looking at variance of chick masses within broods, which will increase with brood size.

In summary, prevalence of runts in young broods was influenced by provision of supplementary feeding when conditions were less favourable, but not in older broods.

### **Brood survival**

Incidence of whole or partial brood losses were low, with 74% of the nests fledging the full number of chicks. There was no effect of supplementary feeding on chick survival within the nest.

## **Chick survival**

There was no effect of supplementary feeding on survival of chicks to the next breeding season. The only thing to affect chick survival was date, with chicks from broods which were 9 days old earlier in May having a lower survival than chicks from later broods.

## **Later Reproductive Output**

Overall, 22% of experimental birds went on to have a second brood, and 15% to have a third brood. BTO data for the year 1980-1981 showed that 46% of birds (n=276) went on to have a second clutch, and 12% a third clutch (Summers-Smith, 1995). Values from Rutland Water could be underestimates, as identification of parents was done at the chick-feeding stage, so failed nesting attempts at the clutch or young chick stage are unlikely to have been detected.

Supplementary feeding had no effect on a parent's reproductive output that year.

There was a significant effect of the (parental age) x (number of chicks fledged in brood 1) interaction term on a parent's likelihood of having further clutches after brood 1. For first-year parents, the more chicks they fledged in brood 1, the more likely they were to have further clutches, whereas for older birds, the relationship was reversed. This could be because, as it would seem that first-year birds are generally less efficient at provisioning their broods, there is a quality/experience effect for them, with parents which are more successful at their first brood being more likely to have more clutches. For older birds, where birds have more experience (or are 'better' in terms of some other age-related quality, such as size) there is a trade-off effect, with investment in the first brood being at a cost to a parent's chances of having later clutches. A similar trade-off to that found for



older parents here was found for a population of Tree Sparrows in Hungary (Sasvari & Hegyi, 1993). Adults which produced fewer than the average number of fledglings in previous broods produced more than average in broods 2 and 3. They also found evidence for a reproductive trade-off between years, with females that produced fewer offspring in years 1 and 2 surviving longer (however, its not clear whether these results include adults which have had failed nests). As theirs was just a correlational study, the causes of these trade-offs were not clear.

## **Conclusions**

Supplementary feeding had no effect on provisioning rate, but affected chick mass and prevalence of runts when conditions were unfavourable. This was contrary to expectations, which were that supplementary feeding would cause a reduction in provisioning rate, as parents would be maximising provisioning rates and trying to compensate for possibly low invertebrate abundance, as Tree Sparrows are relatively short-lived.

This could be because parents are provisioning their broods at (an age-related) maximum rate. Lack of invertebrate food thus appears to be having a detrimental effect on chick mass under certain circumstances. Firstly, chicks from 'fed' broods early in May had a higher mass than unfed broods, secondly chicks with first-year parents had a higher mass when provided with supplementary food but there was no difference for chicks of older pairs, and lastly chicks with first-year parents had a lower mass early in May than late May, with there being no difference for chicks of older birds. Control broods were also more likely to contain a runt on day 5 than 'fed' broods early in May, but not late in May. This implies that lack of invertebrate food may be limiting chick condition when parents are first-year (and thus less effective provisioners), and also early in May, when invertebrate food is presumably scarcer. Chicks which were from broods which were nestlings early in May

had a significantly lower survival to the next breeding season than chicks from later broods. Due to the differences in condition, we might also expect parental age, or supplementary feeding to affect chick survival, but this was not the case, perhaps due to lack of statistical power.

Fifty percent of birds in this study were first-years. As the Tree Sparrow population at Rutland Water is provided with supplementary seed food all year, it is possible that the proportion of first-year birds in other populations will be higher. Parents will also need to spend more time foraging for themselves in other populations. Therefore, the fact that there is some evidence for lack of chick food limiting chick mass and survival in this population has potentially serious implications for other populations.

Thus it would seem that low chick food abundance could have been partly responsible for Tree Sparrow declines by causing decreased first-year survival.

Källander (1974) found that providing a population of Great Tits with trays of meal worms meant that the previously late laying date of first-years was brought forwards to be the same as that of older birds, implying that providing easily accessible invertebrate food could overcome the fact that first-years may have poorer foraging efficiency, and also lay later on average. This is similar to a result found for Sandwich Terns that when food was super-abundant the usually lower fishing abilities of first-winter birds were the same as those of older birds. Although it is clearly not feasible to hand-feed chicks as a conservation management option, it may be beneficial in some cases, for example where there is risk of local extinction, to provide some easily accessible source of high-protein supplementary chick food.

Other recommendations would be measures to increase abundance and availability of invertebrate food on farmland, particularly early in the season. Chapter 3 suggests that winter oilseed rape and set-aside are relatively invertebrate rich crop types in May, with

winter wheat having higher invertebrate abundance than spring barley. Provision of rough field boundaries, a relatively invertebrate rich habitat on farmland, which are protected from excessive cutting or spray drift, and reduced pesticide inputs, particularly spring and summer insecticide applications, would also be beneficial. Accessibility of invertebrates within cereal fields to farmland birds could be improved by measures such as such as wider drill row spacing, reduced fertiliser inputs, and the provision of bare patches created by momentarily turning off seed drills.



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## **Chapter 6:**

# **The effect of supplementary chick-food on a population of Yellowhammers, *Emberiza citrinella***

### **Abstract**

The Yellowhammer, *Emberiza citrinella*, is Britain's most rapidly declining farmland bird species, but the specific causes of its decline are unknown. During the period of population decline breeding performance has increased at the national scale, but there have been decreases in both first-year and adult survival. Results of a study to investigate whether these decreases in survival could be attributed to lack of invertebrate chick food during the breeding season are presented here. This was done by supplementary feeding of chicks in the nest, and comparing provisioning rates and chick condition for fed and control broods. There was no effect of supplementary feeding on provisioning rate. Provisioning rate significantly decreased with increasing chick age, and also through the season. It is suggested that both of these effects are due to increasing load sizes. Supplementary feeding significantly increased chick condition (mass) early in the season, but not for later broods. Analysis of data on Yellowhammer populations in Oxfordshire showed that partial or whole brood losses due to starvation were more common early in the season. Condition of chicks was also lower early in the season, and this result was true also when just looking at broods which did not suffer partial or whole brood losses. Thus it appears that invertebrate chick food abundance is limiting Yellowhammer chick condition and survival early in the season, and that this is also leading to parents having to make more forays at this time.

## **Introduction**

Many species of farmland birds have shown huge declines in numbers or range over the last few decades (Fuller *et al.*, 1995), and these declines have been attributed to agricultural intensification (Chamberlain *et al.*, 2000). Agricultural intensification has occurred as a suite of changes in farming practices since the 1970s, such as increased agrochemical input, the switch from spring sown to winter sown cereals, the switch from hay to silage, and the loss of unfarmed structures such as hedgerows and ponds. These changes have affected farmland birds by reducing nesting habitat and/or abundance of food. Worst affected by the changes in farming practices have been granivorous passerines (Fuller *et al.*, 1995), and their declines are often attributed to lower seed food abundance during the winter leading to a reduction in survival (Peach *et al.*, 1999, Robinson & Sutherland, 1999, Donald, 1997). However, most of these 'granivorous' passerines feed their chicks invertebrates as a source of high-protein food (Baillie *et al.*, 1997). Abundance of invertebrates on farmland has also declined (with the possible exception of aphids) since the onset of agricultural intensification (Sotherton & Self, 2000). The decline of the Grey Partridge has been attributed to lack of invertebrate chick food due to the indirect effects of herbicides (Potts, 1986), and lack of invertebrate chick food is also likely to have contributed to the decline of at least three other farmland passerine species in the UK (Skylark: Poulsen *et al.*, 1998; Cirl Bunting: Evans *et al.*, 1997; Corn Bunting: Brickle *et al.*, 2000).

The Yellowhammer, *Emberiza citrinella*, is Britain's fastest declining farmland bird (Bradbury *et al.*, 2000), having declined rapidly since the late 1980s both in Britain (Fuller *et al.*, 1995, Crick *et al.*, 1998, Siriwardena *et al.*, 1998) and much of western Europe (Tucker and Heath, 1994). The timing of the Yellowhammer's decline is unusual amongst

granivorous farmland bird populations, which mainly began to decline in the 1970s (Siriwardena *et al.*, 1998, Fuller *et al.*, 1995). On farmland, Yellowhammers nest in herbaceous vegetation next to ditches or in rough margins, or in the shrubby vegetation of hedgerows (Stoate *et al.*, 1998, Bradbury *et al.*, 2000). Adults are predominantly granivorous, but chicks are fed a large proportion (at least 50%) of invertebrates (Wilson *et al.*, 1996, Stoate *et al.*, 1998, Moreby & Stoate, 2001). The exact reasons for the Yellowhammer's decline are unknown, but the removal of hedgerows, poor management of hedgerows, loss of ditches, and loss of field margins have all been named as possible causes (Bradbury *et al.*, 2000, Kyrkos *et al.*, 1998). Whilst these could have led to a lack of invertebrate food for chicks, field boundary features being the Yellowhammer's preferred foraging habitat during the breeding season (Morris *et al.*, 2001), a model developed to predict presence of Yellowhammer territories in Oxfordshire suggested that the population is not limited by a lack of suitable nesting habitat (Bradbury *et al.*, 2000). Intensification of grassland management leading to loss of floral and invertebrate diversity and lower invertebrate abundance, and loss of winter feeding sites such as over-winter stubbles are likely to have had an adverse effect on Yellowhammer populations (Bradbury *et al.*, 2000). Losses of Yellowhammers from the north and west of England, as well as Wales, Ireland and parts of Scotland, could also be associated with the decline of cereals in these areas, the preferred nesting habitat of the Yellowhammer (Kyrkos *et al.*, 1998).

Lack of invertebrate chick-food could have affected the Yellowhammer population via a number of mechanisms:

1. It could have reduced chick growth and survival in the nest;
2. Number of breeding attempts made per year may have decreased;
3. Chick condition at fledging may have been reduced, leading to poor first-year survival;



4. Parental effort during the breeding season could be higher, leading to poor post-breeding season condition, and thus reduced adult survival.

Yellowhammer breeding performance per attempt has been higher during the period of population decline (Siriwardena *et al.*, 2000). Yellowhammers make a maximum of two successful breeding attempts per season (Bradbury *et al.*, 2000). There are no long-term data on number of breeding attempts per year. However, the fact that a study which compared Yellowhammer breeding performance on organic and conventional farms found a double-peaked distribution of first egg dates on organic farms, but not intensive farms, may suggest that a more limited number of breeding attempts are made on intensive farms (Bradbury *et al.*, 2000), which suggests that agricultural intensification may have led to a decrease in number of breeding attempts made. Survival is generally suggested as the most likely demographic cause of Yellowhammer declines (Siriwardena *et al.*, 2000, Bradbury *et al.*, 2000), with both adult and first-year survival having decreased by 10% between the periods 1960-1988 and 1988-1994 (Siriwardena *et al.*, 2000). Decreases in survival such as this are often assumed to be due to a drop in over-winter survival; however this is an assumption, as they are based on Common Birds Census data, which does not discriminate between breeding season and winter survival.

The 'reproductive cost' hypothesis states that investment in current reproduction by iteroparous species is made at a cost to future reproductive success and survival (Williams, 1966, Charnov & Krebs, 1974, Stearns, 1976, Ricklefs, 1981). This results in conflicting interests between what is optimal for parents to invest in current reproduction, and the level of investment which is optimal to offspring, as parents must trade-off the benefits of investment in current offspring with the potential costs to their own future reproduction and survival. The outcome of this trade-off will depend on a number of factors, including average life span of the species in question. In a short-lived species, such as the

Yellowhammer, life-history theory predicts that this trade-off will favour the current offspring (Linden & Moller, 1989). Thus, we predict that as invertebrate abundance has decreased, parents will have increased their effort (in the form of their provisioning rate) as much as possible, in order to maintain chick condition. If invertebrate abundance was sufficiently low, it could be that parents are working at maximum rate to provision chicks, with chick condition still suffering. We investigate how low invertebrate abundance may have affected the Yellowhammer population by a supplementary feeding experiment, and its possible role in causing the observed declines in Yellowhammer survival.

Yellowhammer broods on farmland near Stirling, Scotland, were provided with supplementary food, and comparisons of chick condition and growth rate, and parental effort were made with control broods. It is inferred that parental effort, measured as provisioning rate, will affect post-breeding season condition, and thus potentially over-winter survival and/or future reproduction. Chick condition is known to affect subsequent survival for many bird species. Attempts were made to mist-net adult Yellowhammers just prior to their chicks fledging, in order to measure adult condition, but these attempts had a low success rate. High-protein hand rearing food was used in place of invertebrates.

## **Methods**

### **Study Area**

The study area was a lowland mixed farming landscape in Stirling, Scotland. The experiment was carried out between April and August 2002 and 2003.

Yellowhammer nests were found by mapping territories using Common Birds Census methods (Marchant *et al.*, 1990) and then watching for signs of breeding behaviour. If found at the egg stage, nests were checked every other day for hatching to determine hatch

date accurately. If found at the chick stage, chick age was estimated by comparing feather development with known age broods.

### **Supplementary Feeding**

Chicks from every other nest found were assigned to the 'fed' group. Chicks from 'fed' nests were given high-protein hand-rearing food (Low energy Gold Label Hand Rearing Food from the Birdcare Company) using a 1mm plastic syringe. Chicks were fed four times a day, leaving at least 2 hours between consecutive feeds, from days 4 to 8 inclusive. Chicks were fed in the nest until they stopped begging. Chicks from control nests were disturbed at the same frequency, and for the same duration, as fed nests, in order to control for any effects of nest-visiting.

The mean daily amount of supplementary food ingested per chick per day was 2.7cm<sup>3</sup>, This is about 27% of a chick's average daily metabolised energy (ADME) on day 6. This was calculated using the value of the Chaffinch nestlings' ADME of 1.88 KJ per g per day (Dolnik & Yablonkevich, 1982), as a value could not be found for Yellowhammer nestlings. The estimate was thought to be suitable due to the two species' similar size, diet and nesting habits. The calculation was based on the mean Yellowhammer chick mass of 15.6g on d6, the mid-point of feeding, giving an overall ADME of 29.3 KJ per chick per day.

### **Chick Measurements**

Chicks were marked on their feather pins using a colour marker when the first measurements were taken so that individuals could be identified later. Where possible, a series of measurements were taken on days 4, 6 and 8, when chicks were weighed (to the nearest 0.05g) using a Pesola spring balance. The age, in days, of chicks, where not known



from hatch date, was estimated by comparison of feather development with known-age broods.

## **Provisioning Rate**

Provisioning rate was estimated by conducting hour-long feeding watches at a safe distance from the nest. A minimum of two feeding watches were conducted, one in the morning, and one in the afternoon, on two separate days, when the chicks were aged between 4 and 8 days. Morning watches were conducted between 0600 and 1100, and afternoon watches between 1400 and 1800. Provisioning watches were not carried out in wet or windy (> Beaufort force 4) weather.

## **Data Analysis**

Effects of supplementary feeding were examined using three types of model; generalised linear models (GLMs) in S-PLUS; and residual maximum likelihood models (REMLs) and generalised linear mixed models (GLMMs) in GENSTAT. GLMs allow the analysis of non-normal error distributions through the use of linearising transformations specified by link functions. REMLs and GLMMs are both forms of mixed model, so allow the inclusion of random effects, such as blocking factors, to account for non-independence of data points (e.g. for repeat measurements, or measures of chicks from the same brood). REMLs only allow for normal error distributions, whereas GLMMs allow analysis of non-normal error distributions, again by use of linearising link functions.

Unless stated otherwise, minimum adequate models were found by stepwise deletion from the maximal model. Model residuals were checked for normality. Predicted means or fits were used to display results while controlling for other terms in the minimum adequate model. Mean values presented in the text are given in the form 'mean +/- standard error'.

## **Provisioning rate**

Analysis was conducted to see whether supplementary feeding affected provisioning rate. Provisioning rates were measured by conducting hour-long watches, with three or four being done for each nest. Mixed models were run, with provisioning rate as the dependent variable, and 'nest' as a random factor, in order to avoid pseudoreplication. Mixed models were used, rather than just analysing mean provisioning rate for each nest using GLMs, so that variables which were specific to a particular watch could be included in the analysis (i.e. time and chick age).

GLMMs with Poisson errors and log link were run in GENSTAT. Whether the nest was provided with supplementary food and year were included as factors in the model, with brood size, chick age, day and time of day included as variables. Two-way interaction terms to be included were supplementary feeding x brood size, supplementary feeding x chick age, supplementary feeding x day and supplementary feeding x year.

## **Chick Condition**

Models were run to see whether supplementary feeding affected chick condition (mass). REMLs were conducted in GENSTAT with chick mass as the dependent variable. Terms included in the model were brood size, chick age and hatch date (May 1<sup>st</sup> = '1'), which were included as variables, and supplementary feeding and year which were included as factors. All two-way interaction terms including the 'supplementary feeding' term were included.

## **Growth rate**

Growth rates of fed and control chicks were compared. GLMs with Poisson errors and log link were conducted in S-PLUS, with mean daily increase in mass as the dependent

variable. Terms included in the model were supplementary feeding which was a factor, and chick age (at the mid-point between the two measurements), brood size and day (where May 1<sup>st</sup> = '1') which were included as variables. Two-way interactions including the 'supplementary feeding' term were added two at a time, due to the low sample size.

## **Results**

### **Provisioning rate**

The mean hourly provisioning rate for control nests was 7.8 +/- 0.5 (n = 11 nests), whereas for fed nests it was 4.9 +/- 0.8 (n = 5 nests). Despite this relatively large distance in means, there was no significant effect of supplementary feeding on provisioning rate (table 1).

Provisioning rate was affected by brood size; with larger broods being fed more frequently (table 1, figure 1). Provisioning rate decreased with increasing chick age (table 1, figure 2) and also with day (table 1, figure 3).



**Table 1. GLMM relating provisioning rate to supplementary feeding.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	34	-21.09	
Minimum adequate model:			
<b>Day</b>	<b>1</b>	<b>34.11</b>	<b>&lt;0.001</b>
<b>Brood size</b>	<b>1</b>	<b>6.93</b>	<b>0.008</b>
<b>Age</b>	<b>1</b>	<b>9.04</b>	<b>0.003</b>
Excluded terms:			
Supplementary food	1	0.23	0.631
Year	1	0.00	0.996
Time	1	0.00	0.990

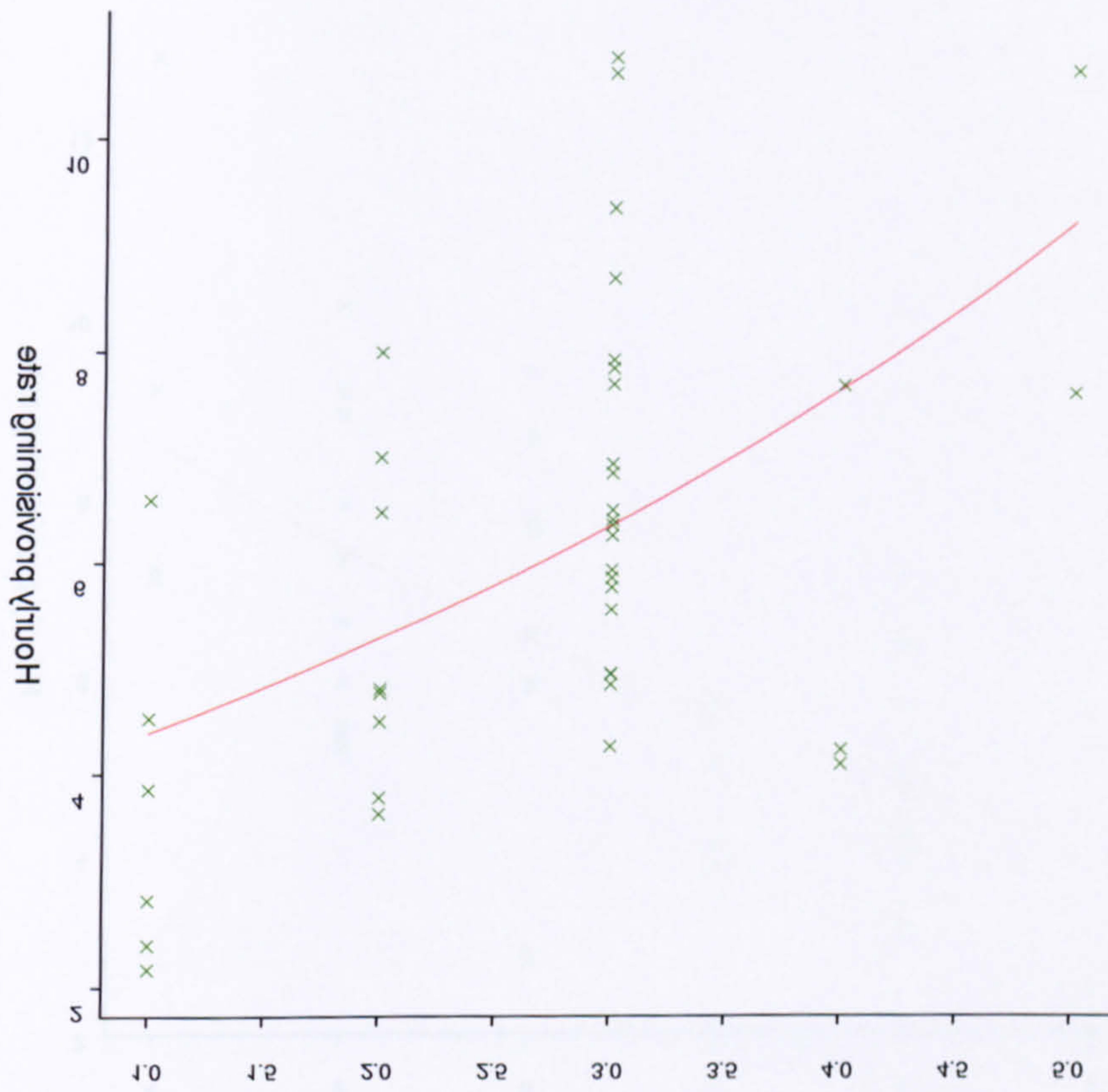
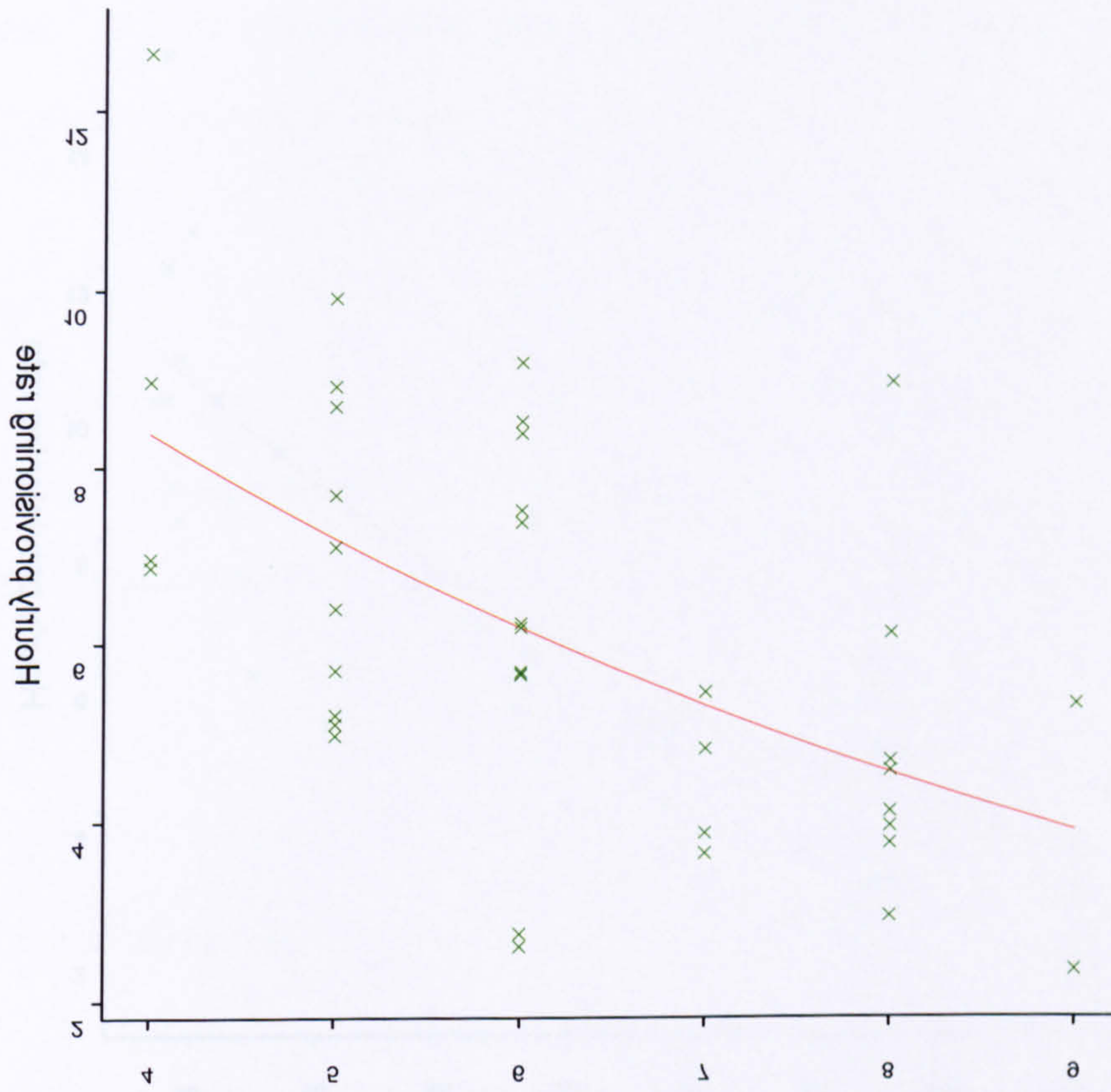


Figure 1. Predicted hourly provisioning rate in relation to brood size



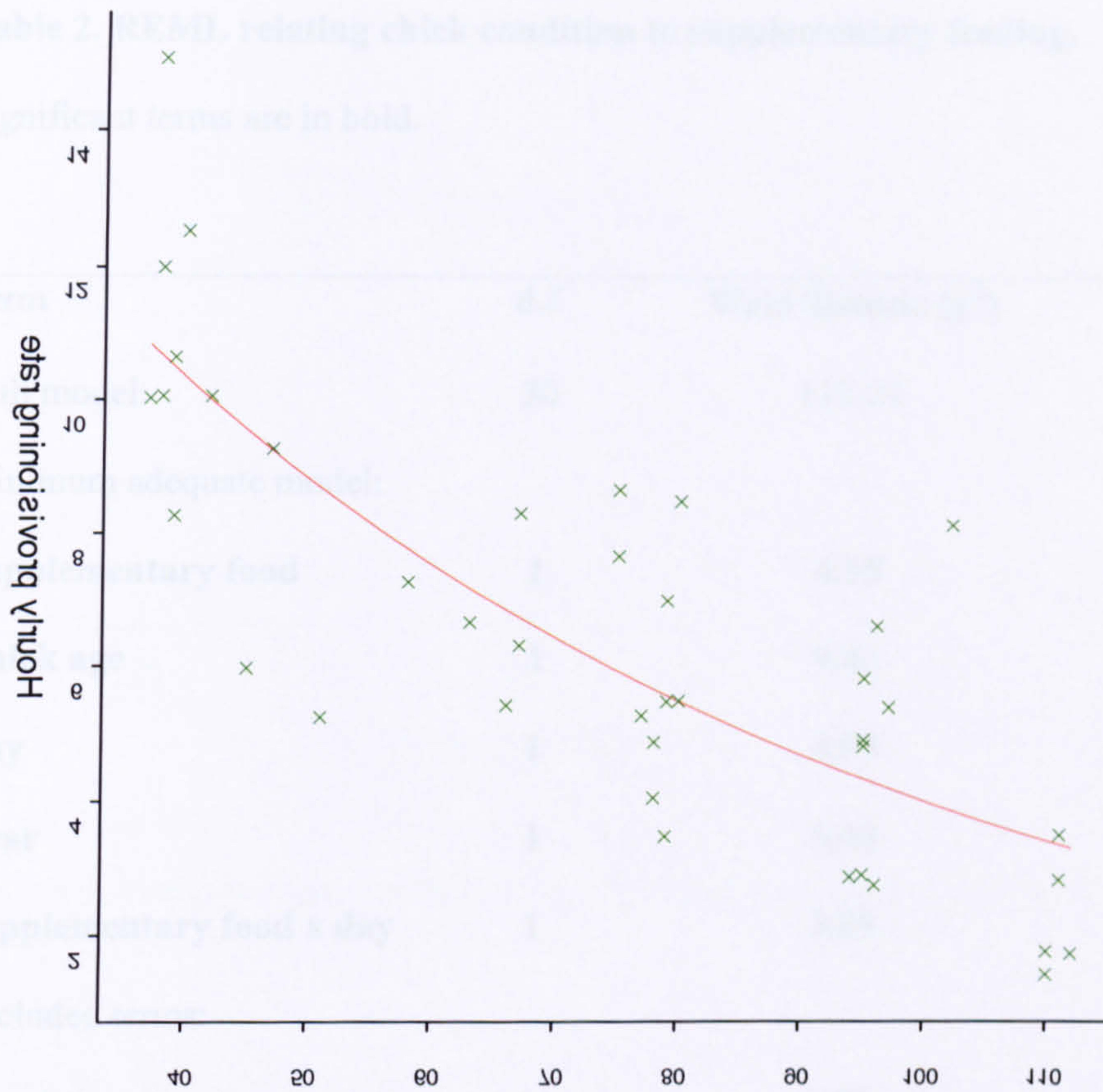


**Figure 2. Predicted hourly provision rate in relation to chick age**

**Chick condition**

Supplementary feeding was provided to the chicks in the first 10 days depending on day (table 2). The amount of supplementary feeding increased the mass of chicks daily in 2001 and 2002. Somewhat unsurprisingly, the 2 age chicks were significantly heavier (weighing more table 2). Extra feeding was provided to the chicks weighing more in 2002 than in 2001 days.





**Figure 3. Predicted hourly provisioning rate in relation to date**

### **Chick condition**

Supplementary feeding significantly affected chick mass, with the effect differing depending on day (table 2, control nests:  $n = 11$ , fed nests:  $n = 5$ ). Supplementary feeding increased the mass of chicks early in the season, but not late in the season (figure 4). Somewhat unsurprisingly, chick age had a significant effect on mass, with older chicks weighing more (table 2). Year also had a significant effect on chick mass, with chicks weighing more in 2002 than in 2003 (table 2).



**Table 2. REML relating chick condition to supplementary feeding.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	30	116.21	
Minimum adequate model:			
<b>Supplementary food</b>	<b>1</b>	<b>4.15</b>	<b>0.042</b>
<b>Chick age</b>	<b>1</b>	<b>9.43</b>	<b>0.002</b>
<b>Day</b>	<b>1</b>	<b>4.99</b>	<b>0.026</b>
<b>Year</b>	<b>1</b>	<b>5.48</b>	<b>0.019</b>
<b>Supplementary food x day</b>	<b>1</b>	<b>3.89</b>	<b>0.049</b>
Excluded terms:			
Brood size	1	1.86	0.173

Table 3. GLM relating chick growth to mean daily temperature

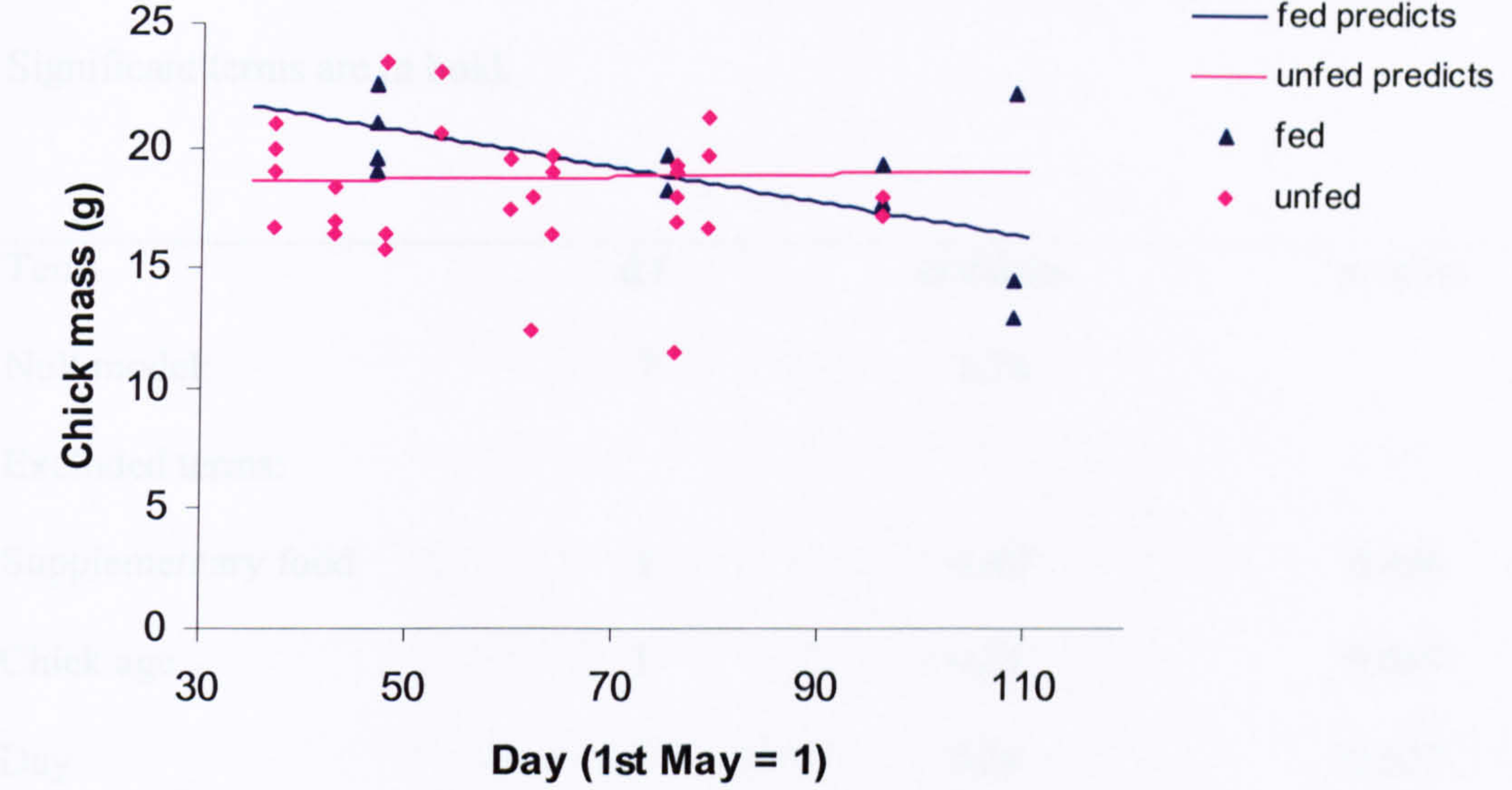


Figure 4. Predicted mass of fed and unfed chicks through the season

### Growth rate

Supplementary feeding had no effect on mean daily chick mass increase (table 3, control nests: n = 4, fed nests: n = 4).



**Table 3. GLM relating chick growth rate (in mass) to supplementary feeding.**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	7	1.74	
Excluded terms:			
Supplementary food	1	0.40	0.496
Chick age	1	0.22	0.639
Day	1	0.24	0.627
Year	1	0.63	0.506
Brood size	1	0.25	0.616

### **Brood Fates**

Looking just at nests which were found before day 4, and where chicks survived beyond day 4 (so that any effect could be possibly attributed to feeding), four out of five fed nests fledged a full brood, with the other suffering a partial brood loss. Seven out of ten control nests fledged a full brood, with two of the others suffering partial brood losses and one suffering whole brood loss.

## **Discussion**

### **Provisioning rate**

Supplementary feeding chicks had no effect on provisioning rate.

Provisioning rate increased with brood size. This has also been found for European Starlings, where increased provisioning rate and increased load size both occurred as a result of experimentally increased brood size (Wright *et al.*, 1998).

Provisioning rate decreased with increasing chick age. This is probably as older chicks are able to take more food at a time, allowing parents of older chicks to bring larger loads and make fewer visits. This is demonstrated by the fact that the mean amount of supplementary food taken per chick per day increased from 2.4g on day 4 to 4.3g on day 8. There is evidence that for Wood Warblers load size increases with chick age (Temrin *et al.*, 1997), however this was associated with increased, rather than decreased, provisioning rate.

Provisioning rate also decreased through the season. This could also be an effect of load size, as invertebrates become more abundant or larger invertebrate prey becomes available through the season so parents may be able to increase the amount of food brought back per foray. Optimal load size may depend upon distance travelled (with large loads being favoured when distance travelled is large) or food abundance (with large loads being taken when food is plentiful) (Orrians & Pearson, 1979). There is some evidence for a positive correlation between load size and distance travelled in a number of species (Blackbirds: Orrians & Pearson, 1979, House Martins, Sand Martins: Bryant & Turner, 1982, Shags: Wanless *et al.*, 1993). However, a study of Skylarks comparing foraging habits of birds nesting in different crop types showed that load sizes and provisioning rates were higher when the shortest distance was travelled (Poulsen *et al.*, 1996), this presumably being due

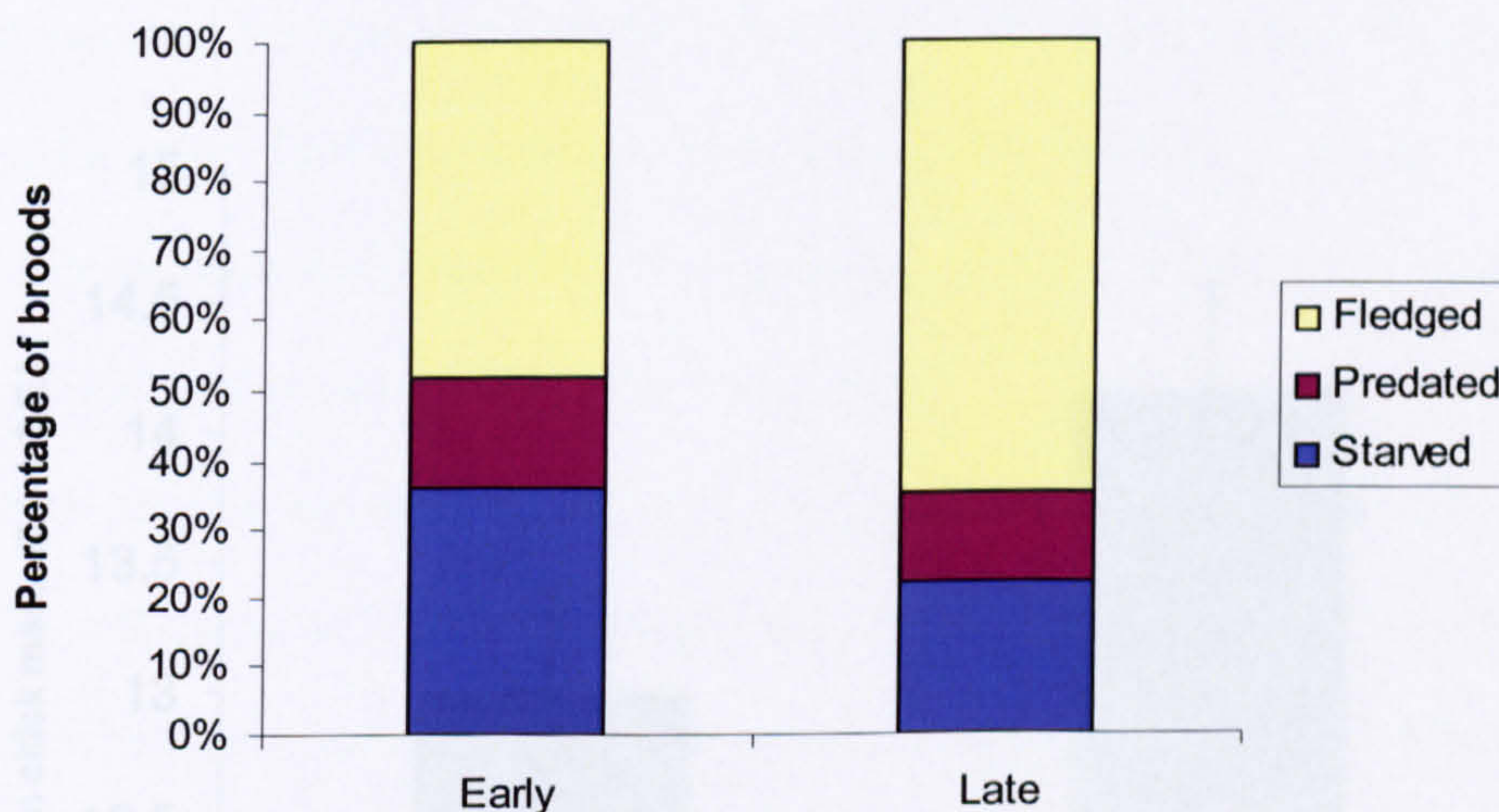
to food availability. Food availability rather than distance travelled has also been shown to be a predictor of load size in the Swallow (Bryant & Turner, 1982). Some studies have shown increased load size to be associated with increased provisioning rate (Reed Warblers: Sejberg *et al.*, 2000, European Starlings: Wright *et al.*, 1998, Wood Warblers: Temrin *et al.*, 1997, Skylarks: Poulsen *et al.*, 1996, House Finch: Stoeckl *et al.*, 2001). However, the fact that in this study Yellowhammer chick condition was increased by supplementary feeding only early in the season would suggest that chicks were receiving less food at this time, and thus we deduce that parents are bringing smaller load sizes more frequently early in the season, as invertebrate food abundance, or abundance of larger prey items, is low. Other possible explanations are that parents are having to make more frequent trips early in the season to try to compensate for the fact that chicks are losing more energy as the weather is colder, or as they are constrained as to how far they can go from the nest as they do not want to leave chicks for too long in case they chill.

### **Chick condition**

Supplementary feeding increased the mass of chicks early in the season, but not later on, when it actually appears to reduce it. However, this decrease in chick condition late in the season is due to one brood of two chicks with low masses, and there are no control broods for this late in the season. Possible reasons for the fact that supplementary food increased chick mass early in the season but not later are due to poorer weather early in the season, or that abundance of preferred invertebrate food is lower early in the season. A study of Yellowhammers in Oxfordshire found that a higher proportion of nestlings were fledged later in the season (Bradbury *et al.*, 2000). Further analysis of the Oxfordshire data shows that the number of nests suffering whole or partial brood losses as a result of starvation significantly decreased through the season (figure 5; Appendix, table 4). There was no



seasonal effect on the number of nests predated. Nest failure due to starvation and predation in British Cirl Buntings also decreases through the season, and it was suggested that the decreased predation rates were due to decreased begging as invertebrate food became more abundant, as chicks in predated nests were of poorer condition than those in successful nests (Evans *et al.*, 1997). Low abundance of Orthoptera early in the season was suggested as a possible mechanism for this (Evans *et al.*, 1997), and it is possible a similar seasonal change in invertebrate abundance or availability of a preferred large prey item is affecting the Yellowhammer chicks in this study. However, in this case it is unlikely that an increase in abundance of Orthoptera is the mechanism, as Orthoptera make up a relatively low proportion of Yellowhammer chick diet (0.23%, Moreby & Stoate, 2001).

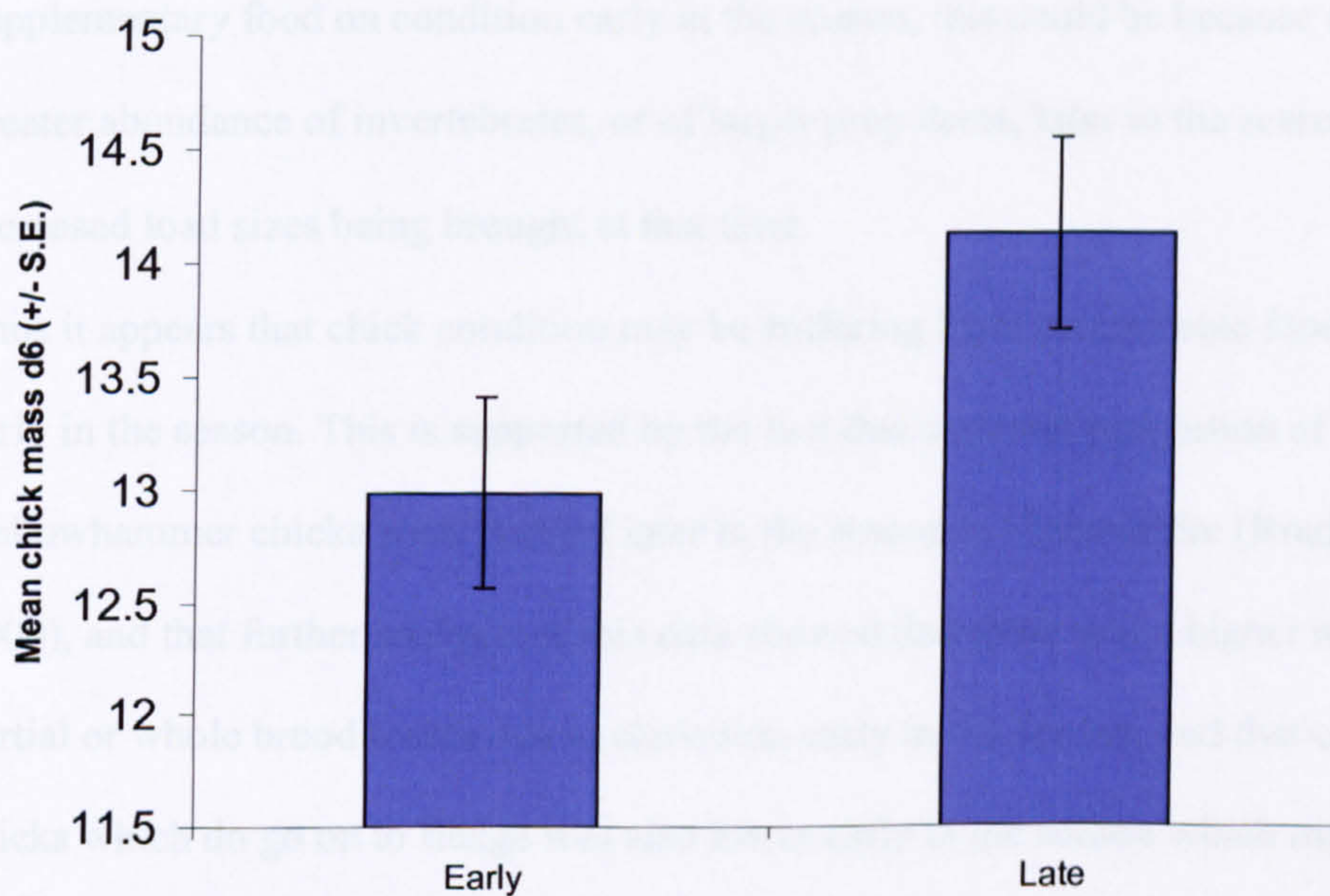


**Figure 5. Percentage of Yellowhammer broods in Oxfordshire which suffered whole or partial brood losses through starvation, whole brood losses through predation, or were successful ('early', broods which hatched before July 1<sup>st</sup> (n = 163), 'late', hatched after this date (n = 128)).**

The fact that there are increased partial and whole brood losses early in the season is unlikely to have contributed to Yellowhammer declines, however, as breeding performance per attempt has not decreased during periods of population decline (Siriwardena *et al.*,



2000). However, further analysis of the Oxfordshire data shows that chick mass on day 6 is also lower early in the season, and that this is true when nests which suffered partial or whole brood losses were excluded from the analysis (figure 6, Appendix: tables 5 & 6). Chicks which are fledged in poorer condition have lower survival rates, and thus chicks fledged early in the season may be suffering higher first-year mortality due to lower invertebrate abundance during their nestling period. A different analysis of Yellowhammer chick condition at chicks from the same areas, but in a larger number of years, found no relationship between chick condition and date (Bradbury *et al.*, 2002). This could be because the measure of condition was different to that used in this study, being the residual of a regression of mass on tarsus, rather than mass on day 6.



**Figure 6. Predicted mean d6 masses of Yellowhammers in Oxfordshire early and late in the season ('early', from broods which hatched before July 1<sup>st</sup> (n = 163), 'late', from broods hatched after this date (n = 128)).**



## **Growth rate**

Supplementary food had no effect on chick growth rate, however this could be due to the small sample size preventing an effect from being detected.

## **Conclusions**

There was no significant effect of supplementary food on provisioning rate. This could be due to the low sample size, as there was a non-significant trend for fed nests to be provisioned less. Chick mass was increased by the provision of supplementary food early in the season, but not later on. This concurs with other studies looking at Yellowhammers and Cirl Buntings which show effects of low invertebrate abundance early season.

Provisioning rate was significantly lower early in the season, given the effect of supplementary food on condition early in the season, this could be because there is a greater abundance of invertebrates, or of larger prey items, later in the season, resulting in increased load sizes being brought at that time.

Thus it appears that chick condition may be suffering from invertebrate food limitation early in the season. This is supported by the fact that a greater proportion of Yellowhammer chicks were fledged later in the season in Oxfordshire (Bradbury *et al.*, 2000), and that further analysis of this data showed that there was a higher number of partial or whole brood losses due to starvation early in the season, and that condition of chicks which do go on to fledge was also lower early in the season which may in turn lead to lower first year survival of chicks which are produced during this period.

Thus it seems that Yellowhammers are suffering from lack of invertebrate chick food early in the breeding season, and would benefit from measures to increase invertebrate abundance at this period. Chapter 3 suggests that winter oilseed rape and set-aside are relatively invertebrate rich crop types in May, with winter wheat having higher



invertebrate abundance than spring barley. Other measures which could improve breeding season conditions for Yellowhammers are provision of rough field boundaries, their preferred foraging habitat (Morris *et al.*, 2001) which are protected from excessive cutting or spray drift, and reduced pesticide inputs, particularly spring and summer insecticide applications, and also measures to increase invertebrate availability such as wider drill spacing in cereal crops and provision of bare patches created by momentarily turning of seed drills (Morris *et al.*, 2002) .

## Appendix

**Table 4. GLM relating likelihood of whole or partial brood loss through starvation to time in season (defined as ‘early’, broods which hatched before July 1<sup>st</sup>, ‘late’, hatched after this date).**

Significant terms are in bold.

Term	d.f.	deviance	p-value
Null model:	286	348.75	
Minimum adequate model:			
<b>Early/late season</b>	<b>1</b>	<b>5.99</b>	<b>0.014</b>
Excluded terms:			
Year	3	3.84	0.279
Brood size	1	0.56	0.453
Site	8	3.98	0.859

**Table 5. REML relating chick mass d6 to time in season (defined as ‘early’, broods which hatched before July 1<sup>st</sup>, ‘late’, hatched after this date) for all chicks.**

Significant terms are in bold.

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	300	877.48	
Minimum adequate model:			
<b>Early/late</b>	<b>1</b>	<b>6.61</b>	<b>0.010</b>
<b>Brood size</b>	<b>1</b>	<b>7.08</b>	<b>0.008</b>
<b>Site</b>	<b>8</b>	<b>16.37</b>	<b>0.037</b>
Excluded terms:			
Year	3	6.98	0.072

**Table 6. REML relating chick mass d6 to time in season (defined as ‘early’, broods which hatched before July 1<sup>st</sup>, ‘late’, hatched after this date) for chicks from nests which did not suffer partial or whole brood losses only.**

Term	d.f.	Wald Statistic ( $\chi^2$ )	p-value
Null model:	161	464.60	
Minimum adequate model:			
<b>Early/late</b>	<b>1</b>	<b>9.89</b>	<b>0.002</b>
<b>Site</b>	<b>8</b>	<b>19.41</b>	<b>0.013</b>
Excluded terms:			
Brood size	1	0.53	0.468
Year	3	4.05	0.256



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## Chapter 7: General Discussion

### Introduction

Many species of farmland birds have shown huge declines in numbers and range since the 1970s (Fuller *et al.*, 1995) due to agricultural intensification (Chamberlain *et al.*, 2000, Benton *et al.*, 2003). Agricultural intensification has also led to a decrease in other farmland biodiversity, such as plants and invertebrates (Campbell *et al.*, 1997, Sotherton & Self, 2000). Agricultural intensification has taken form as a suite of changes in farming practice, such as the loss of mixed farming, the switch from spring to autumn sowing of cereals and associated loss of over-winter stubbles, the switch from hay to silage, increased agrochemical input, and loss of unfarmed structures such as ponds and hedgerows (Evans *et al.*, 1995, O'Connor & Shrub, 1986).

Amongst farmland bird species, granivorous passerines have shown the worst declines (Fuller *et al.*, 1995). The breeding performance of many of these granivorous species has actually increased during periods of decline (Siriwardena *et al.*, 2000), and survival, either first-year or adult, is thought to be the predominant driver of declines (Siriwardena *et al.*, 1998, 1999). This decrease in survival has often been referred to as a decrease in 'over-winter survival'; however, this is an assumption as Common Birds Census data does not discriminate between mortality occurring in different seasons. Thus, lack of seed food during the winter is often suggested as the main cause of the declines (Peach *et al.*, 1999, Robinson & Sutherland, 1999, Donald, 1997). However, most of these 'granivorous' species feed their chicks invertebrates during the breeding season (Baillie *et al.*, 1997). Lack of invertebrate chick food has only been proved as the cause of the decline of one

species in the UK, the Grey Partridge, for whom a lack of invertebrate chick food due to the indirect effects of herbicides has led to a reduction in chick survival (Potts, 1986). Lack of invertebrate chick food has, however, been suggested as playing a role in the declines of at least three species of granivorous passerines (Skylark: Poulsen *et al.*, 1998; Cirl Bunting: Evans *et al.*, 1997; Corn Bunting: Brickle *et al.*, 2000).

It is worth noting here that the Grey Partridge has precocial young, whereas those of granivorous passerines are altricial. The 'reproductive cost' hypothesis states that investment in current reproduction by iteroparous species is made at a cost to future reproductive success and survival (Williams, 1966, Charnov & Krebs, 1974, Stearns, 1976, Ricklefs, 1981). This results in conflicting interests between what is optimal for parents to invest in current reproduction, and the level of investment which is optimal to offspring, as parents must trade-off the benefits of investment in current offspring with the potential costs to their own future reproduction and survival. The outcome of this trade-off will depend on a number of factors, including average life span of the species in question. As passerines are relatively short-lived, life-history theory predicts that this trade-off will favour the current offspring (Linden & Moller, 1989). Thus it could be that parents of granivorous passerine chicks have increased their provisioning effort and managed to absorb the decrease in invertebrate chick food which has occurred since the 1970s, at a possible cost to their own future survival and reproductive output.

This PhD aimed to investigate the relative importance of invertebrate chick food in the breeding season in causing declines of granivorous farmland birds. Unlike farmland birds, which have been monitored since the 1960s under the Common Birds Census, there are few monitoring schemes for invertebrates. Suction traps were introduced in 1964 as a method of predicting pest outbreaks in order to use pesticides more efficiently. The Stirling Suction Trap has been collecting insects daily since 1972. However, these traps are on a



variety of different habitats, and collect aerial invertebrates. Thus it is not clear how their catches relate to what is available on local farmland to a ground-feeding passerine species such as the Yellowhammer. Chapter 2 aimed to investigate this. Chapter 3 looked at how invertebrates are distributed on farmland spatially and temporally, with the aim of making recommendations for how to increase invertebrate abundance for farmland birds during the breeding season.

The rest of the PhD aimed to investigate the predictions that low invertebrate abundance may be impacting on adult survival of granivorous farmland passerines, by looking at how low invertebrate abundance may have affected Tree Sparrow and Yellowhammer populations. This was investigated firstly by looking for evidence of reproductive tradeoffs in a population of Tree Sparrows, with the assumption that these may be caused by low invertebrate abundance. Secondly, supplementary feeding experiments were conducted on Tree Sparrows and Yellowhammers, providing chicks directly with high protein food in the nest, in order to look at how low invertebrate abundance might be impacting on these populations.

### **Relating suction trap catches to farmland invertebrate abundance**

Despite the conservation importance of farmland invertebrates, and the recognised importance of long-term monitoring schemes, there is relatively little long-term national data on invertebrate abundance on farmland (see Sotherton & Self, 2000, for review), with there being little long-term data generally, and much of this being restricted to one location. Long-term monitoring schemes for insects include one for butterflies (Pollard *et al.*, 1995), moths and aphids (Woiwod & Harrington, 1994).

The first aim of this study was to look at whether data from a long-running suction trap could be used to draw conclusions about invertebrates available to farmland birds with different foraging habits.

The daily catch of a 2m high portable suction trap correlated with the catch of the Stirling suction trap. This was not very surprising, as suction trap catches have already been related to a number of breeding factors in hirundines, which are aerial feeders (Bryant, 1973, Bryant, 1975, Turner, 1980, Johnston 1990).

Given the constraints of the sampling programme (for example that G-vac samples taken over a short time period were being compared to 24 hour Stirling suction trap samples), the existence of relationships between Stirling suction trap samples and epigeal invertebrates, and the fact that there were positive relationships between invertebrates caught within fields of the most predominant crop types in the area (spring barley and pasture, which together accounted for 56% of fields) suggests that the suction trap does provide a measure of invertebrate abundance on farmland; both in the field and above it.

### **Spatial and temporal distribution of invertebrates on farmland**

Abundances of aerial invertebrates were higher in winter oilseed rape, set-aside and winter wheat than silage or spring barley, with there being more differences in April and May.

Abundance of epigeal invertebrates, caught by a vacuum sampler, were lowest early in the season. This corresponds with the fact that many species of farmland birds seem to find breeding conditions hard early in the season (Cirl Bunting: Evans *et al.*, 1997;

Yellowhammer: this thesis: chapter 6). Most differences in abundances between different crop types occurred at this time. Spring sown crops (spring oilseed rape and spring barley) had a very low invertebrate abundance early in the season (particularly May), probably due to their low sward height. Winter oilseed rape supported high numbers of invertebrates

through out the season, as did set-aside. Winter wheat was a better crop type for invertebrates early in the season than spring barley.

Within fields, uncropped margins supported 60% more invertebrates than the centres of fields. Margins next to all of the crop types examined were invertebrate rich. They also seemed to act as source for invertebrates in the field later in the season, making them important to a range of species, and not just those which preferentially forage in margins. The outer field (4m from the edge) supported more of some invertebrate orders in some crop types. Thus, recommendations of Conservation Headlands from this study would be less certain than the recommendation of extending uncropped margins, with other studies suggesting that they may be beneficial in spring sown cereal fields, but actually detrimental in winter sown cereals where the resultant denser vegetation may lead to problems of accessibility (Green *et al.*, 1994).

Recommendations from this study to increase invertebrate abundance on farmland would be firstly to increase field margin habitat, as this was by far the most invertebrate rich habitat sampled in this study. Secondly, to ensure that winter oilseed rape is maintained in the landscape after production subsidies have been phased out under reform of the Common Agricultural Policy, maintenance of set-aside also being beneficial. Areas of winter and spring sown cereals should be sown in close proximity in order to provide food throughout the breeding season, as there were indications that winter wheat may be of importance early season when invertebrates are scarce.

### **Effects of previous reproductive effort on Tree Sparrow parents and chicks**

The Tree Sparrow, *Passer montanus*, has shown one of the greatest population declines amongst farmland bird species in the UK, however, little is known about the causes of this



decline. We looked for evidence of reproductive trade-offs in a population of Tree Sparrows, both within one breeding season, and also between years. If found, such trade-offs could be evidence of invertebrate chick food limitation, particularly as the study population has year round access to supplementary seed food.

There was no evidence of reproductive trade-offs within years, instead an effect of individual quality was found. There was a non-significant trend for parents which fledged more chicks in brood 1 to also fledge more in brood 2, and parents which fledged more chicks in brood 1 fledged significantly more chicks in broods 2 plus 3. This is converse to what was found in a population of Tree Sparrows in Hungary, where adults which produced fewer than the average number of fledglings in previous broods produced more than average in broods 2 and 3 (Sasvari & Hegyi, 1993).

There was some evidence for reproductive trade-offs between years; there was a non-significant trend for parents which fledged more chicks one year to fledge fewer the next.

There was also a strong effect in one of the three years for parents which invested more to invest less the following year, with there being a milder trend in the other two years. These results could be due to birds actually having lower reproductive output in the following year, or to breeding season mortality (that is, parents having a lower reproductive output due to them dying during or between breeding attempts). Males which invested more in reproduction one year invested less the next year. Males also had a higher survival rate than females (72% as oppose to 51%). This is not uncommon amongst avian populations, and could be due to the higher reproductive investment made by females. This could also help to explain why there was more evidence for reproductive trade-offs amongst males than females, as there may be higher selective mortality of poorer quality females. The fact that there was some evidence of trade-offs when looking at reproductive output (with parents which invested more in reproduction one year investing less the next year in some

years), but none when looking at survival to the next breeding season is somewhat surprising, and could be due to the fact that there is a peak in breeding season mortality, which leads to the observed trade-offs, or because survival is too crude a measure, thereby requiring a large sample size to detect small effects; perhaps had it been possible to measure adult condition during the winter, a trade-off would have been apparent.

As this population has year-round access to supplementary seed food, these trade-offs could be due to lack of invertebrate chick food. Perhaps if conditions were easier during the breeding season high reproductive output could be maintained between years. The fact that trade-offs were found in this population, which has seed food provided, means that there may have been even more evidence of trade-offs in other populations living in harder conditions.

### **The effect of supplementary feeding Tree Sparrow chicks**

The effect that lack of invertebrate food might be having on Tree Sparrow populations was further investigated by a supplementary feeding experiment. Low invertebrate abundance could be affecting Tree Sparrow populations via chick survival or growth in the nest, first-year survival (by reducing chick condition at fledging), adult survival (by parents having to invest more effort in provisioning), or the number of breeding attempts a parent is able to make in a year. Providing a brood with supplementary food had no effect on its parents provisioning rate, reproductive output later that season, or likelihood of survival to the following breeding season. Provisioning rate of first-year birds was lower than that of older birds.

Supplementary feeding increased chick mass when the brood's parents were first-years, as first-year birds had a generally lower provisioning rate. Provision of supplementary food also increased the mass of chicks early in May, but not later in May. Chicks of first year

parents were of lower condition in early May, but not later in May. Thus, it would seem that invertebrate chick food abundance is limiting chick condition under certain conditions, such as early in May and sometimes when chicks have first-year parents. There was no difference in the incidence of whole or partial brood losses between fed and unfed nests. Chicks from early broods had a lower survival rate to the following breeding season than chicks from later broods. Supplementary feeding had no effect on the likelihood of a chick surviving to the following breeding season. This could be due to lack of statistical power, as there were effects of feeding on chick mass under certain conditions, and mass at fledging is known to relate to a chick's subsequent chances of survival for a number of species. Older parents tended to have earlier first-brood hatch dates than first-years, and this is presumably because first-years are constrained by their poor foraging ability. This suggests that low invertebrate abundance is affecting Tree Sparrow chicks, and not parents, and is having an effect on their first-year survival. The fact that provision of 27% of a chick's average daily metabolised energy had no effect on survival, whereas hatch date did, shows just how harsh conditions must be early in May.

A study of Great Tits also found that first-year laying dates were later than those of older birds, and found that they could be advanced by provision of trays of mealworms at breeding sites. It is possible that the condition and survival of chicks from early nests could be helped by provision of supplementary invertebrate food near the nest in emergencies, such as when a local extinction may be imminent. Alternatively, measures to increase invertebrate rich habitats such as beetle banks, and extensive field margins, in the vicinity of Tree Sparrow colonies could have the same effect. When conservation measures to provide nest sites and seed food for Tree Sparrows are being considered, where possible these should be established in places with high availability of chick food invertebrates early in the breeding season. An experiment at Rutland Water looking at colonisation of



different nest boxes would suggest that boxes sited close to water features are preferable (Field & Anderson, 2004).

### **The effect of supplementary feeding Yellowhammer chicks**

The Yellowhammer, *Emberiza citrinella*, is Britain's most rapidly declining farmland bird species, but the specific causes of its decline are unknown. During the period of population decline breeding performance has increased at the national scale, but there have been decreases in both first-year and adult survival.

The effect of low invertebrate chick food abundance on Yellowhammer populations was investigated by a supplementary feeding experiment. Supplementary feeding a brood had no effect on its parent's provisioning rate, although this could be due to the low sample size, as there was a non-significant trend for parents of 'fed' broods to have lower provisioning rates than those of control broods. Provisioning rate decreased with increasing chick age and also through the season, this was attributed to increased load sizes.

Supplementary feeding increased chick mass early in the season, but not later on. This is presumably as invertebrate abundance is lower or there are fewer preferred large prey items early on. Previous studies have suggested that conditions are harder for Yellowhammers early in the season, with a study in Southern England finding more Yellowhammers fledged later in the season than early on (Bradbury *et al.*, 2000). Further analysis of this data showed that this was due to more individuals starving early in the season than later on. Chick mass of these Yellowhammers was also lower early in the season, even when just looking at mass of chicks which went on to fledge. This would suggest that low invertebrate abundance early in the season is leading to decreased survival in the nest, but the lower chick masses of chicks which went on to fledge would suggest that these chicks may also have a lower first-year survival.

## **Conclusions and recommendations**

There was some evidence for reproductive trade-offs in the Tree Sparrow population, and these could be due to low invertebrate abundance. Overall, however, the supplementary feeding experiments on Tree Sparrows and Yellowhammers would seem to suggest that, contrary to predictions, low invertebrate abundance is more likely to be affecting chick condition and first-year survival than adult survival. Both experiments highlighted the importance of early breeding season conditions, with survival being lower for early first broods than late first broods for Tree Sparrows, and early season broods being more likely to starve for Yellowhammers. Supplementary feeding increased chick mass during both of these early periods; both within the first-brood for Tree Sparrows, and within the whole season for Yellowhammers. However, Tree Sparrow first-brood chicks which fledged early in May still had lower survival than chicks which fledged later, whether they were supplementary fed or not. There is some evidence to suggest that early breeding season conditions are relatively harsh for other granivorous passerine chicks in farmland bird species (Evans *et al.*, 1997), however this is contrary to what is found for other passerines such as the Great Tit, where chicks fledged later have a lower recruitment rate (Verboven & Visser, 1998) and males which fledge later also go on to have a lower lifetime reproductive success (Visser & Verboven, 1999).

In light of this, recommendations from this study to increase invertebrate abundance early in the season would be to increase field margin habitat, which was relatively invertebrate rich throughout the season, and next to all crop types. Secondly, a mixture of spring sown and winter sown cereals in close proximity may help to provide invertebrate food throughout the breeding season for farmland birds, as spring sown crops have very low invertebrate abundance early season (May) when the sward height is very low. Winter

oilseed rape and set-aside were invertebrate rich habitats, and measures to maintain winter oilseed rape in the landscape after the cessation of production subsidies under Common Agricultural Policy reforms may therefore be beneficial to granivorous farmland passerines. Where local extinctions are likely emergency measures where live invertebrate food is provided near nests could also help. When providing nest boxes and seed food for Tree Sparrows, these should, where possible, be placed near to areas of high invertebrate abundance, such as water features.

Other measures which would increase invertebrate abundance, but which were outwith the scope of this study, would be a reduction of pesticide input, especially spring and summer insecticides, and measures to improve accessibility of invertebrates, such as wider drill spacing in cereals and provision of bare patches created by momentarily turning off seed drills (Morris *et al.*, 02).



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