CHAPTER 6
General Discussion

As introductions of non-native species continue in biological communities and cause biodiversity loss worldwide, it is increasingly important for ecologists to understand the spread mechanisms and potentials of invaders and to be able to predict the impacts that a given invasion will have on native species (Parker et al. 1999). However, the complexity of multispecies communities and the novelty of each invader within them make it difficult to anticipate the course of invasion and the ecological impacts. The paucity of detailed information about the interactions between non-native and native species has also been a major limitation, though some researchers have made predictions using correlative analyses of other successful invasive species (e.g. Rejmánek 1996; Reichard & Hamilton 1997). In the present thesis, I combine detailed, quantitative field data on the life histories and interactions of the introduced *Bombus terrestris* and native bumblebee species, and demonstrate the high possibility of competitive exclusion of native bumblebees by assessing potential niche overlaps in flower resources and nest sites (Chapter 2), resources limitation for bumblebees (Chapter 2), and the reproductive ability per successful colony (Chapter 3) and the potential population growth (Chapter 4).

Ecological impacts of *Bombus terrestris* on the native bumblebees

Potential niche overlaps in flower resources and nest sites

Morphological measurements relating to flower use in bumblebees demonstrated that

there were significantly potential overlaps in flower use between *B. terrestris* and three native species, *B. hypocrita sapporoensis*, *B. ardens sakagamii* and *B. hypnorum koropokkrus* (Chapter 2: Inoue et al. 2008).

Field surveys also revealed that the niche overlaps in flower resources and nest sites between *B. terrestris* and five native species. The niche overlap index (Horn 1966) in flower use, taking account of foraging habitat use, flower visit and active season, was especially large between *B. terrestris* and *B. hypocrita sapporoensis* (0.48) / *B. pseudobaicalensis* (0.60), while particularly high similarity in nest site selection was appreciated between *B. terrestris* and *B. hypocrita sapporoensis* / *B. diversus tersatus* (Chapter 2: Inoue et al. 2008).

Resources limitation for bumblebees

Some researchers (Wilms et al. 1996; Minckley et al. 2003) reported that abundant flower resources provided by plants may buffer native bees from competition for food with introduced species. In the study area, the great abundance of non-native plants also supplies sufficiently food for all bumblebees through their active season, and thus the competition for flower resources may be trivial (Chapter 2: Inoue et al. 2008).

Nest usurpation by queens commonly occurs and will be concluded when one queen successfully stings and kills the other (Sladen 1912; Alford 1975; Richards 1978). In the study area, the number of nest usurpers found in *B. terrestris* nests, which markedly increased between 2003 and 2005, indicated the restricted availability of nest sites and strong competition among queens for nest sites (Chapter 2: Inoue et al. 2008).

The reproductive ability and the potential population growth

I conducted the investigation of 25 feral nests of *B. terrestris* collected in the agricultural landscape in the Iburi region to examine colony growth and reproductive ability (Chapter 3). The excavated nests were assigned to one of the three stages according to Katayama and Takamizawa (2004): seven nests to the 'growing' stage (worker production stage); 17 nests to the 'mature' stage (sexual production stage); and one nest to the 'senescent' stage (the end of colony activity). The features for the seasonal development of a success *B. terrestris* colony in the study area, which were revealed in the present study, are summarized as follows: slow development in the 'growing' stage, followed by rapid development in the 'mature' stage, and the terminal decline after sexuals have been produced. Consequently, successful nests of *B. terrestris* in the study area produced 109.5 ± 73.9 gynes and the high reproductive ability of the species was shown.

I performed the investigation of the natural selection on *B. terrestris* queens during the solitary phase and quantified the success rates of queens in hibernation and subsequent nest founding (Chapter 4). The success rate of *B. terrestris* queens during solitary phase was estimated by multiplying the success rate in hibernation (44.0 %) by the success rate in nest founding (11.8 %). In combination with the result in Chapter 3, which indicates the potential productivity of gyne in a successful nest, 5.7 of 110 queens (5.2 %) potentially initiate nest foundation in the following year. Direct extrapolation of the data by Cumber (1953), which assumed the success rate of colony in gyne production (approximately 30 %), 1.8 queens (1.6 %) from a single colony are supposed to be successful in reproduction. This success rate of queens per colony is coincided well with the population growth rate (approximately 1.5 per year) estimated by the

census in Chapter 2 (Inoue et al. 2008). Since *B. terrestris* population in the study area has become almost saturated (Inoue et al. 2008: Chapter 2), the potential intrinsic rate of natural increase of the species is estimated to be approximately 20 per year by excluding success rate in nest founding (11.8 %) when density effect operates.

Displacement of native bumblebees through competitive exclusion

By the examinations for the possibilities of competitive exclusion, native bumblebee species, which overlap in flower resources and nest sites with *B. terrestris*, were detected. Furthermore, it was demonstrated that availability of nest sites was limited and *B. terrestris* showed high ability of reproduction and population growth. As results, the risk of competitive exclusion of native bumblebees was considered to be high.

To demonstrate that *B. terrestris* actually has the ecological impacts on native bumblebees via competitive exclusion, the abundance of bumblebee species was surveyed in the monitoring area during 2003 to 2005. During three-year monitoring, *B. hypocrita sapporoensis* and *B. diversus tersatus,* which overlap with *B. terrestris* in nest site selection, largely declined in their number, associated with the increase of *B. terrestris*. By contrast, *B. pseudobaicalensis*, which prefers different nest sites from *B. terrestris*, showed no noticeable change. Therefore, the findings in the present study suggested that *B. terrestris* displaced these two native species through competition for a limited resource, that is, nest sites.

Potential impacts of *Bombus terrestris* in the important regions and implication for management of established population

Currently, occurrence of *B. terrestris* was reported from the conservationally important

region, Notsuke-Furen Prefectural Natural Park, eastern Hokkaido (Chapter 5; Inoue et al. 2007). This region is characterized by the following features: (1) a rich variety of vegetation associations; and (2) a rich bumblebee fauna including a rare native species, *B. florilegus* (Sakagami and Ishikawa 1969; Nakatani 1999b). Considering outperforming native conspecifics (Chapter 2: Inoue et al. 2008) and its reproductive ability (Chapter 3), *B. terrestris* is considered to negatively affect native bumblebee communities through competitive exclusion, potentially leading to displacement of some species. Since a large number of native plants in these regions are pollinated predominantly or exclusively by native bumblebees, negative impacts on the mutualistic pollination systems is highly concerned (Chapter 5).

For the effective management of its growing populations, extermination is needed not only in such valuable regions but also in the surrounding regions where potential source populations of *B. terrestris* are established (Chapter 4). The two following ways are considered to be effective as *B. terrestris* exclusion: (1) exhaustive collection of hibernated queens in spring and (2) destroying natural nests (Yokoyama et al. 2004). Based on the seasonal developed pattern of *B. terrestris* colonies (Chapter 3) can be proposed as follow: post-hibernating queens (especially pollen-carrying queens) should be captured during late May to early June before first workers emerge, and nests should be destroyed till at least as late as August before sexuals emerge. The *B. terrestris* exclusion project during two days was carried out in the study area in 2004, and 484 of 603 *B. terrestris* queens were captured (Kojima 2006). Although some decline of *B. terrestris* queens was observed in 2004, its number increased more than twice in 2005 (Chapter 2: Inoue et al. 2008). Since 2005, the bumblebee monitoring activity collaborating with citizen volunteers has started in aim of *B. terrestris* exclusion,

directed by Hokkaido Government and the University of Tokyo (Kikuchi et al. 2006). During 2007, more than 23,000 *B. terrestris* individuals including 7,152 queens were collected and 26 nests were detected in Hokkaido (Laboratory of Conservation Ecology 2007). It is hoped that this activity will continue to pressure the *B. terrestris* population leading to reduce in its number.

Conclusion

In this thesis, I assessed the ecological impacts of the invasion of *B. terrestris* in terms of the possible competitive exclusion of native bumblebees. In terms of niche overlaps in limited resources, that is, nest sites, *B. hypocrita sapporoensis* and *B. diversus tersatus* were detected as the native species, which were potentially affected through competitive exclusion. In fact, the field surveys demonstrated that these species have declined accompanied by increase of *B. terrestris*. Prediction and evaluation of competitive exclusion of native species is considered to appropriate. Therefore, the method developed in this study to assess the ecological impacts on native species will be available for other invasive alien species.

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