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Författare
Author Elin Jansson

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Final Thesis

Phenology, landscape utilisation and monitoring of bumblebees

Elin Jansson

LiTH-IFM-Ex—06/1635—SE

Table of contents

1. Abstract

The last decades the abundance of many *Bombus* species in Europe has declined, likely as a result of agricultural intensification. The aim of this study was to improve monitoring methods, study the phenology and to see the importance of various landscape elements for bumblebees. The impact of weather and daily variation in bumblebee abundance was also examined. A total of 1053 bumblebees of 17 species were found. This study shows that flower-rich landscape elements like unfertilised pastures, undisturbed wood verges and uncropped field verges are important for bumblebee abundance and species-richness. However, the results also point out the importance of a diverse landscape, because bumblebee species preferred different landscape elements and showed a clear seasonal variation in habitat preferences. The bumblebees were not much affected by different weather and monitoring can be performed over the whole day as long as it is not raining, the temperature is above 17 ˚C and the wind speed is below five on Beaufort's scale. The number of bumblebees and species were relatively stable between the middle of June and the middle of July and peaked at the beginning of August. It is recommended that the seasonal visit is carried out at the beginning of the summer due to lower variation in bumblebee abundance. Power analyses showed that in order to detect a significant change in abundance, large-scale monitoring with many visited sites is needed. To detect a 50% change in abundance of *B. pascuorum*, the most common species, 295 sites must be monitored.

Keywords: *Bombus,* daily variation, plant preferences, landscape use, monitoring, phenology, weather impact.

2. Introduction

The last 50 years the abundance of many bumblebee species (*Bombus* spp.) in Europe has declined (Goulson et al. 2004). The major cause of this decline is thought to be the recent agricultural intensification leading to habitat destruction and fragmentation (Stoate et al. 2001, Jansson 2004), as well as exposure to various pesticides (Thompson & Hunt 1999). Bumblebees are generally associated with various habitats characterised by a high diversity and abundance of flowers, habitats that have declined strikingly in Europe (Goulson 2003a). Because bumblebees do not store nutrients as honeybees, they require a continuous succession of flowers during the summer to survive (Goulson 2003a). Uncropped areas of farmland, like for example roadside verges, shelter zones, hedgerows and borders of streams and ponds, which can provide flowers throughout the season, tend to support a greater number of bumblebees than cultivated areas (Mänd et al. 2002).

The decline in bumblebee abundance and species-richness may have serious consequences for plant community compositions and thus negatively affect other species in the pollination systems (Kearns et al. 1998). Bumblebees are not only important pollinators of wild flowers, but also of crops, and the decline in bumblebee abundance could have long-term economic as well as ecological implications (Allen-Wardell et al. 1998). Recently there have been attempts in the agricultural landscape to maintain and restore habitats that enhance the number of bumblebees (Bignal 1998, Goulson 2003b, Pywell et al. 2005). In order to efficiently achieve these goals, accurate monitoring of bumblebees must be implemented. Monitoring is important in order to evaluate the condition of a certain area in terms of species occurrence, species-richness and changes in abundance.

Previous studies have shown (Comba 1999) that the number of active bees is positively correlated with temperature, and this suggests that monitoring of bumblebees only under certain times of the day or in certain weather might not give an accurate picture of the number of bumblebees. Information about the phenology of different bumblebee species, how they use different landscape elements for foraging and to understand differences in plant preferences between species, would be valuable for conservation measures and management plans.

The aim of this study was to examine the phenology of bumblebees during the season, to improve monitoring methods, examine plant preferences and to see how different landscape elements differ in bumblebee species-richness and population sizes. Impact of weather and daily variation in bumblebee abundance was also examined.

3. Material and methods

3.1 Study area

The study was conducted in Sturefors, approximately 17 km south of Linköping in Östergötland, Sweden. Within the 2 km^2 study area, six different landscape elements were identified: unfertilised pasture, ley, uncropped field verge, wood verge and two kinds of road verges, all differing in vegetation structure and floral availability. The roads differed in size and maintenance, one small gravel road and a larger asphalt road. For each landscape element, there were three replicates, which gave a total of 18 sites. Each site was represented by one line transect, placed to give a good estimate of the particular landscape element.

3.2 Study period

Data was collected between 10th of June and 9th of September and each site was visited at least once a week. A rotating scheme allowed the 18 sites to be investigated during different times of the day each visit, with a return to the first time period after approximately three weeks. This was to eliminate the possible effect of daily fluctuation in number of observed bumblebees when comparing different landscape elements.

In order to investigate the variation in bumblebee abundance over the day, an intense shorter period of 15 days in the middle of July was dedicated to the three sites of pasture, which earlier in the season had proven to hold a high abundance of bumblebees. These three sites were then visited once a day during different times of the day (morning: 8:30-09.30, midday: 12:30-13.30 and afternoon: 16:30-17.30), which allowed a return to the first time period after three days. During this period the effect of different weather parameters on bumblebee abundance was examined. In this short period of time the variation seen in number of bumblebees was not likely caused by seasonal changes and therefore conclusions about the effect of weather and time of the day could be made. During this period the other sites were visited with a longer time-span in between, once every two weeks instead of every week, but with the same division into times of the day as before. After these 15 days the rotation of all the 18 sites returned to the original scheme.

3.3 Bumblebee monitoring

Bumblebees were recorded using a line transect method, which has been shown in previous studies to give a good estimate of the abundance of bumblebees in an area (Banaszak 1980, Teräs 1985). The transect length of 400 m was walked in a steady pace, approximately 16 min per transect, and every bumblebee within one metre from the transect line, in front or to the sides, was recorded and named to species. Bumblebee species were identified by eye on the basis of their colouring. In some cases a bumblebee had to be caught in order to be identified. In those cases the inventory was temporarily paused and later resumed from the same spot. The bumblebees' activities were recorded as either 'flying' or 'feeding'. 'Feeding' means that the bumblebee was positioned on a flower. The plant species that the bumblebee visited during feeding was recorded. Walks were carried out between 9.00 am and 18.00 pm. Every site was visited at least 15 times during the study period.

Nomenclature of the *Bombus* species followed Alford (1975). Because of their similar colour pattern the species *Bombus terrestris* (Linnaeus) and *Bombus lucorum* (Linnaeus) are difficult to distinguish in the field and were treated as a single species as in Dramstad & Fry (1995). A total of 17 species were found during the study period (Table 1) and the species were classified in two tongue-length classes by the length of the proboscis (Pekkarinen 1979, Teräs 1985).

Table 1. *Classification of the 17 observed* Bombus *species in short- and long-tongued species by the length of the proboscis, according to Pekkarinen (1979) and Teräs (1985).*

Short-tongued spp.	N	Long-tongued spp.	N
B. lapidarius (Linnaeus)	118	*B. pascuorum* (Scopoli)	289
B. terrestris/B. lucorum (Linnaeus)	80	*B. ruderarius* (Müller)	165
B. pratorum (Linnaeus)	49	*B. sylvarum* (Linnaeus)	119
B. soroeensis (Fabricius)	40	*B. hortorum* (Linnaeus)	111
B. barbutellus (Kirby)	23	*B. humilis* (Illiger)	5
B. hypnorum (Linnaeus)	14		
B. rupestris (Fabricius)	11		
B. bohemicus (Seidl)	8		
B. norvegicus (Sparre-Schneider)	8		
B. campestris (Panzer)	6		
B. quadricolor (Lepeletier)	4		
B. sylvestris (Lepeletier)	3		

3.4 Vegetation and plant survey

Transect surroundings were described by recording vegetation height and frequency of flowering plants after each transect walk, as described by Jansson (2004). Vegetation height was measured ten times along the transects, giving a mean for each walk. Frequency of flowering plants was recorded in order to give a measure of the forage resource availability. This was done by placing 1x1 m squares every 10th m (in total 20 squares) along the transects after every walk and recording all flowering plants rooted within each square. The total number of plant species as well as the number of flowering plants of each species was recorded. Plant specimens with more than one inflorescence were recorded as one plant. Nomenclature of the plant species followed Karlsson (1998).

3.5 Weather conditions

At the end of each transect walk, temperature; wind speed; percentage of sky covered by clouds and percentage of transect in direct sunshine (part of transect not shaded from e.g. trees or clouds) were recorded. As in Comba (1999), the temperature was measured about 70 cm above ground and five recordings, taken with short succession to allow for short-term fluctuations, gave a mean for each walk. Wind speed was estimated by observing the swaying vegetation using the Beaufort-scale. In strong wind (seven or above on the Beaufort-scale) or in rain, no recording took place. After a rainfall no recording was performed for ½-1 hour.

Part of transect in direct sunshine was classified into three categories: no sunshine (0%), intermediate sunshine (1-50%) and much sunshine (51-100%), which were later used to test the differences in bumblebee abundance with different amount of sunshine. Part of the sky covered by clouds was also classified into three similar categories: no clouds (0%), intermediate cloudiness (1-50%) and many clouds (51-100%).

3.6 Data analyses

For calculations and data analyses SPSS 12.0.1 statistical software was used except for the power analyses (see below), which were calculated in Excel. All statistical analyses in this study were made using a 0.05 significance level.

Although 17 *Bombus* species were observed in this study, only eight were caught in high enough numbers to be included in the statistical analyses based on individual species: *B. pascuorum, B. sylvarum, B. ruderarius*, *B. pratorum, B. hortorum, B. lapidarius, B. terrestris/B. lucorum* and *B. soroeensis.* All species were included in calculations on short- and long-tongued species and total number of species and individuals. During the 15-days intensive study period (see paragraph 3.2) conducted in the pastures, eleven *Bombus* species were observed and seven in numbers high enough to be used in statistical analyses concerning individual species: *B. pascuorum, B. sylvarum*, *B. ruderarius, B. pratorum, B. hortorum, B. lapidarius* and *B. terrestris/B. lucorum.*

Power analyses were made as in Glimskär et al. (2005) to estimate how many samples that are needed in order to detect a certain change in bumblebee abundance of different *Bombus* species. As in Glimskär et al. (2005) the statistical power settled as acceptable was 0.8, which means that the probability is 0.8 that a change of a certain size is statistically significant. This is a recommended level of, among others, Cohen (1988). Some modifications of the original statistical formulas from Glimskär et al. (2005) were made for this study. Instead of PPS selection (probability proportional to size) as in Glimskär et al. (2005), SRS (simple random sampling) was used in the following calculations, which means that all sites have the same probability of being selected. In Glimskär et al. (2005) transects of different lengths were used and the number of observations per hectare was estimated. In this study however, all transects were of the same length so instead the number of observations per transect was estimated. The following calculations are based on the assumption that the samples are drawn from an infinite population.

With an SRS selection of sites and transects of the same size, a mean for the number of observations in a transect can be estimated as follows:

$$\bar{y} = \frac{1}{n}\sum_{i=1}^{n}\bar{y}_i = \frac{1}{n}\sum_{i=1}^{n}\frac{1}{t}\sum_{j=1}^{t}y_{ij} \qquad (1)$$

where n is the number of examined sites, t is the number of inventory visits and y_{ij} is the number of observations of a certain species in the transect in site i at inventory visit j.

The variance of this mean can be estimated as follows:

$$Var(\bar{y}) = \frac{Var(\bar{y}_i)}{n} + \frac{1}{nt}\frac{\sum_{i=1}^{N}Var(\bar{y}_{ij})}{N} \qquad (2)$$

where $Var(\bar{y}_i)$ is the variance between the mean (for the *t* visits) of all sites and $Var(\bar{y}_{ij})$ is the variance between the number of observations at the different inventory visits in site *i* and *N* is the total number of sites from which a random sample is drawn.

The variance for an estimation of the difference between time 1 and 2, can be calculated as follows:

$$Var(\bar{d}) = 2 \cdot \left(\frac{Var(\bar{y}_i)}{n}(1-\rho) + \frac{1}{nt}\frac{\sum_{i=1}^{N} Var(\bar{y}_{ij})}{N} \right) \quad (3)$$

with designations as above and where *ρ* is the correlation between the number of observations at time 1 and 2 in the different sites. This is an approximate formula, based on the assumption that the variance for the estimation of the mean number of bumblebees in a transect is the same between the two observation times. Because this study was conducted during one year only, the same correlation (ρ=0.5) between years as in the study by Glimskär et al. (2005) was used for all *Bombus* species and between species.

All data for these analyses derive from pastures, field verges and wood verges, the three most bumblebee-rich landscape elements. The most abundant species, *B. pascuorum,* was used to examine the timing and the number of visits and sites needed to reach a probability of 0.8 to detect a 50% change in abundance.

4. Results

A total of 1053 bumblebees belonging to 17 species were observed in the six landscape elements. During the 15-days intensive study period conducted in the pastures, 224 bumblebees of eleven species were observed.

4.1 Weather and daily variation

No significant variation was found in number of observed bumblebees during different time periods of the day ($F_{(2, 42)}$=1.07, P=0.35), although there was a small increase during the day (Fig. 1a). The mean number of bumblebees in the morning was 4.5, at midday 5.1 and in the afternoon 5.9.

Overall, there was a significant effect of wind speed on the number of bumblebee observations (Fig. 1b) ($F_{(3, 41)}$=2.87, P=0.048). However, the mean number of observed bumblebees per transect was not affected as long as the wind was light (4.9 bumblebees/transect), gentle (5.5 bumblebees/transect) or moderate (4.7 bumblebees/transect). Not until the wind speed reached the level of fresh wind (five on Beaufort’s scale) and the mean number of bumblebees was as low as 1.3, a significant reduction in the number of bumblebees was detected. Tukey's Honest Significant Difference test showed that the effect of fresh wind differed significantly from both light (P=0.025) and gentle (P=0.006) winds, but not from moderate wind (P=0.044). During the study period no wind speeds above five on Beaufort's scale (fresh wind) were measured.

Number of observed bumblebees was not affected ($F_{(2, 42)}$=0.73, P=0.49) by the percentage of transect in sunshine (Fig. 1c). Mean number of observations at 0% sunshine was 4.3, and at both 1-50% and 51-100% it was 5.3.

The amount of sky covered by clouds (Fig. 1d) did not affect the number of observed bumblebees ($F_{(2, 42)}$=0.14, P=0.87). The mean number of bumblebees at 0% clouds was 5.2, at 1-50% the number of observations was 5.3 and at 51-100% it was 4.8.

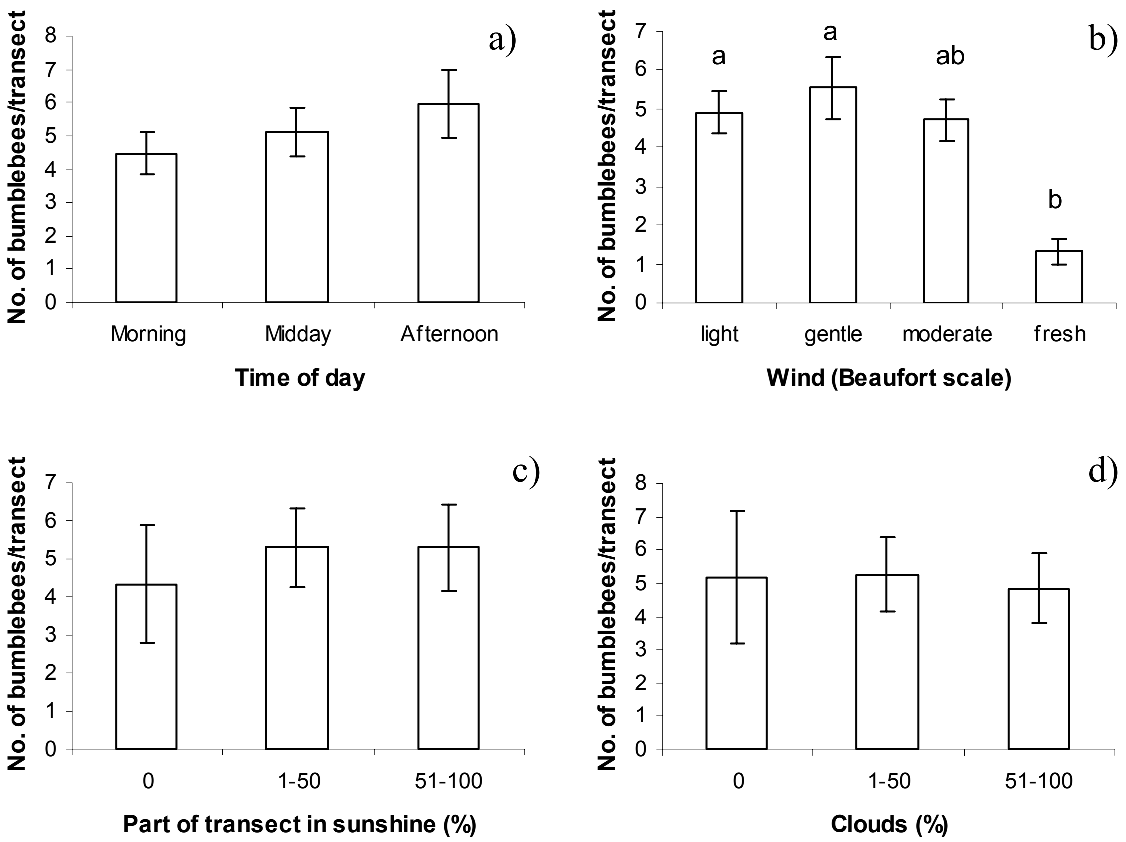

Figure 1. *a) Mean daily variation in bumblebee observations. Morning: 8:30-09.30. Midday: 12:30-13.30. Afternoon: 16:30-17.30. b) Mean number of bumblebees per transect in different wind speeds. Light wind is two on the Beaufort scale, gentle wind three and so on. Letters indicate differences (P<0.05) following Tukey's Honest Significant Difference test. c) Mean number of bumblebees per transect at different percentages of transect in sunshine (not shaded from e.g. trees or clouds). d) Mean number of bumblebees at different percentages of the sky covered by clouds. a-d) Error bars show 95% confidence interval for the mean. Data comes from the landscape element pasture. N=224.*

No significant correlation between temperature and number of bumblebees was found (Fig. 2) ($R^2_{(1, 43)}=0.04$, P=0.18). In temperatures below 17 ˚C, few or no observations were made. Above that temperature the mean number of bumblebees were 5.5, varying from 2 to 14 individuals per transect walk. During the study period no temperature below 15 ˚C or above 36 ˚C was measured.

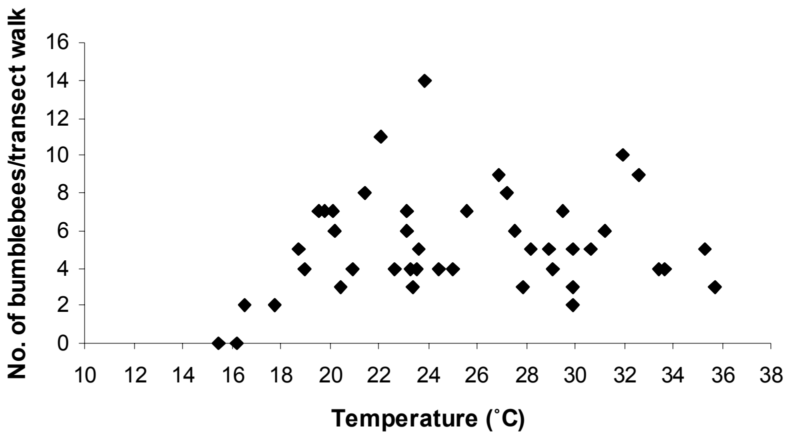

Figure 2. *Relation between number of observed bumblebees and temperature in the pastures. Each data point represents one transect.* $R^2_{(1, 43)}=0.04$, *P=0.18. N=224.*

Bumblebees were generally not affected by different weather conditions (Fig. 1). This was also clear when studying individual *Bombus* species (Table 2). One species however, *B. ruderarius,* seemed to be sensitive to different weather conditions. It had a strong (P<0.001) positive correlation with both temperature and percentage sunshine and also a strong negative correlation with percentage cloudiness. *Bombus ruderarius* was not correlated with any of the wind speeds measured in this study, as was neither of the other species. The total number of observed individuals was somewhat negatively correlated with wind and the total number of species had a positive correlation with temperature and sunshine, although neither was significant at the P<0.05 level.

Table 2. *Correlation between* Bombus *species and weather parameters. Numbers represent Pearson correlation coefficients. Numbers in brackets are the number observed bumblebees during the 15 days of intense study of the pastures. L=long-tongued species. S=short-tongued species. N=224. ***P<0.001.*

Species (N)	Temperature	Sunshine	Clouds	Wind
B. pascuorum (93) L.	-0.14	-0.22	0.20	-0.19
B. ruderarius (36) L.	0.49***	0.48***	-0.62***	-0.07
B. sylvarum (34) L.	0.11	0.02	0.03	0.04
B. hortorum (20) L.	-0.11	0.00	0.13	-0.08
B. pratorum (17) S.	0.03	0.11	-0.13	-0.25
B. terrestris/B. lucorum (15) S.	0.20	0.16	-0.15	-0.03
B. lapidarius (9) S.	0.21	0.11	-0.17	-0.02
Long-tongued spp. (183)	0.11	0.03	-0.05	-0.20
Short-tongued spp. (46)	0.29	0.25	-0.28	-0.20
Total no. of bumblebees (224)	0.20	0.12	-0.15	-0.25
Total no. of spp. (11)	0.29	0.25	-0.24	-0.21

4.2 Phenology

The number of individuals (Fig. 3a) and species (Fig. 3b) followed the same basic pattern over the season, although the number of individuals significantly changed over the 15 sampling dates during the season ($\chi^2_{(14)}$=389.35, P<0.001) and the number of species did not ($\chi^2_{(14)}$=15.45, P=0.35). Between the middle part of June and the end of July the numbers were rather stable with about 60-80 observed individuals and 8-10 species. At the beginning of August both the number of individuals and species increased and reached a peak at 167 individuals and 16 species. The number of species had a broader peak and did not decrease until the end of August, whereas the number of individuals decreased directly after peaking and continued to decrease until the first part of September, when only a few individuals remained.

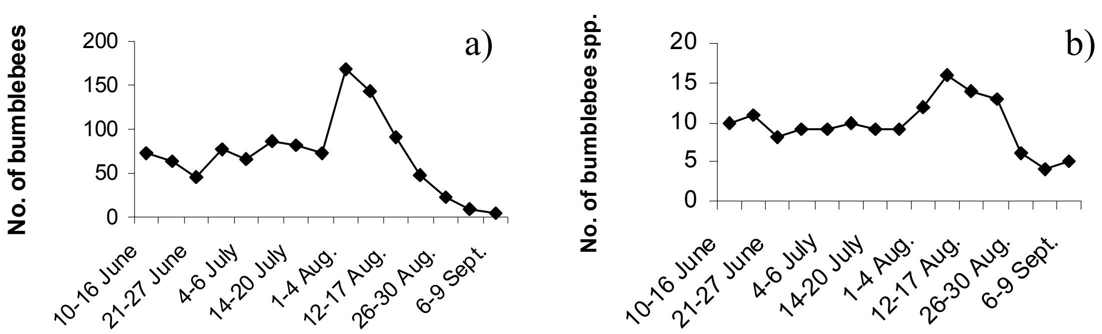

Figure 3. *Seasonal change in number of bumblebees and bumblebee species, from the 10th of June until the 9th of September. a) Seasonal change in number of bumblebees. $\chi^2_{(14)}$=389.35, P<0.001. N=1053. b) Seasonal change in number of observed bumblebee species. $\chi^2_{(14)}$=15.45, P=0.35. N=17 species.*

All landscape elements experienced significant variation in number of bumblebees over the season (Fig. 4). Three of the six landscape elements; field verge, wood verge and pasture, had a similar pattern of seasonal change in bumblebee abundance. All three had relatively stable numbers from the middle part of June until the end of July and reached their peaks at the beginning of August. Field verge had a narrow peak and already in the middle of August the number of bumblebees was back to the same level as before the peak and continued to decrease. Wood verge and pasture experienced broader peaks that continued until the end of August. Gravel road verge was fluctuating more in bumblebee abundance than the landscape elements above and reached its peak about one week after the others. Asphalt road verge was rather stable in the number of bumblebees until the end of July when the abundance decreased. It reached its original level again in the middle of August and started to decrease again after approximately two weeks. The leys were cut at the beginning of the research period and almost no bumblebees were observed the first two weeks. At the end of June bumblebees were observed and the abundance reached a peak in the middle part of July. After that, the abundance decreased again before reaching a smaller peak at the end of August.

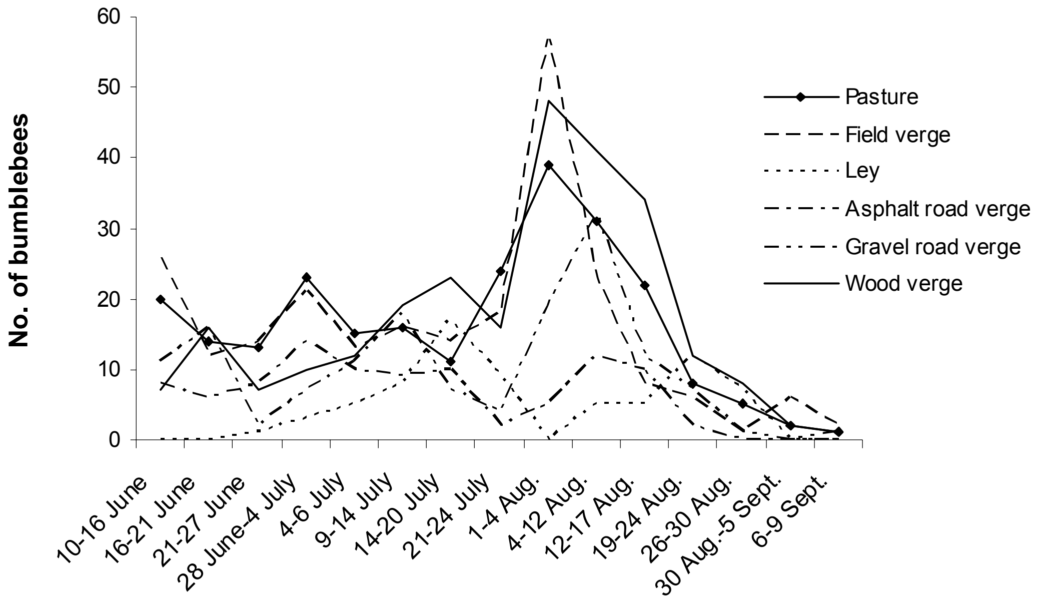

Figure 4. *Change in number observed bumblebees in the six different landscape elements, from the 10th of June until the 9th of September. Pasture:* $\chi^2_{(14)}=96.08$, $P<0.001$. *Field verge:* $\chi^2_{(14)}=163.06$, $P<0.001$. *Ley:* $\chi^2_{(14)}=76.33$, $P<0.001$. *Asphalt road verge:* $\chi^2_{(14)}=47.44$, $P<0.001$. *Gravel road verge:* $\chi^2_{(14)}=107.41$, $P<0.001$. *Wood verge:* $\chi^2_{(14)}=159.90$, $P<0.001$. $N=1053$.

All bumblebee species varied significantly in number over the season, although the relative proportion of the different species did not change much (Fig. 5). *Bombus pascuorum* represented a large part of the total number of bumblebees the whole season and was overall the most common species in this study. Most species experienced a peak in abundance in the first part of August, *Bombus pratorum* was, however, unlike the other species, most numerous in the middle part of July. *Bombus sylvarum* differed from the other species in the respect that it did not experience a peak in abundance. Instead the abundance was relatively stable the whole season until the end of August when the number decreased.

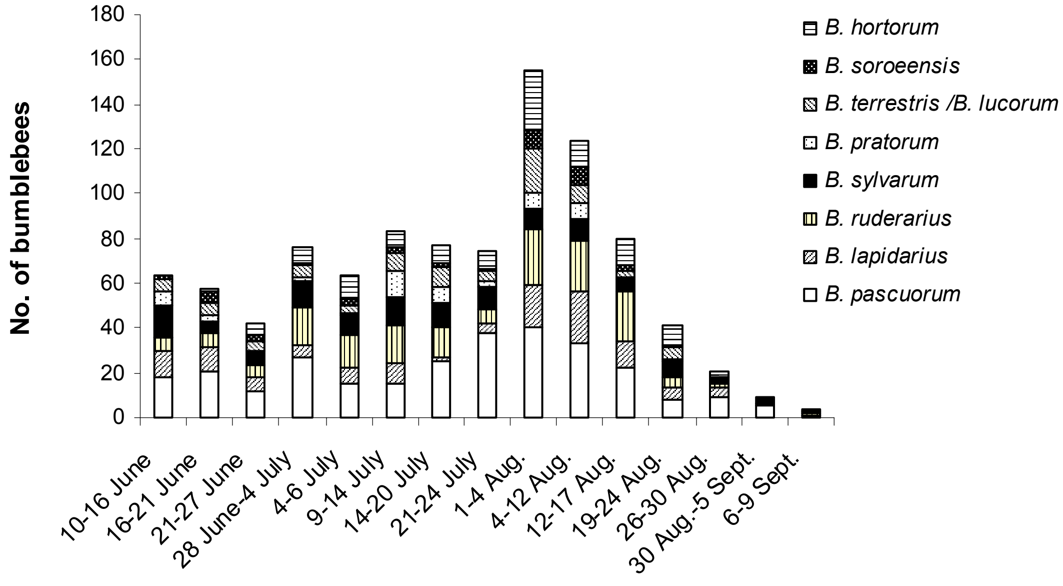

Figure 5. *Change in bumblebee species composition over the season, from the 10th of June until the 9th of September.* B. hortorum: $\chi^2_{(14)}$*=89.14, P<0.001*. B. soroeensis: $\chi^2_{(14)}$*=35.00, P<0.01*. B. terrestris/B. lucorum: $\chi^2_{(14)}$*=63.63, P<0.001*. B. pratorum: $\chi^2_{(14)}$*=51.71, P<0.001*. B. sylvarum: $\chi^2_{(14)}$*=28.35, P<0.05*. B. ruderarius: $\chi^2_{(14)}$*=88.36, P<0.001*. B. lapidarius: $\chi^2_{(14)}$*=76.49, P<0.001*. B. pascuorum: $\chi^2_{(14)}$*=100.33, P<0.001. N=1053.*

4.3 Differences between landscape elements

The total number of bumblebees, as well as the number of *Bombus* species, differed between the six landscape elements (Table 3). Most bumblebee individuals were found in wood verges, pastures and field verges, where 70% of all bumblebee observations were made. The lowest number of observations was found in leys. The highest number of species was also found in pastures, wood verges and field verges and the lowest in leys, but the asphalt road verges were also found to be species-poor.

No clear difference in habitat preferences was found between short- and long-tongued species; both groups were most common in wood verges, pastures and field verges and least numerous in leys and asphalt road verges. For individual species, wood verges were the first or second most popular landscape elements for the majority of species (*B. hortorum*, *B. soroeensis*, *B. pascuorum* and *B. pratorum). Bombus soroeensis* was almost only found in wood verges and the number differed significantly (P<0.05) from the other landscape elements. For the two species *B. sylvarum* and *B. lapidarius* wood verges were the least visited landscape element; instead *B. sylvarum* was most numerous in field verges and *B. lapidarius* in pastures. Leys were the least or among the least visited landscape element for all species. No individuals of *B. soroeensis* or *B. pratorum* were found in leys. Gravel road verges were the most visited landscape elements for *B. pratorum*, but among the least visited for *B. sylvarum* and *B. soroeensis*. Asphalt road verges were the least visited landscape element for *B. pascuorum* and not much visited by the other species. No significant difference in abundance between landscape elements was found for *B. ruderarius* and *B. terrestris/B. lucorum.*

Table 3. *Mean number of bumblebees per transect in the six different landscape elements, with confidence intervals in brackets. Letters indicate differences (P<0.05) following Tukey's Honest Significant Difference tests. L=long-tongued species. S=short-tongued species. *P<0.05, **P<0.01, ***P<0.001.*

Species (N)	Wood verge	Gravel road verge	Field verge	Ley	Pasture	Asphalt road verge	$F_{(5, 264)}$	Significance
B. pascuorum (289) L.	**2.16 c** (0.62)	**1.04 ab** (0.43)	**1.31 bc** (0.12)	**0.27 a** (0.08)	**1.40 bc** (0.48)	**0.24 a** (0.16)	9.996	***
B. ruderarius (165) L.	**0.42** (0.19)	**0.42** (0.42)	**0.91** (0.33)	**0.53** (0.13)	**1.00** (0.21)	**0.38** (0.15)	2.094	ns
B. sylvarum (119) L.	**0.11 a** (0.07)	**0.16 a** (0.12)	**1.02 c** (0.13)	**0.31 ab** (0.17)	**0.69 bc** (0.14)	**0.36 ab** (0.13)	9.925	***
B. hortorum (111) L.	**0.93 b** (0.49)	**0.27 a** (0.17)	**0.38 ab** (0.29)	**0.11 a** (0.14)	**0.38 ab** (0.22)	**0.40 ab** (0.24)	3.668	**
B. pratorum (49) S.	**0.33 ab** (0.24)	**0.38 b** (0.24)	**0.13 ab** (0.12)	**0.00 a**	**0.13 ab** (0.12)	**0.11 ab** (0.11)	3.038	*
B. terrestris/B. lucorum (80) S.	**0.33** (0.20)	**0.24** (0.15)	**0.53** (0.45)	**0.16** (0.15)	**0.31** (0.17)	**0.20** (0.12)	1.235	ns
B. soroeensis (40) S.	**0.62 b** (0.21)	**0.00 a**	**0.07 a** (0.06)	**0.00 a**	**0.16 a** (0.12)	**0.02 a** (0.04)	13.760	***
B. lapidarius (118) S.	**0.16 a** (0.12)	**0.47 ab** (0.25)	**0.56 ab** (0.28)	**0.18 a** (0.14)	**0.98 b** (0.38)	**0.29 a** (0.21)	5.980	***
Long-tongued spp. (689)	**3.67 c** (1.03)	**1.91 ab** (0.66)	**3.64 bc** (1.19)	**1.22 a** (0.57)	**3.47 bc** (0.91)	**1.40 a** (0.44)	7.315	***
Short-tongued spp. (364)	**1.78 b** (0.88)	**1.18 ab** (0.47)	**1.42 ab** (0.73)	**0.36 a** (0.29)	**1.64 b** (0.55)	**0.71 ab** (0.29)	3.542	**
Total no. of bumblebees (1053)	**5.71 b** (1.86)	**3.24 ab** (1.02)	**5.18 b** (1.89)	**1.62 a** (0.84)	**5.42 b** (1.32)	**2.13 a** (0.55)	6.813	***
Total no. of spp. (17)	**2.93 b** (0.68)	**1.98 ab** (0.49)	**2.82 b** (0.57)	**1.09 a** (0.47)	**3.00 b** (0.56)	**1.67 a** (0.38)	8.384	***

There was some variation over the season in which landscape elements that were most important for different *Bombus* species (Table 4). Overall, the wood verges were the most important landscape element for the majority of species during the season. In June however, both field verges and pastures were important and in September the field verges were important for the few species that remained. The highest number of observed bumblebees varied over the season between pastures, wood verges and field verges. Both long- and short-tongued species most often preferred wood verges, field verges and pastures, although the short-tongued were most common in wood verges a larger part of the season. Except for *B. soroeensis*, who almost exclusively preferred wood verges, species showed a large variation between preferred landscape elements over the season.

***Table 4.** Landscape elements where* Bombus *species were most numerous over the season, from the 10th of June until the 9th of September. F=field verges, W=wood verges, G=gravel road verges, A=asphalt road verges, L=leys, P=pastures. L=long-tongued species. S=short-tongued species.*

Species (N)	10-16 June	16-21 June	21-27 June	28 June-4 July	4-6 July	9-14 July	14-20 July	21-24 July	1-4 Aug.	4-12 Aug.	12-17 Aug.	19-24 Aug.	26-30 Aug.	30 Aug. - 5 Sept.	6-9 Sept.
B. pascuorum (289) L.	W	W	F / W	F	G	P	W	P	W	W	W	W	W	F	G
B. ruderarius (165) L.	F / P	P	F	W	P	F / L	L	L	F / P	G	W / P	G	W / L	P	F
B. sylvarum (119) L.	F	F / P	P	P	F	F	L	F	P	A	F	L	L	F	-
B. hortorum (111) L.	-	P	A	F / A	W / A	G	A	W	W	W	W	L	F / L / P	-	F
B. pratorum (49) S.	G	G	-	G / A	A	W / G	F / W / P	W	W	G	W	W	-	-	-
B. terrestris/B. lucorum (80) S.	P	A	F	F / P	W / G / L	F / G / L	F / L	F / W / A / L	F	W	W / G	W	-	-	W
B. soroeensis (40) S.	W / A	W	W	W	W	W	W	W	W	W	W	P	-	-	-
B. lapidarius (118) S.	F	G	P	P	P	F / W / G	L	L	P	P	P	P	P	-	-
Long-tongued spp. (689)	F	W	F	P	F / P	P	W	P	F	W	W	L	W / L	F	F
Short-tongued spp. (364)	P	G	F	P / A	W	W	F / W	W	F	W	W	P	W / P	W	W
Total no. of bumblebees (1053)	F	W	F / P	P	P	W	W	P	F	W	W	W / L	W	F	F

4.4 Plant preferences

A total of 94 flowering plant species were recorded in this study; of these 50 species were visited by bumblebees. The 19 most visited plant species accounted for 89.7% of all visits. Five plant species were the overall most important food sources; in order of importance they were *Serratula tinctoria, Trifolium pratense, Centaurea jacea, Trifolium medium* and *Knautia arvensis* (Table 5) and accounted for over 50% of all visits. The five most visited plant species were the same for both long- and short-tongued *Bombus* species, although in different order. Short-tongued bumblebees preferred *S. tinctoria* and *C. jacea,* while long-tongued preferred *T. pratense* and *T. medium.* Long-tongued bumblebees also visited *Trifolium repens* and *Vicia cracca* to a greater extent.

Bumblebee species preferred partly different plant species (Table 5). With little exception however, the five overall most visited plant species, *S. tinctoria, T. pratense, C. jacea, T. medium* and *K. arvensis,* were among the most visited also for individual bumblebee species. *Trifolium repens* was another important plant species, especially for *B. ruderarius, B. sylvarum* and *B. terrestris/B. lucorum.* Even though most *Bombus* species preferred the overall top five plant species some of them visited other plant species to a great extent. *Bombus lapidarius* was the only species that visited *Leontodon autumnalis* and it was one of the few species that did not have *S. tinctoria* as one of the top five most visited plants. *Bombus sylvarum* was another species that did not have *S. tinctoria* on the top five and it had *Vicia sepium* and *T. repens* as the second most visited plant species. *Bombus pratorum* was unique in having *Hypericum maculatum* and *Geum rivale* as the second and third most visited plant species respectively and *B. terrestris/B. lucorum* was the only species that used *Helianthemum nummularium. Bombus soroeensis* had *Campanula persicifolia* as second most visited and *V. sepium* and *Campanula rotundifolia* as third most visited plant species. *Bombus pascuorum* was the only species that did not have *C. jacea* as one of the five most visited plant species and it had *V. cracca* as the third most visited plant.

4.5 Correlation between plants and bumblebees

Some of the plant species examined in this study showed a positive correlation with and received a high percentage visits from certain *Bombus* species (Table 5). *Serratula tinctoria* and *C. jacea* had a strong positive correlation with and received many visits from both long- and short-tongued species. However, there was no clear relation between plant occurrence and *Bombus* visits. In some cases plant species that had a strong correlation with a particular *Bombus* species received few or no visits at all from that species, for example *B. lapidarius* and *C. rotundifolia*. In other cases, as with *B. pascuorum* and *T. pratense,* plant species that received a high percentage of visits from a *Bombus* species did not have any significant correlation with that species. *Trifolium pratense* received a high percentage of visits from both long- and short-tongued species but was not correlated with either. It did correlate with *B. sylvarum, B. hortorum* and *B. pratorum* but only received a few visits from the latter and it was not correlated with *B. pascuorum, B. lapidarius* or *B. ruderarius* from which it received a high percentage of visits.

4.6 Proportion of plant visits

In Table 6 the relative proportion of visits to the 19 most visited plant species for different *Bombus* species are shown. This is only meant as a relative comparison of proportion visits of *Bombus* species and should not be interpreted as a true value of exploitation because the number of bumblebee visits derived from line transects and the number of plants from 1x1 m squares placed along the transects. The results showed that *S. tinctoria* and *C. vulgare* had the highest proportions of visits, followed by *C. jacea, K. arvensis* and *Succisa pratensis. Trifolium repens* and *Lathyrus pratensis* had overall the lowest proportions of visits, but generally all plant species with high number of observed plants had a low proportion of visits.

The general pattern of proportion of visits was rather similar among all *Bombus* species (Table 6), although some differences were notable. All *Bombus* species showed a relatively high proportion of visits to *S. tinctoria*, *C. jacea* and *K. arvensis*. *Succisa pratensis* was not visited by *B. hortorum* and *B. soroeensis* but had a high proportion of visits from the other species. *Trifolium pratense, T. medium* and *T. repens* had overall a low proportion of visits from all species. *Bombus lapidarius* had a high proportion visits to *L. autumnalis, B. sylvarum* to *V. sepium, B. terrestris/B. lucorum* to *H. nummularium* and *B. soroeensis* to *C. persicifolia.* Long-tongued bumblebees had a higher proportion of visits to *T. pratense, T. medium, K. arvensis, T. repens, V. cracca, V. sepium, L. pratensis* and *Prunella vulgaris* than short-tongued bumblebees did, who preferred *C. persicifolia, C. rotundifolia* and *L. autumnalis.*

Table 5. *Percentage of the total number of bumblebee visits to the 19 most visited plant species. Correlation between plant abundance and individual bumblebee species are indicated by stars (*P<0.05, **P<0.01, ***P<0.001). Plants with >5% visits, the five most visited plant species for each bumblebee species and those with significant correlations are included. Ranking of the five most visited plant species for the individual bumblebee species are written in bold. L=long-tongued species. S=short-tongued species. *=positive correlation. -*=negative correlation.*

Plant species (% of total number of visits)	*B. pascuorum* L. N=241	*B. ruderarius* L. N=139	*B. sylvarum* L. N=99	*B. hortorum* L. N=107	*B. pratorum* S. N=43	*B. terrestris/ B. lucorum* S. N=70	*B. soroeensis* S. N=35	*B. lapidarius* S. N=89	Long-tongued spp. N=591	Short-tongued spp. N=263	Total no. of bumblebees N=889
S. tinctoria (13.72)	**4.** 9.54***	**2.** 14.39***		**2.** 17.76***	**1.** 22.93***	**1.** 20.00***	**1.** 20.00***	5.62	**3.** 11.17***	**1.** 16.73***	**1.** 13.72***
T. pratense (13.61)	**1.** 19.92	**4.** 10.79	**1.** 23.23*	**3.** 15.89*	2.33**	5.71		**3.** 10.11	**1.** 17.60	**5.** 5.70	**2.** 13.61
C. jacea (12.71)	3.32*	**1.** 24.46***	**3.** 8.08	**4.** 10.28***	**4.** 6.98	**2.** 15.71	**2.** 17.14***	**1.** 20.22***	**4.** 10.32***	**2.** 15.97***	**3.** 12.60***
T. medium (12.26)	**2.** 12.86*	**5.** 5.76	**2.** 11.11**	**1.** 36.45		**4.** 7.14		**2.** 11.24	**2.** 15.23**	**3.** 6.46	**4.** 12.26*
K. arvensis (6.52)	**5.** 8.71*	5.03	7.07	**5.** 3.74	**4.** 6.98		5.71	**4.** 8.99	**5.** 6.77	**4.** 6.08	**5.** 6.52
T. repens (5.06)		**3.** 11.51***	**2.** 11.11***			**3.** 8.57		5.62*	5.58*		5.06
V. cracca (3.94)	**3.** 10.79		3.03*						5.58		
V. sepium (3.60)			**2.** 11.11				**3.** 8.57*				
L. pratensis (2.14)											
L. linifolius (2.02)	4.15*							6.74			
P. vulgaris (1.91)		0.72**		2.80*					2.70**		1.91*
C. vulgare (1.91)		2.88*		0.93*				5.62***	1.35*	2.66**	1.91**
H. maculatum (1.91)	0.41***			0.00***	**2.** 13.95**		2.86***		1.18***	3.80**	1.91***
S. pratensis (1.80)							0.00*				
G. rivale (1.57)					**3.** 9.30*						
C. persicifolia (1.12)				0.93*	2.33**		**2.** 17.14*				
H. nummularium (1.12)			0.00**			**3.** 8.57		0.00*			
C. rotundifolia (1.01)	0.00**					5.71	**3.** 8.57*	0.00**	0.34*	2.66*	1.01*
L. autumnalis (1.01)	0.00 -*							**5.** 7.87*	0.17 -*		

Table 6. *Proportion of visits to the 19 most visited plant species for different* Bombus *species. Number of bumblebee visits derive from line transects and number of plants from 1x1 m squares placed along the transect. L=long-tongued species. S=short-tongued species.*

Plant species (total number of observed plants)	*B. pascuorum* L. N=241	*B. ruderarius* L. N=139	*B. sylvarum* L. N=99	*B. hortorum* L. N=107	*B. pratorum* S. N=43	*B. terrestris/ B. lucorum* S. N=70	*B. soroeensis* S. N=35	*B. lapidarius* S. N=89	Long-tongued spp. N=591	Short-tongued spp. N=263	Total no. of bumblebees N=889
S. tinctoria (91)	0.25	0.22	0.044	0.21	0.099	0.15	0.077	0.055	0.73	0.48	1.3
T. pratense (9219)	0.0052	0.0016	0.0025	0.0018	0.00011	0.00043	-	0.00098	0.011	0.0016	0.013
C. jacea (193)	0.042	0.18	0.042	0.057	0.016	0.057	0.031	0.093	0.32	0.22	0.58
T. medium (7277)	0.0043	0.0011	0.0015	0.0054	0.00014	0.00069	0.00010	0.0014	0.012	0.0023	0.015
K. arvensis (184)	0.11	0.038	0.038	0.022	0.016	0.011	0.011	0.044	0.22	0.087	0.32
T. repens (6839)	0.00073	0.0023	0.0016	0.00015	-	0.00088	-	0.00073	0.0048	0.0016	0.0066
V. cracca (2549)	0.010	0.0016	0.0012	-	-	-	-	0.00078	0.013	0.00078	0.014
V. sepium (875)	0.0091	0.0023	0.013	0.0011	-	0.0023	0.0034	0.0034	0.026	0.010	0.037
L. pratensis (3158)	0.0038	0.00032	0.00095	0.00032	-	0.00032	-	-	0.0054	0.00032	0.0060
L. linifolius (627)	0.016	0.0016	-	-	-	-	0.0016	0.0096	0.018	0.011	0.029
P. vulgaris (681)	0.013	0.0015	0.0044	0.0044	0.0015	-	-	-	0.024	0.0015	0.025
C. vulgare (14)	0.21	0.29	-	0.071	-	-	0.071	0.36	0.57	0.50	1.2
H. maculatum (794)	0.0013	0.0050	0.0025	-	0.0076	0.0013	0.0013	0.0025	0.0088	0.013	0.021
S. pratensis (80)	0.088	0.013	0.013	-	0.013	0.013	-	0.025	0.13	0.075	0.20
G. rivale (351)	0.0028	0.0085	0.0028	0.0028	0.011	0.0028	-	0.0057	0.017	0.020	0.040
C. persicifolia (112)	-	0.0089	-	0.0089	0.0089	0.0089	0.054	-	0.018	0.071	0.089
H. nummularium (694)	0.0029	0.0014	-	-	-	0.0086	-	-	0.0043	0.0086	0.014
C. rotundifolia (483)	-	-	0.0021	0.0021	-	0.0083	0.0062	-	0.0041	0.015	0.019
L. autumnalis (515)	-	0.0019	-	-	-	-	-	0.014	0.0019	0.014	0.018

4.7 Landscape elements and plant abundance

All landscape elements experienced a significant variation in number of flowering plants over the season (Fig. 6). The total plant abundance was high already in June and reached a peak at the beginning of July, about a month before the peak in bumblebee abundance. Pastures, field verges, gravel road verges and wood verges were relatively flower abundant the whole season. Asphalt road verges held a high number of flowering plants until the end of July when the flower abundance drastically decreased. Leys were a flower-poor landscape element the whole season with almost no flowering plants until the end of June.

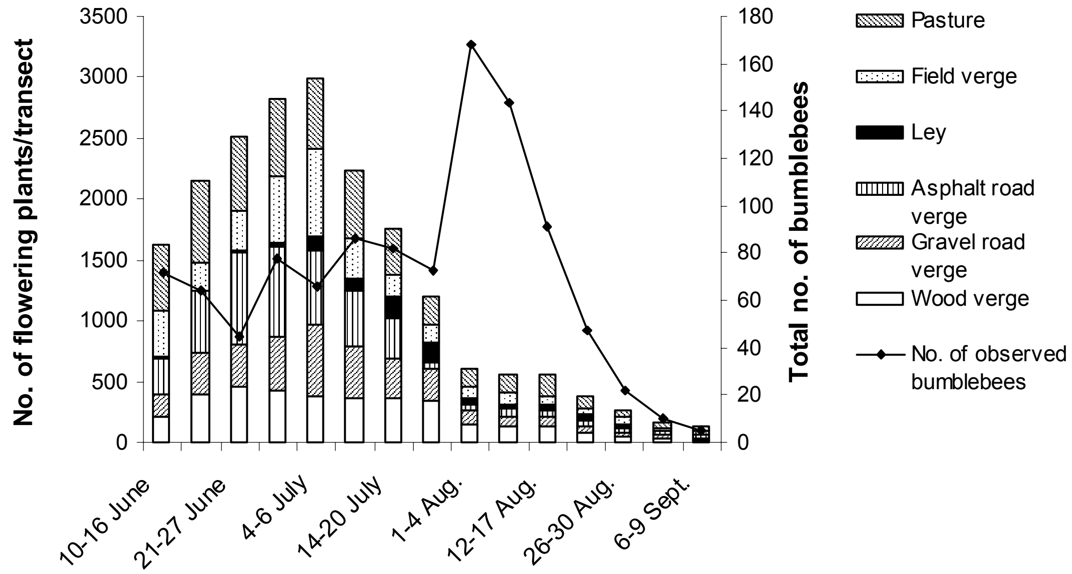

Figure 6. *Change in total number of flowering plants in the six landscape elements and the total number of bumblebees over the season, from the 10th of June until the 9th of September. Pasture: $\chi^2_{(14)}$=2575.77, P<0.001. Field verge: $\chi^2_{(14)}$=2672.26, P<0.001. Ley: $\chi^2_{(14)}$=809.02, P<0.001. Asphalt road verge: $\chi^2_{(14)}$=3942.93, P<0.001. Gravel road verge: $\chi^2_{(14)}$=2185.24, P<0.001. Wood verge: $\chi^2_{(14)}$=1472.18, P<0.001. Bumblebees: $\chi^2_{(14)}$=389.35, P<0.001. $N_{(Bumblebees)}$=1053. $N_{(Plants)}$=1198080.*

The 19 most visited plant species differed in abundance between landscape elements (Table 7), although most species were most numerous in the pastures. *Serratula tinctoria,* the most visited plant species, was found in wood verges, gravel road verges and field verges and was most numerous in field verges. *Trifolium pratense* was mostly found in pastures and asphalt gravel road, *C. jacea* in pastures, *T. medium* in field verges and *K. arvensis* in gravel road verges and pastures. The leys were a species-poor landscape element where only *T. repens* and *T. pratense* grew. These species were also found in asphalt road verges together with *V. sepium* and *V. cracca.* Some plant species were almost only found in a specific landscape element. *Prunella vulgaris, H. nummularium* and *L. autumnalis* grew almost exclusively in pastures and *H. maculatum* and *S. pratensis* in wood verges.

Table 7. *Mean number of flowering plant species per transect (within 1x1 m-squares) in the different landscape elements, with confidence intervals in brackets. Letters indicate differences (P<0.05) following Tukey's Honest Significant Difference tests. *P<0.05, **P<0.01, ***P<0.001.*

Plant species (N)	Wood verge	Gravel road verge	Field verge	Ley	Pasture	Asphalt road verge	$F_{(5, 264)}$	Significance
S. tinctoria (91)	**0.67 ab** (0.62)	**0.40 ab** (0.39)	**0.96 a** (0.73)	**0.00 b**	**0.00 b**	**0.00 b**	3.594	**
T. pratense (9219)	**12.40 a** (10.67)	**29.82 ab** (16.87)	**39.36 ab** (21.36)	**9.29 a** (6.00)	**56.00 b** (25.05)	**58.00 b** (30.04)	4.158	**
C. jacea (193)	**0.69 ab** (1.06)	**1.09 ab** (0.90)	**0.00 a**	**0.00 a**	**2.33 b** (1.46)	**0.18 a** (0.21)	4.567	***
T. medium (7277)	**36.13 ab** (18.97)	**24.71 ab** (16.23)	**74.89 a** (52.45)	**0.00 b**	**15.64 b** (10.29)	**10.33 b** (10.10)	4.527	***
K. arvensis (184)	**0.38 ab** (0.31)	**0.98 ab** (0.50)	**0.29 a** (0.23)	**0.00 a**	**0.96 ab** (0.51)	**1.49 b** (1.10)	3.745	**
T. repens (6839)	**3.91 a** (2.01)	**1.62 a** (0.84)	**1.87 a** (0.89)	**44.24 b** (29.49)	**52.20 b** (20.17)	**48.13 b** (28.24)	7.029	***
V. cracca (2549)	**11.09 ab** (4.66)	**10.24 ab** (6.11)	**5.53 a** (3.22)	**0.00 a**	**5.02 a** (2.96)	**24.76 b** (18.49)	3.969	**
V. sepium (875)	**5.04 ab** (3.31)	**4.33 ab** (2.58)	**1.20 a** (1.26)	**0.00 a**	**1.56 a** (1.08)	**7.31 b** (4.77)	4.126	**
L. pratensis (3158)	**9.24 ab** (5.21)	**26.82 c** (10.89)	**19.04 bc** (8.29)	**0.00 a**	**0.29 a** (0.29)	**14.78 bc** (6.95)	9.916	***
L. linifolius (627)	**7.93 b** (6.19)	**1.04 a** (0.80)	**2.47 ab** (2.84)	**0.00 a**	**2.49 ab** (1.95)	**0.00 a**	3.983	**
P. vulgaris (681)	**3.18 a** (1.29)	**0.58 a** (0.59)	**0.67 a** (0.38)	**0.00 a**	**10.71 b** (8.44)	**0.00 a**	5.491	***
C. vulgare (14)	**0.02** (0.04)	**0.00**	**0.07** (0.13)	**0.00**	**0.16** (0.16)	**0.07** (0.07)	1.565	Ns
H. maculatum (794)	**10.27 b** (3.76)	**2.82 a** (1.00)	**2.44 a** (1.19)	**0.00 a**	**1.36 a** (0.85)	**0.76 a** (0.62)	18.244	***
S. pratensis (80)	**1.51 b** (0.78)	**0.00 a**	**0.02 a** (0.04)	**0.00 a**	**0.24 a** (0.24)	**0.00 a**	12.386	***
G. rivale (351)	**0.82 a** (0.60)	**4.20 b** (3.25)	**1.13 ab** (1.13)	**0.00 a**	**1.64 ab** (1.80)	**0.00 a**	3.633	**
C. persicifolia (112)	**1.04 b** (0.57)	**0.49 ab** (0.39)	**0.56 ab** (0.37)	**0.00 a**	**0.31 a** (0.34)	**0.09 a** (0.10)	4.380	***
H. nummularium (694)	**0.00 a**	**0.00 a**	**0.00 a**	**0.00 a**	**15.42 b** (9.76)	**0.00 a**	9.598	***
C. rotundifolia (483)	**2.80 b** (1.57)	**0.38 a** (0.36)	**1.40 ab** (0.94)	**0.00 a**	**5.04 c** (1.66)	**1.11 ab** (0.69)	11.947	***
L. autumnalis (515)	**0.42 a** (0.46)	**0.00 a**	**1.51 a** (1.15)	**0.00 a**	**6.47 b** (3.17)	**3.04 a** (1.34)	10.923	***

4.8 Vegetation parameters

The vegetation parameters examined in this study affected the *Bombus* species to different extents (Table 8). The total number of *Bombus* species, individuals and both long- and short-tongued species were positively correlated with the number of flowering plant species and the total number of flowers. All species except *B. ruderarius* and *B. terrestris/B. lucorum* were positively correlated with number of plant species. *Bombus pascuorum, B. lapidarius, B. sylvarum* and *B. ruderarius* had a positive correlation with the total number of flowers. The only species that was affected by vegetation height was *B. lapidarius*, which had a negative correlation with vegetation height.

The landscape elements clearly differed in the vegetation parameters measured (Table 9). The highest number of flowering plant species was found in pastures and wood verges and the lowest in leys. Leys also had a significantly lower number of flowers than the other landscape elements. The highest number of flowering plants was found in pastures, although it did not differ significantly from the other landscape elements except for leys. The vegetation was highest in field verges and shortest in pastures.

Table 8. *Correlation between* Bombus *species and vegetation parameters. Numbers represents Pearson correlation coefficients. L=long-tongued species. S=short-tongued species. *P<0.05, **P<0.01, ***P<0.001.*

Species (N)	No. of flowering plant species	Total no. of flowering plants	Vegetation height
B. pascuorum (289) L.	0.35***	0.12*	
B. ruderarius (165) L.		0.14*	
B. sylvarum (119) L.	0.15*	0.23***	
B. hortorum (111) L.	0.22***		
B. pratorum (49) S.	0.22***		
B. terrestris/B. lucorum (80) S.			
B. soroeensis (40) S.	0.23***		
B. lapidarius (118) S.	0.23***	0.13*	-0.12*
Long-tongued spp. (689)	0.34***	0.22***	
Short-tongued spp. (364)	0.30***	0.13*	
Total no. of bumblebees (1053)	0.36***	0.20**	
Total no. of spp. (17)	0.48***	0.35***	

Table 9*. Differences in vegetation parameters between landscape elements. Letters indicate differences (P<0.05) following Tukey's Honest Significant Difference tests. Numbers in brackets are confidence intervals. ***P<0.001.*

Landscape Element	Mean no. of flowering plant species	Mean total no. of flowering plants	Mean vegetation height
Wood verge	13.3 (1.1) c	235.1 (51.3) b	11.8 (0.7) bc
Gravel road verge	11.9 (1.2) bc	220.7 (57.0) b	11.9 (0.9) c
Field verge	10.9 (0.8) b	220.4 (64.8) b	14.5 (0.7) d
Ley	1.4 (0.4) a	55.2 (29.0) a	9.8 (1.2) b
Pasture	13.7 (1.2) c	327.7 (73.5) b	4.7 (0.4) a
Asphalt road verge	10.3 (1.2) b	271.9 (83.6) b	12.1 (1.5) c
$F_{(5.264)}$	75.68	8.24	44.93
Significance	***	***	***

4.9 Detecting changes in bumblebee abundance

Bombus pascuorum, the most abundant species in this study, was used in the following calculations to examine the timing and the number of visits and sites needed to reach a probability of 0.8 to detect a 50% change in abundance.

The probability of detecting a certain change in abundance of *B. pascuorum* with one visit per year to 785 sites (number of sites needed to detect a difference of 50% with a probability of 0.8, see Table 10) was found to be greatest when the visit occurred at the beginning of the summer, between 10th of June and 20th of July (Fig. 7a). In that case a change of 30% could be detected with a probability of approximately 0.8. If the visit occurred at the end of the summer instead, it was only possible to detect a 40% change in abundance and when considering the whole season there had to be a 50% change. These and the following calculations derive from field verges, wood verges and pastures, where most bumblebees were found.

Considering the beginning of the summer, when the probability of detecting a change in abundance of *B. pascuorum* was greatest (Fig. 7a), about 300 sites were needed in order to detect a change of 50% with a probability of 0.8 (Fig. 7b). If instead 200 sites were used the probability went down to approximately 0.6, if 100 sites were used the probability was 0.4 and if 50 sites were used the probability was only 0.2.

Varying the number of visits per season did not have a large effect on the probability of detecting a certain change in abundance of *B. pascuorum* (Fig. 7c). When visiting the sites one time during the season the probability was 0.81 that a change in 50% abundance was detected. When instead three visits were made the probability went up to 0.87; with ten visits to 0.89; and with 30 visits the probability was 0.90.

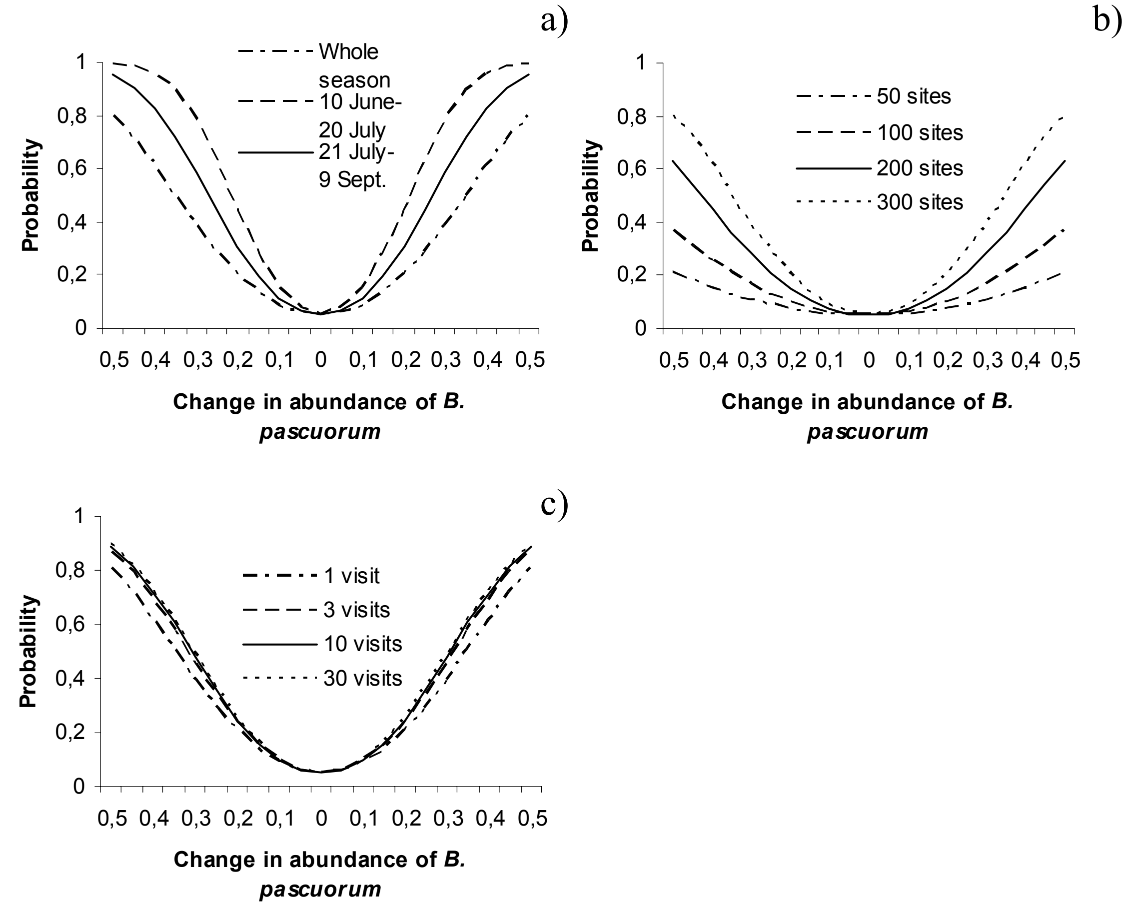

***Figure 7**. Probability to detect a certain change in abundance of* Bombus pascuorum, *the most common species in this study. Data comes from the landscape elements field verge, wood verge and pasture. a) Probability at which a certain change in abundance can be discovered at different times of the season. Number of sites=785. Number of visits=1. b) Probability at which a certain change in abundance can be discovered at different number of sites. Number of visits=1. Visit between 10th of June and 20th of July.* c) *Probability at which a certain change in abundance can be discovered at different number of visits. Number of sites=300. Visit between 10th of June and 20th of July.*

The number of sites necessary to detect a 50% change in abundance with a probability of 0.8 varied between *Bombus* species and also depended on at what time the one visit occurred (Table 10). Generally, visiting the sites the first part of the summer resulted in fewer sites needed. One species however, *B. hortorum,* required fewer sites if the visit was to occur the last part of the summer. As long as the visits occurred at the beginning of the summer, the following species required the least number of sites: *B. pascuorum* with 295 sites; *B. ruderarius* with 640; *B. terrestris/B. lucorum* with 900 and *B. sylvarum* with 940 sites.

In order to detect a change of 50% in the number of observed species with a probability of 0.8 only a few sites were needed. Least sites were required if the visit was at the beginning of the summer (15 sites) and most if the visit was at the end of the summer (90 sites).

***Table 10**. Number of sites necessary to reach a probability of 0.8 to detect a 50% change in abundance for different* Bombus *species and for the total number of species. Data comes from the landscape elements field verge, wood verge and pasture. Number of visits=1. Numbers in brackets are as follows: observed numbers of bumblebees the whole season/observed numbers between 10th of June and 20th of July/observed numbers between 21st of July and 9th of September.*

Species	The whole Season	10 June-20 July	21 July-9 Sept.
B. pascuorum (219/99/120)	785	295	465
B. ruderarius (105/51/54)	3415	640	2000
B. sylvarum (82/51/31)	4710	940	2060
B. hortorum (76/18/58)	8490	3555	2250
B. pratorum (27/13/14)	7865	2315	5845
B. terrestris/B. lucorum (53/24/29)	5065	900	3305
B. soroeensis (38/17/21)	10810	2990	3715
B. lapidarius (76/30/46)	4315	1140	1725
No. of species (17/13/17)	55	15	90

5. Discussion

The last decades the number of bumblebees in Europe has declined, most likely because of more intense farming and forestry that causes habitat destruction and fragmentation (Stoate et al. 2001). This study has shown that flower-rich landscape elements like unfertilised pastures, undisturbed wood verges and uncropped field verges are important for bumblebee abundance and species-richness. In this study 17 bumblebee species were observed, which is a high figure compared with studies in for example Germany and UK. In UK six to seven species are commonly found (Croxton et al. 2002, Carvell et al. 2004, Pywell et al. 2005) and in a German study by Steffan-Dewenter & Tscharntke (2000) six species were found. The difference may be caused by the high degree of agricultural intensification in these countries (Stoate et al. 2001).

5.1 Impact of weather and daily variation

In order to perform monitoring work, it is important to identify the impact of weather factors. No effect of light to moderate wind, temperature, or amount of sunshine or cloudiness was found in this study. This is in conclusion with other studies, such as Carvell (2002) where no significant correlation between bumblebee abundance and weather conditions were found. However, see Comba (1999). In the present study, fresh wind (five on Beaufort's scale) was found to have a negative effect on the number of observed bumblebees. At temperatures below 17 ˚C few or no observations were made, which may indicate that temperatures below this level have a negative effect on bumblebee abundance. Only *B. ruderarius* was found to be significantly affected by the weather parameters, showing a strong positive correlation with temperature and sunshine and a strong negative correlation with cloudiness. According to Goulson (2003a) it is possible that different *Bombus* species, which vary in size, hairiness and the climate to which they are adapted, differ in minimum body temperatures at which flight can occur, however most species have not been studied. Bumblebee's hairy coat is an effective insulator, which reduces heat loss considerably and heat loss tend to be greater in smaller bumblebees (Alford 1975). *Bombus ruderarius* is, however, not one of the smallest bumblebees so size could not adequately explain its sensitivity to weather parameters. The reasons for bumblebees' relative indifference to weather conditions are several. They are able to produce heat in preparation for flight by shivering, which involves repeated contraction of flight muscles while functionally uncoupling them from the wings (Prŷs-Jones & Corbet 1987). Bumblebees also appear to be able to generate heat without shivering by an energy-releasing biochemical substrate cycle under control of the bumblebee (Newsholme et al. 1972). The activity of the enzyme needed for the substrate cycle, fructose bisphosphatase, vary to some extent between species (Newsholme et al. 1972). However there are no indications that *B. ruderarius* would have a considerably lower enzyme activity that could explain its sensitivity to low temperatures.

It has been suggested that the abundance of bumblebees reach a peak in the mid-morning (Alford 1975) and that in warm weather there is a decline during the middle of the day to prevent over-heating (Prŷs-Jones & Corbet 1987). However, no such fluctuations over time of the day were found in this study, although some of the summer days reached a temperature of above 30 ˚C in the sun. According to Goulson (2003a), workers of different size are likely to differ in their optimal ambient temperature range for activity so that smaller workers would be better suited for foraging in warm weather and in the middle of the day and larger workers in colder weather and in early mornings and evenings. If it is indeed so, it could explain the lack of fluctuation in number of bumblebee observations over the day.

Findings of this study show that monitoring of bumblebees can be performed between 9 am and 18 pm independent of temperature, cloudiness and wind speed as long as the temperature is above 17 ˚C and the wind speed below five on Beaufort's scale. The fact that bumblebees are so indifferent to weather conditions and not affected by time of the day make them easy to monitor in the field, which considerably facilitates survey and follow-ups on different bumblebee species and habitat conditions.

5.2 Phenology, landscape use and plant preferences

Both the number of bumblebee individuals and species followed the same basic pattern over the season. Between the middle of June and the end of July the numbers were rather stable and at the beginning of August they peaked. This was somewhat later than found in other studies (Dramstad & Fry 1995) and because this study was conducted over one season only, the exact dates must be interpreted with care.

The season ended at the beginning of September when only a few individuals and species remained. The peak in bumblebee abundance was probably caused by the fact that colonies of several species start to rear reproductives (males and queens) at the end of the summer, which means that workers, queens and males can be observed in August (Alford 1975, Teräs 1985, Nisbet 2005). The increase in number of species in August could be caused by the strong decrease in flower abundance. This may force workers to seek forage over larger distances, and so more species could be observed in the study area.

Most *Bombus* species experienced a peak in abundance in the first part of August; *B. pratorum* was, however, most numerous in the middle part of July. It is well known that *B. pratorum* has a short life-cycle that starts earlier in the season than most other species (Alford 1975, Teräs 1985, Prŷs-Jones & Corbet 1987), which would explain the earlier peak in abundance. In this study, *B. pratorum* was observed until the middle of August, which is later than found in other studies (Alford 1975, Teräs 1985). It appears that a few young queens of *B. pratorum* and *B. hortorum*, which also have a short life-cycle, go on to produce a second cycle in some years (Prŷs-Jones & Corbet 1987), which may be the case in this study. *Bombus terrestris* and *B. lucorum* colonies are known to reach high numbers of individuals but have a rapid development and in Britain they often die out in mid- or late August (Alford 1975), which was also seen in this study. *Bombus pascuorum* is one of the most long lived species and can often be seen well into September (Alford 1975); also in this study it was one of the latest species to be seen in significant numbers.

Abundance of flowering plants reached a peak at the beginning of July, about a month before the bumblebee abundance peaked. The total developmental process from egg to adult bumblebee takes about four to five weeks (Alford 1975), so it is possible that the colony produces a numerous offspring when the food resources are abundant but that the result is not visible until about a month later. Colonies usually start to rear reproductives only when adequate food stores are available for feeding the brood (Alford 1975).

Clear differences both in bumblebee abundance and species-richness between landscape elements were found. The landscape elements with most bumblebees and species were pastures, field verges and wood verges while leys were the landscape element with the least numbers of species and bumblebees. Wood verges, field verges and pastures all had similar patterns of seasonal change in bumblebee abundance with a peak at the beginning of August. These three landscape elements were abundant in flowering plants the whole season and had high numbers of plant species, which may explain why the highest number of bumblebee individuals and species were found there. All *Bombus* species were found to be positively correlated with number of plant species except for *B. ruderarius* and *B. terrestris/B. lucorum.* These species, however, did not differ significantly in abundance between landscape elements. Previous studies have found a correlation between number of bumblebees and plant species-richness (Kells et al. 2001, Bäckman & Tiainen 2002, Carvell 2002). Several of the 19 most visited plant species were most abundant in pastures although *S. tinctoria,* the most visited species, was more abundant in field- and wood verges. Uncropped field verges and undisturbed wood verges have been found to be important landscape elements for bumblebees in several studies (Dramstad & Fry 1995, Kells et al. 2001, Bäckman 2002, Meek et al. 2002).

The reason for the low numbers of bumblebees in leys and asphalt road verges was probably because they were cut, causing almost all flowers to disappear for some time. Leys contained the lowest number of flowering plant species as well as number of plants. The leys reached a peak in bumblebee abundance in the middle part of July and the number would probably have continued to increase if the leys had not been cut at that point. Asphalt road verges contained a fairly high number of flowering plants before they were cut and after recovering again, and the number of bumblebees were rather stable until the end of July when they were cut. Road verges are otherwise known to be important landscape elements for several bumblebee species (Teräs 1985).

Gravel road verges were fluctuating in bumblebee abundance over the season but were relatively flower-rich the whole season. It is possible that the fluctuation in the number of bumblebees are caused by changes in flower supply in nearby landscape elements, especially in leys and asphalt road verges because the bumblebee abundance tended to be higher in gravel road verges when it was low in leys and asphalt road verges and vice versa. Gravel road verges were together with wood verges the preferred landscape element for *B. pratorum.* This could be explained by its use of *G. rivale*, that were most abundant in gravel road verges, and *H. maculatum* that almost only grows in wood verges.

As previously found in a study by Teräs (1985), the various *Bombus* species differed somewhat in habitat preferences, although most preferred wood verges, field verges and pastures. *Bombus soroeensis* was the most habitat-specific species and was almost exclusively found in wood verges. This is also in conclusion with Teräs' study (1985), where *B. soroeensis* was considered a forest species. *Bombus soroeensis* also used *C. persicifolia* and *C. rotundifolia*, two common species in wood verges, to a greater extent than any other *Bombus* species. *Bombus lapidarius* and *B. sylvarum* differed from the other species in being least numerous in wood verges. Both species are known to have a wide habitat use and have been found to prefer open terrains (Teräs 1985). *Bombus lapidarius* was most abundant in pastures and was also the only species that used *L. autumnalis,* a plant species that was almost exclusively found in pastures. *Bombus lapidarius* was also the only species that had a negative correlation with vegetation height. Even though *B. lapidarius* was most common in pastures, where the vegetation was lowest, the number was not significantly different from that found in field verges, the second most common landscape element for *B. lapidarius.* This suggests that even though a negative correlation exists between *B. lapidarius* and vegetation height, it does not affect the habitat preferences.

Were an intensification of agriculture or forestry to be adopted in this area, it would probably lead to decline and destruction of pastures, wood verges and field verges, the most bumblebee-rich landscape elements in this area, which would have a serious negative impact on abundance of bumblebees. However, preserving these landscape elements are not enough in terms of maintaining viable populations of bumblebees. As also found by Teräs (1985), there was a clear seasonal variation in bumblebee habitat preferences. During some part of the season each of the six landscape elements held the highest number of at least one bumblebee species. This demonstrates the importance of a diverse landscape. If the landscape elements with fewer bumblebees, as road verges and leys, were to disappear it could cause gaps in the flower supply, leading to a decline in bumblebee abundance. Bumblebees require a continuous succession of flowering plants during the summer, because they do not store nutrients as honeybees do (Goulson 2003a).

Most bumblebee species show a preference for certain plant species, but they are flexible in their preferences according to availability over the season (Goulson 2003a). As found in other studies, not all plant species available were used by bumblebees and a few species received almost all visits (Teräs 1985, Dramstad & Fry 1995). The five most visited plant species (*S. tinctoria, T. pratense, C. jacea, T. medium* and *K. arvensis*) were the same for both long- and short-tongued *Bombus* species and for most individual species. These plant species must therefore be considered important food sources for bumblebees in this area. However, for some *Bombus* species the importance of other food sources were apparent and that bumblebee species differ in their flower preferences is well known (Alford 1975, Teräs 1985, Goulson 2003a, Nisbet 2005). Long-tongued *Bombus* species visited plants of the family Fabaceae to a greater extent than short-tongued species did. This is in accordance with previous studies where long-tongued species prefer plant species with longer corolla (Harder 1985, Teräs 1985, Graham & Jones 1996). As noted by Carvell (2002), it was found that not all *Bombus* species were constrained by their tongue-lengths, most likely because of the known behaviour of short-tongued species as *B. lucorum* and *B. terrestris* to 'rob' nectar from plants with long corolla (Alford 1975, Teräs 1985). All of the 19 most visited plant species were perennials and it has been shown in several studies that bumblebees prefer perennials above annual species, probably because they are more stable in time and space than annuals and divert more resources into attracting pollinators (Fussel & Corbet 1992, Dramstad & Fry 1995).

Some plant species, like *S. tinctoria* and *C. jacea,* received a high percentage of visits and showed a correlation with certain *Bombus* species. This means that the plant species were most numerous at the same time as the bumblebees were and that they were used to a great extent. There was, however, no clear relation between plant occurrence and *Bombus* visits. When plant species that had a strong correlation with a particular *Bombus* species received few or no visits from that species, it meant that those plant species had available resources that were not used as forage. It is known that not all plant species available during the season are used as food sources (Alford 1975). However, when plant species that received a high percentage of visits from a certain *Bombus* species did not have any significant correlation with that species, it is most likely because the plant species were used at another part of the season than when the bumblebees or plant species were as most abundant. It may also be because the plant species were abundant the whole bumblebee season and therefore had no correlation with the occurrence of bumblebees. In any case, those plant species must still be considered important food sources despite lack of correlation because of the high percentage of visits they received.

Serratula tinctoria and *C. vulgare* were the plant species that had the highest proportions of visits, followed by *C. jacea, K. arvensis* and *S. pratensis.* These plant species were all found in relatively low numbers, and when plant species with low abundance receives many visits it can be assumed that the species is important as a food source or effectively attracts pollinators (Teräs 1985). *Trifolium repens* and *L. pratensis* had overall the lowest proportions of visits, but generally all plant species with a high number of observed flowers were used to a small proportion. This is likely because the high plant abundance makes it difficult for bumblebees to visit more than a small fraction of the plants even though they receive a high percentage of visits.

5.3 Detecting changes in abundance by monitoring

In order to detect changes in abundance by monitoring, it is important to know the appropriate number of sites that must be sampled as well as when and how often inventories must be carried out. The probability of detecting a certain change in abundance of *B. pascuorum* (the most numerous species in this study), with one visit per year and 785 sites, was greatest when that visit occurred at the beginning of the summer. In that case a 30% change in abundance could be detected with a probability of approximately 0.8. This is because bumblebee abundance was rather stable during the first part of the summer before reaching a peak in the beginning of August and the variation is therefore small. This results in a larger probability of discovering changes in abundance than if the visit occurred at the end or at any time during the summer, in which case it was only possible to detect a 40% respectively 50% change.

Varying the number of visits per season had little effect on the probability of detecting a 50% change in abundance. When visiting the sites one time during the season the probability was 0.81 that a 50% change in abundance was detected; with three visits the probability went up to 0.87; with ten visits to 0.89 and with 30 visits the probability was 0.90. This is because the number of bumblebees was rather stable at the beginning of the summer, on which these calculations were based, and more visits each season therefore does not result in a substantially better probability of detecting changes.

The probability of detecting a certain change in bumblebee abundance varied with the number of sites visited each season, with more sites resulting in a higher probability. In *B. pascuorum,* approximately 300 sites were needed in order to detect a 50% change in abundance with a probability of 0.8. If instead 200 sites were used, the probability went down to 0.6 and if only 100 were to be monitored the probability was 0.4. These results point out the need for large-scale monitoring, with a great number of visited sites, if significant changes in bumblebee abundance are to be detected.

The numbers of sites necessary to detect a 50% change in abundance with a probability of 0.8 varied between *Bombus* species and at what time the single visit occurred. As in Glimskär et al. (2005) changes in the most common species were easier to detect than changes in less common species. For most species, visiting the sites the first part of the summer resulted in fewer sites needed. *Bombus hortorum* however, required fewer sites if the visit was to occur in the last part of the summer. This was because at the beginning of the summer, only a small fraction of the observations made of *B. hortorum* occurred. The species that required least number of sites, as long as the visit occurred at the beginning of the summer, were *B. pascuorum* with 295 sites; *B. ruderarius* with 640 sites; *B. terrestris/B. lucorum* with 900 sites and *B. sylvarum* with 940 sites. This is because species with a high abundance or low variation between sites or visits require lower number of sites for a change in abundance to be detected. These species, except for *B. terrestris/B. lucorum,* were the most numerous in this part of the summer and *B. terrestris/B. lucorum* had a relative low variation between visited sites.

In order to detect a change of 50% in the number of observed species with a probability of 0.8, only few sites are needed. This was because both the variation between sites and between visits was low when it came to species abundance. Only 15 sites were needed if the visit occurred at the beginning of the summer and 90 if the visit was at the end of the summer. However, the number of species was higher at the end of the summer, so in order to examine species-richness, monitoring at that time would still be preferred.

It must be pointed out, however, that the above calculations are based on the assumption that the samples are drawn from an infinite region. This means that the results are applicable on very large populations only, for example at national level. For inventories at local levels, where the total number of sites are known, not all sites must be visited to detect a difference in abundance, but a finite population correction factor ((N-n)/N, where N is the total number of sites and n is the number of sampled sites) can be multiplied with the variance term of the in-between site variance to calculate the total number of samples needed.

The correlation between the number of observations at time 1 and 2 in the different sites is another important factor in power analyses that affect the number of sites that need to be monitored. Because this study was conducted during one year only, the same correlation (ρ=0.5) between years as in the study by Glimskär et al. (2005) was used in the calculations. If the correlation is in fact much stronger than that, considerably fewer sites will have to be monitored in order to detect a significant change in abundance.

5.4 Conclusions

The most bumblebee-rich landscape elements in this study were pastures, wood verges and field verges, where 70% of all observations were made. These sites contained the highest amount of flowering plant species and number of plants as well as a large proportion of the plant species most preferred by bumblebees. If these landscape elements disappeared due to agricultural intensification it would have serious implications on the bumblebee abundance in this area. These landscape elements alone are, however, not enough to support viable bumblebee populations. The results of this study point out the importance of a diverse landscape with different landscape elements, because bumblebee species prefer different landscape elements and all species showed a clear seasonal variation in habitat preferences. Therefore it is important to preserve and protect even less bumblebee-rich landscape elements, like road verges and leys.

Monitoring is important in order to evaluate the condition of a certain area in terms of species occurrence, species-richness and changes in abundance. This study has shown that bumblebees can forage under poor weather conditions and that they have clear preferences in terms of forage plants and habitat requirements which facilitate monitoring. In order to detect a significant change in abundance, large-scale monitoring with many visited sites is needed. To detect a 50% change in abundance of *B. pascuorum*, the most common species, 295 sites must be monitored. It is recommended that the visit each season is carried out at the beginning of the summer due to lower variation earlier in the season.

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