Foraging and Nesting Ecology of Bumblebees *(Bombus Spp.)* in Agricultural Landscapes in Sweden

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Abstract

Svensson, B. 2002. *Foraging and nesting ecology of bumblebees (Bombus spp.) in agricultural landscapes in Sweden.* Doctoral thesis.
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The aim of the thesis was to investigate in what way different agricultural landscapes and management routines affect the abundance and performance of bumblebees. The studies were conducted in the surroundings of Uppsala, in mid Sweden. The area consists of both intensive, large-scale farming and small agricultural fields surrounded by pastures, forests and lots of boundaries. Both the local habitat type and the amount of forest in the surrounding agricultural landscape affected bumblebee queens searching for nesting sites.

Boundaries, together with other uncultivated areas, showed the highest densities of nest-seeking queens. Different bumblebee species chose nesting sites in different habitats. Few of the available plant species were used as foraging source for the bumblebees. The highest frequency of foraging bumblebees was found in clearings, road boundaries and pastures. There was a negative correlation between the number of nest-seeking bumblebees in spring in a habitat and the number of foraging bumblebees there the following summer. The most frequently visited plant species for bumblebees in general were preferred by all observed bumblebee species. Differences "castes" were found to prefer different plants.

Two declining bumblebee species in the agricultural landscape, *Bombus sylvarum* and *B. subterraneus*, both forage on plant species preferably growing in boundary habitats. For prevalence of these species, such habitats have to be conserved in the modern agricultural landscape. A greater abundance of foraging bumblebee queens in spring was estimated in areas with a high volume of *Salix caprea* per ha (>1000 m^3 crown volume). In areas with low volumes of *S. caprea* per ha (<100 m^3), there is higher competition for food resources. Thus, it is recommended that even small willows, which can have high flowering percentage, be preserved in the agricultural landscape. Plantations of short-rotation energy forests can also be used by bumblebees as a complementary foraging source.

Trees and juniper shrubs (*Juniperus communis*) have a positive effect on the species richness of foraging bumblebees within semi-natural pastures and the proportion of arable fields and urban elements per km^2 surrounding area affected the bumblebee community structure positively. Bumblebees and butterflies were negatively affected by increasing grazing pressure. These results led to a recommendation to conserve management heterogeneity, *i.e.* grazing pressure and tree and shrub layer, within the semi-natural pastures.

Key words: bumblebees, *Bombus*, nesting sites, foraging, willows, *Salix caprea*, habitat selection, agricultural landscape, semi-natural pastures, heterogeneity, Sweden.

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Contents

Appendix

Papers I-VI

This thesis is based on the following papers, which will be referred to in the text by the corresponding Roman numerals:

I. Svensson, B., Lagerlöf, J. and Svensson, B. G. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. *Agriculture, ecosystems & environment 77*, 247-255.

II. Svensson, B. Foraging preferences of bumblebees (Hymenoptera: Apidae) in a diverse agricultural landscape. Manuscript.

III. Svensson, B. Do bumblebees (Hymenoptera: Apidae) use the same plant species, regardless of species or caste? Manuscript.

IV. Svensson, B. The willow, Salix caprea L. - a key stone species for bumblebees (*Bombus* spp.). Submitted manuscript.

V. Söderström, B., Svensson, B., Vessby, K. & Glimskär, A. 2002. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation 10 (11)*, 1839-1863.

VI. Vessby, K., Söderström, B., Glimskär, A. & Svensson, B. 2002. Species richness correlations of six different taxa in Swedish semi-natural grasslands. *Conservation Biology*, in press.

Introduction

Swedish agricultural landscape

The Swedish agricultural landscape has changed radically during the past fifty years. Since 1980, the number of farming units has decreased by almost one third (Statistics Sweden, 2000). Farming practice has changed to being dominated by larger farming units with a concentration on cereal production on large fields, use of pesticides and monocultures. Many minor habitats like ditches, field islands and different types of boundaries have disappeared. In addition, the number of cattle has declined by one third since the 1930s (Statistics Sweden, 1990). As a consequence, the number of semi-natural pastures has decreased by one half between 1920 and 1989.

Basic ecology of bumblebees

Bumblebees (*Bombus* spp.) belong to the social insects (Hymenoptera, Apidae). Only inseminated females (queens) overwinter to the following season (Heinrich, 1979). Depending on species and location, they spend about seven to eight months hibernating in a cavity, mostly underground (Alford, 1975). In central Sweden, the queens emerge from hibernation in April and May and start foraging and searching for a suitable place to build a nest. Competition for suitable nesting sites can sometimes be so intense that one of the fighting queens dies (Heinrich, 1979).

When a queen succeeds in finding a nesting site, she starts to collect pollen and nectar, and on the pollen brood she deposits the first brood of eggs. She keeps the brood warm with her body until the first workers are hatched (Heinrich, 1979). The workers help the queen to collect pollen and nectar that are stored in wax pots in the nest. The food is primarily intended for the larvae, but is also eaten by adults during periods of bad weather. After two or three broods of workers are produced, the queen does not leave the nest. Her only mission is to produce eggs (Heinrich, 1979). Towards the end of the summer, the new reproductive generation of males and queens are hatched and the old queen dies. Males and new queens mate outside the nest, usually in the air (Svensson, 1979). Shortly thereafter, males and workers die and the new queens seek out a place for hibernation.

A number of cleptoparasitic bumblebee species, cuckoo bumblebees (in the past *Psithyrus* spp., now *Bombus* spp.), invade the nests of bumblebees. Queens of these species lay their eggs in their host's egg chambers and the host's workers feed the larvae as their own. Only queens and males are hatched from the eggs of cuckoo bumblebees (Heinrich, 1979).

Bumblebees are vital for agriculture and conservation because they pollinate crops, fruit trees and wildflowers. However, for bumblebees to be effective they must have local access to suitable nesting and hibernation sites, as well as to alternative good food sources (*i.e.* wildflowers) during periods when crop plants are not in flower (Fridén, 1967; Fussell & Corbet, 1992a).

The distinction between castes (queens, workers and males) is important for a proper understanding of the occurrence and activities of bumblebees and their use of resources over time and species (Svensson & Lundberg, 1977).

Nesting sites

A majority of the bumblebee species found in Sweden have their nests under ground, in cavities or abandoned nests of small mammals (Løken, 1973; Svensson & Lundberg, 1977; Harder, 1986). Some species always or often have their nests above ground (*e.g. B. hypnorum* and *B. lucorum*) or on the surface of the ground (*e.g. B. pascuorum* and *B. pratorum*; Løken, 1973; Svensson & Lundberg, 1977). Bumblebee queens searching for a nesting site characteristically fly in a zigzag pattern close to the ground within a small area, occasionally going down to investigate the ground surface (Lundberg & Svensson, 1975). This behaviour can be used to predict preferred nesting sites (Skovgaard, 1936; Richards, 1973; Svensson & Lundberg, 1977).

Foraging sources

Bumblebees are totally dependent on the availability of nectar and pollen resources. They have a long flight season with the production of many individuals, and thus depend on a continuous food supply (Prys-Jones & Corbet, 1991). In early spring, willows (*i.e. Salix caprea* L.) are almost the only food supply for the first emerging bumblebee species (Vatchev, 1996). After hibernation, the queens need nectar to get energy. Then they must have access to large amounts of protein-rich pollen in order to develop their ovaries for egg production (Heinrich, 1979). Willows are dioecious, thus, females produce nectar and males provide both nectar and pollen (Elmqvist *et al.*, 1988). Willows are, therefore, of great value to the bumblebees.

Perennial herbs are important foraging sources for bumblebees throughout the foraging season (Fussell & Corbet, 1991; Dramstad & Fry, 1995). Such plants are found particularly in uncultivated areas, such as boundaries, small field islands and pastures, all of which are becoming less common in the modern agricultural landscape (Banaszak, 1992).

Species composition

In Sweden, 30 species of bumblebees (*Bombus* spp.) and 9 species of cuckoo bumblebees (past *Psithyrus* spp., now *Bombus* spp.) have been recorded (Janzon *et al.*, 1991). In central Sweden 14 species of bumblebees can be found, according to Løken (1973). The different bumblebee species generally can be identified in the field by their colour, size and sound.

The tongue length (or the length of proboscis) also differs between the species (Pekkarinen 1979). Bumblebees are often divided into short-tongued (*e.g. B. lucorum* and *B. terrestris*) and long-tongued (*e.g. B. hortorum* and *B. subterraneus*). Depending on their tongue length, they can use flowers with different depths of corolla. Some of the short-tongued species (*e.g. B. terrestris*) use to rob nectar from flowers with deep corolla (*e.g. Trifolium pratense*). This behaviour does not leads to pollination of the flower.

Bumblebee queens, workers and males

The queen is the largest individual in the bumblebee colony. The proboscis lengths of queens of the species represented in the present papers are between 8.5 mm (*B. lucorum*) and 14.6 mm (*B. hortorum*; Pekkarinen, 1979). The number of workers (*i.e.* the colony size) varies between different bumblebee species. The body size of the workers hatched within a colony increases during the season. Compared to the queen, the workers of the first brood are much smaller while those of the last brood are almost equal in size. At the end of the colony season, queens and workers often come into conflict and workers try to lay their own, unfertilised, eggs, which develop to males. The new queens are allowed to remain in the colony for a while, helping in the nest and sometimes foraging (Heinrich, 1979).

Male individuals, unlike females, do not collect any food for the benefit of the colony. Soon after they are hatched, the males leave the colony and never come back. Instead, they start searching for an area where they, with help of pheromones, can mark out a route to which they attract the new queens. These routes are often placed in wooded areas. The vertical placing of the routes differ from species to species (Svensson, 1979). Males are intermediate between queens and workers in body size. Their colour pattern and some morphological details (e.g. absence of pollen-collecting hairs) differ from that of female individuals in most of the species studied (*cf.* Løken, 1973).

Boundaries in the agricultural landscape

Field margins, roadsides and forest edges are examples of boundaries occurring in the agricultural landscape. During the modernisation of agriculture, covered drains have replaced a lot of open ditches between crop fields. The remaining ditches and field margins serve as a valuable refuge for many different organism groups (Mineau & McLaughlin, 1996) *e.g.* pollinating insects (*e.g.* Lagerlöf *et al.*, 1992), arthropods (*e.g.* Dennis & Fry, 1992; Lagerlöf & Wallin, 1993) and plants (*e.g.* Fischer & Milberg, 1997).

Roadsides can harbour many plant species that were common in the widespread meadows of the past (Persson, 1995). Forest edges have many ecological functions (Fry, G. & Sarlöv-Herlin, I, 1997). For example, they are important habitats for a lot of animals, *e.g.* birds (Söderström, 1999) and beetles (Dennis et al., 1994).

Semi-natural pastures

Swedish semi-natural pastures are very heterogeneous and have sometimes been managed for centuries (Swedish Environmental Protection Agency, 1997). With a decreasing number of cattle on the farms, this kind of habitat has drastically declined during the last decades. In addition, the increasing use of artificial fertilisers even in pastures leads to decreasing richness in plant species. Many of the plant and animal species on the Swedish Red data list depend on semi-natural pastures (Gärdenfors, 2000).

Aims of the thesis

The aim of the thesis was to investigate in what way different agricultural landscapes and management routines affect the abundance and performance of bumblebees in Sweden. The following questions were asked (each numeral refers to the corresponding paper I-VI):

I. How are bumblebee queens affected by landscape type and habitat when searching for a nesting site?

II. Which are the most frequently visited plant species in the agricultural landscape in the summer? Are foraging bumblebees distributed in different habitat types? Do habitats used for nesting sites and foraging correlate?

III. Do bumblebees use the same plant species regardless of their species or caste?

IV. How is the abundance of bumblebee queens in the agricultural landscape in spring affected by the abundance of willows (*Salix caprea*)?

V. Is the species richness and abundance of bumblebees in semi-natural pastures affected by habitat variables within the pastures and the surrounding agricultural landscape?

VI. Is the number of bumblebee species in semi-natural pastures correlated with the species richness of other groups of organisms? How does grazing pressure in the pastures affect the number of bumblebee species?

Papers I, II and III: Nest-seeking and foraging

Material and Methods

These studies were conducted in a 30-km^2 area about 20 km southeast of Uppsala, Sweden (59°51´N, 17°41´E). The area consists of both intensive, large-scale farming and small agricultural fields surrounded by pastures, forests and lots of boundaries.

In these studies the transect method ("belt method" Banaszak, 1980) were used to count the number of bumblebees (*Bombus* spp.). Twelve transects, each with a length of 500 metres, were randomly placed in different types of agricultural landscapes. The landscape types were classified according to the percentage of forest in a one km^2 square surrounding the centred transect. The classifications used were open landscape (with < 15% forest per km^2), relatively open landscape (15-50% forest), relatively wooded landscape (50-85% forest) and wooded landscape (with > 85% forest per km^2).

Within each of the twelve transects, different habitats were intermingled. In total, eight habitats were included in the present studies. Of these, three were different types of boundaries (*i.e.* field margins, roadsides and forest edges). The other investigated habitats (*i.e.* fields, pastures, open uncultivated areas, clearings and forests) represented connected areas in the agricultural landscape. Concerning the crops on the studied fields, none of the transects included rape or clover fields. Walking speed during a transect inspection was 20 metres per minute. Transect walks were done twice a week. No inspections were made in rainy weather.

The statistical analysis was performed using SAS® (1996). All tests for significant differences were conducted in the GLM procedure. Correlation analyses were performed with Pearson's correlation test in the CORR procedure. To analyse differences among species and castes, Principal Component Analysis (PCA) was used (Paper III).

Some of the comparisons needed compensation for the difference in length between landscape types and habitats. Therefore, the number of bumblebee observations was transformed to a "number of observations per 100 metres"-value. All data were log10(x+1) transformed prior to the analysis in order to transform the residuals into a normal distribution. In all analyses, the least significant values were * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Paper I

Bumblebee nests are difficult to find in numbers large enough to allow statistical analysis. Therefore, queens performing nest-seeking behaviour were used as an indication of their relative preference for nesting in a certain area. The study was carried out during April to June 1991. All bumblebees observed within 5 metres on either side of a transect were noted. At each observation event the bumblebee species, the habitat type and the characteristics of the environment adjoining the nest-seeking area were recorded. Eight bumblebee species were noted in this study: *B. lucorum* L., *B. terrestris* L., *B. pratorum* L., *B. pascuorum* Scop., *B. lapidarius* L., *B. sylvarum* L., *B. subterraneus* L. and *B. hortorum* L. The investigation time of day varied randomly between 0900 and 1900 hours (Swedish Summer Time; GMT +one hour).

Papers II and III

These studies were carried out during July to September 1991. All foraging bumblebees observed within one metre on either side of the transect were recorded. In addition, bumblebee species, bumblebee caste, plant species visited and habitat type for each observation was noted. Nine bumblebee species were recorded in these studies: *B. lucorum* L., *B. terrestris* L., *B. pratorum* L., *B. pascuorum* Scop., *B. lapidarius* L., *B. sylvarum* L., *B. subterraneus* L., *B. hortorum* L. and *B. hypnorum* L. Within most of these species, four bumblebee castes were represented: queens, workers, males and new queens. The investigation time of day varied randomly between 1000 and 1800 hours (Swedish Summer Time; GMT +one hour).

Results

Paper I

A significant difference concerning the number of nest-seeking bumblebee queens was found between the four studied landscape types ($P < 0.05$, $n = 12$). A majority of the 147 queens in this study were recorded in a relatively open landscape (with 15-50% forest per km^2). Also between the studied habitats, a significant difference concerning nest-seeking queens was found ($P < 0,01$, $n=96$). The habitat with most bumblebee observations (independent of landscape type) was forest boundary, followed by open uncultivated area and field boundary. In forest, no nest-seeking bumblebees were observed and in clearings the number of observations were few. In each of the three types of boundaries represented, both the number of observations and the species richness were higher than in any of the connected areas (except for the open, uncultivated area).

The bumblebee species recorded could be divided into those which prefer open areas (*i.e. B. terrestris*, *B. lapidarius*, *B. sylvarum* and *B. subterraneus*) and those which prefer wooded areas (*B. lucorum* and *B. pascuorum*) when searching for a nesting site. The number of observed *B. pratorum* and *B. hortorum* was too low to be used in the analysis. For all species observed, the amount of withered grass and tussocks were crucial for where the queens were nest seeking.

Paper II

Bumblebees were observed foraging on 48% of the 126 potentially insect-pollinated, flowering plant species recorded. Half of the visited plant species had less than ten visits. A majority (64%) of the 2 610 observed bumblebee visits were performed on the following eight plant species: *Calluna vulgaris*, *Carduus crispus*, *Trifolium pratense*, *Trifolium medium*, *Vicia cracca*, *Centaurea jacea*, *Cirsium arvense* and *Succisa pratensis*. A couple of plant species with patchy occurrence (*i.e.* *Lythrum salicaria*, *Epilobium hirsutum*, *Medicago sativa*, *Lamium album*, *Trifolium repens*, *Melampyrum pratense* and *Trifolium hybridum*) had, after compensation by counting an obs/transect value, also high frequency of foraging bumblebees.

Among the investigated habitats in this study, pasture, open uncultivated area and clearings had the highest plant species richness (*i.e.* potentially insect-pollinated, flowering plant species). The number of foraging bumblebees differed significantly between the habitats ($P < 0.01$, $n = 96$) and the highest number of bumblebees was found in clearings and on the road boundary. Habitats with a high frequency of nest-seeking bumblebee queens (Paper I) were negatively correlated with habitats used by foraging bumblebees ($n = 6$, $r = -0.86$**).

Paper III

The bumblebee species *B. lucorum* and *B. terrestris* were treated as one species in this study, since there are difficulties in distinguishing between workers in the field. In addition, the number of observed *B. hypnorum* was too low to be used in the analysis. Generally, a majority of the records within each bumblebee species were observed foraging on about ten plant species (*i.e.* 7-11 species).

More than half of the number of bumblebees within each species were foraging on the plant species *Calluna vulgaris*, *Carduus crispus*, *Trifolium pratense*, *Trifolium medium*, *Vicia cracca*, *Centaurea jacea*, *Cirsium arvense* and *Succisa pratensis*. No significant difference among the bumblebee species in their choice between these plants was found ($F_{5, 18} = 1.48$ n.s.). A couple of other plant species were more frequently visited by some bumblebee species than by others: *Filipendula ulmaria* and *Campanula rotundifolia* (mostly visited by *B. lucorum* / *B. terrestris*), *Cirsium palustre* and *Melampyrum pratense* (*B. pratorum*), *Trifolium hybridum* (*B. pascuorum*), *Sonchus arvensis* (*B. lapidarius*), *Medicago sativa* (*B. sylvarum*) and *Galeopsis speciosa* (*B. hortorum*).

A significant difference was found between the number of foraging visits by the bumblebee castes to the plant species *C. vulgaris*, *C. crispus*, *T. pratense*, *T. medium*, *V. cracca*, *C. jacea*, *C. arvense* and *S. pratensis* ($F_{3, 20} = 9.18$***). Foraging males were more often found on thistles and *C. vulgaris*, while queens (both old and new) foraged on clover.

The bumblebee species *B. sylvarum* (documented as declining in Europe) was represented mainly by workers in this study. The plant species *V. cracca*, *T. pratense* and *L. pratensis* account for 43% of the observed foraging visits of this bumblebee species. These three plant species are all typically found in boundaries in the agricultural landscape. Thus it can be concluded that such habitats have to be conserved for the prevalence of *B. sylvarum*.

Paper IV: Importance of willows

Material and Methods

This study was carried out in a 2400 km^2 area in the surroundings of Viksta, about 35 km north of Uppsala, Sweden (60°05´N, 17°40´E). The area consists of both large-scale agriculture and smaller, habitat-diverse farming units with lots of pastures, forests and boundaries.

During the period April 27th to May 6th 2001, the influence of willow (*i.e. Salix caprea* L.) abundance, sex ratio, crown volume, flowering intensity and growing habitat on foraging bumblebees (*Bombus* spp.) was investigated. Forty willows were used in the comparison between male and female *S. caprea*. For the comparison between areas with high and low abundance of willows, six willows which could not be used in the male-female study were added. To investigate the importance of crown volume, flowering intensity and growing habitat to the visiting rate of foraging bumblebees, all 46 willow individuals were used.

The flowering intensity was counted as the number of catkins per dm^3 leaf-holding crown. Flowering percentage approximated the amount of the crown volume that was flowering. The crown volume of the individual *S. caprea* was estimated in cubic metres (m^3). Willows in three types of boundary habitats were studied: field margin, roadside and forest edge.

In the abundance study, female individuals from 12 of the *S. caprea* pairs were used together with the six single willows. All *S. caprea* individuals in a one ha circular area surrounding the centred focal willow were recorded and the number, crown volume and sex of each individual were noted.

Four field plantations with short-rotation energy forest (*S. viminalis*) were compared with the *S. caprea* concerning abundance of foraging bumblebees. A twelve cubic metres (m^3) plot of each plantation was used as study area.

The recording of bumblebee foraging visits started as soon as the first bumblebee queen had been observed in the study area. Bumblebee visits on each of the studied willows (and plots) were recorded during five minutes on five different days. Investigation time of day was randomised between 0800 and 2000 hours.

Five bumblebee species were represented in this study: *B. lucorum* L., *B. terrestris* L., *B. hypnorum* L., *B. pratorum* L. and *B. sylvarum* L. The flowering of *S. caprea* was almost over when the study was finished.

The statistical analysis was performed using SAS® (1996). All tests for significant differences were conducted in the GLM procedure. Correlation analyses were performed with Pearson's correlation test in the CORR procedure. Some of the comparisons needed compensation for the difference in volume. Therefore, the number of bumblebee observations was transformed to a "number of observations per m^3"-value. All data were log10(x+1) transformed prior to the analysis in order to transform the residuals into a normal distribution. In all analysis, the least significant value were * $P < 0.05$, ** $P < 0.01$ and *** $P<0.001$.

Results

In the comparison between male and female willows, the recorded bumblebee visits were not significantly different between the sexes. This was also the case when comparing clones of energy forests. No differences between the sexes of *S. caprea* were found concerning their flowering or volume. The sex ratio of the willows in the surrounding areas had a female bias (80% were females; 20 males/80 females).

Flowering percentage, but not the crown volume, affected the number of foraging bumblebees per m^3 of willow crown (n = 18, r = 0.52* and r = 0.17 n.s., respectively).
The volume of the focal willows and also the number of bumblebee visits per m^3 leaf-holding crown differed significantly between willows growing in different types of boundary habitats ($F_{2, 43} = 21.96$*** and $F_{2, 15} = 4.13$*, respectively). Willows in forest boundaries were larger and had the lowest number of bumblebee visits per volume unit.

Willows with high crown volume were correlated with high total volume of surrounding *S. caprea* (n = 18, r = 0.58*). The total crown volume of the surrounding *S. caprea* affected the number of bumblebee visits per m^3 on the focal willow (n = 18, r = – 0.76***). Individual willows surrounded by < 100 m^3 *S. caprea* per ha had the highest densities of foraging bumblebees per volume unit. Small willows (< 10 m^3 leaf-holding crown) in the surrounding area also led to a higher number of visits on the studied individual.

The investigated plots of energy forest had more visits per m^3 than all other compared groups, except the studied willows surrounded by < 100 m^3 *S. caprea.*
On the landscape level, a higher abundance of bumblebees were estimated in areas with a high total volume of willows (> 1000 m^3) per ha. Hence, the amount of willows seems to regulate bumblebee abundance.

Paper V and VI: Semi-natural pastures

Material and methods

These studies were conducted in 31 semi-natural pastures in the agricultural landscape surrounding Uppsala, Sweden (59°52′N, 17°39′E). The selected pastures were representative for the region with regard to the proportion of trees and shrubs within the pasture as well as the proportion of arable fields and forest in the landscape surrounding the pasture.

During the months of July 1996 and 1997, the number of bumblebees (*Bombus* spp.) were counted using the transect method ("belt method" Banaszak, 1980). One 400-metre transect, formed as a 100 m x 100 m square, was placed in a representative part of each pasture. All bumblebees observed within one metre on either side of the transect were counted and determined to species and visited plant species, and the location on the transect were noted.

Nine bumblebee (*Bombus* spp.) species were recorded in these studies: *B. lucorum* L., *B. terrestris* L., *B. pratorum* L., *B. pascuorum* Scop., *B. lapidarius* L., *B. sylvarum* L., *B. subterraneus* L., *B. hortorum* L. and *B. hypnorum* L. In addition, three species of cuckoo bumblebees (previously named *Psithyrus* spp., now *Bombus* spp.) were observed: *B. barbutellus*, *B. bohemicus* and *B. rupestris*.

The pastures were visited on the same day and the investigation time of day varied randomly between 0900 and 1900 hours (Swedish Summer Time; GMT +one hour). Walking speed during a transect inspection was 20 metres per minute. Transect walks were done three to four times a week. No inspections were made in rainy weather.

Paper V

Within each pasture, a "tree cover"-value was calculated. Using maps and during field visits, the proportion of the pasture area covered by single trees or tree groups was recorded. In addition, the volume of juniper shrubs (*Juniperus communis*) and thorny shrubs (*i.e. Prunus spinosa* and *Rosa* spp.) per ha were calculated. The proportion of fields (*vs.* forest), pastures and urban elements were recorded in a one km^2 square surrounding the centred pasture.

Partial correlations were used to examine the effects of tree cover, shrub volume and surrounding landscape composition on species richness. To examine the effects on community structure, partial canonical correspondence analysis (CCA) on abundance data were used.

The statistical analyses were performed using SPSS 6.1 (Norusis, 1994) and Canoco for Windows 4.0 (ter Braak and Smilauer, 1998). Species richness, abundance and non-proportional independent variables were log10(x+1) transformed prior to analyses. Proportional variables were arcsine transformed in order to transform the residuals into a normal distribution.

Paper VI

The species richness of six groups of organisms (taxa) was studied concerning covariation. Apart from bumblebees, the species richness of plants, birds, butterflies, dung beetles (*Scarabaeoidae*) and ground beetles were recorded.

Within each pasture, grass height (reflecting grazing pressure) was estimated visually during the last week of June. In a grid of one-ha quadrates covering the entire pasture, the proportion of the open area where the height of the grass was <5 cm was recorded.

Pearson correlation analysis was used to test covariation between species richness of different taxa. To investigate patterns of species composition among taxa, the Mantel test (PC-ORD for Windows 3.19, McCune & Mefford, 1997) was used. Multiple linear regression was used to analyse associations between species richness and grass height.

The statistical analyses were performed using SPSS 6.1 (Norusis, 1994). Species richness and non-proportional independent variables were log10(x+1) transformed prior to analyses. Proportional variables were arcsine transformed in order to transform the residuals into a normal distribution.

Results

Paper V

Bumblebee species richness was positively correlated with both the tree cover and the volume of juniper shrubs in the investigated pastures (n = 31, r = 0.29* and r=0.31*, respectively). No correlation was found between bumblebee species richness and the volume of thorny shrubs.

Also the community structure (species diversity and total abundance of bumblebees) was positively correlated with tree cover in the pastures (CCA-analysis; n = 31, r = 59*) while the volume of shrubs was not correlated with the community structure of bumblebees. At the landscape level, the proportion of arable fields and urban elements per km^2 were positively correlated with the community structure (CCA-analysis; n = 31, r=94*** and r=90***, respectively). The proportion of pastures per km^2 showed no significant correlation with the community structure of bumblebees.

In this study, local habitat quality seems to have stronger effects on species richness than the composition of habitats in the surrounding landscape. In contrast to species richness, the community structure of bumblebees in semi-natural pastures seems to differ in relation to the structure of the surrounding agricultural landscape.

Paper VI

In this study, bumblebee species richness was positively correlated only with species richness of butterflies, both with the total number of species of butterflies and the number of grassland species ($n = 31$, $r = 0.52$* and $r=0.49$*, respectively). No correlation between species richness of bumblebees and plants were found. The species richness of bumblebees (as of butterflies) was negatively influenced by increasing grazing pressure in the pastures ($n = 31$, $r = - 0.36$*). In addition, species composition between bumblebees and butterflies in the pastures showed a significant relationship (Mantel test; $n = 31$, $r = 2.19$*). For example, the occurrence of several butterfly (e.g. *Lycaena hippothoe*, *Lasiommata maera*, *Issoria lathonia*) and bumble bee (*B. pratorum*, *B. lapidarius*) species was negatively associated with grass height in semi-natural pastures.

General discussion

Bumblebee abundance and species richness

The number of bumblebee species (*Bombus* spp.) is relatively constant throughout the continent of Europe (Pekkarinen, 1984). Eight (Paper I) to nine (Papers II, III, V and VI) bumblebee species were recorded in the agricultural landscapes studied in this thesis. Compared with early studies in Scandinavia, this number is low. Løken (1973) reported 14 species in central Sweden. In Denmark, 13 species have been recorded in agricultural landscapes (Skovgaard, 1936) and in Finland, ten to twelve species were recorded fifteen years ago (Ranta & Tiainen, 1982; Teräs, 1985).

Several authors have reported on a decline of several bumblebee species in Scandinavia (Dramstad & Fry, 1995; Saville et al., 1997; Cederberg, 1999; Calabuig, 2000; Pekkarinen et al., 2001), in other European countries (Williams, 1986; Banaszak, 1992; Carvell, 2002) and in North America (Allen-Wardell et al., 1998).

Five bumblebee species are found on the Swedish Red data list (Gärdenfors, 2000). One of these species, *Bombus subterraneus*, is relatively often observed in the open agricultural landscape surrounding Uppsala. This species is rare or not recorded in several European countries (Walther-Hellwig & Frankl, 2000b). *Bombus sylvarum* is another species that has been reported as declining during the past years in many European countries (Pekkarinen et al., 2001; Carvell, 2002), but it is quite abundant in the investigated agricultural landscape.

In the present studies, species specific differences concerning nesting site characteristics, nesting sites habitats and landscape types were found (Paper I). Bumblebee species richness in pastures was affected by the amount of trees and shrubs (Paper V), but species richness in the agricultural landscape could not be explained by plant species richness (Paper II, III and VI). Concerning plant species preferred as foraging sources, no differences between bumblebee species were found (Paper III). Since the preferred plant species occurred in different habitats, recording of foraging queens and workers is a less valuable indicator of the bumblebee species' distribution within the agricultural landscape. Instead, the best indicator is probably their nesting sites. In addition, males performing patrolling routes give valuable information about the distribution of the species (Svensson, 1980).

Characteristics of suitable nesting sites

All the species in the present study (Paper I) preferred nesting sites with a lot of withered grass and tussocks. These characteristics are typically found in uncultivated areas. Such areas are for example boundaries, which (together with the connected habitat type called "other uncultivated area") account for a majority of the observations of nest-seeking queens. Compared to the large number of studies concerning foraging of bumblebees, few studies have been made of bumblebee nesting site preferences. The preference of bumblebee queens for uncultivated areas is also documented in *e.g.* Skovgaard (1936), Løken (1973), Svensson & Lundberg (1977), Richards (1978), Harder (1986) and Fussell & Corbet (1992b).

Together with withered grass and tussocks, characteristics such as fresh grass, stones and moss were noted in patches where bumblebee queens performed nest-seeking behaviour. The amount of these characteristics varied between the species. Late-emerging species (*e.g. B. lapidarius* and *B. subterraneus*) often were nest-seeking in areas with a lot of fresh grass, which probably is a consequence of their late appearance. Species nesting on the surface of the ground (*e.g. B. pascuorum*) prefer nesting sites with moss, where they place the nest in a moss cavity (Skovgaard, 1936) or use moss as bedding material in the nest (Fussell & Corbet, 1992b).

Bombus subterraneus

This species was mostly found searching for nesting sites in open agricultural landscapes with less than 15% forest per km^2. No observations were made in areas with more than 50% forest. Also Reinig (1972) characterised this species as preferring an open terrain. In this open landscape, the connected uncultivated area seems to be the most valuable habitat as a nesting site for *B. subterraneus*. Also road boundaries and field boundaries are used, but not forest boundaries. Stones and moss were not present near their nesting site. These special demands are surely the major reason why this species is on the Swedish Red data list. In the open agriculture landscape of today, with modern intensively farmed fields, there is little place for large, connected, uncultivated areas and boundaries are scarce.

Bombus sylvarum

Agricultural landscape with a small amount of forest (15-50% per km^2) harbours (despite its species name (Skovgaard, 1936)), the largest amount of nest-seeking queens of this species. Both boundaries (roadsides and forest edges) and connected areas (*e.g.* pastures) were used as nesting sites. If this species is declining, as reported by several authors, one possible reason may be the loss of boundaries and pastures suitable as nesting habitats in the agricultural landscape.

Forage plant preferences

In general, bumblebees in the present studies (Paper II and III) used only a few of the plant species occurring in the agricultural landscape. The same behaviour (but not the same preferred specific plant species) has been observed by bumblebees in other Scandinavian countries (Ranta *et al.*, 1981; Dramstad & Fry, 1995; Bäckman & Tiainen, 2002). A majority of the preferred plant species are perennial, and probably used because of a higher amount of nectar in these plants (Fussell & Corbet, 1992a). Although the most visited plant species by bumblebees in separate studies differ, it can be concluded that bumblebees in general prefer species of *Trifolium*, different species of thistles, *Vicia cracca*, *Centaurea jacea*, *Melamphyrum pratense*, *Lythrum salicaria*, *Epilobium spp.*, *Medicago spp.*, *Galeopsis speciosa* and *Lamium album.*

Willows (*e.g. Salix caprea*) are valuable for all bumblebees which are active in the early spring (Paper IV). High flowering intensity (but not the crown volume) of the willow increased the number of bumblebee visits. It is of great value to preserve even small willows, especially in the modern agricultural landscape, since they can have high flowering intensity and also because all willows do not flower each year.

Bombus sylvarum and *B. subterraneus* have almost the same preference of usage of plants: *Lathyrus pratensis*, *Trifolium pratense* and *Vicia cracca* accounted for almost half of their foraging visits (Paper III). These plants grow preferably in boundary habitats and these habitats, therefore, need special attention and should be preserved in the open agricultural landscape.

Since the old "mother-queens" almost exclusively forage during spring and early summer, their foraging sources are somewhat different from the other castes in the colony. Queens have longer proboscises (Pekkarinen, 1979) and can, therefore, use some plant species (*e.g. Trifolium pratense* and *T. medium*) more efficiently than workers. Males forage for their own needs and use different plant species than the females, preferably thistles and *Calluna vulgaris*, which provide plenty of nectar.

Some weather conditions influenced the abundance of foraging bumblebees in the spring (Paper IV). Rising temperatures increased the number of bumblebee visits, as also was found by Comba (1999). Wind speed and light intensity did not influence the number of bumblebee visits in the present study.

Impact of landscape structure and habitat diversity

Boundaries in the modern agricultural landscape (*e.g.* field margins, roadsides and forest edges) are valuable for bumblebees because: 1) a majority of the nest-seeking queens were found here (indicating that these habitats are preferred as nesting sites; (Paper I)), 2) forest edges in particular harbour a great amount of willows (i.e. *Salix caprea*), a valuable foraging source in early spring (Paper IV), 3) they serve as refuges for a lot of the preferred bumblebee foraging plant species (Paper II) and 4) they serve as major foraging habitats for the declining species *B. subterraneus* and *B. sylvarum* (Paper III).

Semi-natural pastures, connected uncultivated areas and clearings (in early succession) are also important habitats for many of the preferred forage plant species. Uncultivated areas also serve as valuable habitats as bumblebee nesting sites.

Preferred foraging habitats (Paper II and III) were not identical with the habitats where bumblebee queens performed nest-seeking behaviour (Paper I). Bumblebees in general perform foraging at least 250-300 metres from their nest, even if there are suitable foraging sources quite near (*i.e.* 50 m) the nest (Dramstad, 1996; Osborne *et al.*, 1999). This gives a circular foraging area of about 28 ha (nest site centred). However, other studies have shown that some species (*i.e. B. muscorum*) are dependent on a close connection between the nesting and foraging habitat (Walther-Hellwig & Frankl, 2000a).

All together, these results lead to the conclusion that it is of great importance to study bumblebees on a landscape scale if we want to preserve a species rich bumblebee fauna in the agricultural landscape; *i.e.* to serve the species with nesting sites and foraging sources, but also mating habitats and hibernation places, according to their individual requirements. The structure of the surrounding landscape (*i.e.* the amount of forest per km^2) influenced the abundance of nest-seeking queens in the spring (Paper I) and also the species community (species diversity and total abundance) of foraging bumblebees in semi-natural pastures during summer (Paper V).

Banaszak (1992) suggests that the share of farmland should not exceed three-quarters of the total surface. The remaining part of the landscape should be made up of refuge habitats for wild bees: a mosaic structure of the landscape, consisting of meadows and residues of natural and semi-natural plant communities. A heterogeneous agricultural landscape will not only preserve bumblebees, but also other pollinating insects, as solitary bees (Calabuig, 2000) and butterflies (*e.g.* Weibull *et al.*, 2000).

Management of boundaries and semi-natural pastures

The management of both boundaries and semi-natural pastures influences the plant species diversity and community (*e.g.* Glimskär, 1999; Kleijn & Verbeek, 2000), and thus their value as foraging habitats for bumblebees. To preserve a species-rich flora, the vegetation needs to be mown regularly.

Cutting and removal of roadside vegetation leads to an increase in species richness (Parr & Way, 1988). In grass-dominated roadsides, the establishment of new plant species was increased when the habitat was mown (Milberg & Persson, 1994). But, on the other hand, if the habitats are harvested in an unsuitable period (*i.e.* at the peak of flowering) their value as foraging habitats for bumblebees is lost.

Sowing meadow plant species can increase species richness in field margins in intensively farmed areas. Most of the sown species can survive in field boundaries where annual mowing and taking away of the cuttings are the only measures taken (Bokenstrand *et al.*, in manuscript). Small areas with flowering plants can create highly positive effects on the abundance of pollinating insects in the intensively farmed agricultural landscape (Lagerlöf *et al.*, 1992).

The abundant use of pesticides and fertilisers is also responsible for the decreasing number of plant species in the agricultural landscape (and thus for the decrease in bumblebee fauna). For example, Pyretroides seems to have been responsible for the poisoning of honeybees in western Sweden (Stark, 1999).

Intensively grazed pastures (*e.g.* with a large number of grazing animals) are of minor importance as foraging habitats for bumblebees (and butterflies) as compared to pastures where the grass height is at least 5 cm (Paper VI). Calabuig (2000) found grasslands grazed by cattle to be the best for foraging bees. Cattle-grazed pastures are also necessary for other insect groups, e.g. dung beetles (Vessby, 2001). Also trees and shrubs in the semi-natural pasture increased the species richness of foraging bumblebees (Paper V), but only during the first steps in the succession. If there are too many trees and shrubs, the species richness declines.

A large amount of willows (*e.g. Salix caprea*) are needed in the agricultural landscape to provide foraging sources to the early emerging bumblebee species (Paper IV). An estimated value of >1000 m^3 crown volume per ha is preferred. This corresponds to about 2% of the estimated foraging area of 28 ha calculated on the basis of bumblebee foraging flights (Dramstad, 1996).

In addition to all these managed habitats, bumblebees preferred nesting sites located in uncultivated areas. These results point out the importance of preserving a heterogeneous agricultural landscape, not only as regards the number and location of different habitats, but also in the management of the habitats.

Investigation methods

In the studies presented in this thesis, the bumblebees were identified visually in the field. Since not only colouring, but also size and sound differ from species to species and the bumblebees were recorded from a short distance, no confusion with other, less common species (*e.g. B. soroeensis*, *B. jonellus*, *B. muscorum*) was likely to occur. If confusion occurred, it was to an extent that did not affected the main results in this thesis.

Weather and time parameters were recorded in all studies. Temperature and time of day influenced the number of bumblebee observations, but not wind speed and light intensity. Therefore, randomising the investigation time of day on the transect walks and investigating all study transects on the same day is important.

Conclusions

The thesis can be summarised by answering the questions asked in the Aims:

I. Both the local habitat type and the amount of forest in the surrounding agricultural landscape affected bumblebee queen's search for nesting sites. Boundaries, together with other uncultivated areas, showed the highest densities of nest-seeking queens and are, therefore, worth conserving in the modern agricultural landscape. Since the nesting sites of different bumblebee species varied, maintaining a habitat-diverse landscape is recommended in order to preserve a species-rich bumblebee fauna.

II. A very small number of the available plant species were used as foraging sources for the bumblebees. The preferred plant species (most of them perennial) were growing in different habitats. Semi-natural pastures and open uncultivated areas had the highest numbers of visited plant species. The highest frequency of foraging bumblebees was found in clearings, road boundaries and pastures. Habitats with the highest number of nest-seeking bumblebees in spring (Paper I) were negatively correlated with the foraging habitats the following summer. However, the pollinating bumblebee fauna needs to have a great many habitats in the agricultural landscape to supply the needs of the bumblebee colonies during the whole season.

III. The preferred plant species for bumblebees in general (Paper II) were preferred by all observed bumblebee species. Between castes, differences in preferred plants were found. Males mostly visited thistles and *Calluna vulgaris*, while queens preferred clover. Two declining bumblebee species in the agricultural landscape, *Bombus sylvarum* and *B. subterraneus*, both foraged on plant species preferably growing in boundary habitats. For prevalence of these species, such habitats have to be conserved in the modern agricultural landscape.

IV. Higher abundance of foraging bumblebee queens was estimated in areas with a high volume of *Salix caprea* per ha. In areas with low volume of *S. caprea* per ha (< 100 m^3) or with small individuals (< 10 m^3 leaf-holding crown), there was greater competition for food resources. Therefore, all willows, even the small ones, that can have high flowering percentage, are of value for bumblebees and should be protected in the intensively used agricultural landscape. Plantations of short-rotation energy forests can also be used by bumblebees as a complementary foraging source during early spring.

V. Both percentage of tree cover and volume of juniper shrubs (*Juniperus communis*) within semi-natural pastures have a positive effect on the species richness of foraging bumblebees. Also the community structure of the bumblebees was positively correlated with the tree cover density. At the landscape level, the proportion of arable fields and urban elements (but not pastures) per km^2 surrounding area affected the bumblebee community structure positively.

VI. Butterflies were the only one of the studied organism groups (taxa) that was correlated with bumblebees. These taxa were positively correlated concerning both species richness and species composition. Both bumblebees and butterflies were negatively affected by increasing grazing pressure. These results, together with the results in Paper V, lead to a strong recommendation to conserve heterogeneity within the semi-natural pastures. This heterogeneity should also concern management, as grazing pressure, together with variation in the tree and shrub layer in the pastures .

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