Invasion Status and Potential Ecological Impacts of an Invasive Alien Bumblebee, *Bombus terrestris* L. (Hymenoptera: Apidae) Naturalized in Southern Hokkaido, Japan

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Abstract

In 1996, a naturally occurring nest of an introduced bumblebee, *Bombus terrestris* L., was found in Monbetsu in the Hidaka region of southern Hokkaido, indicating that it had become naturalized in Japan. In this region, monitoring of *B. terrestris* has been continued at two sites. The numbers of *B. terrestris* captured or observed have increased rapidly during the eight years since the evidence of its naturalization was found. Seasonally, the queens of naturalized *B. terrestris* have appeared as early as mid-April each spring. Queens were observed continuously during the period from April to October, workers from May to October, and males from July to October. *B. terrestris* was shown to forage among various flowering plants, 40%–70% of the species of flowering plants upon which native bumblebees fed. Nine of ten natural nests of *B. terrestris* discovered during the study were found in abandoned underground rodent nests. The nest sites of this species were similar to those of *B. hypocrita sapporoensis* Cockerell, and *B. diversus tersatus* Smith. *B. terrestris* clearly has the potential to compete with native bumblebees for floral resources and nest sites. The mean number of new queens born in the colonies of *B. terrestris* was 4.4 times larger than that of the native bumblebees. This strongly suggested superior reproductive ability of *B. terrestris* compared with native bumblebees in the region.

Key words: biological invasions, *Bombus terrestris,* ecological impacts, invasive alien bumblebee, monitoring, pollination

1. Introduction

Claims of widespread declines in populations of animal pollinators have recently captured public and scientific attention (Buchmann & Nabhan, 1996; Allen-Wardell *et al*., 1998; Keans *et al*., 1998). Invertebrates, particularly native bees, are essential for reproduction by seed of most wild and agricultural plants that require pollinators. During their flights between flowers of conspecific plants in search of nectar, pollen, oil, or mates, bees and other insects often move pollen to floral stigmas, thereby enhancing fruit set and size, seed production and viability, seedling vigor, and genetic diversity of plant populations (Cane & Tepedino, 2001). Declines in the abundance and distribution of bee populations are thought to have far-reaching effects on natural plant communities and on the economic viability of some agricultural practices (Williams, 1995).

Over the last few decades local extinction of bumblebee species has been prevalent in agricultural areas of Europe (Williams, 1986; Rasmont *et al.,* 1992; Williams, 1995; Corbet, 2000). In particular, long-tongued bumblebee species which are irreplaceable pollinators of flowers with long corollas have markedly declined (Rasmont *et al*., 1992). Decreasing numbers of plants with long-tubed flowers due to human disturbance, the loss of nesting areas (Corbet *et al*., 1994), and their restricted foraging radius compared to short-tongued generalist bumblebees (Walther-Hellwig & Frankl, 2000) might be among important factors in the loss of long-tongued bumblebee species.

In contrast to these long-tongued species, the large earth bumblebee, *Bombus terrestris* L. (Fig. 1) is still a widespread species in its native range (Williams, 1986). *B. terrestris* is a palaearctic species which is widely distributed west of the Urals and also occurs in the Mediterranean basin (Dafni & Shmida, 1996). This short-tongued bumblebee shows several types of adaptation which render it as a generalist, able to harvest floral resources from a large spectrum of plant species in various habitats. The adaptations include: earlier seasonal emergence, particularly of queens (Sladen, 1912; Prys-Jones & Corbet, 1991), longer mean foraging distances (Walther-Hellwig & Frankl, 2000; Ne'eman *et al*., 2000; Kreyer *et al.,* 2004), and a variety of effectual behavioral skills for nectar and pollen gathering, including nectar robbing and buzz pollination, i.e., vibratory pollen collecting (Prys-Jones & Corbet, 1991; Proctor *et al*., 1996).

Since 1988 this efficient generalist pollinator has been used commercially in many countries beyond its natural range to improve pollination of greenhouse crops, particularly tomatoes *Lycopersicon esculentum* Mill. (de Ruijter, 1997). Colonies of the species have been imported into Korea, Japan, China, Taiwan, Mexico (Dafni, 1998), Chile, Argentina, Uruguay, South Africa, Morocco and Tunisia (Hingston *et al*., 2002). In Japan, *B. terrestris* colonies were first commercially introduced for crop pollination in 1991 (Ono, 1998). Today colonies of the species have been used for pollination in almost all parts of Japan and the annual importation is 60,000 colonies (Goka & Japanese Bumblebee Companies Association, 2003).

Japanese ecologists have continued to warn of the high risks of biological invasion of the species since the first commercial introduction was considered by industry (Kato, 1993; Washitani & Morimoto, 1993), because *B. terrestris* is known to have great ecological flexibility and highly polylectic foraging habits enabling it to flourish in various habitats (Dafni & Shmida, 1996; Hingston & McQuillan, 1998; Hingston *et al.*, 2002).

Fig. 1 *Bombus terrestris* (Hymenoptera, Apidae) visiting flowers of *Hylotelephium cauticolum* (Crassulaceae) in the Hidaka region of southern Hokkaido, Japan.

The invasive potential of *B. terrestris* has been demonstrated by its successful naturalization into New Zealand (Donovan & Wier, 1978), Israel (Dafni & Shmida, 1996), and the Australian southern island of Tasmania (Semmens *et al.*, 1993). In Israel, Dafni and Shmida (1996) reported that the numbers of honeybees and solitary bees declined during the last two decades on Mt. Carmel where the range of *B. terrestris* had expanded. There are indications of competition for resources between *B. terrestris* and other bee species (Dafni & Shmida, 1996). *B. terrestris* arrived in Tasmania in 1992 (Semmens *et al.*, 1993). Since then one study (Semmens, 1996) recorded *B. terrestris* workers foraging on 170 species of flowering plant, of which 156 were introduced and 14 were native. Another investigation reported that foraging of *B. terrestris* ranged over 66 native plant species from 21 families (Hingston & McQuillan, 1998), and concluded that the species therefore clearly has the potential to compete with native pollinators, including bees and nectivorous birds in Tasmania.

There is also evidence for novel life history evolution in introduced *B. terrestris*. In its native range, this species is univoltine, that is, there is one cycle of colony foundation and sexual reproduction per year, interrupted between years by the death of all individuals except for the young, newly mated queens that enter hibernation (Alford, 1975; Prys-Jones & Corbet, 1991). Bivoltinism, the occurrence of two cycles of colony foundation and reproduction per year is very rare in the native range of the species (Prys-Jones & Corbet, 1991). However, studies of *B. terrestris* in New Zealand and Tasmania have suggested that bivoltinism is much more frequent (Donovan & Weir, 1978; Buttermore, 1997). In its introduced range, *B. terrestris* appears to have rapidly evolved to adapt to new environments, since its newly obtained traits greatly enhance its productivity and hence presumably expand its ecological niche (Chapman & Bourke, 2001).

Japan is home to 15 species of native bumblebees (Ito, 1991), which form key elements in the coevolved pollination guilds which service the native flora (Kato, 1988; Suzuki, 1992; Kato *et al*.,1993; Washitani *et al.* 1995; Matsumura & Washitani, 2000; Suzuki & Akazome, 2000). Invading *B. terrestris* may compete with the native species for vital resources, i.e., nectar, pollen and nest sites. Ecological theory (Elton, 1958) suggests that the strongest effects will be exerted on closely related species, i.e., native Japanese bumblebees (Thomson, 1997; Washitani, 1998). Laboratory experiments showed that queens of *B. terrestris* usurped nest sites from queens of native bumblebees (Ono, 1997).

In addition to competition, there are possibilities of reproductive and genetic interferences that can have negative impacts on the populations of native bumblebee species (Washitani, 1998; Goka, 1998). Laboratory experiments have shown that males of *B. terrestris* can mate with queens of Japanese native species. On rare occasions, *B. terrestris* and *B. hypocrita sapporoensis Cockerell* can produce hybrids (Mitsuhata & Ono, 1996).

Another potential threat from introduced *B. terrestris* is the transmission of disease organisms to native bees (Washitani, 1998). The endoparasitic mite *Locustacarus buchneri* Stammer (Podapolipidae) was found in commercially introduced colonies of *B. terrestris* (Goka *et al.*, 2000, 2001). *L. buchneri* mites of European genotype have been found on wild Japanese native bumblebees (Goka, 2002).

Indirect effects on plant reproduction that currently rely on Japanese bees for pollination depend on the mechanisms by which the Japanese bees are affected through competition with *B. terrestris* (Thomson, 1997). Thomson (1997) pointed out the following possibilities. If *B. terrestris* reduces native bee populations through competition for nectar and pollen, the invading bees may partially compensate for the role of the natives playing in pollination. However, this species' habit of nectar robbing, i.e., taking nectar by biting a hole in the corolla tube of longer flowers without effective pollination, may negatively affect seed production in the plants it exploits. Moreover, if the invaders usurp limited nest sites or introduce diseases, their negative effects may spread to bees other than those with which they share floral hosts. Therefore, *B. terrestris* has influences on the reproductive success of the long-tubed flowers that depend on long-tongued bumblebees such as *B. diversus* Smith for successful pollination, not only directly by nectar robbing, but also indirectly through reducing effectual pollinators.

In 1996, a naturally occurring nest of *B. terrestris,* i.e., the first evidence of the naturalization of the species in Japan, was found in Monbetsu (site A) in the Hidaka region of Hokkaido prefecture, the northern part of Japan (Washitani, 1998). Since then a total of more than 4,300 bees have been recorded captured or witnessed from one half of the 47 Japanese prefectures (Washitani, 1997; Washitani & Matsumura, 1998; Japanese Society of Conservation Ecology, 2004). *B. terrestris* has been escaped in the wide range of the Japanese Archipelago.

In census studies performed in Shizuoka prefecture of central Japan and Hokkaido, where a large number of colonies of this species have been commercially introduced for agricultural pollination, in 2002, *B. terrestris* was ascertained to visit *Rhododendron* × *obtusum* (Lindl.) Planch. and *Elaeagnus multiflora* Thunb. var. *hortensis* (Maxim.) Servettaz, respectively (Matsumura *et al.*, 2003). The study was a part of a long-term nationwide monitoring program that has been in progress since 1997 to monitor the invasion of *B. terrestris* in Japan (Japanese Society of Conservation Ecology, 1997). These monitoring activities have revealed that *B. terrestris* has escaped and/or become naturalized in at least two districts of Japan. In particular, an accelerated increase in the number of *B. terrestris* captured in Monbetsu (sites A and B) from 1996 to 2002 indicates that *B. terrestris* has become firmly established in this region (Matsumura & Washitani, 2002).

In the present study, we attempted to document the magnitude of the recent invasion by *B. terrestris* in the Hidaka region according to several lines of data including those obtained by monitoring, and to assess the possible ecological impact of the invasive alien bee on native bumblebees and plants with bumblebee-pollinated flowers.

2. Methods

2.1 Study area

The study area was located in Tomikawa in the municipality of Monbetsu (42˚30'N, 142˚0'E, at an elevation of 10–40 m a.s.l.), and Nina, Shiunkotsu, and Saruba in the municipality of Biratori (42˚31'N, 142˚03'E, at an elevation of 10−100 m a.s.l.) in southern Hokkaido, Japan (Fig. 2). The annual mean air temperature and annual precipitation as recorded at the standard meteorological station in Monbetsu in 2002 were 7.3˚C (max. 27.1˚C, min. −20.1˚C), and 845 mm year^{-1}, respectively. In Nina, Shiunkotsu, and Saruba, rice fields and other cultivated fields extend on an alluvial fan formed by the River Saru. In the area, *B. terrestris* has been introduced for pollination of greenhouse tomatoes during the past 10 years. Tomatoes are cultivated in plastic-covered greenhouses that are ventilated by simple windows through which the bees can freely leave the enclosure. Therefore, certainly there have been many escapes of *B. terrestris*. Since 2003, the tomato-cucumber section of one agricultural cooperative association of Biratori has put union members under an obligation to put up nets on their greenhouses to prevent bees from escaping.

Tomikawa is a more urban residential area with intermingling of pastures and windbreak forests of *Quercus dentata* Thunb. *B. terrestris* bees observed in Tomikawa are regarded as naturalized bees, because Tomikawa is 5−6 km away from the area where *B. terrestris* has been mass introduced.

2.2 Monitoring and censuses for *Bombus terrestris* and native bumblebees

2.2.1 Long-term monitoring in Monbetsu

Monitoring of *B. terrestris* and native bumblebees has been performed during their active seasons from 1996 to 2002 in Monbetsu, mainly in private gardens, site A (7,398 m^2) and B (4,624 m^2) in Tomikawa area. The garden owners have voluntarily participated in our monitoring program and whenever they found *B. terrestris* in their garden or its surrounding area, on the flowers (including *Rhododendron* spp., *Prunus* spp., *Pieris japonica* (Thunb.) D. Don, *Elaeagnus*

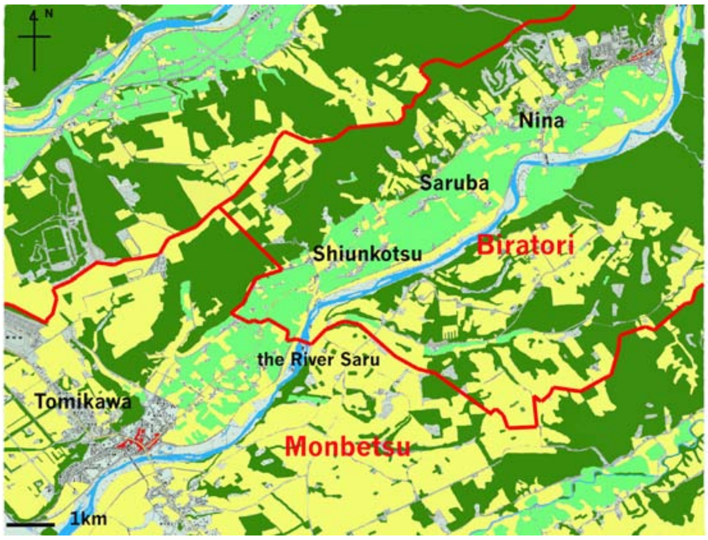

Fig. 2 Land use map of the study area of municipalities Biratori and Monbetsu in the Hidaka region of southern Hokkaido. Pale green, pale yellow, dark green, red, and blue areas are dominated by rice fields, other cultivated fields and pastures, broad-leaved and coniferous forests, densely residential areas, and rivers, respectively. Red lines indicate borders between municipalities.

multiflora var. *hortensis*, *Ligustrum obtusifolium* Siebold et Zucc., *Dahlia pinnata* Cav., *Salvia officinalis* L., *Helianthus annuus* L., and *Cosmos bipinnatus* Cav., and vegetable flowers such as, *Cucurbita* spp. and *Phaseolus coccineus* L.), they captured the bees and sent the frozen specimens to the authors. During the bees' active seasons, such a voluntary census was continued almost everyday, as long as the weather permitted.

The authors also performed censuses on *B. terrestris* and native bumblebees over a wider area of Monbetsu for 14–21 days each month during May, June, and July from 1996 to 2001. In 1996 and 1997, C. Matsumura took the census of native bumblebees from May to October in the area.

The censuses were performed in and around remnant woodlands of *Quercus dentata*, *Q. crispula* Blume and *Q. serrata* Thunb. The date, location, and the species and caste (workers, males and queens) of bumblebees witnessed were recorded with information on plant species upon which they fed, the presence or absence of pollen in their corbiculae, the presence or absence of nectar robbing behavior. The bees of *B. terrestris* were captured. For native bees, we captured the bees to identify the species and caste, and released them after identification.

In addition to these censuses, Yokoyama *et al.* (2003, 2004) took a census of *B. terrestris* at sites A and B, with an effort of 2.6 man-days and 0.4 man-days in 2002, and 3.7 man-days and 0.7 man-days in 2003, respectively.

2.2.2 *B. terrestris* census in Monbetsu and Biratori

In 2002, a census of *B. terrestris* and native bumblebees by a relatively large group of observers was initiated in the Tomikawa area of Monbetsu and mainly in Nina, Shiunkotsu, and Saruba of southern Biratori (Yokoyama *et al*., 2003). The census was performed during May to October on the flowers of exotic and native plant species by the road, in deciduous forests and its edges, and in gardens. The same kinds of information as in the above monitoring were recorded in this survey. The total amount of effort made each month during May to October was 6.9, 0.4, 1.7, 0.5, 1.8, and 0.5 man-days in Monbetsu, and 2.9, 8.0, 2.2, 0.1, 3.0, and 1.3 man-days in Biratori. Data from Monbetsu include the data collected at sites A and B.

2.3 Foraging overlap with native bumblebees

We compared the ranges of flower utilization between *B. terrestris* and native bumblebee species. Data were collected in Monbetsu and Biratori from 1996 to 2002 (Appendix 1) on the occasion of the censuses described above. The number of plant species visited by a given bumblebee species was compiled from all the observation data. The potential degree of competition for flower resources between two bumblebee species was evaluated according to patterns of the proportion of plant species foraged by both bumblebees among the total number of plant species foraged by either of the bumblebee species.

2.4 Analyses of pollen load collected from one *B. terrestris* nest

Forty pollen loads were collected from a total of 40 workers captured at the entrance to one *B. terrestris* nest (Bt-2 in Table 1) during various periods of time on four days from 29 June to 2 July 2002 (Matsumura *et al.,* unpublished).

Pollen grains from every load were acetolyzed and mounted in silicon oil on a slide. The slides were observed under a light microscope. From each of the slides, 200 pollen grains were randomly chosen and identified into plant species. According to the method of O'Rourke and Buchmann (1991), the proportion of pollen volume represented by plant species in every sample was calculated.

2.5 Nest sites and colony productivity

Ten *B. terrestris* nests have been found in the Hidaka region from 1996 to 2003 (Table 1). Eight among ten feral nests were found during one growing season in 2003. For the common native *Bombus* species in the study region (Table 2), seven *B. hypocrita sapporoensis* nests, three *B. diversus tersatus* Smith nests, seven *B. pseudobaicalensis* Vogt nests, and two *B. schrenck albidopleuralis* Skorikov nests were found in 2003. For the individual nests, nest site characteristics and/or bee productivity were compared and compiled according to Washitani (1998), Matsumura *et al.* (unpublished), Nakajima *et al.* (2004), and Matsumura *et al.* (2004).

3. Results

3.1 Numbers of *B. terrestris* recorded at long-term monitoring sites in Monbetsu

At both monitoring sites A and B, the yearly summed number of *B. terrestris* showed a marked increase especially in 2002 and 2003 (Fig. 3). At site A, the number increased from 0 in 1997 to 642 and 565 in 2002 and 2003, respectively; and at site B, the number increased from 0 in 1996 to 203 in 2003. At both sites, the number of queens increased steadily during 1999 to 2003.

3.2 Seasonal flight activities of castes of *B. terrestris* and native bumblebees

In 2002, *B. terrestris* was recorded in both Monbetsu and Biratori during the months from April to October (Fig. 4). In Biratori 996 *B. terrestris* individuals were collected. Possibly, most were reared bees which had escaped from greenhouses. Workers and males were collected from May to October, and queens, every month except August (Fig. 4). Although we could not collect queens of *B. terrestris* in August, they foraged on the flowers of *Phaseolus coccineus* L. (Leguminosae) in crop fields. In Monbetsu 687 *B. terrestris* individuals were collected. Most of them were assumed to be naturalized bees, because Tomikawa is 5-6 km away from the mass introduction site of southern Biratori. Queens were captured every month from April to October; workers, from May to October; and males, from July to October (Fig. 4).

Seasonal patterns of flight activities of *B. terrestris* in Monbetsu and four common native *Bombus* species in Monbetsu and southern Biratori are shown in Fig. 5. For *B. terrestris* and native bumblebees, data on 862 and 689 observations were compiled from the long-term monitoring and censuses in Monbetsu during 1996 to 2002 and the censuses in Biratori in 2002. The queens of *B. terrestris* were found from early spring when queens of no other species appeared. The flight activity period of *B. terrestris* was longer than that of any native species. The period when males of *B. terrestris* were active overlapped with those of new queens of all the native species, i.e., *B. ardens sakagamii* Tkalců, *B. hypocrita sapporoensis, B. diversus tersatus,* and *B. pseudobaicalensis* .

3.3 Foraging flower resources

During the seven-year monitoring program in Monbetsu and Biratori, we recorded 168 plant species visited by *B. terrestris* and four common native bumblebees (Appendix 1). *B. terrestris* visited the flowers of 100 species across 26 families, 58% of which were 12 alien wild plant species and 46 cultivated plant species. However, *B. terrestris*

Table 1 Nest sites of *Bombus terrestris* in the Hidaka region of southern Hokkaido, Japan. 'Bt' indicates *B. terrestris*. Blank indicates 'lack of data.'

Nest ID	Site	Surroundings	Entrance tunnel length (cm)	Elevation from the ground level (cm)
Bt-1	Cavity in a roll of fiber glass insulation on ground below the floor of a house	Residential area		
Bt-2	Rodent nest underground in a bank of an irrigation channel	Rice fields, fields	125	-28
Bt-3	Rodent nest underground in a ridge between rice fields	Rice fields		
Bt-4	Rodent nest underground in a bank of an irrigation channel	Rice fields, fields	33	-20
Bt-5	Rodent nest underground in a bank	A dry riverbed	70	-15
Bt-6	Rodent nest underground in a bank of an irrigation channel	Rice fields	140	-20
Bt-7	Rodent nest underground in a bank of an irrigation channel	Rice fields		
Bt-8	Rodent nest underground in a bank of an irrigation channel	Rice fields		
Bt-9	Rodent nest underground in a bank of an irrigation channel	Rice fields		
Bt-10	Rodent nest underground in a ridge between rice fields	Rice fields	33	-20

Table 2 Nest sites of the four common native bumblebee species in the Hidaka region of southern Hokkaido, Japan. ‘Bhs’, ‘Bdt’, ‘Bp’, ‘Bsa’ indicate *Bombus hypocrita sapporoensis, B. diversus tersatus, B. pseudobaicalensis, B. schrenck albidopleuralis,* respectively.

Nest ID	Site	Surroundings
Bhs-1	Rodent nest underground in a small bank	Deciduous forest edge, dwarf bamboo community
Bhs-2	Rodent nest underground in a small bank	Deciduous forest edge, dwarf bamboo community
Bhs-3	Rodent nest underground in a small bank	Rice fields
Bhs-4	Rodent nest underground in a ridge between rice fields	Rice fields
Bhs-5	Cavity in leaf litter and moss	Deciduous forest floor
Bhs-6	Rodent nest underground in a bank of an irrigation channel	Rice fields, fields
Bhs-7	Rodent nest underground in a riverbank	Rice fields, weed community
Bdt-2	Rodent nest underground in a bank of an irrigation channel	Rice fields, fields
Bdt-3	Rodent nest underground in a small bank	Deciduous forest edge
Bdt-4	Rodent nest underground in a small bank	Deciduous forest edge, dwarf bamboo community
Bp-1	Under litter at a bank of in irrigation channel	Rice fields
Bp-2	On ground at a dry riverbed	*Festuca arundinacea-Trifolium repens-T. pratense* community
Bp-3	Under litter at a dry riverbed	*Festuca arundinacea* community
Bp-4	Under litter on ground	Deciduous forest edge
Bp-5	Under litter on ground in a riverbank	weed community
Bp-6	Under litter on ground	Dwarf bamboo community, grassland
Bp-7	Under moss on ground	Dwarf bamboo community, deciduous forest floor
Bsa-1	Under litter on ground	Deciduous forest edge, dwarf bamboo community
Bsa-2	Under moss on ground	Deciduous forest edge, dwarf bamboo community

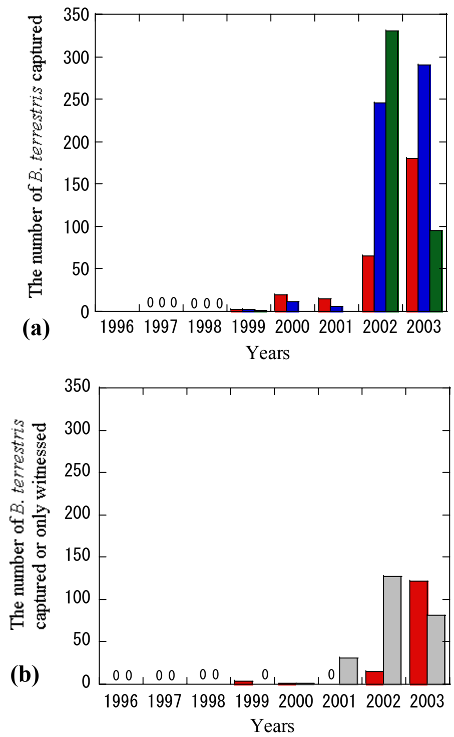

Fig. 3 The numbers of *Bombus terrestris* captured or witnessed during 1996 to 2003 in the gardens at site A (a) and site B (b), in Monbetsu. Red columns are for queens; blue columns, for workers; green columns, for males; and gray columns, for workers and males. At site A, one natural nest of *B. terrestris* was found in 1996. In the summer and autumn seasons of this year, many *B. terrestris* workers were observed at site A, but the number was not counted.

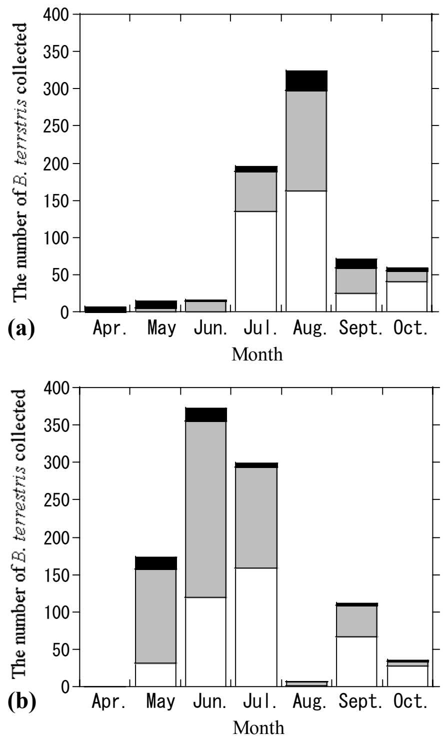

Fig. 4 Seasonal changes in the number of *Bombus terrestris* collected in Monbetsu (a) and southern Biratori (b) in 2002. Black columns are for queens; shaded columns, for workers; and white columns, for males. Blank indicates ‘lack of data.’

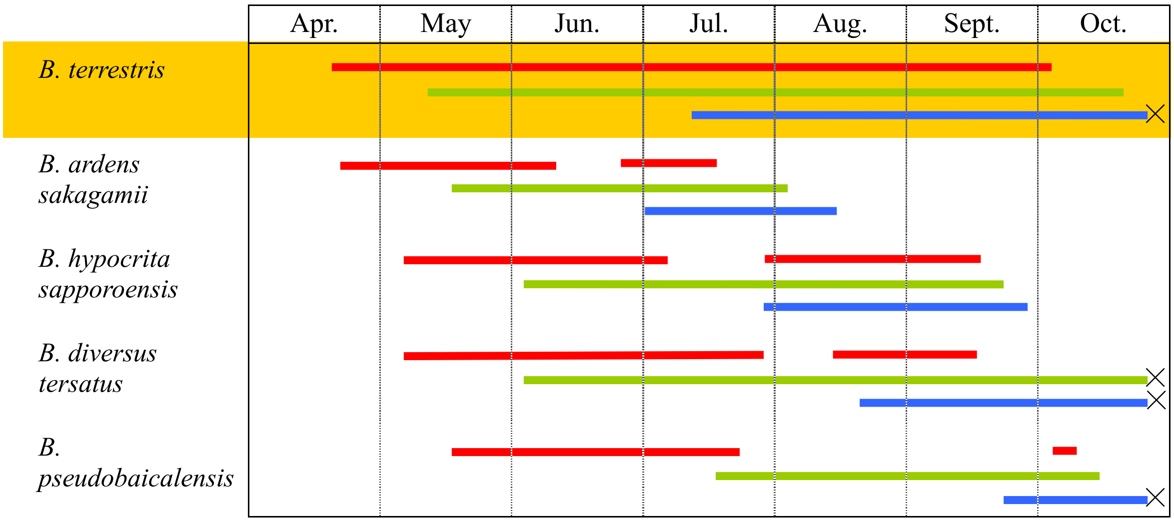

Fig. 5 Seasonal occurrence of castes of *Bombus terrestris* in Monbetsu compared with four common native *Bombus* species in Monbetsu and southern Biratori during 1996 to 2002. Red lines are for queens; green lines, workers; and blue lines, males. '×' indicates the end of the survey.

frequently visited native wild plant species in deciduous forests, such as *Staphylea bumalda* (Thunb.) DC. (Staphyleaceae).

Figure 6 shows flower resource sharing patterns among bumblebee species observed in Monbetsu and Biratori. Those comparisons indicate that 39.8% − 68.1% of plant species foraged by native bumblebee species were used as flower resources by B. terrestris, while 73.3% − 61.6% of plant species used by B. terrestris were not included in the diet menu of native bumblebee species.

Figure 7 shows the proportions of pollen volume of plant species, including native, alien naturalized, and cultivated plants, in pollen loads collected from the workers of one *B. terrestris* nest. A total of 80% by volume of the pollen grains was comprised by native wild plant species, *Actinidia arguta* (Siebold et Zucc.) Planch. ex Miq. (Actinidiaceae) and *Chelidonium majus* L. var. *asiaticum* (H. Hara) Ohwi (Papaveraceae).

3.4 Nectar robbing

B. terrestris was occasionally observed to perforate long corolla tubes and rob the nectar (i.e., primary nectar-robbery) from flowers of various wild and cultivated plant species. Nectar robbing by *B. terrestris* was recorded for a native plant species, *Vicia cracca* L. (Leguminosae), some exotic cultivated plant species, *Aquilegia vulgaris* L. (Ranunculaceae), *Lonicera sempervirens* L. (Caprifoliaceae), an alien naturalized plant species, *Symphytum officinale* L. (Boraginaceae), and several agricultural crop species, *Phaseolus coccineus* L., *P. vulgaris* L. (Leguminosae) (Fig. 8(a)), and *Lonicera caerulea* L. subsp. *edulis* (Turcz.) Hult var. *amphhyllocalyx* (Maxim.) Nakai (Caprifoliaceae) (Fig. 8(b)).

3.5 Nest sites

Among ten *B. terrestris* nests (Table 1), only one (Bt-1) was located in man-made fiber glass insulation above ground (Fig. 9 (a)) and was not furnished with a

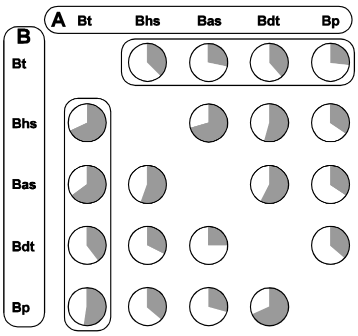

Fig. 6 Flower resource sharing patterns between two bumblebee species. The shaded portions in the pies indicate the proportion of plant species foraged by both A and B bumblebee species among the plant species used by B bumblebee species. Surrounded pies represent the sharing patterns between introduced *Bombus terrestris* and native bumblebees. 'Bt,' 'Bhs,' 'Bas,' 'Bdt,' and 'Bp' indicate *B. terrestris, B. hypocrita sapporoensis, B. ardens sakagamii, B. diversus tersatus, and B. pseudobaicalensis,* respectively.

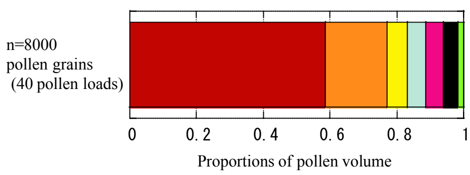

Fig. 7 The proportions of pollen volume of nine plant species in pollen loads collected from the workers of one *Bombus terrestris* nest (Bt-2) on four days from 29-June to 2-July 2002. Red and orange indicate native wild plant species, *Actinidia arguta* (Actinidiaceae) and *Chelidonium majus* var. *asiaticum* (Papaveraceae), respectively. Pink, black, and green indicate alien naturalized plant species, *Lupinus perenis*, *Trifolium pretense*, and *T. repens* (Leguminosae), respectively; pale blue, a cultivated plant species, *Weigela florida* (Caprifoliaceae); yellow, one species in the family Liliaceae. Small proportions of pollen grains, 0.0007 and 0.0001 were occupied by a native wild plant species, *Syringa reticulata* (Oleaceae) and an alien naturalized plant species, *Symphytum officinale* (Boraginaceae), respectively.

(a)

(b)

Fig. 8 (a) *Phaseolus vulgaris* (Leguminosae) and (b) *Lonicera caerulea* subsp. *edulis* var. *amphyllocalyx* (Caprifoliaceae) flowers that were robbed of their nectar by *Bombus terrestris* through a bitten hole in the corolla tube of the flowers without effective pollination. Arrows indicate holes formed by biting.

(a)

(b)

Fig. 9 *Bombus terrestris* nests located in (a) fiber glass insulation above ground below the floor of a private house (Bt-1, Table 1), and in (b) a rodent nest underground in a bank of an irrigation channel between rice fields (Bt-2, Table 1) in the Hidaka region of southern Hokkaido.

tunnel. The other nine nests were made in abandoned rodent nests with entrance tunnels underground in ridges between rice fields or other cultivated fields, and a dry riverbed (Fig. 9 (b)). Similarly, six *B. hypocrita sapporoensis* nests and three *B. diversus tersatus* nests were found to be built in abandoned rodent nests with entrance tunnels underground in ridges between rice fields or other cultivated fields and in deciduous forest edges (Table 2). Only one nest of *B. h. sapporoensis* was built in a cavity in leaf litter and moss (Bhs-5, Table 2). All nine nests of *B. pseudobaicalensis* and *B. schrenck albidopleuralis* were under litter or moss on the ground (Table 2).

3.6 Colony reproductive success inferred from collected nests

The total number of cocoons of the five *B. terrestris* nests collected (Table 3) ranged from 89 to 582 (mean ± s.d., 335.4 ± 179.7) and the total number of individuals at collection ranged from 334 to 911 (mean ± s.d., 548.2 ± 250.4). Among seven *B. terrestris* nests observed, five nests produced new queens (Table 4). In Bt-2, 5, 6, and 10, new queen production ranged from 78 to 151 (mean ± s.d., 110.00 ± 30.32). These nests were collected just before their cycles completed. Bt-2 produced new queens as early as mid-July. In Bt-5 a live foundress queen and a dead body of queen were present.

The total number of cocoons of the four *B. pseudobaicalensis* nests and one *B. schrenck albidopleuralis* nest (Table 3) rangedfrom 49 to 376 (mean ± s.d., 191 ± 120.8) and the total number of individuals at collection ranged from 6 to 63 (mean ± s.d., 40.6 ± 24.4). Among 19 nests of native bumblebees, 12 nests produced new queens (Table 4). In Bhs-4, Bdt-2, and Bp-4, 5, the numbers of new queens produced ranged from 19 to 36 (mean ± s.d., 25.00 ± 7.79).

Although there was no significant difference in the proportion of colonies with new queen production between *B. terrestris* and native bumblebees (Fisher's exact probability test: $p > 0.9999$), the mean number of new queens in the colonies of *B. terrestris* was significantly larger (Mann-Whitney *U* test: $p = 0.021$), and 4.4 times that of the native bumblebees (Matsumura *et al*., 2004).

4. Discussion

4.1 Presumable rapid population growth

The discovery of eight feral colonies of *B. terrestris* discovered during one growing season as well as the accelerated increase in the number of *B. terrestris* captured in the Tomikawa area of Monbetsu during the past eight years strongly suggests that *B. terrestris* has already established a feral population in the study region. The mean number of new queens produced per mature nest of *B. terrestris* was shown to surpass 100, and such reproductive success is comparable to that observed for laboratory-reared nests of the species (Goodwin & Steiner, 1997). Such a high reproductive advantage of *B. terrestris* coincides with the accelerated increase in the number of *B. terrestris* bees captured in the study area. On forty days from 26-April to 5-June 2004 in the study area and surroundings, 976 newly emerged queens of *B. terrestris* were collected. One hundred forty five of them carried pollen loads in their corbiculae, indicating that they had established colonies (Matsumura *et al*., unpublished). It is likely that the rapid population growth of *B. terrestris* continues in the study region.

Among the *B. terrestris* feral nests studied, one reached full maturity and produced new queens in as early as mid July. Such early summer maturation suggests the possibility of production of a second generation in the year, since Beekman *et al.* (1999) and Beekman and van Stratum (2000) showed the possibility of production of a second generation without a period of diapause under laboratory conditions. In New Zealand (Donovan & Weir, 1978) and Tasmania (Buttermore, 1997), yearly second generations are not exceptional during warmer months. However, the egg-laying capability of the new queens produced early in summer should be examined before any firm conclusion on the possibility of two yearly generations in the study area is drawn.

4.2 Potential for floral resource competition with native bumblebees

B. terrestris was shown to be highly polylectic in the study region, as is the case within its native range (Fussell & Corbet, 1992; Dafni & Shmida, 1996) and in Tasmania (Hingston & McQuillan, 1998). At Mt. Carmel in Israel, the species was reported to forage on almost all plants with nectar-producing flowers (Dafni & Shmida, 1996).

The analyses of pollen loads collected from a *B. terrestris* nest in the present study demonstrated that some native plant species are important pollen resources for *B. terrestris* colonies. Most plant species that were foraged by native bumblebees were utilized also by *B. terrestris*, whereas *B. terrestris* was shown to forage on a range of plant species less likely to be used by native bumblebees. Moreover, native plant species utilized by *B. terrestris* are increasing year after year (Yokoyama *et al.*, 2003, 2004). Frequent visitations by *B. terrestris* queens to the flowers of native forest plant species, *Erythronium japonicum* Decne. (Liliaceae), *Corydalis ambigua* Lidén et Zetterlund (Papaveraceae), and *Prunus sargentii* Rehder (Rosaceae) were recorded from observations in 2003 in the study area (Yokoyama *et al.,* 2004). These plant species are important resources for queens of *B. ardens sakagamii* and *B. h. sapporoensis* newly emerged from hibernation (Yokoyama *et al.,* 2004). In 2003, a springtime forest herb *Corydalis incisa* Pers. (Papaveraceae) frequently foraged by newly emerged queens of *B. d. tersatus* were used as flower resources by *B. terrestris* queens in the study area (Matsumura *et al.,* unpublished).

These results suggest that all the native bumblebee species may be affected by the competition for plant resources from *B. terrestris,* and that they will suffer from resource deficiency if the rapid population growth of *B. terrestris* continues.

4.3 Potential for nest site competition with native bumblebees

Most of the nests of *B. terrestris* discovered in this study were found under the ground. Similarly, most Japanese native bumblebee species use underground nests abandoned by small mammals (Katayama & Ochiai, 1980; Ito, 1991). Similarity in nest site selection with *B. terrestris* was noted for the short-tongued *B. h. sapporoensis*, and long-tongued *B. d. tersatus* in the present study. It is likely that *B. terrestris* will compete for nest sites at least with these species. Furthermore, *B. terrestris* queens have a marked advantage in occupying suitable nest sites over native queens because of their early emergence from hibernation. Preemption of the nest sites by *B. terrestris* queens, the population of which is rapidly growing, will inevitably pose a serious threat to the native species.

On the other hand, according to Prys-Jones and Corbet (1991), *B. terrestris* is more adaptable for taking advantage of man's artifacts (*e.g*., rolled-up carpets and heaps of coal). In the present study, a *B. terrestris* nest was found in a cavity of a fiberglass insulation roll left on the ground. In Shimane prefecture of western Japan, a *B. terrestris* nest was found in a fold of a vinyl tarpaulin on the floor of a greenhouse (Hosoda, 1999). These facts indicate that *B. terrestris* chooses nest sites more flexibly than most native bumblebee species and is presumably less susceptible to nest site shortage.

Nest invasion by queens of either the same or another species is rather common in bumblebees (Sladen, 1912), and the habit was ascertained for *B. terrestris* in the present study. Of the five nests of *B. terrestris* collected and dissected, one had two

Table 3 Nest size and the number of individuals of *B. terrestris* and native bumblebee nests in the Hidaka region of southern Hokkaido. 'No. of cocoons' indicates total numbers of opened and un-opened cocoons. 'No. of individuals' indicates total number of live eggs, larvae, cocoons, and bees at time of collection. '.' indicates 'not collected' and blank indicates 'lack of data.' Symbols as in Tables 1 and Table 2.

			Nest size (cm)				
Nest ID	Date found	Date collected	Length	Width	Height	No. of cocoons	No. of individuals
Bt-1		20-Oct-96					
Bt-2	4-Jun-02	17-Jul-02	20	20	5	582	405
Bt-3	4-Jun-03	.					
Bt-4	3-Jul-03	2-Aug-03	11	8	6	89	334
Bt-5	8-Jul-03	2-Aug-03	20	13	8	321	708
Bt-6	4-Aug-03	23-Aug-03				403	911
Bt-7	4-Aug-03	.					
Bt-8	5-Aug-03	.					
Bt-9	5-Aug-03	.					
Bt-10	27-Aug-03	28-Aug-03	20	13	8	282	383
Bhs-1	5-Jul-03	.					
Bhs-2	5-Jul-03	.					
Bhs-3	8-Jul-03	.					
Bhs-4	8-Jul-03	.					
Bhs-5	25-May-03	.					
Bhs-6	4-Aug-03	.					
Bhs-7	6-Aug-03	.					
Bdt-2	3-Jul-03	.					
Bdt-3	20-Sept-03	.					
Bdt-4	21-Sept-03	.					
Bp-1	4-Jul-03	.					
Bp-2	7-Jul-03	.					
Bp-3	9-Jul-03	.					
Bp-4	25-Aug-03	12-Oct-03	11	10	10	180	60
Bp-5	29-Aug-03	23-Sept-03	13	11	13	376	63
Bp-6	16-Sept-03	12-Oct-03	7	6	4	49	6
Bp-7	17-Sept-03	12-Oct-03	11	8	6	216	25
Bsa-1	21-Sept-03	.	10	10			
Bsa-2	23-Sept-03	24-Sept-03	10	9	6	134	49

conspecific foundress queens (a live queen and a dead queen body). One might be the original foundress, and another, a usurper.

4.4 Presumable impacts on plant-pollinator mutualisms

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). Considering the high competitive abilities of *B. terrestris,* displacement of short- and long-tongued native bumblebee species by *B. terrestris* through competition will be highly likely in near future.

Reduction in the long-tongued bumblebee species population will cause reproductive failure of long-tubed flowers that depend on these bumblebee species. Furthermore, nectar robbing by *B. terrestris,* which was recorded in several wild plant species, may disturb the reproduction of these plants. Nectar robbing by *B. terrestris* was also ascertained for some crop plants, *Phaseolus coccineus*, *P. vulgaris*, and *Lonicera caerulea* subsp. *edulis* var. *amphhyllocalyx*. Nectar robbing by *B. terrestris* from the flowers of the Field Bean (*Vicia fava* L.) has been frequently observed in Europe and New Zealand (Newton & Hill, 1983). Therefore, the bees have the potential to negatively influence seed production not only of wild plants but also of agricultural crops by hindering normal pollination.

As discussed above, enhanced negative impacts of the rapidly growing population of *B. terrestris* on native bumblebees and bumblebee-pollinated plants are anticipated. To avoid such impacts, not only prevention of further escape, but also control of established populations is urgently needed.

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Table 4 The number of live un-opened new queen cocoons and adult new queens in individual nests of *Bombus terrestris* and native bumblebees. Blank indicates 'lack of data.' Symbols as in Tables 1 and Table 2.

Nest ID	No. of new queens			Cause of nest demise
	Un-opened cocoons	Adults	Total	
Bt-2	33	118	151	Cycle complete
Bt-3		+	+	Cycle complete
Bt-4	0	0	0	Queen absence/ Nest collection
Bt-5	108	0	108	Nest collection
Bt-6	103	0	103	Nest collection
Bt-7	0	0	0	Mites
Bt-8				Destruction of nest entrance and tunnel
Bt-9				Destruction of nest entrance and tunnel
Bt-10	24	54	78	Nest collection
Bhs-1		+	+	Cycle complete
Bhs-2	0	0	0	Unknown
Bhs-3		+	+	Cycle complete
Bhs-4		36	36	Cycle complete
Bhs-5	0	0	0	Unknown
Bhs-6		+	+	Cycle complete
Bhs-7		+	+	Cycle complete
Bdt-2		25	25	Cycle complete
Bdt-3		+	+	Cycle complete
Bdt-4		+	+	Cycle complete
Bp-1	0	0	0	Unknown
Bp-2	0	0	0	Flooding
Bp-3	0	0	0	Unknown
Bp-4	9	10	19	Cycle complete
Bp-5	0	20	20	Cycle complete
Bp-6	0	0	0	Queen absence
Bp-7	0	0	0	Queen absence
Bsa-1	+	+	+	Cycle complete
Bsa-2	+	4	+	Cycle complete

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Appendix 1 Plant species visited by bumblebees from 1996 to 2002 in Monbetsu and Biratori in the present study. 'Bt', 'Bas', 'Bhs', 'Bdt', 'Bp' indicate *Bombus terrestris, B. ardens sakagami, B. hypocrita sapporoensis, B. diversus tersatus, B. pseudobaicalensis,* respectively. Q indicates queens; W, workers; M, males; and U, unidentified caste. 'p' indicates 'pollen carrying bees were observed.' *Alien naturalized plant species, **cultivated plants, ***cultivated varieties of native plants. Plant family arrangement is based on Melcheior 'A. Engler's Syllabus der Pflanzenfamilien' (1964).

			Bumblebee species				
Month	Family	Species	Bt	Bas	Bhs	Bdt	Bp
	(Herbaceous plant species)						
8,9	Caryophyllaceae	*Silene latifolia* subsp. *alba**				W	
8,9	Ranunculaceae	*Aconitum yesoense*				Wp, M	W
7	Ranunculaceae	*Aquilegia flabellate*		W	W		
6	Ranunculaceae	*Aquilegia vulgaris***	Qp,Wp				
7	Ranunculaceae	*Thalictrum minus* var. *hypoleucum*			Wp		
8	Guttiferae	*Hypericum erectum*					W
5	Papaveraceae	*Chelidonium majus* var. *asiaticum*	Qp,Wp			Q	
5	Papaveraceae	*Corydalis ambigua*				Q	
5,6	Papaveraceae	*Corydalis incise*		Q	Q	Q	Q
9	Papaveraceae	*Eschscholzia californica***	Wp				
7	Papaveraceae	*Papaver rhoeas***	Wp				
5,6	Cruciferae	*Barbarea vulgaris**	Q,Wp,M		Q		Q
7,8,9	Cruciferae	*Brassica oleracea***	W			W	
6	Cruciferae	*Cardamine leucantha*				Q	
9	Cruciferae	*Lobularia maritima***	Q				
8,9	Cruciferae	*Raphanus sativus***				W	
9	Crassulaceae	*Hylotelephium cauticolum*	Wp		W,M	Wp,M	W
9	Crassulaceae	*Hylotelephium telephium*	Q,M				
8	Saxifragaceae	*Astilbe* × *arendsii***	Wp,M				
7	Saxifragaceae	*Astilbe thunbergii* var. *congesta*	W				

Appendix 1 Continued.

7	Rosaceae	*Filipendula yezoensis*			W		
5	Rosaceae	*Potentilla discolor*				Q	
9	Rosaceae	*Sanguisorba tenuifolia* var. *alba*	Wp				
6	Leguminosae	*Lathyrus japonicus* subsp. *japonicus*					Q
7,8,9	Leguminosae	*Phaseolus coccineus***	Qp,Wp,M	M	W,M	W	
8	Leguminosae	*Phaseolus vulgaris***	W,M				
6	Leguminosae	*Thermopsis lupinoides*					Q
6	Leguminosae	*Trifolium hybridum**	Wp				
6,7,8,9,10	Leguminosae	*Trifolium pretense**	Qp,Wp,M		Q,Wp	Qp,Wp,M	Q,Wp,M
6,7,8,10	Leguminosae	*Trifolium repens**	Qp,Wp,M		Q,Wp,M	Qp,Wp	Q,Wp
8	Leguminosae	*Vicia amoena*				Wp	
7,8	Leguminosae	*Vicia cracca*	W,M			Wp	W
8	Leguminosae	*Vicia nipponica*					W
8	Leguminosae	*Vicia unijuga*				Wp	Wp
6,7	Leguminosae	*Lupinus perrenis**	Wp		Wp	W	
9	Geraniaceae	*Geranium nepalense* subsp. *thunbergii*				W	
5	Geraniaceae	*Geranium phaeum***	Q,W				
9	Balsaminaceae	*Impatiens glandulifera***				W	
7,8,9	Balsaminaceae	*Impatiens noli-tangere*			W	Q,Wp,M	
8,9	Balsaminaceae	*Impatiens textori*				W,M	
9	Balsaminaceae	*Impatiens walleriana***				Q,W,M	
5,6	Violaceae	*Viola hirtipes*				Q	Q
5	Violaceae	*Viola* × *wittrockiana***				Q	
7,9	Tropaeolaceae	*Tropaeolum majus***	W			Q,W	
7	Cucurbitaceae	*Cucumis sativus***	W,Q				
7,8	Cucurbitaceae	*Cucurbita maxima***	W			W	
7,8	Cucurbitaceae	*Cucurbita maxima* × *moschata***	W,M			W	
5,6	Primulaceae	*Primula sieboldii*		Q		Q	Q
9	Convolvulaceae	*Ipomoea purpurea***				Q	
5,6,7,9	Boraginaceae	*Symphytum officinale**	Qp,Wp,M	Wp	Q,Wp	Qp,W,M	Q
7,8	Labiatae	*Agastache rugosa*				Wp	
8	Labiatae	*Clinopodium chinense* subsp. *grandiflorum* var. *parviflorum*				W	W
8	Labiatae	*Clinopodium sachalinense*			W		
9	Labiatae	*Elsholtzia ciliate*				W,M	M
5,6	Labiatae	*Glechoma hederacea* subsp. *grandis*					Q
7	Labiatae	*Hissopus officinalis***					W
7	Labiatae	*Lamium maculatum***	W				
7	Labiatae	*Mentha* sp.**	M				
9	Labiatae	*Origanum vulgare***	W,M				W
8	Labiatae	*Physostegia virginiana***	W				
7	Labiatae	*Prunella vulgaris* subsp. *asiatica*	M		Qp		
8,9	Labiatae	*Rabdosia inflexa*				W,M	W
7	Labiatae	*Salvia officinalis***	Wp,M				
7	Labiatae	*Scutellaria strigillosa*					W
7	Labiatae	*Stachys riederi* var. *intermedia*				W	
7	Labiatae	*Thymus serpyllum* subsp. *quinquecostatus*			W		
8,9	Solanaceae	*Lycopersicon esculentum***	Wp			Wp	
9	Scrophulariaceae	*Antirrhinum majus***	Q			W	
7	Scrophulariaceae	*Digitalis purpurea***	Wp				
7	Scrophulariaceae	*Mimulus hybridus***	Wp				
7	Scrophulariaceae	*Verbascum thapsus**	Wp				
7	Scrophulariaceae	*Veronicastrum sibiricum* subsp. *japonicum*	Wp				

Appendix 1 Continued.

7	Orobanchaceae	*Phacellanthus tubiflorus*				Qp	
8	Phrymaceae	*Phryma leptostachya* var. *asiatica*				W,M	
8	Campanulaceae	*Adenophora triphylla* var. *japonica*				W,M	W
8	Campanulaceae	*Codonopsis ussuriensis*				W	
7	Campanulaceae	*Platycodon grandiflorum*	U				
9	Compositae	*Ammobium alatum***	W				
9	Compositae	*Aster ageratoides* subsp. *ovatus* var. *yezoensis*	W				
9,10	Compositae	*Aster novae-angliae**	M			Wp,M	Wp,M
9	Compositae	*Aster novi-belgii**					W,M
7	Compositae	*Breea setosa*	Q,Wp,M				
6	Compositae	*Cacalia hastata* subsp. *orientalis*				Q	
7	Compositae	*Centaurea cyanus***	Wp,M	M			W
6,7,8	Compositae	*Cirsium kamtschaticum*		M,Wp	Qp,Wp	Qp,Wp	
8,9,10	Compositae	*Cirsium oligophyllum* subsp. *aomorense*	Wp,M			Wp,M	M,U
9	Compositae	*Cirsium pendulum*				Wp	
9	Compositae	*Cirsium vulgare**	M				
9,10	Compositae	*Cosmos bipinnatus***	Q,Wp,M		Q,U	W,M	U
7	Compositae	*Cosmos sulphureus***	M				Wp
7,8,9,10	Compositae	*Dahlia hybrida***	Q,Wp,M			Wp,M	Wp
7	Compositae	*Helianthus annuus***	W,M				
7	Compositae	*Helianthus debilis***	Wp,M				Wp
7	Compositae	*Leucanthemum × superbum***	W				
8,9	Compositae	*Rudbeckia laciniata**	Q,Wp,M		W,U	Q,Wp,M	Wp,U
7,8,9	Compositae	*Solidago gigantea* var. *leiophylla**	Wp,M	M	Wp,M,U	Wp	W
9	Compositae	*Tagetes erecta* **				Q,W,M	W
5,6	Compositae	*Taraxacum hondoence*				Q	Q
5,6	Compositae	*Taraxacum officinale**	Q,Wp,M	Q	Q	Q	Q
8	Compositae	*Liatris spicata***	W				
9	Compositae	*Zinnia elegans***	Q				
8	Liliaceae	*Cardiocrinum cordatum* var. *glehnii*				Wp	
6	Liliaceae	*Disporum sessile*				Q	
6	Liliaceae	*Disporum smilacinum*				Q	
5	Liliaceae	*Erythronium japonicum*			Q		
8	Liliaceae	*Hosta albo-marginata*				Wp	
7	Liliaceae	*Hosta sieboldiana* var. *sieboldiana****	Q			W	
8	Liliaceae	*Hosta* sp.***	W	M			
6	Liliaceae	*Polygonatum odoratum* var. *maximowiczii*	Wp	W	W	Q	Q
7	Iridaceae	*Iris sanguinea*				Qp	
5	Iridaceae	*Iris setosa*	Q				
9	Commelinaceae	*Commelina communis*				Wp	
6	Poaceae	*Dactylis glomerata**			Wp		
9	Cannaceae	*Canna indica hybrid***				U	
	(Woody plant species)						
5	Berberidaceae	*Berberis canadensis***	Q,Wp				
6	Berberidaceae	*Berberis* sp.**		Q	Q	Q	Q
7	Actinidiaceae	*Actinidia arguta*	Wp			W	
7	Saxifragaceae	*Hydrangea paniculata*	W,M		U		
8	Saxifragaceae	*Hydrangea* sp.**	Q				
5	Rosaceae	*Chaenomeles speciosa*	Q				
5,6	Rosaceae	*Kerria japonica*	Wp				
5,6	Rosaceae	*Malus baccata*		Qp,Wp		Q	Q
5	Rosaceae	*Prunus maximowiczii*	Qp	U	U		

Appendix 1 Continued.

5	Rosaceae	*Prunus sargentii*		W	Q		
5	Rosaceae	*Prunus* sp.***	Q				
7	Rosaceae	*Rosa multiflora*	W	W	Qp,W	Q	
7	Rosaceae	*Rosa rugosa*				Wp	
8	Rosaceae	*Rosa* sp.**		W			
6,7	Rosaceae	*Rubus crataegifolium*				Q	
6	Rosaceae	*Rubus idaeus***	W				
6	Rosaceae	*Rubus parvifolius*		M	W	W	
7	Rosaceae	*Rubus phoenicolasius*		M			
5	Rosaceae	*Sorbus sambucifolia*	W				
6,8	Rosaceae	*Spiraea salicifolia*	Qp,Wp			Wp	
8,9	Leguminosae	*Lespedeza bicolor*	Wp		W	Wp	Wp
7	Leguminosae	*Lespedeza* sp.***	Wp				
6,7	Leguminosae	*Robinia pseudoacacia**	Wp	W	Q,Wp	Q,W	
6	Leguminosae	*Wisteria floribunda*	Wp	W	W		Q
5	Aceraceae	*Acer japonicum*		W	Q		
5	Aceraceae	*Acer mono*		W			
6	Hippocastanaceae	*Aesculus turbinata*	Wp,M	Wp	Wp		
6	Celastraceae	*Celastrus orbiculatus*				Q	
6	Staphyleaceae	*Staphylea bumalda*	Q,Wp,M	Q,W	Q,Wp	Q	
10	Malvaceae	*Hibiscus moscheutos***	W				
9	Malvaceae	*Hibiscus syriacus***	W				
5,6	Elaeagnaceae	*Elaeagnus multiflora* var. *hortensis*	Q,Wp,M	Wp	Q,W	Q	Q
6	Ericaceae	*Enkianthus campanulatus*	Q				
5	Ericaceae	*Enkianthus perulatus*	Qp	Q	Q		
8	Ericaceae	*Erica* sp.**	Wp,M				
5	Ericaceae	*Pieris japonica*	Qp	Q	Q		
5	Ericaceae	*Rhododendron aureum* × *brachycarpum*	Qp,Wp		Q		
7	Ericaceae	*Rhododendron brachycarpum*	Wp,M	M	W	W	W
4,5	Ericaceae	*Rhododendron dauricum*	Q,W	Q,Wp	Q	Qp	Q
5	Ericaceae	*Rhododendron dilatatum*	Qp			Q	
6	Ericaceae	*Rhododendron japonicum*	W	W	Q	Q	
5,6	Ericaceae	*Rhododendron kaempferi*		Wp	Q,W	Qp	
5	Ericaceae	*Rhododendron kiusianum*	Wp	M			
5,6	Ericaceae	*Rhododendron* × *mucronatum*	Q,Wp	M			
5	Ericaceae	*Rhododendron obtusum****	Q	M			
5	Ericaceae	*Rhododendron yedoense* var. *yedoense***	Q	Q			
5	Ericaceae	*Rhododendron* sp.***	Qp				
6,7,8	Oleaceae	*Ligustrum obtusifolium*	Wp,M	M	Wp	Wp	
6	Oleaceae	*Syringa reticulata*	Wp		Wp		
6	Oleaceae	*Syringa vulgaris***				Q	
5,6	Caprifoliaceae	*Lonicera caerulea* subsp. *edulis* var. *amphyllocalyx*	Qp,Wp,M		Q		
7	Caprifoliaceae	*Lonicera sempervirens***	W				
7	Caprifoliaceae	*Weigela coraeensis*	W		Qp		
7	Caprifoliaceae	*Weigela decora*				W	

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