Distribution and forage use of exotic bumblebees in South Island, New Zealand

D. Goulson and M.E. Hanley

Division of Biodiversity and Ecology, School of Biological Sciences, University of Southampton, Biomedical Sciences Building, Bassett Crescent East, Southampton SO16 7PX. United Kingdom. (E-mail: DG3@soton.ac.uk)

Abstract: The rapid decline in bumblebee populations within Europe has been linked to habitat loss through agricultural intensification, and a consequential reduction in the availability of preferred forage plants. The successful introduction of four European *Bombus* species to the South Island of New Zealand from England (in 1885 and 1906) provides an opportunity to determine how important different forage plants (also introduced from the U.K.) are to two severely threatened European bumblebee species (*Bombus ruderatus* and *B. subterraneus*). In January 2003 we conducted a survey of bumblebee populations across 70 sites in the central and southern South Island, recording which plant species were being used as pollen and nectar sources for each *Bombus* species. All four bumblebee species showed a clear preference for plants of European origin. Only *B. terrestris*, the most polylectic species, was recorded feeding on native plant species. The longer-tongued bumblebees, *B. hortorum*, *B. ruderatus*, and *B. subterraneus*, foraged predominantly on just two plant species; *Trifolium pratense* for both nectar and pollen, and *Echium vulgare* for nectar. These plant species are now declining in abundance in the U.K. Our results provide support for the hypothesis that the loss of flower-rich meadows, particularly those containing populations of Fabaceae species with long corollae, is responsible for the decline of bumblebee species across Europe. Comparison with earlier bumblebee surveys suggests that long-tongued bumblebees may also be in decline in New Zealand, particularly *B. subterraneus* which is now very localised and scarce.

Keywords: alien weeds; *Bombus*; nectar; pollen; rarity; *Trifolium pratense*.

Introduction

Following a series of introductions from England in the late nineteenth and early twentieth century, four native European bumblebees (*Bombus* spp.) became established in New Zealand. These species, *B. hortorum*, *B. terrestris*, *B. subterraneus*, and *B. ruderatus* were released on the South Island to improve pollination of the forage plant *Trifolium pratense* (Hopkins, 1914). Following their introduction, each species spread throughout large areas of the South Island, and by 1960 all but *B. subterraneus* had successfully colonised the North Island (Gurr, 1964). The most recent survey (MacFarlane and Gurr, 1995) suggested that *B. terrestris* and *B. ruderatus* were ubiquitous throughout New Zealand, while the distributions of *B. hortorum* and *B. subterraneus* were more restricted, the latter only occurring in central South Island.

One of these species, *B. subterraneus* is now probably extinct in the U.K., while *B. ruderatus* is exceedingly rare. The former was once found throughout southern England, but by the period 1960-1980 both species had almost disappeared. *Bombus subterraneus* was last recorded in England from Dungeness, Kent in 1988 and also appears to be declining throughout much of its native range in Europe. Similarly, *B. ruderatus* was once common throughout England (its common name is the Large Garden Bumblebee), but by 2001 it was thought to be extinct. It has since been rediscovered at a handful of sites in East Anglia. Both *B. terrestris* and *B. hortorum*, by contrast, remain common throughout most of North-western Europe (Goulson, 2003a).

It seems likely that, in Europe at least, agricultural intensification is primarily responsible for the decline of many bumblebee species (Rasmont, 1988; Osborne and Corbet, 1994; Goulson, 2003a), although it is difficult to provide unequivocal evidence. More specifically, it is likely that the large-scale loss of species-rich grasslands in Europe has significantly reduced forage availability for wild bees (Rasmont, 1988; O'Toole, 1994; Gathmann *et al.*, 1994). However, it is not clear why some bumblebee species have declined greatly, while others remain abundant. There is some evidence that common bumblebee species

such as *B. terrestris* tend to have broader foraging preferences than co-occurring rare species (such as *B. humilis*), and are thus perhaps better able to cope with declines in habitat quality (Goulson and Darvill, 2003). Our knowledge of the ecology of very rare bumblebee species such as *B. subterraneus* and *B. ruderatus* is limited by the obvious practical difficulties in studying them, at least within their native range.

The successful colonisation and spread of European bumblebees in New Zealand provides an excellent opportunity for ecologists to examine the foraging and habitat requirements of these rare species, and to shed light on some of the causes of decline in their native range. Furthermore, since it is potentially possible to reintroduce *B. subterraneus* and *B. ruderatus* to England from New Zealand, a detailed understanding of the ecology of these species in New Zealand is valuable.

In this study we surveyed the current distributions of the four introduced bumblebee species in the central and southern South Island, and attempt to determine whether their distributions have altered by comparison with an earlier study. We test whether particular bee species are associated with particular habitat types. We also recorded the foraging activities of each species in order to determine the variety of plant species visited (both native and introduced), their relative importance in terms of supplying pollen and nectar, and to test the hypothesis that rarer species have narrower diets.

Materials and methods

Bumblebee abundance and foraging preference was determined from 1-hour searches conducted within each of 70 sites located in central and southern South Island (Figure 1). Surveys were conducted between 2-23 January 2003 and were concentrated within the Canterbury and Otago regions where *B. subterraneus* had previously been recorded and where *B. ruderatus* is also abundant (MacFarlane and Gurr, 1995). Within this region, sites were selected to cover as broad an altitudinal range as possible (5 to 931 m. a.s.l.), and to include all vegetation types. Sites were only searched if at least some bumblebee forage plants were present. Searches were carried out between 8am and 7pm, and only in weather favourable to bumblebee activity. Site position and altitude was measured using a hand-held GPS, and habitats were broadly classified as: lake margins (all lakes were surrounded by rough pasture and scrub, and most had lush marginal vegetation containing Fabaceae); native vegetation (scrub or forest with few introduced weeds, only found at high altitude and/or in the far south and west); river beds and margins (invariably rich in weeds such as *Lupinus*

arboreus); rough pasture and scrub (usually rich in weeds such as *Echium vulgare* and *Cirsium* species); semi-improved or improved pasture (often containing sown Fabaceae); gardens. All bumblebees seen at each site were recorded; where the species could not be identified, the bee was caught and killed for later identification. Relationships between abundance of each bumblebee species and habitat type were examined with Kruskal Wallis tests, and between abundance and altitude and latitude with Spearman's rank correlations (altitude and latitude are each likely to be crudely correlated with climate).

For every bee that was observed foraging, we recorded the flower species they were visiting, and whether they were collecting pollen or nectar. Bees were recorded as pollen collectors if they were seen to groom pollen into their pollen baskets and if the baskets contained pollen of an appropriate colour for the flower being visited. Many bees classed as pollen collectors were also collecting nectar.

To compare the diet breadth of the species recorded, a Simpson's index was calculated for the diversity of flowers visited (Simpson, 1949):

$$D_s = \sum_{i=1}^{s} \frac{(n_i(n_i - 1))}{(N(N-1))}$$

where n_i is the number of flowers of the *i*th species that were visited, N is the total number of flowers visited, and s is the total number of flower species visited. Results are presented as $1/D_s$, so that larger values indicate higher diversity. This index is insensitive to sample size (Magurran, 1988), important because samples are inevitably larger for the more common species.

Results

Bumblebee distribution and abundance

The most abundant species by far were *B. terrestris* (882 bees recorded) and *B. hortorum* (771 bees). *B. ruderatus* was locally abundant (293 bees), while *B. subterraneus* was restricted in distribution and always scarce. Although searches were targeted at areas where *B. subterraneus* had previously been recorded, only 38 individuals of this species were found. *Bombus terrestris* was the only species recorded in areas of native vegetation.

Bombus terrestris was found at nearly all sites and altitudes (Fig. 1) and no relationships were found between abundance and altitude or latitude (Spearman's $r = 0.02$ and -0.05, respectively, $P > 0.05$). For example, large populations were found at Milford Sound (annual rainfall approx 7000 mm) and throughout the Canterbury Plains (annual rainfall as
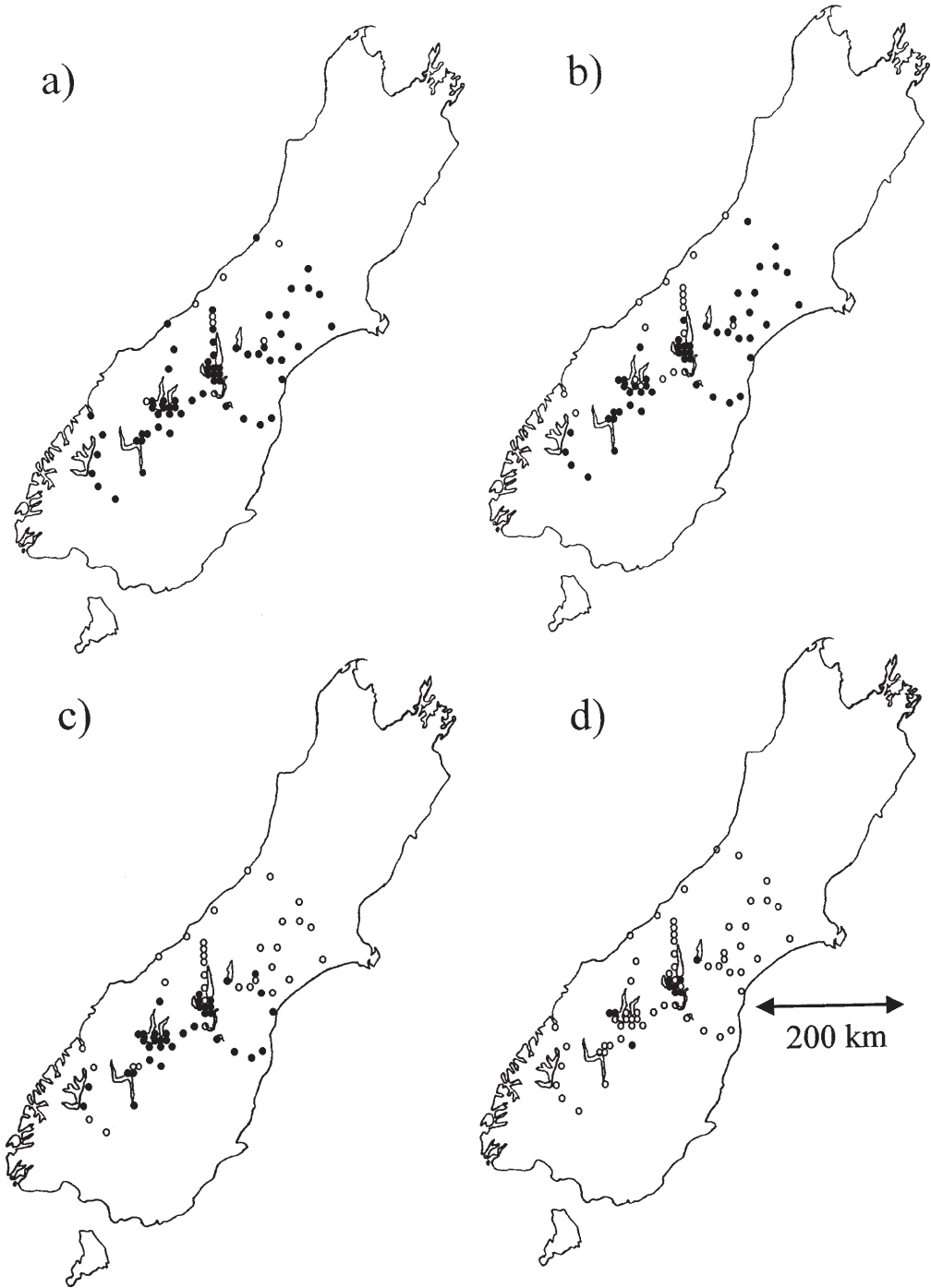
Figure 1. The distribution of four bumblebee species recorded within 70 sites across central and southern South Island, New Zealand: a) *B. terrestris,* b) *B. hortorum,* c) *B. ruderatus,* d) *B. subterraneus*. Each site was searched for 1 hour. Closed circles indicate sites where each species was found; open circles indicate sites where they were absent.

Table 1. Numbers of each bumblebee species observed, according to habitat type (means for a 1-hour search). Differences in abundance between habitat types were examined using a Kruskal Wallis test.

| | B. terrestris | | B. hortorum | | B. ruderatus | | B. subterraneus | | Number |
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	of sites
Lake margins	14.2	4.8	7.1	1.9	5.9	1.6	3.3	1.3	10
Native vegetation	3.0	2.1	0	0	0	0	0	0	8
River margins	20.0	4.2	6.6	2.2	2.6	1.7	0	0	11
Rough pasture and scrub	16.8	3.8	8.5	2.4	6.7	2.1	0.3	0.2	20
Improved/semi-improved pasture	7.5	1.8	23.2	6.2	3.8	1.5	0	0	19
Gardens	11.0	10.0	0	0	0	0	0	0	2
Kruskal Wallis χ^2, d.f. = 5	15.5**		24.7***		16.6**		32.6***		

low as 300 mm). However, abundance showed a marked relationship to habitat type, with the highest numbers recorded along river margins, lakes, and in rough pasture (Table 1). Very few *B. terrestris* were present in areas of native vegetation.

Bombus hortorum was also widespread, but was generally more common at higher latitudes (Spearman's $r = 0.24$, $P = 0.05$). It was also absent at the very highest sites, although the relationship between altitude and abundance was not statistically significant ($r = 0.22$). *Bombus hortorum* was not found on the West Coast. Abundance varied greatly between habitats, with *B. hortorum* being three times more abundant in areas of semi-improved and improved pasture than in any other habitat (Table 1).

Bombus ruderatus was largely confined to the hilly country of the central South Island, between about 100 and 930 m altitude and was absent from the Canterbury Plains and the West Coast. There was no significant correlation between abundance and altitude ($r = -0.04$), but this species was significantly more common in the southern ($r = 0.52$, $P < 0.001$) and eastern ($r = -0.33$, $P = 0.006$) parts of our study area. *Bombus ruderatus* exhibited marked habitat preferences (Table 1), being most abundant in rough pasture (particularly arid, overgrazed and infertile pasture in which *E. vulgare* was invariably abundant), as well as lake margins.

Bombus subterraneus was confined to a small region of the central South Island between 44° 00' and 44° 58' S, 168° 56' and 170° 282' E, and between 210 and 710 m in altitude. Perhaps because of the restricted distribution of *B. subterraneus*, there were no significant relationships evident between abundance and altitude or latitude ($r = 0.19$ and 0.03, respectively). *Bombus subterraneus* was notably more abundant in lake margins than elsewhere (Table 2). All sites where *B. subterraneus* was recorded were <2 km from a lake. The largest populations were found on the southern

shore of Lake Tekapo, and around two smaller lakes, Wairepo Arm and Lake Ruataniwha, near Twizel. Another modest population was located further south near Lake Wanaka. These lakes are in areas that were otherwise fairly arid and infertile. The lake margins provided flushes of *T. pratense* and *L. corniculatus*, while *E. vulgare* was abundant in the surrounding areas. Wherever *B. subterraneus* was found the other three species were also present.

Our survey was conducted in January which would appear to be towards the beginning of the bumblebee colony cycle, since worn queens of all four species were observed (*Bombus hortorum* queens were rare, whereas queens of *B. terrestris* and *B. ruderatus* were often common). At one high altitude site (603 m) *B. ruderatus* queens were the most common bumblebees. *Bombus subterraneus* queens were only recorded at Lake Tekapo, the highest site where this species was found (710 m), suggesting that elsewhere nest-founding queens of this species had stopped foraging. Males of *B. terrestris* and *B. hortorum* were observed in small numbers, particularly in the lowlands, but no males of *B. ruderatus* or *B. subterraneus* were recorded.

Forage use

A large proportion of visits by all four bumblebee species were made to just two introduced plants species, *Trifolium pratense* and *Echium vulgare* (44.7% and 26.7% of visits, respectively). Almost all visits were to introduced plants; of the 39 plant species on which bumblebees were recorded, only 3 were native to New Zealand. Only *B. terrestris* was recorded foraging on these native flowers [*Hebe canterburiensis, Metrosideros excelsa* (in a garden) and *Phormium tenax*], and did so only rarely. The majority (27) of the introduced plant species visited by bumblebees were of European origin, the remainder (9) being native to South Africa, North America, and Australia. *Bombus terrestris* was by far the most polylectic bumblebee

Table 2. Bumblebee visits to flowers when collecting nectar (n) or pollen (p), summed for 70 sites in the South Island of New Zealand. Figures are the percentage of all visits to each plant species. Only the twelve most-visited plant species are shown. These account for 96% of all visits to flowers. Simpson's Index provides a measure of the diversity of flowers visited (and is based on all flower species visited).

Forage plant	B. terrestris worker p	n	queen p	n	male n	B. hortorum worker p	n	queen p	n	male n	B. ruderatus worker p	n	queen p	n	B. subterraneus worker p	n	queen n	Total no. of visits
Trifolium pratense	9.6	22.9	16.7	32.0	22.7	85.5	47.6	33.3	30.0	42.9	76.2	34.4	50.0	27.3	66.7	46.7	0.0	887
Echium vulgare	22.1	35.9	25.0	42.0	63.6	4.1	37.5	0.0	30.0	7.1	7.1	55.9	0.0	62.1	0.0	26.7	100.0	530
Lotus corniculatus	24.3	4.8	0.0	2.0	0.0	3.2	0.0	0.0	0.0	0.0	6.3	1.1	0.0	0.0	23.8	0.0	0.0	119
Trifolium repens	8.5	15.6	0.0	7.0	0.0	0.6	1.1	0.0	0.0	0.0	0.8	1.1	0.0	0.0	0.0	6.7	0.0	110
Cirsium vulgare	0.0	4.4	0.0	2.0	9.1	0.0	3.3	0.0	10.0	7.1	0.0	1.1	0.0	0.0	0.0	0.0	0.0	38
Hypericum perforatum	7.0	0.0	8.3	0.0	0.0	0.9	0.0	0.0	0.0	0.0	7.9	0.0	12.5	0.0	9.5	0.0	0.0	37
Lupinus polyphyllus	5.1	0.0	8.3	3.0	0.0	0.2	0.4	33.3	0.0	0.0	0.0	0.0	12.5	9.1	0.0	0.0	0.0	28
Cirsium arvense	0.4	4.6	8.3	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.7	0.0	25
Lupinus arboreus	5.5	1.1	16.7	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	12.5	0.0	0.0	0.0	0.0	25
Digitalis purpurea	0.0	0.2	0.0	0.0	0.0	1.3	3.6	0.0	30.0	0.0	0.8	3.2	0.0	1.5	0.0	0.0	0.0	25
Medicago sativa	4.4	1.5	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	20
Cytisus scoparius	7.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	19
others:	6.3	8.8	16.7	11.0	2.3	3.8	6.5	33.3	0.0	42.9	0.8	3.2	12.5	0.0	0.0	13.3	0.0	121
Total visits	272	454	12	100	44	469	275	3	10	14	126	93	8	66	21	15	2	1984
Simpson's Index	7.2	4.7	NA	3.6	2.2	1.4	2.7	NA	NA	NA	1.7	2.3	NA	2.2	2.1	NA	NA	

species, visiting 36 of the 39 plant species, the workers showing the highest Simpson's index for both pollen and nectar use (Table 2). *Bombus hortorum* was recorded on 19 plant species, *B. ruderatus* on 13 plant species, and *B. subterraneus* on 7 plant species.

When collecting pollen, three species (*B. hortorum, B. ruderatus* and *B. subterraneus*) all appeared to depend largely on *T. pratense* (Table 2). In the areas where *B. ruderatus* and *B. subterraneus* were found, *T. pratense* is rarely grown as a fodder crop, but was frequently associated with road verges, lake margins and rough pasture. Besides *T. pratense*, the main pollen sources for *B. ruderatus* workers were *Hypericum perforatum*, *E. vulgare* and *L. corniculatus* (Table 2). *Bombus subterraneus* workers were only recorded collecting pollen from three plant species; *T. pratense*, *L. corniculatus* and *H. perforatum* (Table 2). Few queens of any species were recorded collecting pollen. Like workers, *B. terrestris* queens had the broadest range of pollen sources, while of the eight pollen-collecting *B. ruderatus* queens observed, half were visiting *T. pratense*.

When collecting nectar, *E. vulgare* and *T. pratense* were the preferred source for all four bumblebee species (Table 2). *B. hortorum, B. ruderatus* and *B. subterraneus* made very few nectar-collecting visits to any other flowers. Nectar-foraging preferences of queens largely followed those of workers. *Bombus terrestris, B. hortorum* and *B. ruderatus* queens collected nectar largely from *T. pratense* and *E. vulgare*,

while the only two queens of *B. subterraneus* observed were collecting nectar on *E. vulgare*.

Discussion

In terms of numerical abundance and range, the four bumblebee species in New Zealand have broadly the same ranking as they do in England (where *B. terrestris* is ubiquitous, *B. hortorum* is widespread but generally less abundant, *B. ruderatus* is exceedingly rare and *B. subterraneus* is extinct; Fussell and Corbet, 1992; Kells *et al.,* 2001; Goulson and Darvill, 2003). The similarity in distribution and abundance patterns for the four bumblebee species in New Zealand and the U.K. supports the hypothesis that habitat carrying capacity is low for rare bumblebee species (Williams, 1986, 1988). One possible explanation for this relationship might be that rare species, such as *B. subterraneus,* are more specialized in their habitat requirements. *Bombus terrestris* is more generalized in its foraging behaviour than other bumblebee species (Goulson and Darvill, 2003). By exploiting a greater range of flowers, it can persist in a wider range of habitats and maintain a higher population size within habitats.

As expected, *B. terrestris* in New Zealand is found across a greater geographical range, occurs in more habitat types, and forages on more plant species, including native taxa, than other introduced bumblebees. *Bombus hortorum*, *B. ruderatus* and

B. subterraneus were all very much more specialized in their foraging preferences in this study, showing a clear dependence on one species, *T. pratense*, as a source of both pollen and nectar. What is not clear from this or other studies is why *B. hortorum*, a seemingly specialized, long-tongued bumblebee, remains fairly widespread and abundant in both Europe and New Zealand, while other species with similar foraging preferences are less widespread. At present there are no known, clear ecological differences between, for example, *B. hortorum* and *B. ruderatus*, yet they differ greatly in abundance and distribution in Europe as well as in New Zealand. Similarly, *B. subterraneus* remains very restricted in New Zealand and is extinct in the U.K., yet its forage requirements appear very similar to those of *B. hortorum*. There are clear differences in habitat preferences, but these do not obviously relate to availability of forage. We have no indication why *B. subteranneus* should be closely associated with lake margins.

The role of Fabaceae species with long corollae as an important food source for long-tongued bumblebees is well established. *Trifolium pratense* is an important forage species in both the U.K. and northern Europe (Teräs, 1985; Jennersten *et al.,* 1988; Carvell, 2002). Rasmont (1988) argued that the decline of long-tongued bumblebees in France and Belgium is largely attributable to a decline in leguminous fodder crops once grown to feed horses. The importance of forage availability in limiting bumblebee abundance is also suggested in our study. Although *H. perforatum* is believed to be increasing in abundance in the U.K., the other main forage plants we identified in New Zealand (*E. vulgare, L. corniculatus* and *T. pratense*) are all declining (Grime *et al.,* 1988; Rich and Woodruff, 1996). The loss of these species, particularly the two members of the Fabaceae, is likely to have had severe repercussions on rare, long-tongued *Bombus* species in the U.K.

Our results suggest that the decline in rare *Bombus* species in the U.K. is mirrored in New Zealand. Compared with the distribution of *B. subterraneus* described by MacFarlane and Gurr (1995), we found a much more restricted range in the South Island. Their survey recorded *B. subterraneus* further north and east than ours, notably in the areas of Lake Coleridge and Fairlie. Despite conducting several searches in these areas, we found no *B. subterraneus*. Similarly, MacFarlane and Gurr (1995) found *B. ruderatus* throughout the Canterbury Plains. Today it is absent from much of that area.

Agricultural changes have occurred in New Zealand as they did in Europe. The use of *T. pratense* as a forage crop, for instance, has greatly declined in New Zealand. Both *L. corniculatus* and *T. pratense* were widely sown during the subsidised agricultural

development phase in New Zealand from the 1950s to the late 1980s. However, both species need the continual addition of phosphorous in order to maintain high populations. Once the subsidies stopped, this became too expensive for farmers to maintain and consequently, both species have declined (W. Lee, Landcare Research Ltd., Dunedin, *pers. comm.*). As we observed in this study, both *T. pratense* and *L. corniculatus* now tend to form only small local populations in natural grasslands, along roadside verges, and lake margins. It is likely that the loss of key forage plants that drove *B. subterraneus* to extinction in the U.K. may similarly be affecting populations of the species in New Zealand.

In addition to the close relationship between bumblebee distribution and forage availability, it is interesting to note the close association between pollinators and the successful spread of exotic weed species. Our survey showed that all four introduced bee species forage almost exclusively on introduced weed species. Previous studies in New Zealand have recorded *B. terrestris* visiting 400 exotic plants, but only 19 native species (MacFarlane, 1976). The three other introduced *Bombus* species feed exclusively on exotic plant species (Donovan, 1980). Honeybees also rely, almost exclusively, on introduced plants for pollen during most of the season (Pearson and Braiden, 1990). These preferences presumably occur because bees tend to gain higher rewards by visiting flowers with which they are co-adapted.

Although the preference for exotic weed species shown by introduced pollinators would seem to be one reason for the successful spread of weeds, this view has been challenged (Butz Huryn and Moller, 1995; Butz Huryn, 1997). Butz Huryn (1997) argues that most weeds do not rely on insect pollination, either because they are anemophilous, self-pollinating, apomictic or primarily reproduce vegetatively. In addition to *T. pratense* and *L. corniculatus*, both of which are highly dependent on insects for pollination (Grime *et al.,* 1988), we found substantial numbers of bumblebees visiting lupin (*Lupinus arboreus* and *L. polyphyllus*), thistles (*Cirsium vulgare*), and broom (*Cytisus scoparius*). Each of these species is known to depend substantially or wholly on bee pollinators in order to reproduce (Grime *et al.,* 1988; Stout, 2000; Stout *et al.,* 2002). Our results lend further support to the claim that exotic (bumble- and honey-) bees are important pollinators of various weeds (Sugden *et al.,* 1996; Stout *et al.,* 2002; Goulson, 2003b; Hanley and Goulson, 2003).

Whether or not introduced weeds do indeed depend on introduced bees for their establishment and spread in New Zealand, it is clear that bumblebee occurrence is closely linked to the availability of preferred forage species. Our results support the view that the loss of forage plants due to agricultural change has probably

been a major factor in the decline of many bumblebee species in Europe (Rasmont, 1988; Osborne and Corbet, 1994; Carvell, 2002), and potentially in New Zealand. Artificial nests placed in intensively managed agroecosystems in New Zealand had a very low take-up rate (2%), compared to those placed in less-disturbed, more floristically diverse sites (Barron *et al.,* 2000), which also supports this view. It seems likely that further agricultural changes in New Zealand, particularly the move away from the cultivation of *T. pratense* as a forage crop, will have important consequences for populations of long-tongued bumblebees such as *B. ruderatus* and *B. subterraneus*.

Acknowledgements

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