Austral Ecology (2002) **27**, 162–172

Extent of invasion of Tasmanian native vegetation by the exotic bumblebee *Bombus terrestris* (Apoidea: Apidae)

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Abstract Observations of the large earth bumblebee, *Bombus terrestris* (L.), in native vegetation were collated to determine the extent to which this exotic species has invaded Tasmanian native vegetation during the first 9 years after its introduction. The range of *B. terrestris* now encompasses all of Tasmania's major vegetation types, altitudes from sea level to 1260 m a.s.l., and the entire breadth of annual precipitation in the state from more than 3200 mm to less than 600 mm. Observations of workers carrying pollen, together with the presence of large numbers of bumblebees at many localities across this range indicate that colonies are frequently established in native vegetation. Evidence that colonies are often successful was obtained from repeated observations of the species during more than 1 year at particular sites. Unequivocal evidence of colonies was obtained from six National Parks, including four of the five in the Tasmanian Wilderness World Heritage Area (WHA). Indeed, the species has been present in the WHA for at least as long as it has in the city of Hobart, where it was first recorded. In south-western Tasmania, evidence of colonies was obtained up to 40 km from gardens, 61 km from small towns and 93 km from large towns. Hence, contrary to previous suggestions, the species is established in the most remote parts of Tasmania and is not dependent on introduced garden plants. Given their strong record of invasion, it is likely that *B. terrestris* will form feral populations on the mainland of Australia and in many other parts of the world if introduced. Because of their likely negative impacts on native animals and plants, and potential to enhance seed production in weeds, the spread of bumblebees should be avoided.

Key words: Australia, biological invasions, bumble bees, colonial insects, introduced species, social Hymenoptera.

INTRODUCTION

The rate at which living organisms move across the world's geographical barriers has risen to unprecedented levels as a result of human assistance (Low 1999; Mack *et al.* 2000; Mooney & Hobbs 2000). Many imported species are beneficial to human welfare and cause little environmental harm (Williamson 1999; Mooney & Hobbs 2000). Others, however, become highly invasive in their new environment and collectively pose a serious threat to the world's ecosystems, including those upon which humans depend for their basic needs (Moyle & Light 1996; Low 1999; Mack *et al.* 2000; Mooney & Hobbs 2000). For this reason, any proposed introductions must be carefully scrutinized for their potential to become invasive

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Accepted for publication August 2001.

and harmful (Moyle & Light 1996; Mack *et al.* 2000; Mooney & Hobbs 2000).

The most reliable predictor of an organism being invasive in a new area is it being invasive in other regions where it has been introduced (Carlton 1996; Mack 1996; Moller 1996; Williamson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997; Pheloung *et al.* 1999; Williamson 1999; Daehler & Carino 2000; Mooney & Hobbs 2000; Rejmánek 2000). Other characteristics are poorer predictors of invasive potential because of the idiosyncratic nature of invasions (Mack 1996; Moller 1996; Williamson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997; Mack *et al.* 2000). Hence, invasive organisms appear to possess certain characteristics that facilitate their survival and reproduction in a wide range of habitats, but these characteristics differ between organisms (Reichard & Hamilton 1997; Williamson 1999; Rejmánek 2000). For success to be possible in a wide range of habitats, these characteristics must enable the invasive species to tolerate a wide range of biotic and abiotic conditions (Moller 1996; Mack *et al.* 2000; Rejmánek 2000).

One organism that requires assessment of its potential to invade areas beyond its natural range is the large earth bumblebee, *Bombus terrestris* (L.). Since 1988 this Eurasian colonial bee has been used in many countries to improve pollination of greenhouse crops, particularly tomatoes *Lycopersicon esculentum* Mill. (Goodwin & Steiner 1997; Buttermore *et al.* 1998; Dafni 1998). Colonies of *B. terrestris* have already been imported into Korea, Japan, China, Taiwan, Mexico (Dafni 1998), Chile, Argentina, Uruguay, South Africa, Morocco and Tunisia (A. Dafni, pers. comm.) for deployment in greenhouses. An application to import *B. terrestris* into the mainland of Australia for use in greenhouses has also been made (Goodwin & Steiner 1997). In spite of approval being denied by the relevant government agencies, some horticulturists continue to lobby for their introduction (Goodwin & Steiner 1999; Wilson 1999). The introduction of bumblebees, including *B. terrestris*, to islands in the Pacific, Atlantic, and Indian Oceans, has also been proposed as a means of enhancing pollination in several field crops (Macfarlane 1995; Macfarlane *et al.* 1995).

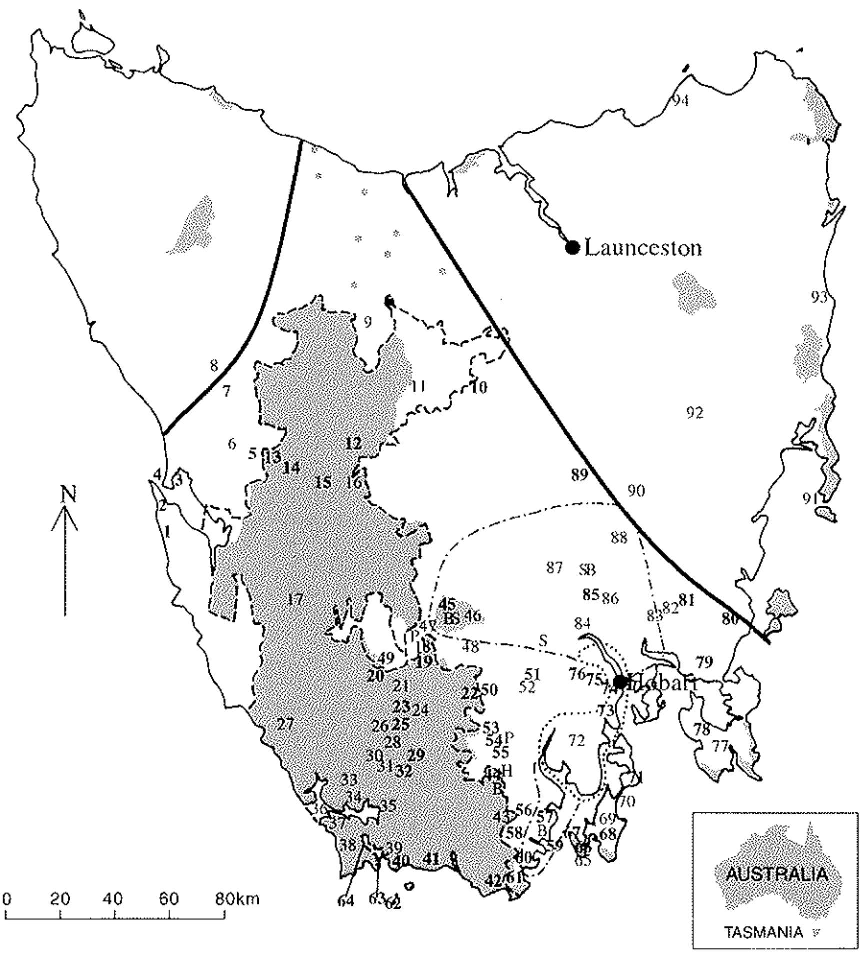

Fig. 1. Tasmania, showing the distributions of *Bombus terrestris*, the World Heritage Area (WHA), National Parks, and the two largest cities. (▩), National Parks; (---), WHA boundary; (—), limit to areas where *B. terrestris* is common. Number codes indicate locations where *B. terrestris* has been observed in native vegetation. Bold numbers represent locations where evidence of breeding populations of *B. terrestris* was found, in the form of bees carrying pollen in their corbiculae or where more than one bee was seen in 1 day. Stars (*) indicate locations where *B. terrestris* has been seen in gardens and agricultural areas during 2000–2001 outside the area where evidence of colonies has been found in native vegetation (B. Hingston, J. Nelson, J. Dudley and G. de Burgh-Day, pers. comm.). The previously known distribution of *B. terrestris* is shown as broken lines for 1995 and 2000: (– · –), distribution of *B. terrestris* according to Stout and Goulson (2000); (·····), distribution of *B. terrestris* according to Semmens (1995). Additional observations during the intervening period are indicated by letters as follows: S, Semmens (1996); B, Buttermore (1997); H, Hingston and McQuillan (1998); P, Parker (1999).

A number of lines of evidence suggest that *B. terrestris* is likely to be invasive in many areas where it is introduced. First, social insects, including bees, are a particularly invasive group (Moller 1996). Second, all colonial bees must be able to forage from a very wide range of different types of flowers (polylecty) because the activity period of the colony exceeds the flowering periods of most plant species (Moldenke 1975; O'Toole & Raw 1991; Westerkamp 1991). Third, bumblebees suffer very little predation while foraging (Davies 1977; Pyke 1979; Morse 1986). Fourth, *B. terrestris* has successfully invaded New Zealand, where it was introduced in 1885 for the pollination of red clover (Hopkins 1914; Macfarlane & Gurr 1995), and has recently colonized Japan, where it escaped from greenhouses in 1996, after its introduction in 1991 (Dafni 1998; Goka 1998).

Bombus terrestris has also recently colonized the Australian continental island of Tasmania. It was first discovered in the capital city of Hobart (Fig. 1) in February 1992, after being introduced without government approval (Semmens *et al.* 1993), and rapidly spread into surrounding populated areas (Semmens 1995; Fig. 1). It was initially predicted that *B. terrestris* would probably spread throughout Tasmania, and possibly southern Australia, because of the similarities in climate and vegetation between these areas and New Zealand (Semmens *et al.* 1993). This view of the potential distribution of *B. terrestris* was supported by Hingston and McQuillan (1998), based on their observations of large numbers of *B. terrestris* foraging on a wide range of native plants in several native vegetation types within 5 km of urban areas near Hobart. Evidence of invasion of native vegetation in more remote areas of Tasmania was provided by Semmens (1996), Buttermore (1997), Hingston and McQuillan (1998), Parker (1999) and Stout and Goulson (2000), all of whom recorded *B. terrestris* in or near national parks and the Tasmanian Wilderness World Heritage Area (WHA; Fig. 1).

In spite of this, doubts have subsequently been expressed regarding the ability of *B. terrestris* to invade native vegetation in Tasmania. Hergstrom (1999) questioned whether *B. terrestris* could survive in areas more than 8 km from urban gardens. In addition, the most recent survey of bumblebee distribution asserted that *B. terrestris* was largely restricted to gardens, urban parks and pastures (Stout & Goulson 2000). Stout and Goulson (2000) argued that *B. terrestris* may never colonize the WHA (Fig. 1), because of insufficient European plant species and the high altitude and rainfall in this area, and, if it did, that this would be the last part of Tasmania to be invaded (Stout & Goulson 2000).

In the present paper, we investigate the extent of the invasion of Tasmania by *B. terrestris* in the 9 years after it was first observed. Specifically, we test the hypotheses that the range of *B. terrestris* is limited by the biotic factor of the availability of garden plant species (Hergstrom 1999; Stout & Goulson 2000) and the abiotic factors of altitude and rainfall (Stout & Goulson 2000). From this we infer its capacity to invade habitats in which it has not evolved and, hence, the nature of its likely feral distribution and impact if introduced to the Australian mainland or other parts of the world.

METHODS

Several of the authors of this paper had noted the presence of *B. terrestris* in Tasmanian native vegetation in areas distant from urban areas, including the WHA, between 1992 and 1999. Following the doubts raised by Hergstrom (1999) and Stout and Goulson (2000) about the capacity of *B. terrestris* to invade such areas, we decided that it would be useful to publish our earlier sightings if they could be verified by further observations in these areas. Consequently, from early December 1999, a large group of observers, including

Table 1. Details of observations of *Bombus terrestris* in native vegetation before mid-1999 in areas where the species was not found during Stout and Goulson's (2000) survey in January 1999

Site	Date	*n*
16	March 1992	Q
41	1995–1996	N
41	1996–1997	W
54	March 1998	W
24	January 1999	W
34	January 1999	Q
58	17 January 1999	W
22	6 March 1999	3 W
1	13 March 1999	N

Locations of sites are shown in Fig. 1. N, numerous bees; S, several bees; Q, queens; W, workers and/or drones.

Table 2. Numbers of *Bombus terrestris* seen in Tasmanian native vegetation in areas according to mean annual precipitation (Bureau of Meteorology 2001)

Precipitation (mm per year)	Bumblebees seen
400–600	Q, 6W
600–900	$11Q^{1P, 2N}$, $305W^{8P, 8N}$, 4U
900–1200	Nest, N, S, $31Q^{1P}$, $212W^{29P, 31N}$, 2U
1200– 1800	4N, 12Q, $79W^{15P, 4N}$, 4U
1800–2400	5N, 2S, $14Q^{1N}$, $186W^{34P, 29N}$
2400–3200	3N, S, 3Q, $9W^{2P}$, 2U
> 3200	N, $7W^{3P, 1N}$

N, numerous bees; S, several bees; Q, queens; W, workers and drones; U, unidentified caste. Superscripts: P, numbers of bees seen carrying pollen; N, the numbers of bees seen not carrying pollen.

scientists working in areas of native vegetation, people employed by land management agencies, and amateur naturalists, commenced a survey of the distribution of *B. terrestris* in Tasmanian native vegetation.

Observers recorded the date and location of the bumblebee sighting, whether they were workers/drones or queens, any species of plants upon which they fed, and the presence or absence of pollen in their corbiculae. However, in some cases *B. terrestris* was seen while conducting other research. In such circumstances it was not possible to collect all these details, and we simply recorded the presence of several (5–10) or numerous (> 10) bumblebees. It is unlikely that we mistook other insects for bumblebees, as there are no other similar insects in Tasmania. Australian native bees in the genus *Xylocopa*, which are of similar size and shape to bumblebees, have not been recorded from Tasmania (Hingston 1999; Leys 2000). Queens of *B. terrestris*, at 30–35 mm in length, can be easily differentiated from the other castes, which are only 8–22 mm long. However, workers and drones are similar in size and, for this reason, we did not differentiate between these two castes.

Observations of *B. terrestris* in native vegetation between December 1999 and April 2001 were collated and mapped, along with any unpublished records we had made prior to this period. The extent of breeding populations in native vegetation was determined by

Table 3. Numbers of *B. terrestris* seen in Tasmanian native vegetation types

Vegetation type	Altitude (m a.s.l)	Bumblebees seen
Beach or sea	0–10	N, 7W
Coastal scrub	0–60	6N, 4Q, 30W$^{9P, 2N}$, 2U
Heathy woodland	0–110	5Q, 87W, U
Sedgeland	0–10	Nest
Buttongrass moorland	0–450	3S, 2Q, 99W$^{5P, 26N}$, U
Wet scrub	0–380	2N, 5Q, 15W^{2P}
Bush gardens	10–150	N, 2Q^{1P}, W
Grassy woodland/grazing land	140–460	Q, 7W^{1N}
Eucalypt plantation	0–500	7Q, 2W
Dry sclerophyll forest	0–600	5Q, 202W$^{3P, 1N}$, U
Wet sclerophyll forest	0–530	2Q^{2N}, 21W$^{5P, 6N}$, 2U
Mixed forest	60–775	N, 8Q^{1N}, 16W$^{5P, 4N}$
Rainforest	0–760	2N, Q, 10W$^{3P, 1N}$
Subalpine sclerophyll forest	720–1100	23Q^{1P}, 171W$^{24P, 29N}$, 3U
Subalpine shrubbery	660–1180	N, 5Q, 119W$^{34P, 3N}$, 2U
Alpine	950–1260	S, 2Q, 17W^{1P}

Symbols as in Table 2.

Table 4. Numbers of *B. terrestris* seen each year (July 1 – June 30) at locations in Tasmanian native vegetation where they were observed during more than one year

Site	1995–1996	1996–1997	1997–1998	1998–1999	1999–2000	2000–2001
4					W, U	N, 12W
12					Q^{N}	2Q, 2W^{1P}
20					S, 2W^{1P}	Q, 53W$^{2P, 2N}$
26					Q	W
41	N	W				
44					65W$^{26P, 1N}$	N, 3Q, W^{P}
45			W		2Q, 18W^{2P}	N, 8W^{1P}
49					Q, W^{P}	2Q, 40W^{24N}
50					Q, W	3 W
54			W		Q, 6W^{1N}	
58				W	W	3Q
59				Q	W	2Q, 2W
64					N, W	Q, W
68					Nest, W	W
71					W	Q, U
75					4Q^{1P}, 48W$^{11P, 2N}$	11Q, 4W
79					3W^{1P}	3W$^{2P, 1N}$
80					4W$^{3P, 1N}$	2Q^{2N}, 10W$^{2P, 5N}$

Locations of sites are shown in Fig. 1. Symbols as in Table 2.

mapping the sites where bees were seen carrying pollen in their corbiculae, or where more than one bee was observed in 1 day.

We emphasize that comparisons of the numbers of *B. terrestris* observed between different climatic conditions, vegetation types, altitudes, distances from gardens, species of plants and months of the year cannot be conducted because search effort levels were not constant across any of these variables.

RESULTS

Current distribution of *Bombus terrestris*

Bombus terrestris has invaded extensive parts of Tasmania in the 9 years since it was first reported in Hobart. Large numbers of bumblebees were observed frequently in native vegetation in southern Tasmania, and in the central west of the island (Fig. 1). Evidence of breeding populations in native vegetation was found across an area of approximately 30 000 km^2 (Fig. 1). Bumblebees were also common in the agricultural areas in the central-north, and were observed occasionally in the central-east and north-east of the island (Fig. 1).

Rate of spread by *Bombus terrestris*

If it is assumed that the Tasmanian population of *B. terrestris* originated in Hobart in 1991–1992 (Semmens *et al.* 1993), *B. terrestris* has spread through western Tasmania at a rate of approximately 25 km per year. Large numbers were present on the south coast (site 41) after four years (Table 1), on the west coast (site 1) after 7 years (Table 1), and on the north coast after 9 years (Fig. 1).

Habitat types invaded by *Bombus terrestris*

Bombus terrestris is breeding in Tasmanian native vegetation under a very wide range of conditions. Pollen-gathering workers were found in areas with annual precipitation ranging from 600 mm to more than 3200 mm (Table 2), altitudes ranging from sea level to 1180 m a.s.l., and in all of Tasmania's major types of native vegetation (Table 3). Several bumblebees were also observed in areas receiving 400–600 mm of annual rainfall (Table 2).

Breeding in native vegetation appears to be successful, as bumblebee populations are persistent in many areas, being observed at several localities during more than one season (Table 4).

Invasion of national parks by *Bombus terrestris*

Bombus terrestris workers were observed in large numbers and/or carrying pollen in six national parks in southern and western Tasmania, including four of the five national parks in the WHA (Table 5, Fig. 1). This is convincing evidence of colony establishment in these conservation areas. One worker was also observed in the Freycinet National Park in eastern Tasmania (Table 5, Fig. 1).

Moreover, *B. terrestris* has been observed in the WHA for many years. The earliest sighting was of a queen in March 1992 at Mount King William 1 (site 16), and the species was common at Turua Beach (site 41) by the summer of 1995–1996 (Table 1).

Independence of *Bombus terrestris* from urban gardens

Frequent observations of more than 10 bumblebees per day and/or workers collecting pollen, at sites remote from urban areas and other places where exotic plants are cultivated, indicate that *B. terrestris* is breeding in native vegetation (Table 6). Strong evidence of colonies was found in far south-western Tasmania up to 61 km from small towns and 93 km from larger urban areas (Table 6). There are gardens containing a few exotic plant species at the two most remote locations where large numbers of *B. terrestris* were seen (sites 62 and

Table 5. Numbers of *B. terrestris* seen in Tasmanian national parks

National parks	Sites	Bumblebees seen
Cradle Mountain – Lake St Clair NP	12	$3Q^{1N}$, $2W^{1P}$
Franklin – Gordon Wild Rivers NP	14–17	Q, $2W^{2P}$, U
South-west NP	18–43	3 N, 3S, 4Q, $84W^{5P, 4N}$, U
Hartz Mountains NP	44	N, 3Q, $66W^{27P, 1N}$
World Heritage Area	12–44	4 N, 3S, $11Q^{1N}$, $160W^{38P, 6N}$, 2U
Mount Field NP	45–46	N, 2Q, $28W^{3P}$
South Bruny NP	66–67	N, W^{P}, U
Freycinet NP	91	W

Locations of sites are shown in Fig. 1. Symbols as in Table 2. NP, National Park.

64). Nevertheless, if these two locations and those nearby are excluded, strong evidence was still found of colonies up to 40 km from areas where exotic plants are cultivated (sites 25 and 29; Table 6).

Foraging profile of *Bombus terrestris*

Bombus terrestris was observed foraging on a wide range of plants in native vegetation. The range encompassed 16 plant families and included 26 species of Tasmanian native plants, another species native to mainland Australia (*Eucalyptus nitens*), and eight species of exotic plants occurring as weeds within native vegetation (Table 7). *Bombus terrestris* was frequently observed foraging on plants in the families Myrtaceae and Epacridaceae, the native species *Banksia marginata*, *Leptospermum* spp., *Bursaria spinosa* and *Eucryphia* spp., and the weed species blackberry *Rubus fruticosus*, American sea rocket *Cakile edentula,* white clover *Trifolium repens*, trefoil *Lotus* spp., and scotch thistle *Onopordum acanthium* (Table 7).

Annual activity patterns of *Bombus terrestris*

Bombus terrestris was encountered in native vegetation during every month of the year (Table 8). Queens were observed during every month except June, and workers/drones in every month except July and August. However, large numbers of individuals and pollen collecting were only observed between December and March (Table 8).

DISCUSSION

Bombus terrestris is highly invasive in Tasmania. This, together with its extensive invasion of New Zealand

Table 6. Locations where strong evidence of *B. terrestris* colonies was found in native vegetation, and the distance from small and large urban areas

Site	Bumblebees seen	Distance from urban gardens (km) < 1000 people	> 1000 people
64	N, Q, 2W	61	84
63	N, W	56	84
62	N, W	51	93
40	N	46	81
29	N	40	55
25	W^{P}	38	57
23	$7W^{1P, 1N}$	32	57
41	N, W	31	72
1	N	25	42
15	W^{P}	19	42
49	3Q, $41W^{1P, 24N}$	18	64
20	S, Q, $55W^{3P, 2N}$	17	79
14	W^{P}	17	21
44	N, 3Q, $66W^{27P, 1N}$	14	30
2	$2W^{2P}$	13	34
53	$3W^{2P}$	13	28
55	$2W^{2P}$	13	24
66	W^{P}	12	54
45	N, 2Q, $27W^{3P}$	12	42
13	$6W^{3P, 1N}$	12	16
67	N, U	10	43
80	$2Q^{2N}$, $14W^{5P, 6N}$	9	24
68	Nest, 2W	8	47
4	N, 13W, U	8	29
51	7Q, $145W^{16P, 29N}$	8	15
7	N	8	13
5	N, W	8	10
12	$3Q^{1N}$, $2W^{1P}$	6	56
79	$6W^{3P, 1N}$	4	14
76	$5W^{1P}$	4	7
75	$15Q^{1P}$, $52W^{11P, 2N}$	3	4
61	3Q, $9W^{6P, 1N}$	2.5	63
73	Q, 85W	2	2
3	N, 2U	1	21
74	2Q, 192W	0.3	0.3

Locations of sites are shown in Fig. 1. Symbols as in Table 2.

(Macfarlane & Gurr 1995) and recent colonization of Japan (Goka 1998), suggests that it is likely to be invasive in many other regions into which it is introduced (Carlton 1996; Mack 1996; Moller 1996; Williamson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997; Pheloung *et al.* 1999; Williamson 1999; Daehler & Carino 2000; Mooney & Hobbs 2000; Rejmánek 2000).

Its invasiveness in Tasmania can be attributed to its tolerance of a wide range of biotic and abiotic conditions. *Bombus terrestris* workers are not known to forage at distances of more than a few kilometres from their nest (Dafni & Shmida 1996; Osborne *et al.* 1999; Walther-Hellwig & Frankl 2000). Therefore, large numbers of *B. terrestris* and/or workers carrying pollen, up to 40 km from gardens, 61 km from towns with fewer than 1000 residents, and 93 km from larger towns and cities, indicates that its range is not limited by the availability of garden plant species (cf. Hergstrom 1999; Stout & Goulson 2000). This, together with the general absence of exotic plants in the WHA (Parks and Wildlife Service 1999) and their broad range of native host plants (see also Hingston & McQuillan 1998), suggests that the range of *B. terrestris* is not limited by the availability of introduced plant species. Observations of *B. terrestris* from the coast to high on mountains, and across Tasmania's entire range of annual rainfall, indicates that neither of these abiotic factors is limiting the range of *B. terrestris* in Tasmania (cf. Stout & Goulson 2000). In fact, its abiotic tolerance range is even greater than that observed in Tasmania, as it forages up to an altitude of 2500 m a.s.l. in New Zealand, and is distributed across the entire annual rainfall gradient in New Zealand from 339 mm to more than 10 000 mm (Macfarlane & Gurr 1995).

The wider distribution reported in the present study, in comparison with that reported by Stout and Goulson (2000) following their survey in January 1999, may reflect recent range expansion. However, range

Table 7. Species of plants upon which *B. terrestris* was observed foraging during this study

Species	Family	Bumblebees seen
Banksia marginata Cav.	Proteaceae	7Q, 238W$^{42P, 26N}$
Leptospermum scoparium J. R. & G. Forst.	Myrtaceae	N, Q, 176W
Bursaria spinosa Cav.	Pittosporaceae	Q, 102W
Rubus fruticosus L.*	Rosaceae	2N, 2W^{1N}
Eucryphia lucida (Labill.) Baill.	Eucryphiaceae	N, 4Q^{1N}, 4W
Cakile edentula (Bigelow) Hook.*	Brassicaceae	N, 8W$^{6P, 1N}$
Leptospermum lanigerum (Ait.) Sm.	Myrtaceae	N, 5Q
Eucryphia milliganii Hook. f.	Eucryphiaceae	N, 2W
Trifolium repens L.*	Fabaceae	N, W^{P}
Pentachondra involucrata R. Br.	Epacridaceae	27W$^{11P, 7N}$
Lotus spp.*	Fabaceae	11W$^{9P, 2N}$
Onopordum acanthium L.*	Asteraceae	8W$^{7P, 1N}$
Prostanthera lasianthos Labill.	Lamiaceae	Q^{N}, 6W$^{1P, 2N}$
Nematolepis squamea (Labill.) Paul G. Wilson	Rutaceae	6Q
Hakea microcarpa R. Br.	Proteaceae	S
Ozothamnus sp.	Asteraceae	S
Epacris impressa Labill.	Epacridaceae	4Q
Cirsium arvense (L) Scop.*	Asteraceae	4W$^{3P, 1N}$
Digitalis purpurea L.*	Scrophulariaceae	Q^{N}, 3W^{2N}
Eucalyptus viminalis Labill.	Myrtaceae	4 W
Leucopogon parviflorus (Andr.) Lindl.	Epacridaceae	Q, W
Eucalyptus johnstonii Maiden	Myrtaceae	Q^{P}, W
Persoonia gunnii Hook. f.	Proteaceae	2W^{1P}
Leptospermum sp.	Myrtaceae	2W
Melaleuca ericifolia Sm.	Myrtaceae	Q^{P}
Eucalyptus delegatensis R. T. Baker	Myrtaceae	Q
Eucalyptus obliqua L'Herit.	Myrtaceae	W^{P}
Goodenia ovata Sm.	Goodeniaceae	W^{P}
Richea gunnii Hook. f.	Epacridaceae	W^{P}
Plantago lanceolata L.*	Plantaginaceae	W^{P}
Acacia verticillata (L'Herit.) Willd.	Mimosaceae	W
Oxylobium ellipticum (Labill.) R. Br.	Fabaceae	W
Cyathodes parvifolia R. Br.	Epacridaceae	W
Richea dracophylla R. Br.	Epacridaceae	W
Carpobrotus rossii Schwartes	Aizoaceae	W
Eucalyptus nitens (Deane & Maiden) Maiden*	Myrtaceae	W

Symbols as in Table 2. *Exotic species.

expansion cannot account for all of the differences, because our study included records of *B. terrestris* between 1992 and early 1999 in areas outside the distribution documented by Stout and Goulson (Table 1). If it is assumed that the Tasmanian population has spread from a founder population in Hobart in 1991–1992 (Semmens *et al.* 1993), its rate of spread appears to have been fairly constant at approximately 25 km per year. This is double the rate suggested by Buttermore (1997).

The international spread of *B. terrestris* should be limited by three major factors: (i) the extent of its dispersal by humans; (ii) the availability of nectar and pollen; and (iii) the climatic tolerance of the species. The ability of *B. terrestris* to forage on a very wide range of flowers with which it has not coevolved (see also Macfarlane & Gurr 1995; Dafni & Shmida 1996; Hingston & McQuillan 1998) suggests that it will be able to adapt to forage effectively wherever sufficient floral resources are available. Indeed, *B. terrestris* is regarded as being one of the most opportunistic of all bumblebees (Olesen 1985). The best indicator of the climatic tolerance limits of *B. terrestris* is its natural distribution, which is restricted to non-arid regions within the latitudinal range of 28–58° (Dafni & Shmida 1996; Estoup *et al.* 1996; Goodwin & Steiner 1997). Based on this, *B. terrestris* could potentially colonize non-arid regions in Australia as far north as southern Queensland, South Africa, Chile, Argentina, Uruguay, Japan, Korea, a large part of China and most of North America. However, the southern limit of its natural distribution is marked by a hot arid, rather than hot humid, climatic zone (Goodwin & Steiner 1997). It is therefore not possible to predict the lower latitudinal limits of the species in non-arid regions with certainty (Goodwin & Steiner 1997).

Populations of *B. terrestris* may be particularly successful at lower latitudes because of their capacity to remain active for a greater part of the year when not constrained by severe winters (Cumber 1954; Estoup *et al.* 1996). Bumblebees were observed during every month of the year in the present study, consistent with the situation in New Zealand (Cumber 1954; Donovan & Macfarlane 1984). Although evidence of colony activity was only found between December and March in the present study, active colonies have been observed as late as May in Tasmania (Buttermore 1997; Hingston 1997) and throughout the year in New Zealand (Cumber 1954). This prolonged breeding season in Tasmania results in two generations being produced each year (Buttermore 1997), in contrast to the single generation in England (Cumber 1953).

The potential for *B. terrestris* to invade many regions around the world raises concerns that this species will have similar harmful environmental impacts to those caused by the earlier international spread of another polylectic social bee, the European honeybee, *Apis mellifera* L. Numerous studies have demonstrated that *A. mellifera* displaces native anthophiles (nectar and pollen feeders) in Japan (Sakagami 1959), the Americas (Roubik 1978, 1980; Brown *et al.* 1981; Schaffer *et al.* 1983; Roubik *et al.* 1986; Dobson 1993; Wenner & Thorp 1994; Roubik 1996) and Australia (Pyke & Balzer 1985; Paton 1993; Bailey 1994; Paton 1997; Gross & Mackay 1998). The displacement of native bees by *A. mellifera* in French Guiana adversely affects seed production in *Mimosa pudica* (Roubik 1996). Research in Australia has also found that *A. mellifera* is sometimes ineffective in transferring pollen between conspecific native plants (Pyke 1990; Carthew 1993; Paton 1993, 1997; A. Hingston, unpubl. data), and in one study was shown to reduce seed set by removing pollen from stigmas (Gross & Mackay 1998). *Apis mellifera* also contributes to the pollination of weeds in North America (Barthell *et al.* 1994; Parker 1997).

Hence, if *B. terrestris* is exported around the world to enhance the pollination of greenhouse tomatoes, it may result in widespread displacement of native pollinators, reduced pollination of native plants, and increased pollination of weeds. Competitive displacement of native bees by *B. terrestris* has already been recorded in Tasmania (Hingston & McQuillan 1999) and in parts of Israel where *B. terrestris* has recently expanded its natural range (Dafni & Shmida 1996). Seed production also appears to be adversely affected in some native Israeli plants in areas where *B. terrestris* outnumbers other pollinators (Dafni 1998; Ne'eman *et al.* 2000). The potential for *B. terrestris* to increase seed production in weeds is apparent from the status of foxglove *Digitalis purpurea* L. as a serious weed in New Zealand (Webb *et al.* 1988; Roy *et al.* 1998), where it is pollinated by bumblebees (Goodwin & Steiner 1997; Roy *et al.* 1998). In contrast, in the absence of bumblebees at similar latitudes in the Australian mainland, foxglove is regarded as a useful ornamental plant rather than as a weed (Parsons 1973).

Table 8. Numbers of *B. terrestris* seen in each month in Tasmanian native vegetation

Month	Bumblebees seen
January	6N, S, 5Q, 40W$^{8P, 1N}$, U
February	6N, 2S, 17Q$^{1P, 1N}$, 301W$^{69P, 35N}$, 2U
March	3N, S, 9Q, 146W$^{8P, 29N}$, 4U
April	2Q, 13W^{1N}, U
May	Q, W
June	W
July	4Q
August	Q
September	8Q, W
October	3Q, 2U
November	3Q, 2W
December	Nest, 19Q$^{1P, 2N}$, 298W$^{6P, 7N}$, 2U

Symbols as in Table 2.

Moreover, the environmental threats posed by introductions of *B. terrestris* to new areas are not restricted to the areas of importation. All new populations of invasive species are potential sources of propagules that may invade other areas (Carlton 1996). For this reason, the governments of Canada and the USA oppose the introduction of *B. terrestris* to Mexico (J. Golubov, pers. comm.). In addition, there is concern that the Tasmanian population will spread to the Australian mainland by island-hopping across Bass Strait (Donovan 1994).

However, it may be possible to eradicate populations from small islands to prevent bumblebees from island-hopping from Tasmania to the Australian mainland. Osborne *et al.* (1999) followed the movements of *B. terrestris* workers up to 610 m from their nests by fitting small radar transmitters to the bees as they left the nest. If such transmitters were attached to foraging bees, it might be possible to follow them back to the nests, which could then be destroyed. Natural spread from Tasmania to the Australian mainland is, therefore, not inevitable.

In view of the proof that *B. terrestris* is highly invasive, and the evidence suggesting that it will displace native pollinators, reduce pollination of native plants, and increase the invasability of exotic weed species, there are firm grounds for preventing this species from being introduced or spreading into new areas. Most species of social insects that have formed feral populations have become permanent additions to invaded communities (Moller 1996). Therefore, the only means of ensuring that *B. terrestris* will not become established in more areas around the world is the prevention of its importation.

ACKNOWLEDGEMENTS

Much gratitude goes to Greg Lehman and Jim Nelson for distributing the request for data to their colleagues, and to Jonah Gouldthorpe, Rob Beedham, Matt Bradshaw, John Reid, Kete Rowe, Catherine Davis, Wally Herrmann, Mike Driessen, Kate Bassano, Cathy Young, Helen Crawford, Graham Edgar, Douglas Grubert, David James, Jane Elek, Jean Jackson, Mike Burns, Philipa Varris, John Watts, Mark Holdsworth, Pakinee Hingston, Helen Dunn, Nick Mooney, Holli Howard, Lisa McCarthy, Dianne Gee, Bev Armstrong, Brian Hingston, Jim Nelson, John Dudley and Geraldine de Burgh-Day for their bumblebee sightings. We are also grateful to Jane Stout, University of Southampton, for providing us with a copy of her paper prior to its publication. Thanks also go to the Tasmanian and Central North Field Naturalists Groups, who kept their collective eyes and ears open for bumblebees during their outings.

REFERENCES

Bailey W. J. (1994) Feral bees: Their potential effect on the native insect fauna. In: *Impact and Control of Feral Animals in South-Western Australia* (eds R. Siewert, N. Robinson & P. Horwitz) pp. 19–28. Conservation Council of Western Australia, Perth.

Barthell J. F., Randall J. M., Thorp R. W. & Wenner A. M. (1994) Invader-assisted invasion: Pollination of yellow star-thistle by feral honey bees in island and mainland ecosystems. *Suppl. Bull. Ecol. Soc. Am.* **75**, 10.

Brown J. H., Kodric-Brown A., Whitham T. G. & Bond H. W. (1981) Competition between hummingbirds and insects for the nectar of two species of shrubs. *Southwest. Nat.* **26**, 133–45.

Bureau of Meteorology (2001) Average Annual Rainfall. Available from: www.bom.gov.au/cgi-bin/climate/cgi_bin_scripts/annual_rnfall.cgi.

Buttermore R. E. (1997) Observations of successful *Bombus terrestris* (L.) (Hymenoptera: Apidae) colonies in southern Tasmania. *Aust. J. Entomol.* **36**, 251–4.

Buttermore R. E., Pomeroy N., Hobson W., Semmens T. & Hart R. (1998) Assessment of the genetic base of Tasmanian bumble bees (*Bombus terrestris*) for development as pollination agents. *J. Apic. Res.* **37**, 23–5.

Carlton J. T. (1996) Pattern, process, and prediction in marine invasion ecology. *Biol. Conserv.* **78**, 97–106.

Carthew S. M. (1993) An assessment of pollinator visitation to *Banksia spinulosa*. *Aust. J. Ecol.* **18**, 257–68.

Cumber R. A. (1953) Life cycle of the humble bee. *NZ Sci. Rev.* **Aug**, 92–8.

Cumber R. A. (1954) The life-cycle of humble-bees in New Zealand. *NZ J. Sci. Technol.* **36**, 95–107.

Daehler C. C. & Carino D. A. (2000) Predicting invasive plants: Prospects for a general screening system based on current regional models. *Biol. Invas.* **2**, 93–102.

Dafni A. (1998) The threat of *Bombus terrestris* spread. *Bee World* **79**, 113–14.

Dafni A. & Shmida A. (1996) The possible ecological implications of the invasion of *Bombus terrestris* (L.) (Apidae) at Mt Carmel, Israel. In: *The Conservation of Bees* (ed. A. C. Matheson) pp. 183–200. The Linnean Society of London and The International Bee Research Association, London.

Davies N. B. (1977) Prey selection and the search strategy of the spotted flycatcher (*Muscicapa striata*): A field study on optimal foraging. *Anim. Behav.* **25**, 1016–33.

Dobson H. E. M. (1993) Bee fauna associated with shrubs in two California chaparral communities. *Pan-Pac. Entomol.* **69**, 77–94.

Donovan B. J. (1994) *Bombus terrestris* in Tasmania (Australia). *Bumblebee Quest* **1**, 3.

Donovan B. J. & Macfarlane R. P. (1984) Bees and pollination. In: *New Zealand Pest and Beneficial Insects* (ed. R. R. Scott) pp. 247–58. Lincoln University College of Agriculture, Canterbury, New Zealand.

Estoup A., Solignac M., Cornuet J.-M., Goudet J. & Scholl A. (1996) Genetic differentiation of continental and island populations of *Bombus terrestris* (Hymenoptera: Apidae) in Europe. *Molec. Ecol.* **5**, 19–31.

Goka K. (1998) Influences of invasive species on native species: Will the European bumble bee, *Bombus terrestris*, bring genetic pollution into the Japanese native species? *Bull. Biogeogr. Soc. Jap.* **53**, 91–101.

Goodwin S. & Steiner M. (1997) Introduction of *Bombus terrestris* for pollination of horticultural crops in Australia. A submission to AQIS and Environment Australia. Available from: http://www.tmag.tas.gov.au/workshop/append2.html.

Goodwin S. & Steiner M. (1999) Workshop on possible introduction of bumblebees (*Bombus terrestris*) for pollination of horticultural crops in Australia. Background to a submission to Environment Australia. In: *Workshop on Possible Introduction of Bumblebees* (Bombus terrestris) *for Pollination of Horticultural Crops in Australia* (ed. R. E. Buttermore). Tasmanian Museum and Art Gallery, Hobart, Tasmania. Available from: www.tmag.tas.gov.au/workshop/proceedings.html.

Gross C. L. & Mackay D. (1998) Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biol. Conserv.* **86**, 169–78.

Hergstrom K. (1999) Bumblebee EIS proposed methodology. In: *Workshop on Possible Introduction of Bumblebees* (Bombus terrestris) *for Pollination of Horticultural Crops in Australia* (ed. R. E. Buttermore). Tasmanian Museum and Art Gallery, Hobart, Tasmania. Available from: www.tmag.tas.gov.au/workshop/proceedings.html.

Hingston A. B. (1997) The impact of the Large Earth Bumblebee, *Bombus terrestris* (L.) (Apidae: Apoidea) on Tasmanian ecosystems. Honours Thesis, Department of Geography and Environmental Studies, University of Tasmania, Hobart, Tasmania.

Hingston A. B. (1999) Affinities between southern Tasmanian plants in native bee visitor profiles. *Aust. J. Zool.* **47**, 361–84.

Hingston A. B. & McQuillan P. B. (1998) Does the recently introduced bumblebee *Bombus terrestris* (Apidae) threaten Australian ecosystems? *Aust. J. Ecol.* **23**, 539–49.

Hingston A. B. & McQuillan P. B. (1999) Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Aust. J. Zool.* **47**, 59–65.

Hopkins I. (1914) History of the humble-bee in New Zealand: Its introduction and results. *NZ Dept. Agric. Ind. Comm. Bull.* **46**, 5–29.

Leys R. (2000) A revision of the Australian carpenter bees, genus *Xylocopa* Latreille, subgenera *Koptortosoma* Gribodo and *Lestis* Lepeletier & Serville (Hymenoptera: Apidae). *Invert. Taxon.* **14**, 115–36.

Low T. (1999) *Feral Future.* Penguin Books Australia, Ringwood, Victoria, Australia.

Macfarlane R. P. (1995) Applied pollination on tropical and subtropical oceanic islands. In: *Pollination of Cultivated Crops in the Tropics* (ed. D. W. Roubik) pp. 40–8. Food and Agriculture Organization, United Nations, Rome, Italy.

Macfarlane R. P. & Gurr L. (1995) Distribution of bumble bees in New Zealand. *NZ Entomol.* **18**, 29–36.

Macfarlane R. P., Lipa J. J. & Liu H. J. (1995) Bumble bee pathogens and internal enemies. *Bee World* **76**, 130–48.

Mack R. N. (1996) Predicting the identity and fate of plant invaders: Emergent and emerging approaches. *Biol. Conserv.* **78**, 107–21.

Mack R. N., Simberloff D., Lonsdale W. M., Evans H., Clout M. & Bazzaz F. A. (2000) Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecol. Appl.* **10**, 689–710.

Moldenke A. R. (1975) Niche specialization and species diversity along a Californian transect. *Oecologia* **21**, 219–42.

Moller H. (1996) Lessons for invasion theory from social insects. *Biol. Conserv.* **78**, 125–42.

Mooney H. A. & Hobbs R. J. (2000) *Invasive Species in a Changing World.* Island Press, Washington.

Morse D. H. (1986) Predatory risk to insects foraging at flowers. *Oikos* **46**, 223–8.

Moyle P. B. & Light T. (1996) Biological invasions of fresh water: Empirical rules and assembly theory. *Biol. Conserv.* **78**, 149–61.

Ne'eman G., Dafni A. & Potss S. G. (2000) The effect of fire on flower visitation rate and fruit set in four core-species in east Mediterranean scrubland. *Plant Ecol.* **146**, 97–104.

O'Toole C. & Raw A. (1991) *Bees of the World.* Blandford Publishing, London.

Olesen J. M. (1985) The Macaronesian bird-flower element and its relation to bird and bee opportunists. *Bot. J. Linn. Soc.* **91**, 395–414.

Osborne J. L., Clark S. J., Morris R. J. *et al.* (1999) A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* **36**, 519–33.

Parker I. M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch Broom), an invasive exotic shrub. *Ecology* **78**, 1457–70.

Parker C. (1999) Comments on introduction of *Bombus terrestris* to Tasmania. In: *Workshop on Possible Introduction of Bumblebees (*Bombus terrestris*) for Pollination of Horticultural Crops in Australia* (ed. R. E. Buttermore). Tasmanian Museum and Art Gallery, Hobart, Tasmania. Available from: www.tmag.tas.gov.au/workshop/proceedings.html

Parks and Wildlife Service (1999) *Tasmanian Wilderness World Heritage Area Management Plan.* Parks and Wildlife Service, Hobart.

Parsons W. T. (1973) *Noxious Weeds of Victoria.* Inkata Press, Melbourne, Australia.

Paton D. C. (1993) Honeybees in the Australian environment. Does *Apis mellifera* disrupt or benefit the native biota? *Bioscience* **43**, 95–103.

Paton D. C. (1997) Honey bees *Apis mellifera* and the disruption of plant-pollinator systems in Australia. *Vic. Nat.* **114**, 23–9.

Pheloung P. C., Williams P. A. & Halloy S. R. (1999) A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *J. Environ. Manage.* **57**, 239–51.

Pyke G. H. (1979) Optimal foraging in bumblebees: Rule of movement between flowers within inflorescences. *Anim. Behav.* **27**, 1167–81.

Pyke G. H. (1990) Apiarists versus scientists: A bittersweet case. *Aust. Nat. Hist.* **23**, 386–92.

Pyke G. H. & Balzer L. (1985) *The Effects of the Introduced Honeybee (*Apis mellifera*) on Australian Native Bees.* National Parks and Wildlife Service Occasional Paper no. 7. NSW National Parks and. Wildlife Service, Sydney.

Reichard S. H. & Hamilton C. W. (1997) Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* **11**, 193–203.

Rejmánek M. (2000) Invasive plants: Approaches and predictions. *Austral Ecol.* **25**, 497–506.

Roubik D. W. (1978) Competitive interactions between neotropical pollinators and Africanized honeybees. *Science* **201**, 1030–2.

Roubik D. W. (1980) Foraging behaviour of competing Africanized honeybees and stingless bees. *Ecology* **61**, 836–45.

Roubik D. W. (1996) African honey bees as exotic pollinators in French Guiana. In: *The Conservation of Bees* (eds A. Matheson, S. L. Buchmann, C. O'Toole, P. Westrich & I. H. Williams) pp. 173–82. Linnean Society of London and the International Bee Research Association, London.

Roubik D. W., Moreno J. E., Vergara C. & Wittman D. (1986) Sporadic food competition with the African honey bee: Projected impact on neotropical social bees. *J. Trop. Ecol.* **2**, 97–111.

Roy B., Popay I., Champion P., James T. & Rahman A. (1998) *An Illustrated Guide to Common Weeds of New Zealand.* New Zealand Plant Protection Society, Canterbury, New Zealand.

Sakagami S. F. (1959) Some interspecific relations between Japanese and European honeybees. *J. Anim. Ecol.* **28,** 51–68.

Schaffer W. M., Zeh D. W., Buchmann S. L., Kleinnans S., Schaffer M. V. & Antrim J. (1983) Competition for nectar between introduced honey bees and native North American bees and ants. *Ecology* **64,** 564–77.

Semmens T. (1995) The buzzzzz on bumble bees!. *Agric. Tas.* **1,** 19.

Semmens T. D. (1996) Flower visitation by the bumblebee *Bombus terrestris* (L.) (Hymenoptera: Apidae) in Tasmania. *Aust. Entomol.* **23,** 33–5.

Semmens T. D., Turner E. & Buttermore R. (1993) *Bombus terrestris* (L.) (Hymenoptera: Apidae) now established in Tasmania. *J. Aust. Entomol. Soc.* **32,** 346.

Stout J. C. & Goulson D. (2000) Bumblebees in Tasmania: Their distribution and potential impact on Australian flora and fauna. *Bee World* **81,** 80–6.

Walther-Hellwig K. & Frankl R. (2000) Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *J. Appl. Ent.* **124,** 299–306.

Webb C. J., Sykes W. R. & Garnock-Jones P. J. (1988) *Flora of New Zealand, IV. Naturalised Pteridophytes, Gymnosperms, Dicotyledons.* Botany Division, Department of Scientific and Industrial Research, Christchurch, New Zealand.

Wenner A. M. & Thorp R. W. (1994) Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In: *The Fourth California Islands Symposium: Update on the Status of Resources* (eds W. L. Halvorson & G. J. Maender) pp. 513–22. Santa Barbara Museum of Natural History, Santa Barbara, CA, USA.

Westerkamp C. (1991) Honeybees are poor pollinators: Why? *Plant Syst. Evol.* **177,** 71–5.

Williamson M. (1996) *Biological Invasions.* Chapman & Hall, London.

Williamson M. (1999) Invasions. *Ecography* **22,** 5–12.

Williamson M. H. & Fitter A. (1996) The characters of successful invaders. *Biol. Conserv.* **78,** 163–70.

Wilson A. (1999) Bumblebee workshop presentation. In: *Workshop on Possible Introduction of Bumblebees (*Bombus terrestris*) for Pollination of Horticultural Crops in Australia* (ed. R. E. Buttermore). Tasmanian Museum and Art Gallery, Hobart, Tasmania. Available from: www.tmag.tas.gov.au/workshop/proceedings.html.