

Forage use and niche partitioning by non-native bumblebees in New Zealand: implications for the conservation of their populations of origin

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Abstract Bumblebees were introduced into New Zealand from the UK approximately 120 years ago and four species became established. Two of these, *Bombus terrestris* and *B. hortorum*, are common in Europe whilst two, *B. ruderatus* and *B. subterraneus*, have experienced declines, and the latter is now extinct in the UK. The presence of these species in New Zealand presents an opportunity to study their ecology in a contrasting environment. Forage visits made by bumblebees in New Zealand were recorded across a season. Ninety-six percent of visits were to six non-native forage plants (*Cirsium vulgare*, *Echium vulgare*, *Hypericum perforatum*, *Lotus corniculatus*, *Lupinus polyphyllus* and *Trifolium pratense*). All but *L. polyphyllus* are European plant species, and three are noxious weeds in New Zealand. Several of these plants have decreased in abundance in the UK, providing a potential explanation for the declines of *B. ruderatus* and *B. subterraneus* in Britain. In contrast to studies conducted elsewhere, *B. ruderatus*, *B. terrestris* and *B. hortorum* did not differ in diet breadth and overlap in forage use was high, probably due to the reduced diversity of bumblebee forage plants present in New Zealand. Diel partitioning of forage use between the species was observed, with foraging activity of *B. hortorum* greatest in the morning and evening, *B. ruderatus* greatest in the middle of the day and *B. terrestris* intermediate between the two. These patterns correspond to the climatic preferences of each species as evidenced by their geographic ranges. Implications for bumblebee conservation in the UK are discussed.

Keywords *Bombus* · Competition · Hymenoptera · Invasive weeds · Species introduction

Introduction

Bumblebees were introduced into South Island, New Zealand from the UK in 1885 and 1906 for the pollination of *Trifolium pratense*, which was widely cultivated as a fodder crop (Hopkins 1914). Four species (*Bombus terrestris*, *B. hortorum*, *B. ruderatus* and *B. subterraneus*) became established and spread rapidly (MacFarlane and Gurr 1995). *B. terrestris* is now ubiquitous throughout the North and South Islands, *B. ruderatus* and *B. hortorum* are widely distributed and at least locally common and *B. subterraneus* persists only in central South Island.

In the British Isles, *B. terrestris* and *B. hortorum* are common and widespread, but *B. ruderatus* has suffered severe declines in recent decades and *B. subterraneus* was declared extinct in the UK in 2000 (Edwards and Jenner 2005). The decline of these two species and of several others in the UK has been attributed to habitat degradation as a result of agricultural intensification (Williams 1986; Goulson et al. 2008a) and particularly to associated declines in the availability of the wild flowers on which these species feed (Carvell et al. 2006a).

Many factors may have facilitated the successful invasion of British bumblebees into New Zealand, including the similar climate and freedom from natural enemies (Donovan and Weir 1978). However, the most important factor is likely to have been the abundance of non-native plant species that have evolved alongside bumblebees in Europe and elsewhere. Bumblebees in New Zealand are rarely observed visiting native plant species (MacFarlane 1976; Donovan 1980; Goulson and Hanley 2004).

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Understanding why *B. ruderatus* and *B. subterraneus* persist in New Zealand when they have done so poorly in the UK could provide important insights for future conservation efforts for these species. This is of particular relevance since a project is currently underway to reintroduce *B. subterraneus* into the UK from New Zealand (Goulson, 2009). A major component of this project involves management of land for bumblebees adjacent to the proposed reintroduction sites, which currently support several rare British bumblebee species including *B. ruderatus*. In order for this to be successful, the forage requirements of these species throughout the season must be understood and met.

The exact details of the introduction of bumblebees to New Zealand are unknown but it is reported that at least six British bumblebee species were released in New Zealand (Hopkins 1914). Although *B. ruderatus* and *B. subterraneus* would have been more common in the UK than today, it seems likely that random selection of British bumblebees would have resulted in equal if not greater representation of other common species such as *B. lucorum* and *B. lapidarius*. It is not clear why the four existing species in New Zealand should have survived whilst others did not.

Bombus terrestris is a generalist, short-tongued bumblebee species that is able to make use of a wide range of different plant species for forage (Goulson and Darvill 2004; Goulson et al. 2002, 2005) and has shown high invasiveness, having become established in Tasmania, Japan and Israel (Semmens et al. 1993; Goulson 2003; Matsumara et al. 2004). However, *B. ruderatus*, *B. hortorum* and *B. subterraneus* are all long-tongued Fabaceae specialists (Goulson et al. 2005). All three have a known preference for *T. pratense* and studies have reported strong overlaps in forage use between these species (Goulson et al. 2005, 2008b). Therefore, it might be predicted that competition between these three species should be high, particularly when introduced into a novel environment which is likely to provide a limited breadth of resources in comparison to those available within their native range.

Data collected by Goulson and Hanley (2004) indicate that the diet breadth of New Zealand bumblebee populations are indeed reduced compared with figures calculated within their native ranges and that forage visits by all four species are largely restricted to a handful of non-native forage plants. Overlap in forage use was evident between the species, and as might be expected, this was particularly true for the three long-tongued species.

These findings were based on records collected over a 3 week recording period beginning towards the end of early colony foundation, providing only a snapshot view of the forage requirements of these species. However, in order to thrive, bumblebees require a continuous supply of forage throughout the spring and summer. Changes in forage use

across the season are currently unknown for New Zealand bumblebees. In this study, forage visits were recorded across a whole season in order to provide a more complete picture of forage use by European bumblebees in New Zealand. These data could help to inform management practices for the conservation of rare bumblebees and may be of particular relevance to the development of suitable strategies for the reintroduction of *B. subterraneus* in the UK. Aspects of niche partitioning between the three most abundant bumblebee species in New Zealand are also investigated in order to assess how competitive interactions might be reduced by differences in forage use and/or timing of foraging.

Methods

Field work

Field work was carried out in the MacKenzie District and Central Otago regions of South Island, New Zealand between the 11th December and the 15th February 2008–2009. These regions were selected because they are the only areas of New Zealand within which the four bumblebee species coexist (Goulson and Hanley 2004).

Searches of one man hour were conducted at 121 sites across the study area, following an established technique which has been used for a number of previous studies of forage use by bumblebees, facilitating comparisons across studies (Goulson and Darvill 2004; Goulson and Hanley 2004; Goulson et al. 2005, 2008b). All sites were at least 1 km away from neighbouring sites and the locations of the sites were chosen at random so that all areas were represented across the full temporal range of the study. The sites searched were approximately 100 m in radius and were selected based on habitat type and the presence of known bumblebee forage plants. Sites were either lake or river margins or areas of rough pasture or scrub, since these habitat types were found by Goulson and Hanley (2004) to attract all four bumblebee species present in New Zealand. Searches were conducted between 9am and 7 pm, during warm, dry weather and the exact location, date and time of day was recorded for each search. All bumblebees observed were identified to species and caste and their behaviour was recorded as either pollen collecting (if active brushing of pollen into the corbicula was observed) or nectar collecting. The plant species on which the bee was foraging was also recorded. At each site, the number of open flowers or inflorescences of each plant species present was estimated. The recording period was chosen such that it would span the full range of bumblebee activity in the region: from emergence of spring queens through colony development and growth, to the production of new queens and males at the end of the season. As a result, all castes

were represented and the requirements of each species across a whole season could be identified.

Dawn until dusk studies were also carried out to look for differences in activity patterns throughout the day between the four bumblebee species. Ten surveys were conducted between the 2nd and the 19th February 2009. These were conducted at distant sites spread across the study area and only in dry weather. At each survey site transects of 110 m in length were marked out through high quality patches of forage, chosen to include plants known to be attractive to all four of the species present. The transect was walked at a constant speed at sixteen regular intervals between first light (approximately 6am) and sundown (approximately 9.30 pm) and any foraging worker bumblebees seen within a distance of three metres on either side of the transect were recorded to species level. Prior to each transect walk, the temperature and relative humidity were recorded. Transects were walked alternately by two observers.

Analysis

Statistical analyses were conducted using SPSS 16.0. *B. subterraneus* was excluded from all analyses due to low numbers of observations of this species, although data are presented on forage use for this species.

A chi-square test of independence was used to examine species-specific differences in forage use. Only the six most commonly visited plant species were included in this analysis since number of visits to other species was low. The proportions of visits (all species combined) to each of the six most commonly visited plant species for the collection of pollen versus nectar were also compared in order to assess the relative usage of these plants by bumblebees for the provision of each resource.

Simpson's index of diversity (Simpson 1949) was calculated for the forage plants visited by each species at each site in order to provide a measure of diet breadth. Data were summed across caste and foraging behaviour and only those sites in which five or more individuals of that species were recorded were included. All plant species were included in this analysis. A Kruskal-Wallis test was used to compare diet breadths among species.

Niche overlap was calculated (following Colwell and Futuyma 1971) between every species pair for each site in which both species in the pair were represented by five or more individuals. Again, all plant species were included in this analysis.

In order to assess changes in forage availability and use over time, the study period was divided into four recording periods (11th–31st December, 1st–15th January, 16th–31st January, 1st–18th February). The proportion of total forage plant availability represented by each of the most frequently visited six species was calculated for each recording period.

A plant species was classified as a forage plant if five or more visits were observed during the course of the study (“Appendix”). The aim of this was to remove plants such as those belonging to *Heracleum* spp. which were abundant but despite occasional visits were not commonly used for forage. The proportion of bumblebee visits (all species combined) to each of the six most commonly visited plant species was also calculated per recording period.

Bee visits recorded during dawn until dusk sampling were summed over each two consecutive transect walks to control for observer bias, resulting in the division of the day into eight regular recording periods. Bee visits within each period were then expressed as proportions of the total visits observed across the day for each species. Data were normalised using an arcsine transformation and a repeated measures analysis of variance was carried out with recording period as a covariate and species as a factor such that a test for an interaction effect between species and recording period allowed a comparison of temporal influence on daily activity patterns among species. A Pearson product moment correlation was used to assess the relationship between temperature and relative humidity across all sites and time points.

Results

A total of 7,612 foraging bees were recorded including queens, workers and males of all four bumblebee species present in New Zealand (Table 1). *B. ruderatus* and *B. terrestris* were by far the commonest bumblebee species, constituting 95% of all observations and found throughout the study area. *B. subterraneus* was also found throughout the study area, but in very low numbers (constituting <1% observations), whilst observations of *B. hortorum* were largely restricted to the south-west and north-east of the study area (Fig. 1).

Forage use

Bumblebees were recorded visiting 28 different introduced and one native plant species (appendix 1) but 96% of all

Table 1 Numbers of bumblebee forage visits observed divided by species, caste and pollen or nectar collection

	Queen		Worker		Male	Total
	Nectar	Pollen	Nectar	Pollen	Nectar	
<i>B. hortorum</i>	4	0	228	23	73	328
<i>B. ruderatus</i>	120	9	1,628	222	534	2,513
<i>B. subterraneus</i>	2	0	16	1	14	33
<i>B. terrestris</i>	164	37	2,431	941	1,165	4,738
Total	290	46	4,303	1,187	1,786	7,612

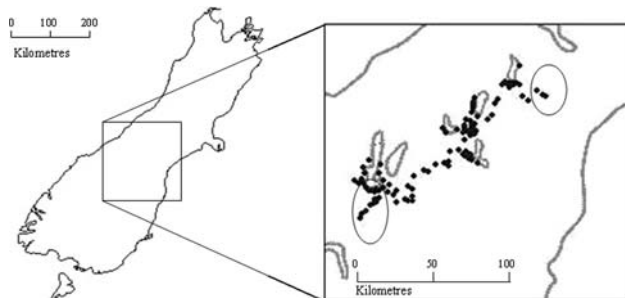


Fig. 1 Sites within South Island, New Zealand at which hour bumblebee searches were conducted. Circled areas indicate areas where *B. hortorum* were commonly observed

forage visits were to just six introduced plant species (*Cirsium vulgare*, *Echium vulgare*, *Hypericum perforatum*, *Lotus corniculatus*, *Lupinus polyphyllus* and *T. pratense*). Visits to *E. vulgare* made up the majority of observations (74%). *B. terrestris* was the only species to be observed foraging on a native plant species (*Acaena saccaticupula*) and these visits accounted for just 0.2% of total visits by this species. When forage visits were combined across sites and castes, no species-specific differences were observed in visitation rates to the six most commonly used forage plants ($\chi^2_{10} = 0.65$, $P \approx 1$; Fig. 2).

There was no evidence for differences in diet breadth between *B. terrestris*, *B. ruderatus* and *B. hortorum* ($\chi^2_2 = 1.30$, $P = 0.523$; Table 2) and diet breadths calculated for all three species were low compared to values calculated for the same species in previous studies (Table 2). Niche overlaps for forage use were high for all possible pairs of species (Table 2) suggesting that all three species are utilising very similar resources.

Though too few *B. subterraneus* were sampled to include in any analysis, all visits by this species were to four of the six plant species most commonly used by other

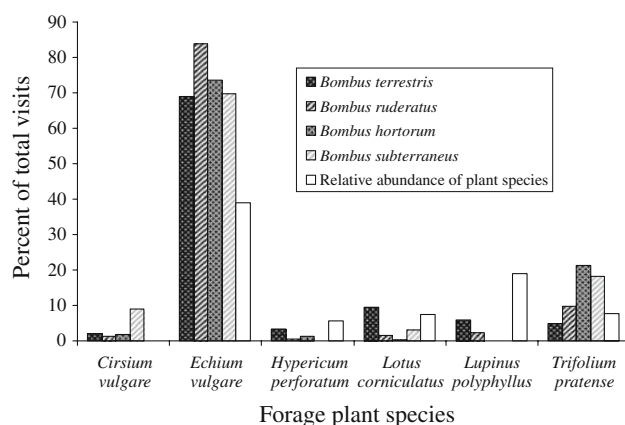


Fig. 2 Percentages of forage visits made by four European bumblebee species in New Zealand to the six most commonly visited wild flower species

bumblebees in New Zealand (*E. vulgare*, *C. vulgare*, *L. corniculatus* and *T. pratense*).

Nectar collecting bumblebees demonstrated different patterns of forage use compared to pollen collecting bumblebees (Fig. 3). *E. vulgare* accounted for 80% of nectar collecting visits but only 44% of pollen collecting visits. Conversely, *L. corniculatus* and *L. polyphyllus* (both belonging to the Fabaceae family) were rarely visited by nectar collectors but attracted many more pollen collecting bumblebees. *C. vulgare* was only ever visited for nectar whilst *T. pratense* accounted for approximately 7% of visits by both pollen and nectar collecting bees.

Forage use over time

In December, the six preferred forage plants made up just 46% of total forage plant availability (Fig. 4a), but accounted for 96% of foraging visits (Fig. 4b). Visitation to *E. vulgare* was always high (accounting for between 54 and 86% of total visits) regardless of the abundance of this species in relation to that of other forage plants. The proportion of visits to *L. corniculatus* and *T. pratense* generally reflected the relative abundance of these species, whilst use of *L. polyphyllus* reflected the relative abundance of this plant early in the season, but decreased as other plant species increased in relative abundance over the season. Use of *H. perforatum* showed a peak in early January, when the relative contribution of this species to overall forage was at its highest, but visits to this species decreased in late January and February. *C. vulgare* was always relatively uncommon, and being late flowering, contributed greater than 1% to overall forage availability only in February during which the contribution of this species was almost 3%. During this time, visits to this species were disproportionately high, mainly as a result of the preference of males for feeding on this species (“Appendix”). It was not uncommon to see multiple individuals on a single inflorescence of *C. vulgare*.

Differences in daily activity patterns between species

Activity of all bumblebee species was affected by time of day ($F_{7,140} = 8.09$, $P < 0.001$) but there were also species-specific differences in activity patterns across a day (interaction effect, $F_{14,140} = 2.12$, $P = 0.014$). Both *B. terrestris* and *B. ruderatus* demonstrated low levels of activity in the early morning and late evening, but showed a peak of activity in the afternoon (Fig. 5a). This pattern was more pronounced for *B. ruderatus* which showed a very steep activity curve with a high peak activity rate. Activity of *B. terrestris* was more evenly distributed with activity remaining high across time points 4–6 (approximately 12 noon until 5.30 pm). *B. hortorum* showed very

Table 2 Indices of diet breadth and niche overlap calculated for the three bumblebee species present in New Zealand in different studies (Indices calculated with data collected in this study include standard error in brackets)

Diet breadth				
Reference	Country	<i>B. ruderatus</i>	<i>B. hortorum</i>	<i>B. terrestris</i>
Goulson and Hanley (2004)	New Zealand	2.07 ^a	2.05 ^a	4.43 ^a
Goulson and Darvill (2004)	UK	NA	2.57 ^a	7.27 ^a
Goulson et al. (2008b)	Poland	3.5	3.02 ^a	8.63 ^a
Current study	New Zealand	1.56 (± 0.101)	1.36 (± 0.096)	1.67 (± 0.097)
Overlap in forage use				
Reference	Country	<i>B. rud/B. hort</i>	<i>B. rud/B. terr</i>	<i>B. terr/B. hort</i>
Goulson and Darvill (2004)	UK	NA	NA	0.19 ^a
Goulson et al. (2008b)	Poland	0.78	0	0.02
Current study	New Zealand	0.83 (± 0.047)	0.7 (± 0.036)	0.67 (± 0.085)

^a Where values were calculated separately for caste or foraging behaviour, the average value is presented

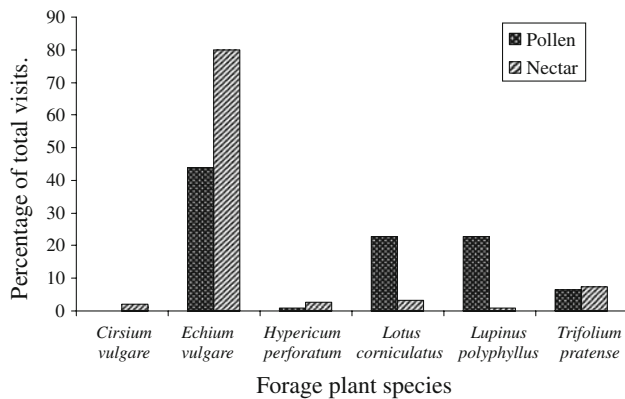


Fig. 3 Percentages of forage visits made by European bumblebees in New Zealand to the six most commonly visited wild flower species split by pollen and nectar collecting visits

different patterns of activity compared to the other two species, being most active early in the morning and at time points 4 and 7 (approximately 1 and 6.30 pm, respectively), either side of the peak of activity for *B. ruderatus*.

Temperature increased throughout the day until time point 6 (approximately 5.30 pm) and then began to drop off towards the end of the recording period (Fig. 5b). Relative humidity was negatively correlated with temperature (Pearson correlation coefficient = -0.73, $P < 0.001$).

Discussion

As in previous studies (Goulson and Hanley 2004; Donovan 1980), bumblebee populations in New Zealand were found to rely almost entirely on non-native plant species for forage and just six of these constituted the majority of forage visits across all four species within the study area.

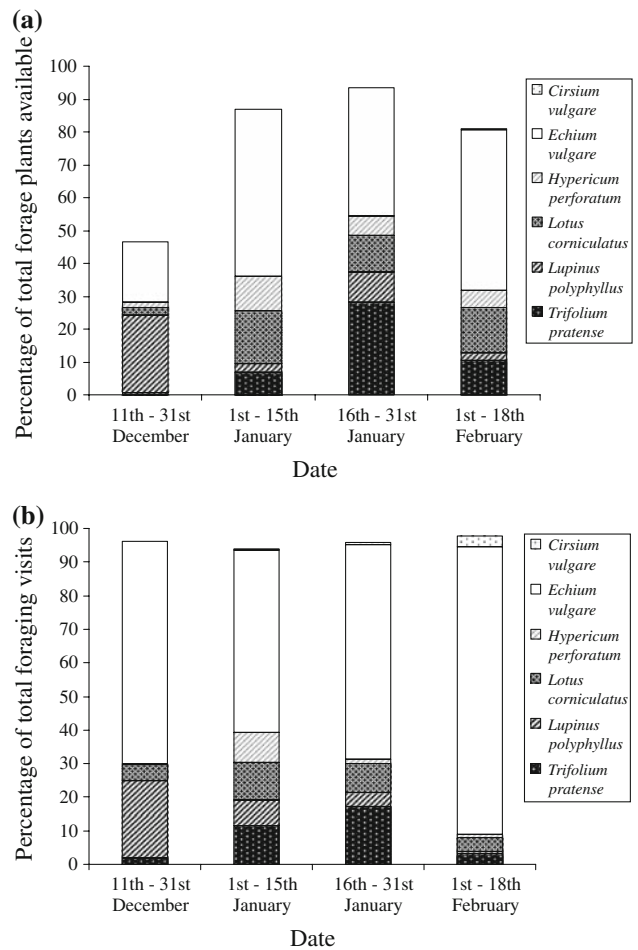


Fig. 4 Percentages of **a** available forage attributable to the six most commonly visited forage plant species and **b** foraging visits made to these six species by date

Despite the diverse life-history stages encompassed, patterns of forage use were fairly consistent across the study period, although the importance of *C. vulgare* increased

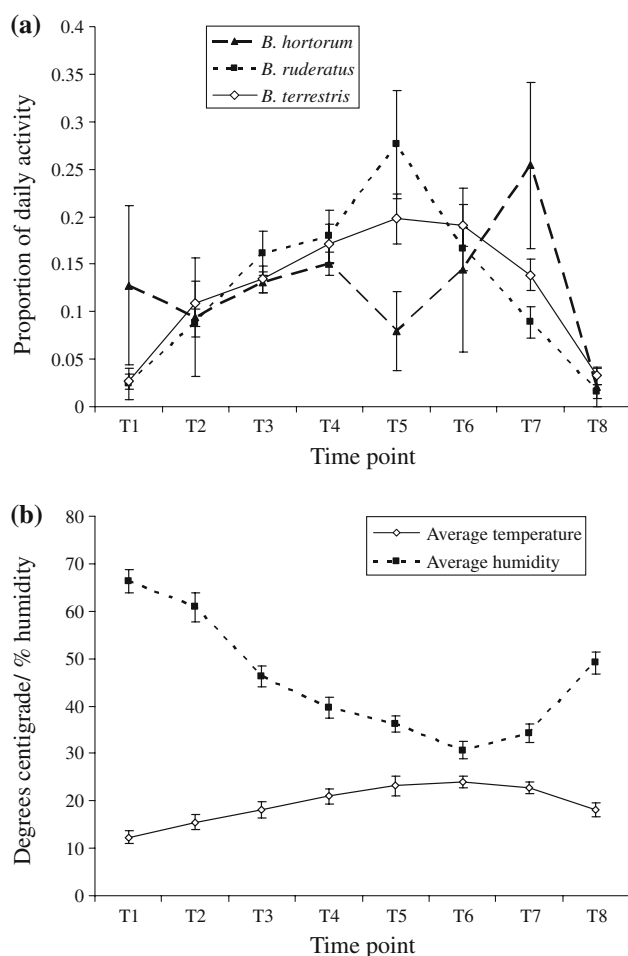


Fig. 5 Average **a** proportion of daily foraging activity of three bumblebee species and **b** daily temperature and humidity at eight evenly spaced (average 114 min) time points over a day (\pm standard error). Points represent the average of two transects per time period across ten sites. Times are not given since the exact times of each time point vary depending on the day length

towards the end of the study, apparently providing an important source of forage for males. That males may differ in forage requirements to workers and queens has previously been shown in the UK (Carvell et al. 2006b) and is an important consideration for the development of management strategies for bumblebees. In this study, *E. vulgare* was a particularly important forage plant species, accounting for the majority of visits observed. The phenology of this species is such that it continued to flower for the duration of the study and the availability of this favoured forage plant throughout the period during which bumblebees are active may be at least partially responsible for the success of bumblebees in New Zealand.

Whilst *E. vulgare* made up the majority of nectar collecting visits, *L. polyphyllus*, *L. corniculatus* and to a lesser extent, *T. pratense* were also commonly visited for pollen. This reflects their high quality pollen in terms of both

protein content and provision of essential amino acids (Hanley et al. 2008; Weiner et al. 2010). *L. polyphyllus* flowered early in the season and in December, foraging visits to this species were numerous. *L. corniculatus* and *T. pratense* flowered later in the season and when these species became more abundant, *L. polyphyllus* was visited proportionately less. *L. corniculatus* and *T. pratense* are important sources of forage for bumblebees in the UK (Goulson and Darvill 2004; Carvell et al. 2004, 2007) whilst *L. polyphyllus* originates from North America (Hanley and Goulson 2003). This study suggests that *L. polyphyllus* may also provide an important source of high quality pollen early in the season in New Zealand.

In contrast to findings presented here, Goulson and Hanley (2004) found that *T. pratense* was more commonly visited than *E. vulgare*. Additionally, diet breadth indices calculated by Goulson and Hanley (2004) were larger than those calculated here. These differences can be accounted for by the fact that the previous study included a wider range of habitat types and covered a wider area of New Zealand than did the current study. In this study, and in that of Goulson and Hanley (2004), diet breadth indices were low for all species compared to those reported elsewhere (Goulson and Darvill 2004; Goulson et al. 2008b). This is particularly notable for *B. terrestris* which is a very generalist species and is typically observed foraging on a wide range of different plant species including many that are not native within its natural range (Hingston and McQuillan 1998; MacFarlane 1976). Since New Zealand's native bees are generally much smaller than bumblebees (Donovan 1980), native plant species are unlikely to be suitable for exploitation by bumblebees, rendering them almost entirely dependent on introduced plant species.

The finding that both long and short-tongued bumblebee species can thrive on a narrow spectrum of plants has important consequences for conservation strategies. That bumblebee communities may often make use of very few plant species for the majority of forage visits has been demonstrated in many studies elsewhere (Thomson 2006; Goulson et al. 2005; Carvell et al. 2007) and it is clear from data presented here that a diverse floral community is not necessarily required to support declining species such as *B. ruderatus*.

A strong overlap in forage use between *B. ruderatus* and *B. hortorum* is consistent with the findings of Goulson et al. (2008b), but high levels of overlap between *B. terrestris* and the two long-tongued species are in contrast to values presented elsewhere (Goulson and Darvill 2004; Goulson et al. 2008b). Within their native range, overlap in forage use between long- and short-tongued species is often low since bumblebees tend to visit flowers with corolla-lengths that correspond to the length of their tongue (Ranta and Lundberg 1980; Harder 1985). This may provide a

mechanism of niche partitioning, reducing competitive interactions and facilitating the coexistence of several bumblebee species (Inouye 1978; Pyke 1982; Goulson et al. 2008b). Findings presented here suggest that the limited diversity of suitable bumblebee forage plants present in New Zealand forces long-tongued and short-tongued species to share the same floral resources. An associated increase in competitive pressure between bumblebee species in New Zealand may provide a partial explanation for the failure of some species to persist following their initial introduction.

The findings of this study suggest that those bumblebee species that do persist in New Zealand may avoid competition by partitioning forage use throughout the day such that each species makes use of floral resources at different times. In particular, *B. ruderatus* was found to forage predominantly in the middle of the day when conditions were hot and dry, whilst *B. hortorum* foraged early in the morning and either side of the peak activity time for *B. ruderatus* when temperatures were cooler and humidity higher. *B. ruderatus* has a more southerly distribution than *B. hortorum* in Europe (MacFarlane and Gurr 1995) and shorter hair than that of *B. hortorum* (Sladen 1912), suggesting that *B. ruderatus* is adapted to warmer and drier environmental conditions than *B. hortorum*. Since many other sympatric bumblebee species do not share identical geographic ranges (Williams 2005), differences in environmental tolerances leading to differential patterns of activity may be widespread and could provide an additional explanation for coexistence. Indeed, similar patterns were reported in Sweden by Hasselrot (1960) who found that nest traffic commenced earlier and continued until later in *B. hypnorum* than *B. terrestris* (as found here for *B. hortorum*) and that *B. lapidarius* demonstrated a pattern of activity that was very similar to that observed here for *B. ruderatus*.

Another possibility is that floral availability does not limit bumblebee populations in New Zealand but that other ecological parameters are more important in determining bumblebee success. For example, nest site availability for bumblebees may be low in New Zealand (Fussell and Corbet 1992) and may therefore limit bumblebee numbers.

Implications for the conservation of bumblebees in the UK

Both this study and that of Goulson and Hanley (2004) demonstrate a heavy reliance of New Zealand bumblebees on a small number of plant species. Of these, several (including *E. vulgare*, *L. corniculatus* and *T. pratense*) have shown marked declines in the UK (Grime et al. 1988; Rich and Woodruff 1996; Carvell et al. 2006a) perhaps explaining the current rarity of *B. ruderatus* and the

extinction of *B. subterraneus* in the UK. The promotion or supplementation of populations of these plant species in the proposed area of release of *B. subterraneus* in the UK (Dungeness in Kent—Goulson 2009) may be beneficial for the survival of reintroduced individuals and is also likely to confer benefits to other bumblebee species currently persisting within these areas.

The low numbers of *B. subterraneus* recorded in this study are of concern considering the current plans to reintroduce this species into the UK. Goulson and Hanley (2004) report that this species appeared to be present within a more restricted range than that reported by MacFarlane and Gurr (1995) in their survey of the distribution of bumblebees in New Zealand (based on records from 1969 to 1991) and suggested that this species may be declining in New Zealand. Whilst *B. subterraneus* was found throughout the study site, this species made up proportionately fewer observations than in Goulson and Hanley's study (2004), suggesting that this apparent decline is ongoing. The mechanisms behind the decline of *B. subterraneus* in New Zealand are likely to be similar to those acting in the UK. The withdrawal of government subsidies for the sowing of leguminous crop plant species such as *T. pratense* and *L. corniculatus* on agricultural land in New Zealand is likely to have dramatically reduced forage availability in the rural environment (Goulson and Hanley 2004).

It is notable that three of the six most commonly visited plant species (*E. vulgare*, *H. perforatum* and *C. vulgare*) were listed as pest plants under the New Zealand Noxious Weed Act in 1950 (<http://www.maf.govt.nz/mafnet/rural-nz/sustainable-resource-use/land-management/emerging-weeds/appendices/appendix-a.htm>) and several studies demonstrate that the spread of weeds is often facilitated by the presence of non-native pollinator species (Barthell et al. 2001; Stout et al. 2002; Goulson and Derwent 2004). The high rate of visitation to these plants by bumblebees in New Zealand indicates that they may play an important role in the pollination and/or out-crossing of these weed species, potentially facilitating their spread throughout New Zealand and acting as a threat to native ecosystems.

Conclusions

British bumblebees in New Zealand rely on a small number of non-native plant species on which to forage. Several of these species have declined in the UK, perhaps providing an explanation for the declines of two out of the four New Zealand bumblebee species in Britain. The provision of these plant species should be considered in management targeted towards the conservation of these species and could form a basis for habitat management strategies associated with the reintroduction of *B. subterraneus* into the UK.

An understanding of mechanisms of coexistence is vital for the effective conservation of communities of related species. *B. ruderatus* and *B. hortorum* may exhibit temporal partitioning of resources throughout the day and this can be explained as a result of differences in environmental tolerances of these two, otherwise very similar, species. This suggests that the balance between these species may be maintained by environmental conditions and that alteration in climatic conditions could shift the balance such that one species is favoured and may exclude the other. This phenomenon may be widespread and further investigation is required.

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Appendix

See Table 3.

Table 3 All forage visits by bumblebees to different flower species split by species, caste and pollen (P) or nectar (N) collection

	<i>B. hortorum</i>			<i>B. ruderatus</i>			<i>B. subterraneus</i>			<i>B. terrestris</i>			Total								
	Queen		Worker	Queen		Worker	Queen		Worker	Queen		Worker									
	N	P	N	N	P	N	N	P	N	N	P	N									
	N	P	N	N	P	N	N	P	N	N	P	N									
<i>Acaena saccaticupula</i> ^a	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	0	8			
<i>Buddleja davidii</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	3	4		
<i>Calystegia sepium</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1		
<i>Cirsium palustre</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	8	31	56		
<i>Cirsium vulgare</i>	0	0	1	0	5	0	0	10	0	20	0	0	0	0	3	0	0	12	84	135	
<i>Digitalis purpurea</i>	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0	1	2	0	0	6	
<i>Echium vulgare</i>	2	0	173	9	57	103	5	1,399	124	476	1	0	11	0	11	150	21	1,755	381	960	5,638
<i>Eschscholzia californica</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Heracleum</i> spp. ^b	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	3
<i>Hypericum perforatum</i>	0	0	4	0	0	0	0	15	1	0	0	0	0	0	0	1	0	149	11	1	182
<i>Leontodon</i> spp.	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	20	0	17	41
<i>Linarea purpurea</i>	0	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4	7
<i>Lotus corniculatus</i>	0	0	0	1	0	1	0	17	16	2	0	0	0	1	0	0	0	151	264	34	487
<i>Lupinus arboreus</i>	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	2	0	6
<i>Lupinus polyphyllus</i>	0	0	0	0	0	8	2	19	28	1	0	0	0	0	0	3	13	25	239	1	339
<i>Medicago sativa</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	38	9	0	47
<i>Mentha × piperita</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Origanum vulgare</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<i>Papaver rhoeas</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Prunella vulgaris</i> ^b	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
<i>Reseda luteola</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	1	9
<i>Rosa rubiginosa</i>	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	2	1	6
<i>Rubus fruticosus</i> ^b	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	4
<i>Silene vulgaris</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Trifolium pratense</i>	2	0	49	12	7	2	0	160	49	33	1	0	5	0	0	10	0	183	20	17	550
<i>Trifolium repens</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	32	4	5	43
<i>Trifolium vesiculosum</i> ^b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
<i>Verbascum thapsus</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	15	1	2	20
<i>Verbascum virgatum</i>	0	0	0	0	0	2	0	4	1	0	0	0	0	0	0	0	1	4	0	0	12
Total	4	0	228	23	73	120	9	1,628	222	534	2	0	16	1	14	164	37	2,431	941	1,165	7,612

^a Plant species native to New Zealand

^b Plant species that were not classified as forage plant species due to low visitation rates by bumblebees

References

- Barthell JF, Randall JM, Thorp RW, Wenner AM (2001) Promotion of seed set in yellow star-thistle by honey bees: evidence of an invasive mutualism. *Ecol Appl* 11:1870–1883
- Carvell C, Meek WR, Pywell RF, Nowakowski M (2004) The response of bumblebees to successional change in newly created arable field margins. *Biol Conserv* 118:327–339
- Carvell C, Roy DB, Smart SM, Pywell RF, Preston CD, Goulson D (2006a) Declines in forage availability for bumblebees at a national scale. *Biol Conserv* 132:481–489
- Carvell C, Westrich P, Meek WR, Pywell RF, Nowakowski M (2006b) Assessing the value of annual and perennial forage mixtures for bumblebees by direct observation and pollen analysis. *Apidologie* 37:326–340
- Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficiency of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *J Appl Ecol* 44:29–40
- Colwell RK, Futuyama DJ (1971) On the measurement of niche breadth and overlap. *Ecol* 52:567–576
- Donovan BJ (1980) Interactions between native and introduced bees in New Zealand. *NZ J Ecol* 3:104–116
- Donovan BJ, Weir SS (1978) Development of hives for field population increase, and studies on the life cycle of the four species of introduced bumble bees in New Zealand. *NZ J Agric Res* 21:733–756
- Edwards M, Jenner M (2005) Field guide to the bumblebees of Great Britain and Ireland. Ocelli, UK
- Fussell M, Corbet SA (1992) The nesting places of some British bumble bees. *J Apic Res* 31:32–41
- Goulson D (2003) Effects of introduced bees on native ecosystems. *Annu Rev Ecol Evol Syst* 34:1–26
- Goulson D (2009) Short-haired bumblebee reintroduction project storms ahead!. Buzzword: Newslett Bumblebee Conserv Trust 11:8–9
- Goulson D, Darvill B (2004) Niche overlap and diet breadth in bumblebees. Are rare species more specialized in their choice of flowers? *Apidologie* 35:55–64
- Goulson D, Derwent LC (2004) Synergistic interactions between an exotic honeybee and an exotic weed: pollination of *Lantana camara* in Australia. *Weed Res* 44:195–202
- Goulson D, Hanley ME (2004) Distribution and forage use of exotic bumblebees in South Island, New Zealand. *NZ J Ecol* 28:225–232
- Goulson D, Stout JC, Kells AR (2002) Do alien bumblebees compete with native flower-visiting insects in Tasmania? *J Insect Conserv* 6:179–189
- Goulson D, Hanley ME, Darvill B, Ellis JS, Knight ME (2005) Causes of rarity in bumblebees. *Biol Conserv* 122:1–8
- Goulson D, Lye GC, Darvill B (2008a) Decline and conservation of bumble bees. *Annu Rev Entomol* 53:191–208
- Goulson D, Lye GC, Darvill B (2008b) Diet breadth, coexistence and rarity in bumblebees. *Biodivers Conserv* 17:3269–3288
- Grime JP, Hodgson JG, Hunt R (1988) Comparative plant ecology. Unwin Hyman, London
- Hanley ME, Goulson D (2003) Introduced weeds pollinated by introduced bees: cause or effect? *Weed Biol Manag* 3:204–212
- Hanley ME, Franco M, Pichon S, Darvill B, Goulson D (2008) Breeding system, pollinator choice and variation in pollen quality in British herbaceous plants. *Funct Ecol* 22:592–598
- Harder LD (1985) Morphology as a predictor of flower choice by bumblebees. *Ecol* 66:198–210
- Hasselrot TB (1960) Studies on Swedish bumble bees (genus *Bombus* Latr.); their domestication and biology. *Opusc Entomol Suppl* 17:1–192
- Hingston AB, McQuillan PB (1998) Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Aust J Ecol* 23:539–549
- Hopkins I (1914) History of the bumblebee in New Zealand: its introduction and results. *NZ Dep Agric Ind Commer* 46:1–29
- Inouye DW (1978) Resource partitioning in bumblebees: experimental studies of foraging behaviour. *Ecol* 59:672–678
- MacFarlane RP (1976) Bees and pollination. In: Ferro DN (ed) *New Zealand insect pests*. Lincoln University College of Agriculture, New Zealand, pp 221–229
- MacFarlane RP, Gurr L (1995) Distribution of bumble bees in New Zealand. *NZ Entomol* 18:29–36
- Matsumara C, Nakajima M, Yokoyama J, Waishitini I (2004) High reproductive ability of an alien bumblebee invader, *Bombus terrestris*, L., in the Hidaka region of southern Hokkaido, Japan. *Jpn J Conserv Ecol* 9:93–102
- Pyke GH (1982) Local geographic distributions of bumblebees near Crested Butte, Colorado: competition and community structure. *Ecol* 63:555–573
- Ranta E, Lundberg H (1980) Resource partitioning in bumblebees: the significance of differences in proboscis length. *Oikos* 35:298–302
- Rich TCG, Woodruff ER (1996) Changes in the vascular plant floras of England and Scotland between 1930–1960 and 1987–1988: The BSBI monitoring scheme. *Biol Conserv* 75:217–229
- Semmens TD, Turner E, Buttermore R (1993) *Bombus terrestris* (L.) (Hymenoptera: Apidae) now established in Tasmania. *J Aust Entomol Soc* 32:346
- Simpson GH (1949) Measurement of diversity. *Nat* 163:688
- Sladen FWL (1912) *The humble-bee, its life history and how to domesticate it*. Macmillan, UK
- Stout JC, Kells AR, Goulson D (2002) Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biol Conserv* 106:425–434
- Thomson DM (2006) Competitive interactions between the invasive European honey bee and native bumble bees. *Ecol* 85:458–470
- Weiner CN, Hilpert A, Werner M, Linsenmair KE, Blüthgen N (2010) Pollen amino acids and flower specialisation in solitary bees. *Apidologie* (in press). doi:10.1051/apido/2009083
- Williams PH (1986) Environmental change and the distribution of British bumblebees (*Bombus* Latr.). *Bee world* 67:50–61
- Williams PH (2005) Does specialization explain rarity and decline among British bumblebees? A response to Goulson et al. *Biol Conserv* 122:33–43