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Spatial and temporal pattern of introduced *Bombus terrestris* abundance in Hokkaido, Japan, and its potential impact on native bumblebees

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Abstract A commercial colony of *Bombus terrestris* (L.) was introduced to Japan in 1992 for crop pollination in greenhouses. Since then wild colonies have developed and spread in some regions. In the present study, we measured the spatial distribution and temporal change in abundance of *B. terrestris* in the Chitose River Basin, Hokkaido, Japan to elucidate the relation of greenhouses to the bee's distribution and to evaluate its potential effects on native bumblebees. Bumblebees were collected with window traps in windbreak forests roughly 1, 2, 4, and 6 km NNW and SSE of a large greenhouse. The peak catch of *B. terrestris* queens occurred in early June, suggesting that they had successfully hibernated in the field. The distributions of *B. terrestris* and the native *B. ardens* were mutually exclusive, while the native *B. hypocrita* appeared at all sites. Catches of *B. terrestris* were restricted to within 4 km of the nearest greenhouse, suggesting that the invasion was still in the initial phase in this area. The reduction in abundance of the native bumblebees in the sites of high *B. terrestris* abundance suggests the presence of interspecies competition between *B. terrestris* and the native bumblebees during the early part of the

colony activity, although such reduction in *B. ardens* can be explained by habitat suitability.

Keywords *Bombus ardens* · *Bombus hypocrita* · Chitose River Basin · Introduced species · Interspecies competition

Introduction

The large earth bumblebee, *Bombus terrestris* (L.), which is indigenous to Europe, has been artificially introduced throughout the world. In New Zealand, four European bumblebee species including *B. terrestris* were released for pollination of crops, such as meadow grass, starting in the 19th century (Macfarlane and Gurr 1995). Since 1988, colonies of *B. terrestris* in portable boxes have been available commercially from European companies. The bees are used for pollination of crops grown in greenhouses, particularly the tomato *Lycopersicon esculentum* Mill. In some countries, queens escaped from the introduced colonies, and founded wild colonies, and these colonies produced reproductive individuals (Semmens et al. 1993; Washitani 1998; Hingston et al. 2002). This exotic bumblebee has the potential to affect native bees and plants in four ways. First, exotic parasites and pathogens may be transmitted from *B. terrestris* to native bumblebees (Goka et al. 2001). Second, if native bumblebees hybridize with *B. terrestris*, pure strains of native bumblebees will decrease due to introgression (Goka 1998). Third, competition with *B. terrestris* for nest sites and food resources may decrease the species richness and abundance of native bees (Hingston and McQuillan 1999). Finally, if *B. terrestris* interferes with the pollination of native plants by native bees or facilitates pollination of alien plants, reproductive success of native plants may decrease and natural pollination systems may be altered (Dafni and Shmida 1996).

Visual observations throughout Tasmania, Australia, have suggested that *B. terrestris* had reached locations more than 230 km distant from the town where it had first

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been observed (Hingston et al. 2002). On the other hand, a quantitative survey of *B. terrestris* using sticky traps (Goulson et al. 2002) clearly showed that *B. terrestris* colonization was restricted to a narrower range than that suggested by Hingston et al. (2002). Although the impacts of *B. terrestris* on native bees and plants have been studied in Tasmania (Goulson et al. 2002), Tasmania lacks native bumblebees, which would probably be the ones most strongly affected by the invasion of *B. terrestris*.

B. terrestris was introduced into Japan in 1992, and the first reproductive colony was found in 1996 (Washitani 1998). In the Chitose River Basin, Hokkaido, commercial *B. terrestris* colonies have been used since 1992, and their use has rapidly increased since 1997 (Matsumura and Washitani 2002; Nakajima et al. 2004). Thus, this area is suitable for studying the initial phase of the invasion process of *B. terrestris*. To obtain data, we used traps instead of direct observation or marking and recapturing because trapping is particularly appropriate for quantitative assessment of bumblebees at numerous sampling sites and requires relatively little labor (Goulson et al. 2002).

We investigated the spatial distribution and temporal seasonal changes in the abundance of *B. terrestris* in the Chitose River basin in relation to the abundance and performance of native bumblebees in order to address the following questions: (1) Is *B. terrestris* naturalized? (2) How far has the range of *B. terrestris* spread?

Materials and methods

Study area

This study was conducted in an approximately 270 km² area surrounding a 7-ha greenhouse for tomato cultivation (hereafter the “large greenhouse”) in Chitose River Basin, Hokkaido Island, Japan (42°54′N, 141°38′E, 0–40 m in altitude; Fig. 1). The large greenhouse was about 3 km away from the nearest urban area. Several small greenhouses in which tomatoes were cultivated (“small greenhouses”) were located within the area (Fig. 1). The study area consisted mainly of rice, potato, and wheat fields and meadows. Many windbreak forest belts approximately 20 m in width run through the study area (Fig. 1). Most of them are remnants of cool-temperate deciduous broad-leaved forests dominated by *Quercus crispula* Blume, *Acer mono* Maxim., and *Fraxinus mandshurica* Maxim., usually with dwarf bamboo, shrubs, and herbs in the understory. Residential and industrial areas lie along the western and southern boundaries of the agricultural area.

Native bumblebees

Six native *Bombus* species are distributed in this region (Ito 1991), *Bombus ardens sakagamii* Tkalcu, *Bombus hypnorum koropokkurus* Sakagami and Ishikawa,

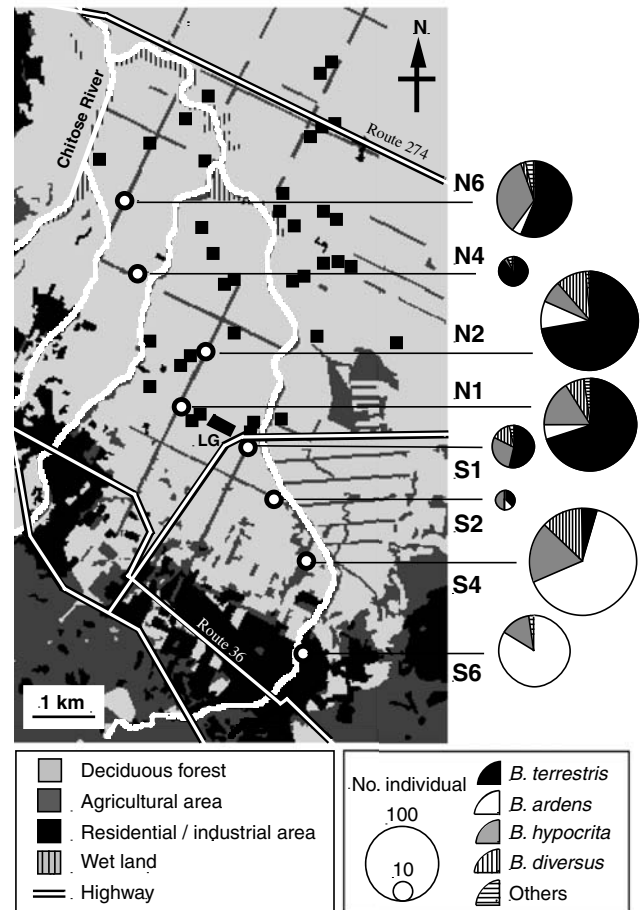


Fig. 1 Abundance and species composition of bumblebees collected at each trapping site. Distributions of five types of vegetation or development and the greenhouses in which commercial *B. terrestris* colonies were used in 2003 are marked. LG is the large greenhouse and closed squares indicate small greenhouses

Bombus hypocrita sapporoensis Cockrell, *Bombus diversus tersatus* Smith, *Bombus pseudobaicalensis* Vogt, *Bombus deuteronymus deuteronymus* Schulz, and *Bombus schrenki albidopleuralis* Skorikov. *Bombus hypocrita* appears over a wide range of altitudes from sea level to alpine meadows, but the other five species are mainly distributed in lowlands (Ito 1991). *B. ardens* may have a more selective preference for broadleaf forests than the other five species (Ito and Munakata 1979). *B. ardens* is characterized by an early and short duration of colony activity, and *B. diversus* is the latest to appear and survives the longest of the six species (Inoue and Kato 1992). Subgenus *Diversobombus* including *B. diversus* has the longest proboscis compared with body length, while subgenus *Bombus* including *B. terrestris* and *B. hypocrita* has the shortest relative proboscis length of the other subgenera in the study area (Ito 1991; Inoue and Kato 1992).

Distribution of *B. terrestris* commercial colonies

In order to locate invasion sources of *B. terrestris*, we first located all greenhouse-like constructions using

aerial photographs (approximately 1:30,000, Geographical Survey Institute of Japan). Then we visited all marked constructions $\geq 900 \text{ m}^2$ to check whether they were greenhouses for farming, and, in November and December 2003, searched for smaller (400–900 m^2) greenhouses in the study area that had not been found on the aerial photographs. We excluded greenhouses of less than 400 m^2 because commercial *B. terrestris* colonies are not used in such small greenhouses due to low profitability. We visited owners of all the greenhouses more than 400 m^2 in area and inquired (1) whether they used commercial *B. terrestris* colonies or not, and if so, (2) when they had started using them, (3) how many colonies they used each year, and (4) in which seasons they maintained the commercial colonies. Commercial colonies were introduced into the small greenhouses in late April or early May and disposed of in August, September, or October. Windows of these greenhouses were frequently opened during this period to moderate the temperature. In the large greenhouse, tomatoes were cultivated throughout the year using various stages of commercial colonies continuously; the windows of the greenhouse were opened from late April to October. The large greenhouse has been using commercial colonies since 1997. Since 2001 it has used 200–300 colonies per year. The numbers of colonies used from 1997–2000 was not recorded. All the small greenhouses using commercial colonies were located north of the large greenhouse (Fig. 1). In 2003, a total of 101 commercial colonies were used in 36 small greenhouses. The small greenhouses have been using from one to ten colonies per year for periods ranging from 1–11 years.

Trapping of bumblebees

We arranged trapping sites around the large greenhouse assuming that it was the main invasion source in the study area. We set window traps at sites roughly 1, 2, 4, and 6 km distant from the large greenhouse along two imaginary transects in each direction, NNW (northern transect, hereafter) and SSE (southern transect) (site names: N1, 2, 4, 6 and S1, 2, 4, 6) (Fig. 1). A window trap is a kind of interception trap, which has a roof, transparent vanes perpendicularly crossed, and a plastic white tray (Inari 2001). Water (2 liter) with a little odorless detergent was placed in the tray. After samples were collected, the tray was filled with freshly made detergent water.

In early May 2003, we set a total of 34 traps at two heights (1 m above the ground and in the canopy stratum) on two trees at seven sites (N1, 2, 4, 6 and S1, 2, 6), and on three trees at S4. The height of the canopy traps ranged from 7–15 m, according to the canopy height of the forests. The lowest trap was tied directly to a tree branch, while the others were suspended by a rope through a pulley fixed to a canopy branch. Trapped bumblebees were collected once a week from 31 May to 19 September 2003, and in total 510 samples [(7

sites \times 2 trees) + (1 site \times 3 trees)] \times 2 heights \times 15 weeks) were obtained. To minimize the impact of trapping, we reduced the number of traps at each site at the end of 2003.

Trapped bumblebees were preserved in 99.5% ethanol in the laboratory, and were classified by species, sex, and caste. We could not distinguish between *B. pseudobaicalensis* and *B. deuteronymus* females (queens and workers) because of the low quality of collected specimens, and hereafter refer to them as *B. pseudobaicalensis*.

Data analyses

Owing to damage to the traps or loss of the detergent water by strong wind, 35 out of 510 samples in 2003 contained no bumblebees. However, these losses were considered negligible, and so the catches were treated as zero. Seasonal variation in the abundance of trapped bumblebees was described separately for each sex or caste of each species. The species composition was compared between directions (north and south), among distances (1, 2, 4, and 6 km), and between strata of traps (canopy and ground). The differences in these compositions were examined using Fisher's exact probability test. Two rare species, *B. pseudobaicalensis* and *B. hypnorum*, were pooled as one category in these tests.

We summed up the numbers of colonies used in greenhouses for 0.5-km intervals from each trapping site for distances from 0–6 km. The relationship between the numbers of *B. terrestris* individuals collected at trapping sites and the numbers of commercial colonies used around the sites was examined by Kendall's rank correlation analysis. Correction of tied values followed Sokal and Rohlf (1995).

Results

Seasonal pattern

B. terrestris showed two peaks. The earlier one was dominated by queens, and the later one mainly consisted of workers (Fig. 2). There were some differences in the timing and the duration of appearance of each caste between *B. terrestris* and the native bumblebees. *B. ardens* queens seemed to start their activity earliest, producing workers before and during early June and producing sexuals from mid-June. *B. ardens* colonies also terminated approximately 1 month earlier than the colonies of other species. Worker populations of both *B. terrestris* and *B. hypocrita* peaked in late July. However, workers of *B. terrestris* were collected longer, until mid-September, than those of *B. hypocrita*. *B. diversus* seemed to start its activity latest: workers appeared in early July and their numbers peaked in early August. Only three workers of *B. hypnorum*, and five queens and three workers of *B. pseudobaicalensis* were trapped in June and July.



Fig. 2 Seasonal changes in the number of trapped individuals of bumblebees for each sex and caste of each species in 2003

Spatial distribution

Bumblebee species composition was significantly different between northern and southern sites (Fisher's exact probability test, $P < 0.001$; Table 1). *B. terrestris* dominated in the northern five sites (N6, N4, N2, N1 and S1; Fig. 1), whereas *B. ardens* dominated in the two southernmost sites (S4 and S6; Fig. 1).

The species composition also varied significantly among sites at different distances from the large greenhouse (Fisher's exact probability test, $P < 0.001$; Table 1). *B. terrestris* decreased in both absolute and relative abundance in the southerly direction and eventually disappeared at S6, but a similar declining trend

was not observed in the northern transect (Fig. 1). *B. hypocrita* was trapped at every site, but did not dominate at any of the sites.

All species were more abundant (1.3–6.4 times more abundant) on the canopy than on the ground. The species composition significantly differed between the two strata (Fisher's exact probability test, $P < 0.001$; Table 1).

B. terrestris abundance in relation to commercial colony distribution

The number of trapped *B. terrestris* individuals at each site was positively correlated with the number of commercial colonies used within 1.0–4.0 km (Kendall's rank correlation; Fig. 3). The value of the correlation coefficient, τ , sharply increased from 0.5 to 1.0 km, attained a peak at 2 km, and decreased after 2 km (Fig. 3).

Discussion

Seasonality of *B. terrestris*

The seasonal pattern of *B. terrestris* was similar to that of *B. hypocrita*, which belongs to the same subgenus (*Bombus* s. str.). However, *B. terrestris* colonies seemed to last longer than *B. hypocrita* colonies owing to the earlier appearance of queens and prolonged activity of workers. Because the active period of *B. terrestris* spanned that of native species, there is at least the potential for competition between *B. terrestris* and the native bumblebees. The early appearance and long duration of *B. terrestris* observed in Hokkaido, Japan, are consistent with reports on this species in other regions. Among all sympatric species except *B. pascuorum* in London (MacDonald 2001), *B. terrestris* queens were observed to appear the earliest, and *B. terrestris* colonies lasted the longest. In Tasmania, which has no native bumblebees, *B. terrestris* queens were observed throughout the year except in June, and workers and males were also found in all months except July and August (Goulson et al. 2002).

The seasonality of *B. terrestris* suggests that most of the trapped *B. terrestris* individuals originated from a wild population rather than from commercial colonies in

Table 1 Number of trapped bumblebees in 2003, in sites in different directions, distances from the large greenhouse, and strata

Species	Distance										Stratum		Total
	North					South					Canopy	Ground	
	1 km	2 km	4 km	6 km	Subtotal	1 km	2 km	4 km	6 km	Subtotal			
<i>B. terrestris</i>	117	135	15	65	332	18	3	10	0	31	274	89	363
<i>B. ardens</i>	8	16	0	4	28	0	1	145	85	231	198	61	259
<i>B. hypocrita</i>	26	15	1	39	81	10	4	41	13	68	125	24	149
<i>B. diversus</i>	12	20	0	3	35	5	0	28	0	33	38	30	68
Others	3	1	1	4	9	1	0	1	1	3	8	4	12
Total	166	187	17	115	485	34	8	225	99	366	643	208	851

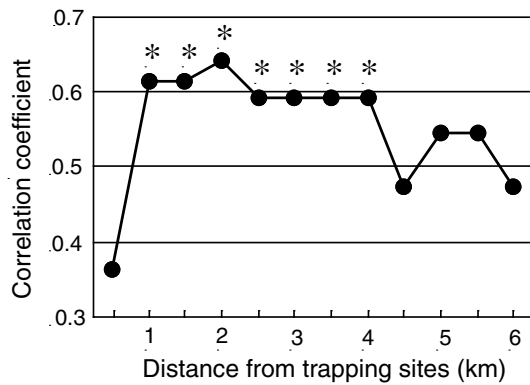


Fig. 3 Kendall's rank correlation coefficient, τ , between the number of *B. terrestris* individuals trapped in a site and the number of commercial colonies used in greenhouses within 0.5–6.0 km from the trap sites. * $P < 0.05$

the greenhouses. *B. terrestris* may have escaped from the greenhouses between late April and mid-October, when windows of the greenhouses were frequently opened. In this period, commercial colonies at various stages were simultaneously maintained in the large greenhouse. If most of the trapped *B. terrestris* had escaped from the large greenhouse, all sexes and castes should be trapped concurrently. However, different sexes and castes of the trapped *B. terrestris* clearly appeared in different seasons, as was observed in native bumblebees (Fig. 2). Since commercial colonies were introduced into the small greenhouses in late April and early May, reproductive individuals (new queens and males) were likely to increase after the peak of workers in the commercial colonies, probably after July. However, the abundance of trapped queens peaked in early June, while males emerged after the time of the peak worker abundance. In addition, the number of commercial colonies used in the large greenhouse in a year was more than twice the total number used in all the small greenhouses that were assessed. These results suggest that most *B. terrestris* queens trapped in June overwintered in the field.

Spatial range of *B. terrestris* invasion

There are three observations that support the idea that *B. terrestris* invades the area mainly around the greenhouses. First, *B. terrestris* abundance was positively correlated with the number of commercial colonies used around the trap sites (Fig. 3). Second, *B. terrestris* dominated in the north region where most of the greenhouses are located (Table 1). Third, the proportion of *B. terrestris* in the catches decreased with increasing distance from the large greenhouse (Table 1). The invasion appeared to be most intense within 2 km of the greenhouses (Fig. 3). Since S4 was the farthest southern trap to catch *B. terrestris*, the invasion front in SSE of the study area was between sites S4 and S6 (Fig. 1). This suggests that the active

invasion range is limited to less than 6 km from greenhouses. However, we cannot exclude the possibility that a less intense invasion is in progress beyond a range of 6 km.

Relationship between *B. terrestris* and native bumblebees

The distributions of *B. ardens* and *B. terrestris* were mutually exclusive. The possible reasons for these differences are habitat preference and interspecific competition. These hypotheses are not mutually exclusive. All the sites in which *B. terrestris* dominated were agricultural areas. Although our results strongly suggest that the abundance of *B. terrestris* is due to the proximity to the greenhouses (which are the original source of *B. terrestris* in the field), the low abundance of *B. ardens* in this area cannot be explained only by the abundance of *B. terrestris*. Restricted distribution of *B. ardens* is consistent with the results of a previous study on the distribution of this species in Hokkaido (Ito and Munakata 1979). It is possible that agricultural areas are unsuitable environments for *B. ardens* and that this is the reason for their low abundance. On the other hand, *B. terrestris* is far more abundant in gardens or cultivated areas with substantial amounts of floral resources of introduced plants than in native vegetation (Goulson et al. 2002).

In this study we could not distinguish the effects of habitat suitability and interspecific competition. Competition possibly reinforces different habitat suitability and/or floral resource partitioning. Field experiments conducted in the early season of colony activity would be an effective way to examine each hypothesis. Determining the effect of translocation of native colonies between different habitats would clarify the habitat suitability of the native species, and determining the effects of adding or removing *B. terrestris* colonies on native species would verify the effect of interspecific competition on native species.

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