CSIRO PUBLISHING
www.publish.csiro.au/journals/ajz Australian Journal of Zoology, 2005, **53**, 29–34

Does the introduced bumblebee, *Bombus terrestris* (Apidae), prefer flowers of introduced or native plants in Australia?

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Abstract. Proponents of importation of the European bumblebee, *Bombus terrestris* (L.), into Australia for pollination of commercial greenhouse crops argue that this species will have little impact on Australian native ecosystems because it prefers to forage on flowers of introduced species of plants rather than Australian native plants. However, data presented as evidence of preference for introduced plants have been equivocal. This study compared the attractiveness of introduced and Australian native plants to free-foraging *B. terrestris* in a garden at the interface between an urban area and native vegetation in the Australian island of Tasmania, where a feral population of *B. terrestris* had been established for over 10 years. No evidence was found to support the proposal that *B. terrestris* forages on flowers of introduced plants in preference to those of Australian native plants. The numbers of *B. terrestris* seen foraging per 1000 flowers did not differ significantly between introduced plants and Australian native plants, and the preferred food sources of *B. terrestris* included flowers of both introduced and Australian native species. Because *B. terrestris* forages frequently on many species of both introduced and native plants, assessments of its ecological impacts must include the effects of altered pollination on recruitment rates in both introduced weeds and native plants, and reduced quantities of nectar and pollen of native plants on recruitment rates of dependent fauna.

Introduction

During the past decade there has been much interest in importing the European bumblebee, *Bombus terrestris* (L.), into Australia to pollinate commercial crops (Goodwin and Steiner 1997, 1999; Buttermore *et al*. 1998; Wilson 1999; Cooke 2001; Hergstrom *et al*. 2002; Carruthers 2003). This species is used in many countries to improve pollination of greenhouse crops, particularly tomatoes, *Lycopersicon esculentum* Mill. (Asada and Ono 1996; Goodwin and Steiner 1997; Buttermore *et al*. 1998; Hergstrom *et al*. 2002). Within three years of the discovery in 1992 of a feral population of *B. terrestris* in the Australian island of Tasmania (Semmens *et al*. 1993) an application for permission to import more genetic material into the population was made by an organisation representing Tasmanian tomato and vegetable growers (Hergstrom *et al*. 2002), and within another two years a private company applied for permission to import *B. terrestris* to the Australian mainland in order to establish a commercial rearing unit (Goodwin and Steiner 1997). Both of those applications were unsuccessful, at least partly because of concerns that *B. terrestris* may harm native ecosystems (Hergstrom *et al*. 2002; Carruthers 2003). However, aspiring commercial bumblebee producers and some horticulturalists continue to press for permission to import *B. terrestris* to the Australian mainland (e.g. Goodwin and Steiner 1999; Wilson 1999; Cooke 2001; Carruthers 2003).

The potential harmful impacts of *B. terrestris* on Australian ecosystems, following effective quarantine to prevent importation of their parasites and pathogens, include: (1) competition with native animals for nectar and/or pollen of native plants; (2) reduced seed production and/or altered gene flow in native plants; and (3) increased seed production in introduced weed species (Hingston *et al*. 2002; Goulson 2003; Thorp 2003). The first two of these potential impacts are serious concerns only if *B. terrestris* forages frequently on native plants, while the third could result from regular foraging on introduced plants.

Proponents for introduction of *B. terrestris* to the Australian mainland have argued that *B. terrestris* prefers to forage on introduced plants and will, therefore, have little impact on Australian native ecosystems (Goodwin and Steiner 1997; Carruthers 2003). However, even if *B. terrestris* does concentrate its foraging on introduced plants, it could still have serious impacts on native plants and the native animals that feed from their flowers if some introduced plants produce more seeds as a response to pollination services by *B. terrestris* and consequently become more invasive and outcompete the native plants. Moreover, enhanced pollination of weeds could in itself be a major impact because weeds already cost Australia $3.3 billion per annum in control and lost production (Commonwealth of Australia 1997). As stated by Goulson (2003) ‘If even one

10.1071/ZO04048 0004-959X/05/010029

new major weed occurs in Australia due to the presence of bumblebees, the economic and environmental costs could be substantial'.

Although introduction of *B. terrestris* could harm Australian ecosystems, regardless of any preference for introduced or native plants, assessment of these foraging preferences will help determine which of the three aforementioned potential harmful impacts warrant further investigation. It is often stated that *B. terrestris* prefers to forage on the flowers of introduced plants rather than on those of native Australian plants (Goodwin and Steiner 1997; Stout and Goulson 2000; Goulson *et al*. 2002; Hergstrom *et al*. 2002; Carruthers 2003). However, data presented in support of statements of preference for flowers of introduced species have been equivocal, because foraging records of *B. terrestris* have not been accompanied by quantification of the relative abundances of flowers of introduced and Australian native species at the foraging sites (Semmens 1996; Goulson *et al*. 2002; Hergstrom *et al*. 2002). As pointed out by Williams (2005), it is inappropriate to use the term 'preference' under such circumstances because it may simply be an artefact of bees encountering the most abundant flowers in the area more frequently by chance alone.

This study investigates whether all three of the aforementioned potential ecological impacts of *B. terrestris* warrant further research. To do this, the null hypothesis that *B. terrestris* exhibits no preference between flowers of introduced species and those of native species in Australia is tested. This is done by comparing the numbers of *B. terrestris* seen foraging per 1000 open flowers on introduced plants and Australian native plants, and the proportions of flowering introduced and Australian native species that were visited by *B. terrestris.*

Methods

Study site

The study site was a garden of approximately 140 m^2 containing a wide variety of both Australian native (mostly Tasmanian) and introduced plants, situated on the interface between suburban Hobart and native vegetation in Tasmania. Thus, the study site and surrounding area carried many species of introduced and native plants, making it an ideal situation to test the null hypothesis.

Data collection

The foraging preferences of *B. terrestris* were investigated during study periods, separated by ~10 days, throughout the time of year when *B. terrestris* was common (15 November 2003 – 27 March 2004). During each study period, the study site was sampled by walking through it at 30-min intervals between dawn and dusk over the greater part of two days. The species of the first flower contacted by each free-foraging *B. terrestris* seen in each sample was recorded. Although it is possible that one bee was counted more than once in the same sample because it flew between plants, the effect of this on the data was probably minor because bees were rarely seen flying away from the plants where they were first seen foraging during the sample period of ~1 min and, if a bee did fly away, it was usually possible to see where it went to within the small L-shaped study site and to differentiate bees that had been counted from those that hadn't been counted because of differences among individuals in body size and the quantity and colour of pollen carried in corbiculae.

Flowering intensity of each plant species in the garden during each study period was determined by counting the open flowers. In species in which the flowers were clustered so tightly in inflorescences that the individual open flowers could not be counted, mostly Asteraceae, the number of inflorescences with open flowers was used as the measure of flowering intensity. For some individual plants that bore more than 500 open flowers, the number was estimated by extrapolating from the number of flowers on a subsection of the plant. Sedges and grasses were excluded from the analysis because they are mostly wind-pollinated.

Data analysis

The intensity of foraging was calculated as the number of *B. terrestris* observed foraging during each study period per 1000 flowers for both native and introduced plants. The intensity of foraging was compared between native and introduced plants using paired *t*-tests, with the study periods as replicates. Because the number of flowers present sometimes influences the frequency with which individual flowers are visited by bumblebees (Andersson 1988; Klinkhamer *et al*. 1989; Klinkhamer and de Jong 1990; but see Geber 1985; Robertson and Macnair 1995; Ohashi and Yahara 2002), these analyses were conducted four times: (1) with all plant species bearing open flowers; (2) without plant species bearing fewer than 10 open flowers; (3) without plant species bearing fewer than 50 open flowers; and (4) without plant species bearing fewer than 200 open flowers. These four analyses were repeated on two modified datasets. The first was analysed to ensure that the results were not dominated by a small number of species with very large numbers of flowers. This modified dataset consisted of all plant species in the original dataset except those with more than 10 000 open flowers during the study period, because there was a median of 6507 open flowers (2616 introduced + 3891 native) per study period. The second modified dataset comprised all plant species in the original dataset except those with floral abundance measured as the number of open inflorescences, rather than individual flowers, because the use of inflorescences comprising many flowers as a measure of flowering intensity would have inflated their attractiveness per flower.

The percentages of flowering introduced and native species that were visited by *B. terrestris* were also compared using paired *t*-tests, with the study periods as replicates. This analysis was done using the original dataset and, as described above for comparisons of foraging intensity, was conducted four times.

To compare intensity of foraging among individual species, the confounding factor of seasonal variation in abundance of *B. terrestris* was controlled for by dividing the number of *B. terrestris* seen foraging per 1000 flowers on each species by the number of *B. terrestris* seen foraging per 1000 flowers across all species during that study period. These analyses were conducted on the original dataset, and both modified datasets. Species were included in this analysis if they carried at least 50 open flowers during at least three study periods, and ratios for study periods were included only when the species carried at least 50 open flowers.

Results

The numbers of *B. terrestris* seen foraging per 1000 flowers did not differ significantly between introduced plants and Australian native plants (Table 1). This result was not altered by removal of plant species with small or large numbers of flowers, or those with measures of floral abundance based on inflorescences rather than individual flowers, from the dataset (Table 1). However, *B. terrestris* did visit signifi-

Table 1. Mean (±s.e.) number of *Bombus terrestris* seen foraging per 1000 introduced and 1000 native flowers in each study period, and the statistical significance of the difference in foraging intensity on introduced and native flowers
Significance determined using paired *t*-tests, with study periods as replicates, on raw data or following square-root transformation to meet normality

Plants in dataset	Data type	Introduced	Native	Significance
All with flowers				
With flowers	Raw	3.68 ± 1.26	3.70 ± 1.05	T_{12} = 0.01, P = 0.99
With ≥10 flowers	Raw	3.69 ± 1.28	3.56 ± 1.03	T_{12} = 0.07, P = 0.94
With ≥50 flowers	Square-root	2.42 ± 0.86	2.58 ± 0.77	T_{12} = 0.41, P = 0.69
With ≥200 flowers	Square-root	2.27 ± 1.18	1.11 ± 0.24	T_{12} = 1.43, P = 0.18
All with <10 000 flowers				
With flowers	Raw	3.96 ± 1.21	4.44 ± 0.94	T_{12} = 0.27, P = 0.79
With ≥10 flowers	Raw	3.98 ± 1.23	4.28 ± 0.94	T_{12} = 0.17, P = 0.87
With ≥50 flowers	Square-root	2.71 ± 0.82	3.31 ± 0.73	T_{12} = 0.85, P = 0.41
With ≥200 flowers	Square-root	2.58 ± 1.16	1.72 ± 0.38	T_{12} = 1.37, P = 0.19
All with no. individual flowers counted				
With flowers	Raw	3.44 ± 1.05	3.88 ± 0.90	T_{12} = 0.28, P = 0.78
With ≥10 flowers	Raw	3.48 ± 1.07	3.75 ± 0.90	T_{12} = 0.17, P = 0.87
With ≥50 flowers	Raw	2.71 ± 0.91	2.91 ± 0.72	T_{12} = 0.16, P = 0.87
With ≥200 flowers	Square-root	2.45 ± 1.22	1.88 ± 0.38	T_{11} = 0.65, P = 0.53

cantly greater percentages of flowering Australian native, than flowering introduced, plant species (Table 2). This difference was statistically significant except when plant species bearing fewer than 200 open flowers during the study period were excluded from the analysis (Table 2).

Common species of plants varied greatly in their attractiveness to *B. terrestris*, but there was no clear difference between introduced and Australian native species (Table 3). The most attractive species included both introduced and Australian native species (Table 3). Species of plants that were not visited by *B. terrestris* also included both introduced and Australian native species (Table 3). The major species of plant for which *B. terrestris* is hoped to be imported as a commercial pollinator – tomato, *Lycopersicon esculentum* – was intermediate in attractiveness (Table 3).

Discussion

In this study, *B. terrestris* exhibited no statistically significant preference between flowers of introduced plants and those of Australian native plants. Plants preferred by *B. terrestris* as food sources included both introduced and Australian native species. This finding is consistent with previous observations in Tasmania of *B. terrestris* foraging regularly on both introduced (Semmens 1996; Goulson *et al*. 2002; Hergstrom *et al*. 2002; Hingston *et al*. 2002; Stout *et al*. 2002) and native (Hingston and McQuillan 1998*a*, 1998*b*, 1999; Olsson *et al*. 2000; Hingston *et al*. 2002, 2004*a*, 2004*b*) species of plants. It is also consistent with Prŷs-Jones and Corbet (1991), who noted that almost all species of British bumblebees, including *B. terrestris*, readily forage in parts of Britain where the native vegetation has been replaced by plants from all over the world.

The findings of this study are contrary to frequent statements that *B. terrestris* forages on introduced species of plants in preference to native plants in Australia (Goodwin and Steiner 1997; Stout and Goulson 2000; Goulson *et al*. 2002; Hergstrom *et al*. 2002; Carruthers 2003). Indeed, in this study, flowers of several species of native Tasmanian plants were more attractive to *B. terrestris* than were those of tomatoes, the major species of plant for which *B. terrestris* is hoped to be imported as a commercial pollinator (Goodwin and Steiner 1997; Carruthers 2003).

Most statements that *B. terrestris* forages on introduced species of plants in preference to native plants in Australia are

Table 2. Mean (± s.e.) percentage of introduced and native flowering plant species on which *Bombus terrestris* foraged during each study period, and the statistical significance of the difference between introduced and native species of plants
Significance determined using paired *t*-tests, with study periods as replicates, on raw data or following square-root transformation to meet normality

Plants in dataset	Data type	Introduced	Native	Significance
All with flowers				
With flowers	Raw	14.1 ± 1.6	19.4 ± 2.3	T_{12} = 2.71, P = 0.019
With ≥10 flowers	Square-root	21.4 ± 2.8	32.4 ± 4.7	T_{12} = 3.01, P = 0.011
With ≥50 flowers	Raw	26.8 ± 4.5	39.8 ± 5.2	T_{12} = 2.37, P = 0.035
With ≥200 flowers	Raw	35.8 ± 9.9	42.2 ± 5.7	T_{12} = 0.70, P = 0.50

not well supported by data, because they have been based on foraging records in the absence of any quantification of relative abundance of introduced and native flowers. These observations could, therefore, be an artefact of flowers of introduced plants being more common in the study sites (Williams 2005). Goodwin and Steiner (1997) and Stout and Goulson (2000) argued that *B. terrestris* prefers to forage on the flowers of introduced plants rather than those of native plants in Tasmania, on the basis of observations made by Semmens (1996) of *B. terrestris* visiting flowers of 156 introduced species and only 14 native species. However, Semmens (1996) provided no information regarding how his list of forage plants was obtained. Hergstrom *et al*. (2002) presented two lines of evidence in support of their argument: (1) the general public reported more observations of *B. terrestris* foraging on introduced plants than on native plants; and (2) *B. terrestris* was encountered more frequently on introduced plants than on native plants while the observers walked around a variety of urban, rural and bushland sites. However, both of those studies may have been confounded by the relative abundances of introduced and native flowers in the areas surveyed, which were not recorded (Hergstrom *et al*. 2002), casting doubt on their interpretation.

The only previous study to incorporate flowering intensity of plants with foraging records of *B. terrestris*, when comparing foraging preference between introduced and Tasmanian native plants, produced equivocal results (Goulson *et al*. 2002). That study found that, although it was estimated that 63.2% of inflorescences across 67 sites of ~8000 m^2 each were of native plants, only 16.5% of individuals of *B. terrestris* seen foraging in 36 of those sites visited native plants. From this, Goulson *et al*. (2002) concluded that *B. terrestris* preferred flowers of introduced plants to those of native plants. This conclusion is justified if the proportion of inflorescences that were of native species at the 36 sites where they saw *B. terrestris* was similar to, or larger than, the proportion of inflorescences that were of native species across all 67 sites. However, their conclusion is not justified if the proportion of inflorescences that were of native species at the 36 sites where they saw *B. terrestris* was much smaller than the proportion of inflorescences that were of native species across all 67 sites.

Table 3. Mean (± s.e.) ratios of the number of *B. terrestris* seen foraging per 1000 flowers on each plant species to the number of *B. terrestris* seen foraging per 1000 flowers across all species during that study period

Values greater than 1.00 indicate plants that are more attractive than average for plants flowering concurrently. Species are listed in order of attractiveness according to the grand mean of the ratios from the three datasets. Only species that carried at least 50 open flowers during at least three study periods, and ratios for study periods when the species carried at least 50 open flowers, were included. The number of replicates per species was insufficient for statistical analysis

Plant species	Plants in dataset: All with flowers	All with <10 000 flowers	All with no. individual flowers counted
Xerochrysum papillosum (Labill.) R. J. Bayer	42.62 ± 39.08	7.33 ± 4.08	
Xerochrysum bracteatum (Vent.) Tzvelev	30.96 ± 11.20	14.10 ± 5.20	
Brassica oleracea L. var. *acephala*[A]	22.63 ± 15.12	7.07 ± 0.60	18.29 ± 10.88
Leptospermum scoparium J. R. & G. Forst.	11.22 ± 7.03	1.50 ± 0.49	5.73 ± 3.07
Philotheca verrucosa (A. Rich.) Paul G. Wilson	5.62 ± 5.62	5.62 ± 5.62	6.72 ± 6.72
Pelargonium australe Willd.	6.46 ± 3.29	1.77 ± 0.40	4.08 ± 1.53
Allium schoenoprasum L.[A]	2.83 ± 2.83	2.83 ± 2.83	3.86 ± 3.86
Campanula poscharskyana Degen[A]	4.58 ± 3.34	1.43 ± 0.45	2.41 ± 1.10
Trifolium repens L.[A]	3.73 ± 2.43	1.14 ± 0.52	1.96 ± 0.87
Goodenia ovata Sm.	1.96 ± 1.57	0.48 ± 0.13	1.61 ± 1.15
Petroselinum crispum (Miller) Nyman ex A. W. Hill[A]	1.65 ± 0.98	0.66 ± 0.44	0.99 ± 0.60
Lycopersicon esculentum Mill.[A]	0.76 ± 0.76	0.76 ± 0.76	1.03 ± 1.03
Sonchus oleraceus L.[A]	0.39 ± 0.26	0.39 ± 0.26	
Viola hederacea Labill.	0.17 ± 0.13	0.17 ± 0.13	0.21 ± 0.15
Hypochaeris radicata L.[A]	0.15 ± 0.15	0.15 ± 0.15	
Beta vulgaris L. ssp. *maritima* (L.) Arcangeli[A]	0.11 ± 0.07	0.02 ± 0.02	0.05 ± 0.03
Rheum X*hybridum* Murray[A]	0.02 ± 0.02	0.02 ± 0.02	0.02 ± 0.02
Cassinia aculeata (Labill.) R. Br.	0.00 ± 0.00	0.00 ± 0.00	
Chrysocephalum apiculatum (Labill.) Steetz in Lehm.	0.00 ± 0.00	0.00 ± 0.00	
Fumaria muralis Sonder ex Koch[A]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Galium aparine L.[A]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Lobelia anceps L.f.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Prostanthera lasianthos Labill.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Stackhousia monogyna Labill.	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Trifolium dubium Sibth.[A]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
Veronica hederifolia L.[A]	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00

[A]Introduced species.

A definitive answer to the question of whether *B. terrestris* prefers flowers of introduced or native species of plants in Australia seems unlikely because of the large numbers of species that must be tested, and because studies such as this are so time-consuming. In this 140-m^2 study site, it took 2–4 h to determine the approximate number of flowers present during each study period. The only comparisons between the propensity for *B. terrestris* to forage on introduced and native plants that produced statistically significant results in this study showed that *B. terrestris* foraged on greater proportions of species of Australian native plants, than of introduced plants, that carried open flowers. However, it would be imprudent to claim that *B. terrestris* prefers to forage on Australian native plants than on introduced plants on this basis, because this study was limited to one location during one season and the plants studied here comprise only small proportions of the introduced and native plant species in Australia (median number of species bearing flowers per study period: introduced = 19, native = 21). Similarly, the data of Goulson *et al*. (2002) do not provide a definitive answer to the question of whether *B. terrestris* prefers flowers of introduced or native species of plants in Australia because their observations of *B. terrestris* were restricted to 1100–1500 hours between 15 November and 10 December during one season, and they did not state which species of plants were involved.

Continued debate over the relative foraging preferences of *B. terrestris* for flowers of introduced and native species in Australia appears somewhat irrelevant to assessment of the potential impacts of *B. terrestris* because, irrespective of any overall preference, it is clear from this and other studies that *B. terrestris* forages on a wide variety of both introduced and native species of plants in Australia. Because *B. terrestris* forages in large numbers on many introduced species of plants, the effect that this has on seed production in many existing and potential species of weeds requires investigation. Frequent foraging by *B. terrestris* on many species of Australian native plants could alter seed production in these plants and food availability to native animals, and this must also be investigated as part of any assessment of the ecological impact of *B. terrestris* in Australia. However, to determine the current impact of *B. terrestris*, it will be necessary to go beyond previous assessments of the effectiveness of *B. terrestris* as a pollinator of introduced (e.g. Stout *et al*. 2002) and native (e.g. Hingston *et al*. 2004*b*) plants, and the effects of *B. terrestris* on foraging behaviour of native flower-visiting animals (e.g. Hingston and McQuillan 1999). Future studies must investigate the effects that any alteration in seed production, food availability or foraging behaviour have on recruitment rates in the relevant plant and animal populations. However, several recent reviews have highlighted the difficulty of designing experiments that investigate the effects of introduced bees on reproductive success or population sizes in native flower-visiting animals (Paton 1996; Moller and Raffaelli 1998; Roubik 2001; Williams *et al*. 2001; Goulson 2003; Paini 2004). Because of the huge numbers of both introduced and native species of plants visited by *B. terrestris*, and the complexity of interactions between non-native pollinators, plants and native pollinators, quantification of the potential impacts associated with importation of this bee will require a great deal more research.

Acknowledgments

I thank Alex Buchanan for advice on nomenclature of plant species, an anonymous referee for helpful comments, and Maj-Britt di Folco for discussions on statistical techniques.

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Manuscript received 17 June 2004, accepted 15 December 2004