

NORWEGIAN UNIVERSITY OF LIFE SCIENCES



Preface

I have always been fascinated by social insects, especially social bees. I therefore started to work with my fieldwork and thesis with great joy, motivation and excitement. Even though rainy days and incomprehensible statistics have had severe effects on this motivation at times; this study has been an overall good experience for me.

First of all I would like to express my appreciation to my supervisors Tone Birkemoe, Anne Sverdrup Thygeson and Anne Lene Thorsdatter Orvedal Aase. I am grateful for all help the help, ideas and guidance I have received through the entire process of writing my thesis.

Thank you so much for funding my thesis and for believing in me.

I would also like to thank Harald Kvaalen for his guidance and valuable points of view about statistics. Thanks to the farmers and landowners for their hospitality and co-operation.

Last but not least, I would like to thank Even, Helmer, my family and friends which have given me their support and valuable input during my studies.

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Abstract

Bumblebees are important pollinators of crops and wild flowers, and the observed decrease in natural bumblebee populations are therefore an increasing cause of concern. The aim of this thesis was to evaluate how bumblebees are affected by different variables in the fragmented landscape. The questions raised were if the density of flowering plants and habitat configuration could explain the species richness, abundance and size of bumblebees. Questions about preferred forage plant species were also addressed. The study was conducted during the summer of 2012 in south-east Norway, which has a landscape dominated by a mixture of intensive cereal production and coniferous forests. 13 different species of bumblebees were found in this area and the results showed that the total abundance and species richness of social bumblebees were positively influenced by the density of flowering plants. Results show no significant effects of area, circumference or type of remnant on species richness, abundance or size of bumblebees. The preferred plant species for bumblebees in general were preferred by all observed species. Between casts, differences in preferred plant species were found. The results also indicate that bumblebees prefer perennial plants over annuals.

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1. Introduction

There is evidence that many bumblebee species have declined dramatically in Europe, Britain and North America in recent decades (Goulson et al. 2008; Goulson 2010; Westrich 1996; Williams 1982; Williams 1986). Especially the declines in the natural populations of bumblebee species are an increasing cause for concern. The first worries about the changes in the status of bumblebee species were expressed in Britain by Free and Butler in 1959; “*It is commonly supposed that the bumblebee population has declined in recent years*” .

Of the 34 species known in Norway, six species are listed on the Norwegian redlist: *Bombus distinguendus* – endangered, *B. humilis* – vulnerable, *B. muscorum* – near threatened, *B. ruderarius* – near threatened, *B. subterraneus* – critically endangered, *B. quadricolor* – data deficient (Kålås et al. 2010). Species in the groups critically endangered, endangered and vulnerable are characterized as threatened species, which means that the best available information about the species indicates a high risk of extinction. These species are confined to a handful of sites, and have uncertain futures. The near threatened species do not have a high risk of extinction at the present time, but are close to meet some of the criteria for threatened species in the near future (Kålås et al. 2010).

Several factors might explain the decline in bumblebees, of which land use changes are believed to be the most important (Goulson et al. 2006; Goulson 2010; Westrich 1996). Intensification of farming practices and changing agricultural policy has often been identified as driving land-use changes. Throughout Europe the change and rationalization in farming practices have led to two contrasting trends (Fjellstad & Dramstad 1999). Management of fertile land has been progressively intensified, with mechanization leading to increased intensively managed field sizes, large monocultures, removal of a wide variety of landscape features considered to represent obstacles to production, such as remnant islets of semi-natural vegetation and boundary vegetation, and increased application of agrochemicals. On the other hand, marginal areas have been abandoned, and successively transformed into forest or replanted for forestry (Fjellstad & Dramstad 1999; Framstad et al. 1998). The intensification of farming practices have reduced the agricultural landscapes biodiversity and led to poorer quality of life for many different species of animals, insects and plants. Progressive loss, destruction and fragmentation of permanent grassland and semi-natural habitats to arable cultivation in Europe between 1900 and 1970 reduced the amount and quality of habitat for bees. Documented regional losses of certain bumblebee species in United Kingdom, France and Belgium are attributed to ploughing of undisturbed habitats and reduction in the areas of legume-rich forage crops and semi-natural vegetation (Corbet et al.

1991). As a consequence of habitat loss, bumblebees are often confined to small remnants of semi-natural vegetation within the fragmented agricultural landscape (Banaszak 1992).

Bumblebees need habitats that provide nest sites and a seasonal succession of flowers from April to August. They prefer flower-rich open grassland, heath, unimproved grassland, undisturbed areas on farmland (hedges, field boundaries and margins, roadside verges) and woodland edges (Carvell 2002). Many studies deal with the effects the destruction and fragmentation of semi-natural habitats have on bees. The decline of many bumblebee species is probably influenced by the loss of unimproved flower-rich grasslands (Goulson et al. 2005). It has been shown that decreasing size and increasing isolation of habitat patches leads to a decline in species richness and abundance as well as to changes in community structure (Steffan-Dewenter & Westphal 2008). On farmland, the crops themselves may provide an abundance of food during their brief flowering periods, but crops alone are unlikely to provide the continuous succession of flowers that the bumblebees need to thrive. Uncropped areas of farmland, such as hedgerows, roadside verges, shelterbelts and unimproved grassland can provide flowers throughout the season, and tend to support far greater numbers of foraging bumblebees than cultivated areas (Banaszak 1983).

Growing evidence for declines in bee populations has caused great concern because of the valuable ecosystem services they provide. In general, bumblebees have flexible floral preferences and visit a range of flowers of different plant species (generalist pollinators). They have a very high work rate, and are among the more efficient and well-adapted pollinators of many wild flowers and crops (Banaszak 1983), and vital components of ecosystems. Large numbers of wild plants are pollinated predominantly or exclusively by bumblebees, sometimes by particular species of bumblebee (Corbet et al. 1991). The loss of bumblebee diversity and richness may therefore have serious implications for the pollination of crops and wild flowers. For example, bumblebees are able to forage in weather conditions in which honeybees are inactive, they have greater tongue lengths enabling visitation to a wider range of plant species, and they are not susceptible to the mite *Varroa jacobsoni*, which has led to declines in honeybee numbers (Corbet et al. 1991).

Bumblebees are entirely dependent on flowers, because they feed almost exclusively on nectar and pollen. Several studies have demonstrated a direct correlation between floral density and the number of bee species (Banaszak 1983; Goulson 2010). Studies in Finland, Poland, Britain and the Netherlands have also shown a parallel decline in bee and plant species richness (Biesmeijer et al. 2006; Goulson 2010). Biesmeijer et al. (2006) could not

show if the decline in floral abundance explained the decline in bee populations, if the decline in pollinators led to the decline of plants, or if both the plants and their pollinators were responding to some other factor. Corbet et al. (1991) on the other hand argue that it seems likely that reductions in the abundance and richness of bumblebees can lead to widespread changes in plant communities. If the floral resources are few, and the number of bumblebees decline, the plants they pollinate set less seeds, and as a result there will be even less food for the bumblebees. This positive feedback is described as an extinction vortex, and changes like these can in turn have further effects for other animals dependent on plant resources.

Fragmentation leads to reduced connectivity, the degree to which the landscape facilitates or hinders movement among resource patches (Taylor et al. 1993). Connectivity is particularly important in agricultural landscapes since habitat patches are typically small (Fjellstad & Dramstad 1999). Each patch alone may be too small to support a stable population, but dispersal amongst a network of patches may enable long-term survival of a species. Many bumblebees are very flexible in their utilization of floral resources. They are probably buffered against some level of fragmentation and patchiness by their ability to forage quite far away from the colony (Osborne et al. 2008), by their communication and by their accurate memory of forage sites (Williams & Osborne 2009). Bumblebees often use different habitats for nesting and foraging (Goulson 2010). The richness and abundance of floral resources available to bumblebees will therefore depend on the distance from their nests that they forage. Species with large foraging range may be able to cope in a landscape with a few patches of forage that are widely dispersed, whereas species with shorter foraging range need forage patches to be close together.

Various species of bumblebee tend to be found everywhere, in other words they are ubiquitous, while others tend to be very locally restricted (Williams 1986). In Europe six species are widespread and common, *B. terrestris*, *B. lucorum*, *B. lapidarius*, *B. pratorum*, *B. hortorum*, and *B. pascuorum* (Goulson et al. 2008; Williams 1982). These species are called the “mainland ubiquitous” by Williams (1982) and have, with the exception of *B. hortorum*, a broad diet (Goulson et al. 2005; Williams 1982). Studies from both Norway and other countries show that bumblebees in general prefer flowers from biennial and perennial plants rather than annuals (Dramstad 1996a). In addition to their general preference for perennials, the different species of bumblebees also have more specific preferences to what flower species they choose to utilize. These preferences are linked to the species differences in tongue length.

Another interesting feature about bumblebees is the wide range of sizes they show within and between species and colonies (Knee & Medler 1965; Peat et al. 2005). Bumblebees exhibit great size variation within the worker caste, with up to a tenfold variation in mass within single nests (Goulson et al. 2002), though the largest workers are noticeably smaller than the queen of their species. The workers of different sizes engage in different tasks (alloethism). Larger workers tend to engage in foraging, while smaller workers tend to forage less/ remain in the nest and carry out within-nest tasks.

Summing up, bumblebees provide valuable and unique ecosystem services, being among the most well-adapted and efficient pollinators of many wild flowers and crops. As a consequence of the removal of remnant biotopes and fragmentation in intensively managed agricultural landscapes the bumblebees' resources are increasingly fragmented. A decline in bumblebees on isolated remnants may lead to reduced seed set for several plant species, which again could change the local plant species composition. Increased awareness and knowledge about bumblebees in the agricultural landscape and the consequences changes in the landscape have for the richness and abundance of bumblebees are important. Only with this knowledge there can be developed action plans with the object to stop the decline in bumblebees that we see today. The aim of this study was to evaluate how bumblebees are affected by different variables in the fragmented agricultural landscape. The study was conducted in south-east Norway, which has a landscape dominated by a mixture of intensive cereal production and coniferous forests. Hence the following questions were asked:

1. Can the density of flowering plants explain species richness, abundance or size of bumblebees?
2. Can surface area, circumference and grade of isolation of the patches studied explain species richness, abundance or size of bumblebees?
3. What are preferred forage plants for bumblebees and do they choose the same plant species regardless of their species and caste?

2. Methods

2.1. The study species

Bumblebees (bee genus *Bombus*, Fam. Apidae) belong to the large and exceedingly successful insect order Hymenoptera, and are classified as primitively eusocial bees (Goulson 2010; Gullan et al. 2005). There are 249 known bumblebee species in the world. They are largely confined to temperate, alpine and arctic zones, and found throughout Europe, North

America and Asia. In Norway 34 different species are found, which represents about 14 % of all bumblebee species in the world. In this study 13 different species were recorded.

Table 1. The 13 bumblebee species recorded in this study.

	<i>Bombus</i> species Latin name	<i>Bombus</i> species Norwegian name
'True bumblebees'	<i>B. hortorum</i>	Hagehumle
	<i>B. humilis</i>	Bakkehumle
	<i>B. hypnorum</i>	Trehumle
	<i>B. lapidarius</i>	Steinhumle
	<i>B. lucorum/terrestris</i>	Lys jordhumle
	<i>B. pascuorum</i>	Åkerhumle
	<i>B. pratorum</i>	Markhumle
	<i>B. subterraneus</i>	Slåttehumle
	<i>B. sylvarum</i>	Enghumle
'Cuckoo bumblebees'	<i>B. bohemicus</i>	Jordgjøkhumle
	<i>B. campestris</i>	Åkergjøkhumle
	<i>B. rupestris</i>	Steingjøkhumle
	<i>B. sylvestris</i>	Markgjøkhumle

2.1.1 'True bumblebees'

Social bumblebees generally have similar annual lifecycles. The queens that have mated in late summer hibernate usually in the soil, and emerge in late winter and spring, timing depends on species (Alford 1975; Free & Butler 1959). She will then search for a suitable nest site. Colonies are founded by one single queen, often after a deadly fight between several queens due to competition for the best nest site. Once she has found a suitable site she makes a lump of pollen where she places her eggs. The different species of bumblebees are divided in two groups according to how they store their pollen and how their larvae are fed. These two groups are called pollen-storers and pocket-makers (Alford 1975; Free & Butler 1959; Goulson 2010). The pocket-makers form little pockets or pouches of wax at the side of the wax-covered group of growing larvae, so the larvae can feed directly on the pollen which is plastered into the pockets adjoining them. As the larvae grow the whole group expands in size and comes to have a mass of pollen both beside and underneath it. In addition the larvae of such a group may also feed on pollen that is regurgitated into their cells from time to time by the workers. The pollen storers on the contrary store pollen into waxen cells. Their larvae are so fed individually on a mix of pollen and nectar regurgitated to them by the workers (Free & Butler 1959; Goulson 2010). The first batch of offspring consists only of workers (females) that are dominated by the queen physically, with aggression and pheromones that modify the workers behavior. Within a few days of their emergence the queen stop to forage and the duty

of foraging are taken over by some of the new workers, while some help her tend to new and developing broods. Several more batches of workers are reared and the nest grows rapidly as the work force expands. Depending on the size of the colony, sometime between June and August the nest starts to produce new queens and males. The main factor that triggers the shift is thought to be the density of workers, although it is probably under the influence of the queen (Goulson 2010). In Hymenoptera, the males are haploid and females diploid, so the males are produced from unfertilized eggs. Workers can also lay eggs, for example in absence of the queen or late in season when the queen's physical and chemical influence decrease. The offspring of workers will always be males, since the workers haven't mated. The number of males and queens reared by a colony varies greatly, and is determined by nest size. Once the young queens and males have left the nest to mate and the young queens begin their search for suitable hibernating sites, the nest rapidly degenerates.

*2.1.2 Cuckoo bumblebees (subgenus *Psithyrus*)*

Cuckoo bumblebees, sometimes called parasitic bumblebees, have annual life cycles similar to those of typical temperate bumblebees, except that instead of founding their own nest and rearing workers they steal a nest from a 'true' bumblebee. *Psithyrus* females emerge from hibernation later than their host, and search young nests of other *Bombus* species. Once located, they kill the queen and take over her role. When the *Psithyrus* female have taken over the nest she will lay eggs which will be reared by the bumblebee workers as their own. The eggs develop into either new breeding females or males. Mate location and hibernation are similar to other *Bombus* species.

2.2. The study site

The study was conducted during the summer of 2012 in Ås, Frogn and Vestby in Akershus county, south-east Norway. Agriculture occupies approximately 40% of the land area of Ås, 15% of Frogn and 30% of Vestby (Office of agriculture in Follo, personal communication 4th March 2013). Arable fields, mostly grain-growing and spruce forest dominate the area. Despite agricultural intensification, remnants of uncropped habitat exist scattered throughout the landscape between crop fields and forests. They remain because they cannot be cultivated and are too large or difficult to be removed. These areas are characterized by a cover of semi-natural vegetation harboring a high diversity of plants and animals (Dramstad & Fry 1995) . In an intensively managed area in Akershus, close to 300 different vascular plant species was found, comprising 15 % of the total Norwegian flora (Framstad et al. 1998). The remnants of uncropped area comprise uncultivated "habitat islands" associated with small rocky outcrops

(called “åkerholmer” in Norwegian) that lie completely surrounded by arable fields (variously covered with trees, herbs and areas of bare rock). Linear elements in the landscape, such as road verges, field margins and forest edges, act as a network linking habitat patches together and habitats for several species.

2.3. Data Collection (Field Work)

2.3.1. Study design

Twenty-three different experimental plots, previously used in a different study (Aase, ALTO, personal communication May 10th 2012) were chosen. These experimental plots were patches of semi-natural vegetation (remnants) isolated from similar habitat by different types of unsuitable habitat. The patches were divided in two different types:

1. There were 11 rocky outcrops (“åkerholmer”) completely surrounded by arable fields, which are called ‘islands in arable fields’.
2. The other 12 patches were habitat islands with semi-natural vegetation like meadows, field margins, forest edges and roadsides surrounded by unsuitable habitat. These islands are called ‘islands in matrix’.

The following habitat measurements were recorded from each of the patches:

1. Flower cover. The density of flowering plants at each island were sorted in classes where: class one = 0-40%, class two = 40-70% and class three = 70-100%. The percent density of flowering plants was determined through a visual estimation of the overall coverage and was performed by the same person at all study sites.
2. Surface area and circumference (obtained from the previous study (Aase, ALTO, personal communication May 10th 2012)).
3. Patch type, either an island in arable fields or an island in matrix.

2.3.2. Bumblebee recording

Bumblebees were sampled in five periods of two weeks between June and August 2012. To control for differences in *Bombus* numbers with the time of day, the order in which the different island were visited was changed randomly during the summer. Bumblebees can fly in overcast and rain, but they fly most intensely in sunny weather, weak wind and temperatures above 12° C. The bumblebees were therefore recorded in dry weather, with temperatures above 12° C, between 09.00 and 18.00. Each island was searched with a method called ‘the one man hour’ (Goulson & Darvill 2004; Goulson & Hanley 2004; Goulson et al. 2005; Goulson et al. 2008), which is a timed one hour search within a defined patch. A

stopwatch was used to time the one hour, and every time a bumblebee was caught the clock was stopped. The clock was started when the search continued, which was after the previous bumblebee caught had been recorded and released. The islands were searched systematically; to reduce the chance of recording the same bees more than once to a minimum.

To catch the bumblebees an insect net was used. The bumblebees were then transferred from the net to a small lab glass (“dramsglass” in Norwegian) where they were anaesthetized with CO₂, using an SKS Airgun. For every single bumblebee caught, the following was recorded:

1. Species and cast (queen, worker or male)
2. Weight and length over thorax (measured with a JS-VG 20g x 0,002g spring balance and a Cocraft Digital Vernier caliper: measuring range 150 mm, accuracy 0,03 mm).
3. Forage plant species utilized. Flower identification follows Lid (1979) and Grey-Wilson et al. (2005).

All bumblebees were released immediately after the recordings were taken. Bumblebee identification followed Holmström(2009) and Løken (1985). *B. lucorum* and *B. terrestris* were grouped as *B. lucorum* due to the difficulties in separating the species in the field (Goulson & Darvill 2004; Kwak 1978).

2.4. Data Analysis

Data from the five sampling periods were pooled for analysis. To test for effects of the predictor variables, the data analysis proceeded in several steps. First simple frequency diagrams were produced to inspect the distribution of the dependent variables. Thereafter the independent variables were subjected to mixed model analysis of variance using flower cover score and sampling time and whether the patch was an island in matrix or arable field as independent fixed factors. Covariates, such as the area and circumference length of the patches were also included in the model. It was also conceivable that there were random effects of patch that were not related to the above mentioned attributes of the patch. The random effect of patch and relevant interactions with patch were therefore included in the models. However, the flower cover at each patch was classified into three classes at each sampling time. Flower cover varied with season and the classification of each patch could therefore change and influence the test of the main effect of flower cover. The main effect of flower cover was therefore also analyzed for each sampling time to check that the conclusions concerning this effect did not change. The analysis was performed with the Mixed procedure in the SAS™ System, using Satterthwaite’s approximation to calculate the degrees of freedom for the various effects. The sampling distribution(s) of the residuals were checked with the

univariate procedure for deviations from normality. The same analytical procedure was used with regards to the bumblebees' thorax width and weight. In a few cases it was necessary log transform the independent variable. This is indicated in the various ANOVA tables.

3. Results

3.1 Overall bumblebee species richness and abundance

In total 13 different bumblebee (*Bombus*) species were observed and recorded, reaching a total of 2437 individuals. Of these 13 species 9 species were non-parasitic bumblebee species, with a total of 2370 individuals. *B. pascuorum* and *B. lucorum* dominated with 64% of the observations, followed by *B. hortorum*, *B. pratorum* and *B. lapidarius* with 28% and *B. sylvarum* and *B. hypnorum* with 7% of the observations (Fig. 1). Very low numbers of *B. humilis* (5 individuals) and *B. subterraneus* (3 individuals), were observed, with 0,34% of the observations (Fig. 1).

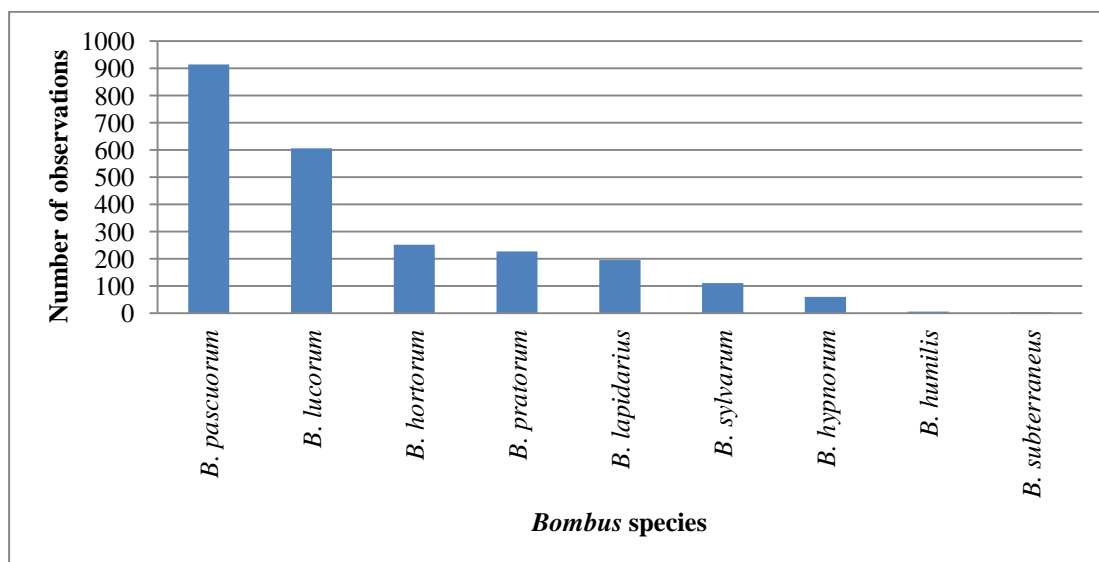


Fig. 1. Total abundance of the social *Bombus* species recorded.

Four parasitic species, ‘cuckoo’ bumblebees (*Psithyrus*) were observed and recorded, reaching a total of 67 individuals (Fig. 2).

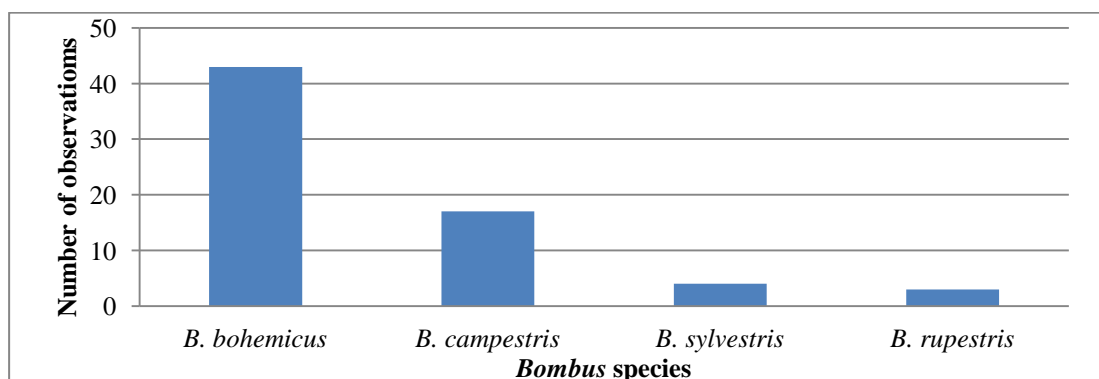


Fig. 2. Total abundance of the parasitic *Bombus* species recorded.

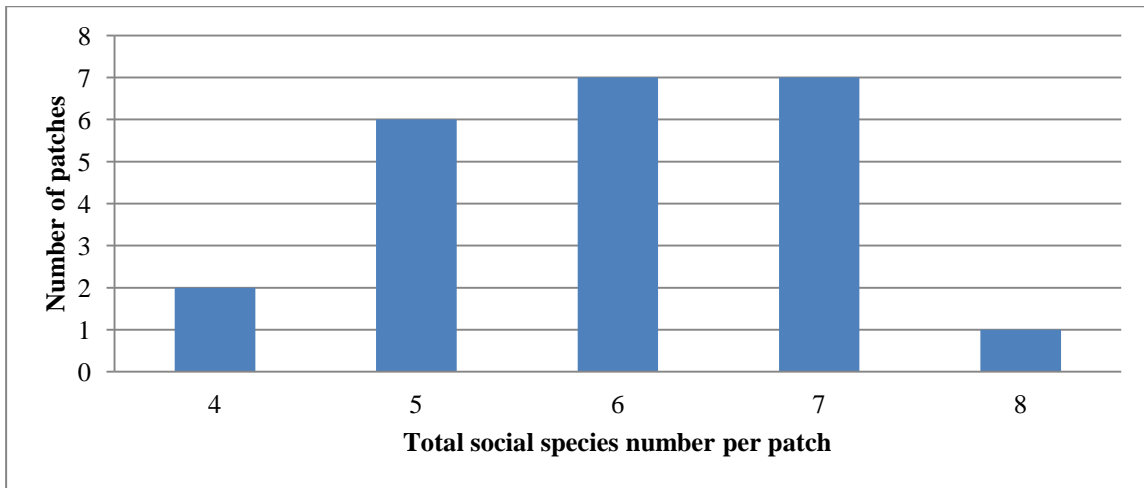


Fig. 3. Distribution of social species number

The bumblebee communities at each patch were composed of four to eight social species (Fig. 3). 20 of the 23 patches were composed of five to seven species.

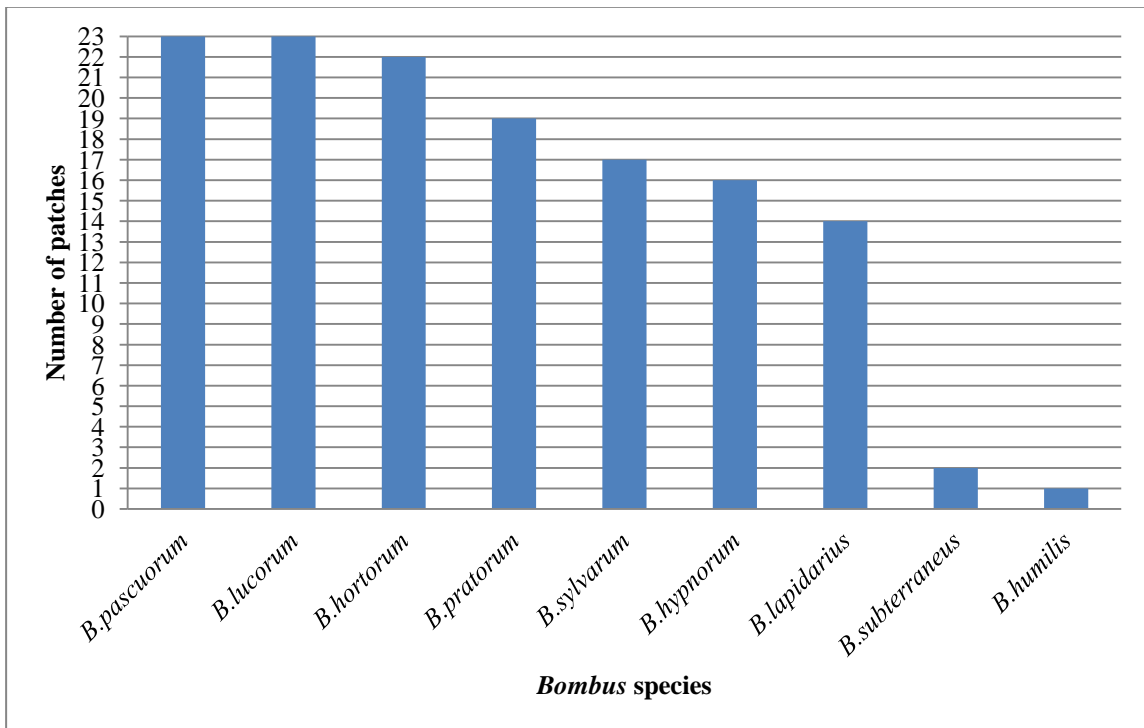


Fig. 4. Distribution of social bumblebee species in the 23 patches.

B. pascuorum and *B. lucorum* were observed in all 23 patches. *B. subterraneus* was only observed at two patches and *B. humilis* was only observed at one patch (Fig. 4).

3.2 Importance of patch quality for bumblebee species richness and abundance

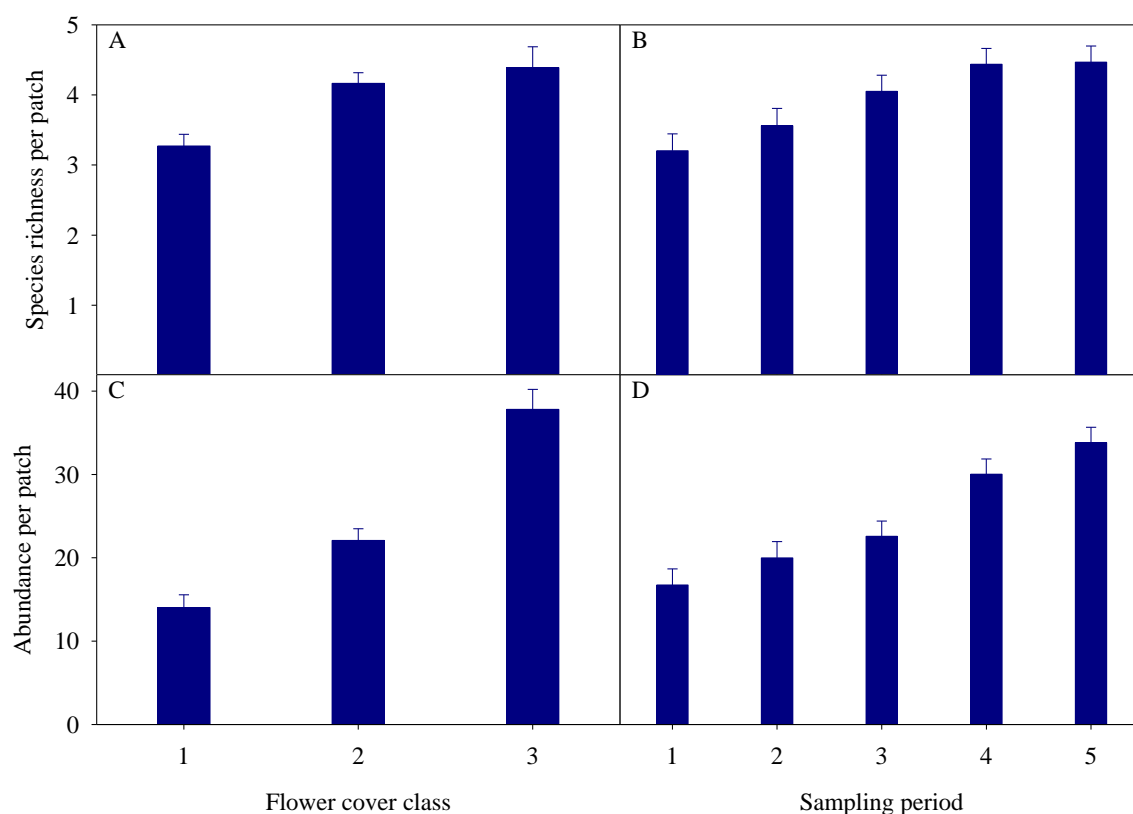


Fig. 5. A) Flower cover class. B) Flower cover class. C) Sampling period. D) Sampling period.

Species richness and abundance of the social bumblebees increased with flower cover and season (Fig. 5). When entering both variables into an analysis of variance (Table 2) the Flower cover significantly explained the total number of social species and abundance of social species. In addition the abundance of social species differed significantly between the sampling periods. There was also a tendency of social species number to change with period, but this was not significant ($p=0.0721$ Table 2). Neither of the variables could explain the species number and abundance of the parasitic bumblebee species (Table 2).

As for the landscape parameters, neither had any significant effect on abundance and species number of social or parasitic bumblebee species.

Table 2. Analysis of variance for fixed effects of various traits.

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
Number of social species	Flower cover	2	92	10,75	<.0001
	Period	4	92	2,23	0,0721
	Flower cover*period	7	92	1,25	0,2817
	Island	1	92	0,81	0,3697
	Flower cover*island	2	92	0,23	0,7938

Table 2. Continued

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
	Period*island	4	92	1,7	0,1567
	Circumference	1	92	2,26	0,1362
	Area	1	92	1,14	0,2888
Number of parasitic species	Flower cover	2	10	0,51	0,6177
	Period	4	10	1,01	0,4487
	Flower cover*period	6	10	0,63	0,7018
	Island	1	10	0,02	0,8931
	Flower cover*island	1	10	1,82	0,2069
	Period*island	3	10	1,15	0,3764
	Circumference	1	10	0,02	0,8815
	Area	1	10	0	0,9671
Abundance of social species	Flower cover	2	90,8	30,26	<.0001
	Period	4	77,6	12,05	<.0001
	Flower cover*period	7	85,9	1,62	0,1414
	Island	1	26,6	1,9	0,1799
	Flower cover*island	2	90,3	0,22	0,8021
	Period*island	4	77,2	0,48	0,7493
	Circumference	1	21,3	0,52	0,4778
	Area	1	21,7	1,03	0,3204
Abundance of parasitic species	Flower cover	2	10	0,12	0,8891
	Period	4	10	0,38	0,8204
	Flower cover*period	6	10	0,24	0,9519
	Island	1	10	0,35	0,5679
	Flower cover*island	1	10	0,13	0,7256
	Period*island	3	10	0,02	0,997
	Circumference	1	10	0,75	0,407
	Area	1	10	0,27	0,6137

The mean flower cover was overall higher at the islands in arable fields (Fig. 6). When entering the variables into an analysis of variance there is a significant effect of the patch being an island in arable fields ($p=0,0098$ Table 3). Neither of the other parameters had any significant effect on flower cover.

Table 3. Analysis of variance for fixed effects on flower cover.

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
Flower cover	Island	1	18,6	2,28	0,0098
	Period	4	76,9	0,77	0,548
	Circumference	1	19	1,61	0,2201
	Area	1	18,2	2,54	0,128

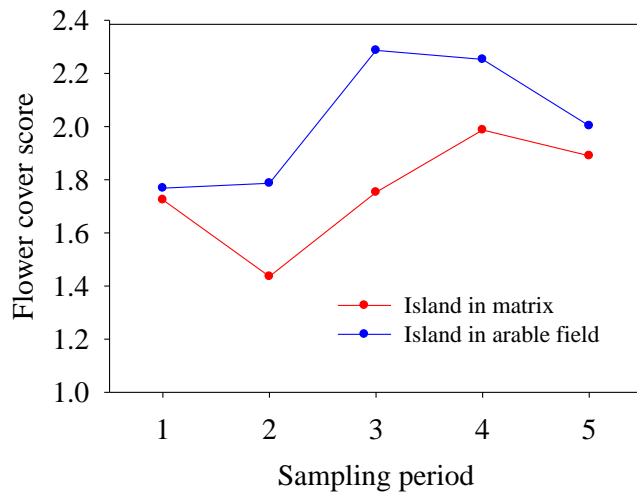


Fig 6. Mean flower cover in the five sampling periods from June to August.

3.3 Abundance of the six most common bumblebee species in relation to patch quality

When entering all variables into an analysis of variance for the workers of each species (Table 4), the flower cover significantly explained the abundance of *B. hortorum*, which had highest mean abundance in flower cover class three (Fig. 7). The effect of flower cover also changed with period in *B. hortorum*, the number of individuals in all flower cover classes increased from period one to three, before it declined in period three to four. There was a tendency towards change in abundance of *B. pascuorum* ($p=0,0573$ Table 4) and *B. lapidarius* ($p=0,0535$ Table 4) with flower cover. The mean abundance of *B. pascuorum* was highest in patches with flower cover class three, while the data for *B. lapidarius* are more difficult to interpret (Fig. 7). Looking closer at *B. pascuorum*, mean abundance increased in flower cover classes two and three relative to class one from period two to three and had the highest mean number of individuals relative to the other species in from period three to five. Sampling period significantly explained the abundance of *B. pascuorum*, *B. hortorum*, *B. pratorum* and *B. sylvarum*. *B. pascuorum* and *B. sylvarum* had highest mean abundance in period five, while *B. hortorum* and *B. pratorum* had highest mean abundance in period three (figure 7). Sampling period had a weak effect on the abundance of *B. lucorum* ($p=0,0845$ table 4), but this was not significant. As for the landscape parameters neither had any significant effect on abundance of the six most common species, with a possible exception of area, which had a weak effect on the abundance of *B. lapidarius* ($p=0,0641$ Table 4).

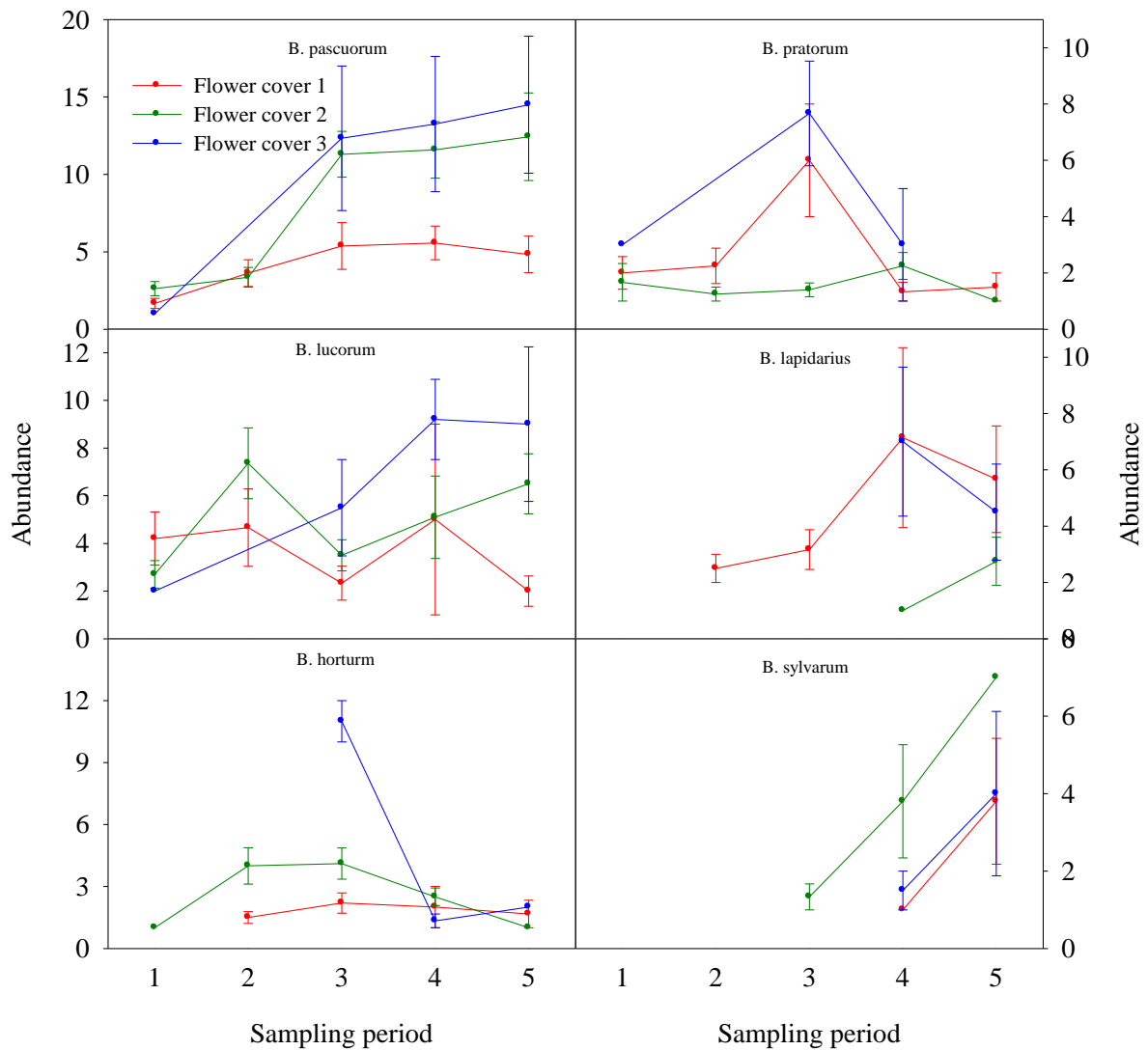


Fig. 7. Mean (\pm SE) abundance at the five sampling times from June to August for the six most common bumblebee species.

Table 4. Analysis of variance for fixed effects of various traits on the abundance of the six most common bumblebee species observed.

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
Abundance of <i>B. pascuorum</i>	Flower cover	2	75,1	2,97	0,0573
	Period	4	66,5	9,59	<.0001
	Flower cover*period	7	71,4	1,48	0,1893
	Island	1	30,0	4,86	0,0357
	Flower cover*island	2	74,3	0,01	0,9903
	Period*island	4	65,5	0,61	0,6603
	Circumference	1	21,5	0,01	0,9341
	Area	1	21,3	0,15	0,7070
Abundance of <i>B. lucorum</i>	Flower cover	2	58,4	1,74	0,1848
	Period	4	57,0	2,17	0,0845
	Flower cover*period	7	58,8	1,02	0,4268
	Island	1	21,2	3,32	0,0826
	Flower cover*island	2	62,6	0,39	0,6766

Table 4. Continued

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
	Period*island	4	53,3	0,77	0,5512
	Circumference	1	21,4	0,16	0,6975
	Area	1	26,4	0,09	0,7642
Abundance of <i>B. hortorum</i>	Flower cover	2	27,6	3,46	0,0456
	Period	4	22,9	5,16	0,0041
	Flower cover*period	5	25,6	3,56	0,0141
	Island	1	26,3	0,04	0,8490
	Flower cover*island	2	27,1	0,13	0,8816
	Period*island	3	24,3	0,05	0,9853
	Circumference	1	20,8	1,15	0,2968
	Area	1	23,9	0,57	0,4585
Abundance of <i>B. pratorum</i>	Flower cover	2	17,0	0,84	0,4508
	Period	4	17,0	3,91	0,0199
	Flower cover*period	6	17,0	2,47	0,0662
	Island	1	17,0	0,77	0,3913
	Flower cover*island	2	17,0	1,76	0,2025
	Period*island	4	17,0	0,51	0,7320
	Circumference	1	17,0	0,14	0,7095
	Area	1	17,0	0,00	0,9550
In(Abundance) of <i>B. lapidarius</i>	Flower cover	2	16,9	3,58	0,0535
	Period	3	15,3	2,06	0,1564
	Flower cover*period	2	14,6	0,82	0,4610
	Island	1	15,4	0,29	0,5983
	Flower cover*island	2	17,0	2,92	0,0844
	Period*island	3	14,2	1,77	0,2079
	Circumference	1	15,3	1,66	0,2173
	Area	1	15,2	3,94	0,0641
Abundance of <i>B. sylvarum</i>	Flower cover	2	6,2	2,10	0,2007
	Period	2	6,9	7,44	0,0190
	Flower cover*period	3	2,6	1,25	0,4436
	Island	1	6,2	0,85	0,3922
	Flower cover*island	2	6,4	2,44	0,1631
	Period*island	2	2,7	3,64	0,1734
	Circumference	1	5,4	4,90	0,0738
	Area	1	5,3	3,73	0,1079

3.4 Size of the six most common bumblebee species in relation to patch quality

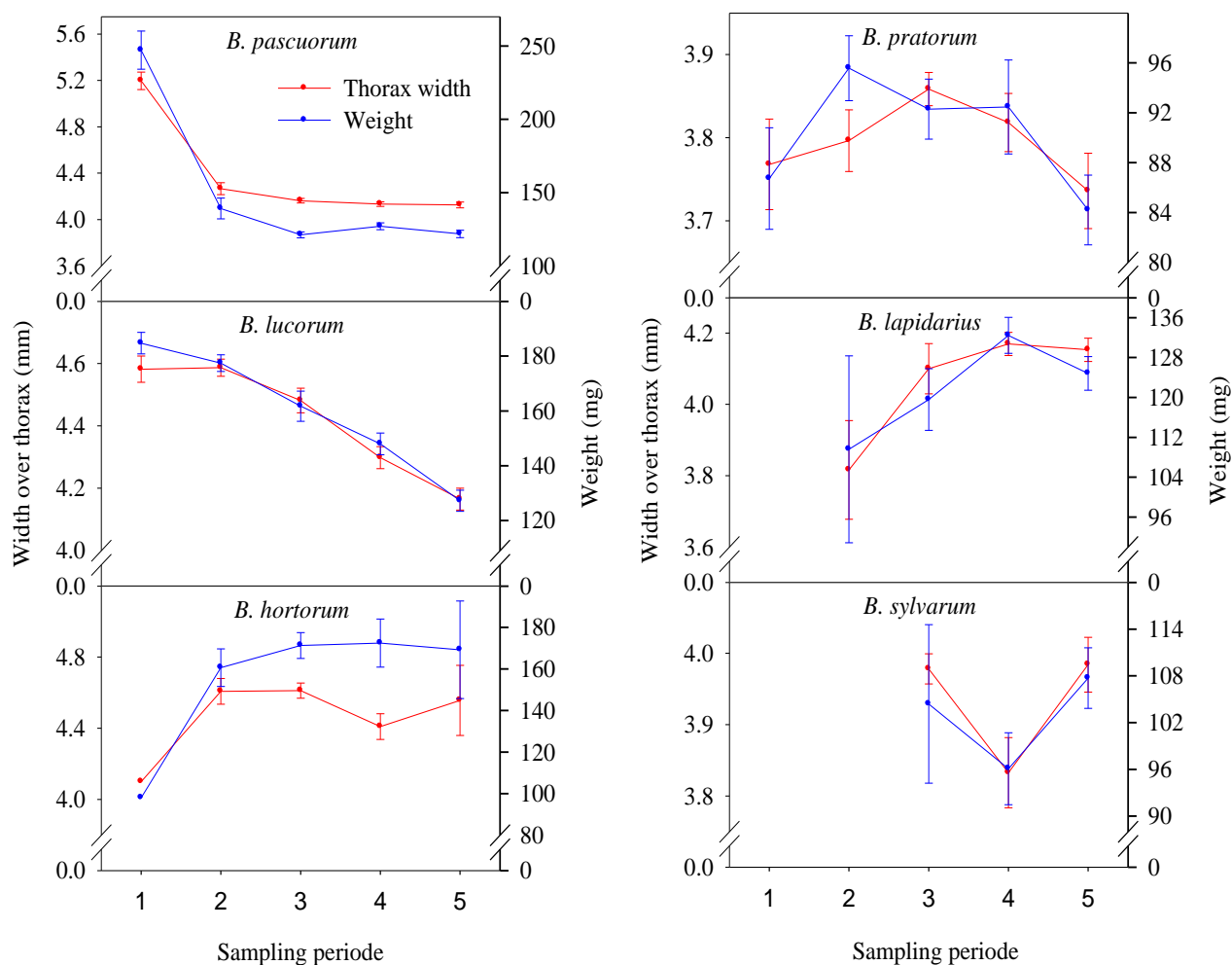


Fig. 8: Mean (\pm SE) thorax width and weight at the five sampling times from June to August for the six most common bumblebee species.

When entering all the variables into an analysis of variance for the workers of each species (Table 5 and 6), sampling period significantly explained the thorax width of *B. pascuorum* and *B. lucorum*. The mean thorax width of these two species was highest in period one, the thorax width of *B. pascuorum* rapidly declined from period one to two, while the thorax width of *B. lucorum* steadily declined from sampling period one to five (Fig. 8). Sampling period had a weak effect on the thorax width of *B. lapidarius* ($p=0,0581$ Table 6), but was not significant. The mean thorax width of *B. lapidarius* increased from period two to five. Sampling period significantly explained the weight of *B. pascuorum*, *B. lucorum* and *B. lapidarius*. The weight of *B. pascuorum* and *B. lucorum* declined parallel with the length. The weight of *B. lapidarius*, on the other hand, increased from period one to two, before it declined from period two to three and period four to five (Fig. 8).

Flower cover class had a weak effect on the thorax width of *B. lapidarius* ($p=0,0519$ Table 5). However there was a significant interaction in the model between flower cover class and sampling period. Flower cover class had a significant effect on the weight of *B. pascuorum* and *B. lapidarius*. There was a significant interaction in the model between flower cover class and period for *B. lapidarius*. There was also a tendency towards an interaction between flower cover class and period for *B. pascuorum* ($p=0,0560$ Table 6), but this was not significant.

There was a significant effect of island on the weight of *B. lapidarius* ($p=0,0456$). Individuals of *B. lapidarius* recorded on islands in arable fields were significantly heavier compared to those recorded on islands in matrix. As for the other parameters, neither had any significant effect on the worker size of the six most common bumblebee species (Table 5 and 6).

Table 5. Analysis of variance for fixed effects of various traits on the thorax width of the six most common bumblebee species observed.

Dependent variable	Effect	Numerator		Denominator	
		DF	DF	F Value	Pr > F
Thorax width <i>B. Pascuorum</i>	Flower cover	2	119,6	1,27	0,2859
	Period	4	78,6	12,74	<.0001
	Flower cov*period	7	68,8	1,27	0,2767
	Island	1	69,2	1,65	0,2030
	Flower cover*island	4	74,9	0,68	0,6073
	Period*island	2	55,9	0,47	0,6254
	Circumference	1	82,3	2,55	0,1144
	Area	1	72,2	0,93	0,3376
Thorax width <i>B. lucorum</i>	Flower cover	2	79,6	0,00	0,9955
	Period	4	71,8	7,87	<.0001
	Flower cov*period	7	67,7	1,43	0,2062
	Island	1	57,6	0,18	0,6740
	Flower cover*island	4	71,7	1,78	0,1424
	Period*island	2	69,0	0,14	0,8668
	Circumference	1	98,2	0,37	0,5427
	Area	1	82,8	0,67	0,4170
Thorax width <i>B. hortorum</i>	Flower cover	2	45,2	2,00	0,1473
	Period	4	53,8	1,56	0,1996
	Flower cov*period	5	41,7	0,80	0,5578
	Island	1	47,1	0,09	0,7677
	Flower cover*island	3	29,5	0,85	0,4797
	Period*island	2	43,4	1,96	0,1528
	Circumference	1	43,3	1,95	0,1697
	Area	1	39,1	2,75	0,1055
Thorax width <i>B. pratorum</i>	Flower cover	2	9,6	0,88	0,4448
	Period	4	9,7	0,91	0,4966

Table 5. Continued

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
	Flower cov*period	6	8,1	0,23	0,9538
	Island	1	7,7	0,04	0,8385
	Flower cover*island	4	9,3	0,40	0,8073
	Period*island	2	7,5	0,66	0,5456
	Circumference	1	14,3	0,75	0,4019
	Area	1	13,7	0,60	0,4504
Thorax width <i>B. lapidarius</i>	Flower cover	2	17,0	3,54	0,0519
	Period	3	17,4	3,01	0,0581
	Flower cov*period	2	16,5	3,86	0,0420
	Island	1	13,1	3,41	0,0876
	Flower cov*island	3	15,3	1,09	0,3846
	Period*island	2	13,3	1,03	0,3838
	Circumference	1	13,5	0,50	0,4904
	Area	1	12,0	0,30	0,5927
Thorax width <i>B. sylvarum</i>	Flower cover	2	22,1	1,15	0,3354
	Period	2	21,3	1,39	0,2695
	Flower cov*period	3	22,1	0,55	0,6532
	Island	1	23,4	0,79	0,3820
	Flower cover*island	2	18,5	0,92	0,4165
	Period*island	2	14,7	1,12	0,3540
	Circumference	1	22,8	2,06	0,1645
	Area	1	21,9	2,87	0,1044

Table 6 Analysis of variance for fixed effects of various traits on the weight of the six most common bumblebee species observed.

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
Weight <i>B. pascuorum</i>	Flower cover	2	90,0	3,41	0,0373
	Period	4	62,7	8,61	<.0001
	Flower cov*period	7	56,0	2,12	0,0560
	Island	1	54,6	3,44	0,0690
	Flower cover*island	4	59,5	1,88	0,1261
	Period*island	2	46,1	0,11	0,8972
	Circumference	1	65,0	1,48	0,2277
	Area	1	58,0	0,68	0,4113
Weight <i>B. lucorum</i>	Flower cover	2	82,2	0,44	0,6471
	Period	4	72,5	8,19	<.0001
	Flower cov*period	7	67,7	0,46	0,8612
	Island	1	56,3	0,30	0,5866
	Flower cover*island	4	72,5	1,51	0,2084
	Period*island	2	69,4	0,24	0,7883
	Circumference	1	102,5	1,15	0,2852
	Area	1	85,1	1,71	0,1943
Weight <i>B. hortorum</i>	Flower cover	2	36,1	2,36	0,1086

Table 6. Continued

Dependent variable	Effect	Numerator DF	Denominator DF	F Value	Pr > F
	Period	4	42,1	1,46	0,2323
	Flower cov*period	5	34,9	0,65	0,6662
	Island	1	37,1	0,01	0,9167
	Flower cover*island	3	29,9	0,96	0,4232
	Period*island	2	35,8	0,65	0,5279
	Circumference	1	38,9	1,25	0,2699
	Area	1	37,2	2,26	0,1412
<i>Weight B. Pratorum</i>	Flower cover	2	12,5	0,32	0,7300
	Period	4	12,8	0,51	0,7294
	Flower cov*period	6	11,5	0,54	0,7666
	Island	1	11,0	0,21	0,6561
	Flower cover*island	4	12,5	0,19	0,9367
	Period*island	2	10,6	0,37	0,6973
	Circumference	1	17,2	0,08	0,7743
	Area	1	16,4	0,30	0,5936
<i>Weight B. lapidarius</i>	Flower cover	2	17,3	4,30	0,0305
	Period	3	17,7	4,09	0,0227
	Flower cov*period	2	16,7	5,09	0,0187
	Island	1	13,1	4,87	0,0456
	Flower cover*island	3	15,4	1,41	0,2788
	Period*island	2	13,3	1,22	0,3252
	Circumference	1	13,5	0,78	0,3932
	Area	1	11,9	0,43	0,5232
<i>Weight B. sylvarum</i>	Flower cover	2	19,6	1,06	0,3659
	Period	2	18,9	0,59	0,5662
	Flower cov*period	3	19,7	0,90	0,4567
	Island	1	20,5	1,46	0,2404
	Flower cover*island	2	16,5	1,26	0,3088
	Period*island	2	13,8	1,48	0,2616
	Circumference	1	20,4	1,36	0,2575
	Area	1	19,7	1,94	0,1795

3.5 Flower preferences of the six most common bumblebee species

In total, 1588 foraging workers were observed visiting 45 flowering plant species over the study period. Seven of the 45 utilized plant species received 1225 (77%) of the total visits, common cow wheat (*Melampyrum pratense* L.) received 469 visits, bird vetch (*Vicia cracca* L.) received 175 visits, raspberry (*Rubus idaeus* L.) received 150 visits, alsike clover (*Trifolium hybridum* L.) received 145 visits, common hemp-nettle (*Galeopsis tetrahit* L./*bifida* Boenn.) received 122, red clover (*Trifolium pratense* L./*medium* L.) received 94 visits and white clover (*Trifolium repens* L.) received 70 visits.

Of the 45 utilized flower species 85 % were perennial, and this suggests a tendency for bumblebees to visit perennial plant species rather than annuals. One should still note that since plant species not were recorded if they did not receive any visits, the data from this study can't demonstrate this rigorously. Two of the most visited plant species, *Melampyrum pratense* and *Galeopsis tetrahit/bifida*, are annuals and received 38 % of the total visits.

Flower preferences for each of the six most abundant bumblebee species were calculated. Fig. 9, 10 and 11 show what plant species the different species preferred. *B. pascuorum* utilized 33 of the 45 different plant species, with a clear preference for *Melampyrum pratense* (181 visits), *Vicia cracca* (126 visits), *Galeopsis tetrahit/bifida* (96 visits) and *Trifolium hybridum* (79 visits). *B. lucorum* utilized 35 different plant species, with a clear preference for *Melampyrum pratense* (170 visits) and *Rubus idaeus* (57 visits). All the other plant species *B. lucorum* visited received less than 16 visits each. *B. hortorum* utilized 21 different plant species and showed a clear preference for *Melampyrum pratense* (67 visits), *Trifolium pratense/medium* (25 visits) and *Vicia cracca* (18 visits). *B. pratorum* utilized only 9 different plant species, and showed a clear preference for *Rubus idaeus* (46 visits) and *Melampyrum pratense* (39 visits). These two plant species comprised almost 90% of all recorded visits by *B. pratorum*. *B. lapidarius* utilized 20 different plant species, and showed a preference for *Trifolium hybridum* (42 visits), *Cirsium* spp. (18 visits), *Asteràceae* spp. (17) and *Trifolium repens* (16 visits). *B. sylvarum* utilized 14 different plant species, and preferred *Trifolium pratense/medium* (16 visits), *Trifolium hybridum* (14 visits), *Galeopsis tetrahit/bifida* (10 visits) and *Vicia cracca* (9 visits).

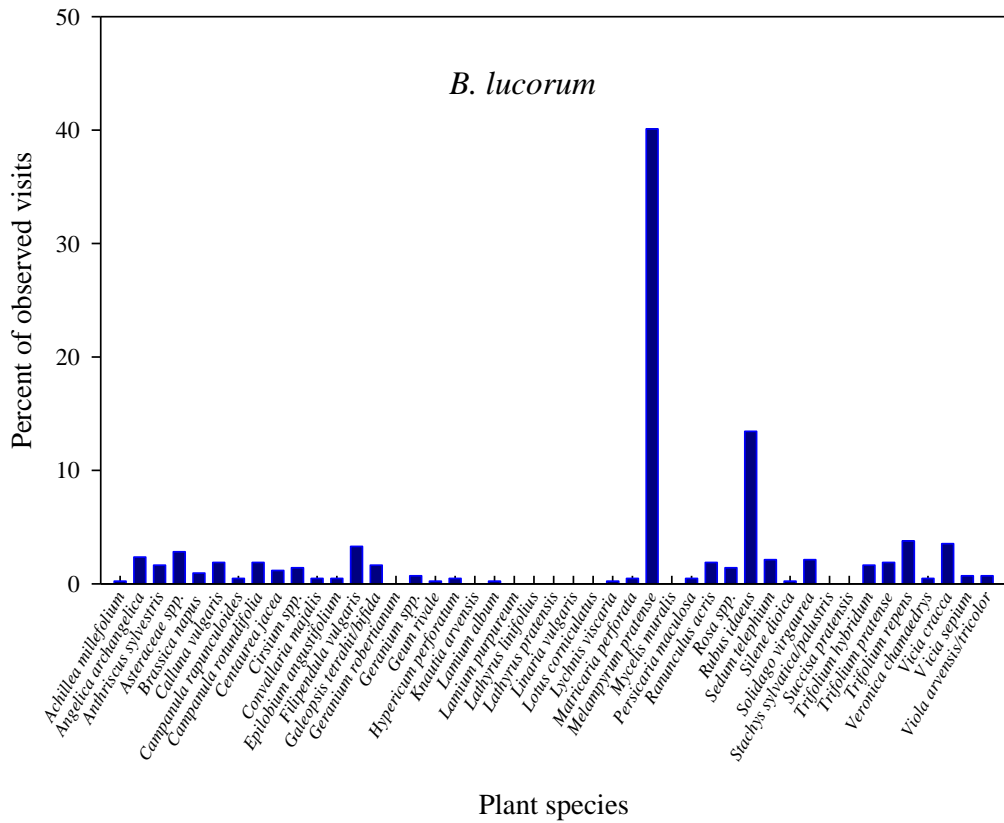
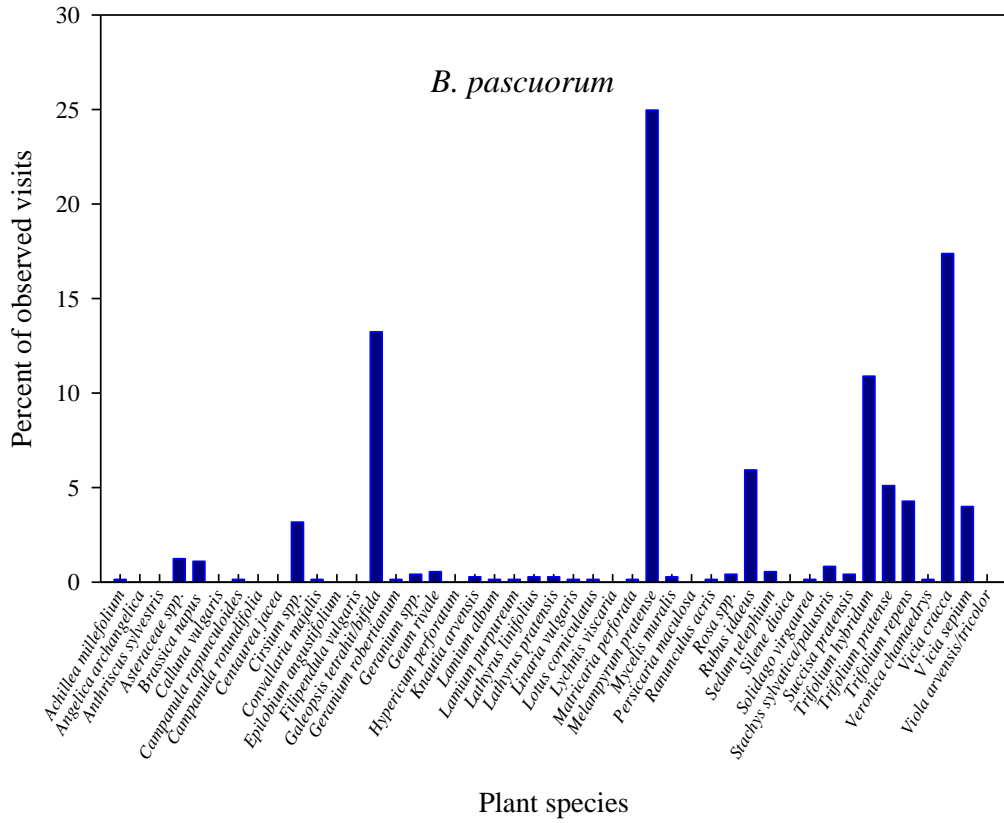


Fig. 9. Percent of observed visits to the different plant species by workers from June to August. *B. pascuorum*, upper, and *B. lucorum*, lower.

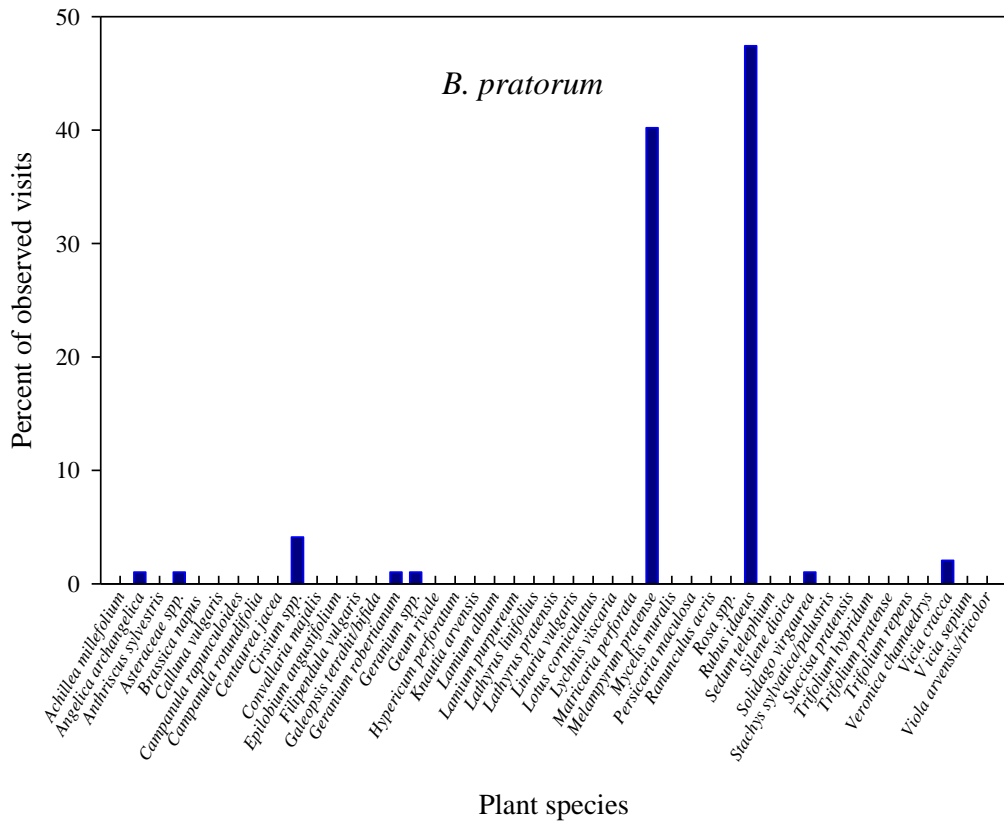
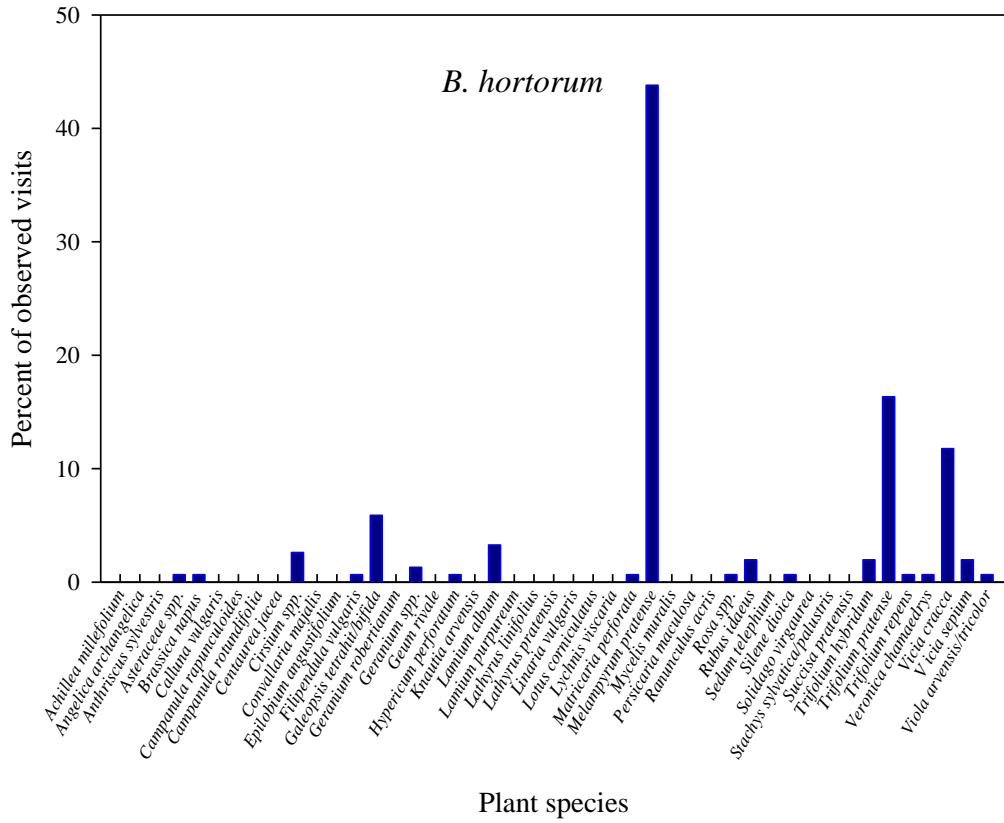


Fig. 10. Percent of observed visits to the different plant species by workers from June to August. *B. hortorum*, upper, and *B. pratense*, lower.

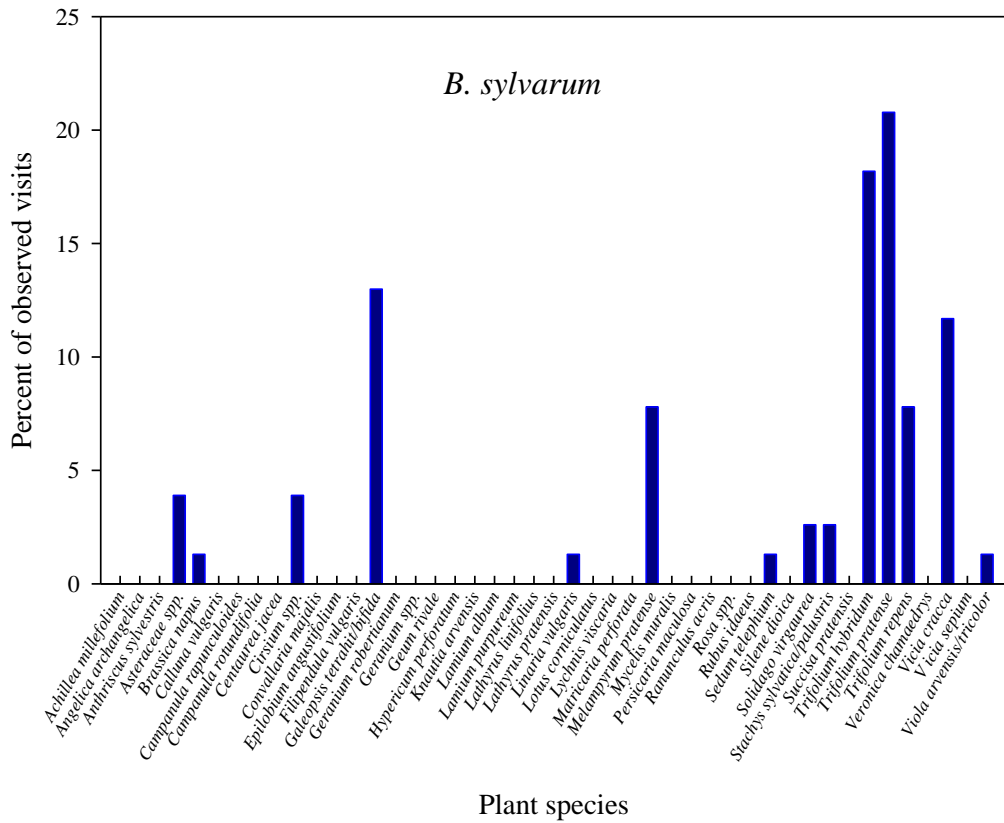
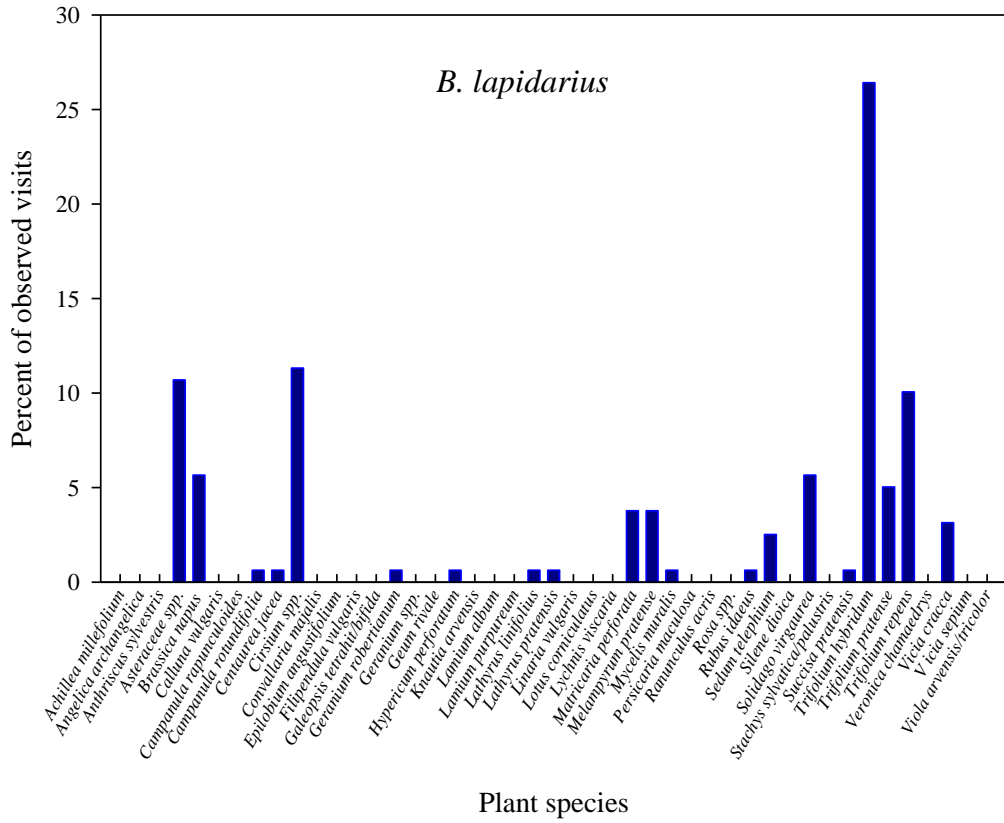


Fig. 11. Percent of observed visits to the different plant species by workers from June to August. *B. lapidarius*, upper, and *B. sylvarum*, lower.

In total 372 males of the six most abundant species were observed visiting 24 different flower species (Fig. 12). *Cirsium* spp. were the most visited plant species, with 28% of the total visits.

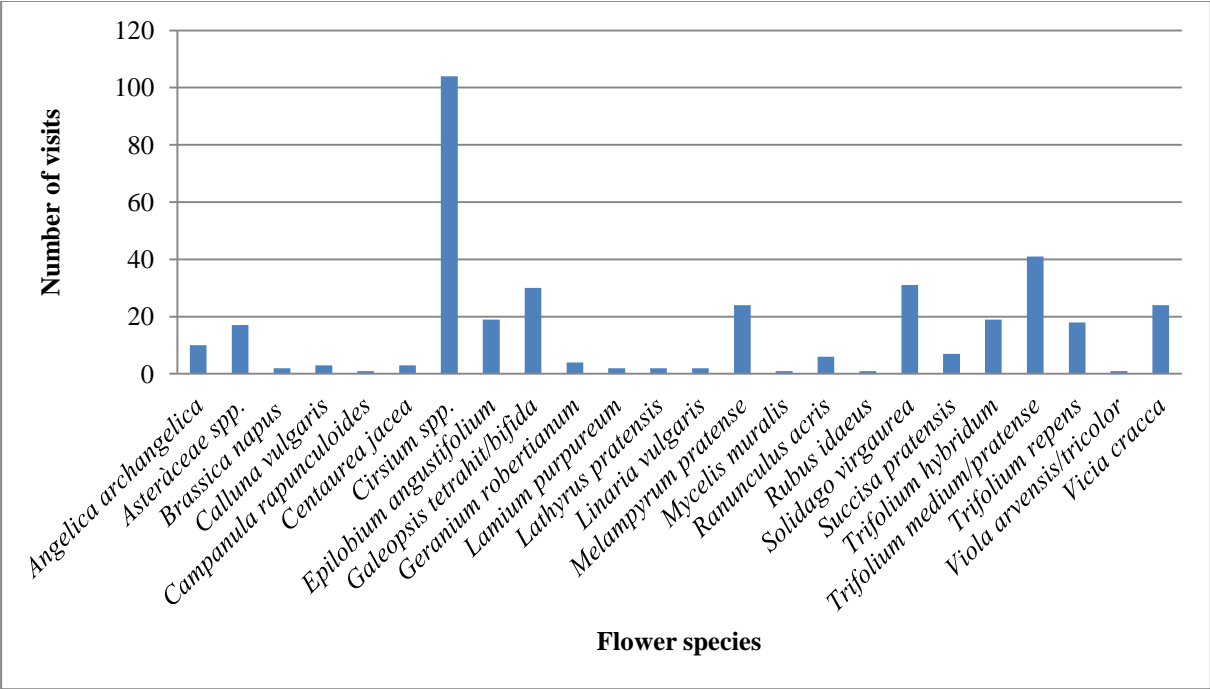


Fig. 12. The different plant species utilized by the males of the six most abundant bumblebee species.

244 queens of the six most common bumblebee species were observed visiting 30 different flowers (Fig. 13). *Rubus idaeus* and *Melampyrum pratense* were the queens preferred plant species, comprising 47% of the total visits.

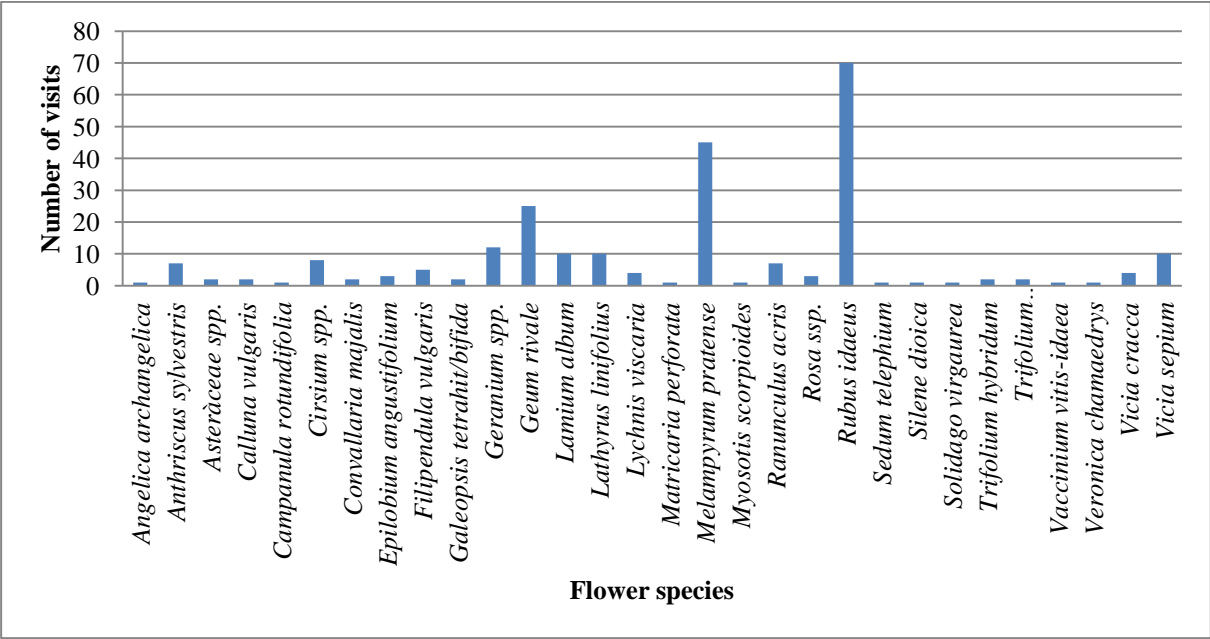


Fig. 13. The different plant species utilized by the queens of the six most abundant bumblebee species.

4. Discussion

4.1 Overall bumblebee species richness and abundance

The number of social bumblebee species recorded in this study (9) seems low in comparison with the 14-17 species recorded in this region (Løken 1973; Ranta 1982), but in a study from the same agricultural area Dramstad and Fry (1995) recorded only seven social bumblebee species. Dramstad and Fry (1995) also found that *B. lucorum* and *B. pascuorum* dominated the records, comprising 71% of the total number of observations.

Løken (Løken 1973) lists six species as widely distributed throughout Scandinavia, namely *B. lucorum*, *B. pascuorum*, *B. hortorum* and *B. lucorum*, *B. jonellus* and *B. hypnorum*. *B. jonellus* was the only one of these not found in this study, maybe because this species avoid intensively cultivated areas (Løken 1973). All the species found in this study, except *B. humilis* and *B. subterraneus*, is reported to be widely distributed in this part of Norway, and do not seem to be affected so hard by habitat loss and fragmentation. The species that are declining the most and are most negatively affected by habitat loss and fragmentation are those with long tongues foraging perennials with deep corollas (Ødegaard et al. 2009). *B. humilis* is reported to have a scattered distribution in southeastern lowlands, while *B. subterraneus* is reported to be rare in Norway and to have scattered localities in the southeastern lowlands, restricted to the areas around the Oslofjord. Both *B. humilis* and *B. subterraneus* are on the Norwegian Redlist, listed as vulnerable and critically endangered respectively (Kålås et al. 2010). *B. subterraneus* is known to decline in Norway as well as the rest of Europe. *B. subterraneus* was last seen in the United Kingdom in Dungeness National Nature Reserve in 1988 and declared regionally extinct in 2000. *B. sylvarum* is also highly endangered and in the late stages of a similar process in UK, and likely to go extinct in the near future (Goulson et al. 2008; Williams 1982). The reasons to why there is such a difference between bumblebee populations in Norway and the UK might be that the present situation in Norway is somewhat different from more intensively cultivated areas of United Kingdom. Even though the trends concerning changes in agricultural practice are the same throughout Europe, topography, climate and politics have limited the agricultural intensification in many areas in Norway (Fjellstad & Dramstad 1999). Norway differs from most European countries in the low proportion of farmland. Just 3,3% of the total land area in Norway are registered as agricultural area (Framstad et al. 1998), compared with around 75% in the United Kingdom (Robinson & Sutherland 2002). Since 1960 almost half of the agricultural holdings in Norway have been closed down, while the remaining running agricultural holdings have more than doubled its area (Framstad et al. 1998). However, the

average farm size in Norway is still small compared with the average farm size in the UK (Fjellstad & Dramstad 1999). It is therefore likely that the removal of remnant biotopes and use of agrochemicals in the agricultural landscape in the UK has had a higher impact on bumblebees than in Norway.

The five most common and widespread bumblebee species found in this study are the same as those Williams called the “mainland ubiquitous”(1982). *B. lucorum/terrestris*, *B. pascuorum*, *B. hortorum*, *B. pratorum* and *B. lapidarius* dominated the different communities. Since the study area in Ås, Vestby and Frogn is influenced by intensive agricultural activity and don't have a high habitat diversity, it is no surprise that the bumblebee records were dominated by ubiquitous species, rather than habitat specialists with restricted distributions (Dramstad & Fry 1995; Williams 1986). The findings also follow reports that local species richness in bumblebee communities in Northern and Central Europe typically consists of six to eleven species (Ranta & Vepsäläinen 1981).

4.2 Importance of patch quality for overall bumblebee species richness and abundance

The results from this study clearly show that the total abundance and species richness of social bumblebees were affected by the flower cover. Several studies at the landscape level have found positive relationships between the richness and abundance of floral resources and pollinator richness and abundance (Hegland & Boeke 2006; Steffan-Dewenter & Tscharrntke 1999; Steffan-Dewenter et al. 2002; Westphal et al. 2003; Öberg et al. 2010). Hegland and Boeke (2006) found that the abundance of flowering plants was more important for bumblebees than plant species richness. Since many of the bumblebees are generalists, increased diversity and richness of flower species may not cause increased floral resources for the bumblebees. Bumblebees choose patches with high flower cover because this obviously will increase the possibilities for high rewards, and they want to maximize their rate of resource acquisition (Goulson 2010). This corresponds with the findings in this study that there is a positive relationship between flower cover within patches and abundance of bumblebees. Bumblebees have high energetic demands, and therefore have a search pattern that resembles the blossom density. When the rewards decrease or fall below a critical threshold they will switch resources or leave the patch (Chittka et al. 1997; Dukas & Real 1993).

There was no difference in the social bumblebee abundance and richness between islands in arable land and islands in matrix (forest edges, field margins and road verges). According to the result of this study one would maybe expect the richness and abundance of bumblebees to

be higher in the habitat remnants completely surrounded by arable fields due to the results that the flower cover was higher here. Since this is not the case one could argue the bumblebee abundance and richness to be higher in habitat remnants not completely surrounded by arable land. Here the bumblebees would have better possibilities to disperse through corridors like field margins and road edges, and therefore have better foraging possibilities. Landscape heterogeneity has been shown to increase species richness and abundance of bumblebees in agricultural landscapes (Rundlöf et al. 2008). Bäckman and Tiainen (2002) found that of all non-arable habitats, field margins are the most important ones for bumblebees in agricultural environment, especially as they are wide-spread and offer food resources, but they are also places for reproduction and overwintering. Osgathorpe et al. (2012) found that both agricultural and adjacent non-agricultural habitats were utilized by foraging bumblebees, but off-farm habitats were of greater importance to long-tongued species. Similarly, Mänd et al. (2002) found greater diversity of foraging bumblebees within non-agricultural habitats adjacent to farmland in Estonia. Track edges and road verges are outside the direct influence of farm management practices, although they are still subject to indirect influences from the adjacent agricultural land.

The results showed no significant effect of habitat size or circumference and bumblebee abundance and richness. Theories about the relationship between area and number of species state that the number of species in a habitat can be viewed as a function of area and that this is the a good predictor of species number (Simberloff 1974). This would mean that a larger area gives higher number of plant species, although which species that occurs depends on the environment on the habitat remnants (Framstad et al. 1998). This means that a large area, compared to a smaller, not necessarily have a higher number of plants that bumblebees prefer to utilize. In general one also finds the highest plant species richness around the edges of remnant biotopes such as islands surrounded by crops (Framstad et al. 1998), though as with number of plant species in relation to area, this does not mean that the number of plant species preferred by bumblebees are any higher here.

That the period significantly affected the total abundance of the social bumblebees is no surprise. The successful bumblebee colony grows all through the season, and will have the highest number of individuals in the end of the season before the colonies degenerates. The total number of individuals will therefore be highest in late June to August. The weak tendency for period affecting the social species richness can be explained with the queens timing of emergence from hibernation. The timing of emergence differ between the queens

of the different species, and this influence which species that were observed in the first periods.

4.3 Abundance of the six most common bumblebee species in relation to patch quality

The six most abundant species were *B. pascuorum*, *B. lucorum*, *B. hortorum*, *B. pratorum*, *B. lapidarius* and *B. sylvarum*. The abundance of the different species in this study differs greatly, with *B. pascuorum* and *B. lucorum* being the most abundant (Fig. 1).

The flower cover significantly explained the abundance of *B. hortorum*. Of the six most abundant species this is the one with the longest tongue and the most specialized diet, preferring flowers with deep corollas, like *Trifolium medium/pratense* (Goulson & Darvill 2004; Goulson et al. 2005), while the species with shorter tongues have broad foraging preferences and exploit a wider range of floral resources. This could explain the observed differences in abundance between the species, because species with narrow diet breadth have access to fewer resources. Sowig (1989) showed that the long tongued bumblebee species tend to visit flowers in small patches, whereas short tongued species favored the same species growing in large patches. In this study on the contrary the mean abundance of *B. hortorum* was highest in patches with flower cover three in sampling period three. There were however a significant effect of period, and in sampling period four the number of observed *B. hortorum* were smallest in patches with flower cover three, which correlates to Sowigs (1989) results. Flower cover did not significantly explain the abundance of any of the other species, although mean abundance of *B. pascuorum*, *B. lucorum*, *B. hortorum* and *B. pratorum* was highest in patches with Flower cover class three. This corresponds with the findings of several other studies showing that there is a positive relationship between flower cover within patches and the abundance of bumblebees (Banaszak 1983; Hegland & Boeke 2006; Westphal et al. 2003; Öberg et al. 2010).

The differences in mean abundance between the workers of the different species in the five sampling periods can be explained by the different times in which the queens emerge from hibernation and the workers flight season. The timing of emergence differs greatly between the queens of the different species, which again makes the flight season of the workers different. Studies of bumblebees in Norway by Løken (1973) and Bollingmo (2012) shows the differences in emergence and flight season for *B. terrestris/lucorum* (queen: ultimo March; workers: medio April-ultimo September), *B. pascuorum* (queen: medio April; workers: medio May-October), *B. hortorum* (queen: May; workers: ultimo May-primo September), *B. pratorum* (queen: ultimo March; workers: ultimo April-primo September),

B. lapidarius (queen: ultimo March-primo May; workers: medio June-medio September) and *B. sylvarum* (queen: medio April; workers: ultimo May-medio September). The findings of this study have three differences from those of Løken and Bollingmo; the first observations of *B. sylvarum* workers were done in July and there were a rapid decline in the number of *B. hortorum* and *B. pratorum* workers in July. The reasons for this can be many and the failure rate of colonies seems to be quite high. Bumblebees are attacked in various stages of their life cycle by a diverse range of predators, parasites and parasitoids (Goulson 2010). Agricultural practices are also a danger, for example mowing of hay or the cutting of road edges and field margins. Studies have also shown that some species reach maturity, produce queens, and die out much earlier in the season than others (Free & Butler 1959). It has long been suspected that *B. pratorum* sometimes have more than one generation per year, their colony being finished already in July, yet fresh workers are seen foraging late in the summer (Free & Butler 1959; Goulson 2010). The changes in weather from year to year may also affect the queens timing of emergence. The differences in abundance through the different sampling periods can also be explained by the different flowers being available in the different sampling periods, and the bumblebee's ability to switch resources and forage patch when the rewards decrease or fall below a critical threshold (Chittka et al. 1997; Dukas & Real 1993).

One could explain the differences in abundance between the species with the different species forage range. Many studies have focused on the question about foraging range, and it has been shown that the foraging range vary among the different bumblebee species (Darvill et al. 2004; Knight et al. 2005). Dramstad (1996b) showed that bumblebees in general forage at least 250-300 meters from their nest, even if there is suitable foraging resources closer. Other studies have shown that some species are dependent on a close connection between nest and foraging habitat (Walther-Hellwig & Frankl 2000). The differences in foraging range seems to correspond to nest size (Goulson 2010), which make sense since a large colony needs to forage over a larger area to find enough pollen and nectar. A thriving colony of *B. lapidarius* and *B. terrestris/lucorum* (in this study noted as *B. lucorum*) can rear as many as 300-400 workers during the season, whereas colonies of *B. pascuorum*, *B. sylvarum*, *B. hortorum* and *B. pratorum* rarely rear more than 100-200 workers (Free & Butler 1959; Goulson 2010). This fits with studies showing that species such as *B. terrestris* (in our case noted as *B. lucorum*) and *B. lapidarius* forage further away from the nest than so-called doorstep foragers such as *B. pascuorum* and *B. sylvarum* which only fly within an area of about 500 meters (Darvill et al. 2004; Goulson et al. 2008; Knight et al. 2005). In theory, a larger foraging range gives the colony a greater chance to survive in areas where the average density of floral resources is

highly patched, while species with a shorter range need the forage patches to be close together to thrive. Whether or not resources are available to bumblebees depends on flight distances from the nest and landscape characteristics. This theory is supported by Osborne et al. (2008) which found that the scale at which landscape context affects bee populations will depend on the species' foraging range. This means that the bumblebees with the largest foraging range to some extent will be buffered against fragmentation and heterogeneity in the agricultural landscape, while bumblebees with shorter foraging ranges can be more vulnerable to changes in the agricultural landscape, having problems reaching available forage. With this said Dramstad (1996b) found that bumblebees marked on isolated patches of forage, like small remnant habitat islands, appeared to disperse more widely across discontinuities in the landscape like cereal fields. The results of Dramstad (1996b) further showed that bumblebees are able to fly over barriers like cereal fields and forests to reach preferred forage. *B. pascuorum* is the most abundant and common species in this study, and remain so in much of Europe, so foraging range alone is not a good predictor of which species that will survive and thrive in fragmented landscapes.

4.4 Size of the six most common bumblebee species in relation to patch quality

The results of this study show that the workers of the six most abundant species exhibit intraspecific size variation. It has long an assumption that the workers are significantly smaller in the beginning of the season and that they grow in size through the season, as forage resources increase. However several studies have examined changes in worker size during the season with variable results, which is consistent with this study as no clear pattern emerges. *B. pascuorum* and *B. lucorum* shows a steady decrease in mean worker size, both thorax width and weight, as the season progresses. *B. hortorum* shows an increase in weight, while the thorax width increase before it has a slight decrease in the middle of June. *B. lapidarius* shows an increase in worker size as the season progresses. Workers of *B. pratorum* show a small increase in size early in the season, before it starts to decline in June, while *B. sylvarum* decline rapidly before it increase again towards the last sampling period. In the beginning of the 20th century one observed that the workers increased in size as the season progressed, and food became more abundant (Knee & Medler 1965). The first data to support this observation was published by Richards (1946). Cumber (1949) however, concluded that there was no gradual increase during the season as previously thought. Knee and Medler (1965) found an increase in worker size for three American species as the season progressed. Early increases however were small and not significant. This was explained by few workers being available for measurements early in the season, and that real differences, if any, could not be detected.

Knee and Medler (1965) also showed that disruptions to the colony, like parasitism, resulted in subsequent age groups of workers being significantly smaller. Plowright and Jay (1968) found an increase in worker size as the season progressed in some species but not in others, while Roseler (1970) described an initial decline in the mean size followed by a general increase in *B. terrestris*. Couvillion et al. (2010) showed that the average size of the workers did not consistently increase or decrease during the season, and that the colonies even though the feeding regime was standardized, exhibited significant variation in the worker size. With this Couvillion et al (2010) demonstrated that the maintenance of worker size polymorphism is independent of variation in or limitation of available resources. Bumblebees could have unlimited resources and still there would be a variation in worker size. Small colony size did neither limit the production of workers of a particular size, the average size even decreased with the size of the colony in some cases. This shows that the production of small workers is not a result of an insufficient forager force.

The reason for the size-variation in bumblebee workers has not been adequately explained. The size of any individual is being determined by nutrition, so the primary factor contributing to the difference in size seems to be unequal food provisioning during the larval stage (Plowright & Pendrel 1977). The size attained by each larvae is directly proportional to the amount of food they receive, this implies that the size of each larvae probably is determined by the adults. The cost to a colony to rear a worker is therefore approximately proportional to the worker's size. Bumblebees are divided in two groups, according to how they store their pollen and how they feed their larvae, which are called pollen-storers and pocket-makers (Free & Butler 1959; Goulson 2010). *B. hortorum*, *B. pascuorum* and *B. sylvarum* belong to the group pocket-makers. Larvae of these species feed themselves on pollen plastered into pockets adjoining them. In addition the larvae of such a group may also feed on pollen that is regurgitated into their cells from time to time by the workers. *B. lucorum*, *B. pratorum* and *B. lapidarius* belong to the group pollen-storers. The larvae of these species are fed individually on a mix of pollen and nectar regurgitated to them by the workers (Free & Butler 1959; Goulson 2010). Both pocket-making species and pollen-storers show variation in size. No clear pattern emerges showing the size of the pollen-storers increasing throughout the season, while the pocket-makers size decrease, and vice versa. It is likely that the in-nest spatial organization of workers and larvae is the proximate mechanism maintaining variation in worker size. This is because workers working as nurses tend to be more in the center of the nest, and larvae developing there receive more food, and therefore develop into larger workers, whereas larvae in the periphery are fed less and develop into smaller workers. The

spatial organization of workers and larvae could therefore directly lead to variation in feeding rate over the nest surface and thus to worker size polymorphism (Free & Butler 1959). The pollen-storers *B. lucorum/terrestris* and *B. lapidarius* are known to have large colonies, while the pocket-maker *B. pascuorum* has a medium sized nest. One would therefore expect that for these species the nest surface would be larger, and that there are more larvae in the periphery which receive less food. Maybe this can explain why both *B. pascuorum* and *B. lucorum* shows such a steady decrease in mean size through the season. It correlates with the results of Couvillion et al. (2010), who showed that the average size of workers decreased with colony size in some colonies. If this is the case, why does not the mean size of *B. lapidarius* decrease? Maybe *B. lapidarius* in this area don't produce such large colonies, and manage to feed all their larvae with approximately the same amount of food.

Type of island had no significant effect on the size of bumblebees, except for *B. lapidarius*. Workers of *B. lapidarius* observed on islands in arable fields were significantly heavier than those observed on islands in matrix. Earlier studies have shown that *B. lapidarius* seemingly prefer islands in arable fields (Dramstad 1996a). The reason why they prefer islands in arable fields can be because their preferred flowers grow more abundant here, but it does not explain how it affects their weight. The explanation could be that islands in matrix are not ideal and this makes the workers of *B. lapidarius* smaller. Couvillion and Dornhaus (2010) found that the smaller workers were significantly more resilient to starvation than larger workers. They might be more robust, meaning they can continue to perform under non-ideal conditions (Bonabeau et al. 2000). If there is a shortage of nectar, small workers would remain alive significantly longer than their larger nest-mates. The presence of small workers, which might be less efficient under normal conditions, can allow colonies to survive during times where the colony undergoes high colony stress. Total colony fitness may be maximized by balancing the trade-off between the expensive, non-robust but very efficient large workers and the inexpensive, non-efficient but robust small workers.

4.5 Flower preferences of the six most common bumblebee species

More than half the number of bumblebees within each species (with the exception of *B. lapidarius*) were foraging on: *Galeopsis tetrahit/bifida*, *Melampyrum pratense*, *Rubus idaeus*, *Trifolium hybridum*, *Trifolium pratense/medium*, *Trifolium repens* and *Vicia cracca*. This shows that preferred plant species for bumblebees in this area in general were preferred by all observed species.

There is strong evidence that perennials are more valuable to bumblebees foraging in farmland than annuals. 85 % of all the visited plant species were perennials, and this suggests a tendency for bumblebees to visit perennial plants rather than annuals. Although one should remember that just plant species receiving visits were recorded, which implies that this can only be a tentative conclusion. With this in mind, there was no surprise that most of the plants visited were perennials. Studies have shown that bumblebees only use a few of all the plant species occurring in the agricultural landscape (Dramstad & Fry 1995; Ranta et al. 1981). Dramstad and Fry (1995) found that all flowering species positively selected by bumblebees in a study done in the same area were perennials, except *Melampyrum pratense*.

Why bumblebees prefer flowers from perennials rather than annuals is not entirely known. Most of the flowers in an intensively used arable landscape belong to the annual species. Perennial plants are characteristic for unploughed areas such as field margins (Marshall 1989). One therefore suspects that annuals, maybe because they lack reserves, in general produce less nectar (Dramstad 1996a). The quality of nectar is obviously important, and bumblebees are known to visit the plants that are most rewarding. However the number of flowers available is of great importance for the bumblebees since they want to maximize the reward of a forage trip (Heinrich 1979). Choosing patches with high blossom density will obviously increase the possibility for high rewards. Dramstad (1996a) means that bumblebees can utilize annuals very intensely when they have a high flowering density, although the densities of flowering annuals need to pass a threshold for the bumblebees to switch from perennials to annuals. In this study the bumblebees' utilized two annual plant species intensively, especially *Melampyrum pratense*. Although *Melampyrum pratense* produce small volumes of nectar, it has very high sugar content and is a very good pollen source (Jennersten & Kwak 1991). This is probably important for the developing colony, since both nectar and pollen can be collected during the same foraging trip (Jennersten & Kwak 1991). *Galeopsis tetrahit/bifida* is an herbaceous annual plant which can be found in large densities in arable land and on disturbed sites like field margins and road verges.

The relation between tongue length and flower depth is an important factor affecting flower selection. Long-tongued bumblebees do not usually visit flowers with short corolla tubes. On the other hand, robbing is a method short-tongued bumblebees use to obtain nectar from flowers with deep corollas. Because of differences in the flowers available, small bumblebees can sometimes visit deeper flowers than larger bumblebees. Even though they have shorter tongues they also have smaller heads, giving them the possibility to insert their head deeper into the flowers. The three most dominant species in this study, *B. pascuorum*, *B. lucorum* and

B. hortorum, have short, medium and long proboscis respectively (Aase, ALTO, personal communication January 14th 2013). These three species all have *Melampyrum pratense* as their main forage. *Melampyrum pratense* has a long corolla, and *B. lucorum* probably rob these flowers to get a hold of the nectar. *B. pascuorum* and *B. hortorum* shows a greater preference for *Vicia cracca*, *Galeopsis tetrahit/bifida* and *Trifolium pratense/medium* than *B. lucorum*, plant species which all have the nectar deep in their corolla. *B. lucorum* shows a higher preference for *Rubus idaeus* which have shorter corolla. *B. lucorum* and *B. pascuorum* utilized 35 and 33 different plant species respectively, while *B. hortorum* only utilized 21, where only 4 species received more than eight visits. *B. pascuorum* and *B. lucorum* are both known to be generalists, able to utilize several different species, while the long tongued *B. hortorum* needs flowers with a long corolla like *Trifolium pratense/medium* to thrive.

There are some differences in preferred plant species between the different cast. Since queens almost exclusively forage during spring and early summer, their foraging sources are often different from the other casts of the colony. Queens also have longer tongues, and can therefore use some plant species more efficiently than workers. In this study the queen's flower preferences was almost the same as the workers, both casts preferring *Rubus idaeus* and *Melampyrum pratense*. Bumblebee recording started in June, and since queens emerge from hibernation early in the spring, the lack in data from March, April and May makes these results somewhat incomplete. Studies (Svensson et al. 2002) have shown that willows (*Salix caprea* L.) are valuable for all bumblebees in the early spring, and that the number of foraging queens in the spring were higher in areas with a high volume of *Salix caprea*. The differences in preferred forage plants between males and workers/queens can be explained by the fact that males forage for their own needs, and therefore use different plant species than the females. They prefer plants which have a high content of nectar like different species of thistles (*Cirsium* spp). It is also reasonable to believe that period and season have an impact on preferred plant species between casts, since plant species communities' change throughout the season.

4.6 Sampling methodology

To sample the bumblebees, the method 'one man hour' was chosen, a method previously been used by Goulson et al. (Goulson & Darvill 2004; Goulson & Hanley 2004; Goulson et al. 2005; Goulson et al. 2008) . This method was chosen because it has the advantage over methods such as a fixed transect in that it allows the searcher freedom to go to the places where bees are most likely to be found, e.g. patches of flowers, whereas on a fixed transect

one might count very few bees because the pre-defined route missed the places where all the bees are concentrated. The disadvantage is that a degree of subjectivity is involved, choosing where to go (Goulson, D, personal communication October 24th 2012). Using this method each patch was searched systematically to avoid recording the same bumblebee several times.

The flower cover at each patch could be classified into three different classes at each sampling time. Flower cover varied with season, and the classification of each patch could therefore influence the statistical tests. It would probably be good to find an alternative way to measure floral cover. One should also do a total count of all flower species at each patch, because it would give better data on the hypothesis that bumblebees prefer perennial plants over annuals.

For further research in this area it could also be suggested to use a higher number of patches, since this would give the data a higher degree of validness. Having a defined radius for all the patches could also give the results a higher degree of validness.

5. Conclusions

The aim of this thesis was to evaluate how bumblebees are affected by different variables in the fragmented landscape. The questions raised were if the density of flowering plants and habitat configuration could explain the species richness, abundance and size of bumblebees in a fragmented agricultural landscape. Questions about preferred forage plant species were also addressed. The results of this study show that the total abundance and species richness of social bumblebees were positively affected by the density of flowering plants (flower cover). This correlates with the results of several other studies. On the species level there is no statistical significant effect of flower abundance on bumblebee abundance, except for *B. hortorum*, though the other species had the highest number of individuals in patches with Flower cover three. For the size of the bumblebees the results gave no unambiguous answers. And it seems that the intra specific size difference continue to be somewhat of a mystery. There no clear effects of area, circumference or type of remnant that significantly explained species richness, abundance or size of bumblebees. The preferred plant species for bumblebees in general were preferred by all observed species. Between casts, differences in preferred plant species were found. Males mostly visited different species of thistle (*Cirsium ssp*), while queens preferred raspberry (*Rubus idaeus*) and common cow wheat (*Melampyrum pratense*). It seems that the bumblebees prefer perennials over annuals, with the exception of annuals like common cow wheat and common hemp-nettles in high densities, though the data obtained in this study didn't make it possible to demonstrate this rigorously.

We know for certain that bumblebees are declining all over Europe. Increased awareness and knowledge about bumblebees in the agricultural landscape and about the consequences changes in the landscape have for the richness and abundance of bumblebees are therefore important. Management to enhance bumblebee populations might involve maintaining undisturbed perennial vegetation along field boundaries and elsewhere, e.g. by conserving the spring willows and allowing a flora with high diversity and density. Bumblebee species richness and abundance has been shown to be lower in areas where grassy field margins were common in comparison with flowery field margins. In order to be of value for bumblebees the vegetation should therefore be dominated by perennials and annuals with a high content of nectar and diverse enough to provide flowers through the entire season.

6. References

- Alford, D. V. (1975). *Bumblebees*. London: Davis-Poynter (352 s.).
- Banaszak, J. (1983). Ecology of bees (Apoidea) of agricultural landscape. *Polish Ecological Studies*, 9: 421-505.
- Banaszak, J. (1992). Strategy for conservation of wild bees in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 40 (1-4): 179-192.
- Biesmeijer, J. C., Roberts, S. P. M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A. P., Potts, S. G., Kleukers, R., Thomas, C. D., et al. (2006). Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science*, 313 (5785): 351-354.
- Bollingmo, T. (2012). *Norges Humler med Humleskolen*. Trondheim: Brains Media.
- Bonabeau, E., Dorigo, M. & Theraulaz, G. (2000). Inspiration for optimization from social insect behaviour. *Nature*, 406 (6791): 39-42.
- Bäckman, J.-P. C. & Tiainen, J. (2002). Habitat quality of field margins in a Finnish farmland area for bumblebees (Hymenoptera: Bombus and Psithyrus). *Agriculture, Ecosystems & Environment*, 89 (1-2): 53-68.
- Carvell, C. (2002). Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation*, 103 (1): 33-49.
- Chittka, L., Gumbert, A. & Kunze, J. (1997). Foraging dynamics of bumble bees: correlates of movements within and between plant species. *Behavioral Ecology*, 8 (3): 239-249.
- Corbet, S. A., Williams, I. H. & Osborne, J. L. (1991). Bees and the pollination of crops and wild flowers in the European community. *Bee World*, 72 (2): 47-59.
- Couvillon, M. J. & Dornhaus, A. (2010). Small worker bumble bees (*Bombus impatiens*) are hardier against starvation than their larger sisters. *Insectes Sociaux*, 57 (2): 193-197.
- Couvillon, M. J., Jandt, J. M., Duong, N. H. I. & Dornhaus, A. (2010). Ontogeny of worker body size distribution in bumble bee (*Bombus impatiens*) colonies. *Ecological Entomology*, 35 (4): 424-435.
- Cumber, R. A. (1949). The biology of humble-bees, with special reference to the production of the worker caste. *Transactions of the Royal Entomological Society of London*, 100 (1): 1-45.
- Darvill, B., Knight, M. E. & Goulson, D. (2004). Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos*, 107 (3): 471-478.

- Dramstad, W. & Fry, G. (1995). Foraging activity of bumblebees (*Bombus*) in relation to flower resources on arable land. *Agriculture, Ecosystems & Environment*, 53 (2): 123-135.
- Dramstad, W. E. (1996a). *Der humlene fremdeles surrer*. FAFnytt Naturforvaltning 3(4):1-4.
- Dramstad, W. E. (1996b). Do bumblebees (Hymenoptera: Apidae) really forage close to their nests? *Journal of Insect Behavior*, 9 (2): 163-182.
- Dukas, R. & Real, L. (1993). Effects of recent experience on foraging decisions by bumble bees. *Oecologia*, 94 (2): 244-246.
- Fjellstad, W. J. & Dramstad, W. E. (1999). Patterns of change in two contrasting Norwegian agricultural landscapes. *Landscape and Urban Planning*, 45 (4): 177-191.
- Framstad, E., Lid, I. B., Moen, A., Ims, R. A. & Jones, M. (1998). *Jordbrukets kulturlandskap: forvaltning av miljøverdier*. Oslo: Universitetsforlaget (285 s.).
- Free, J. B. & Butler, C. G. (1959). *Bumblebees*. London: Collins (208 s.).
- Goulson, D., Peat, J., Stout, J. C., Tucker, J., Darvill, B., Derwent, L. C. & Hughes, W. O. H. (2002). Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Animal Behaviour*, 64 (1): 123-130.
- Goulson, D. & Darvill, B. (2004). Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie*, 35 (1): 55-63.
- Goulson, D. & Hanley, M. E. (2004). Distribution and forage use of exotic bumblebees in South Island, New Zealand. *New Zealand Journal of Ecology*, 28 (2): 225-232.
- Goulson, D., Hanley, M. E., Darvill, B., Ellis, J. S. & Knight, M. E. (2005). Causes of rarity in bumblebees. *Biological Conservation*, 122 (1): 1-8.
- Goulson, D., Hanley, M. E., Darvill, B. & Ellis, J. S. (2006). Biotope associations and the decline of bumblebees (*Bombus* spp.). *Journal of Insect Conservation*, 10 (2): 95-103.
- Goulson, D., Lye, G. C. & Darvill, B. (2008). Decline and conservation of bumble bees. *Annual Review of Entomology*, 53: 191-208.
- Goulson, D. (2010). *Bumblebees: behaviour, ecology and conservation*. New York: Oxford University Press (317 s.).
- Grey-Wilson, C., Blamey, M., Faarlund, T. A. & P., S. (2005). *Damms store flora for Norge og Nord-Europa*. Oslo: Damm.
- Gullan, P. J., Cranston, P. S. & McInnes, K. H. (2005). *The insects: an outline of entomology*. Malden, Mass.: Blackwell (505 s.).
- Hegland, S. J. & Boeke, L. (2006). Relationships between the density and diversity of floral resources and flower visitor activity in a temperate grassland community. *Ecological Entomology*, 31 (5): 532-538.

- Heinrich, B. (1979). "Majoring" and "Minoring" by Foraging Bumblebees, *Bombus Vagans*: An Experimental Analysis. *Ecology*, 60 (2): 246-255.
- Holmström, G. (2009). *Humlor : Alla Sveriges arter : så känner du igen dem i naturen - och i trädgården*. 2 ed.
- Jennersten, O. & Kwak, M. (1991). Competition for bumblebee visitation between *Melampyrum pratense* and *Viscaria vulgaris* with healthy and *Ustilago*-infected flowers. *Oecologia*, 86 (1): 88-98.
- Knee, W. J. & Medler, J. T. (1965). The Seasonal Size Increase of Bumblebee Workers (Hymenoptera: *Bombus*). *The Canadian Entomologist*, 97 (11): 1149-1155.
- Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A. & Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology*, 14 (6): 1811-1820.
- Kwak, M. M. (1978). Pollination, Hybridization and Ethological Isolation of *Rhinanthus minor* and *R. serotinus* (Rhinanthoideae: Scrophulariaceae) by Bumblebees (*Bombus* Latr.). *Taxon*, 27 (2/3): 145-158.
- Kålås, J. A., Viken, Å., Henriksen, S. & Skjelseth, S. (2010). *The 2010 Norwegian Red List for Species*. Norway: Biodiversity Information Centre.
- Lid, J. (1979). *Norsk og Svensk Flora*: Det Norske Samlaget.
- Løken, A. (1973). Studies on Scandinavian Bumble Bees. *Norwegian Journal of Entomology*, 20 (1).
- Løken, A. (1985). Norske insekttabeller 9. Humler. *Norsk Entomologisk Forening*.
- Marshall, E. J. P. (1989). Distribution Patterns of Plants Associated with Arable Field Edges. *Journal of Applied Ecology*, 26 (1): 247-257.
- Mänd, M., Mänd, R. & Williams, I. H. (2002). Bumblebees in the agricultural landscape of Estonia. *Agriculture, Ecosystems & Environment*, 89 (1-2): 69-76.
- Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J. & Sanderson, R. A. (2008). Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, 77 (2): 406-415.
- Osgathorpe, L., Park, K. & Goulson, D. (2012). The use of off-farm habitats by foraging bumblebees in agricultural landscapes: implications for conservation management. *Apidologie*, 43 (2): 113-127.
- Peat, J., Darvill, B., Ellis, J. & Goulson, D. (2005). Effects of climate on intra- and interspecific size variation in bumble-bees. *Functional Ecology*, 19 (1): 145-151.
- Plowright, R. C. & Jay, S. C. (1968). Caste differentiation in bumblebees (*Bombus* Latr.: Hym.) I. The determination of female size. *Insectes Sociaux*, 15 (2): 171-192.

- Plowright, R. C. & Pendrel, B. A. (1977). Larval growth in bumble bees (Hymenoptera: Apidae). *The Canadian Entomologist*, 109 (7): 967-973.
- Ranta, E., Lundberg, H. & Teräs, I. (1981). Patterns of Resource Utilization in Two Fennoscandian Bumblebee Communities. *Oikos*, 36 (1): 1-11.
- Ranta, E. & Vepsäläinen, K. (1981). Why Are There So Many Species? Spatio-Temporal Heterogeneity and Northern Bumblebee Communities. *Oikos*, 36 (1): 28-34.
- Ranta, E. (1982). Species Structure of North European Bumblebee Communities. *Oikos*, 38 (2): 202-209.
- Richards, O. W. (1946). Observations on *Bombus agrorum* (Fabricius)(Hymen, Bomhidae). *Proceedings of the Royal Entomological Society of London. Series A, General Entomology*, 21 (7-9): 66-71.
- Robinson, R. A. & Sutherland, W. J. (2002). Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology*, 39 (1): 157-176.
- Roseler, P. F. (1970). Differences in caste determination between bumblebee species *Bombus-hypnorum* and *Bombus-terrestris*. *Zeitschrift Fur Naturforschung Part B-Chemie Biochemie Biophysik Biologie Und Verwandten Gebiete*, 25 (5).
- Rundlöf, M., Nilsson, H. & Smith, H. G. (2008). Interacting effects of farming practice and landscape context on bumble bees. *Biological Conservation*, 141 (2): 417-426.
- Simberloff, D. S. (1974). Equilibrium Theory of Island Biogeography and Ecology. *Annual Review of Ecology and Systematics*, 5: 161-182.
- Sowig, P. (1989). Effects of flowering plant's patch size on species composition of pollinator communities, foraging strategies, and resource partitioning in bumblebees (Hymenoptera: Apidae). *Oecologia*, 78 (4): 550-558.
- Steffan-Dewenter, I. & Tschardtke, T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia*, 121 (3): 432-440.
- Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tschardtke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83: 1421-1432.
- Steffan-Dewenter, I. & Westphal, C. (2008). The interplay of pollinator diversity, pollination services and landscape change. *Journal of Applied Ecology*, 45 (3): 737-741.
- Svensson, B., Lagerlöf, J. & G. Svensson, B. (2002). Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, Ecosystems & Environment*, 77 (3): 247-255.
- Taylor, P. D., Fahrig, L., Henein, K. & Merriam, G. (1993). Connectivity Is a Vital Element of Landscape Structure. *Oikos*, 68 (3): 571-573.

- Walther-Hellwig, K. & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, 124 (7-8): 299-306.
- Westphal, C., Steffan-Dewenter, I. & Tschardt, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6 (11): 961-965.
- Westrich, P. (1996). Habitat requirements of central European bees and the problems of partial habitats. In Matheson, A., Buchmann, I.H., O Toole, C., Westrich, P., Williams, I.H (ed.) *The Conservation of Bees*, pp. 2-16. London: Academic Press.
- Williams, P. & Osborne, J. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie*, 40 (3): 367-387.
- Williams, P. H. (1982). The distribution and decline of British bumblebees (*Bombus* Latr.). *Journal of apicultural research*, 21 (4): 236-245.
- Williams, P. H. (1986). Environmental change and the distribution of British bumble bees (*Bombus* Latr.). *Bee World*, 67: 50-61.
- Öberg, S., Gjershaug, J. O., Certain, G. & Ødegaard, F. (2010). Utvikling av metodikk for arealrepresentativ overvåking av utvalgte invertebratgrupper. Pilotprosjekt Naturindeks for Norge. *NINA, Rapport 555* (50 s.).
- Ødegaard, F., Gjershaug, J. O., Öberg, S. & Mjelde, A. (2009). Status for humler (Hymenoptera, Apidae, *Bombus* spp.) i Norge i 2010. *Fauna* 62(4): 94-104.

7. Appendix

Appendix 1. List of all plant species which received visits from the workers of the six most common bumblebee species

Plant species		
Latin name	English name	Norwegian name
<i>Achillea millefolium</i> L.	Yarrow millefolium	Ryllik
<i>Angelica archangelica</i> L.	Garden angelica/Norwegian angelica	Kvann
<i>Anthriscus sylvestris</i> L.	Cow parsley	Hundekjeks
<i>Asteraceae</i> spp.	Yellow aster ssp.	Gul kurvplante
<i>Brassica napus</i> L.	Rape	Raps
<i>Calluna vulgaris</i> L.	Heather	Røsslyng
<i>Campanula rapunculoides</i> L.	Creeping bellflower	Ugressklokke
<i>Campanula rotundifolia</i> L.	Harebell	Blåklokke
<i>Centaurea jacea</i> L.	Cornflower	Knoppurt
<i>Cirsium</i> spp.	Thistle	Tistel
<i>Convallaria majalis</i> L.	Lily of the valley	Liljekonvall
<i>Lotus corniculatus</i> L.	Bird's-foot trefoil	Tiriltinge
<i>Epilobium angustifolium</i> L.	Rosebay willowherb/Fireweed	Geiterams
<i>Filipendula vulgaris</i> L.	Dropwort	Mjødurt
<i>Galeopsis tetrahit</i> L./ <i>bifida</i> Boenn.	Common hemp-nettles	Kvassdå/vrangdå
<i>Geranium robertianum</i> L.	Herb Robert	Stankstorknebb
<i>Geranium</i> spp.	Cranesbill	Storknebb
<i>Geum rivale</i> L.	Water avens	Enghumleblom
<i>Hypericum perforatum</i> L.	St. Johns-wort	Prikkperikerikum
<i>Knautia arvensis</i> L.	Field scabious	Rødknapp
<i>Lamium album</i> L.	White deadnettle	Dauvnesle
<i>Lamium purpureum</i> L.	Red dead-nettle	Rødtvetann
<i>Lathyrus linifolius</i> Reichard.	Bitter Vetch	Knollertknapp
<i>Lathyrus pratensis</i> L.	Meadow vetchling	Gulflatbelg
<i>Linaria vulgaris</i> Miller.	Yellow toadflax	Torskemunn
<i>Lychnis viscaria</i> L.	Sticky catchfly	Tjæreblom
<i>Matricaria perforata</i> Mèrat.	Scentless mayweed	Balderbrå
<i>Melampyrum pratense</i> L.	Common cow wheat	Marimjelle
<i>Mycelis muralis</i> L.	Wall lettuce	Skogsalat
<i>Persicaria maculosa</i> L.	Redshank	Hønsegress
<i>Ranunculus acris</i> L.	Meadow buttercup	Smørblomst
<i>Rosa</i> ssp.	Rose ssp.	Nyperose
<i>Rubus idaeus</i> L.	Raspberry	Bringebær
<i>Sedum telephium</i> L.	Orpine	Smørbutikk
<i>Silene dioica</i> L.	Red campion	Jonsokblom
<i>Solidago virgaurea</i> L.	Goldenrod	Gullris
<i>Stachys sylvatica/palustris</i> L.	Hedge/Marsh Woundwort	Skogsvinerot/åkersvinerot
<i>Succisa pratensis</i> L.	Devil's bit	Blåknapp
<i>Trifolium hybridum</i> L.	Alsike clover	Alsikekløver
<i>Trifolium pratense/medium</i> L.	Red clover	Rødkløver
<i>Trifolium repens</i> L.	White clover	Hvitkløver

Appendix 1. Continued.

Plant species		
Latin name	English name	Norwegian
<i>Veronica chamaedrys</i> L.	Speedwell	Veronica
<i>Vicia cracca</i> L.	Bird vetch	Fuglevikke
<i>Vicia sepium</i> L.	Bush Vetch	Gjerdevikke
<i>Viola arvensis</i> Murray./ <i>tricolor</i> L.	Field/wild pansy	Stemorsblomst