Foraging activity of bumblebees (Bombus) in relation to flower resources on arable land: A follow-up 13 years later

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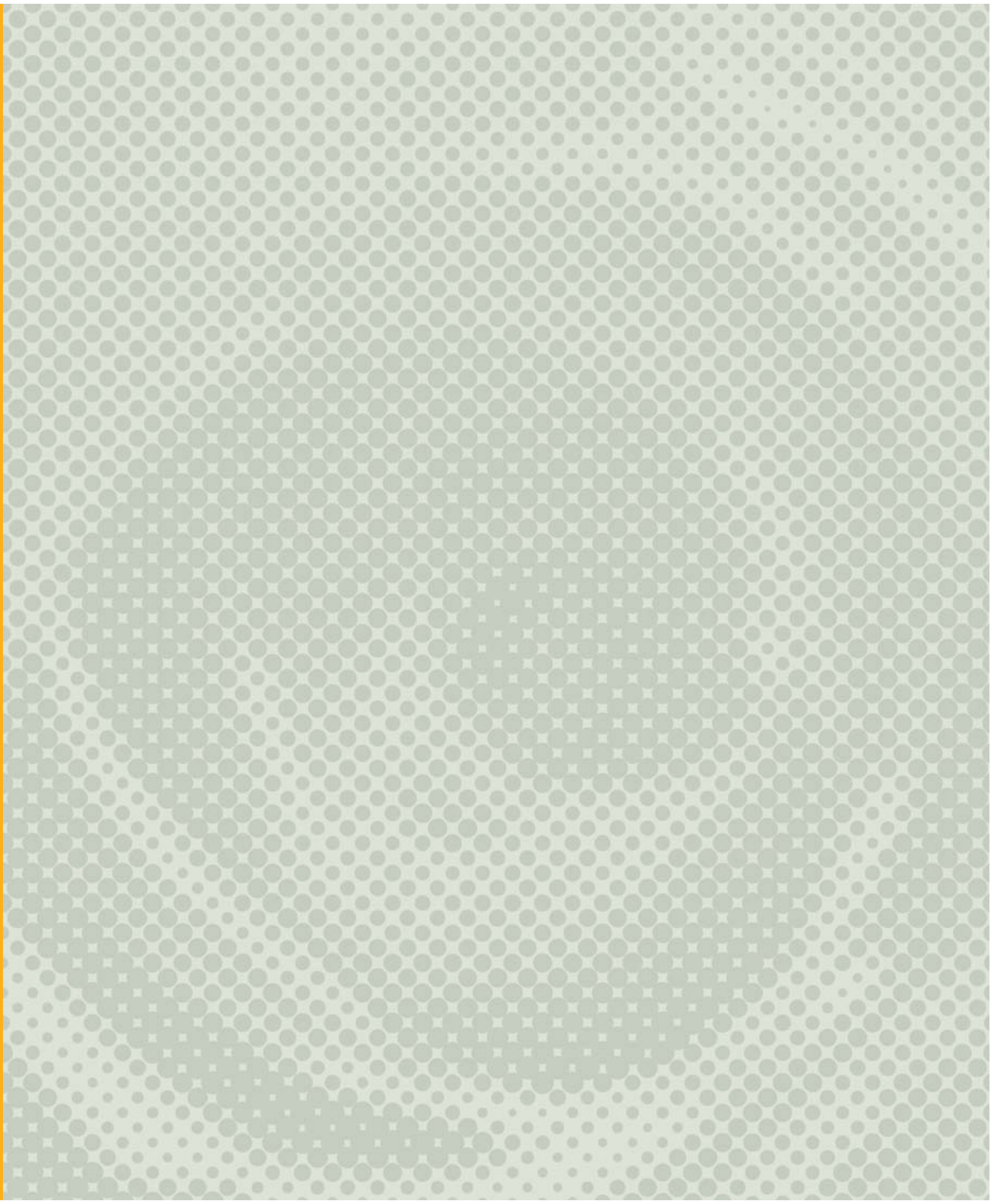

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Preface

Studying bumblebees was not an obvious choice to start with. Because I wanted a thesis that would be useful in teaching at high-school, I wanted it to cover as much of the curriculum as possible. I realized that geology and limnology would be difficult to include.

I chose this topic after a lecture held by Wenche Dramstad: I had found what I was looking for. Everybody knows what a bumblebee is, but very few people have looked close enough to realize that there are different species. Bumblebees may be approached in the field, and a teacher can plan an outdoor lesson and be almost certain to find them, unlike with birds or mammals. Bumblebees are generally well thought of. If there was a popularity contest, I think bumblebees would be second, only beaten by large and colorful butterflies.

Most of all, I chose to spend a year with this because I thoght it would be fun. It was.

I would like to thank the employees at the institute collectively for inspirational lectures during the studies. My plan was to study biology for one year, I ended up with four. Especially, I thank Eline B. Hågvar for teaching me that "bugs" are so exciting, and that she has kept her head cool and guided me through this work. Wenche Dramstad has offered crucial assistance and inspiration by turning quantity into some degree of quality in this thesis.

I also thank Emil and Håkon. They have been very patient and understanding when their father had to count "weeds and bugs", and only taking them to holydays when it was raining.

Dag Kristiansen, University of Life Science 15/5-2006

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Abstract

Observations of bumblebees (*Bombus*, Apoidea, Hymenoptera) were done in the same transects using the same method of bee-walks in Frogn community in the southeastern part of Norway in 1992 and 2005. The transects were chosen to represent different types of remnant habitats in an intensively cultivated agricultural area. This study showed differences between 1992 and 2005 in species` composition of both flowers and bumblebees, differences in flower preferences, and different times of peak activity of bumblebees. Much of the differences are most likely due to the different weather the two years. *Bombus hortorum* L. was not observed in 2005, *Bombus sylvarum* L. and *Bombus ruderarius* Müller were registered as new. *B.lapidarius* L., *B.wurfleini* Radoszkowski , *B.lucorum* L. */B.terrestris* L., *B.pascuorum* Scopoli, *B.pratorum* Radoszkowski., and *B.hypnorum* L. were observed both years.

The quality of remnant habitats to bumlebees is highly variable. Edges along cereal fields shaded by spruce forest are less attractive as foraging habitat than edges in full or partial sun. Some edges provided large amounts of resources a short period, others provided less resources, but more continuous.

The most evident differences from 1992 to 2005 are that:

1) *B.lapidarius* and partially *B.wurfleini* replaced *B.lucorum* and *B.pascuorum* as the most abundant species in total numbers for the entire season.
2) The weather delayed the season in 2005, giving a peak in bumblebee activity 6 weeks later than in 1992.
3) One transect lost its importance to bumblebees from 1992 of mass-flowering of *Vicia* spp, but maintained its importance in 2005 during the mass-flowering of *Cirsium vulgare*, but to other species and at a different time.
4) Flower preferences differed substantially between years.
5) There has been a large species turnover in flowers, with an increase in perennials.

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2 Materials and methods

4 Results

5 Discussion

The CD contains this thesis with appendices, and Excel-files with all of the observations, sorted in different ways. In addition, there are files where the flora is sorted by Latin, Norwegian, and English names. The recordings of temperature and relative humidity are included both as numbers and as graphs.

1 Introduction

1.1 Biology of bumblebees

Taxonomy

Bumblebees (*Bombus* Latreille, Apoidea, Hymenoptera) are closely related to other bees and belong to the same taxonomic superfamiliy called Apoidea. Apoidea belong to the order Hymenoptera, that includes social ants and wasps, among others. In Norway, there are 180 known species from 8 families that belong to Apoidea (Sundby 1995), in addition to bumblebees. Most of them are solitary, only the honeybee (*A. mellifera*) and the true bumblebees are eusocial. As honeybees have a far more complex society, bumblebees are called primitively eusocial.

Species

Of the "true" (eusocial) bumblebees, there are 34 species in Norway (Sundby 1995). In addition, the coockoo bumblebees are now included in the *Bombus*-genus (formerly the *Psithyrus*-genus, Lepeletier), with 8 species in Norway (Sundby 1995). Worldwide, it is estimated to exist a little more than 250 species (Goulson 2003). As bumblebees are large, active at daytime, and mostly live close to humans, it is believed that all species are discovered (Goulson 2003). The different species have different adaptations, and there is no site in Norway were all Norwegian species co-exist (Løken 1973).

Colony establishment

True bumblebees live in colonies, or nests, and they are called social because they care for and feed their offspring and divide the labor (Hågvar 1998). The founder of a colony is a single, mated queen that has hibernated through the winter. In spring she has to find a site to found the colony, and the species differ in their preferences for nest-sites; Species like *Bombus terrestris* and *Bombus lucorum* like burrows and abandoned nests made by rodents, other use tussocks, and some use open spaces in stone walls, houses (especially *Bombus hypnorum*), hollow trees, or abandoned bird nests (Goulson 2003). In her new nest, the queen makes a cell from wax (secreted from glands) and fill it with a mixture of pollen and nectar. In addition, she makes another cell to store some honey. Honey is "dried" nectar, concentrating the sugars to raise the osmotic pressure to prevent yeasts from fermenting sugars into alcohol (Villumstad 2004). Nectar contains 40-70 % water, while honey contains about 20% (Villumstad 2004). Further, enzymes both in the insect and from the flower itself, turns complex sugars into glucose (Villumstad 2004). This honey is to be used when the weather does not allow her to forage outside. The queen mated the previous autumn, so she can begin to lay eggs that will result in the first batch of workers.

Colony development

When the eggs hatch, the larvae are feed on pollen and nectar. Female bumblebees collect pollen from flowers and place it on her pollen baskets on the hind legs, and collect nectar in their honey stomach. Back in the nest, the pollen is scraped off, and nectar is regurgitated. Pollen provides amino acids and proteins, and some other elements such as starch and fatty acids. Nectar provides mainly carbohydrates, i.e. energy. Later, the larvae pupate and transform into adult, female adult, female workers. From the eggs are layed, it takes 4-5 weeks until they are ready to help the queen to raise new batches of workers (Goulson 2003). The youngest workers work inside the nest, by tending the queen and the larvae, older workers forage outside and provide the colony, including the queen and the young workers, with pollen and nectar. Foraging is dangerous, as the bumblebees are more exposed to predators when they are outside the nest.

The colonies will in mid-summer reach the maximum number of workers (50-400, depending on the species). Then the colony will produce sexual offspring. The workers are not physiologically sterile, but pheromones produced by the queen prevent them from laying eggs.Young queens are fed with more nutritious food than workers, and late in the season the queen nearly stops producing supressing pheromones. In addition, she lays eggs that are not fertilized, that turns into males. They are haploid, that is, they have no father. As a consequence, all genes are expressed, and the queen`s genes are not “diluted”. Sometimes workers lay eggs that turn into males as they are not fertilized. Males do not forage for the colony, but they leave to mate. In the autumn, all workers, males, and the old queen die. Mated young queens then find a place to hibernate, but first she has to build up a storage of fat in her body by eating pollen (Williams and Christian 1991), giving both energy and insulation. Hibernation sites are believed to most often be in a north-facing slope (Goulson 2003).

Cockoo bumblebees

Coockoo bumblebees have earned their name by being social parasites. Different species of coockoo bumblebees are specialized to parasitize one or few species of true bumblebees, and have similar coloration as their hosts. A coockoo bumblebee queen takes over a colony of true bumblebees, most often by killing the founder-queen. Then she lays her own eggs. The offspring will all become males and queens, and no workers. The workers from the original colony of true bumblebees raise them. This implies that no more workers are produced in nests, and it is unlikely that reproductives of the founder-queen ever will leave the nest.

Honeybees

In honeybees, many workers also live through the winter, but they do not hibernate. Instead they survive by producing heat. To do so, they stick close together and let the muscles work. This costs energy, so the colony has to store plenty of honey for the winter. The honey humans take from the honeybees, therefore, has to be replaced by ordinary sugar (sucrose) dissolved in water. The number of workers that live through the winter is low, normally about 2000. When the workforce peaks in the summer, the number has increased to about 40000. With each bee weighing cirka one tenth of a gram, the colony can be compared to the body mass of a rabbit in the winter and a row deer in mid summer. Reducing the numbers in the autumn reduce the need for energy during the winter.

The old workers that are going to die, feed larvae with proteins secreted from their bodies, limiting the loss of colony resources as workers die. Some call the colonies “super-organisms” as the individuals cooperate and divide the tasks. In my opinion, it would be more correct to regard the queen as the only individual, and the workers and males as dispersed and expendable body-parts.

Bumblebees as pollinators

Bumblebees play an important, ecological role as pollinators as do many other insects too. The insect orders Hymenoptera, Lepidoptera (butterflies), Diptera (flies), and Coleoptera (beetles) are known to have many pollinating species (Pellmyr 2002). Bumblebees are large insects, giving a high volume:body-surface ratio compared to most invertebrates. They also have fur, and many species living north and in montaneous areas are black and red, colors that absorb solar radiation efficiently. Bumblebees also produce internal heat by muscle-shivering, not always showing externally. Thus, bumblebees are well adapted to live in cold areas where competition from other nectar- and pollen feeding insects is limited. In turn, many flowers are believed to have evolved to be pollinated by bumblebees, and have colors, shapes, sizes, and scents that attract bumblebees. Bumblebees are shown to be especially efficient in pollinating a range of plants, and many plants try to avoid other insects from depleting nectar or other resources (Pellmyr 2002). This way a specialization arises, and the species co-evolve. That is, if the bumblebees went extinct, species of flowers might go extinct too, at least at some places or regions.

Pollination syndromes and flower constancy

Pollination syndromes is a term that describes how different pollinators and flowers seems to have co-evolved into groups of similar characteristics. Flowers preferred by bumblebees are often yellow or blue, have a sweet scent, complex shape, concealed nectar, have nectar guides, and pendant flowers (Pellmyr 2002). White flowers may indicate that a plant attracts pollinators at night (as moths, Lepidoptera). It is often assumed that red flowers are adapted to be pollinated by birds (mainly hummingbirds), as their color vision is more similar to the human perception of light. It is shown that bees avoid or at least discriminate flowers with carotenoides (Pellmyr 2002). Waser et al. (1996) states that bumblebees are able to see red colors, and can detect radiation from 320 nm (near UV) to 600-650 nm (near red). Naïve workers have innate preferences for some floral traits, but have to experience what flowers that are rewarding at any given time. In a foraging habitat it might be many species of flowers to choose from, and both rewards and the access to the rewards differ. A bumblebee that learn to deplete one species of flowers reduces the handling time and becomes more efficient, and tend to specialize on the chosen flower species. This is given the term flower constancy (e.g. Goulson 2003). Occasionally, the bumblebee will try to sample other flower species, and may switch if new resources are experienced as more rewarding (in quality, quantity, and/or searching time or handling time). There might be a threshold of the density of a new resource before the switch takes place (Dramstad, pers.com.). It is also suggested that some species of bumblebees may establish a fixed route between rewarding flowers (of the same or of different flower species), and thereby reduce the searching time. There is no evidence that bumblebees communicate the location of resources to each other, but most likely they communicate the kind of resources to look (or rather smell) for.

Different plant strategies

Plants are immobile, and need assistance to transport male gamets (pollen) between individual plants within and between populations (Pellmyr 2002). Some plants spread their male gamets by wind or water, but have to produce large amounts of pollen to succeed (Pellmyr 2002). The air may be so saturated with pollen that humans may respond with allergic reactions to for example grasses, some trees, and *Artemisia vulgaris*. This strategy has disadvantages: Pollen contain amino acids that are costly to plants, wind-pollination of course requires wind, and conspecifics can not be too scattered in the landscape (Pellmyr 2002). By using insects to pollinate, plants can produce far less pollen, and instead produce nectar to reward insects. These sugars are synthesized water and carbondioxide produced in the photosynthesis. In addition, these plants accept a loss of pollen to their pollinators: Many pollinating insects eat pollen, or feed their offspring with it, as a source of nitrogen-compounds. Nitrogen is the limiting factor to life in most terrestrial ecosystems, and many other insects have to be predators to get this.

Benefits to bumblebees from pre-industrial agriculture

As bumblebees depend on flowers as food sources, they are more abundant in areas that are not shaded by dense forests. Whithout human impact, this would be montaneous areas, areas that have newly experienced a fire or a storm, edges along rivers and lakes, or areas to dry or poor in nutrients to sustain a closed-canopy forest. Agriculture provided the bumblebees with areas with the required qualities, as trees were cut to grow cereals and to provide grazing fields for live-stock.

Some plants live in symbiosis with anaerobic bacterias (primarily *Rhizobium* spp.) that are able to fixate atmospheric nitrogen into ammonia. These leguminose plants have been used by humans to fertilize the soil (in addition to manure) and yield larger cereal crops (that are seeds of wind pollinated grasses that not offer any resources to bumblebees). The following seasons, cereals containing organic nitrogen-compounds human bodies need, are grown. Leguminosa-fields were especially important to feed horses. Farmers also let their animals graze over large pastures that were of lower quality than the cereal fields, in terms of nitrogen and other measures. This provided the landscape with large areas with sunny conditions, and a diverse community of flowers thrived. It may therefore be argued that bumblebees have good conditions till now because of human activity as many species have thrived in this cultivated landscape.

Bumblebees in present day agricultural landscapes

Agriculture and agricultural landscapes has changed quite a lot since the Norwegians Kristian Birkeland 1867-1917) and Samuel Eyde (1866-1940) invented a method to fixate and mass produce atmospheric nitrogen one hundred years ago. By adding artificial fertilizers to cereal fields, the need for nitrogen fixating plants, such as clovers which are a valued resource to bumblebees, was reduced. Artificial fertilizers were cheap enough to be added to larger areas. Then both the cereal yield increased sharply, and the animals could be fed from smaller areas. Turning relatively undisturbed pastures into ploughed and cropped fields also ment that rodent burrows and tussocks disappeared, so bumblebees` nest-sites may be in shortage. Agriculture also had problems with weeds in the cereal fields, especially *Agrostemma githago* that has seeds that are poisonuos to humans. Some of these weeds could be exploited by bumblebees. As herbicides were introdused to control the weeds (especially herbicides that act specifically on dicotyledons, but not affecting the cereals that are monocotyledons), this resource more or less disappeared. Another problem was aphids and other insects that could feed and reproduce rapidly in these monocultures, and the aim was to develop and add insecticides. Unfortunately, these were not species-specific, and killed a lot of non-target species, bumblebees among them.

Some characteristics of the bumblebees in this study

Table 1 summarizes the following.

Colors

B.lucorum, B.terrestris, and *B.hortorum* have black and yellow bands and a white tail. *B.pratorum* is black with yellow tail and orange collar, with an additional yellow band on the abdomen in England. *B.lapidarius, B.wurfleini, B.ruderarius* and melanic *B.sylvarum* are black with grey-reddish tails. According to Løken (1973 page 172 ff) the melanic form is the typical form in Norway. *B.lapidarius* has bright red tail, *B.wurfleini, B.ruderarius* more brown. These two are distinguished by the color of the hairs on the pollen basket. Melanic *B.sylvarum* has more grey tail, and grey hairs at the base of the legs. If it is not melanic, as in England and most of Sweden, it looks more like *B.pratorum. B.pascuorum* and *B.hypnorum* are mainly brown with a black band at the abdomen. *B.hypnorum* has a white tail, *B.pascuorum* brown. *B.distinguendus* is grey with a black band between the wings. In most of Europe the grey is more or less bright yellow.

Foraging distances

Some species forage close to their nests. This makes sense in terms of time and energy spent on foraging, and it was believed that this was the case for all bumblebees. However, Dramstad et al. (2001) showed that some species have a ”safety zone” around their nests where they normally not forage. Little is known about the actual foraging distances as this is difficult to study (Goulson 2003). Foraging distances for some species are listed in table 1.

Proboscis-length

The proboscis- (or tongue) lengths in a species probably vary between individuals and between populations, as different authors state different lengths (table1). Here the proboscis lengths from Goulson et al. (2004) are used. Flowers with deep corollas in this part of the world are thought to have evolved to be pollinated by bumblebees and butterflies (Lepidoptera). It is believed that insects with different proboscis-lengths divide the floral resources between them (Goulson 2003). Flowers that are more open will most likely be depleted by flies (Diptera) or beetles (Coleoptera). Some bumblebee species, like *B.lucorum* and *B.wurfleini* are known to be nectar robbers, that is, they make a hole in the corolla tube at the rear of deep flowers to reach the nectar (Goulson 2003). Then the bumblebees do not come in contact with the reproductive parts of the flower.

Rearing

Bumblebees are divided into two sections (not taxa) based on the way the larvae are reared. The sections are called Odontobombus Krüger (pocket makers) and Anodontobombus Krüger (pollen storers) (Goulson 2003). In pocket makers, the brood graze pollen collectively, while the pollen storer larvae lay in individual wax-cells. This is shown here because they have different evolutionary histories and may have other characteristics in common as well.

Distribution

The term “northerly advanced southern species” is used by Løken (1973) to describe species that probably have colonized the northern of Europe after the ice age from populations further south on the continent. These species have a distribution with a northern limit. It is possible that cold climate towards higher latitudes and altitudes restrict their further advance. A widespread species live under more different climatic conditions. *B.wurfleini* is a western species, probably spreading from the coastal areas at the western of Norway. *B.wurfleini* is rarely recorded this far east, and never recorded in Østfold (ca 30 kilometers south and east of the study site) (Løken 1973). The species is thought to be univoltine, that is, completes only one life-cycle per season, and with moderate-sized number of workers per nest (80-150) (wildbienen.de/b-wurfle.htm 03.09.2004).

Both *B.lapidarius* and *B.ruderarius* are restricted to the eastern of Norway (Løken 1973). This suggests that they prefer a warm climate, and probably have a low success-rate in seasons with unfavorable weather. Goulson (2003) states that *B.terrestris* and *B.lapidarius* have expanded northwards in Scotland.

Emerging time

The data in table 1 are from Goulson et al. (2004). The data are collected from the UK, the Hebrides, and New Zealand, but also from Løken (1973). More exact timing from Great Britain and the continental Europe is available, but this probably not valid for Norway. Here, I only use the terms early-, mid-, and late-emerging. Only species observed in the two present studies are included in table 1.

Table 1. Some characteristics of different species of bumblebees.
FD=Foraging distance[5]. NR = Nectar robber. Notes: 1.Proboscis lengths at the left are from Goulson et al (2004), at the right calculated from Kawakita et *al*. (2004). 2. Emergence-times are from Goulson et *al*. (2004), except from *B.hypnorum* and *B.wurfleini*. These are fitted in by comparing all species with bombus.de/cgi-bin/bombus.exe/show?steckbrief& hummel. 3. From Goulson (2003). 4. According to Løken (1973). 5. According to Walther-Hellwig and Frankl (2000).

Species	FD[5]	Proboscis length[1]	Emergence[2]	Rearing[3]	Distribution[4]
Black/red					
B.lapidarius	Long	7,7- 7,0	Mid	Pollen storer	Northerly advanced
B.ruderarius	Short	8,5-10,3	Mid	Pocket maker	Northerly advanced
B.wurfleini		?- 8,2 NR	Mid	Pollen storer	Western
B.sylvarum	Short	8,8- ?	Late	Pocket maker	Northerly advanced
Yellow/white/black					
B.lucorum	Long	7,5- 7,6 NR	Early	Pollen storer	Widespread
B.terrestris	Long	7,6- 9,2	Early	Pollen storer	Northerly advanced
B.pratorum		7,3- 7,2	Early	Pollen storer	Widespread
B.hortorum		12,5-14,3	Mid	Pocket maker	Widespread
Brown (-ish)					
B.pascuorum	Short	8,5- 9,6	Mid	Pocket maker	Widespread
B.hypnorum		? - 6,7	Mid	Pollen storer	Widespread

1.2 Decline in bumblebees

Bumblebees are reported to have declined throughout Europe, especially the specialized, long-tongued species like *B.hortorum* (Goulson et al. 2004). This decline may in part be caused by the use of artificial fertilizers, reducing the need for nitrogen-fixating crops, primarily legumes, that are known to be important to bumblebees (Goulson 2003).

Little is known about the causes of the decline, however (Goulson 2003). He does not mention a connection with the decline of the water vole (*Arvicola terrestris*) (Rushton et al. 2000) in England, and thereby the loss of burrows, as a possible cause.

None of the species in Norway is on the Norwegian Red List (1998), except for *Bombus subterraneus* L. that is believed to be extinct.

Foraging distances and dispersal abilities

Bombus pascuorum, B.sylvarum, B.ruderarius, and *Bombus muscorum* L. are "door-step foragers" (Goulson 2003), that is, they do not move far from their nests to forage. Goulson (2003) suggests that this may be a disadvantage when resources are scattered in the landscape and may be a reason for the decline of these species in England. He further mentions that *Bombus terrestris* L. and *B.lapidarius* may travel further to forage. This is consistent with the findings by Dramstad et al. (2003), made on nest-boxes of *B.terrestris* at this study site.

Bumblebees are good dispersers (Dramstad, pers. com.) and will colonize or recolonize suitable habitats from surrounding poulations if they become locally extinct. This is metapopulation dynamics (Krebs 2001, pp 289-290). However, the ability to disperse, in terms of individuals that may colonize an area or spread their genes to another population, is limited to reproductives at the end of a season, and to queens searching for nest-sites in the spring.

Different species of bumblebees probably prefer different habitats for hibernating, nesting, and foraging, and react differently to competition, barriers, and matrix, and have different abilities to disperse.

Climate changes

The last decades, it has become evident that global changes are real, amongst them land use and climate changes, man-made or not. NILU (2002) states findings by Intergovernmental Panel on Climate Change (IPCC), that concludes with a global warming of 0,4-0,8 ºC during the last decade, possibly more close to the sea and close to the ground. Both the horizontal and the vertical directions are important bumblebees. Temperatures are expected to raise additionally 1,4-5,8 ºC within the next 100 years (IPPC 2001). Bumblebees, that generally have a northerly distribution (Goulson 2003), will probably be heavily affected by such changes, altering the species` composition locally. In addition, there can be expected to be an indirect effect on nectar-feeding insects through the flowering vegetation, and vice versa. However, there is likely to be a time-lag in the succession of plants as established perennial plants may live for decades or even centuries. It takes time for new species to establish a population in competition with the "relics", that is, species that most likely will become extinct under the present conditions, but are still present.

A climate change that makes bumblebees less important as pollinators, can affect interactions between plants and pollinators in a series of ways: Galen (1996) states that many flowers that live in a cold climate are adapted to pollination by bumblebees, as the diversity of pollinators is smaller than in warmer areas. The flowers are commonly more rewarding, and will produce larger floral displays. However, this may also be because plants grow older before they bloom if they live in a cold area. Further, she found that corolla size increased by 9 % in the progeny if the flower was pollinated by bumblebees. Larger corollas may have both a shape and a size effect, as larger corollas are better fit to deposit pollen on larger pollinators (Campell et al. 1991). Some flowers vary in color or other attractants within a population, and preferences by pollinators may affect both the fenotypes and possibly the evolution of plants. Stanton et al. (1986) found that in a population of *Raphanus raphanistrum*, where whites are dominant to yellows, insect-pollinator preferences resulted in 80-90 % yellows (homozygotes).
Global warming may cause the plants and insects to move to higher altitudes and latitudes. Warmer climate makes it possible to bumblebees to start the season earlier, making the total life-cycle to shift towards the spring and cease earlier in the summer, or makes it possible for some species to complete, or at least try, a second life-cycle in one summer.

Pesticides

During the last decades, the awareness of environmentally harmful pesticides and agricultural methods have resulted in information and legislative restrictions on farming practice (Fry and Rinde 2002). The aim is to prevent pesticides used in field crops from reaching areas of non-crops. Some pesticides are forbidden, others are made less harmful, spraying is restricted to late in the evening to minimize effects on non-target species, and conservation headlands are treated as valuable to crops (as "beetle banks") and the environment in general. Some of these measures are made to protect honeybees (*Apis mellifera* L.), but will protect other pollinating insects as well (Villumstad 2004). Restrictions in the use of herbicides should improve the conditions to perennial flora and indirectly bumblebees, and restrictions in the use of insecticides should help them directly.

Land use

Changes in human land use is fragmenting the landscape (e.g. Dramstad et al. 1996). Habitat-fragmentation is suggested to cause bumblebees to decline (Goulson 2003), possibly affecting the specialized species most. Fragmentation may be hard to identify from the bumblebees` point of view. The disappearence of unimproved meadows and pastures with nectar- and pollen sources (Goulson 2003) are partially replaced by parks, gardens, and road verges that offer new resources in open habitats.

A part of the intensifications in the agriculture has been to drain wet areas and close ditches to increase the cropped area, and to level the fields and make straighter edges to make the fields easier to manage by modern machinery. Goulson (2003) writes that removal of hedgerows in England has had negative impact on bumblebees, with loss of both floral resources and nest-sites. Hedgerows were originally grown to separate grazing live-stock from cropped fields. It is uncertain if this applies to Norway, as fences are more commonly used for this purpose.

The combined effect

The combined effect on bumblebees from climate change, habitat fragmentation, and less harmful use of pesticides is not intuitively obvious.

This thesis is based on data from a field study in 1992 (Dramstad and Fry 1995), and my own follow-up the summer of 2005, in the same transects, using the same methods. As table 2 shows, the weather was not favorable for bumblebees this season, and the bumblebee activity was low until the end of the season (figure 3, table 6). This is not a complete inventory of all the available resources in the study area, only the narrow transects. The results can not be extrapolated to the all of the non-cropped areas in the region. The idea of using the species` composition of bumblebees as an indicator-group of altered conditions is a long shot, but it is not obvious that it is tested in Norway or Scandinavia.

The flora and possible changes during the last 13 years will not be analyzed in detail here, only commented where it is relevant to the hypotheses and the observations of bumblebees.

1.3 Hypotheses

Based on the mentioned changes in climate and agricultural practice, I hypothesize that some changes have occured in the flora and the bumblebee populations during the last 13 years. As different bumblebee species have different habitat requirements, e.g. climate, nest-sites, and floral resources, the community and abundance of bumblebees may reflect these qualities in an area.

1 The general European trend of decline in bumblebees, whatever the cause, is evident in the southern of Norway too. This has led to a decrease in the number of species and a lower total density of bumblebees, most evident in the long-tongued species.
Predictions: *Bombus hortorum* will be present in very low numbers, if at all. The lesser abundant species from 1992, *Bombus hypnorum* and *Bombus pratorum,* will be absent. *Bombus lucorum* L. and *B.pascuorum* will dominate relatively, but have declined in absolute numbers compared to 1992.

2 Ecological awareness has led to positive changes in agricultural practice. This will give higher numbers of perennial plants (also because the individual plants will have grown larger without disturbance), plants favored by bumblebees. Less disturbance in remnant habitats also leads to more nest-sites. Thereby, there are more resources to bumblebees that will have inceased in total density, and in the number of species.
Prediction 1: Increased floral diversity (measured by the Shannon-Wiener diversity index and by the number of species) since 1992, especially in perennial flowers.
Prediction 2: Increased density of bumblebees through the season, all species from 1992 are present, and some new species will be present. More specialized species with long proboscis, like *B.hortorum* and *Bombus distinguendus* Morawitz will be present in respons to increased floral diversity.

3 Warmer climate alters the bumblebee species` composition, favoring species that are locally close to their northerly distribution limit and excluding species that are close to their southerly distribution limit. In 1973, the northernmost observation of *Bombus ruderatus* Fabricius was in Falkenberg, Halland, Sweden, 320 km south-south-east of Ås (Løken 1973). By moving 10 kilometres as an annual average, it may have reached Ås by now. Cf. Løken (1973) the site is within the distribution range for *B.sylvarum*, but not very far from its western and northern limit, except for coastal areas.
Prediction: *B.muscorum, B.ruderatus* and/or *Bombus veteranus* Fabricius have colonized Frogn/Ås, and *B.terrestris, B.sylvarum, B.ruderarius* and *B.lapidarius* will be abundant. *Bombus consobrinus* Dahlbom is absent.

To address these questions, I used the same transects and the same study methods as used by Dramstad and Fry (1995), and compared the results relevant to the hypotheses.

2 Materials and methods

2.1. Study area

The study area is in Frogn municipality, Akershus county, 25 km south of Oslo. The landscape is dominated by cereal fields with some remnant islands where the moraine soil is too shallow over the rock surface. In addition, there are some linear structures of non-cultivated areas along roads, draining ditches, and ownership boundaries. At the edge of the study area, there is a forest surrounding the cereal field, divided in a deciduous and a spruce forest.

Flowering vegetation was counted within the transects (see 2.3) before the bee walks. They were counted as umbels (e.g. Apiàceae), heads (Asteràceae, except *Achillea millefolium*: umbel), spikes, or individual flowers (e.g. Fabàceae). Identification and Norwegian names in Appendix A follows Lid and Lid (1998), English names follows Rose (1981). Authors of plant species that are not mentioned in the text, are listed in Appendix A. Bee walks followed the method described by Prys-Jones and Corbet (1991): Each transect was walked in a slow and even pace five successive times, recording all foraging bumblebees one metre in front and to each side. When a bee left one plant species to visit another during the counting, only the first plant species was recorded. All transects were walked the same day except for once, but the most of the flora was recorded the day before. Time, temperature, and relative humidity 0,5-1 meter above ground were recorded at the beginning and end of each bee-walk. Temperature was measured in shade. All recordings are on the CD. The earliest recording started at 9.20, and finished at latest at 20.40. The temperatures had a minimum of 14.4ºC and a maximum of 34,5ºC, and I never recorded during rain or the first half an hour after a shower. Relative humidity varied from 24 to 69 %, the highest levels were in the ground vegetation, and this was in mornings after rainfall at night, but with sunny conditions during bee-walks.

The intervals between replicates varied from 3 to 14 days, trying to keep intervals of 7-10 days. The 3-day interval was after three warm days after a longer period with cold and rainy weather, leading to increased bumblebee activity. I did not count flowers at this occasion (19th of June). The 14-day interval (and one 13-days) was caused by cold and/or rainy weather. At the hottest day, registration was stopped when the temperature rose above 35ºC (bumblebee activity almost ceased) and continued in the evening when the temperature fell below 28ºC. This was also the date of the latest recordings. Goulson (2003) defines a body temperature in bumblebees above 44ºC to be lethal. Arial temperature was measured in shade while the transects were partly in direct sunlight. Body temperature will be well above ambient temperature due to metabolism and muscle activity. When I considered the wind to be too strong, recording was stopped, likewise when I considered distant thunder to be close enough to affect bumblebees in the transects.

The bumblebees were classified after Løken (1985), and species` with a northern limit south of Norway in 1985 were based on Swedish and Danish sources (none of these species were found). *B.lucorum* and *B.terrestris* were grouped due to the problem of distinguishing them in the field, and were classified as *B.lucorum* as Løken (1985) raised doubt whether *B.terrestris* exists in this study area.

2.3 The permanent transects

The transect from 1992 were chosen to represent different structures of remnant natural and semi-natural habitats in agricultural landscapes in the region. They were given names to describe their main habitat type. Together with Dramstad, I plotted the transects. To facilitate the recordings, marker sticks were placed each 25 metres in all transects. All transects were 225 square metres, with a 75x3 metres as preferred shape. All written recordings (flowers and bumblebee visitations) are within 25 by 3 metres, but in the presented data it is pooled to whole transects. Where the edge was narrower than 3 metres, it was compensated by lengthening the transect to keep the total edge-area constant.

A) Ditch edge
B) Road verge (replaced from 1992, see below)
C) Deciduous island edge
D) Deciduous island interior
E) Rock outcrop
F) Spruce forest edge
G) Deciduous forest edge (not included in 1992, see below)
H) Spruce forest edge, shadow (not included in 1992, see below)

The transects are presented in more detail below.

2.3 Analyses

The Shannon-Wiener diversity index and equitability index

This index calculates the likelyhood of encountering different objects in two successive events. There are different versions of this index, this one is from Krebs (2001 pp 617-618).The index does not measure spatial distribution of the objects, that is, if the objects are evenly distributed or appear in clusters.

$$H = -\sum_{i=1}^{s} (p_i)(\log_2 p_i)$$

S = The number of species in the community

p_i = The proportion of the total sample that belong to the $_i$ –th species

H = Species diversity index

H_{max} = Maximum species diversity = $\log_2 S$

E = Equitability index (range 0-1, 1 is the most even community)

E-index = H/H_{max}

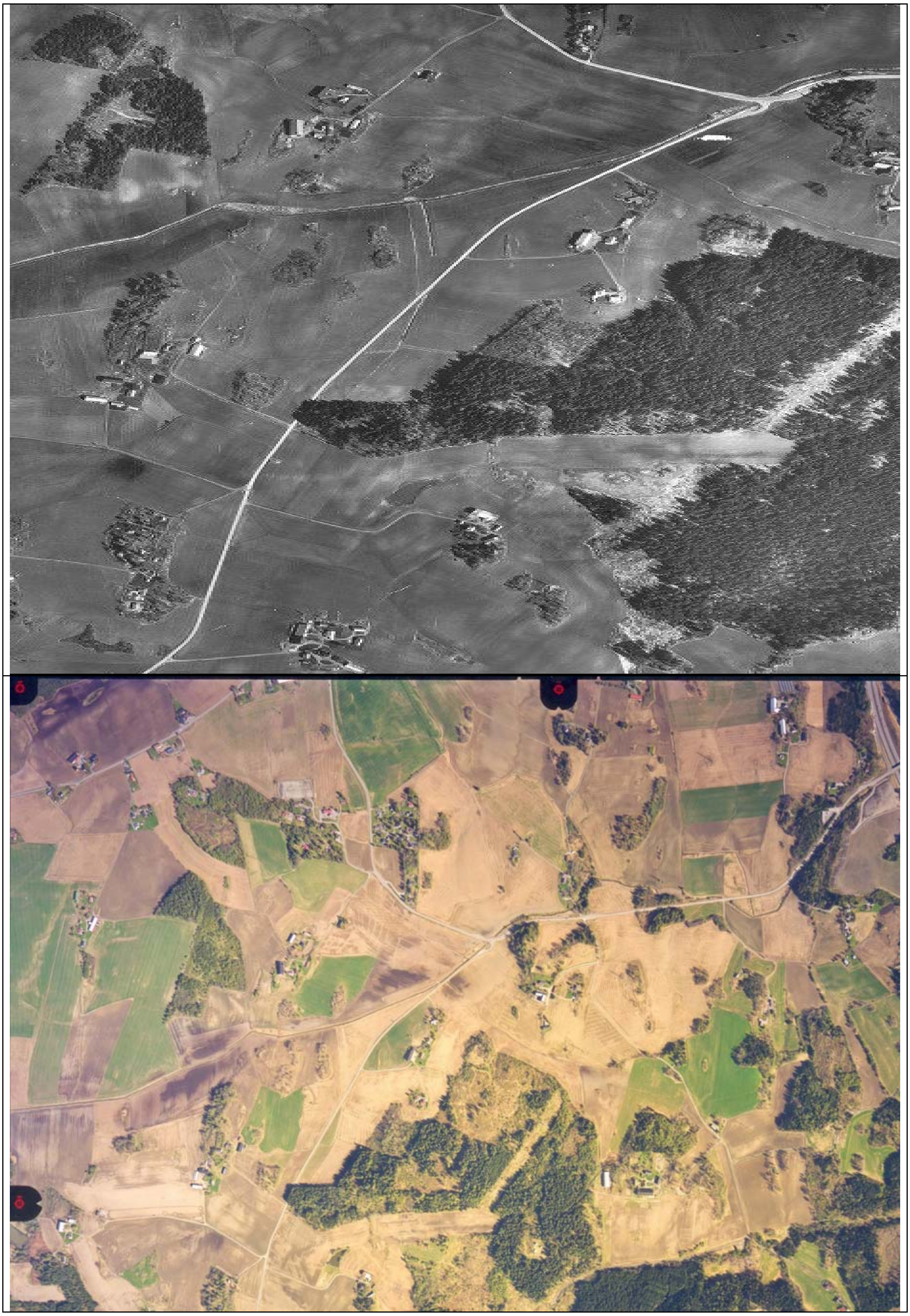
The H-index increases as the number of species increase, and by increased evenness, and the E-idex compares the H-index with the maximum possible equitability, or evenness.

Murdoch`s C-index of flower preferences (Murdoch 1969)

$$C = \frac{\text{Visits to flower A/All visits}}{\text{Number of flower A/All flowers}}$$

The calculations are substantially modified to be statistically valid. The same modifications are used for both years, making the data directly comparable. This is explained further in Appendix B, Appendix C and D includes the results from 2005 and 1992, respectively. The method used here gives a z-value directly without using neither mean or standard deviation. By entering these z-values into standard tables (e.g. in Moore and McCabe 2002), the p-values are given. The p-values gives the statistical probability of an event happening by chance if the data are normally distributed.

The term preference is used when a flower is visited significantly more than expected by chance. A flower is called discriminated if it received significantly less visits than expected, but received at least one visit. Unvisited flowers are not tested.



Arial photos showing the study area. The top picture is from 1992, the bottom picture is from 2003.

Pooling data of all nectar and pollen resources for an entire season (comparing plants that do not co-flower) will most likely not detect the real preferences by bumblebees. To reduce this bias here, I have separated the season into three periods called spring (27th of May till 16th of June), summer (19th of June till 11th of July), and autumn (24th of July till 12th of September). The first period should be when queens are founding nests and are (more or less) sole foragers, the mid period when activity peaks, and the latest period when young reproductives are active and nest activity decreases.

3 The transects in 1992 og 2005

The arial photos at page 20 shows that there are no large-scale physical changes in the landscape from 1992 till 2003.

Transect A, the ditch edge.

In 1992 this was described as a strip with woody and herbaceous vegetation. In 2005 there were no signs of shrubs or even saplings of trees. It was also somewhat narrower than the three metres mentioned in Dramstad and Fry (1995). It had shrunk to about one meter, in addition to the steep banks of this open draining ditch. It is elevated some twenty centimetres above the cropped field, and the crops were grown without any clearing (10-15 centimetres, about the width of my shoes) to this edge and made it difficult to walk this transect without disturbing both the crops and the narrow strip of edge vegetation. The vegetation was too dense to pass through. From half a meter above ground, the crops and the edge vegetation intertwined, making a "canopy".The vegetation was heavily influenced by farming practice in the cropped field: Herbicides probably had its largest effect on annuals and young perennial dicotyledons. The use of artificial fertilizers provided good conditions for herbs like *Urtica dioica* and *Artemisia vulgaris* and some clusters of *Cirsium vulgare*. The dominance of grasses was obvious. The plants were large: *U.dioica* at least 160 cm tall, *A.vulgaris* about 2 metres and *C. vulgare* close to 2,5 metres.

Transect B, the road verge.

Transect B in 1992, a grass bank constituting an ownership boundary, had become so narrow that we decided to substitute it with another linear structure, a road verge passing through the study area. To arrive to transects C, D, and E, I had to walk along the grass bank and could evaluate the decision.

The road verge runs almost parallel to the ditch edge (A), in one of the ends only separated by six metres of cereal field. The transect was cut mechanically by the road authorities four times during this study, possibly because of traffic safety and to avoid the spread of seeds of perennial weeds into the cropped fields and/or gardens. Clearing the verges is considered important to prevent allergic reactions to pollen from *Artemisia vulgaris* (Bjørn-Egil Dehlin, pers.com.) The 27th of May the road verge began to be dominated by *Taraxacum officinale* (for several kilometres), and many *A. mellifera* and some bumblebees foraged along with other nectar-feeding insects (e.g hover-flies and butterflies). I had the impression that bumblebees were just starting to utilize this resource, and that *T.officinale* was just in the beginning of its blossom, but the transect was cut by the 7th of June. This potentially large resource to local pollinators in a time of relative scarcity, turned into matrix, that is, an area unsuited for foraging and increasing the distance between resources (Dramstad et al. 1996). To some degree *Trifolium* spp. were to low to be cut, but never dominated. In addition to grasses, it was primarily *Myosotis* spp. and other small flowers not interesting to bumblebees until late summer. Then, *Leontodon autumnalis* and some other resources became available. This transect was heavily influenced by the use of herbicides in the cropped field.

At the grass bank, the vegetation was dominated by tall grasses, *Anthriscus sylvestris, Artemisia vulgaris,* and *Urtica dioica*, none of which preferred by bumblebees. Later in the season, some scattered *Galeopsis tetrahit/bifida* provided some resources to nectar-feeding insects. Early in the season, the vegetation was heavily influenced by herbicides used in the cereal-field. As a boundary, it probably received herbicides twice as often as the cereal-fields because the neighbouring farmers did not treat their fields simultaneously.

Transect C, the deciduous island edge.

The transect was along the north-eastern side of the island and then turning south. Most of the transect received sunlight till about 10 AM in the north-east after the canopy closed in mid June, and had sun almost all day at the southern part. The edge of small islands has the benefit of always having a side in the shade of wind, and always having both sunny and more and less shady conditions over a short distance. As a result, bumblebees do not only have to choose what flowers to visit, but also the degree of wind and temperature they prefer or tolerate. The abiotic factors may influence bumblebees directly (wind, precipitation, and temperature), and indirectly through the response of the vegetation to these factors. The trees were mainly oak (*Quercus* spp.), and some scattered aspens (*Pòpulus trèmula* L.) and birches (*Betula* spp.). The edge vegetation was primarily herbaceous. There were no signs of logging the last decades, but parts had been used as a dumping spot in a period before the municipality authorities started collecting household waste (tin cans, glass, broken light bowls etc.). Together with transect D, this transect provided most resources early in the season.

Transect D, the decidiuous island interior

The interior of the island was dominated by mature, deciduous trees, and the forest floor was mainly herbaceuos with some scattered bushes (e.g. *Rosa* spp). It provided less and less resources as the season developed, with the exception of *Sedum telèphium*.

Placed between other large islands in a matrix of intensively cropped fields, it seemed to be important to birds and larger mammals like row deer and elk: Faeces and resting places were everywhere inside the island, and tracks of these animals were often seen along the edge. The animal-made lanes through the crops showed how they moved in the landscape, using these remnants as temporary habitats for feeding, resting, and shelter, possibly also mating. These lanes were almost straight lines between islands. Ants were extremely abundant.

Transect E, the rock outcrop

This small island has a thin layer of soil on top of the rock. There are a lot of tussocks, many of which most likely abandoned ant nests. There were many tunnels made by digging animals, probably voles (*Arvicola terrestris*) and mice (*Microtus* spp. and *Apodemus* spp.). These might serve as nesting places to some bumblebee species. The island is sloping with a ridge of rock along the top, so that draining from the fertilized field do not pass through the soil. This gives the island a vegetation adapted to drought and conditions relatively poor in nutrients.

Transect F, the spruce forest edge

This transect runs along the eastern side of a cereal field, and the sun comes in about 14 AM. Together with transect H, that is the southern limit of the field, the spruce forest edges are the corners of the cropped field. Early in the season, the owner cleared shrubs and bushes from the edge. The edge was wide: 5-8 metres of headland, 2-3 metres of uncropped field, and additionally 3-4 metres of elevated edge bank. The outer 10 metres of the field gave little yield, probably due to the combination of shade half of the day and that, as a consequence, it was little to gain by adding fertilizers. Because the farmer may choose to manage the field different in different years, I chose to use the elevated bank for this study. It was dominated by tall grasses. The resources were relatively poor, except for a 3-4 square metre patch of Fabàceae: Clovers (*Trifolium hybridum* and *T.repens*), vetches (*Vicia cracca* and *V.sepium*) and meadow vetchling (*Lathyrus pratensis*). In addition, there were some scattered individuals of thistles that attracted bumblebees.

Transect G, deciduous forest edge

The transect runs north-south, along the eastern side of the cerial field. The deciduous forest was primarily young birch and aspen, probably after a clear-cut some decades ago. Before the canopy closed in mid-June, this area received a lot of light. This transect is narrow, and also serve as a draining ditch in the spring. Young frogs (*Rana temporaria*) were more abundant than bumblebees in this transect, and *Iris pseudacorus* L. (that did not bloom, and therefore not in the list) in the ditch shows that the conditions are moist. This transect was dominated by *Anthriscus sylvestris* in June to mid-July, later by *Angelica sylvestris*. None of these had any visits by bumblebees, and the transect never provided larger amounts of resources.

Transect H, shaded spruce forest edge

This is close to transect F, but has the mature spruce forest to its south, leaving the field edge in shade all day. The vegetation was sparse, providing almost no resources. An exception may be during the flowering of blueberries (*Vaccinium myrtillus*), and that it might be suited as a hibernation site. The transect was dark and chilly, and most of the photosynthetically active radiation (400-700 nm, f.ex. Molles 2002, pp 138) was probably absorbed by the forest. The forest-floor had even less vegetation than the edge, and almost without herbaceous plants, but with some blueberry and ericoide plants (primarily *Calluna vulgaris* (L.) Hull). The intention with this transect is to demonstrate that the area of uncropped margins are of different quality to flora and fauna. The bottom (western end) of the sloping transect was moist, as the forest drained this way, with herbs like *Viola palustris*. At the top it was dry, with blueberry (*Vaccinium myrtillus)*. By the end of October, the Norway spruce (*Picea abies* (L.) Karsten) south of this transect was cut, leaving only scattered deciduous trees (mainly *Betula pubescens* Ehrh.). The changes in light conditions, humidity, acidification, and wind will give raise to a succession the next years in this edge, that the bumblebees probably will benefit from. This clear-cutting will most likely affect the conditions in the adjacent transect too, and the former forest may contribute with resources.

It is remarkable that there are no stone walls or other larger assemblies of stones picked up from the cropped areas over the years in any of the transects. Such structures would offer important nest-sites for some bumblebee species. Even in clay, there are often stones that melted out of floating ice at the end of the ice age.

4 Results

4.1 Weather and seasonal development

Table 2 shows that in 1992, May and June were warm and sunny months, while August had a lot of rain. In 2005, April and the beginning of May were very sunny and warm, and late May till the end of June was cold and rainy compared to 1992. In 2005, August was warmer and much drier than in 1992, so to September compared to the 30-years normal period.

Table 2. Temperature (°C) and precipitation (mm) in 1992 and 2005, and the 30-year normal period. The data are from Det Norske Meteorologiske Institutt.

Temperature	April	May	June	July	August	September
1961-1990	4,1	10,3	14,8	16,1	14,9	11,0
1992	3,8	12,8	17,3	16,2	13,9	
2005	5,9	8,9	13,7	17,6	15,1	12,9

Precipitation	April	May	June	July	August	September
1961-1990	39,0	60,0	68,0	81,0	83,0	100,0
1992	66,4	49,0	16,7	88,4	153,5	
2005	29,8	72,4	59,4	87,0	66,6	18,8

Figure 1. Bumblebee with longitudinal yellow band

4.2 Floral diversity

Table 3 shows that all transects from 1992 have more flower species in 2005. The flowers were also present in more equal numbers (higher values in the E-index, and the Shannon-Wiener diversity index), except for the rock outcrop (E). The largest difference in E-index values between years is for the ditch edge (A), but it is still the least diverse in both number of species and in species` diversity and evenness. Grasses and other monocotyledons are not included, neither are mosses or lichens. See Materials and methods for how data were collected; The number of flowers does not equal the number of “individual” plants, but rather units of possible resources to bumblebees.

Table 3. Number of flower species from each transect studied in both 1992 and 2005, and calculations of the Shannon-Wiener diversity index (H) and species` evenness (E-index) by the. See Materials and methods for formulas.

Transect	Species 1992	Species 2005	H_{max} 1992	H_{max} 2005	H-value 1992	H-value 2005	E-index 1992	E-index 2005
A	19	23	4,248	4,524	0,778	2,711	0,183	0,599
C	39	47	5,285	5,555	3,506	4,124	0,663	0,742
D	37	46	5,209	5,524	2,410	4,156	0,463	0,752
E	47	53	5,555	5,728	4,259	4,198	0,767	0,733
F	29	41	4,858	5,358	2,766	3,928	0,569	0,733

Table 5 lists plant species that were observed in a transect only one of the years, and in table 4 they are divided in annuals, biennials, and perennials. Table 4 shows that plants of all life-strategies have increased, but with a trend of relatively more perennials in all transects. This only apply to the narrow transects, lost species may still be present in the area.

Table 4. Floral changes by life-strategies. Flower species lost from 1992, and species new in 2005. Vertical letters are codes for transects, horizontal letters are life-strategy of the plants: A=annuals, B=biennials, and P=perennials.

	Lost			New		
	A	B	P	A	B	P
A	1	1	3	3	1	5
C	4		6	4	1	13
D	1	1	7	1	1	17
E	2	1	8	1	1	15
F	2		7	4	1	16
	10	3	31	13	5	66

Table 5. Differences in floral composition between 1992 and 2005 in transects that were studied both years

Transect A		Transect C		Transect D		Transect E		Transect F
Lost from 1992	New in 2005	Lost from 1992	New in 2005	Lost from 1992	New in 2005	Lost from 1992	New in 2005	Lost from 1992
Sonchus oleraceus	*Lysimachia vulgaris*	*Chamomilla suaveolens*	*Barbarea vulgaris*	*Campanula persicifolia*	*Succisa pratensis*	*Hypericum montanum*	*Campanula rotundifolia*	*Myosotis spp*
Carduus crispus	*Leontodon autumnalis*	*Euphrasia spp*	*Carum carvi*	*Leontodon autumnalis*	*Urtica dioica*	*Campanula persicifolia*	*Arthemisia vulgaris*	*Vicia spp*
Ranunculus repens	*Lathyrus pratensis*	*Galium boreale*	*Centaurea jacea*	*Hieracium pilosella*	*Rubus idaeus*	*Leontodon autumnalis*	*Viola spp*	*Solidago virgaurea*
Lamium purpureum	*Lapsana communis*	*Knautia arvensis*	*Galium aparine*	*Centaurea jacea*	*Viola spp*	*Pimpinella saxifraga*	*Vicia spp*	*Tussilago farfara*
Angelica sylvestris	*Epilobium montanum*	*Lamium purpureum*	*Lotus corniculatus*	*Ranunculus auricomus*	*Vicia spp*	*Sonchus oleraceus*	*Ranunculus flammula*	*Galium boreale*
	Taraxacum officinale	*Melampyrum sylvaticum*	*Lychnis viscaria*	*Knautia arvensis*	*Veronica serpyllifolia*	*Anemone nemorosa*	*Carum carvi*	*Spergula arvensis*
	Chenopodium album	*Pimpinella saxifraga*	*Myosotis* spp	*Lamium purpureum*	*Stellaria graminea*	*Spergula arvensis*	*Epilobium montanum*	*Ranunculus auricomus*
	Cuscuta europaea	*Ranunculus auricomus*	*Prunella vulgaris*	*Galium uliginosum*	*Ranunculus flammula*	*Ranunculus auricomus*	*Selinum carvifolia*	*Sonchus asper*
	Impatiens noli-tangere	*Rubus idaeus*	*Ranunculus acris*	*Crepis tectorum*	*Carum carvi*	*Melampyrum pratense*	*Alchemilla spp*	*Veronica chamaedrys*
		Taraxacum officinale	*Ranunculus flammula*		*Geum urbanum*	*Potentilla argenta*	*Rumex acetosa*	
			Rubus saxatilis		*Lapsana communis*	*Arabis thaliana*	*Filipendula ulmaria*	
			Rumex acetosa		*Prunus padus*		*Knautia arvensis*	
			Silene dioica		*Alchemilla spp*		*Rumex acetosella*	
			Succisa pratensis		*Rumex acetosa*		*Galium uliginosum*	
			Trifolium campestre		*Filipendula ulmaria*		*Veronica chamaedrys*	
			Trifolium hybridum/repens		*Leucanthemum vulgare*		*Barbarea vulgaris*	
			Veronica serpyllifolia		*Silene dioica*		*Euphorbia helioscopia*	
			Vicia sepium		*Angelica sylvestris*			
			Euphorbia helioscopia		*Valeriana sambucifolia*			
			Fragaria vesca					

4.3 Bumblebee diversity and abundance in 2005

Eight bumblebee-species were recorded in the transects in 2005 (*Bombus lapidarius, B.wurfleini/ wurflenii, B.ruderarius, B.pratorum, B.pascuorum, B.lucorum/B.terrestris, Bombus sylvarum* L. *and B.hypnorum*) (figure 2).

All the *B.sylvarum* were melanic. On the 12th of September, I collected six specimens and sent them to Björn Cederberg, ArtDatabanken, Uppsala, Sweden for identification. *B.ruderatus* and *B.veteranus* were not found, neither were *B.consobrinus* or *B.muscorum*.

The total number of visits by bumblebees in 2005 is shown in table 6. Comparisons with data from 1992 are made in figure 2. Table 6A shows that *B.lapidarius* made up half of all visits in 2005, and that activity was highest late in the season. Table 6B shows that more than half of all recorded visits was at the ditch edge (A) and very few visits in the transect shaded by spruce forest (H). Table 6B and figure 4 shows that the island edge had many recorded visits early in the season, and then experienced few visits from mid June till the beginning of August. Further, the rock outcrop (E) had a moderate, but continouos, visitation from mid June. On the six dates of recording from the 16th of June till the 24th of July, nearly half of all visits were to the rock outcrop (E) (60 of 126).

Table 6. Visits by dates in 2005. 6A) by bumblebee species, and 6B) by transect.

A) Bumblebee species	27.5.	7.6.	10.6.	16.6.	19.6.	25.6.	6.7.	11.7.	24.7.	5.8.	19.8.	30.8.	12.9.	sum	%
B.pascuorum	2	8	3	3	1	0	2	2	4	5	0	19	11	60	8,11
B.lucorum	5	1	6	5	0	1	1	1	5	6	1	8	1	41	5,54
B.wurfleini	0	0	0	1	2	0	2	1	23	8	45	97	11	190	25,68
B.ruderarius	1	0	0	1	7	7	0	13	0	0	0	0	0	29	3,92
B.lapidarius	2	0	0	4	2	3	2	5	19	30	136	104	68	375	50,68
B.hypnorum	1	1	2	0	2	0	0	0	0	0	0	0	0	6	0,81
B.sylvarum	0	0	0	0	0	0	0	0	7	1	2	13	14	37	5,00
B.pratorum	0	0	1	0	0	0	0	0	0	1	0	0	0	2	0,27
Sum	11	10	12	14	14	11	7	22	58	51	184	241	105	740	100,00

B) Transect	27.5.	7.6.	10.6.	16.6.	19.6.	25.6.	6.7.	11.7.	24.7.	5.8.	19.8.	30.8.	12.9.	sum	%
A, ditch edge	0	0	0	0	0	0	0	8	19	29	134	167	54	411	55,54
B, road verge	8	0	0	0	1	0	0	0	0	0	6	18	33	66	8,92
C, island edge	2	8	11	5	7	1	1	0	0	7	14	25	6	87	11,76
D, island interior	1	2	1	1	1	0	1	1	0	0	4	3	0	15	2,03
E, rock outcrop	0	0	0	7	4	10	4	12	23	2	25	20	4	111	15,00
F, spruce edge	0	0	0	0	0	0	1	1	12	12	1	1	0	28	3,78
G, deciduous edge	0	0	0	1	0	0	0	0	2	1	0	6	8	18	2,43
H, spruce edge, shade	0	0	0	1	0	0	0	0	2	0	0	1	0	4	0,54
Sum	11	10	12	14	14	11	7	22	58	51	184	241	105	740	100,00

Table 7 shows the distribution of bumblebee species in the different transects. *B.lapidarius* and *B.wurfleini* had most recorded visits at the ditch edge (A), whereas *B.pascuorum* and *B.lucorum* were most frequent at the island edge (C). *B.hypnorum* was confined to the deciduous island (C and D). The door-step forager *B.ruderarius* was observed in both the rock outcrop (E) and at the ditch edge/road verge (A and B). These transects were in the opposite ends of the study area (arial photo), about 500 metres apart.

Table 7. Visits by species and transect in 2005. Vertical letters are codes for transects.

	B.lapidarius	*B.wurfleini*	*B.pascuorum*	*B.lucorum*	*B.ruderarius*	*B.pratorum*	*B.hypnorum*	*B.sylvarum*
A	250	114	9	2	3	0	0	33
B	56	4	0	5	1	0	0	0
C	36	5	20	16	5	1	4	0
D	1	4	4	3	0	0	2	0
E	31	50	1	9	20	0	0	1
F	1	11	6	6	0	1	0	3
G	0	2	16	0	0	0	0	0
H	0	0	4	0	0	0	0	0
Sum	375	190	6	41	29	2	6	37

4.4 Changes in bumblebee species composition from 1992 to 2005

Nine species of bumblebees were observed foraging in the area, 7 in 1992 and 8 in 2005 (figure 2). The overlap is 6 species. *B.hortorum* is lost, *B.ruderarius* and *B.sylvarum* may be new. According to Dramstad, she may have excluded *B.ruderarius* and *B.sylvarum* as uncertain observations in 1992. In addition, I observed a single queen of *B.distinguendus* just outside a transect the 7th of June 2005, but it did not forage. In 1992, the most abundant species were *B.lucorum* and *B.pascuorum* (figure 2), totalling 71 % of the observations. In 2005, *B.lucorum* and *B.pascuorum* totalled just 13,6 %, while *B.lapidarius* and *B.wurfleini* totalled over 76 % of all observations. The realtive decline in *B.lucorum* and *B.pascuorum*, however, was not apparent early in the season. By mid June in 2005, *B.lucorum* and *B.pascuorum* comprised 70-75% of all observations, many were queens. From then on till the last week of July, both species were more or less absent until they appeared again in moderate numbers, many of which were males and young queens.

Figure 2 shows that the long-tongued *B.pascuorum* (8,5m/m) and the nectar-robbing *B.lucorum* (7,5m/m) (table 1) have declined at the study site. On the other hand, the nectar-robbing *B.wurfleini* has increased. Figure 2 also shows that *B.lucorum* and *B.pratorum* have decreased, and *B.hortorum* is lost. These species are mainly white, black, and yellow (table1). *B.lapidarius* and *B.wurfleini* have increased, and *B.ruderarius* and melanic *B.sylvarum* are registered as new. These are black and with grey-reddish tail (table 1). *B.pascuorum* and *B.hypnorum* are mainly brown (table 1).

By mid June in 1992, *B.lapidarius, B.hypnorum,* and *B.pratorum* were still not observed. In 2005, all bumblebee species that were recorded during the season, except for *B.sylvarum* (figure 3) were active by this time. In 1992, 25 species of flowers were visited in a total of 627 times. In 2005, 30 species of flowers were visited 740 times.

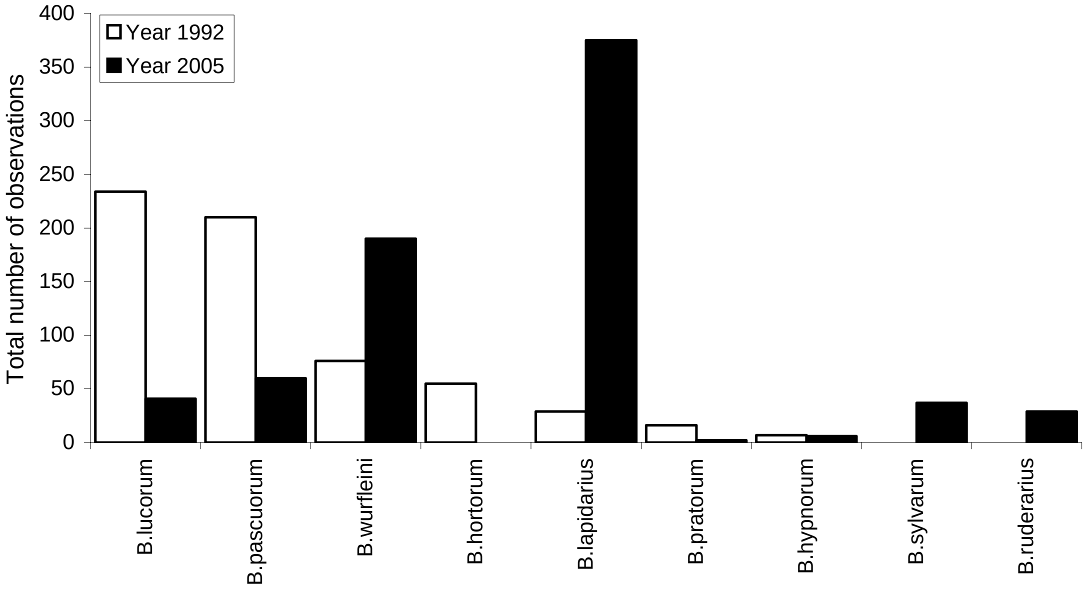


Figure 2. Observed visits in 1992 (open bars) and 2005 (filled bars) by bumblebee species.

The weather (table 2) made these seasons difficult to compare directly. April and the first half of May in 2005 was hot and sunny, with many nest-seeking queens. Then cold and rainy weather set in, with only short periods of weather favorable for foraging until August. Between the first (27th of May) and the second field work (7th of June), it was really cold and a lot of rain. Around the 11th of July, it was a period with temperatures above 30ºC in the mid-day, that must be considered almost extreme for Norway.

Figure 3 shows that activity peaked the 15th of July in 1992, and the 31th of August in 2005. The 31th of August was the last date of recordings in 1992, with only nine observed visits (Dramstad and Fry 1995).

Figure 4 shows how the different transects were visited by bumblebees during the season of 2005. The numbers are in table 6B. Recorded flowers from the transects are in the CD.

Figure 3 and 4 are shown as graphs to emphasize the trends, the data are not continouos.

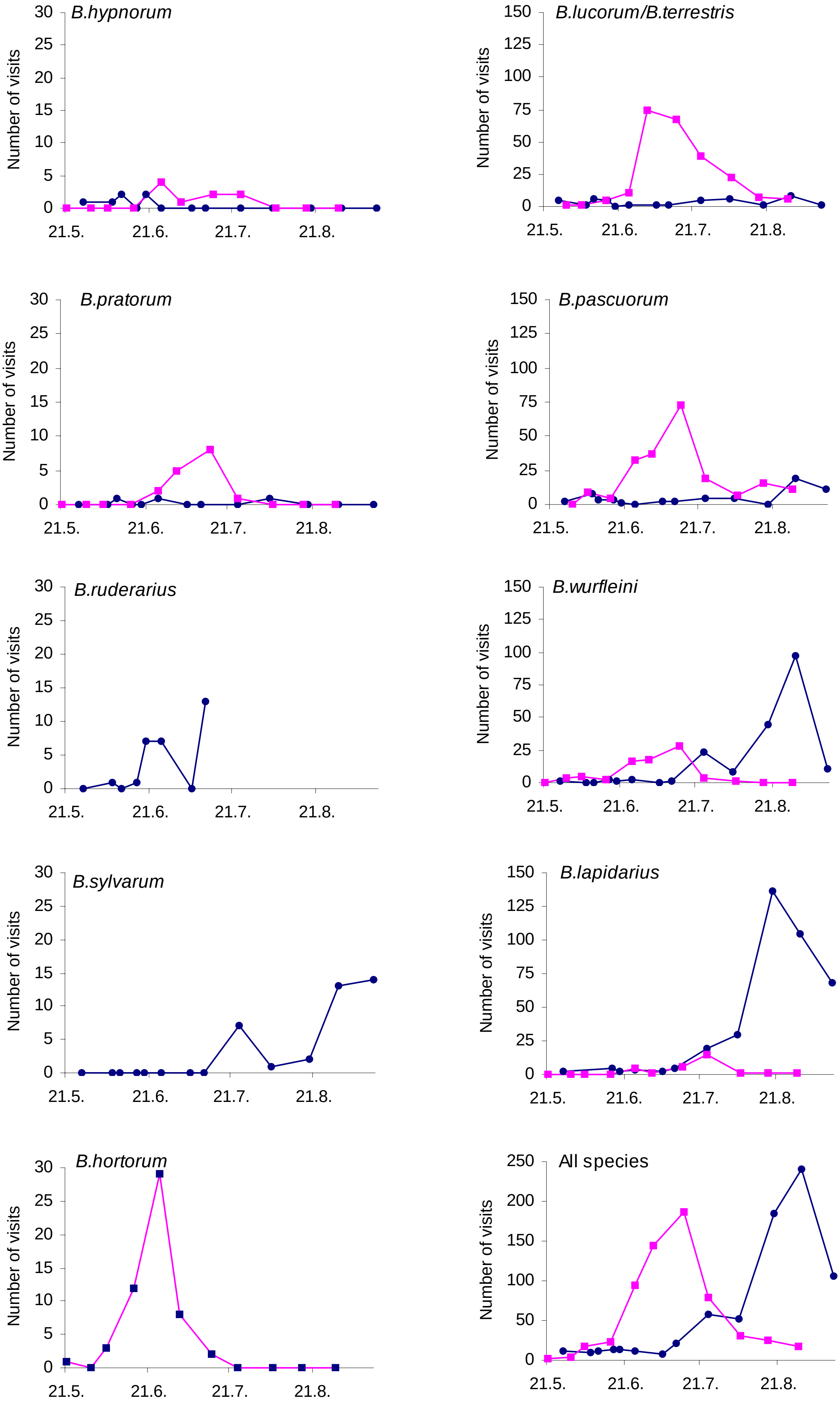


Figure 3. Phenology of the bumblebee species, all transects grouped. 1992 are with squares and 2005 with circles. Note the different vertical scales. The dates are monthly intervals, not dates of recordings

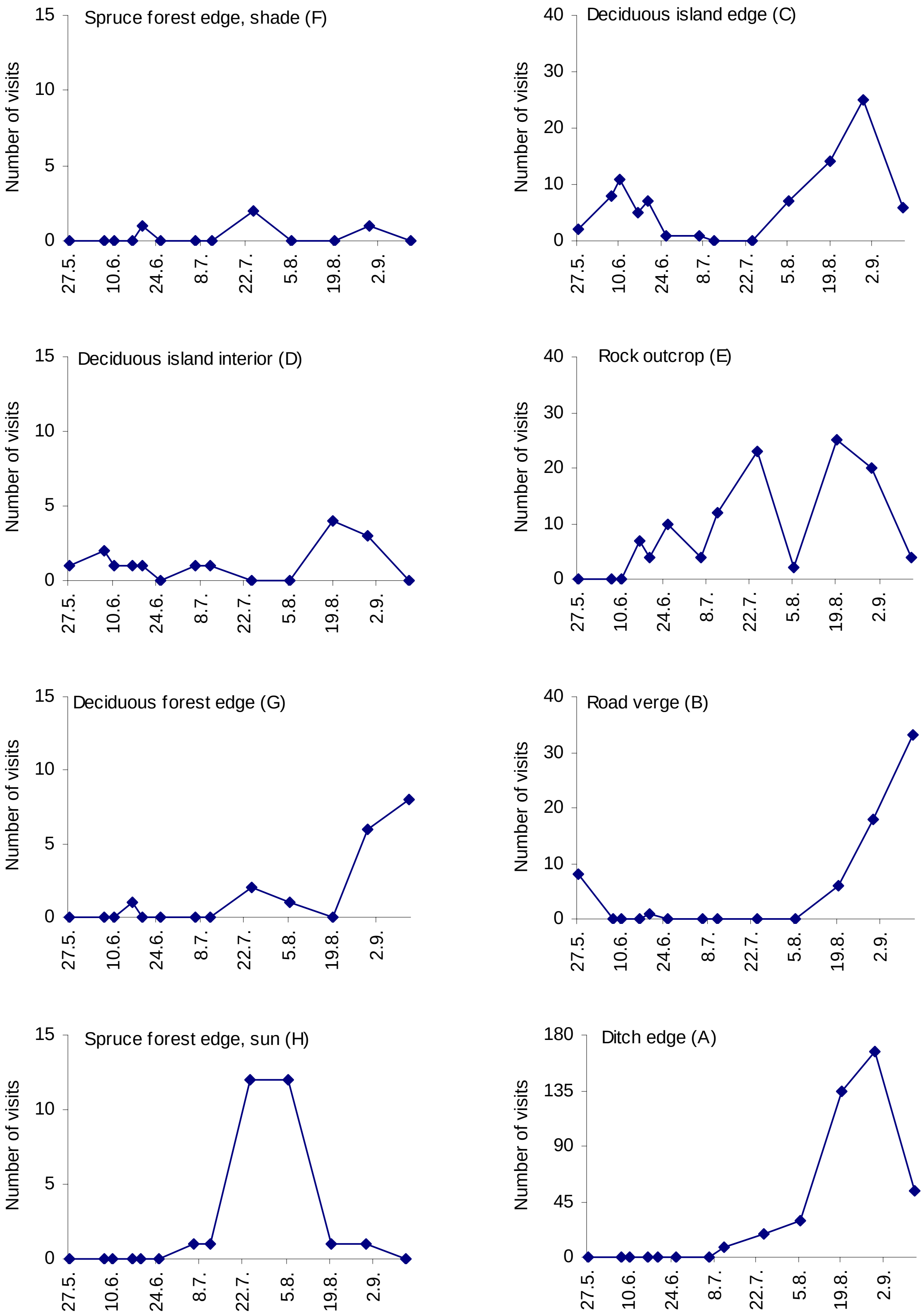


Figure 4. Visits by transects in 2005. Note the different vertical scales.

4.5 Flower preferences

Calculated preferences for both years are in Appendix C and D.

Statistical tests of flower preferences by individual bumblebee species by the C-index turned out to be misleading and/or to violate the tests. There were too many cells in the three-dimensional combinations of bumblebees, flowers, and different dates. The expected value of each cell was on average less than 0,24 visits when unvisited flower-species were excluded. Many of the combinations do not make biological sense, e.g. comparing flowers that are not blooming contemporary or testing a bumblebees` preference for a flower that bloomed before or after the bumblebee was active. This was somewhat improved by dividing the season into three periods, but the two first periods had so low visitation rates that even a single visit to a flower species turned out as a significant preference. The data are included in the CD.

Table 8 shows that flower preferences may vary during a season. For example, *L.corniculatus* was significantly preferred in the period from 19th of June till 11th of July, but was significantly discriminated later in the season. Pooling the data for the entire season does not reveal this, as it turned out insignificant.

Table 8. Differences in flower preferences between a period and the entire season. All bumblebee species are pooled. Spring: 27th of May till 16th of June, Summer: 19th of June till 11th of July, and autumn: 24th of July till 12th of September. Only flowers that loose or gain significance between the methods are mentioned here, see Appendix C for details. Abbreviations: NS= Not significant, neg=negative (discriminated), pos=positive (preferred).

Flower species	Spring	Summer	Autumn	Season
Ajuga pyramidalis	p<0,0560 Pos			NS
Galeopsis tetrahit/bifida		p<0,0749 Pos	NS (Neg)	p<0,0239 Pos
Hieracium umbellatum			NS (Neg)	p<0,0002 Pos
Hypericum maculatum		NS	p<0,001 Neg	p<0,0516 Neg
Lathyrus montanus/vernus	p<0,0005 Pos	p<0,0002 Pos		p<0,0516 Pos
Lathyrus pratensis		p<0,0002 Pos	NS (Neg)	NS (Neg)
Leontodon autumnalis			NS (Neg)	p<0,0002 Pos
Lotus corniculatus		p<0,0002 Pos	p<0,0045 Neg	NS
Lychnis viscaria	p<0,0002 Pos	p<0,0008 Pos		NS
Trifolium medium/pratense		p<0,0192 Pos		NS
Vicia cracca/sepium	p<0,0002 Pos	p<0,0002 Pos	NS	NS

Flower preferences for the entire season

Table 10 shows visits of bumblebee species to the different plant species. *B.pratorum*, *B.hypnorum* and *B.ruderarius* visited only two, three, and eight flower-species, respectively. For *B.pratorum*, there were only two observations. *B.hypnorum* made three out of six visits to *Rubus saxatilis* (table 10), that also imply that the observations mainly were done early in the season (figure 3). The same phenomenon goes for *B.ruderarius*, as this species disappeared from the study-area before many of the flowers did blossom.

B.lapidarius, B.pascuorum, B.wurfleini, and *B.lucorum* visited 16, 15, 14, and 13 species of flowers, respectively (table 10). These bumblebee-species were present through the season, with a peak in late summer (figure 3).

The vegetation at the ditch edge (A) and the road-verge (B) was highly different, despite the short distance between them. Of flowers visited by bumblebees, the ditch edge (A) is dominated by *C.vulgare* (see the presentation of the transects above), while the road verge (B) is dominated by *Leontodon autumnalis* and *Mycèlis muralis*. The 12th of September, both the ditch edge (A) and the road verge (B) still offered floral resources, but especially the *C.vulgare* had started to wither. The road verge (B) was studied only twenty minutes after the ditch edge (A). The pattern of visitation was obvious: Both sites pooled had 31 visits by *B.lapidarius,* but all of the total of 14 males visited *C. vulgare* at the ditch edge (A). The 17 females females appeared in almost equal numbers at the ditch edge (A) and the road verge (B). *B.wurfleini* was represented at the ditch edge (A) with 19 observations (all castes present), the road verge (B) with only two. *B.pascuorum* and *B.terrestris* visited the ditch edge (A) (3 and 1, respectively), but not the road verge (B) (table 6, figure 4).

Flower preferences in the spring and early summer of 1992 and 2005

The largest differences in statistical preferences by dividing the season into three periods, was the early period from the 27th of May till the 16th of June. The main differences are shown in table 9. Table 9 shows that *B.pascuorum* visited all species of flowers that received one or more visits this early, except *Geranium* spp. The five last species of flowers in table 9 were visited exclusively by *B.pascuorum*. *Lychnis viscaria* was visited by all bumblebee species except for *B.hypnorum* (table 10). *Trifolium medium/pratense* were in 1992 visited only by the long tongued species *B.hortorum* and *B.pascuorum* (table 10). In 2005, *T.medium/pratense* is recorded with only 15 flowers this early, but with more than 4500 later in the season. In 1992, *Melampyrum pratense* received more than half of all visits early in the season, but was not visited in 2005. In 1992, *M. pratense* was especially important to the long tongued *B.hortorum* and *B.pascuorum,* with 10 out of 16 and 11 out of 15 visits to *M.pratense,* respectively. *R.idaeus* was just starting to provide resources this early in 2005, but these were mainly depleted by honeybees *(A.mellifera)*. *R.idaeus* was significantly positive for the entire season in 2005. Lily-of-the-valley (*Convallaria majalis*) received some visits in 1992 (though significantly less than expected), but none in 2005 despite an intense blooming. The number of flowers in 1992 were only available as totals for the entire season, so the numbers are not presented for any of the years. *M. pratense* was registered with 15301 flowers in 1992, and 2925 in 2005.

Table 9. Visits in spring and early summer (27th of May till 16th of June) in 1992 and 2005 by bumblebee species on plant species. Below the bumblebee species, number of visits are described as 1992+2005. If no visits any of the years, the space is left open. Abbreviations: *hort: B.hortorum, pasc: B.pascuorum, lapi: B.lapidarius, rude: B.ruderarius, hypn: B.hypnorum, luco: B.lucorum, wurf: B.wurfleini,* and *prat: B.pratorum*. See the CD for details.

Flower species	1992	2005	*hort*	*pasc*	*lapi*	*rude*	*hypn*	*luco*	*wurf*	*prat*
Melampyrum pratense	27	0	10+0	11+0				5+0	1+0	
Rubus idaeus	8	0	2+0	1+0					5+0	
Geranium spp	4	1					0+1	1+0	3+0	
Trifolium medium/pratense	3	0	2+0	1+0						
Lychnis viscaria	3	24	1+0	0+6	0+4	0+1		1+11	1+1	0+1
Taraxacum officinale	2	8	1+0	1+0	0+2	0+1		0+5		
Rubus saxatilis	0	7		0+3			0+3	0+1		
Convallaria majalis	1	0		1+0						
Fragaria vesca	0	1		0+1						
Vicia spp	0	1		0+1						
Lathyrus spp	0	4		0+4						
Ajuga pyramidalis	0	1		0+1						.
Total	48	47	16+0	15+16	0+6	0+2	0+4	7+17	10+1	0+1

Flower preferences in mid summer

Table 8 shows that *Galeopsis tetrahit/bifida, Lathyrus pratensis, and Lotus corniculatus* were preferred in the summer, but were visited less than expected in the autumn. Table 8 also shows that *Lychnis viscaria, Trifolium medium/pratense, and Vicia cracca/sepium*of flowers were preferred in this period, but calculated preferences for the entire season turned out insignificant.

Flower preferences in the autumn

Table 8 shows that several flowers that were significantly preferred earlier in the season or for the entire season, were visited less than expected when looking at this period isolated. In this period, there were many visits to *C.vulgare* (table 10), mainly at the ditch edge (A) (figure 4).

As figure 4 shows, it was an abrupt decline in the curve of visitations for the rock outcrop (E) on the 5th of August. This coincides with a down-slope for *B.wurfleini* at the same day (figure 3). The same pattern is not shown in any other species in bumblebees, and is inconclusive in the other transects. There were thunder clouds in a distance the 5th of August, and shifting winds (both in strength and direction). At 14 AM this day, there was a sudden increase in temperature and a steep fall in relative humidity (that was not just an inverse reaction to the change in temperature). The rock outcrop (E) was studied 17.30 to 18.00 AM, and both temperature and relative humidity had stabilized more than two hours earlier.

Figure 4 shows that the rock outcrop (E) was the only transect that received visits all the time from mid June. Both the deciduous forest edge (G) and the road verge (B) got their highest recorded number of visits at the last day of observations, the 12th of September. All visits in the shaded spruce forest edge (H) were by *B.pascuorum* (table 6 and figure 4).

Flower preferences in 1992 versus 2005

38 species of flowers were visited these two seasons (table 10), 25 in 1992, 33 (30 in table 10) in 2005, with an overlap of only 16 species. Separating the grouped (see discussion) *T.hybridum/repens*, *L.montanus/vernus* and *V.cracca/sepium* gives the additional 3 species. All these 33 species were present and all were visited in 2005. Bumblebees may land without actually foraging, they sample, and naïve workers have to experience what flowers that are rewarding. I regarded less than 0,5 % of the total visits as coincidental. These flowers are hardly a resource to any bumblebee species at any date in any transect. This group was made up by 17 species of flowers that received 47 visits in total for both years, or 3,4 % of all visits. It should be noted, however, that all 5 visits to *Cirsium arvense* and all 3 visits to *Campanula persicifolia* were by *B.lucorum* and that all 4 visits to *Mycelis muralis* were by *B.lapidarius.* Flowers with visitation-rates between 0,5 % and 2 % (7 and 28 visits, respectively), may be of some value, at least to some species in some transects in some periods in some years. This group had 8 flower-species. They received 107 visits in total, or 7,8 % of all visits.
Flowers with more than 2 % (29 visits) of the total visits can be regarded as important to the entire community of bumblebees, some as a direct resource, others by diverting competitors. This group included 13 species of flowers, two of which received more than 10% of the total visits (*Vicia cracca* and *C. vulgare* with 17,2 % and 29,3 % of the total visits for both years pooled, respectively). These 13 species received 1237 visits, or 90,5 %. *H.umbellatum* is the only species that varied less than 100 % in visitation between years (11 visits in 2005 and 21 visits in 1992).

Results from 1992 for *Geranium* spp showed that bumblebees significantly discriminated these flowers. Four visits and 1379 flowers were recorded. In 2005, however, only one visit was recorded, but that turned out insignificant because only 100 flowers were recorded.

Note that flowers visited in spring and early summer by *B.pascuorum* in 1992 received no visits in 2005, and vice versa (table 9).

Galeopsis tetrahit/bifida received no visits in 1992 (table 10), but received 5,3 % of all visits in 2005 (table 10). It was preferred in the period from 16th of June till 11th of July (table 9), but not preferred later in the season. *R. saxatilis* (in transects C and D) got no visits in 1992 (table 10) in 2005. It flowered till the end of June and received 7 visits, nearly 10 % of all visits during the same period. It was significantly preferred in the spring (p<0,0002) but barely significant for the season (p=0,0526). On the deciduous island, *R. saxatilis* received 6,9 % of all visits the entire season.

Flowers visited in 1992 but not in 2005

Angelica sylvestris was significantly preferred (18 visits) in 1992, but the plant was abundant and attracted large numbers of flies (Diptera) in 2005. Especially transect G was dense with *A. sylvestris* in 2005. *Achillea ptarmica, Lamium purpureum, Lythrum salicaria,* and *Sonchus arvensis* received some visits in 1992, but were either discriminated or insignificant.

Flowers visited in 2005 but not in 1992

Ajuga pyramidalis, Fragaria vesca, Linaria vulgaris, Matricaria perforata, and *Viola arvensis/tricolor* received 4 or less visits and turned out as dicriminated or insignificant. *Linaria vulgaris* received 11 visits, but was insignificant. *Mycèlis muralis* and *Succhisa pratensis* was not recorded from any transect in 1992, both were preferred in 2005 (z=4,40, p<0,0002, and z=20,54, p<0,0002, respectively).

C. vulgare was the most preferred flower in 2005 with 400 of all the 740 recorded visits through the entire season (z=104,39, p<0,0002 for the season, and z=74,19, p<0,0002 for the autumn). The first visit to *C. vulgare* was at the 11th of July at the edge of the spruce forest (F), and the first recorded visits at the ditch edge (A) were two weeks later.

Other flowers that were visited in only 2005 (number of visits; z-value; p-value): *Galeopsis tetrahit/bifida* (38; z=2,76; p<0,003), *Lathyrus montanus/vernus* (7; z=1,63; p<0,052), *Lathyrus pratensis* (11; z=-0,07; NS), *Rubus saxatilis* (7; z=1,62; p<0,053), and *Trifolium hybridum/repens* (24; z=2,85; p<0,0022).

Table 10. Visits by bumblebee species in 1992 and 2005. At the right the percentages are calculated as visits to each species of flowers for the two years pooled. 0,5 % = 6 or less visits, 0,5 % -2 % = 7-28 visits, 2 % - 10 % = 29-136 visits, and 10 %+ = 137 or more visits. Abbreviations: *B.sylv=B.sylvarum*, *B.rude=B.ruderarius*, and *B.hort=B.hortorum.*

	B.lapidarius		*B.wurfleini*		*B.pratorum*		*B.pascuorum*		*B.hypnorum*		*B.lucorum*		*B.hort*	*B.sylv*	*B.rude*	Sum		Total	0,5%	0,5%-2%	2%-10%	10% +
	1992	2005	1992	2005	1992	2005	1992	2005	1992	2005	1992	2005	1992	2005	2005	1992	2005					
Achillea ptarmica	1										1					2		2	x			
Ajuga pyramidalis								1									1	1	x			
Angelica sylvestris					7				1		10					18		18		x		
Cirsium arvense											4	1				4	1	5	x			
Centaurea jacea	18	10		6			10				20			1		48	17	65			x	
Convallaria majalis							1									1		1	x			
Campanula persicifolia											3					3		3	x			
Campanula rotundifolia												1					1	1	x			
Cirsium vulgare		247		107				10				6		30			400	400				x
Filipendula ulmaria											2					2		2	x			
Fragaria vesca								1									1	1	x			
Galeopsis tetrahit/bifida		8		19				6				1		5			39	39			x	
Geranium spp			3							1	1					4	1	5	x			
Hypericum maculatum		3	1	1			11		2		60	2	2			76	6	82			x	
Hieracium umbellatum	1	5		16			7				3					11	21	32			x	
Knautia arvensis							4				1				1	5	1	6	x			
Leotodon autumnalis		42		4			1	11								1	57	58			x	
Lotus corniculatus		3						1							6		10	10		x		
Lathyrus montanus/vernus								5							2		7	7		x		
Lathyrus pratensis		1		4											6		11	11		x		
Lamium purpureum	1															1		1	x			
Lythrum salicaria			1				2		1							4		4	x			
Lychnis viscaria		8	1	1		1		6			1	12	1		4	3	32	35			x	
Linaria vulgaris							1					4				1	4	5	x			
Mycelis muralis		4															4	4	x			
Matricaria perforata				1													1	1	x			
Melampyrum pratense			3		7		40	2			30		20			100	2	102			x	
Rubus idaeus			17				10			2	1		12		4	40	6	46			x	
Rubus saxatilis								3		3		1					7	7		x		
Sonchus arvensis							1									1		1	x			
Succisa pratensis		25		5				7				4					41	41			x	
Sedum telephium	2	5		6			9		1		20	2				32	13	45			x	
Solidago virgaurea		2			2		7		1		21					31	2	33			x	
Trifolium hybridum/repens		7		15				1				1					24	24		x		
Trifolium medium/pratense							11	1				1	7			18	2	20		x		
Taraxacum officinale		2					1					5	1		1	2	8	10		x		
Viola arvensis/tricolor				1		1		1						1			4	4	x			
Vicia cracca/sepium	6	3	50	4			94	4	1		56		12		5	219	16	235				x
Sum	29	375	76	190	16	2	210	60	7	6	234	41	55	37	29	627	740	1367	17	8	11	2

5 Discussion

5.1 Weather and seasonal development

The large differences in the weather between the seasons of 1992 and 2005, makes comparisons on bumblebees difficult. The weather in May and June 2005 did probably not allow colonies of all present bumblebee species to build up a large force of workers. In turn, they could not respond in high numbers to rich resources that became available at the end of the season. A bumblebee colony stores little honey, only enough for one or two days without foraging (Corbet et al.1996). Several colonies of early and mid emerging species may have starved in the cold and wet period in May and June 2005. My impression is also that workers late in the season were extremely small, even smaller than workers of the first batch in the spring. This might indicate that some species tried (or even succeeded) a second life cycle this season. If so, reproductives should have been observed earlier in the season. Discussing this with Dramstad, she suggests that the small workers may be a consequence of lack in resources, whereas Goulson (2003) claims that the size of workers are due the temperature at which the worker brood is raised. If resources are constraining, like in the early spring when the queen must forage alone, this may indicate that the colonies had few workers or that they were unable to forage efficiently. This view is supported by the observations of reproductives, emerging late in the season. Long periods of cold and rainy weather may have caused the colonies of *B.hypnorum* and *B.ruderarius* to perish. No reproductives of these two species were observed, but it is possible that it occurred between replicates, even if I doubt it. According to Løken (1973) both species are active till mid September. *B.hypnorum* was seen for the last time the 19th of June, and the last observations of *B.ruderarius* were the 11th of July (table 6A). Most of the observations of *B.ruderarius* were at the rock outcrop (E) (20 out of 29, table 6), which is consistent with the characteristic of being a door-step forager (table 1). In 1992, July and August were rainy (table 2), and the bumblebees declined rapidly from mid July (figure 2). The results indicate that the weather each season may explain much of the variations in bumblebees, perhaps being the most important factor. After several days of bad weather in 2005 (rainy, cold, or windy), bumblebees often visited different flower-species, indicating that they had to sample from different resources to choose what flower to specialize on. Displaying this behavior of non-flower-constancy, might suggest that bumblebees forget after a period without foraging. If so, there will be a period of less efficient foraging. Unfavorable weather may restrict the searching distances. In shorter periods of better weather conditions, it is likely that bumblebees act more like door-step foragers than they would otherwise do. Bumblebees then may miss the entire blossom of one or more distant plant species and this resource, and the plant risks not being pollinated that season. This seemed to be true for at least apple-trees this year.

Climatic factors as wind, temperature, and solar radiation will often vary a lot over short time, making conclusions regarding any observed trend dubious.
The rapid decline in observations in September is most likely due to decreasing nest-activity, but at the same time also the blooming of preferred flowers was ceasing in the study area.

5.2 Floral diversity

There is a problem of comparing annual and non-annual plants for the entire season when most annuals are blooming relatively late. The different life-strategies (Appendix A) of the plants affect the importance they have to nectar- and pollen-feeding insects. When queens are founding nests in the spring and early summer, annuals are still not offering any resources. This alone shows the importance of early-blooming perennials and a continuous supply of resources as the season develop.

The rock outcrop had 53 species of flowers (transect E, table 3). The transects C and D at the adjacent forested island had 47 and 46 species of flowers, respectively. The rock outcrop (E) did not offer resources to bumblebees at the earliest dates, but had a continuous flowering the rest of the season. Transect C experienced a period with few flowers in June, but offered plenty of resources at the earliest dates and at the end of the season and then received more visits again (figure 4). It is possible that the island edge, the island interior, and the rock outcrop are complementary in temporal supply of floral resources. My impression was that these islands were the least disturbed transects, it is possible that no humans had set foot there since Dramstad in 1992. The apparent influence of pesticides and fertilizers from the cereal field was very low, if any at all. At the rock outcrop (E), I found *Selinum carvifolia* L., and brought one back to be identified by Kåre Lye. Such remnant biotopes, isolated in cereal fields, have to be considered as important to the biodiversity in large, not only bumblebees.

In comparison, the ditch edge (A) and the road verge (B) were the least diverse, with 23 and 26 flowering species, respectively (table 3). These transects were highly influenced by pesticides and fertilizers applied to the cereals, and both were mechanically disturbed: The ditch edge (A) by tractors and occasional ploughing, the road verge (B) by cutting. Transects

F, G, and H were intermediates, with 41, 33, and 33 species, respectively. These transects showed little sign of influence by chemicals, except for early in the spring. However, they were obviously mechanically disturbed to some degree in some years. 14 of the 28 observed bumblebee visits in transect F were to a single, large plant of *C.vulgare*. This plant had many inflorescences, though. Being a biennial, it is coincidental where resources like this will occur in different years.

It seems clear that a diverse flora provides resources that are preferred in different years. To a plant, the presence of another plant-species may act as a competitor for light, space, and other resources in much of a plants life-history. However, increased diversity may be crucial to its ability to reproduce sexually in some years by contributing to high levels of pollinators. Studies of interactions should therefore not be limited to a single season, probably not even in an “average” season.

There was a high rotation in annual species between 1992 and 2005. The increase in perennials suggests that conditions have been relatively stable the last years. Severe impact from herbicides or mechanical disturbance would probably have resulted in more annuals. That supports the hypothesis that conditions have been relatively stable, allowing long-lived plants to thrive. I have not analyzed if floral changes may shade light on the hypothesis of a warmer climate.

It can be argued that plant species that are know to be anemophilious (as *Urtica dioica* and *Artemisia* spp) should not be counted, especially as grasses and anemophilious trees are ignored. It would be an advantage to save time during the process of mapping floral resources to get as equal climatic conditions as possible between transects when counting bumblebees. If some plants are excluded, care must be taken: Bumblebees may visit flowers that does not advertize their rewards through colors that look bright to the human eye (as *Sedum telèphium* and *R.idaeus*), and plants bumblebees visit may vary between years and over time, and spatially in the same year (as experienced here).

Misidentification of species

The reason for grouping certain species of flowers, is due to misidentification. For example, *Lathyrus vernus* was identified correctly, and counted at several occasions. Later, I discovered that some of the flowers were different, and identified them as *Lathyrus montanus*. This made previous recordings uncertain, and I had to group these species. Some of the differences between the two years in this study, may be due to misidentifications. *Galium boreale* may have been confused with *G.aparine, Carum carvi* with *Pimpinella saxifraga, Euphrasia* spp with *Veronica serpyllifolia,* and *Ranunculus auricomus/R.acris* with *R.flammula.* Therefore, some flower species I suspect to have been confused, are grouped here. This indicates that other misidentifications occurred too, but without being detected.

Seasonal timing of study

Tussilago farfara was not registered in 2005 (and only 1 in 1992, at the 21th of May, unvisited), and *Vaccinium myrtillus* did not receive any visits. Both of these might be because my first day of field work was at the 27th of May, a little late for these species.

Year to year variations in flowers

Comparing vegetation between years will be biased of a number of reasons. The number of days with recordings are not equal, making the number of flowers within species varying. The timing of counts relative to the time of peak flowering of the individual species of flowers may be skewed between the years. Microclimatic variations may lead to seasonal variations in flowering (both timing and number of flowers, and duration).

Some flowers recorded in 1992 were not counted in 2005, but at least one of these species, *Lamium purpureum,* was seen after blooming in 2005. One transect was straight through some rose-bushes (*Rosa* spp.). These roses only gave three counted flowers in 1992, and 23 in 2005. It was obvious in 2005 that the main flowering occurred between two counts as there were many buds at one date and a lot of sheded flowers the next. When recordings are done with intervals of 7-14 days, important trends may be missed. Differences may further partially be because the transects did not overlap exactly between years. Even a small change in starting-point in the length or width direction will cause differences in vegetation recorded. However, some of the changes can not be discarded. *Trifolium campestre* and *Myosotis* spp grew in ploughed, unsowed areas. For the *Vicia cracca/sepium* at the ditch edge (A), I can not rule out the possibility that these species were loosing in the competition against grasses and tall herbs, due to succession. The data would be more powerful and easier to interpret if the study was repeated.

5.3 Bumblebee diversity and abundance in 2005

At least three specimens of *B.terrestris* were observed, all very late in the season. According to Løken (1973), this site should be north and too far inland of its average distribution limit. Together with Dramstad, I observed many more at the campus, indicating that the species was relatively abundant in this area this year. However, some of the observations may be due to migrating reproductives, and it is possible that some are escaped from green-houses using commercially produced nests for pollination of e.g. tomatoes.

The observations of *B.lucorum* reproductives may indicate that their colonies were successful despite few observations in the transects. This can be explained if this species can react quickly to short periods of acceptable weather conditions, or if they tolerate lower temperature, longer foraging distances, or can store more food. However, one would expect that this would lead to strong colonies with many workers being active at some point. More probable is that the reproductives are dispersing from surrounding sources, but too far away to make this area interesting to workers to forage for the colony.

It should be noted that *B.hypnorum* seemed to prefer the interior (D) to the edge (C) at the deciduous island (table 7).

Species` characteristics

Non of the black and red species are widespread or early-emerging, and did possibly not start rearing workers before the weather became more favorable in mid June. Early-emerging species experienced set-backs in May and June, possibly with some colonies dying.

It seems to be a tendency in this study that the widespread species have declined, while the northerly advanced species have increased along with *B.wurfleini* which is a western species (table 1 and figure 2). Both of the new species (*B.ruderarius* and *B.sylvarum*) and the two species that have increased (*B.lapidarius* and *B.wurfleini*) are black with red (-ish) or grey tail (table 1). It is also a tendency that early emerging species (table 1) did worse and that the late emerging species did well, while there is a mix in the mid-emerging group. On the other hand, *B.ruderatus* and *B.veteranus* were not found. In fact, these species seem to have retreated from its formerly northern range of the south-western coast of Sweden (Bjørn Cederberg, pers.com.).

Climate changes

Observations of *B.ruderatus* or *B.veteranus*, with a northern distribution limit of the south-western of Sweden (Løken 1973, page 192), would be an indication of an effect of global warming on bumblebees. The large numbers of *B.lapidarius* and the observations of *B.terrestris* and *B.sylvarum* are interesting in this sense: If these species are characteristic of a warmer environment, their distribution and numbers would be interesting to monitor.

Choosing to use the absence of *B.consobrinus* to indicate that distribution limits were moving northwards, was not suited for this study. *B.consobrinus* is found in areas with *Aconitum septentrionale* (Løken 1973), a plant not seen in the study area.

As no coockoo bumblebees were seen, there are no strong indication of sosial parasitism as explanation for the results in 2005.

Within a given area, there are too few flowers with deep corollas to sustain more than one colony of long-tongued bumblebees (Goulson et al. 2004). If so, *B.ruderarius* and *B.sylvarum* may have out-competed both *B.pascuorum* and *B.hortorum* from the islands, before also *B.ruderarius* perished. Then one would expect at least some observations of *B.hortorum* early in the season, but I did not record any activity at all. However, there may be important foraging places outside the narrow transetcs, but well within the range of the bumblebees. A landscape ecology approach is necessary to understand the dynamics of a system like this one, and it would be interesting to study a landscape that has more in common with an actual island.

Some of the differences in flower species visited between the two seasons, may be explained as more or less “accidental” landings by naïve workers, as both years recorded a range of flowers that received six or less visits by bumblebees (table 10).

The grass bank (transect B in 1992, not included in 2005, see Materials and methods) received one visit in mid august (a *B.pascuorum* worker) and some 5-6 visits in late August and the first half of September, all to *Galeopsis tetrahit/bifida*. As shown in the results this is a low number, but better than transect H.

Bee-walks

The method of walking the same transects five successive times without a delay, that is, within a short time, will not necessarily give a representative impression of the community. The possibility of overestimating the relative number of visits by a certain bumblebee species to some species of flowers is high. The same individual bumblebee may stay within the transect and be counted repeatedly. Likewise, a bumblebee of another species, that may have other flower preferences, may just have left, and possibly return when the recording is completed. Individual markings would provide additional information when bumblebee activity is low. On the other hand, the method of measuring activity gives a good measure of the quality of a patch: The bumblebees do not have to stay. The largest error will probably appear when the total is low. As for the ditch edge (A) under peak activity, bumblebees were constantly leaving and arriving, making the bias less. The peak diurnal activity of some species may be at different times than the mid-day hours of this work. Bumblebees have longer working hours than e.g. honybees (Goulson 2003) (which is also a problem as legislation regarding use of pesticides are based on the diurnal period honeybees are active).

Misidentification of species

The first observations of *B.sylvarum* were identified as “*B.wurfleini* with pale tails”. As this species emerged late, the mind was set on the known species, but these notes made it possible to reconstruct correct data.

A "strange" bumblebee (figure 1) was detected at the rock outcrop (E), and brought to the lab. It had a yellow longitudinal thorax-band in the wrong direction. Using a stereomicroscope, Hågvar and I saw that the band was lumps of pollen on a *B.wurfleini*. Later, I discovered more *B.wurfleini* with this pollen-load on their backs. I followed two of them, as they foraged. Both visited *Linaria vulgaris*. The morphology of this flower makes the bumblebees crawl into a narrow tube, and thereby pressing their back towards the vertically placed anthers of the flower. According to Bjørn Cederberg (pers. comm.) this is quite common, and the bumblebees are able to unload this pollen-load. Whether this pollen is utilized by the colony is unclear, however.

5.4 Changes in bumblebee species composition from 1992 to 2005

Metapopulation dynamics

A source population means that the reproduction rate exceeds the mortality rate, leading to a surplus (e.g. Krebs 2001 pp 299-300). Then the population can have emigrants without declining over time. A sink population has a higher mortality rate than reproduction rate, and the population would go extinct without immigration. A metapopulation is two or more populations that are spatially apart, but close enough to exchange genes (frequent or occasionally), often by migrating individuals.

The bumblebee populations in this area my be in a process of constant extinctions and recolonizations, at least for some species. Further, some years may act as “temporal sources”, producing large numbers of young, mated queens, while other years may have lower success-rates. I interpret the observation of a *B.distinguendus* as that this species may colonize the area from nearby populations if they find the conditions acceptable.

Changes in bumblebees caused by climatic conditions

Løken (1973) writes that the distribution of *B.ruderarius* is local, but frequent, in this part of Norway. As bumblebee nests are annual, it is likely to be some changes in the species` composition locally between years. It is interesting that *B.hortorum* was totally absent in 2005, but it does not prove that it is "extinct" from the area: They may still forage in gardens or other patches they find rewarding, even close to or within the study area as only the narrow transects were studied.

Changes in bumblebees caused by predation

A *Lanius collurio* L. was observed in the dense *R.idaeus* at the rock outcrop (E). Literature suggest that bumblebees are not very susceptible to predation, but in birds of the *Lanius*-genus bumblebees can make up 40 % of the food intake (Goulson 2003). Another, far-fetched possible explanation of the reduction of *B.lucorum/B.terrestris* and *B.hortorum* can be a web of interactions: Müllerian mimicry in bumblebees is thought to scare predators off through encounters with stinging bees and wasps. If this system is parasitized enough by hover-flies with the same color-patterns (Batesian mimicry), a predator (as a bird) may experience occasional stings as exceptions. If so, the color-pattern does not offer the "intended" protection, but render bumblebees more susceptible to predation.

Birds start nesting and raising offspring in the spring when protein-supply from invertebrates is still scarce. Then young queens of bumblebees are vulnerable, as they seek nest-sites and have to forage alone. Taking young queens will, of course, lead to the loss of entire colonies even before really getting started. At the campus of the University of Life Science in Ås, Norway, just some kilometres from the study area, *B.terrestris* appeared in large numbers the whole season. This indicates a site-specific explanation for the low numbers of this species at the study site. At a holiday-trip to the western coast of Norway, I saw that *B.lucorum* was extremely abundant. Together, this points at a biological explanation of the differences in bumblebee species` composition and abundance between the two years studied. That is, the different climatic conditions through the seasons is not the only possible explanation, at least there may have been an interaction of biotic and abiotic factors.

Estimating the populations of bumblebees

Counting bumblebee workers gives little information to the total effective population size in terms of individuals actually reproducing. A colony would be a more correct unit for measuring population size. Because each colony may vary in the number of workers (even within species, or within a colony during the season), and the uncertainty in how large proportion of the workers that forage at a given time, and where they forage, it is virtually impossible to estimate the number of colonies from observed workers. When nests are difficult to locate, factors as sink-source dynamics, bottle-necks in the life-cycles, and more, are difficult to study. A single founder-queen more or less in an area can lead to a difference of many workers.

There is an urgent need to invent a method to localize nests in the field, especially because almost all of the present research is done by using "domesticated" *B.terrestris*. I would be surprised if results from *B.terrestris* can be extrapolated to every other bumblebee species and in every sense.

5.5 Flower preferences

I have to stress that flower preference is different from the importance a flower represents to the bumblebees. Some flowers may be important for a short period, and some may be present in very large numbers and thereby loose significance.

Foraging on concentrated resources can be explained as a beneficial adaptation for pollinators. In many cases concentrations occur as perennials grow large and produce many and large inflorescences, often on many stalks over several square metres due to vegetative growth. As this can occur with stolons (on the ground) and rhizomes (in the soil), and the connections can be broken later, it is virtually impossible to detect which plants that are clones. To a hermaphroditic plant, the risk of inbreeding between flowers on a genetic individual (geitonogamy) may increase as it is more preferred by bumblebees, but reduces the risk of heterospecific pollen-transfer by pre-stigma (e.g. spatial or temporal offset between the male and the female phase) or post-stigma mechanisms (recognize and prohibit pollen tubes from its own pollen) (Pellmyr 2002). If a flower species is present in different degrees of concentrations in an area, it is possible that the flower may provide resources to a wider range of pollinators. As competition increases in the centre (e.g. bumblebees vs honeybees vs butterflies), the less competitive may forage the outer or the scattered flowers. Holmes (1964) reported that in the presence of many honeybees on a resource, bumblebees were excluded. Large butterflies are supposed to display their wings as protection from predators, but the effect on potential competitors might be just as important.

If the view is changed from protecting bumblebees to also protecting rare plants, it is obvious that rich food resources that attract many bumblebees (and other pollinators) may drain neighboring areas for a lot of pollinators. Efforts in e.g. England to grow flowers in gardens to help the pollinating insects, is not necessarily a way to help the ecosystem. Over time, it is likely that pollinators will increase the density of their most preferred plants. This is not only the case between flower species, but also variations within species as they display differences in colors, nectar production, petal size, or other floristic measures. Waser et al. (1996) write that surrounding plants can interact in a beneficial or detrimental way through overlap in pollinators. *Mycèlis muralis*, a new species to the study area at the road verge (B), turned out to be a preferred resource. This may in part be an effect of the proximity to the ditch edge (A). Bumblebees may have been attracted by *C.vulgaris*, but sampled the area as competition hardened. If so, it shows that plants providing a lot of resources may facilitate pollination in neighbouring plants. Another new-commer that was preferred, was *Succhisa pratensis*. This flower gave many visits to the deciduous island edge (D) when this transect otherwise would be more or less without resources to bumblebees, but it is likely that less preferred flowers now were discriminated. On the other hand, helping the pollinators through a time of scarcity, the pollinators survive to pollinate late-blooming flowers.

The numerous visits at the ditch edge (A) by *B.lucorum* on *Vicia* spp. in 1992 and by *B.lapidarius* and partly by *B.wurfleini* on *C.vulgare* in 2005 probably reflect that these plants attracted bumblebees from a large area. In 1992, the mass flowering of *Vicia* spp. never came to be, and the weather made the now smaller resource unavailable for long periods. *C. vulgare* got no visits in 1992, but was clearly the most preferred resource in 2005 with 54 % of all visits. It should be noted that *B.lucorum, B.lapidarius,* and *B.wurfleini* have long foraging distances (table 1). Then the results can not be interpreted as a description of how many colonies of such species a study area may sustain during an entire season. I observed that many bumblebees took off from this transect, heading out of the study area. As it is assumed that bumblebees prefer perennials (Prys-Jones and Corbet 1991), it was surprising that *C.vulgare*, a biennial (Lid and Lid 1998) received so many visits. *C.vulgare* blooms late. By the time of blossom in 1992 (if equal to 2005) both *B.lapidarius* and *B.wurfleini* had disappeared weeks earlier.

The difference in visitation by *B.lapidarius* castes between the road verge (B) and ditch edge (A) , where the males preferred *C. crispus* at the ditch edge (A), can at least partially be explained by that *C. crispus* were the tallest points in the area. The males also had a tendency to visit flowers at or near the top of the plants. This behavior can be interpreted as a mating-strategy (Goulson 2003), not only preferences in foraging.

The patch of *C.vulgare* in the ditch edge (A) comprised less than one fourth of the total length of this transect, but the visits at the 19th of August totalled 34 % of all bumblebee visits of all transects during the entire season to that date. Further, all visits here that day were made up by two species, even when other species were observed in the transect earlier in the season, and that other species utilized this flower in other transects this day. This also leads to the possibility that foraging distances may be a lot longer than generally assumed. Other personal observations also indicate this: In my garden, I watched three *B.lapidarius*-queens in my *Allium schoenòprasum* L. They foraged for 15-20 minutes, then they took off and raised to 4-6 metres above ground and oriented themselves before they flew off in a more or less straight line, in high speed, and in an altitude well above the telephone poles. I observed them till they were too far away to be seen, heading for the nearest possible place for nesting at least 500 metres away. 20-40 minutes later, they appeared at the *A. schoenòprasum* to forage again.

It is difficult to interpret the causality in a community like this. Changes in preferences may be a consequence of changes in species` composition in bumblebees, but the flora itself may lead to differences in what species of bumblebees that are present in an area. Further, there are no evidences that observed activity equal the peaks in the total number of workers in an area. Especially for 2005, the large number of observed bumblebees late in the season is probably not a numerical response by the colonies to a large resource, as the resource was not lasting long enough. It is then more likely that another resource was abundant outside the study site earlier, allowing the colonies to build up many workers. This is partially supported by the observation of large areas of *Carduus crispus* about 500 metres north of the study site, but this patch was discovered after blooming. I can not confirm if this resource was actually utilized.

Separating the season of 2005 into three periods did not result in large differences compared to levels of significance for the whole season. However, I recommend this method to be applied to similar studies, because some detected trends may be important. For example, *Lychnis viscaria* was, when looking at the pooled data, discriminated in 1992 and insignificantly preferred in 2005 (table 8). In June 2005, however, 32 of the 71 recorded visits were to this flower. Table 9 shows that it was preferred for this period. *L. viscaria* provided resources to almost all species of bumblebees in 2005 (table 8). Further, *L.corniculatus* (table 8) is an example of switching in preferences as the season develop. It was preferred at the beginning of its blooming period, but was avoided later. This may be because new flower species went into blooming, and diverted the bumblebees. From the bumblebees point of view, they make the best choice at hand. From the flower`s point of view, it is important to get the timing right to have a high probability of getting pollinated.

Different plants possibly respond differently to the seasonsal development in a year. Which plant species that co-flower will therefore probably vary between years. That is, results in one year can not be extrapolated to be valid for another year, even within the same site and with the same species of bumblebees and flowers.

Certain flowers were preferred in the spring and early summer, but lost statistical significance later in season (table 8), because some flower species withered before bumblebee activity was high and others were no longer preferred as new floral resources became available. The relatively large number of flowers and bumblebees later in the seasons diluted the numbers from the spring. This may give a wrong impression, as the activity and numbers of bumblebees late in the season is dependent on the foraging success of the colony in the spring and early summer. The early stages of the colony are crucial, but on the other hand the colonies are still small and need less resources than later in the season.

B.pascuorum may be an important pollinator to a wider range of flower species than the other bumblebees. It can be extracted from table 10 that *B.pascuorum* visited 27 species of flowers, 5 of these exclusively by *B.pascuorum*. In comparison, *B.lapidarius* visited 18 species of flowers, and only two of these were not visited by any other bumblebee species.

Sundby (1995) mentions that pollen from different plants differ in both quality and quantity. The most collected resource may be poor in one or more substances important to the colony in one sense or another. Pollen from another plant may provide this substance. If pollen from two or more plants are complementary to the colony, but in different quantities, the relative importance of the plants to bumblebees may be misinterpreted. This could be a parallel to the fact that males collect different substances than workers do, as they need scents from flowers and do not collect pollen. The pollen used to feed the larvae may have other qualities than pollen the queen needs to produce eggs. If so, one would expect some visits to other flowers than the one that is most preferred and that seems to offer enough resources. Thus, a diversity of plant species may be more important than observed from which flowers that have the highest numbers of visits.

Bumblebees may actually use different flowers in different years. Whatever the reasons may be, it stresses the importance of a degree of diversity in the flora. A loss of diversity will probably be most disadvantageous to bumblebees that are specialized in their habitat- or food-resource requirements.

The switch in flower preferences between years indicate that some flowers may be efficiently pollinated by bumblebees in certain years, but be more or less avoided in other years. If so, perennials are less vulnerable to lack of pollinators in one season as they can be successful some other years, while annual species that are also obligate out-crossers depend on producing offspring every year. A counter-strategy by the latter is the “soil seed-bank” (e.g. Milberg and Hansson 1993).

The high attractiveness of *Melampyrum pratense*, an early-blooming species, in 1992 compared to 2005 (table 9), may indicate that it is only depleted by bumblebees when floral resources are low. In 1992, *M.pratense* may have been flowering relatively early, in a time of relative scarcity. As *M.pratense* has declined sharply and that *B.hortorum* was not observed in 2005, there might be a connection.

Some observations indicate that the importance of vision by bumblebees to find resources, may be overestimated. For example, *R.idaeus* does not advertice with flowers that are large, zygomorfic, or to our eyes, colorful. Nontheless, they are preferred. *R.saxatilis* has small and white flowers, but they are hidden under the leaves. This does not seem to be an adaptation to attract flying insects. The bumblebees had no problem of finding these flowers, however, indicating that scent is an important attractant.

In transect E the 24th of July, suspiciously many bumblebees switched between flower species in successive visits. This may be explained as sampling, but also that individual workers in a small patch may be able to remember several flowers or establish a fixed route between rewarding flowers.

5.6 Recommendations for management, methods, and further studies

The maintenance practice of roadside verges should undergo revision, considering the importance of certain perennial flowers to wild invertebrates and domestic honeybees. In areas where the bottle-neck to some species is a lack of resources in the period of flowering in dandelions, different interests should be able to compromise. Rich resources close to a road leads to many road kills, however. The loss of a young queen is obviously devastating, a loss of workers later in the season adds to the risk involved in foraging and consequently leads to a loss of resources to the nest.

The demand for organically produced food is increasing, and farmers get higher prices for this than for conventionally produced food. It is likely that bumblebees will benefit from the absence of pesticides, and the presence of nitrogen-fixating plants. Farms that produce organically have a signinficant higher diversity in bumblebee species compared to convetionally grown areas (Risberg 2004). If the grazing fields are left unploughed, perennials preferred by bumblebees will establish. In addition, there will be more rodent burrows and tussocks for nesting. There will be benefits to the human population too: The landscape will appear softer and friendlier. This effect will be largest close to densly populated areas, and thereby good patches for bumblebees will be connected to gardens, parks, and road verges. I suppose that butterflies and bumblebees are less political controversial than wolves, and may be used as flag-ship species for conservational interests.

Planting flowers to help bumblebees should not be done in a large scale before the impact on the ecosystem at hand is well understood, including plants and different insects.

To bumblebees, it is possible that a resource can be too large, mainly through attracting honeybees and other competitors. In addition, door-step foragers with small colonies may risk the competition from other species of bumblebees. If it is an aim to provide resources to bumblebees by providing flower-resources, it may be done indirectly through planting resources that divert honeybees and/or butterflies away from resources bumblebees can exploit (reduce competiton). The distribution of resources on a spatial scale may have different consequences to different species of bumblebees. Door-step foragers may be more dependent on a continuous supply of resources on small spatial scale than species that exploit resources over longer distances. The latter can thereby tolerate temporary gaps in food-supply locally. To address questions like these, it would be an advantage to study different species in an archipelago of actual islands of different sizes and with different floral resources.

Agricultural pesticides are mentioned in the litterature, but little, if any, is said about insecticides used against ants in or near buildings. These chemicals are designed to attract nectar feeding insects that bring the poison back to the nest and thereby kill the queen. At least in Norway, such chemicals can be bought in most grocery stores. Chemicals as powder to fight ants should be prohibited from ordinary sale. The effect on honeybees and bumblebees from some substances for this use, e.g. deltametrin, is not even tested (Trond Gjessing, pers.comm.). There are also tiny boxes that conceal the chemicals available, with entrances that are to small for bumblebees and honeybees. The boxes also decrease the risk of children eating the poison.

Without knowing the location of nests in the area, it is very difficult to assess what options the bumblebees have, and how they respond. A better approach to the study of bumblebees would be to localize the majority of nests within an area and mark bumblebees individually. This can be done by gluing marks produced to mark honeybee queens on the back, available in six different colors, each numbered from 1 to 100. It is not necessary to use anaesthesia. In Norway, equipment for this is available at Honningcentralen. Many have stated the fact that it is difficult to find the nests, but some people succeed in finding some. If they have different ways to discover nests the knowledge should be gathered to increase the rate of findings. When most of the bumblebees within an area are marked, it would be easier to locate the rest by attatching transponders to bumblebees and track them with harmonic radar (Goulson 2003) or, as I suggest, even with trained dogs. I propose trials where bumblebees are caught and scent-marked with some meat (as salami or some other spicy meat) or other scents that dogs would want to find. The scent-marking may be done by using queen-bee tubes for marking, and then brush scent at the bumblebees` back, or by releasing bumblebees into a chamber were the exit-hole is narrow and covered with scent. The search would have to be done at night, when the bumblebees are inside their nests. There are many questions to be asked and answered with data collected from known nests of different species, so in my opinion many under-graduates could be engaged to overcome the vast amount of fieldwork necessary. For example, for many species the foraging distances are not known (even if they are door-step foragers or not), the competition between species and cooperation within colonies is unclear, predation rates, success rates, colony sizes, diurnal activity, maximum foraging distances in different species, maximum of time spent away from the nest, colony density within an area, and many more questions. Such data can also be used to answer questions in botany.

5.7 Conclusions

Hypothesis 1, that bumblebees are declining in Norway, is not supported. However, rare species were not studied or observed. Both in the number of species and the total number of observations, there is an increase compared to 1992. It seems that the trend is the opposite from the British isles (Goulson 2003): The widespread species, except for *B.lapidarius*, have declined here, *B.hortorum* was even lost. That bumblebees have not declined in total numbers at this site, may be explained by that agricultural intensification has not progressed. There are many small farms, all have gardens, all have relatively long driveways with edge vegetation at both sides, many islands of remnant biotopes (as the rock outcrop, E), and linear structures like road verges, ditch edges, ownership boundaries, and forest edges. This site is therefore not representative for the ongoing intensification in agricultural practice.

Hypothesis 2 predicts that increased floral diversity would give more niches and therefore more species of specialized bumblebees. The results by the Shannon-Wiener index, shows an increase in the number of flower species in all transects, and in species diversity and species evenness in all transects except for the rock outcrop (table 3). The trend is a larger increase in perennials than annuals and biennials (table 4). This indicates more stable conditions in the transects the last 13 years. It is difficult to read any causality out of these data, but I interpret it as a strong support to hypothesis: Political aims to reduce negative impact from farming practice on wildlife may have had an effect.

The second prediction was an increase in bumblebee species` abundances and in number of species present. New species were indeed found (*B.sylvarum* and *B.ruderarius*), but the loss of *B.hortorum* and the fact that a *B.distinguendus* chose not to stay here, points in the opposite direction. The low numbers of *Trifolium medium/pratense* may be important, but the counted flowers in 1992 and 2005 were almost equal. Further, the number of observed bumblebees was very low until the 19th of August (figure 2). This indicates that the total supply of resources was low, or unavailable due to the weather conditions.

The large differences in the bumblebees` flower preferences in 1992 and 2005, however, indicates that a diverse flora provides resources in different quantities or qualities in different years (table 9). The change in species` composition and abundance may have contributed to the differences in flower preferences.

The hypothesis, as formulated here, must be rejected.

Hypothesis 3, that the climate is warmer and has shifted the distribution limits of different bumblebee species northwords, is both supported and contradicted by the data. The presence of *B.ruderarius* and *B.terrestris,* in addition to the large increase in *B.lapidarius,* indicates warmer conditions compared to 1992. The retreat of *B.veteranus* from the southern of Sweden points in the opposite direction. However, *B.veteranus* may have vanished for other reasons, as the habitat-requirements are special as they prefer sandy fields (Løken 1973 page 180). If the differences in species` composition between 1992 and 2005 are the results of a trend rather than year to year variations, this indicates that the bumblebee community reflects the local climate.

My intention with this hypothesis was partly to provide a practical, easy, and fast method to map the qualities of an area, but my experienceses from the field tells me otherwise: The likelyhood of discovering all bumblebee species that live within an area at a single day and in a narrow transect is very low.

The data are inconclusive in relation to the formulated hypothesis.

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Appendix A

Flower species by Latin names with authors, includes names in Norwegian and English, and life strategy

Life strategy: PE=perennial, A=annual, B=biennial, Par=parasitic

Latin with authors, following Lid & Lid (1998) Abbreviations of authors: see e.g. Lid & Lid pp 971-981 for full names	Norwegian	English	Life strategy
Achilléa millefólium L.	Ryllik	Yarrow	PE
Achilléa ptármica L.	Nyseryllik	Sneezewort	PE
Ájuga pyramidális L.	Jonsokkoll	Pyramidal bugle	PE
Alchemilla L.ssp	Marikåpe	Lady`s mantle	PE
Anemóne nemorósa L.	Hvitveis	Wood anemone	PE
Angélica sylvéstris L.	Sløke	Angelica	PE/B
Anthríscus sylvéstris (L.) Hoffm.	Hundekjeks	Cow parsley	PE
Árabis thaliána L. (Arabidópsis thaliána (L.) Heynh.)	Vårskrinneblom	Thale cress	A
Artemísia vulgáris L.	Burot	Mugwort	PE
Barbaréa vulgáris R.Br.	Vinterkarse	Winter-cress	PE
Caltha palústris L.	Soleihov/Bekkeblom	Marsh-marigold	PE
Campànula persicifòlia L.	Fagerklokke	Peach-leaved bellflower	PE
Campànula rotundifòlia L.	Blåklokke	Harebell	PE
Capsélla bursa-pastóris (L.) Medicus	Hyrdetaske	Shepherd`s purse	A
Cárduus crispus L.	Krusetistel	Welted thistle	B
Carum carvi L.	Karve	Caraway	B
Centauréa jácea L. (Jácea praténsis Lam.)	Engknoppurt	Brown knapweed	PE
Cerástium arvénse (L.)	Storarve	Field Mouse-ear	PE
Chamomilla suavéolens (pursh) Rydb. (Matricária matricarioides (Less.) Porter, M.discoidea DC.)	Tunbalderbrå	Pineapple mayweed	A
Chenopódium album L.	Meldestokk	Fat-hen	A
Chrysosplénium alternifólium L.	Maigull	Alternate-leaved Golden-saxifraga	PE
Cirsium arvénse (L.) Scop.	Åkertistel	Field thistle	A
Cirsium vulgáre (Savi) Ten. (C.lanceolátum (L.) Scop.)	Veitistel	Spear thistle	B
Convallária majális L.	Liljekonvall	Lily-of-the-valley	PE
Crepis tectorum	Takhaukeskjegg	Hawk`s beard	AB
Cuscúta europaéa L.	Neslesnyltetråd	Greater Dodder	A/Par
Epilóbium montánum L.	Krattmjølke	Broad-leaved Willowherb	PE
Erýsimum cheiranthoides L.	Åkergull	Treacle mustard	A
Euphórbia helioscópia L.	Åkervortemelk	Sun Spurge	A
Filaginélla uliginósa (L.) Opiz (Gnaphálium uliginósum L.)	Åkergråurt	Marsh Cudweed	A
Filipéndula ulmária (L.) Maxim.	Mjødurt	Meadow-sweet	PE
Fragária vesca L.	Markjordbær	Wild strawberry	PE
Fumária officinális L.	Jordrøyk	Common fumitory	A
Galeópsis tetrahit L.*/bifida* Boenn.	Kvass-/vrangdå	Hemp-nettles	A
Gálium boreále L. */aparíne* L.	Hvit-/klengemaure	Northern bedstraw/Cleavers	PE/A
Gálium uliginósum L.	Sumpmaure	Fen bedstraw	PE
Ghéranium L. spp	Storkenebb	Cranesbills	PE
Geum urbánum L.	Kratthumleblomst	Wood Avens	PE
Hierácium (L.) *umbellátum*	Skjermsveve	Leafy hawkweeds	PE
Hierácium pilosélla L. (Pilosélla officinárum F.W.Schmidt & Schultz Bip.)	Hårsveve	Mouse-ear hawkweed	PE
Hypericum montànum L.*/maculàtum* Crantz	Bergperikum	Imperforate St.John`s-wort	PE
Impátiens noli-tángere L.	Springfrø	Touch-me-not Balsam	A
Knaútia arvénsis (L.) Coulter	Rødknapp	Field scabious	PE
Lámium purpúreum L.	Rødtvetann	Red Dead-nettle	A
Lápsana commúnis L.	Haremat	Nipplewort	A
Láthyrus linifólius (Reichard) Bässler (L. Montanus Bernh.*)/vernus* (L.) Bernh.	Knoll-/vårerteknapp	Bitter vetchling/Spring pea	PE
Láthyrus praténsis L.	Gul flatbelg/gulskolm	Meadow vetchling	PE
Leóntodon autumnális L.	Følblom	Autumn hawkbit	PE
Leucánthemum vulgáre Lam. (Chrysánthemum leucánthemum L.)	Prestekrage	Ox-eye daisy	PE
Linária vulgáris Miller	Lintorskemunn	Yellow toadflax	PE
Lotus corniculátus L.	Tiriltunge	Birdsfoot trifoil	PE
Lychnis viscária L. (Viscária vulgáris Bernh., V.viscósa Ascherson)	Tjæreblom	Sticky catchfly	PE

Lýcopus europaéus L.	Klourt	Gipsywort	PE
Lysimáchia vulgáris L.	Fredløs	Yellow loosestrife	PE
Lythrum salicária L.	Kattehale	Purple loosestrife	PE
Maiánthemum bifólium (L.) F.W.Schmidt	Maiblom	May lily	PE
Matricària perforàta Mèrat	Balderbrå	Scentless mayweed	A
Melampýrum praténse L.	Stormarimjelle	Common cow-wheat	A/H-Par
Melampýrum sylváticum L.	Småmarimjelle	Small cow-wheat	A/H-Par
Mycélis murális (L.) Dumort. (Lactúca murális (L.) Gaertner)	Skogsalat	Wall Lettuce	PE
Myosótis arvénsis (L.) Hill/*scorpoídes* L. (*M.palustris* (L.) Hill)	Forglemmegei	Forget-me-nots	PE
Óxalis acetosélle L.	Gaukesyre	Wood-sorrel	PE
Persicária lapathifólia (L.) S.F.Gray (Polýgonum lapathifólium L.)	Rødt hønsegress	Redshank	A
Pimpinélla saxifraga L.	Gjeldkarve	Burnet saxifrage	PE
Polygonum maculósa S.F.Gray (Polýgonum persicária L.)	Vanlig hønsegress	Pale Persicaria	A
Potentilla argéntea L.	Sølvmure	Hoary cinquefoil	PE
Potentilla erécta (L.) Räuschel (P.tormentilla Stokes)	Tepperot	Tormentil	PE
Prunèlla vulgàris L.	Blåkoll	Selfheal	PE
Prunus padus L. (Padus ávium Miller, Padus racemósa (Lam.) Gilib., Cérasus padus (L.) Delarbre	Hegg	Bird Cherry	PE
Ranunculus acris L.	Engsoleie	Meadow buttercup	PE
Ranúnculus aurícomus L.	Nyresoleie	Goldilocks buttercup	PE
Ranúnculus ficária L.	Vårkål	Lesser celandine	PE
Ranunculus flámmula L.	Grøftesoleie	Lesser spearwort	PE
Ranunculus repens L.	Krypsoleie	Creeping buttercup	PE
Rosa L.spp	Nyperoser	Rose spp	PE
Rubus idaéus L.	Bringebær	Raspberry	PE
Rubus saxátilis L.	Teiebær	Stone bramble	PE
Rumex acetósa L.	Matsyre	Common Sorrel	PE
Rumex acetosélla L.	Småsyre	Sheep`s Sorrel	PE
Sambúcus racemósa L.	Rødhyll	Red-berried Elder	PE
Saxifraga granuláta L.	Nyresildre	Medow saxifrage	PE
Sedum acre L.	Bitterbergknapp	Biting stonecrop	PE
Sedum teléphium L.	Smørbukk	Orpine	PE
Selinum carvifólia (L.) L.	Krusfrø	Cambridge Milk-parsley	PE
Senecio vulgáris L.	Åkersvineblom	Groundsel	AB
Siléne dioica (L.) Clairv. (Meléndrium dioicum (L.) Cosspm & Germ., M.rubrum (Weigel) Garcke)	Rød jonsokblom	Red Campion	PE
Siléne rupéstris L.	Småsmelle	White Campion	PE
*Solidágo virgaúrea*L.	Gullris	Golden-rod	PE
*Sonchus arvénsis*L.	Åkerdylle	Perennial sow-thistle	PE
Sonchus asper (L.) Hill	Stivdylle	Prickly sow-thistle	A
Sonchus oleráceus L.	Haredylle	Smooth sow-thistle	PE
Spérgula arvénsis L.	Linbendel	Corn spurrey	A
Stachys sylvática L.	Skogsvinerot	Hedge Woundwort	PE
Stellária graminea L.	Gress-stjerneblomst	Lesser stitchwort	PE
Succisa pratènsis Moench	Blåknapp	Devil`s-bit Scabious	PE
Taraxácum (L.) *officinále*	Løvetann	Dandelion	PE
Trientális europaéa L.	Skogstjerne	Chickweed Wintergreen	PE
Trifolium campestre Schreber (*T.procùmbens* L.)	Krabbekløver	Hop trefoil	A
Trifòlium hýbridum L./*repens* L.	Alsike-/hvitkløver	Alsike clover	PE
Trifólium medium L./*pratense* L.	Skog-/rødkløver	Zig-zag/Red clover	PE
Tussilágo fárfara L.	Hestehov	Coltsfoot	PE
Urtica dioica L.	Stornesle	Common nettle	B/PE
Vaccinium myrtillus L.	Blåbær	Bilberry	PE
Valeriána sambucifólia Mikan fil. (V.officinális ssp.sambucifólia (Mikan fil.) Celak.)	Vendelrot	Valerian	PE
Verónica chamaèdrys L.	Tveskjeggveronika	Germander speedwell	PE
Verónica serpyllifólia L./*Euphrásia* spp L.	Glattveronika/ Øyentrøst	Thyme-leaved Speedwell/Eyebrights	PE/A
Vicia cracca L./*sépium* L.	Fugle-/gjerdevikke	Tufted /bush vetch	PE
Viola arvénsis Murray/*tricolor* L.	Stemorsblomst	Field/Wild Pansy	AB
Viola palústris L.	Myrfiol	Marsh Violet	PE
Viola riviniána Reichenb./*canina* L.	Fioler (eng-, skog-)	Violet spp	PE

Appendix B

Murdochs C-index with modifications

To be able to compare my results with the data Dramstad published from her study in 1992, I had to use the same way to calculate the statistic values. Unfortunately, the old data were not readable by modern computers, but I received a paper version. All the formulas were hidden, so I had to reconstruct the whole data to insure that I got it right.

Murdoch (1968) constructed a formula for flower preferences. Here it is modified to give z-values. The formula has a lot in common with the chi-square test.

Murdochs index:
A: All visits to all flowers by bumblebeespecies A
B: All visits by all bumblebeespecies to all species of flowers
C: Number of flowers of species A
D: All flowers of all species

C-index: (A/B)/(C/D)

An example from Dramstad and Fry (1995): They counted 1379 *Geranium* spp (C), and 100757 flowers in total (D). They observed four visits to *Geranium* spp (A), and 627 visits in total (B). This gives the value 0,466 by the C-index.

To calculate the chi-square (sum (Expected-Observed)^2/Expected), a minimum of 5 as expected values is needed for every cell, what we do not have here. Modifications weaken the significance by +/- 0,5. Expected values are calculated as C*B/D (1379*627/100757 here). This gives 8,58, more than observed. Modified, observed value then becomes 4+0,5=4,5.

Expected values are also modified:
Here: (B-C*B/D)(C/D), (627-1379*627/100757)(1379*100757)=8,46

Now the z-values are calculated directly, whithout calculating standard deviations:
The formula z=(L - E)/square root of V, see for example Barnard et al. (2001 page 77-78).
L is the expected value before modification (8,58 in the example), E is the modified, observed value, and V is the modified, expected value (8,46 here). Dramstad and Fry (1995) used the letters V for L, U for E, and had no symbol for V (the denominator).

If the numerator is squared, as normally with the chi-square, all numbers turn out positive. Here we need to keep also the negative signs to detect whether flowers are discrimated or preferred: Calculate E-L and not L-E in the numerator, and divide by the squared root of the denominator. Further, the chi-square statistic gives a single measurement for a complete set of data, not for the individual cells. By squaring all the z-values here, sum them, and finally calculate the square root of the sum, it approximates the chi-square.

Probabilities for the z-values are taken from Moore and McCabe (2002), table A.
This example gives a z-value of –1,40 that gives a p-value less than 0,01, that is, *Geranium* spp received significantly fewer visits than expected, and were dicriminated by bumblebees.

Appendix C. Flower preferences 2005

All season

Flower species	Blomsterart	Number	Number/sum	Visits observed	Visits expected: L		Visits observed mod:E	Visits expected modified=V	Sqrt V	z-value (E-L)/sqrt V	Significance
Ajuga pyramidalis	Jonsokkoll	49	0,000274562	1	0,20317596	-0,5	0,5	0,203120171	0,450689	0,6586013	NS
Campanula rotundifolia	Blåklokke	329	0,001843488	1	1,36418141	0,5	1,5	1,36166656	1,166905	0,1163922	NS
Centaurea jacea	Knoppurt	464	0,002599935	17	1,9239519	-0,5	16,5	1,918949751	1,385262	10,522235	**** Pos
Cirsium arvense	Åkertistel	461	0,002583125	1	1,91151256	0,5	1,5	1,906574881	1,380788	-0,2980274	NS
Cirsium vulgare	Veitistel	3370	0,018883149	400	13,97353	-0,5	399,5	13,70966573	3,702657	104,12158	**** Pos
Fragaria vesca	Markjordbær	230	0,001288761	1	0,95368305	-0,5	0,5	0,952453985	0,975937	-0,464869	NS
Galeopsis tetrahit/bifida	Vrangdå	5824	0,032633667	38	24,1489135	-0,5	37,5	23,36084592	4,833306	2,7623094	*** Pos
Geranium spp	Storkenebb	100	0,000560331	1	0,41464481	-0,5	0,5	0,414412468	0,643749	0,1325908	NS
Hieracium umbellatum	Skjermsveve	2639	0,01478713	21	10,9424764	0,5	21,5	10,78066861	3,283393	3,2154311	**** Pos
Hypericum maculatum	Bergperikum	2922	0,016372867	6	12,1159212	0,5	6,5	11,91754888	3,45218	-1,6267752	* Neg
Knautia arvensis	Rødknapp	12	6,72397E-05	1	0,04975738	-0,5	0,5	0,049754031	0,223056	2,0185173	** Pos
Lathyrus montanus/vernus	Knoll-/vårerteknapp	836	0,004684366	7	3,46643058	-0,5	6,5	3,450192552	1,857469	1,6331733	* Pos
Lathyrus pratensis	Gul flatbelg	2586	0,014490155	11	10,7227147	-0,5	10,5	10,56734089	3,250745	-0,0685119	NS
Leontodon autumnalis	Følblom	7362	0,041251555	57	30,5261506	-0,5	56,5	29,26689946	5,409889	4,8011797	**** Pos
Linaria vulgaris	Lintorskemunn	2144	0,012013493	4	8,88998465	0,5	4,5	8,783184881	2,963644	-1,4812794	* Neg
Lotus corniculatus	Tiriltunge	2800	0,015689263	12	11,6100546	-0,5	11,5	11,42790138	3,380518	-0,0325555	NS
Lychnis viscaria	Tjæreblomst	7039	0,039441686	32	29,1868479	-0,5	31,5	28,03566941	5,294872	0,4368665	NS
Matricaria perforata	Balderbrå	13350	0,074804164	1	55,3550816	0,5	1,5	51,21429101	7,156416	-7,5254263	**** Neg
Melampyrum sylvaticum	Småmarimjelle	747	0,004185671	2	3,0973967	0,5	2,5	3,084432019	1,756255	-0,3401537	NS
Mycèlis muralis	Skogsalat	114	0,000638777	4	0,47269508	-0,5	3,5	0,472393132	0,687309	4,4045788	**** Pos
Rubus idaeus	Bringebær	552	0,003093026	6	2,28883933	-0,5	5,5	2,281759891	1,51055	2,1258228	** Pos
Rubus saxatilis	Teiebær	841	0,004712382	7	3,48716282	-0,5	6,5	3,470729977	1,86299	1,6172056	* Pos
Sedum telèphium	Smørbukk	292	0,001636166	13	1,21076283	-0,5	12,5	1,208781825	1,099446	10,268113	**** Pos
Solidago virgaurea	Gullris	470	0,002633555	2	1,94883059	-0,5	1,5	1,943698237	1,394166	-0,3219349	NS
Succisa pratensis	Blåknapp	795	0,00445463	41	3,29642621	-0,5	40,5	3,281741851	1,811558	20,536785	**** Pos
Taraxacum officinale	Løvetann	892	0,004998151	8	3,69863167	-0,5	7,5	3,680145353	1,91837	1,9815611	** Pos
Trifolium hybridum/repens	Hvitkløver	3193	0,017891363	24	13,2396087	-0,5	23,5	13,00273402	3,60593	2,8454214	*** Pos
Trifolium medium/pratense	Skog-/rødkløver	394	0,002207703	2	1,63370054	-0,5	1,5	1,630093811	1,276751	-0,1047193	NS
Vicia cracca/sepium	Vikker	4120	0,02308563	15	17,083366	0,5	15,5	16,68898576	4,085216	-0,3875845	NS
Viola arvensis/tricolor	Stemorsblomst	457	0,002560712	4	1,89492676	-0,5	3,5	1,890074403	1,3748	1,167496	NS
Sum		178466		740							
										Probability	* 0,1
										less than	** 0,05
											*** 0,01
											**** 0,001

Appendix D

Preferences 1992

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Dramstad & Fry 1992	B	C	D	E	F	G	H	I	J	K	L	M
Flower species	Numbers	Visits	Flower/100757	D*All visits	Visits/627	visits	E rounded	G+/- 0,5	G+I	C-index	1/c-index	Chi
Achillea ptarmica	8986	2	0,089184871	55,91891382	0,003189793	2	56	0,5	2,5	-0,9552924	-1,0467999	3,8231684
Angelica sylvestris	159	18	0,001578054	0,98943994	0,028708134	18	1	-0,5	17,5	16,6867734	16,6867734	246,07486
Campanula rotundifolia	89	3	0,000883313	0,55383745	0,004784689	3	1	-0,5	2,5	3,51395982	3,51395982	6,31999399
Centaurea jacea	368	48	0,003652352	2,290024514	0,076555024	48	2	-0,5	47,5	19,742136	19,742136	351,267663
Cirsium arvense	192	4	0,001905575	1,194795399	0,006379585	4	1	-0,5	3,5	1,92937184	1,92937184	0,86373202
Convallaria majalis	4006	1	0,039759024	24,92890817	0,001594896	1	25	0,5	1,5	-0,9398289	-1,0640235	3,76293613
Filipendula ulmaria	245	2	0,002431593	1,524608712	0,003189793	2	2	-0,5	2	0,311812	0	0,47360273
Geranium sp.	1379	4	0,013686394	8,581369036	0,006379585	4	9	0,5	4,5	-0,4756081	-2,1025712	2,17741941
Hieracium umbellatum	1551	11	0,015393471	9,651706581	0,01754386	11	10	-0,5	10,5	0,08789051	11,3777926	0,83194372
Hypericum maculatum	2299	76	0,022817273	14,30643032	0,121212121	76	14	-0,5	75,5	4,2773472	4,2773472	10,7410047
Knautia arvensis	49	5	0,000486319	0,304921742	0,007974482	5	0	-0,5	4,5	13,757885	13,757885	162,763629
Lamium purpureum	417	1	0,00413867	2,594946257	0,001594896	1	3	0,5	1,5	-0,4219533	-2,3699303	2,02195132
Leontodon autumnalis	162	1	0,001607829	1,008108618	0,001594896	1	1	0,5	1	-0,0080434	0	1,01615149
Lotus corniculatus	601	1	0,005964846	3,739958514	0,001594896	1	4	0,5	1,5	-0,598926	-1,6696553	2,55656446
Lychnis viscaria	1411	3	0,01400399	8,780501603	0,004784689	3	9	0,5	3,5	-0,6013895	-1,6628158	2,56444838
Lythrum salicaria	491	4	0,004873111	3,055440317	0,006379585	4	3	0,5	4,5	0,47278282	2,11513609	0,27795796
Melampyrum pratense	15191	100	0,150768681	94,53196304	0,159489633	100	95	-0,5	99,5	0,05255404	19,0280314	0,89765384
Rubus idaeus	1345	40	0,013348948	8,369790685	0,063795853	40	8	-0,5	35,5	3,24144418	3,24144418	5,02407202
Sedum telephium	555	32	0,005508302	3,45370545	0,051036683	32	3	-0,5	31,5	8,12063882	8,12063882	50,7034972
Solidago virgaurea	1468	31	0,014569707	9,135206487	0,049441786	31	9	-0,5	30,5	2,33873132	2,33873132	1,79220154
Sonchus arvensis	32	1	0,000317596	0,199132566	0,001594896	1	0	-0,5	0,5	1,51089015	1,51089015	0,26100875
Taraxacum officinale	59	2	0,000585567	0,367150669	0,003189793	2	0	-0,5	1,5	3,08551618	3,08551618	4,34937773
Trifolium medium/pratense	837	18	0,008307115	5,208561192	0,028708134	18	5	-0,5	17,5	2,35985301	2,35985301	1,84920021
Vicia cracca	24469	217	0,242851613	152,2679615	0,346092504	217	152	-0,5	216,5	0,42183554	2,37059208	0,33427414
Vicia sepium	12	2	0,000119098	0,074674712	0,003189793	2	0	-0,5	1,5	19,0871212	19,0871212	327,143954
Total	100757	627	0,658743313	413,0320573	1	627	413	-4,5	618,5	96,9975013	124,627424	1189,89227

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N	O	P	Q	R	S	T	U	V	W
Sqrt chi	J-E	Rounded	Squared	Exp mod	Sqrt previuos	Rounded squared	z-value	Chi square	significance
1,95529241	-53,4	-53	2809	50,93179273	7,136651367	2809	-7,485151099	51,99044597	*** Neg
15,6867734	16,51	17	289	0,98787855	0,993920797	289	16,61154502	292,4474159	*** Pos
2,51395982	1,946	2	4	0,553348239	0,743873805	4	2,616253638	10,80409281	*** Pos
18,742136	45,21	45	2025	2,28166054	1,510516647	2025	29,93014052	912,3927913	*** Pos
0,92937184	2,305	2	4	1,192518627	1,092025012	4	2,110944874	6,58620954	** Pos
1,93982889	-23,4	-23	529	23,9377591	4,892622927	529	-4,788619216	22,96902224	*** Neg
0,688188	0,475	0	0	1,520901484	1,233248347	0	0,385478958	0,148232707	NS
1,47560815	-4,08	-4	16	8,463921039	2,909281877	16	-1,402878514	2,445873398	* Neg
0,91210949	0,848	1	1	9,503133312	3,08271525	1	0,275177352	0,188349607	NS
3,2773472	61,19	61	3721	13,97999659	3,738983364	3721	16,36636586	266,0409658	*** Pos
12,757885	4,195	4	16	0,304773453	0,552062907	16	7,598913465	72,29317159	*** Pos
1,42195335	-1,09	-1	1	2,58420663	1,607546774	1	-0,681128708	0,980310693	NS
1,0080434	-0,01	0	0	1,006487752	1,003238632	0	-0,008082442	6,52208E-05	NS
1,59892603	-2,24	-2	4	3,717650237	1,928120908	4	-1,161731354	2,007341159	NS
1,60138952	-5,28	-5	25	8,657539548	2,942369716	25	-1,794642452	3,805499992	** Neg
0,52721718	1,445	0	0	3,040550818	1,743717528	0	0,828436751	0,292001447	NS
0,94744596	4,968	5	25	80,27950365	8,959883016	25	0,55447565	0,316289086	NS
2,24144418	27,13	27	729	8,25806278	2,87368453	729	9,440914279	119,5334721	*** Pos
7,12063882	28,05	28	784	3,434681397	1,853289345	784	15,13325193	235,9468531	*** Pos
1,33873132	21,36	21	441	9,002109202	3,000351513	441	7,120763491	52,33260967	*** Pos
0,51089015	0,301	0	0	0,199069323	0,446171853	0	0,674330824	3,22091287	NS
2,08551618	1,133	1	1	0,366935678	0,605752159	1	1,870153187	7,261860479	** Pos
1,35985301	12,29	12	144	5,165293074	2,272728113	144	5,408231077	31,41383978	*** Pos
0,57816446	64,23	64	4096	115,2894414	10,73729209	4096	5,982145026	27,51883431	*** Pos
18,0871212	1,425	1	1	0,074665819	0,273250469	1	5,216186062	49,64033128	*** Pos
					0				
101,305835	205,5	203	15665	354,733881	68,13329894	15665	3,015675828	2172,576792	