Studies on aspects of the ecology of some hole nesting birds

Catrina Faith Barrett

STUDIES ON ASPECTS OF THE ECOLOGY OF SOME HOLE NESTING BIRDS

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..... being a thesis presented in candidature for the degree of Master of Science in the University of Durham, 1994.

This is to certify that none of the material contained in this thesis has previously been submitted for a degree in this or any other University.

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ABSTRACT

The breeding success of four species of small, hole-nesting woodland birds, the Blue, Great and Coal Tits and Pied Flycatcher utilising nestboxes was examined. Three study areas in County Durham were selected, Hamsterley Forest (largely a plantation) and Backstone Bank and Horsleyhope Ravine, both of which are semi-natural oak woods. Some data were also collected in Kielder Forest, Northumberland. When the density of nestboxes was increased at a semi-natural woodland site Pied Flycatcher numbers increased but Blue Titi numbers did not change and the same effect was discovered in broadleaved sites in Hamsterley, however, no change in any bird species was found in the conifer areas. A significant negative relationship was found between the occupation percentage of all species and the altitude and a significant positive relationship between the coefficient of variation of the annual occupancy rate of all species and altitude. The same relationship was found for Blue Tit. Great and Coal Tit and Pied Flycatcher did not show a significant relationship between occupancy and altitude, however, Coal Tit showed a significantly negative relationship between the coefficient of variation of the occupancy and altitude, whilst Great Tit and Pied Flycatcher did not show a significant relationship. A significant negative relationship between first egg date and clutch size was found for all four species. Blue Tits were found to have a significant negative relationship between first egg date and altitude. The differences in food availability shown by invertebrate sampling partially explained between year differences in productivity.

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Michelle Bews kindly typed the thesis.

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CHAPTER ONE

INTRODUCTION

Woodland birds have attracted many research workers in the past and their studies have varied from feeding ecology (eg Gibb, 1954; Peck, 1989), surveys of singing birds to estimate breeding populations in different woodland types (eg Yapp, 1962; Watson, 1969; Simms, 1971; Moss, 1978a) to detailed studies of one or more species (eg Gibb, 1950; Kluijver, 1951; Perrins, 1963; van Balen, 1973; Dhondt et al., 1984).

Many of the detailed studies of the tits (Paridae) have been carried out as part of long-term population studies at a range of study sites in Europe. These include the Edward Grey Institute's work in Oxford, where Lack, Perrins and many others have worked; the Dutch Institute for Ecological Research where Kluijver and van Balen led the research; Dhondt and his co-workers in Belgium and von Haartman (eg 1971) and others have worked in Scandinavia. Shorter-term studies such as those by Campbell (eg 1968) in the Forest of Dean have also contributed to our knowledge of the tits and the Pied Flycatcher Ficedula hypoleuca. The majority of the breeding studies have depended upon the use of nestboxes as these facilitate access to the clutch, brood and the capture of the adult birds. The Great Tit Parus major has attracted the most research because almost all the breeding Great Tits will move into nestboxes if enough are provided, while only about two-thirds of the Blue Tits Parus caeruleus behave in this way (Perrins, 1979).

Conservation concerns about afforestation with exotic conifers centre around the loss of existing habitat such as peat bog and their characteristic breeding bird communities (Nature Conservancy Council, 1986); however, the management of these forests as a wildlife habitat has recently become an issue of interest for both foresters and conservationists and has resulted in much debate such as the Institute of Chartered Foresters' Wildlife

Management in Forests' discussion meeting at the University of Lancaster in 1987 (Jardine, 1988). This co-operative attitude was preceded by critical conservation comment on forest design such as that by Williamson (1970).

Some studies have been made on the passerines of conifer plantations. Thirty years ago serious consideration was given to the provision of nestboxes in commercial plantations in order to increase the number of broods of insectivorous birds and so reduce insect pests. Bruns (1960) was a keen advocate of this and showed that the breeding density of birds could be increased using nestboxes. Gibb and Betts (1963) examined the use of Scots Pine Pinus sylvestris and Corsican Pine Pinus nigra laricio in the Brecklands by tits all year round, some of which bred in nestboxes. They compared the feeding of the nestling tits and winter food in the different pine species with that in broadleaved trees. Many recent studies have involved censusing songbird populations in plantations (eg, Moss, 1978b; Bibby et al., 1985) and whilst these have indicated that a diversity of birds may occur in conifer plantations, few have examined individual breeding performances or compared them with broadleaved woodlands. Currie and Bamford (1982) carried out some experimental work in North Wales in plantations. The nestboxes that they erected in Sitka Spruce Picea sitchensis did not attract many breeding birds but those in broadleaves and larch Larix sp. did successfully attract birds, especially Pied Flycatchers.

This study investigates some of the passerines living in two large upland forests (Kielder and Hamsterley), the small hole nesting birds Great Tit, Blue Tit, Coal Tit Parus ater and the migratory Pied Flycatcher. It examines their breeding success and productivity, using nestboxes. Data from two semi-natural ancient woodland sites in County Durham (Horsleyhope Ravine and Backstone Bank) are compared with the results from the plantations.

CHAPTER TWO

STUDY SITES AND METHODS

2.1 Introduction

During the breeding season, studies of small hole nesting birds, breeding in nestboxes were made at Hamsterley Forest (1985-91), Backstone Bank Wood and Horsleyhope Ravine (1988-91) in County Durham. Data were also collected from nestbox studies in Kielder Forest, Northumberland (1986-90). The locations of these study areas are shown in Figure 2.1 and details of the areas given later in this chapter. Boxes were erected at a height of 3m with the entrance hole facing east.

2.2 Hamsterley Forest

Hamsterley Forest is a Forestry Commission plantation near Barnard Castle, County Durham (grid reference: NZ 060290). It is approximately 2000 ha in size and its altitude ranges from 150 to 430m above sea level. The higher ground is largely planted with conifers, with Sitka Spruce being the most frequent, but the lower ground includes some mixed plantations and some areas of almost pure broadleaved trees.

Records exist of a nestbox scheme in the forest from 1952, the boxes were then situated almost only along the becks which run through the forest (Kime, 1964). The bird species were the same as they are now but in different proportions, generally there were more Redstarts then than at present, more Great than Blue Tits and large numbers of Coal Tits. The present scheme was started in 1985 with 11 sites (separate groups of nestboxes in distinct blocks of woodland/plantation). Figure 2.2 shows the location of all 30 eventual sites. In the first two years, boxes were largely sited in

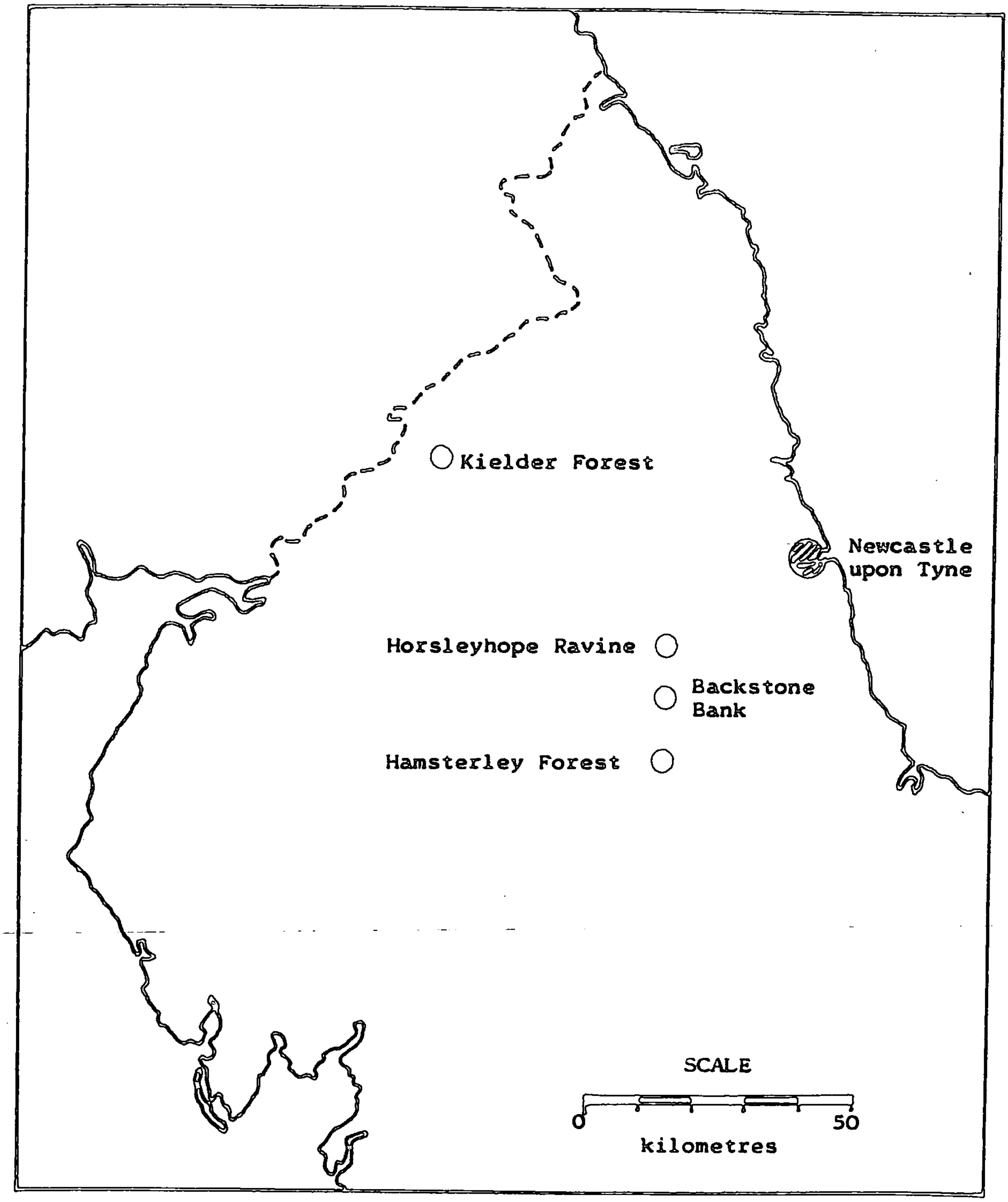


Figure 2.1: Location of study areas.

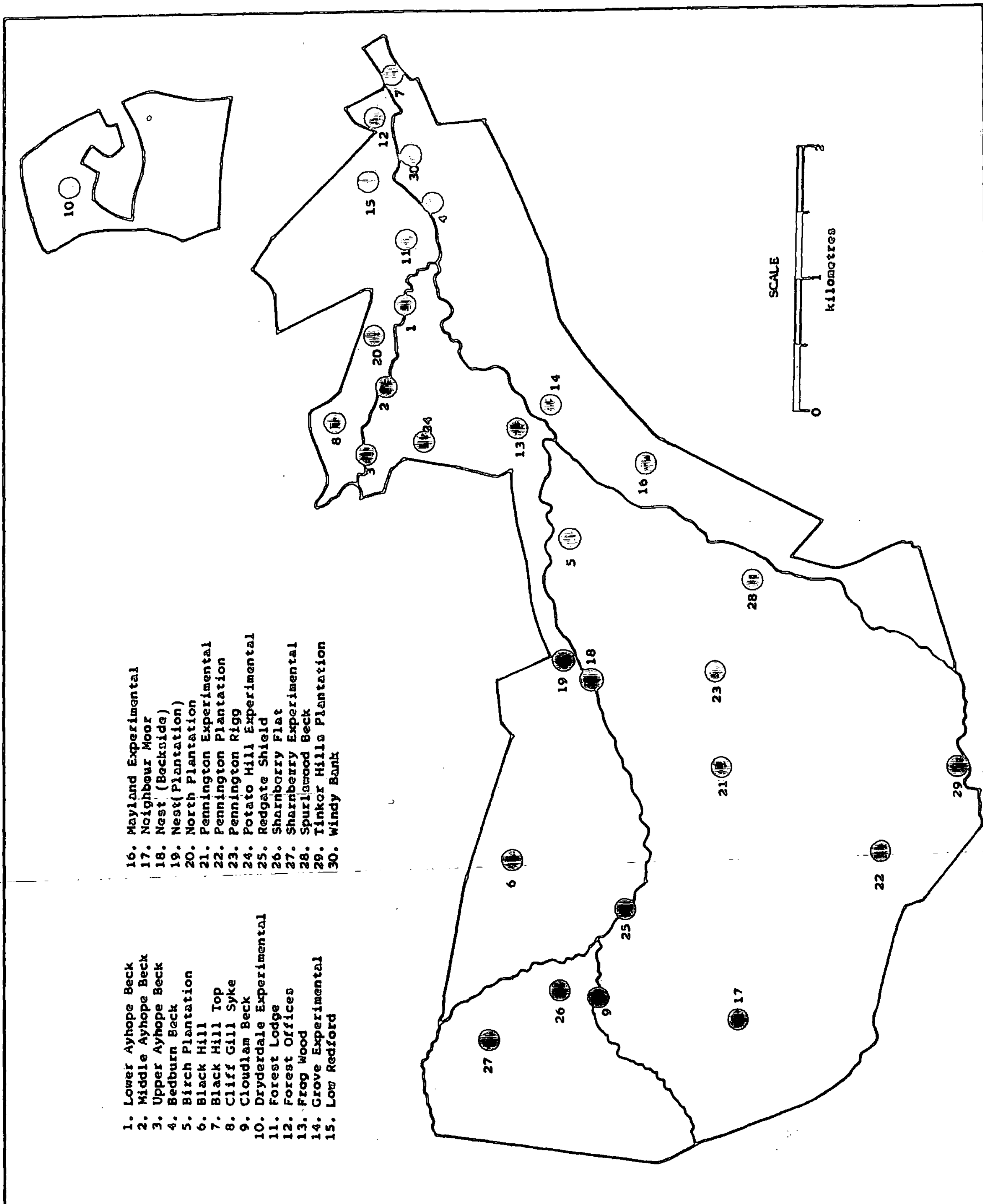


Figure 2.2: Location of study sites within Hamsterley Forest, County Durham.

what appeared to be 'good' areas for birds, ie mostly in the lowland part of the forest and generally in broadleaved trees and along becksides. As the scheme has progressed, it has extended to include sites on the higher ground along becksides and in conifer blocks. Table 2.1 shows the number of (small hole) boxes available in each breeding season from 1985-91 in the forest and the number and percentage of these which were occupied.

By 1990 there were 30 sites with nestboxes and for some statistical comparisons these have been divided into five categories with three sites remaining which fail to fit into the definitions of any of the categories and/or are distinct in some way. The categories and sites are outlined below.

2.2.1 Hamsterley - Categories and Sites

The date in brackets following the site name, in the list below, is the first breeding season in which boxes were available at that site. Several of the sites have been extended or the density of boxes increased since this initial breeding season. Table 2.2 gives an outline description of the sites including percentage of broadleaved trees, size of site, final density of nestboxes and the mean occupation percentage at that density. The nestboxes varied in final density (density established following the expansion in nestbox numbers at each site) from 0.8 to 8.8 boxes/ha with a mean density of 3.5 boxes/ha. Further details of the sites, including grid references, are given in the Appendix.

Table 2.1

Small hole nestboxes available in Hamsterley Forest during the breeding seasons 1985-91 and the number and percentage of these which were occupied.

YEAR							
	1985	1986	1987	1988	1989	1990	1991
Number of boxes	111	220	302	362	362	456	438
Boxes occupied	50	52	88	162	124	181	193
% boxes occupied	45	24	29	45	34	39	44

Table 2.2

Outline description of the Hamsterley sites including size in hectares, percentage broadleaves (established in 1991), density of nestboxes per hectare, mean occupation percentage and number of boxes.

Name of Site	Size (ha)	% Broadleaves	Density of Nestboxes/ha	Mean % Occupation	Number of Nestboxes
Ayhope Beck Lower	4	10.9	1.8	61.9	7
Ayhope Beck Middle	5.4	4.4	1.7	44.0	9
Ayhope Beck Upper	4.1	5.3	2.2	25.8	9
Bedburn Beck	4.4	13.5	2.7	66.7	12
Birch Plantation	4.0	0	5.0	10.0	20
Black Hill	2.0	0	5.0	6.7	10
Black Hill Top	2.6	65.2	7.3	64.7	19
Cliff Gill Syke	3.5	1.1	4.0	15.5	14
Cloudlam Beck	3.7	8.7	2.7	18.0	10
Dryderdale	2.5	0	4.0	60.0	10
Forest Lodge	1.3	95.7	5.4	53.6	7
Forest Offices	2.4	100	3.8	58.3	9
Frog Wood	4.7	69.0	2.3/4.5*	77.3/66.7*	11/21*
Grove	2.5	0	4.0	35.0	10
Low Redford Wood	18.9	64.0	1.6/1.6-4.2*	91.7/77.0*	30/50*

Table 2.2 (Continued)

Name of Site	Size (ha)	% Broadleaves	Density of Nestboxes/ha	Mean % Occupation	Number of Nestboxes
Mayland	2.5	0	4.0	15.0	10
Neighbour Moor	3.9	0	3.6	9.5	14
Nest (beckside)	11.6	8.0	0.8	38.9	9
Nest (plantation)	2.0	0	3.0	16.7	6
North Plantation	8.5	42.4	4.5	50.8	38
Pennington	2.5	0	4.0	25.0	10
Pennington Plantation	4.8	97.2	4.2	21.7	20
Pennington Rigg	3.4	0	2.9/5.9*	15.0/10.0*	10/20*
Potato Hill	2.5	0	4.0	40.0	10
Redgate Shield	12.0	9.4	2.4	22.6	29
Sharnberry Flat	3.5	0	2.9/5.4*	23.3/21.1*	10/19*
Sharnberry	2.5	0	4.0	5.0	10
Spurlswood Plantation	3.2	98.5	8.8	20.3	28
Tinker Hills Plantation	6.4	87.4	2.0	44.6	13
Windy Bank Wood	1.7	19.9	2.9	80.0	5

*Note Figures show before/after the experimental increase in nestbox density in certain sites (Section 2.7)

a. Low Altitude Sites with a Large Broadleaved Element

These sites vary between 150 and 200m with a mean box altitude of 185m.

Forest Lodge (1985)

Forest Offices (1985)

Frog Wood (1988)

Low Redford Wood (1987)

North Plantation (1985)

b. Low Altitude Beckside Sites

These sites include a narrow band of scattered broadleaves along becksides within the forest. The surrounding crop trees are coniferous. These sites vary in altitude between 175 and 210m, with a mean box altitude of 186m.

Ayhope Beck Lower (1985)

Ayhope Beck Middle (1985)

Ayhope Beck Upper (1985)

Bedburn Beck (1985)

Cliff Gill Syke (1985)

Nest Plantation (1985)

Windy Bank Wood (1985)

c. High Altitude Beckside Sites

These sites are as (b) but at a higher altitude, varying between 260 and 275m, with a mean box altitude of 264m.

Cloudham Beck (1987)

Redgate Shield (1987)

Tinker Hills Plantation (1987)

d. High Conifer Sites

These sites are largely on the higher ground within the forest, altitudes vary between 225m and 360m, with a mean box altitude of 307m.

Birch Plantation (1986)

Black Hill (1986)

Neighbour Moor (1988)

Nest Plantation (1986) an extension of the Low Beckside site

Pennington Rigg (1988)

Sharnberry Flat (1987)

e. Conifer Sites Erected for an Experiment

These sites were all erected in 1990 as part of an experiment which has not been included within this study. The altitude varies between 185m and 270m, with a mean box altitude of 273m.

Dryderdale (1990)

Grove (1990)

Mayland (1990)

Pennington (1990)

Potato Hill (1990)

Sharnberry (1990)

f. Remaining Sites

Black Hill Top (1985) a remnant of ancient woodland with non-native tree species introduced.

Pennington Plantation (1986) Beech plantation at high altitude (365m), over 100 years old.

Spurlswood Plantation (1986) mixed plantation with very high wood ant Formica lugubris density.

2.3 Backstone Bank Wood

Backstone Bank Wood lies about 5km from Wolsingham, on a west-facing slope above Tunstall Reservoir (NZ 068414). It is an ancient, largely oak, woodland and has been declared a Site of Special Scientific Interest on botanical grounds by the Nature Conservancy Council for England, who lease the site. Nestboxes were erected here for the 1988 breeding season. Nestboxes were established at 2.5 boxes/ha. Table 2.3 shows the number of nestboxes available in each breeding season and the number and percentage occupied at Backstone Bank Wood, Co Durham. The site altitude is 230m.

2.4 Horsleyhope Ravine

Horsleyhope Ravine lies approximately 3km south west of Consett, County Durham on a west-facing slope above Horsleyhope Burn (NZ 063485).

It is an ancient, largely oak, woodland and has been declared a Site of Special Scientific Interest on botanical grounds by the Nature Conservancy Council for England, who own the site. Nestboxes were erected here for the 1988 breeding season. Nestboxes were originally at 3.2 boxes/ha and later increased (see section 2.7 for details) to 6.3 boxes/ha. Table 2.4 shows the number and percentage of boxes occupied. The site altitude is 200m.

Table 2.3

The number of nestboxes available in each breeding season and the number and percentage occupied in Backstone Bank Wood, County Durham.

	YEAR			
	1988	1989	1990	1991
Number of boxes	20	20	20	20
Boxes occupied	19	17	18	19
% boxes occupied	95	85	90	95

Table 2.4

The number of nestboxes available in each breeding season and the number and percentage of boxes occupied at Horsleyhope Ravine, County Durham.

	YEAR			
	1988	1989	1990	1991
Number of boxes	20	20	40	40
Boxes occupied	18	19	26	35
% boxes occupied	90	95	65	88

2.5 Kielder Forest

Kielder Forest is a massive (50,000 ha), largely conifer forest in Northumberland. Nestboxes were erected in the spring of 1986 throughout the Forest and the success and occupation of 491 boxes was monitored by the Forest Rangers and the results used for this study. The forest district is sub-divided into three areas and boxes were erected in each: Kielder (220 boxes), Falstone (121 boxes) and Redesdale (150 boxes). These nestboxes were then divided into sites around each area by the ranger who would be monitoring them. They were erected in the places that the rangers felt were most likely to attract birds and so a high proportion of the sites were in broadleaved trees, except in Redesdale which is largely coniferous and where large, mature conifers were chosen. The nestboxes were generally spaced randomly within each site and the density of the nestboxes is unknown. Table 2.5 shows the number of nestboxes available in each breeding season up until 1990 and the number and percentage occupied in Kielder Forest, Northumberland. The occupancy is far lower than that in the other areas. This may be due to the habitat and food availability and is discussed further in Chapter 4.

2.6 Data Collected from Nestboxes

The boxes were monitored during the breeding season and the following data collected whenever possible (except at Kielder where only occupancy, numbers of eggs, chicks and fledged young data were collected and some of the chicks ringed):

Table 2.5

The number of nestboxes available in each breeding season and the number and percentage occupied in Kielder Forest, Northumberland.

	YEAR				
	1986	1987	1988	1989	1990
Available boxes	491	491	491	491	491
Boxes occupied	56	72	98	83	62
% boxes occupied	11	15	20	17	13

a. <u>Occupancy</u>

The number and percentage of nestboxes used by all species of birds attempting to breed (building a nest and laying at least one egg) in each year. Measurements used in the results include:

Occupation percentage - mean percentage of nestboxes occupied over a period of years with the same number of nestboxes available at a site; thus some sites may have more than one occupation percentage as the number of nestboxes at a site may have been at two different levels over the time of the study (this means that each figure represents the occupancy at a certain nestbox density).

The coefficient of variation of the occupation percentage is calculated by dividing the annual occupation percentages into their standard deviations and multiplying the result by 100 to produce percentages. This figure indicates the degree of variation between years at the same site with the same number of nestboxes available. These figures were produced for all and for individual species.

b. <u>The Date of Laying of The First Egg of Each Clutch</u>

The first egg date. The clutch was observed when incomplete and as one egg is generally laid each day, generally in the early morning, it was then possible to calculate the date on which the first egg of the clutch was laid.

c. Adult female tits and Pied Flycatchers were caught on their full clutch, about half way through incubation. Redstarts were not caught as they have a reputation for deserting their nests when disturbed. Any existing ring number was noted or the bird ringed. Tits were aged as one year old birds or adults using plumage characteristics (Svensson, 1984).

Pied Flycatchers cannot be aged at this time of the year.

d. The number of eggs in the full clutch was recorded.

e. The number of chicks hatching was noted.

f. The chicks were ringed.

g. After the young had finally left the nest, it was checked for dead chicks (dead chicks were noted and removed when seen during earlier visits) and then the old nest cleared from the box and thrown to the ground to reduce the retention of nest parasites.

A number of correlations are made (in chapter 3) between these data and other factors. The percentage of variation described by a particular correlation can easily be explained by squaring the correlation coefficient to get the coefficient of determination and multiplying it by 100.

2.7 Experiments to Investigate the Effects of Nestbox Density

In 1990 the density of boxes in several sites was increased. The number of nestboxes at Horsleyhope Ravine was doubled and the density increased from 3.2 to 6.3 boxes/ha. Four sites at Hamsterley were also involved:-

a. Low Redford

The density in a block of nestboxes in the centre of Low Redford was increased from 1.6 to 4.2 boxes/ha and the number of nestboxes tripled. The remaining 60% of the area remained at its previous spacing of 50m between boxes. Low Redford was one of the highest occupancy sites before this experiment. In 1988 all of the boxes had been occupied and occupancy was always above 70%.

b. Frog Wood

Another high occupancy site where the number of boxes was doubled and density increased from 2.3 to 4.5 boxes/ha.

c. Sharnberry Flat

A high altitude conifer site with low occupancy, the number of boxes was doubled and density increased from 2.9 to 5.4 boxes/ha.

d. Pennington Rigg

A high altitude conifer site with low occupancy, where the box number was doubled and the density increased from 2.9 to 5.9 boxes/ha.

2.8 Collection of Invertebrates

Between the 26 April and 21 July 1990, invertebrates were collected from six tree species:-

Oak Quercus spp

Birch Betula pubescens

Alder Alnus glutinosa

Scots Pine Pinus sylvestris

Sitka Spruce Picea sitchensis

European Larch Larix decidua

Fifteen sub-samples were collected from each tree species at approximately ten-day intervals (or as close to that time as weather allowed). Each sub-sample was taken from a terminal branch, 67cm (approximately) of which was enclosed in a muslin bag (52 x 42cm), which was closed with a drawstring and then cut from the tree. Samples were collected at approximately 5m above the ground, from a ladder, except for Alder and Birch which were far smaller trees and were sampled at 3m. The invertebrates were then killed with ethyl acetate before the bags were opened and the invertebrates separated from the plant material by hand. The invertebrates were then stored in 70% ethyl alcohol. Sampling took place on eight dates for each tree species. At a later stage the invertebrates were sorted into size categories and identified to order and sometimes further. In 1989, a 25 June sample was taken from three tree species (15 sub-samples of each) and two of these species were amongst those used in 1990 and so were available for comparison. In 1991, samples were collected on 28 and 29 June and these were taken from all six tree species for comparison with the 1990 samples.

CHAPTER 3

BREEDING BIOLOGY

3.1 Occupation of Nestboxes

There are considerable variations in both numbers and proportions of species of birds using the nestboxes between different woods, sites and years and these basic data are shown in Tables 3.1-3.4 which are further analysed below. Table 3.1 shows the overall occupancy levels and bird species at Hamsterley Forest over the period of the study (1985-91), Tables 3.2-3.4 show the same information for Kielder Forest (1986-90), Horsleyhope Ravine and Backstone Bank Woods (1988-1991) respectively. Table 3.1 shows the increasing number of boxes at Hamsterley and the variation in the occupancy rates during the study, with a minimum in 1986 (following a cold winter) for all species except Pied Flycatcher. Table 3.2 reveals the very low occupancy rates for Kielder with a surprisingly low proportion of Coal Tit (2%) and high proportion of Great Tit (54%). Tables 3.3 and 3.4 show the semi-natural woodland sites, Backstone Bank and Horsleyhope Ravine, had high occupancy levels. Pied Flycatchers only occurred in numbers once the number of nestboxes at Horsleyhope Ravine had been doubled. Figures 3.1-3.4 present the percentage of species by years for Hamsterley, Kielder, Horsleyhope Ravine and Backstone Bank, respectively. The increase in Pied Flycatchers at Horsleyhope Ravine, following the increase in the number of nestboxes, can clearly be seen when compared with Backstone Bank where levels stayed at similar level without an increase in density of boxes. The very irregular occurrence of Pied Flycatcher in Kielder, compared with the other areas is very noticeable. Figure 3.5 gives the numbers of the five main bird

Table 3.1 Nest Box Occupancy at Hamsterley Forest - 1985-91

	YEAR						
	1985	1986	1987	1988	1989	1990	1991
Boxes available	111	220	302	362	362	458	441
Number occupied	50	52	88	*162	124	*181	*194
% occupied	45.1	23.6	29.1	44.8	34.3	39.0	44.0
Number Blue Tit	20	15	38	89	54	76	83
% of occupied	40.0	28.9	43.2	54.9	43.6	42.0	42.8
% of available	18.0	6.8	12.6	24.6	14.9	16.6	18.8
Number Great Tit	20	12	13	27	14	21	31
% of occupied	40.0	23.1	14.8	16.7	11.3	11.6	16.0
% of available	18.0	5.5	4.3	7.5	3.9	4.6	7.0
Number Coal Tit	0	3	10	7	12	22	21
% of occupied	0	5.8	11.4	4.3	9.7	12.2	10.8
% of available	0	1.4	4.3	1.9	3.3	4.8	4.8
Number Pied Flycatcher	10	19	23	28	33	48	51
% of occupied	20.0	36.5	26.1	17.3	26.6	26.5	26.3
% of available	9.0	8.6	7.6	7.7	9.1	10.5	11.6
Number Redstart	0	2	4	9	11	12	7
% of occupied	0	3.9	4.6	5.6	8.9	6.6	3.6
% of available	0	0.9	1.3	2.5	3.0	2.6	1.6

Notes

* In 1988, 1990 and 1991 additional species nested in the nestboxes; in 1988 a Treecreeper and a Nuthatch, in 1990 two Treecreepers and in 1991 a Nuthatch.

% of occupied: percentage of the occupied boxes that were occupied by this species.

% of available: percentage of the total boxes available that were occupied.

Table 3.2 Nestbox Occupancy at Kielder Forest 1986-1990

	YEAR				
	1986	1987	1988	1989	1990
Boxes available	491	491	491	491	491
Boxes occupied	56	72	98	83	62
% occupied	11.4	14.7	20.0	16.9	12.6
Number Blue Tit	14	20	44	35	21
% of occupied	25.0	27.8	44.9	42.2	33.9
% of available	2.9	4.1	9.0	7.1	4.3
Number Great Tit	37	47	47	31	32
% of occupied	66.1	65.3	48.0	37.3	51.6
% of available	7.5	9.6	9.6	6.3	6.5
Number of Coal Tit	0	2	0	2	3
% of occupied	0	2.8	0	2.4	4.8
% of available	0	0.4	0	0.4	0.6
Number Pied Flycatcher	5	2	1	4	4
% of occupied	8.9	2.8	1.0	4.8	6.5
% of available	1.0	0.4	0.2	0.8	0.8
Number of Redstart	0	1	1	8	1
% of occupied	0	1.4	1.0	9.6	1.6
% of available	0	0.2	0.2	1.6	0.2
Number of unidentified	0	0	5	3	1
% of occupied	0	0	5.1	3.6	1.6
% of available	0	0	1.0	0.6	0.2

% of occupied: percentage of the occupied boxes occupied by this species.

% of available: percentage of the total available boxes occupied by this species.

Table 3.3 Nestbox Occupancy at Horsleyhope Ravine 1988-1991

	YEAR			
	1988	1989	1990	1991
Boxes available	20	20	40	40
Boxes occupied	18	19	26	35
% occupied	90.0	95.0	65.0	87.5
Number Blue Tit	14	14	12	17
% of occupied	77.8	73.7	46.2	48.6
% of available	70.0	70.0	30.0	42.5
Number Great Tit	1	0	0	3
% of occupied	5.6	0	0	8.6
% of available	5.0	0	0	7.5
Number Coal Tit	0	1	0	0
% of occupied	0	5.3	0	0
% of available	0	5.0	0	0
Number of Pied Flycatcher	3	4	14	15
% of occupied	16.7	21.1	53.8	42.9
% of available	15.0	20.0	35.0	37.5

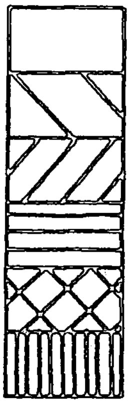
% of occupied: percentage of occupied boxes occupied by this species.

% of available: percentage of the total available boxes occupied by this species.

Table 3.4 Nestbox Occupancy at Backstone Bank 1988-1991

	YEAR			
	1988	1989	1990	1991
Boxes available	20	20	20	20
Boxes occupied	19	17	18	19
% occupied	95.0	85.0	90.0	95.0
Number Blue Tit	16	12	14	15
% of occupied	84.2	70.6	77.8	79.0
% of available	80.0	60.0	70.0	75.0
Number Great Tit	1	1	1	1
% of occupied	5.3	5.9	5.5	5.3
% of available	5.0	5.0	5.0	5.0
Number of Pied Flycatcher	2	4	3	3
% of occupied	10.5	23.5	16.7	15.8
% of available	10.0	20.0	15.0	15.0

Key to figures 3.1 - 3.4



Blue Tit

Great Tit

Coal Tit

Pied Flycatcher

Redstart

Other species (Treecreeper and Nuthatch)

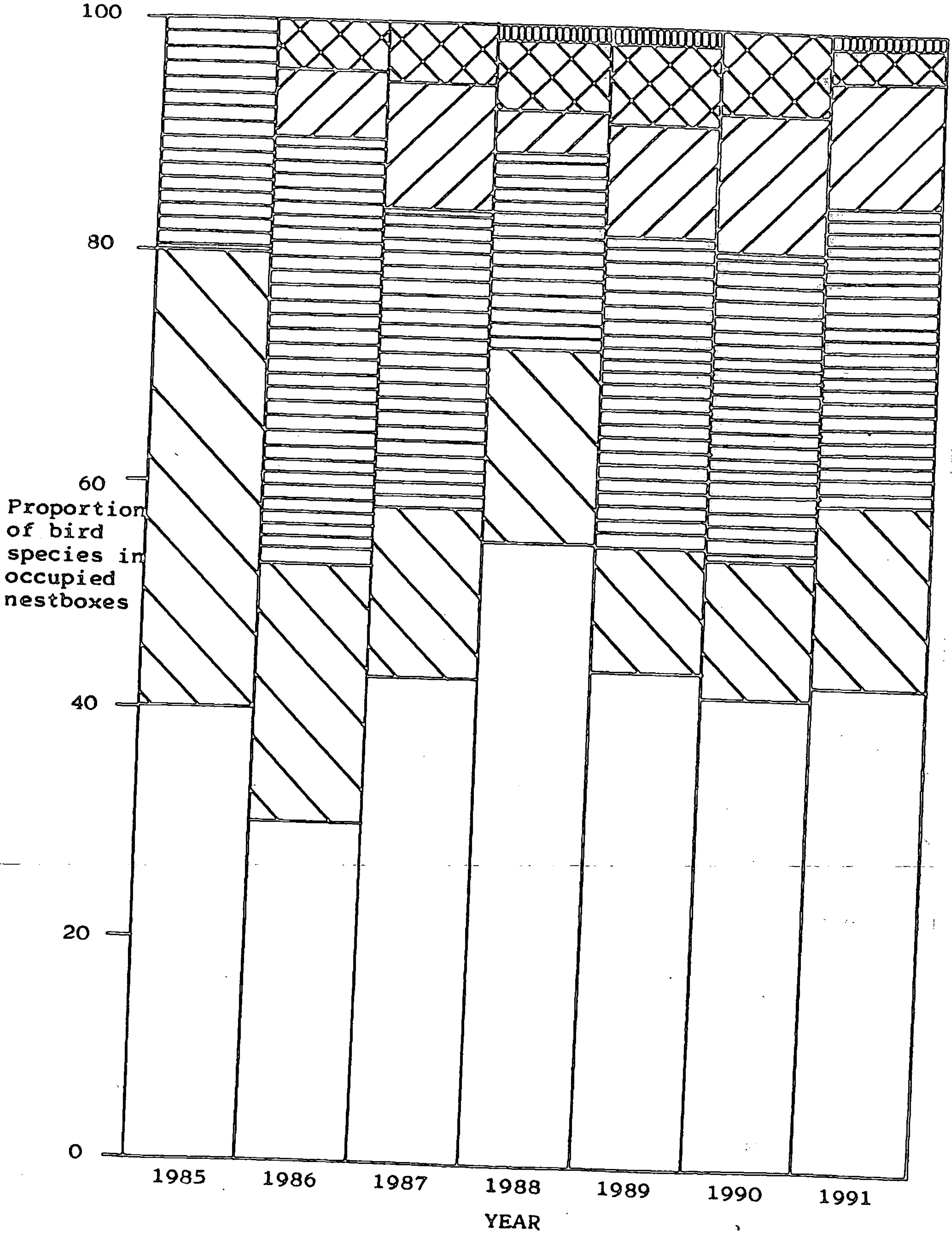


Figure 3.1: The proportion of each bird species in occupied nestboxes in Hamsterley Forest, County Durham, 1985-1991.

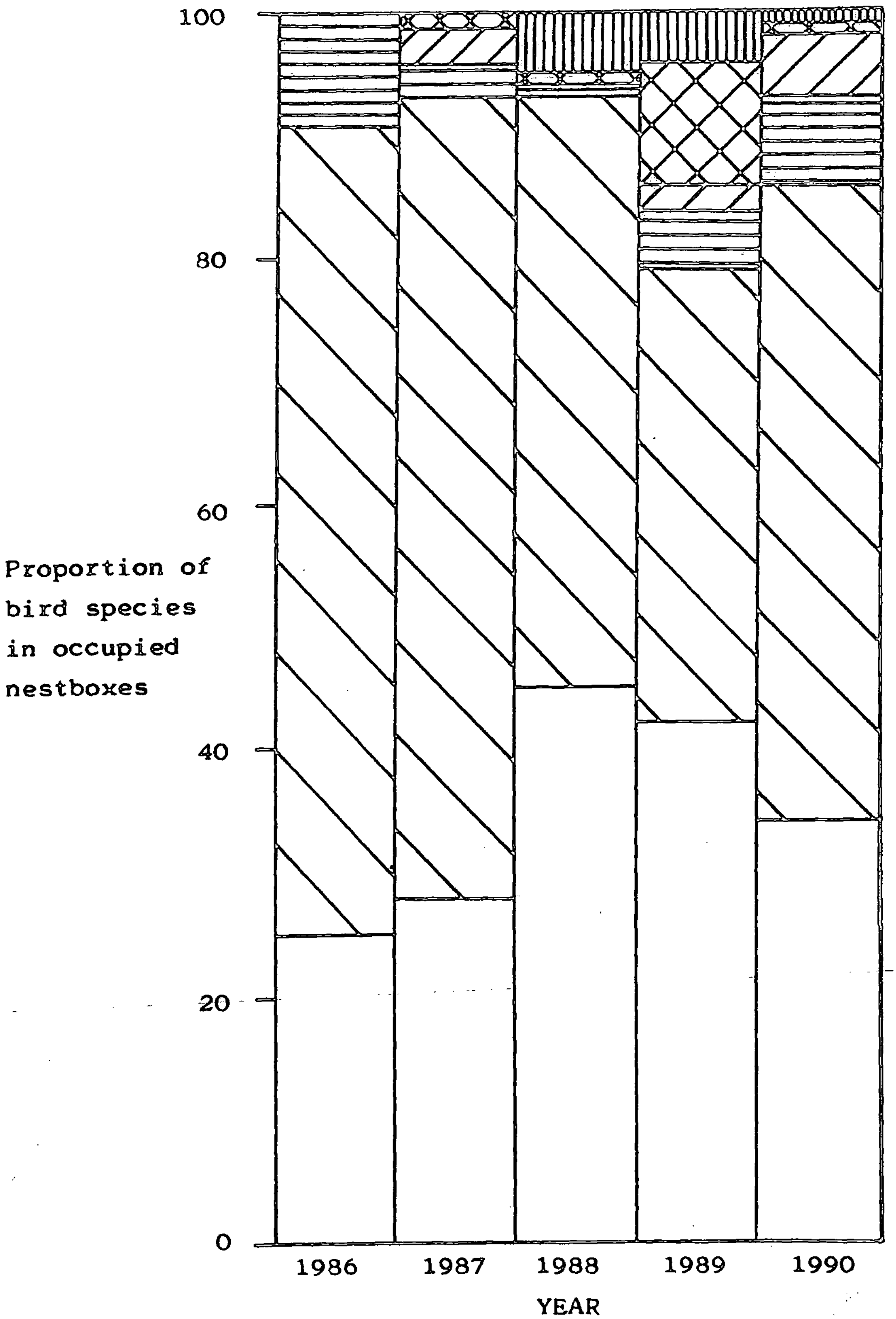


Figure 3.2: The proportion of each bird species in occupied nestboxes in Kielder Forest, Northumberland, 1986–1990.

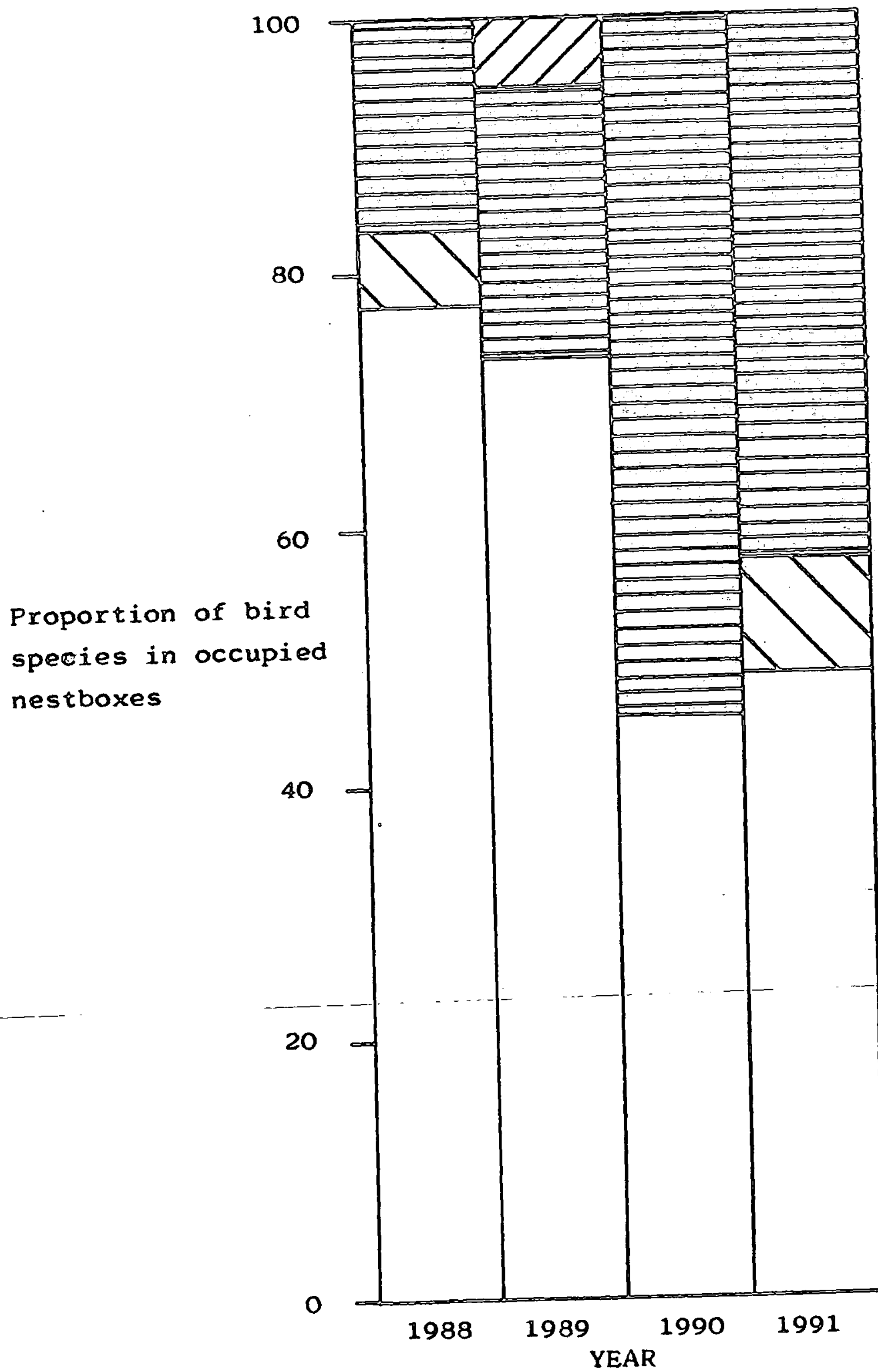


Figure 3.3: The proportion of each bird species in occupied nestboxes in Horsleyhope Ravine, County Durham, 1988-1991.

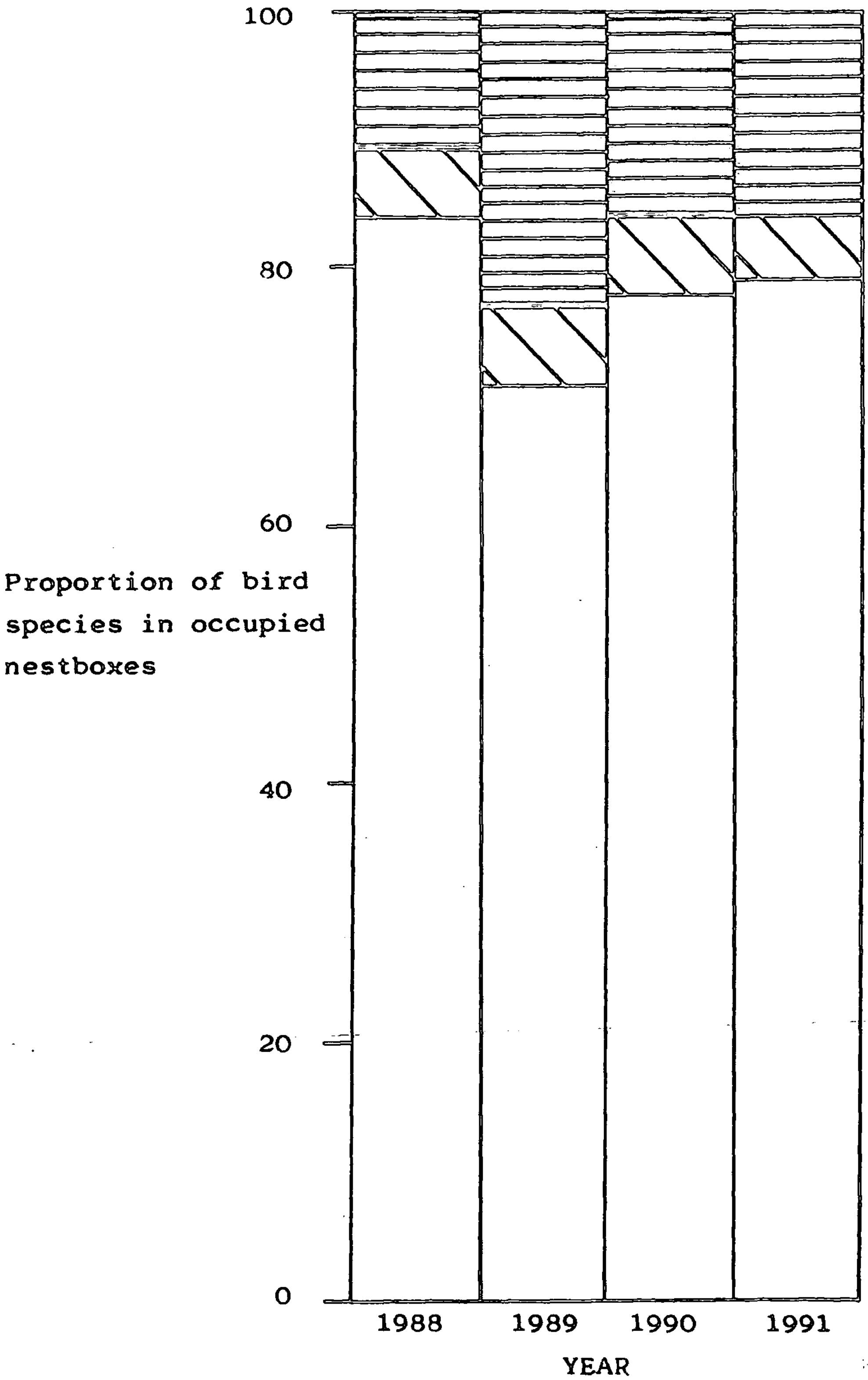


Figure 3.4: The proportion of each bird species in occupied nestboxes in Backstone Bank, County Durham, 1988-1991.

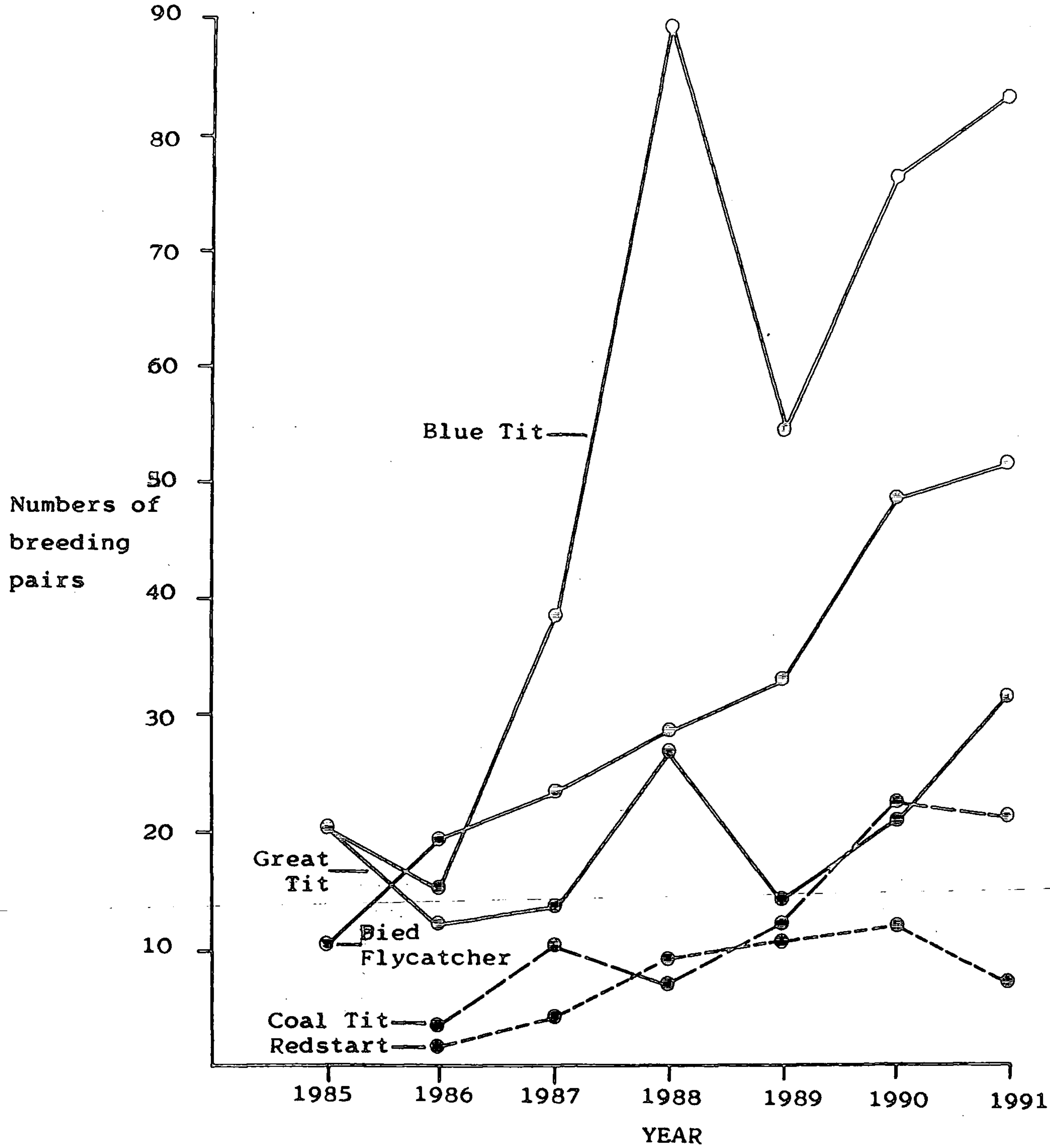


Figure 3.5: The number of breeding pairs of each bird species in nestboxes in Hamsterley Forest, County Durham, 1985-1991.

species breeding in nestboxes in Hamsterley Forest by year and shows the peak of Blue Tit numbers (in nestboxes) in 1988 when there were only 362 nestboxes available (the number of boxes varied between years, as shown in Section 2.2). The figure also shows the parallel, smaller rise in Great Tit numbers in 1988. The other bird species appear to vary independently of each other and the Blue and Great Tit. Pied Flycatcher numbers rose throughout the study. Figure 3.6 displays the same information for Kielder Forest and Figure 3.7 the percentage occupation by Blue Tits in all the areas, showing the 1988 peak in all areas. The mean percentage of occupation of the five main bird species are compared between Hamsterley and Kielder Forest (1986-90) in Table 3.5 which shows the low numbers of Coal Tit and high numbers of Great Tit in Kielder, compared with Hamsterley.

Occupancy is influenced by a combination of factors. Differences between sites include: density of nestboxes, altitude, tree species and origins, ie plantation or semi-natural.

3.1.1 Box Density

An obvious effect on occupancy is the density of the boxes at the site. Unfortunately these data are only available for the County Durham sites. When the occupation percentage for all species was regressed on the density of nestboxes, the relationship was not significant (r=-0.27, df=32). When this was examined in more detail by examining individual regressions for the Hamsterley categories and semi-natural sites, the Low Altitude category proved negatively significant (Table 3.6).

The figures suggest that both High Beckside and Semi-natural sites might have been significant, had the sample sizes been larger. It would be expected that only categories with high occupation levels, at some sites at least, would show such an effect presumably caused by birds interacting with their neighbours.

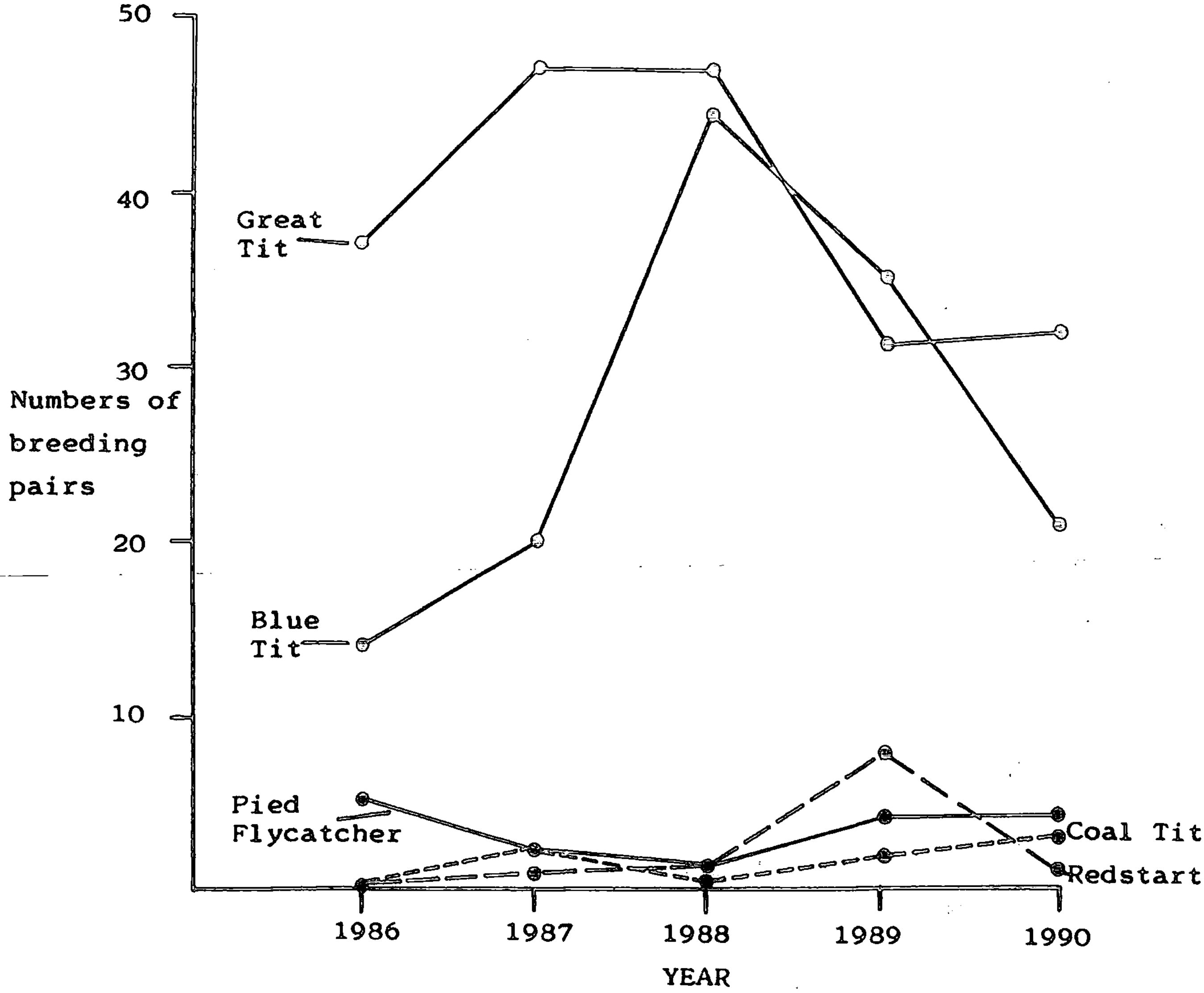


Figure 3.6: The number of breeding pairs of each bird species in nestboxes in Kielder Forest, Northumberland, 1986-1990.

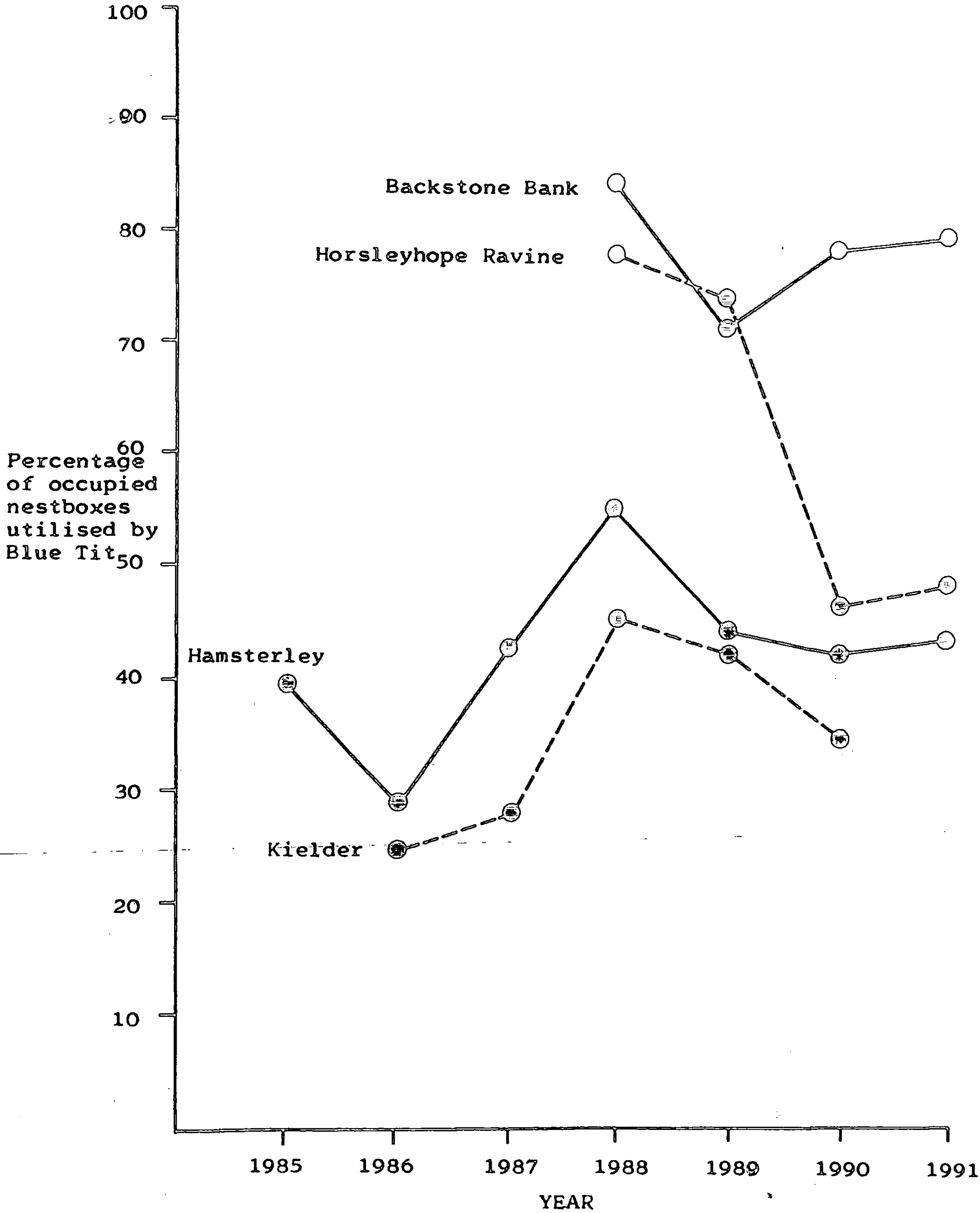


Figure 3.7: The percentage of occupied nestboxes utilised by Blue Tits in Hamsterley Forest (1985-1991), Backstone Bank (1988-1991), Horsleyhope Ravine (1988-1991) and Kielder Forest (1986-1990).

Table 3.5

Results of a comparison between the mean percentage of occupation of nestboxes for five bird species between Hamsterley (Ham) and Kielder Forest (Kiel) (1986-90). There are eight degrees of freedom, ie n-2, in all cases.

	%	95% confidence limits	%	95% confidence limits		
	Ham		Kiel		t	P<
Species:						
Blue Tit	42.8	34.5-51.4	34.6	27.0-42.7	1.28	NS
Great Tit	15.4	9.8-22.0	53.8	42.8-64.6	5.39	0.01
Coal Tit	8.4	5.6-11.6	1.2	0.03-4.0	3.09	0.02
Pied Flycatcher	26.6	20.5-33.2	4.3	1.9-7.7	5.91	0.01
Redstart	5.8	4.2-7.6	1.7	0.09-5.4	1.82	NS

Note: The % occupation data was transformed using arcsine before the t value was calculated in each case.

Table 3.6

The results of regressions of box density on percentage occupation in the Hamsterley categories and semi-natural sites.

Category	r	df	P<
Low Beckside	-0.12	5	NS
Low Altitude	-0.85	5	0.02
High Conifers	-0.36	5	NS
High Beckside	-0.96	1	NS
Semi-natural	-0.97	1	NS

Experiments to investigate the effects of nestbox density on occupancy were carried out at Hamsterley and Horsleyhope Ravine in 1990 and 1991 (see Section 2.7). Considering the semi-natural sites first, Backstone Bank was used as a control site (Table 3.7) for occupancy of all birds combined to compare with Horsleyhope Ravine. When Blue Tit numbers are compared for both Horsleyhope Ravine and Backstone Bank from 1988 to 1991 there is no apparent difference between the years. However, when Pied Flycatcher numbers are examined, it is obvious that the numbers rose at Horsleyhope Ravine but not at Backstone Bank following the increase in nestbox numbers (1990). It was noticeable that annual occupancy percentage levels had quickly reached a high level again in 1991 after dropping in 1990 (Table 3.7). This was tested when the annual occupation percentage of all species for the two sites were compared and only one significant difference found and that was in 1990 ($t=2.44$, $df=58$, $P<0.05$).

The number of nestboxes in the centre of Low Redford was trebled in 1990. The rest of the site was used as a control. Occupation figures for before and after the increase in nestbox density are given in Table 3.8.

The numbers of all species, Blue Tit and Pied Flycatcher were compared between years for both experimental and control areas. The control area produced no significant results (X^2 = 0.38, 0.54, and 0.4 respectively with 3 degrees of freedom). The experimental areas produced some significant results X^2 = 10.07 ($df=3$, $P<0.05$) for all species, $X^2=5.58$ ($df=3$, NS) for Blue Tit and $X^2=10.05$ ($df=3$, $P<0.05$) for Pied Flycatcher. This showed a significant increase in the numbers of Pied Flycatchers and all species and an increase for Blue Tit in the experimental

Table 3.7

Occupancy levels at the semi-natural sites: Backstone Bank (BB) and Horsleyhope Ravine (HR) (1988-1991) for Blue Tit and Pied Flycatcher. Percentages expressed as proportions of total boxes available shown on the line beneath. 1988-1989 were prior to the increase (in 1990).

	1988		1989		1990		1991	
	BB	HR	BB	HR	BB	HR	BB	HR
Number of boxes	20	20	20	20	20	40	20	40
Species								
All	19 95%	18 90%	17 85%	19 95%	18 90%	26 65%	19 95%	35 88%
SE	±5.0	±6.9	±8.2	±5.0	±6.9	±7.6	±5.0	±5.2
Blue Tit	16 80%	14 70%	12 60%	14 70%	14 70%	12 30%	15 75%	17 43%
Pied Flycatcher	2 10%	3 15%	4 20%	4 20%	3 15%	14 35%	3 15%	15 38%

Table 3.8

Occupancy levels for Blue Tit and Pied Flycatcher in Low Redford Wood before (1988-89) and after (1990-91) the increase is nestbox density, in both the control and experimental areas.

YEARS								
	Control		Experimental		Control		Experimental	
	1988	1989	1988	1989	1990	1991	1990	1991
<u>Species</u>								
All	18	16	12	9	15	15	25	21
Blue Tit	7	10	9	4	9	9	11	14
Pied Flycatcher	5	4	1	5	6	5	11	4
Number of Nestboxes	18	18	12	12	18	18	32	32

area. When the annual occupation percentages were compared between the control and experimental areas for each year, none was found to be significant (t=0, 0.93, 0.17 and 1.2). This is mostly due to the large standard errors.

The number of nestboxes in Frog Wood was also increased in 1990 and Pied Flycatcher numbers increased but not enough to produce a significant X^2 test. Table 3.9 gives the occupancy levels, before (1988 and 1989) and after (1990 and 1991) the increase in nestbox density.

In the higher, coniferous parts of the forest in Pennington Rigg Plantation and Sharnberry Flat, the increased density of the boxes made little difference to the number of birds nesting there and numbers were too small for statistical tests.

3.1.2 Altitude

Sites examined during the study vary in altitude between 150 and 370m. The occupation percentage (transformed using the arcsine) (for all species) and altitude (at all sites and areas in County Durham) showed a significant negative relationship, ($r=-0.74$, df=34, $P<0.01$) (Fig 3.8) so that as altitude increases, occupancy decreases. This relationship appears curvilinear when a scattergram is drawn, but is not improved by making a log transformation of altitude, producing a similar correlation co-efficient ($r=-0.75$, df=33, $P<0.01$). Therefore, the original regression line was retained. When the coefficient of variation of the annual occupancy rate

Table 3.9

The occupancy levels for all species, Blue Tit and Pied Flycatcher before (1988 and 1989) and after (1990 and 1991) the increase in nestbox density in Frog Wood, Hamsterley Forest.

	YEARS			
	1988	1989	1990	1991
Species				
All species	9	8	13	15
Blue Tit	4	4	6	5
Pied Flycatcher	1	1	4	7
Number of Nestboxes	11	11	21	21

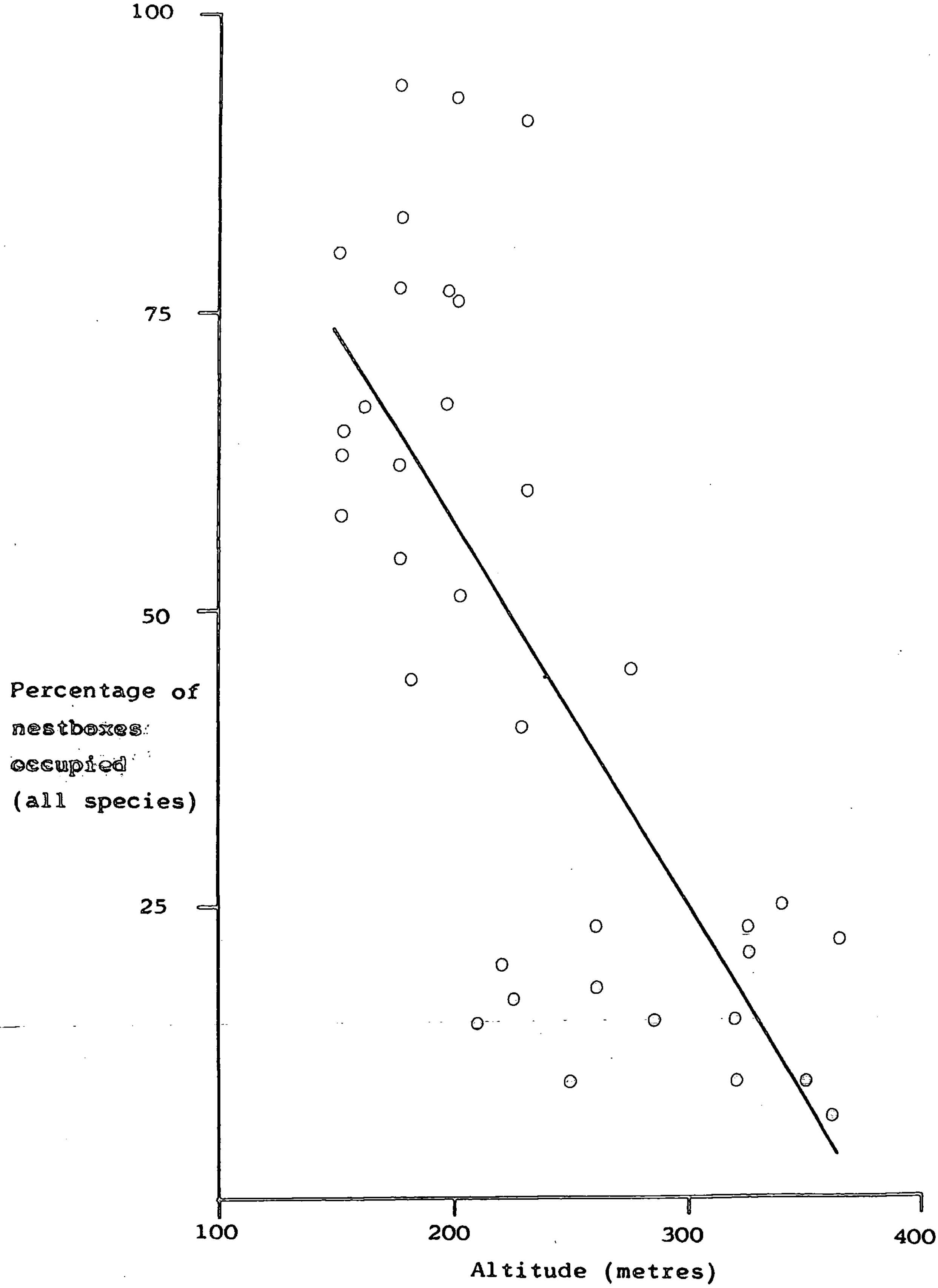


Figure 3.8: The relationship between percentage nestboxes occupied (all species) and altitude at all study sites in County Durham (1985-1991).

was regressed on the site altitude, a significant positive relationship ($r=0.34$, $df=33$, $P<0.05$) was found. This indicates that as altitude increased, the variation in the level of occupation between years increased. This suggests that in years of low total occupancy, proportionately fewer birds nest at higher altitudes in the forest and only in years of high total occupancy do they nest there in numbers. This follows the pattern described by Dhondt et al (1992) as the response to poor breeding sites, which are avoided in years of low density. When the examination is extended to individual species (sites where none of that species were recorded were excluded) Blue Tits also show a significantly negative relationship ($r=-0.59$, $df=28$, $P<0.01$) between altitude and occupation percentage, giving a decrease of 19% occupation for every 100m increase in altitude in the forest, and a significantly positive relationship ($r=0.61$, $df=28$, $P<0.01$) between altitude and the coefficient of variation, of the occupation % such that for a 100m rise in altitude, the variation increases by 66%. In contrast, the Great Tit (occupation percentage/altitude $r=-0.27$, $df=23$, and coefficient of variation $r=0.10$, $df=23$) and Pied Flycatcher ($r=-0.37$, $df=17$ and $r=0.18$, $df=19$, respectively) showed no significant relationships between these factors. The Coal Tit did not show a significant relationship with the percentage of occupation ($r=0.44$, $df=15$) but there is a significant negative relationship between the coefficient of variation and altitude ($r=-0.54$, $df=16$, $P<0.05$) suggesting that as altitude increased, the variation in occupation levels from year to year decreased, in contrast with the Blue Tit.

3.1.3 Tree Species

The number of tree and shrub species was negatively related to altitude ($r=-0.54$, $df=31$, $P<0.01$) such that as altitude increased, the number of tree and shrub species was reduced. When the occupation percentage for all bird species is correlated with the number of tree and shrub species for each site, a significant correlation coefficient ($r=0.54$, $df=34$, $P<0.01$) is obtained, with a coefficient of determination (r^2) of 29%. However, individual bird species except Blue Tit did not show significant relationships. The Blue Tit showed a significant correlation coefficient ($r=0.39$, $df=34$, $P<0.05$) with a coefficient of determination of 15% whilst that for Blue Tit occupation and altitude was 30.3% and so that relationship explained more of the variation in Blue Tit occupation than the number of tree species.

3.1.4 Origins

When differences in occupation between the broadleaved plantations (Low Altitude Broadleaves category at Hamsterley) and the semi-natural sites were examined, a significant difference was found in 1988 but not in 1989, 1990 or 1991. Table 3.10 shows the numbers of boxes occupied by the main species in common for those years (1988-91). When a comparison (using X^2 test) is made between years by adding the semi-natural and Low Altitude broadleaved category, a significant difference is found ($X^2 = 7.98$, $df=3$, $P<0.05$) in 1990 where the number of Pied Flycatchers is greater than expected and Blue Tits less than expected which appears to be a factor of the increase in nestbox numbers in that year. When the two areas are compared before and after the increase in nestboxes, both show more Pied Flycatchers and less Blue Tits than expected following the increase ($X^2 = 8.88$, df=3, $P<0.05$). However, before the increase in nestboxes the semi-natural sites have more Blue Tits and less Pied Flycatchers than expected whilst the Low Altitude sites are as expected.

The presence of shrubs could be taken as an indication of more natural woodland, however, only Horsleyhope Ravine of the two semi-natural sites shows a high percentage of shrubs (32.7). The site with the next highest percentage is Black Hill Top which is partially ancient semi-natural woodland. Blue Tit was the only bird species to show a significant correlation coefficient between occupation and the percentage of shrubs ($r=0.40$, df=28, $P<0.05$).

3.2 Timing of Breeding

Timing of breeding was measured by the date on which the first egg of the clutch was laid and called the first egg date (FED). This aspect of breeding is examined in relation to clutch size and altitude.

Other studies show that the timing of breeding is related to the age of the female tit with young birds tending to lay a few days later than those birds which have bred before (Perrins 1965). At Hamsterley, no differences in first egg date were found between first year females (mean FED=4 May, SE=0.44, n=112) and adult females (mean FED=2 May, SE=0.51, n=95).

Differences were found in the timing of breeding between study areas. Due to the large between year variations, comparisons were only made within the same year.

Table 3.10

Comparison between the numbers of nestboxes occupied by Blue Tit and Pied Flycatcher in the Low Altitude Broadleaves (LA) and the semi-natural sites (SN) (1988-91).

	YEAR							
	1988		1989		1990		1991	
	LA	SN	LA	SN	LA	SN	LA	SN
Number of boxes	94	40	95	40	126	60	126	60
Species								
Number of Blue Tit	40	30	31	26	43	26	49	32
% of available boxes	42.6	75	32.6	65.0	34.1	43.3	38.9	53.3
Number of Pied Flycatcher	15	5	20	8	30	17	27	18
% of available boxes	16.0	12.5	21.1	20.0	23.8	28.3	21.4	30.0

The figures for Great Tit have not been included in this table due to their small size (the figures would read: 16, 2, 3, 1, 5, 1, 7, 4 across).

When the semi-natural sites were compared with Hamsterley (all categories) for the Blue Tit (1988-91) the semi-natural sites were significantly earlier (t=3.32, 3.76, 2.78 and 2.09 respectively and df=96, 74, 85 and 120 respectively with $P<0.01$, 0.01, 0.01 and 0.05 respectively) and the mean difference was 4.1 days (SE=0.72). There was no difference for the Pied Flycatcher data. When the Low Altitude sites from Hamsterley were compared with the semi-natural sites a very similar result was found. There was no significant difference in 1988, but there were for 1989-91 (t=3.15, 3.36 and 3.68 respectively and df=55, 52 and 72 respectively and $P<0.01$ in all cases) and the difference was the semi-natural sites were earlier by a mean of 4.1 days (SE=0.18). These differences are not explained by the differences in altitude (section 3.2.2) as the semi-natural sites are at greater altitudes than the Low Altitude Hamsterley sites (see Chapter 2). There were differences in the timing of breeding between the Hamsterley categories but these may be correlated with altitude and so these are not investigated further here.

3.2.1 Clutch Size and First Egg Date

Kluijver (1951) and Lack (1955, 1958 and 1966) found that clutch size in the Great and Blue Tit declined progressively through the breeding season. Blue Tit clutch (y) size was regressed on first egg date (x) for Hamsterley Forest for each of the five years that the data were available (1987-91). Each year produced a significant negative relationship with a larger clutch size in early breeding birds. The Hamsterley data were compared for intercept and slope between years. Four significant differences (in the slopes) were found (Table 3.11). No significant differences were found in the constant.

Similar data were also produced for the combined semi-natural sites (Horsleyhope Ravine and Backstone Bank). Only in 1991 (of the four years, 1988-91) was there a significant difference (in slope) between the Horsleyhope Ravine and Backstone Bank regression lines ($t=2.22$, $df=29$, $P<0.05$) and so these data are combined in Table 3.11. There were no between year differences in the semi-natural sites' slope.

The semi-natural Blue Tit data was combined with the Hamsterley data on an individual year basis as no significant differences were found between the slopes or intercepts of the two. Consideration was given to producing a single regression line covering all years, however, when the data was examined graphically (by plotting mean first egg date for each year of data against the slope of the first egg date/clutch size regression line), it was noted that the points tend to a positive relationship with later first mean egg date years having a steeper slope. This needs to be examined further but precluded combining inter-year data and is discussed further in the final chapter. A regression line was produced using first egg dates which had been adjusted to eliminate between year differences (in the same way as in Section 3.2.2). This regression line was $y=16.03-0.22x$ ($r=-0.556$, $df=335$, $P<0.01$, SE of slope $= 0.02$). The coefficient of determination is 30.9% for this regression. This line avoided the problems of combining the raw individual year data by adjusting the first egg dates to bring them closer together and reducing the scatter of points.

Pied Flycatcher data were similarly analysed where sample size permitted. The results of the regressions for Hamsterley and the semi-natural sites (1987-91) are shown in Table 3.12, with combined year regression lines as no between year differences were found (Snedecor, 1946).

Table 3.11

Relationship between First Egg Date (x) and clutch size (y) in the Blue Tit (1987-91) in Hamsterley Forest, the semi-natural sites and the combined figures.

Hamsterley Forest

Year	r	df	P<	Regression Line	SE of Slope
1987	-0.365	30	0.05	y=12.8-0.09x	0.04
1988	-0.644	77	0.01	y=20.4-0.26x	0.04
1989	-0.322	49	0.05	y=15.9-0.15x	0.06
1990	-0.513	73	0.01	y=14.6-0.16x	0.03
1991	-0.621	89	0.01	y=18.6-0.23x	0.03

Semi-Natural Sites

Year	r	df	Signif	Regression Line	SE of Slope
1988	-0.725	17	P<0.01	y=24.8-0.39x	0.09
1989	-0.690	23	P<0.01	y=18.1-0.23x	0.05
1990	-0.555	24	P<0.01	y=14.7-0.17x	0.05
1991	-0.408	29	P<0.05	y=15.6-0.16x	0.07

Combined Hamsterley/Semi-natural Sites

Year	r	df	P<	Regression Line	SE of Slope
1988	-0.656	96	0.01	y=20.5-0.27x	0.03
1989	-0.403	74	0.01	y=15.6-0.16x	0.04
1990	-0.528	99	0.01	y=14.5-0.16x	0.03
1991	-0.589	120	0.01	y=18.1-0.22x	0.03

When the regressions from Hamsterley were compared with those from the semi-natural sites in the same years, no significant differences were found so the data were combined (Table 3.12).

Using the Hamsterley Coal Tit data, the regression lines in Table 3.13 were obtained. No significant difference was found between them when the slopes and intercept were compared. A combined year regression line is also shown in the table. Only this and the 1991 regressions were found to be significant.

The Hamsterley Great Tit data produced no significant annual regression lines (1987-91) and only a single, combined data regression line was found to be significant, $y=10.0-0.06x$ ($r=-0.25$, $df=85$, $P<0.05$, SE of the slope$=0.03$). The Redstart data did not produce any significant regression lines, even when the 1988-91 data were combined ($r=0.03$, $df=26$).

3.2.2 Altitude

The mean first egg date of Blue Tit for each site was regressed against the site altitude for each year with available data (from all areas) with samples greater than one. The results are given in Table 3.14.

From these regressions, a first egg date can be given for each year for any altitude, the results for the altitude of 200m are given in Table 3.15.

In order to produce a single trend line to describe all of the data, from all the years, the first egg data have been standardised. This process eliminates between year differences and merely describes the change in timing of breeding with altitude. Standardisation was carried out by taking

Table 3.12

Relationship between first egg date (x) and clutch size (y) in the Pied Flycatcher (1987-91) in Hamsterley Forest and the semi-natural sites.

Hamsterley Forest

Year	r	df	P<	Regression Line	SE of Slope
1987	+0.193	14	NS	y=5.3+0.02x	0.03
1988	-0.461	20	0.05	y=11.0-0.10x	0.04
1989	-0.350	26	NS	y=11.0-0.09x	0.05
1990	-0.507	41	0.01	y=11.9-0.12x	0.03
1991	-0.591	49	0.01	y=10.0-0.07x	0.01
1987-91	-0.453	158	0.01	y=9.3-0.06x	0.009

Semi-Natural Sites

Year	r	df	P<	Regression Line	SE of Slope
*1989	-0.017	6	NS	y=7.3-0.004x	0.09
1990	-0.591	14	0.05	y=11.3-0.11x	0.03
1991	-0.326	15	NS	y=9.3-0.04x	0.03
1988-91	-0.332	43	0.01	y=9.0-0.09x	0.03

Combined Hamsterley/Semi-natural Sites

Year	r	df	P<	Regression Line	SE of Slope
1988	-0.478	24	0.02	y=11.2-0.1x	0.04
1989	-0.322	34	NS	y=10.7-0.09x	0.04
1990	-0.522	57	0.01	y=11.6-0.1x	0.02
1991	-0.562	63	0.01	y=10.2-0.07x	0.01

* The sample size in 1988 was too small for statistical analysis.

Table 3.13

Relationship between first egg date (x) and clutch size (y) in the Coal Tit, Hamsterley Forest (1987-91).

Year	r	df	P<	Regression Line	SE of Slope
1989	+0.037	9	NS	y=8.5+0.01x	0.10
1990	-0.430	19	NS	y=13.9-0.15x	0.07
1991	-0.491	15	0.05	y=15.2-0.19x	0.09
1987-91	-0.370	52	0.01	y=11.9-0.09x	0.03

Table 3.14

Relationship between altitude (x) and the mean first egg date (y) for Blue Tit for Hamsterley Forest and the semi-natural sites (1987-91).

Year	r	df	P<	Regression Line	SE of Slope
1987	0.843	6	0.05	y=8.6+0.11x	0.03
1988	0.765	13	0.01	y=31+0.06x	0.01
1989	0.316	10	NS	y=37+0.03x	0.03
1990	0.582	17	0.05	y=19+0.07x	0.02
1991	-0.423	12	NS	y=46-0.02x	0.01

Table 3.15

The mean first egg date for each year at an altitude of 200m for the Blue Tit, using the formulae from Table 3.14 and the combined data (1987-91) regression lines using both actual first egg date and standardised first egg date.

Year	First Egg Date
1987	29 April
1988	7 May
1989	13 May
1990	3 May
1991	12 May
Standardised First Egg Date	1 May

the earliest year and calculating the mean difference between that and each other year. The first egg dates for the later years are then standardised by having the appropriate mean difference subtracted from them. The single line thus produced is y=25.4+0.03x (r=0.46, df=69, P<0.01, SE of the slope=0.009) where y=first egg date and x=altitude in metres and the expected first egg date from this formula at 200m is also displayed in Table 3.15. Following the method of Snedecor (1946) the relationship between altitude and first egg date for individual years (as shown in Table 3.14) were compared. It was found that there was sufficient difference between them (F=17.85) to consider them as coming from different populations and so the data could not be merged to form a single line.

The Great Tit and Coal Tit data sets are too small for each year to produce reliable statistical results and so only the standardised first egg dates were regressed against the altitude. For Great Tits, this produced the line y=39.3-0.04x (r=-0.44, df=19, P<0.05, SE of the slope=0.02) and for Coal Tits y=24.7+0.02x (r=0.30, df=14, NS, SE of the slope=0.02).

None of the annual first egg date/altitude regressions were significant for the Pied Flycatcher. The single line produced by regressing the standardised first egg date on altitude is y=35.6+0.02x (r=0.26, df=37, NS, SE of the slope=0.01).

3.3 Clutch Size

Older tits are known to lay slightly larger clutches than younger birds (Perrins, 1979), but at Hamsterley the data did not support this and there was no difference in the clutch size between first year (mean clutch size 9.27, SE=0.16, n=112) and older birds (mean clutch size 9.26, SE=0.20, n=95).

Comparisons in clutch size between years in the same category and between categories in the same year were made. Figures 3.9-3.12 demonstrate these differences, where there was sufficient data for Blue Tit, Great Tit, Coal Tit and Pied Flycatcher respectively in the Hamsterley categories 1985-91. There were many significant differences within categories between years. When the individual species clutch size data were analysed, using two-way anova techniques with year and Hamsterley categories as the variables, several significant results were obtained, all the results are shown in Table 3.16. It is noticeable that the between year differences are the most important factor in all three species affecting clutch size. The overall mean clutch size for individual bird species for each category was taken and then these were compared. The only bird species which occurs in all of the categories in any numbers is the Blue Tit. The mean clutch size for each category and the significant comparisons are given in Table 3.17. Comparisons were only made including the data from years where those data were available for both categories, eg the high altitude categories did not exist in 1985 and so the comparison with low altitude sites did not include any data from that year in either clutch size mean.

Clutch size data were analysed, within individual years, between the categories of sites for Hamsterley and the semi-natural sites in order to obtain sufficient sample sizes. Blue Tit numbers were very high in 1988 (see Section 3.1) and this is the only year in which the mean clutch size for the Low Altitude Broadleaved, category of sites, was statistically higher than for other categories and sites for Blue Tit and, in one case, Great Tit. In 1991, Horsleyhope Ravine proved to have higher Blue Tit clutch sizes than other sites. The results of these comparisons using the t test are shown in Table 3.18.

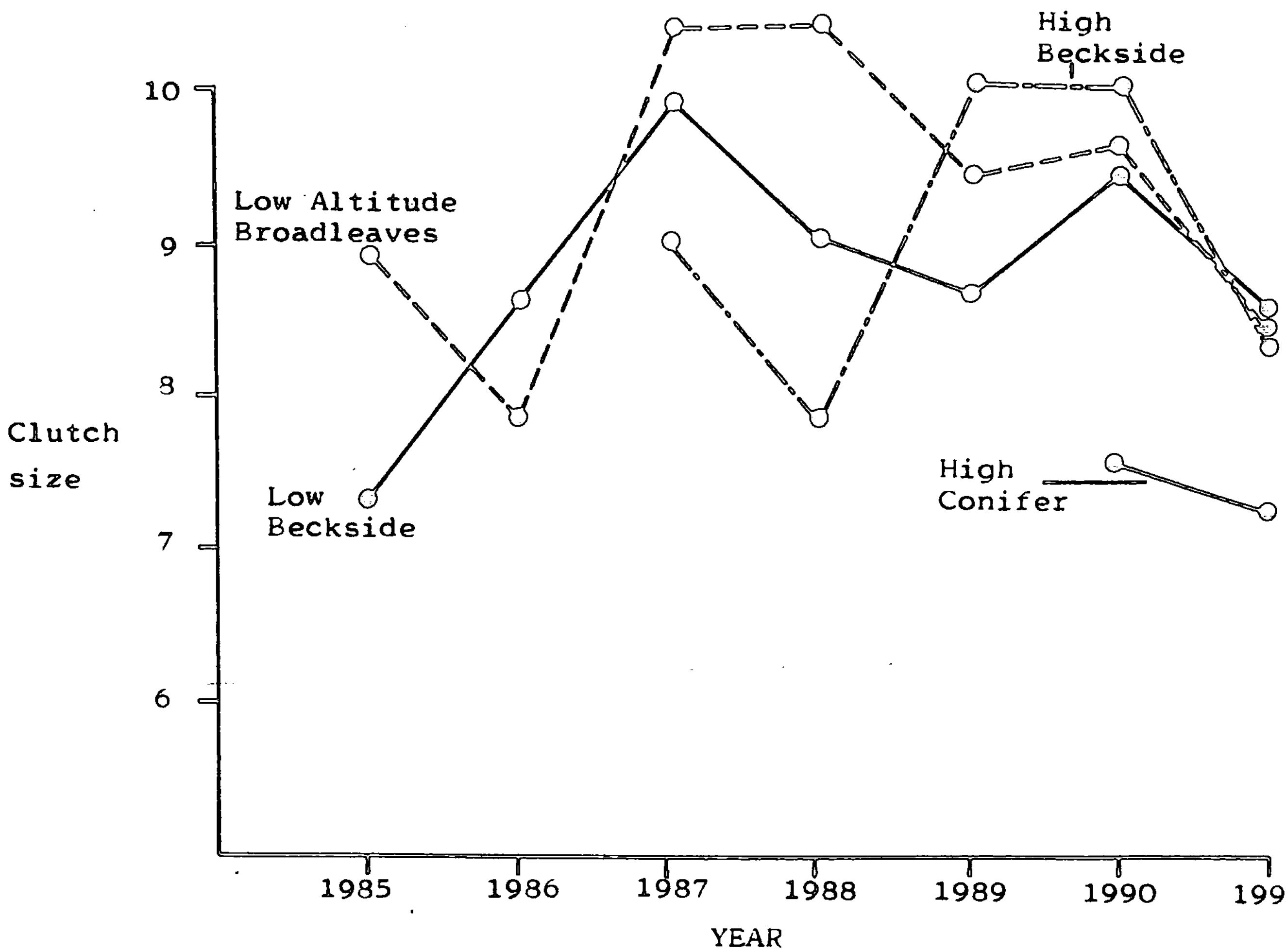


Figure 3.9: The clutch size of Blue Tit 1985-1991 (where sufficient data available) For the different habitats in Hamsterley Forest.

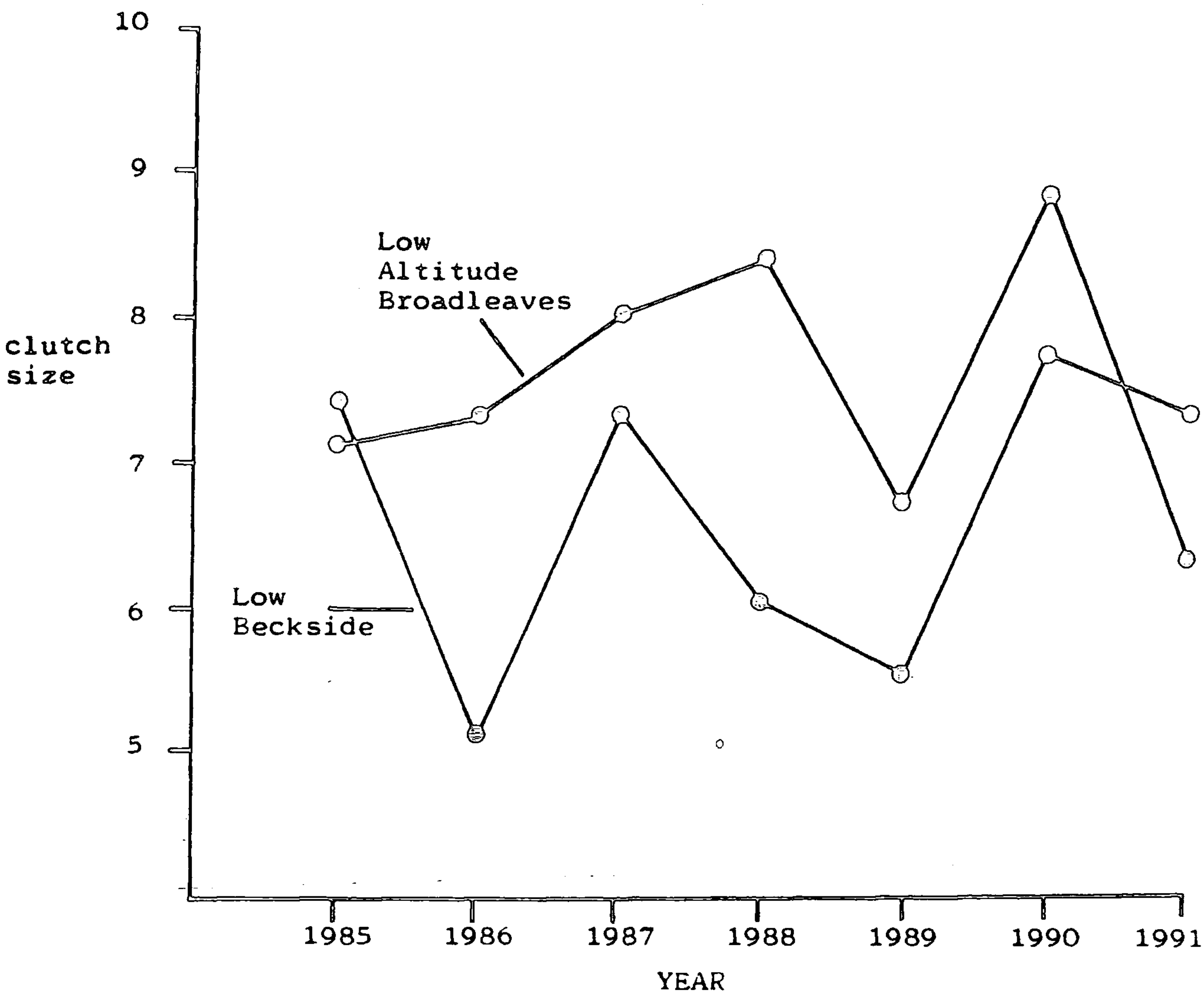


Figure 3.10: The clutch size of Great Tit 1985-1991 (where sufficient data available) for the different habitats in Hamsterley Forest.

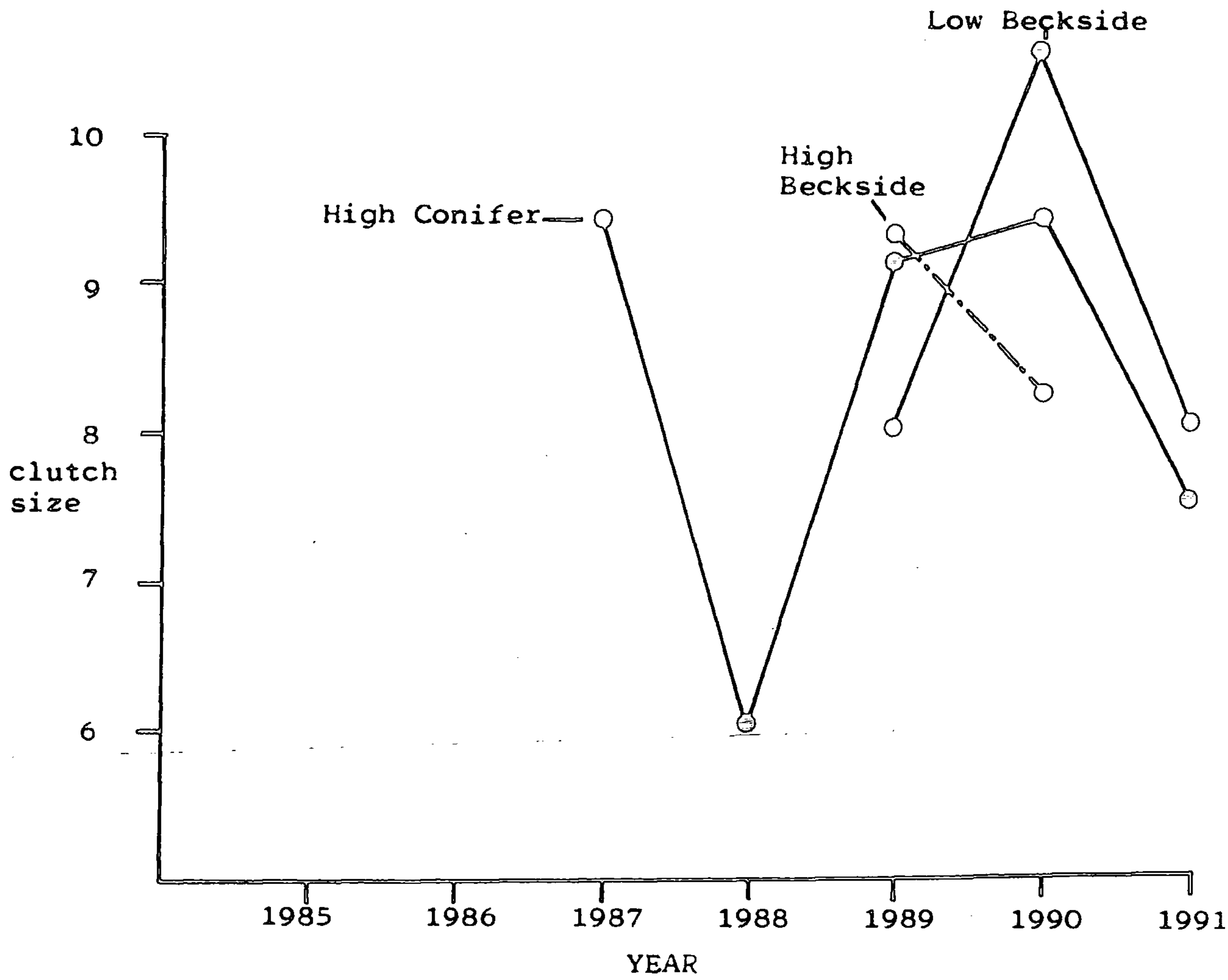


Figure 3.11: The clutch size of Coal Tit 1985-1991 (where sufficient data available) for the different habitats in Hamsterley Forest.

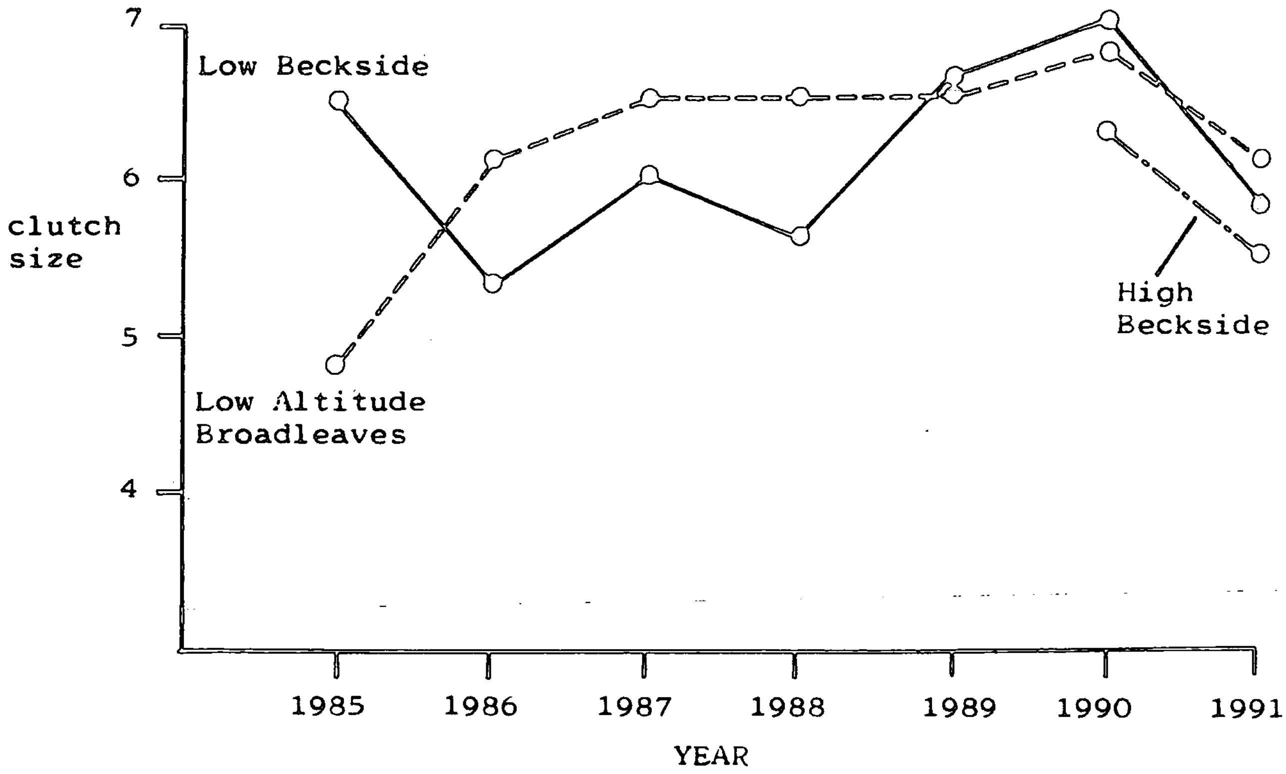


Figure 3.12: The clutch size of Pied Flycatcher 1985-1991 (where sufficient data available) for the different habitats in Hamsterley Forest.

Table 3.16

Analysis by two-way anova of the clutch size data by year in Hamsterley categories.

Species	Source of Variation	F	df	Probability
Blue Tit	Year	5.48	3	0.01
	Category	1.90	2	NS
	Interaction between year and category	2.51	6	0.05
Great Tit	Year	2.80	6	0.05
	Category	7.17	1	0.05
	Interaction between year and category	0.93	6	NS
Pied Flycatcher	Year	3.09	6	0.01
	Category	2.94	1	NS
	Interaction between year and category	1.20	6	NS

Table 3.17

The overall mean clutch size for Blue Tit for each Hamsterley category and the significant comparisons between categories.

	Mean clutch size	n	SE
Low Altitude Broadleaves	9.4	163	0.16
Low Beckside	8.9	57	0.26
High Beckside	8.7	27	0.38
High Conifers	6.8	8	0.70

Comparisons	t	df	P<
Low Altitude/High Conifer	3.18	169	0.01
Low Beckside/High Conifer	2.88	63	0.01
High Beckside/High Conifer	2.53	33	0.02

Table 3.18

Significant comparisons of clutch size between categories and sites in 1988 and 1991.

Year	Sp	Sites/Cats	t	df	P<
1988	BT	Low Alt/Low Beck	2.67	57	0.01
1988	GT	Low Alt/Low Beck	3.40	20	0.01
1988	BT	Low Alt/High Con	4.98	43	0.01
1988	BT	Low Beck/High Con	2.26	22	0.05
1988	BT	High Beck/Low Alt	4.49	48	0.01
1988	BT	Low Alt/Penn	4.64	43	0.01
1988	BT	Low Alt/Back	3.08	48	0.01
1991	BT	Hors/Back	3.48	30	0.01
1991	BT	Hors/Low Alt	3.09	64	0.01
1991	BT	Hors/Low Beck	3.86	25	0.01
1991	BT	Hors/High Con	4.83	24	0.01
1991	BT	Hors/High Beck	2.82	22	0.01
1991	BT	Hors/Penn Exp	4.38	18	0.01

BT = Blue Tit

GT = Great Tit

Low Alt = Low Altitude

High Con = High Conifers

Penn = Pennington Plantation

Penn Exp = Pennington Experimental

Back = Backstone Bank

Hors = Horsleyhope Ravine

df = degrees of freedom

NB: In 1988, Low Altitude mean clutch was the largest and Low Beck second largest mean clutch size. In 1991, the mean Horsleyhope Ravine Blue Tit clutch size was largest.

These data do not suggest that clutch size is directly related to altitude for the Blue or Great Tit. However, as these tits lay their clutches later at high altitude and the later in the season the clutch is laid the smaller it is there is an indirect relationship. The main difference between Low Altitude and Low Beckside is the number of broadleaves near the nestboxes, with far more in the Low Altitude sites. Horsleyhope Ravine is a very rich site botanically with a good shrub layer in addition to the, mainly oak, canopy trees. Invertebrate availability may be a factor in these differences (see Section 3.6).

3.4 Productivity

Productivity is defined in this study as the number of fledged juveniles produced in a nest. It is far more difficult to make statistical comparisons between areas for their productivity because a high standard deviation is almost inevitable. The only significant comparison was for Blue Tit between Low Altitude Broadleaves, mean of 8.8 juveniles fledging and Low Beckside, with a mean of 6.6 juveniles fledging ($t=2.19$, $df=57$, $P<0.05$). Comparisons between years for the same categories are possible. Figures 3.13-3.15 show the clutch size and number of juveniles fledging for each year that data are available 1985-91 in the Low Altitude Broadleaves category in Hamsterley for Blue Tit, Great Tit and Pied Flycatcher, respectively. There are many between year differences for categories. The data were analysed by two-way anova for individual species and the results are summarised in Table 3.19. It can be seen that only the variation between years produced significant differences, while the variation between categories and the interaction between year and categories did not. Therefore the differences in the numbers of chicks fledging can only be proven as resulting from between years differences.

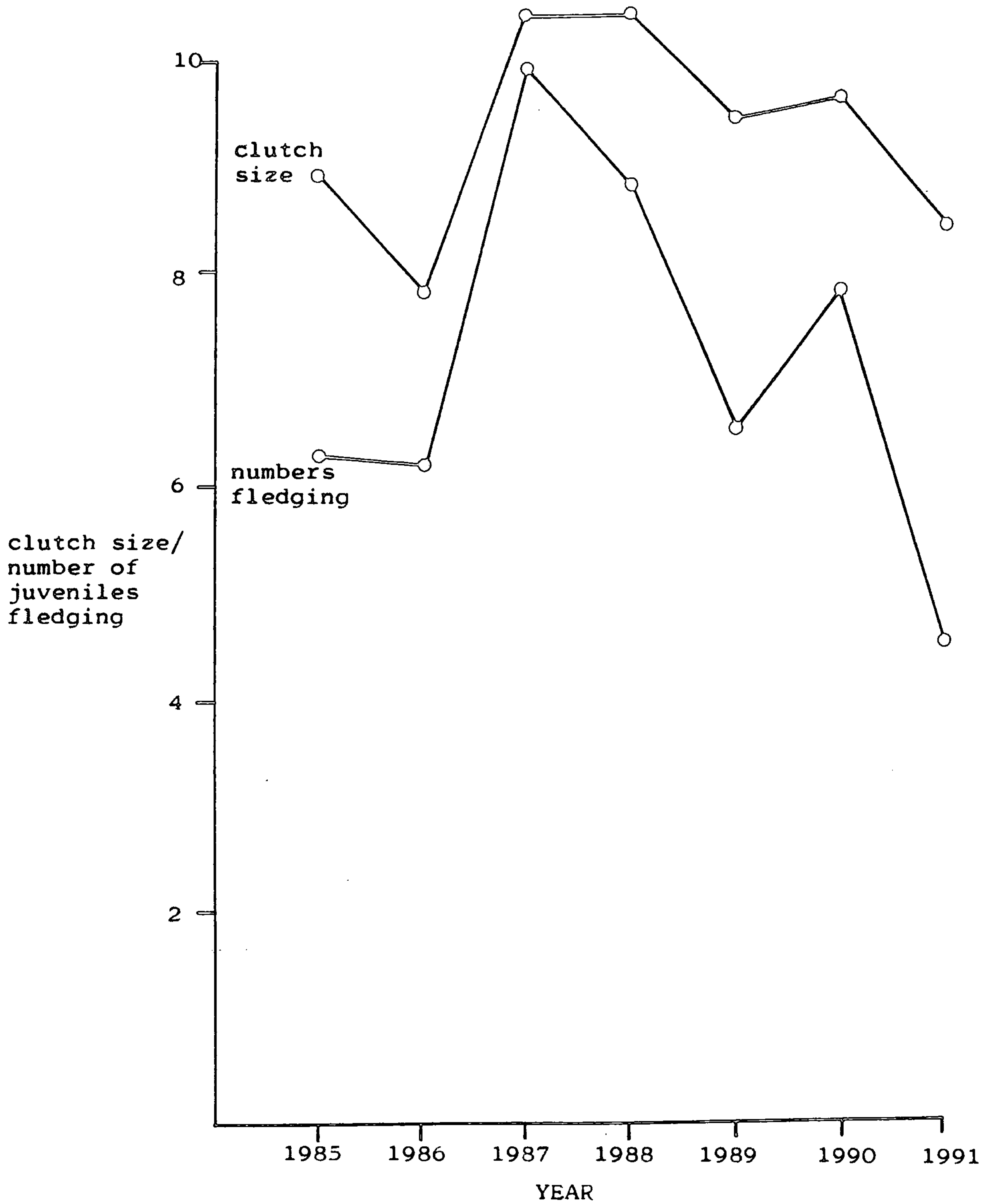


Figure 3.13: The clutch size and number of Blue Tits fledging each year (1985-1991) in the Low Altitude Broadleaved sites in Hamsterley Forest, County Durham.

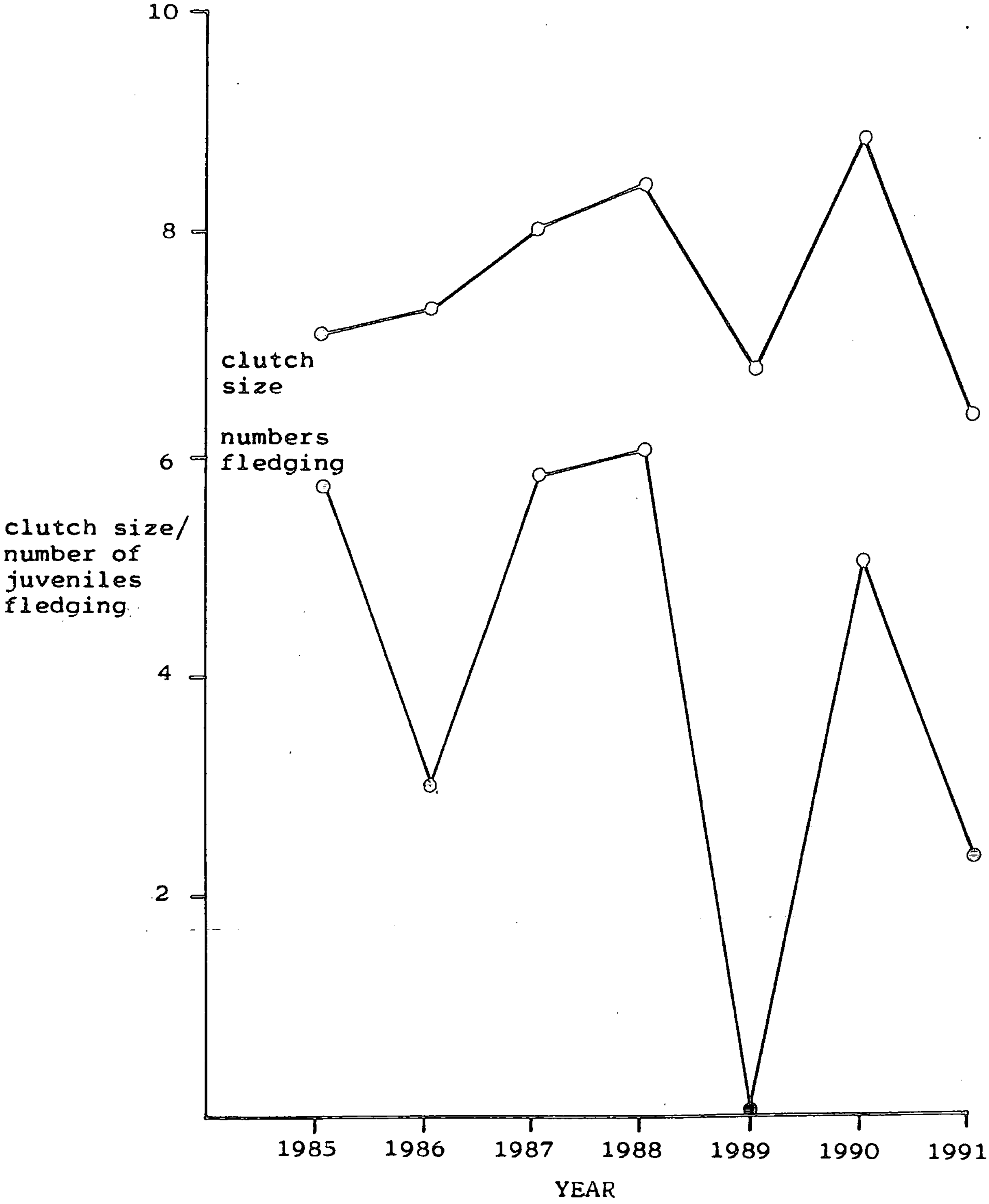


Figure 3.14: The clutch size and number of Great Tits fledging each year (1985-1991) in the Low Altitude Broadleaved sites in Hamsterley Forest, County Durham.

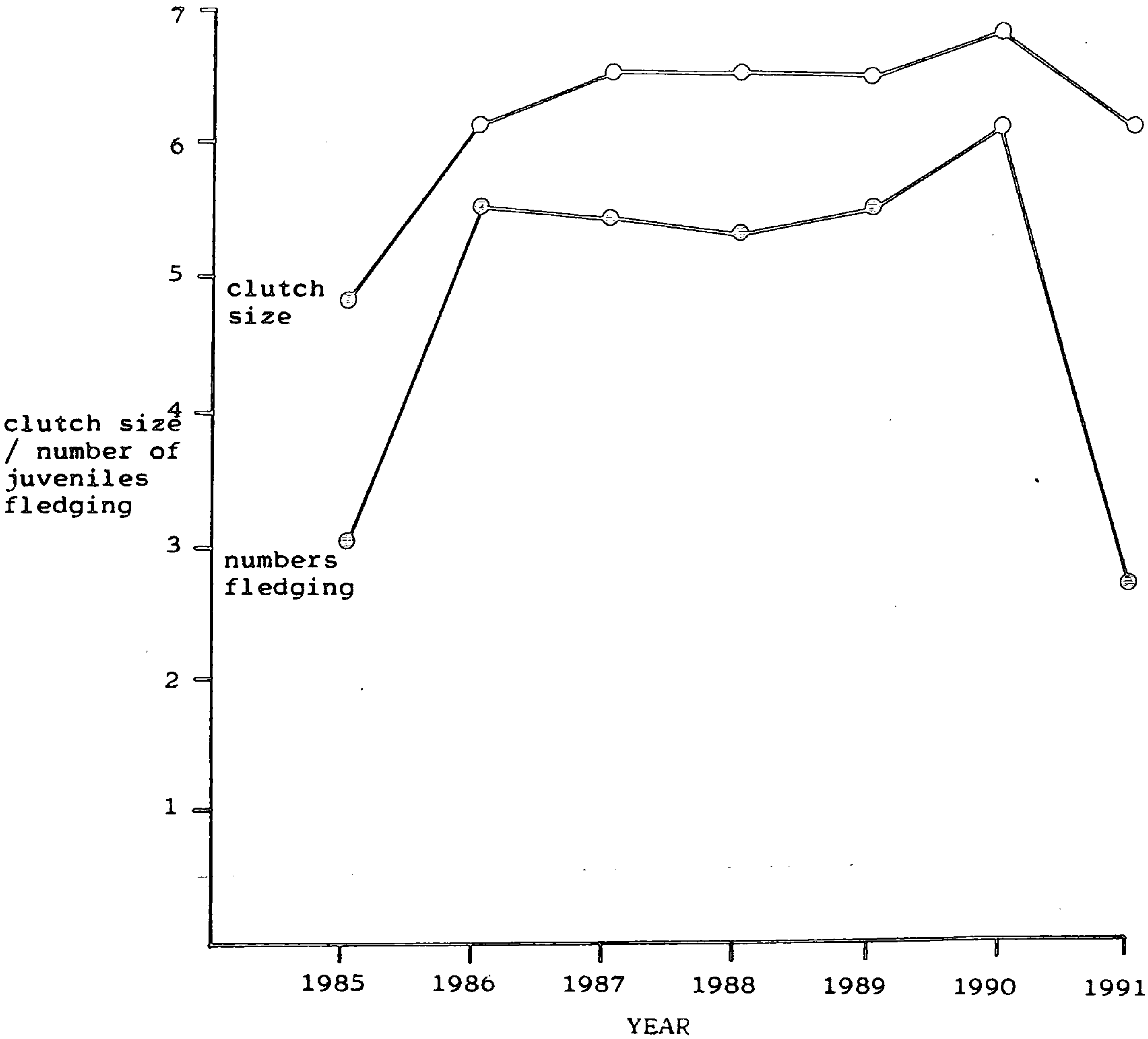


Figure 3.15: The clutch size and number of Pied Flycatchers fledging each year (1985-1991) in the Low Altitude Broadleaved sites in Hamsterley Forest, County Durham.

3.5 Success

There are two main ways of measuring success, the first is to consider any nest which produces at least one fledged juvenile a success and so the percentage of success is the percentage of the nests which achieve that. The other method is to divide the number of juveniles fledging by the number of eggs laid and multiply by 100 to give a percentage. Only the latter method is used, allowing easier comparison with other studies in the next chapter.

Table 3.20 shows the success rate (calculated as percentage of eggs laid producing fledged juveniles) for each Hamsterley category (1985-1991).

3.6 Invertebrates

Invertebrate samples were compared using both the mean number of individuals and biomass (wet weight) of a sub-sample (15 of which make up a sample, for one tree species, for a particular date). When biomass and the number of invertebrates per sample are correlated, no significant relationship results. The reason for this is evident when Figure 3.16 (the number of large (>5mm) invertebrates for each sample shown against date of sampling) is examined and compared with 3.17 (the biomass (mg) of each sample shown against date of sampling). It can be seen that a few large invertebrates are responsible for most of the peak weights. Figure 3.18 shows the number of invertebrates per sample against date of sampling showing that some of these peaks, such as the early Sitka Spruce one was largely due to smaller invertebrates. At each sampling date, the trees may be ranked differently, according both to biomass and mean number of individuals per sub-sample.

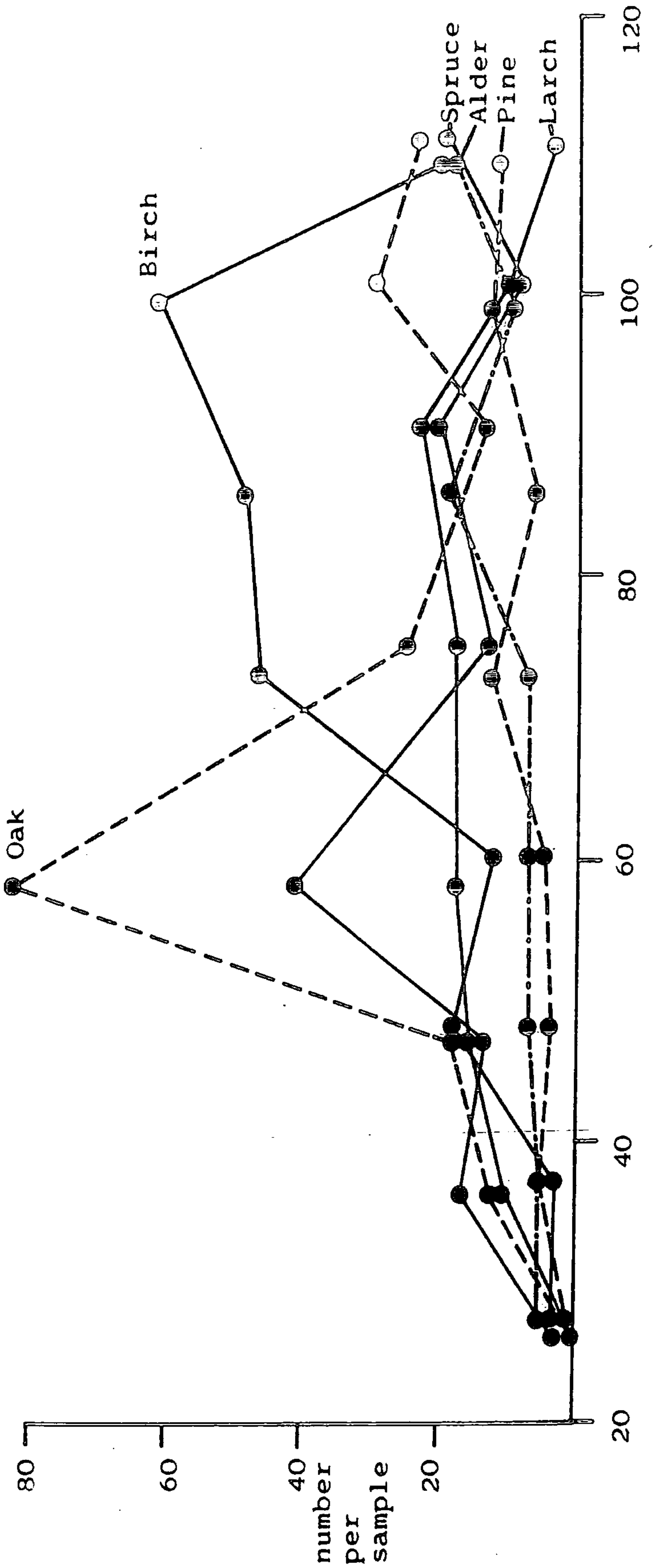


Figure 3.16: The numbers of large invertebrates collected from six tree species in Hamsterley Forest, County Durham in 1990 (1st April = 1).

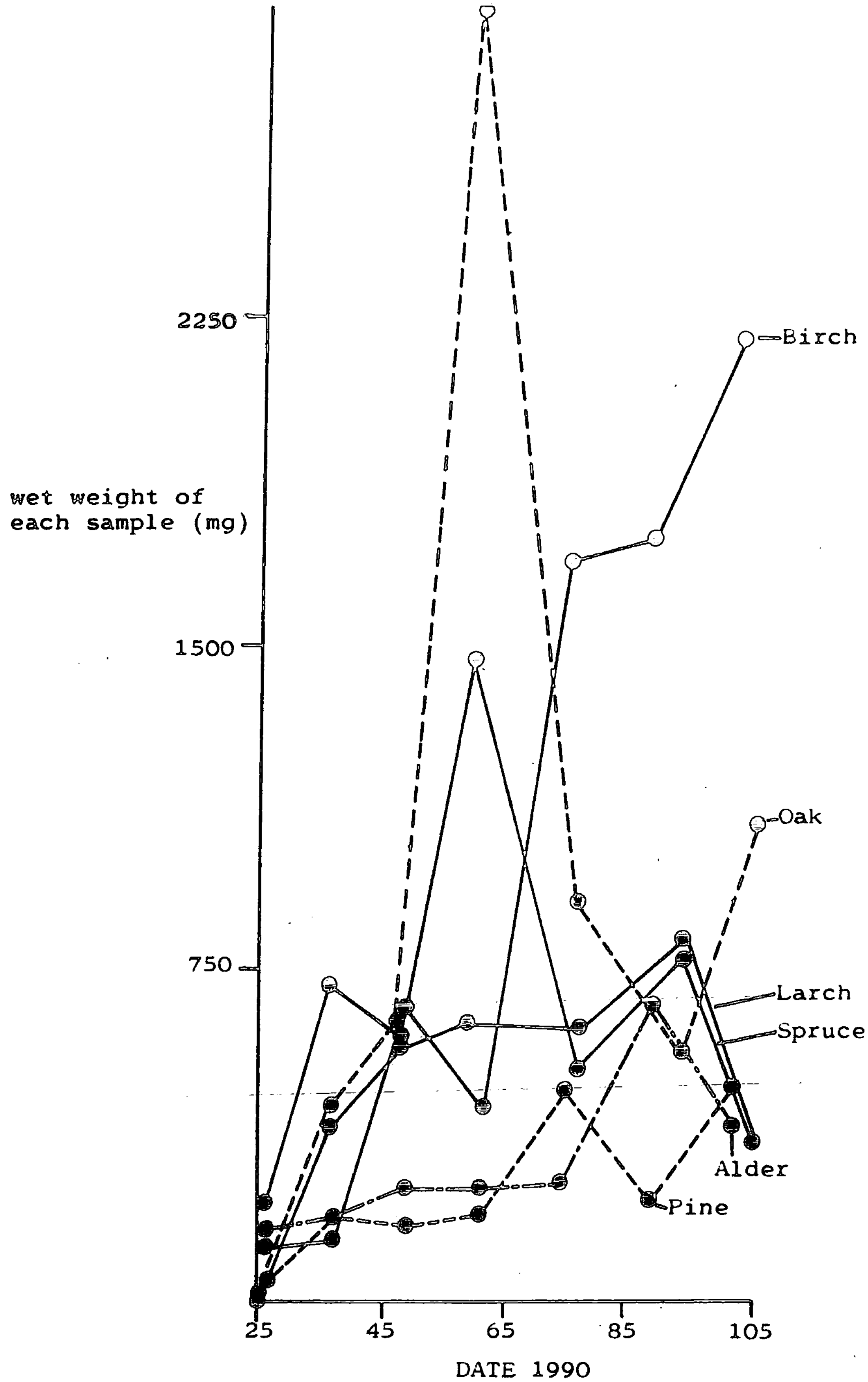


Figure3.17: The biomass (wet weight in miligrams) of each sample collected from six tree species in Hamsterley Forest, County Durham in 1990 (1st April = 1).

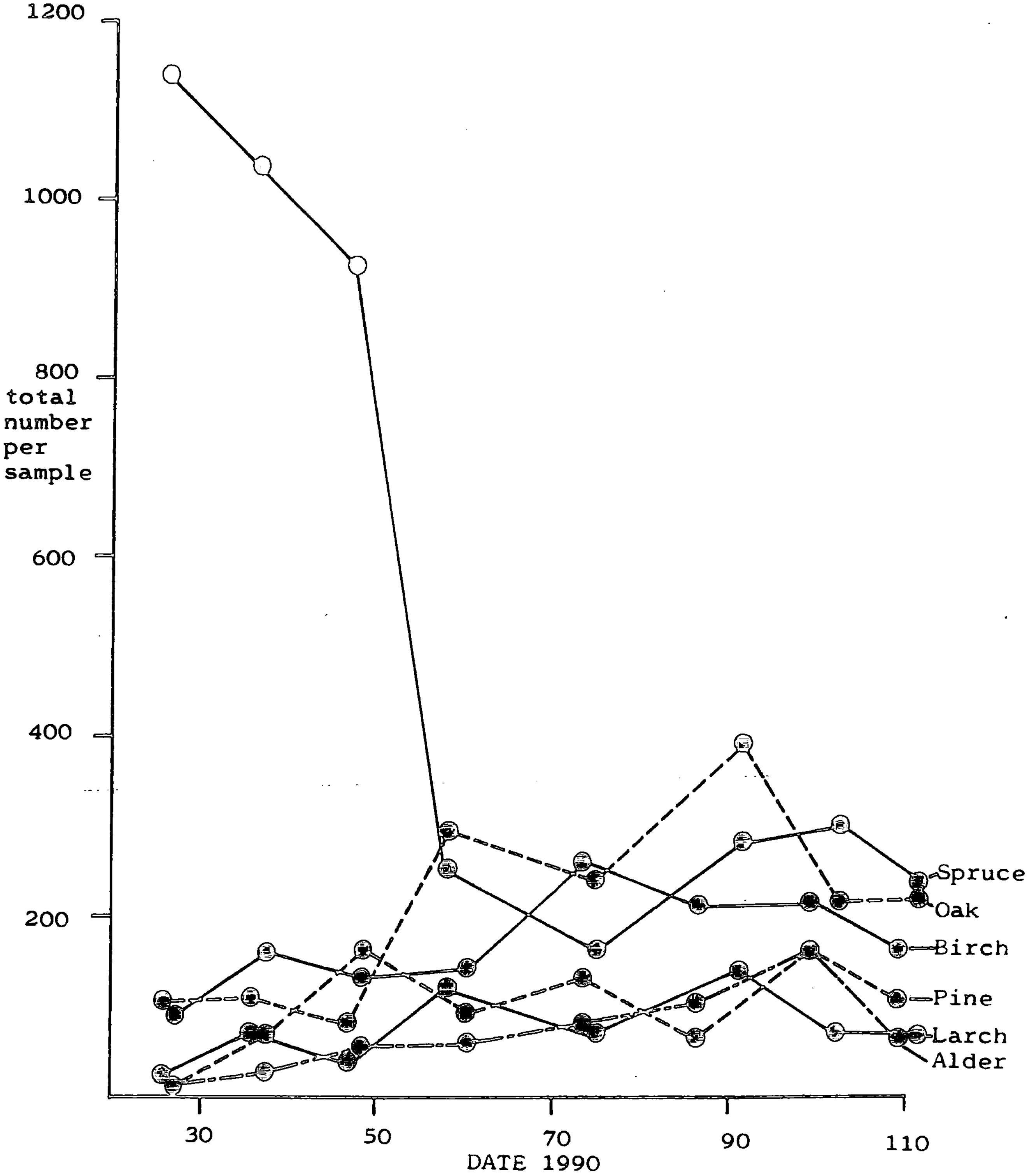


Figure 3.18: The total numbers of invertebrates collected from six tree species in Hamsterley Forest, County Durham in 1990 (1st April=1).

Samples taken on similar dates for certain tree species were collected in 1989 (25 June), 1990 (25 and 30 June) and 1991 (28 and 29 June) and the results are shown in Table 3.21.

The number of invertebrates have been compared between years using t test on the sub-sample data. Sitka Spruce was the only tree which showed a significant difference ($t=2.32$, $df=28$, $P<0.05$) between 1989 and 1990, with three times the number of invertebrates in 1990. Comparisons between 1990 and 1991 produced four significant results and these are given in Table 3.22. The 1991 results were always the lower density.

Table 3.19

Analysis by two-way anova of the number of chicks fledging data by year in Hamsterley categories.

Species	Source of Variation	F	df	Probability
Blue Tit	Year	9.42	3	0.01
	Category	1.20	2	NS
	Interaction between year and category	1.27	6	NS
Great Tit	Year	3.43	6	0.01
	Category	0	1	NS
	Interaction between year and category	0.80	6	NS
Pied Flycatcher	Year	7.38	6	0.01
	Category	0.11	1	NS
	Interaction between year and category	1.35	6	NS

Table 3.20

Success rate (calculated as percentage of eggs laid producing fledged juveniles) for each area.

Hamsterley Forest

YEARS							
	1985	1986	1987	1988	1989	1990	1991
Number of boxes occupied	50	51	88	160	124	181	193
Species							
Blue Tit	74	73	90	83	73	80	61
Great Tit	73	49	86	68	54	76	37
Coal Tit	-	100	98	71	73	87	81
Pied Flycatcher	76	57	81	82	81	83	54
Redstart	-	78	80	56	77	90	98

Backstone Bank

YEARS				
	1988	1989	1990	1991
Number of occupied boxes	19	17	18	19
Species				
Blue Tit	64	78	87	80
Pied Flycatcher	50	93	65	25

Table 3.20 (Continued)

Horsleyhope Ravine

YEARS				
	1988	1989	1990	1991
Number of occupied boxes	18	19	26	35
Species				
Blue Tit	87	84	93	66
Pied Flycatcher	63	82	84	81

Table 3.21

Comparisons between mean numbers of invertebrates in sub-samples taken in 1989, 1990 and 1991 in late June. There were 15 sub-samples taken in each year.

YEAR						
	1989	(SE)	1990	(SE)	1991	(SE)
Tree Species						
Alder	6.5	(1.4)	6.5	(1.1)	3.8	(0.7)
Birch			14.0	(1.3)	6.2	(1.1)
European Larch			7.8	(1.5)	3.9	(1.0)
Oak			26.0	(4.1)	9.6	(1.8)
Scots Pine			4.1	(1.0)	2.5	(0.6)
Sitka Spruce	5.7	(1.1)	18.7	(5.5)	8.1	(2.0)

Table 3.22

Comparisons between the number of invertebrates in samples in late June 1990 and 1991, shown as the 1991 figure expressed as a percentage of the 1990 figure. There are 28 degrees of freedom in all cases.

Tree Species	t	P<	% 1991/1990
Alder	2.06	0.05	50.5
Birch	4.55	0.01	44.3
Larch	2.21	0.05	50.0
Oak	3.64	0.01	36.9
Pine		NS	61.0
Spruce		NS	43.3

CHAPTER FOUR

DISCUSSION

The main theme of the study was the breeding success of the birds nesting in upland woodland and this chapter discusses the findings in depth.

As defined in Chapter 3, breeding success has been considered as the percentage of eggs laid producing fledged juveniles. This definition involves both the clutch size and the number of chicks fledged. Breeding success encompassed several different forms of failure: whole clutches and broods abandoned (generally thought to be as a result of the death of one or both parents), infertile eggs, predated eggs and juveniles and juveniles dying in the nest for various reasons, including starvation. Breeding success varied considerably between years (Table 3.20) with 1991 being a particularly bad year. The ranges of breeding success at Hamsterley and the semi-natural sites are shown in Table 4.1.

Follows (1990), in his North Yorkshire study from 1974-1989 in a mixed conifer and Ash (Fraxinus excelsior)/Elm (Ulmus procera) wood with riverside Alder (Alnus glutinosa), recorded an overall breeding success of 74% in the Pied Flycatcher, although there were considerable differences between years. This figure is similar to the results in this study. In another study on the Pied Flycatcher between 1948-58 in the Forest of Dean, the overall success was 87% (Harvey et al., 1985) in oak woodland.

Habitat preference may influence the breeding success in different wood types as well as the numbers breeding thus explaining the difference between the Forest of Dean and the present study and Follows' Yorkshire Study. Stowe (1987) states that Pied Flycatchers showed a preference for woods predominantly, but not entirely, with an oak canopy and a poorly developed shrub layer in his survey of 31 woods with breeding Pied Flycatchers in western Britain.

Table 4.1

The ranges and mean of breeding success at Hamsterley and at the Semi-natural sites.

	Years	% Range	Mean %	Sd
HAMSTERLEY				
Blue Tit	1985-91	61-90	76	9.2
Great Tit	1985-91	37-86	63	17.2
Coal Tit	1986-91	71-100	85	12.3
Pied Flycatcher	1985-91	54-83	73	12.5
Redstart	1986-91	56-98	81	14.2
SEMI-NATURAL SITES				
Blue Tit	1988-91	72-90	80	7.8
Pied Flycatcher	1988-91	58-88	75	12.8

Alatalo and Lundberg (1984) found that there was a negative effect on success of Pied Flycatchers breeding at high density in years of poor weather conditions, overturning Tompa's (1967) suggestion that fledging success was unaffected by density although clutch size does not appear to be affected.

As can be seen in Table 4.1, Great Tit breeding success at Hamsterley was the most variable (sd=17.2) and almost twice that of the Blue Tit. However, in some other studies, a higher and more consistent level of success has been found. Kluijver (1951) in the Netherlands found a success rate of 82% for 2022 Great Tit clutches during his long-term study. Gibb (1950) in his 3 years of research in Wytham Wood, Oxford found a range of 78-81% for Great Tit and 73-86% for Blue Tit. Perrins (1979) gives the percentage loss of eggs and young for Wytham as 17% (equivalent to success of 83%). Perrins (1979) states that Great Tits are birds of open, broadleaved, deciduous woodland with a shrub layer and the Blue Tit a bird of broadleaved, deciduous woodland with a preference for oak, although both species are found over a variety of habitats. Their preferences may also be reflected in their breeding success in woodland types other than the preferred one.

Campbell (1968) described a mystery disease which affected chicks of all the species in his study in 1948, 51 and 60. The disease caused diarrhoea and a displacement of the lower mandible and no such symptoms were seen during the present study. Despite this, disease could have been a factor affecting the success of some of the clutches, both affecting the parents and chicks.

Flegg and Cox (1975) demonstrated how high losses could be, due to predation, in their 10-year study in Northward Hill National Nature Reserve, Kent. Overall success for the Great Tit was 64% and 62% for the Blue Tit. Predators in their study included Grey Squirrel (Sciurus carolinensis), Weasel (Mustela nivalis) and Great Spotted Woodpecker (Dendrocopos major) all of which occur at Hamsterley. At Hamsterley Grey Squirrel numbers have risen sharply during the study, although still at relatively low levels and there was little evidence of them predating nests. Although predators took both eggs and young and so reduced the success rate, the majority of losses (approximately 60%) in the years of particularly low success appeared to be due to starvation. Cowie and Hinsley (1987) found that in suburban gardens in Cardiff (1981-83) the breeding success rate was very low (44.3% for Blue Tit and 28.4% for Great Tit) which was largely due to nestling mortality through starvation.

Other factors which could have affected the success rates include the absence of the female, while feeding (or of course predated) during cold or damp weather.

Although breeding success is an important factor in the productivity of birds, it is only able to reflect the adult birds ability to feed the young and the effects of predation. It is, if predation is excluded, a measure of the birds' ability to assess in advance the quality of the breeding season. In years such as 1991, birds did not anticipate the potential of the breeding season well; many laid large clutches and the level of abandoned nests and juveniles starving to death was high leading to a low success rate. Invertebrate samples were not collected early in the breeding season in 1991 and so the numbers of available invertebrates then are unknown. It seems likely that there were sufficient to trigger the birds to lay relatively large clutches which later invertebrate numbers could not support. Invertebrate samples collected then (late June) were at a far lower density than at the same time in the previous years (Table 3.21) suggesting that this may be responsible for the very low success rate of Blue and Great Tits and Pied Flycatcher in that year. Coal Tit success was not significantly reduced. Despite the fact that the number of invertebrates per sample was reduced to 43.3% of the 1990 number on Sitka Spruce and 61% on Scots Pine neither of these reductions was significant. The main tree species where the Coal Tits nest in nestboxes in Hamsterley Forest are Sitka Spruce and Scots Pine. The density of breeding birds in this area is far less than in the lower parts of the forest and presumably this lack of competition for food is also an important factor in their success. Other factors affect the clutch size and these are now examined and compared with other studies.

4.1 Clutch Size

There is variation in clutch size both between years and between sites in the present study. Table 4.2 shows the mean clutch sizes found in studies on the Blue and Great Tits and Pied Flycatcher and the present one for comparison. In addition, Järvinen (1989b) found that in Finland the clutch size of the Pied Flycatcher varied between 4.88 and 6.22 (1966-87) but did not present an overall mean.

Table 4.2 shows that there is very little difference between the figures. The number of fledged chicks produced, however, are very different (calculated from the success figures given in Table 3.1 and earlier in this chapter).

When table 3.16 is examined, it can be seen that a major difference between figures for clutch size in the three species analysed was the difference between different years and in fact for Pied Flycatcher this was the only significant result. However, Blue Tits showed that the interaction between year and the habitat within Hamsterley (category) was also important and for Great Tit the category was an important factor. Table 3.19 shows that only between year differences were significant in terms of the number of chicks fledged, this is probably due to the large variances involved in the calculations allowing only very large differences to be statistically significant.

Another feature which varies between sites is the ratio of Blue to Great Tits. Lack (1955) noted that Great Tits were more abundant in rich broadleaved woods than in conifers or broadleaved parkland with conifers or in an oak wood in a large industrial town. The density of the Blue varied similarly with habitat but this species was more than twice as numerous as the Great Tit in rich broadleaved woods and decidedly scarcer in conifers. In the Cardiff study, the ratio was over 3 Blue Tits to 1 Great Tit, in the present study the Hamsterley ratio was 2.7:1 and the semi-

Table 4.2

Mean clutch sizes found in published papers and the present study of the Blue and Great Tits and Pied Flycatcher.

Source	Dates	Blue Tit	Great Tit	Pied Flycatcher	Site
Perrins, 1965	1958-63	9.7	8.7		Marley Wood, Oxford
East & Perrins, 1988	1983-84	8.9	8.1		Wytham Wood, Oxford
Follows, 1990	1974-89	9.3	8.3	6.6	North Yorkshire
Cowie & Hinsley, 1987	1981-83	8.8	7.4		Suburban gardens, Cardiff
Petty, 1989	1988	10.1	8.2	6.4	Broadleaved Woods, Argyll
Present Study	1988	10.4	8.4	6.5	Low Altitude Sites
" "	1988	9.8		6.5	Semi-natural Sites
" "	1985-91	9.2	7.6	6.4	Hamsterley

natural sites ratio 14.3:1 and in Argyll 1.9:1 (Petty, 1989). This seems to infer that Great Tits are less adaptable or perhaps less competitive than Blue Tits. However, if the low altitude Hamsterley categories are compared, a more complicated picture emerges. The Low Altitude broadleaved sites give a ratio of 4.4 Blue Tit: 1 Great Tit and the Low Beckside 1.3 Blue Tit: 1 Great Tit. The Kielder ratio is similar to the latter at 1.4 Blue Tit: 1 Great Tit which may reflect the beckside nature of many of the broadleaves selected as sites there. This aspect would benefit from further research.

4.2 Timing of Breeding

Timing of breeding appears to be related to spring temperature and food availability (Perrins, 1965). Migratory birds such as the Pied Flycatcher do not arrive on the study area until early May but the resident tit species are available to take advantage of early warm weather and food abundance, therefore the onset of breeding in the tits tends to vary more widely between years.

There is considerably between-year variation in the timing of breeding and, if possible, it is far preferable to make comparisons between sites in the same year. However, when comparing the results of one study with another, this can usually not be done. The work of Petty (1989) in Argyll was carried out in 1988 and so direct comparison may be made. The Argyll study was carried out in broadleaved woods and so comparison with the low altitude broadleaved sites from Hamsterley and the semi-natural sites of the present study are appropriate and these comparisons are presented in Table 4.3.

The breeding of both Blue and Great Tits is considerably earlier in Argyll than in the present study in County Durham. Petty's less complete presentation for the Pied Flycatcher gives a mean first egg date in the Argyll study of approximately 20 May, while that for Hamsterley was 19 May, Low Altitude sites 17 May and

Table 4.3

Comparison between first egg dates in the Argyll study (Petty, 1989) and the Hamsterley, Low Altitude sites and semi-natural sites in the present study in 1988.

BLUE TIT			
	First Egg Date	Sample Size	SE
Argyll	3 May	97	0.51
Hamsterley	13 May	79	0.63
Low Altitude	10 May	40	0.58
Semi-natural	9 May	19	1.08

Significant comparisons with Argyll Blue Tits:			
Hamsterley	t=12.09	df=174	P<0.01
Low Altitude	t=9.41	df=135	P<0.01
Semi-natural	t=4.73	df=114	P<0.01

GREAT TIT			
	First Egg Date	Sample Size	SE
Argyll	6 May	52	0.71
Hamsterley	13 May	22	1.20
Low Altitude	11 May	15	1.52

Significant comparisons with Argyll Great Tits:			
Hamsterley	t=5.09	df=72	P<0.01
Low Altitude	t=3.34	df=65	P<0.01

semi-natural sites 19 May so no significant differences are likely.

Other studies can only be compared using mean first egg dates from several different years in each. Dunn (1976) gives the mean first egg dates from Wytham Wood for Blue and Coal Tits as 27 April and 1 May respectively for 1962-75. These were compared with the Hamsterley dates (1985-91) of 9 May, a difference of 12 days and 9 May, a difference of 8 days for Blue and Great Tits respectively.

4.3 The Effect of Timing of Breeding on Clutch Size

As shown in Section 3.2.1, clutch size declined as the breeding season progressed for the Blue, Great and Coal Tits and Pied Flycatcher. Perrins (1965) found a reduction of 0.09 eggs for each day later that breeding began in the Great Tit in Wytham Wood, Oxford. This does not differ significantly from the figure of 0.06 eggs for Hamsterley ($t=0.632$, $df=370$). Perrins and McCleery (1989) found a reduction of only 0.07 eggs for each day of delay by the Great Tit at Wytham Wood and this is even more similar to the Hamsterley figure of 0.06. Lack (1958) showed a difference of 0.12 eggs for each day, but this is still not significantly different.

The suggestion (Section 3.2.1) that the relationship between the annual mean first egg date and the slope of the original annual first egg date/clutch size for the Blue Tit is positive requires further study. It implies that in a late breeding season, breeding is confined to a period where clutch size declines at a faster rate than during an early season. This is presumably related to a reduced utilisable invertebrate availability.

If the adjusted Blue Tit first egg date/clutch size regression from the present study at Hamsterley is used, it predicts a clutch size of 10.4 eggs when the Wytham mean first egg date (Dunn, 1976) is inserted. The actual Wytham clutch size (1983-84) was 8.9 (East and Perrins, 1988). This suggests that although breeding is significantly earlier in Wytham Wood, the equation line between clutch size and first egg date is situated to the left (ie earlier) of the Hamsterley equation line, with a similar slope. In contrast if the Wytham Great Tit first egg date is entered into the Hamsterley regression for first egg date on clutch size, a clutch size of 8.1 is predicted which is the same as that found in the East and Perrins (1988) study. These results suggest that whereas the same regression can be applied for Great Tits in Wytham and County Durham, the same regression cannot be used for both sites for Blue Tits. It would appear that the relationship in Blue Tits is relative to the starting of laying, whereas in the Great Tit it is related to actual calendar date. This difference needs further research.

The large differences in timing of breeding in Blue and Great Tits may be related to latitude in this case, although this does not explain the differences between the Argyll study and the present one. In suburban Cardiff gardens (Cowie and Hinsley, 1987) found that the timing of breeding was very similar to Wytham Wood. Dhondt et al. (1984) found a gradient in laying dates from urban, through suburban to rural in the Great Tit but not in the Blue Tit. Within the rural habitats, they did not find any differences between 'good' and 'poor' habitats. This contrasted with the work of Lack (1955 and 1958) who suggested that laying would be later in poorer habitats in the same way as he found it to be in the Corsican Pine plantations compared with the adjacent Scots Pine plantations. Food seems to be a likely cause of differences in the breeding dates and success of these birds.

Previous work on breeding tits (Kliujver 1951, Lack 1958, Perrins 1965, van Balen 1973) have shown that spring temperatures are the major effect on the timing of breeding. This effect is thought to be effected through the availability of insects.

Lundberg et al. (1981) reported a decrease of 0.07 eggs per day for the Pied Flycatcher in central Sweden. The figures for Hamsterley and the Semi-natural sites were 0.06 and 0.09 respectively, which are both very similar to the Swedish result. Järvinen and Väisänen (1983) also found a decline of about 0.07 eggs per day in Finland. When Järvinen (1989a) considered the relationship between clutch size and laying date over the whole of Europe, he did not find it to be a significant relationship. This is presumably due to the spread of breeding dates within this area and the differences in the rate of decline in clutch size relative to the date of the start of breeding. The decline in clutch size with the advance in the breeding season is approximately the same between different parts of Europe, but the equation line is shifted earlier or later by differences such as latitude, spring temperatures etc.

Crick et al (1993), using data from the British Trust for Ornithology nest record cards, support the view that single brooded bird species have a clutch size which declines throughout the breeding season. They found that single brooded species start to lay when the optimal clutch size is greatest thus maximising the number of chicks produced in their single brood which are likely to fledge. Upon that pattern, certain constraints are imposed. Perrins (1970) suggested that the chicks may be dependent upon a short period of food abundance for survival and so the clutch cannot be laid at the energetically optimal time. These energy levels drop through the season. As mentioned in the previous chapter, the date of breeding and clutch size have been shown (in other studies) to be related to the age of the breeding pair with younger, less experienced birds, laying smaller clutches, later in the season. Habitat quality may also constrain the date of breeding and clutch size as shown in the present study. Migrants, such as the Pied Flycatcher, are restricted by the date of arrival of both birds of the pair on to the breeding ground. Pied Flycatchers are largely insectivorous, throughout their lives, and sufficient food must be available on the breeding site before their energy requirements for breeding are met. In general they lay eggs very soon after finding a mate and settling on a nesting site.

4.4 The Effects of Altitude on the Timing of Breeding

The reason for the delay in breeding with increasing altitude is difficult to elucidate. It is likely that the temperature is lower at higher altitude and so the invertebrate numbers may increase later. In the present study some of the habitat at Hamsterley was probably poorer (ie, less food available) than the lower altitude sites. However, the semi-natural sites have been included in the figures and these are at relatively high altitude and are of high quality.

Altitude has been shown to have an effect on the timing of breeding in the Pied Flycatcher by other researchers. Stowe (1987) found that, in 31 woods which support Pied Flycatcher populations in western Britain, the mean first egg date was delayed by one day for every 42m gain in elevation. Using the standardised first egg date/altitude equation from the present study, a one-day delay was caused by a rise of 50m. These figures are close enough to suggest that this sort of delay is an effect throughout Britain.

Järvinen (1989a) discovered a decrease in Pied Flycatcher clutch size with increasing altitude which was approximately the same in coniferous, mixed and deciduous forests. However, he did find that the clutches were generally larger in deciduous and mixed than in coniferous forests. Lundberg et al. (1981) found that Pied Flycatchers started breeding about 4 days earlier in deciduous compared with coniferous woods and the final breeding success was higher in the deciduous. In the present study, it was the Pied Flycatchers which did not appear to alter their first egg date with site whilst other species did. However, this may at least in part be due to the competition for food and nesting holes with the tits, in the present study, which encouraged the Pied Flycatchers to breed as soon after their return to the area as possible.

4.5 Occupancy

This is not a factor discussed by other researchers and the large differences between Kielder Forest and the areas in County Durham can only at present be explained by food availability and further research is required to clarify the picture.

Campbell (1968) noted the competition for nesting holes between the migratory Pied Flycatchers and the resident tits. He blocked the entrance holes to the nestboxes until the flycatchers arrived in 1958 and 1959 with an apparent increase and maintenance of that in the occupation level of Pied Flycatcher. However, when he repeated the operation in 1964 no such increase occurred. Campbell felt that the effect of the experiment had been inconclusive. No such experiment was carried out in the present study and nestboxes were generally provided in excess but the increase in nestboxes, particularly in Horsleyhope Ravine showed that (at least in some years) there is a considerable potential for expansion in the numbers of Pied Flycatchers. Male Pied Flycatchers only defend their nesting hole and so nesting density levels can be increased with increased nestbox density (von Haartman, 1971). This can, however, affect breeding success (Alatalo and Lundberg, 1984).

Section 3.1.2 shows that Blue Tits were reluctant to breed at high altitude in the County Durham sites and only appear to do so when overall numbers were high (eg, 1988). Coal Tits, on the other hand, preferred to breed at the higher altitude sites and only at the lower altitudes ones in years of high population (eg, 1990). Thus, in most years, there is no competition between the two species, particularly as the two populations do not appear to follow the same trend in numbers.

SUMMARY

1. The occurrence and breeding success of four species of small, hole-nesting woodland birds (Blue, Great and Coal Tit and Pied Flycatcher) were examined in areas by erecting nestboxes in woodland in County Durham. The chosen areas were Hamsterley Forest which has low altitude broadleaved planations as well as high altitude conifers, and two semi-natural oak woods, Backstone Banks and Horsleyhope Ravine. Some data were also derived from a nestbox scheme in Kielder Forest, Northumberland.

2. Comparisons between the study areas shows large differences in the levels of occupancy of the nestboxes from Kielder at 15% to Backstone Bank 91%. Kielder supported a significantly greater ($t=6.51$, $P<0.01$, $df=8$) proportion of Great Tits (54%) than would have been expected compared to Hamsterley (16%), other species (Coal Tit and Pied Flycatcher) occurred in significantly larger proportions in Hamsterley (8 and 27% respectively) than Kielder (2 and 5% respectively) $t=3.71$, $P<0.01$, $df=8$ and $t=6.53$, $P<0.01$, $df=8$. Almost all of the Horsleyhope Ravine and Backstone Bank nestboxes were occupied by Blue Tits (77%) until the number of nestboxes at Horsleyhope Ravine was doubled and the proportion dropped to 47% there as Pied Flycatchers increased their proportion from 19% to 48%. Similarly at Low Redford (a Hamsterley site) the number of Pied Flycatchers increased significantly in the area where the box density was increased (X^2 10.05, $df=3$, $P<0.05$).

3. The County Durham study sites varied between 150 and 370m. A significant negative relationship $y=89.0-0.20x$ ($r=-0.74$, $df=34$, $P<0.01$) was found when the

occupation percentage for all species was regressed on site altitude. A significant positive relationship $y=4.0 + 0.11x$ ($r=0.34$, $df=38$, $P<0.05$) was found when the coefficient of variation of the annual occupancy rate of all species was regressed on site altitude. Blue Tit showed similar significant relationships for both regressions. Great Tit and Pied Flycatcher did not have significant relationships for either. The Coal Tit did not have a significant regression for occupancy and altitude, but a significant ($r=-0.54$, $df=16$, $P<0.05$) negative relationship between the coefficient of variation and altitude.

4. Clutch size was shown to decline as the first egg date increased in Blue Tit in both the Hamsterley and semi-natural sites. At Hamsterley, a regression line using adjusted first egg dates was produced to eliminate between year differences and the line was $y=16.03-0.22x$ ($r=-0.56$, $df=335$, $P<0.01$). Pied Flycatcher produced a similar regression lines in Hamsterley and the semi-natural sites, $y=9.3-0.06x$ ($r=-0.45$, $df=158$, $P<0.01$) for Hamsterley (1987-91) and $y=9.0 -0.09x$ ($r=-0.33$, $df=43$, $p<0.01$) for the semi-natural sites. The Great Tit regression line was $y=10.0-0.06x$ ($r=-0.25$, $df=85$, $P<0.05$) and Coal Tit $y=11.9-0.09x$ ($r=-0.37$, $df=52$, $P<0.01$) both from the Hamsterley data. The level of decline of clutch size with the breeding season was similar to that in other studies.

5. The mean adjusted first egg date of Blue Tit was regressed on site altitude to produce the line $y=25.4 + 0.03x$ ($r=0.46$, $df=69$, $P<0.01$). The Great Tit actual first egg date regression was significant $y=39.3-0.04x$ ($r=-0.44$, $df=19$, $P<0.05$) but Coal Tit and Pied Flycatcher did not produce significant regressions. The increase in Pied Flycatcher first egg date with altitude (1 day for 50m) was similar to that found by Stowe (1987), 1 day for every 42m.

6. Invertebrates samples were collected from 6 tree species in 1990 at 10-day intervals through the bird breeding season. In 1991 a late season sample was taken to compare with 1990. Four of the 6 tree species had significantly lower densities of invertebrates and the other 2 were also lower in 1991 than 1990.

7. The breeding success of Pied Flycatcher at Hamsterley was similar to that found in North Yorks by Follows (1990) at 74%, however, in the Forest of Dean a level of 87% was found 1948-58 (Harvey et al, 1985).

8. Great Tit success was the most variable at Hamsterley. The success of both Great Tit and Blue Tit was low compared to most other studies except Flegg and Cox (1975) where predation levels were very high and Cowie and Hinsley's (1987) study in gardens when many juveniles starved to death. Starvation was the major reason for failure in poor years such as 1991 rather than predation.

9 It is proposed that success is a measure of the birds' ability to assess in advance the quality of the breeding season. In 1991 many birds laid large clutches (which may indicate that invertebrate levels prior to egg laying were high). Success levels were very low and corresponded with low invertebrate levels late in the breeding season.

10. The timing of breeding, measured by the first egg date, was far later in this study than in Argyll (Petty, 1989) and in southern England studies.

11. This study showed the importance of invertebrate density to the productivity of small hole-nesting bird species.

12. The effects of altitude on these small, hole-nesting bird species has not been shown previously in Britain.

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APPENDIX

Site	Grid Reference	Area (ha)	Altitude (metres)	Age of Stand (years)	Number of Tree-Shrub Species	Density (No trees-shrubs/ha)	% Broadleaved Species	% Conifer Species	% Shrubs	% Open Space	Ground Flora	
											Species-Rich	Species-Poor
Low Ayhope Beck	NZ080310	4.0	175	51	12	1155	10.9	89.1	1.3	20.0	*	
Middle Ayhope Beck	073311	5.4	180	51	11	1435	4.4	95.6	0.1	0		*
Upper Ayhope Beck	069313	4.1	185	21	7	1188	5.3	94.7	0.1	45.0		*
Bedburn Beck	087310	4.4	160	50	18	1605	13.5	86.5	1.0	0		*
Birch Plant	055299	4.0	250	60	1	816	0	100	0	0	*	
Black Hill	038302	2.0	360	41	2	2500	0	100	0	0		*
Black Hill Top	095311	2.6	150	100+	9	523	65.2	34.8	12.9	0	*	
Cliff Gill	069314	3.5	210	22	7	2275	1.1	98.9	0	0		*
Cloudlam Beck	029297	3.7	260	40	9	1314	8.7	91.3	1.3	0	*	
Dryderdale Exp.	086335	5.0	230	34	1	1100	0	100	0	0		*
Forest Lodge	082310	1.3	175	53	5	350	95.7	4.3	8.4	35.0	*	
Forest Offices	091312	2.4	150	54	3	400	100	0	9.5	0	*	
Frog Wood	069301	4.7	195	53	8	384	69.0	31.0	6.0	0	*	
Grove Exp.	071301	5.0	185	56	1	625	0	100	0	0		*
*Low Redford North)	086312	9.3	175	53	5	541	64.0	36.0	1.5	0	*	
*Low Redford South)	087311	9.6	175	53	6	541	64.0	36.0	1.5	0	*	
Mayland Exp.	065292	5.0	285	62	1	918	0	100	0	0		*
Neighbour Moor	026290	3.9	350	42	2	2500	0	100	0	0		*
Nest Plant. (beck)	053299	11.6	200	51	11	1050	8.0	92.0	0.9	12.0		*
Nest Plant. (conifer)	053300	2.0	225	52	1	625	0	100	0	0		*
North Plant.	080311	8.5	200	52	6	570	42.4	57.5	0.5	0	*	
Pennington Exp.	047289	5.0	340	51	1	772	0	100	0	0		*
Pennington Plant.	038275	4.8	365	111	5	246	97.2	2.8	3.8	0	*	
Pennington Rigg	051289	3.4	320	59	2	625	0	100	0	0		*
Potato Hill Exp.	068310	5.0	230	61	1	641	0	100	0	0		*
Redgate Shield	029298	12.0	260	41	7	1324	9.4	90.6	0.9	10.0		*
Sharnberry Flat	027299	3.5	325	40	2	1658	0	100	0	0		*
Sharnberry Exp.	022304	5.0	370	40	2	2500	0	100	0	0		*
Spurlswood Beck	060289	3.2	220	91	6	337	98.5	1.5	1.8	0	*	
Tinker Hills	042269	6.4	275	91	8	95	87.4	12.6	5.2	30.0	*	
Windy Bank	089311	1.7	160	50	13	668	19.9	80.1	2.6	0		*
Backstone Bank	067410	8.0	230	100+	8	247	99.2	0.8	1.6	0	*	
Horsleyhope Ravine	063485	6.3	200	100+	11	675	95.9	4.1	32.7	0	*	

* Low Redford North and Low Redford South are the 2 sections of Low Redford

TREE SPECIES PRESENT IN EACH SITE (AS PERCENTAGE) - HAMSTERLEY AND THE SEMI-NATURAL SITES

Site	Alder	Ash	Beech	Birch	Bird Cherry	Blackthorn	Crab Apple	Elm	Gean	Hawthorn	Hazel	Holly	Lime	Oak	Rowan	Sycamore	Willow	Yew	European Larch	Japanese Larch	Scots Pine	Norway Spruce	Sitka Spruce	Western Hemlock
Low Ayhope Beck	4.6	0.5		0.7				0.1		0.3	0.9	0.1		3.4		0.3			29.7		29.7	29.7		
Middle Ayhope Beck	2.6	0.4	0.1	0.4						0.1				0.1	0.1	0.5				47.8	23.9	23.9		
Upper Ayhope Beck	4.2	0.2	0.1	0.4								0.1			0.3								94.7	
Bedburn Beck	2.9	3.7	2.9	1.3		0.1	0.1		0.4	0.1	0.6	0.1	0.1	0.4	0.5	0.4			1.2		6.8	23.4		55.1
Birch Plant.																					100			
Black Hill																					30.0		70.0	
Black Hill Top	1.1		2.5	26.4 (40%)							0.6	1.7		22.7	10.1						0.6	34.2		
Cliff Gill	0.7	0.2												0.1	0.1					24.7	24.7		49.5	
Cloudlam Beck	4.3			2.5	0.7					0.1	0.3				0.7		0.2			27.9		63.4		
Drydersdale Exp.																				100				
Forest Lodge				34.9 (20%)					1.4	1.4				58.0							4.3			
Forest Offices												2.0		90.5	7.5 100%									
Frog Wood				2.1							0.5	1.6		56.5	3.9	1.0		3.4	31.0					
Grove Exp.																						100		
Low Redford North)				5.0 (10%)								1.0		58.0					35.0		1.0			
)																								
L. R. South)				5.0 (10%)								1.0		57.0		1.0			35.0		1.0			
Mayland Exp.																					100			
Neighbour Moor																					30.0		70.0	
Nest Plnt. (beck)	4.7	0.5		1.2						0.1					0.8		0.3			15.5	15.5	20.5	40.5	
Nest Plt. (conifer)																					100			
North Plant.			1.0	1.0								0.5		40.0					54.5		3.0			
Pennington Exp.																							100	
Pennington Plant.			76.4 (5%)	5.3										5.3	10.2						2.8			
Pennington Rigg																					50.0		50.0	
Potato Hill Exp.																					100			
Redgate Shield	2.4			5.4	0.2										0.6		0.7			62.9		22.7		
Sharnberry Flat																				75.4	24.6			
Sharnberry Exp.																					50.0		50.0	
Spurlswood Beck			41.2	1.8								1.8		51.9	1.8				1.5					
Tinker Hills			21.1	15.8 (10%)								2.1		28.4	14.7 (10%	5.3			6.3		6.3			
Windy Bank	6.3	1.0	0.7	1.7	1.7					0.3	0.6			3.7	1.7	2.2					44.5	9.0		26.6
Backstone Bank	11.3	4.1		18.2								1.6		58.3	3.2	2.4						0.8		
Horsleyhope Ravine		2.2	3.3	8.7						2.7	20.2	9.8		41.8	5.9	1.3			3.5		0.6			

NOTES: The figures in brackets represent the proportion of the species forming the shrub layer.