INTRODUCTION

Interspecific interactions such as competition may affect species survival and the stability of ecological communities. In general, two or more species vying for a limited common resource in a community are separated by differences in temporal activity patterns, habitat use, or foraging behavior, and competition leads to a partitioning of these resources to minimize niche overlap (Schoener, 1974). If, however, there is no such differentiation, then competition may cause a reduction in fecundity, survivorship, or growth of one or both species. Thus, a newly invading species may restructure the ecological community; if the invading species has a competitive advantage, this may cause suppression or even extinction of native species (Mack et al., 2000).

Terrestrial invertebrates are often successful invaders of new regions around the world, owing to their rapid reproduction and dispersal abilities (e.g. Moller, 1996; Chapman and Bourke, 2001). The majority have probably been accidentally introduced along with human activities, such as the highly successful invasive species, the red imported fire ant Solenopsis invicta Buren, which has replaced its ecological equivalents, presumably by competitive exclusion, in the southern United States (Porter and Savignano, 1990; Morris and Steigman, 1993; Holway et al., 2002). Other invasive species are intentionally introduced as biological agents, such as predatory arthropods and pollinators. Introduced bees, including the honeybee Apis mellifera (L.) and the alfalfa leaf-cutter bee Megachile rotundata (Fabr.), are generally thought to be beneficial for their roles in honey production.
and the pollination of crops and wild plants. Because of these economic benefits, these introduced bees were not regarded as potentially damaging to the environment until the 1980s (Goulson, 2003).

The European bumblebee *Bombus terrestris* (L.) was also initially considered to be beneficial because of its pollination services, and this species has been intentionally introduced as a pollinator for various crops worldwide (Velthuis and van Doorn, 2006). In recent years, however, grave concerns have arisen over the potential ecological impacts of using non-native bumblebee species (e.g., Dafni and Shmida, 1996; Goka et al., 2001; Goulson et al., 2002a) and subspecies (e.g., Ings et al. 2005, 2006). In Japan, *B. terrestris* was also reported to visit a wide range of plants for nectar and/or pollen: 100 species across 26 families, of which 40 were native (Matsumura et al., 2004b). The polylectic diet of *B. terrestris* means that this species might compete for flower resources with many native species collecting nectar and pollen from the same flower resources. In fact, some studies noted high niche overlap in flower visits between *B. terrestris* and native flower visitors (Hingston and McQuillan, 1998; Matsumura et al., 2004b). Interspecific competition between flower visitors does not appear to be a problem in flower-rich habitats (Goulson and Darvill, 2004), but resource depletion by introduced bees is likely to become more pronounced when resources are more limiting (Goulson, 2003). In the latter case, *B. terrestris* can influence the foraging patterns of native flower visitors, competing for foraging time on the rich flower resources. In Tasmania, Hingston and McQuillan (1999) reported that native bees spent less time at each flower when *B. terrestris* foraged simultaneously.

**SUGGESTED IMPACTS OF BOMBUS TERRESTRIS ON NATIVE ECOSYSTEMS**

**Competition with native species for floral resources**

*Bombus terrestris* visits a substantial proportion of flowering plants both within its natural range (Prys-Jones and Corbet, 1991) and in areas where colonies are introduced. The regional use is often up to 100 or more species of plants, according to lists of plants visited by *B. terrestris* in New Zealand (Goodwin and Steiner, 1997; Goulson and Hanley, 2004) and Tasmania (Semmens, 1996; Hingston and McQuillan, 1998; Goulson et al., 2002b). In Japan, this species was also reported to visit a wide range of plants for nectar and/or pollen: 100 species across 26 families, of which 40 were native (Matsumura et al., 2004b). Competition with native species for nest sites

*Bombus terrestris* nests are generally constructed in existing cavities below ground, often using abandoned rodent holes in both its natural range (Sladen, 1912; Alford, 1975; Prys-Jones and Corbet, 1991) and in introduced areas (Donovan and Wier, 1978; Buttermore, 1997; Matsumura et al., 2004a, b). Donovan (1980) considered it unlikely that bumblebees compete with native bee species for nest sites in New Zealand because their requirements for nest sites differ so markedly; however, there are no native bumblebees in New Zealand. In contrast, particularly high similarity in nest site selection was found between *B. terrestris* and some native bumblebee species in Japan (Matsumura et al., 2004a, b). In the laboratory experiments, Ono (1997) found that *B. terrestris* queens succeeded in usurping the nests of native bumblebees within artificial nest boxes. In addition, *B. terrestris* queens appear to have a marked advantage over native
queens in occupying suitable nest sites because of their earlier emergence from hibernation (Pry-Jones and Corbet, 1991; Matsumura et al., 2004b).

**Effects of Bombus terrestris on native bee populations**

On Mt. Carmel in Israel, Dafni and Shmida (1996) showed declines in abundance of medium- and large-sized native bees, including honeybees, following the arrival of *B. terrestris* in 1978. In Japan, Kawahara (2004) reported that *B. hypocrita sapporoensis* Cockerell has decreased since *B. terrestris* became established in eastern Hokkaido. A quantitative survey conducted in 2003 using window traps demonstrated that the distributions of *B. terrestris* and *B. ardens sakagamii* Tkalců were mutually exclusive (Inari et al., 2005). Subsequent investigation in 2004, however, showed that the local abundance of *B. terrestris* was not associated negatively with the number and body size of the two native bumblebees *B. hypocrita sapporoensis* and *B. ardens sakagamii*, and the authors could not demonstrate any evidence of competitive interaction between them (Nagamitsu et al., 2006).

Abundance of the introduced species, high levels of niche overlap, and some declines of native bees suggested that competitive exclusion may be occurring in Japan and other countries. However, there is no indisputable evidence that the establishment of *B. terrestris* has caused a decline or even local extinction of native bees through competitive exclusion, and thus the ecological impacts of *B. terrestris* are still controversial. In addition, most overseas studies have focused on competition for flower resources but not for nest sites between introduced and native bees.

**ASSESSING ECOLOGICAL IMPACTS OF BOMBUS TERRESTRIS ON NATIVE BUMBLEBEE SPECIES IN HOKKAIDO, NORTHERN JAPAN**

The probability of competitive exclusion is enhanced when niche overlap occurs between an invader and native species, their common resources are limited, and the invader has a competitive advantage. In this section, we discuss our work to assess the likelihood of competitive exclusion by *B. terrestris* in terms of niche overlap, resource limitation, and reproductive capacity, in the agricultural region of Hokkaido, Japan (for details of the study area, see Inoue et al., 2008).

**Niche overlaps in flower resources and nest sites**

We examined potential niche overlaps in flower resources between *B. terrestris* and mainly four native bumblebees (*B. hypocrita sapporoensis*, *B. schrencki albidopleuralis* Skorikov, *B. pseudobaicalensis* Vogt, and *B. diversus tersatus* Smith) in terms of morphological characteristics, seasonal cycles of flight activity, foraging habitat use, and flower visits. We also investigated nesting habitat selection among the species to determine the likelihood of competition for nest sites.

First, proboscis length was compared to investigate the potential overlap of flower resource use between *B. terrestris* and native bumblebees, using the data from Inoue et al. (2008). Proboscis length is frequently used as a morphological character in the study of bumblebee-flower interactions because the length is assumed to determine the accessible depth of flowers that bumblebees use (Brian, 1957; Heinrich, 1976; Inouye, 1980; Barrow and Pickard, 1984; Plowright and Plowright, 1997). Compared with the native bumblebee species, *B. terrestris* had a shorter proboscis than most, although its proboscis length overlapped considerably with *B. hypocrita sapporoensis* and partly with *B. pseudobaicalensis* and *B. schrencki albidopleuralis* (Fig. 1).

We investigated of foraging niche overlap in habitat use, flower visits, and active season between *B. terrestris* and native bumblebees in 2004, using the transect method (Inoue et al., 2008). All five bumblebees were long-lived, first appearing from late May to June and lasting into October. *Bombus terrestris* and *B. pseudobaicalensis* foraged throughout open habitats, whereas *B. schrencki albidopleuralis* was almost exclusively found in woodlands. *Bombus hypocrita sapporoensis* and *B. diversus tersatus* were observed in both habitats, but the latter foraged more in the wooded habitats. Based on this transect data, the similarity of flower resource use between *B. terrestris* and native bumblebees (i.e., the plant species visited during a given study period in a given habitat) was calculated according to Horn (1966). The niche overlap index ranges from zero in the case of no overlap to one in the case of full overlap between species. Niche overlap was especially large between *B. terrestris* and *B. hypocrita sapporoensis*.
restris and B. hypocrita sapporoensis (0.48) and B. pseudobaicalensis (0.60) (Table 1). By contrast, B. diversus tersatus showed a relatively small overlap (0.26) and B. schrencki albidopleuralis showed no overlap (0.00).

Nest sites of B. terrestris and native bumblebees were investigated during the 2003–2005 censuses (Inoue et al., 2008). We found 30 B. terrestris nests, eight B. hypocrita sapporoensis nests, seven B. pseudobaicalensis nests, and one B. diversus tersatus nest in the study area. Most B. terrestris nests were constructed in abandoned underground rodent nests with entrance tunnels in ridges between rice paddies or other cultivated farmland or in dry riverbed sites. The nests of B. hypocrita sapporoensis and B. diversus tersatus were also found underground in similar microhabitats. In contrast, all nests of B. pseudobaicalensis were above-ground, covered with grass litter or a moss layer.

The niche overlap demonstration by Inoue et al. (2008) suggests that B. terrestris may compete for flower resources and nest sites with B. hypocrita sapporoensis, for flower resources with B. pseudobaicalensis, and for nest sites with B. diversus tersatus.

**Resource limitation for bumblebees**

During nest initiation by bumblebees, it is common for other queens to attempt to usurp the nest (Sladen, 1912; Alford, 1975; Richards, 1978; Paxton et al., 2001), and the fights between the foundress and intruder usually conclude when one queen escapes or one successfully stings and kills the other (Alford, 1975). Queens (both alive and dead) found in and around nests are presumably the successive usurpers and foundresses. We thus counted the number of queens in a collected nest as an indicator of competition for nest sites (Inoue et al., 2008). The number of queens found in and around the B. terrestris nests increased markedly between 2003 and 2005 (Fig. 2). We also observed that B. terrestris and B. hypocrita sapporoensis simultaneously used the same nesting holes (Nakajima et al., 2004). These findings suggested that the availability of nest sites was restricted and competitive exclusion of B. hypocrita sapporoensis and B. diversus tersatus, which overlap with B. terrestris in nest sites, likely occurred.
Reproductive capacity of *Bombus terrestris*

To investigate reproductive capacity, we examined 25 feral nests of *B. terrestris* collected between 2003 and 2006 (Inoue et al., 2010). Of the excavated nests, 17 contained sexuals, producing a mean of 376.5±168.6 cocoons in total and 90.2±81.5 gyno cocoons (22.1% of the total).

Compared with the proportion of gynes in *B. terrestris* nests in the species’ natural range (8.6%, Cumber, 1949) and in other introduced areas (16.4%, Donovan and Wier, 1978; 18.7%, Buttemore, 1997), *B. terrestris* nests in our study were characterized by a higher proportion of gynes, suggesting that this non-native species is well suited to conditions in Japan. *Bombus terrestris* also produced more gynes than the consubgeneric native Japanese species (*Bombus s. str.*), *B. ignitus* Panfilov (8.5%, Sakagami and Katayama, 1977) and *B. hypocrita hypocrita* Pérez (9.9%, Katayama and Takamizawa, 2004). Some recent studies show that commercially imported *B. terrestris* outperformed native conspecifics in reproduction, probably as a result of commercial selective pressure (Gösterit and Gürel, 2005; Ings et al., 2006). Therefore, the higher proportion of gynes that we observed might have resulted from artificial selection experienced by the bees through commercialization. In addition, propagule pressure (i.e., the number of individuals released into a new region) plays an important role in the establishment of invasive species (Cassey et al., 2004, 2005; Lockwood et al., 2005; Mikheyev et al., 2008). *Bombus terrestris* may prevail over native species in usurpation contests due to its large propagule size, allowing it to occupy more of the available nest sites.

Displacement of native bumblebees through competitive exclusion

Native bumblebee species were found to overlap in flower resources and/or nest sites with *B. terrestris*. Furthermore, we demonstrated a limited availability of nest sites, and *B. terrestris* showed a high reproductive capacity. Therefore, we consider the risk of competitive exclusion of native bumblebees in Japan to be high.

To investigate whether *B. terrestris* actually has ecological impacts on native bumblebees via competitive exclusion, the abundance of bumblebee species was surveyed (Inoue et al., 2008). Between 2003 and 2005, *B. hypocrita sapporoensis*, which overlaps with *B. terrestris* in nest site selection, markedly declined in number, associated with an increase of *B. terrestris* (Fig. 3). *Bombus diversus tersatus* also tended to decrease during three years. Conversely, *B. pseudobaicalensis*, which overlaps in flower resource but prefers different nest sites than *B. terrestris*, showed no noticeable change. These findings suggested that *B. terrestris* displaced *B. hypocrita sapporoensis* and *B. diversus tersatus* through competition for a limited resource, that is, nest sites.

CONCLUSION

In terms of niche overlap for limited resources (i.e., nest sites), *B. hypocrita sapporoensis* and *B.
*Bombus terrestris* were the native species potentially most likely to be affected through competitive exclusion. In fact, field surveys demonstrated that these species have declined accompanied by an increase in *B. terrestris*. The present study provides strong circumstantial evidence for competitive exclusion of native bumblebees owing to the establishment of *B. terrestris*. Further studies of these interactions are urgently needed to elucidate mechanisms by which the impacts of *B. terrestris* can be mitigated.

**ACKNOWLEDGMENTS**

We thank Professor I. Washitani for her advice throughout the study. We are also grateful to Dr. M. Ajima, Dr. I. Dohzono, Mr. A. Goto, Mr. T. Inoue, Dr. T. Kadoya, Dr. C. Matsumura, Dr. C. Nakano, Dr. J. Nishihiro, Ms. Y. Nakatsuka, Dr. M. Ohtani, Dr. A. Shimono, Dr. S. Takagawa, and Mr. M. Tamura for their helpful comments on the studies and assistance with the investigations. Finally, we thank the farmers and homeowners who allowed us to collect bee nests on their land. This work was partly supported by the Pro Natura Foundation and the Global Environment Research Fund (F-3; Leader: K. Ohtani, Dr. A. Shimono, Dr. S. Takagawa, and Mr. M. Tamura). We thank Professor I. Washitani for her advice throughout the study. We are also grateful to Dr. M. Ajima, Dr. I. Dohzono, Mr. A. Goto, Mr. T. Inoue, Dr. T. Kadoya, Dr. C. Matsumura, Dr. C. Nakano, Dr. J. Nishihiro, Ms. Y. Nakatsuka, Dr. M. Ohtani, Dr. A. Shimono, Dr. S. Takagawa, and Mr. M. Tamura for their helpful comments on the studies and assistance with the investigations. Finally, we thank the farmers and homeowners who allowed us to collect bee nests on their land. This work was partly supported by the Pro Natura Foundation and the Global Environment Research Fund (F-3; Leader: K. Ohtani, Dr. A. Shimono, Dr. S. Takagawa, and Mr. M. Tamura).

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Oecologia 144: 508–516.


