



Floral abundance and bee density affect species-specific foraging patterns of alpine bumble bees

Akari Shibata¹ · Gaku Kudo¹

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Abstract

In response to the qualitative and quantitative changes in floral resources, bumble bees flexibly forage multiple plant species throughout the growing season. During the short summer in an alpine ecosystem, the activity of worker bees is maximized in the middle of the season, when the competition for floral resources may be intense. We predicted that the foraging patterns of bumble bees are affected by both relative floral abundance and interactions between bumble bee species. We recorded the floral abundance of individual plant species and the foraging frequency of bumble bees in an alpine meadow during the major flowering period over 3 years. Two bumble bee species were common during the major flowering period. Although they tended to visit abundant floral species, the shorter-tongued species (*Bombus hypocrita*) showed a more diverse and flexible floral choice than the longer-tongued species (*Bombus beaticola*). The degree of floral use overlap between two bumble bee species tended to decrease when the foraging density of the longer-tongued species was high. These results indicated that multiple bumble bee species are able to coexist when certain bee species can flexibly change targeting flowers in response to the temporal variations in flowering species and the density of competing bee species. The extent of foraging flexibility is related to the morphological traits of bee species and availability of floral resources.

Keywords *Bombus* · Floral choice · Flowering phenology · Pollination · Seasonal dynamics · Visitation frequency

Introduction

Bumble bees (*Bombus* spp.) are the most common and effective pollinators in cool-temperate, alpine, and subarctic ecosystems (Heinrich 1979; Bingham and Orthner 1998; Kudo 2016). They are eusocial insects with an annual life cycle, and their colony growth and reproductive success depend on the availability of floral resources (Schmid-Hempel and Schmid-Hempel 1998; Pelletier and McNeil 2003; Inari et al. 2012). Reflecting the annual cycle of colony development, the activity of worker bees is maximized in the middle of summer. In the short growing season of alpine environments,

floral visits by worker bees drastically increase after mid-July (Kudo 2016). Intensive floral use by worker bees may cause the partitioning of floral resources among bee species, but the pattern of interspecific resource partitioning was not consistent in the previous studies (Goulson 2010; Miller-Struttmann and Galen 2014).

Interspecific competition for resource acquisition is one of the most important factors affecting community structure (Schoener 1974; Schaffer et al. 1979). Foraging patterns of bumble bees were surveyed several times in the previous studies in order to evaluate the existence of resource competition (Heinrich 1976a; Inouye 1978; Pyke 1982; Thomson 2004). Foraging bees obtain nutrients from nectar and/or pollen, and the floral use period of multiple species can overlap. When floral resources are abundant, the bees can share the preferable floral species; otherwise, they have to shift to other available floral species to reduce the competition. One of the mechanisms for resource partitioning is morphological matching between floral shape and tongue length of bees in which bumble bee species having different tongue length can coexist due to small foraging niche overlap (Heinrich 1976a; Pyke 1982; Inoue and Yokoyama 2006;

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✉ Akari Shibata
aka.11mbbc28@gmail.com

¹ Faculty of Environmental Earth Science, Hokkaido University, Sapporo, Hokkaido 060-0810, Japan

Pyke et al. 2012). However, this pattern was not always clear. Some studies reported that bumble bee species with similar tongue length coexisted irrespective of large niche overlap (Ranta and Lundberg 1980; Goulson et al. 2008). Therefore, resource partitioning between bumble bee species needs to be explained not only by morphological matching but also by species composition and abundance of bumble bees and floral resources in each site.

Previous studies have shown that bumble bees tend to visit abundant floral species, which is termed ‘frequency-dependent foraging’ (Smithson and Macnair 1996). However, the pattern of floral choice is also affected by the preference and foraging experience of individual bees (Heinrich 1979; Dukas and Real 1993; Raine and Chittka 2005). They potentially prefer floral species with the corolla shape matching their body shape and those with more floral rewards. After learning which floral species possess specific traits associated with floral rewards, individual bees tend to have their own flower constancy (Heinrich 1976b; Gegeer and Thomson 2004). In addition, the relative importance of floral resources for bee colonies changes depending on the stage of colony development. Pollen, which contains proteins and lipids, is used for larva development, and nectar is used as energy source for adult bees also (Tasei and Aupinel 2008; Nicolson 2011). The composition of pollen and nectar varies among different floral species (Somme et al. 2015). In natural plant communities, available floral species are replaced quickly and bee abundance is also variable as the season progresses. When the density of foraging bees is high, individual bees may behave in a more generalist manner having wider floral diet (Fontaine et al. 2008). Therefore, seasonal changes in abundance and diversity of floral species and species-specific population dynamics of bumble bees across the season should be taken into account when trying to understand the competitive situation of bumble bees. However, analytical studies on the foraging patterns of bumble bees responding to the seasonal dynamics of floral resources are scarce.

In this study, we evaluated the factors affecting foraging patterns of bumble bees in an alpine meadow on Mt. Asahidake in Hokkaido, northern Japan. Several bumble bee species having different body size and tongue length, such as *Bombus beaticola moshkarareppus*, *B. diversus tersatus*, *B. hypnorum koropokkrus*, *B. hypocrita sapporoensis*, and *B. yezoensis*, were recorded in the alpine zone of this mountain area (Kudo 2014). This provided us an opportunity to analyze the effects of floral dynamics and bee density on foraging patterns of bumble bees in the field. We used data on foraging frequency of worker bees and floral abundance throughout the active foraging season during 3 years. We addressed the following questions: (1) How extent do species composition of bumble bees and availability of floral resources vary as the season progresses in the alpine

meadow? (2) Do bumble bees tend to visit floral species with large abundance at any given time? (3) Does the floral resource partitioning between bee species occur intensively at the time of high bee density? If so, does the pattern of resource partitioning reflect the morphological difference between the bee species?

Materials and methods

Study site and survey

This study was conducted in an alpine meadow (1610–1745 m a.s.l.) on Mt. Asahidake in the Taisetsu Mountains, Hokkaido, northern Japan (43° 39′ 49″ N, 142° 51′ 15″ E). In this area, the treeline is located at around 1600 m a.s.l., and snowmelt progresses gradually from early June to late July. The mean annual temperature at 1700 m a.s.l. is -1.9°C , ranging from -16.1°C in January to 12.5°C in August (average of the period 2002–2018; Kudo unpublished data). The flowering of alpine plants usually occurs from early June to the middle of September. We recorded visitation frequency of bumble bees, flowering phenology of insect-pollinated plant species, and the amount of floral resources along the 2.6 km trail, which was divided into four transects (Fig. S1). Observation was conducted at approximately 10-day intervals throughout the active season of worker bees (from mid-July to early September) in 2015 and 2016 (in total, 10 surveys each summer). Furthermore, additional observations were conducted three times at the peak of the season in 2018.

Bee observation

We recorded the number of bumble bees that were visiting the flowers as well as the number of plant species foraged by bumble bees within about 5 m on both sides of the trail. On each observation day, one to three observers walked slowly along the trail for about 30 min in each transect. In total, 37, 36, and 12 observations were made in 2015, 2016, and 2018, respectively. Species and castes of bumble bees were identified in the field. Observations were conducted under conditions of no rain, air temperature higher than 9°C , and with wind speed lower than 6 m/s.

Floral abundance and flowering phenology

We recorded the number of open flowers within 2×2 m quadrats. We arbitrarily set quadrats on floral patches in order to cover every insect-pollinated plant species that was flowering on each day of the investigation. In total, around 35 (ranging 8 to 48) quadrats were set depending on the flowering conditions of individual plant species in each

survey. The flowering species and abundance largely change across the season (Kudo 2019; Fig. 2a). Because a half of the transect was still covered with snow in early season, we conducted the survey only at the snow-free area. In late season, flowering periods of the most plant species had finished and the amount of flowering species was small. As a result, the number of quadrats was small early and late in the season. Therefore, flower density and diversity were evaluated at floral patch scale in this study. Average number of flowers per 4 m² (total flower number of each species divided by the number of quadrats) was used as an index of floral abundance at community scale. Instead of counting the actual number of florets, we used the number of capitula for Asteraceae species, number of small units of umbels for Apiaceae species, and number of inflorescences for *Spiraea* species. Plant species that were visited by two dominant bee species, *B. hypocrita sapporoensis* and/or *B. beaticola moshkararepus*, at a frequency of > 1% of total visits in 2015 and 2016 were defined as major plant species (Table 1).

Data analyses

In order to assess the diversity of flowering plant species (floral diversity) and the diversity of plant species visited by bumble bees (foraging diversity), the Simpson's diversity index D (Simpson 1949) was calculated as follows:

$$D = 1 - \sum_{k=1}^s \left(\frac{n_i(n_i-1)}{N(N-1)} \right),$$

where s is the number of plant species, n is the total flower number of plant species i , and N is total number of flowers in all plant species.

For the evaluation of floral use overlap between two dominant bumble bee species (j and k), the Morisita's niche overlap index C between j and k (Morisita 1959) was calculated as follows:

$$C = \frac{2 \sum_i p_{ij} p_{ik}}{\sum_i p_{ij} [(n_{ij}-1)/(N_j-1)] + \sum_i p_{ik} [(n_{ik}-1)/(N_k-1)]},$$

where p is the proportion of flower number of plant species i to total number of flowers visited by bee species j or k , n is the number of bee species j or k that visited plant species i , and N is the total number of bee species j or k .

In order to evaluate the relationship between total floral abundance and total number of observed bumble bees in each survey of 2015 and 2016, we performed generalized linear model (GLM) postulating negative binomial error distribution with log-link function. Total floral abundance available for each bee species was expressed as the cumulative flower number of the plant species visited by the focal bee species at least once. Total number of bumble bees was

set as the response variable, and total floral abundance, bee species, and year were set as the explanatory variables with inclusion of their interactions.

In order to evaluate the floral preference of bumble bees among major plant species, we used GLMs to evaluate the relationships between relative floral abundance of specific plant species and foraging frequency to the top five most-visited floral species by worker bees. Relative floral abundance of a specific plant species in each survey time was calculated by dividing the flower number of the species by the cumulative flower number of the top five plant species. GLMs postulating binomial error distribution with logit-link function were performed independently for each plant species. The foraging frequency was set as the response variable, and relative floral abundance was set as the explanatory variable. Survey data including the plant species visited by > 5 worker bees were used for the analyses.

We used generalized linear mixed models (GLMMs) to test the effects of floral diversity, another bee species, and own species on floral use patterns of two dominant bee species, *B. hypocrita* and *B. beaticola*. GLMMs postulating beta error distribution with logit-link function were performed using the glmmTMB package in R (Mollie et al. 2017). Foraging diversity was set as the response variable, and floral diversity, number of heterospecific worker bees, and number of conspecific worker bees in each survey were set as the explanatory variables. Survey data including the plant species visited by > 10 conspecific worker bees were used for the analyses. The number of bees was log-transformed to reduce overdispersion. We classified the survey periods into three colony developing stages in each bumble bee species, i.e., stage-1: early stage of colony development in which only small number of worker bees were observed; stage-2: middle stage of colony development in which the number of worker bees increased or remained at high level; stage-3: late stage of colony development in which the number of worker bees decreased, and males and new queen bees appeared. For each GLMM model, colony stage nested by year was set as random factor in the GLMMs.

In order to test the effects of heterospecific and conspecific worker bees and floral diversity on floral use overlap between two dominant bee species, *B. hypocrita* and *B. beaticola*, we performed GLMM postulating beta error distribution with logit-link function. In the GLMM, niche overlap index was set as the response variable, and floral diversity, the number of *B. hypocrita* workers, and the number of *B. beaticola* workers foraging in each survey were set as the explanatory variables. Survey data including > 10 worker bees of each species were used for the analyses. The number of bees was normalized to reduce overdispersion. Survey period was divided into 10-day intervals starting from June 20th in order to reflect seasonal changes in the species composition of flowers and foraging bees, and divided

Table 1 Plant species visited by bumble bees, the number of observed bees for each bee species and caste (Q: queen, W: worker, M: male), total number of observed bees, and visited plant species number in 2015 and 2016

| Plant species | Family | Flower shape/inflorescence type | Observed bee no. | | | | | | | | | | | | | | |
|--|------------------|---------------------------------|---------------------|-----|-----|--------------------|---|----|--------------------|---|-----------------|---------------------|----|----|---------------------|----|---|
| | | | <i>B. beaticola</i> | | | <i>B. diversus</i> | | | <i>B. hypnorum</i> | | | <i>B. hypocrita</i> | | | <i>B. yezoensis</i> | | |
| | | | Q | W | M | Q | W | M | Q | W | M | Q | W | M | Q | W | M |
| <i>Rhododendron aureum</i> | Ericaceae | Funnel/corymb | | 3 | | | | | | | | 2 | 4 | | | | |
| <i>Phyllodoce caerulea</i> | Ericaceae | Urceolate/corymb | 2 | 19 | 1 | | | | 1 | | | | 22 | | | | |
| <i>Vaccinium ovalifolium</i> | Ericaceae | Urceolate/corymb | 1 | 2 | | | | | | | | | | | | | |
| <i>Vaccinium vitis-idaea</i> | Ericaceae | Campanulate/corymb | | 1 | | | | | | | | | | | | | |
| <i>Ledum palustre</i> | Ericaceae | Cup/corymb | | | | | | | 1 | | | | 1 | | | | |
| <i>Sieversia pentapetala</i> | Rosaceae | Cup/uniflowered | | 21 | 1 | | | | 1 | | | | 88 | | | | |
| <i>Phyllodoce caerulea</i> var. <i>yezoensis</i> | Ericaceae | Urceolate/corymb | | 190 | 3 | | | | 7 | | 1 | | 59 | | | | |
| <i>Spiraea betulifolia</i> | Rosaceae | Cup/corymb | | 15 | | | | | 18 | | | | 40 | | 2 | | |
| <i>Gaultheria miqueliana</i> | Ericaceae | Urceolate/corymb | | 26 | 1 | | | | | | | | 1 | | | | |
| <i>Primula cuneifolia</i> | Primulaceae | Tubular/umbel | | 2 | | | | | | | | | 6 | | 1 | | |
| <i>Phyllodoce aleutica</i> | Ericaceae | Urceolate/corymb | | 228 | 54 | | | | 23 | | 1 ^a | | 76 | | 7 | | |
| <i>Penstemon frutescens</i> | Scrophulariaceae | Campanulate/raceme | | 4 | | | | | | | | | | | | | |
| <i>Peucedanum multivittatum</i> | Apiaceae | Cup/umbel | | 8 | | | | | | | 1 ^a | | 32 | | | | |
| <i>Gentiana nipponica</i> | Gentianaceae | Campanulate/corymb | | 3 | 8 | | | | 1 | | | | 5 | | 2 | | |
| <i>Solidago virgaurea</i> | Asteraceae | Ligulate + tubular/panicle | | 5 | 10 | | | | | | 1 ^a | | 2 | | | | |
| <i>Gentiana triflora</i> | Gentianaceae | Campanulate/uniflowered | 5 ^a | 92 | 87 | 3 | 3 | | | | 22 ^a | | 64 | 45 | 2 ^a | 49 | 2 |
| <i>Cirsium pectinellum</i> | Asteraceae | Tubular/capitulum | | 1 | 11 | | | | | | | | | | | | |
| Total observed bee number | | | 8 | 620 | 176 | 3 | 3 | 52 | | | 28 | 400 | 45 | 2 | 61 | 2 | |
| Visited plant species number | | | 3 | 16 | 9 | 1 | 1 | 7 | | | 6 | 13 | 1 | 1 | 5 | 1 | |

The bold numbers indicate major plant species for workers of *Bombus hypocrita* and *B. beaticola*^aNew queen

survey period nested by year was set as random factor in the GLMMs. The best-fit model was selected based on AIC values in all GLMs and GLMMs. All analyses were conducted using R 3.5.1 (R Core Team 2018).

Results

Composition of bumble bee species

In total, 1680 bees were recorded foraging flowers during 3 years (396, 1004, and 280 individuals in 2015, 2016, and 2018, respectively). Among five recorded *Bombus* species, *B. beaticola* (48.6%) and *B. hypocrita* (43.8%) were the most dominant species, followed by *B. yezoensis* (3.9%), *B. hypnorum* (3.3%), and *B. diversus* (0.4%). The two most dominant species, *B. beaticola* and *B. hypocrita*, were recorded

almost throughout the whole observation period, while the other three species were recorded only during a short period or occasionally. Overall, the highest number of worker bees was recorded in the middle of summer (late July to mid-August), and males and new queen bees appeared after mid-August (Fig. 1). We recorded species-specific yearly variation in colony development, which was estimated from the appearance of worker and reproductive bees. The timing of colony development of *B. hypocrita* seemed to be late in 2016, while the observed number of *B. beaticola* workers was very low in 2018.

Composition of floral species and flowering phenology

Throughout the 3-year survey, we recorded 37 flowering insect-pollinated plant species belonging to 14 families.

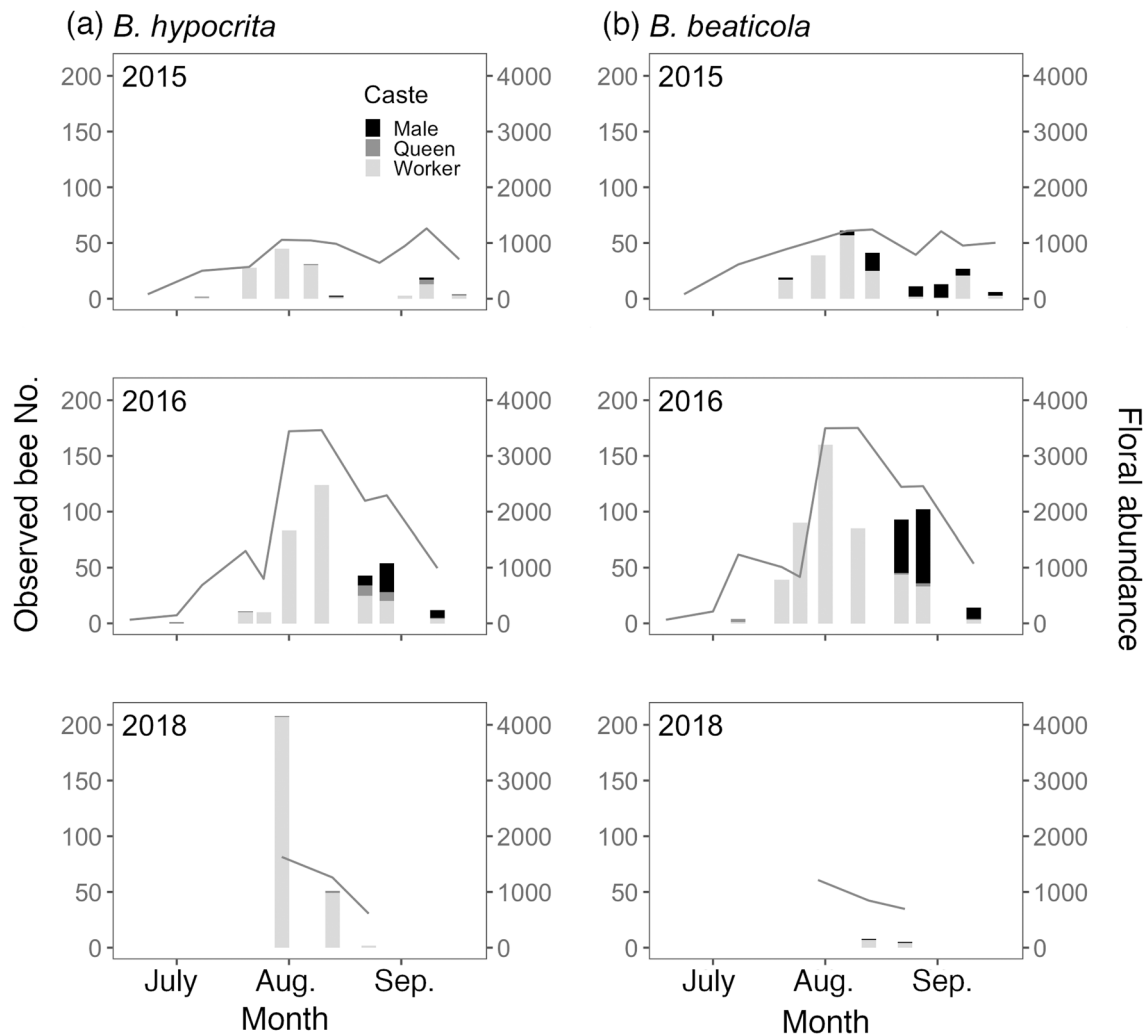


Fig. 1 Seasonal trends of the frequency of observed bees (histogram) and floral abundance (line) in 2015, 2016, and 2018 for **a** *Bombus hypocrita* and **b** *B. beaticola*

Among them, 18 species were shrubs, including 13 erica-ceous species. Snowmelt proceeded gradually across the area, and flowering of individual species occurred in response to the time of snowmelt in individual habitats (Fig. 2a). Three *Phyllodoce* species, two *Gentiana* species, *Solidago virgaurea*, and *Spiraea betulifolia* continued to flower for long periods at regional scale. The amount of *Phyllodoce* flowers highly varied from year to year (Fig. 2b).

Floral visits of bumble bee species

In total, we recorded 17 plant species that were visited by bumble bees. In 2015 and 2016, the most-visited species was *Phyllodoce aleutica* (27.8%), followed by *Gentiana triflora* (26.7%) and *Phyllodoce caerulea* var. *yezoensis* (18.1%). Workers of *B. hypocrita* and *B. beaticola* visited 13 and 16 plant species throughout the whole study period, respectively

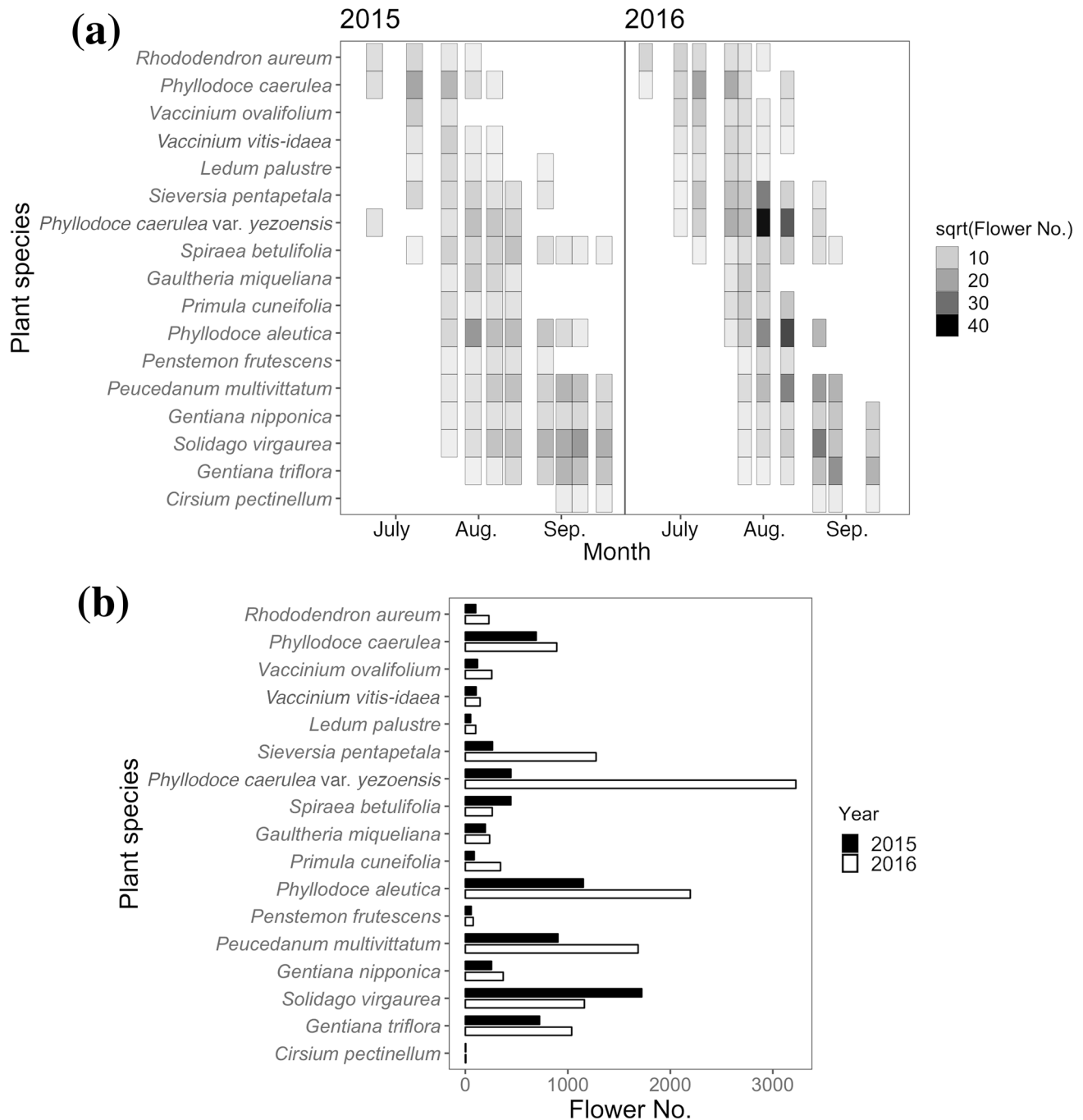


Fig. 2 **a** Flowering phenology and **b** flower number of 17 plant species visited by bumble bees in 2015 and 2016

(Table 1). A big difference in the floral use patterns between the two bee species was that the flowers with shallow corollas were more frequently visited by *B. hypocrita* than by *B. beaticola* [the ratio of visits on cup-shaped flowers was 0.40 (= 161/400) in *B. hypocrita* and 0.07 (= 44/620) in *B. beaticola*]. Workers of both of these bee species showed a high diversification of floral use, i.e., Simpson's diversity indices for *B. hypocrita* and *B. beaticola* were 0.68 and 0.61 in 2015, and 0.82 and 0.74 in 2016, respectively.

Total number of workers was positively correlated with the total floral abundance in both species ($z=5.18$, $P<0.001$ for *B. hypocrita* and $z=3.35$, $P<0.001$ for *B. beaticola*; Figs. 1, 3). There was no significant difference in the number of *B. hypocrita* workers between years ($z=-1.74$, $P=0.08$) and interaction between explanatory variables was excluded by the AIC model selection. The number of *B. beaticola* workers was significantly increased in 2016 ($z=2.79$, $P<0.01$), and the significant interaction between total floral abundance and year was detected ($z=-2.78$, $P<0.01$). We recorded positive correlations between relative floral abundance and foraging frequency in *Sieversia pentapetala*, *P. aleutica*, and *Peucedanum multivittatum* for *B. hypocrita* workers, and in *P. aleutica*, *P. caerulea* var. *yezoensis*, and *G. triflora* for *B. beaticola* workers (Fig. 4a). In *B. hypocrita* workers, foraging frequency to *P. caerulea* var. *yezoensis* was independent of the floral abundance. They choose other floral species than *P. caerulea* var. *yezoensis* late in the flowering season.

In the GLMM for the foraging diversity of *B. hypocrita*, worker bees tended to visit more plant species when floral

diversity was high ($z=1.93$, $P=0.054$; Fig. 5), while the numbers of conspecific (*B. hypocrita*) and heterospecific bees (*B. beaticola*) were excluded by the AIC model selection (Table S1). In the GLMM for the foraging diversity of *B. beaticola*, all explanatory variables were excluded by the AIC model selection (Table S1), indicating that the foraging pattern was independent of both of floral diversity and bee density (Fig. 5).

The degree of floral use overlap between *B. hypocrita* and *B. beaticola* decreased in the middle season of 2016 compared to that in the middle season of 2015 (Fig. 6). The GLMM result showed that the floral use overlap was negatively correlated with the number of *B. beaticola* workers ($z=-3.55$, $P<0.001$), while floral diversity and the number of *B. hypocrita* workers were excluded by the AIC model selection (Table S1).

Discussion

Two common bumble bees, *B. hypocrita* and *B. beaticola* visited similar plant species, while the foraging pattern was different between them. *Bombus hypocrita* tended to visit diverse flowers more frequently than *B. beaticola*. Furthermore, resource partitioning was detected under the condition of high bee density. In the following sections, we discussed the mechanisms underlying these findings considering the differences in morphological traits, colony cycle, and floral choice between the investigated bee species.

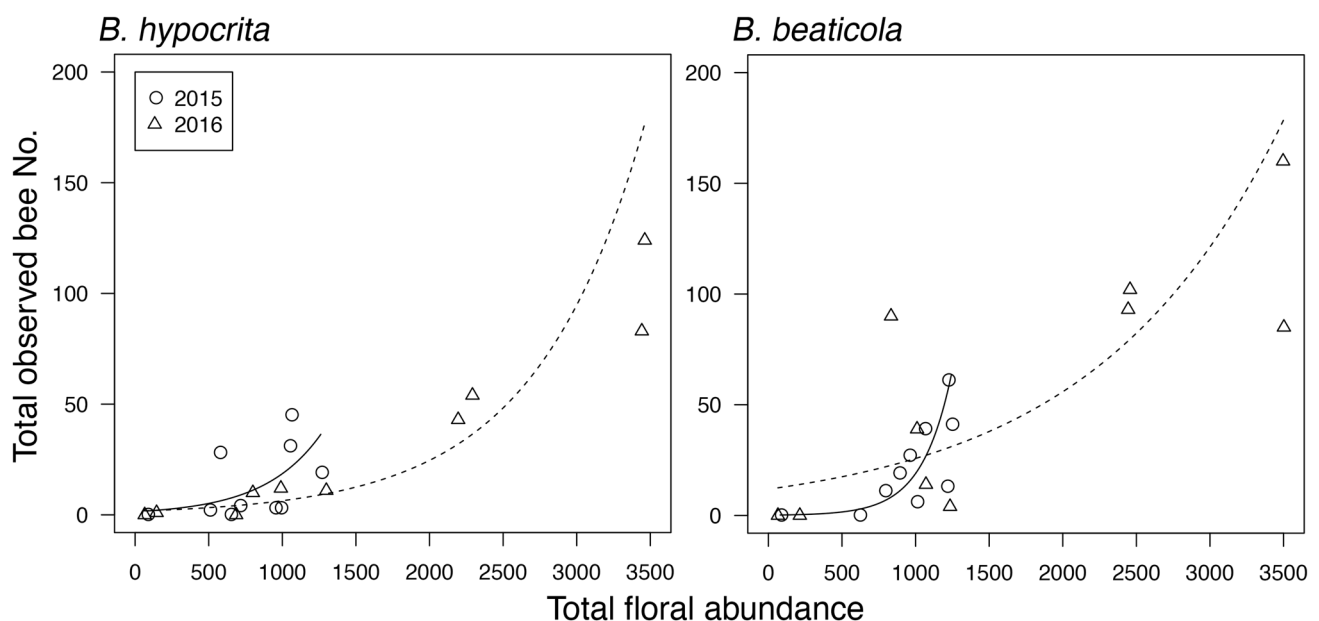


Fig. 3 Relationships between total floral abundance and total observed number of *Bombus hypocrita* and *B. beaticola* workers. Solid and broken regression lines represent 2015 and 2016, respectively

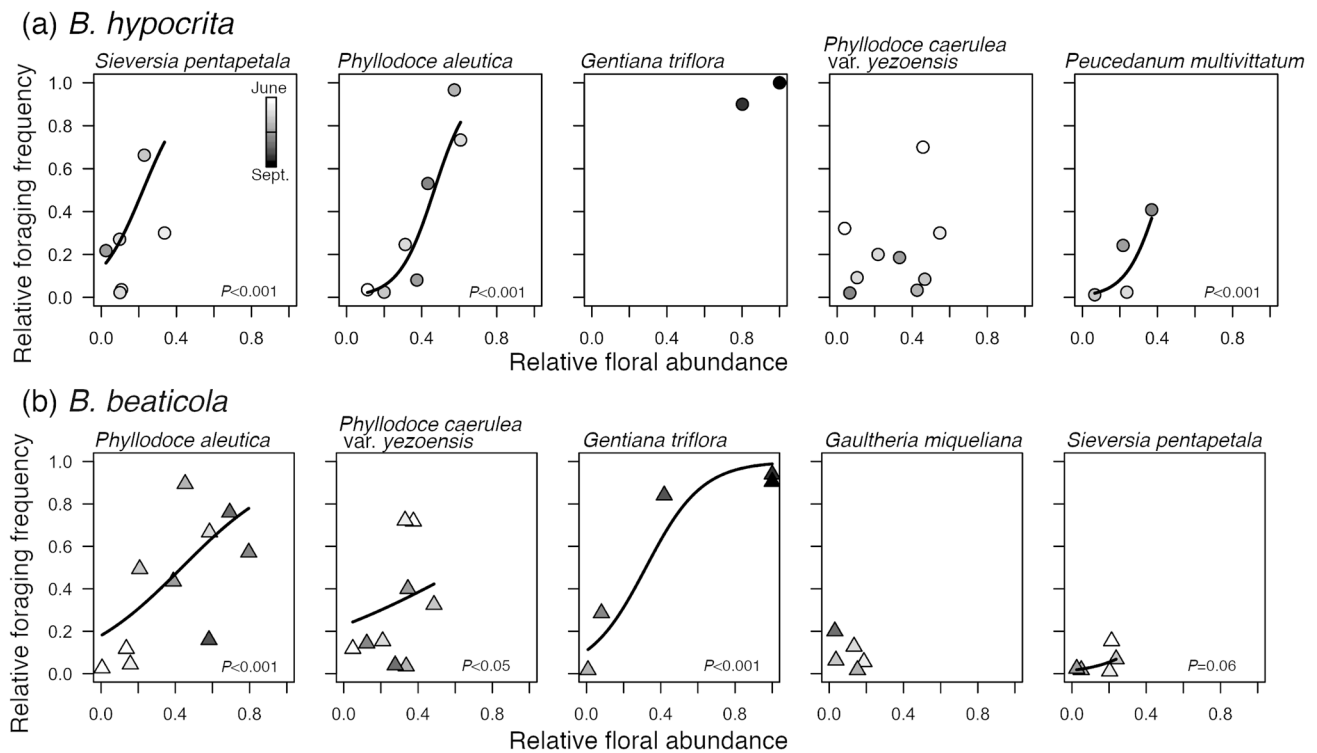


Fig. 4 Relationship between relative floral abundance and relative foraging frequency of worker bees in **a** *Bombus hypocrita* and **b** *B. beaticola* for top five most-visited floral species. The lines indicate the prediction by GLM

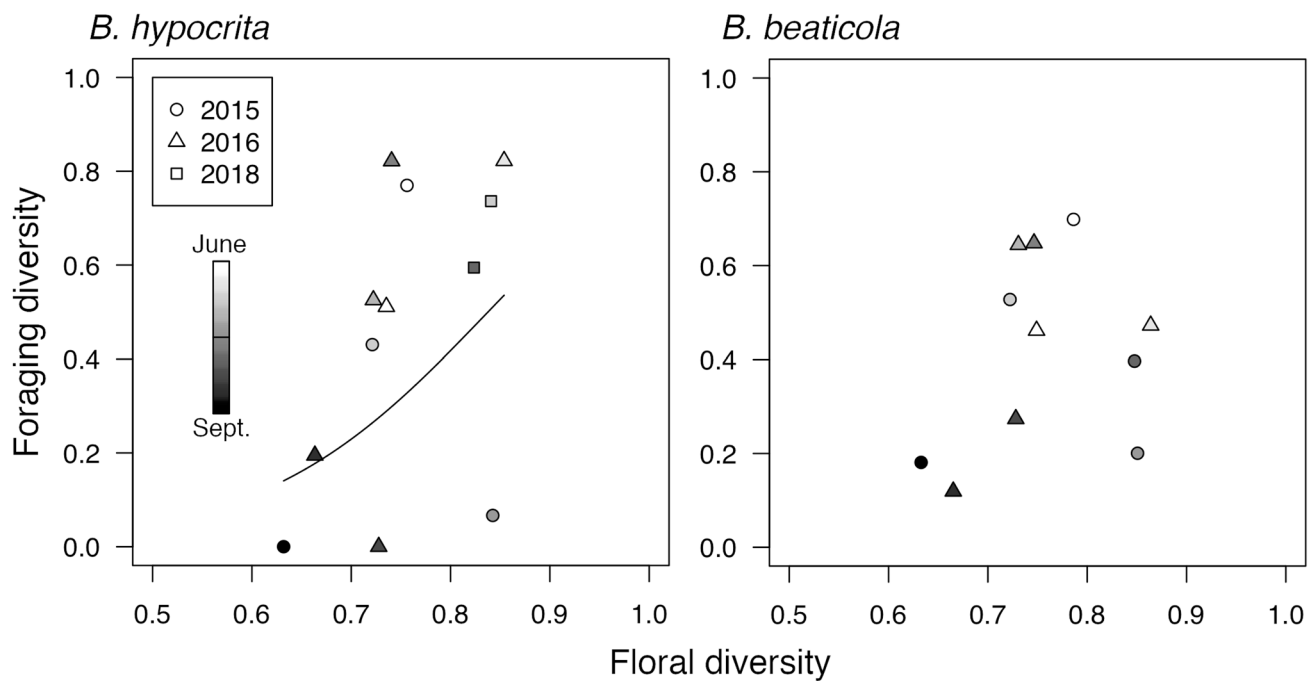
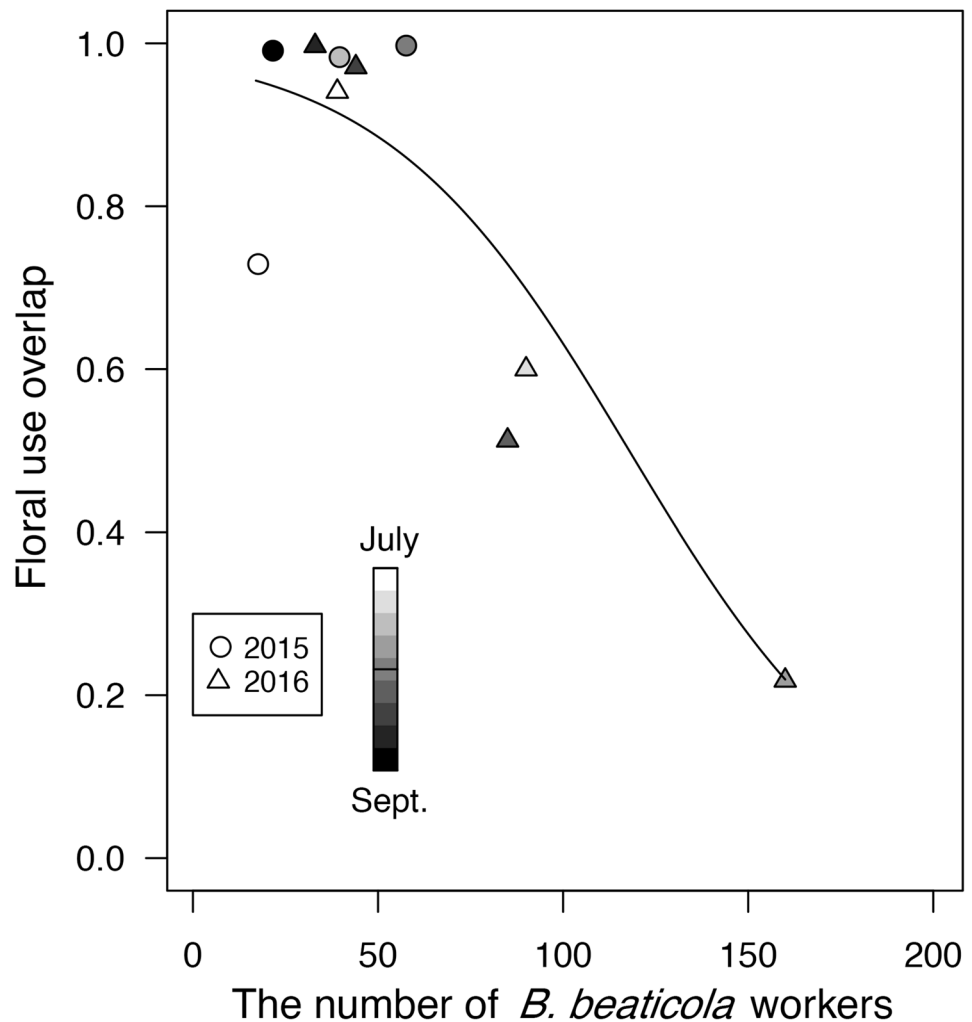


Fig. 5 Relationship between floral and foraging diversity of *Bombus hypocrita* and *B. beaticola* workers. A positive correlation was detected only for *B. hypocrita* ($P=0.05$ by GLMM)

Fig. 6 Relationships between the number of *Bombus beaticola* workers and floral use overlap index between *B. hypocrita* and *B. beaticola* workers. The line indicates the prediction by GLMM



Seasonal trends of bumble bees and flowering plants

In the present research, the two dominant species, *B. hypocrita* and *B. beaticola*, were continuously recorded during the summer, indicating that these species are residents of the alpine site. *Bombus hypocrita* is the most common bumble bee species in Hokkaido, distributed from the coastal grasslands to the alpine areas, and all castes (overwintered queens, workers, new queens, and males) were observed in the investigated alpine site, suggesting the existence of sedentary populations in this alpine environment. *Bombus beaticola* is the second dominant species in the Taisetsu Mountains and this species nests in alpine areas, but overwintered queens are rarely observed in early summer (Tomono and Sota 1997; Kudo 2014). This indicates that queen bees may overwinter below timberline and migrate to the alpine site for nesting. In contrast, other bee species were sporadically recorded at low frequency in the alpine site. These less abundant species may be residents of lower elevations

and visit the alpine site for foraging when floral resources are abundant. Bumble bees are able to fly long distances (> 1.5 km) for foraging across diverse plant communities (Walther-Hellwig and Frankl 2000; Kreyer et al. 2004; Osborne et al. 2008; but see also Geib et al. 2015). Therefore, alpine meadow can be a foraging site also for bumble bees inhabiting at lower elevations (Tomono and Sota 1997).

Although *B. hypocrita* workers were recorded most frequently during the 3 survey years, *B. beaticola* workers were scarce in 2018. The same trend was also observed in other sites in this mountain region (personal observation by A. Shibata and G. Kudo). One possible reason for this is the occurrence of an unusual severe frost period in mid-June of 2018, during which the mean daily temperature was 5 °C lower than that in the usual year and freezing night time temperatures persisted for a week. Such cold weather conditions might restrict survival of overwintered queens, migration to alpine area or establishment of colonies in *B. beaticola*. In 2015 and 2016, colony development was presumed to be successful for both species. Positive correlations between

floral abundance and the number of worker bees in both species indicated that colony development was correlated with the progress of flowering during these years. Such a species-specific population dynamics of bumble bees between years was reported previously in this mountain region (Kudo 2014), indicating that the factors affecting population dynamics differ among bumble bee species. Further studies are required to reveal the mechanism of colony development and to predict population dynamics of bumble bees.

The flowering of 17 plant species commonly foraged by bumble bees progressed sequentially during the summer, and species richness and floral abundance reached maximum levels in the middle of summer. The flowering of individual species lasted for several weeks at regional scale. Spatiotemporally diverse flowering patterns in alpine ecosystem is created by the existence of snowmelt gradient by which flowering of alpine plants persists continuously at landscape scale (Kudo 2016, 2019). Plant species inhabiting snowbeds, such as *Phyllodoce* spp. and *S. pentapetala*, continued to flower for long periods across the investigated sites owing to the difference in snowmelt time, although the flowering period in each population was relatively short (10–14 days). In contrast, flowering of several plant species, such as *Gentiana* spp., *S. virgaurea*, and *S. betulifolia*, progresses successively within individuals, resulting in longer flowering periods in each population. The floral abundance and foraging frequency of *Phyllodoce* spp. and *G. triflora* were high in the investigated site, and their peak flowering periods were different: flowering of *Phyllodoce* spp. commonly occurred about 10–14 days after the snowmelt, while *G. triflora* was the latest bloomer in the snow meadow. Thus, these species are important floral resources for bumble bees in this area. The flowers of *Phyllodoce* spp. were abundant in 2016, which might have allowed bees to succeed in colony growth, resulting in larger number of foraging worker bees. A large yearly variation in the abundance of *Phyllodoce* flowers was previously observed in the same region (Kasagi and Kudo 2003; Kameyama and Kudo 2009; Kudo 2014). Therefore, the quantity and quality of floral resources vary greatly from year to year in the alpine environment, which may affect the development of bumble bee colonies.

Effects of floral abundance and diversity on foraging patterns

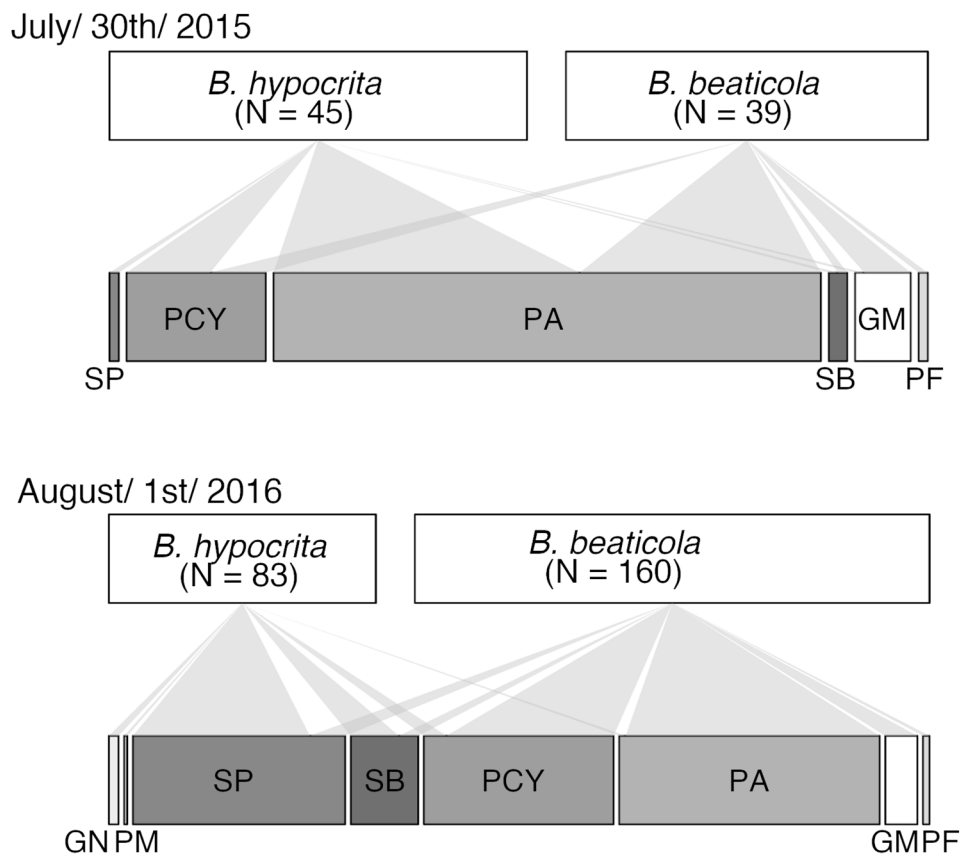
The workers of both dominant bee species tended to forage on abundant floral species. However, the trends and foraging patterns were different between the species. *Bombus hypocrita* workers frequently foraged on both shallow and deep corolla flowers, whereas *B. beaticola* workers mostly foraged on deep corolla flowers. Furthermore, *B. hypocrita* workers had a more general floral use pattern when floral diversity was high, whereas the species richness of visited

flowers through the season was higher in *B. beaticola* workers. Target floral species are often determined by the extent of morphological matching between flowers and bees (Heinrich 1976a; Inoue and Yokoyama 2006). *Bombus hypocrita* workers have larger body size, shorter tongue length, and larger head width (body size = 14.22 ± 1.96 SE mm; proboscis length = 7.82 ± 0.83 mm; head width = 3.97 ± 0.43 mm) than those of *B. beaticola* workers (11.04 ± 0.95 mm; 8.03 ± 0.63 mm, nd 3.30 ± 0.21 mm) (Kinota 2012). Although the difference in proboscis length was small between them, the ratios of proboscis length to head width of *B. hypocrita* and *B. beaticola* workers are 1.97 and 2.43, respectively. Not only the proboscis length but also the combination of morphological traits can affect the floral choice in bumble bees (Inoue and Kato 1992). Therefore, the ratios of proboscis length to head width may be an important determinant factor of floral preference. *Bombus hypocrita* workers avoided foraging on flowers with narrow and deep corollas, resulting in lower species richness of visited flowers throughout the season. *Bombus hypocrita* workers preferred cup-shaped and urceolate-shaped flowers, whereas *B. beaticola* workers did not prefer cup-shaped flowers. The abundance of cup-shaped flowers (*S. pentapetala* and *P. multivittatum*) was relatively high in the investigated site. Such a floral composition might result in higher foraging diversity for shorter-tongued *B. hypocrita*. In addition, *B. hypocrita* workers have larger intraspecific size variation than *B. beaticola* workers. Generally, bumble bee workers have large intraspecific size variation (Johnson 1986; Goulson et al. 2002). A previous study reported that larger workers of *B. terrestris* with longer tongues tended to visit deeper flowers more frequently than smaller workers did (Peat et al. 2005). Because of their high size variability, *B. hypocrita* workers might be able to forage on various floral species.

Effects of bee density on foraging pattern

The number of different bee species was independent of the foraging diversity in both bee species, whereas the degree of floral use overlap decreased with the increase in the number of *B. beaticola* workers. Under conditions of high density of foraging bees on August the 1st, 2016 (the number of *B. beaticola* workers was 160), *B. hypocrita* workers visited *S. pentapetala* more frequently than they visited *Phyllodoce* flowers, which were frequently foraged on by *B. beaticola* workers (Fig. 7). In contrast, when the density of foraging bees was low on July the 30th, 2015 (the number of *B. beaticola* workers was 39), workers of both bee species predominantly visited *Phyllodoce* flowers. Therefore, *B. hypocrita* workers were more flexible than *B. beaticola* workers in choosing target flowers. Individual bumble bees commonly change target flowers in response to the availability of floral resources (Heinrich 1979; Chittka et al. 1997; Wiegmann

Fig. 7 Foraging frequency of *Bombus hypocrita* and *B. beaticola* workers observed in each floral species on two observation days; low bee density on July 30th, 2015 (top) and high bee density on August 1st, 2016 (bottom). Floral species are *Gaultheria miqueliana* (GM), *Gentiana nipponica* (GN), *Penstemon frutescens* (PF), *Peucedanum multivittatum* (PM), *Phyllodoce aleutica* (PA), *Phyllodoce caerulea* var. *yezoensis* (PCY), *Sieversia pentapetala* (SP), *Spiraea betulifolia* (SB)



et al. 2003). These results suggest that resource level of *Phyllodoce* flowers decreases as the number of foraging workers increases, and the competition for the floral resource should be intensify, resulting in a shift to subsequently preferred floral species in short-tongued *B. hypocrita*.

The stage of colony development also affects floral choice of worker bees via changes in the nutrition demand of colonies. Nutritional compositions of pollen and nectar differ among different floral species (Somme et al. 2015), and bees collect pollen and nectar for different purposes (Nicolson 2011). During the survey on August the 1st, 2016, when the number of *B. hypocrita* workers was still increasing, pollen resources might have been highly required for their larvae growth (Fig. 1). In contrast, during the same period, the number of *B. beaticola* workers reached maximum level, indicating that the demand for pollen resources might have decreased. Although *Phyllodoce* flowers provide both pollen and nectar to bumble bees, *S. pentapetala* flowers provide only pollen because of low nectar production. Seasonal variations in colony development of each bee species might have resulted in different floral use patterns in *B. hypocrita* and *B. beaticola*.

In this study, we found that the relative floral abundance and foraging bee frequency affected the foraging patterns of bumble bee workers, and that *B. hypocrita* had a more

diverse and flexible floral choice than that of *B. beaticola*. This difference might reflect the differences in morphological traits and/or colony developmental cycles. When a competition for floral resources exists between bumble bees, the possibility of resource partitioning can be a key issue for the coexistence of multiple bumble bee species. The intensity of competition depends on the both of the availability of floral resources and bee densities, and the possibility of resource partitioning highly depends on the flexibility of floral usage of competing bee species. Therefore, coexistence mechanism of multiple bee species is highly situation-dependent.

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Author contributions AS and GK designed the study. AS and GK collected field data, analyzed the data, discussed, and wrote the manuscript.

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