UNIVERSITY OF SOUTHAMPTON

THE CONSERVATION AND FORAGING ECOLOGY OF BUMBLEBEES (*Bombus* spp.) IN AGRO-ECOSYSTEMS

Andrea R. Kells M.A., M.Sc.

Thesis submitted for the degree of Doctor of Philosophy

RESEARCH DIVISION OF BIODIVERSITY AND ECOLOGY
SCHOOL OF BIOLOGICAL SCIENCES
FACULTY OF SCIENCE

MARCH 2002

"Ye must perdonne my wyttes, for I tell you plaine, I have a hive of humble bees swarmynge in my brain"

Unknown; *Republica*

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF SCIENCE

RESEARCH DIVISION OF BIODIVERSITY AND ECOLOGY

Doctor of Philosophy

THE CONSERVATION AND FORAGING ECOLOGY OF BUMBLEBEES (*Bombus* spp.) IN AGRO-ECOSYSTEMS

by Andrea R. Kells

The aim of this project was to provide a framework for future habitat management schemes aimed at conserving bumblebee populations in agro-ecosystems. I focused on the identification of landscape components that could be of value in the implementation of future conservation schemes. Specifically, two areas where individual bumblebees display ecological 'choice' were investigated; forage choice, and nest-site choice. The availability of suitable forage resources and nest sites are two important components in the continued survival of bumblebee populations on agricultural land, and must be considered in planning any conservation scheme.

One way in which increased melliferous forage can be provided in agro-ecosystems having impoverished floral diversity is through allowing natural regeneration along field margins, or sowing these with a wildflower seed mix. I found that margins of both types attracted a higher density and diversity of foraging bumblebees than corresponding edges managed as conservation headlands. Floral diversity was found to be a much more important component of overall attractiveness than floral density, and perennials were a much more attractive resource than annuals; the preferences of different bee species for different forage plants indicates that conservation schemes could have a species-specific component. Growing certain crop species could greatly supplement the floral resources provided by areas of semi-natural vegetation, especially such nectar-rich 'novel' crops as *Onobrychis viciifolia*.

Newly emerged queens displayed interspecific site preferences when nest searching along field boundaries. Subterraneous nesting species (*B. terrestris, B. lapidarius, B. lucorum*) showed a strong preference for searching along banks, whilst *B. pascuorum, B. hortorum* and *B. ruderarius* searched preferentially along edges with tussocky vegetation. *B. lapidarius* in particular was most frequently observed searching along exposed boundaries; this species has a higher temperature threshold, and nests along exposed edges may maximise the heat reservoir effect of the soil. It is clear that a range of different boundary types need to be provided if nesting requirements of a variety of bumblebee species are to be met.

These findings are discussed in detail, with reference to the implications for conservation of bumblebees in agro-ecosystems. The possible effects on other species of flora and fauna are also considered.

INDEX

Abstract i
Index ii
List of tables vi
List of figures vii
List of plates viii
Acknowledgements ix

1. GENERAL INTRODUCTION 1-27

1.1 The plant-pollinator system 1
- 1.1.1 The mechanisms of pollination and fertilisation 1
- 1.1.2 Floral resources and rewards 2
- 1.1.3 Co-evolution and co-adaptation of plants and their pollinators 3
- 1.1.4 Pollinators exert selective pressures on floral morphology 5
- 1.1.5 Potential benefits of pollinators 6
- 1.1.6 Summary 6

1.2 Bee pollination 7
- 1.2.1 General behavioural differences between *Apis mellifera* and *Bombus* species 7
- 1.2.2 Floral constancy 9
- 1.2.3 Ambient temperature requirements 10
- 1.2.4 Sonication 10
- 1.2.5 Summary 11

1.3 The bumblebee life-cycle 12

1.4 U.K. Bumblebee species 15
- 1.4.1 The foraging ranges of *Bombus* species 18
- 1.4.2 Differences in nest site requirements 18
- 1.4.3 Geographical distribution 18
- 1.4.4 *Psithyrus* species 20

1.5 The decline of U.K. bumblebee populations 21
- 1.5.1 Agricultural intensification and subsequent environmental impact 21
- 1.5.2 Competition with honeybees 23
- 1.5.3 Other possible contributing factors 24
- 1.5.4 Impacts for agriculture 24
- 1.5.5 The wider picture 25

1.6 Conservation of bumblebee populations 26
- 1.6.1 Field margins as conservation priorities 26
- 1.6.2 Aims of this project 27

2. THE VALUE OF UNCROPPED FIELD MARGINS FOR FORAGING BUMBLEBEES 28-46

2.1 Abstract 28

2.2 Introduction 29

2.3 Methods 34
- 2.3.1 Study sites 34

  2.3.2 Sampling methods 34
  2.3.3 Floral preferences 35
  2.3.4 Statistical analysis 36

2.4 Results 36
  2.4.1 Numbers of foraging bees recorded on both margins 36
  2.4.2 Flower numbers through time 37
  2.4.3 Bee species 39
  2.4.4 Floral preferences of foraging bees 40

2.5 Discussion 42

3. THE VALUE OF WILDFLOWER STRIPS FOR FORAGING BUMBLEBEES 47-67

3.1 Abstract 47

3.2 Introduction 48

3.3 Methods 52
  3.3.1 Study sites 52
  3.3.2 Sampling methods 53
  3.3.3 Statistical analysis 54
  3.3.4 Floral preferences and niche overlap 55

3.4 Results 56
  3.4.1 Numbers of foraging bees recorded on both margins 56
  3.4.2 Flower numbers through time 57
  3.4.3 Bee species 57
  3.4.4 Floral preferences of foraging bees 60
  3.4.5 Niche overlap 62

3.5 Discussion 62

4. COMMON AND ‘NOVEL’ CROPS – NECTAR PRODUCTION AND BUMBLEBEE FORAGING BEHAVIOUR 68-89

4.1 Abstract 68

4.2 Introduction 69
  4.2.1 *Vicia faba* 71
  4.2.2 *Brassica napus* 72
  4.2.3 *Linum usitatissimum* 72
  4.2.4 *Glycine max* 72
  4.2.5 *Onobrychis viciifolia* 73

4.3 Methods 73
  4.3.1 Experimental set-up 73
  4.3.2 Nectar measurements: standing crop and secretion rates 74
  4.3.3 Microclimate 75
  4.3.4 Analysis 75

4.4 Results 76
  4.4.1 Microclimate 76
  4.4.2 Standing crop and secretion rates 76

4.4.3 Forager visitation patterns 80

4.5 Discussion 85

5. SAINFOIN (*Onobrychis viciifolia*); A NOVEL CROP FOR BEES 90-94

5.1 Fact Box 90

5.2 Description 91

5.3 Habitat 92

5.4 Cultural notes 92

5.5 Association with bees 92

6. EVIDENCE FOR HANDEDNESS IN FORAGING BUMBLEBEES 95-104

6.1 Abstract 95

6.2 Introduction 96

6.3 Methods 97
  6.3.1 Study site and sampling methods 97
  6.3.2 Analysis 99

6.4 Results 99

6.5 Discussion 101

7. PREFERRED NESTING SITES OF BUMBLEBEE QUEENS (HYMENOPTERA: APIDAE) IN AGRO-ECOSYSTEMS IN THE U.K. 105-130

7.1 Abstract 105

7.2 Introduction 106

7.3 Methods 108
  7.3.1 Study site 108
  7.3.2 Study design 108
  7.3.3 Analysis 111

7.4 Results 111
  7.4.1 Total numbers of bumblebee species observed 111
  7.4.2 Timing of emergence 112
  7.4.3 Habitat preferences 113
  7.4.4 *B. terrestris* 114
  7.4.5 *B. lapidarius* 115
  7.4.6 *B. lucorum* 115
  7.4.7 *B. pascuorum* 115
  7.4.8 *B. hortorum* 116
  7.4.9 *B. ruderarius* 116

7.4.10 *B. pratorum* 116

7.5 Discussion 124
7.5.1 Individual species preferences 124
7.5.2 Parasitism 126
7.5.3 Timing of emergence 127
7.5.4 Spatial patterns of nest founding 128
7.5.5 Availability of suitable nest sites 129

8. GENERAL DISCUSSION **131-142**

8.1 Project summary 131

8.2 Implications 134

8.3 Future directions 138

8.4 Concluding remarks 141

9. REFERENCES **143-169**

GLOSSARY 170

APPENDIX 1: LATIN AND ENGLISH SPECIES NAMES: FAUNA 172

APPENDIX 2: LATIN AND ENGLISH SPECIES NAMES: FLORA 173

LIST OF TABLES

Table 1.1: Examples of U.K. crops which require bees for pollination 7

Table 1.2: Mean proboscis and body lengths of the common bumblebee species in the U.K. 15

Table 1.3: U.K. bumblebee species grouped according to geographical distribution 19

Table 1.4: Habitat and species change in Britain 1947-1980 22

Table 1.5: The different types of arable field-boundary management, and their conservation objectives 27

Table 2.1: Dates of observations 35

Table 2.2: Flower species present in control and experimental margins across the duration of the experiment 38

Table 2.3: Total number of observations of each bee species across all timepoints, expressed as a percentage 39

Table 3.1: Annual and biennial/perennial species present in the wildflower strips, and numbers of flowers of each species 52

Table 3.2: Dates of observations 54

Table 3.3: Pearson correlation values for individual bee species numbers and number of open flowers on wildflower strips through time 58

Table 3.4: Total number of observations of each bee species across all timepoints, expressed as a percentage 59

Table 3.5: Total number of observations of each bee species on each flower species 60

Table 3.6: Spearman's correlation coefficients showing correlations between relative preferences of *A. mellifera* and *Bombus* spp. 60

Table 3.7: Morisita's measure of total niche overlap between species pairs 62

Table 4.1: Dates of observations 74

Table 4.2: Microclimate readings during the observation periods 76

Table 4.3: Results of two-way ANOVA showing influence of time, secretion rate and crop species on bee visitation. 81

Table 6.1: Mean numbers of anti-clockwise and clockwise visits made by each bee species, and Monte-Carlo simulation values 109

Table 7.1: Total number of observations of nest-searching queens of each species, expressed as a percentage 112

Table 7.2: Summary of references containing information on the preferred nesting sites of British *Bombus* species 126

LIST OF FIGURES

Figure 1.1: Generalised life-cycle of a typical British bumblebee species 13

Figure 1.2: Map of Britain illustrating the post-1960 distribution of bumblebee species groups 20

Figure 2.1: The principle components of a generalised arable field margin 30

Figure 2.2: Average number of bees observed foraging on experimental and control margins 37

Figure 2.3: Total number of open flowers on uncropped field margins and control margins through time 38

Figure 2.4: Numbers of each bee species observed on all uncropped field margins through time, expressed as a percentage 39

Figure 2.5: The preferences of bee species for each flower species 41-42

Figure 3.1: Average number of bees observed foraging on experimental and control margins 56

Figure 3.2: Total number of open flowers on wildflower strips and control margins through time 57

Figure 3.3: Patterns of abundance of the different bee species through time 58

Figure 3.4: Numbers of each bee species observed on all wildflower strips through time, expressed as a percentage 59

Figure 3.5: Scatter graphs showing relationships between preference indices 61

Figure 4.1: Standing crop and secretion rate of crops in terms of sugar content (mg) throughout a 14 hour period 77-79

Figure 4.2: Correlations between crop secretion rate and visitation rate 80

Figure 4.3: Forager visitation patterns 06:00-20:00 82-84

Figure 6.1: The frequency of switches between clockwise and anti-clockwise rotation on inflorescences 101

Figure 7.1: Schematic of plate 7.1 111

Figure 7.2: Patterns of abundance of nest-searching queens of the different species through time 113

Figure 7.3: Total numbers of each *Bombus* species queen observed in each of the two habitats 114

Figure 7.4: Boundary and edge type preferences for nest-searching *B. terrestris* queens 117

Figure 7.5: Boundary and edge type preferences for nest-searching *B. lapidarius* queens 118

Figure 7.6: Boundary and edge type preferences for nest-searching *B. lucorum* queens 119

Figure 7.7: Boundary and edge type preferences for nest-searching *B. pascuorum* queens 120

Figure 7.8: Boundary and edge type preferences for nest-searching *B. hortorum* queens 121

Figure 7.9: Boundary and edge type preferences for nest-searching *B. ruderarius* queens 122

Figure 7.10: Boundary and edge type preferences for nest-searching *B. pratorum* queens 123

LIST OF PLATES

Plate 1.1: The 6 common U.K. bumblebee species 17

Plate 2.1: A typical naturally regenerated field margin, year 1 33

Plate 3.1: A typical wildflower strip, year 1 51

Plate 5.1: A sainfoin crop (*Onobrychis viciifolia*) in flower 94

Plate 6.1: *B. lapidarius* foraging on sainfoin 98

Plate 7.1: Some examples of typical field boundaries 110

All photos A.R. Kells

ACKNOWLEDGEMENTS

This work was funded by a MAFF studentship with a CASE award from the Game Conservancy Trust. Many thanks go to Dave Goulson, my primary supervisor, for encouragement, general cheerfulness, and many words of wisdom over the last three years. I'm also grateful to my second supervisor, John Holland, for advice and help. Thanks to the many farmers who allowed access to their land, especially to Henry Edmunds and Viv at The Cholderton Estate for help, encouragement and enthusiasm, and for providing me with such a wonderful place to work. A mention must also go to David Allen at ADAS, who helped lots with the logistics involved, and also to Peter Hillier who always managed to find me transport from somewhere. Patrick Doncaster and Tas Crowe have my gratitude for helping with all manner of statistical nightmares, and Ray Comick was always there when my computer and I didn't quite see eye to eye.

My time in Southampton has been made all the more enjoyable by the people I've met and worked alongside, especially Mairi, Rikka, Tas, Alan, Bill, Nigel, Sue, Mick, George, Andy, Dan and co., and not least of all Jane, who was always there to offer advice over a pint. Wendy and Steve may not have been familiar with the subject matter, but offered many words of encouragement and kept me smiling. I'd also like to say thanks to Andrew for providing a welcome distraction from thesis writing.

Lastly, but most importantly, a huge thank you to my family for all their love, support and help over the years.

1. GENERAL INTRODUCTION

The aim of this introduction is to give the reader an overview of pollination biology and how it relates to bumblebees; bumblebees rely on floral rewards for food, and these are a product of many evolved pollination systems. It is hoped that such information will provide a context for the work that follows. This section will open with some information on plant-pollinator systems in general, including co-evolution of such systems and their pollinators. There will then follow specific information pertaining to pollination by bees, as these are the most important pollinators at temperate latitudes. The introduction will then concentrate on the general ecology of the bumblebees, giving some detail on their life-cycle, distribution, and habitat requirements. I will outline the main proposed reasons behind the declines in numbers documented across temperate Europe, and explore possible impacts that this may have, hopefully convincing the reader of the validity of conducting the research which follows.

1.1 The plant-pollinator system

Plant propagation, except where vegetative, is dependent on the systems of pollination and fertilisation. Pollination, the transfer of mature pollen to a receptive stigma on the same or another intraspecific plant, may be limited by the absence of pollen transfer vectors, of which there are many types. Simple systems rely on wind (anemophilous species), and less commonly water (hydrophilous species), for pollen dispersal, and have evolved adaptive features accordingly. The majority of plant species utilise animal vectors (zoophilous species), and these have evolved in such a way as to be attractive to their potential pollinators.

1.1.1 The mechanisms of pollination and fertilisation

Worldwide there are estimated to be 250,000 species of angiosperms (Heywood 1993), and at least 90% of these are pollinated by animals (Buchmann and

Nabhan 1996). Typically, a pollinator will work upwards on a stem or inflorescence of protandrous species, depositing pollen from conspecifics on the mature stigmas of the lower flowers, and collecting pollen from the ripe anthers of the younger, uppermost flowers (Price and Waser 1979). Sexual systems have evolved within most flowering plant species to ensure intraspecific outcrossing, and to minimise interspecific pollen flow, and therefore wastage. The receipt of pollen by a mature stigma is followed by the growth of a pollen tube from the intraspecific grain down the style to the ovary, fertilisation of the embryo sac with the male genetic material, and development of this ovule to seed. Various mechanisms prevent hybrid formation e.g. prevention of interspecific pollen tube growth (Heslop-Harrison *et al.* 1975, Hogenboom 1975). Protandry and protogyny (respectively the maturation of anthers prior to the stigma becoming receptive and vice versa; this temporal separation is known as dichogamy (Lloyd and Webb 1986)) act to limit self-fertilisation within a single flower, and combined with sequential flower opening on a stem can prevent self-fertilisation within an inflorescence or plant (Snow 1986, Klinkhamer and de Jong 1993). Other self-incompatibility mechanisms include heterostyly (Proctor and Yeo 1973, Barrett 1990, Bjorkman 1995), dioecy (Proctor and Yeo 1973, Bawa 1990), herkogamy (Webb and Lloyd 1986), selective post-zygotic abortion (Casper 1988, Stephenson *et al.* 1988; but see Andersson 1990) and selection for heterozygosity (Levin 1981), as well as the S-gene pollen-recognition complexes (Lewis and Crowe 1958, Barrett 1990), which are a feature of homomorphic self-incompatible species.

1.1.2 Floral resources and rewards

Anemophilous and hydrophilous plant species often have small, inconspicuous white or green flowers. There is no production of attractants, for example scent or nectar (Dafni 1992), and pollen grains are generally small and smooth (Proctor and Yeo 1973, Faegri and van der Pijl 1979, Whitehead 1983, Crane 1986). On the other hand, zoophilous plant species usually possess colourful and frequently scented flowers (Williams 1994). Scent is released either as a direct attractant from specialised osmophores, in the case of dung and carrion insect pollinated flowers, and also hawk-moth and bat pollinated blossoms (Vogel 1990), or, in the majority of blossoms, as a diffuse signal which is coupled with simultaneously offered nectar and pollen to induce attractiveness and promote floral constancy (Vogel 1990). These nutrient-rich rewards may also act to attract potential pollinators.

Nectar is composed of 3 main sugars (sucrose and the hexoses, glucose and fructose) in differing ratios (Sihag and Kapil 1983). In addition, the solution may contain a selection of the following - lipids, amino-acids, proteins, anti-oxidant organic acids, alkaloids, glycosides, saponins and phenolics (Baker and Baker 1979, Walter 1997). It provides energy for the forager, and perhaps also for their brood. Most zoophilous plant species contain one or more nectaries within the flowers, usually at the base of the corolla, with nectar guide marks on the petals to direct pollinators to the nectar source (Frankel and Galun 1977).

As well as being the currency of pollination, pollen is also rich in nutrients, including carbohydrates, proteins, amino-acids, lipids, and minerals, and is used by many pollen foragers as food for themselves and their brood. In addition to nectar and pollen, flowers may offer other rewards to pollinators, such as stigmatic exudates, floral tissues, mating sites, and shelter (Simspon and Neff 1983).

1.1.3 Co-evolution and co-adaptation of plants and their pollinators

Animals that act as potential pollinators through utilisation of floral resources include birds, bats, and individuals of many insect groups. Varying degrees of co-evolution exist within these plant-pollinator systems; this is more marked between some species than others. Pollinator specialisation is thought to be an adaptation within evolutionary time, with pollinator constancy being an adaptation within ecological time (Levin 1978). Floral hybridisation and speciation may also be pollinator-mediated, for example, pollen transfer by bumblebees between *Lycium ciliatum* and *L. cestroides* (Solanaceae) occasionally results in the formation of a hybrid cross (Bernadello *et al.* 1995). Indeed, many theories of angiosperm evolution implicate the behaviour of foragers as a mechanism for speciation (Waddington 1983). Co-adaptation, i.e. a facultative or obligate reciprocal relationship between two organisms, where the benefits are mutual (Macior 1984), can be observed seasonally in some species. Members of the bumblebee-pollinated *Pedicularis* genus produce queen-adapted nectariferous flowers vernally, and nectarless worker-adapted pollen-producing flowers aestivally (Macior 1984). An apparent obligate mutualism has been demonstrated between two species of Colletidae (Hymenoptera: Apidae) and *Verticordia* spp. (Myrtaceae) (Houston *et al.* 1993).

Pollinator flower constancy to a 'patch' of flowers may provide a barrier to cross-pollination; this can lead to speciation through ethological isolation (Grant 1994a, b, Bradshaw *et al.* 1995, Macior 1995, Goulson and Jerrim 1997) as the majority of pollen grains inadvertently collected from a flower are deposited on the subsequent 4 or 5 flowers visited (Cresswell and Robertson 1994, Cresswell *et al.* 1995). Deposition of marked pollen has been observed up to the eleventh plant (Rasmussen and Brødsgaard 1992), but the fluorescent tracing method used in that study has been criticised elsewhere (e.g. Thomson *et al.* 1986).

As flowers of different species diverge in similarity (Rathcke 1983), specialist pollinators may become more constant to particular species (Wilson and Stine 1996). Flowers of different species may be positively selected to be dissimilar from others (Grant 1949) in order to encourage pollinator flower constancy. Hybridisation and pollen wastage are therefore avoided.

Some plant species demonstrate mimicry. Often a mimetic species does not offer rewards itself, but attracts the potential pollinator due to its resemblance to a 'rewarding' species (Boyden 1982, Dafni 1983, Little 1983, Ackerman 1986, Johnson 1994). This is thought to be analogous to Batesian mimicry in animals (Johnson 1994, Johnson 2000), although the theory has been contested in the literature (Malcolm 1990, Joron and Mallet 1998). Mimicry may also take the form of sexual deception or brood-site mimicry (Dafni 1984, Nilsson 1992). The phenomenon of mimicry in plants is especially evident in the Orchidaceae, where more than one third of species (>8,000 spp.) do not offer rewards (Nilsson 1992). The absence of nectar is thought to reduce the risk of geitonogamy (see 1.1.4), as it shortens pollinator visit length to the individual flowers, and to the plant as a whole (Johnson and Nilsson 1999).

That co-evolution exists between some bee and plant species has been noted at least since Darwin (1859, 1876). Bees are a feature of the fossil record from the

Oligocene[1] (Walter 1997), and so the relationship between these and the plant species they utilise as sources of forage has had many years to evolve.

1.1.4 Pollinators exert selective pressures on floral morphology

At first glance it would seem that pollen transfer to conspecifics, and therefore fitness, is enhanced by attracting as many pollinators as possible. It follows that zoophilous plants should maximise attractiveness through copious nectar secretion and production of large numbers of showy flowers. However, this is often not the case, due to the physiological costs to the plant, and also through selective pressures imposed by the pollinating species.

Pollinators visiting a high proportion of flowers available within a plant on a single visit act to increase within-plant pollen transfer (geitonogamy) (de Jong *et al.* 1992, de Jong *et al.* 1993, Klinkhamer and de Jong 1993). As a pollinator moves around a plant it accumulates self pollen (pollen from that plant) and loses outcross pollen (pollen from other plants). Increased length of flower visitation sequence acts to increase the ratio of self to outcross pollen, and, consequently, the rate of geitonogamy. This has a negative effect on female fitness through interference with any outcross pollen present, or, in self-compatibles, through inbreeding depression (Klinkhamer and de Jong 1993, Ramsey and Vaughton 2000). Male fitness is also affected, as the amount of pollen exported to conspecifics is determined by levels of geitonogamy (Klinkhamer and de Jong 1993). Plants attract potential pollinators through presenting increased nectar rewards and/or producing a large number of flowers, but both these increase visitation time on the target plant, and act to increase geitonogamy. Therefore, especially in self-incompatible species, there is selection for an intermediate number of flowers and lower levels of nectar secretion.

Certain features of plant morphology may be attributed to the action of certain pollinators. Deep corollas in some moth-pollinated species are known to be co-evolutionary adaptations; deeper nectaries within the flower result in increased contact between the anthers and the pollinator's body when the pollinator attempts to reach the nectar (Nilsson 1988). Galen (1989, 1996) concluded that pollinator-mediated

---

[1] 35 million years ago

selection by bumblebees can alter floral form and explain morphological shifts in *Polemonium viscosum* (Polemoniaceae) along habitat gradients.

Mapping experiments of quantitative trait loci (QTL's) in monkeyflowers (*Mimulus*) (Bradshaw *et al.* 1995) suggest the evolution of reproductive isolation between sympatric species may involve genes with wide-reaching morphological effects, and therefore morphological change and ultimately speciation may occur much more rapidly than previously thought.

1.1.5 Potential benefits of pollinators

Pollinators provide a valuable service to plants, with the transferral of mature pollen to the receptive female parts of the same (self pollination) or other (cross pollination) plants of that species. They are necessary for the pollination of largely self-incompatible species, partially self-incompatibles, and self-fertile but non-self-pollinating species (Corbet *et al.* 1991).

Proposed benefits of insect-mediated pollination include increased fruit/seed yields, improved fruit quality and metaxenia, synchronised seed ripening resulting in reduced losses at harvest (*Brassica* spp.) and increased seed oil content (*Helianthus annus*) (Riedel and Wort 1960, Barbier 1962, Langridge and Goodman 1974, Williams and Free 1975, Barbier and Nadir 1976, Williams *et al.* 1987, Williams *et al.* 1990). Cross pollination eliminates inbreeding depression in self-compatible species, resulting in maintained vigour of the next generation of crop. That cross pollination results in hybrid vigour was noted as early as the turn of the 19th century (Knight 1799).

1.1.6 Summary

Pollination is a vital process, with many plant species dependent on animal vectors. Different animal species fill this niche in different parts of the world; in Europe most zoophilous plant species utilise insects as pollination vectors. Indeed, eighty-four percent of the European Union crops whose pollination requirements have been investigated and reported are dependent on, or benefit from entomophilous pollination (Williams 1994).

1.2 Bee pollination

At temperate latitudes, the social bees (Hymenoptera: Apidae) are commonly observed pollinators. Frequent, consistent, flower visiting behaviour and pubescent bodies make bees the most effective pollinators of many plant species (Corbet *et al.* 1991, Batra 1995), and they are necessary for the pollination of almost 40 species of crop in the U.K. alone (table 1.1).

Bees essential	Bees important	Bees beneficial
apple	broad bean	aubergine
blackcurrant	buckwheat	blackberry
celery	field bean	gooseberry
coriander	mustards	grapevine
fennel	plum	peach
gherkin	raspberry	peppers
kiwifruit	sunflower	redcurrant
marrow	turnip rape	strawberry
melon		swede rape
pear		tomato
pumpkin		white currant
sweet cherry		

Table 1.1: Examples of U.K. crops (grown for fruit or seed) which require bees for pollination (after Osborne and Williams 1996)

In the U.K., bumblebees (*Bombus* spp.) and honeybees (*Apis mellifera*) are the most economically important pollinators. Although bumblebees and honeybees are superficially similar, they have very different physiological and life-history traits, which influence their relative effectiveness as pollinators.

1.2.1 General behavioural differences between *Apis mellifera* and *Bombus* spp.

Honeybees visit most types of flower dependant upon insect pollination, and colonies are active year-round (Donovan 1990). However, honeybees are now known not to be “queens of pollinators” as was once thought (Percival 1950). The evolution of a highly eusocial lifestyle and relative colony longevity has necessarily resulted in an ‘extreme generalist’ foraging strategy (Donovan 1990), which has restricted the evolution of specific adaptations to individual plant species. Indeed, in flowers where specific ‘complex’ mechanisms have evolved to ensure cross-pollination, it is common for honeybees to circumvent these, and manipulate the flower to access the nectar without being dusted with pollen (Giurfa and Nuñez 1993). The outcome is that honeybees are less efficient pollinators of these species than co-evolved pollinators (such as some bumblebee species), and there appear to be no flowers that are specifically adapted to pollination by honeybees (Westerkamp 1991). Honeybees have shorter tongues than most bumblebee species, so although generalist, they are limited to foraging on flower species with relatively shorter mean corolla depths (Holm 1966).

Both bumblebee and honeybee workers feed on nectar, and collect and store pollen, on which to feed the brood. Pollen collection for colony utilisation has been shown to decrease the chances of pollination (Westerkamp 1991), as flowers are only pollinated if pollen is carried inadvertently (Westerkamp 1996). As pollen-foragers only visit male-stage flowers on dioecious plants (Paton 1993, Vaughton 1996), intraspecific pollination of such species by these individuals is unlikely to occur. As honeybee colonies function year-round, they must store food in order to survive the winter, wheras the transient nature of bumblebee colonies (see 1.1.3) means that their pollen requirements are much less. Individual honeybees are thought to remove more pollen than *Bombus* spp. during a foraging bout, but deposit less, and it is thought that in some cases they can act as antagonists to male reproductive success (Wilson and Thomson 1991), c.f. "floral parasitism" (McDade and Kinsman 1980, Batra 1995). However, honeybees are prolific pollinators of many crop and wildflower species, and they are the most valuable agricultural pollinator worldwide (Carreck and Williams 1998, Kevan 1999).

Honeybee colonies have proved to be fully manageable, i.e. they can be produced and utilised on a commercial scale (Williams *et al.* 1993). This is something that has proved elusive in the past for bumblebees, although some species are now beginning to be managed with varying success rates (van Heemert *et al.* 1990 [*B. terrestris*]). At present, however, managed honeybees remain the only readily available insect pollinators in the U.K. that can be moved to field crops to supplement declining populations of wild bees (Williams *et al.* 1993).

1.2.2 Floral constancy

Due to the division of labour, selection of floral resources in honeybee colonies has become the responsibility of a 'scout' caste. Once a potential food resource has been located, scout bees return to the nest and perform a 'waggle dance' before the workers to recruit foragers (Corbet *et al.* 1993). As many as 90% of the foragers from one nest have been observed at only 9.7% of the potential resources in natural habitats (Visscher and Seeley 1982), and honeybees will remain constant to a chosen resource until it expires. All other flower species receive few or no visits, which is deleterious to the pollination of the plant concerned as it limits outcrossing, and is further intensified with increasing length of the flowering period, especially if the plant is self-incompatible or a clone (Westerkamp 1991).

Faegri and van der Pijl (1979) have suggested that 'pollinators that collect both pollen and nectar may exhibit separate degrees of even types of constancy for the two activities'. It has been shown that although honeybees may take nectar from more than one flower species during a foraging trip, generally they will only collect pollen from one of these species (Zahavi *et al.* 1984). It has been suggested that this is indicative of 'pollen constancy' rather than 'flower constancy'. The benefit is that pure pollen loads seem to pack together in the corbiculae more efficiently than mixed loads (Zahavi *et al.* 1984).

Although individual bumblebees are relatively constant on a single flower species per foraging trip, bumblebee colonies as a whole are less constant in their flower choices than honeybees (Thomson 1981, Estes *et al.* 1983). Individuals may also include more than one flower species in a foraging strategy (Heinrich 1976a, 1979), which has implications for the likelihood of pollination of rare species. Recent research indicates that bumblebees may have a system of sorts that communicates, by production of certain pheromones, the presence of valuable resources to nest-mates (Chittka and Dornhaus 1999). However, it is obvious that this does not induce the level of recruitment (if indeed recruitment is induced at all) seen in honeybees. This lack of recruitment (Heinrich 1976b) has resulted in bumblebees being successfully used to pollinate commercial crops of tomatoes in glasshouses (Banda and Paxton 1991, Duchateau 1991, Velthuis and Cobb 1991); use of honeybees has limited success in greenhouses because as daily temperatures increase towards the summer months the windows need to be opened to prevent heat stress, and the honeybees will desert the commercial crop through recruitment to more attractive species outside (van Heemert *et al.* 1990). Disorientation, excitation, and the lack of sufficient food resources for such large numbers of insects are also thought to exacerbate the high levels of mortality and alterations in normal pollinating behaviour exhibited by honeybees in greenhouses (Doualt 1981, Free 1993); bumblebees do not seem to be affected in the same way.

1.2.3 Ambient temperature requirements

In order to fly, the thoracic temperature of Apidae must be raised to a certain threshold, above which it can be maintained metabolically (Heinrich and Raven 1972, Stone and Willmer 1989). This ambient thoracic temperature threshold is higher in honeybees relative to bumblebees. Both can generate some heat through 'shivering', but this is energetically expensive (Prys-Jones and Corbet 1991). Bumblebees have evolved a much less costly chemical means of heat generation through substrate cycling of fructose diphosphatase (Newsholme *et al.* 1972, Surholt and Newsholme 1981), where heat is produced as a by-product of ATP hydrolysis by fructose diphosphatase-phosphofructokinase cycling. There is no detectable fructose diphosphatase activity in honeybee flight muscles (Newsholme *et al.* 1972).

Bumblebees are bigger and better insulated, and are active at lower temperatures than other foraging insects including honeybees (Hippa *et al.* 1981); the species able to fly at the lowest minimum air temperatures have the densest insulating pubescence (Stone and Willmer 1989), which consequently increases pollen carry-over (Willmer *et al.* 1994). That there are temperature-dependent patterns of activity throughout the day in both *Apis* and *Bombus* species has been well documented (see Herrera 1990).

1.2.4 Sonication

The syndrome of sonication, or buzz pollination, is represented in many angiosperm families (Buchmann 1983), and is thought to represent a method of pollen conservation. It necessitates a distinctive behaviour pattern (Buchmann 1983, Corbet 1987), in which pollen-collecting bees embrace mature anthers, fold their wings, and emit brief and audible buzzes caused by vibration of the indirect flight muscles (Westerkamp and Gottsberger 2000). This applied vibration results in forcible discharge of a pollen cloud from the staminal pores at a critical frequency and its harmonics. Bumblebees and some solitary bee species perform sonication; honeybees cannot. Plant species which require buzz pollination are therefore reliant on visitation from such species, e.g. tomatoes, kiwifruit (King and Ferguson 1994), rhododendron (King and Buchmann 1995), and others (Prys-Jones and Corbet 1991, Batra 1993, King 1993, King and Lengoc 1993, Harder and Barclay 1994).

1.2.5 Summary

There have been problems in the past with growers selecting honeybees for managed pollination regardless of the crop grown, because of centuries worth of beekeeping knowledge pertaining to honeybees (Corbet 1987). However, increased knowledge of the physiological and morphological differences between honeybees and bumblebees has led in recent years to bumblebees being acknowledged as more important for pollination than honeybees for many plant species. The devastating impact the *Varroa destructor* mite has had, and indeed continues to have, on honeybee colonies, has emphasised the problems associated with reliance on a single species for pollination. Originally a parasite of *Apis cerana* (the Asian hive bee), where it primarily parasitises drone broods (Kevan *et al.* 1990), *V. destructor* attacks all *A. mellifera* castes and infestation results in the destruction of the colony through ingestion of the haemolymph of individuals by adult *V. destructor* females (Wanatabe 1994). Bumblebees do not appear to be susceptible to *V. destructor.*

The behavioural plasticity of bumblebees with respect to foraging repertoires (Zimmerman 1982), and their lower ambient temperature requirements allows efficient foraging under a much wider variety of environmental conditions than honeybees.

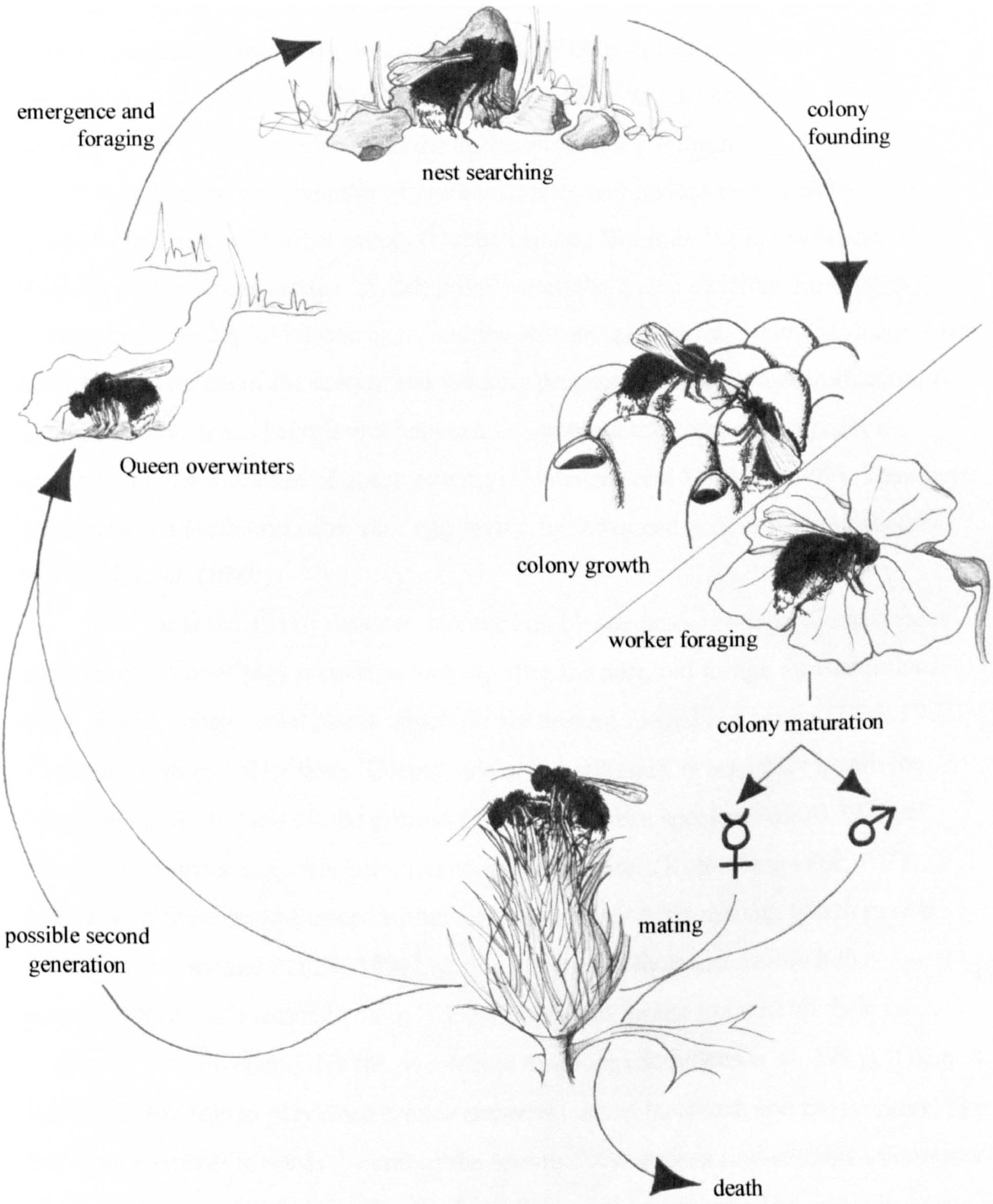
1.3 The bumblebee life-cycle

When soil temperature reaches a certain threshold, mated queen bumblebees emerge from the subterranean holes where they over-winter, and initiate nest building. Initially a queen will forage on pollen and nectar to meet the energetic requirements of ovary development. She may then spend up to a week (or longer) searching for a suitable nest site (Alford 1975), a behaviour typified by low flight over banks and rough uncultivated land, punctuated with investigation of small cavities and tussocks (Prys-Jones and Corbet 1991). When a suitable site has been chosen, the queen forages for pollen, which is moulded into a mass in the nest to form a clump on which she lays her first batch of eggs. The wax that is used to construct brood cells (and also food storage vessels, and the comb) is secreted from glands located beneath tergites 3-6, and sternites 3-6[2]; these are present in all female *Bombus* individuals. Bumblebee eggs are brooded for 4-6 days by contact with the underside of the queen's abdomen, after which time they hatch into larvae. These feed on the pollen mass, and are supplied with nectar and pollen in a fashion dependant on the species. 'Pocket maker' species construct waxen 'pockets' close to the brood clump. Returning foragers (the queen in the initial brood) deposit pollen masses into the pockets, and the larvae feed from these. The larvae remain together in a common chamber, and share a common food source. The larvae of 'pollen storer' species spin separate cells for themselves, and are fed individually by regurgitation by the queen (and later, workers) of a mixture of nectar and stored pollen through a hole in the wax covering of the larval cell. Size variability is less marked among the larvae of the 'pollen storers' as these receive more equal shares of food. 'Pocket-makers' and 'pollen-storers' are not distinct monophyletic groups (Koulianos and Schmid-Hempel 2000). After 10-12 days, larvae form cocoons and pupate. Further egg cells are constructed between or on top of these cocoons; these may or may not be primed with a pollen mass (Free and Butler 1959). After approximately 14 days as pupae, adult workers emerge, and after a short period commence foraging. This commencement of foraging is thought to be a light dependent reaction; Doualt (1981) found that newly hatched bumblebees exhibited a photonegative response, which gradually became photopositive over several days.

---

[2] tergites are the dorsal segmented plates of the abdomen, and sternites the ventral

Figure 1.1: Generalised diagram of the life-cycle of a typical British bumblebee species



Pollen and/or nectar are collected, depending on plant species, time of day, time of year, and foraging preferences of the individual worker (Cresswell and Robertson

1994). Nectar is imbibed by a foraging bee through its proboscis, and stored in a distensible honey stomach. That which is not used as fuel during flight is regurgitated in the nest. Nectar may also provide a source of water for bumblebees, as they do not collect water on its own (Prys-Jones and Corbet 1991). Pollen is necessary for provisioning the brood, as well as being essential for ovary development in newly emerged queens, and is collected in the corbiculae during foraging.

It is thought that the ratio of workers, males and queens produced by a colony is determined by two distinct events (Duchateau and Velthuis 1988, Duchateau and Velthuis 1992). These are the 'switch point' when the queen switches from laying fertilised eggs to haploid drone eggs, and the 'competition point' when the queen loses pheromonal control of the colony and workers prepare for their own reproduction. A strong correlation has been found between the moment the competition point is reached, and the initiation of queen rearing (Duchateau and Velthuis 1992). That there is pheromonal inhibition of worker egg-laying by the queen has been established by van Honk *et al.* (1980).

Towards the end of summer, mature bumblebee nests produce young queens and drones. Drones play no part in looking after the nest, but forage for themselves, often on tall, conspicuous plants which do not require specialised access (Lack 1982). They may also patrol habitats (Corbet 1992a, Fussell and Corbet 1992c), with the height of the flight path off the ground differing between species (Alford 1975). Drones scent-mark to attract potential conspecific mates (Kullenberg *et al.* 1973); queens visit these scent-marked routes and mate there. After mating, which may be multiple (Crozier and Pamilo 1996), young queens fill their distensible honey-stomachs from the maternal colony's food stores and forage to build up their fat bodies, to provide energy for the overwinter diapause (Semmens *et al.* 1993). The nest has no further role to play once drones and new queens have left, and the workers, like the drones, die off towards the end of the season. New queens find suitable overwinter sites, generally in north-facing banks that will not become warmed by any winter sun (Prys-Jones and Corbet 1991), until the task of nest building can begin with emergence in the spring. There is of course considerable variation within and between species in colony characteristics such as founding date, growth rate, and colony size when reproductives are produced (see Oster and Wilson 1978); many colonies fail before reaching this stage.

1.4 U.K. bumblebee species

There are approximately 50 species of bumblebee in Europe (Løken 1973), 19 of which are resident in the U.K., although 3 of these have not been sighted for many years, and may be extinct. Six U.K. species, namely *Bombus hortorum*, *B. lapidarius*, *B. pascuorum*, *B. terrestris*, *B. pratorum* and *B. lucorum*, are common and widespread, whilst the others are more localised in their distributions. Bumblebee names used throughout this study follow those of Prys-Jones and Corbet (1991). *Bombus* spp. differ in their patterns of hair colouration (plate 1.1); often drones (and in some species, queens) have slightly different markings to the workers. There may be several species with similar colouration patterns, and often such species are not closely related; these are thought to be examples of Müllerian mimicry (Prys-Jones and Corbet 1991). Interspecific differences in mean proboscis length and body size (table 1.2) result in observed differences in foraging strategies between species, although absolute proboscis length is related to individual body size (Pekkarinen 1979).

Species	Mean proboscis length (mm)	Mean body length (mm)
B. hortorum	13.1	11-16
B. pascuorum	8.97	9-15
B. lapidarius	7.55	11-17
B. terrestris	7.45	12-16
B. lucorum	7.4	9-16
B. pratorum	7.4	9-14

Table 1.2: Mean proboscis and body lengths of the common bumblebee species in the U.K. (after Brian 1957, Alford 1975, Prys-Jones 1982, Williams 1989).

Daily patterns of foraging activity are controlled mainly by weather conditions and light intensities, and also by the rewards offered by suitable food sources (Teräs

1985). It appears that temperature is the limiting factor for the commencement of foraging, and light intensity is limiting in the evening (Løken 1949, Lundberg 1980).

Plate 1.1: The 6 common U.K. bumblebee species

B. terrestris

B. lucorum

B. lapidarius

B. pascuorum

B. hortorum

B. pratorum

1.4.1 The foraging ranges of *Bombus* species

A search of the literature pertaining to bumblebee foraging ranges reveals that most of the early research concluded that bumblebees forage close to their nests (e.g. Mosquin 1971, Heinrich 1976a, Teräs 1976b, 1983, Kevan and Baker 1983, Bowers 1985, Rotenberry 1990). However, more recent work indicates that foraging may take place at much greater distances from the nest, and that such behaviour could potentially be due to avoidance of predators and intra-colony competition between foragers (Dramstad 1996). The use of harmonic radar (Riley *et al.* 1996) has revealed that bumblebees may forage at least 700m from their nests, even if suitable forage is available closer to the nest (Osborne *et al.* 1999), whilst in a more recent study, marked *B. lapidarius* and *B. terrestris* workers were observed foraging up to 1750m from their nests (Walther-Hellwig and Frankl 2000a).

1.4.2 Differences in nest site requirements

Bumblebee queens require a dry, well-insulated nest site in which to found a colony. Most bumblebee species predominantly favour one or two types of nest site. Some prefer to build a nest on or just below the surface, underneath grassy tussocks or similar (*B. hortorum*, *B. pascuorum*, *B. sylvarum*, *B. humilis*, *B. muscorum*, *B. ruderarius*), whilst others prefer an underground nest approached by a tunnel varying in length from a few centimetres to more than a metre (*B. terrestris*, *B. lucorum*, *B. ruderatus*, *B. lapidarius*) (Fussell and Corbet 1992b). Often in these cases, small abandoned mammal nests make ideal domiciles. The more adaptable species (*B. terrestris*, *B. lucorum*, *B. pratorum*, *B. lapidarius*) will readily take advantage of anthropogenic artefacts.

1.4.3 Geographical distribution

Bumblebee species in the U.K. can be classified into three groups on the basis of their distributions, analogous to the distribution groups in other parts of northern Europe (Løken 1973, Pekkarinen *et al.* 1981, Williams 1986). These three groups are termed 'mainland ubiquitous species', 'southern localised species', and 'widespread localised species', (after Williams 1982) (table 1.3, figure 1.2).

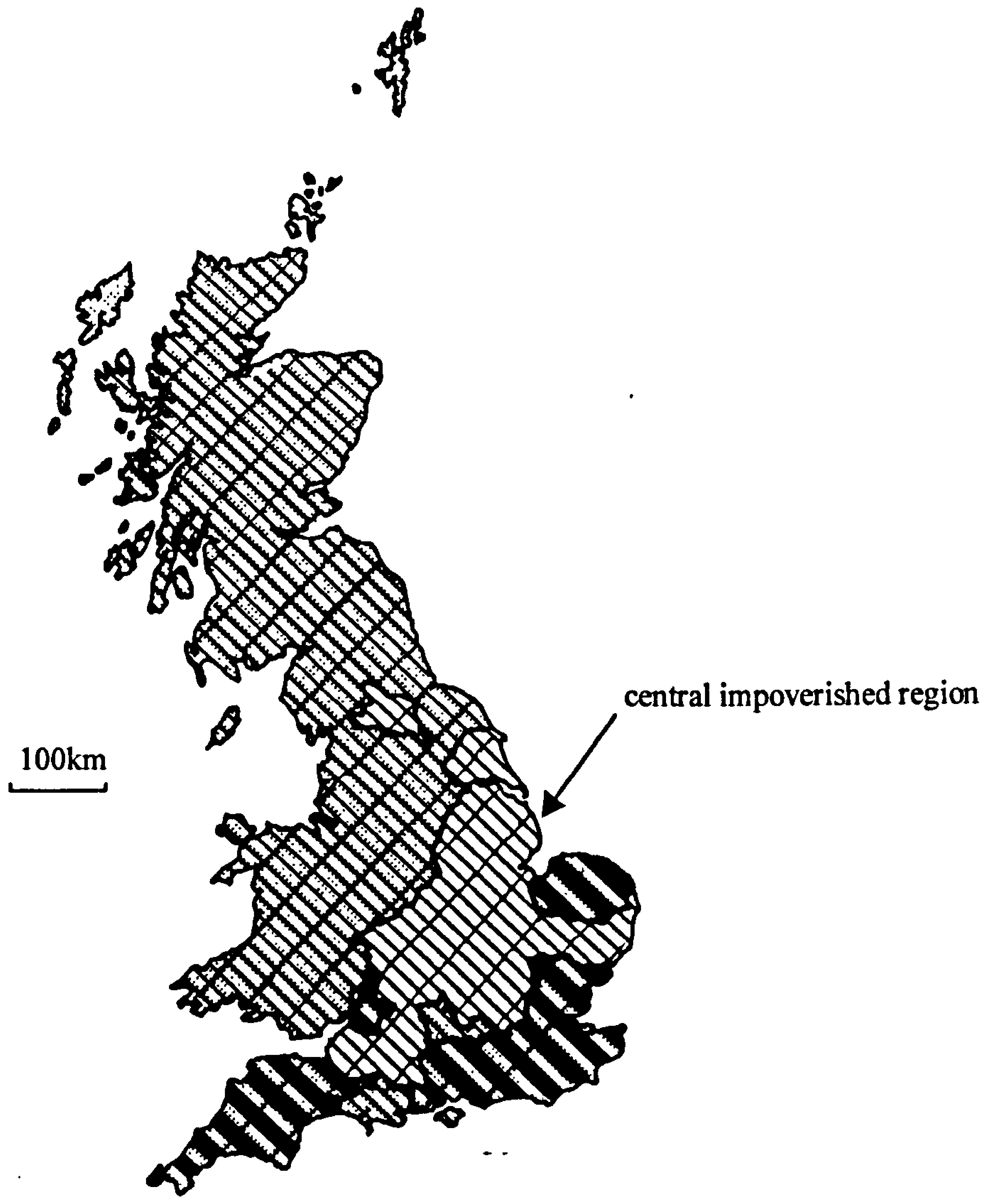
Mainland ubiquitous species	**Southern localised species**	**Widespread localised species**
B. hortorum (L.)	*B. ruderatus* (F.)	*B. laevis* (Vogt)
B. ruderarius (Müller) *	*B. muscorum* (L.)/*B. humilis* (Ill.)	*B. soroeensis* (F.)
B. pascuorum (Scop.)	*B. sylvarum* (L.)	*B. jonellus* (Kirby)
B. pratorum (L.)	*B. subterraneus* (L.)	*B. monticola* (Smith)
B. terrestris (L.)/*B. lucorum* (L.)		
B. lapidarius (L.)		

Table 1.3: U.K. bumblebee species grouped according to geographical distribution (after Williams 1986)

* Although *B. ruderarius* is a member of the mainland ubiquitous speices group according to Williams (1986), its distribution is much more localised than that of the other members of this group.

Members of the mainland species group are not generally at the latitudinal limits of their distribution throughout Britain. Members of the other two groups are localised, and are much less common. The southern localised species are restricted to southern counties and some parts of East Anglia, while the widespread localised species group is found in the same areas as the southern group, and also in Wales and to the north. Only the mainland species occur in central parts, an area termed the 'central impoverished region' (Williams 1986) (figure 1.2). This distribution pattern is very different from that pre-1960, when both the southern and widespread species groups were found throughout what is now the central impoverished region.

Figure 1.2: Map of Britain illustrating the post-1960 distribution of bumblebee species groups. Dots represent 'widespread local species', narrow lines 'mainland ubiquitous species', and broad stripes 'southern local species'. After Williams (1986)



1.4.4 *Psithyrus* species

The closest relatives of bumblebees are members of genus *Psithyrus* ('cuckoo bumblebees'), of which 6 species are resident in the U.K. The genus is thought to be monophyletic in origin (Plowright and Stephen 1978), and have evolved from a *Bombus*-type ancestor; morphologically they are very similar. However, the exoskeleton of *Psithyrus* spp. is tougher, thicker, and much less flexible than that of the bumblebees (Alford 1978), and during the evolutionary process they have lost the corbiculae and worker caste, as well as the ability to secrete wax from between the segmented plates of their abdomens (Prys-Jones and Corbet 1991). This renders *Psithyrus* spp. unable to construct brood cells of their own (Alford 1975), and instead, the queens invade *Bombus* spp. nests where they lay their eggs in cells constructed with wax taken from other parts of the comb (Alford 1975). The *Psithyrus* eggs and larvae are then raised to maturity by the *Bombus* colony workers (Fisher 1987). *Psithyrus* queens show behavioural control over the host workers, and there may also be pheromonal control (Fisher 1984, Fisher and Sampson 1992), although interactions between parasite and host appear to be species-specific (see e.g. Kupper and Schwammberger 1995). Each of the six British *Psithyrus* species shows a similar colouration pattern to one or several native species of *Bombus* (e.g. *B. lapidarius*, *B. ruderarius*, *P. rupestris*); as well as being examples of Müllerian mimicry (Prys-Jones and Corbet 1991), each *Psithyrus* species most closely resembles those *Bombus* spp. whose nests they normally parasitise. This may be an evolutionary attempt to circumvent visual systems of *Bombus* nest-mate recognition.

1.5 The decline of U.K. bumblebee populations

Bumblebee populations in the U.K. are in decline. It appears to be species nearest the edges of their distribution ranges that are most at risk of extinction (Williams 1986). Long-term patterns of climate change may have an impact, but a more major influence is likely to be the intensification of agricultural practices over most parts of the country.

1.5.1 Agricultural intensification and subsequent environmental impact

The roots of agricultural intensification can be traced to the beginning of the 20th century, but the real explosion in intensification occurred during the second world war (1939-1945), when self-sufficiency for food was at a premium. This was enforced by the 1947 Agriculture Act, and later by the Common Agricultural Policy, with its network of development grants and market subsidies (Williams 1986) (table 1.4).

The up-rooting of hedgerows, the development of waste ground, and the levelling of banks and ditches to provide maximal field sizes for crop production and to facilitate mechanisation (Pollard *et al.* 1974) have resulted in a reduction of suitable nest sites for *Bombus* species (Westrich 1989, Ortiz-Sánchez 1995). There is some disparity in estimates of hedgerow loss in this country (e.g. since 1938 there has been a 30% reduction in hedgerows (Park 1988); 50% have been lost since 1984 (Chapman and Sheail 1994)); nonetheless it is apparent that the decline has been great.

	% loss	**% gain**
Hedgerows	22	--
Broadleaved woodland	40	--
Semi-natural vegetation	25	--
Crop production	--	30
	Extinct	**Endangered**
Flowering plants	10	149
Dragonflies	3?4	11
Butterflies	1	13
Birds	0	36

Table 1.4: Habitat and species change in Britain 1947-1980 (after Nature Conservancy Council 1984)

Changing land uses and a trend towards annually disturbed anemophilous monocultures have resulted in decreased floral diversity, both spatially and temporally (Torchio 1991). Much nectar-rich perennial herbaceous vegetation has disappeared as a result (Williams 1982, Corbet *et al.* 1991) (anemophilous species do not produce nectar); this has been exacerbated by increasing applications of herbicides targeting broad-leaved weeds, which are a valuable nectar source for foraging insects (Torchio 1991). Some herbicidal sprays are also known to be directly toxic to bees (Moffett *et al.* 1972, Thompson 2001). Colin and Belzunces (1993) have shown that toxicity of pyrethroids (insecticides) to bees is strongly synergised when applied alongside fungicides.

Application of fertiliser may be contributory to the decline in nectivorous farmland plant species. Levels of nitrogen applied to highly competitive modern crop varieties have increased by up to 900% between 1943 and 1988 (Chalmers *et al.* 1990). It is thought that vigorous species such as modern crops out-compete all others in nitrogen-rich environments, and it has been found that fertilised crops suppress weed growth almost as effectively as applications of herbicide (Wilson 1993). Most species of arable weed are becoming restricted to the extreme edges of fields where agricultural inputs are less efficient (Wilson and Aebischer 1995).

The recent practice of omitting leguminous crops from crop rotation is also thought to be detrimental for bumblebees. These are especially important as a food plant for long-tongued species, and their floral conformation renders such flowers inaccessible to short-tongued pollinators (Rasmont and Mersch 1988, Rasmont 1995). The cutting of large areas of agricultural grassland for silage is carried out before most herbaceous species, with their valuable rewards, have flowered (Ellenberg 1988, Williams 1994). Grazing of any remaining semi-natural grassland all at one time (i.e. no rotation of animals) is potentially the single-most destructive management action that can be carried out on this potentially resource-rich habitat type (Edwards 1998).

Different authors have reached varying conclusions on which of the above constitute the main factors behind bumblebee species decline on agricultural land. The reality is that all the above-mentioned factors are likely to have some impact, albeit to different degrees in different situations.

1.5.2 Competition with honeybees

It is thought that competition with honeybees is unlikely to be a factor in bumblebee decline. The majority of bumblebee visits in the region of most bumblebee species impoverishment within the U.K. are to plants not utilised by honeybees (Williams 1986), although this could be due to evolutionary avoidance of competition - the 'ghost of competition past' hypothesis of Connell (1980). Competition with honeybees may be avoided by foraging early in morning before honeybees are active, and ingesting nectar that has accumulated overnight within the flowers, and also by foraging later in the evening (Corbet *et al.* 1991).

Bombus species that forage on flower species with deep corollas may be utilising a refuge free from competition, or they may keep nectar levels sufficiently depleted in such flowers to exclude *Apis mellifera* and solitary species (Corbet *et al.* 1995). Morse (1978) demonstrated within-species resource partitioning with respect to body size in one bumblebee species, although this has not been demonstrated between honeybees and *Bombus* spp.

1.5.3 Other possible contributing factors

Other anthropogenic sources may also be impacting on bumblebee decline, including planting of forestry, pollution, drainage and irrigation, and weed invasions (Batra 1995). Although specialist pollinators would appear to be most at risk, generalists can be specialists on high-density resources (Rathcke and Jules 1993). If fragmentation decreases the abundance of plant species which generalists rely on for forage, these may also become vulnerable.

It must be noted at this point that natural succession of landscapes is known to be at least partly responsible for the decline of some bumblebee species. Bumblebees are known to prefer fauna of early secondary succession (Fussell and Corbet 1992a). Banaszak (1997) found a decrease in Apidae numbers and diversity on xerothermic grasslands in western Poland over a 10-year period due to natural successional changes such as overgrowth of the grassland by maple.

1.5.4 Impacts for agriculture

Seed oil content is increased in some oilseed crops with cross rather than self pollination e.g. in sunflower (Langridge and Goodman 1974), safflower (Barbier and Nadir 1976) and lavender (Barbier 1962). In other crops, prolific insect activity ensures the pollination and set of early flowers, resulting in short, compact plants with well-filled pods low on the early racemes, which ripen to give an early, more uniform harvest e.g. oilseed rape (Williams *et al.* 1987), field bean (Riedel and Wort 1960), and lupin (Williams *et al.* 1990). In runner beans, pollination and set of the early flowers result in an early crop which commands a high price (Williams and Free 1975).

A decrease in bumblebee numbers within agricultural systems will lead to a decrease in, or increased variability of, seed yields and reproductive success of crops and wild flowers, as many are dependent on bees for pollination (Osborne and Williams 1996). Poor yields may cause farmers to abandon growing bee-pollinated crops unless these can be grown economically using imported seed. Wildflower species that obtain an inadequate pollination service will gradually disappear in a negative feedback loop, leading to an 'extinction vortex'[3] (Gilpin and Soule 1986, Guerrant 1992) for both plant and pollinator species, at least at a local level. Research has shown that abundance and diversity of all insect pollinators decreases with decreasing habitat area (Rathcke and Jules 1993), so conservation measures beneficial to bumblebees should also safeguard survival of those crops (and wildflowers) that rely on other species for pollination.

The decline of co-evolved pollinator and plant systems will also have knock-on effects on fauna which feed on the seeds, exudates, or vegetative parts of such plants, or which rely on these for shelter, egg-laying sites etc. Also, many semi-natural vegetation types are at risk because their flora is dominated by bee-pollinated plants, and many of these are very valuable habitats in terms of conservation e.g. Atlantic and Mediterranean heathland, garigue, and ancient meadows (Corbet 1992b).

1.5.5 The wider picture

A decline in bumblebee species and abundance is not solely a U.K. phenomenon. Range contraction and declines in numbers and diversity have also been reported in France and Belgium ([up to 40% decline in long-tongued Apoidea species in some areas] Rasmont 1988, [68% of *Bombus* taxa studied in regression] Rasmont *et al.* 1992), The Netherlands (Haeck and Hengeveld 1981, Kwak and Tieleman 1994), Russia (Berezin *et al.* 1995), and southern Poland (Kosior 1995). Banaszak (1984) working in western Poland found the density of bees increased in cultivated fields due to a high food density, but diversity decreased due to homogeneity of the resource present.

---

[3] extinction vortices progressively lower population sizes, resulting in local extinctions. Once a species enters a vortex, population size becomes progressively lower, which in turn, enhances the negative effects of the vortex.

1.6 Conservation of bumblebee populations

The prime objective for both conservationists and farmers is to halt further bumblebee decline both for the conservation of flowering plants and their dependant species, and to safeguard yields of commercial crops (Proctor and Yeo 1973, Osborne and Williams 1996). This can best be achieved through development of habitat management schemes that consider both the food and nest-site requirements of bumblebees, and the ease of implementation for farmers.

1.6.1 Field margins as conservation prioritites

The identification of arable field boundaries as possible refugia for plant and animal species initially attracted interest in the UK in grey partridge conservation (Rands 1985). Since then, different types of margin management have been identified (table 1.5), and MAFF (now DEFRA) has instigated the Arable Stewardship pilot scheme in two areas, where farmers are offered payments for managing arable field boundaries in ways which encourage wildlife (MAFF 1999). As part of this scheme, the relative environmental benefits posed by different types of margin and management are being monitored. Although thus far there has been little quantification of the value of such schemes for bumblebees, margins have been found to be of positive value to beneficial arthropods, spiders, insectivorous birds, and species of rare arable weeds (de Snoo 1995). It is thought that some types of margin could be beneficial in providing a continuum of nectar and pollen resources in what may otherwise be a relatively barren landscape in terms of these two resources. They may also be a source of potential nest sites for bumblebee queens.

Management type	Conservation Objective
conservation headland (unsprayed crop edge)	enhancement of dicotyledonous weeds, rare weeds, insects, and gamebirds
uncropped wildlife strip	enhancement of rare arable weeds
buffer strip	environmental protection of watercourses
perennial herbaceous strip - - grasses only - grasses and flowers - flowers only - legumes	protection of pre-existing boundary, increased habitat for perennial flora, beneficial insects, pollinators, some birds
annual herbaceous strip	enhancement of some predatory insects and pollinators
set-aside margin	production control, weed control, secondary wildlife benefits particularly seed-feeding birds

Table 1.5: The different types of arable field-boundary management, and their conservation objectives (after Marshall & Moonen 1998)

1.6.2 Aims of this project

Specifically, the main aim of this thesis was to provide a basis for the development of conservation strategies for *Bombus* spp. within arable landscapes, based on field margin management. The following questions were addressed –

1) Can naturally regenerated field margins (chapter 2) and wildflower strips (chapter 3) offer valuable alternative forage resources for bumblebees?
2) Which nectar producing crops do bumblebees prefer to forage on (chapter 4)? An example of foraging behaviour on the 'novel' crop sainfoin, *Onobrychis viciifolia* (Fabaceae) is then given (chapter 5, chapter 6)
3) Where are the preferred nesting sites of bumblebee queens on farmland (chapter 7)?

2. THE VALUE OF UNCROPPED FIELD MARGINS FOR FORAGING BUMBLEBEES

A.R. Kells, J.M. Holland and D. Goulson. 2001. *Journal of Insect Conservation* 5: 283-291

2.1 Abstract

The intensification of agriculture has led to declines in species diversity and abundance within groups of certain flora and fauna. Bumblebees (*Bombus* spp.) are one group where a decline has been documented, and it is thought to be attributable to a decrease in forage resources and potential nest sites. As bumblebees play an important role in the pollination of many entomophilous crops, this decline could impact on agricultural productivity. I examined the role of naturally regenerated field margins in providing forage plants on land where nectar resources are otherwise impoverished. The following question was addressed - Are naturally regenerated unsprayed field margins more attractive to foraging bumblebees and honeybees than cropped field margins managed as conservation headlands? Significantly more bees visited naturally regenerated field margins than cropped field margins. Honeybees (*Apis mellifera*), *Bombus terrestris* and *Bombus lapidarius* were the most commonly observed bee species. Different wildflower species within the naturally regenerated margins varied greatly in relative number of visits received, and bumblebee species were found to prefer different flower species to honeybees. The potential role that naturally regenerated field margins could play in the conservation of bumblebee species and the implications for other species of flora and fauna are discussed.

2.2 Introduction

In recent years there have been attempts to introduce conservation measures into arable systems (Firbank *et al.* 1991, Dennis and Fry 1992, Saunders *et al.* 1992; Dramstad and Fry 1995), and to reverse the detrimental effects of agricultural intensification on such species as rare arable weeds (Wilson *et al.* 1999), chickfood insects (Aebischer 1991), beneficial insects (MAFF 1999), bumblebees and solitary bees (Williams 1982, O'Toole 1994), butterflies (Thomas 1995), songbirds (Fuller *et al.* 1995) and gamebirds (Potts 1986). As field edges produce lower yields than any other part of the field (Boatman 1998), often require increased effort for lower economic return (de Snoo and Chaney 1999), and generally contain the greatest floral diversity (Marshall 1989, de Snoo 1995, Wilson and Aebischer 1995), it is unsurprising that these are the areas which have become the focus of the conservation effort. The U.K. has seen the introduction of the Countryside Stewardship Scheme (CSS), and more recently the Arable Stewardship Scheme (ASS), both of which recognise the potential importance of field margins in agro-ecosystem conservation (MAFF 1998, 1999).

There are currently three main management regimes applied to land between the crop and the field boundary (see figure 2.1). Firstly, a narrow sterile strip immediately adjacent to the crop, created by ploughing or herbicide application (Fielder 1987), may act as a defence against weed ingress from the field boundary. Secondly, the outer strip of the crop may be maintained free from herbicide and pesticide application; such strips are known as conservation headlands. These encourage survival of certain broad-leaved annuals, and their associated insects. Thirdly, an uncropped strip, usually 6-12m wide, may be left around the edge of the field. Uncropped strips can be naturally regenerated, or sown with a seed mixture (Critchley 1996b, MAFF 1999). Naturally regenerated, regularly cultivated, uncropped margins were primarily designed to conserve rare local arable flora and their associated fauna by providing an area free from both agrochemicals and competition from other species (Schumacher 1987, Boatman 1998). Sowing an uncropped margin with a grass or wildflower seed mixture can meet particular objectives, e.g. grass margins can provide winter cover for game birds, flowering plant margins can be used to enhance integrated pest management regimes (de Snoo and Chaney 1999).

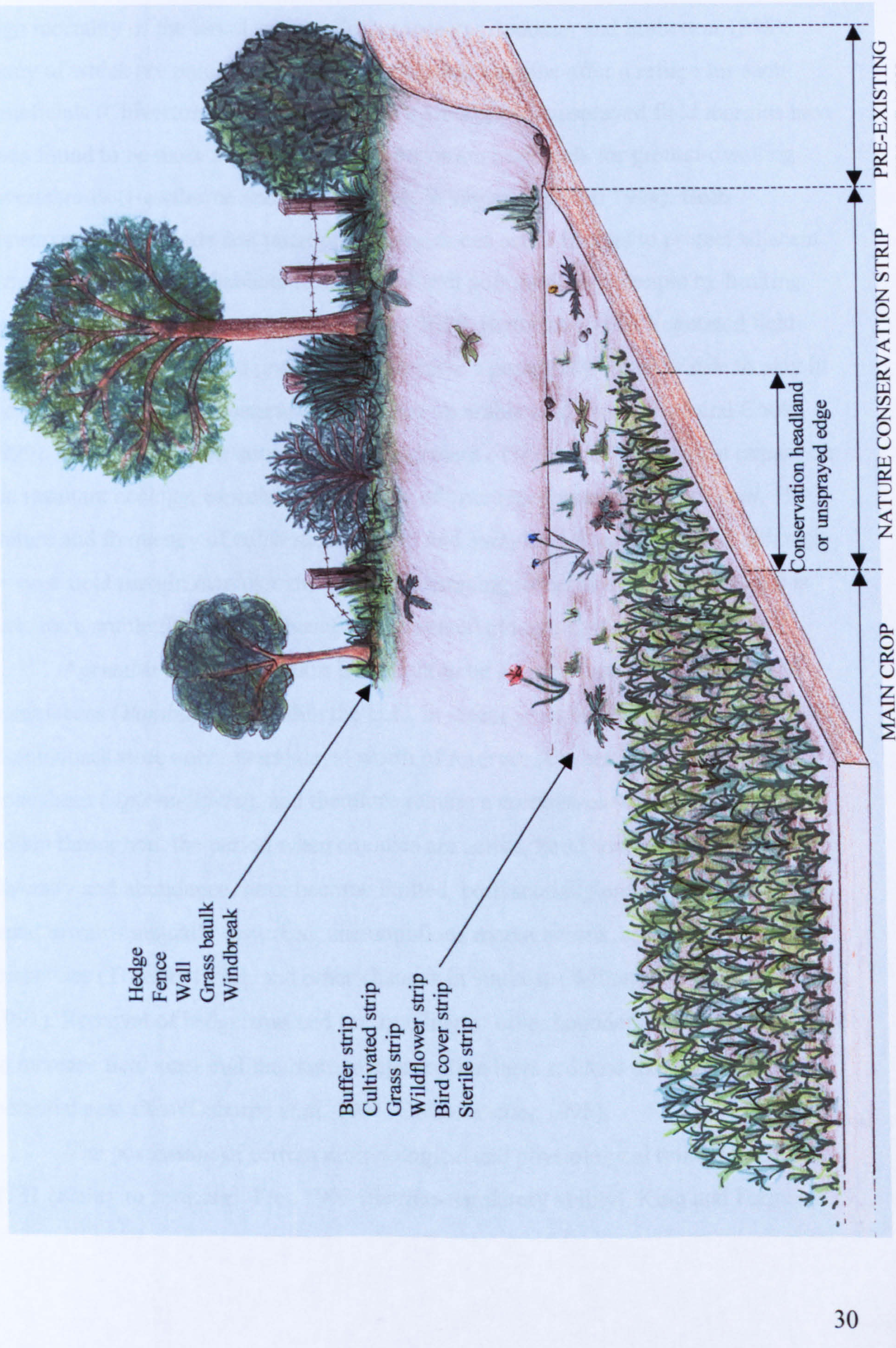


Figure 2.1: The principal components of a generalised arable field margin

The nature of vegetated margins makes them valuable habitats for invertebrates (Moreby and Southway 1999), birds (Rands 1985, Stoate 1999), and small mammals (Tew *et al.* 1994). Broad-spectrum insecticides used on crops to control aphids cause high mortality of the larval stages of other insects (Boatman and Sotherton 1998), many of which are parasitic on aphids; unsprayed margins offer a refuge for such beneficials (Chiverton and Sotherton 1991). Uncropped, unsprayed field margins have been found to be more attractive than conservation headlands for ground-dwelling invertebrates (Hawthorne and Hassall 1994, White and Hassall 1994). Both conservation headlands and uncropped margins can act as buffers to protect adjacent terrestrial and riparian habitats from agricultural pollution, for example by limiting pesticide drift and surface run-off (de Snoo 1995, Boatman 1998). Vegetated field margins, both cropped and uncropped, thus have a potentially valuable role to play in the implementation of conservation schemes on arable land (Smallshire and Cooke 1999). However, it is the subsequent management of these that has greatest impact on the resultant ecology, especially in the case of uncropped margins (Smith *et al.* 1993). Nature and frequency of cultivation, cutting and spraying all have an effect, although in most field margin management schemes, spraying (other than spot treatments) is rare. Rare arable flora tend to benefit from annual ploughing (Critchley 1996a).

Agricultural intensification is thought to be a major factor in the decline of bumblebees (*Bombus* spp.) within the U.K. in recent years (see Williams 1982, 1986). Bumblebees store only several days' worth of reserves (Corbet 1996), unlike honeybees (*Apis mellifera*), and therefore require a continuous supply of nectar and pollen throughout the period when colonies are active. Food sources, in terms of floral diversity and abundance, have become limited, both spatially and temporally, by the trend towards annually disturbed, anemophilous monocultures, application of herbicides (Torchio 1991), and other changes in land use (Williams 1982, Corbet *et al.* 1991). Removal of hedgerows and the levelling of other boundary features in the drive to increase field sizes and facilitate mechanisation have reduced the availability of potential nest sites (Osborne *et al.* 1991, Ortiz-Sánchez 1995).

The possession of certain morphological and physiological traits (Hippa *et al.* 1981 [ability to sonicate], Free 1993 [thermo-regulatory ability], King and Ferguson

1994 [pubescence], Batra 1995 [comparatively long-tongued]) mean that bumblebees are the most effective pollinators of many plant species (Colbert and de Oliveira 1990, Corbet *et al.* 1991, Batra 1995), and, along with the other members of the family Apidae, they are necessary for the pollination of approximately 40 crop species grown in the U.K. (Osborne and Williams 1996). As such they are an integral component of agricultural landscapes, and their continued presence is important for safeguarding yields. Bumblebees also act as pollination vectors for numerous wildflower species, and have the ability to maintain small fragmented populations of rare plants (Kwak *et al.* 1991, Petanidou *et al.* 1991).

Little work has been done thus far on the possible contribution field margins may make to the conservation of bumblebee populations on arable land (although see Fussell and Corbet 1992a, Lagerlof *et al.* 1992). Under the pilot Arable Stewardship Scheme, a MAFF initiative (MAFF 1999), I undertook a preliminary study into the potential that naturally regenerated unsprayed field margins might have in providing forage resources to *Bombus* spp. in a landscape identified as being relatively impoverished in terms of these. I specifically looked at nectar provision, as I was interested in determining if there was resource partitioning between individual *Bombus* species, and between *Bombus* species and honeybees, based on differences in morphology (here avaerage tongue length). I aimed to establish if naturally regenerated unsprayed field margins are more attractive to foraging bumblebees and honeybees than corresponding cropped field margins managed as conservation headlands. This was addressed by studying bee abundance and behaviour in an experimental field margin set-up in central England.

Plate 2.1: A typical naturally regenerated field margin after establishment, year 1

2.3 Methods

2.3.1 Study sites

This study was carried out on five arable farms centred around Newport, the west Midlands, from June 29th until August 9th, 1999. All farms were located within a 12.5 kilometre radius, at similar elevations, and had introduced field margins for the first time in 1999. Prior to that, these areas had been subject to the same treatment as the rest of the field.

Fields in which the experiments took place were planted with spring-sown cereals, and were matched for size as closely as possible. Two uncropped field margins, which had been allowed to undergo natural regeneration following spring cultivation, and a control margin managed as conservation headland were studied on each farm, each within a different field; controls were as similar in terms of height and density of vegetation to the naturally regenerated field margins as possible. No management other than the spring cultivation was undertaken on these areas for the duration of the experiment. Both naturally regenerated margins and control margins were 4-6 metres wide, and adjacent to the field boundary, which was a hedgerow in all cases. Hedgerow nectar was not a factor in these experiments as adjacent boundaries were chosen to be relatively flower-free. Plant names follow Stace (1997).

2.3.2 Sampling methods

Observations of bee numbers, species, and chosen forage plants were made following an adaptation of Pollard's method of butterfly surveying (Pollard 1977, Pollard *et al.* 1975). Only workers were recorded as the foraging patterns of queens and drones may differ from those of the workers, and few of either of these castes were observed. Those workers collecting pollen only were removed from the data set as I wished to carry out analysis comparing floral choice to average tongue length of the different species (2.4.4); tongue length is presumably not a factor in choosing pollen resources. Observations were made along a 0.5 x 50 m^2 transect through the centre of field margins and controls, parallel with the edge of the crop. All transects were laid out along the straight edges of fields; corners were not included. Three sets of observations, taken at 30-minute intervals, were made at each margin at 8-10 day intervals over a 40 day period, depending on ambient conditions, giving 5 'timepoints' of observations. The actual dates of these timepoints are given in table 2.1. Sets of observations were averaged for each margin for each day. Individual farms, and the margins within a farm, were visited in a random order for each observation period. Transects were only walked on days when ambient temperature was 18°C or above, and it was not raining. All walks were completed between 09:30 and 18:00 hours; all sites were visited within a 72-hour period. Number of individual flowers of each species were counted for each flower species along the transects at each time observations were made, except in the case of e.g. *Matricaria* spp., where number of flowerheads were counted.

Timepoint	Date of observations
1	28-30 June
2	7-9 July
3	17-19 July
4	27-29 July
5	8-10 August

Table 2.1: Actual dates on which observations were carried out, and the timepoints these correspond to

2.3.3 Floral preferences

A preference index (PI) was constructed to show preferences of individual *Bombus* species and *A. mellifera* for each flower species present –

$$\mathrm{PI} = (V_{ik}/V_{it})/(A_k/A_t)$$

where V_{ik} is the number of foraging visits of species *i* to plant species *k*, V_{it} is the total number of visits of species *i* to all plant species, A_k is the total number of flowers of species *k*, and A_t is the total number of flowers of all species (Colwell and Futuyama 1971). Flower counts and average numbers of bee visits for each observation period were summed across all sites and all dates for the purposes of this index.

2.3.4 Statistical analysis

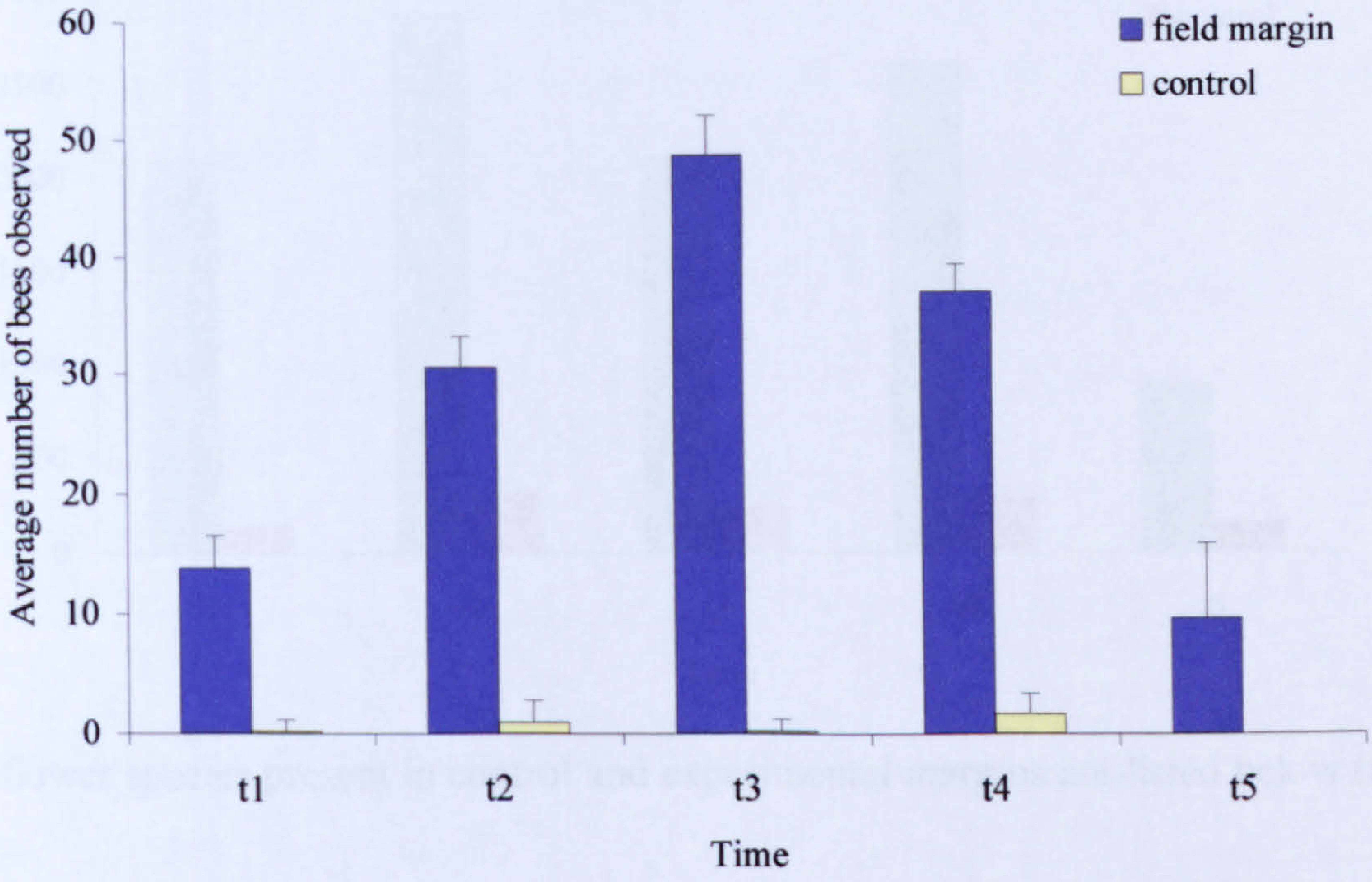
Repeated measures ANOVA using SPSS9.0 for Windows (SPSS 1998), was used to determine if bee and flower numbers varied between experimental and control treatments. 'Timepoints' (i.e. dates) were treated as replicates as the gap between observations was enough to allow sufficient turnover of bees and flowers to justify this. Repeated measures ANOVA was also used to determine whether time had a significant effect on total bee numbers.

2.4 Results

2.4.1 Numbers of foraging bees recorded on both margins

Significantly more bees were recorded in uncropped field margins than in control margins ($F_{1,5}$=31.3, p=0.003) (figure 2.2). Of the five sampling timepoints, most bees were recorded at timepoints 2-4, fewer at the beginning and the end (figure 2.2). The response of bee numbers to time is best described as a quadratic relationship ($F_{1,5}$=51.5, p=0.001). This response occurred primarily in naturally regenerated margins, but not in controls, leading to a significant interaction between timepoint and treatment for bee numbers ($F_{1,5}$=34.8, p=0.002). *A. mellifera* accounted for 87.5% of all observations on the control plots, and *B. lapidarius* accounted for the other 12.5%. No other *Bombus* species were observed foraging on the control plots.

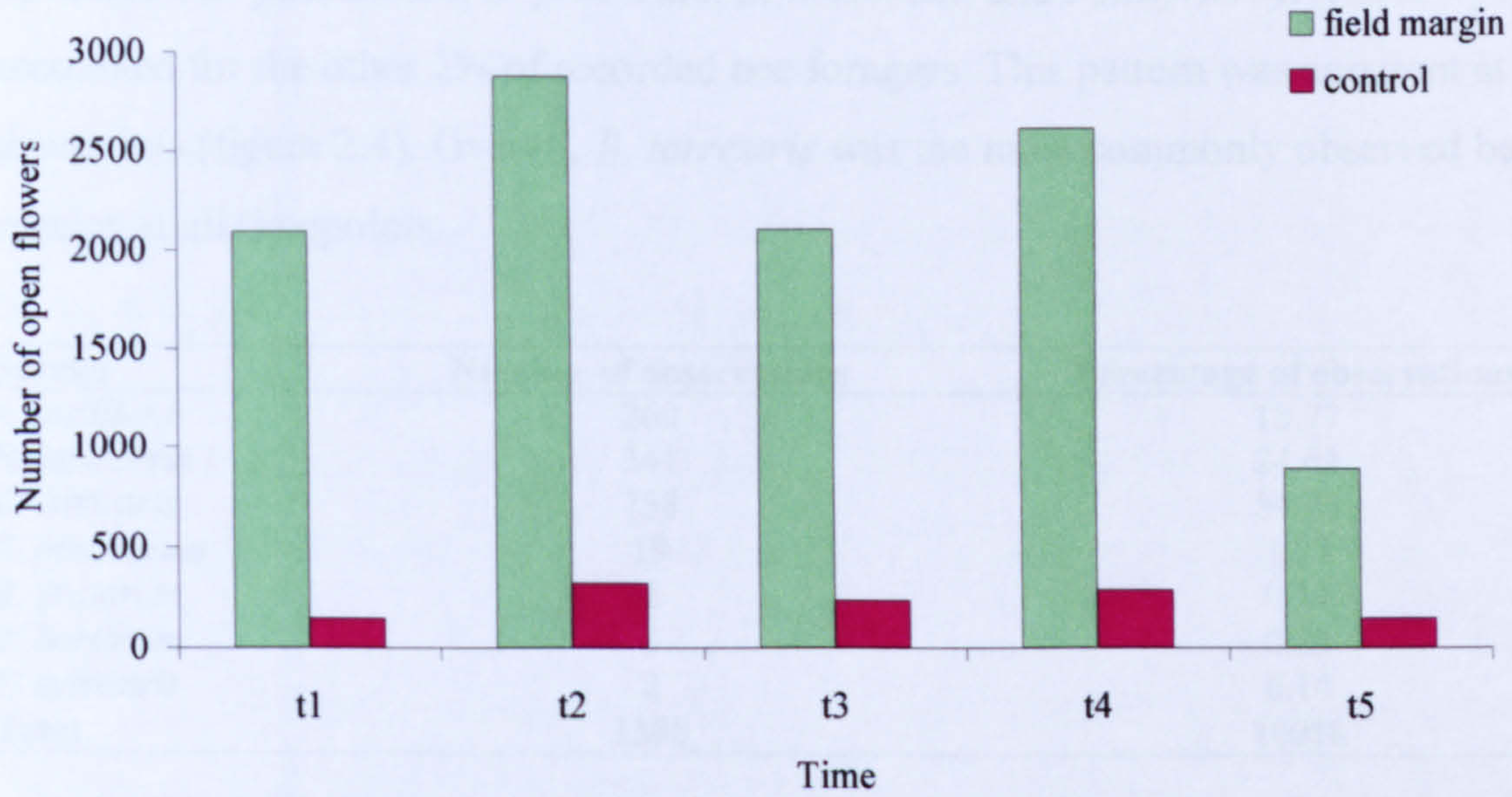
Figure 2.2: Average number of bees (*Bombus* + *Apis*) observed foraging on experimental and control margins across the duration of the experiment. Interval between time-points was approximately 10 days. n=10 for experimental plots, and n=5 for controls. Error bars indicate SEM



2.4.2 Flower numbers through time

Many more open flowers were recorded on naturally regenerated field margins compared with controls ($F_{1,13}=11.26$, $p<0.005$) (figure 2.3). There was a significant interaction between date and treatment for open flowers ($F_{4,52}=2.74$, $p=0.038$); this is expected due to the temporal nature of the flowering period. Differences between sites were not found to be significant ($F_{4,5}=0.15$, $p=0.957$). No significant association was found between numbers of foraging bees and temporal variation in floral density ($r=0.64$, $p>0.05$).

Figure 2.3: Total numbers of open flowers on uncropped field margins and control margins through time



The flower species present in control and experimental margins are listed below (table 2.2) –

	Control margins	**Experimental margins**
Flower species	*Matricaria* spp. *Chaemerion angustifolium*	*Viola arvensis* *Matricaria* spp. *Brassica* spp. *Lamium purpureum* *Linum usitatissimum* *Phacelia tanacetifolia* *Persicaria maculosa* *Cirsium* spp. *Dipsacus fullonum* *Chaemerion angustifolium* *Trifolium repens* *Pentaglottis sempervivens*
Total number of flowers	**1128**	**10529**

Table 2.2: Flower species present in control and experimental margins over the duration of the experiment. For relative numbers of different flower species in the experimental margins see figure 2.5

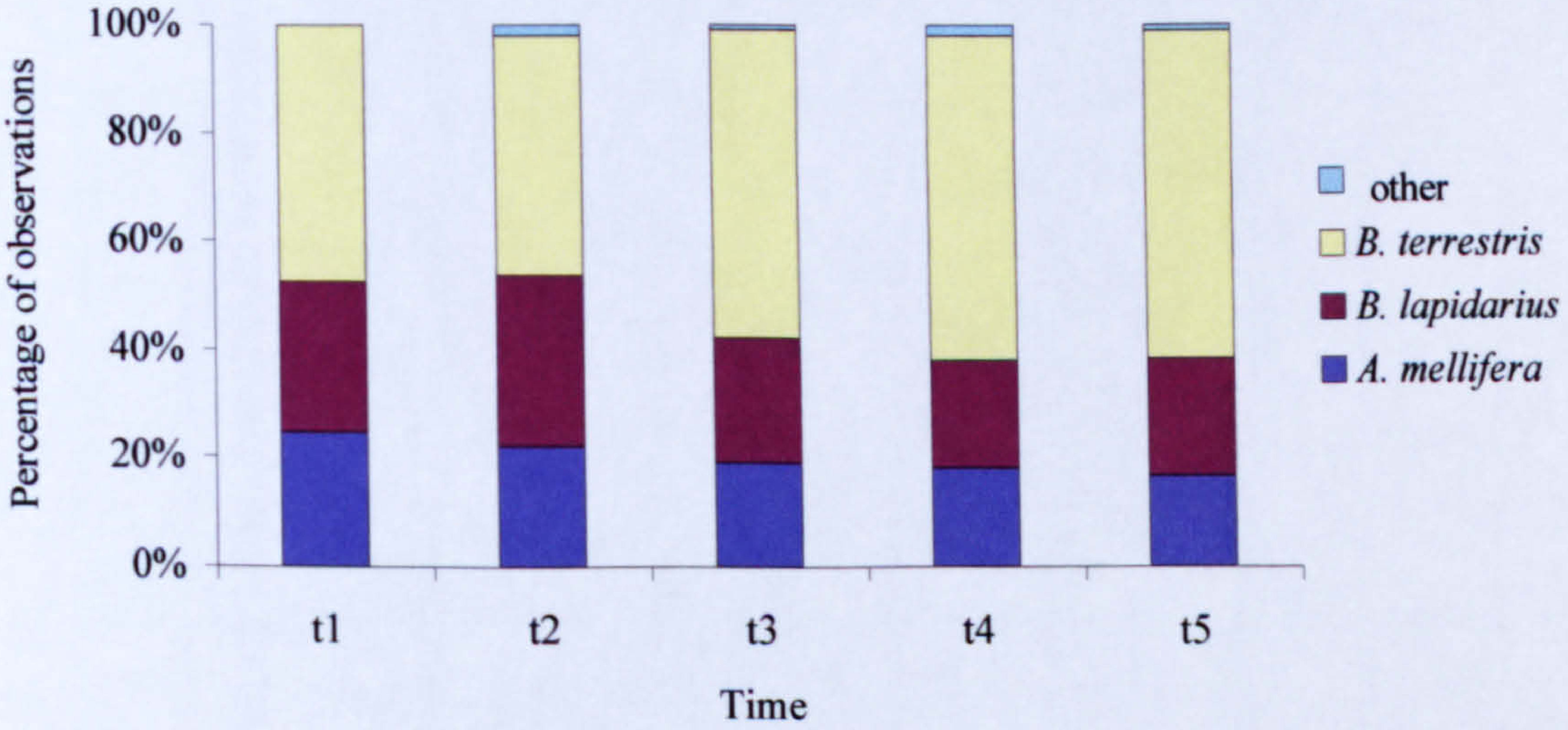
2.4.3 Bee species

Three species accounted for more than 98% of all observed visits across all timepoints (table 2.3). These were *A. mellifera*, *B. terrestris/lucorum*, and *B. lapidarius*. *B. pascuorum*, *B. pratorum*, *B. hortorum*, and *Psithyrus sylvestris* accounted for the other 2% of recorded bee foragers. This pattern was apparent at all timepoints (figure 2.4). Overall, *B. terrestris* was the most commonly observed bee species at all timepoints.

Species	**Number of observations**	**Percentage of observations**
A. mellifera	260	18.77
B. lapidarius	341	24.62
B. terrestris	758	54.73
B. pascuorum	19	1.37
B. pratorum	2	0.14
B. hortorum	3	0.23
P. sylvestris	2	0.14
Total	**1385**	**100%**

Table 2.3: Total number of observations of each bee species across all timepoints, expressed as a percentage of the total number of observations of all species

Figure 2.4: Numbers of each bee species observed on all field margins through time, expressed as a percentage of the total number of bees observed. Other observed species were *B. pascuorum*, *B. pratorum*, *B. hortorum* and *P. sylvestris*



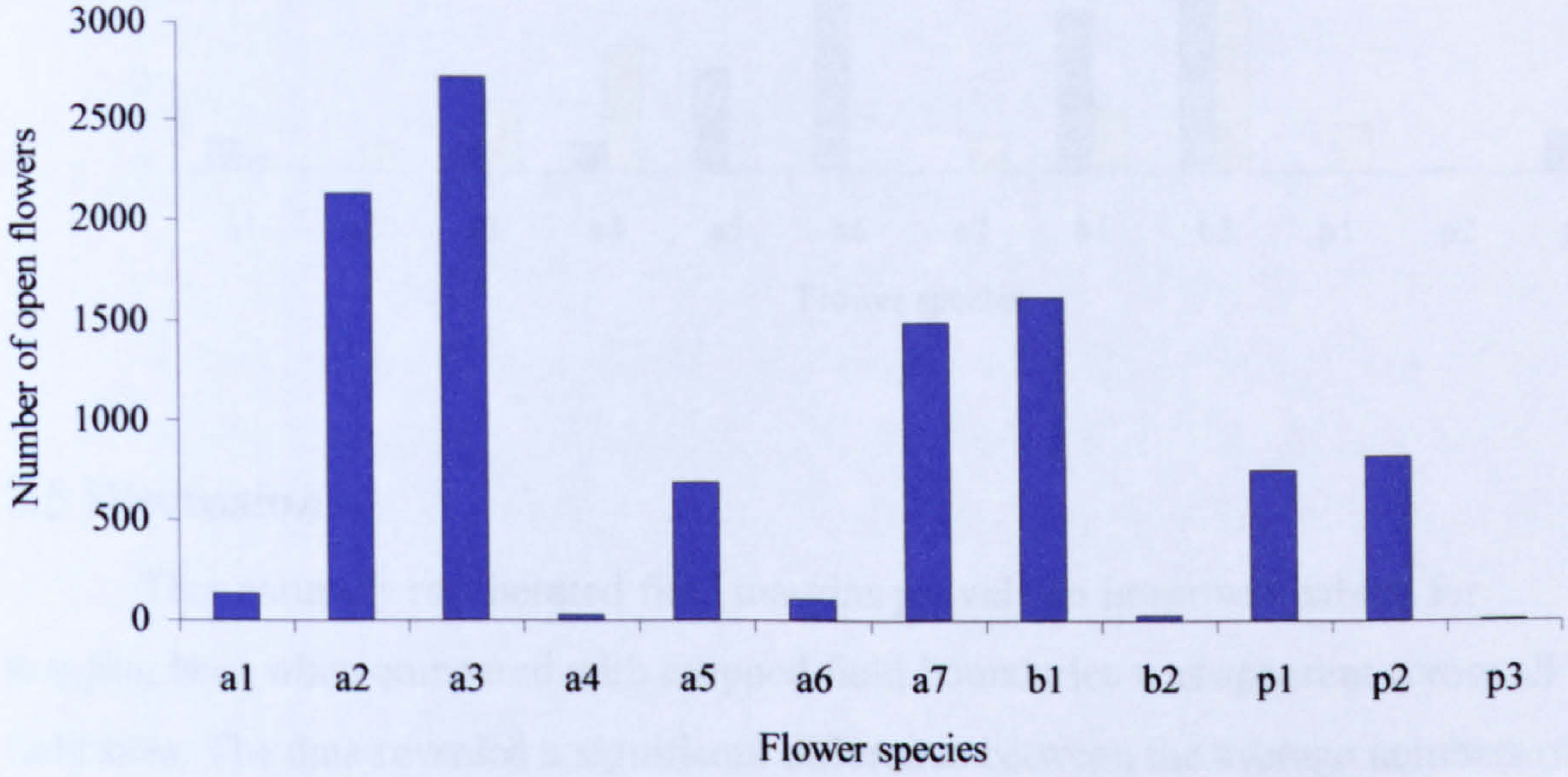
2.4.4 Floral preferences of foraging bees

There was great variation in the total number of open flowers of the different plant species on naturally regenerated margins (figure 2.5a). Those species that were most numerous were not necessarily the species that received the highest proportion of foraging visits. Volunteer *Brassica* spp. were the most numerous inflorescences in the naturally regenerated margins, but did not score highly on the preference indices for honeybees and bumblebees when compared with species present at lower densities. *Matricaria* spp. (a2) and *Persicaria maculosa* (a7) were abundant, but were not visited at all by bumblebees, although honeybees were observed foraging on these (figure 2.5b). Conversely, *Phacelia tanacetifolia* (a6) and *Dipsacus fullonum* (b2) which were present in very small numbers at one site, received a disproportionately large number of bee visits.

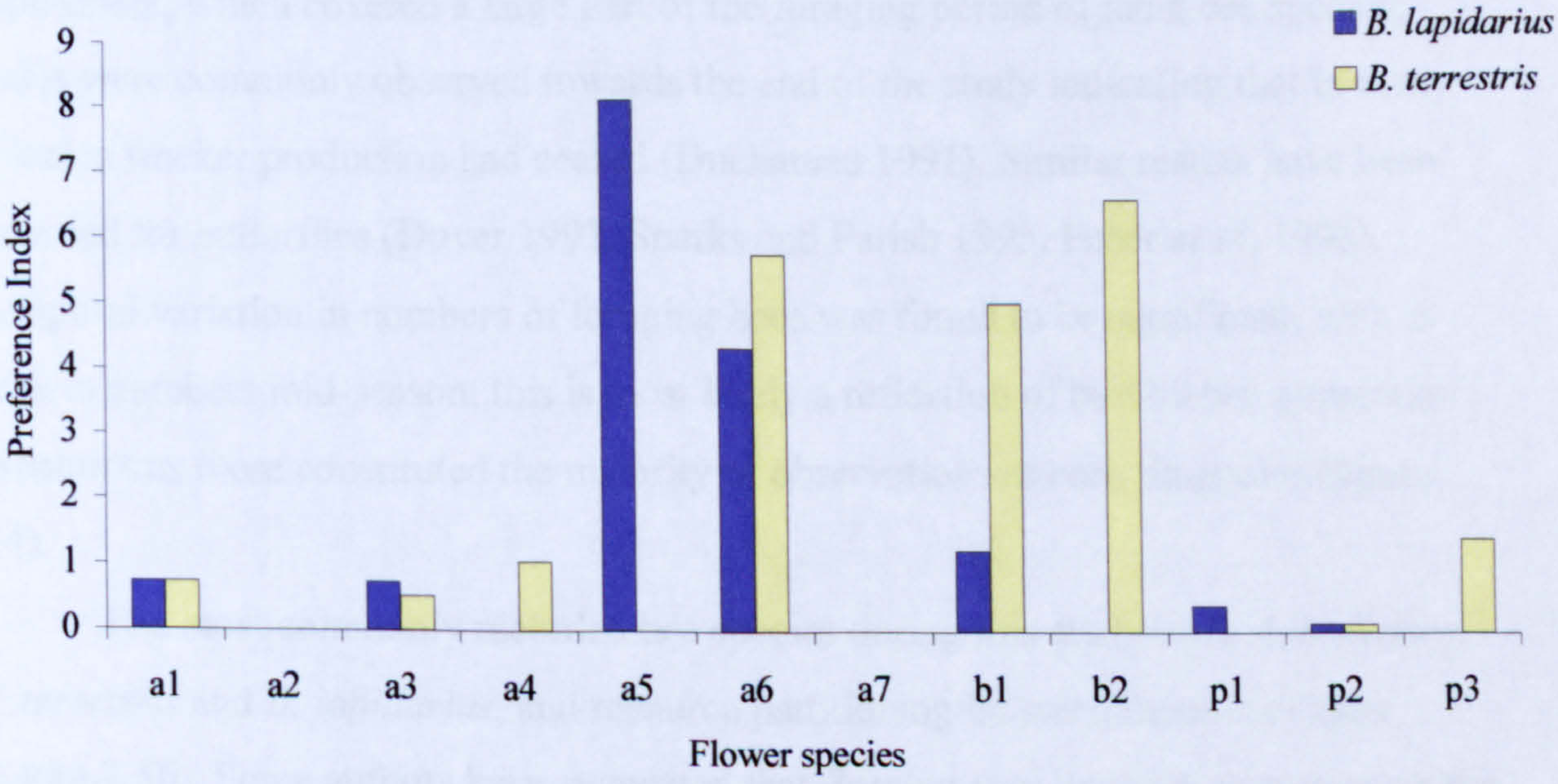
The individual species preferences of *B. lapidarius* and *B. terrestris* were found to be quite different (figure 2.5c), although both exhibited a high preference for *P. tanacetifolia*. *B. lapidarius* also exhibited a high preference for *Linum usitatissimum*, while *B. terrestris* preferentially foraged on *Cirsium* spp., and *D. fullonum*. *B. terrestris* was also recorded foraging on *Pentaglottis sempervivens* and *Lamium purpureum*; there were no recorded visits of *B. lapidarius* to either of these plant species.

Figure 2.5: The preferences of bee species for each flower species. Flower species are the annuals a1) *Viola arvensis*, a2) *Matricaria* spp., a3) *Brassica* spp., a4) *Lamium purpureum*, a5) *Linum usitatissimum*, a6) *Phacelia tanacetifolia*, a7) *Persicaria maculosa*; biennials b1) *Cirsium* spp., b2) *Dipsacus fullonum*; and perennials p1) *Chaemerion angustifolium*, p2) *Trifolium repens*, p3) *Pentaglottis sempervivens*. a) total number of open flowers of each species summed across all timepoints; b) relative preferences of *Bombus* spp. and *A. mellifera*; c) relative preferences of *B. lapidarius* and *B. terrestris*. Data is taken from experimental margins only; for formula see text

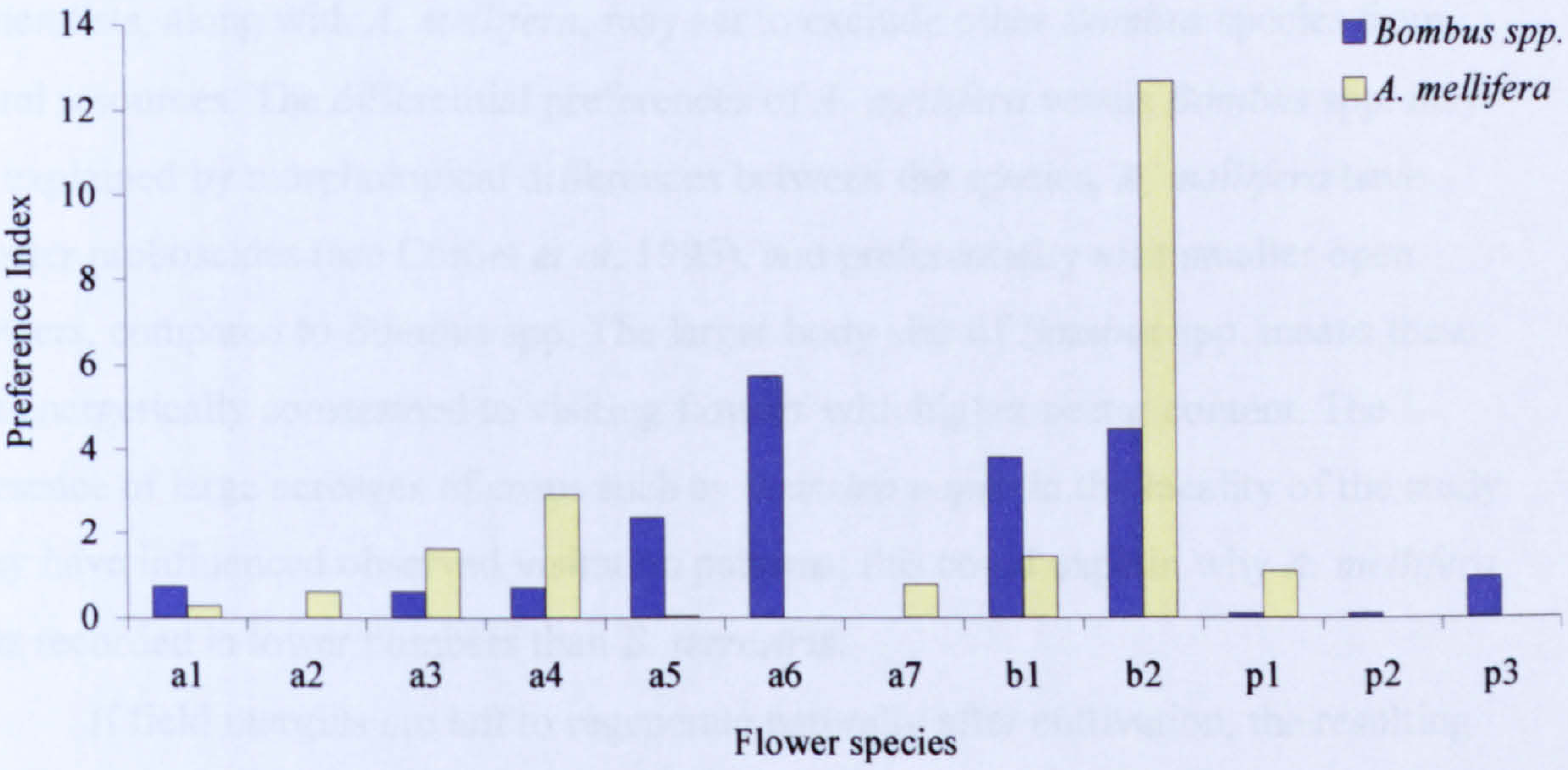
2.5a)



2.5b)



2.5c)



2.5 Discussion

That naturally regenerated field margins provide an improved habitat for foraging bees when compared with cropped field boundaries was apparent across all field sites. The data revealed a significant difference between the average numbers of bees foraging on naturally regenerated margins and controls for the duration of this experiment, which covered a large part of the foraging period of most bee species; males were commonly observed towards the end of the study indicating that in many colonies worker production had ceased (Duchateau 1991). Similar results have been recorded for butterflies (Dover 1992, Sparks and Parish 1995, Feber *et al*. 1996). Temporal variation in numbers of foraging bees was found to be significant, with a peak in numbers mid-season; this is most likely a reflection of bumblebee population dynamics as these constituted the majority of observations at each timepoint (figure 2.4).

The most commonly recorded bee species during this study were *A. mellifera*, *B. terrestris* and *B. lapidarius*, and resource partitioning between these is evident (figure 2.5b). Some authors have suggested that *Bombus* spp. partition resources on the basis of proboscis length (Inouye 1977, 1978, Ranta and Lundberg 1980, Pyke 1982).

However, *B. terrestris* and *B. lapidarius* have similar proboscis lengths (Prys-Jones and Corbet 1991), but exhibited different preferences for the flowers present; these generalists, along with *A. mellifera*, may act to exclude other *Bombus* species from floral resources. The differential preferences of *A. mellifera* versus *Bombus* spp. may be explained by morphological differences between the species. *A. mellifera* have shorter proboscides (see Corbet *et al.* 1995), and preferentially visit smaller open flowers, compared to *Bombus* spp. The larger body size of *Bombus* spp. means these are energetically constrained to visiting flowers with higher nectar content. The presence of large acreages of crops such as *Brassica napus* in the locality of the study may have influenced observed visitation patterns; this could explain why *A. mellifera* was recorded in lower numbers than *B. terrestris.*

If field margins are left to regenerate naturally after cultivation, the resulting habitat diversity is probably influenced by years of intensive agriculture. The outcome of such natural regeneration will depend on species already present, either as plants along the field boundary, or in the seed or bud banks. Certain species in either of these may affect establishment of the successive vegetation (Egler 1954, Connell and Slayter 1977). The persistence of seeds in the seed bank varies between species (Feber *et al.* 1996), so seed bank age is potentially important. In this study similar wildflower species were found across all the naturally regenerated margins, most of which are common and widespread within the U.K. It was not therefore surprising to find that the dominant bumblebee fauna belonged to the mainland ubiquitous species group of Williams (1982), rather than habitat specialists or those with restricted ranges. Dramstad and Fry (1995) found a similar dominance of ubiquitous species on land subjected to intensive agricultural practices in Norway. However, along with *B. terrestris (B. lucorum)* and *B. lapidarius, B. pascuorum, B. pratorum*, and *B. hortorum* also belong to the ubiquitous species group, and yet there were few recorded sightings of any of these. It is known that *B. pascuorum* and *B. hortorum* preferentially visit flowers with deeper corollas than *B. lapidarius* and *B. terrestris* (Prys-Jones and Corbet 1991); it is disturbing that the two ubiquitous members of the longer-tongued species group (Williams 1986) should account for such a low proportion of observations here. Corbet *et al.* (1995) have suggested that frequent disturbance has most affected the longer-tongued *Bombus* spp. as it has enabled shallower annual species to displace the deeper-flowered perennials that this sub-compartment of the pollination web preferentially feed on (Corbet 2000). The disappearance of this species group would have serious implications for flower species with deep corollas. However, diversity and density of perennials should increase in field margins with time, and with lack of disturbance; many perennials are highly attractive to all *Bombus* spp. (Fussell and Corbet 1992a). This also has the advantage of causing failure of either germination or establishment of annual weeds (Greaves and Marshall 1987, Smith *et al.* 1993), most of which require an open sward for germination. Butterflies also prefer to forage on perennial species (Feber *et al.* 1996).

Control plots consistently contained lower densities of flowers than naturally regenerated margins (figure 2.3). There was also lower floral diversity, with *Matricaria* spp. and *Chaemerion angustifolium* the only entomophilous species present, compared with twelve entomophilous species on the naturally regenerated margins (see figure 2.5). *A. mellifera* and *Bombus* spp. were shown to exhibit little or no foraging affinity in this case for either *Matricaria* spp. or *C. angustifolium*. Flowers that scored highly on the preference index (figure 2.5) were absent from control plots, so the increase in number of foragers on naturally regenerated margins is not solely a function of increased flower density, but of the presence of more 'attractive' flower species. Floral species richness has been correlated with abundance of bees (Tscharntke *et al.* 1998), and butterflies (Sparks and Parish 1995). The increased floral diversity found on the naturally regenerated margins may result from an initial lack of competition during establishment.

The naturally regenerated margins used in this study were all in the initial year of establishment. Some contained volunteer crop species (for example *Brassica* spp., *P. tanacetifolia*), whilst others were comparatively bare. Edges produce lower yields than any other part of the field (Boatman and Sotherton 1998), and often require increased effort (de Snoo and Chaney 1999). Losses are therefore minimized by preferentially removing these areas from production (Rands 1985). Field edges are also likely to be the area of the field containing the most diverse flora and fauna, although Fielder (1987) has noted that seedbed quality at the field edge is likely to be poor. Where there is a diverse local flora and weed populations are small then natural regeneration should be the preferred option. However, Smith *et al.* (1993, 1994) found that sowing a grass/wildflower mixture produced better control of annual grass weeds, and increased butterfly and overall invertebrate abundance. This should be considered in areas where the outcome of natural regeneration is likely to be unacceptable. However, although the sowing of a wildflower seed mixture may provide better cover, particularly during establishment, and a wider variety of nectar-producing plants, these can be expensive, and species from the local flora tend to be excluded from the resultant border (Smith *et al.* 1993). Management of either a naturally regenerated or a sown field margin should ensure that the herbaceous flora is not degraded through shading or herbicide application, and also that ploughing is limited to allow development of a mid-successional community, and its constituent deep-flowered perennials. Timing and depth of cultivations are also likely to influence the outcome of natural regeneration (Critchley *et al.* 1999). Naturally regenerated species in field margins have been maintained for at least three years in the absence of fertiliser application (Smith *et al.* 1993); the addition of fertiliser is likely to promote growth of a few of the most competitive species at the expense of all others (Wilson 1993, Wilson *et al.* 1999).

Although the flight ranges of *Bombus* spp. remain to be quantified, observations suggest that bumblebees are not economically constrained to forage close to their nests (Dramstad and Fry 1995, Saville *et al.* 1997), and various models of bumblebee foraging have proposed that flight ranges in the order of kilometres can be economically viable (Dukas and Edelstein-Keshet 1998, Cresswell *et al.* 2000). This has implications for the spatial and temporal organisation of appropriate conservation measures.

That naturally regenerated margins benefit other species has already been noted (Hawthorne and Hassall 1994, Tew *et al.* 1994, Moreby and Southway 1999, Stoate 1999). I would advocate from the results of this study that naturally regenerated field margins, with careful management, have the potential to supply a continuum of nectar and pollen to foraging bumblebees on agricultural land across the active period of colonies. With the development of a mid-successional community (here meaning open herbaceous vegetation that has been free from disturbance for at least 5 to 10 years), they should prove valuable in conserving the longer-tongued bumblebee species, which are most under threat (Corbet 2000). Also, as such margins become established, tussocks will form, which may be utilised as nest sites (Alford 1975). This should aid stabilization of bumblebee numbers on agricultural land, and safeguard the yields of certain crops. Management of naturally regenerated field margins for bumblebees should have a positive effect on other species traditionally associated with farmland, many of which are also in decline.

3. THE VALUE OF WILDFLOWER STRIPS FOR FORAGING BUMBLEBEES

---

submitted to *Agriculture, Ecosystems and Environment*

3.1 Abstract

Agricultural intensification is known to be directly responsible for declines in the diversity and abundance of flora and fauna associated with arable land. Amongst other things, the reduction in field boundary habitat due to 'improvements' and field enlargement has had deleterious effects on many species. This study investigated the potential that re-vegetated field margins could have in reversing the declines shown within the bumblebees, *Bombus* spp., an important component of the pollinator guild within agricultural systems. Margins were sown with a wildflower seed mixture in an attempt to provide a continuum of forage resources on land where nectar sources are otherwise impoverished. I found that wildflower strips did offer an attractive resource, with significantly more bees foraging on these than on control margins. Honeybees (*Apis mellifera*), and two generalist bumblebee species, *Bombus terrestris* and *Bombus lapidarius,* were common; however, more specialised bumblebee species formed only a small proportion of observations. This has implications for native arable flora, and for the future establishment and management of wildflower strips.

3.2 Introduction

There has always been a degree of conflict between agricultural systems and areas of natural and semi-natural habitat. This has become more apparent in the last fifty years, with the drive towards land improvement, monocultures, and field expansion, resulting in many areas of natural and semi-natural habitat becoming increasingly fragmented or destroyed altogether (Smallshire and Cooke 1999, Ricketts *et al.* 2001). Fragmentation has also led to a decrease in the natural diversity of such habitats (Hinsley and Bellamy 2000). Flora is affected as inbreeding reduces heterozygosity (Young *et al.* 1996); clonal species may be more affected as the opportunity for re-invasion by vegetative growth is reduced (Robinson *et al.* 1992). Also, disturbance can alter nutrient cycling within the system (Saunders *et al.* 1991), leading to gradual changes in soil composition, and potential alteration of patterns of succession (McCollin *et al.* 2000). Such modification impacts on associated fauna by affecting availability of certain faunal habitat requirements, such as nest-sites, foodstuffs, and refugia from predation. Alteration in microclimate (increased exposure, reduction of cover) is known to have a potentially destabilising influence on competitive, predator-prey, and parasitic interactions (Saunders *et al.* 1991). Insectivorous and granivorous bird species associated with arable land have declined (Aebischer 1991, Wilson *et al.* 1999), with detrimental effects also noted for small mammals (Tew *et al.* 1994), and many insect species (e.g. see Williams 1982, O'Toole 1994, Thomas 1995).

Field edges are known to accommodate many species of flora and fauna, but many such areas have been lost or degraded in recent years. Between 1984 and 1993, approximately one third of hedgerows and associated vegetation in Britain were lost (McCollin 2000). Remaining edges have been found to have decreased floral species richness, and contain an increased number of annual grasses than was the case in the 1970's (Barr *et al.* 1993). However, they have recently become the focus for agro-ecosystem conservation schemes across Europe as they are still generally the sites of greatest floristic diversity on farmland (Marshall 1989, de Snoo 1995, Wilson and Aebischer 1995). These field margins are also recognised as facilitating linear wildlife movement by acting as corridors (McCollin *et al.* 2000). The establishment and management of vegetated field margins along field edges (MAFF 1998, 1999) is a relatively cost-effective way in which to create areas of semi-natural vegetation on farmland (Fry and Main 1993), and to increase habitat diversity and complexity (Kiss *et al.* 1997). Initially, conservation schemes focused on managing margins as 'conservation headlands' (Sotherton 1991), to increase survival of the grey partridge, *Perdix perdix* L. (Rands 1985). More recently, some schemes have focused on removing the margin area from production altogether (e.g. MAFF 1998, 1999, Marshall and Moonen 1998). Yields along field edges are lower than from any other part of the field (Boatman and Sotherton 1998), and these often require increased effort for lower economic return (de Snoo and Chaney 1999), so removal from production minimises potential conflict between environmental benefits and degree of acceptability to farmers (Smallshire and Cooke 1999). Specific conservation objectives can then be targeted on these uncropped field margins, depending on the set-up and management regimes implemented (Smith *et al.* 1993). Naturally regenerated margins can offer a valuable habitat for rare arable weeds and their associated fauna (Critchley 1996a, Critchley *et al.* 1999). Margins sown with tussock-forming species such as cocks-foot (*Dactylis glomerata*), red fescue (*Festuca rubra*), or timothy (*Phleum pratenese*) provide nesting cover for game birds (Aebischer and Blake 1994), and are a suitable habitat for many arthropod species (e.g. Haughton *et al.* 1999). Seeding margins with flowering plants promotes an insect fauna rich in nectar-feeding species, such as those belonging to the orders Hymenoptera, Lepidoptera and Diptera (Carreck and Williams 1999).

Bumblebees (*Bombus* spp. Latreille, Hymenoptera, Apidae) are one example of an insect group associated with agro-ecosystems that have undergone a decline, both in terms of absolute numbers, and species diversity (Williams 1982, 1988b). Increasing acreages of annually disturbed, anemophilous crops, application of herbicides, and other land use changes, have led to spatial and temporal alterations in the composition of the flora associated with agro-ecosystems. Nectar-rich flora on which bumblebees feed has become limited as a result (Williams 1982, Corbet *et al.* 1991, Torchio 1991). As bumblebees represent a major component of the pollinator guild (Osborne and Williams 1996), any change in local populations has the potential for feedback effects on entomophilous flora (Kwak *et al.* 1991, Petanidou *et al.* 1991). In order to survive within an environment, bumblebees require suitable nesting habitats as well as appropriate forage plants (Westrich 1996). The majority of nest-sites on arable land are provided by such habitats as uncultivated field boundaries (Banaszak 1983, von Hagen 1994); these are often the first areas to be lost in agricultural intensification.

The possible contribution of field margins to bumblebee conservation within agro-ecosystems remains relatively un-documented (although see Lagerlof *et al.* 1992, Carreck and Williams 1999, Kells *et al.* 2001). Kells *et al.* (2001) found that naturally regenerated wildflower strips provided a more attractive resource than conservation headlands, but that initial cover was patchy, and that the seedbed may need to be supplemented with additional seed to increase floral diversity. Here, an investigation was undertaken into the attractiveness of uncropped field margins to nectar-foraging Apidae, when compared with corresponding margins managed as conservation headlands. Specifically, experimental margins were sown with wildflower mixes, according to guidelines given under the Arable Stewardship Scheme, a pilot MAFF (now DEFRA) initiative (MAFF 1999) as part of the Countryside Stewardship Scheme. Current requirements for pollen/nectar rich wildflower mixes established through Countryside Stewardship are that such mixes contain at least 4 nectar-rich species that will flower in continuum, and at least 4 non-competitive grasses; if the pollen/nectar component fails it must be replaced (MAFF 1999). In establishing such margins, the aim is to create an open sward of flowering plants which provide a nectar source for foraging insects, and which also provide cover for other insects and small mammals (MAFF 1999). The comparison of these 'wildflower strips' and conservation headlands was undertaken by studying bee abundance and behaviour in an experimental field margin set-up in central England.

Plate 3.1: A typical wildflower strip after establishment, year 1

3.3 Methods

3.3.1 Study sites

This study was carried out on five arable farms centred around Newport, the west Midlands, from June 30th until August 8th, 2000. All farms were located within a 15 km radius, at similar elevations, and had introduced field margins into their management plans for the first time in 1999. In 2000, experimental margins were cultivated and sown with wildflower seed mixtures (according to MAFF guidelines) or crop in early spring. All experiments took place in fields which were planted with spring-sown cereals, and which were matched for size as closely as possible. Following the spring cultivation, no other management was undertaken on the wildflower strips or controls for the duration of this experiment. Prior to 1999, all experimental areas had been subject to the same treatment as the rest of the field.

Although the same seed mix was sown at each farm, differences in date of sowing, soil seed bank and previous crop grown along the margin area, and several uncontrolled 'additions' to the seed mix by individual farmers, resulted in differences in the established vegetation between sites. However, as all data was summed across sites, these differences do not affect the overall findings of this chapter. The number of flowers of the different species recorded is shown below (table 3.1).

Annuals	**Number of flowers**	**Biennials/perennials**	**Number of flowers**
Brassica napus	1798	*Melilotus officinalis*	14654
Lamium purpureum	43	*Centaurea nigra*	175
Linum usitatissimum	71	*Chaemerion angustifolium*	70
Papaver rhoeas	1154	*Cichorium intybus*	63
Sinapsis arvensis	99	*Cirsium arvense*	917
Tripleurospernum inodorum	7342	*Lotus corniculatus*	44
		Pentaglottis sempervivens	74
		Prunella vulgaris	149
		Silene dioecia	7
		Stachys sylvatica	107
		Trifolium pratense	322
		Trifolium repens	390
		Trifolium hybridium hybridium	1622
Total number	**10507**		**18594**

Table 3.1: Annual and biennial/perennial species present on the wildflower strips following establishment, and number of flowers of each species summed across the experiment

The only annual species included in the seed mix were the crops *Brassica napus* and *Linum usitatissimum*. The other annuals that were recorded were highly competitive species presumably present in the soil seed bank. Some of the perennial species recorded were also volunteers (*Pentaglottis sempervivens, Silene dioecia*).

Two wildflower margins and a control managed as a conservation headland were studied on each farm, each within a different field. Both wildflower margins and conservation headlands were 4-6 metres wide and adjacent to the field boundary. Hedgerow nectar was not a factor in these experiments as adjacent boundaries were chosen to be relatively flower-free. Plant names follow Stace (1997).

3.3.2 Sampling methods

Observations of bee numbers, species, and chosen forage plant were made following an adaptation of Pollard's method of butterfly surveying (Pollard 1977; Pollard *et al.* 1975). Only workers were recorded as the foraging patterns of queens and drones may differ from those of the workers, and few of either of these castes were observed. Those workers collecting pollen only were removed from the data set as I wished to carry out analysis comparing floral choice to average tongue length of the different species (3.4.4, 3.4.5); tongue length is presumably not a factor in choosing pollen resources. Recordings were taken along 0.5 x 50 m^2 transects through the centres of the wildflower strips and controls, parallel with the edge of the crop. All transects were walked along the straight edges of fields; corners were not included. Three sets of observations, taken at 30-minute intervals, were made at each margin at 8-10 day intervals over a 40-day period, depending on ambient conditions, giving 5 'timepoints' of observations. The actual dates of these timepoints are given in table 3.2. These were averaged for each site for each day, with individual farms, and the margins within a farm, being visited in a random order for each observation period. All sites were visited within a 72-hour period each time, and transects were walked between 09:30 and 18:00 hours. Transects were only walked on days when it was not raining, and when the ambient temperature was 18°C or above. Number of individual flowers of each species were counted for each flower species along the transects at each time observations were made, except in the case of e.g. *Matricaria* spp., where number of flower heads were counted.

Timepoint	Date of observations
1	27-29 June
2	9-11 July
3	19-21 July
4	28-30 July
5	8-10 August

Table 3.2: Actual dates on which observations were carried out, and the timepoints these correspond to

Due to the total number of farms needed for this study, two farms visited were sites that had been used the previous year in the experiment detailed in chapter 2. However, in no case had a margin planted as a wildflower strip in 2000 been a designated naturally regenerated margin in 1999.

3.3.3 Statistical analysis

Repeated measures ANOVA in GLM using SPSS9.0 for Windows (SPSS 1998) was used to determine if bee and flower numbers varied between experimental and control treatments; time was treated as a within-subject factor, and farm and treatment as between-subject factors. 'Timepoints' (i.e. dates) were treated as replicates as the gap between observations was sufficient to allow turnover of bees and flowers. Repeated measures ANOVA was also used to resolve whether time had a significant effect on total bee numbers. Pearson's correlation was used to determine if there was an association between total number of foragers and temporal variation in floral density, and also between numbers of individual species and temporal variation. As there was no significant difference in terms of bee numbers and flower numbers between different farms (see 3.4.1; 3.4.2), these data were pooled. Repeated measures was used as the three margins (2 experimental and 1 control) on each farm were revisited at each time-point, although it is acknowledged that this method may have some limitations (see e.g. Wilcox *et al.* 2000).

3.3.4 Floral preferences and niche overlap

A preference index (PI) was constructed to show preferences of individual *Bombus* species and *A. mellifera* for each flower species present –

$$\mathrm{PI} = (V_{ik}/V_{it})/(A_k/A_t)$$

where V_{ik} is the number of foraging visits of species *i* to plant species k, V_{it} is the total number of visits of species *i* to all plant species, A_k is the total number of flowers of species k, and A_t is the total number of flowers of all species (Colwell and Futuyama 1971). Flower counts and average number of bee visits for each observation period were summed across all sites and all dates for the purposes of this index, as in some cases, different flower species were present at different sites. Spearman's correlation coefficient was used to compare relative floral preferences between bee species pairs.

Niche overlap (NO) between different species was calculated using the following equation (Morisita 1959) –

$$\mathrm{NO} = \frac{2\sum_i^n p_{ij}p_{ik}}{\sum_i^n p_{ij}[(n_{ij}-1)/(N_j-1)] + \sum_i^n p_{ik}[(n_{ik}-1)/(N_k-1)]}$$

where p_{ij} and p_{ik} represent the proportion of resource *i* of total resources used by species *j* and *k* respectively, n_{ij} and n_{ik} represent number of individuals of species *j* and *k* using resource i, and N_j and N_k represent total numbers of individuals of each species in the sample. This particular index was used as it minimises bias, and can be applied to data expressed in terms of number of individuals.

Data obtained from the Spearman's rank correlation and Morisita's equation were transformed into comparable matrices with values ranging from 0 → 1. These were then compared using a Mantel test (Mantel 1967), which is used to estimate the association between corresponding paris of values in 2 independent matrices. The Mantel statistic, Z, is computed as follows –

$$Z = \sum_{i=1}^{n-1} \sum_{j=i+1}^{n} X_{ij} Y_{ij}$$

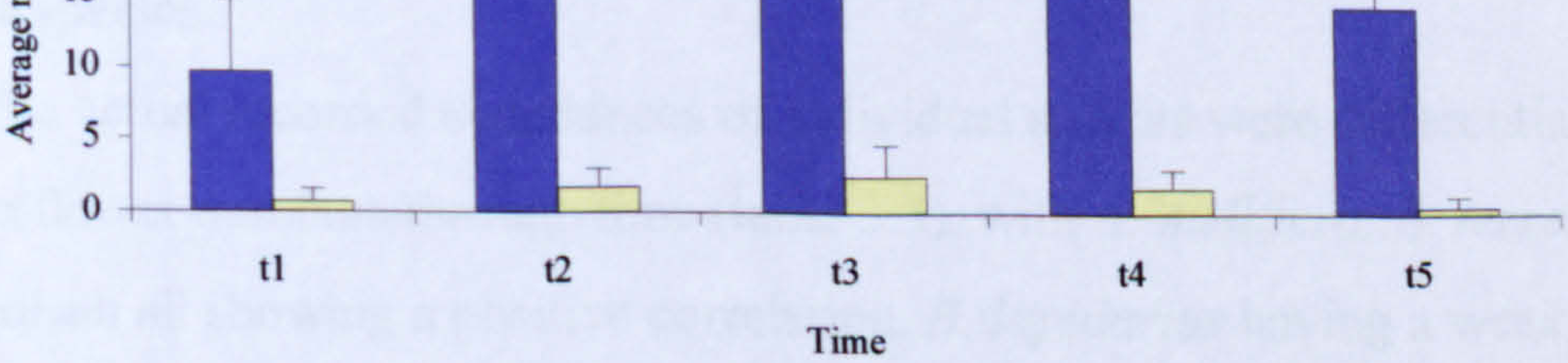
3.4 Results

Due to problems in distinguishing between *B. terrestris* and *B. lucorum*, for the purposes of what follows, these 2 species have been classified together as *B. terrestris*, and are counted as 1 species where number of species recorded is mentioned in the text.

3.4.1 Numbers of foraging bees recorded on both margins

Significantly more bees were recorded foraging in wildflower strips than in control margins ($F_{1,5}$=21.64, p=0.006) (figure 3.1), with a significant interaction also being found between time and treatment ($F_{4,20}$=5.66, p=0.006). The pattern of total bee numbers through time is best described by a quadratic relationship ($F_{1,5}$=9.41, $p<0.05$). Differences between farms were not significant ($F_{1,5}$=1.91, p=0.248).

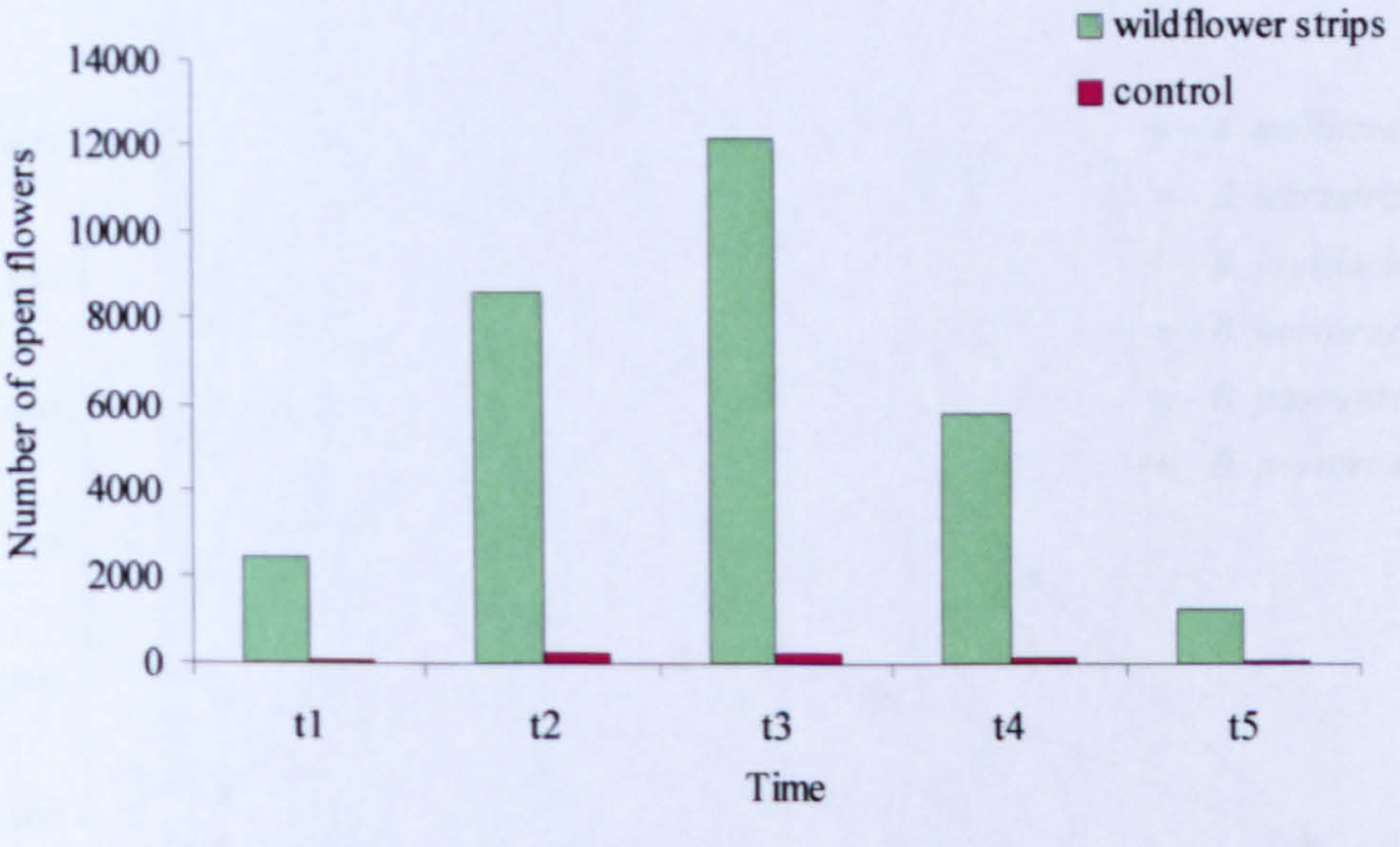
Figure 3.1: Average number of bees (*Bombus* + *Apis*) observed foraging on experimental and control margins across the duration of the experiment. Intervals between timepoints were approximately 10 days. n=10 for experimental plots; n=5 for controls. Error bars indicate SEM



3.4.2 Flower numbers through time

Wildflower strips contained many more open flowers than control margins at all timepoints (figure 3.2). Although between-treatment effects show no significant association due to some wildflower strips not having commenced flowering at t=1 ($F_{1,5}$=5.93, p>0.05), within-treatment effects for time versus treatment does reveal a significant difference ($F_{4,20}$=4.76, p=0.007). Time had a significant effect on number of open flowers ($F_{4,20}$=5.34, p=0.004); this is a reflection of the temporal nature of the flowering period. Again, there was no significant difference between farms ($F_{1,5}$=1.39, p>0.05).

Figure 3.2: Total number of open flowers on wildflower strips and control margins through time. n=10 for experimental plots; n=5 for controls. The data includes only those flower species that bees were observed to forage on



3.4.3 Bee species

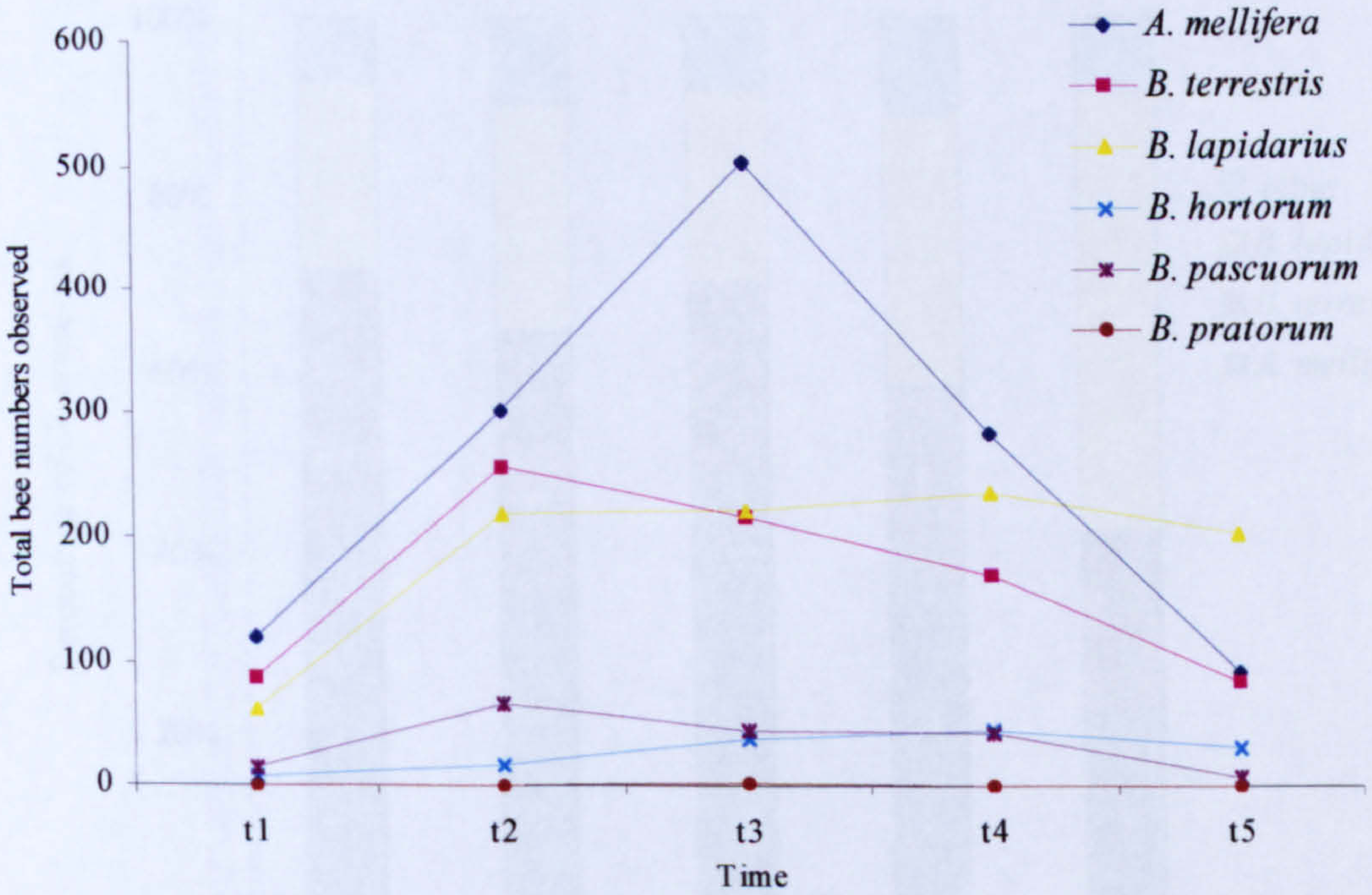
The actual recorded abundances of individual species were differentially related to flower numbers through time (table 3.3), with *A. mellifera, B. terrestris* and *B. pascuorum* all showing a positive correlation, *B. lapidarius* having a weakly positive correlation, and *B. hortorum* being negatively correlated with number of open flowers. There were only 2 recorded observations of *B. pratorum*, so this result can be disregarded.

	r	p
A. mellifera	0.805	<0.001
B. terrestris	0.761	<0.001
B. lapidarius	0.382	0.59
B. hortorum	-0.142	0.498
B. pascuorum	0.569	<0.005
All bee species combined	**0.803**	**<0.001**

Table 3.3: Pearson correlation values for total numbers of individual bee species and open flowers on wildflower strips through time. n=50

Patterns of abundance of observed foragers through time were different for the different species (figure 3.3).

Figure 3.3: Patterns of abundance of the different bee species through time. n=10

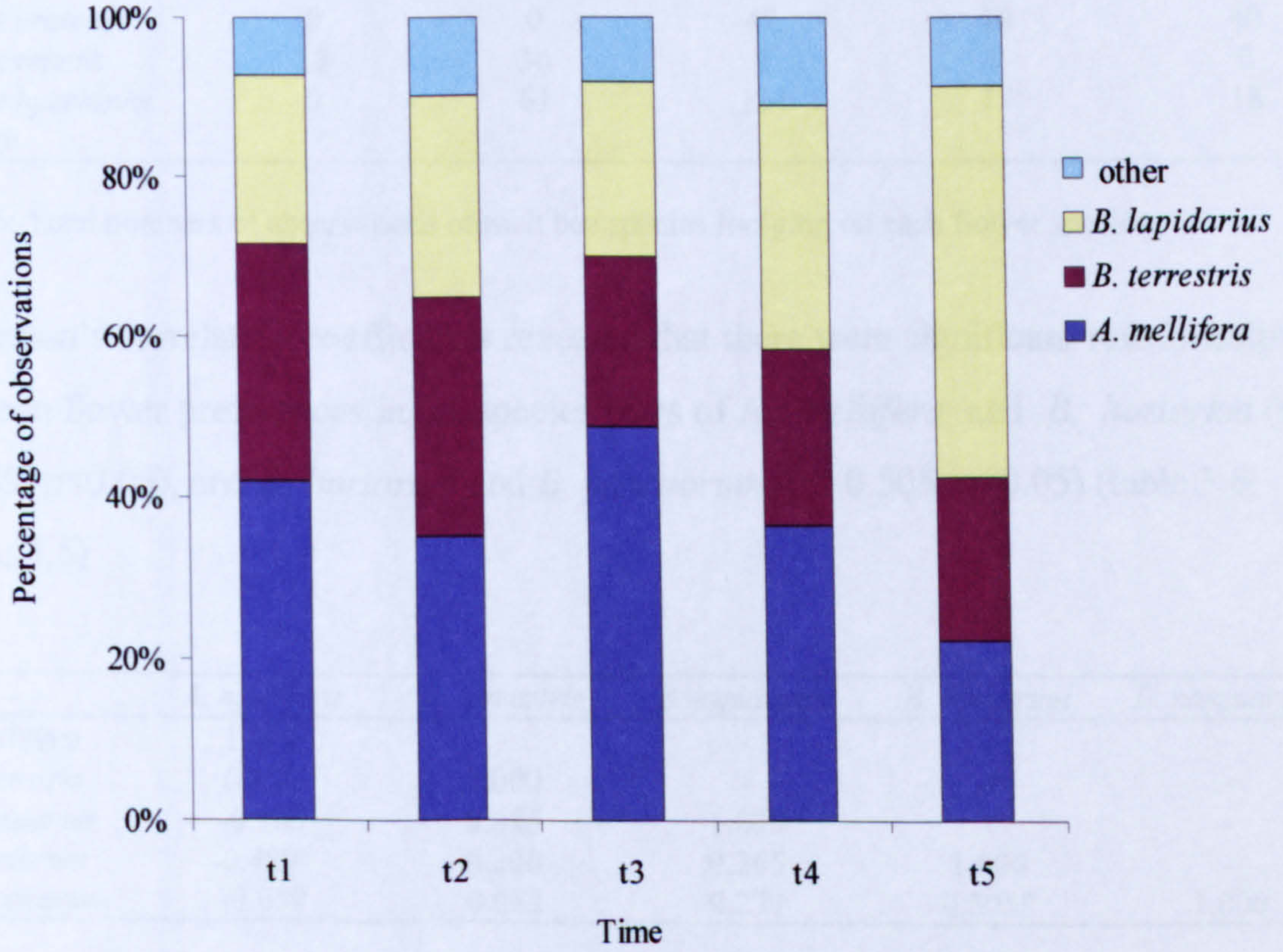


A. mellifera, *B. terrestris*, and *B. lapidarius* accounted for more than 90% of all observed visits to the wildflower strips when data across all timepoints was summed (table 3.4). *B. pascuorum*, *B. hortorum*, and *B. pratorum* made up the remaining proportion of observations. This pattern was apparent across all timepoints. (figure 3.4).

	Number of observations	**Percentage of observations**
A. mellifera	1299	38.63
B. lapidarius	939	27.92
B. terrestris	813	24.18
B. pascuorum	175	5.20
B. hortorum	135	4.01
B. pratorum	2	0.06
Total	**3363**	**100%**

Table 3.4: Total numbers of observations of each bee species across all timepoints on wildflower margins, expressed as a percentage of the total number of observations of all species

Figure 3.4: Numbers of each bee species observed on all wildflower strips through time, expressed as a percentage of the total number of bees observed. n=10. Other observed species were *B. pascuorum*, *B. hortorum* and *B. pratorum*



3.4.4 Floral preferences of foraging bees

There were interspecific differences in flower choice by bee species (table 3:5).

Flower species	Bee species				
	A. mellifera	*B. terrestris*	*B. lapidarius*	*B. hortorum*	*B. pascuorum*
Brassica napus	94	105	54	1	10
Lamium purpureum	10	4	0	32	7
Linum usitatissimum	35	0	0	85	0
Papaver rhoeas	2	0	0	3	12
Sinapsis arvensis	24	0	4	2	14
Tripleurospernum inodorum	1	0	0	0	0
Melilotus officinalis	17	342	238	0	36
Centaurea nigra	30	62	42	1	15
Chaemerion angustifolium	17	8	4	0	0
Cichorium intybus	1	11	2	0	0
Cirsium arvense	0	148	341	52	11
Lotus corniculatus	0	7	1	4	0
Pentaglottis sempervivens	331	6	0	5	19
Prunella vulgaris	0	1	4	6	21
Silene dioecia	46	0	0	0	0
Stachys sylvatica	617	4	5	26	2
Trifolium pratense	0	0	42	18	40
Trifolium repens	18	36	0	0	0
Trifolium hybridium hybridium	0	61	134	17	18

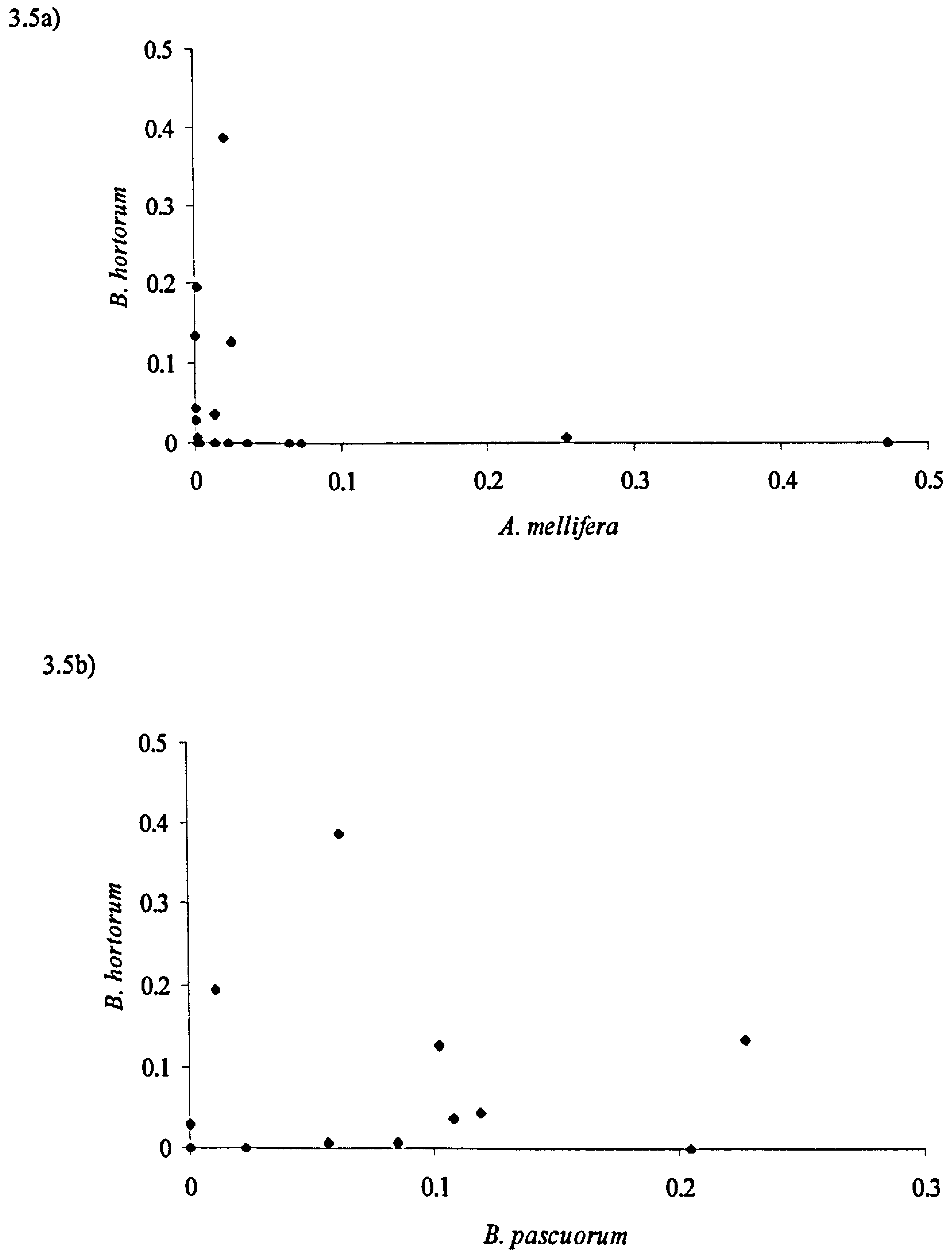
Table 3.5: Total numbers of observations of each bee species foraging on each flower species

Spearman's correlation coefficients revealed that there were significant relationships between flower preferences in the species pairs of A. *mellifera* and *B. hortorum* (r = -0.489, $p<0.05$), and *B. hortorum* and *B. pascuorum* (r = 0.505, $p<0.05$) (table 3.6; figure 3.5)

	A. mellifera	*B. terrestris*	*B. lapidarius*	*B. hortorum*	*B. pascuorum*
A. mellifera	1.000	-	-	-	-
B. terrestris	0.154	1.000	-	-	-
B. lapidarius	-0.163	0.385	1.000	-	-
B. hortorum	-0.489*	0.300	0.265	1.000	-
B. pascuorum	-0.059	0.082	0.277	0.505*	1.000

Table 3.6: Spearman's correlation coefficients showing correlations between relative preferences of *A. mellifera* and *Bombus* spp. across all flower species. n=19, * indicates significance at 0.05

Figure 3.5: Scatter graphs showing relationship between preference indices for a) *A. mellifera* and *B. hortorum*, and b) *B. hortorum* and *B. pascuorum*. n=50



3.4.5 Niche overlap

Morisita's measure of total niche overlap is shown below (table 3.7).

	A. mellifera	*B. terrestris*	*B. lapidarius*	*B. hortorum*	*B. pascuorum*
A. mellifera	1.000	-	-	-	-
B. terrestris	0.297	1.000	-	-	-
B. lapidarius	0.433	0.838	1.000	-	-
B. hortorum	0.462	0.362	0.749	1.000	-
B. pascuorum	0.389	0.635	0.589	0.444	1.000

Table 3.7: Morisita's measure of total niche overlap between species pairs

A Mantel test of transformed Spearman's rank correlation (preference indices), and Morisita's measure (niche overlap) resulted in Z=2.168676, p=0.175, with 999 permutations. This indicates that there is no correlation between floral preference and niche overlap for pairs of bumblebee species.

3.5 Discussion

In this experiment wildflower strips offered a much more attractive habitat to foraging bees than controls managed as conservation headlands. They contained many more open flowers, and attracted a significantly higher number of bees across the duration of this study. A similar response has been recorded for butterflies (Feber *et al.* 1996), and the syrphid *Episyrphus balteatus* DeGeer (MacLeod 1999). Some temporal variation was found in forager abundance, both overall, and between individual species; this is most likely a reflection of species demographics. Although abundance of most bee species displayed a positive correlation with number of open flowers, numbers of *B. hortorum* were negatively correlated with flower numbers through time (table 3.3). This species has previously been found to preferentially visit small and medium sized patches of flowers above large, densely populated, patches (Teräs 1985, Sowig 1989). Of those bumblebees observed foraging on the conservation headlands (controls), the majority were foraging for pollen from *Papaver rhoeas*; few were observed foraging for nectar.

Observations of *A. mellifera, B. terrestris* and *B. lapidarius* made up the majority of data points in this experiment. *B. terrestris* and *B. lapidarius* have previously been found to be the most numerous *Bombus* species foraging on temporary crop resources of arable land (Walther-Hellwig and Frankl 2000, Kells *et al.* 2001). These two *Bombus* species are generalists (Williams 1986), and can visit shallower flowers than those with longer proboscides. In areas of natural habitat within agricultural landscapes in Germany, Walther-Hellwig (2000) found that along with *B. terrestris* and *B. lapidarius*, 2-3 other bumblebee species accounted for more than 10% of observations at such sites, and a similar pattern of low species diversity is revealed here. All five *Bombus* species observed here belong to the common ubiquitous species group of Williams (1986); there were no recordings of any rarer species, which tend to be more localised in their distributions (Williams 1986).

Although no significant relationship was found between the floral preferences of *A. mellifera* and four of the five *Bombus* species recorded, the floral preferences of *A. mellifera* and *B. hortorum* were found to be significantly negatively correlated. Floral species that were much more highly preferred by *B. hortorum* than *A. mellifera* were *L. purpureum, C. nigra, C. arvense, S. sylvatica, L. corniculatus, T. pratense* and *P.vulgaris*, whilst *Brassica* spp., *S. arvensis, E. montanum, C. intybus, T. repens* and *S. dioica* were preferred by *A. mellifera* much more than *B. hortorum*. Only *P. sempervivens* and *T. hybridium* had similar preference values for both these bee species in this study. *B. hortorum* and *A. mellifera* occupy either end of the morphological scale here; *A. mellifera* is a short-tongued generalist that feeds on shallow, relatively open flowers, whilst *B. hortorum* is long-tongued and best able to manipulate those flowers with the deepest corollas. *B. pascuorum* preferences correlated positively with those of *B. hortorum*; this species has the next-longest tongue length of those observed.

The coexistence of such generalist species as *A. mellifera, B. terrestris*, and *B. lucorum* is presumably at least partly facilitated by super-abundant forage resources throughout much of the flowering period (Den Boer 1980). These species may be able to avoid competition by utilising different floral resources under such conditions. Although one would expect interspecific competition to be greatest between closely related species (e.g. Gordon 2000), it is becoming increasingly realised that coexistence does not necessarily imply competition and therefore a state of competitive equilibrium. Weather, climate and other physical factors (Den Boer 1986), as well as parasitism (Gordon 2000), may be holding bee numbers at below carrying capacity in the environment, so allowing coexistence of morphologically similar species as shared resources are not exhausted (Abrams 1988, Huston and Deangelis 1994); coexistence and abundant resources are evident in temperate ecosystems during the flowering period when bumblebees are active. Other studies have found evidence of competition between bumblebee species (Inouye 1978, Pyke 1982), but these were carried out at altitude in the Rocky Mountains, where resources may be more limited than on agricultural land at much lower altitudes in Western Europe. Numbers may also be held below carrying capacity because of limited forage and potential nest sites. Ranta and Vepsäläinen (1981) have suggested that spatio-temporal unpredictability in floral resources may be a key factor affecting whether or not local interspecific competition occurs between bumblebee species. Although nectar-rich forage has been increased in this study, species demographics are such that there will presumably be a time lag before bee numbers respond to this, if indeed available forage is a limiting factor. Little previous evidence has been found to support theories of competitive exclusion between *A. mellifera* and *Bombus* spp. with respect to floral preferences under natural conditions (Steffan-Dewenter and Tscharntke 2000); results from this experiment would suggest that even where floral preferences are similar between species pairs, total niche overlap is low.

Bumblebees are economically important pollinators of many crop and wildflower species (Colbert and de Oliveira 1990, Corbet *et al.* 1991, Batra 1995); their conservation is important in both aesthetic and economic terms. Results of this study suggest that creation of wildflower strips on farmland can provide important forage resources for *Bombus* spp., and therefore could be utilised in bumblebee conservation schemes. As diversity of naturally regenerated vegetation depends upon flora already present along the field boundary, and those species present in the seed and bud banks (Hartshorn 1978), seed mixes can be used to provide a more diverse flora, with a higher proportion of perennial species than may result from natural vegetation. Localised seed dispersal may have limited seeds available (Kollmann and Bassin 2001), and seed bank diversity may have become impoverished following years of cultivation and herbicide application (Wilson 1994, Ford 1996). Perennial vegetation typical of a mid-successional community is thought to be more attractive to bumblebees, with bumblebees visiting perennials more often than annuals (Parrish and Bazzaz 1979, Fussell and Corbet 1992a, Corbet 2000). In this study, perennials accounted for 64.84% of all flowers, and received 86.30% of all recorded visits by *Bombus* spp. Seeding disturbed land with plants typical of a more advanced successional stage has previously been found to accelerate succession (Wilcox 1998). Other benefits of using seed mixes as opposed to natural regeneration include increased cover during establishment, and possibly enhanced control of annual grass weeds (Smith *et al.* 1993, Smith *et al.* 1994).

Sufficient and suitable resources to support an insect fauna rich in Apidae can only be offered by florally diverse habitats; on arable land these will mostly be represented by areas of semi-natural vegetation. The diverse flora and more complex structure of such habitats are also known to support a generally more species-rich insect fauna (Pollard 1968, Thomas and Marshall 1999) and avifauna (e.g. O'Connor and Shrubb 1986, Shrubb *et al.* 1997). There is some evidence that complex landscapes with a high density and connectivity of uncultivated, perennial habitats may increase populations of natural enemies, which can reduce pest populations in neighbouring fields to economically significant levels (Thies and Tscharntke 1999). Only mobile and abundant natural enemies can operate in fragmented systems (Kruess and Tscharntke 1994); one result of restoring connectivity should be increased levels of bio-control. Connectivity has also been shown to maintain population dispersal within habitat specialists (Mech and Hallett 2001), something that becomes more important with increasing habitat fragmentation. Field margins, whether naturally regenerated or seeded, have the potential to act as corridors for movement of both flora and fauna (Fry 1991, Allen-Wardell *et al.* 1998, Wossink *et al.* 1999, Mech and Hallett 2001), and also to provide cover against predation for small mammal species (Mech and Hallett 2001). They offer refuges for those arthropod species whose diversity and abundance the toxic effects of herbicides and pesticides have altered (Chiverton 1999), and buffer adjacent hedgerows and watercourses from drift and run-off (Cutherbertson and Jepson 1988, de Snoo and de Wit 1998).

There are ecological and economic problems to overcome in creating wildflower strips, and returning land to semi-natural vegetation (Fry and Main 1993), and it has been argued that the high cost of creating corridors could be better spent on other conservation priorities (Mann and Plummer 1993). Field edges are already an intrinsic component of agricultural landscapes, and the initial set-up costs should be balanced by safeguarding yields and increasing populations of natural enemies, if such margins are managed correctly. The ratio of arable to semi-natural vegetation is flexible, and could be altered by changing the width of the field margin in response to cereal surpluses or deficits (Thomas and Marshall 1999). In any event, the importance of formulating good policy before encouraging widespread implementation of such conservation measures is paramount (Oglethorpe and Sanderson 1988).

I would advocate from the results of this study that field margins sown with a wildflower seed mix rich in nectar-producing species offer a potentially valuable means of conserving bumblebee species numbers and diversity on agricultural land. Obviously, careful management will be needed to maintain initial diversity of these habitats; Smith *et al.* (1993) have shown that diversity of sown margins can be maintained for at least 3 years with certain mowing regimes, and in the absence of fertilisers. Wildflower margins can provide a continuum of nectar and pollen throughout the period when bumblebee colonies are active. The seed mix can be manipulated to maintain a high proportion of perennial species, which bumblebees have been identified as favouring. However, in this experiment, both annual and perennial flora were included in the mixes as annual species have been documented as having a positive effect on other insect fauna within agro-ecosystems (Kruess and Tscharntke 1994, Krause 1997). As more work is carried out into field margins, increasing knowledge will allow further manipulation and refinement of margin mixes, which should result in these containing those floral species most preferred by different *Bombus* species; they may then be used to target conservation of specific *Bombus* species within the foraging guild. The implementation of such nectar-rich margins across agro-ecosystems should have a positive role to play in the conservation of many species associated with arable land.

4. COMMON AND 'NOVEL' CROPS – NECTAR PRODUCTION AND BUMBLEBEE FORAGING BEHAVIOUR

submitted to *Apidologie*

4.1 Abstract

Bumblebees (*Bombus* spp.) are important pollinators of many crop species in the U.K. Their presence is essential for seed production in some species, whilst for many others, their presence increases either quantity or quality of yields. In return, many entomophilous crops provide bumblebees with a source of nectar and/or pollen. With the potential increase in crop diversity within the U.K., driven by a desire for new products, and to reduce the importation of vegetable protein into the E.U., it is important that native pollinator diversity is maintained if commercial yields of such crops are to be maximised. The increased floral resources resulting from the introduction of such crops could also greatly benefit bumblebees. This study investigated the nectar secretion patterns of five crop species, and corresponding visitation of both bumblebees and honeybees. Three of these species are commonly grown in the U.K. at present, and two are 'novel' crops. It was found that nectar secretion patterns differed between crops, and that nectar secretion rates were positively correlated with visitation rates of bee species. Particular bee species seemed to favour certain crop species over others. The implications of increasing diversification on farmland for bumblebee conservation are discussed.

4.2 Introduction

The arable landscape across the lowland U.K. broadly conforms to a mosaic pattern of cropped land, interspersed within a matrix of semi-natural areas, most of which remain uncultivated (Marshall 1993). The area under intensive management has been substantially increased in recent years (Barr *et al.* 1993), at the expense of semi-natural habitats, and there has been a general trend towards landscape homogeneity. There is also increased homogeneity in the cropping pattern, with less overall variety in crop species grown, and the almost total disappearance of crop rotation practises. As a result, there is now little continuum to the flowering period across arable landscapes, and changes have led to many species of flora and fauna that were once common on agricultural land becoming scarce or even endangered (Nature Conservancy Council 1984, Sotherton 1998).

Bumblebees (*Bombus* spp.) are a major component of the pollinator guild across Europe (Corbet *et al.* 1991), where 84% of crops grown depend on bees for pollination (Williams 1994). They are important pollinators of the many crop species grown in the U.K. that do not have anemophilous-based pollination systems. For some crop species, the presence of bumblebees is essential (e.g. McGregor 1976, Free 1993), for example, in some species, bee pollination is necessary in order to obtain seed (e.g. brassicas (*Brassica* spp.)) (Crane and Walker 1983, 1984, Free 1993). Other crops require insect movement of the pollen within the flower (e.g. rape, (*Brassica napus*), brown mustard (*Brassica juncea*), tomato (*Lycopersicon esculentum*)), or cross-pollination in those species that are self-incompatible (e.g. alfalfa (*Medicago sativa*), clover (*Trifolium* spp.)). Although bumblebee visits are not essential for other species, they can augment yield in terms of quantity or quality (e.g. Erickson 1975, Erickson *et al.* 1978, Parker *et al.* 1987). Bumblebees are such effective pollinators due to certain physiological, morphological and behavioural characteristics that they possess (Newsholme *et al.* 1972, Heinrich 1976b, Hippa *et al.* 1981, Surholt and Newsholme 1981, Thomson 1981, Buchmann 1983, Estes *et al.* 1983, Willmer *et al.* 1994), and they are highly effective in terms of pollen dispersal (Jennersten *et al.* 1992, Steffan-Dewenter and Tscharntke 1997).

Cropped land represents a temporary foraging habitat, which has been found to attract a high density of bumblebees, but a low diversity, when compared with surrounding semi-natural vegetation (Walther-Hellwig and Frankl 2000). There is also low diversity of floral species within cropped fields as a result of modern agricultural practise, which contributes to the low diversity of pollinators present (Banaszak 1984). In Poland, the diversity of wild bees in stands of annual crops was found to be positively correlated with degree of contact between these stands and areas of semi-natural vegetation (Banaszak and Cierzniak 1994, Banaszak 1996). Schwenninger (1992) found higher numbers of bee species in those agricultural areas that contained higher proportions and a higher quality of small, semi-natural landscape elements. Although cropped areas can offer an abundant food source for bees during the flowering period, a diversity of habitats are required for formation and maturation of successful colonies (see e.g. Banaszak 1984). If colonies are to succeed, they require amongst other things a continuous supply of nectar and pollen. Large-scale monocultures alone cannot provide this (Martin and McGregor 1973), and so there must be augmentation from flowering species in semi-natural habitats (Corbet 1995). Alternatively, planting a range of crop species with differing flowering periods could provide the necessary food resources, although this would have to be economically acceptable to farmers. This could be especially important in areas where much of the semi-natural vegetation has already disappeared, and where excessive use of herbicides and other forms of weed control has further decreased bee forage (Martin and McGregor 1973).

The U.K. generalist species *Bombus lapidarius* and *Bombus terrestris* are known to be the two main beneficiaries of the temporary peak of nectar availability provided by flowering crops (Fussell and Corbet 1991). There is some evidence that these two species have larger foraging ranges than many of the other British species, and they have been termed 'spatial generalists' (Witte *et al.* 1989, Hedtke 1996), as well as being known to be generalists in terms of flower choice (Williams 1986). The ability to forage over greater distances from the nest, and the less conservative flower choice displayed by these species means that they are probably less affected by landscape change than species such as *B. pascuorum*, *B. sylvarum* and *B. ruderarius* which are thought to have much smaller foraging ranges, and those such as *B. hortorum* and *B. muscorum* which are physiologically constrained in their floral choice (Fussell and Corbet 1991, Fussell and Corbet 1992a, Corbet *et al.* 1995, Walther-Hellwig and Frankl 2000). Nonetheless, it is important that the native pollinator diversity is preserved so that the economic value of entomophilous crop species is not affected (Corbet 1995), and that the existing aesthetic and environmental quality of the landscape is maintained (Moonen and Marshall 2001). The huge levels of mortality caused to honeybee populations by the *Varroa destructor* mite have already highlighted potential problems related to over-reliance on one or a few pollinators. Also, maintaining pollinator diversity should increase the likelihood of obtaining economically successful yields from any 'novel' crops that may be introduced into the U.K. in the light of the production surpluses of major cereal and oilseed crops faced by the E.U. (Williams 1994).

This study was set up to determine the nectar secretion patterns of a variety of common and novel entomophilous crops, and the visitation patterns of Apidae to these. The following 5 crop species were studied – *Vicia faba* (field beans), *Brassica napus* ssp. *oleifera* (oilseed rape), *Linum usitatissimum* (linseed), *Glycine max* (soya), and *Onobrychis viciifolia* (sainfoin). *V. faba*, *B. napus* and *L. usitatissimum* are commonly grown in the U.K., whilst *G. max* and *O. viciifolia* are 'novel' crop species at present, with few hectares under cultivation.

4.2.1 *Vicia faba*

V. faba is an annual belonging to the Fabaceae family. Members of this family have 5 petals arranged in a distinctive 'standard (1) wings (2) keel (2)' formation, and are often white, pink or purple in colour. The petal bases are fused to form a deep corolla, and this structure renders the flowers attractive to long-tongued bumblebee species. When these land on the keel of the flower, their body weight causes the anthers to be pressed against their ventral surface, and nototribic pollen transfer to occur. Shorter tongued species act as nectar 'robbers'; species such as *B. terrestris* (primary robbers) will bite a hole in the base of the corolla in order to gain access to the nectar, and other bee species will also utilise these holes (secondary robbers)

(Poulsen 1973). Obviously, those species involved in nectar robbing do not contribute to pollination. Although unable to reach the nectar down the corolla, honeybees and shorter tongued bumblebees do collect pollen from the flowers by landing on the keel. Longer tongued bee species also collect pollen from *V. faba.*

4.2.2 *Brassica napus*

B. napus is a member of the Brassicaceae family. The plants are annual when sown early in the season to flower later in the summer, or biennial when sown late in the year as these flower the following spring. The flowering period itself is approximately 4-5 weeks long. Plants produce small yellow flowers (~1.5cm in diameter) with 4 petals. Although primarily self-pollinating, *B. napus* is highly attractive to Apidae as a source of both nectar and pollen. Honeybees are particularly numerous foragers on this species (Pierre *et al.* 1999).

4.2.3 *Linum usitatissimum*

The pale blue or white *L.usitatissimum* flowers have 5 petals, and open to form a shallow dish shape, 2-3 cm in diameter. New flowers open in the morning and the anthers start to dehisce almost immediately. When the flower is pollinated, the petals are dropped; most flowers have lost their petals by the afternoon (personal observation). The flowering period of *L. usitatissimum* is 2-3 weeks in June. Both bumblebees and honeybees visit *L. usitatissimum,* and forage for both nectar and pollen from the flowers (Gubin 1945), although it is unsure how much these contribute to pollination as the rate of selfing is thought to be high (Williams 1988a).

4.2.4 *Glycine max*

As a Fabaceae, *G. max* has the same floral structure as *V. faba.* It is an annual, and ensures high levels of self-pollination through the anthers opening while the florets are still buds, and shedding pollen directly onto the stigma. The flowering period is approximately 6 weeks during July and August, although individual flowers only stay open for one day. The inflorescence takes the form of a raceme of 1-35 white or purple flowers, each about 1cm long. Both bumblebees and honeybees will visit soya for nectar and pollen, although attractiveness does vary according to cultivar (Erickson 1982).

4.2.5 *Onobrychis viciifolia*

O. viciifolia is also a member of the Fabaceae family, and as such its' flower structure is similar to that of the other members of this family. It is a perennial, and in this country the flowering period is June-early July.The flowers are present in whorls of 6-7, with many whorls on each raceme. The flowers in each whorl open at the same time, and flowering is in a sequential fashion up the stem. *O. viciifolia* flowers are small, with the corolla between 2-3mm in depth (unpublished data), and robbing is unnecessary in order for bumblebee species to reach the nectar. The nectar contains a high concentration of sugar, and is highly attractive to bees; the pollen is also collected by both bumblebees and honeybees (personal observation).

4.3 Methods

This experiment was carried out at two farms in southern central England during summer 1999 and summer 2000. All observations were taken in crops that were being grown for commercial purposes, and in fields of no less than 2 hectares. *V. faba* was a spring-sown crop which flowered mid-summer, *B. napus* was winter-sown and flowered early in the flowering period, *L. usitatissimum* was in flower mid-June to early July, *G. max* was in flower mid-July to early August, and *O. viciifolia* flowered for a 4-week period in June and July; it had been grown at the same site for the preceeding 8 years and the seed present in the seed bank was supplemented by commercial seed in the previous winter.

4.3.1 Experimental set-up

A series of 5, 50m long transects were set out through the crop, parallel to each other, and 10m apart. These commenced 10m in to the crop to eliminate possible edge effects. Observations were made on a dawn-to-dusk basis (06:00-20:00), and a randomly assigned transect was walked at each observation period. The workers present on each crop were assessed by walking along a transect and noting density and diversity of bee species present in a 0.5m wide strip at 30 minute intervals. Observed queens and drones were not recorded as the foraging patterns of these may differ from that of the workers. Only those individuals that were actively foraging for nectar on the crop were recorded in order to allow for comparisions between pollinator visitation rate and nectar secretion patterns of the crop. For *V. faba,* only those species visiting the flower in 'normal' fashion were recorded (i.e. not either primary or secondary robbers). Visitation of species which rob are presumably not related to floral morphology (except perhaps for ease of biting through floral tissue in the case of primary robbers such as *B. terrestris*).

Crop species	Date of observations
V. faba	12th July
B. napus	30th May
L. usitatissimum	28th June
G. max	2nd August
O. viciifolia	24th June

Table 4.1: Dates of experimental observations for each of the 5 crop species

4.3.2 Nectar measurements: standing crop and secretion rates

Nectar measurements were taken at two-hour intervals over one fourteen hour period (06:00 – 20:00) for each crop, at the peak of the flowering period; this was also the period when bee counts were taken. Either 0.1µl or 0.5µl glass micro-capillary pipettes (Drummond) were used throughout.

To calculate standing crop, fifteen different fully open flowers from separate primary stems were sampled at each two hour interval. Nectar concentration (grams sucrose/100 grams solution) was measured using either 0-50% or 40-80% refractometers (Bellingham and Stanley, Tunbridge Wells), modified for small volumes. Milligrams of sugar was calculated using the following equation (Prys-Jones and Corbet 1991) –

$$p = 0.0037291C + 0.0000178C^2 + 0.9988603$$

where *C* is the weight of sucrose per 100g nectar solution (from the refractometer), and *p* is an estimate of the density of *C*. As sampling may have damaged secretory tissue, sampled flowers were marked with a dot of Humbrol paint to avoid resampling.

To measure secretion rate, fifteen fully open flowers from separate primary stems were marked, and then emptied of nectar using micro-capillaries. The stems were then covered with fine mesh bags that were tied at the bottom to prevent forager access during the period of the experiment. After 90 minutes, bags were removed, and the nectar sampled using the same protocol as for standing crop. The same flowers were sampled throughout the day.

4.3.3 Microclimate

Microclimate was recorded on each day of observations. Equipment was set up at flower-height in a site adjacent to the experimental plot, and exposed to similar ambient conditions as the crop. Ambient temperature (Ta) was recorded with a thermometer out of direct sunlight. Relative humidity (RH) was recorded using a hand-held hygrometer. Five Ta and RH readings were taken at 15s intervals once every 30 minutes, and averaged. Wind speed was estimated arbitrarily on a scale of 0→4 (0= calm; 4=strong breeze), and cloud cover was estimated as a percentage (to the nearest 10%). These data were purely for comparative purposes, in order to establish that conditions were similar for the different sets of observations.

4.3.4 Analysis

A two-way ANOVA using SPSS9.0 for Windows (SPSS 1998) was used to establish if secretion rate and crop type affected visitation pattern of the observed bee species. Data were transformed (ln + 1) due to their non-normal distribution. Time was omitted from the analysis, as its effect on visitation rate is not separate from that of secretion rate.

4.4 Results

4.4.1 Microclimate

Comparison of microclimate data revealed that temperatures ranges were within a similar range between different days of observation, between sites and between the two years when the data for this study was collected. Experimental days were pre-selected to be good weather with low wind conditions. Ambient temperature and relative humidity are likely to be the major microclimatic factors influencing bee foraging, and the averages of these at 5 times throughout the day at each observation period are shown below for comparison (table 4.2).

Time	T_a					RH				
	1	2	3	4	5	1	2	3	4	5
06:00	9	11	10	8.5	11	85	80	85	85	90
09:30	20.5	17	21	21	18.5	60	70	55	50	65
13:00	24	23	20	25.5	23.5	40	55	50	40	40
16:30	23.5	19.5	21	23	23	45	50	45	60	50
20:00	17	18.5	15	18.5	18	80	75	65	80	75

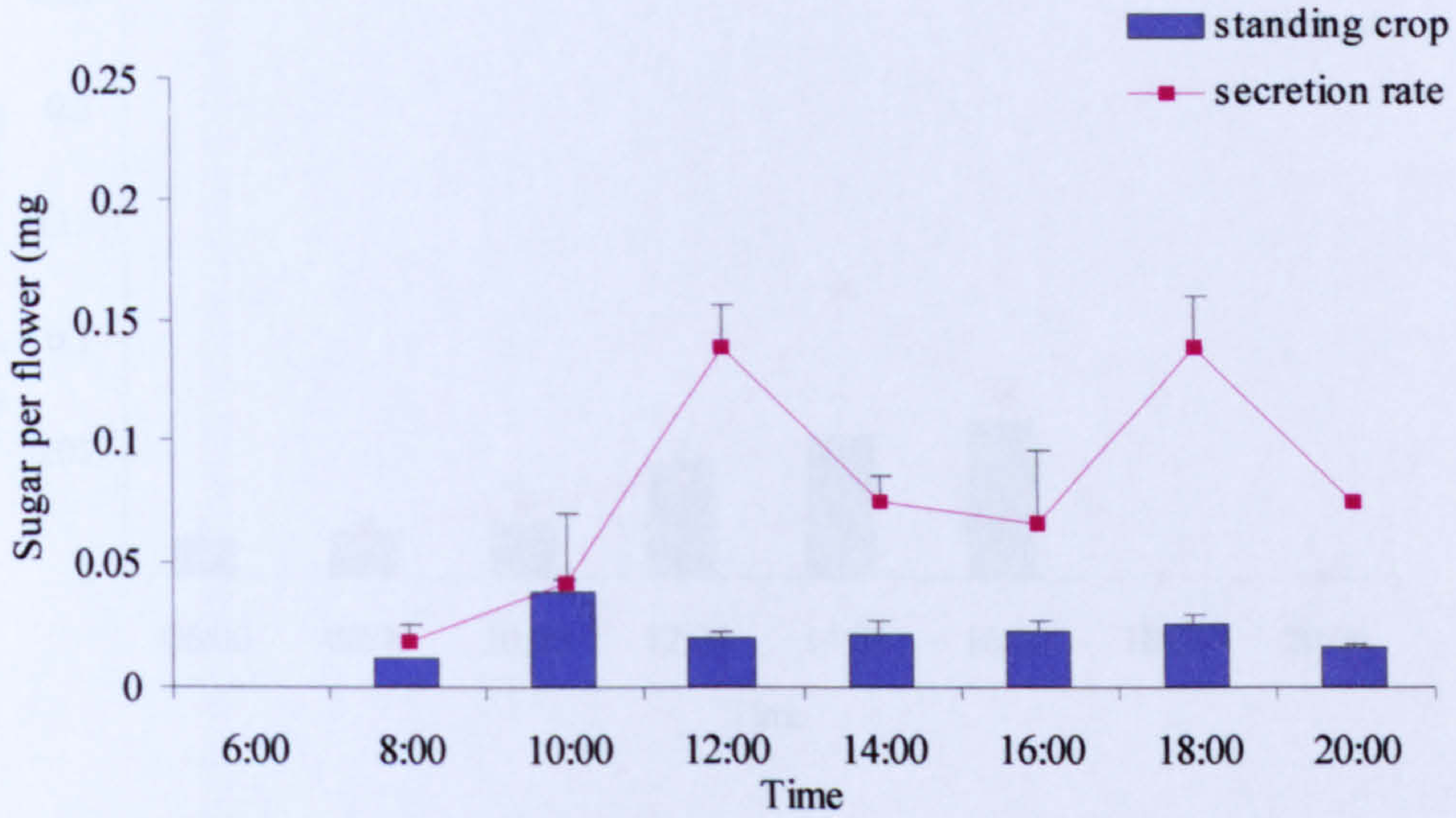
Table 4.2: Ambient temperature (T_a) and relative humidity (RH) at 5 timepoints during the observation periods on each of the 5 crops for comparison. Each figure is an average of 5 readings for that time (see section 4.3.3)

4.4.2 Standing crop and secretion rates

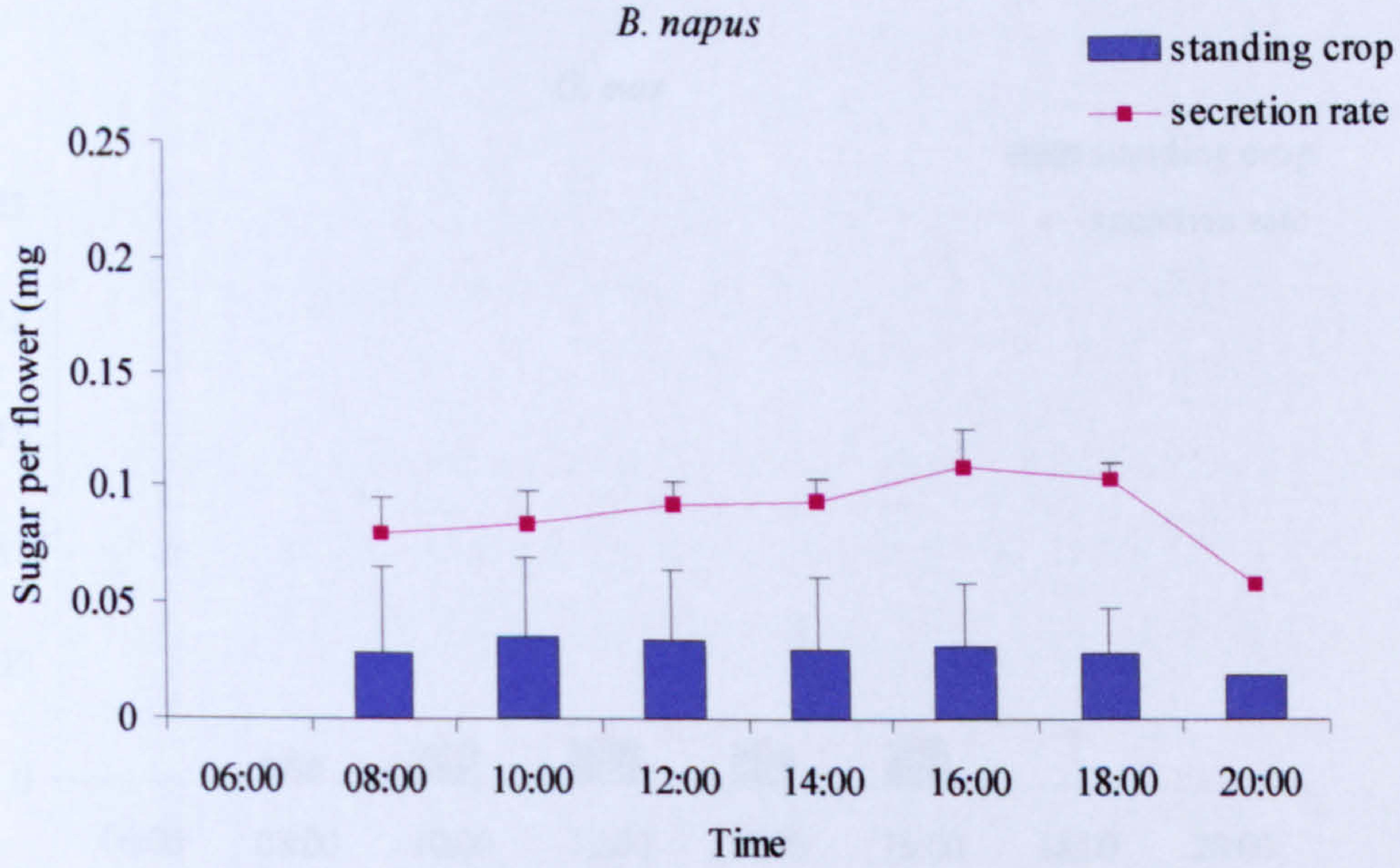
The standing crop and secretion rates of the five crop species under investigation are shown below (figure 4.1). Both these are plotted in terms of amount of sugar per flower in mg (see Prys-Jones and Corbet 1991).

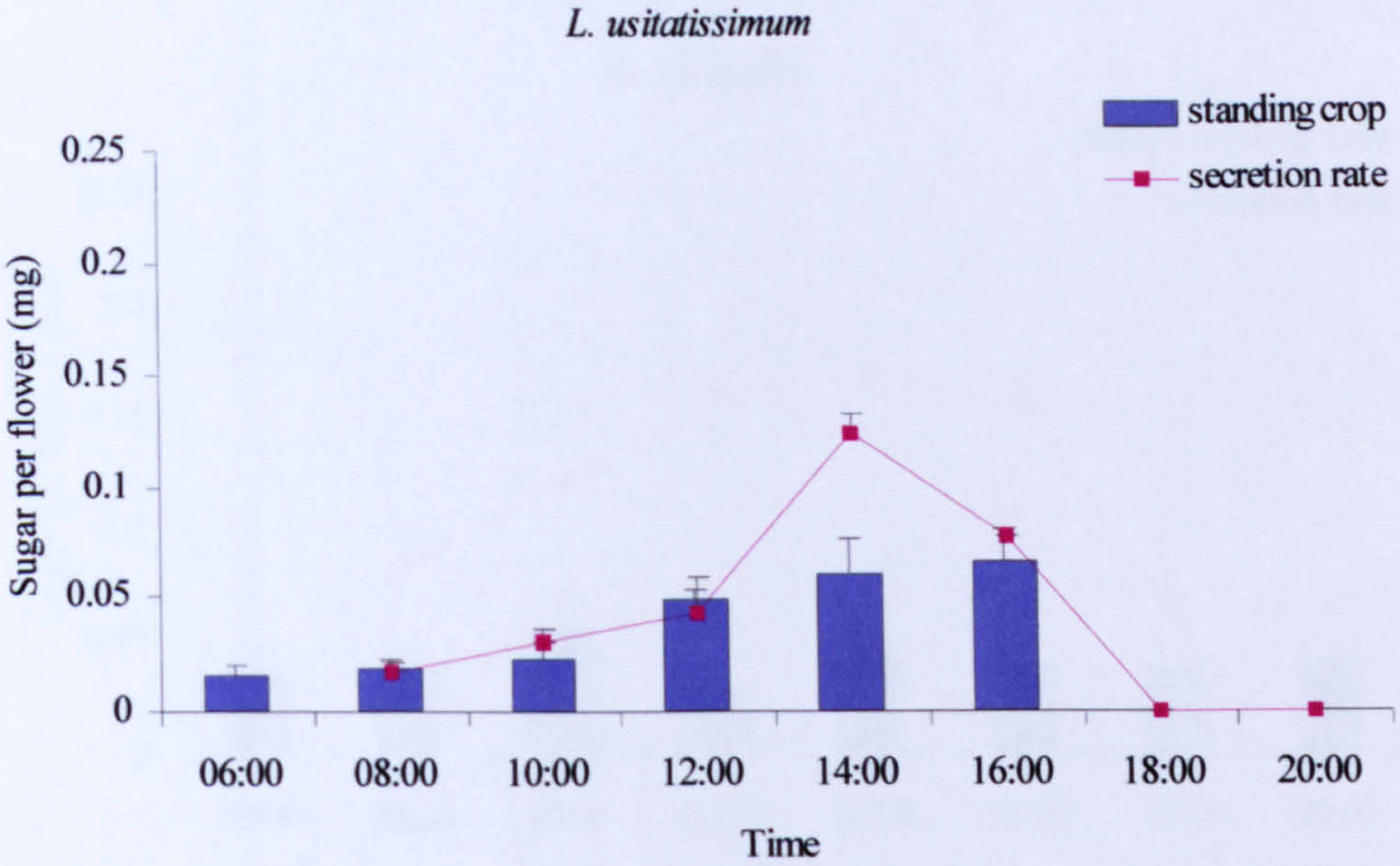
Figure 4.1: Standing crop and secretion rate of crops in terms of sugar content (mg) throughout a 14 hour period. Where no standing crop was recorded at 06:00, nectar production had not commenced. Secretion rates could only be measured from 08:00 onwards as 2 hours needed to elapse before initial measurements could be taken. n=15

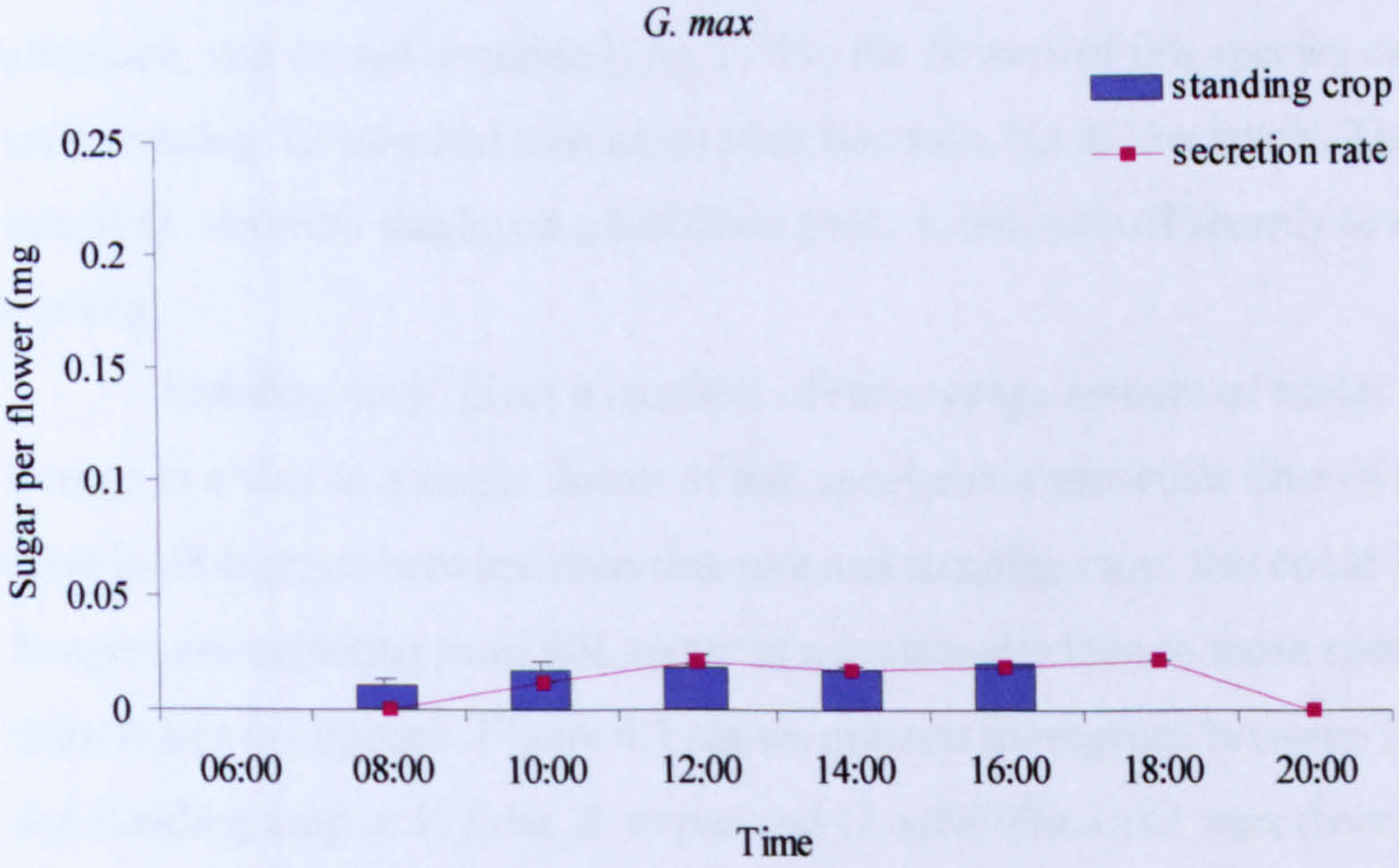
V. faba

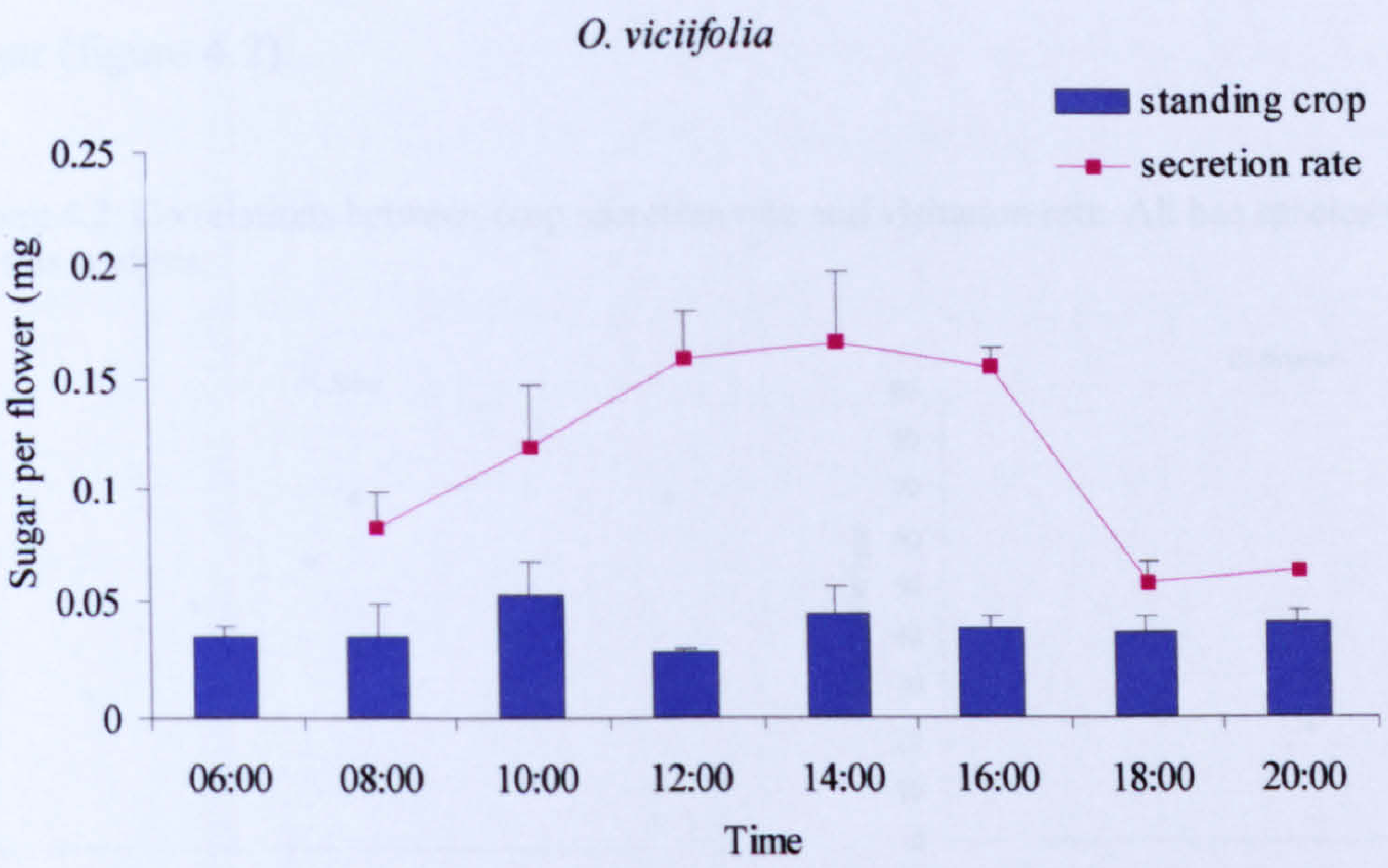


B. napus




L. usitatissimum
standing crop
secretion rate
Sugar per flower (mg)
0.25
0.2
0.15
0.1
0.05
0
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
Time


G. max
standing crop
secretion rate
Sugar per flower (mg
0.25
0.2
0.15
0.1
0.05
0
06:00
08:00
10:00
12:00
14:00
16:00
18:00
20:00
Time



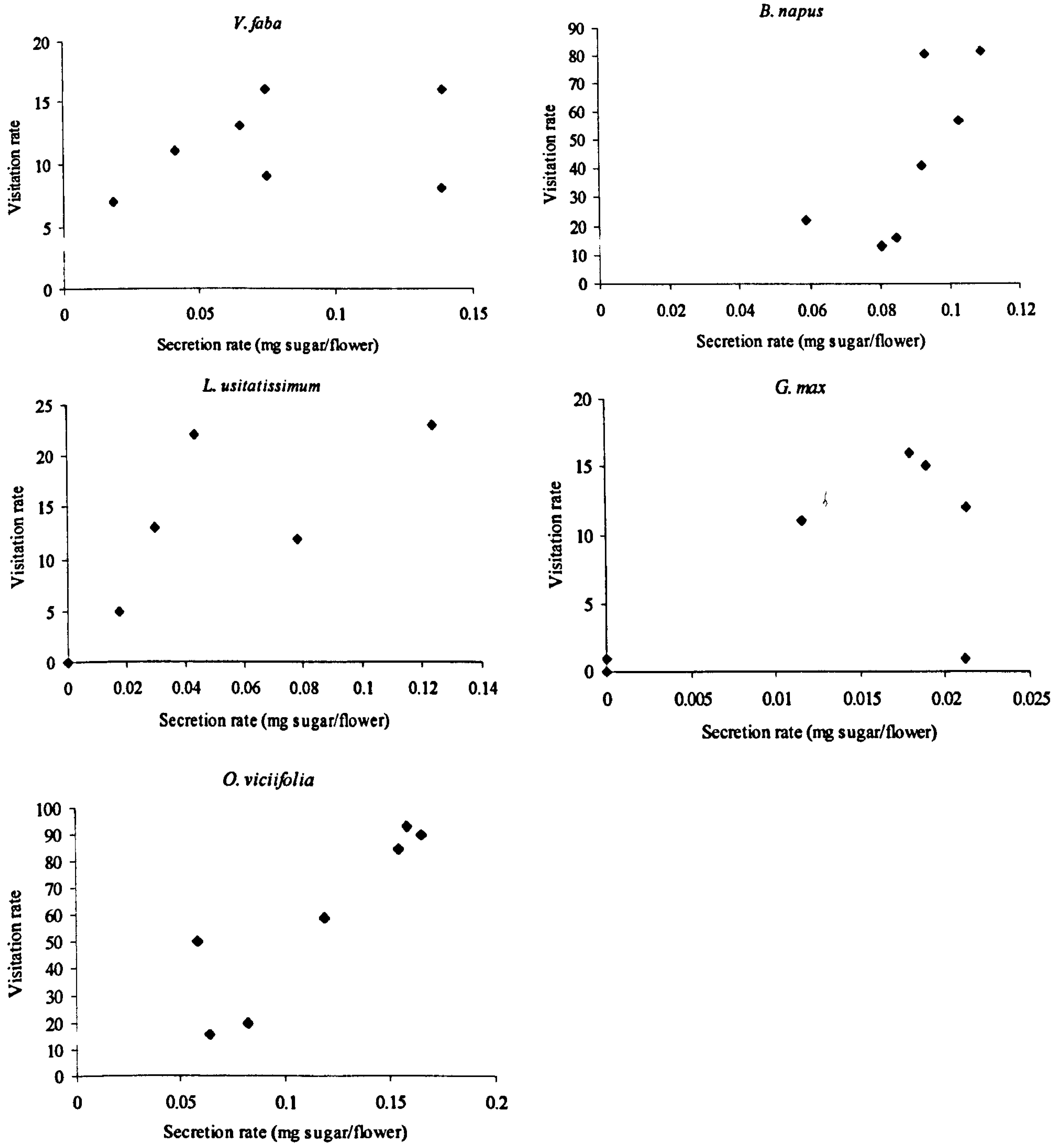
V. faba was found to exhibit 2 peaks of nectar secretion, one in the morning, and one late in the afternoon, whilst *B. napus* secretion rates remained relatively constant throughout the day. *L. usitatissimum* nectar secretion peaked in the early afternoon, and ceased completely by 17:00; the flowers of this species close in the early evening. *G. max* had a constant secretion rate, but at low levels. The secretion rate of *O. viciifolia* displayed a sustained peak, which fell off sharply towards early evening.

'Standing crop' gives a measure of the average amount of nectar available to a forager in a visit to a single flower of that species at a particular time of day. Where there is divergence between secretion rate and standing crop, this could indicate that foragers are depleting available nectar at a greater rate than in those species where there is less divergence. Figure 4.1 shows greatest divergence between secretion rate and standing crop in *V. faba, B. napus* and *O. viciifolia*. In *G. max* there is little divergence between the two values.

4.4.3 Forager visitation patterns

Forager visitation rate (for all bee species combined) was plotted against secretion rate for each crop to determine if this was affected by potential available sugar (figure 4.2).

Figure 4.2: Correlations between crop secretion rate and visitation rate. All bee species were combined for this analysis

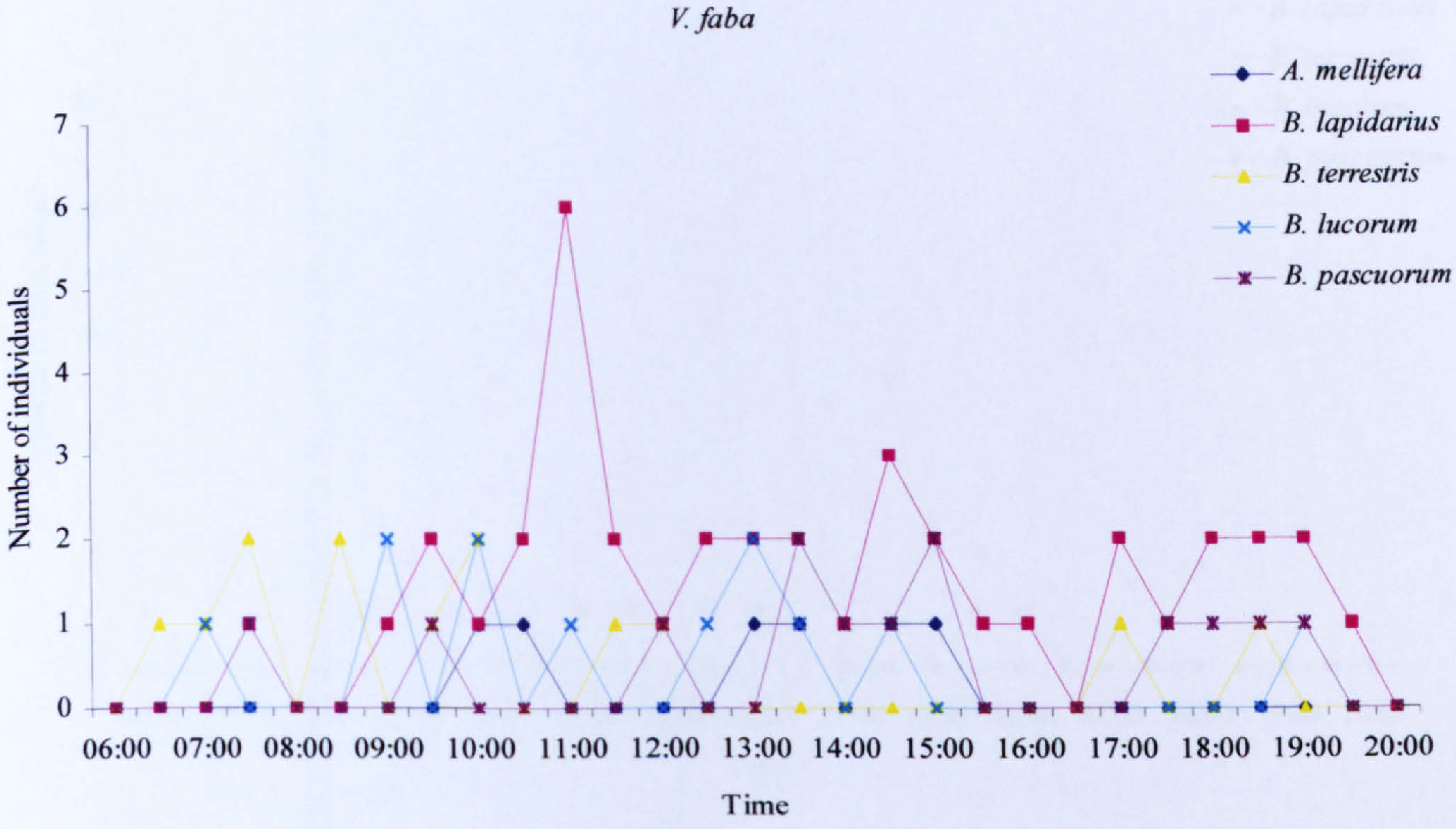


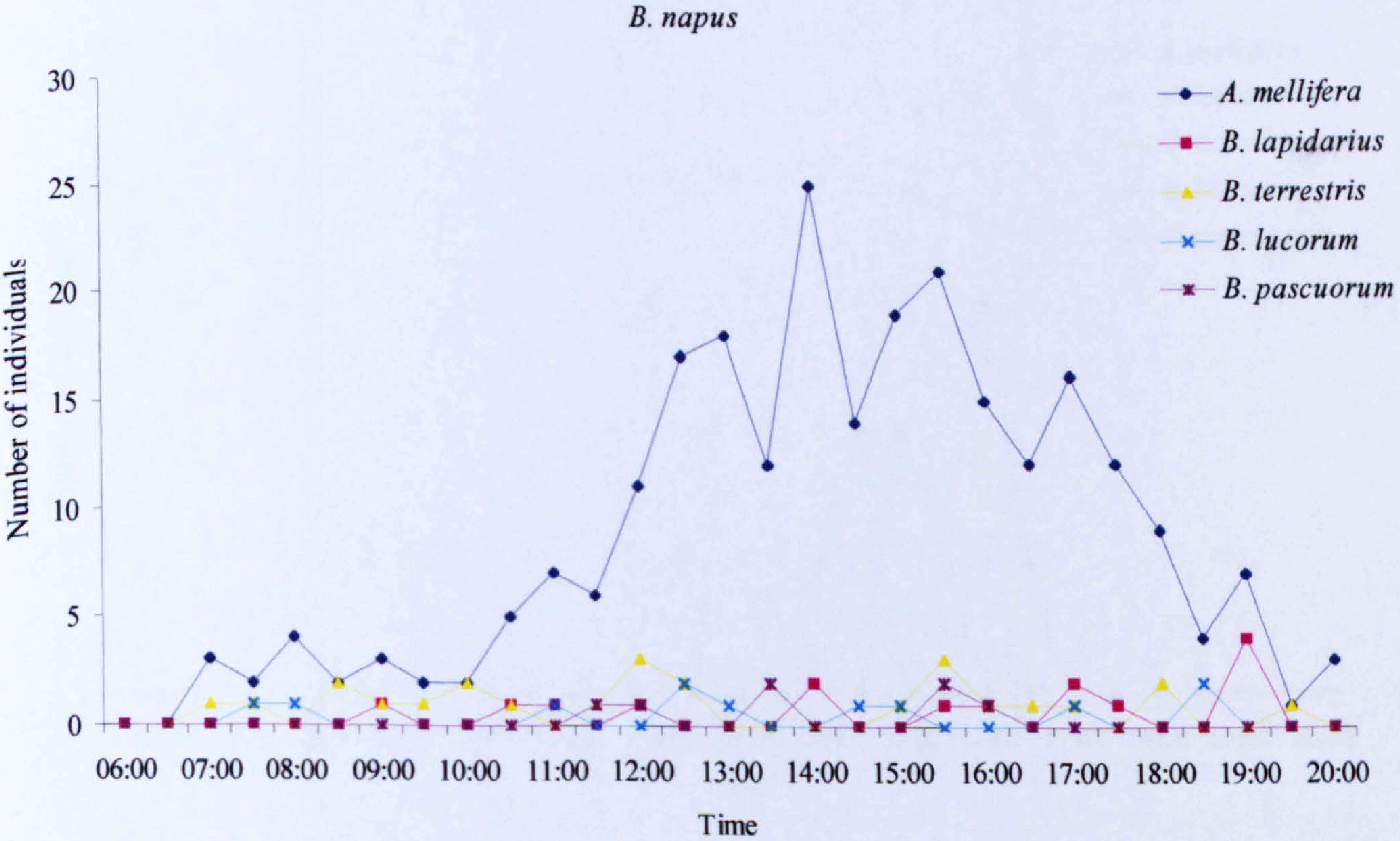
A positive relationship can be observed between secretion rate and visitation rate for all crop species, although this is more marked for some species than others (figure 4.2). In total there were only 7 recorded observations of *B. pratorum* and 3 of *B. hortorum*, and so these species were removed from the data set prior to statistical analysis (this data was also removed from the graphs that follow as figure 4.3). When individual bee species visitation rates were analysed, secretion rate was found to significantly affect visitation rate in *B. lapidarius* and *B. pascuorum* across all crop species (table 4.3). All species showed a significant preference in terms of crops visited; *Bombus* spp. preferences relative to each other and to crop species can be seen in figure 4.3.

	Secretion Rate	Crop
A. mellifera	$3.764^{\text{n.s.}}$	20.892^{**}
B. lapidarius	20.277^{**}	7.084^{**}
B. terrestris	$0.022^{\text{n.s.}}$	5.530^{*}
B. lucorum	$1.495^{\text{n.s.}}$	6.782^{**}
B. pascuorum	9.473^{*}	6.596^{**}
All species	11.299^{*}	$2.156^{\text{n.s.}}$
d.f.	1,34	4,34

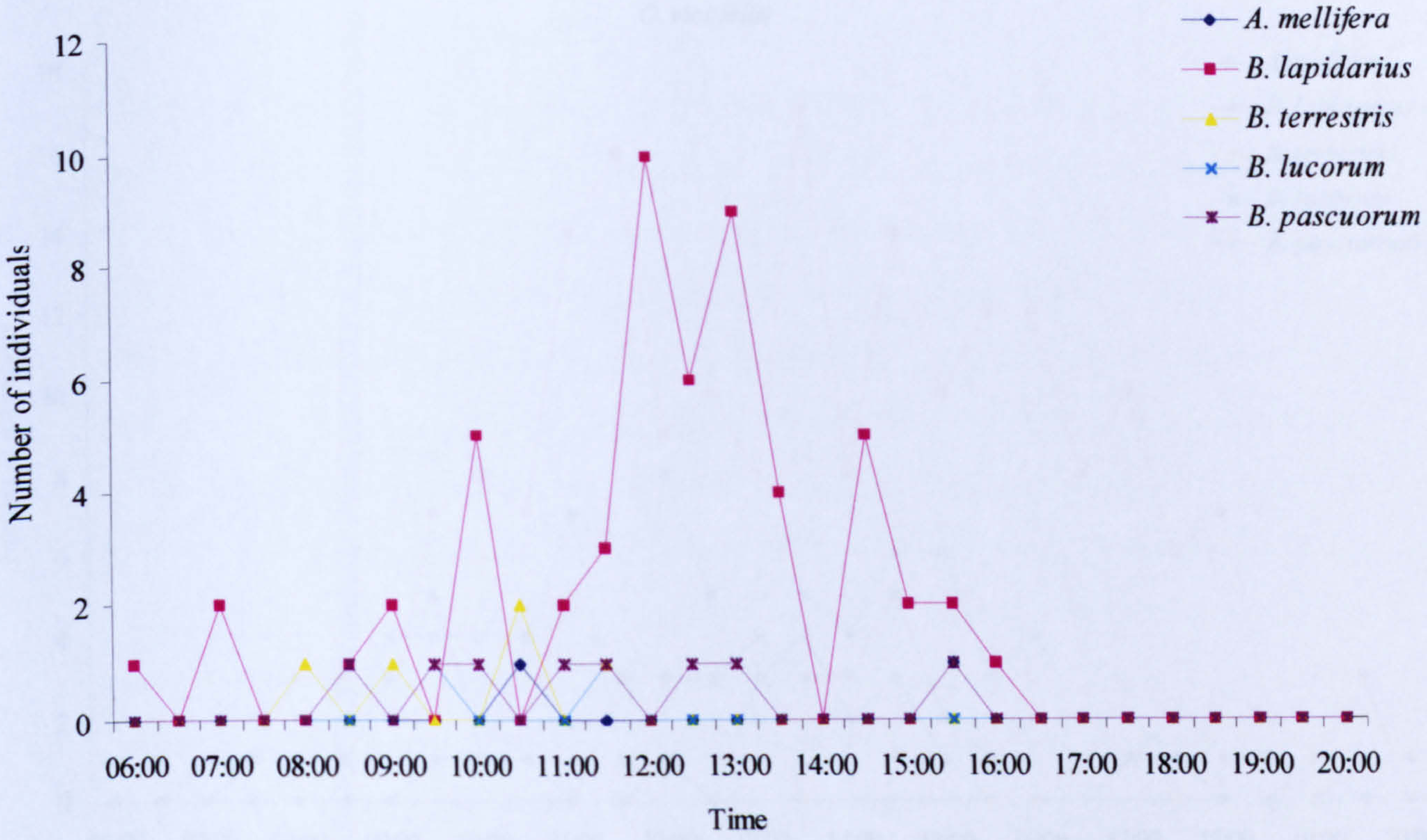
Table 4.3: Results of two-way ANOVA (SPSS 1998), showing influence of secretion rate and crop species on bee visitation. Numbers represent F-values. *$p<0.05$, ** $p<0.001$

Figure 4.3: Forager visitation patterns 06:00-20:00. Data points represent total observations for that time

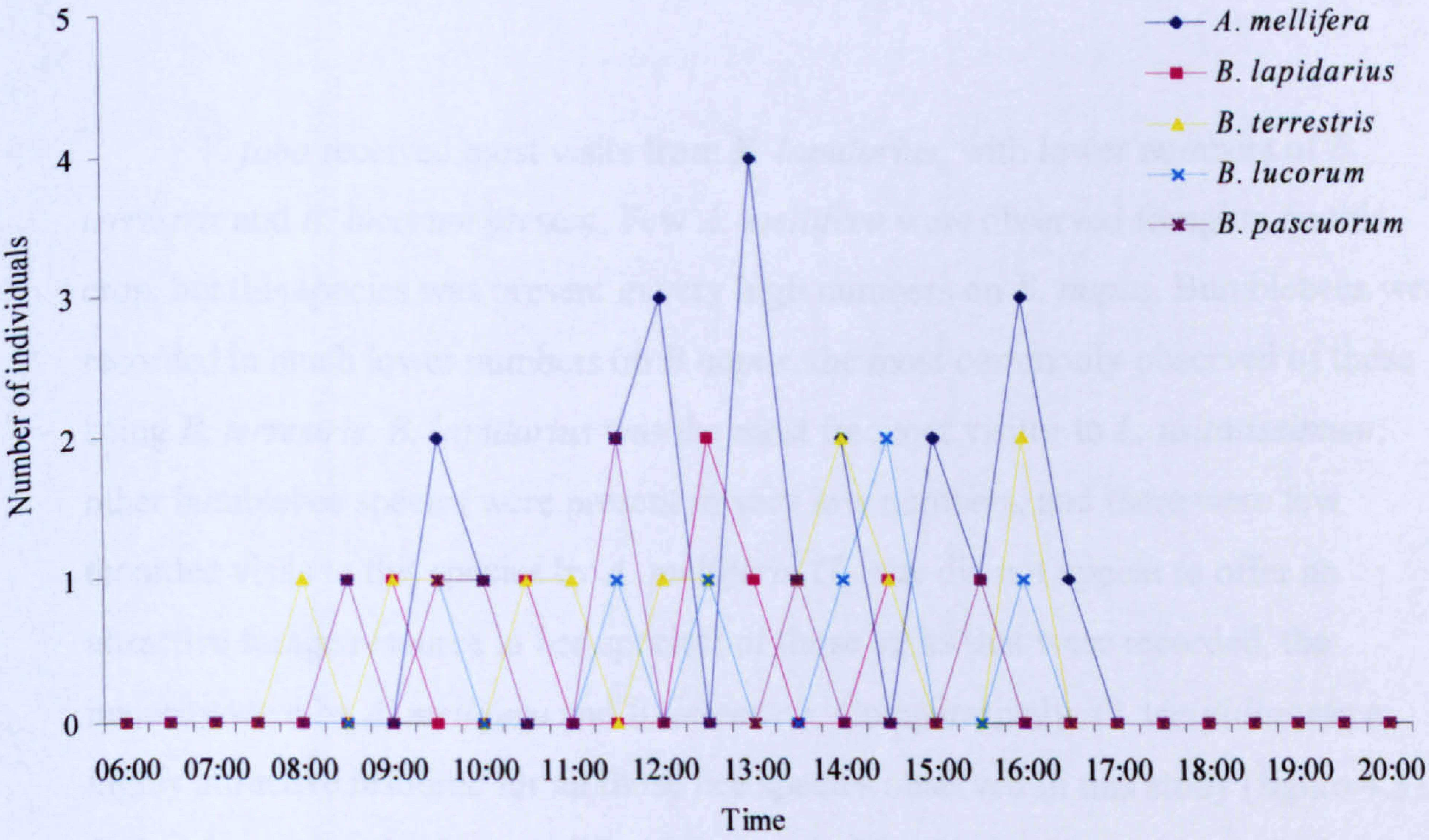


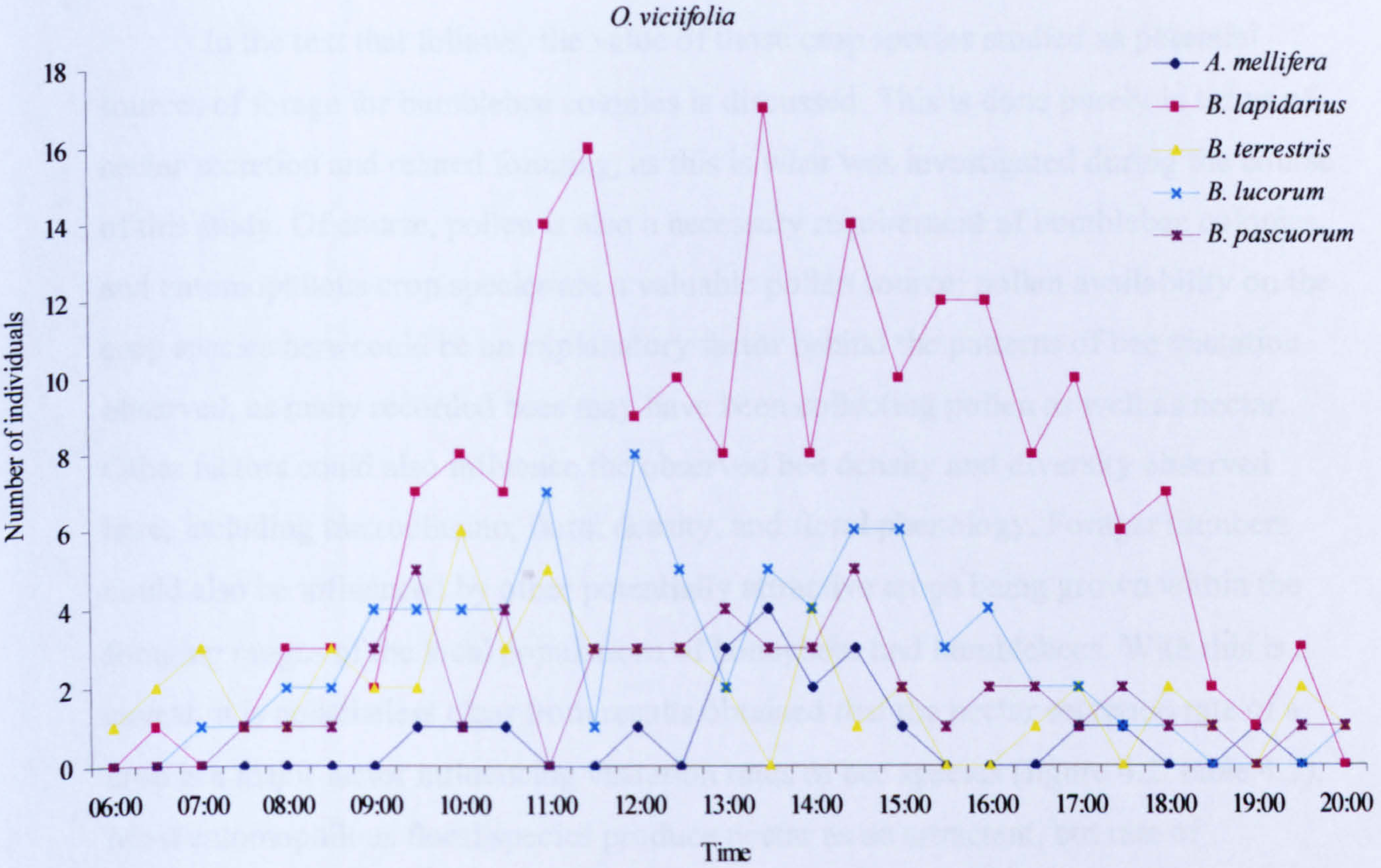


L. usitatissimum



G. max





V. faba received most visits from *B. lapidarius*, with lower numbers of *B. terrestris* and *B. lucorum* present. Few *A. mellifera* were observed foraging on this crop, but this species was present in very high numbers on *B. napus*. Bumblebees were recorded in much lower numbers on *B.napus*, the most commonly observed of these being *B. terrestris*. *B. lapidarius* was the most frequent visitor to *L. usitatissimum*; other bumblebee species were present in very low numbers, and there were few recorded visits to this species by *A. mellifera*. *G. max* did not appear to offer an attractive forage resource to bee species; of those visits that were recorded, the majority were by *A. mellifera* and *B. terrestris*. Comparatively, *O. viciifolia* was a highly attractive resource for all those bee species observed in this study (figure 4.3). *B. lapidarius* was the most prolific visitor, and visitation by *B. terrestris, B. lucorum* and *B. pascuorum* was recorded at higher levels than on the other crop species. There was also some visitation by *A. mellifera*.

4.5 Discussion

In the text that follows, the value of those crop species studied as potential sources of forage for bumblebee colonies is discussed. This is done purely in terms of nectar secretion and related foraging, as this is what was investigated during the course of this study. Of course, pollen is also a necessary requirement of bumblebee colonies, and entomophilous crop species are a valuable pollen source; pollen availability on the crop species here could be an explanatory factor behind the patterns of bee visitation observed, as many recorded bees may have been collecting pollen as well as nectar. Other factors could also influence the observed bee density and diversity observed here, including microclimate, floral density, and floral phenology. Forager numbers could also be influenced by other potentially attractive crops being grown within the foraging ranges of the local populations of honeybees and bumblebees. With this is a caveat, it is nonetheless clear from results obtained that the nectar secretion rate of a crop is a major factor influencing visitation rates of bee species (figure 4.2, table 4.2). Most entomophilous floral species produce nectar as an attractant, but rate of secretion, and composition of sugars within it, vary between species, and it is these factors that determine how 'valuable' the nectar is relative to that being produced by other species. Nectar provides the main energy source for adult bees (in the form of 3 main sugars, sucrose, glucose and fructose (Sihag and Kapil 1983)); foragers regurgitate nectar not consumed during flight into specially constructed cells, or empty pupal cells, on return to the nest (Prys-Jones and Corbet 1991). All life-stages of the colony utilise energy from these stores, and a continuous supply of this food source is necessary.

Several of the crop species studied here were found to support a high density of bees, but in all cases, species diversity was low, with only *A. mellifera* and four ubiquitous bumblebee species commonly observed (figure 4.3). These were *B. lapidarius, B. terrestris, B. lucorum* and *B. pascuorum*, and these species are all relatively short-tongued generalist foragers, except for *B. pascuorum* which is medium-tongued. There were few observations of *B. hortorum* and *B. pratorum*, and none of any more localised species (Williams 1982, 1986). Short-tongued generalist species are the most commonly observed foragers on entomophilous crops (Walther-

Hellwig and Frankl 2000); many commonly grown crops are annuals, and these generally produce smaller, shallower flowers that are attractive to generalist foragers (Fussell and Corbet 1991).

In this study, *V. faba* was found to be reasonably attractive to bumblebees, especially to *B. lapidarius*. Other studies have also recorded it as being an attractive resource (e.g. Poulsen 1973, Williams and Free 1975). In *V. faba*, plants from seeds formed as a result of bee pollination are known to set seed autogamously, whilst plants resulting from autogamous seed do not themselves set seed unless insect pollinated (Stoddard and Bond 1987). With prolific pollinator visitation, seed pods set lower on the stems, causing the plant to ripen more evenly, which assists with harvesting and drying of the crop (Scriven *et al.* 1961, Poulsen 1975). Thus, maintaining pollinator populations is economically important if production of this crop on a commercial scale is to continue in the U.K.

B. napus is grown to produce rapeseed meal or oils for human consumption. Floral morphology promotes initial cross-pollination, but mechanisms for self-pollination are induced in older flowers (Delapane and Mayer 2000). However, even though flowers are self-fertile, they do not always self-pollinate (Eisikowitch 1981), and rely on pollinators for pollen transfer. Some studies indicate that increased pollinator visitation increases seed set, evenness of ripening and ease of harvest (Williams *et al.* 1986a, 1987). In this study, *B. napus* offered a relatively constant source of nectar throughout the day. The vast majority of recorded visits were by *A. mellifera*, but the crop was visited by the four commonly observed species of bumblebee in lower numbers. As the fuel (diester) potential of *B. napus* is becoming realised, acreages of this crop may increase; this will be beneficial to bumblebees if it replaces fields of anemophilous crops.

Linum spp. (linseed and flax) are grown for seed and for fibre. The seed is used whole as horse and bird feed, or is crushed to give oil and cake, a high-protein animal feed. Although *Linum* spp. are generally self-pollinated with the flowers self-fertilising within a few hours of opening (Williams 1988a), most commercial varieties are highly attractive to bee species. Previous studies have found that honeybees are the most prolific visitors, followed by bumblebees (Dillman 1938, Gubin 1945). However, in this study, *B. lapidarius* was by far the most commonly observed visitor (figure 4.3), which may be as a result of different cultivars being used.

It is unclear from other studies whether increased pollinator visitation increases seed yields in *G. max* (Delapane and Mayer 2000), and self-fertilisation is thought to be the norm. The results of this study suggest it is not very attractive to bees (figure 4.3). However, *G. max* has an extremely high seed protein content (44%) (Hymonwitz 1990), and the development of hybrid lines to increase this further will require development of parental strains that are attractive to potential pollinators. As such, it could be an important entomophilous crop species in the future.

O. viciifolia also has a high seed protein content, but unlike *G. max*, is obviously highly attractive to bees (figure 4.3). The nectar has a high sugar content, and is secreted at plentiful levels throughout the day (figure 4.1). Little *O. viciifolia* is currently grown in the U.K., but it could become both an economically important crop, and a valuable forage resource for many different bee species (see chapter 5 for more detail on this crop).

Crop diversification is gradually increasing across Europe with the introduction of 'novel' crop species, helped by a system of E.U. grants. Lupins, chickpeas, lentils and navy beans are all currently being encouraged in order to fulfil the E.U. deficit in vegetable protein (Lutman *et al.* 1991), although lupins are only of value to bees for pollen as they do not secrete nectar (Putnam 1993, Rasheed and Harder 1997). An increased interest in alternative medicines may lead to the planting of borage and evening primrose, which are rich sources of GLA (gamma linolenic oil) (Williams 1994). Obviously, the presence of adequate pollination vectors for any species to be commercially produced is vital; equally, if these crops do require pollination vectors, then they are likely to have evolved to be attractive to bees, and to provide forage resources.

Introducing novel entomophilous crop species to U.K. agriculture has the potential to increase floral diversity on agro-ecosystems, and there are conservation implications not only for bees, but also for other fauna. Other methods of increasing diversity on farmland include sympathetic management of uncropped areas (see chapters 2 and 3), or managing the area within the crop itself. Such methods of diversification include within-crop aggregated diversification (inter-cropping/inclusion of strips of non-crop plants); and interspersed diversification (diversification below or amongst the crop). However, the highly competitive nature of modern crops (Wilson 1994b) means that many modern cultivars support low levels of floral diversity within the crop; diversity may be best improved at this level by increasing the variety of entomophilous crops grown. Diversification at the crop level could see a return to rotation systems involving legumes, especially with mounting concerns over the environmental impacts of nitrogen-rich fertilisers (Williams 1994). Diversification can also interfere with the ability of pests to locate host plants, which has a direct effect on crop yields (Sunderland and Samu 2000). There will also be an indirect effect on pests through the promotion of populations of natural enemies (see Sunderland and Samu 2000).

Honeybees were once thought to be the most important pollinators of economically important crops in this country (Percival 1950). However, it is now recognised that other bee species are potentially equally as important in crop pollination (e.g. see Dag and Kammer 2001). The primary pollen harvesting behaviour of honeybees is detrimental to pollination success; other bee species tend to practise secondary pollen harvesting, which is much more likely to result in successful pollination (Westerkamp 1991). Many of these have an important service to offer in the pollination of many species of arable crops (Free 1993, O'Toole 1994, Wanatabe 1994). In this study, bumblebee species were more prolific visitors than *A. mellifera* to three out of the five crop species studied (*V. faba, L. usitatissimum* and *O. viciifolia*; figure 4.3). This indicates that they may be a necessary part of the pollination web on agro-ecosystems.

The density of foraging bees of various species can give a misleading representation of habitat quality (van Home 1983); bee density in the area may represent a temporary state, especially where they are being studied on crop resources, and such observations cannot give a long-term measure of habitat quality. Also, in today's modern agricultural landscape, large areas of unrewarding (anemophilous) crops must be crossed to reach fields offering enough nectar (and pollen) to fulfil colony requirements. Isolated patches of highly rewarding crops are probably only visited by those bumblebee species with the largest mean foraging distances, e.g. *B. terrestris* (Walther-Hellwig and Frankl 2000), and observed interspecific differences in number of foragers may be influenced by different mean foraging distances (Fussell and Corbet 1991). The relative numbers of each bee species on a crop type is also dependant on the background numbers of those species in the environment. The crop species under consideration in this study have different flowering periods, and the constitution of the local bee fauna changes over the duration of the foraging season; these factors may contribute to differences in the number of bees attracted to each crop type. Therefore care must be taken in the interpretation of results from studies such as this. However, the results of this study reveal that bumblebees are prolific visitors to certain crops, and that visitation rate depends on the nectar secretion rate of those crops. Entomophilous crops, both traditional and novel, could potentially provide an important way of increasing floral diversity on agro-ecosystems, and aiding in the conservation of a range of bumblebee species.

5. SAINFOIN (*Onobrychis viciifolia*) – AN ALTERNATIVE FORAGE CROP FOR BEES

A.R.Kells. 2002. *Bee World* **82**: 192-194

(The following chapter follows the format of the journal where it was published)

5.1 Fact Box

Species: *Onobrychis viciifolia*

Family: Fabaceae

Common names: sainfoin (UK, France); esparcette (France); esparceta (Spain); lupinella (Italy); esparcet, holy clover (USA)

Distribution: has grown wild in various forms in temperate Europe and Asia for centuries. Introduced to N. America around 1900.

Flowering period: June to early September.

Pollen: grains have 3 long, narrow furrows along their length, are reticulate, and are rectangular in equatorial view

Value to bees: the flowers produce nectar with a high sugar content; this is collected by honeybees and many species of bumblebee. When grown for forage, sainfoin is mown late, so the flowering period has finished; forage yields for bees are therefore maximized

Honey: sainfoin is thought to yield more honey than any other temperate plant. Honey is very clear, and mixes well with honey from other sources

Other uses: once a popular forage legume for cattle and sheep, as it does not induce bloat

5.2 Description

Sainfoin is a perennial temperate forage legume. The plant has a deep taproot (Fearn 1987), and one primary stem, which branches into one to three secondary stems. Stems are sub-erect and can grow to 80 cm. Leaves consist of 13-39 imparipinnate leaflets (pinnate with an odd terminal leaflet), with tendrils (Stace 1997).

Florets are numerous, grow in whorls of six to seven around the erect racemes, and vary in colour from pale pink to deep red-purple. Darker-coloured stripes lead down the petals, directing insect visitors towards the nectary. The calyx tube measures 2-3mm in depth (ARK, unpublished data), so most melliferous insects can reach the nectar, and the nectary produces nectar with medium to high sucrose concentration (42-70g/100g solution) (Rosov 1952, Petkov 1958, Haragsimova-Neprasova 1960, Fomina 1961, Kropacova and Haslbachova 1969, Bogoyavlenskii *et al.* 1976). Individual flowers remain open for 1-2 days (Tereshchenko 1949), with flowering commencing at the base of the raceme and taking two to three weeks to reach the tip (Richards and Edwards 1988). There are ten stamens, nine of which are fused to form a tube, with the tenth free. Out-crossing is promoted by protandry, i.e. a temporal separation in maturation of the sexual parts, with the pollen being released prior to the stigma becoming receptive. The stigma protrudes beyond the anthers, so cross-pollination is assured if bee visits occur. The style becomes gradually more erect as anthesis progresses, and ultimately projects 1-1.5mm beyond the cleft in the keel (Knuth, 1908). The large, brown, single-seeded pods have a distinctive raised network of venation. They often have spines along one edge. When mature, the pods shatter from the plant with the seeds still enclosed. Seeds are smooth, kidney shaped, olive- to dark-brown, and approximately 6.5mm in length.

Self-fertility of sainfoin has been found to range from zero to 37 percent (Bosca and Hejja 1963). Seed production of exposed plants has been found to be 10-25 times as great as that from plants caged to exclude bee visits (Kropacova and Haslbachova 1969).

5.3 Habitat

Sainfoin grows best in open, grassy places, on dry calcareous soils, within an optimum soil pH range of 6.0-7.5 (Fearn 1987). Nectar secretion ceases below 14°C (Rosov 1952), which probably accounts for the plant's geographic distribution in Europe falling mostly within the 15°C July isotherm. It is cold hardy, and drought-resistant (Ayers 1993).

Most of the plants today derive from the time when sainfoin was widely grown as a fodder crop, but there is a native form that is semi-prostrate and has deeper pink flowers. This form is found especially on chalk grassland in eastern England (Fearn 1987).

5.4 Cultural notes

Sainfoin is cold hardy, and drought resistant, and has few serious pests of crop or seed (Hanna *et al.* 1977). Plants are capable of cropping well for up to seven years, although some U.K. leys are still providing yields after 40 years (Fearn 1987). However, a high seeding rate is required for successful establishment of a sainfoin crop (Doyle *et al.* 1984), and plants have a low dry matter yield when compared with other forage legumes, so production costs are high (Wilkinson 1984). It is uncompetitive with common agricultural weeds, especially during the seedling period. Although it is presently uneconomic to grow sainfoin in the U.K., trials with new varieties in Canada have shown that dry matter yield can be substantially increased (Doyle *et al.* 1984).

As a forage crop, sainfoin is highly palatable to horses, cattle, and sheep. Also, unlike red clover and alfalfa, it does not induce bloat in these animals. Current interest centres on its' potential use as a high-protein feed for racehorses, especially as it could replace expensive imports such as the currently used soya-bean meal (Fearn 1987).

5.5 Association with bees

The high sugar concentration of the nectar makes sainfoin very attractive to bees. A bee landing on a flower causes the stigma and anthers to protrude from the keel, brushing pollen onto the back of the bee (nototribic pollen transfer); these then return inside the keel when the weight of the bee is removed (personal observation). Nectar robbing via lateral access is impossible, so foraging visits always result in pollen transfer. As sainfoin is self-sterile, it relies on bees and other flower visitors for cross-pollination. It has been reported that individual sainfoin flowers require multiple visits to maximise pollination (Bogoyavlenskii 1955, Kropacova and Haslbachova 1969, Bogoyavlenskii 1974). Bees also collect pollen from sainfoin.

It has been reported that honeybees are the main visitors to sainfoin (e.g. Richards and Edwards 1988). However, during a study in summer 1999 I found that cultivated sainfoin was visited mostly by bumblebees, and more infrequently by honeybees (see chapter 4), who took on average twice as long to visit the open flowers. Richards and Edwards (1988) also found that bumblebees visited sainfoin flowers at a much greater rate than honeybees in Canada. I found that flower visiting by both bumblebees and honeybees commenced before 08:00, and continued after 20:00. Numbers of bee visitors peaked in the early afternoon with as many as 29 bumblebees and honeybees observed foraging in $1m^2$ of crop at a given time (see chapter 4). When grown as a forage crop, sainfoin is mown late so flowering has normally finished; therefore its' value as a bee forage crop is maximised (Ayers 1993).

Plate 5.1: A sainfoin crop (*Onobrychis viciifolia*) in flower

6. EVIDENCE FOR HANDEDNESS IN FORAGING BUMBLEBEES

A.R. Kells and D. Goulson. 2000. *Journal of Insect Behaviour* **14**: 47-55

6.1 Abstract

This chapter describes a simple study of how bumblebees (*Bombus* spp.) behave when visiting florets that are arranged in a circle around a vertical inflorescence. In four different species of bee, individuals tended to rotate in the same direction around each inflorescence on successive visits i.e. each individual tended to rotate either clockwise or anti-clockwise. Similar behaviour has also been observed in mammals including humans. The implications of this tendency to repeat tasks in the same way are discussed, particularly in relation to our understanding of the phenomenon known as flower constancy. In humans, the tendency for individuals to turn in a particular direction is strongly related to handedness. In three of the four bee species, there was a strong overall tendency towards rotation in a specific direction. This suggests that bumblebees too may exhibit handedness.

6.2 Introduction

Bee foraging behaviour has proved to be a fruitful and popular area of research, and studies in this area have greatly improved our understanding of the learning and memory capacities of insects (Menzel *et al.* 1993, Chittka 1998, Menzel 1999). Bees have the ability to learn associations between sensory stimuli, such as visual and olfactory cues, and rewards, so that they can recognise rewarding flowers (Menzel and Erber 1978). They learn appropriate motor skills for handling often complex floral structures (Laverty 1980, 1994). New associations and motor skills can be learned when needed (Woodward and Laverty 1992, Chittka and Thomson 1997). Bees can distinguish and avoid recently visited flowers using traces of odour deposited by the previous visitor (Goulson *et al.* 1998, Stout *et al.* 1998). They learn the relative spatial positions of landmarks and use these to navigate complex routes to and from their nest (Southwick and Buchmann 1995, Menzel *et al.* 1996, Menzel *et al.* 1997).

One aspect of bee foraging, that of flower constancy (which is also found in other flower-visiting insects), has not yet been adequately explained. It is one of the few areas in which bee behaviour appears to be less than optimal. The various explanations for flower constancy that have been suggested all tend to argue that foraging is constrained by some aspect(s) of the capacity and temporal dynamics of the bumblebee brain (reviews by Chittka *et al.* 1999, Goulson 1999b). For example bees may be unable to remember motor skills for several flowers at the same time, or they may be unable to quickly recall a succession of different motor skills from their long-term memory. They may simply not be aware of the rewards offered by many of the flower types present. Recently Chittka *et al.* (1999) argued that bees have a large long-term memory and that the most probable limitation is the stability and capacity of short-term memory; cues for recognition of a rewarding flower or for motor skills to handle that flower can be down-graded from the short-term to the long-term memory if replaced by other information. This is rather similar to an hypothesis proposed by Goulson (1999a), that constancy may reflect use of a search image to find a rewarding flower type: search images are thought to occur due to a limited ability to recognise several 'prey' types at once. This 'non-adaptive behavioural persistence' also appears evident in the phenomena of site-fidelity and trap-lining (Thomson *et al.* 1982, Thomson *et al.* 1987).

In this study I examined the behaviour of bumblebees (*Bombus* spp.) when foraging on vertical inflorescences of *Onobrychis viciifolia* (Fabaceae), in which the florets that are open at any one time form a circle around the raceme. Bumblebees may forage by visiting florets in a clockwise or an anti-clockwise sequence. I demonstrate that bees tend to use the same direction of rotation on successive inflorescences, revealing that bees appear to have an innate tendency to repeat tasks in the same way even when the rewards provided by alternative behaviours are exactly the same.

6.3 Methods

6.3.1 Study site and sampling methods

This study was carried out during June 1999 in Hampshire, U.K., in a field of *O. viciifolia* planted to provide forage for bees. Four species of bumblebee were present in abundance; *Bombus lapidarius* (L.), *Bombus terrestris* (L.), *Bombus lucorum* (L.) and *Bombus pascuorum* (Scopoli). *B. terrestris* and *B. lucorum* were distinguished on the basis of colour which is not absolutely reliable. Between 11 and 17 individuals of each bee species (see table 6.1) were selected at random and observed as they foraged on ten successive inflorescences. The direction in which they rotated around each inflorescence was recorded. A different bee species was chosen each time to minimise the likelihood of observing the same bee twice, but the bee population was so large that this is likely to have occurred very rarely if at all. I moved around the field when making observations, so risk of pseudo-replication was minimal. Where a bee probed fewer than three florets on an inflorescence, or was forced to alter direction due to obstacle (leaves, stem of another flower, interference from another pollinator), that individual was excluded from the data set. For the duration of the data collection period, weather conditions were constant (temperature 23.5°C ± 0.5; relative humidity 35% ± 5).

Plate 6.1: *B. lapidarius* foraging on sainfoin

6.3.2 Analysis

The null hypothesis here is that the direction of rotation on each flower is random, so that I would expect equal numbers of clockwise and anti-clockwise visits. The mean numbers of anti-clockwise and clockwise visits made by each bee species were compared with critical values obtained from a simple Monte Carlo simulation model. This simulation was used to calculate threshold values for significant departures from random.

To determine whether the four bee species differed in the frequency with which individual bees switched between clockwise and anti-clockwise visits, the proportion of switches made by each bee was analysed according to species in GLIM with binomial errors (Crawley 1991).

Since bee species did not differ in the frequency with which they switched between clockwise and anti-clockwise foraging, the four species were combined for subsequent analysis. To examine whether the frequency of switches was significantly lower than would be expected from a random forager (i.e. 50%), a paired *t* test was conducted on the number of switches made by each bee versus the number of times the bee rotated around an inflorescence in the same direction as on its previous visit. The GLIM analysis was also used to estimate the overall mean and standard error of the frequency of switching.

To examine whether there were differences between individual bees in their propensity to switch between clockwise and anti-clockwise foraging, the number of switches made on the first four transitions between inflorescences was correlated with the number of transitions made in the following five transitions. If some bees tended to switch, while others consistently exhibited either clockwise or anti-clockwise foraging, I would expect a positive correlation.

6.4 Results

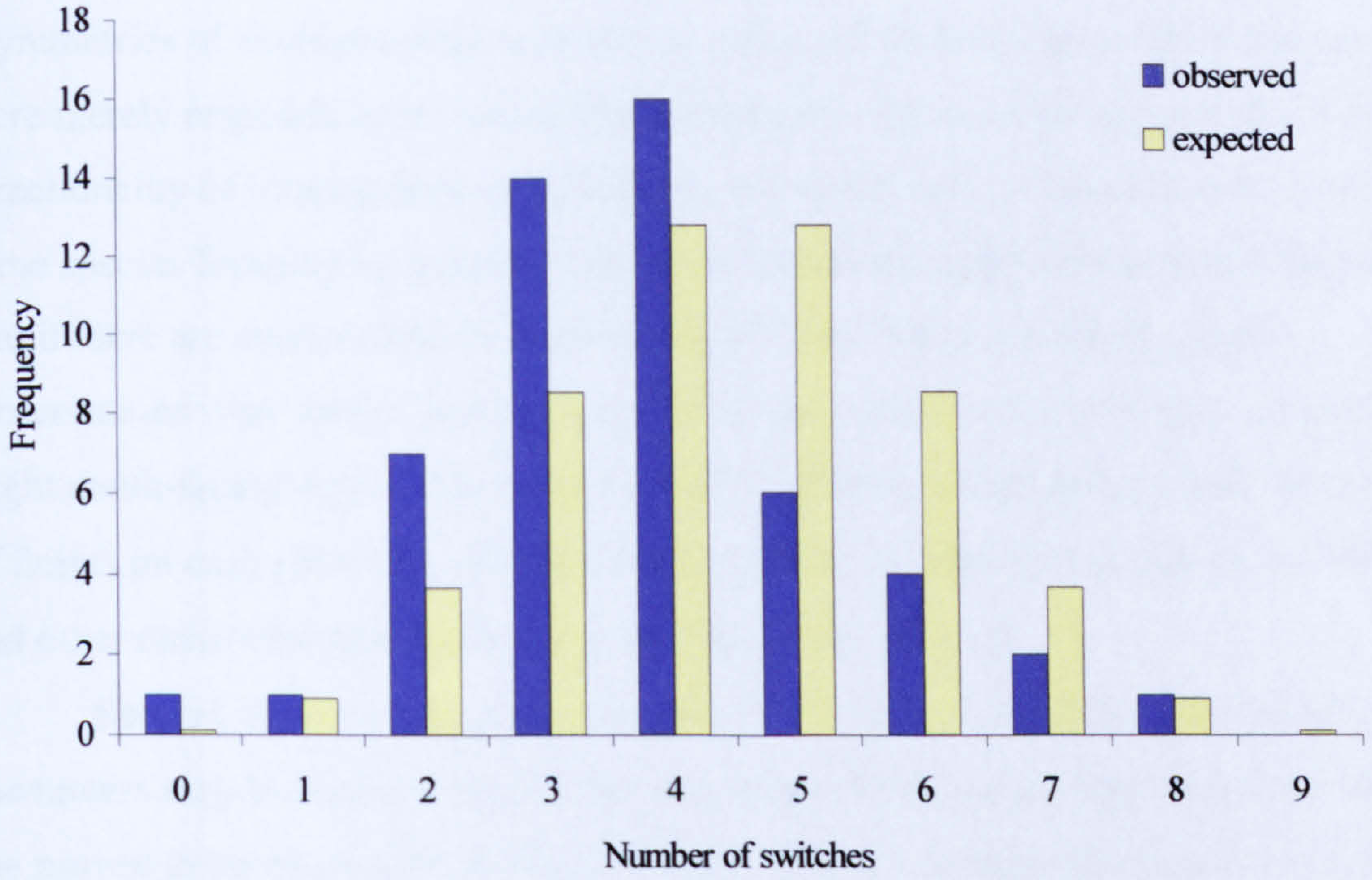
Comparing average numbers of anti-clockwise versus clockwise visits for each species against the values expected if this was random indicates significant overall handedness for three of the four species studied (table 6.1). Two species preferentially foraged in an anti-clockwise direction (*B. pascuorum, B. lucorum*), while *B. lapidarius* displayed a significant tendency to visit flowers in a clockwise direction. Only *B. terrestris* did not exhibit a tendency to handedness in either direction.

The GLIM analysis of the proportion of switches between clockwise and anti-clockwise visits exhibited by each bee indicated no differences between the four bee species ($\chi^2 = 4.86$, d.f. = 3, p>0.05). Overall, bees tended to forage on consecutive inflorescences by rotating in the same direction. The number of switches between directions was significantly lower than the number of times a bee continued to forage by rotating in the same direction (t=3.34, d.f. = 51, p=0.001). This is clearly illustrated by comparing the frequency distribution of switches with that which would be expected if the direction of foraging was random on each visit to an inflorescence (figure 6.1). Overall, bees rotated around inflorescences in the same direction as on their previous visit on 68.6% of visits (all bee species combined, S.E. = 9.34).

				Monte Carlo simulation value			
Bee species	**N**	**Anti-clockwise**	**Clockwise**	**0.05**	**0.01**	**0.001**	**P**
B. lapidarius	17	4.18	5.82	5.70	5.94	6.24	<0.5C
B. terrestris	11	4.91	5.09	5.91	6.09	6.46	n.s
B. lucorum	11	6.09	3.91	5.91	6.09	6.46	0.01A
B. pascuorum	13	6.46	3.62	5.77	6.08	6.39	0.001A

Table 6.1: Mean numbers of anti-clockwise (A) and clockwise visits (C) made by each bee Species, and Monte Carlo simulation values (two-tailed test)

Figure 6.1: The frequency of switches between clockwise and anti-clockwise rotation on inflorescences, based on 10 visits to inflorescences. The expected distribution is calculated assuming random foraging, so that the probability of switching between directions is 0.5. Data are for 52 bees (all 4 species combined).



There was no indication that some individual bees were more likely to switch than others. No correlation was apparent between the number of switches made in the first four transitions between inflorescences, and the number of switches made in the following 5 transitions (r = -0.046, d.f.=51, p>0.05).

6.5 Discussion

When faced with a choice of two possible ways of handling an inflorescence, individual bees tended to repeatedly move in the same direction around successive inflorescences. Presumably a bee which exhibited random rotation would receive the same rate of reward, and hence just as much reinforcement of its behaviour, as a bee with a fixed direction of rotation. Ecologically, the direction of rotation is trivial, since it has no consequence for either the bee or plant.

There are several possible causes of the observed tendency for bees to rotate in the same direction on successive inflorescences. First, there could be an asymmetry of the flower which may have induced the directionality of the rotation. If flowers visited in succession were located in close proximity, they may have been exposed to similar asymmetries of environmental factors (e.g. shade, illumination), to which the bees were merely responding. However, that asymmetry is the reason behind the observed directionality of rotation here is unlikely. It was common to observe two bees of the same species foraging in opposite directions around the same flower, which implies that if there are asymmetries in flowers, these do not influence directionality. Observations were carried out in a large field, surrounded by low hedges, which had a slight south-facing aspect. The similarity of sward height and density, and the number of florets on each plant (unpublished data), tends to indicate that drainage, soil fertility, and other environmental factors were similar across the crop.

Second, the direction in which a naïve bee turns on the first inflorescence it encounters may be random, but the bee may then simply repeat this behaviour since it has proved to be successful. If this is so, then flower constancy too could result from a bee simply repeating whatever was previously successful. In a sense, this is equivalent to the 'costly information' hypothesis (Chittka *et al.* 1999), which argues that if information as to the profitability of other strategies is costly to obtain, and so long as the forager is gaining at least a moderate rate of return, then the forager should continue with its current strategy. Menzel (1999) found with sensory learning that learned handling abilities can fade from short-term memory if not frequently reinforced. It is likely that this phenomenon could apply to motor learning. The direction in which an individual tends to rotate could depend on its earliest foraging experiences or could be relearned every day if motor skills are lost from the memory overnight. Either way, I would expect the observed frequencies of rotation in either direction to be approximately equal in the population on any given day. However, three of the four species exhibited an overall tendency for rotation in a particular direction, which would seem to discredit this hypothesis in this instance.

Corbet *et al.* (1981) suggested that insect posture during a visit to a floret might influence directionality. Subsequent movement in one direction requires less time and energy than movement in the other, hence directionality within an inflorescence may act to decrease foraging costs. If the initial posture of the bee on the first floret of an inflorescence influences the direction it moves in around that inflorescence, I would expect rotation on subsequent inflorescences to be random and related to the initial posture of the bee on the floret. Even if there were reinforcement of this behaviour, resulting in a bias in direction of rotation of individuals, I would still expect an equal distribution of individuals following either strategy within the population.

Another possible explanation for the phenomenon of individual bees exhibiting constancy to rotation in one direction is that these are exhibiting something akin to 'handedness' in humans, i.e. individuals have an innate preference for rotating in one direction or another. It may be possible to distinguish between these possibilities by examining behaviour over longer periods. If, for example, it were found that there is no correlation between the preferred directions used by an individual bee on different days, this would suggest that they do not exhibit handedness, but, rather, just tend to repeat the direction of rotation that was tried initially on that day.

Giurfa *et al.* (1995), working on colour choice in *A. mellifera,* concluded that evaluation of a floral signal in this instance is jointly controlled by innate and experience-dependant processes. If motor memory functions in a similar way, it could be that a naïve forager is innately programmed for 'handedness' but, with experience (encountering an obstacle, interference from another forager), learns that there is no difference in reward if flowers are visited in the opposite direction. Therefore the age of the forager could at least partly explain the varying degrees of stereotypy found between individual foragers, although this does not account for a species exhibiting an overall preference for rotation in one direction or another.

The history of flower visitation may also affect the direction the forager moves around a particular flower. It is known that both honeybees and bumblebees deposit volatile scent marks when visiting flowers (Stout *et al.* 1998, Williams 1998). It could be that the direction of rotation is influenced by the relative strength of the scent mark on either side of the forager when it lands; this is more likely to be of importance in those flowers where many florets make up an inflorescence. However, this explanation fails to explain why bees tend to rotate in the same direction around successive flowers.

Three of the four species observed displayed an overall tendency for individuals of that species to rotate in one direction as opposed to the other. Individuals of *B. pascuorum* and *B. lucorum* tended to exhibit a preference for left-handed movement around an inflorescence, while those of *B. lapidarius* displayed a right-handed preference. It would appear that the most likely explanation for such behaviour is that it is the result of non-adaptive behavioural persistence, although why *B. terrestris* did not exhibit this is unclear. Parallels toward a tendency for rotation in a given direction are also evident in higher organisms. In behaviours that require body rotation, children exhibit a tendency to turn in one direction or another, and just as in two of the bee species here, most children tend to rotate anti-clockwise. This tendency becomes more pronounced with age (Day and Day 1997), and preferred directions are correlated with handedness (Yazgan *et al.* 1996). Similar rotational preferences have been found in other mammals including capuchin monkeys (Westergaard and Suomi 1996) and mice (Nielsen *et al.* 1997), but apparently these do not occur in goats (Ganskopp 1995).

To my knowledge, these data represent the first study into constancy in turning direction in an insect. Further studies are needed, chiefly the marking of emergent foragers, to establish if age affects the degree of stereotypy, and records of how the visitation history of the plant affects subsequent foragers. Observations of bees foraging on more plant species may also be useful in helping to establish the generality of the phenomenon. Its existence suggests that there is an innate constancy in bee foraging behaviour, which need not relate to memory constraints or to rewards.

7. PREFERRED NEST SEARCHING SITES OF BUMBLEBEE QUEENS (HYMENOPTERA: APIDAE) IN AGRO-ECOSYSTEMS IN THE U.K.

A.R. Kells and D. Goulson. *Biological Conservation* – in press

7.1 Abstract

Bumblebees (*Bombus* spp.) have undergone a documented Europe-wide decline in recent years, mostly attributable to destruction of forage and nest sites caused by agricultural intensification. This study was set up to quantify the species-specific nest-site preferences of observed U.K. species for various types of field and forest boundary habitat. In total, 1287 observations were made of seven common bumblebee species; nest searching behaviour was taken as being indicative of nest site preference. There was interspecific variation in preferred habitat, with some species found to be much more specific in their choice of nest site than others. A strong association was found between those species that are known to prefer subterraneous nesting and those habitats that contained banks (*Bombus terrestris*, *B. lapidarius* and *B. lucorum*); other species were strongly associated with tussock-type vegetation (*B. pascuorum*, *B. hortorum* and *B. ruderarius*). In order to safeguard the continued existence of bumblebee species it is clear that a variety of field and forest boundary types need to be conserved; this has positive implications for the conservation of other species of flora and fauna associated with agro-ecosystems.

7.2 Introduction

That nest-choice preference is species specific amongst bumblebees has been demonstrated in previous studies (see e.g. Sladen 1912, Skovgaard 1936, Svensson and Lundberg 1977, Richards 1978, Harder 1986, Fussell and Corbet 1992b, Svensson *et al.* 2000). Some species are known to prefer to nest subterraneously, (e.g. *B. terrestris, B. lucorum, B. lapidarius, B. ruderatus*), whilst others prefer to nest on or just below the soil surface (e.g. *B. hortorum, B. pascuorum, B. sylvarum, B. humilis, B. muscorum, B. ruderarius*). Species such as *B. lapidarius* and *B. pratorum* can be very opportunistic in their nest choice, and utilise objects such as birds' nests and anthropogenic artefacts (see Fussell and Corbet 1992b and references therein; Svensson *et al.* 2000). Bowers (1985) has suggested that queen nest site selection is governed by different evolutionary forces to those that influence the success of the resultant colony. Intrinsic factors determining acceptability as a nest site include degree of shelter, soil drainage, heat absorption, and those factors that are species specific. There may be a trade-off between shelter and degree of warmth from direct sunlight (i.e. more exposed sites), and Skovgaard (1945) has suggested that south-facing banks may be least popular.

In recent years there has been a documented decline in bumblebee species numbers and species diversity across Europe (Rasmont *et al.* 1992 [France], Kwak and Tieleman 1994 [The Netherlands], Berezin *et al.* 1995 [Russia], Kosior 1995 [southern Poland]). Within the U.K., local species diversity and density have become altered; a huge central area of the country now contains only 6 resident species (out of a total of 19) (Williams 1982, 1989). Agricultural intensification is known to be responsible for a decline in forage resources (see chapters 2 and 3); increased mechanisation and 'improvements' of previously uncultivated areas in a drive to increase field sizes have also decreased the area available for nest sites (e.g. Pollard *et al.* 1974, Williams 1986, Ricketts *et al.* 2001). The abandoned burrows of small mammals and tussocky areas where the different bumblebee species commonly build their nests are generally found along field boundaries; this is where queens are often found in nest-searching flight

(Svensson *et al.* 2000), but these habitat types are amongst the first to be lost in any intensification of the farming system.

Finding existing nests in the field is difficult, and only a small proportion of nests are ever located (Svensson and Lundberg 1977, Donovan and Wier 1978, Fussell and Corbet 1992b). Previous studies of bumblebee nesting behaviour have placed artificial nest boxes in the field, but the uptake rates of these are generally very poor (Norgaard Holm 1966, Richards 1973, 1978, MacFarlane *et al.* 1983; Fussell and Corbet 1992b). Alternatively, observed nest-searching behaviour of bumblebee queens has been used as an indicator of preferred nest site, as a larger amount of data can be generated in this way. This method of extrapolating nest-site preference from search data has previously been used in similar studies in other countries (see Plath 1922; Skovgaard 1936; Svensson and Lundberg 1977; Richards 1978; Svensson *et al.* 2000). It is important to note here that this technique does have limitations; if a queen immediately locates a suitable nest-site she may only be briefly visible on the soil surface before disappearing into the nest. Subsequently, many 'successful' searches may go unrecorded. Related to this, queens observed searching could be an indicator of lack of suitable nest sites. However, queens are likely to search in habitats where they are likely to nest, and there is no evidence to suggest that queens immediately enter the first suitable site that they find, especially without searching the surrounding area, or that they do infact nest in the first site they find. As a comparative method of species preferences, I believe that the methodology is valid as long as these points are borne in mind, and no inference is drawn between numbers observed searching, and number of nests successfully founded.

Nest searching queens display a typical behaviour pattern very different from that of foraging individuals. This comprises a characteristic zigzag flight trajectory, low over the ground, with stops to investigate potential nest sites (Lundberg and Svensson 1975). This study was set up to compile detailed information on the relative nest-site searching preferences of those British bumblebee species recorded across different habitats along field edges. Although species do nest in other places (rough grassland, anthropogenic artefacts, etc.) the time scale of this project, and the number of habitats to be covered restricted data collection to field edges. Sufficient data was obtained from these areas to indicate that they do play an important part in providing nest sites to many species. It is hoped that results will give a basis for field boundary management, which could be used in conjunction with studies of foraging preference to enable farmers to manage these habitats to encourage bumblebees.

7.3 Methods

7.3.1 Study site

This study was carried out on the Cholderton Estate, near Andover, on the Wiltshire/Hampshire border, U.K. The estate is managed in a way that is beneficial to wildlife. Most of the study area is chalk downland, and a mixed farming system is in place. The estate also contains stands of mixed deciduous woodland, and many fields are bounded by this on at least one side.

7.3.2 Study design

Two different habitat types were studied in this experiment -

1. Habitat 1: field-field edges. Borders running between 2 large agricultural fields
2. Habitat 2: field-forest edges. Borders running between a large agricultural field and mixed woodland

Within each of the habitat types, 3 different boundary types were characterised –

1. Fence. Fields or field and forest separated by a fence with no associated hedge-type vegetation.
2. Hedgerow. A continuous boundary of dense, shrubby, vegetation separating fields, or field and forest, and containing typical hedgerow flora.
3. Gapped out hedgerow. Older hedge banks where the flora has become impoverished through lack of management. These generally consisted of a row of mature trees typical of hedgerow species, such as hawthorn (*Crataegus monogyna*), with gaps in between.

These 3 boundary types could be sub-divided into 4 distinct edge types –

1. Nothing. No associated vegetation in the case of fences, or no vegetation except that which constitutes the hedgerow in the other 2 boundary types.
2. Bank. Edges where the boundary was located on top of a bank at least 15cm high (maximum bank height included was 30cm).
3. Tussock. An edge containing a densely vegetated, grass-dominated strip.
4. Bank and tussock. Edges containing a combination of types 2 and 3 above.

The occurrence of nest-searching queens was quantified along 100m transects laid out along field edges. An adaptation of Pollard's transect method for butterfly recording was used (Pollard 1977, Pollard *et al.* 1975), with all queens searching 0.5m either side of the transect recorded. Queens exhibiting both typical nest-searching flight low over the ground, and those observed crawling on the ground (Lundberg and Svensson 1975), were included in the analysis. Every effort was made to avoid pseudo-replication.

Observations were carried out during a 6-week period from 25th April until 1st June 2001, with 3 days of observations being made each week. There was no replication of transects walked within the weeks, but there was replication between the weeks. Equal numbers of edge types were studied within each boundary type, and equal numbers of boundary types within each habitat. 432 transects in total were walked along each habitat type, 24 per day of observations. This represented 36 transects of each of 12 different edge types (4 different edge types within each of 3 different boundary types in each habitat).

Bumblebee nomenclature follows Prys-Jones and Corbet (1991). Female bumblebees that are capable of egg laying, but which have not founded a nest are properly known as gynes (Michener 1974). However, this is interchangeable with 'queen' in the literature, and so queen will be the term used here.

Plate 7.1: Some examples of typical field boundaries studied in this experiment. For detail of which boundary types these represent see figure 7.1

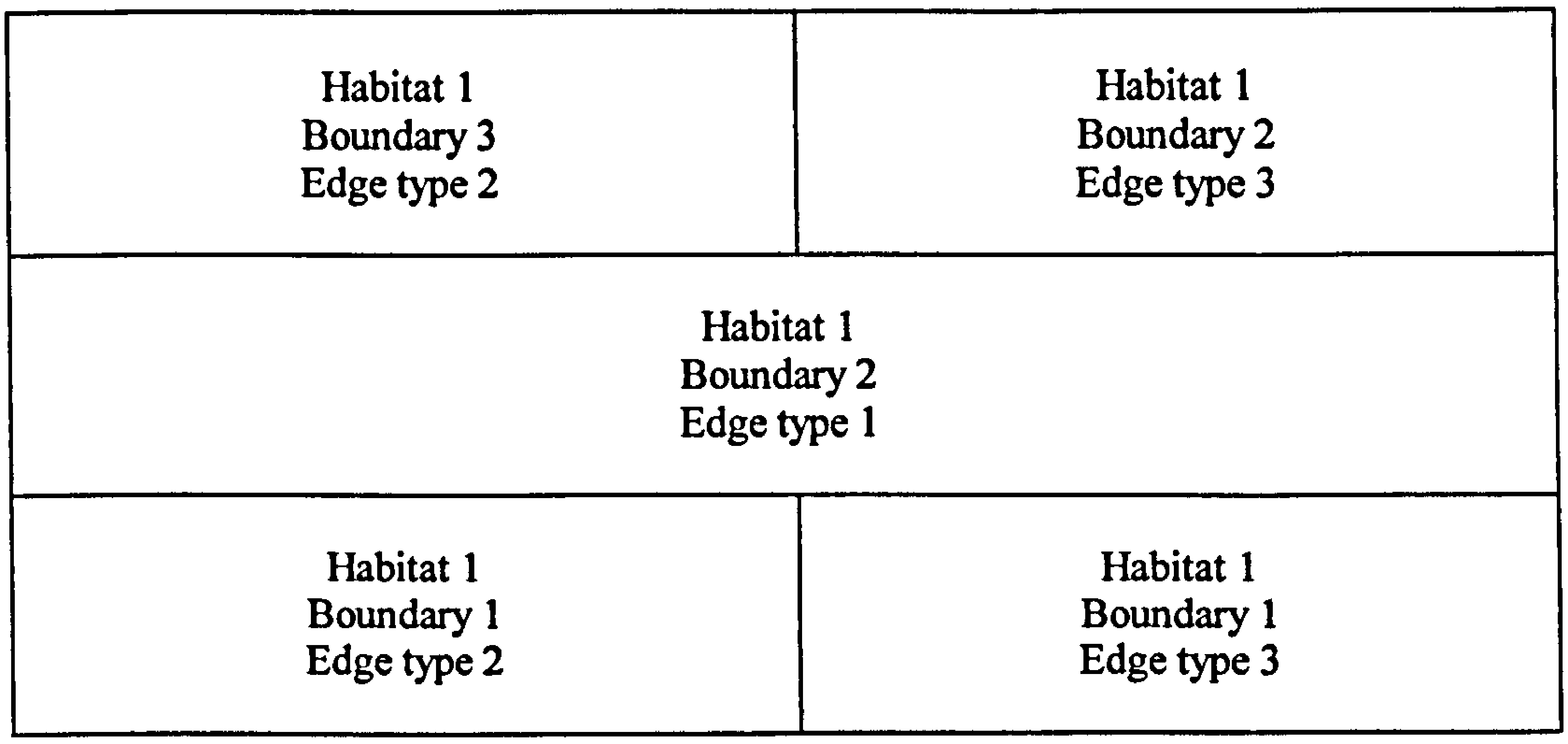


Figure 7.1: Schematic showing which habitat, boundary, and edge types the photographs in plate 7.1 represent

7.3.3 Analysis

Univariate ANOVA using GLM (SPSS 1998) was used to analyse the data from this study, with each edge type entered as fixed factors. Observations within and between weeks were summed for the purpose of this analysis.

7.4 Results

7.4.1 Total numbers of bumblebee species observed

A total of 1287 observations of nest-searching queens were made during this study (table 7.1). The most commonly recorded species were *B. terrestris* and *B. pascuorum*, accounting for 44.83% of all observations, whereas observations of *B. ruderarius* made up only 6.60% of the total number (table 7.1).

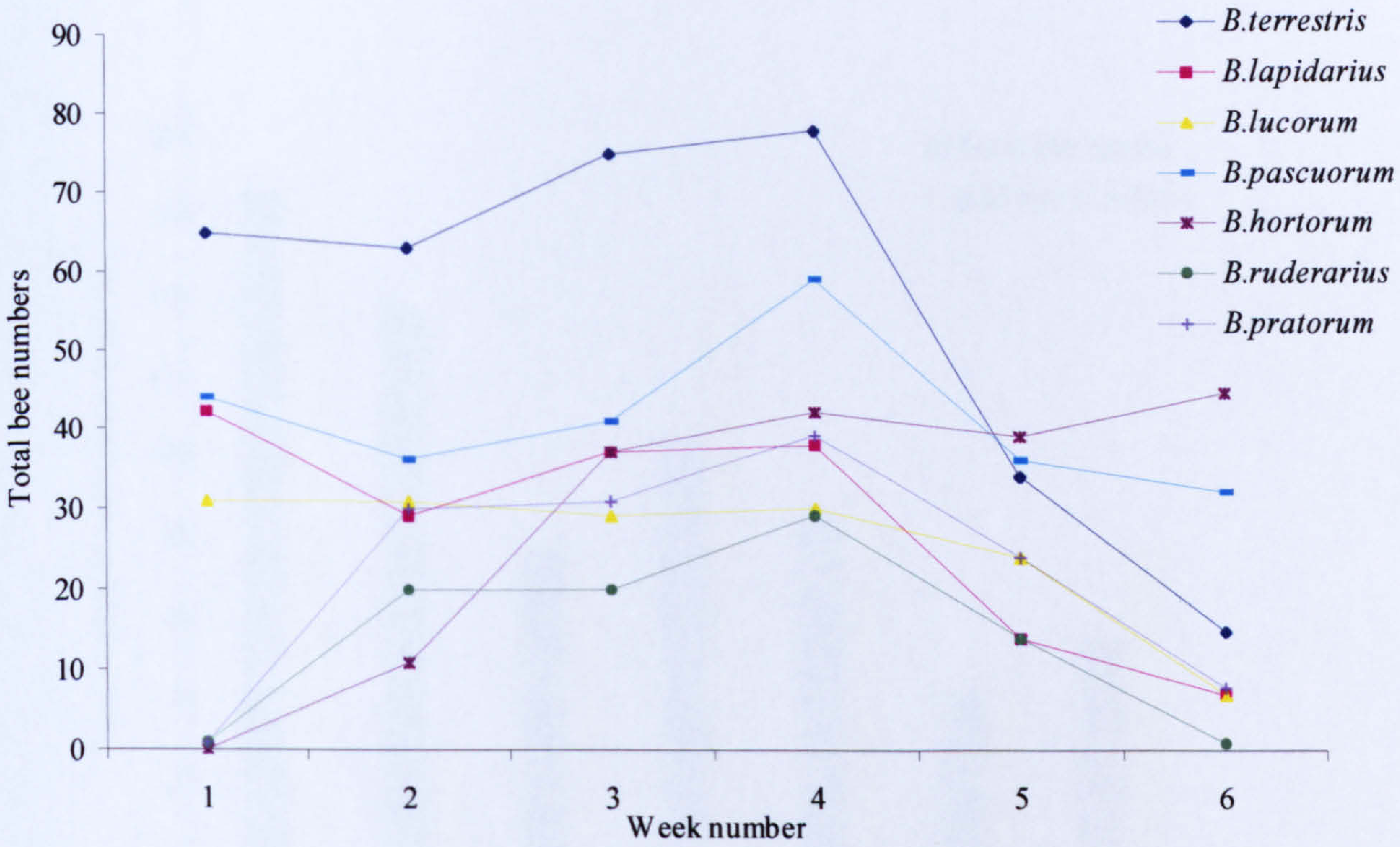
Species	Number of observations	Percentage of observations
B. terrestris	329	25.56
B. lapidarius	167	12.98
B. lucorum	152	11.81
B. pascuorum	248	19.27
B. hortorum	174	13.52
B. ruderarius	85	6.60
B. pratorum	132	10.26
Total	**1287**	**100%**

Table 7.1: Total number of observations of nest-searching queens of each species for the duration of this study, expressed as a percentage of the total number of observations of all species

7.4.2 Timing of emergence

Emergence of *B. terrestris*, *B. lapidarius*, *B. lucorum* and *B. pascuorum* queens had commenced prior to the initiation of this study (the start date was delayed because of restricted access to farmland nationwide following a foot-and-mouth outbreak). *B. terrestris* numbers peaked in week 4 (16-18 May), and then underwent a sharp decline; *B. pascuorum* exhibited a similar pattern, though the decline was not as steep, and numbers were still relatively high at the end of the study. *B. lapidarius* and *B. lucorum* numbers remained relatively constant for the first 4 weeks of observations, but declined towards zero over the next 2 weeks. Emergence of *B. hortorum*, *B. ruderarius* and *B. pratorum* queens was evident by week 2 (2-4 May); *B. ruderarius* and *B. pratorum* numbers peaked at week 4, and had declined to low levels by week 6 (30 May-1 June), whilst *B. hortorum* numbers were still increasing at this point (see figure 7.2).

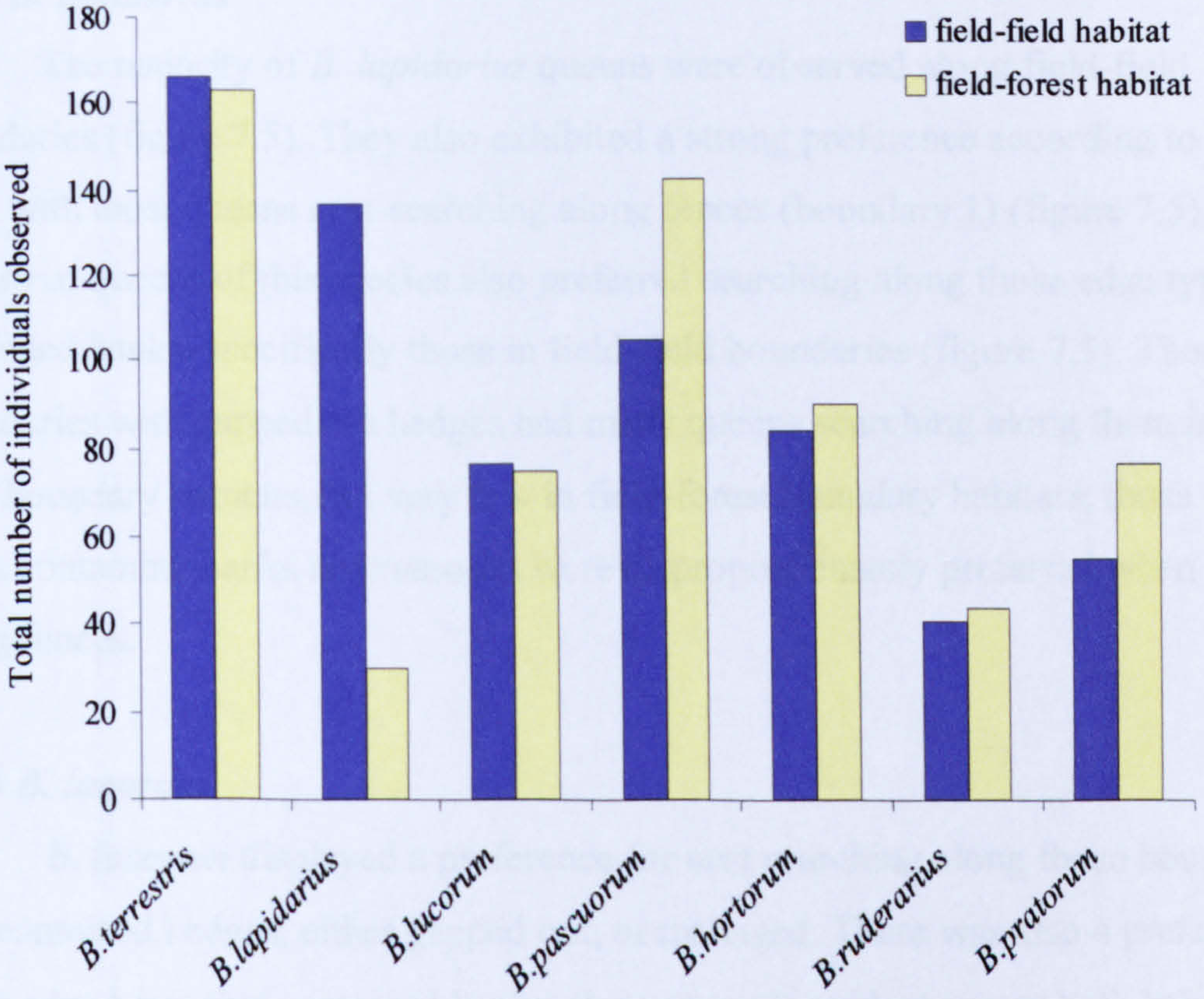
Figure 7.2: Patterns of abundance of nest-searching queens of the different species through time



7.4.3 Habitat preferences

A two-way ANOVA reveals that there is no overall difference between the two habitats in terms number of total individuals observed searching in each when all species are considered together ($F_{1, 154}$=0.120, p=0.741). Neither is there a significant interaction between species and habitat most commonly observed in ($F_{6, 154}$=1.753, p=0.112); 4 of the 7 species recorded were observed in similar numbers in both habitats (figure 7.3).

Figure 7.3: Total numbers of each *Bombus* species queen observed in the two habitats across the duration of this study. Habitat 1 denotes field-field boundaries; habitat 2 denotes field-forest boundaries



Considering boundary type and edge type within habitats it does become clear that different *Bombus* species had specific preferences in terms of investigation of potential nest sites. The seven species that were observed are now considered in turn.

7.4.4 *B. terrestris*

B. terrestris queens showed no preference for nest searching in either field-field or field-forest habitats, or according to boundary type (figure 7.3). However, edge type does appear to be a significant factor, with queens preferring to nest-search in edge types 2 and 4 (figure 7.4). Both these edge types contained banks, with type 4 also containing a tussocky grass strip. This pattern is apparent across both habitat and boundary types.

7.4.5 *B. lapidarius*

The majority of *B. lapidarius* queens were observed along field-field boundaries (figure 7.5). They also exhibited a strong preference according to boundary type, with most queens nest-searching along fences (boundary 1) (figure 7.5). Like *B. terrestris*, queens of this species also preferred searching along those edge types that contained banks, specifically those in field-field boundaries (figure 7.5). Those boundaries with gapped out hedges had many queens searching along them in field-field boundary habitats, but very few in field-forest boundary habitats; those edge types containing banks and tussocks were disproportionately preferred when occurring along fences.

7.4.6 *B. lucorum*

B. lucorum displayed a preference for nest searching along those boundaries that contained hedges, either gapped out, or managed. There was also a preference for those edge types that contained banks: this pattern is evident across both habitats (figure 7.6). The preference of nest-searching queens for banks along those boundaries with hedges was not displayed along fenced boundaries.

7.4.7 *B. pascuorum*

B. pascuorum queens were observed much more often along field-forest habitats (figure 7.3). Those boundaries with hedges were preferred over boundaries with fences. In both habitats and across all boundary types, many more individuals were observed along those edge types that contained tussocks (types 3 and 4) (figure 7.7). With the exception of fenced boundaries along forest edges, more *B. pascuorum* queens were recorded from those tussocky habitats not containing banks, than from those that did. Along field-forest habitats there were more observations of *B.*

pascuorum queens along those edges with bank and tussock, than along these same edge types in field-field habitats. There also appears to be an interaction between boundary type and edge type; more queens were observed along tussocky edges (types 3 and 4) next to hedges (boundary types 2 and 3) than next to fences (type 1) in both habitats (figure 7.7).

7.4.8 *B. hortorum*

B. hortorum queens were not found to exhibit a preference for nest sites based on habitat type or on boundary type as quantified in this study. However, these queens were observed searching much more often along those edge types that contained tussocks (types 3 and 4); this behaviour was evident across all boundary and habitat types (figure 7.8).

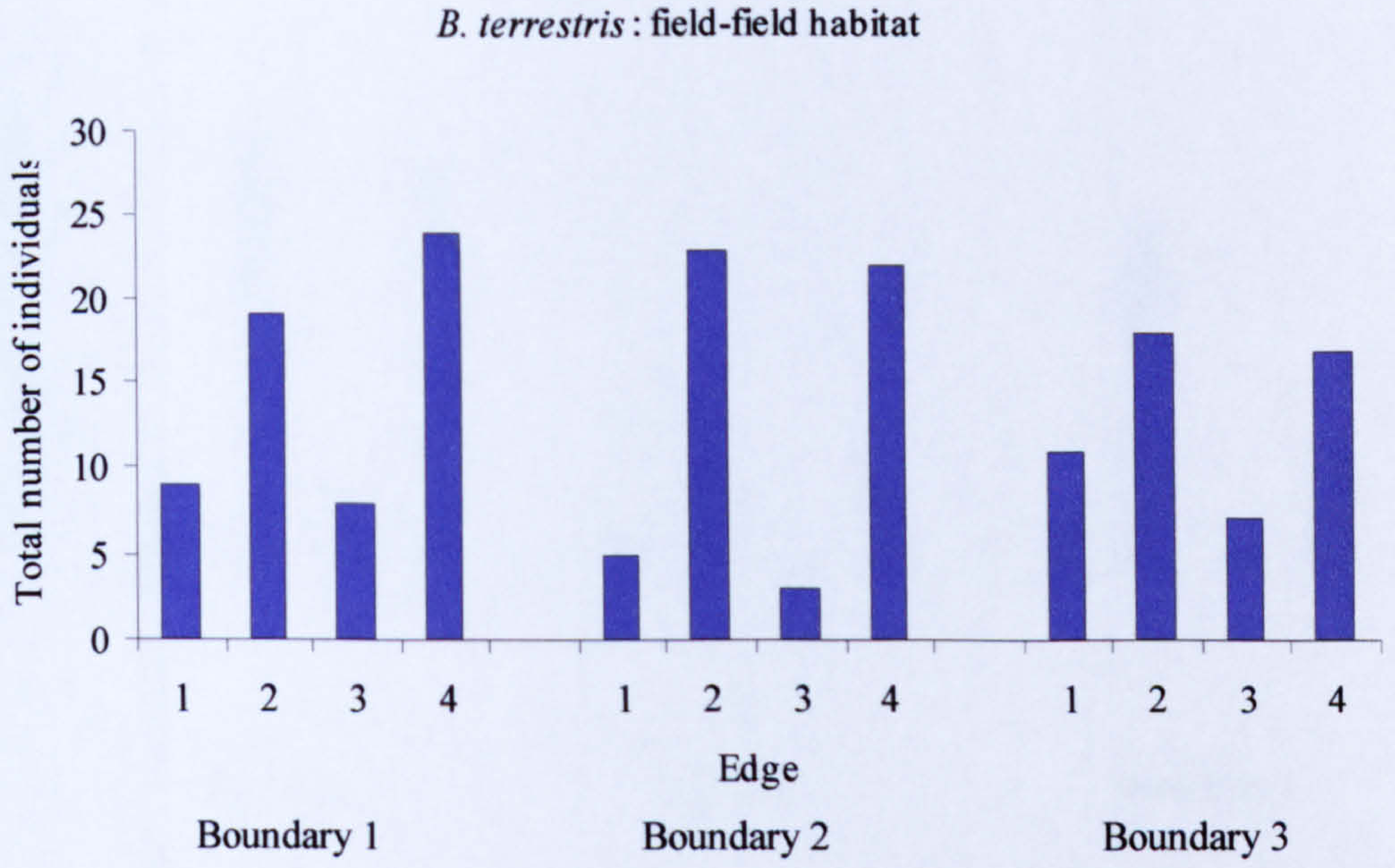
7.4.9 *B. ruderarius*

No difference is apparent between numbers of nest searching *B. ruderarius* queens between habitats and between boundary types (figure 7.3). However, edge type did appear to be a factor in terms of numbers of queens observed. Most queens of this species were recorded along tussocky edges (types 3 and 4) (figure 7.9), with more *B. ruderarius* queens observed nest searching along tussocky edges with banks in field-forest habitats, and more observed nest searching along tussocky edges without banks in field-field habitats (figure 7.9). There were also more queens recorded along type 1 edges (no banks or tussocks) in field-forest than field-field habitats, although numbers were much lower than those observed along edge types with tussocks (figure 7.9).

7.4.10 *B. pratorum*

More *B. pratorum* queens were recorded from field-forest habitats than field-field habitats (figure 7.3). Boundary type and edge type did not seem to affect the occurrence of nest-searching queens; figure 7.10 illustrates that nest-searching queens of this species were observed across all boundary and edge types in approximately equal numbers.

Figure 7.4: Boundary and edge type preferences for nest-searching *B. terrestris* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



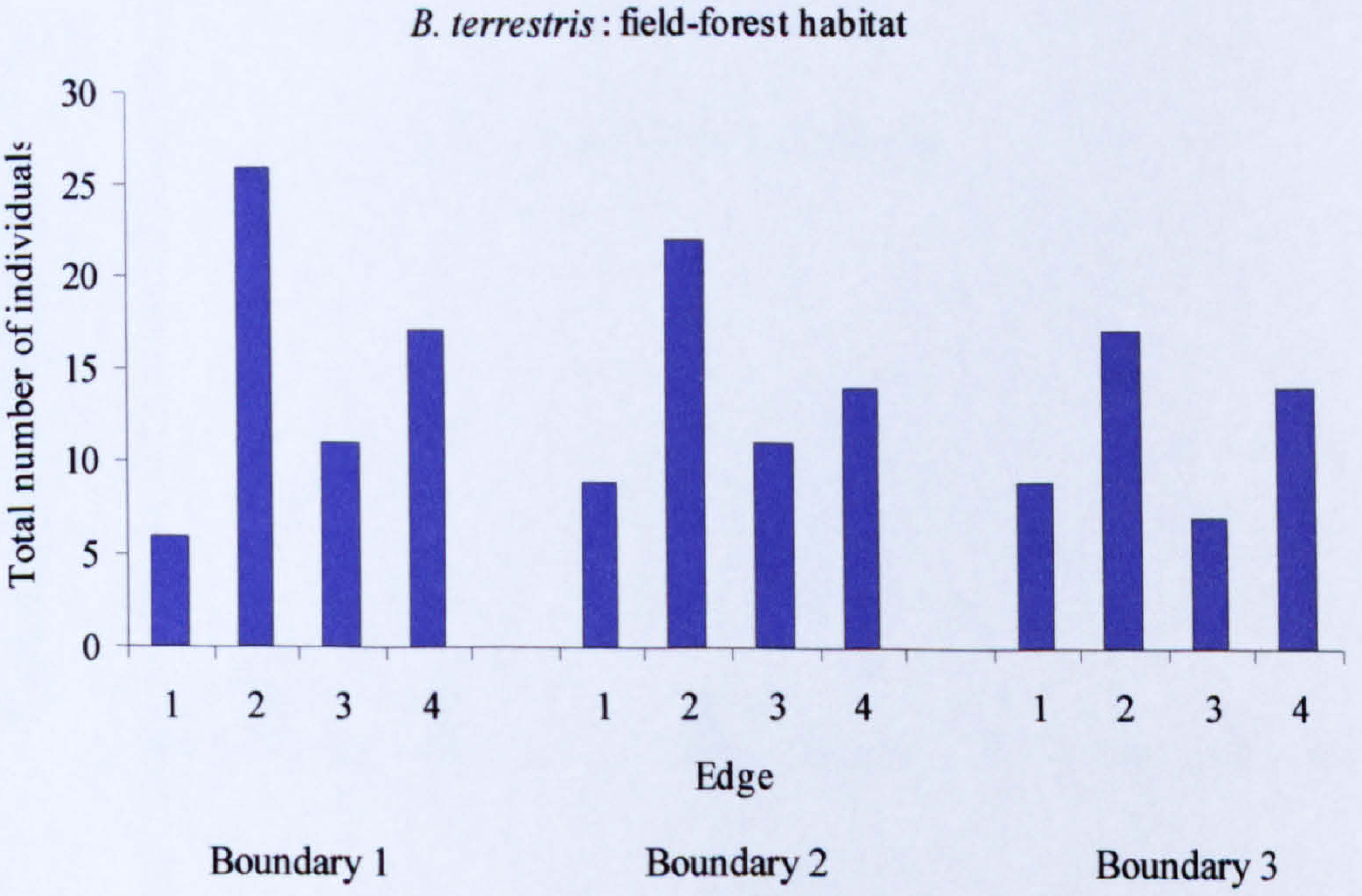
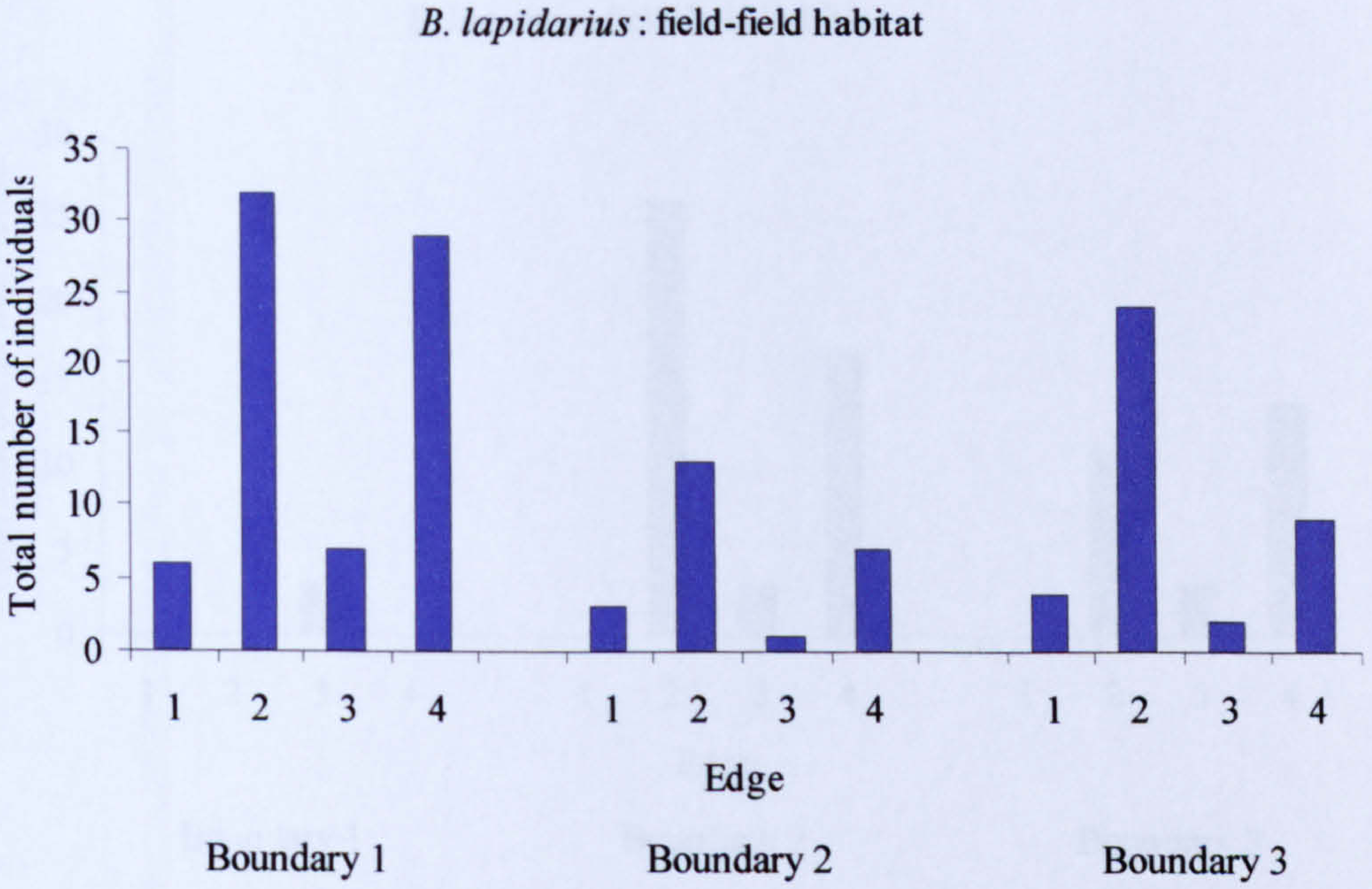


Figure 7.5: Boundary and edge type preferences for nest-searching *B. lapidarius* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



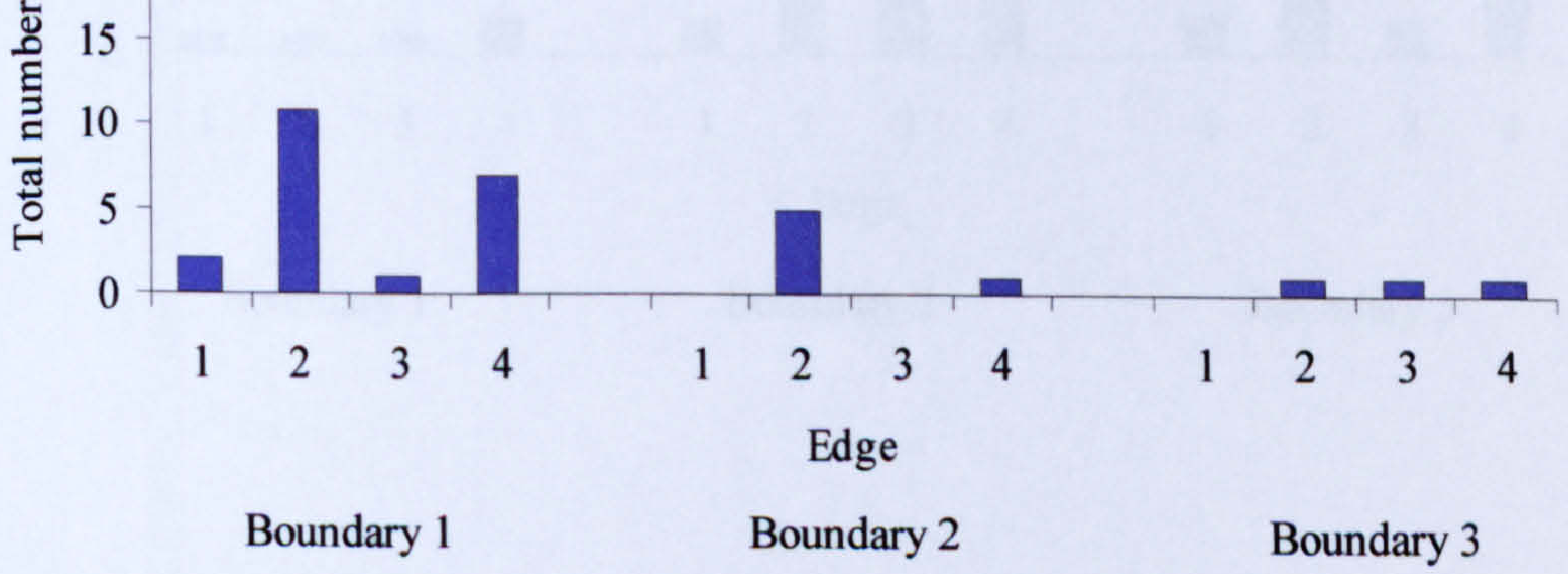
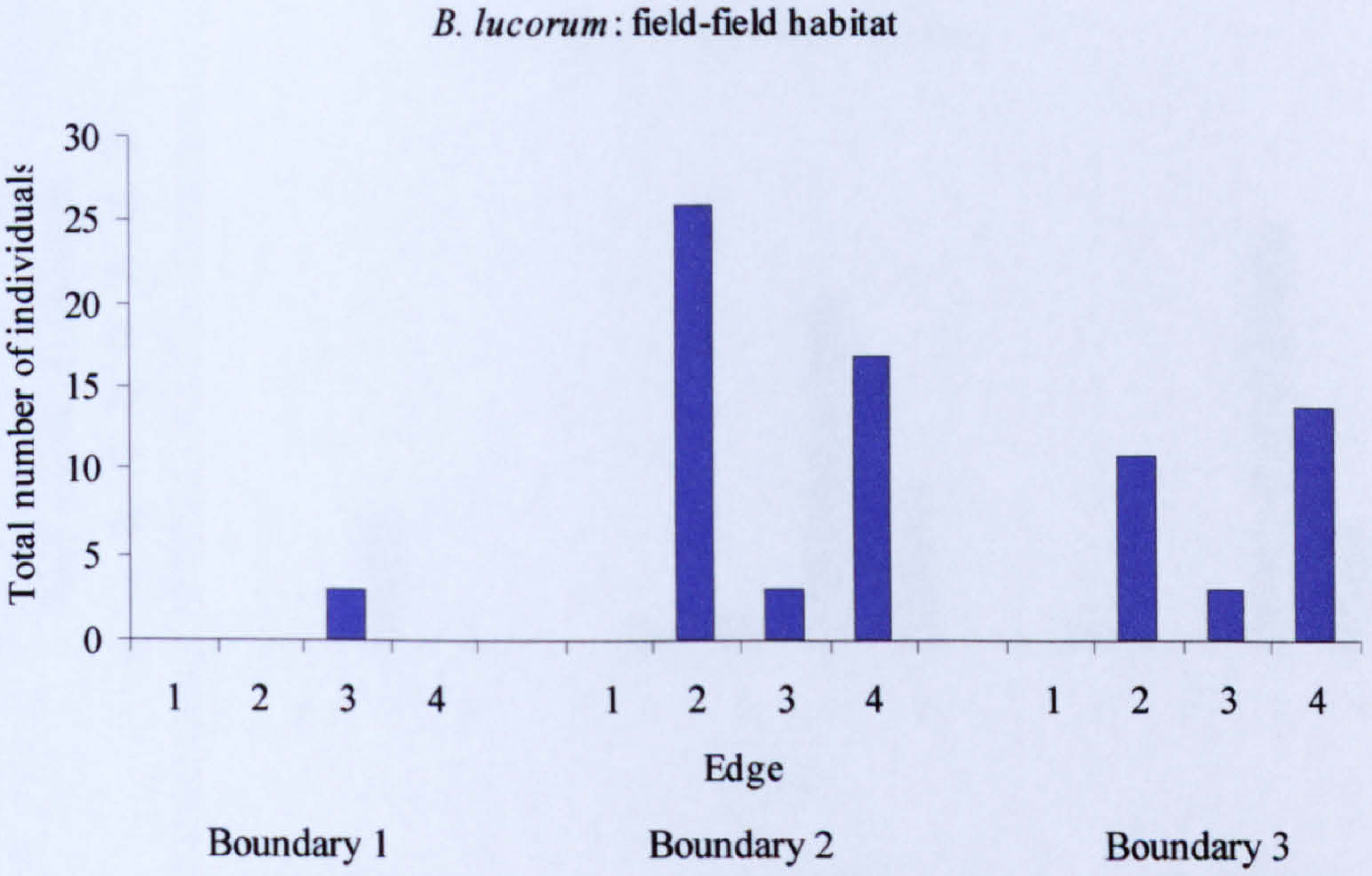


Figure 7.6: Boundary and edge type preferences for nest-searching *B. lucorum* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



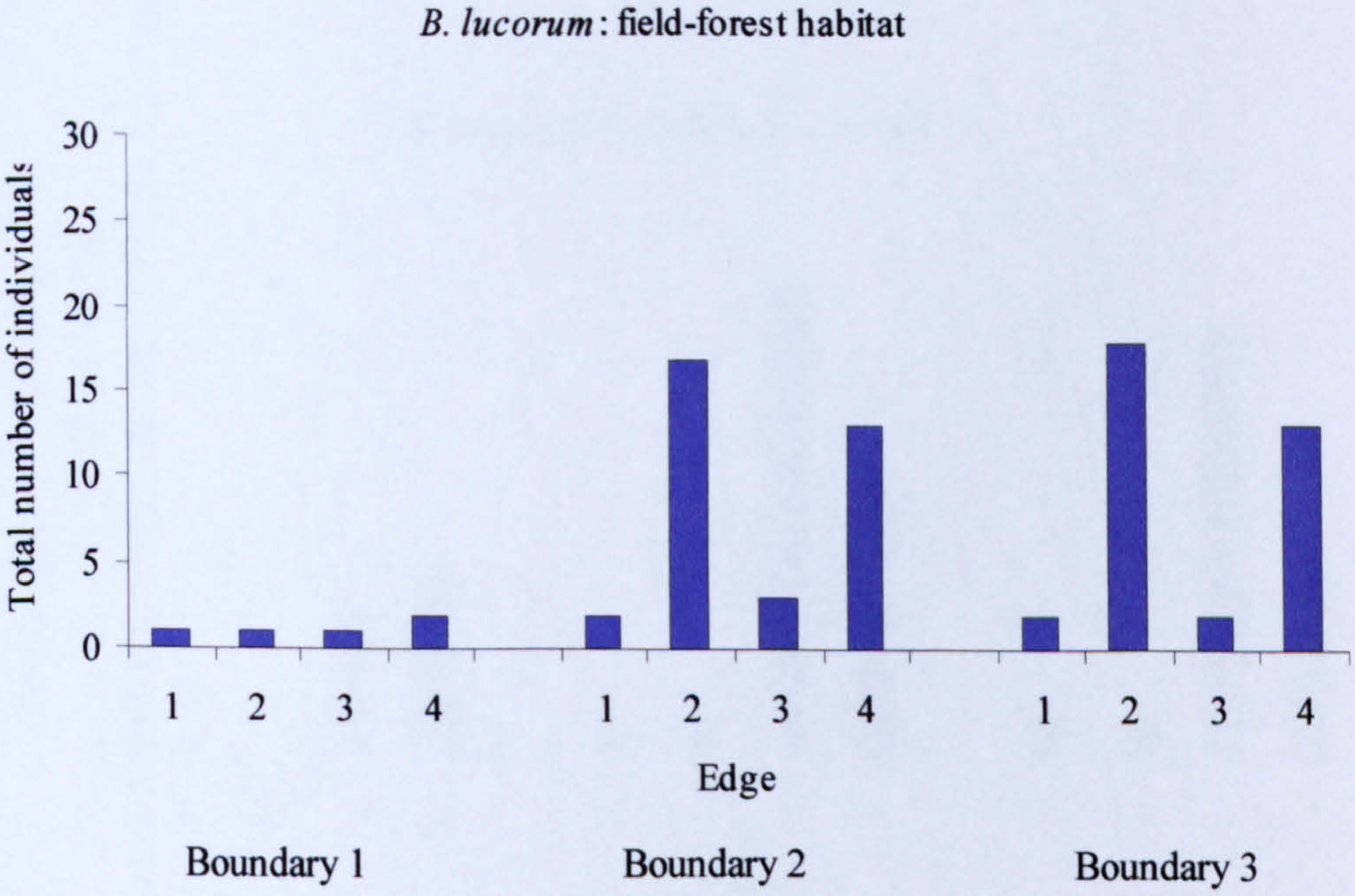
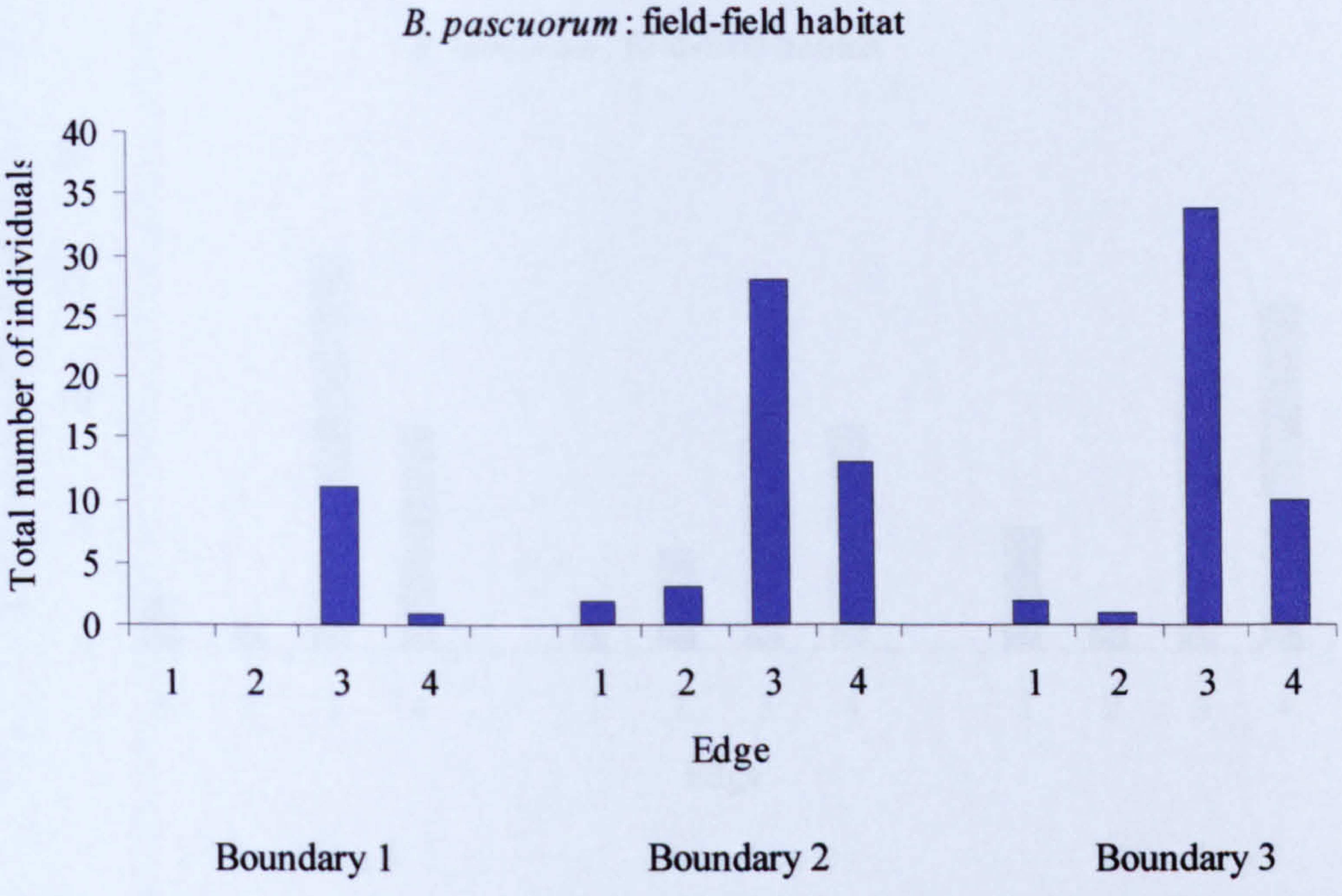


Figure 7.7: Boundary and edge type preferences for nest-searching *B .pascuorum* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



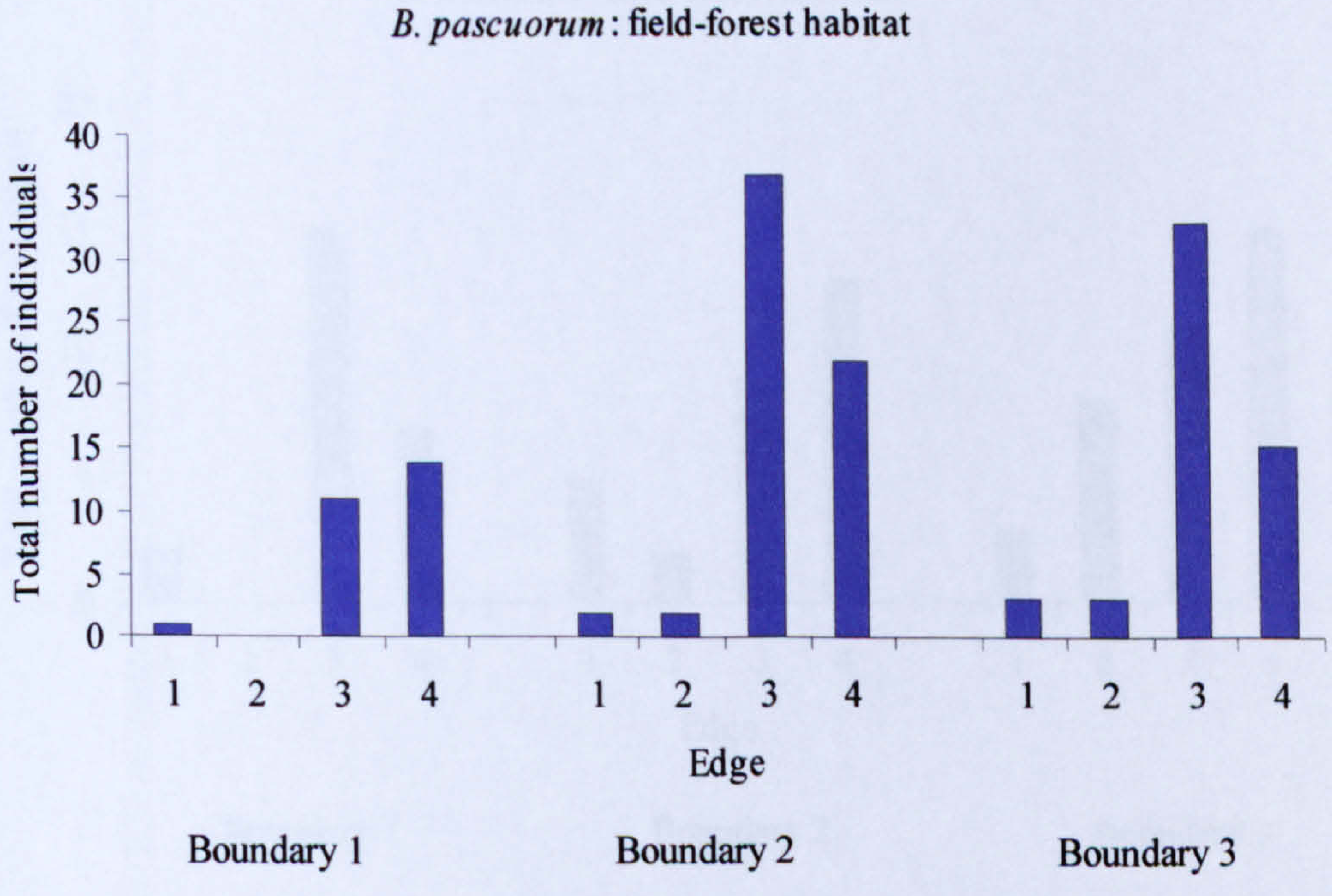
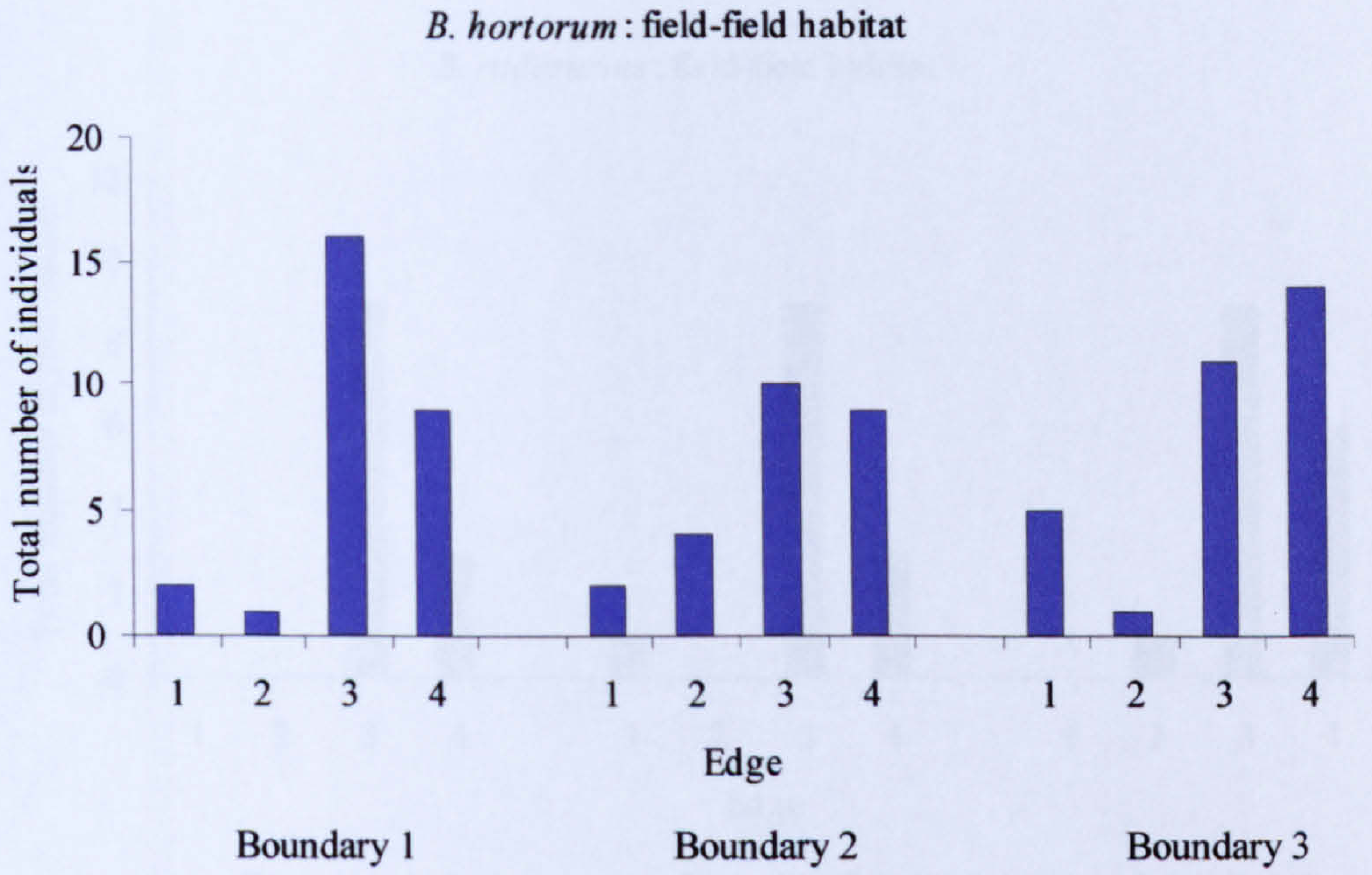


Figure 7.8: Boundary and edge type preferences for nest-searching *B. hortorum* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



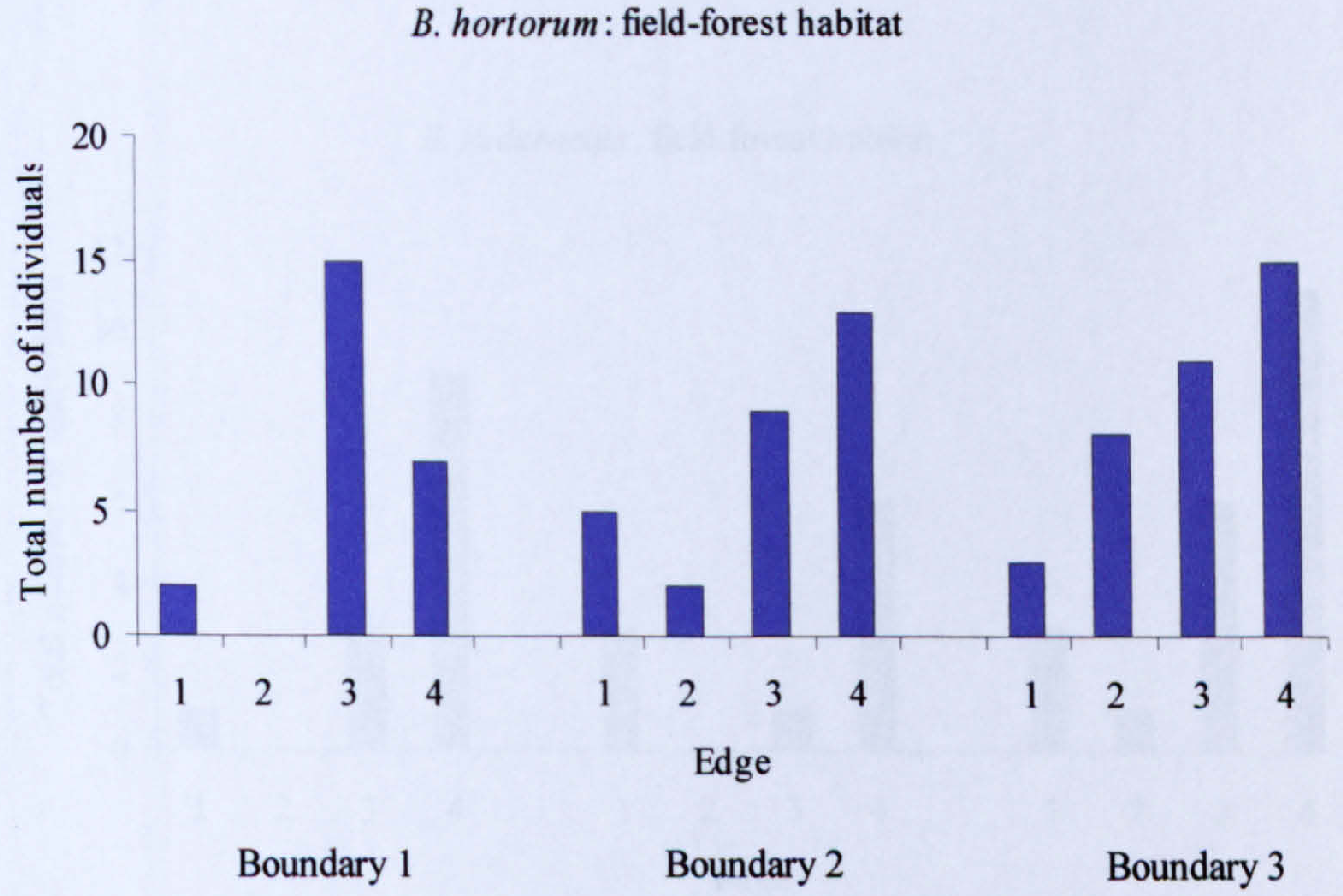
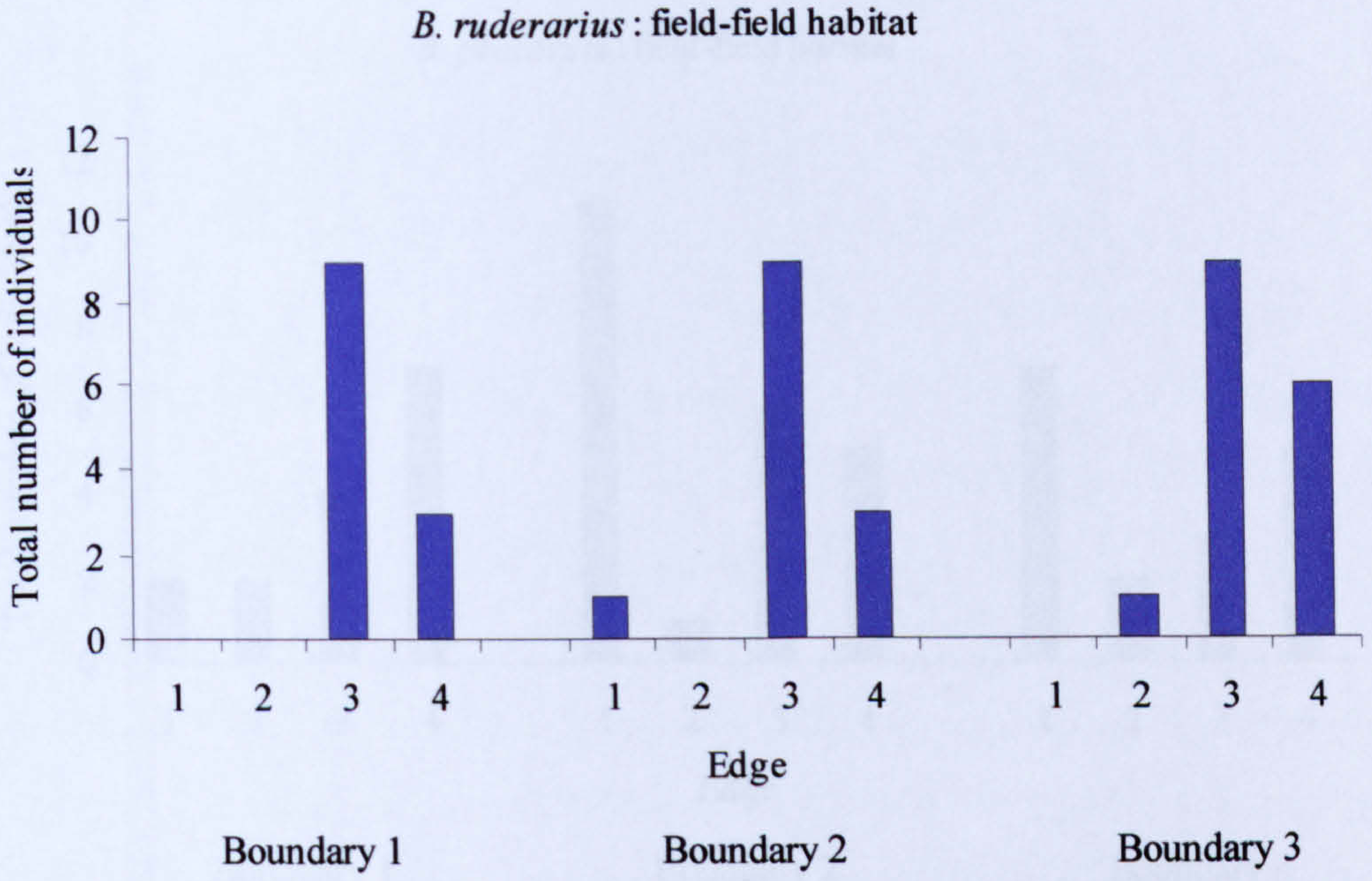


Figure 7.9: Boundary and edge type preferences for nest-searching *B. ruderarius* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock



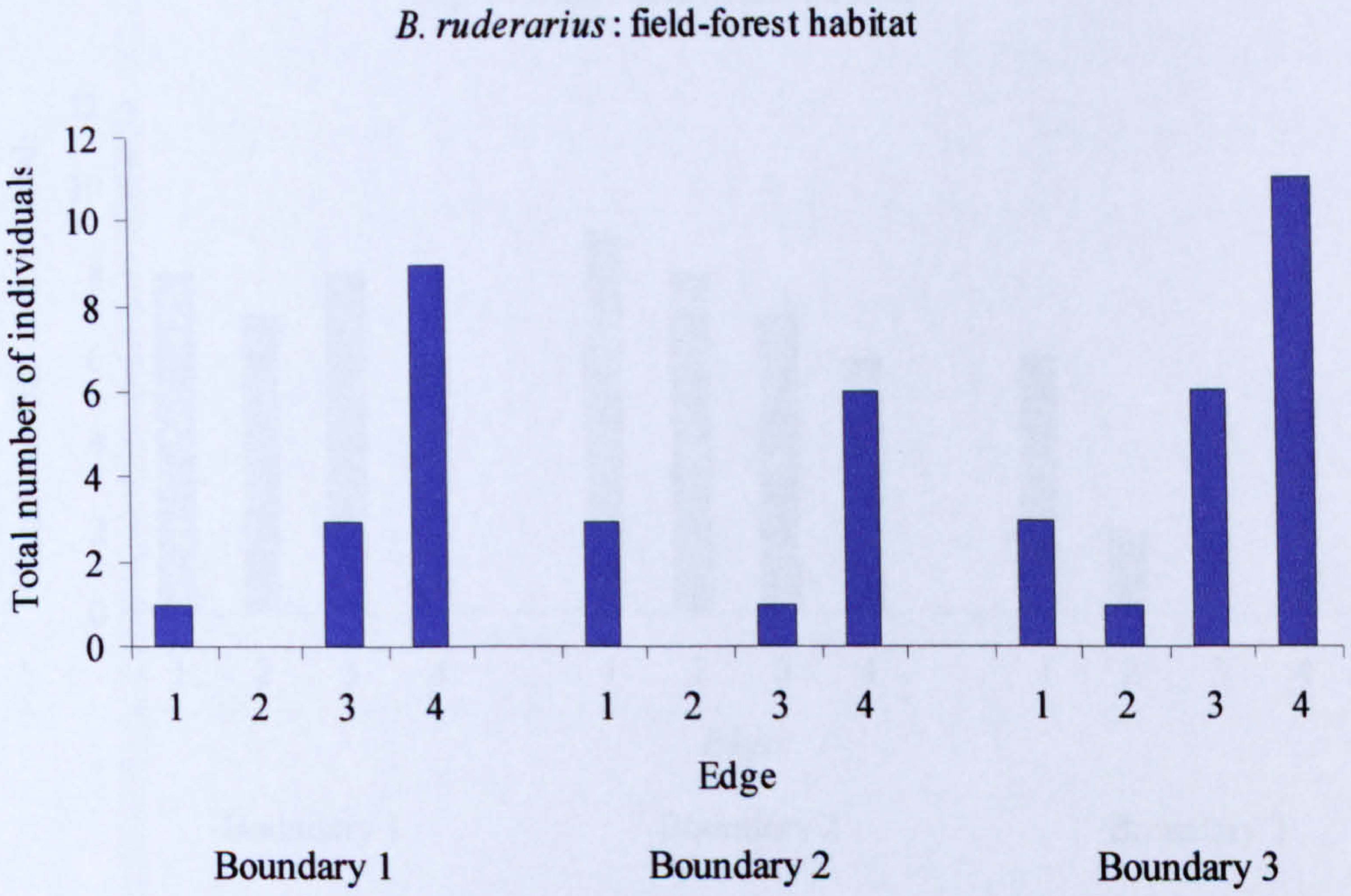
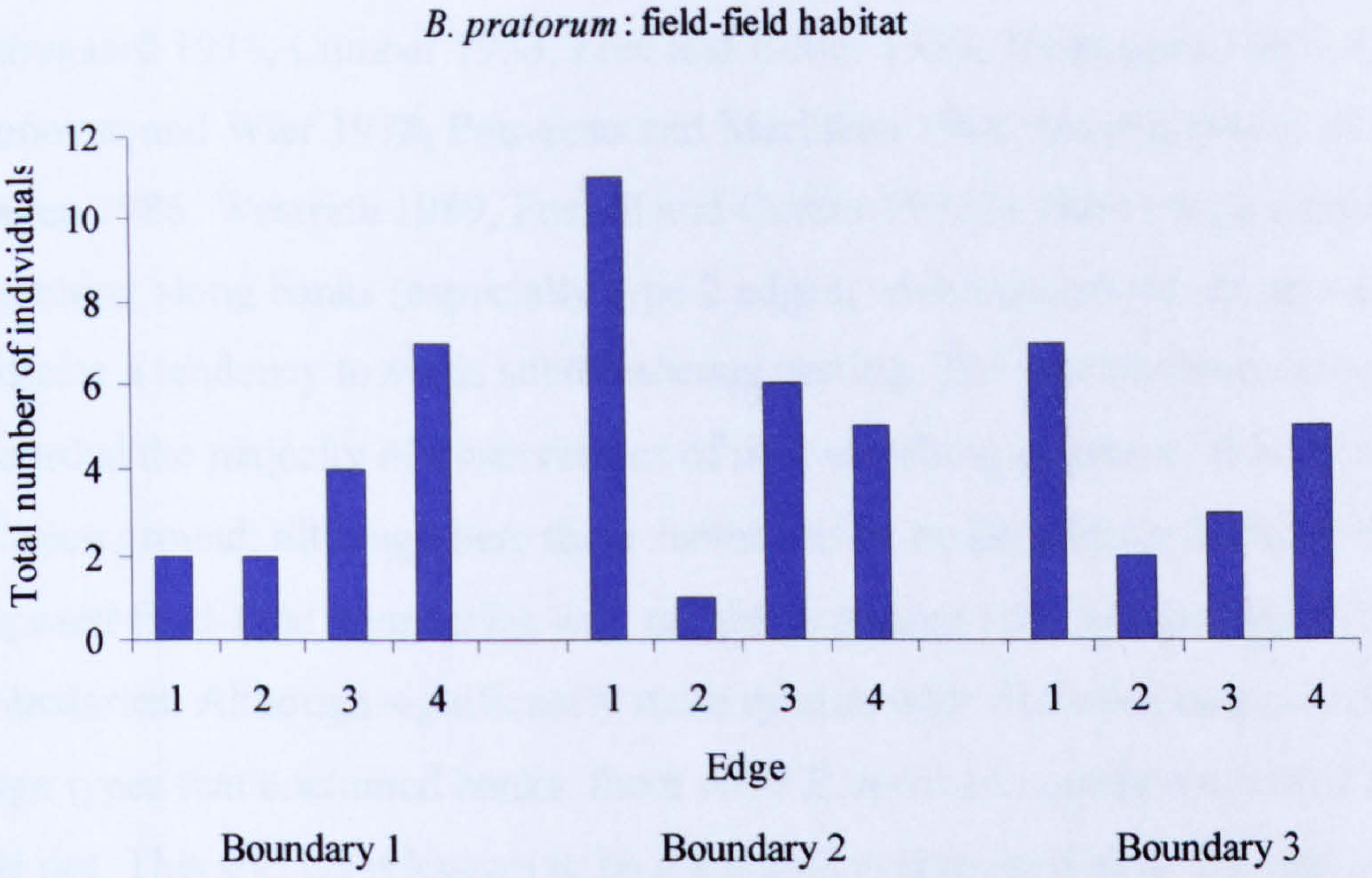
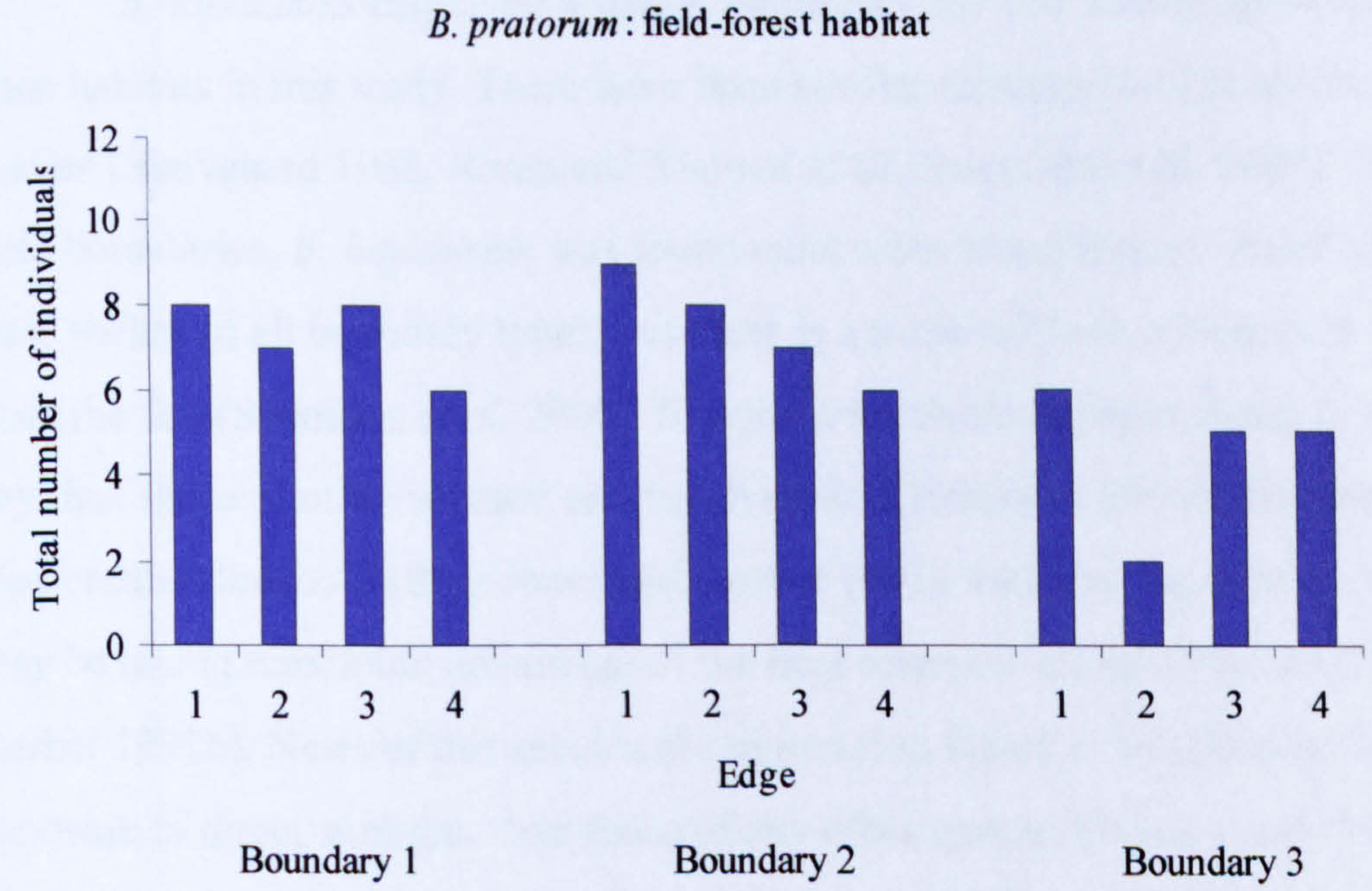


Figure 7.10: Boundary and edge type preferences for nest-searching *B. pratorum* queens in 2 different habitats. Boundary types were as follows – 1) fenced; 2) managed hedge; 3) gapped out hedge. Edge types were 1) no bank or vegetation; 2) bank only; 3) tussock only; 4) bank and tussock





7.5 Discussion

7.5.1 Individual species preferences

B. terrestris is known from previous studies to nest subterraneously, something which can be inferred from its' Latin name, *terra*, meaning of the earth (Sladen 1912, Skovgaard 1936, Cumber 1953, Free and Butler 1959, Wojtowski 1963, Alford 1975, Donovan and Wier 1978, Pouvreau and Marilleau 1980, MacFarlane *et al.* 1984, von Hagen 1986, Westrich 1989, Fussell and Corbet 1992b). Here I took a preference for searching along banks (especially type 2 edges, which contained no tussocks), to indicate a tendency towards subterraneous nesting. The work of Svensson *et al.* (2000) recorded the majority of observations of nest searching queens of this species in areas of open ground, although here there seemed to be no preference between those exposed field-field boundaries with no hedge present and the most shaded field-forest boundaries. Although significantly more queens were observed nest searching in those edge types that contained banks, there were *B. terrestris* queens recorded in edges that did not. This species is known to be adaptable in choice of nest site, and can utilise anthropogenic artefacts (Fussell and Corbet 1992b).

B. lapidarius displayed a strong preference for nest searching along the more open habitats in this study. There have been similar findings for this species from other studies (Skovgaard 1936, Ranta and Tiainen 1982, Svensson *et al.* 2000). On the field-field boundaries, *B. lapidarius* was found most often along fences, which afford the least shelter of all boundary types, but there is a trade-off here with degree of warmth from the sun (Svensson *et al.* 2000). *B. lapidarius* workers begin foraging later in the day than those of other species, and finish earlier (Hasselrot 1960); they have a higher temperature threshold (Prys-Jones and Corbet 1991), and nest location in open areas may be taking maximum advantage of the heat reservoir effect of the soil (Fussell and Corbet 1992b). Nests of this species are more often found in locations with all-day exposure to direct sunlight, than those of any other species (Fussell and Corbet 1992b). Svensson *et al.* (2000) found that *B. lapidarius* queens did not nest search along habitats containing tussocks; results here were similar, indication that this species rarely founds nests in above-ground vegetation. There may be an avoidance of nesting in heavily vegetated areas, as nests here are likely to be shaded. Alford (1975), von Hagen (1986), and Westrich (1989) all mention that *B. lapidarius* may nest above ground; this species is known to take advantage of anthropogenic artefacts (Prys-Jones and Corbet 1991), and sites such as wall cavities may offer ideal unshaded nest sites.

No difference was found between occurrence of nest searching on open ground and on forest boundaries for *B. lucorum*, although there was a preference towards boundaries with a hedge structure; these may be more sheltered than boundaries that only have fences along their length. Svensson *et al.* (2000) also found that although this species displayed variety in terms of where individuals searched, overall there was a preference for sheltered boundaries. Those *B. lucorum* queens recorded in southern Sweden (Svensson *et al.* 2000) were also associated with the presence of tussocks, but here the presence of banks seemed to play an important part in nest site choice.

The majority of *B. pascuorum* queens were observed along boundaries that afforded some degree of shelter, a pattern that was apparent in both habitats. There was a strong preference towards those edges that contained tussocky vegetation within these boundary types. Svensson *et al.* (2000) found that *B. pascuorum* queens were most prevalent along forest boundaries in southern Sweden, however Svensson and Lundberg (1977), working in northern Sweden found a preference for open areas with tussocks. This may depend on the degree of shelter and the amount of direct sunlight afforded by the location (Svensson *et al.* 2000). The common name of this species is the 'carder bee' because of its distinctive habit of combing (or 'carding') material from around the nest into a covering for the cells (Sladen 1912); it is no surprise then that it has been found to prefer to nest on the soil surface in areas containing tussocks, which provide material to cover the nest (Sladen 1912, Skovgaard 1936, Cumber 1953, Richards 1946, Free and Butler 1959, Panfilov and Zimina 1962, Wojtowski 1963, Alford 1975, Fussell and Corbet 1992b).

B. hortorum queens were observed searching for nests in either habitat in approximately equal numbers. This species also did not seem to exhibit a preference for boundary type. However, significantly more observations were made along those edges that contained tussocks. The literature suggests that *B. hortorum* nests are found in a diversity of sites (table 7.2), with some studies reporting an association between these and the presence of hedges and banks (Skovgaard 1936; Fussell and Corbet 1992b); this was not the case here.

Although *B. ruderarius* belongs to the mainland ubiquitous species group of Williams (1982, 1986), it is less common than the other members of this species group, although it may be locally abundant. This species is known to nest on the soil surface (Alford 1975), and it is another 'carder' species; here it was seen to search along field and forest edges that had tussocks.

B. pratorum is known to be one of the most opportunistic bumblebee species in terms of where it builds its nests (Sladen 1912; Cumber 1953; Free and Butler 1959; Alford 1975; von Hagen 1986; Fussell and Corbet 1992b). There is some evidence in this study of a slight preference towards forest boundaries, but queens were observed nest searching along the whole range of boundary and edge types.

Species	**Preferred nesting place**		
	Usually underground	Usually at or above the surface	Either
B. terrestris	1-2, 4-5, 7-8, 10-16		
B. lapidarius	1, 2, 4-7, 15-16		8, 13-14
B. lucorum	1, 4, 8, 11, 13-16		
B. pascuorum		1-8, 11, 15-16	13-14
B. hortorum	1, 2, 11	12	4, 8, 10, 13-16
B. ruderarius		16	
B. pratorum	2, 11	14	1, 4-5, 8, 13, 15-16

Table 7.2: Summary of references containing information on the preferred nesting sites of British *Bombus* spp. 1: Sladen (1912); 2:Skovgaard (1936); 3: Richards (1946); 4: Cumber (1953); 5: Free and Butler (1959); 6: Panfilov and Zimina (1962); 7: Wojtowski (1963); 8: Alford (1975); 9: Svensson and Lundberg (1977); 10: Donovan and Wier (1978); 11: Pouvreau and Marilleau (1980); 12: MacFarlane *et al.* (1984); 13: von Hagen (1986); 14: Westrich (1989); 15: Fussell and Corbet (1992b); 16: this paper. Table compiled from Fussell and Corbet (1992b)

7.5.2 Parasitism

It is important to remember that the findings of this study can only give an indication of individual species nest-site preference, and are not necessarily indicative of the abundance of successful nests. Spring queen numbers may bear very little relationship to the number of viable nests founded. The nematode *Sphaerularia bombi*, which acts to arrest ovary development (Pouvreau 1962, McCorquodale *et al.* 1998), may disrupt the mechanism of female orientation and affect nest-seeking behaviour (Lundberg and Svensson 1975). Parasitised queens remain on the wing for much longer than conspecific healthy queens, and are found on typical hibernation sites (north-facing banks) appearing to try to dig into the soil, or to force themselves under vegetation (Alford 1975); parasitised queens do not found nests. Queens in this study exhibited characteristic nest-searching behaviour, and not that of parasitised individuals. Large numbers of nests founded by queens free from *S. bombi* parasitism fail before workers and/or reproductives are produced. This can be due to factors such as predation, disturbance from both human and environmental stochastic events, and usurpations, from both conspecifics and *Psithyrus* spp. Hobbs *et al.* (1962) and Richards (1978) found that approximately 15% of nests of one species within their study area in western Canada experienced usurpation attempts. As the season progresses, local extinctions and the successful production of reproductives are highly correlated with local floral diversity and density (Pyke 1979, 1980, Bowers 1985).

7.5.3 Timing of emergence

The earlier a species emerges from hibernation, the more choice one would imagine it has in terms of possible nest sites. However, later emergence has advantages in that new nest sites may become available as the season progresses, and weather and resources may be more favourable to colony founding at this time. There may also be lower pressure from parasitism by *Psithyrus* spp. There is probably a degree of trade-off between early and late establishment (Richards 1978). Here, the 3 species that preferentially searched along banks (*B. terrestris, B. lapidarius, B. lucorum*) were already abundant by the start of the study, whilst of the 3 species that preferred tussocks (*B. pascuorum, B. hortorum, B. ruderarius*), *B. hortorum* and *B. ruderarius* were only beginning to emerge (figure 7.1). Potential nest sites along banks are likely to be more visible earlier in the season, before becoming covered with vegetation, whilst tussocks are likely to offer better cover later in the season. Emergence patterns of queens of all species were slightly later in this study than may be expected in southern England; the study site was located on elevated chalk downland and relatively exposed, and ambient temperatures would have been lower than those on surrounding land with a greater degree of shelter.

7.5.4 Spatial patterns of nest founding

There is considerable spatial variation in the patterns of *Bombus* nest founding. Harder (1986) found a random pattern of dispersion of 35 bumblebee nests of 5 different species within one field in Ontario, Canada. Nest-site abundances, both relative and absolute, vary from year to year (Bohart and Knowlton 1952, Stephen 1955, Teräs 1976a, 1983, Thomson 1978, Ranta 1982). The pattern of establishment of subterranean nests is likely to be a reflection of the nesting habits of the local small mammal population. The density of small mammals is independent of the density of nest-seeking queens (Harder 1986). Svensson and Lundberg (1977) working on bumblebee nests in northern Sweden found that all excavated subterraneous nests were located in what were previously rodent nests. They suggested that with peaks in rodent population dynamics, many ‘extra’ nests are created; these are then left empty when numbers fall below peak levels, and *Bombus* species can colonise these without competition or parasitism from rodents (Svensson and Lundberg 1977). Individual *Bombus* species success is highly variable between years, and some years are more favourable overall for *Bombus* spp. than others. All this influences the numbers of queens produced at the end of the colony life cycle, and the numbers emerging from hibernation in the spring. Some authors believe that there may be competition for nest sites (Ranta 1982), but this has been refuted by others (Pyke 1982). If competition does occur, it probably differs between habitats, and between years. Discrepancies between the results of different studies may be attributable to location-specific adaptations of the extant *Bombus* species to differing environmental conditions.

7.5.5 Availability of suitable nest sites

Although recent work has indicated that bumblebees forage further from their nests than previously thought (Riley *et al.* 1996, Osborne *et al.* 1999, Walther-Hellwig and Frankl 2000a), the maximal observed home range is no more than 1750m (Walther-Hellwig and Frankl 2000a), and on average may be much less than this (Kevan and Baker 1983, Bowers 1985, Rotenberry 1990, Dramstad 1996). Successful nests will require a continuum of forage resources from crops or other food sources within the home range of the colony (Dukas and Edelstein-Keshet 1998, Cresswell *et al.* 2000).

The availability of nest sites is obviously important to the survival of *Bombus* spp. (Tscharntke *et al.* 1998). Many potential nest sites have been destroyed by landscape modification (Rasmont *et al.* 1992, Ortiz-Sánchez 1995), as most bumblebee nest sites are found along uncultivated field boundaries (Banaszak 1983, von Hagen 1994). Those habitats that have been much disturbed and cultivated are of least value to bumblebee queens as potential nest sites (Fussell and Corbet 1992b). Remaining potential nest sites exist mainly on scattered remnants of semi-natural habitat (Saville *et al.* 1997), and it is important that these are conserved, along with habitats such as field and forest boundaries that contain banks and tussock-type vegetation. As an initial step, priority may be given to habitat conservation depending on the crop grown. Those *Bombus* species with the longest tongues (*B. hortorum, B. pascuorum*) are necessary for the pollination of crops such as beans and red clover, and tend to prefer nest sites containing tussocks, whilst those short-tongued species (*B. terrestris, B. lapidarius*) that preferentially nest along banks are successful pollinators of crops with smaller, more open flowers, such as rape and apples (Ranta and Lundberg 1980, Fussell and Corbet 1991, Fussell and Corbet 1992a).

Field boundaries have become a major refuge for many arthropod species once common on farmland (Lagerlof and Wallin 1993). Many widely distributed bird species utilise hedgerows, and areas that are otherwise inhospitable to woodland bird species may contain hedgerows that are used as winter habitats or as dispersal routes

(Fuller *et al.* 2001). Conservation of such areas should aid not only bumblebees, but many other species of fauna as well (Kells *et al.* 2001).

8. GENERAL DISCUSSION

The main aim of this project was to provide a basis for the development of conservation strategies for *Bombus* spp. within intensively farmed habitats (see page 25). Specifically, I investigated the potential that both naturally regenerated field margins and sown wildflower strips could have in providing forage resources for bumblebees, how foraging behaviour differed on different crop species, and which boundary features of agricultural land were the preferred nesting sites of bumblebee queens of different species. I also investigated the physiological and morphological characteristics of the 'novel' crop, sainfoin (*Onobrychis viciifolia*), and observed bee foraging behaviour in detail on this species. The discussion that follows brings together the conclusions (and limitations) of the work undertaken for this thesis, and examines the implications of these, as well as outlining some future directions for bumblebee conservation research, and indeed agro-ecosystem research in general.

8.1 Project summary

The introduction of naturally regenerated field margins and sown wildflower strips along the edges of cropped fields unsurprisingly increases the availability of nectar-rich vegetation in agro-ecosystems (chapters 2 and 3). Both these management schemes had a positive effect on the density and diversity of foraging bumblebee species in the landscape. Other studies have found that increasing the numbers of florally rich field margins within the landscape positively influences *Bombus* spp. density (Backmann and Tiainen 2002). One Dutch study (Kleijn *et al.* 2001) has shown small increases in bee species richness on fields under agri-environment legislation, when compared with those that are not. In the present study, although species richness was increased on the experimental margins, all recorded bumblebees were species that are relatively common across the lowland U.K., and by far the most commonly observed species were the generalist foragers, *B. terrestris* and *B.*

lapidarius, along with *A. mellifera*. These experiments were carried out in the west Midlands, an area where the bumblebee fauna belongs to the mainland ubiquitous species group (Williams 1986); perhaps a higher diversity of species would have been observed in experimental margins in an area known to have more diverse bumblebee species representation. It is difficult to compare the results from these two chapters as the experiments were carried out in consecutive years; nonetheless it is apparent from the results that both these management schemes have a positive effect on the apifauna of agro-ecosystems, even in areas where species diversity is low to start with.

These two chapters suggest that floral diversity rather than floral density is the determining factor as to whether an area is attractive to bumblebees. Those flower species that scored highest on the preference indices were those that were not found in the study area prior to the introduction of the management regimes. Different floral species differed in their degree of attractiveness to different bee species; this relationship is best illustrated by the significant negative correlation between floral preferences of *A. mellifera* and *B. hortorum* (chapter 3), two species at divergent ends of the morphological spectrum. Obviously, the seed mix in sown wildflower strips can be manipulated to include those species most attractive to whichever bumblebee species are being targeted by the conservation effort, whilst floral diversity in naturally regenerated margins is dependant on that of the seed and bud bank (Hartshorn 1978). This seed and bud bank diversity will influence whether the outcome of natural regeneration is likely to be a valuable habitat in conservation terms. The outcome of natural regeneration on former arable land has been found to offer particularly valuable foraging habitats to some less common *Bombus* spp. in some areas (Carvell 2002), so it is clear that this can be successful where seed and bud bank diversity is adequate, and it is the least expensive option. In either case, subsequent management regimes need to conserve initial floral diversity if any long-term benefit is to be seen. It is also important to research what the farmers in an area find acceptable or desirable before they are expected to introduce conservation schemes across their land (Wossink *et al.* 1999).

The measured increase in bumblebees in the experimental margins represents a short-term increase in bumblebee numbers, with migration of foragers into these habitats from elsewhere. Any effect on absolute bee numbers in an area will only be evident after a time lag of several colony generations, and if any increase in density and/or diversity is to be sustained, a commitment to long-term management schemes is required.

The introduction of nectar-rich crop species can provide a supplementary floral resource, at a higher density, and more importantly cover a much larger area, when compared to wild flowers on agro-ecosystems. Although traditional crops such as beans and linseed are attractive to bumblebees (chapter 4), some potential 'novel' crops are highly attractive, and could become economically important, e.g. *Onobrychis viciifolia* (chapter 5). As with wildflowers, different crop species vary hugely in their degree of attractiveness to different bumblebee species (chapters 2-5), which is of importance if consideration is being given to crop species grown when designing conservation schemes. The observation of the foraging behaviour of bumblebees on novel crops can reveal behavioural patterns not studied previously (chapter 6).

The availability of potential nest sites is obviously also important to the survival of *Bombus* spp. Spring queens were found to have interspecific nest-site preferences when nest searching along field boundaries (chapter 7), and some species were much more specific in the types of habitat they searched than others. *B. terrestris, B. lapidarius*, and *B. lucorum* are subterraneous-nesting species, and had a strong preference for nest-searching along banks, whilst *B. pascuorum, B. hortorum* and *B. ruderarius* were most frequently observed searching along edges with tussock-type vegetation. This chapter only recorded nest-searching behaviour along field edges, and it is entirely possible that bumblebees could nest in significant numbers in other areas, such as in open fields, on rough ground, under trees and shrubs, and even in anthropogenic artefacts. However, field edges are obviously utilised to some extent, and by a range of difference species with different preferences (Svensson *et al.* 2000).

This thesis draws the conclusion that field margins can provide valuable forage and nest-site habitats for bumblebees on agro-ecosystems, with entomophilous crop species providing a supplementary floral resource. However, when nest-searching, *B. lapidarius* in particular seemed to favour exposed field edges, so the universal introduction of field margins along field edges is not recommended. Also, some species nest in banks; these landscape features should be retained where possible. It is important that a variety of field edge habitats are maintained to cater for the life-history requirements of the maximum number of species. If crops dependant on pollination by longer-tongued bumblebee species are being grown (e.g. *T. pratense, V. faba*) (e.g. Richards 2001), it is probably advantageous to provide tussocks along field margins to encourage nearby nesting of these species (Walther-Hellwig and Frankl 2000a). There is some evidence that following hibernation newly emerged queens return to the vicinity of the maternal nest (Donovan and Wier 1978, Pomeroy 1981); if correct margin management increases the availability of suitable nest sites, in conjunction with enriching the floral resources of an area, then the return of daughter queens in subsequent years should boost local species numbers.

Although this study was set up to investigate foraging and nest-site preferences of all *Bombus* spp. observed on agro-ecosystems, the majority of observations were of common species, with the only rare species sited in significant numbers being *B. ruderarius*, and this only in the nest-searching study. It is important to identify the preferred forage plants and nesting habitats of those species causing most conservation concern. However, although these findings can only be taken in the context of the project, some implications for the conservation of bumblebees and other species using field margins can be drawn in conjunction with other research.

8.2 Implications

Although it is often stated that 84% of all crop species grown within the E.U. depend on insect pollination to some extent (see Corbet *et al.* 1991), in some of these species the crop is produced vegetatively with pollination only necessary to produce small areas of seed crop (e.g. *Trifolium repens, T. pratense* (clovers), *Medicago sativa* (alfalfa), *Daucus carota* (carrot), some *Brassica* spp.). Many other crops dependent on insect pollination are not grown intensively (Richards 2001). However, bee visitation does increase the quality of the fruits set in species such as oil-seed rape (*B. napus* ssp. *Oleifera)*, flax and linseed (*Linum usitatissimum*), sunflowers (*Helianthus annus*), cotton (*Gossypium* spp.), field beans (*Vicia faba*), soya (*Glycine max*), strawberry (*Fragaria* x *ananassa*), aubergine (*Solanum melanocarpum*), pepper (*Capsicum* *annuum*), tomato (*Lycopersicon esculentum*), olives (*Olea europea*), and grapes (*Vitis vinifera*) (Free and Ferguson 1983, Williams *et al.* 1986a, Williams *et al.* 1986b, Stoddard and Bond 1987, Corbet *et al.* 1991, Richards 2001), and therefore bees still have economic importance even though they are not essential for crop production in these species. As well as this economic value, bee pollination also contributes to the aesthetic component of the landscape through wildflower pollination; fauna associated with certain flower species are dependant on the successful pollination of these. Obviously, any crop where there is a positive response to insect-assisted pollination will benefit if there are high levels of biodiversity in the surrounding landscape to support insect populations.

Three ecological concepts have been identified within the mosaic pattern of the agricultural landscape; these are biodiversity, spatial heterogeneity, and island biogeography (Marshall 1993). Biodiversity is primarily species richness (diversity) and equitability (species density relative to one another). On agro-ecosystems, biodiversity is generally poor, with populations of flora and fauna that are generally ubiquitous and generalist, tolerant to disturbance (or indeed require it for successful germination), and highly competitive (especially in the case of flora) (Hinsley and Bellamy 2000). Introducing management schemes for field margins has the potential to increase the biodiversity in these systems. Thomas and Marshall (1999) found that both wildflower strips and naturally regenerated field margins contained more diverse arthropod assemblages than field margins sown with rye grass (*Lolium perenne*) or with the main field crop. Field margins where the leaf litter is allowed to build up are beneficial habitats for pseudoscorpions and spiders (Bell *et al.* 1999); vegetational structural complexity is more important for these orders than actual floral diversity (Baines *et al.* 1998). The introduction of field margins across agricultural systems is likely to see these becoming important sources of seeds and invertebrates for many bird species (Wilson *et al.* 1999), although margins are unlikely to contribute to an increase in avian species diversity unless these are associated with structurally complex hedgerows or windbreaks (Jobin *et al.* 2001).

Agricultural intensification has led to a decrease in the spatial heterogeneity of agro-ecosystems (Smallshire and Cooke 1999, Ricketts *et al.* 2001), and remaining areas of semi-natural vegetation have become increasingly fragmented (Hinsley and Bellamy 2000). Spatial heterogeneity is important; the more heterogeneous and complex an environment, the more requirements of various species' life-stages that can be meet. It is clear from this study that bumblebees require a range of habitats to meet their forage and nest-site requirements. Many insect and arachnid species that benefit crops by acting as pollinators or natural enemies (Corbet 1995) also depend on the existence of a variety of semi-natural habitats for at least some of their life-history stages (Chiverton and Sotherton 1991, Hawthorne and Hassall 1994, White and Hassall 1994, de Snoo and Chaney 1999, Sunderland and Samu 2000). Heterogeneous environments may also provide refugia for rare arable weeds (Critchley 1996a, Critchley *et al.* 1999), and for those species of flora and fauna that are susceptible to disturbance (Chiverton 1999, Mech and Hallett 2001). As well as being directly beneficial in terms of increasing heterogeneity and complexity, naturally regenerated or sown wildflower strips can enhance the conservation potential of hedge-bottom vegetation (Moonen and Marshall 2001).

Species surviving in remnant areas of semi-natural vegetation can act as 'source' populations for the surrounding habitat, according to theories of island biogeography (MacArthur and Wilson 1967). However, these areas need to be of sufficient size and complexity to support and maintain a source population. Field margins containing wildflowers can act as sources for species important in integrated pest management schemes, such as *Episyrphus balteatus* (Diptera: Syrphidae) (MacLeod 1999). Spiders are another important bio-control agent which depend on habitats such as those provided by field margins (Alderweireldt 1994, Haughton *et al.* 1999); large diverse populations are fostered by such habitats, and these can act as source populations for aerial immigrations into adjacent fields (Sunderland and Samu 2000). Similarly, the presence of old field margins in fields planted with *B. napus* were associated with increased mortality of the rape pollen beetle (*Meligethes aeneus*), which is an important economic pest of this species (Thies and Tscharntke 1999). Booij and Noorlander (1992) found that natural sources of pest control were reduced in conditions of low biodiversity. Connectivity may be important in population dispersal of both flora (Kleijn *et al.* 2001), and fauna (Mech and Hallett 2001), whilst proximity certainly will be; hedge intersections are already known to be 'hot-spots' for certain bird and carabid species (Lack 1988, Joyce 1997).

The value of field margins in increasing the biodiversity and spatial heterogeneity of agro-ecosystems, and providing source populations of natural enemies will depend on the relative size and complexity of these, and their proximity to and connectedness with similar habitats.

Field margin management systems that take into account both the margin and the hedgerow vegetation can therefore only have a positive effect on many species of flora and fauna found on agro-ecosystems. These are the areas on agro-ecosystems where conservation management is most valuable to the majority of species, and where it is least costly in economic terms (Wossink *et al.* 1999). Managing field margins in ways that are beneficial for wildlife is unlikely to increase weed invasion from the field edge into the crop (Smith *et al.* 1999), and therefore economic value of the crop is also maintained. The conservation benefits of introducing and maintaining field margins should be long lasting (Delapane and Mayer 2000), and presumably also self-perpetuating. Man-made habitats do offer suitable substitutes for degraded natural habitats if management is correctly implemented (Day 1991, Klemm 1996). If yields from lands under production are optimised through increased pollinator services as a result of the introduction of field margins, then there is less likelihood of land being taken back out of conservation schemes to increase yields at a later date (Delapane and Mayer 2000).

Management schemes pertaining to field margins will be directly involved with maintaining floral density and diversity. However, it is important that management of the surrounding cropped area is also taken into account if conservation benefits are to be maximised. Although modern generations of pesticides are more directly targeted to specific pest species than their predecessors, and application methods have been refined to limit toxicity to bees, these may still be having both direct and indirect effects on bumblebee populations. Many pesticide applications occur in the early morning or late evening, outside the period of *A. mellifera* activity, but *Bombus* spp. are still active at these times. High levels of bumblebee mortality may therefore go unrecorded. *Bombus* spp. colonies are much smaller than those of *A. mellifera,* and, as a result, any loss of workers will have a greater effect, especially in the early spring when colonies contain few workers (Thompson 2001). Although most of the industrialised world has now introduced measures to limit pollinator poisonings through pesticide application (Kevan 1998), such legislation is many years from being introduced in developing countries (Crane and Walker 1983). As well as direct mortality, sub-lethal effects of pesticide exposure are known to include a disruption in homing behaviour and decreased longevity (Thompson 2001), although Tasei *et al.* (2001) found no perceptible effect on *B. terrestris* homing behaviour when foragers were exposed to the systemic insecticide imidacloprid on *Helianthus annus*. These factors need to be taken into account when planning suitable management regimes for introduced field margins on agro-ecosystems.

8.3 Future directions

I believe that the future of conservation schemes on agro-ecosystems lies in firstly maintaining existing biodiversity and spatial heterogeneity, and then improving this. Extensive and traditional systems will be favoured, as these are more ecologically 'valuable' than intensive systems. Although various agri-environment schemes managing land in an environmentally conscious fashion now cover approximately 20% of farmland within the E.U. (E.U. 1998), not all of this has been properly targeted, and in those cases where land under environmental management has been compared with land which is not, little difference has been found in terms of biodiversity (Kleijn *et al.* 2001). Price-support legislation such as the Common Agricultural Policy (C.A.P.) is responsible for high levels of agricultural intensification across lowland areas of E.U. member countries (Pain and Pienkowski 1997), and it is important that those countries next in line for membership are not driven down the same road. In light of this, C.A.P. policy needs further revision than the 'Agenda 2000' package of amendments (Donald *et al.* 2001). Bumblebee species richness in Estonia has been found to be lower on agricultural land than on adjacent semi-natural vegetation, even though a similar abundance of wildflowers were found on the two habitat types (Mand *et al.* 2002), and species differences in the floral community between these two habitats are thought to be responsible. Estonian agriculture is much less intensive than western European systems, and the agricultural landscape is more of a mosaic. This illustrates that maintaining biodiversity on a within-field basis is as important as maintaining spatial heterogeneity on a landscape scale. The introduction of environmental cross compliance schemes (through Agenda 2000) whereby farmers are given support payments to manage their land in ways that protect and enhance the rural environment (Russell and Fraser 1995, Mitchell 1999) whilst potentially curbing over-production (Wossink *et al.* 1999), is a step in the right direction, but current legislation can only be used to achieve very basic goals (Mitchell 1999). Recent E.U. agreements with GATT partners (General Agreement on Trade and Tariffs) provide a political as well as ecological framework for improving the targeting of environmental support schemes for farmland (Bignal 1998).

There may be abiotic constraints to floral regeneration on intensively farmed land (Bakker and Berendse 1999). These include increased soil nitrogen content through nitrogen accumulation from inorganic sources, and atmospheric deposition of nitrogen (Berendse 1998, Bakker and Berendse 1999). Possible biotic constraints include impoverished seed banks and limited dispersal of 'good' species of flora and fauna from surrounding habitats (Zobel *et al.* 1998, Bakker and Berendse 1999). Those sites that have the greatest potential for regeneration to florally diverse habitats are those where agricultural intensification is recent (Bekker *et al.* 1997), as seed longevity of grassland species is low (Rice 1989, Thompson *et al.* 1997, Bekker *et al.* 1998). It is obvious then that great importance should be placed upon the maintenance of remaining areas of high floral diversity, and on identifying those areas where regeneration potential can be maximised.

The development and use of micro-satellites markers for *B. terrestris* and *B. pascuorum* is already revealing information about *Bombus* spp. not evident from behavioural studies. Work by Pirounakis *et al.* (1998) suggests that the Alps have acted as a barrier and caused intra-specific divergence in *B. pascuorum* populations north and south. *B. terrestris* populations did not display divergence, possibly because the queens of this species are larger and the Alps do not act as a barrier to flight in this species (Estoup *et al.* 1996). Application of the techniques used in these studies should be able to reveal how many nests contribute workers to forage patches, whether daughter queens return to the vicinity of the maternal nest following hibernation, and if populations are at risk from inbreeding depression. Conservation techniques can be refined in the light of such information.

Of course, genetic work is also currently being used to modify various forage resources of *Bombus* spp. There are several ways in which genetic modification could have an impact on pollination systems, but it is important to stress at this point that research is at an early stage, and little has been proven as yet. Proteins expressed through modification for an insecticidal toxin may prove to be directly toxic to bees if present in nectar or pollen (Picard-Nizou *et al.* 1997). Even if such proteins are not directly toxic, they may have a neurological or other behavioural effect following ingestion (Picard-Nizou *et al.* 1995). Experiments have shown that conditioned foraging responses in *A. mellifera* have been markedly affected following ingestion of several expressed proteins from genetically modified *B. napus* in sugar solution (Picard-Nizou *et al.* 1997). Such proteins may also cause disorientation, resulting in disruption of trap-lining and navigation systems. Alternatively, application of herbicides to crops which have had resistance conferred by modification may further impoverish the fauna of arable landscapes. Careful assessment needs to be made of the risks and benefits before genetically modified crops are introduced on anything other than an experimental scale.

People have attempted to quantify the monetary value of pollination services to the world economy (see references in Kearns *et al.* 1998), but when the figures talked about are estimated at $200 billion, this is meaningless except as an exercise in pedantics. It would be more worthwhile to concentrate efforts in this direction towards providing accurate figures for the differences in crop yields for each species, with and without adequate pollinator visits. Hard evidence that crop yields are reduced in the absence of bumblebees would surely assist in the attraction of finance for research into valid conservation schemes. At present there is a general lack of finance for such schemes; concentrating available resources on those which will benefit most species in an 'all-inclusive' approach should allow maximum conservation gains. It is clear that focussing grant aid on the development of an inter-linked network of naturally regenerated field margins, wildflower strips and other typical boundary features will benefit not only bumblebees, but many other species of flora and fauna associated with agro-ecosystems. However, good scientific research still needs to be carried out to ensure that appropriate management schemes are identified and implemented (Ovenden *et al.* 1998).

8.4 Concluding remarks

Although there is a general trend towards regression of *Bombus* spp. ranges across western Europe, there are some examples where species are actually expanding their ranges. Rasmont and Mersch (1988) found that of 31 Belgian species, 5 had increased their abundance since 1950. Also, of the 14 species that had decreased in abundance, one of these was increasing its range in Finland (Pekkarinen *et al.* 1981). The decreasing species were those that preferred open habitats and to forage on Fabaceae, whilst increasing species preferentially foraged on species from the Ericaceae, Asteraceae and Rosaceae, and were more often found in forest habitats. Suggested reasons for this pattern included climate change related to different heat tolerances of the species from fields or forests. Range contractions as a result of climatic change and the 'marginal mosaic model' of Williams (1988b) may partially explain bumblebee decline in some species, and in such cases conservation schemes are likely to make little difference to the survival of these in areas at the edge of their thermodynamic range. In such locations, species decline through gradual changes in resources and temperature, and subsequent thermoregulatory costs (Williams 1988b).

However, for many species of bumblebee (and other Apoidea) there has been a documented decline in both species density and diversity, attributable to alteration of the agricultural landscape (Williams 1982, Rasmont 1988, Westrich 1989, Corbet *et al.* 1991, Torchio 1991, Ortiz-Sánchez 1995, Rasmont 1995). Intensification, and the removal or disturbance of pollinator habitat, are together thought to be responsible for 64% of those cases where pollination of a crop species has been found to be inadequate (Richards 2001). The resilience of pollination webs (Kearns *et al.* 1998) to loss of constituent plants or pollinators will determine their survival in many cases. If we are to ensure survival of these constituent plants and pollinators, along with crop yields, and other associated flora and fauna, then we need to implement wellresearched and ecologically optimised conservation schemes on farmland. The conservation of bumblebee populations on agro-ecosystems is both necessary and desirable.

9. REFERENCES

Abrams, P. 1988. Resource productivity-consumer species diversity: simple models of competition in spatially heterogeneous environments. *Ecology* 69:1418-1433

Ackerman, J. D. 1986. Mechanisms and evolution of food-deceptive pollination systems in orchids. *Lindleyana* 1:108-113

Aebischer, N. 1991. Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. pp 305-331 in *The Ecology of Temperate Cereal Fields* (LG Firbank, N Cartar, JF Darbyshire, GR Potts, editors). Blackwell Science Publications, Oxford

Aebischer, N. J., and K. A. Blake. 1994. Field margins as habitats for game. pp 95-104 in *Field margins: Integrating Agriculture and Conservation. BCPC Monograph 58* (N. Boatman, editor). British Crop Protection Council, Farnham, Surrey

Alderweireldt, M. 1994. Habitat manipulations increasing spider densities in agroecosystems: possibilities for biocontrol? *Journal of Applied Entomology* 118:10-16

Alford, D. V. 1975. *Bumblebees*. Davis-Poynter, London

Allen-Wardell, G., P. Bernhardt, R. Bitner, A. Burquez, *et al.* 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology* 12:8-17

Andersson, S. 1990. No evidence for selective seed maturation in *Ancusa officinalis* (Boraginaceae). *Oikos* 57:88-93

Ayers, G. S. 1993. Return of information about sainfoin. *American Bee Journal* 133:257-259

Backmann, J.-P. C., and J. Tiainen. 2002. Habitat quality of field margins in a Finnish farmland are for bumblebees (Hymenoptera: *Bombus* and *Psithyrus*). *Agriculture Ecosystems and Environment*, in press

Baines, M., C. Hambler, P. J. Johnson, D. W. Macdonald, and H. Smith. 1998. The effects of arable field margin management on the abundance and species richness of the Araneae (spiders). *Ecography* 21:74-86

Baker, H. G., and I. Baker. 1979. Sugar ratios in nectars. *Phytochemical Bulletin* 12:43-45

Bakker, J. P., and F. Berendse. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* 14:63-68

Banaszak, J. 1983. Ecology of bees (*Apoidea*) of agricultural landscape. *Polish Ecological Studies* 9:421-505

Banaszak, J. 1984. Pattern of distribution of Apoidea in an agricultural landscape. pp 223-227 in *Vème Symposium International sur la Pollinisation, Versailles, 27-30 Sept. 1983*. Les Colloques de l'INRA 21. INRA Publishing

Banaszak, J. 1986. Impact of agricultural landscape structure on diversity and density of pollination in insects. *Les Colloques de l'INRA* 36:75-84

Banaszak, J. 1992. Strategy for conservation of wild bees in an agricultural landscape. *Agriculture Ecosystems and Environment* 40:179-192

Banaszak, J. 1996. Ecological bases of the conservation of wild bees. pp 55-62 in *The Conservation of Bees* (A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. WIlliams, editors). Academic Press, London

Banaszak, J. 1997. Local changes in the population of wild bees. I) Changes in the fauna 10 years later. *Ochrona Przrody* 54:119-130

Banaszak, J., and T. Cierzniak. 1994. The effect of neighbouring environments and the acreage of winter rapeseed plantation on the diversity and density of Apoidea (Hymenoptera). *Studia Przyrodnicze* 10:25-38

Banda, H. J., and R. J. Paxton. 1991. Pollination in greenhouse tomatoes by bees. *Acta Horticulturae* 288:194-198

Barbier, E. 1962. Quelques facteurs de la productivite quantitative et qualitative des essences chez les lavandes (*Lavandula tarin*). *Annals Abeille* 5:265-279

Barbier, E., and M. Nadir. 1976. Pollinisation du carthame (*Carthamus tinctorius*), ses effects sur la formation et la germination des semences. *Apidologie* 7:85-104

Barr, C. J., R. G. H. Bunce, R. T. Clarke, R. M. Fuller, M. T. Furse, M. K. Gillespie, G.B.Groom, C. J. Hallam, M. Hornung, D. C. Howard, and M. J. Ness. 1993. *Countryside Survey 1990 Main Report*. HMSO, London

Barrett, S. C. H. 1990. The evolution and adaptive significance of heterostyly. *Trends in Ecology and Evolution* 5:144-149

Batra, S. W. T. 1993. Male-fertile potato flowers are selectively buzz-pollinated only by *Bombus terricola* Kirby in upstate New York. *Journal of the Kansas Entomological Society* 66:252-254

Batra, S. W. T. 1995. Bees and pollination in our changing environment. *Apidologie* 26:361-370

Bawa, K. S. 1990. Evolution of dioecy in flowering plants. *Annual Review of Ecology and Systematics* 11:15-39

Bekker, R. M., G. L. Verweij, R. E. N. Smith, R. Reine, T. P. Bakker, and S. Schneider. 1997. Soil seed banks in European grasslands: does land use affect regeneration perspectives? *Journal of Applied Ecology 34*:1293-1310

Bekker, R.M., J.H.J. Schaminee, J.P. Bakker, and K. Thompson. 1998. Seed bank characteristics of Dutch plant communities. *Acta Botanica Neerlandica* 47: 15-26

Bell, J. R., S. Gates, A. J. Haughton, D. W. Macdonald, H. Smith, C. P. Wheater, and W. R. Cullen. 1999. Pseudoscorpions in field margins: Effects of margin age, management and boundary habitats. *Journal of Arachnology* 27:236-240

Berendse, F. 1998. Organic matter accumulation and nitrogen mineralisation during secondary succession in heathland ecosystems. *Journal of Ecology* 78:413-427

Berezin, M. V., V. B. Beiko, and N. V. Berezina. 1995. Bumblebees of the Moscow region. *Entomologist's Monthly Magazine* 131:259-268

Bernadello, L., I. Rodriguez, L. Stiefkens, and L. Galetto. 1995. The hybrid nature of *Lycium ciliatum* x *cestroides* (Solanaceae): Experimental, anatomical and cytological evidence. *Canadian Journal of Botany* 73:1995-2005

Bignal, E.M. 1998. Using an ecological understanding of farmland to reconcile nature conservation requirements, EU agriculture policy and world trade agreements. *Journal of Applied Ecology* 35: 949-954

Bjorkman, T. 1995. The effectiveness of heterostyly in preventing illegitimate pollination in dish-shaped flowers. *Sexual Plant Reproduction* 8:143-146

Boatman, N. D. 1998. The value of buffer zones for the conservation of biodiversity. pp 939-950 in *Proceedings of the 1998 Brighton Crop Protection Conference - Pests and Diseases.* British Crop Protection Council, Farnham, Surrey

Boatman, N. D., and N. W. Sotherton. 1998. The agronomic consequences and costs of managing field margins for game and wildlife conservation. *Aspects of Applied Biology* 17:47-55

Bogoyavlenskii, S. G. 1955. Bees and sainfoin. *Pchelovodstvo Mosk* 32:10-14

Bogoyavlenskii, S. G. 1974. The multiplicity of visits to sainfoin by honey bees and its importance for the yields of seeds. pp 121-127 in *Proceedings of the 3rd International Symposium on Pollination.* Les Colloques de l'INRA 19. INRA Publishing

Bogoyavlenskii, S. G., S. A. Rosov, and A. K. Tereshchenko. 1976. *Espartset i opylenie ego pchelani (Pollination of sainfoin by bees).* Naucho-Issledovatel'skii Institut Pchelovodstva, Ryazan, USSR

Bohart, G. E., and G. F. Knowlton. 1952. Yearly population fluctuation of *Bombus morrisoni* at Freedonia, Arizona. *Journal of Economic Entomology* 45:890-891

Booij, C. J. H., and J. Noorlander. 1992. Farming systems and insect predators. *Agriculture Ecosystems and Environment* 40:125-135

Bosca, I., and S. Hejja. 1963. Data on fertilisation in sainfoin (*Onobrychis viciifolia* Scop.). *Novenytermeles* 12:137-142

Bowers, M. A. 1985. Bumblebee colonisation, extinction and reproduction in subalpine meadows in north-eastern Utah. *Ecology* 66:914-927

Boyden, T. C. 1982. The pollination bid of *Calypso bulbosa* var. *americana* (Orchidaceae): initial deception of bumblebee visitors. *Oecologia* 55:178-184

Bradshaw, H. D., S. M. Wilbert, K. G. Otto, and D. W. Schemske. 1995. Genetic mapping of floral traits associated with reproductive isolation in monkeyflowers (*Mimulus*). *Nature* 376:762-765

Brian, A. D. 1957. Differences in the flowers visited by 4 species of bumblebees, and their causes. *Journal of Animal Ecology* 26:71-98

Buchmann, S. L. 1983. Buzz pollination in angiosperms. in *Handbook of Experimental Pollination Biology* (C. E. Jones and R. J. Little, editors). Scientific and Academic Additions, New York

Buchmann, S. L., and G. P. Nabhan. 1996. *The Forgotten Pollinators.* Island, Washington D.C.

Carlson, J. B., and N.R. Lersten. 1987. Reproductive morphology. pp95-134 in *Soybeans: Improvement, Production, and Uses*; Second Edition (J. R. Wilcox, editor). American Society of Agronomy. Madison, Wisconsin

Carreck, N. L., and I. H. Williams. 1998. The economic value of bees in the U.K. *Bee World* 79: 115-123

Carreck, N. L., and I. H. Williams. 1999. Enhancing farmland for insect pollinators using flower mixtures. pp 101-108 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103:33-49

Casper, B. B. 1988. Evidence for selective embryo abortion in *Cryptantha flava*. *American Naturalist* 132:318-326

Chalmers, A., C. Kershaw, and P. Leach. 1990. Fertiliser use on farm crops in Great Britain: results from the survey of fertilising practice 1969-1988. *Outlook on Agriculture* 19:269-278

Chapman, J., and J. Sheail. 1994. Field margins - An historical perspective. pp 3-12 in *Field margins: Integrating agriculture and conservation: BCPC Monograph 58* (N. Boatman, editor). British Crop Protection Council, Farnham, Surrey

Chittka, L. 1998. Sensori-motor learning in bumblebees: Long term retention and reversal training. *Journal of Experimental Biology* 201:515-524

Chittka, L., and J. D. Thomson. 1997. Sensori-motor learning and its relevance for task specialization in bumble bees. *Behavioural Ecology and Sociobiology* 41:385-398

Chittka, L., and A. Dornhaus. 1999. Comparisons in physiology and evolutions, and why bees can do the things they do. *http://www.ciencia.cl/CienciaAlDia/volumen2/numero2/articulos/articulo5.html*

Chittka, L., J. D. Thomson, and N. M. Waser. 1999. Flower constancy, insect physiology, and plant evolution. *Naturwissenscahten* 86:361-377

Chiverton, P. A. 1999. Buffer zones of different floral composition - effects on the beneficial arthropod fauna. pp 307-314 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Chiverton, P. A., and N. W. Sotherton. 1991. The effects on beneficial arthropods of exclusion of herbicides from cereal crop edges. *Journal of Applied Ecology* 28:1027-1039

Colbert, S., and D. de Oliveira. 1990. Influence of pollen variety on raspberry (*Rubus idaeus* L.) development. *Journal of Heredity* 81:434-437

Colin, M. E., and L. P. Belzunces. 1993. Impact of the synergism of pesticides on bees: Biological effect of a combination of an insecticide with a fungicide. pp 167-170 in *Bees for pollination. Proceedings of an EC workshop. Brussels, 2-3 March 1992* (E. Bruneau, editor). Commission for the European Communities, Brussels

Colwell, R. K., and D.J. Futuyma. 1971. On the measurement of niche breadth and overlap. *Ecology* **52**: 567-576

Connell, J. H. 1980. Diversity and the co-evolution of competitors, or the ghost of competition past. *Oikos* **35**:131-138

Connell, J. H., and R. O. Slayter. 1977. Mechanisms of succession in natural communities and their in-community stability and organization. *The American Naturalist* **111**:1119-1144

Corbet, S. A. 1987. More bees make better crops. *New Scientist* 23rd July: 40-43

Corbet, S. A. 1992a. Bumblebees and their flowers. *Bee World* **73**:213-215

Corbet, S. A. 1992b. Wild bees for pollination in the agricultural landscape. pp 175-188 in *Bees for pollination. Proceedings of an EC workshop. Brussels, 2-3 March 1992* (E. Bruneau, editor). Commission for the European Communities, Brussels

Corbet, S. A. 1995. Insects, Plants and Succession - Advantages of Long-Term Set- Aside. *Agriculture Ecosystems and Environment* **53**:201-217

Corbet, S. A. 1996. Why bumblebees are special. pp 2-11 in *Bumblebees for Pleasure and Profit* (A. Matheson, editor). IBRA, Cardiff

Corbet, S. A. 2000. Conserving compartments in pollination webs. *Conservation Biology* **14**:1229-1231

Corbet, S. A., I. Cuthill, M. Fallows, T. Harrison, and G. Hartley. 1981. Why do nectar-foraging bees and wasps work upwards on inflorescences? *Oecologia* **51**:79-83

Corbet, S. A., I. H. Williams, and J. L. Osborne. 1991. Bees and the pollination of crops and wild flowers in the European Community. *Bee World* **72**:47-59

Corbet, S. A., M. Fussell, R. Ake, A. Fraser, C.Gunson, A. Savage, and K. Smith. 1993. Temperature and the pollinating activity of social bees. *Ecological Entomology* **18**:17-30

Corbet, S. A., N. M. Saville, O. E. Prys-Jones, and D. M. Unwin. 1995. The competition box: a graphical aid to forecasting pollinator performance. *Journal of Applied Ecology* **32**:707-719

Crane, E., and P. Walker. 1983. *The Impact of Pest Management on Bees and Pollination.* International Bee Research Association, Tropical Development and Research Institute, London

Crane, E., and P. Walker. 1984. *Pollination Directory for World Crops.* International Bee Research Association, London

Crane, P. R. 1986. p179 in *Pollen and Spores: Symposium Series 12.* Academic Press, London

Crawley, M.J. 1991. *GLIM for Ecologists.* Blackwell, Oxford

Cresswell, J. E., and A. W. Robertson. 1994. Discrimination by pollen-collecting bumblebees among differentially rewarding flowers of an alpine wildflower, *Campanula rotundifolia* (Campanulaceae). *Oikos* **69**:304-308

Cresswell, J. E., A. P. Bassom, S. A. Bell, S. J. Collins, and T. B. Kelly. 1995. Predicted pollen dispersal by honeybees and 3 species of bumblebees foraging on oilseed rape: a comparison of 3 models. *Functional Ecology* **9**:829-841

Cresswell, J. E., J. Osborne, and D. Goulson. 2000. An economic model of the limits to foraging range in central place foragers with numerical solutions for bumblebees. *Ecological Entomology* 25:249-255

Critchley, C. N. R. 1996a. Monitoring as a feedback mechanism for the conservation management of arable plant communities. pp 239-244 in *Aspects of Applied Biology 44. Vegetation management in forestry: amenity and conservation areas.* Association of Applied Biologists, Warwick

Critchley, C. N. R. 1996b. *Vegetation of Arable Field Margins in Breckland.* PhD thesis. University of East Anglia, Norwich

Critchley, C. N. R., J. A. Fowbert, I. A. Diack, and A. J. Sherwood. 1999. Cultivation regimes to conserve annual plant communities in uncropped arable field boundary strips. pp139-146 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Crozier, R. H., and P. Pamilo. 1996. *Evolution of Social Insect Colonies.* Oxford University Press, Oxford.

Cumber, R. A. 1953. Some aspects of the biology and ecology of humble-bees bearing upon the yields of red clover seed in New Zealand. *New Zealand Journal of Science and Technology* B 34:227-240

Cutherbertson, P. S., and P. J. Jepson. 1988. Reducing pesticide drift into the hedgerow by inclusion of an unsprayed field margin. pp 747-751 in *Proceedings of the 1988 Brighton Crop Protection Conference - Pests and Diseases.* British Crop Protection Council, Farnham, Surrey

Dafni, A. 1983. Pollination of *Orchis caspia* - a nectarless plant species which deceives the pollinators of nectariferous species from other plant families. *Journal of Ecology* 71:467-474

Dafni, A. 1984. Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15:259-278

Dafni, A. 1992. *Pollination Ecology; a practical approach.* Oxford University Press, Oxford

Dag, A., and Y. Kammer. 2001. Comparison between the effectiveness of honey bee (*Apis mellifera*) and bumble bee (*Bombus terrestris*) as pollinators of greenhouse sweet pepper (*Capsicum annuum*). *American Bee Journal* 141:447-448

Darwin, C. 1859. *The Origin of Species: Washington Square Press Edition (1963) edition.* Washington Square Press, Washington

Darwin, C. 1876. *The effects of cross and self fertilisation in the vegetable kingdom.* Murray, London

Day, H. D., and K. C. Day. 1997. Directional preferences in the rotational play behaviours of young children. *Developmental Psychobiology* 30:213-223

Day, M. C. 1991. *Towards the conservation of aculeate Hymenoptera in Europe.* Council of Europe Press, Strasbourg

de Snoo, G. 1995. *Unsprayed field margins: implications for environment, biodiversity, and agricultural practice. The Dutch field margin project in the Haarlemmermeerpolder.* PhD thesis. Leiden University, Wageningen de Snoo, G. R., and K. Chaney. 1999. Unsprayed field margins - What are we trying to achieve? pp1-12 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

de Snoo, G. R., and P. J. de Wit. 1998. Buffer zones for reducing pesticide drift to ditches and risks to aquatic organisms. *Ecotoxicology and Environmental Safety* 41:112-118

Delapane, K. S., and D. F. Mayer. 2000. *Crop Pollination by Bees.* CABI Publishing, Wallingford, U.K.

Den Boer, P. J. 1980. Exclusion or coexistence and the taxonomic or ecological relationship between species. *Netherlands Journal of Zoology* 30:278-306

Den Boer, P. J. 1986. The Present Status of the Competitive Exclusion Principle. *Trends in Ecology and Evolution* 1:25-28

Dennis, P. D., and G. L. A. Fry. 1992. Field-margins: Can they enhance natural enemy population densities and general arthropod diversity on farmland? *Agriculture Ecosystems and Environment* 40:95-115

Dillman, A. C. 1938. Natural crossing in flax. *Journal of the American Society of Agronomy* 30:279-286

Donald, P. F., R. E. Green, and M. F. Heath. 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London* Series B-Biological Sciences 268:25-29

Donovan, B. J. 1990. Selection and importation of new pollinators to New Zealand. *New Zealand Entomologist* 13:26-32

Donovan, B. J., and S. S. Wier. 1978. Development of hives for field population increase, and studies on the life-cycles of the four species of introduced bumblebees in New Zealand. *New Zealand Journal of Agricultural Research* 21:733-756

Doualt, P. 1981. Influence of the microclimate on the survival and activity of domestic bees used for crop pollination in plastic structures. *Plasticulture* 49:32-36

Dover, J. 1992. The conservation of insects on arable farmland. pp 294-318 in *The Conservation of Insects and their Habitats* (J. Thomas and N.W. Collins, editors). Academic Press, London

Doyle, C. J., D. J. Thompson, and J. E. Sheehy. 1984. The future of sainfoin in British agriculture: an economic assessment. *Grass and Forage Science* 39:43-51

Dramstad, W. E. 1996. Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behaviour* 9:163-182

Dramstad, W. E., and G. Fry. 1995. Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture Ecosystems and Environment* 53:123-135

Duchateau, M. J. 1991. Regulation of colony development of the bumblebee. *Netherlands Acta Horticulturae* 288:139-143

Duchateau, M. J., and H. H. W. Velthuis. 1988. Development and reproductive strategies in *Bombus terrestris* colonies. *Behaviour* 107, 186-207

Duchateau, M. J., and H. H. W. Velthuis. 1992. How to make a good tomato pollinator from a common earth-bumblebee: solved and unsolved problems in bumblebee biology in relation to the use of bumblebees in agriculture. pp 113-119 in *Bees for pollination. Proceedings of an EC workshop. Brussels, 2-3 March 1992* (E. Bruneau, editor). Commission for the European Communities, Brussels

Dukas, R., and L. Edelstein-Keshet. 1998. The spatial distribution of colonial food provisioners. *Journal of Theoretical Biology* 190:121-134

E.U. 1998. *Working Document 'State of Application of Regulation (EEC) no. 2078/92. Evaluation of Agri-Environment Programmes', VI/7655/98, 9.11.1998.* http://europa.eu.int/comm/agriculture/envir/programs/evalrep/text_en.pdf.

Edwards, M. 1998. *UK Biodiversity Action Plan Working Group Report.*

Egler, F. 1954. Vegetation science concepts I. Initial floristic composition - a factor in old-field vegetation development. *Vegetation* 4:412-417

Eisikowitch, D. 1981. Some aspects of pollination of oil-seed rape (*Brassica napus* L.). *Journal of Agricultural Science* 96:321-326

Ellenberg, H. 1988. *Vegetation Ecology of Central Europe*, 4th edition. Cambridge University Press, Cambridge

Erickson, E. H. 1975. Effect of honeybees on yield of three soybean cultivars. *Crop Science* 15:84-86

Erickson, E. H., G. A. Berger, J. G. Shannon, and J. M. Robins. 1978. Honeybee pollination increases soybean yields in the Mississippi Delta region of Arkansas and Missouri. *Journal of Economic Entomology* 71:601-603

Estes, J. R., B. B. Amos, and J. R. Sullivan. 1983. Pollination from two perspectives; the Agricultural and Biological Sciences. pp 536-554 in *Pollination Perspectives: Agricultural and Biological Sciences. Volume 8: Applied Population Ecology*, Springer, New York

Estoup, A., M. Solignac, J.-M. Cornuet, J. Goudet, and A. Scholl. 1996. Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Molecular Ecology* 5:19-31

Faegri, K., and L. van der Pijl. 1979. *The principles of pollination ecology*, 3rd edition. Pergamon, Oxford

Fearn, G. M. 1987. Sainfoin. *Biologist* 34:93-97

Feber, R. E., H. Smith, and D. W. MacDonald. 1996. The effect on butterfly abundance of the management of uncropped edges of arable fields. *Journal of Applied Ecology* 33:1191-1205

Fielder, A. G. 1987. Management options for field margins - an Agricultural Advisor's view. pp 85-94 in *Field margins* (P. W. Greig-Smith and J.M. Way, editors). British Crop Protection Council, Farnham, Surrey

Firbank, L. G., N. Cartar, J. F. Derbyshire, and G. R. Potts (editors). 1991. *The Ecology of Temperate Cereal Fields.* Blackwell, Oxford

Fisher, R. M. 1984. Dominance by a bumble bee social parasite (*Psithyrus citrinus*) over workers of its host (*Bombus impatiens*). *Animal Behaviour* 32:304-305

Fisher, R.M. 1987. Queen-worker conflict and social parasitism in bumble bees (Hymenoptera: Apidae). *Animal Behaviour* 35: 1026-1036

Fisher, R. M., and B. J. Sampson. 1992. Morphological specializations of the bumble bee social parasite *Psithyrus ashtoni* (Cresson) (Hymenoptera, Apidae). *Canadian Entomologist* 124:69-77

Fomina, K. Y. 1961. Effect pf shelter belts on nectar production and seed yield of sainfoin and sunflower. *Dokl TSKHA* 62:531-536

Ford, M. A. 1996. The transformation of surplus farmland into semi-natural habitat. I. Effect of seed supply on the conservation value of Scottish set-aside exemplified by the vegetation at a site near Elgin. *Aspects of Applied Biology* 44:179-184

Frankel, R., and E. Galun (editors). 1977. *Pollination mechanisms, reproduction and plant breeding.* Springer-Verlag, Berlin

Free, J. B. 1993. *Insect Pollination of Crops.* Academic Press, London

Free, J. B., and C. G. Butler. 1959. *Bumblebees.* Collins, London

Free, J. B., and A. W. Ferguson. 1983. Foraging behaviour of honeybees on oilseed rape. *Bee World* 64:22-24

Fry, G., and A. R. Main. 1993. Restoring seemingly natural communities on agricultural land. pp 225-241 in *Reconstruction of Fragmented Ecosystems: local and global perspectives* (D. A. Saunders, R. J. Hobbs, and P. R. Erlich, editors). Surrey Beatty, Chipping Norton

Fry, G. L. A. 1991. Conservation in Agricultural Ecosystems. pp 415-443 in *The Scientific Management of Temperate Communities for Conservation. 31st Symposium for BES, Southampton, 1989* (I. Spellerberg, F. Goldsmith, and M. Morris, editors). Blackwell Scientific Publications, Oxford

Fuller, R. J., D. E. Chamberlain, N. H. K. Burton, and S. J. Gough. 2001. Distributions of birds in lowland agricultural landscapes of England and Wales: How distinctive are bird communities of hedgerows and woodland? *Agriculture Ecosystems and Environment* 84:79-92

Fuller, R. J., R. D. Gregory, D. W. Gibbons, J. H. Marchant, J. D. Wilson, S. R. Baillie, and N. Cartar. 1995. Population declines and range contractions among lowland farm birds in Britain. *Conservation Biology* 96:1425-1441

Fussell, M., and S. A. Corbet. 1991. Forage for Bumble Bees and Honey-Bees in Farmland - a Case-Study. *Journal of Apicultural Research* 30:87-97

Fussell, M., and S. A. Corbet. 1992a. Flower usage by bumblebees: A basis for forage plant management. *Journal of Applied Ecology* 29:451-465

Fussell, M., and S. A. Corbet. 1992b. The nesting places of some British bumblebees. *Journal of Apicultural Research* 31:32-41

Fussell, M., and S. A. Corbet. 1992c. Observations on the pollinating behaviour of male bumblebees (Hymenoptera). *Entomologist's Monthly Magazine* 128:229-235

Galen, C. 1989. Measuring pollinator-mediated selection on morphometric floral traits - bumblebees and the alpine sky pilot *Polemonium viscosum. Evolution* 43:882-890

Galen, C. 1996. Rates of floral evolution - adaptation to bumblebee pollination in an alpine wildflower, *Polemonium viscosum. Evolution* 50:120-125

Ganskopp, D. 1995. Free-ranging Angora goats - left-handed or right-handed tendencies while grazing. *Applied Animal Behaviour Science* 43:141-146

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: processes of species extinction. pp 19-34 in *The Science of Scarcity and Diversity* (M. E. Soule, editor). Sunderland Associates, Sunderland, M.A

Giurfa, M., and J. A. Nuñez. 1993. Efficient floret inspection by honeybees in capitula of *Carduus acanthoides. Ecological Entomology* 18:116-122

Giurfa, M., J. A. Núñez, L. Chittka, and R. Menzel. 1995. Colour preferences of flower-naive honeybees. *Journal of Comparative Physiology* A 177:247-259

Gordon, C. E. 2000. The coexistence of species. *Revista Chilena de Historia Natural* 73:175-198

Goulson, D. 1999a. Are insects flower constant because they use search images to find flowers? *Oikos* 88:547-552

Goulson, D. 1999b. Foraging strategies for gathering nectar and pollen in insects. *Perspectives in Plant Ecology, Evolution and Systematics* 2:185-209

Goulson, D., S. A. Hawson, and J. C. Stout. 1998. Foraging bumblebees avoid flowers already visited by conspecifics or by other bumblebee species. *Animal Behaviour* 55:199-206

Goulson, D., and K. Jerrim. 1997. Maintenance of the species boundary between *Silene dioeca* and *S. latifolia* (red and white campion). *Oikos* 79:115-126

Grant, V. 1949. Pollination systems as isolating mechanisms in angiosperms. *Evolution* 3:82-97

Grant, V. 1994a. Mechanical and ethological isolation between *Pedicularis groenlandica* and *P. attollens* (Scrophulariaceae). *Biologicisches Zentralblatt* 113:43-51

Grant, V. 1994b. Modes and origins of mechanical and ethological isolation in angiosperms. *Proceedings of the National Academy of Sciences of the USA* 91:3-10

Greaves, M. P., and E. J. P. Marshall. 1987. Field margins: definitions and statistics. pp 3-9 in *Field Margins: BCPC Monograph 35* (J. M. Way and P. W. Greig-Smith, editors). British Crop Protection Council, Thornton Heath

Gubin, A. F. 1945. Cross-pollination of flax. *Bee World* 26:30-31

Guerrant, E. O. 1992. Genetic and demographic considerations in the sampling and re-introduction of rare plants. pp 321-344 in *Conservation Biology: The Theory and Practise of Nature Conservation, Preservation and Management* (P. L. Fielder and S. K. Jain, editors). Chapman and Hall, New York

Haeck, J., and R. Hengeveld. 1981. Changes in the occurrences of species of the Dutch flora in relation to their geographical range. *Biological Conservation* 19:189-197

Hanna, M. R., D. H. Cooke, S. Smoliak, B. P. Goplen, and D. B. Wilson. 1977. *Sainfoin for western Canada.* Agricultural Canadian Publications Volume 1470. Agricultural Canadian Publications, Ottawa

Haragsimova-Neprasova, L. 1960. Zjistovani nektarodarnosti rostlin. *Ved Pr vyzk, Ust vcelar. CSAZV* 2:63-79

Harder, L. D. 1986. Influences on the density and dispersion of bumble bee nests (Hymenoptera, Apidae). *Holarctic Ecology* 9:99-103

Harder, L. D., and R. M. R. Barclay. 1994. The functional significance of poricidal anthers and buzz pollination - controlled pollen removal from dodecathon. *Functional Ecology* 8:509-517

Hartshorn, G. H. 1978. Tree falls and tropical forest dynamics. pp 617-638 in *Tropical Trees as Living Systems* (P. B. Tomlinson and M. H. Zimmerman, editors). Cambridge University Press, Cambridge

Hasselrot, T. B. 1960. Studies on Swedish bumblebees (genus *Bombus* Latr.): their domestication and biology. *Opuscula Entomologica Supplementum* 17:1-192

Haughton, A. J., J. R. Bell, N. D. Boatman, and A. Wilcox. 1999. The effects of different rates of the herbicide glyphosate on spiders in arable field margins. *Journal of Arachnology* 27:249-254

Hawthorne, A., and M. Hassall. 1994. Effects of management techniques on carabid communities of cereal field margins. in *Field Margins: Integrating Agriculture and Conservation* (N. Boatman, editor). British Crop Protection Council, Farnham, Surrey.

Hedtke, C. 1996. Heimfinden von *Apis mellifera* und 4 *Bombus*-Arten im Vergleich. *Apidologie* 27:320-323

Heinrich, B. 1976a. The foraging specialisations of individual bumblebees. *Ecological Monographs*:105-128

Heinrich, B. 1976b. Resource partitioning among some eusocial insects: bumblebees. *Ecology* 57:874-889

Heinrich, B. 1979. 'Majoring' and 'minoring' by foraging bumblebees, *Bombus vagans*: An experimental analysis. *Ecology* 60:245-255

Heinrich, B., and P. Raven. 1972. Energetics and pollination ecology. *Science* 176:597-602

Herrera, C. M. 1990. Daily patterns of pollinator activity, differential pollinating effectiveness and floral resource availability in a summer flowering Meditteranean shrub. *Oikos* 58:277-288

Heslop-Harrison, J., Y. Heslop-Harrison, and J. Barber. 1975. The stigma surface in incompatibility responses. *Proceedings of the Royal Society of London* B 188:287-297

Heywood, V. H. (editor). 1993. *Flowering plants of the world.* Oxford University Press, New York

Hinsley, S. A., and P. E. Bellamy. 2000. The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *Journal of Environmental Management* 60:33-49

Hippa, H., S. Koponen, and O. Osmonen. 1981. Diurnal activity of flower visitors to the cloudberry (*Rubus chamaemorus* L.). *Report of the Kevo Subarctic Research Station* 17:55-57

Hobbs, G. A., W. O. Nummi, and J. F. Virostek. 1962. Managing colonies of bumble bees (Hymenoptera: Apidae) for pollination purposes. *Canadian Entomologist* 94:1121-1132

Hogenboom, N. G. 1975. Incompatibility and incongruity: two different mechanisms for the non-functioning of intimate partner relationships. *Proceedings of the Royal Society of London* B **188**:361-375

Holm, S. N. 1966. The utilisation and management of bumblebees for red clover and alfalfa seed production. *Annual Review of Entomology* **11**:155-182

Houston, T. F., B. B. Lamont, S. Radford, and S. G. Errington. 1993. Apparent mutualism between *Verticordia nitens* and *V. aurea* (Myrtaceae) and their oil-ingesting bee pollinators (Hymenoptera, Colletidae). *Australian Journal of Botany* **41**:369-380

Huston, M. A., and D. L. Deangelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist* **144**:954-977

Hymonwitz, T. 1990. Grain legumes. pp 154-158 in *Advances in New Crops* (J. Janick and J. E. Simon, editors). Timber Press, Portland, Oregon

Inouye, D. W. 1977. Species structure of bumblebee communities in North American and Europe. pp 35-40 in *The role of arthropods in forest ecosystems* (W. I. Mattson, editor). Springer, New York

Inouye, D. W. 1978. Response partitioning in bumblebees. Experimental studies in foraging behaviour. *Ecology* **59**:672-678

Jennersten, O., J. Loman, A. P. Moellar, J. Robertson, and B. Widen. 1992. Conservation Biology in agricultural habitat islands. pp 394-424 in *Ecological Principles of Nature Conservation* (L. Hansson, editor). Elsevier Applied Science, London

Jobin, B., L. Choiniere, and L. Belanger. 2001. Bird use of three types of field margins in relation to intensive agriculture in Quebec, Canada. *Agriculture Ecosystems and Environment* **84**:131-143

Johnson, S. D. 1994. Evidence for Batesian mimicry in a butterfly-pollinated orchid. *Biological Journal of the Linnean Society* **53**:91-104

Johnson, S. D. 2000. Batesian mimicry in the non-rewarding orchid *Disa pulchra*, and its consequences for pollinator behaviour. *Biological Journal of the Linnean Society* **71**:119-132

Johnson, S. D., and L. A. Nilsson. 1999. Pollen carryover, geitonogamy, and the evolution of deceptive pollination systems in orchids. *Ecology* **80**:2607-2619

Joron, M., and J. L. B. Mallet. 1998. Diversity in mimicry: paradox or paradigm. *Trends in Ecology and Evolution* **13**:461-466

Joyce, K. 1997. *The role of hedgerows in the ecology of invertebrates in arable landscapes*. PhD Thesis. University of Southampton, Southampton

Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics* **29**:83-112

Kells, A. R., J. M. Holland, and D. Goulson. 2001. The value of uncropped field margins for foraging bumblebees (*Bombus* spp.). *Journal of Insect Conservation* **5**:283-291

Kevan, P. G. 1998. Pollinators in agroecosystems: their keystone role in sustainable productivity and bioindication. in *Biodiversity in Agroecosystems Role of Sustainability and Bioindication* (M. G. Paoletti, editor). Elsevier, New York

Kevan, P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture, Ecosystems and Environment* 74: 373-393

Kevan, P. G., and H. G. Baker. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28:407-453

Kevan, P.G., Laverty, T.M., and Denmark, H.A. (1990). Association of *Varroa jaobsonii* with organisms other than honeybees and implications for its dispersal. *Bee World* 81, 119-121

King, M. J. 1993. Buzz foraging mechanism of bumblebees. *Journal of Apicultural Research* 32:41-49

King, M. J., and S. L. Buchmann. 1995. Bumblebee initiated vibration release mechanism of Rhododendron pollen. *American Journal of Botany* 82:1407-1411

King, M. J., and A. M. Ferguson. 1994. Vibratory pollen collection of *Actinidia deliciosa* (kiwifruit) pollen. *Annals of Botany* 74:479-482

King, M. J., and L. Lengoc. 1993. Vibratory pollen collection dynamics. *Transactions of the Asae* 36:135-140

Kiss, J., K. Penksza, F. T. Toth, and F. Kadar. 1997. Evaluation of fields and field margins in nature protection capacity with special regard to plant protection. *Agriculture Ecosystems and Environment* 63:227-232

Kleijn, D., F. Berendse, R. Smit, and N. Gilissen. 2001. Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413:723-725

Klemm, M. 1996. Man-made bee habitats in the anthropogenous landscape of central Europe - substitutes for threatened or destroyed riverine habitats? in *The Conservation of Bees* (A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors). Academic Press, New York

Klinkhamer, P. G. L., and T. J. de Jong. 1993. Attractiveness to pollinators - a plants' dilemma. *Oikos* 66:180-184

Knight, T. A. 1799. An account of some experiments on the fecundation of vegetables. *Philosophical Transactions of the Royal Society of London* 1:195-204

Kollmann, J., and S. Bassin. 2001. Effects of management on seed predation in wildflower strips in northern Switzerland. *Agriculture Ecosystems and Environment* 83:285-296

Kosior, A. 1995. Changes in the fauna of bumblebees (*Bombus* Latr.) and cuckoobees (*Psithyrus* Lep.) of selected regions in southern Poland. pp 103-111 in *Changes in Fauna of Wild Bees in Europe* (J. Banaszak, editor). Pedagogical University, Bydgoszcz

Koulianos, S., and P. Schmid-Hempel. 2000. Phylogenetic relationships among bumble bees (*Bombus*, Latreille) inferred from mitochondrial cytochrome b and cytochrome oxidase I sequences. *Molecular Phylogenetics and Evolution* 14:335-341

Krause, U. 1997. Populationsdynamik und Uberwinterung von Schwebfliegen (Diptera, Syrphidae) in zwei underschiedlich strukturierten Agrarlandschaften Nord-deutschalnds. *Agrarokologie* 22:1-150

Kropacova, S., and H. Haslbachova. 1969. Study of the honey bee foraging on sainfoin plants (*Onobrychis viciaefolia*, Thell). pp 476-477 in *Proceedings of the 22nd International Apicultural Congress, Munich.* IBRA, Cardiff

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss and biological control. *Science* 264:1581-1584

Kullenberg, B., G. Bergstrom, B. Bringer, B. Carlberg, and B. Cederberg. 1973. Observations on scent marking by *Bombus* (Latr.) and *Psithyrus* (Lep.) males (Hymenoptera: Apidae) and localisation of site of production of the secretion. *Zoon. Suppl.* 1:23-30

Kupper, G., and K. H. Schwammberger. 1995. Social parasitism in Bumble Bees (Hymenoptera, Apidae) - Observations of *Psithyrus sylvestris* in *Bombus pratorum* nests. *Apidologie* 26:245-254

Kwak, M., C. van den Brand, P. Kramer, and E. Boerrigter. 1991. Visitation, flight distances and seed set in the rare species *Phyteuma nigra* (Campanulaceae). *Acta Horticulturae* 288:303-307

Kwak, M. M., and I. Tieleman. 1994. *Het Hommelleven.* Jeugdbondsuitgeverij en strichting Uitgeverij KNNV, Utrecht, Netherlands

Lack, A. J. 1982. The ecology of flowers of chalk grassland and their insect pollinators. *Journal of Ecology* 70:773-790

Lack, P. C. 1988. *Farmland habitat features for birds. BTO Research Report 29.* BTO, Cambridge

Lagerlof, J., J. Stark, and B. Svensson. 1992. Margins of agricultural fields as habitats for pollinating insects. *Agriculture Ecosystems and Environment* 40:117-124

Lagerlof, J., and H. Wallin. 1993. The abundance of arthropods along two field margins with different types of vegetation composition: an experimental study. *Agriculture Ecosystems and Environment* 43:141-154

Langridge, D. F., and R. D. Goodman. 1974. A study on pollination of sunflowers (*Helianthus annuus*). *Australian Journal of Experimental Agriculture and Animal Husbandry* 14:201-204

Laverty, T. M. 1980. Bumble bee foraging: Floral complexity and learning. *Canadian Journal of Zoology* 58:1324-1335

Laverty, T. M. 1994. Bumblebee learning and flower morphology. *Animal Behaviour* 47:531-545

Levin, D. A. 1978. Pollinator behaviour and the breeding structure of plant populations. in *The pollination of flowers by insects* (A. J. Richards, editor). Academic Press, New York

Levin, D. A. 1981. Dispersal versus gene flow in plants. *Annals of the Missouri Botanical Garden* 68:233-253

Lewis, D., and L. K. Crowe. 1958. Unilateral interspecific incompatibility in flowering plants. *Heredity* 12:233-256

Little, R. J. 1983. A review of floral food deception mimicries with comments on floral mutualism. pp 294-309 in *Handbook of Experimental Pollination Biology* (C.E. Jones and R.J. Little, editors). Van Nostrand Reinhold, New York

Lloyd, D. G., and C. J. Webb. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms. I. Dichogamy. *New Zealand Journal of Botany* 24:123-162

Løken, A. 1949. Bumblebees in relation to *Aconitum septentrionale* in central Norway (Øyer). *Nytt Mag Naturvidenskap* 87:1-60

Løken, A. 1973. Studies on Scandinavian bumblebees (Hymenoptera: Apidae). *Norsk Ent. Tidskr* 20:1-218

Lundberg, H. 1980. Effects of weather on foraging flights of bumblebees (Hymenoptera: Apidae) in a subalpine area. *Holarctic Ecology* 3:104-110

Lundberg, H., and B. G. Svensson. 1975. Studies on the behaviour of *Bombus* Latr. species (Hym., Apidae) parasitized by *Sphaerularia bombi* Dufour (Nematoda) in an alpine area. *Norwegian Journal of Entomology* 22:129-134

Lutman, P. J. W., B. D. L. Fitt, and I. H. Williams. 1991. Alternative Crops. pp 51-54 in *AFRC Institute of Arable Crops Research Report for 1991*. AFRC, London

MacArthur, R.H., and E.O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton

MacFarlane, R. P., R. P. Griffen, and P. E. C. Read. 1983. Bumblebee management options to improve "Grasslands Pawera" red clover seed yields. *Proceedings of the New Zealand Grassland Association* 44:47-53

MacFarlane, R. P., R. P. Griffen, and P. E. C. Read. 1984. Hives for management of bumblebees in New Zealand. pp 435-441 in *V^{ème} Symposium International sur la Pollinisation, Versailles, 27-30 Sept. 1983*. Les Colloques de l'INRA 21. INRA Publishing

Macior, L. W. 1984. Behavioural co-adaptation of *Bombus* pollinators and *Pedicularis* flowers. pp 257-261 in *V^{ème} Symposium International sur la Pollinisation, Versailles, 27-30 Sept. 1983*. Les Colloques de l'INRA 21. INRA Publishing

Macior, L. W. 1995. Pollination ecology of *Pedicularis parryi* spp. *purpurea* (Parry) Carr (Scrophulariaceae). *Plant Species Biology* 10:163-168

MacLeod, A. 1999. Attraction and retention of *Episyrphus balteatus* DeGeer (Diptera : Syrphidae) at an arable field margin with rich and poor floral resources. *Agriculture Ecosystems and Environment* 73:237-244

MAFF. 1998. *The Countryside Stewardship Scheme*. MAFF Publications, London

MAFF. 1999. *Arable Stewardship*. MAFF Publications, London

Malcolm, S. B. 1990. Mimicry: status of a classical evolutionary paradigm. *Trends in Ecology and Evolution* 5:57-62

Mand, M., R. Mand, and I. H. Williams. 2002. Bumblebees in the agricultural landscape of Estonia. *Agriculture Ecosystems and Environment* in press

Mann, C. C., and M. L. Plummer. 1993. The High Cost of Biodiversity. *Science* 260:1868-1871

Mantel, N. 1967. The detection of disease clustering and a generalised regression approach. *Cancer Research* 27:209-220

Marshall, E. J. P. 1989. Distribution of plants associated with arable field edges. *Journal of Applied Ecology* 26:247-257

Marshall, E. J. P. 1993. Exploiting semi-natural habitats as part of good agricultural practise. pp 95-100 in *Scientific Basis for Codes of Good Agricultural Practise.* Commission of the European Community, Brussels, Luxembourg

Marshall, E. J. P., and A. C. Moonen. 1998. *A review of field margin conservation strips in Europe.* IACR Long Ashton Research Station, Bristol

Martin, E. C., and S. E. McGregor. 1973. Changing trends in insect pollination of commercial crops. *Annual Review of Entomology* **18**:207-226

McCollin, D. 2000. (editorial): Hedgerow policy and protection - changing paradigms and the conservation ethic. *Journal of Environmental Management* **60**:3-6

McCollin, D., J. I. Jackson, R. G. H. Bunce, C. J. Barr, and R. Stuart. 2000. Hedgerows as habitat for woodland plants. *Journal of Environmental Management* **60**:77-90

McCorquodale, D. B., R. G. Beresford, J. M. Francis, C. E. Thomson, and C. M. Bartlett. 1998. Prevalence of *Sphaerularia bombi* (Nematoda : Tylenchida : Sphaerulariidae) in bumble bee queens (Hymenoptera : Apidae) on Cape Breton Island, Nova Scotia, Canada. *Canadian Entomologist* **130**:877-882

McDade, C. A., and S. Kinsman. 1980. The impact of floral parasitism in two neo-tropical hummingbird-pollinated plant species. *Evolution* **34**:944-958

Mech, S. G., and J. G. Hallett. 2001. Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology* **15**:467-474

Menzel, R. 1999. Memory dynamics in the honeybee. *Journal of Comparative Physiology* A **185**:323-340

Menzel, R., and I. Erber. 1978. Learning and memory in bees. *Scientific American* **239**:102-110

Menzel, R., K. Geiger, L. Chittka, J. Joerges, J. Kunze, and U. Muller. 1996. The knowledge base of bee navigation. *Journal of Experimental Biology* **199**:141-146

Menzel, R., U. Greggers, and M. Hammer. 1993. Functional organization of appetitive learning and memory in a generalist pollinator, the honey bee. pp 79-125 in *Insect learning: Ecological and Evolutionary Perspectives* (D. R. Papaj and A. C. Lewis, editors). Chapman and Hall, London

Menzel, R., A. Gumbert, J. Kunze, A. Shmida, and M. Vorobyev. 1997. Pollinators' strategies in finding flowers. *Israeli Journal of Plant Science* **45**:141-156

Michener, C. D. 1974. *Social Behaviour of the Bees.* Harvard University Press, Cambridge, M.A.

Mitchell, K. 1999. European policies for field margins and buffer zones. pp 13-18 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Moffett, J. O., H. L. Morton, and R. H. Macdonald. 1972. Toxicity of some herbicidal sprays to honey bees. *Journal of Economic Entomology* **65**:475-476

Moonen, A. C., and E. J. P. Marshall. 2001. The influence of sown margin strips, management and boundary structure on herbaceous field margin vegetation in two neighbouring farms in southern England. *Agriculture Ecosystems and Environment* **86**:187-202

Moreby, S. J., and S. Southway. 1999. The importance of the crop edge compared to the mid-field, in providing invertebrate food for farmland birds. pp 217-222 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. *Memoirs of the Faculty of Science of Kyushu University* Series E Biology 3:65-80

Morse, D. H. 1978. Size-related foraging differences of bumblebee workers. *Ecological Entomology* 3:189-192

Mosquin, T. 1971. Competition for pollinators as a stimulus for evolution of flowering time. *Oikos* 22:398-402

Nature Conservancy Council. 1984. *Nature Conservation in Great Britain.* Nature Conservancy Council, Peterborough

Newsholme, E. A., B. Crabtree, S. J. Higgins, S. D. Thornton, and C. Start. 1972. The activities of fructose di-phosphatase in flight muscles from the bumblebee, and the role of this enzyme in heat production. *Biochemical Journal* 128:89-97

Nielsen, D. M., K. E. Visker, M. J. Cunningham, R. W. Keller, S. D. Glick, and J. N. Carlson. 1997. Paw preference, rotation and dopamine function in Collins HI and LO mouse strains. *Physiology and Behaviour* 61:525-535

Nilsson, L. A. 1988. The evolution of flowers with deep corolla tubes. *Nature* 334:147-149

Nilsson, L. A. 1992. Orchid pollination biology. *Trends in Ecology and Evolution* 7:255-259

Norgaard Holm, S. 1966. The utilisation and management of bumble bees for red clover and alfalfa seed production. *Annual Review of Entomology* 11:155-182

O'Connor, R. J., and M. Shrubb. 1986. *Farming and Birds.* Cambridge University Press, Cambridge

Oglethorpe, D. R., and R. Sanderson. 1988. Farm characteristics and the vegetative diversity of grasslands in the North of England: a policy perspective. *Biodiversity and Conservation* 7:1333-1347

Ortiz-Sánchez, F. J. 1995. Diversity of bees (Hymenoptera: Apoidea) in several Spanish ecosystems. pp 147-163 in *Changes in Fauna of Wild Bees in Europe* (J. Banaszak, editor). Pedagogical University, Bydgoszcz

Osborne, J., I. Williams, and S. Corbet. 1991. Bees, pollination and habitat change in the European Community. *Bee World* 72:99-116

Osborne, J. L., and I. H. Williams. 1996. Bumblebees as pollinators of crops and wild flowers. pp 24-32 in *Bumblebees for Pleasure and Profit* (A. Matheson, editor). IBRA, Cardiff

Osborne, J. L., S. J. Clark, R. J. Morris, I. H. Williams, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1999. A landscape-scale study of bumblebee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 38:519-533

Oster, G. F., and E. O. Wilson. 1978. *Caste and Ecology in Social Insects.* Princeton University Press, Princeton

O'Toole, C. 1994. Who cares for solitary bees? in *Bumblebees for Pleasure and Profit* (A. Matheson, editor). IBRA, Cardiff

Ovenden, G.N., A.R.H. Swash, and D. Smallshire. 1998. Agri-environment schemes and their contribution to the conservation of biodiversity in England. *Journal of Applied Ecology* **35**, 955-960

Pain, D. J., and M. W. Pienkowski (editors). 1997. *Farming and birds in Europe. The common agricultural policy and its implications for bird conservation.* Academic Press, London

Panfilov, D. V., and L. V. Zimina. 1962. Some data on the nesting and behaviour of bumblebees (Hymenoptera, *Bombus*). Byulleten' *Moskovskogo Obshchestva Ispytatelei Prirody* (Biol.) 67:38-44

Park, J. R. (editor). 1988. *Environmental management in agriculture (European Perspectives).* Belhaven Press, London

Parker, F. D., S. W. T. Batra, and V. J. Tepedino. 1987. New pollinators for our crops. *Agricultural Zoology Reviews* 2:279-304

Parrish, J. A. D., and F. A. Bazzaz. 1979. Difference in pollination niche relationships in early and late successional plant communities. *Ecology* 60:597-610

Paton, D. C. 1993. Honeybees in the Australian environment: does *Apis mellifera* disrupt or benefit the native biota? *Bioscience* 43:95-103

Pekkarinen, A. 1979. Morphometric, colour and enzyme variation in bumblebees (Hymenoptera, Apidae, *Bombus*) in Fennoscandia and Denmark. *Acta Zoologica Fennica* 158:1-60

Pekkarinen, A., I. Teräs, J. Viramo, and J. Paatela. 1981. Distribution of bumblebees (Hymenoptera, Apidae: *Bombus* and *Psithyrus*) in eastern Fennoscandia. *Notulae Entomologicae* 61:71-89

Percival, M. S. 1950. Pollen presentation and pollen collection. *New Phytologist* 49:40-63

Petanidou, T., H. C. M. den Nijs, and A. C. Ellis. 1991. Comparative pollination of two rare Dutch *Gentiana* species, in relation to population size. *Acta Horticulturae* 288:308-317

Petkov, V. 1958. An investigation into the nectar yield of sainfoin (*Onobrychis sativa*), phacelia (*Phacelia tanacetifolia*), borage (*Borago officinalis*) and buckwheat (*Fogopyrum esculentum*). *Nauchni Trud Minist Zemed Gorite* 1:211-246

Picard-Nizou, A.L., M.H. Pham-Delegue, V. Kerguelen, P. Douault, R. Marilleau, L. Olsen, R. Grison, A. Toppan, and C. Masson. 1995. Foraging behaviour of honey bees (*Apis mellifera* L.) on transgenic oilseed rape (*Brassica napus* L. *var. oleifera*). *Transgenic Research* 4: 270-276

Picard-Nizou, A.L., R, Grison, C. Pioche, G. Arnold, and M.H. Pham-Delegue. 1997. Impact of proteins used in plant genetic engineering: toxicity and behavioural study in the honeybee. *Journal of Economic Entomology* **90**: 1710-1716

Pierre, J., J. Mesquida, R. Marilleau, M.H. Pham-Delegue and M. Renard. 1999. Nectar secretion in winter oilseed rape, *Brassica napus* - quantitative and qualitative variability among 71 genotypes. *Plant Breeding* **118**: 471-476

Pirounakis, K., S. Koulianos, and P. Schmid-Hempel. 1998. Genetic variation among European populations of *Bombus pascuorum* (Hymenoptera : Apidae) from mitochondrial DNA sequence data. *European Journal of Entomology* 95:27-33

Plath, O. E. 1922. Notes on the nesting habits of several North American bumblebees. *Psyche* 24:189-202

Plowright, R. C., and W. P. Stephen. 1978. A numerical taxonomic analysis of the evolutionary relationships of *Bombus* and *Psithyrus*. *Canadian Entomologist* 105:733-743

Pollard, E. 1968. Hedges II: The effect of removal of the bottom flora of a hawthorn hedgerow on the fauna of hawthorn. *Journal of Applied Ecology* 5:109-123

Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. *Biological Conservation* 12:115-134

Pollard, E., D. O. Elias, M. J. Skelton, and J. A. Thomas. 1975. A method of assessing the abundance of butterflies in Monk's Wood Nature Reserve in 1973. *Entomologist's Gazette* 26:79-88

Pollard, E., M. D. Hooper, and N. W. Moore. 1974. *Hedges*. Collins, London

Pomeroy, N. 1981. Use of natural sites and field hives by a long-tongued bumble bee *Bombus ruderatus*. *New Zealand Journal of Agricultural Research* 24, 409-414

Potts, G. R. 1986. *The Partridge: Pesticides, predation and conservation*. Collins, London

Poulsen, M. H. 1973. The frequency and foraging behaviour of honeybees and bumblebees on field beans in Denmark. *Journal of Apicultural Research* 12:75-80

Poulsen, M. H. 1975. Pollination, seed setting, cross-fertilisation and inbreeding in *Vicia faba* L. *Zeitschrift für Pflanzensuchtung* 74:97-118

Pouvreau, A. 1962. Contribution a l'etude de *Sphaerularia bombi* parasite des reines de bourdons. *Annals Abeille* 5:181-199

Pouvreau, A., and R. Marilleau. 1980. *L'elevage des bourdons. Leur utilisation pour la pollinisation des plantes*. OPIE, France

Price, M. V., and N. M. Waser. 1979. Pollen dispersal and optimal outcrossing in *Delphinium nelsonii*. *Nature* 277:294-297

Proctor, M., and P. Yeo. 1973. *The Pollination of Flowers*. Collins, London

Prys-Jones, O. E. 1982. *Aspects of life-history and the foraging ecology of bumblebees*. PhD. thesis. University of Cambridge

Prys-Jones, O. E., and S. A. Corbet. 1991. *Bumblebees*. Richmond Publishing Company, Slough

Putnam, D. H. 1993. An interdisciplinary approach to the development of lupin as an alternative crop. pp 266-277 in *New Crops* (J. Janick and J. E. Simon, editors). Wiley, New York

Pyke, G. H. 1979. Optimal foraging in bumblebees: rule of movement between flowers within inflorescences. *Animal Behaviour* 27:1167-1181

Pyke, G. H. 1980. Optimal foraging in bumblebees: calculation of net rate of energy intake and optimal patch choice. *Theoretical Population Biology* 17:232-246

Pyke, G. H. 1982. Local geographic distribution of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecology* 63:555-573

Ramsey, M., and G. Vaughton. 2000. Pollen quality limits seed set in *Burchardia umbellata* (Colchicaceae). *American Journal of Botany* 87:845-852

Rands, M. R. W. 1985. Pesticide use on cereals and the survival of grey partridge chicks. *Journal of Applied Ecology* 22:49-54

Ranta, E. 1982. Species structure of north European bumblebee communities. *Oikos* 38:202-209

Ranta, E., and H. Lundberg. 1980. Resource partitioning in bumblebees: the significance of differences in proboscis length. *Oikos* 35:298-302

Ranta, E., and K. Vepsäläinen. 1981. Why are there so many species? Spatio-temporal heterogeneity and northern bumblebee communities. *Oikos* 36:28-34

Ranta, E., and M Tianen. 1982. Structure in seven bumblebee communities in eastern Finland in relation to resource availability. *Holoarctic Ecology* 5, 48-52

Rasheed, S. A., and L. D. Harder. 1997. Foraging currencies for non-energetic resources: pollen collection by bumblebees. *Animal Behaviour* 54:911-926

Rasmont, P. 1988. *Monographie écologique et zoogéographique des bourdons de France et de Belgique (Hymenoptera, Apidae, Bombinae).* PhD. Thesis. Gembloux, Belgium

Rasmont, P. 1989. Especes de Bourdons en expansion en Belgique (Hymenoptera, Apidae). *Notes fauniques de Gembloux* 18:57-64

Rasmont, P. 1995. How to restore the apoid diversity in Belgium and France? Wrong and right ways, or the end of the protection paradigm! pp 53-63 in *Changes in Fauna of Wild Bees in Europe* (J. Banaszak, editor). Pedagogical University, Bydogoszcz

Rasmont, P., C. Gaspar, J. LeClerq, A. Jacob-Remacle, and A. Pauly. 1992. The faunistic drift of Apoidea in Belgium. pp 65-86 in *Bees for pollination. Proceedings of an EC workshop. Brussels, 2-3 March 1992* (E. Bruneau, editor). Commission for the European Communities, Brussels

Rasmont, P., and P. Mersch. 1988. Première estimation de la dérive faunique chez les bourdons de la Belgique (Hymenoptera: Apidae). *Annals de la Société Royale de Belgique* 118:141-147

Rasmussen, I. R., and B. Brødsgaard. 1992. Gene flow inferred from seed dispersal and pollinator behaviour compared to DNA analysis of restriction site variation in a patchy population of *Lotus corniculatus* L. *Oecologia* 89:277-283

Rathcke, B. J. 1983. Competition and facilitation among plants for pollination. pp 305-329 in *Pollination Biology* (A. L. Real, editor). Academic Press Incorporated, New York

Rathcke, B. J., and E. S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. *Current Science* 65:273-277

Rice, K.J. 1989. Impacts of seed banks on grassland community structure and population dynamics. pp211-230 in *Ecology of Soil Seed Banks* (M.A. Leck, V.T. Parker, and R.L. Simpson, editors). Academic Press, San Diego

Richards, A. J. 2001. Does low biodiversity resulting from modern agricultural practise affect crop pollination and yield? *Annals of Botany* 88:165-172

Richards, K. W. 1973. Biology of *Bombus polaris* Curtis and *B. hyperboreus* Schonherr at Lake Hazen, Northwest Territories (Hymenoptera: Bombini). *Quaestiones entomologicae* 9:115-157

Richards, K. W. 1978. Nest-site selection by bumblebees (Hymenoptera: Apidae) in southern Alberta. *Canadian Entomologist* 110:301-318

Richards, K. W., and P. D. Edwards. 1988. Density, diversity and efficiency of pollinators of sainfoin, *Onobrychis viciaefolia* Scop. *Canadian Entomologist* 120:1085-1100

Richards, O. W. 1946. Observations on *Bombus agrorum* (Fabricius) (Hymen., Bombidae). *Proceedings of the Royal Entomological Society of London* Series A 21:66-71

Ricketts, T. H., G. C. Daily, P. R. Erhlich, and P. R. Fay. 2001. Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats. *Conservation Biology* 15:378-388

Riedel, I. B. M., and D. A. Wort. 1960. The pollination requirements of the field bean (*Vicia faba*). *Annals of Applied Biology* 48:121-124

Riley, J. A., A. D. Smith, D. R. Reynolds, A. S. Edwards, J. L. Osborne, I. H. Williams, N. L. Carreck, and G. M. Poppy. 1996. Tracing bees with harmonic radar. *Letters to Nature* 379:29-30

Robinson, G. R., R. D. Holt, M. S. Gaines, S. P. Hamburg, M. L. Johnson, H. S. Fitch, and E. A. Martinko. 1992. Diverse and contrasting effects of habitat fragmentation. *Science* 257:524-526

Rosov, S. A. 1952. Sainfoin - one of the best honey plants in crop rotation. *Pchelovodstvo Mosk* 29:46-52

Rotenberry, J. T. 1990. Variable flower phenology: Temporal resource heterogeneity and its implications for flower visitors. *Holoarctic Ecology* 13:1-10

Russell, N. P., and A. M. Fraser. 1995. The potential impact of environmental cross-compliance on arable farming. *Journal of Agricultural Economics* 46:70-79

Saunders, D., R. Hoobs, and P. Erhlich. 1992. *Reconstruction of fragmented ecosystems: local and global perspectives*. Surrey Beatty, Chipping Norton

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18-32

Saville, N. M., W. E. Dramstad, G. L. A. Fry, and S. A. Corbet. 1997. Bumblebee movement in a fragmented agricultural landscape. *Agriculture Ecosystems and Environment* 61:145-154

Schumacher, W. 1987. Methods taken to preserve rare arable weeds and their associated communities in central Europe. pp 109-112 in *Field Margins. BCPC Monograph 35* (J. M. Way and P. W. Greig-Smith, editors). British Crop Protection Council, Farnham, Surrey

Schwenninger, H. R. 1992. Untersuchungen zum Einflus der Bewirtschaftungsintensitat auf das Vorkommen von Insektenarten in der Agrarlandschaft, dargestellt am Beispiel der Wildbienen (Hymenoptera: Apoidea). *Zoologisches Jahrbuch, Abteilung für Systematik* 119:543-561

Scriven, W. A., B. A. Cooper, and H. Allen. 1961. Pollination of field beans. *Outlook on Agriculture* 3:69-75

Semmens, T. D., E. Turner, and R. Buttermore. 1993. *Bombus terrestris* (L.) (Hymenoptera - Apidae) now established in Tasmania. *Journal of the Australian Entomological Society* 32:346

Shrubb, M., I. T. Williams, and R. R. Lovegrove. 1997. The impact of changes in farming and other land uses on bird populations in Wales. *Welsh Birds* 1:4-26

Sihag, R. C., and R. P. Kapil. 1983. Foraging strategies of honeybees as determined by quality and quantity of nectar. pp 51-59 in *Vème Symposium International sur la Pollinisation, Versailles, 27-30 Sept. 1983.* Les Colloques de l'INRA 21. INRA Publishing

Simpson, B.B., and Neff, J.L. 1983. Evolution and diversity of floral rewards. pp142-159 in *Handbook of Experimental Pollination Biology* (C.E. Jones and R.J. Little, editors). Van Nostrand Reinhhold, New York

Skovgaard, O. S. 1936. *Rodkloverens bestovning, humlebier og humleboer.* Raekke, Denmark

Skovgaard, O.S. 1945. Rodklovens Bestoving, Humlebier og Humbleboer. *Kl danske vidensk Selsk Nat og mth Ser* 6, 1-140

Sladen, F. W. L. 1912. *The humble-bee: its life history and how to domesticate it.* MacMillan, London, U.K.

Smallshire, D., and A. I. Cooke. 1999. Field margins in UK agri-environment schemes. pp 19-28 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Smith, H., R. E. Feber, P. J. Johnson, K. McCallum, S. Plesner Jensen, and D. W. MacDonald. 1993. *The Conservation and Management of Arable Field Margins.* English Nature, Peterborough

Smith, H., R. Feber, and D. W. MacDonald. 1994. The role of wild flower seed mixtures in field margin restoration. pp 289-294 in *Field margins: Integrating agriculture and conservation* (N. D. Boatman, editor). British Crop Protection Council, Farnham, Surrey

Smith, H., L. G. Firbank, and D. W. Macdonald. 1999. Uncropped edges of arable fields managed for biodiversity do not increase weed occurrence in adjacent crops. *Biological Conservation* 89:107-111

Snow, A. A. 1986. Pollination dynamics in *Epilobium canum* (Onograceae): Consequences for gametophytic selection. *American Journal of Botany* 73:139-151

Sotherton, N. 1991. Conservation Headlands: a practical combination of intensive cereal farming and conservation. pp 373-397 in *The Ecology of Temperate Cereal Fields* (L. G. Firbank, N. Cartar, J. F. Derbyshire, and G. R. Potts, editors). Blackwell Scientific Publications, Oxford

Sotherton, N. W. 1998. Land use changes and the decline of farmland wildlife: An appraisal of the set-aside approach. *Biological Conservation* 83:259-268

Southwick, E. E., and S. L. Buchmann. 1995. Effects of horizon landmarks on homing success in honey-bees. *American Naturalist* 146:748-764

Sowig, P. 1989. Effects of flowering plants patch size on species composition of pollinator communities, foraging strategies and resource partitioning in bumblebees (Hymenoptera: Apidae). *Oecologia* 78:550-558

Sparks, T. H., and T. Parish. 1995. Factors affecting the abundance of butterflies in field boundaries in Swavesey fens, Cambridgeshire, U.K. *Biological Conservation* 73:221-227

SPSS, Inc. 1998. *SPSS for Windows: Advanced Statistics.* Release 9.0. SPSS Inc., Chicago

Stace, C. 1997. *New Flora of the British Isles.* Cambridge University Press, Cambridge

Steffan-Dewenter, I., and T. Tscharntke. 1997. Bee diversity and seed set in fragmented habitats. *Acta Horticulturae* 437:231-234

Steffan-Dewenter, I., and T. Tscharntke. 2000. Resource overlap and possible competition between honey bees and wild bees in central Europe. *Oecologia* 122:288-296

Stephenson, A. G., R. S. Johnson, and J. A. Winsor. 1988. Effects of competition on the growth of *Lotus corniculatus* L. seedlings produced by random and natural patterns of fruit abortion. *American Midland Naturalist* 120:102-107

Stoate, C. 1999. The influence of field boundary structure on breeding territory establishment of whitethroat *Sylvia communis* and yellowhammer *Emberiza citrinella*. pp 125-130 in *Aspects of Applied Biology 54. Field Margins and Buffer Zones: Ecology, Management and Policy* (N. D. Boatman, D. H. K. Davies, C. H. Chaney, R. Feber, G. R. de Snoo, and T. H. Sparks, editors). Association of Applied Biologists, Warwick

Stoddard, F. L., and D. A. Bond. 1987. The pollination requirements of the faba bean. *Bee World* 68:144-152

Stone, G. N., and P. G. Willmer. 1989. Warm-up rates and body temperature in bees: the importance of body size, thermal regime, and phylogeny. *Journal of Experimental Biology* 147:303-328

Stout, J. C., D. Goulson, and J. A. Allen. 1998. Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). *Behavioural Ecology and Sociobiology* 43:317-326

Sunderland, K., and F. Samu. 2000. Effects of agricultural diversification on the abundance, distribution, and pest control potential of spiders: a review. *Entomologia Experimentalis et Applicata* 95:1-13

Surholt, B., and E. A. Newsholme. 1981. Maximum activities and properties of glucose-6-phosphate in muscles from vertebrates and invertebrates. *Biochemical Journal* 198:621-629

Svensson, B., J. Lagerlof, and B. G. Svensson. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture Ecosystems and Environment* 77:247-255

Svensson, B. G., and H. Lundberg. 1977. Distribution of bumble bee nests in a subalpine/alpine area in relation to altitude and habitat (Hymenoptera, Apidae). *Zoon* 5:63-72

Tasei, J. N., G. Ripault, and E. Rivault. 2001. Hazards of imidacloprid seed coating to *Bombus terrestris* (Hymenoptera : Apidae) when applied to sunflower. *Journal of Economic Entomology* 94:623-627

Teräs, I. 1976a. Bumblebees, *Bombus* Latr. (Hymenoptera, Apidae), on red clover in South Savo, Finland. *Annals Agricultur Fennoscandia* 15:116-127

Teräs, I. 1976b. Flower visits of bumblebees, *Bombus* Latr. (Hymenoptera, Apidae) during one summer. *Annals Zool Fennoscandia* 13:200-232

Teräs, I. 1983. Estimation of bumblebee densities (*Bombus*: Hymenoptera, Apidae) in southern Finland. *Acta Zool. Fennoscandia* 179:1-120

Teräs, I. 1985. Flower visits of bumblebees (Hymenoptera: Apidae) during one day in north-western Finland. *Notulae Entomologicae* 65:129-135

Tereshchenko, A. K. 1949. Pollination of sainfoin by honey bees. *Pchelovodstvo Mosk* 26:338-341

Tew, T. E., I. A. Todd, and D. W. MacDonald. 1994. Field margins and small mammals. pp 85-94 in *Field margins: Integrating agriculture and conservation: BCPC Monograph 58* (N. D. Boatman, editor). British Crop Protection Council, Farnham, Surrey

Thies, C., and T. Tscharntke. 1999. Landscape structure and biological control in agroecosystems. *Science* 285:893-895

Thomas, C. F. G., and E. J. P. Marshall. 1999. Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture Ecosystems and Environment* 72:131-144

Thomas, J. A. 1995. The conservation of declining butterfly populations in Britain and Europe: priorities, problems and successes. *Biological Journal of the Linnean Society* 56(S):55-72

Thompson, K., J.P. Bakker, and R.M. Bekker. 1997. *Soil seed banks of North West Europe: Methodology, Density and Longevity.* Cambridge University Press, Cambridge

Thompson, H. M. 2001. Assessing the exposure and toxicity of pesticides to bumblebees (*Bombus* spp.). *Apidologie* 32:305-321

Thomson, J. D. 1978. A local replacement of *Bombus ternarius* by *Bombus terricola* in northern Winsconsin (Hymenoptera: Apidae). *Great Lakes Entomology* 11:101-103

Thomson, J. D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. *Journal of Animal Ecology* 50:49-59

Thomson, J. D., W. P. Maddison, and R. C. Plowright. 1982. Behaviour of bumblebee pollinators of *Aralia hispida* Vent. (Araliaceae). *Oecologia* 54:326-336

Thomson, J. D., S. C. Peterson, and L. D. Harder. 1987. Response of traplining bumblebees to competition experiments: shifts in feeding location and efficiency. *Oecologia* 71:295-300

Thomson, J. D., M. V. Price, N. M. Waser, and D. A. Stratton. 1986. Comparative studies of pollen and fluorescent dye transport by bumblebees visiting *Erythronium grandiflorum. Oecologia* 69:561-566

Torchio, P. F. 1991. Bees as crop pollinators and the role of solitary species in changing environments. *Acta Horticulturae* 288:49-61

Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* 35:708-719

van Heemert, C., A. de Ruitjer, J. van den Eijnde, and J. van den Steen. 1990. Year-round production of bumblebee colonies for crop pollination. *Bee World* 71:54-56

van Home, B. 1983. Density as a misleading indicator of habitat quality. *Journal of Wildlife Management* 47:893-901

van Honk, C. G. J., H. H. W. Velthius, P. F. Roseler, and M. E. Maloteaux. 1980. The mandibular glands of *Bombus terrestris* queens as a source of queen pheromones. *Entomologia Experimentalis et Applicata* 28:191-198

Vaughton, G. 1996. Pollination disruption by European honeybees in the Australian bird-pollinated shrub *Grevillea barklyana* (Proteaceae). *Plant Systematics and Evolution* 200:89-100

Velthuis, H. H. W., and L. Cobb. 1991. Pollination of *Primula* in a greenhouse using bumblebees. *Netherlands Acta Horticulturae* 288:199-203

Visscher, P. K., and T. D. Seeley. 1982. Foraging strategy of honeybee colonies in a temperate deciduous forest. *Ecology* 63:1790-1801

Vogel, S. 1990. *The role of scent glands in pollination*. Smithsonian Institution Libraries and the National Science Foundation, Washington D.C.

von Hagen, E. 1986. *Hummeln*. Neumann-Neudamn, Melsungen, Germany

von Hagen, E. 1994. *Hummeln bestimmen*. Ansiedeln, Vermehren, Schutzen. Naturbuch-Verlag, Augsburg

Waddington, K. D. 1983. Foraging behaviour of pollinators. pp 213-239 in *Pollination Biology* (L. A. Real, editor). Academic Press Incorporated, New York

Walter, K. S. 1997. *Pollination Ecology*. Royal Botanic Garden, Edinburgh

Walther-Hellwig, K., and R. Frankl. 2000a. Foraging habitats and foraging distances in bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology* 124:299-306

Walther-Hellwig, K., and R. Frankl. 2000b. Foraging distances of *Bombus muscorum, Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). *Journal of Insect Behaviour* 13, 239-246

Wanatabe, M. E. 1994. Pollination worries rise as honey bees decline. *Science* 265:1170

Webb, C. J., and D. G. Lloyd. 1986. The avoidance of interference between presentation of pollen and stigmas in angiosperms. II: Herkogamy. *New Zealand Journal of Botany* 24:163-178

Westergaard, G. C., and S. J. Suomi. 1996. Lateral bias for rotational behaviour in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology* 110:199-202

Westerkamp, C. 1991. Honeybees are poor pollinators - why? *Plant Systematics and Evolution* 177:71-75

Westerkamp, C. 1996. Pollen in Bee-Flower Relationships. *Botanica Acta* 109:325-332

Westerkamp, C., and G. Gottsberger. 2000. Diversity Pays in Crop Pollination. *Crop Science* 40:1209-1222

Westrich, P. 1989. *Die Bienen Baden-Wurttembergs, Volumen 1*. Ulmer Verlag, Stuttgart

Westrich, P. 1996. Considering the ecological needs of our native bees and the problems of partial habitats. pp 1-16 in *The Conservation of Bees* (A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich, and I. H. Williams, editors). Academic Press, London

White, P. C. L., and M. Hassall. 1994. Effects of management on spider communities of headlands in cereal fields. *Pedobiologia* 38:169-184

Whitehead, D. R. 1983. p97 in *Pollination Biology*. Academic Press Incorporated, New York

Wilcox, A. 1998. Early plant succession on former arable land. *Agriculture Ecosystems and Environment* 69:143-157

Wilcox, R. R., H.J. Keselman, J. Muska, and R. Cribbie. 2000. Repeated measures ANOVA: Some new results on comparing trimmed means and means. *British Journal of Mathematical and Statistical Psychology* 53: 69-82

Wilkinson, M. 1984. Milk and meat from forage legumes. *Farmer's Weekly* September 21.

Williams, C. S. 1998. The identity of the previous visitor influences flower rejection by nectar-collecting bees. *Animal Behaviour* 56:673-681

Williams, I. H. 1988a. The pollination of linseed and flax. *Bee World* 69:145-152

Williams, I. H. 1994. Dependence of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews* 6:229-257

Williams, I. H., and J. B. Free. 1975. The pollination and set of the early flowers of runner beans (*Phaseolus coccineus* L.). *Journal of Horticultural Science* 50:405-413

Williams, I. H., A. P. Martin, and R. P. White. 1986a. The pollination requirements of oilseed rape. *Journal of Agricultural Science* 106:27-30

Williams, I. H., J. R. Simpkins, and A. P. Martin. 1986b. Effect of insect pollination on seed production in linseed (*Linum usitatissimum*). *Journal of Agricultural Science* 117:75-79

Williams, I. H., A. P. Martin, and R. P. White. 1987. The effect of insect pollination in winter oilseed rape. *Journal of Agricultural Science* 109:135-139

Williams, I. H., A. P. Martin, J. W. Ferguson, and S. J. Clark. 1990. Effect of pollination on flower, pod and seed production in white lupin (*Lupinus albus*). *Journal of Agricultural Science* 115:67-73

Williams, I. H., N. L. Carreck, and D. J. Little. 1993. Nectar sources for honey bees and the movement of honey bee colonies for crop pollination and honey production in England. *Journal of Apicultural Research* 74: 160-175

Williams, P. H. 1982. The distribution and decline of British bumble bees (*Bombus* Latr.). *Journal of Apicultural Research* 21:236-245

Williams, P. H. 1986. Environmental change and the distributions of British bumble bees (*Bombus* Latr.). *Bee World* 67:50-61

Williams, P. H. 1988b. Habitat use by bumble bees (*Bombus* spp.). *Ecological Entomology* 13:223-237

Williams, P. H. 1989. Why are there so many species of bumble bees at Dungeness? *Botanical Journal of the Linnean Society* 101:31-44

Willmer, P. G., A. A. M. Bataw, and J. P. Hughes. 1994. The superiority of bumblebees to honeybees as pollinators: insect visits to raspberry flowers. *Ecological Entomology* 19:271-284

Wilson, J. D., J. Morris, B. E. Arroyo, and S. C. Clark. 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. *Agriculture Ecosystems and Environment* 75:13-30

Wilson, P., and J. D. Thomson. 1991. Heterogeneity among floral visitors leads to discordance between removal and deposition of pollen. *Ecology* 72:1503-1507

Wilson, P., and M. Stine. 1996. Floral constancy in bumble bees: handling efficiency or perceptual conditioning? *Oecologia* 106:493-499

Wilson, P. J. 1993. Conserving Britain's Cornfield Flowers. pp 411-416 in *The 1993 Brighton Crop Protection Conference - Weeds*. British Crop Protection Council, Farnham, Surrey.

Wilson, P. J. 1994a. Botanical diversity in arable field margins. pp 53-58 in *Field margins: Integrating agriculture and conservation. BCPC Monograph Number 55* (N. D. Boatman, editor). British Crop Protection Council, Farnham, Surrey.

Wilson, P. J. 1994b. Managing field margins for the conservation of arable flora. pp 253-258 in *Field margins: Integrating agriculture and conservation. BCPC Monograph Number 55* (N. D. Boatman, editor). British Crop Protection Council, Farnham, Surrey.

Wilson, P. J., and N. J. Aebischer. 1995. The distribution of dicotyledonous arable weeds in relation to distance from the field edge. *Journal of Applied Ecology* 32:295-310

Witte, G. R., J. Seger, and N. Hafner. 1989. *Hummelschauanlagen*. UTRV, Hannover

Wojtowski, F. 1963. Observations on the construction and arrangement of bumble-bee nests (Bombinae). *Zoologica Poloniae* 13:137-154

Woodward, G. L., and T. M. Laverty. 1992. Recall of flower handling skills by bumble bees: a test of Darwin's interference hypothesis. *Animal Behaviour* 44:1045-1051

Wossink, A., J. van Wenum, C. Jurgens, and G. de Snoo. 1999. Co-ordinating economic, behavioural and spatial aspects of wildlife preservation in agriculture. *European Review of Agricultural Economics* 26:443-460

Yazgan, M. Y., J. F. Leckman, and B. E. Wexler. 1996. A direct observational measure of whole body turning bias. *Cortex* 32:173-176

Young, A., T. Boyle, and T. Brown. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends in Ecology and Evolution* 11:413-418

Zahavi, A., D. Eiskowitch, A. Kadman Zahavi, and A. Cohen. 1984. A new approach to flower constancy in honeybees. pp 89-95 in *V^{ème} Symposium International sur la Pollinisation, Versailles, 27-30 Sept. 1983*. Les Colloques de l'INRA 21. INRA Publishing

Zimmerman, M. 1982. Optimal foraging: random movement by pollen collecting bumblebees. *Oecologia* 53:394-398

Zobel, M., E. van der Maarel, and C. Dupre. 1998. Species pool: the concept, its determination and its significance for community restoration. *Applied Vegetation Science* 1:55-66

GLOSSARY

Anemophilous	Plants that are adapted for pollination by wind
Annual	Plants that complete their life-cycle within one year
Batesian mimicry	Where a harmless species resembles the appearance of a poisonous or dangerous species
Biennial	Plants that require 2 growing seasons to complete their life-cycle
Bio-control	The use of natural enemies to control pest populations
Caste	A division whereby the individuals of the colony are specialised to perform specific functions
Corbiculae	An area on the hind tibia that is concave and surrounded by a fringe of hairs; honeybees and bumblebees pack pollen into these for transport to the nest – 'pollen baskets'
Corolla	Collectively, the petals of a flower
Dichogamy	The male and female reproductive parts of a flower mature at different times (dichogamous)
Dioecy	Male and female flowers found on different plants; dioecious species (cf. monoecy)
Drone	A male bee
Entomophilous	Plants that are adapted for pollination by insects
Eusocial	Colonies are composed of 2 generations of the same family, with division of labour and associated caste development
Floral constancy	A tendency for foragers to specialise on one flower species, even when there are a variety of nectar-producing species present
Floret	Small flower in a flower head or other cluster
Geitonogamy	Pollination of flowers by others on the same plant (geitonogamous)
Herkogamy	Spatial separation of the male and female parts in an hermaphrodite plant (herkogamous)
Heterostyly	Flowers of the same species have styles of different lengths
Homomorphic	Plant species where individuals are morphologically similar, e.g. where there is no variation in style length
Hydrophilous	Plants that are adapted for pollination by water
Inbreeding depression	A decline in fitness caused by accumulation of deleterious alleles through breeding with close relatives
Inflorescence	A particular arrangement of flowers on a single main stalk of a plant

Leguminous	Plants having seeds in pods (legumes)
Metaxenia	Whereby the male parent, through its pollen, influences characteristics of the resultant fruit, e.g. earliness, size
Monoecy	Separate male and female flowers on the same plant; monoecious species (cf. dioecy)
Müllerian mimicry	Where two or more distasteful species resemble each other, presumably for reinforcement
Nectivorous	Animals that feed on nectar
Outcrossing	A pollination event between unrelated or distantly related individual plants of the same species
Perennial	Plants that live for a number of years
Pollen baskets	See 'corbiculae'
Pollen carry-over	The pattern of inadvertent pollen deposition on subsequent flowers by a pollinator after a visit to a flower releasing pollen
Pollen constancy	A tendency for foragers to collect pollen from only one flower species, even when several pollen-producing species are present
Proboscis	The elongated mouthparts, in bees specifically the galea, the labial palps, and the glossa
Protandry	Maturation of male flowers before female ones within a single plant (protandrous species)
Protogyny	Maturation of female flowers before male ones within a single plant (protogynous species)
Site-fidelity	The tendency for foragers to gather food from a particular site, until the resource there is exhausted
Sonication	Pollination requires an applied vibration on the anthers of a critical frequency and its harmonics – 'buzz pollination'
Sympatric species	Those species with over-lapping geographical distributions
Trap-lining	Whereby individual foragers follow a regular 'foraging route' through a patch of flowers
Zoophilous	Plants that are adapted for pollination by animals

APPENDIX 1: LATIN AND ENGLISH SPECIES NAMES: FAUNA

Apis cerana	Asian hive bee
Apis mellifera	honeybee
Bombus hortorum	garden bumblebee
Bombus lapidarius	large red-tailed bumblebee
Bombus lucorum	common white-tailed bumblebee
Bombus pascuorum	common carder bumblebee
Bombus pratorum	meadow bumblebee
Bombus ruderarius	small red-tailed bumblebee
Bombus terrestris	buff-tailed bumblebee
Colletidae spp.	carpenter bees
Psithyrus spp.	cuckoo bumblebee spp.
Varroa destructor	the varroa mite

APPENDIX 2: LATIN AND ENGLISH SPECIES NAMES: FLORA

Brassica juncea	brown mustard
Brassica napus	oilseed rape
Brassica spp.	cabbage family
Centaurea nigra	black knapweed
Chaemerion angustifolium	rosebay willowherb
Cichorum intybus	chicory
Cirsium arvense	creeping thistle
Cirsium vulgare	spear thistle
Crataegus monogyna	hawthorn
Dactylis glomerata	cocks-foot
Dipsacus fullonum	teasel
Festuca rubra	red fescue
Lamium purpureum	red deadnettle
Linum usitatissimum	linseed
Lotus corniculatus	birdsfoot trefoil
Lycium spp.	box-thorns
Lycopersicon esculentum	tomato
Matricaria spp.	daisies
Medicago sativa	alfalfa/lucerne
Melilotus officianalis	melilot
Onobrychis viciifolia	sainfoin
Papaver rhoeas	common poppy
Pedicularis spp.	figworts
Pentaglottis sempervivens	green alkanet
Persicaria maculosa	redshank
Phacelia tanacetifolia	phacelia
Phleum pratense	timothy
Polemonium viscosium	phlox
Prunella vulgaris	self-heal
Silene dioecia	red campion
Sinapsis arvensis	charlock
Stachys sylvatica	hedge woundwort
Trifolium pratense	red clover
Trifolium repens	white clover
Trifolium hybridium hybridium	asilke clover

Tripleurospermum inodorum	scentless mayweed
Viola arvensis	field pansy