BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

A thesis submitted as part of the requirements for the Degree of B. Sc. (Hons.) in Ecology at the University of Aberdeen 1996.

by Laura Brodie

To publish this on the Internet I have made the following changes

PLATE 1 in my thesis was made up of scanned images taken from Prys-Jones & Corbet's excellent book. To use these here would be an infringement of copyright, so I have replaced the scanned images with digital photographs of my own that were taken at a later date.

Some of the figures have been re-sized and had their font size reduced and the legend moved, this was done to keep the file size small and to take into account the different shape of the monitor screen from the printed A4 page. The figures have also been integrated more with the text.

Nothing else has been changed; even the mistakes have been left in.

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BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

1 INTRODUCTION

1.1 Economic importance of bumblebees
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1.3 Foraging
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1.1 ECONOMIC IMPORTANCE

Bees are responsible for pollinating plants that provide much of our food; in North America it is believed that 30% of food for human consumption originates from plants pollinated by bees (Heinrich, 1979). Honeybees are generally thought of as the most common pollinator, and they are the most widely studied, but bumblebees are the chief pollinators of red clover, alfalfa, and in some areas cotton, raspberries, apple and plum blossom; and in Norwegian orchards honeybee pollination is usually limited by low temperatures, so bumblebees are the chief pollinators there (Faegri & van der Pijl, 1979). In New Zealand bumblebees were imported (they have no native bumblebees) to pollinate the forage crop clover (*Trifolium pratense*) as the corolla is too long for honeybees, so they cannot act as pollinators (Sladen, 1912; Faegri & van der Pijl, 1979).
Bumblebees are such good pollinators of these crops for three reasons:

- They can fly at much lower temperatures than honeybees.
- Many species have longer tongues than honeybees, so they can pollinate flowers with long, narrow corollas.
- They are very hairy and their hairs are branched and so are perfect for picking up and transferring pollen.

Bumblebees are increasingly used in glasshouse cultivation, where a honeybee hive would be too large, e.g., cabbage pollination in Holland (Free & Butler, 1959), kiwi fruits and tomatoes. So bumblebees are of great economic importance, and with the increase of glasshouse cultivation, and the spread of the mite, *Varroa jacobsoni*, causing a decline in honeybee populations, their importance can only increase. A decrease in the honeybee population would probably lead to an increase in the populations of short-tongued bumblebees, as happened in Colorado recently (Plowright & Laverty, 1984). Consequently it is most important that there is adequate information on the pollination ecology of bumblebees, hence this study.

1.2 LIFE CYCLE

Bumblebee colonies have a yearly cycle. Queens that have mated in late summer hibernate, usually in the soil, and emerge in spring. The queens found the new colony themselves, they search for a suitable nest site, deserted small rodent nests are popular sites, then they build a wax honey pot and fill it with regurgitated nectar (honey). This store will enable them to survive a day or two of bad weather without foraging. The queens also build up a store of pollen, some of this they eat, and the rest they form into a ball mixing it with nectar. The pollen stimulates the ovaries to produce eggs, which the queen lays in batches of 4-16 (Free & Butler, 1959), on the ball of pollen. The ball of pollen with the eggs is placed within reach of the honey pot, this enables the queen to brood the eggs and drink honey at the same time. After this stage the various species differ slightly in the way the larvae are fed. The larvae pupate and emerge as adults, the queen usually lays another batch of eggs while the first batch is still in the larval stage (Sladen, 1912).

When new workers first emerge their hair is silvery in colour, within an hour or two it changes to the colours seen in foraging bees (Sladen, 1912). The workers can start to forage after only two or three days (Heinrich, 1979), this means that the queen can spend more time egg laying. The average worker's life lasts about four weeks, and in that short time she might develop foraging preferences, this thesis aims to record the preferences of the species and of the individuals. Not all adults leave the nest to forage, some of the smallest workers may stay in the nest and perform "household" duties; these small workers may also have weak or deformed wings, but may live longer than the foragers and have less worn coats (Free & Butler, 1959) and wings, as they rarely fly.

The size a colony reaches depends on the species concerned and the food supply, some can have as few as 30 bees, and *Bombus terrestris* can reach as many as 400 (Free & Butler, 1959). Males are usually produced once the stores reach a sufficient quantity, or if the queen dies or loses her influence. When the adult males emerge they spend a few days in the nest, but do no work, then they leave the nest for good and forage for themselves. They can often be seen sheltering under the heads of flowers when it rains or when it gets dark. Not all workers return to the nest every night, some spend the night outside, sheltering under flowers as the males do. New queens emerge about a week or so after the males. They mate, drink lots of nectar to build up their fat body, which will enable them to survive the winter hibernation, then find a suitable place to hibernate.

Not all nests go on to produce males and queens, many fail in the early stages, some are damaged, and some never build up enough reserves to produce reproductives. Some nests produce only queens, others only males, and some nests produce both males and queens. Although it is possible for workers to lay unfertilised eggs that will be males, workers cannot produce queens or other workers.

At about the same time as the queen starts laying unfertilised eggs that will produce males, the ovaries of some workers, usually those performing household duties (Alford, 1975), may develop. When this happens aggression between worker and worker, and worker and queen increases. Some workers try to lay eggs of their own, and may even attempt to eat eggs laid by the queen. In many cases the more persistent workers will succeed in laying some eggs.

The production of males usually signals the beginning of the end of the co-operation and organisation of the nest. The males drink the stores of honey, but do not forage to replace it. The queen is usually old, almost bald and may have lost some of her influence over the persistent or larger workers, and gradually the stores dwindle and the workers die.

There is some evidence that *Bombus pratorum* and *B. hortorum* may, under certain circumstances, be able to go through two colony cycles in a year (Prys-Jones & Corbet, 1987), this would mean that instead of hibernating the new queens would immediately start a colony and the queens that emerge from this colony would then hibernate through the winter. *B. pratorum* and *B. hortorum* usually have quite small colonies, and *B. pratorum* colonies can reach their maximum size earlier in the year than any other species.

There are some very important differences between the bumblebee life cycle and the honeybee life cycle. There is no mouth-to-mouth exchange of food between adult bumblebees, nor do adults groom each other or the queen (Free & Butler, 1959). As yet no "queen substance" has been found (Wilson, 1971); in honeybee hives workers licking the queen and each other pass the queen substance throughout the hive, and this pheromonal control enables the queen to maintain dominance. Bumblebee queens appear to maintain dominance purely by aggressive behaviour. They are usually bigger than the workers and the queen opens her mandibles and head-butts the most dominant worker from time to time (Free & Butler, 1959). This is usually sufficient until

unfertilised eggs are laid, or a worker's ovaries develop.

1.3 FORAGING AND CONSTANCY

Bumblebee larvae eat most of the pollen brought back to the nest, adult bees eat very little (Free & Butler, 1959). Until the end of the final instar the larvae have a blind gut, faeces are voided all at once during the spinning of the cocoon and final instar (Alford, 1975). The highest growth rate occurs during the last instar (Alford, 1975) so most pollen will be consumed during this time. The exine (outer wall) of the pollen grain is made of a tough carotenoid polymer which is highly resistant to decay (Toothill, 1984) and so can be identified in the larval faeces.

A.D. Brian (1951) analysed the larval faeces of three nests, one each of *Bombus pascuorum*, *B. lucorum* and *B. hortorum*. The nests were located quite close to each other, so the bees would have probably been foraging from the same area. She found considerable differences in the kinds of pollen eaten by the larvae of the different species. In a later study (1957) she found that bumblebees prefer to forage from flowers with corollas a little shorter than their tongue length. She thought that this might increase foraging speed, and also it seemed that they did not like pushing their heads into the flowers.

Inouye (1980) found that, in general, shorter-tongued bees foraged faster on short-corolla flowers than long-tongued bees, although he found it difficult to measure the foraging times of long-tongued bees on shorter corolla flowers because of "their apparent reluctance to feed on short corolla flowers". With captive bees feeding from artificial flowers in the laboratory it was found that the probing time increased gradually with depth of flower, providing the flower was shallower than the bee's tongue, but beyond that depth probing time increased much more rapidly, as the bees stretched their tongues but failed to reach the nectar (Harder, 1983).

J.B. Free (1970) measured constancy by analysis of pollen loads of bees returning to the nest, he found that 63% of *B. pascuorum* and 34% of *B. lucorum* loads contained a mixture of pollen from different flower species, however many of these "mixed" loads contained 98% or more pollen from one plant species.

The analysis of pollen indicates some of the plants the bee visits, but it does not necessarily show all the plants visited by bees, as not all bees collect pollen on foraging trips. Some bees specialise in pollen collection, some in nectar, some in both, but all will change according to the needs of the colony (Free & Butler, 1959). Pollen load analysis does not show the foraging patterns of nectar gathering bees.

Heinrich (1976) in the U.S.A. studied bumblebees foraging in an old field. He confirmed the species preferences of earlier studies, but also found that each individual preferred a small subset of the overall species group. He named the main foraging flower the "major" and the secondary flower(s) the "minor(s)".

The foraging environment of the bumblebees is constantly changing. Individual flowers and groups of flowers of the same and different species come into bloom and die at different times with different life-spans. Nectar changes throughout the day in volume and concentration (Prys-Jones & Corbet, 1987) and throughout the life of the flower (Real & Rathke, 1988; Willmer et al., 1994); soil conditions and daily temperature and humidity changes also affect the quantity of nectar available. Worker and queen bees aim to gather more food than they themselves will consume, in order to build up a store of surplus food. Males do not aim to build up a store, they forage only for themselves, so their foraging patterns might be expected to be different. In this constantly changing environment individual bees may get a different perception of which flower species is most rewarding. The best strategy for an individual bee is to forage from whatever species of flower it perceives to be the most rewarding, and change to another species when the

original species is less rewarding and the new species is abundant enough to provide sufficient nectar.

An optimal forager would visit all flowers with rewards above a certain level, in its foraging area, to minimise energy costs and maximise energy gains (Real, 1983), but individual bumblebees regularly ignore apparently rewarding flowers. Sladen (1912) observed a *Bombus lapidarius* queen persistently fly against a closed window in an effort to reach a bunch of bluebells on the other side, while there were plenty of other suitable species outside that she could have foraged from. There may be constraints that limit the number of different types or species of flower that a bumblebee can forage from. Darwin (1891) thought that there might be a limit to the number of types of flower an insect could learn or remember to handle correctly. It has been shown that flower complexity can cause learning problems in bees (Heinrich, 1976; Laverty, 1980) and that bumblebees are often constant to a guild of species with the same morphology (Manning, 1956), or colour (Darwin, 1891). Real (1983), in Costa Rica, found a slightly greater bumblebee constancy in a guild of species differing only slightly in morphology, than in a guild differing only in colour. As the number of different types of flower increases the constancy to one or a few types increases (Waser, 1986). Laverty (1993) found that constancy was higher for the more morphologically complex species than for the simpler species however, even with the simpler species, bumblebees switched to a new species that had a similar corolla length and handling method, more frequently than would be expected if the switch was random.

Tests done in captivity have shown that bumblebees can recognise rewarding flower "types" by their colour, odour, or shape of flower, and that they will accept flowers that are slightly different from the typical type (Dukas & Waser, 1994). However in tests with artificial flowers where one colour was rewarding and the other colour was non-rewarding, bumblebees showed a preference towards blue flowers whether they were rewarding or not (Dukas, 1995). They may also be able to recognise the general shape or outline of the whole plant (Darwin, 1891; Free & Butler, 1959; Faegri & van der Pijl, 1979), as they have been seen attempting to forage on flowers that are not yet open, while others of the same species are open.

No communication system for recruiting workers to rewarding flowers has been discovered in bumblebees (Brian, 1957; Free & Butler, 1959; Heinrich, 1979; Laverty, 1980), there appears to be no bumblebee equivalent of the honeybee waggle dance; however one bumblebee foraging in a group of flowers appears to attract others (Brian, 1957). So flowers chosen for foraging may initially be chosen at random by individual bees and then be retained, providing they are suitably rewarding and the nectar is within easy reach. The choice of the major flower might influence the choice of the minor flower(s), as the minor flower may be of the same colour and/or morphology as the major. Also the nest odour may influence their choice. If there is one species of flower that is visited by many of the bees in the nest the odour will spread throughout the nest (Faegri & van der Pijl, 1979), and so a bumblebee on its initial foraging flight may be influenced to choose a flower having the same smell, and this in turn might further influence its nest mates. This may explain why two nests of the same species, in the same area, might show great differences in the flowers that were foraged on (Free, 1970).

To help to understand the ways that bumblebees are recruited to flowers of plants, so as to maximise the benefits to these plants, we need to have a fuller understanding of the factors influencing foraging. Despite these previous studies, however, we still do not understand the relationship between the foraging patterns of individual bumblebees in relation to those of their nest mates and so to the general foraging of the "nest". This is the topic of this study.

1.4 AIMS

The principle aim of this project was to discover if species and individual bumblebees have similar foraging preferences by recording the flowers that they were observed using during the

course of a bee walk. To acheive this aim it was necessary to devise a way of reliably marking bees without anaesthetising them. If preferences were found it was intended to investigate whether these could be related to tongue and head measurements. To this end the functional proboscis length, and the head length and width for the species encountered in the bee walk were measured. Subsequently to record flowers visited sequentially by marked and unmarked bees during a single foraging trip, and to compare the sequence of visits of a single foraging trip with individual and species preferences over a five day period.

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BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

2 MATERIALS AND METHODS

2.1 Site characteristics
2.2 Pilot study
2.3 Measuring environmental variables
2.4 Bee identification
2.5 The "bee walk"
2.6 Marking bees and measuring tongue length and head width and length
2.7 Preference and constancy of bees
2.8 Measurements and characteristics of flowers foraged by bees during bee walk

2.1 SITE

(FIGURE 1) The site is in north-east Scotland about 10 km south of Stonehaven, at Ordinance Survey Grid Ref. NO 816 795, on a south-west slope at 150 m above sea level. There are few trees in the area, and none near the site, so the effects of the wind on the vegetation can be severe. The bee walk route was about 410 m long. 400 m followed one edge of a lane between two fields, the edge varied in width from 50 cm to 1.5 m. A 10 m strip of garden was also included. Both sides of the lane contained the same mixture of plant species and in similar proportions. The flowers used by bees during the bee walk are listed in TABLE 2. Other flowers present in the lane, but not seen to be foraged by bees were, *Veronica* sp., *Campanula rotundifolia*, *Ulex europaeus* and various grasses. In the garden, flowers used by bees are listed in TABLE 2, other flowers included *Geranium* sp. and some old-fashioned *Rosa* sp.

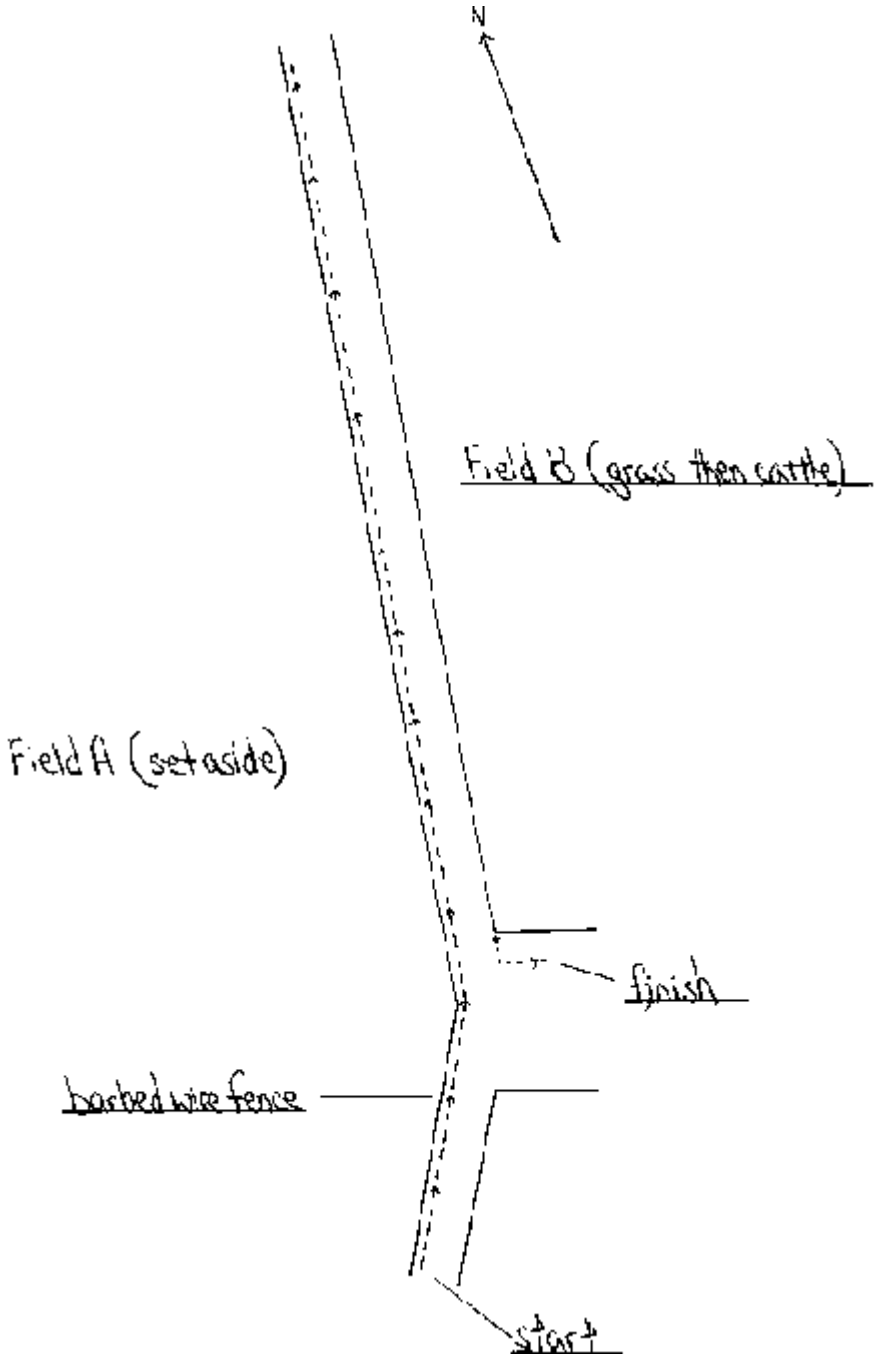


FIGURE 1

The bee walk side was free from the influence of cattle grazing, but parts of the other side of the lane were within reach of cattle which were put into Field B at the end of June. Field A was set-aside this year and grass last year. Field B was grass this year and set-aside last year. The most common flower in the set aside field was *Capsella bursa-pastoris*, there was also a large number of *Lamium purpureum* and various grasses.

2.2 PILOT STUDY

A pilot study was done on the 17th, 18th and 20th of June 1995. This enabled bee marking and measuring techniques to be tried out and perfected, bee identification to be mastered, and the length of the bee walk to be decided.

2.3 MEASURING ENVIRONMENTAL VARIABLES

Temperature was measured by hanging a thermometer from the barbed-wire fence that separated the field from the lane. The thermometer was positioned about 50 cm from the ground surface, approximately bumblebee foraging height for the site, and in full sun, as the bees forage in full sun. Light conditions were recorded either as sun, sun\cloud or cloud. The sky was quartered, then each quarter halved. Sun was recorded when there was cloud in only 0-2 segments, "sun/cloud" when cloud was present in 3-6 segments, and cloud when cloud was present in 7 or 8 segments. Mist and rain were also recorded. Wind speed was recorded using a Ventimeter made by Elvometer Co., Sweden. The ventimeter was held 1.5 m from the ground surface for 20 s, or more if required. The wind speed was taken at approximately the 90 m mark on the bee walk, and the ventimeter was held over the bee walk vegetation. Environmental variables were recorded at the start of every bee walk.

2.4 BUMBLEBEE IDENTIFICATION

Bumblebees were identified using keys in Prys-Jones and Corbet (1987) and Alford (1975). While Bombus terrestris queens and B. lucorum queens are easily distinguishable in the field, their workers are not. So, following the example of Brian (1957), all of the workers were recorded as *B. lucorum*, since *B. lucorum* queens were more numerous than *B. terrestris* queens in 1995. Males of *B. lapidarius* and *B. pratorum* are fairly easily distinguishable and so their caste was recorded; the caste of other species is not so easily distinguished in the field, so was not recorded. The six species regularly seen during the bee walk are on PLATE 1.

2.5 THE BEE WALK

The bee walk was done every 2 hours from 6 a.m. until 8 p.m. on five consecutive days; each session done once in June, July and August 1995. Each walk consisted of:

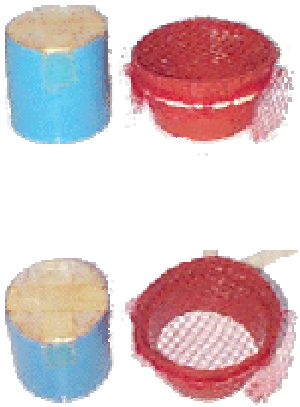
- Measuring the environmental variables.
- Walking down to the start of the bee walk in the lane.
- Walking the 400 m of the lane bee walk, recording each bee foraging, and catching unmarked bees in numbered jars.
- Walking down to the garden area, recording bees foraging and catching unmarked bees in numbered jars.

The bee walk was repeated for one extra day in mid-August 1995 to assess how well the marking had stood up to time. On that day only marked bees were recorded. As the walk progressed, the species of each individual bee and the flower it was foraging from, were recorded on a Sony Professional Walkman. When possible the caste of bee was also recorded. The walk started and ended at the same point every time, and the direction followed was always the same. The walk was done at a slow, regular pace, approximately 0.5 m s for the 6 am walk, when bees were less abundant, 0.4 m s for all other walks. The barbed wire fence was used as one boundary, and the bare ground of the lane as the other. All bees actively foraging in a strip of approximately 20 cm wide stretching from the fence to the bare ground were recorded. If a bee landed and foraged on a flower that had just been passed it was not recorded. When a marked bee was recorded more than once in the same walk, only its first sighting was used in data analysis. Bees foraging on flowers outside the fence around Field A were counted, regardless of whether the roots were also outside the fence. The flower species on either side of the fence were the same, but Centaurea nigra was slightly more common outside (bee walk side) the field than inside, and Cirsium arvense was more common inside the field than outside. It was not possible to include the flowers inside the fence of Field A as the ground in the field sloped sharply downwards.

2.6 MARKING BEES AND MEASURING TONGUE LENGTH, AND HEAD LENGTH AND WIDTH

Unmarked bees were caught in numbered glass jars during the bee walk, the species of bee and flower were recorded as mentioned above, and the jar number was recorded on tape. The bees were measured and marked in the order in which they were caught, as soon as the bee walk ended. After the bee walk, the bees were kept indoors in the shade in the glass jars in which they were caught while waiting to be marked.

Figure 2



It was decided not to anaesthetise the bees, as this might have caused behavioural changes (Prys-Jones & Corbet, 1987). As the bees varied in size and strength a device was made that could restrain any bumblebee, big or small. This was made from the top 3.5 cm of a 6.5 cm wide plastic flower pot and plastic net with a 4-5mm mesh secured over the top of the pot with a length of tape (FIGURE 2). This mesh size was small enough to prevent escape of even small bees and large enough to allow the bee to be marked between the threads. On just one occasion an extremely small Bombus pratorum worker managed to squeeze through the mesh, and, as she was obviously distressed, she was allowed to fly away. The plastic top of an aerosol cap was used to form a base that could be moved up inside the flower pot, to trap the bee between the mesh and the top of the aerosol cap. 1 mm graph paper was sellotaped to the aerosol cap, so that the head measurements could be made.

The conical shape of the restraining device made it possible to fit it over almost any size of glass jar. The bee was persuaded to fly up to the net by excluding light from the sides and base. Once the bee was on the net the jar was removed and the aerosol cap placed under the opening to prevent escape. It was possible to hold the aerosol cap in place with one hand, while offering the bee 30:70 honey and water in a plastic pipette with the other. Not all bees were willing to drink the nectar and, as time was limiting, if they ignored the pipette after it had been within reach for over 10 s it was removed and just their head measurements were taken and they were marked. There was no apparent difference between species in the proportion that drank from the pipette. One noticeable thing was that if their buzzing sound was higher pitched than normal they generally refused to drink and struggled more when being marked, this became known as the "angry buzz". It is not known what caused some bees to emit this higher pitched buzz, but there was certainly a link between it and how co-operatively the bee behaved.

The end of the plastic pipette was marked in 1 mm intervals with a Staedtler fine lumocolor permanent ink pen. With a little practice it was possible to move the meniscus of the nectar up and down the pipette so forcing the bee to extend its tongue to foraging length, which could be seen through the plastic and its length measured. This method is similar to that used by Brian (1957), except that she used capillary tubing, not a pipette. After the tongue length was measured the aerosol top was moved up the inside of the pot until it touched the back of the bee, when the bee turned to walk on the aerosol top the flower pot was moved down with just enough pressure to stop the bee moving its thorax. Its head length and width were now measured, and then the bee could be marked.

The time taken to mark bees varied greatly, the shortest time was about two minutes, but a few bees took as long as five minutes. Waiting for a bee to walk on the surface of the aerosol cap was the main reason for the variation in time taken. Some bees walked over every part of the mesh before they decided to walk on the aerosol cap.

Water based Tipp-Ex in four colours, white, blue, green and pink, was used to paint a disc on the

bee, carefully avoiding the tegulae (wing bases). A small blob of Tipp-ex was placed on the thorax using the brush provided, the blob was then smoothed down with a blunted cocktail stick, this also flattened the hairs on the thorax. Since *Bombus pascuorum* has a very hairy thorax, the layer of Tipp-Ex was insufficient to flatten the hairs, so before marking these hairs were either trimmed using a very small pair of scissors, or scraped off carefully using a scalpel. In August the weather was much hotter and drier and the Tipp-Ex dried much more quickly, so a slightly thicker layer of Tipp-Ex was applied to *B. pascuorum*, this allowed the hairs to be flattened without having to trim or remove them. It was felt that this caused less disturbance to the bee, and made the marking process quicker. Once the Tipp-Ex had dried, a number from 1 to 100 was written on the Tipp-Ex with a Staedtler fine lumocolor permanent ink pen, and the bee was set free.

Marking and measuring were done indoors, the bees were set free out of a window which was about 10 m at right angles from the 100 m mark of the bee walk. Nearly all the bees flew away immediately, but a few sat on the windowsill or below the window. This area was checked periodically and any bees still there were brought indoors, fed and released when they decided to fly.

The number and Tipp-Ex colour of all marked bees seen on the bee walk were also recorded. Occasionally a marked bee was seen but the number could not be read; this was recorded as an unmarked bee.

2.7 PREFERENCE AND CONSTANCY

A highly constant bee ignores or passes over apparently rewarding flowers to forage from flowers of a single species; only occasionally will such a bee forage from another flower species, in other words, the bee is showing a preference for a particular species of flower. Constancy is very important to plants as it means they will have a greater chance of receiving compatible pollen (Faegri & van der Pijl, 1979).

Flower preferences were calculated using the program PREFER in Krebs (1989) which calculates Manly's alpha index of preference. The variables required by the program are:

- The number of species of flower present in the area.
- The number of flowers of each species in the area.
- The number of visits to each species of flower by bumblebees of a particular species.
- Whether the resource was renewable or not.

The number of flowers was calculated by observing how the bees used each flower species, so as to find what could be considered a "functional individual unit", i.e. an area where one bee could forage but not two.

The full list of flowers used by bees during the bee walk is shown in TABLE 2 in the results. During each five day bee walk period, flowers were counted on the morning of the third day. For flowers with inflorescences and umbels, heads were counted; spikes were counted in the *Labiatae*; *Hypericum perforatum* flower clusters were counted; racemes of *Vicia* spp. and *Lathryus pratensis* were counted; and for all others individual flowers were counted or estimated. For *Stachys lanata*, originally spikes, made up of several individual flowers, had been counted but, as the bee walk proceeded, it became obvious that it was common to find two, or even three bees on a spike, but it was also possible to find only one bee on a small spike. Consequently it was eventually decided that on average a spike comprised two functional units. The number of visits to each species of flower by bees was taken from the bee walk data, and the PREFER program was run for each species of bumblebee. It was decided to class the resources as renewable, since few flowers secrete nectar at just one time period and so do renew their nectar. Pollen is not a renewable resource, but no single bumblebee is likely to remove the entire

quantity of pollen from a flower in just one visit.

Originally the program was run with each spike of *Stachys lanata* counted as one unit, the results appeared to greatly over estimate the preference for *S. lanata* and, it was felt, did not reflect what had been seen in the field. Consequently the program was re-run with each spike counted as two "flower units".

To measure flower constancy, bees were picked at random, by following the first bee sighted after stepping outside. The species, caste, number (if marked), and sequence of flowers visited was then recorded on tape. When one bee was lost the next bee sighted was followed as a new sample run. Most of the bee following was within the area of the bee walk, but was not restricted to this area; the bee was followed for as far and as long as was possible.

2.8 MEASUREMENTS AND CHARACTERISTICS OF FLOWERS FORAGED BY BEES DURING THE BEE WALK

The flowers foraged by the bees were counted as mentioned in 2.7, and on the same morning between five and twelve flowers of each species were then examined and vernier callipers used to measure the length the bee would have to extend its tongue to reach the nectar. The presence of nectar was also recorded, as was the accessibility of the nectar, and the width of the opening leading to the nectar. For *Digitalis purpurea* the corolla opening is large enough for even the biggest bee to enter, so the distance to nectar was taken to be the distance from the ovary to nectar, as this is how far the bee must extend its tongue. The handling difficulty of the flowers was estimated, and the flowers that were foraged for nectar were put into four groups, group one being the easiest to handle, and group four the most difficult.

- Group 1. Flowers that had visible nectar.
- Group 2. Flowers that provided a landing platform on which nectar (not visible) could be reached by random probing.
- Group 3. Flowers which do not provide a landing platform, but where the path from the corolla opening to the nectar was straight.
- Group 4. Flowers like Group 3 but where the path from the corolla opening to the nectar was not straight.

The height range of the flowers, the height of the vegetation surrounding the flowers, and the effects of wind on both the flowers and the surrounding vegetation were recorded. The surrounding vegetation was noted as the site is very windy and the movement of the vegetation in the wind might affect foraging preferences. Where most of the vegetation was lower and only the taller grasses were higher, than the flower species being recorded, the surrounding vegetation was classed as mixed, otherwise the surrounding vegetation was classed as higher or lower.

Where possible flowers and inflorescences for identification and examination were picked from various heights and in various places throughout the bee walk. Identification of flowers was made using Rose (1981) and Clapham *et al*. (1993).

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BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

RESULTS

3.1 Species observed
3.2 Proportion of marked bees re-sighted during bee walk
3.3 The relative changes in size of the populations foraging in the bee walk area
3.4 Measurements and characteristics of flowers foraged by bees during bee walk
3.5 Species flower preferences
3.5.1 Caste flower preference
3.6 Tongue and head measurements of each species
3.7 Relationship between tongue length and flower preference
3.8 Flower preferences of individual bees
3.8.1 Constancy
3.9 Environmental variables and their effects on foraging

3.1 SPECIES OBSERVED

Seven species of bumblebee were observed in total, six are shown on PLATE 1. *Bombus lucorum* queens emerged first in late April, followed a few days later by *B. terrestris*, and then *B. pratorum* within a week. All three species were seen foraging on cultivated varieties of spring flowering heather. *B. lapidarius*, *B. pascuorum* and *B. hortorum* queens emerged during May and early June. *B. distinguendus* was observed once on 24th and once on 26th of June, on both occasions it was a queen that was seen, after the 26th *B. distinguendus* was never seen again and has been excluded from the data analysis. In early August the first males were seen; new queens of *B. lucorum* were seen first on 15th August. The last bee, a *B. lapidarius* queen was seen foraging on the 4th of November.

PLATE 1. Six species of *Bombus* seen during bee walk.

Bombus terrestris (queen)

Bombus lucorum

Bombus lapidarius

Bombus pratorum *Bombus hortorum* *Bombus pascuorum*

3.2 RE-SIGHTING OF MARKED BEES (TABLE 1) During June only about ten bees were marked each day, as the effect of the marking on the bees was not yet known. Many queens were still foraging in June, and a few in July, consequently many of the bees marked during June, and some during July were queens. In July there were few bees to be seen, only a very small percentage of the marked bees were re-sighted, and some of those that were foraging in the bee walk area were queens. During August the number of bees marked increased, as did the number re-sighted, some bees were re-sighted over twenty times. The bees marked in August were workers and males, although it is possible that newly emerged Bombus pratorum queens were marked, as there is little difference in size between them and larger workers of the same species.

TABLE 1. The number of bees marked and released during the bee walk and pilot study, and the percentage of bees re-sighted at least once; includes re-sightings made on 15th August.

Date marked	No. of bees marked	No. of bees released	% of released bees re-sighted
18-20 June	*24	**9	0.0
21-25 June	*55	55	16.3
4-8 July	*40	40	7.5
2-6 August	232	232	58.6
Total	351	336	

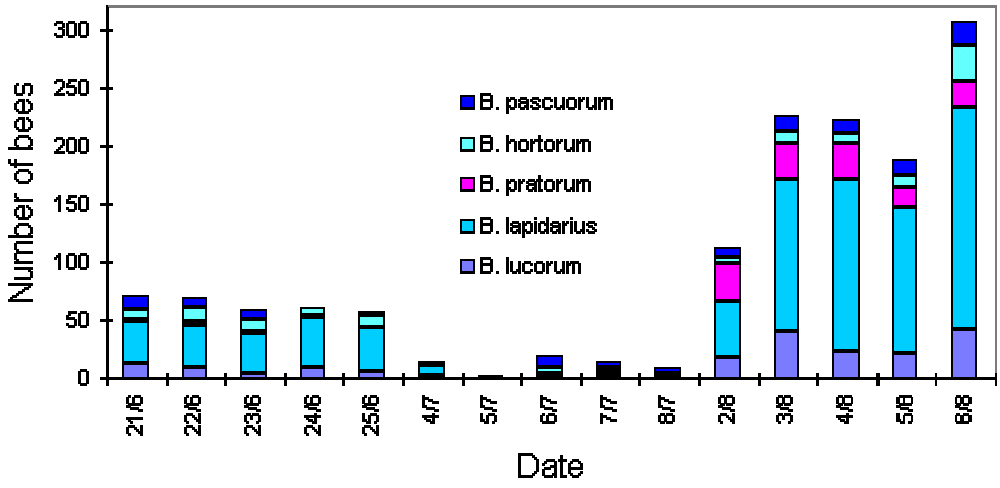
*Many of the bees marked during this period were queens.
**During the pilot study 14 queens were confined to artificial nest boxes in an effort to get them to start a captive colony, one *Bombus lapidarius* worker which refused to fly away was confined with a *B. lapidarius* queen.

3.3 THE RELATIVE CHANGES IN SIZE OF THE POPULATIONS FORAGING IN THE BEE WALK AREA

The total number of bees, both marked and unmarked, of each species recorded during the bee walk is shown in FIGURE 3. In June many queens were still foraging alongside some early workers. On the 24th no *Bombus pascuorum* were seen the entire day, whereas on the three previous days they had been foraging on *Vicia sepium*. In July there were still some queens foraging but very few bees were seen in the bee walk area; on the 5th only one *Bombus*

lapidarius and one *B. hortorum* were seen during the entire day, however many bees were seen flying overhead, possibly to other nectar sources. The numbers foraging in the bee walk area rose considerably in August. *B. lapidarius* was the forager most commonly seen during June and August, but during July *B. pascuorum* was the most common bee. During August 78.8% of the bees recorded foraging during the bee walk were marked bees, many of the individual bees were recorded on more than one walk. When a marked bee was recorded twice during one bee walk, only the first sighting was used in data analysis.

FIGURE 3. The number of each species of bumblebee seen during the bee walk in June, July and August 1995.



3.4 MEASUREMENTS AND CHARACTERISTICS OF FLOWERS FORAGED DURING THE BEE WALK

The data gathered on the various flowers foraged by bees during the bee walk are presented in TABLE 2. Three species were used mainly for their pollen, *Centaurea hypoleuca*, *Hypericum perforatum* and *Hesperis matronalis*, the other species were mainly used as sources of nectar. The flowers fell quite easily into four groups:

- The Labiatae with their gullet-shaped flowers, requiring the bee to bend its tongue down to the nectary once it has entered the corolla. *Digitalis purpurea* is included in this group although it belongs to the Scrophulariaceae, it requires similar handling once the bee has entered the corolla.
- The Leguminosae, all the flowers have a fairly similar morphology with a very small corolla opening, but once that has been entered it is a straight path to the nectar.
- The Compositae which provide good landing platforms where the bee can probe many flowers before flying to the next head.
- A miscellaneous group that have visible nectar and were open or had wide corolla flowers.

TABLE 2. Flower data for species used by bumblebees in the bee walk in June, July and August 1995.

Species	Main resource, pollen or nectar	Corolla opening (mm)	Minimum distance to nectar (mm)	Handling	Flower height (cm)	Clumped or scattered plants	Surrounding vegetation	Other visitors
Digitalis purpurea	N	>10	7	4	50-200	clumped	lower	

Stachys lanata	N	2	3	4	35-65	clumped	lower	m, hf, f
Lavandula angustifolia	N	1-2	6	4	5-60	clumped	lower	f, m
Vicia sepium	N	<1	8	3	0-30	scattered	higher	h, f
Vicia cracca	N	<1	7	3	0-40	scattered	higher	
Lathrus pratensis	N	1	2	3	0-40	scattered	higher	
Trifolium repens	N	<1	3	3	0-15	clumped	higher	h
Trifolium pratense	N	<1	6	3	5-20	clumped	higher	
Centaurea nigra	N	<1	2	2	30-100	clumped	mixed	hf, b
Centaurea hypoleuca	P				10-60	clumped	lower	
Cirsium arvense	N	<1	4	2	50-110	scattered	mixed	h, hf, b
Cirsium vulgare	N	<1	4	2	50-80	scattered	mixed	
Leontodon autumnalis	N	<1	2	2	10-20	scattered	higher	f
Allium schoenoprasum	N	4-7		1	15-50	clumped	lower	f, h
Cotoneaster simonsii	N	open		1	0-80	clumped	mixed	h, w, f
Hypericum perforatum	P				50-70	clumped	lower	f, be
Hesperis	P				10-70	clumped	lower	f

matronalis								

Minimum distance to nectar is the distance from the corolla opening to the nearest nectar (for *Digitalis purpurea* it is the distance the bee has to stretch its tongue past the ovary to reach the nectar).
Handling is the relative difference in handling difficulty of the species encountered in the bee walk.
Other visitors, hf=hover fly, h=honeybee, m=moth, f=fly, b=butterfly, w=wasp, be=beetle

The handling difficulty in TABLE 2 was relative, as there were no truly difficult flowers, such as *Aconitum* spp., present in the walk area. The minimum distance to nectar of *Lathyrus pratensis* is abnormally short, the flowers dissected were full of nectar, but few were foraged (FIGURES 3 and 5). In the corolla of *Centaurea nigra* small beads of nectar were visible with a x10 hand lens 2-4 mm down the corolla tube, although the nectary is about 10 mm from the corolla opening (Knuth, 1906). The nectar status of pollen flowers was not examined. *Centaurea hypoleuca* has very long, showy outer florets which were occasionally probed by the larger queens, on examination it was found that these florets contained no nectar and were sterile, these visits were excluded from the data. The central florets provided copious quantities of pollen which was collected by the workers.

During June and August there were many other visitors besides bumblebees foraging on the flowers, but the bumblebees outnumbered all other insects, except on *Cotoneaster simonsii* in June, where the wasps were more numerous than the bumblebees, and in August on *Hypericum perforatum*, where honeybees by far outnumbered bumblebees; however at no time were the numbers high enough to be considered as competitively excluding bumblebees, as the number of honeybees never exceeded three on the whole plant at any one time.

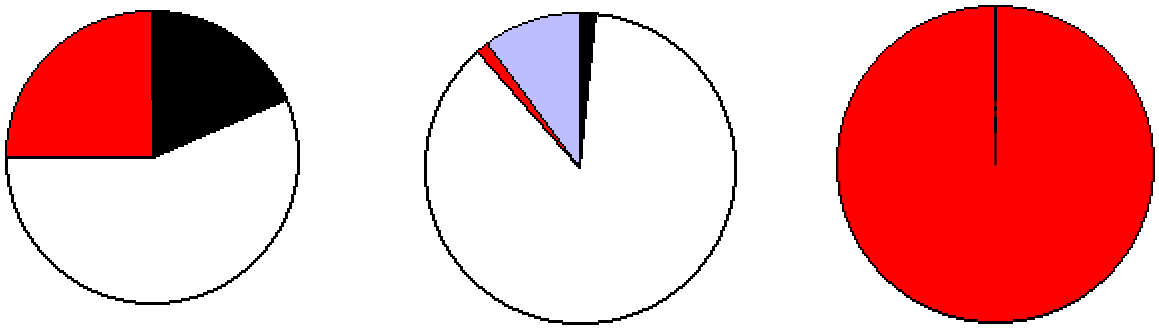
The species of flowers foraged by bumblebees during the bee walk were open before 6 a.m. until after 8 p.m., therefore were available for all eight bee walks in a day.

3.5 SPECIES FLOWER PREFERENCE

FIGURES 4, 5 and 6 show the flower preferences produced by the PREFER program for the bee walk in June, July, and August respectively. The program is such that if no preference was being shown then each species of flower would have an equal proportion of the pie chart. If the proportions are unequal, or if a flower species is not allocated a portion of the chart, this indicates that a preference for one or more species is being shown. It is not possible, using this program, to allocate statistical significance to these preferences. Consequently, in the preferences reported below, only strong deviations have been included.

FIGURE 4. Flower preferences of bumblebees foraging in the bee walk in June 1995. (n = number of observations)

Bombus lucorum (n = 38) *Bombus lapidarius* (n = 187) *Bombus pratorum* (n = 10)



Bombus hortorum (n = 50) *Bombus pascuorum* (n = 30)

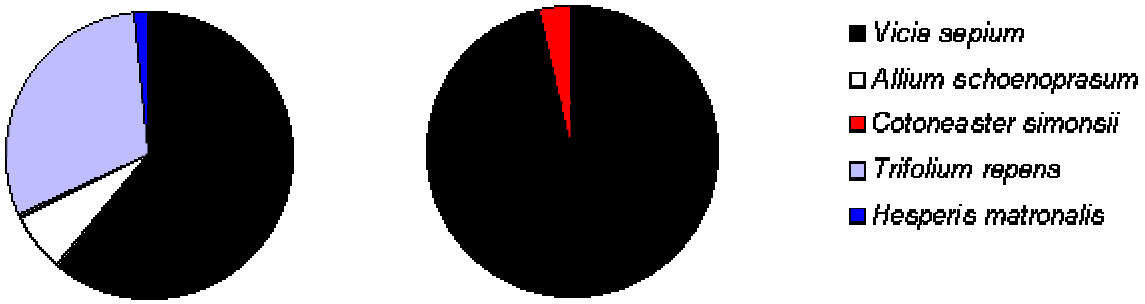
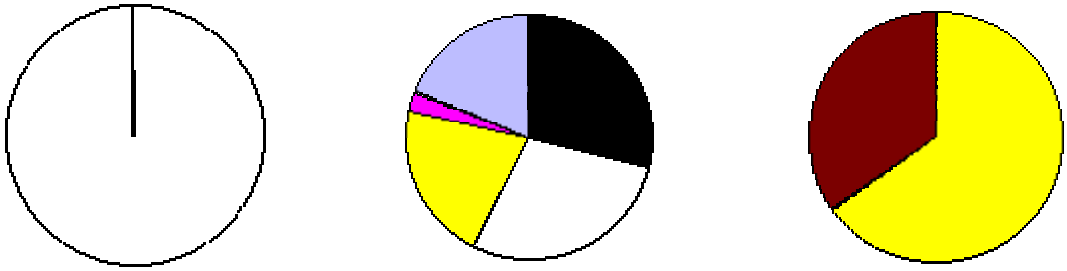


FIGURE 5. Flower preferences of bumblebees foraging in the bee walk in July 1995. (n = number of observations)

Bombus lucorum (n = 1) *Bombus lapidarius* (n = 18) *Bombus pratorum* (n = 2)



Bombus hortorum (n = 16) *Bombus pascuorum* (n = 20)

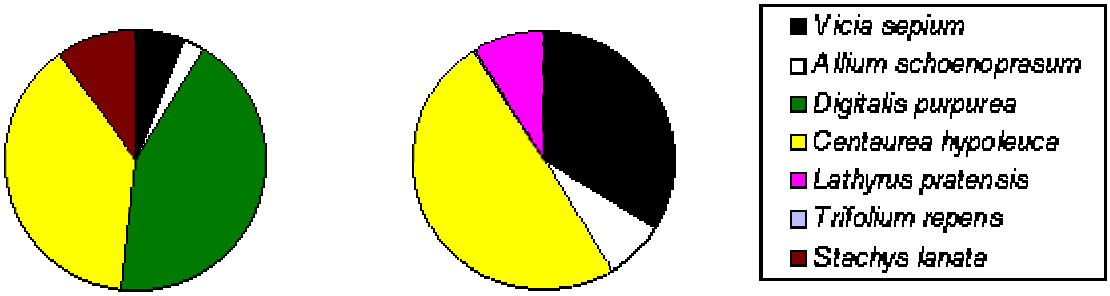
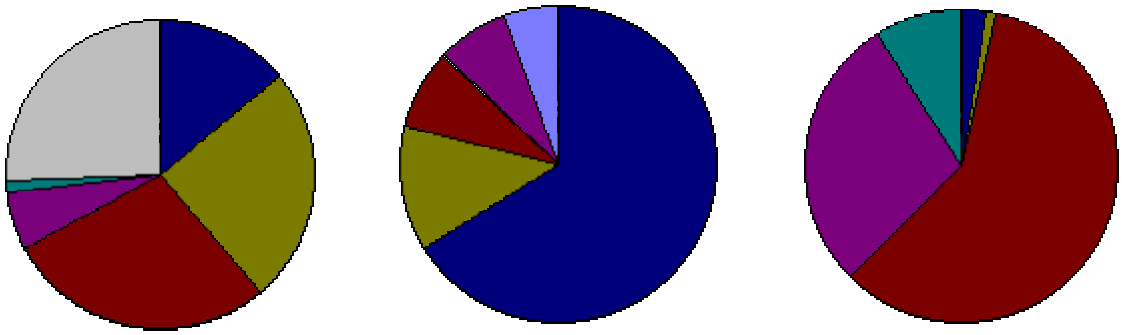
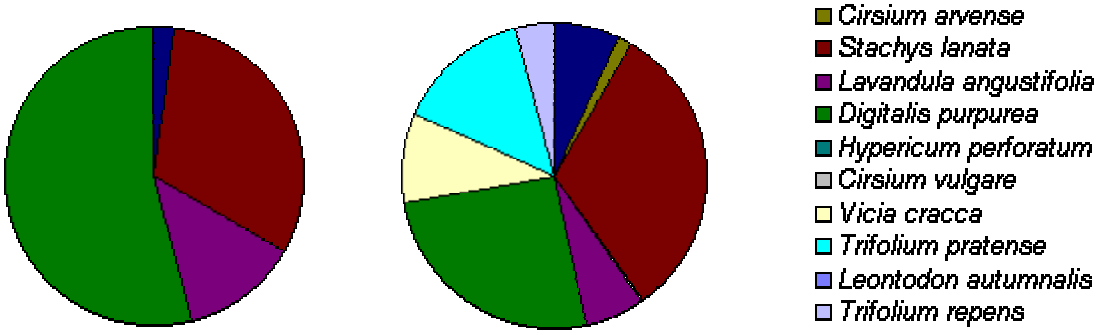


FIGURE 6. Flower prefernces of bumblebees foraging in the bee walk in August 1995. (n = number of observations)

Bombus lucorum (n = 130) *Bombus lapidarius* (n = 645) *Bombus pratorum* (n = 133)



Bombus hortorum (n = 69) *Bombus pascuorum* (n = 67)



In June (FIGURE 4) each species of bee showed a clear preference of one species of flower; *Bombus lucorum* and *B. lapidarius* preferred *Allium schoenoprasum*; *B. pratorum* preferred *Cotoneaster simonsii*; and *B. hortorum* and *B. pascuorum* preferred *Vicia sepium*. Only five species of flower were visited, and no species of bee visited all five species of flower. It was noticed that some *Bombus lucorum* robbed *Vicia sepium* by biting through the calyx to get at the nectar, no other species of *Bombus* was observed to use these holes.

In July (FIGURE 5) there were very few bees foraging in the bee walk area, only one *B. lucorum* was seen foraging just once during the whole five days. Preferences are shown, and those of *Bombus pratorum* and *B pascuorum* for *Centaurea hypoleuca* are quite strong, but the number of observations for all species is quite small.

In August (FIGURE 6) bees returned to forage in the bee walk area, and the number of observations for all species increased. Eleven species of flower were foraged; *Bombus pascuorum* visited eight species and showed a preference for *Stachys lanata* then *Digitalis purpurea*; *B. pratorum* also preferred *S. lanata. B. hortorum* strongly preferred *Digitalis purpurea*, and *B. lapidarius* strongly preferred *Centaurea nigra. B. lucorum* showed almost equal preference for three species, *Cirsium arvense, Stachys lanata* and *Cirsium vulgare*. Throughout June, July and August the most preferred flowers of *B. pratorum* were all situated within a 3-4 m area of the bee walk. In all three months the preferred flowers of *B. hortorum* and *B. pascuorum* belonged to the two groups with the greatest handling difficulty, and have longer distances from corolla opening to nectar.

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BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

RESULTS cont.

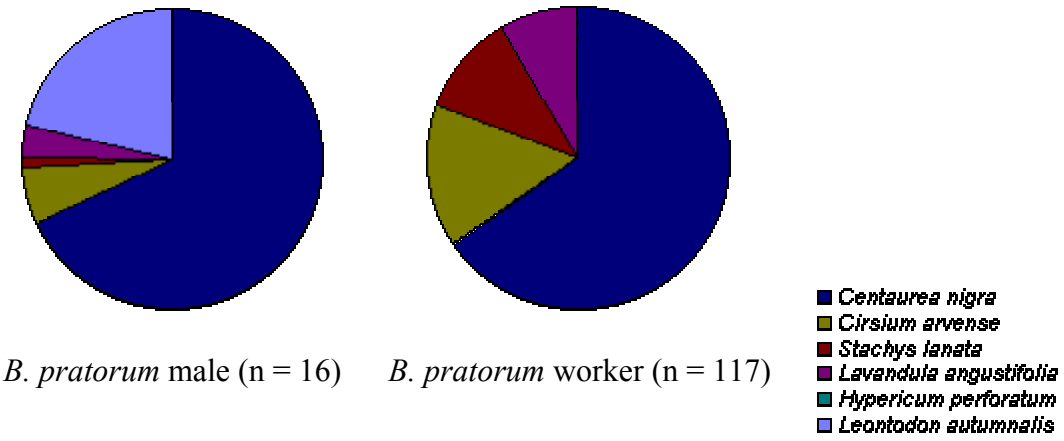
3.5.1 Caste flower preference
3.6 Tongue and head measurements of each species
3.7 Relationship between tongue length and flower preference
3.8 Flower preferences of individual bees
3.8.1 Constancy
3.9 Environmental variables and their effects on foraging

3.5.1 CASTE FLOWER PREFERENCE

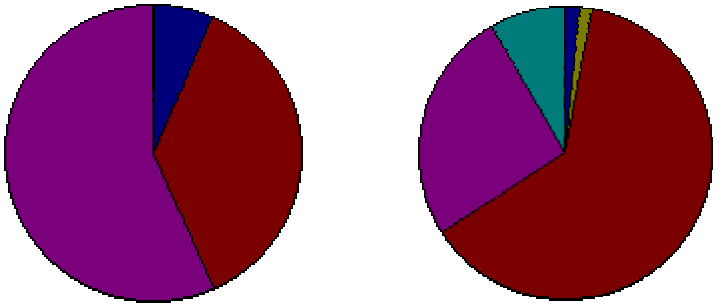
Caste flower preferences were also calculated using the PREFER program using the same variables as Species Flower Preference, and are shown in FIGURE 7. Both male and worker *Bombus lapidarius* show a strong preference for *Centaurea nigra*. They differ slightly in their preferences for minor flowers, though both chose flowers that are similar morphologically to *C. nigra*. Male *B. pratorum* show a strong preference for *Lavandula angustifolia*, while workers show a strong preference for *Stachys lanata*, both these flowers could be considered to be morphologically similar. The males do not visit *Hypericum perforatum*, but, as *H. perforatum* was foraged for its pollen, this is hardly surprising.

FIGURE 7. Male and worker flower preferences of Bombus lapidarius and B. pratorum foraging in the beewalk in August 1995.
(n = number of observations)

B. lapidarius male (n = 159) *B.lapidarius* worker (n = 486)



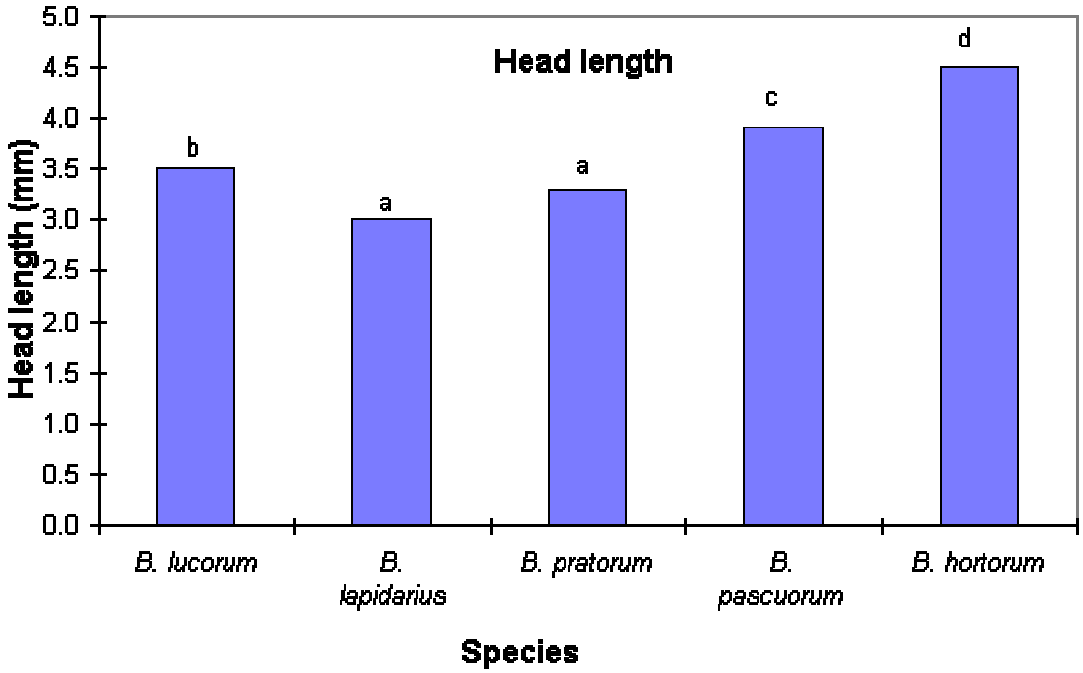
B. pratorum male (n = 16) *B. pratorum* worker (n = 117)

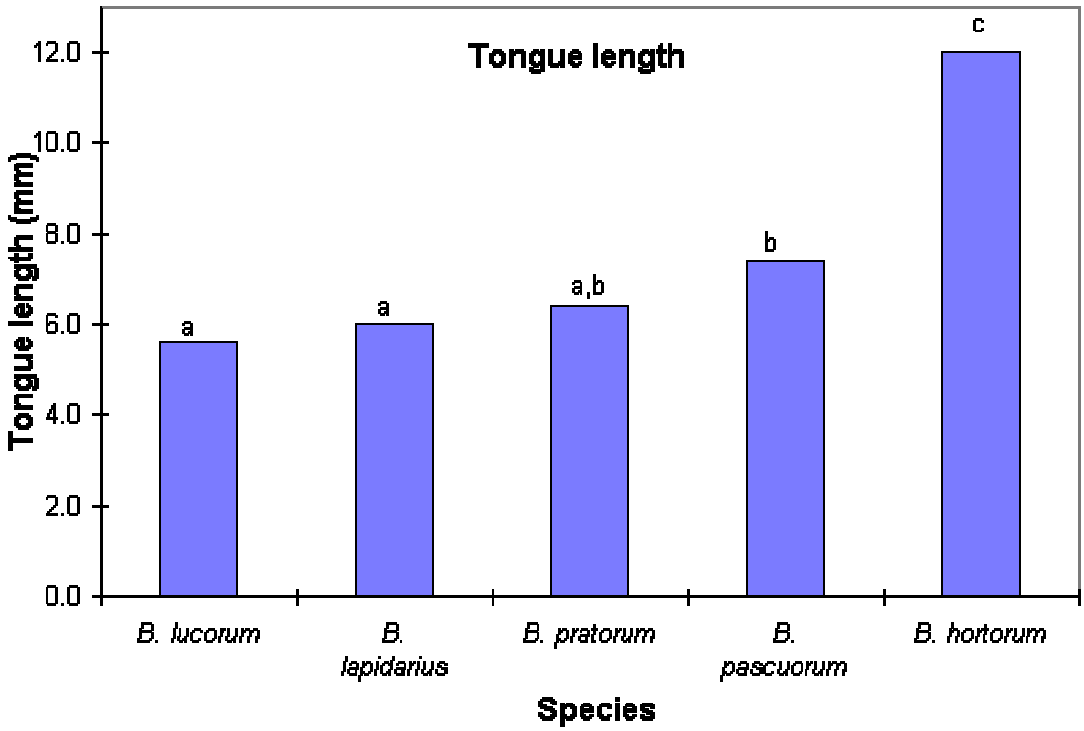


3.6 TONGUE AND HEAD MEASUREMENTS OF EACH SPECIES

The tongue and head measurements made in August were used to test the null hypothesis that there were no significant differences in these dimensions between the different species. The data for each species were compared using ANOVA, then Tukey's Honestly Significant Difference Test to compare between pairs of species, as is shown in FIGURE 8. All of the mean head lengths were significantly different from other species ($P < 0.05$), except for *Bombus lapidarius* and *B. pratorum*. For the mean tongue lengths *B. hortorum* was significantly different ($P < 0.05$) from all other species, and *B. pascuorum* was significantly different ($P < 0.05$) from all except *B. pratorum*. None of the mean head widths were found to be significantly different ($P = 0.06$). The tongue lengths measured were not the maximum lengths, which can really only be found after dissection, but the length that the bees were willing to extend in order to reach a reward during foraging.

FIGURE 8. Mean head and tongue length of bumblebees marked in August 1995. Columns designated with the same letter were not significantly different from each other at $P < 0.05$, all others were significantly different.





None of the head width means were found to be significantly different.

3.7 RELATIONSHIP BETWEEN TONGUE LENGTH AND FLOWER PREFERENCE

There appears to be some relationship between tongue length and flower preference, as the four shorter tongued bee species forage on Compositae for nectar, but *Bombus hortorum* does not, nor does it forage on the open flowers of *Cotoneaster simonsii*. However, the four shorter tongued bees have two distinct foraging patterns, which cannot be explained by tongue length. *B. pratorum* strongly prefers the Labiatae and *C. simonsii*, while *B. pascuorum* shares the preferences of *B. hortorum* and *B. pratorum*. *B. lapidarius* and *B. lucorum* prefer the Compositae, and the more accessible flowers of *Allium schoenoprasum*; these flowers require large numbers of probes for small rewards.

In tongue and head length *B. pratorum* and *B. lapidarius* are not statistically different, yet their preferred flower choices are very different, all of *B. pratorum's* preferred flowers for all three sessions were situated within a 3-4 m patch.

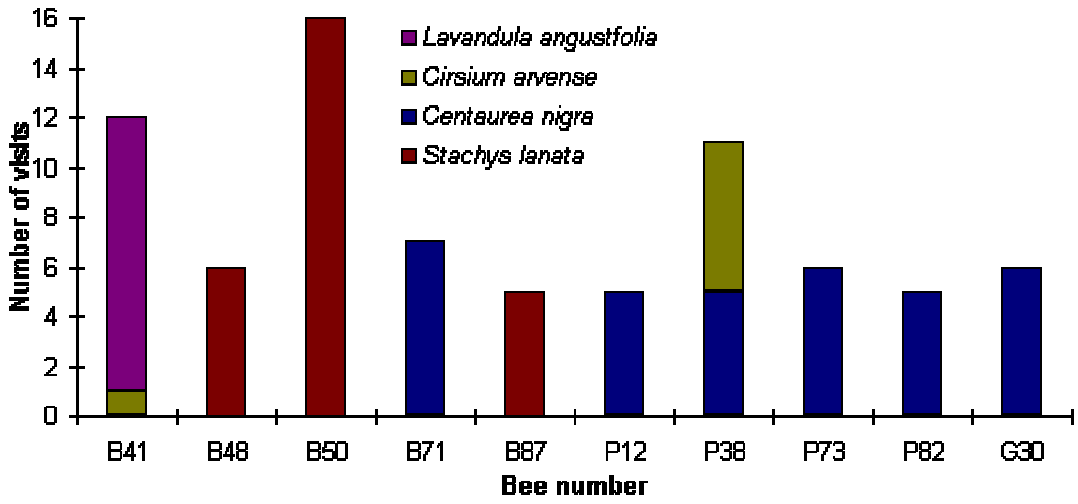
In August *B. lucorum* and *B. lapidarius*, with shorter tongues showed a preference for the Compositae and other "easy" flowers, requiring large amounts of probing for small rewards; this cannot be wholly explained by tongue length, as *B. pratorum*, with a similar tongue length did not show this preference, but strongly preferred the two clumped resources of *Stachys lanata* and *Lavandula angustifolia*, situated within 1.5 m of each other.

3.8 FLOWER PREFERENCES OF INDIVIDUAL BEES

Data gathered on marked bees during the bee walk were used to investigate the flower preferences of individual bees. For all species except *Bombus lapidarius*, data on individuals recorded five or more times were used; for *B. lapidarius*, the most common bee, only bees recorded eleven or more times were used. The individual preferences are shown in FIGURES 9, 10, 11 and 12. The data were gathered during the bee walk from 2nd-6th August, and also on 15th August, when the bee walk was done for one extra day, to record marked bees only. None of the bees recorded in the four graphs were male; although many males were re-sighted, they tended to be re-sighted less often than the workers.

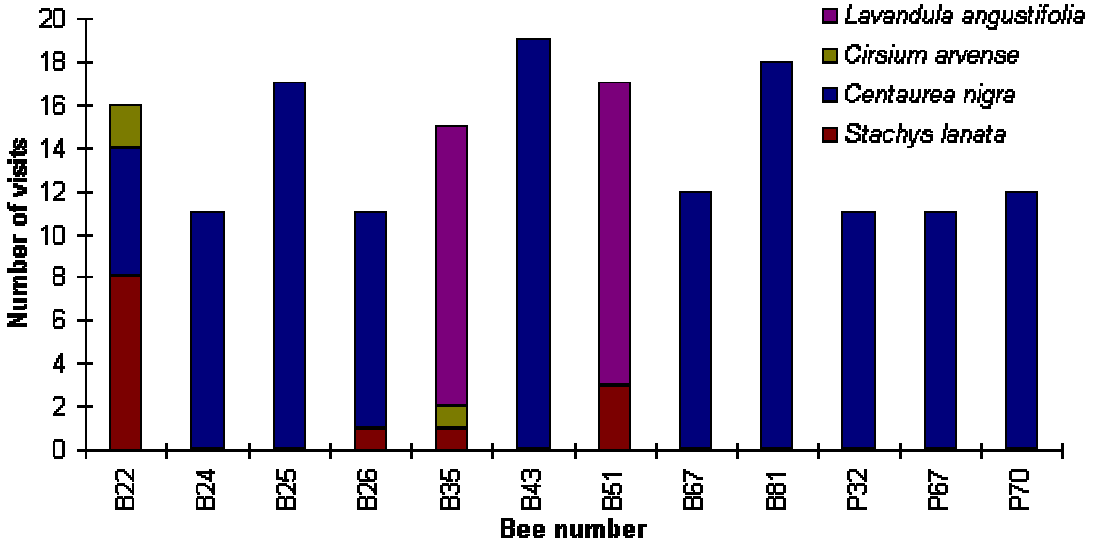
On FIGURE 9 (*B. lucorum*) the most noticeable thing is the constancy of the bees; of the ten bees, eight were recorded on one flower species only, but four different flower species were used overall. No hint of such constancy is apparent in FIGURE 6 showing species flower preferences. Another striking thing is the visits of B41 to *Lavandula angustifolia*. In FIGURE 6 visits to *L. angustifolia* make up less than 6% of the total visits. In all there were twelve recorded visits of *B. lucorum* to *L. angustifolia* during August, B41 made eleven of these.

FIGURE 9. *Bombus lucorum* preferences of individual workers on bee walk in August 1995



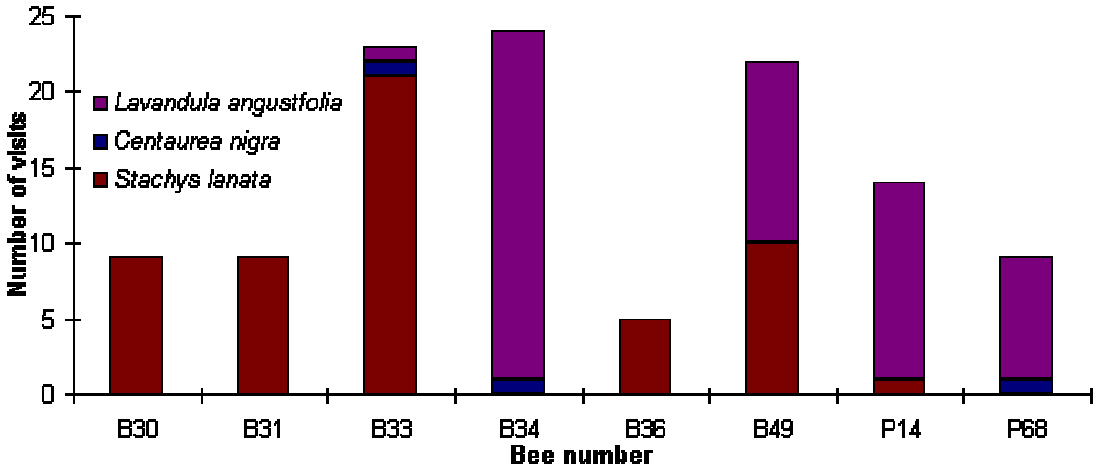
B. lapidarius in FIGURE 10 shows a strong preference for *Centaurea nigra*, as is shown for the species preference in FIGURE 6, however B35 and B51 show a strong preference for *L. angustifolia* and do not pay even one visit to *C. nigra*.

FIGURE 10. *Bombus lapidarius* preferences of individual workers on bee walk in August 1995



The preferences shown by individual *B. pratorum* on FIGURE 11 are the same as the species preference in FIGURE 6, i.e., for the two morphologically similar species, *Stachys lanata* and *Lavandula angustifolia*, although the preference ranges from 100% to almost 50-50% for individual bees.

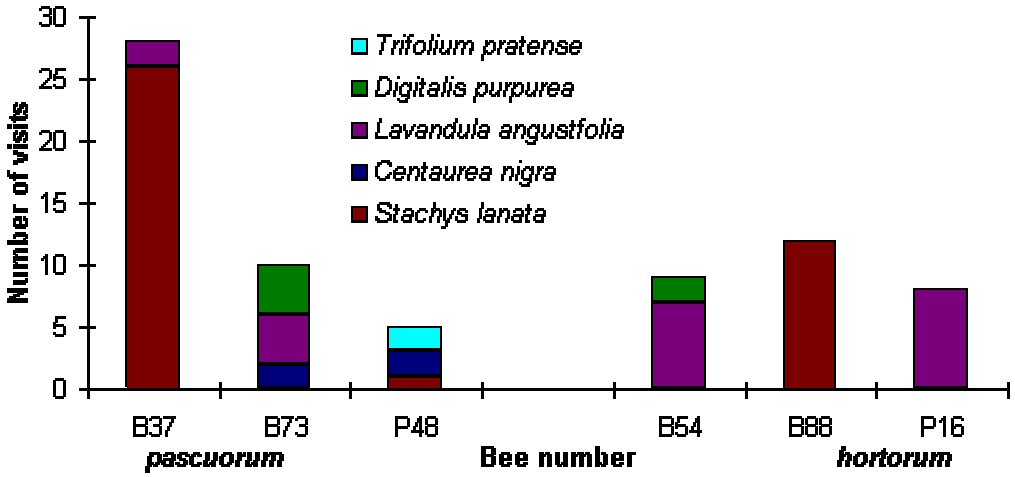
FIGURE 11. *Bombus pratorum* preferences of individual workers on the bee walk in August 1995



In August (FIGURE 6) *B. hortorum* as a species showed a strong preference for *Digitalis purpurea*, but the preferences of frequently seen individuals, (as shown in FIGURE 12), do not indicate any preference for *D. purpurea*. *Stachys lanata* and *Lavandula angustifolia* are the preferred flowers of the three individuals concerned.

Only one *B. pascuorum* individual showed a strong preference in FIGURE 12, the other two visited three flowers each, a high number compared with individuals of other species.

FIGURE 12. *Bombus pasuorum* and *B. hortorum* preferences of individual workers on bee walk in August 1995



The dataset available was too small, and the range of flowers too narrow, to indicate whether the morphology and/or colour of the major flower used by each species and/or individual influenced the choice of the minor flower(s).

3.8.1 CONSTANCY

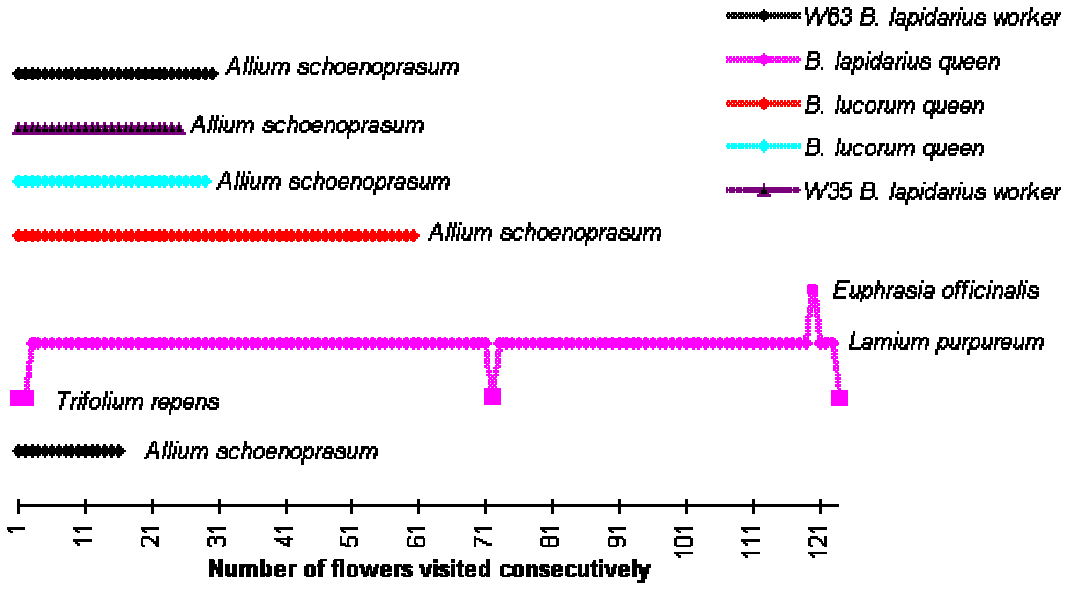
Individual bees were followed for extended periods on two days, 27th June and 7th August. On each day five bees were followed, and on each occasion one bee was followed twice, as it was re-sighted again, as another bee was lost. FIGURE 13 shows the consecutive visits of these bees to flowers. Most of the bees followed stayed within the bee walk area, but one bee, the *Bombus lapidarius* queen, foraged entirely outside the bee walk area on an area of lawn and topsoil on which weeds had grown. In this area there were 2500 heads of *Trifolium repens* and 3000 *Lamium purpureum*. The *T. repens* was a clumped resource but the L. purpureum was spread fairly evenly throughout the area covered by topsoil, and on part of the lawn. there was not a

clear boundary between the lawn and topsoil.

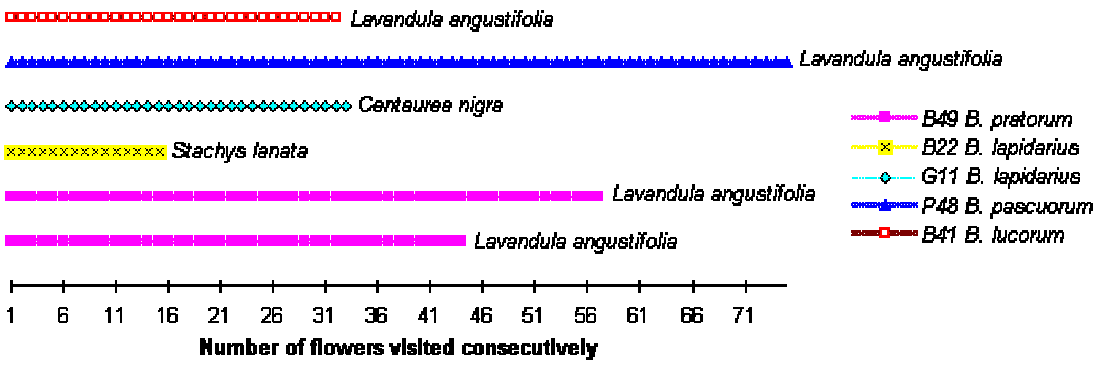
The most striking thing about FIGURE 13 is the almost complete constancy of the bees on a single foraging trip. Only one bee changed its flower use during a foraging episode. The foraging episodes varied in length from only 6-62 minutes. B41 (*B. lucorum*), is also shown in FIGURE 9, where it was recorded eleven times on *Lavandula angustifolia* and just once on *Cirsium arvense*. B49 is recorded twelve times on *L angustifolia* and ten times on *Stachys lanata* in FIGURE 11, whereas in FIGURE 13 it was followed twice and on both occasions it was 100% constant on *L. angustifolia*. P48 (*B. pascuorum*) is constant over a long run to L. angustifolia in FIGURE 13, but in FIGURE 12 it was recorded only twice on *L. angustifolia*.

FIGURE 13. Constancy of bumblebees followed on 27th June and 7th Augst 1995.

27th June 1995



7th August 1995



Too few bees were followed to calculate whether there is a statistical difference in constancy between individuals of different castes or species, but of the ten individuals from four species followed in June and August the constancy to a single species of flower was almost universal.

3.9 ENVIRONMENTAL VARIABLES AND THEIR EFFECTS ON FORAGING

The environmental variables appeared to have little effect on flower preference, there were no very cold periods during observations, and only a little light rain. During the bee walk sessions the temperature ranged from 9°C and 28°C, and the wind speed was between 0.3 and 7.9 m s.

BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

4 DISCUSSION

4.1 Species observed and comparative sizes of foraging populations
4.2 Marking and measuring of bees
4.3 Species flower preference
4.4 Individual flower preference
4.5 Constancy

4.1 SPECIES OBSERVED AND COMPARATIVE SIZES OF THE FORAGING POPULATIONS

Of the six species of bumblebee foraging on the site, *Bombus lapidarius* was the most common. There are no previous data on bumblebees for the site, however *B. lapidarius* with its distinctive colouring is easily recognisable and was certainly the most common bee in 1994 (pers. obs.) and possibly in previous years. *B. pascuorum* was also present on the site in 1994 and was seen foraging on *Digitalis purpurea* (pers. obs.).

On June 24th (FIGURE 3) *Bombus pascuorum* was not seen at all during the bee walk, whereas it had been seen on every previous day. The reason for this may be that Field B was being cut for silage that day and, as *B. pascuorum* is a surface nester preferring to nest in tussocky grass (Sladen, 1912; Alford, 1975), some of its nests were possibly being destroyed. The nests would have been at a very early stage, probably without adult workers. In the surrounding area this field was the best site for tussocky grass, the only other sites being roadside verges and field edges.

B. pascuorum bees did return to the site, but were never very numerous. The bee does not seem to have been resource limited, as *Lathyrus pratensis*, one of its flowers, was brimming with nectar during July, and so it may be that the limiting factor is safe nest sites. *B. pascuorum* is very useful for pollinating various clovers, so provision of safe nest sites should be considered important in areas where clover is an important agricultural crop.

In July all bees almost disappeared from the bee walk area, though many were seen flying overhead. It is believed that the bees were visiting nearby fields of oil seed rape, which must be considered an almost limitless resource during the period it is in flower. One field which had been sown with oil seed rape in 1994 and was fallow in 1995, but a sea of self-seeded rape was situated less than 1 km from the study site. In the same direction but about 1.5 - 2 km away were two fields sown with rape in 1995. Bumblebees forage as far as 2 km from their nests (Alford, 1975), so all of these fields would probably have been within foraging distance.

On the 9th of July almost two hours were spent walking in the set aside field, during that time only three bees were seen, all were *Bombus lapidarius*, two were foraging from *Lamium purpureum*, the other was flying low as if it were about to forage, or had just finished. So it appears that the bees had almost entirely deserted the site.

Bombus lapidarius was by far the most common bee in 1995, and possibly in previous years too; this may be because the site is ideally suited to it both in resources and nesting sites. As its name implies *B. lapidarius* likes to nest under stones (Sladen, 1912; Alford, 1975). In the study area and surrounding countryside most fields have dry stone dykes as their boundaries, many of these

are no longer repaired but they still provide excellent nest sites for *B. lapidarius*.

In the study site bumblebees always outnumbered honeybees, and apart from late April and early May, when honey bees were rare, there always seemed to be sufficient resources, no incidents of aggression or competition were witnessed during the whole study period.

4.2 MARKING AND MEASURING OF BEES

To investigate flower preferences and constancy of bees it is necessary to have a method for marking the bees safely, so that this will not interfere with their future behaviour, and will enable the bee to be recognised for at least the length of the intended observation period. It is also useful to have the opportunity of measuring the tongue and head length.

Brian (1957) had difficulty in persuading *B. hortorum* to drink, and could only get tongue measurements by killing the bees. She may have used sugar and water instead of honey and water, for *B. hortorum* readily drinks honey and water. When the first queens emerged in April and were foraging on heather, both honey and water and sugar and water were offered to them. None of the species could be persuaded to drink sugar and water, but all accepted honey and water. The smell of honey is perhaps more attractive.

Tongue length can be estimated using tongue-wing length regression equations (Morse, 1978) however this requires the tongues of a number of bees to be dissected out and measured when the bee is dead. This method was not suitable for this study, and in any case may not be the length actually extended during natural feeding. The connective tissue in the proboscis can enable the bee to extend its tongue making it 5-10% longer than the measured length when dissected (Inouye, 1980), also many bees do not always extend their tongues fully, especially if their honey stomach already contains a reasonable quantity of nectar (pers. obs.). If the bee is forced to regurgitate its nectar load, perhaps when too much force has been used when marking it, it will often extend its tongue further up the pipette to reach further into the honey and water. This was noticed about five or six times when measuring bees. Consequently it is believed that the correct and most "natural" tongue length is that measured using the pipette method in this study.

Marking bees on the dorsal surface of the abdomen would have given a bigger area to mark, and made identification on re-sighting easier. However, it was decided not to use the abdomen because wax is extruded from between the ventral tergites (Alford, 1975: Heinrich, 1979), and the hardening of the Tipp-Ex on the dorsal surface might have interfered with wax production and/or movement of the abdomen.

The marking technique appeared to work quite well and did not seem to harm the bees in any way, as many were re-sighted over long periods. Laverty (1993) glued plastic discs with numbers on to the thorax with quick drying glue, but never saw any of his marked bees again. Plastic discs with numbers already on them would probably be more easy to read than hand written numbers, so if a method could be found of sticking them to the thorax with a water based glue, or even with Tipp-Ex, this might prove to be an even better method.

The marking seemed to stand up well to wear and tear, and numbers written on 2nd August could still be read on 15th August, although the writing had faded a little. Unfortunately the weather during August was very dry so it is not possible to say how well the marks would stand up to prolonged wet weather.

The *B. lapidarius* worker that would not fly away (TABLE 1) was examined with a x10 hand lens to see if the Tipp-Ex was touching the tegulae or impeding wing movement. Neither was the case. The queens kept in artificial nest boxes were set free on 26th June. Two, a *Bombus terrestris*, and a *B. pratorum*, had reached the stage of building a honeypot, but neither had laid

eggs.

4.3 SPECIES FLOWER PREFERENCE

Each species had its own distinct flower preferences for each of the three sessions (FIGURES 4, 5 and 6). Preferences may be linked to the morphology and method of foraging flowers, as well as the length of corolla.

The Compositae provide the bee with a good landing platform and have many nectar sources, so that bees remain on one flower head for a long time. While on such a flower the bee can allow its temperature to drop, so saving energy, but it must then raise its body temperature before it can fly to the next flower. The usual method of raising the temperature is to shiver, this produces heat without moving the wings, and costs about the same in energy terms as flying. However there is another way the bumblebee can produce heat and this is by substrate cycling (Prys-Jones & Corbet, 1987), the enzyme required is fructose bisphosphate, and the process uses less energy for a given amount of heat produced than shivering does. *B. lapidarius* has over 60% higher fructose bisphosphatase activity than the bee with the next highest activity (*B. lucorum*) (Prys-Jones & Corbet, 1987). So it is possible for *B. lapidarius* to keep warm with greater energy efficiency than other bees, while it is foraging on flowers like Compositae, which require a lot of probing for small amounts of reward. In FIGURE 6 *B. lapidarius*, a short tongue species, shows greater than 75% preference for Compositae. In FIGURE 7 this percentage is increased for males, for whom foraging is not their only task. In FIGURE 4 *Allium schoenoprasum* is very strongly preferred by *B. lapidarius*, and the behaviour of the bees on this flower is similar to that on Compositae, as each head provides a good landing platform for multiple probing before flying off to the next head. Sladen (1912) lists the Composite *Centaurea nigra* as being one of the favourite flowers of *B. lapidarius* and also of *B. terrestris*.

In June (FIGURE 4) *B. lucorum* foraged from *Vicia sepium* by biting through the corolla, or calyx and corolla, to get at the nectar, this was also found by Brian (1957). *B. lapidarius* also foraged from *V. sepium*, but in July. Although the tongue lengths of both species of bee are similar, *B. lapidarius* always foraged from the flower in the correct manner.

The shorter-tongued bees, *Bombus lucorum* and *B. lapidarius*, prefer clumps or elevated flowers that they can land on and probe at random, even though the rewards per probe may be low. Brian (1957) noticed that *B. lucorum* preferred flowers in more exposed places, while *B. pratorum* and *B. pascuorum* preferred flowers in more sheltered places. In this study *B. pascuorum* was the only forager on *Vicia cracca*, and also foraged from *V. sepium* and *Lathyrus pratensis*, which were lower down in the vegetation. Brian (1951) found that *B. pascuorum* specialised in *Vicia* spp. and *Trifolium pratense*. In this study *Vicia* spp., *Trifolium* spp. and *Lathyrus pratensis* have the same handling difficulty (TABLE 2) as they have the same type of flower. *B. hortorum* could have foraged from these flowers, but preferred flowers growing in higher or more clumped situations.

B. hortorum (FIGURE 6) visited the fewest flower species, with its long tongue enabling it to specialise on long-corolla flowers such as *Digitalis purpurea*. The study area does not seem to be well suited to it in that there were rather few long corolla flower species. Tongue length appears to influence flower preference in that short tongues exclude certain species from certain flowers, and the awkwardness of moving a long tongue while standing on a flower make it impracticable for *B. hortorum* to forage from low reward Compositae. Before landing on a flower *B. hortorum* partially extends its tongue (Prys-Jones & Corbet, 1987), and when flying from flower to flower it keeps its tongue extended for longer trips than other species do. *B. hortorum* preferred the more difficult to handle flowers in this study, which may have offered larger rewards. However the range of flower difficulty was not very great in the study area, so this relationship might not exist in other sites with a more diverse range of flowers.

If long-tongued bees could forage profitably on short corolla flowers they would be generalists, and their food niche would overlap with all other bumblebee species, they would also be expected to be more numerous, but that was not the case in this study nor in other places (Ranta & Lundberg, 1980).

B. pratorum, the smallest sized bee, preferred the smaller gullet-shaped flowers (Faegri & van der Pijl, 1979), that possibly provide a greater reward per probe than do the Compositae, but require more movement between probes. During August one *B. pratorum* nest was located inside a water pump cover. The area was surrounded on three sides by clumps of *Centaurea nigra*, yet the bees from this nest flew through, around or over these plants to reach the clumps of *Lavandula angustifolia* and *Stachys lanata* that were located about 4 m away.

It appears that tongue length influences foraging choice by preventing short tongued bees foraging on long corolla flowers, and long tongued bees from foraging on inflorescences that are landing platforms, or open flowers. So tongue length can explain which flowers the bees will not forage on, but not which flowers they will forage on.

In New Zealand the forage crop clover (*Trifolium pratense*) did not set seed when introduced last century, so in 1884 some *B. terrestris* and *B. ruderatus* queens were sent over from England. Both species were well established within a few years (Sladen, 1912). In 1906 and 1907 *B. lapidarius* queens were sent, but five years later no *B. lapidarius* bees could be found (Sladen, 1912). Yet in this study *B. terrestris* (grouped with *B. lucorum*) never foraged on *T. pratense* or any of the other Leguminosae. *T. pratense* was foraged in this study only by *B. pascuorum*.

It was expected that the bees would forage from *Ulex europaeus* (Knuth, 1906) which was found along the bee walk, but they did not. When a bee forages from *U. europaeus* its weight triggers the release of the style and stamens which rise up to hit the underside of the bee, it is fairly easy to see whether a flower has been triggered or not. Neither of the two large *U. europaeus* on the bee walk route had any triggered flowers.

4.4 INDIVIDUAL FLOWER PREFERENCE

The preferences of the individuals are less easy to rationalise in relation to tongue length, they form a subset of the species preferences, but apart from that they do seem to be individual preferences. Why one individual chooses one species of flower, whilst another individual of the same species chooses a different species of flower is not clear. It may be just chance. Laverty (1980) observed that bumblebees found the location of nectar in flowers by trial and error, so the bee might decide to major on the first flower on which it located a reward above a certain threshold, after visiting both rewarding and unrewarding flowers, as Heinrich (1979a) observed. One or two bees decided that the pipette was a suitable resource, and seemed determined to revisit it. It did not resemble a flower, but it did provide a large reward. Perhaps within the guild of preferred flowers of a species, the choice of the individual is as Darwin (1891) said "The cause probably lies in insects being thus enabled to work quicker; they have just learnt how to stand in the best position on the flower, and how far and in what direction to insert their proboscides." Bumblebees ability to discriminate between different types of rewarding flowers decreases as the number of types increases (Dukas & Real, 1993), which would make it more profitable for them to restrict their foraging to only one or two species of flower, bypassing others even if they are also rewarding, as it would save handling time and also learning. This leads to the belief that once the major flower has been chosen it will influence or even limit the choice of the minor flowers, which in time may become majors. Laverty (1994) found that when bees in enclosures were forced to switch from one morphologically similar flower to another, they took only one third as long as naive bees to learn to handle the new flower species. So it is possible for a bee to transfer previous learning experience when switching to a flower that is similar in morphology and handling difficulty. Naive bees may be influenced to forage from a

flower that has an odour they recognise from the nest, they will have been drinking nectar brought back by other foragers, so may have become conditioned to one or a group of odours. More time may be spent trying to learn to handle a flower with a recognised odour. Insufficient data on major and minor flowers were gathered in this study to test this in the field. Waser, (1986) found that constancy to one type of flower increased as the array of flowers on offer increased in dissimilarity of morphology and colour. And Laverty, (1993) found that when bees were offered bouquets of real flowers, they switched to flowers of similar corolla length more often that could be expected if the choice were random.

4.5 CONSTANCY

The remarkable constancy shown by the bees when individuals were followed (FIGURE 13) was quite surprising. Most of the bees were foraging on clumped resources, but as FIGURES 9-12 show, they were aware of other good resources nearby. In particular B49, the *Bombus pratorum* forager who was followed twice within an hour or so, was on both occasions 100% constant to one of her preferred species, *Lavandula angustifolia*. Her other preferred species (FIGURE 11), *Stachys lanata*, was located only 1.5 m from the *L. angustifolia* clump, so it is unlikely that when the bee was lost sight of she was just moving to the *S. lanata*. Heinrich (1976) in a similar experiment of following bees found slightly lower rates of constancy, of sixteen foraging trips six were 100% constant, nine 85-98% constant, and one 57% constant, whereas in this study the figures were 100% for eleven trips, and 96% for one trip.

It was previously thought that bumblebees were relatively inconstant foragers (Brian, 1951; Free & Butler 1959; Real 1983), this belief arose largely through the analysis of pollen and the loose use of the term constancy. From data gathered in this small study it appears that on any one foraging trip, bumblebees are far more constant than was previously expected.

This study also shows that constancy varies according to how it is measured. Constancy has been measured at so many levels in the past that comparisons between different studies are difficult.

- Constancy of species was measured by Brian (1957) and in this study. Distinct preferences for certain species of flower were found, usually each species of bumblebee restricted itself to a few species of flower.
- Brian (1951) measured constancy at nest level by analysis of larval faeces. Again distinct preferences were found, similar to those of species level.
- Caste constancy was measured here and reflected the species preferences.
- Individual preferences were measured by Free, (1970) by pollen analysis of individual loads, who found that about half the loads were mixed, but many of these mixed loads were as much as 98% pure.
- Individual preferences were measured by Heinrich (1976, 1979, 1979a); and in this study, and it was found that bees tend to specialise on one or two species of flower; these flowers are a subset of the species preferences.
- Individual foraging trip was measured by Heinrich (1976, 1979, 1979a); and in this study, and it was found that there was much higher constancy than at any of the other levels.

At each level from species to individual trip the constancy increases. Consequently the use of the term constancy for anything other than an individual foraging trip is misleading. Free (1970) states that constancy should be measured over only one foraging trip, by either pollen analysis or direct observation. He then points out the main difficulty with direct observation, i.e. it is easy to lose sight of the bee. This difficulty can be partly overcome by marking bees and with miniaturisation and technological advances I am sure the day will soon arrive when a transmitter will be fitted to the thorax of a bee, making direct observation even easier. Pollen analysis will never be able to measure flowers visited for nectar, or pollen that has been discarded or eaten by the bee.

Waser (1986) also recognises the confusion caused by the words "constancy" and "preference". He defines two kinds of preference, and proposes using Bateman's index to measure constancy. Bateman's index can be used to measure accurately flower choice in an enclosure where there are two types of flower in equal numbers, of equal handling difficulty, both either with or without honey guides, and/or UV markings, and with equal quantities of reward at equal concentrations; in short, flowers that are identical in all but colour. Such a convenient situation is rarely found in the field, but where it is Bateman's index could be used.

"Constancy" should be restricted in use to the sequential movement of an individual animal from flower to flower, as it feeds or gathers resources. Measurements of flower usage that cover more than one foraging bout, or consider more than one individual, should be considered as "preferences". Waddington (1983) argues that the term "constancy" be replaced with "floral-visitation-sequences" as this term is "neutral", but surely this is just replacing one perfectly good, though misused term, that can be understood by both the scientific and non-scientific community, with a longer, less well understood term that will probably be misused in time.

Measuring constancy is a very difficult problem as there are so many variables that are constantly changing, and the very act of foraging causes some of the variables to change. Some form of sequential comparison index that can measure runs and breaks, but also takes into account the number of different species visited, and also the availability of the various flowers would be needed. Until such an index is available, constancy over one foraging trip can be assessed by presenting the data as a sequence of visits, as is shown by Heinrich (1976), and in FIGURE 13.

BUMBLEBEE FORAGING PREFERENCES: DIFFERENCES BETWEEN SPECIES AND INDIVIDUALS

5 SUMMARY

A simple and reliable marking technique for bumblebees, requiring inexpensive and easily obtainable equipment, was tested and under good weather conditions was found to be adequate, with marks surviving for at least fourteen days, allowing individual bees to be recognised. It appeared to have little or no effect on the behaviour of the bumblebees, as many were re-sighted foraging naturally (TABLE 1). At the same time as marking the bees, a simple field method of measuring the functional proboscis length and head measurements was developed and used.

In the "bee walk" a transect up a lane between two fields (FIGURE 1) was walked at two hour intervals, eight times a day, for five days during each of the three sessions throughout the summer season of 1995. The presence of actively foraging individual bees was recorded to investigate the flower preferences of species, caste and individuals, and whether individual bees or species showed preferences in their choice of flowers.

A program for calculating flower preference of bumblebees seen during the bee walk was used for the species and castes concerned (FIGURES 4-7). It was felt that it truly reflected what had been seen in the field and demonstrated real inter-species preferences.

Tongue length, which differs between some bumblebee species, may partially account for species flower preference, but there appear to be other factors, some physiological, that also contribute to flower preference.

Individual marked bees recorded in the bee walk were found to prefer a subset of the species flower preferences (FIGURES 9-12). There are many suggestions why an individual bee chooses to major on a particular flower species, but insufficient data were available to test any of these suggestions here.

The constancy of bees followed while foraging was remarkably high (FIGURE 13), and was compared to that of marked individuals recorded in the bee walk. In all cases the constancy and flower preference over one foraging trip was a subset of the preferences shown by the individual during the bee walk.

A review of the literature showed that the term constancy is used very loosely, and consequently bumblebees have been regarded as relatively inconstant foragers. This is because there have been studies at a nest and species level, as well as at the level of the individual foraging trip. Constancy is important because it facilitates the passing of pollen from one flower to another of the same species by an animal visitor, leading to successful pollination, so it is suggested that "constancy" should be used when referring to a single foraging trip, and "preference" to the differential use of different flower species on anything more than one foraging trip.

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