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The Life History and Pollination Ecology of Bumblebees in the Alpine Zone of Central Japan

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Abstract We studied the life history and pollination ecology of bumblebees in the alpine (2600–2800 m a.s.l.) and subalpine (1500–2400 m a.s.l.) zones of Mt. Norikura in central Honshu, Japan. *Bombus beaticola* was the only species that nested in the alpine zone, where the nests seemed to have produced few reproductive bees. Their main nest sites were probably in the subalpine zone. *Bombus hypocrita* workers also foraged in the alpine zone. Some foraging workers of *B. beaticola* moved between subalpine and alpine sites, and the mean size of foraging workers in the alpine zone was larger than that in the subalpine zone throughout mid summer. This suggested that larger workers from the subalpine colonies foraged in the alpine zone. In alpine flowers utilized mainly by bumblebees, fruiting rates were significantly decreased when insect pollinators were excluded by bagging, and flowers blooming at the beginning and the end of the season had lower fruiting rates probably because of the reduced numbers of bumblebee-pollinators. Thus, although bumblebees may not complete their life-cycles in the alpine zone, they maintain mutual relationships with alpine flowers through the foraging activity of workers from subalpine and alpine colonies.

Key words: Bumblebees; alpine zone; life history; pollination; ecology.

Introduction

Alpine flowering plants, as well as those in arctic habitats, suffer from low annual productivity. The cost for pollinator attraction is a relatively heavy burden for the plants. The harsh environmental conditions also prevent many insects from colonizing, and the fauna of anthophilous insects is generally poor in the alpine zone. Therefore, natural selection should favor self-fertilization and vegetative reproduction in alpine flowering plants (Mosquin & Martin, 1967; Johnson, 1969; Bliss, 1971). Bumblebees (Hymenoptera: Apidae) unusually are efficient pollinators in cool habitats because of their ability to regulate their body temperature (Heinrich, 1979). Many alpine and arctic flowers depend on bumblebees for pollination (Kenoyer, 1916; Kevan, 1972; Macior, 1974; Bauer, 1983; Yumoto, 1986). Thus, the propagation and survival of some alpine flora depend much on the mutual relationship between

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bumblebees and flowering plants.

In temperate zones, only the inseminated queens of bumblebees overwinter (SAKAGAMI, 1976; HEINRICH, 1979). In the spring, they solitarily construct nests under/on the ground. The colonies develop by producing multiple broods of workers and end in the dispersal of the new reproductive castes from the nest. In the arctic zone, the annual colony cycle is maintained, but only the first brood is produced in the short summer (RICHARDS, 1973). A shift from a social to a solitary life cycle at high altitudes has been reported in a halictine bee, *Lasioglossum duplex* (SAKAGAMI & MUNAKATA, 1972), but such a life-history variation is unlikely in bumblebees at high latitudes (RICHARDS, 1973: MACIOR, 1974; SAKAGAMI, 1976). The life history of alpine bumblebees has scarcely been studied, although there are studies on the alpine bumblebee-flower relationship in North America (*e.g.*, KENOYER, 1916; MACIOR, 1974; PLEASANTS, 1980; PYKE, 1982; BAUER, 1983), and in Japane (*e.g.*, YUMOTO, 1986; SOTA, 1993).

The alpine zone in central Honshu, Japan, is usually defined as the zones above the forest limit at approximately 2500–2700 m a.s.l. The subalpine zone below the alpine zone is mostly evergreen coniferous forest dominated by *Abies mariesii*, *A. veitchii* and *Tsuga diversifolia*. The characteristic vegetation in the Japanese alpine zone is the scrub of the dwarf pine, *Pinus pumila*, which covers a large part of the area above the timberline. The mountains are generally not so high (the highest summit is 3776 m and the second 3192 m), and the alpine meadows are distributed rather sporadically along narrow ridges. Accordingly, alpine flowers bloom in small patches. Bumblebees are the dominant anthophilous insects there, though the number of species is few (*e.g.*, YUMOTO, 1986; Kato *et al.*, 1993; SOTA, 1993).

The purpose of this study is to clarify the life history of bumblebees and their relationship with flowers in the alpine zone of central Honshu, Japan. In this paper, we show that the dominant alpine bumblebee, *Bombus beaticola*, has colonies in the subalpine zone and uses the alpine zone as an alternative foraging site.

Materials and Methods

Study area

This study was carried out on the north and eastern slopes of Mt. Norikura (36°06′ N, 137°33′ E; alt. 3026.3 m), Nagano, central Japan (Fig. 1). Mt. Norikura is located in the southern part of the Hida Mountain Range, included in the Chubu Montane National Park area. In the study area, altitudes above 1500 m are classified as subalpine zone, and above 2500 m as alpine zone. The alpine study sites were one area at 2730–2770 m a.s.l. near Gonoike pond and

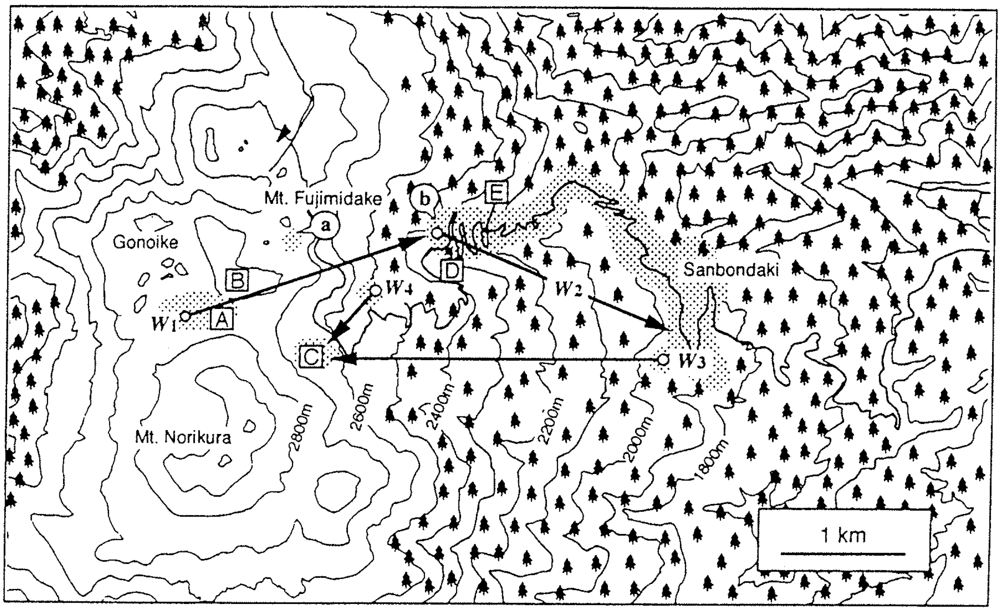

Fig. 1. Study sites in Mt. Norikura area. Dotted areas are study sites. Tree-marks indicate forests. A, Katanokoya; B, Corona Observatory; C, Feeding place where return times of marked workers were recorded; D, Kuraigaharasanso; E, Reisengoya. Arrows indicate the movements of marked workers, w_1–w_4 (open circle, release point; arrow tip, recapture point). "a" and "b" indicate the places where nests were discovered.

another at 2600–2800 m a.s.l. on the eastern slope. The subalpine study sites were at 1500–2400 m a.s.l. along the mountain road and paths. The flora of the Mt. Norikura area is described by SHIMIZU (1990). Figure 2 shows the meteorological conditions at 2870 m a.s.l. of Mt. Norikura and at 610 m a.s.l. of Matsumoto (40 km north east of Mt. Norikura), indicating that the fine or cloudy days which allowed bumblebees to forage were fewer in the alpine zone.

Bumblebee community and seasonal abundance

From June to October, 1993–1995, flower-visiting bumblebees were collected at 1500–2770 m a.s.l. The sampling effort varied according to the altitude and the sampling occasion. The glossa length of bumblebees is defined as the distance from the besiglossal sclerite to the labellum (HARDER, 1982), and is correlated with body size within a species (MORSE, 1977; HARDER, 1982). The glossa length and head width of workers and queens of each species were measured to analyze the bumblebee community in terms of the functional morphology. The specimens for this analysis were also collected outside the study area in the Hida Mountain Range and Matsumoto area.

The seasonal abundance of bumblebees was studied on flowers at the alpine and subalpine study sites. The abundance of each caste was expressed as the number of individuals observed per 1 h in the daytime. The flowering

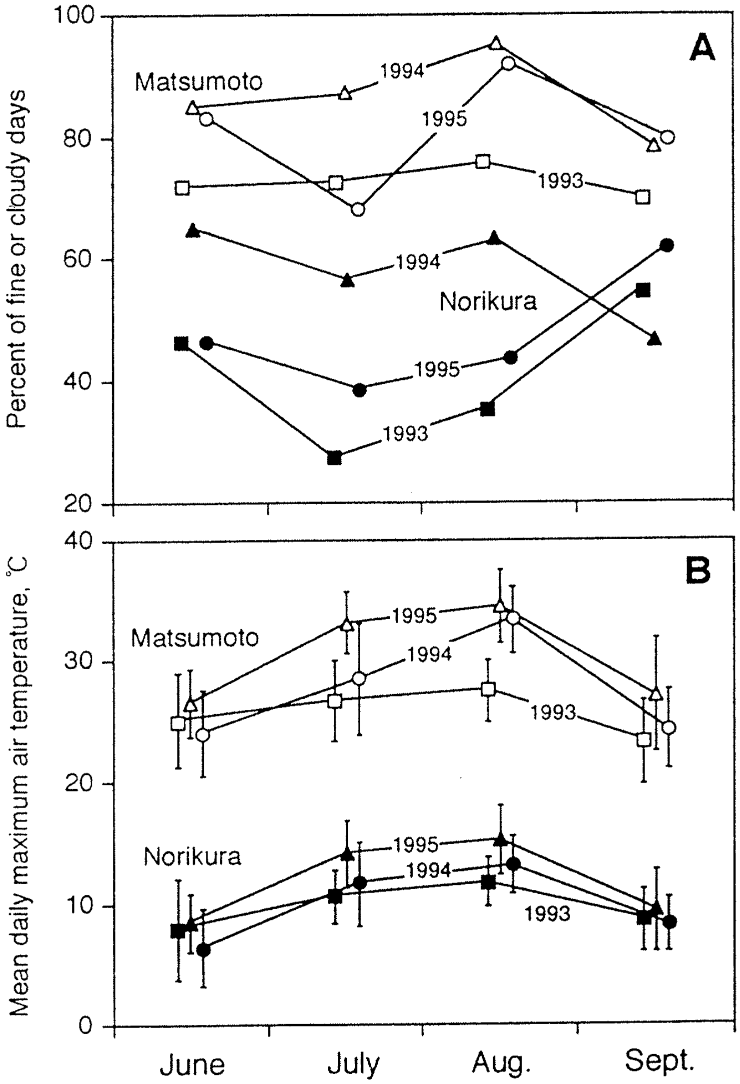

Fig. 2. Percent of fine or cloudy days in each month (A) and monthly mean of daily maximum air temperature (±SD) (B) at MATSUMOTO City (610 m a.s.l.; Nagano Meterological Observatory; open symbols) and at the Corona Observatory, National Astronomical Observatory on Mt. Norikura (2870 m a.s.l.; closed symbols) in 1993–1995.

phenology of plants visited by bumblebees was recorded in the alpine zone. Bumblebee nests discovered were dug out and analyzed (*cf.* KATAYAMA & OCHIAI, 1982).

Movement of workers

To investigate the movement of *Bombus beaticola* workers between altitudes, foraging workers were captured with a silk net and marked individually with color paints (Paint Marker®, Mitsubishi Pencil, Co. Ltd.) at altitudes of 1800 to 2770 m from late June to early September in 1994 and 1995.

To estimate the distance from nests for *B. beaticola* workers foraging at an alpine site, a feeding place (a petri dish with a 40% sugar solution; OCHIAI & MATSUOKA, 1979) was set in a patch of *Phyllodoce aleutica* flowers at 2620 m a.s.l. on August 17 and 20, 1995. Workers attracted there were individually marked with color paints, and the return time to revisit was measured at least three times for each marked bee. The measured time consisted of the time for the round flight between the feeding place and the nest, and the residence time in the nest. Since the flight velocity (v) and residence time (r) were not known for *B. beaticola*, $v=4.1$ m/sec (15 km/h) and $r=101$ sec (1.7 min) for *B. honshuensis* were applied to estimate the distances to the nests for *B. beaticola* workers. These values were obtained from a linear regression of return time on the round trip distance for the data in KATAYAMA & OCHIAI (1980)

Fruiting rate, nectar secretion and insect visits to bumblebee flowers

To study the efficiency of insect pollination and the potentials of self-pollination in some flowers visited by bumblebees, bagging and hand pollination experiments were carried out, and the fruiting rate (or fruit set) was determined as the ratio of the number of ripe fruits with mature seeds to the number of experimental flowers. Because some flowering plants were examined for the fruit set before fully matured, fruits with large immature seeds were also regarded as having been fertilized. The fruit sets were compared between bagged and open (control) flowers of 9 plant species in the alpine zone and 3 species in the subalpine zone. For the bagging of flowers we used paper bags with a paraffin-coating (6 cm by 7.5 cm, or 13 cm by 15.5 cm). Self-compatibility was studied also by hand pollination in 3 species which were bagged to prevent insect visits. Cross pollination by hand was applied for 6 species. The difference in fruit set between control flowers visited by natural pollinators and the flowers which received cross pollination by hand indicated the degree of pollinator limitation in the field. For *Vaccinium ovalifolium*, insect visit and the fruit set were compared among altitudes of 2600, 2360 and 2200 m.

In 1995, altitudinal variations in the frequency of insect visits to flowers and the daily pattern of nectar secretion were studied for three species of Ericaceae with similar bell-shaped flowers: *Vaccinium ovalifolium*, *Menziesia pentandra*, and *Phyllodoce aleutica*. In the subalpine zone, the frequency of insect visits was measured for *M. pentandra* with 456 flowers in 5 stocks at 1950 m a.s.l. on June 17, and for *V. ovalifolium* with ca. 1500 flowers in a plot of 0.45 m by 1.1 m at 2200 m a.s.l. on June 21–22. In the alpine zone, insect visit was studied for *V. ovalifolium* with ca. 1500 flowers in a 1.5 m by 3.0 m plot on July 10 and 15, and for *P. aleutica* with ca. 4500 flowers in a 1.2 by 2.0 m plot on August 12. The insect visits were recorded for 15 min per hour. The

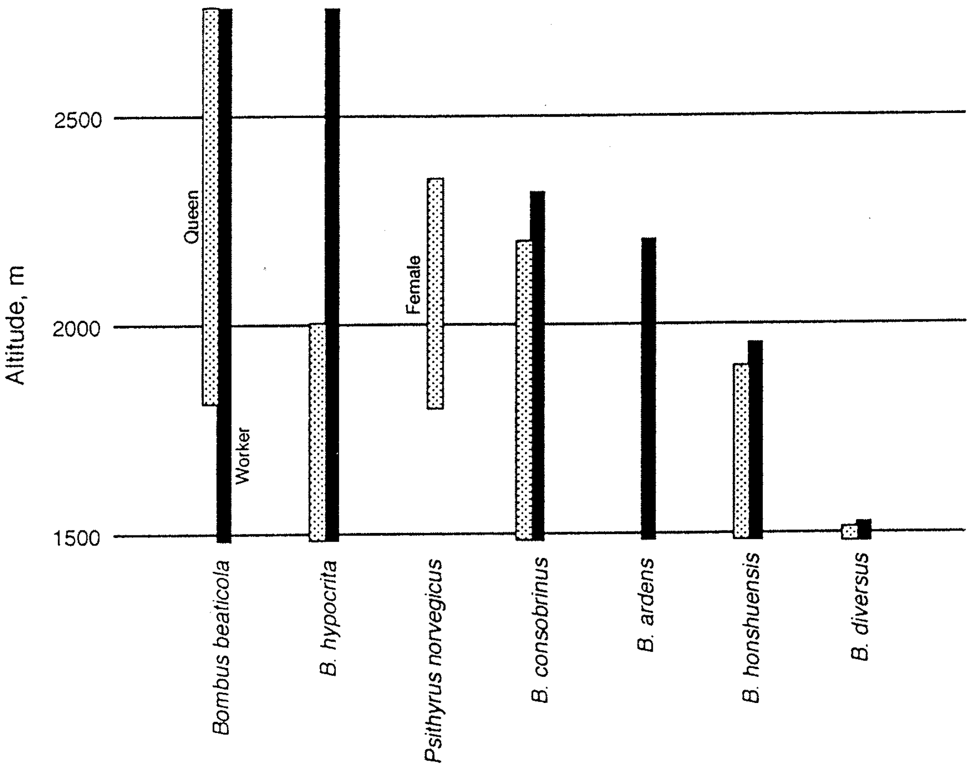

Fig. 3. Altitudinal distributions of *Bombus* and *Psithyrus* species at Mt. Norikura.

amount of nectar was measured by sucking with a micro-pipette (Microcaps®, Drummond Scientific Co.) for flowers with and without nylon nets to exclude insects. The sugar concentration of the nectar was measured with a reflect meter (Bellingham & Stanley Ltd.), and the amount of sugar in terms of the pure sucrose (w) was determined as $w=1.552\,sv/(1.552+s-1.552\,s)$, where s is the concentration and v is the nectar volume.

Results

Bumblebee community and phenology

Seven bumblebee species with various tongue lengths occurred at altitudes above 1500 m (Figs. 3 & 4). Above 1800 m a.s.l., *Bombus beaticola* was the sole dominant species. The cuckoo bumblebee, *Psithyrus norvegicus*, occurred at 1800–2400 m a.s.l. In the alpine zone, all castes of *B. beaticola* and workers of *B. hypocrita*, occurred, which were short-tongued species (Fig. 4). Exceptionally a few individuals of *B. consobrinus* and *P. norvegicus* were obtained.

In the alpine zone, a few queens of *B. beaticola* appeared in July, and workers foraged from mid July; only a few males and new queens were observed in August and early September; workers of *B. hypocrita* appeared from mid July to early August (Fig. 5 A). In the subalpine zone, overwintered *B. beaticola*

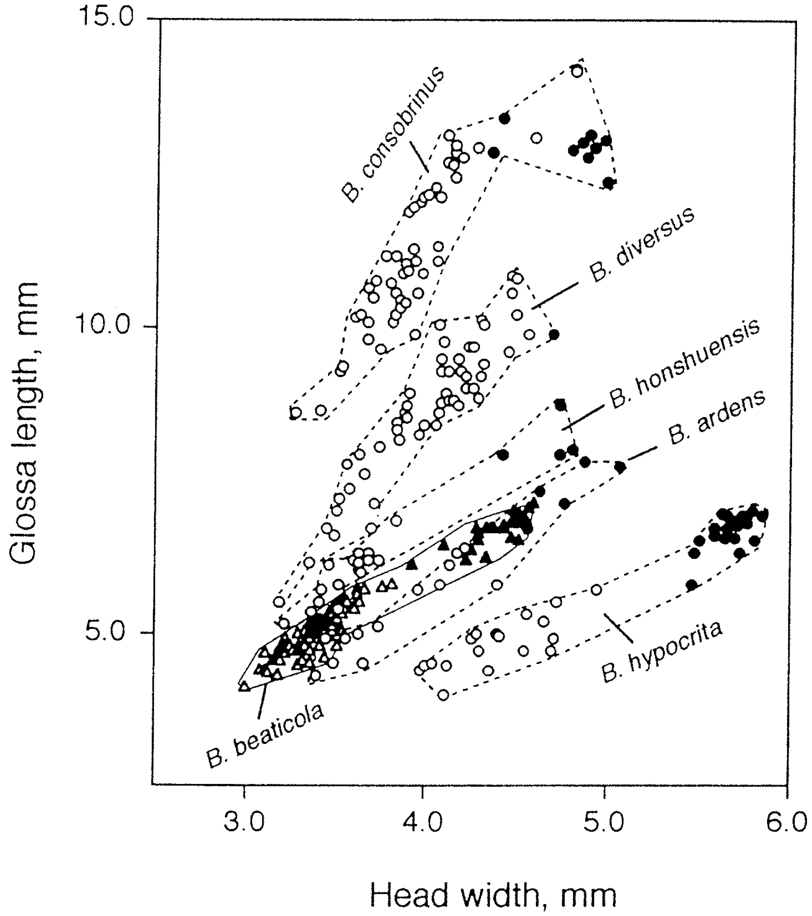

Fig. 4. The relationship between head width and glossa length in bumblebees at Mt. Norikura and the adjacent areas of Nagano Pref. Open and closed symbols represent workers and queens, respectively.

queens visited flowers from early June to mid July, and workers appeared from late June; males were abundant from early August to late September (Fig. 5B).

Table 1 shows the flowering periods in the alpine zone. *Rhododendoron aureum*, *Phyllodoce aleutica* and *Pedicularis yezoensis* bloomed densely and were most frequently visited by *B. beaticola.* These plants bloomed when workers were abundant, and their flowering peaks were segregated. The earliest flowering species was *Vaccinium ovalifolium*, which occurred also in the subalpine zone and was visited by *B. beaticola* queens at 2200 m but by few queens at 2650 m. *R. aureum*, *Schizocodon soldanelloides*, and *P. aleutica* were visited mainly by *B. hypocrita.* Flowers later in the season were visited only by *B. beaticola workers.*

Nests of Bombus beaticola

Two nests of *B. beaticola* were found at 2790 m and 2370 m a.s.l. Both

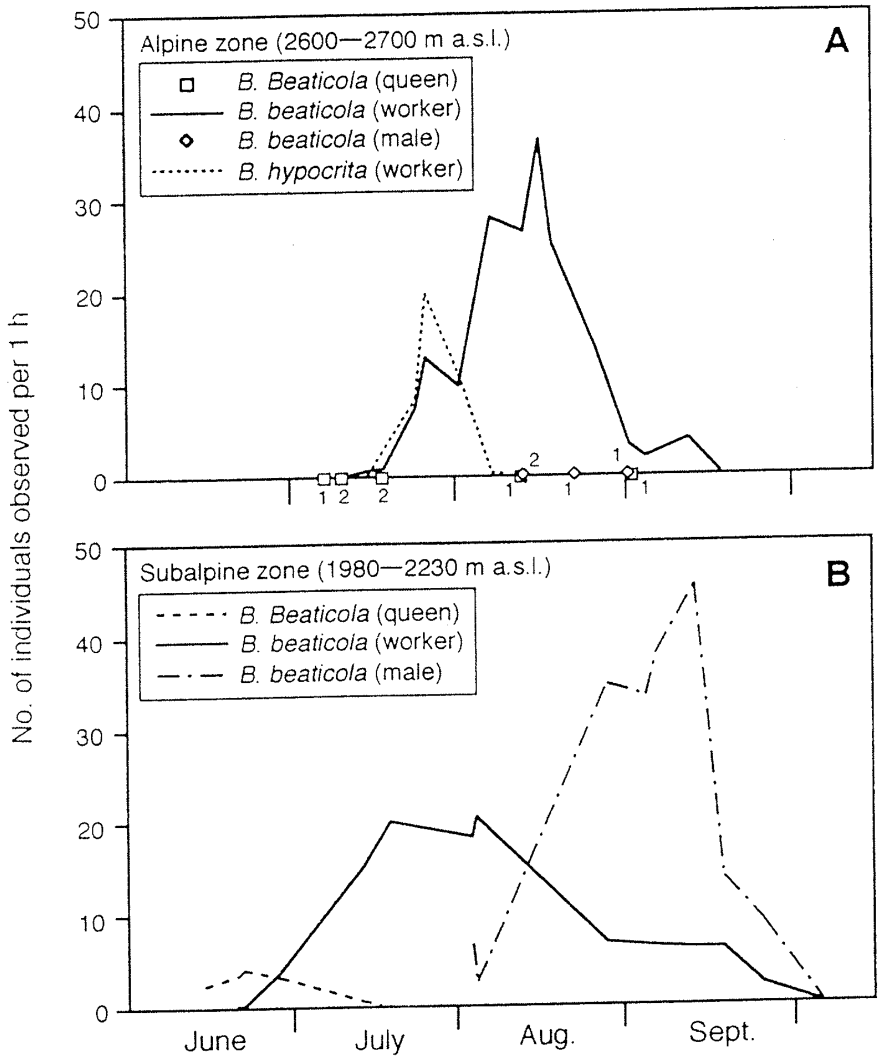

Fig. 5. Seasonal fluctuation in the abundance of flower-visiting bumblebees in the alpine (A) and subalpine zones (B) of Mt. Norikura in 1995. The abundance is the number of individuals observed per 1 h during daytime. In A, the numerals beside the symbols for *B. beaticola* queens and males indicate the numbers observed during the whole census in each day.

nests had collapsed when they were dug out, and produced no reproductive castes. The first nest was discovered by observing the extranidal activity of the queen on the windy ridge of Mt. Fujimidake on July 2, 1993. The first workers were observed on July 26, and probable second brood workers appeared on August 12. The nest taken on August 30 consisted of 3 dead workers, 3 worker pupae, and 11 larvae, with some eggs and 19 vacated cocoons. This colony probably collapsed in mid August because of a heavy rain. There was no significant difference in the cocoon diameter between the first and older broods (WILCOXON two-sample test, $P > 0.05$).

Table 1. Flowering phenology and flower-visit by bumblebees in the alpine zone of Mt. Norikura.

Plant species	Flowering phenology																								Bumblebee visits[a]					
																									B. beaticola			*B. h.*		Others
	June						July						August						September						q	w	m	w	m	
Vaccinium ovalifolium					+	+	⧺	⧺	+	+															+	⧺		+		
Diapensia lapponica						+	⧺	⧺	+																+			+		
Arcterica nana							+	⧺	+	+																		+		
Rhododendron aureum									+	⧺	⧺	+	+												+	⧺		⧺		
Schizocodon soldanelloides									+	⧺	⧺	⧺	+	+												⧺		⧺		*B.c.* w 1
Sorbus matsumurana										+	⧺	⧺	+	+												⧺		+		
Sorbus sambucifolia											+	⧺	+	+												+				
Phyllodoce aleutica											+	⧺	⧺	⧺	⧺	+									+	⧺	+	⧺		
Pedicularis yezoensis														+	+	⧺	⧺	+	+							⧺		+		
Pedicularis chamissonis														+	+	⧺	⧺	+	+							⧺	+	+		
Vaccinium uliginosum															+	+	⧺	+	+							+				
Vaccinium vitis-idaea															+	+	⧺	+	+							+				
Arnica unalaschcensis																+	⧺	⧺	+	+						+		+		*P.n.* m 2
Solidago virga-aurea																+	⧺	⧺	⧺	+	+					+		+	+	
Tripetaleia bracteata																	+	⧺	⧺	+						+				
Hypericum kamtschaticum																	+	⧺	⧺	+						+				
Gaultheria pyroloides																	+	⧺	⧺	⧺	+					+				
Campanula lasiocarpa																	+	⧺	⧺	⧺	+					⧺				
Gentiana algida																	+	+	⧺	⧺	⧺	+				⧺				

[a] *B. h.*, *B. hypocrita*; *B. c.*, *B. consobrinus*; *P. n.*, *P. norvegicus*. q, queen; w, worker; m, visit of male.
⧺ indicate frequent occurrences of flowring and visiting.

The second nest was found among shrubs in a open patch above the subalpine forest at Kuraigahara by observing the extranidal activity of workers on August 11, 1994. When the nest was dug out on August 26, the colony consisted of one live and one dead worker with 31 vacated cocoons (11 of the first brood, 20 of the second and third brood) and 3 pots. No queen or live immatures were found. The size of the second brood cocoons was smaller than that of the first (WILCOXON two-sample test, $P<0.01$). There was no significant difference in the cocoon diameter of the first broods between the two nests (WILCOXON two-sample test, $P>0.05$).

Worker size of Bombus beaticola

The median head width of foraging workers in the subalpine zone was 3.3 mm early in the season, 1993–1994, before foraging workers appeared in the alpine zone (Fig. 6). After that, the median worker size in the alpine zone was significantly larger than that at the alpine zone (3.4 mm *vs.* 3.3 mm in 1993; 3.4 mm *vs.* 3.2 mm in 1994; WILCOXON two-sample test, $P<0.05$). In the autumn, the median head width in the subalpine zone was 3.4 mm in 1993 and 3.2 mm 1994; the head width differed among the three periods significantly in 1994 (KRUSKAL–WALLIS test, $P<0.01$) but insignificantly in 1993 ($P>0.05$).

Foraging distance of Bombus beaticola

In 1994, 286 and 317 workers were individually marked at the alpine and subalpine sites, respectively. Two workers were recaptured at different altitudes; one moved from 2760 m to 2370 m a.s.l. (w_1 in Fig. 1), the other from 2370 m to 1920 m a.s.l. (w_2). The direct distances of these movements were 1990 m and 2320 m. Their head widths were 3.34 mm and 3.45 mm. In 1995, 229 and 271 workers were marked at the alpine and subalpine sites, respectively. One worker marked at 1980 m a.s.l. was recaptured at 2620 m a.s.l. (w_3 in Fig. 1), and another marked at 2530 m a.s.l. was recaptured at 2620 m a.s.l. (w_4). The direct distances of these movements were 2650 m and 560 m. Their head widths were not recorded.

Twenty-two of 27 workers which were individually marked at the alpine feeding site in mid August gave more than 3 data of the return time to the feeding place (Fig. 7). The mean return time to the feeding place of these workers varied from 82 to 849 sec (average, 368 sec). The mean return time was not correlated with head width (SPEARMAN rank correlation, $P>0.05$). With an assumed flight velocity of 4.1 m/s and residence time in the nest of 101 sec, the estimated mean distance to the nest was 547 m. Seven out of 22 workers had estimated distances >800m (maximum, 1533 m) and their nests could have been in the subalpine forests.

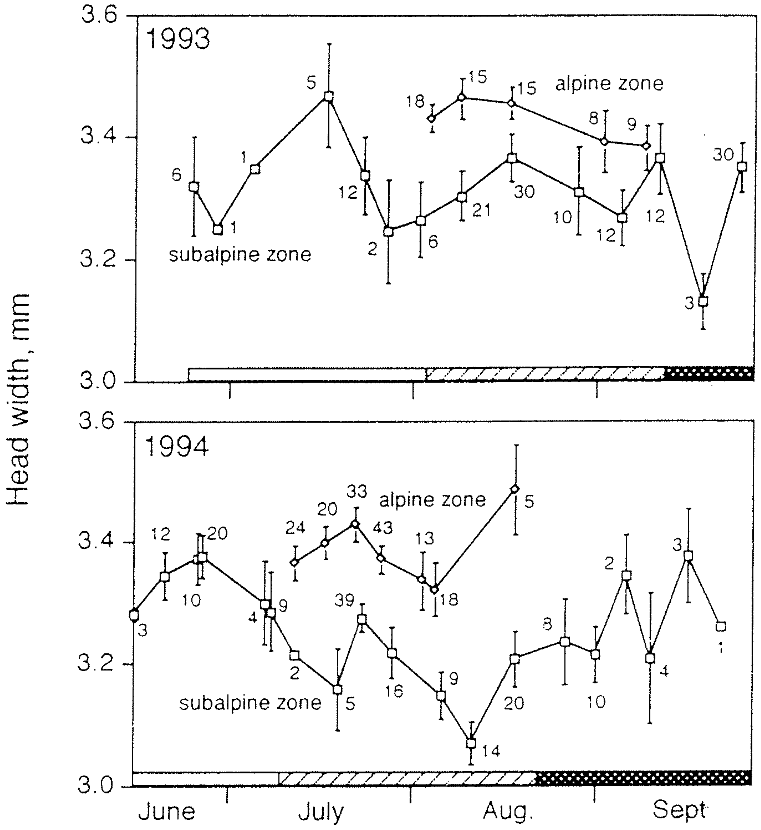

Fig. 6. Seasonal changes in the mean head width (±SE) of *Bombus beaticola* workers at the alpine and subalpine zones of Mt. Norikura in 1993 and 1994. Numerals are sample sizes. Horizontal bars indicate three periods in the statistics (see text): open, before the appearance of workers in the alpine zone; hatched, during the appearance of workers in the alpine zone; dark, after the disappearance of workers in the alpine zone.

Fruiting rate, nectar secretion and insect visits to bumblebee flowers

Bagging experiments showed partial fruiting (2–64%) in 5 flower species out of 11 studied, indicating the possibility of self-pollination (Table 2). Of the fruiting species, *Rhododendron aureum* and *Phyllodoce aleutica* fruited after the artificial self-pollination, whereas *Vaccinium ovalifolium* did not. These results suggested that *V. ovalifolium* was self-incompatible, *R. aureum* was self-compatible but seldom exhibited self-pollination, and *P. aleutica* was self-compatible and selfed in the absence of pollinators. *Gaultheria pyroloides* had no ripe fruit in either the control or the bagged flowers.

In six alpine flowers which received artificial cross pollination, *V. ovalifolium*, *R. aureum* and *Gentiana algida* had higher fruit sets compared with control flowers (Table 2). Thus, the pollinator limitation was indicated for *V. ovalifolium*, *R. aureum* and *G. algida* which flowered earliest and latest in the season; three other species, *Shizocodon soldanelloides*, *P. aleutica* and *Campanula lasiocarpa*, flowered in the intermediate periods when bumblebees were

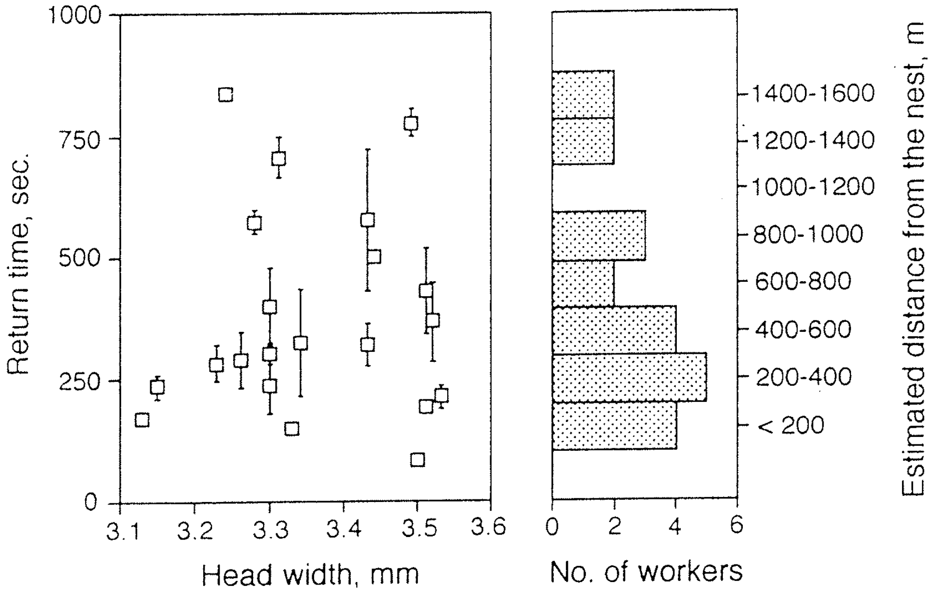

Fig. 7. The relationship between the return time to the alpine feeding site for marked *Bombus beaticola* workers and their head width (left; $n=21$), and frequency distribution of the estimated distance from the feeding site to the nests (right; $n=22$).

abundant (Table 1).

In *Vaccinium ovalifolium*, the fruit set was lower at higher altitudes (Table 2; altitudinal difference, $P<0.01$ by chi-square test; df=2, $\chi^2=86.1$). In the subalpine zone, *V. ovalifolium* was visited mainly by *B. beaticola* queens, *Dolichovespula norvegicoides*, and *Andrena* sp.; they consumed nectar at high rates (Table 3). *B. beaticola* was the sole pollinator in the alpine zone, and their consumption of nectar was negligible probably because of their low population densities (Table 3).

Menziesia pentandra at 1950 m a.s.l. were visited frequently by syrphid flies and *D. norvegicoides*, and less frequently by *B. beaticola*; nectar was consumed by the insects (Table 3). *Phyllodoce aleutica* in the alpine zone bloomed in the peak of bumblebee abundance, and was visited throughout the day by many workers which consumed nectar at high rates (Table 3).

Discussion

Life history of Bombus beaticola

Bombus beaticola was the sole dominant species which foraged and nested in the alpine zone of Mt. Norikura. Workers of *Bombus hypocrita* also occurred in the alpine zone, but they probably do not have nests there. The occurrence of these two species is common in the adjacent alpine zones (YUMOTO, 1986; SOTA, 1993). *Psithyrus norvegicus* occurred in the subalpine zone but seldom in

Table 2. Fruit-set of bumblebee flowers.

Plant species[a]	Treatment								Comparison	
	Control		Bagged		Self-pollinated		Cross-pollinated		Bagged vs. Control χ^2	Cross vs. Control χ^2
	N[b]	fruit-set	N[b]	fruit-set	N[b]	fruit-set	N[b]	fruit-set		
Alpine zone										
Vaccinium ovalifolium[1]	182(40)	0.11	87(25)	0.02	13(6)	0	30(13)	0.50	5.9*	28.4***
Rhododendron aureum	74(5)	0.85	91(5)	0.03	18(5)	0.28	74(5)	0.96	113.9***	5.0*
Schizocodon soldanelloides	22(9)	0.68	20(9)	0.20			18(9)	0.89	12.1***	2.4
Phyllodoce aleutica	33(1)	0.97	36(1)	0.64	19(1)	0.79	33(1)	0.94	11.7***	0.3
Vaccinium uliginosum	45(10)	0.56	12(10)	0					6.2*	
Pedicularis chamissonis	313(21)	0.75	114(7)	0					118.6***	
Gaultheria pyroloides	45(5)	0	44(5)	0						
Campanula lasiocarpa	43(43)	0.49	8(8)	0			28(28)	0.71	6.6**	3.5
Gentiana algida	22(11)	0.77	27(14)	0.11			35(20)	1.00	22.0***	8.7**
Sub-alpine zone										
Pedicularis yezoensis	113(7)	0.81	80(4)	0					52.5***	
Vaccinium ovalifolium[2]	53(11)	0.55								
Vaccinium ovalifolium[3]	42(9)	1.00	54(10)	0.02					92.0***	
Menziesia pentandra	44(9)	0.93	39(9)	0.20					42.4***	

[a] 1, 2, 3 were observed at altitudes of 2600 m, 2350 m, 2200 m, respectively.

[b] Number of flowers observed. Numerals in parenthesis are the number of individuals observed.

* $P<.05$, ** $P<.01$, *** $P<.001$.

Table 3. Nectar secretion and frequency of flower-visit by insects in alpine and subalpine flowers at Mt. Norikura.

Species Altitude Date (time) in 1995	Weather Mean temp., ℃ (range) Mean humidity, % (range)	Nectar secretion time[a] Average sugar weight (LS mean±SE, mg)[b]	Flower-visiting insects	
			Taxon	Frequency of visits/ 1500 flowers/1h
Menziesia pentandra 1950 m June 17 (6:00–17:00)	fine 12.1 (7.5–16.1) 77 (65–93)	Morning and afternoon Bagged: 0.308±0.03* Control: 0.144±0.03	Syrphidae	24.4
			Dolichovespula norvegicoides	22.6
			Bombus beaticola (worker)	5.2
			B. beaticola (queen)	4.5
			Andrena sp.	0.5
Vaccinium ovalifolium 2200 m June 21 (10:00–19:00)	fine/cloudy 12.5 (8.2–14.8) 79 (63–86)	Morning and afternoon* Bagged: 0.508±0.07* Control: 0.235±0.07	*Andrena* sp.	12.3
			D. norvegicoides	4.9
			B. beaticola (queen)	3.9
			B. beaticola (worker)	0.4
			P. norvegicus (queen)	0.3
2200 m June 22 (5:00–16:00)	fine/cloudy 10.6 (3.5–15.5) 88 (71–97)	Continuous Bagged: 0.605±0.07* Control: 0.329±0.07	*B. beaticola* (queen)	3.8
			D. norvegicoides	2.6
			Andrena sp.	0.5
			B. beaticola (worker)	0.3
			B. consobrinus (queen)	0.3
Vaccinium ovalifolium 2650 m July 10 (5:00–18:00)	foggy/cloudy 11.9 (9.8–14.5) 92 (79–99)	Continuous Bagged: 1.62±0.34 Control: 1.51±0.24	*B. beaticola* (queen)	0.3
2650 m July 15 (5:00–18:00)	fine 12.4 (5.1–15) 40.5 (22–79)	Morning* Bagged: 0.286±0.11 Control: 0.398±0.06	*B. beaticola* (worker)	0.3
Phyllodoce aleutica 2620 m Aug. 12 (5:00–18:00)	cloudy/fine 12.1 (8.9–14.2) 90.6 (79–99)	Continuous* Bagged: 0.439±0.02* Control: 0.130±0.02	*B. beaticola* (worker)	15.3

[a] *, diurnal variation in the amount of nectar secretion of bagged flowers was significant ($P<0.05$ by KRUSKAL–WALLIS test).

[b] *, the amout of sugar in control (open) flowers was significantly smaller than that in bagged flowers (treatment effect $P<0.05$ by two-way ANOVA for treatment and time).

the alpine zone. This species is probably parasitic to *B. beaticola* (Ito, 1991). The phenology of *B. beaticola* indicated that the foundress queens were very few and reproductive castes were seldom produced in the alpine zone. In the subalpine zone, the overwintered queens and new males were abundant, and the subalpine forest was probably the main nesting place for *B. beaticola.*

The nests of *B. beaticola* in the present study and in a previous report from 2300 m a.s.l. of Mts. Akaishi (SAKAGAMI & KATAYAMA, 1977) had collapsed before producing reproductive castes. These nests were located in relatively exposed sites, easily accessible by humans. These observations also indicate that reproductive success was low at high altitudes. A mortality factor for the nests may be heavy rain penetrating into the nest. In addition, unstable weather conditions will limit the foraging activity and hinder the development of bumblebee colonies.

Individual bumblebee workers maintain rather fixed routes and areas of foraging (HEINRICH, 1976). However, they may change foraging areas according to the flowering or weather conditions at different places. Our marking experiments showed that the same workers foraged in both the alpine and subalpine zones, and that some workers at the alpine feeding site had long estimated distances from the nest. These facts suggested that some workers came from the subalpine colonies to the alpine meadow. Thus, foraging workers in the alpine zone probably included those from both subalpine and alpine nests.

There was a consistent difference in mean worker size of *B. beaticola* between subalpine and alpine sites. The longevity of bumblebee workers is around two weeks (HEINRICH, 1979; RODD *et al.*, 1980), and multiple broods of workers are usually produced in a colony. Although some bumblebee species produce larger workers later in the season (INOUE & KATO 1992), such a seasonal trend was not found in *B. beaticola.* The altitudinal difference in the worker size in summer can be explained by the following two hypothetical origins of large workers. Firstly, the large workers might be produced in the alpine nests because of their higher efficiency in thermo-regulation (HEINRICH, 1979; RICHARDS, 1973). However, production of large workers in the first brood is costly and will limit the number of workers. In the second, though not mutually exclusive hypothesis, the large workers in the alpine zone might come from the subalpine colonies. The mean worker size in the subalpine zone never exceeded that in the alpine zone after flowering started and workers began to appear in the alpine zone. Thus, larger workers in the subalpine colonies, better suited for long-distance flight, might forage often in the alpine zone, whereas smaller workers might remain in the vicinity of the subalpine nests.

Although some nest-seeking queens of *B. beaticola* remaining in July may colonize the alpine zones where some Ericaceae flowers began to bloom, such

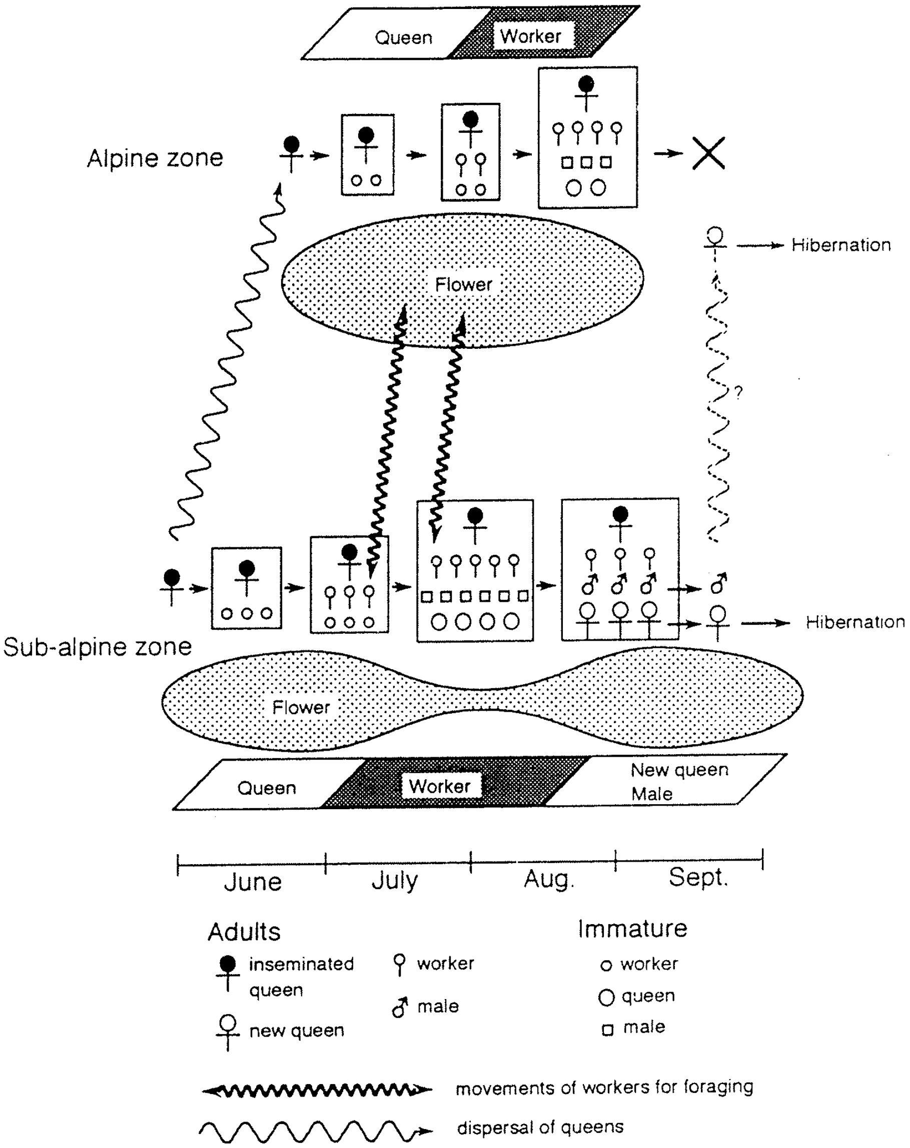

Fig. 8. The life history of *Bombus beaticola* in the subalpine and alpine zones of Mt. Norikura.

behavior will not spread in the population because of low reproductive success in the alpine zone. Nevertheless, the alpine flowers in summer are an attractive resource to bumblebees because flora in the subalpine forest is poor (SHIMIZU, 1990) and flower resources are relatively scarce during mid summer in the subalpine zone.

We hypothesize the life-history strategy of *B. beaticola* as follows (Fig. 8). Because of the longer flowering season and availability of nest sites covered with vegetation in the subalpine zone, most queens colonize there and use flowers in the spring to produce workers. The workers have alternative foraging sites in the alpine zones in summer when the colony development is maximized but the flower resources in the subalpine zone is scarce. The use of alpine flowers is costly in terms of consumption of time and energy for round trips between the nest and alpine site, but may offer the advantage of a relative absence of competitors.

Partnership between bumblebees and flowers in the alpine zone

When multiple bumblebee species occur in an area, they often use different flower species (PLEASANTS, 1980; RANTA *et al.*, 1981a; PYKE, 1982; KATO *et al.*, 1993), though some studies recognized no clear pattern of resource partitioning (BAUER, 1983; OBESO, 1992). The correlation between flower morphology and bumblebee morphology involves resource partitioning (PYKE, 1982; INOUE & KATO, 1992). There is a segregation of flowering period among flower species which share bumblebee species (PLEASANTS, 1980; RANTA *et al.*, 1981b). Thus, the flowering phenology and preference for flowers by bumblebees are influenced both by competition for pollinators among flower species and by competition for flower resources among bumblebee species.

In the alpine zones of central Japan, competition for flower resources among bumblebee species is probably weak or absent because only a few species occur. Although *B. hypocrita* temporally occurred with the dominant *B. beaticola*, there was no clear partitioning of flower species between them. The foraging activity by these bumblebees is limited by the harsh climatic conditions. Reduced interspecific competition among bumblebees in alpine and subarctic habitats has also been suggested by RANTA *et al.* (1981a) and BAUER (1983). On the one hand, flower species may compete for bumblebees (RANTA *et al.*, 1981b). In addition, the paucity of anthophilous insects in the alpine zone may promote the selection for self-fertilization. Some alpine flowers visted by bumbebees have the potentials of self-fertilization (YUMOTO, 1986; Kudo, 1993). In the present study, the bumblebee flowers confined to the alpine zone, *Rhododendoron aureum* and *Phyllodoce aleutica*, were self-compatible. But *Vaccinum ovalifolium* which was distributed in both subalpine and alpine zones was self-incompatible. Despite the possibility of self-fertilization, however, the study plants in the alpine zone depended on pollination by bumblebees for fruit set. Thus, in nine alpine flowers studied, fruit sets were generally reduced when pollinators were excluded. The pollinator dependence in self-compatible flowers will be maintained by the spatial segregation of the stigma and anthers within a flower (herkogamy), dichogamy, etc.

The pollinator limitation in fruiting success significantly occurred in plants flowering early and late in the season when bumblebees were few. This implies that a stabilizing selection acts on the alpine bumblebee flowers for blooming in the middle of the season when the worker density is high. However, the flowering phenology is much constrained by growth form and the time required for preflowering and fruit ripening in the alpine zone which has a short season (KUDO, 1991). For example, shrubs need a long time for fruit-maturation and tend to bloom early in the season. In *Rhododendoron aureum*, later flowering increases the chance of cross-pollination but reduces the chance of seed maturation in habitats where snowmelt is delayed (KUDO, 1993). Thus, different selection pressures on flowering phenology may act in opposite directions. An additional factor for the flowering phenology might be interspecific competition for pollinators (RANTA *et al.*, 1981b). Staggering pattern of flowering among bumblebee flowers in the alpine zone was common at Mt. Norikura and Mt. Kisokomagatake (YUMOTO, 1986). This segregation in flowering time will reduce competition for pollinators among flowers. Thus, it is supposed that there are three selection pressures on flowering phenology: *i.e.*, stabilizing selection for synchronization to the unimodal abundance of bumblebee workers; directional selection for early flowering to ensure seed maturation; and diversifying selection for competitive pollinator partitioning.

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