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Relative abundance, phenology and flower preference of andrenid bees at Hakodateyama, Northern Japan (Hymenoptera, Apoidea) [1][2]

By

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(*With 8 Text-figures and 6 Tables*)

In the previous paper, one of us (T.M.) published some information about relative abundance, phenology and flower preference of andrenid bees in Sapporo, based upon the quantitative periodical sampling (Sakagami and Matsumura, 1967). Following this work, the present paper deals with the biocoenotic structure of andrenid assemblage sampled in 1960∼'62 at Hakodateyama, a small isolated hill within the city of Hakodate.

Before going further, we wish to express our sincere thanks to Prof. M. Yamada and Dr. S. F. Sakagami, Zoological Institute, Hokkaido University, for their kind guidance to the present study. We are also indebted to Dr. Y. Hirashima, Entomological Laboratory, Kyushu University, for his kindness in identifying certain species.

Area studied

Hakodate is the largest city in Southern Hokkaido, located approximately at the middle of the southernmost coastal arc of the Oshima Peninsula, the biota of which is considerably different from that in Central Hokkaido, bearing a tranditional tone to that in Northern Honshu. Hakodateyama (Fig. 1) is a small hill standing at the end of the cape within the city, 335 m high, and, at the foot, longer in SN direction (3.5 km) than in EW (1∼2 km). The narrow neck connecting the hill to the mainland forms now one of the centers of the city, so that the biota of the hill is now strongly isolated. The local flora was precisely surveyed by Sugahara and Komatsu (1958).

The primary vegetation does not essentially differ from that in the submontaneous areas of the southern part of the Oshima Peninsula, that is, represented by the temperate deciduous broad leaf forest with beech, *Fagus crenata* and oaks, *Quercus crispula* and *Q. dentata*, as dominants. The primary vegetation is

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[1] Contribution No. 860 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan, 060

[2] Wild bee biocoenotics in Hokkaido, II

partly still preserved but mostly replaced either by the monoculture of the Japanese cedar, *Cryptomeria japonica*, or by secondary fields.

The sampling was made at the secondary field on the eastern slope, with the extent of about 1.6×0.6 km sq., and ranging 50 to 250 m in altitude. This area is, though facing to the urban districts, quite favorable for bees, protected from cold northenwest wind and provided with various kinds of flowering plants throughout the season. The cedar culture standing nearby also possesses a number of flowering plants as undergrowth, serving as auxillary food sources.

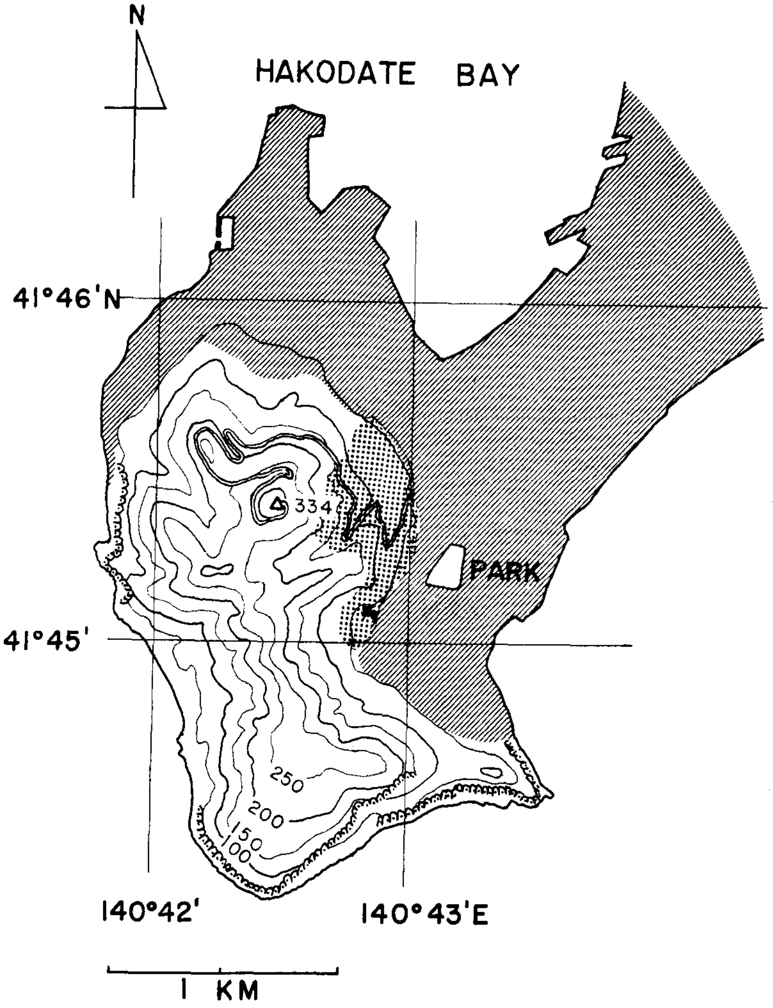

Fig. 1. Topography of Hakodateyama, showing the survey area by dotts and the urban areas by hatching.

The climate of Hakodate is Dfb (Köppen) or A”$_3$ (Kira). Winter is considerably cold but apparently milder than in Central Hokkaido with less snow and with humidity relatively high throughout the year. Some meteorological data are cited from the records taken in 1960 by Hakodate Meteorological Observatory: Annual mean air temperature 8.3°C, annual rainfall 997.6 mm, annual mean moisture 79%, and annual mean rate of fine days 45%. The monthly mean temperature was lowest in January (-5.5°C) and highest in August (22.2°C). Rainfall was relatively abundant throughout the year 1960, with the minimum in February (34.4 mm) and the maximum in September (175.1 mm).

When the area was inspected on April 5, 1960, before the starting sampling, snow patches still remained here and there on the shady grounds.

Sampling procedure

The sampling procedure is the same that given in Sakagami, Laroca and

Table 1. Individual numbers of andrenid

Species (shown with subgeneric names)	Number		
	1960		
	♀	♂	♀ + ♂
1 Micrandrena komachi Hirashima	181	18	199
2 Gymnandrena watasei Cockerell	57	28	85
3 Taeniandrena ezoensis Hirashima	27	23	50
4 Calomelissa mitakensis Hirashima	45	4	49
5 Andrena nawai Cockerell	9	17	26
6 Micrandrena kaguya Hirashima	18	6	24
7 Euandrena stellaria Hirashima[1]	23	0	23
8 Micrandrena hikosana Hirashima	18	4	22
9 Hoplandrena dentata Smith	17	3	20
10 Simandrena opacifovea Hirashima	3	12	15
11 Stenomelissa halictoides Smith	6	1	7
12 Micrandrena brassicae Hirashima	4	0	4
13 Euandrena takachihoi Hirashima[2]	1	1	2
14 Micrandrena sp. 1	0	2	2
15 Andrena brevihirtiscopa Hirashima	1	0	1
16 Andrena sp. 1	1	0	1
17 Andrena hondoica Hirashima	0	0	0
18 Holandrena valeriana Hirashima	0	0	0
19 Habromelissa omogensis Hirashima	0	0	0
20 Micrandrena sp. 2	0	0	0
21 Micrandrena sp. 3	0	0	0
22 Notandrena nitidiuscula Schenck	0	0	0
23 Andrena sp. 2	0	0	0
Total	441	119	530

1) Erroneously identified as *Euandrena hebes* Perez in the previous paper

2) Recorded as *Euandrena* sp. 1 in the previous paper.

Moure (1967), and Sakagami and Matsumura (1967). The regular sampling of wild bees was made by one of us (M.M.) from April to October, 1960, four hours per week. Additional sampling was occasionally undertaken both in 1961 and 1962 with irregular interval.

Actual sampling dates in 1960 are as follows:
April 12, 19, 26; May 3, 10, 17, 24; May 31+June 2, June 5+7, 15, 21, 28; July 5, 12, 18+19, 26; August 2+3, 9+10, 17, 23, 31; September 6, 13, 20, 28; October 4, 11, 18, 26.

These dates are henceforth abbreviated IV-1 (=first sampling in April), IV-2, etc. In VI-1, VI-2, VII-3 and VIII-1, four hour sampling was made on two days, not within one and the same day, owing to adverse weather conditions, and in VIII-2 a total sampling covered 6.5 hours on two days.

Among the results obtained, only andrenid bees are reported here as in the previous paper (Sakagami and Matsumura, '67).

bees sampled in Hakodateyama, 1960–1962

of individuals captured						
		1960+ '61+ '62				
%	♂/♀	♀	♂	♀+♂	%	♂/♀
37.6	0.10	227	30	257	34.3	0.13
16.0	0.49	78	39	117	15.6	0.50
9.4	0.85	44	28	72	9.6	0.64
9.2	0.09	87	5	92	12.3	0.06
4.9	1.89	9	17	26	3.4	1.89
4.5	0.33	20	11	31	4.1	0.55
4.3	0/23	25	1	26	3.5	0.04
4.2	0.22	23	6	29	3.9	0.26
3.8	0.18	21	5	26	3.5	0.24
2.8	4.00	12	14	26	3.5	1.17
1.3	0.17	6	13	19	2.5	2.17
0.8	0/4	6	0	6	0.8	0/6
0.4	1.00	4	2	6	0.8	0.50
0.4	2/0	0	3	3	0.4	3/0
0.2	0/1	2	0	2	0.3	0/2
0.2	0/1	1	0	1	0.1	0/1
0	—	2	2	4	0.5	1.00
0	—	3	0	3	0.4	0/3
0	—	2	0	2	0.3	0/2
0	—	0	1	1	0.1	1/0
0	—	0	1	1	0.1	1/0
0	—	0	1	1	0.1	1/0
0	—	0	1	1	0.1	1/0
	0.27	572	180	752		0.31

(Sakagami & Matsumura, 1967).

Results

1. *Relative abundance*: The individual numbers of all species collected are given in Table 1, the result for 1960 alone and for 1960∼'62 combined separately. The species are given with subgeneric names (henceforth cited by specific names alone) arranged in the descending order of the relative abundance in 1960 (both sexes combined). In total 530 specimens belonging to 16 species were obtained by the regular sampling in 1960. The additional samplings in 1961∼'62 brought in further 222 specimens belonging to 21 species. These later samples do not involve two species (*nawai* and *Andrena* sp. 1) obtained in 1960, while contain seven additional species not collected in 1960. The total species and individual numbers from the samplings 1960∼'62 are 23 and 752 respectively. The data were converted to the percentage ratios in Figure 2, applying the occurrence probability method as in the previous paper. The abundance of *komachi* is remarkable, occupying more than one third. Four species, *komachi*, *watasei*, *ezoensis* and *mitakensis*, are apparently dominant in the area studied, occupying 70% of the total individual number. Six species, *nawai*, *kaguya*, *stellaria*, *hikosana*, *dentata* and *opacifovea*, are relatively abundant species and the other 14 species are rather rare.

2. *Phenology*: Table 2 shows the dates of first and last observations of andrenid flight activities in three successive years, together with the duration of the flight season. The seasonal shift of climatic conditions, as well as that of total species and individual number of bees sampled are given in Fig. 3, and phenology and abundance of each species in 1960, both sexes separately, in Fig. 4.

The flight season of adult andrenid bees in the area seems to be relatively stable, covering about 170 days from middle April to late September or early October. This approximately corresponds to the wild bee season in the area surveyed, although the first appearance of andrenid bees is in average earlier than in other bees, and some bumblebees and halictine bees are seen until late October. Some drops in the seasonal fluctuation of individual number are probably affected by the adverse weather conditions for flight activity as indicated by arrows in Fig. 3, for instance, inhibition by low temperature in V–2, by interaction of low temperature and cloudy weather in VII–2, and by heavy rainfall in the day before sampling in VI–5. The most remarkable instance is observed, however, in VI–1. In this case, the soil temperature at 10 cm under surface dropped from 16.0°C to 10.6°C by the combined influence of low temperature and lasting rains for several days. During this period, flight activities of all wild bees ceased completely. On the other hand, the decreased activity in the first half of August is apparently characteristic to the andrenid assemblage in the area surveyed, on account of its constant appearance throughout three successive years, not accompanied by any adverse weather conditions.

In all abundant species, males appear and disappear ealrier than females, showing the protandry common to most solitary bees. The active period of females lasts for most abundant species one to two months, though very short in *nawai* and *halictoides*. *Dentata* and *kaguya* have exceptionally prolonged active period, 3.5 months in the former and three months in the latter. In both species, some fresh males were captured in the later half of the active period of females, with a delay of 1 to 1.5 months after the disappearance of earlier males. Moreover, fresh females were captured in this later period together with quite worn ones. These facts suggest the probable digoneutric life cycle in these two species.

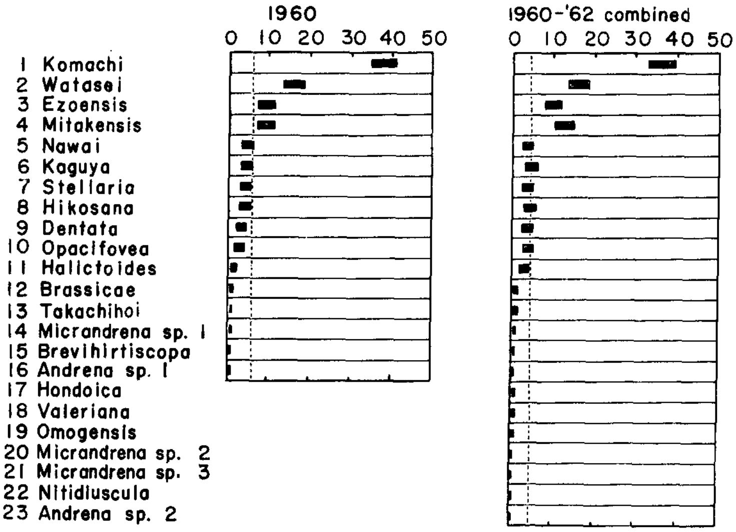

Fig. 2. Assemblage structure of andrenid bees in 1960 and 1960~'62 combined, by occurrence probability method. Ends of each bar show upper and lower limits of statistical confidence and vertical broken line the reciprocal of the number of species captured. The dominant species is defined as those, of which lower confidence limit exceeds the vertical broken line.

As far as the result in 1960 is concerned, the active season of adult andrenid bees begins by male flight of *nawai* and the first generation of *dentata* in middle April, followed by the gradual increase of the numbers of both species and individuals to early May, during which several species, *komachi*, *stellaria*, *kaguya* (first generation), *hikosana*, *watasei*, etc., appear successively. The peak of the flight activities is attained during May to June represented by the maximum numbers of both species and individuals. In May, however, the number of individuals is relatively richer than that of species, mainly caused by the outburst of *komachi*.

Table 2. Start and end of flight activities and duration of flight season in each year.

Year	Start of activities	End of activities	Duration of flight season
1960	April 12	September 28	169 days
1961	〃 21	〃 29	162 〃
1962	〃 17	October 9	176 〃

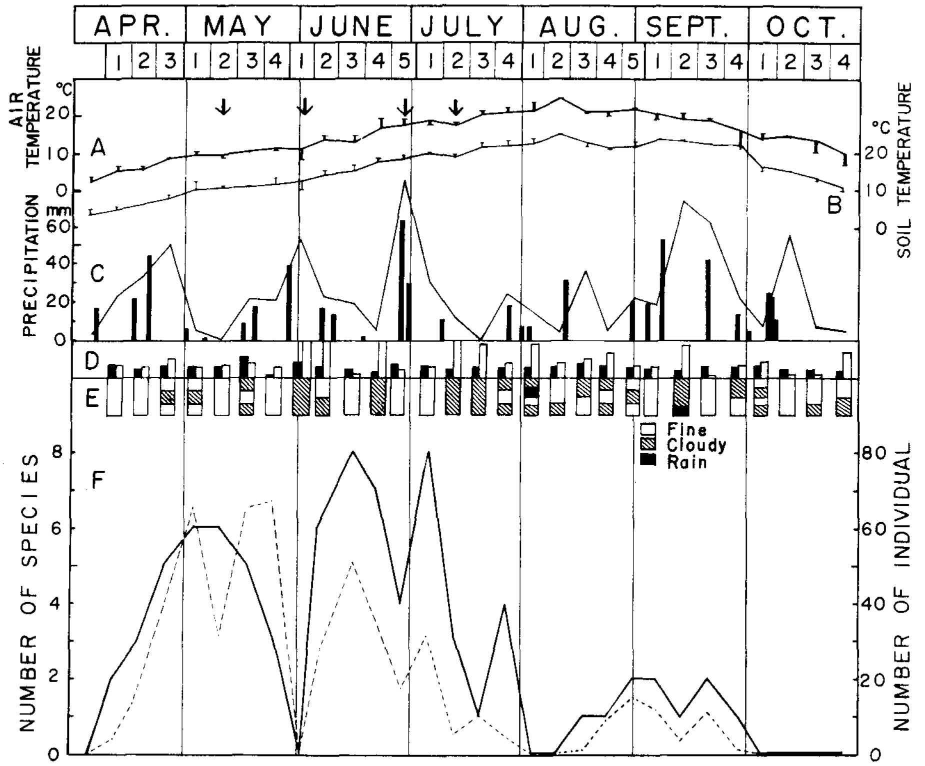

Fig. 3. Climatic conditions and phenology of species and individuals in 1960. A. Mean air temperature in each 7 day period (from the next day of the previous sampling to the sampling day). B. Mean soil temperature at 10 cm under surface in each period. Vertical bars on A and B show deviations of temperature on each sampling day from corresponding mean temperatures in each period. C. Total rainfall in each period and that of heavily rainy day during each period (black bar-histogram). A, B and C from records by Meteorological Observatory. D. Mean wind class (black) and mean cloud amount (white) during sampling. E. General weather condition during sampling. F. Numbers of species (thick solid line) and individuals (thin broken line) in each period.

In June the individual number decreases but the species number attains the peak due to the appearance of additional species. The activities gradually drop in July and practically stop in the first half of August as observed in three successive years. This quiescence is broken in middle August by the appearance of *mitakensis*, which practically monopolizes the andrenid activities in autumn until end of the season in early October. From this seasonal trend, the andrenid species at the area can be divided into the three following groups by their active period:

Spring group: *nawai*, *dentata* and *kaguya* (first generation), *komachi*, *stellaria*, *hikosana*, *watasei*, *brevihirtiscopa*, *brassicae*, *hondoica*, *Andrena* sp. 2, *Micrandrena* sp. 2, *Micrandrena* sp. 3

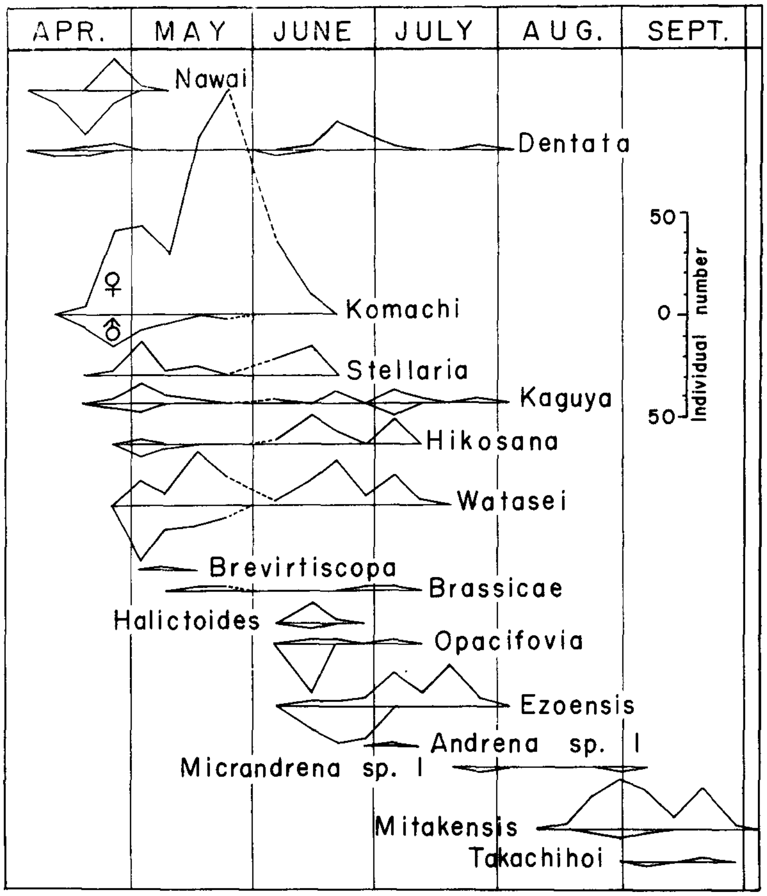

Fig. 4. Phenology of each species shown by individual number captured in both females (upper) and males (below), in 1960.

Summer group: *halictoides*, *opacifovea*, *ezoensis*, *Andrena* sp. 1, *dentata* and *kaguya* (second generation), *valeriana*, *Micrandrena* sp. 1
Autumn group: *mitakensis*, *takachihoi*, *omogensis*, *nitidiuscula*

Correspondingly, the andrenid season in the area has two distinct phases, the spring-summer phase consisted of activities of spring and summer species rich both in species and individuals, and the autumn phase characterized by the virtual monopoly by *mitakensis*.

3. *Flower preference*: The flower preference and its phenology in the area surveyed described briefly based upon 748 specimens captured on 54 flower

Table 3. Fower preference in relatively abundant andrenid species.

Andrenid species		Number of individuals collected	Number of entomophilous species in bloom during flight period (1960)	Number of flower species and genera visited	Flower species visited / Flower species in bloom (Rf)	Index of flower visits		
						λ_s	λ_f	λ_f/λ_s
mitakensis	♀	86	124	24/10	19.3%	0.071	0.348	4.90
	♂	*5*	*105*	*4/ 3*	*3.8*	*0.100*	*0.300*	*3.00*
opacifovea	♀	12	33	4/ 3	12.1	0.546	0.682	1.25
	♂	*14*	*36*	*4/ 4*	*11.1*	*0.308*	*0.308*	*1.00*
hikosana	♀	23	91	10/ 5	11.0	0.146	0.293	2.01
	♂	*6*	*28*	*1/ 1*	*3.6*	*1.000*	*1.000*	*1.00*
watasei	♀	78	128	13/ 6	10.2	0.188	0.254	2.15
	♂	*39*	*51*	*3/ 3*	*5.9*	*0.899*	*0.899*	*1.00*
dentata	♀	20	111	9/ 7	8.1	0.168	0.200	1.19
	♂	*5*	*60*	*3/ 3*	*5.0*	*0.200*	*0.200*	*1.00*
stellaria	♀	25	74	6/ 5	8.1	0.153	0.183	1.20
	♂	—	—	—	—	—	—	—
komachi	♀	225	78	6/ 3	7.7	0.459	0.517	1.13
	♂	*31*	*56*	*3/ 3*	*5.4*	*0.626*	*0.626*	*1.00*
kaguya	♀	19	136	8/ 7	5.9	0.193	0.216	1.12
	♂	*10*	*45*	*4/ 4*	*8.9*	*0.178*	*0.178*	*1.00*
nawai	♀	9	25	1/ 1	4.0	1.000	1.000	1.00
	♀	*17*	*20*	*2/ 1*	*10.0*	*0.767*	*1.000*	*1.30*
ezoensis	♀	44	126	4/ 3	3.2	0.596	0.901	1.51
	♂	*28*	*65*	*2/ 2*	*3.1*	*0.929*	*0.929*	*1.00*
halictoides	♀	6	51	1/ 1	2.0	1.000	1.000	1.00
	♂	*13*	*33*	*2/ 1*	*6.1*	*0.718*	*1.000*	*1.39*
Total	♀	567	252	50/21	19.8	0.131	0.227	1.73
(less abundant species included)	♂	*181*		*26/13*	*10.3*	*0.151*	*0.245*	*1.62*
	♀ + ♂	748		54/21	21.4			

species belonging to 21 families, following the system developed in the previous paper.

3.1. *Relative flower preference of each andrenid species*: Table 3 shows several items basic to the flower preference in each of 11 relatively abundant andrenid species.

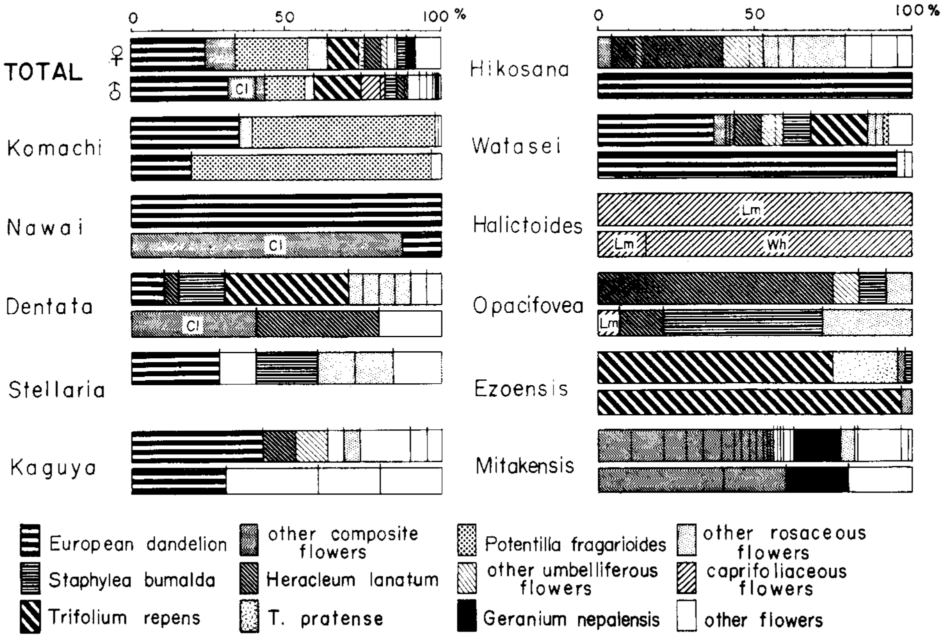

Fig. 5. Flower preference by percentage ratio in certain relatively abundant andrenid species. Females and males separately given by thick and thin bar. Vertical thick lines pretruding above divide families. Cl; coltsfoot. Lc; *Lonicera morrowii*. Wh; *Weigela hortensis*.

Two indices expressing the degree of flower preference at species and family levels, λ_s and λ_f, were used by using Simpson's measure of diversity (Simpson 1949, *cf*. Morisita 1959).

$$\lambda = \frac{\sum_{i=1}^{\infty} n_i (n_i - 1)}{N(N-1)} \qquad 0 \leqq \lambda \leqq 1$$

where N is the total number of andrenid specimens sampled on all flowers and n_i the individual number of specimens captured on flower species i. λ_s gives a measure of poly- and stenotrophy, approaching to 0.0 when the concerned species visits various flowers without any choice, whereas to 1.0 when it shows a strong preference for a single flower species. λ_f gives a similar measure at family level of entomophilous plants.

The higher value of λ_f/λ_s indicates that the concerned species shows a strong preference at family level than at species level, that is, tends to confine their visits to particular families but to visit several flower species indiscriminably within these families.

Some particularities in flower preference of certain abundant andrenid species in the area is given in Table 3, where the species are arranged in the ascending order of stenotrophy, and Fig. 5, which shows the preference in each species by percentage ratios. By a glance at these data, two extremes are soon recognized. One is represented by *mitakensis*, with highest *Rf* and lowest λ_S, indicating its eurytrophic tendency. But the higher ratio of λ_f/λ_S suggests that its preference at family level, especially to Compositae as shown in Figure 5, though this fact partly caused by the predominance of composite flowers in its active period. The other extreme is given by *ezoensis* and *halictoides*, with $\lambda_f=1.0$, showing a distinct stenotrophy to Leguminosae and Caprifoliaceae, respectively, as already mentioned in the previous paper. The preference in *nawai* is also quite high. But this earliest species start the activity when only a limited number of flower species are in bloom, so that, it is still open to the question whether or not the stenotrophy obtained from Table 3 and Figure 5 can be regarded as equivalent to that in *ezoensis* and *halictoides*.

The other species shows the preference intermediate between the two extremes mentioned. Figure 5 shows some marked difference in preference between sexes, such as in *nawai*, *dentata*, *hikosana*, *watasei*, and *opacifovea*. This partly depends on the deviation of active period between sexes (*nawai* and *watasei*, *cf.* Fig. 7), and partly on the absence of pollen foraging in males.

3.2. *Phenology of flower species visited*: Figure 6 shows the monthly phenology of flower-visits by andrenid species in 1960.

The change of predominantly visited flower species from month to month is summarized as follows:

April: Number of species of visited flowers is still low. Most visits are confined to European dandelion (*Taraxacum officinale*), and *Potentilla fragarioides*.

May: The individual number of andrenids attains the peak (=229) owing to the outburst of *komachi*. European dandelion and *P. fragarioides* occupy 89% of all flower visits.

June: Both species and individual numbers of andrenids are relatively high and the number of visited flower species the highest, (=13). White clover (*Trifolium repens*), *Heracleum lanatum* and rosaceous flowers, including *P. fragarioides* are the predominantly visited flower species.

July: The individual number of andrenid bees decreases, but number of visited flower species is still high, (=11). Legumes with white and red clovers, *Astilbe congesta*, and *Angelica edulis* are most important.

August & September: The number of flower species is still rich (12 and 11 respectively), but the andrenids remarkably decrease both in species and individuals with a virtual monopoly by *mitakensis*, which shows, as already mentioned, a high eurytrophy. Compositae occupy the majority (48%, 6 spp. in each month), followed by *Geranium nepalensis* and *Achyranthes japonicus*.

The succession of the predominantly visited flower species is given based upon the results of weekly sampling in 1960, as follows:

Coltsfoot	middle April
European dandelion	Late April — late May
Potentilla fragarioides	Late April — early June
Staphylea bumalda	Early June — middle June
White clover	Middle June — late July
Autumn Compositae	August — September

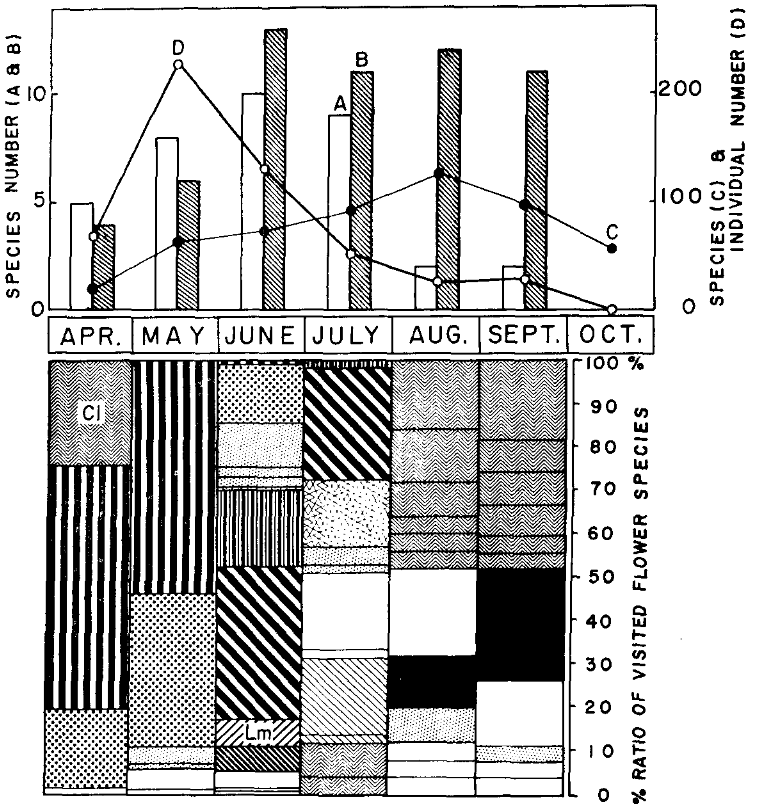

Fig. 6. Phenology of flower visits by andrenid bees. A. Species number of andrenid bees. B. Species number of visited flowers. C. Species number of flowering entomophilous plants. D. Individual number of andrenid bees. Below: Percentage ratio of visited flower species in each month. Various patterns showing flower species are explained in Figs. 5 or 7.

Figure 7 shows the change of flower visits in five relatively abundant andrenid species during their flight period, given by percentage ratio. The seccession of flower visits is distinct in the following three species, in partly depending on the succession of flower blooming.

Nawai:	Coltsfoot ———→ European dandelion
Komachi:	European dandelion ———→ *Potentilla fragarioides*
Watasei:	European dandelion ———→ *Staphylea bumalda* ———→ white clover ———→ composite flowers.

On the other hand, such succession is not seen in *ezoensis* and *mitakensis*, the former continuously attaching to legumes, while the latter, visiting a variety of flowers, especially of Compositae.

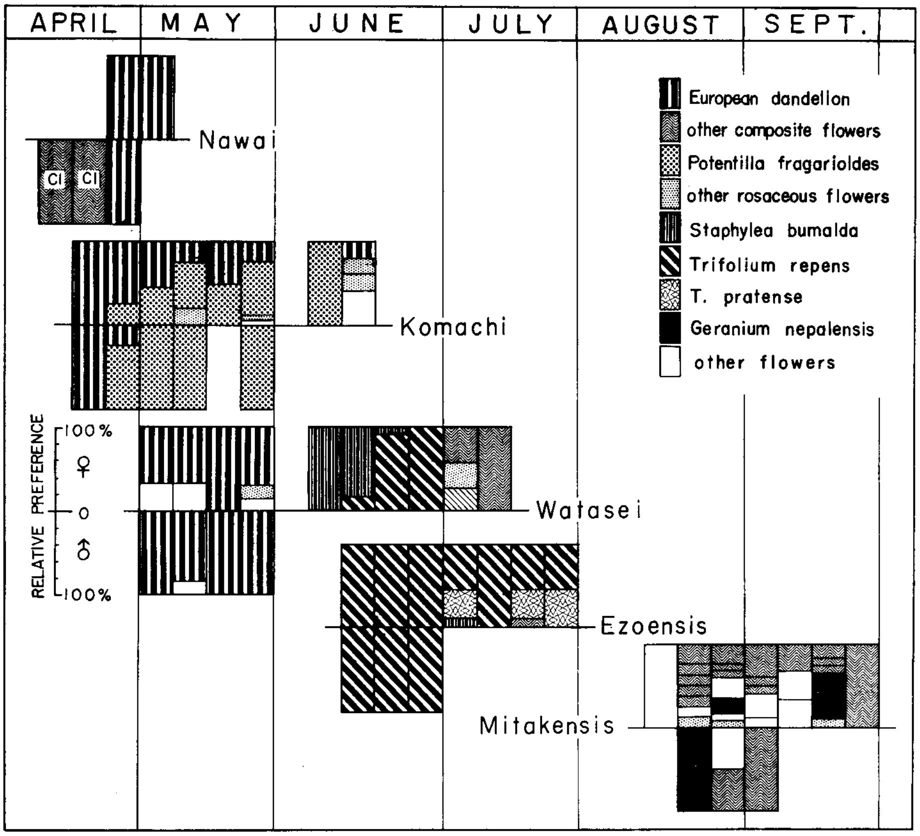

Fig. 7. Phenology of flower visits in five relatively abundant species. Females (above) and males (below) separately given. Cl; coltsfoot.

The flower calendar of the predominant flowering plant species in the area is given as follows:

	Degree of flower visits	Period in bloom
Coltsfoot	+	IV-1——IV-3
Corydalis ambigua	−	IV-1——V-3
Anemone albiflora	−	IV-1——VII-4
European dandelion	⧺	IV-1——X-4
Potentilla fragarioides	⧺	IV-1——VI-2
Stellaria media	+	IV-1——VIII-4
Anemone flaccida	−	IV-2——V-4
Potentilla centigrana	+	IV-3——IX-3
Heracleum lanatum	+	V-3——VI-4
Staphylea bumalda	+	V-3——VI-4
Micromeles alnifolia	+	V-5——VII-1
White clover	⧺	V-5——X-4
Red clover	+	VI-1——X-4
Erigeron annuus	+	VI-3——X-4
Geranium nepalensis	+	VI-4——X-3
Aster ageratoides	±	VII-3——X-4
Reynoutria sachalinensis	−	VIII-1——IX-2
Achyranthes japonica	+	VIII-2——X-1
Aster glehni	−	VIII-2——X-4

Among these species, *Corydalis ambigua*, *Anemone albiflora*, *A. flaccida*, *Reynoutria sachalinensis* and *Aster glehni* are ignored by andrenid bees. This avoidance indicates a negative preference, because the flower of these plants are abundant throughout the area during their blooming periods, which coincide with the flight periods of certain andrenid bees, and they are actually visited by some nonandrenid bees.

3.3. *Flower species and families frequently visited*: Table 4 gives the list of the flower species especially preferred by andrenid bees in the sruvey in 1960, arranged in the descending order of the number of visiting individuals. The first three species, European dandelion, *Potentilla fragarioides* and white clover, absorbed 58% of total visits. Among 54 flower species visited by andrenids, only five (European dandelion, white and red clovers, *Erigeron annuus* and *Aster scaber*), or 9% are exotic. But the visits to these plants reach 40% of total visits, suggesting their importance as food sources.

The flower preference of andrenid bees at family level is shown in Table 5. Compositae, Rosaceae, Leguminosae and Umbelliferae are the most frequently visited families in the area, on which 82% of total andrenid individuals were captured. Compositae and Rosaceae are of special importance in comparison with other families both in flower species and frequency of andrenid visits, absorbing 63% of total visits.

However, the importance of the flower families expressed by the numbers of visiting andrenid individuals in most cases depends on a single flower species

Table 4. Flower species predominantly visited by andrenid bees

Flower species (family)	Number of andrenid individuals visiting				Number of andrenid species visiting			Ratio of individual number of females with pollen load
	♀	♂	♀+♂	%	♀	♂	♀+♂	
Taraxacum officinale (Compositae)*	137	57	194	25.9	8	7	11	48.2
Potentilla fragarioides (Rosaceae)	133	24	157	21.0	3	1	3	84.9
White clover, *Trifolium repens* (Leguminosae)*	58	27	85	11.3	4	1	1	69.6
Heracleum lanatum (Umbelliferae)	28	4	32	4.3	6	2	6	72.2
Staphylea bumalda (Staphyleaceae)	17	7	24	3.2	5	1	5	6.7
Stellaria media (Caryophyllaceae)	15	3	18	2.4	5	2	6	7.7
Geranium nepalensis (Geraniaceae)	16	1	17	2.3	2	1	2	20.0
Coltsfoot, *Petasites japonicus* (Compositae)	0	16	16	2.1	0	2	2	—
Micromeles alnifolia (Rosaceae)	11	4	15	2.0	6	1	6	40.0
Potentilla centigrana (Rosaceae)	15	0	15	2.0	5	0	5	80.0
Achyranthes japonica (Amaranthaceae)	12	2	14	1.9	1	2	2	42.9

* exotic species.

particularly preferred, such as dandelion (occupying 72% of Compositae), *Potentilla fragarioides* (79% of Rosaceae), white clover (90% of Leguminosae), and *Heracleum lanatum* (70% of Umbelliferae).

3.4. *Flower species visited for pollen*: The flower visits of andrenid bees are classified into two types: Visits for self-maintenance and for brood rearing by females. Both nectar and pollen are foraged in the latter case, but the nectar intake is not easily proven externally. On the other hand, the presence of pollen loads on female legs is easily recognized, serving as an indication of their brood rearing activity. Among 54 flower species visited by andrenids, the pollen laden females were captured on 32 species or 59%, occupying 40% of females number captured. The analysis of pollen foraging is rather more important than that of flower visits in general, because of its intimate relation to brood rearing, pollination and preference range usually narrower than in flower visits for self-maintenance. In the present paper, however, only a few comments are given, leaving a detailed analysis elsewhere.

The number of flower species visited for pollen foraging to the total number of flower species visited by females in 11 relatively abundant andrenid species is

Table 5. Plant families preferred by andrenid bees

Plant family	No. of flower species observed	No.of flower species visited			No. of andrenid species visiting			No.of andrenid individuals visiting			Percentage of No. of individuals
		♀	♂	Total	♀	♂	Total	♀	♂	Total	
Compositae	43	14	6	15	11	11	14	192	79	271	36.3%
Rosaceae	22	8	3	9	10	3	11	171	29	200	26.8
Leguminosae	10	2	1	2	4	1	4	67	29	94	12.6
Umbelliferae	13	4	3	5	6	4	8	40	6	46	6.2
Staphyleaceae	1	1	1	1	5	1	5	17	7	24	3.2
Caryophyllaceae	7	2	2	2	5	3	7	19	4	23	3.1
Caprifoliaceae	6	1	2	2	1	2	2	6	14	20	2.7
Geraniaceae	2	1	1	1	2	1	2	16	1	17	2.3
Amaranthaceae	1	1	1	1	1	2	2	12	2	14	1.9
Saxifragaceae	6	2	1	2	4	2	5	7	4	11	1.5
Liliaceae	19	1	1	1	1	4	5	1	6	7	0.9
Labiatae	10	2	0	2	2	0	2	4	0	4	0.5
Polygonaceae	10	2	0	2	2	0	2	4	0	4	0.5
Balsaminaceae	2	2	0	2	1	0	1	3	0	3	0.4
Salicaceae	3	1	1	1	2	1	3	2	1	3	0.4
Areliaceae	2	1	1	1	1	1	2	1	1	2	0.3
Valerianaceae	2	1	0	1	1	0	1	1	0	1	0.13
Oenotheraceae	5	1	0	1	1	0	1	1	0	1	0.13
Anacardiaceae	2	1	0	1	1	0	1	1	0	1	0.13
Cruciferae	6	1	0	1	1	0	1	1	0	1	0.13
Ranunculaceae	11	1	0	1	1	0	1	1	0	1	0.13
Total	252	50	26	54	18	19	23	567	181	748	

shown as follows: *mitakensis* (12/24), *kaguya* (7/8), *watasei* (6/13), *komachi* (6/6), *hikosana* (5/10), *ezoensis* (4/4), *dentata* (3/9), *stellaria* (1/6), *opacifovea* (1/4), *halictoides* (1/1),and *nawai* (0/1). Except for *komachi* and *ezoensis* where the ratio is 1:1, the preference range in pollen foraging is narrower than that in flower visits in general, as already mentioned by Linsley (1958).

Among the flower species given in Table 4, two species of *Potentilla, P. fragarioides* and *P. centigrana*, are specially preferred for pollen foraging. Contrary to this, *Staphylea bumalda* and *Stellaria media* are visited nearly exclusively for nectar intake. Other species in the table are also frequently visited for pollen foraging, except for coltsfoot, the role of which as a pollen source is unknown because only males were collected upon it. Besides the following flowers are also more or less used as relatively important pollen sources: *Lonicera morrowii, Angelica edulis,* red clover (*Trifolium pratense*), *Astilbe thunbergii,* and *Cirsium heiianum.*

Concluding Remarks

The present study forms a part of comprehensive biocoenotic studies on the wild bee assemblages in Hokkaido, the purpose of which is manifold, serving as a basis for life history studies of particular bee species as well as for further biocoenotic analyses. Some general remarks on this approach are given in the previous paper (Sakagami and Matsumura, 1967, *cf.* also Sakagami, Laroca and Moure, 1967). The results described in preceding sections can fully be discussed only after the accumulation of comparative information in various localities in Hokkaido. Therefore, here the discussions are confined to the comparison of the results in the present study (HD) to those given previously as to the andrenid assemblage in Sapporo.

In order to compare the two assemblages, the index measuring the similarity between communities, proposed by Morisita based upon Simpson's measure of diversity was applied (*cf.* Morisita, 1959).

$$C_\lambda = \frac{2\sum_{i=1}^{\infty} n_{1i}\, n_{2i}}{(\lambda_1 + \lambda_2)\, N_1 N_2} \qquad 0 \leqq C_\lambda \leqq 1$$

$$\lambda_1 = \frac{\sum_{i=1}^{\infty} n_{1i}(n_{1i} - 1)}{N_1 (N_1 - 1)} \qquad \lambda_2 = \frac{\sum_{i=1}^{\infty} n_{2i}(n_{2i} - 1)}{N_2 (N_2 - 1)}$$

where N_1 or N_2 is the total number of individuals sampled in area I or II, and n_i or n_{2i} the individual number of species i sampled in area I or II.

The value of C_λ approaches to 0.0 when no or few common species exist between two communities, whereas to 1.0 when community structure is identical or nearly so between them.

In the previous study, the sampling was made at two small areas, the campus of Hokkaido University (UC) and University Botanical Garden (BG), located closely nearby but seemingly relatively well isolated as habitats for wild bees. In calculation, UC and BG were treated either separately or in combination. Further, the results published by Miyamoto on her wild bee survey made in Sasayama, Hyogo prefecture, Southern Honshu (SY), was also used for comparison.

Table 6 presents the value of C_λ obtained from the comparisons of assemblages mentioned above. The highest similarity is found between BG and UC, which is easily understood by their proximity. The similarity in HD–BG and HD–UC is distinctly lower, in part reflecting the faunal difference between Sapporo and Hakodate. However the similarity increases when HD is compared with BG+UC combined, reaching the degree comparable in BG–UC. This indicates that neither BG nor UC can be regarded as an unbiased representative of the andrenid assemblage in Sapporo and the vicinity. Probably the same is true for HD, which

Table 6. Similarity of andrenid assemblages among Hakodateyama, Sapporo and Sasayama

Area	No. of common spp. / No. of total spp.			C_λ		No. of andrenid species in each area
	Hakodateyama (HD)	Sapporo (BG+UC)	BG	UC	Sasayama (SY)	
Hakodateyama		0.316	0.139	0.158	0.079	23
Sapporo (BG+UC)	13/31		—	—	0.104	21
BG	12/30	—		0.376	—	19
UC	9/29	—	13/22		—	15
Sasayama	6/31	6/29	—	—		14

may represent the andrenid assemblage in and near Hakodate only partly. The similarity in SY–(BG+UC) is slightly lower than in HD–BG or HD–UC, but higher than in SY–HD. This does not show the closer relation of Sasayama to Sapporo than to Hakodate, because the numbers of species and individuals (BG+UC) is richer than in HD by the additive effect. Moreover, the value of C_λ between SY and the other assemblages is not directly comparable to those among HD, BG, and UC, because the procedure of survey in SY is different from that in HD, BG, and UC.

Comparing the faunal make up between Sapporo (BG+UC) and Hakodateyama qualitatively, 13 species are common to both areas. The species collected in Sapporo, but not in Hakodateyama, are *benefica*, *sublevigata*, *astragalina*, *haemorrhoa*, *takachihoi*, *sachalinensis* and *knuthi*, among which five species except for *sublevigata* and *astragalina* are collected in the Oshima Peninsula.

The opposite cases are *mitakensis*, *opacifovea*, *brevihirtiscopa*, *A.* sp. 1, *hondoica*, *omogensis*, *Micrandrena* sp. 2, *M.* sp. 3, *nitidiuscula* and *A.* sp. 2, among which *opacifovea* and *hondoica* are collected in and near Sapporo. Therefore, the most conspicuous difference is, for the time being, given only by the presence of *mitakensis*, and the absence of *sublevigata* and *astragalina* in Hakodate. It is still premature to give the precise comparison of these two areas, with respect to the andrenid assemblage. The final conclusion must be postponed until the quantitative faunal makeup in both areas is clarified by the accumulation of further information.

A few words are given concerning the purely faunalistic aspect. According to Hirashima (1962–'66), 63 species of *Andrena* have so far been recorded from Japan. The frequency distribution of species in main islands is as follows: Hokkaido (26), Honshu (48), Shikoku (16), Kyushu (35), Tsushima (2), Yakushima (2), Amami-Oshima (5). From our survey in various localities in Hokkaido, however, at least 17 accurately identified species are added to the fauna of Hokkaido, and there are more than five additional species not yet determined, resulting in the increase of the number of species from 26 to about 48, reaching the same level to that in Honshu. Among 23 species recorded from Hakodateyama, only 18 are the species recorded from Japan by Hirashima. These preliminary figures indicate the rich andrenid fauna in Hokkaido within Japan, and its clarification is of particular importance in the understanding of the origin and evolution of andrenid fauna in the Far East, or the zoogeographical position of Hokkaido as a zone intermediate between the Continent and Southern Japanese islands.

Turning to the phenology, the andrenid season in Hakodateyama continues for about 170 days, about one month longer than in Sapporo, reflecting the warmer climate as shown in Figs. 3 and 8. Another marked difference is the presence of a "summer dearth" lasting about half a month in Hakodateyama. In Sapporo, the the andrenid season is divided into two distinct but not sharply separated phases, spring phase with numerous species visiting various flowers and the rather monotonous summer phase represented by with two oligotrophic species, *ezoensis* and *valeriana*. The first half of August, the dearth period in Hakodateyama, is represented in Sapporo by the later activity of *valeriana*, while there is no predominantly autumn species such as *mitakensis* in Hakodateyama. However, it is still premature to conclude that this difference is essential between Hakodate and Sapporo areas. *Valeriana* is a gregarious species with distinctly patched distribution, for instance, in Sapporo, quite dominant in UC while virtually absent in BG. One of us (M.M.) found a nest aggregation of this species in the other area near the city of Hakodate. Furthermore, in and near Sapporo, there are species such as *A.(Cnemidandrena) seneciorum*, *Euandrena takachihoi*, typically autumnal like as *mitakensis*. Therefore the difference between Hakodateyama and Sapporo, represented here only by BG and UC, may not always represent

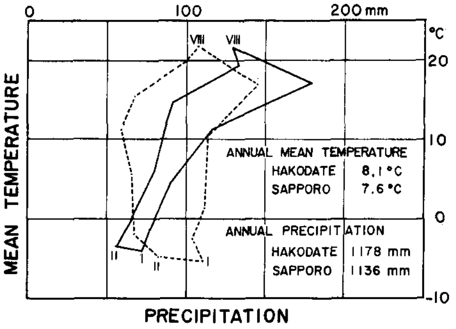

Fig. 8. Hythergraphs of Hakodate and Sapporo (1931～1960, based upon records by Meteorological Observatories).

clear phenological difference, even though the autumn activities would be much prolonged in Hakodate area. Another interesting aspect is the bivoltinism in *dentata* and *kaguya*. In Sapporo, there is no bivoltine species, though the possibility of partial bivoltinism in *ezoensis* is still not completely rejected. Probably Hakodate and the vicinity give the northern limit of definite bivoltinism in Japanese andrenid species.

As to the flower visits, the difference in the importance of Liliaceae is also easily explained. In Sapporo, 15% of their visits to this family depend on a single species *Gagea lutea*, which is in full bloom before the European dandelion and attracts many early spring andrenid species. In Hakodateyama, however, both species burst in bloom nearly synchronously, resulting in the absorption of most individuals to the dandelion. The change of the position of Cruciferae is also not difficult to understand by the absence of rape cultivation in and near Hakodateyama. On the other hand, Umbelliferae occupies there the fourth rank by the abundance of *Heracleum lanatum*. In general, three families, Compositae, Leguminosae and Rosaceae are the most important food sources common to both areas. In the first two families, the predominant role is each played by a single species, European dandelion absorbing 72% of total visits of the family in Hakodateyama and 76% in Sapporo, and white clover 90% in Hakodateyama and 75% in Sapporo, though the role of other composite species is relatively high in Hakodateyama by the autumn activity of *mitakensis*. The family Rosaceae behaves in a little different way. In Sapporo, this is the only plant group attractive to andrenids at family level, with several well visited plants. This tendency is not so conspicuous in Hakodateyama, replaced by the strong preference for *Potentilla*.

Concerning the percentage ratio of flower species visited by andrenids to the total flower species in bloom at corresponding periods (*cf*. Table 3), a strikingly similar tendency is seen both is Sapporo (22.4%) and Hakodateyama (21.4%). The same relation was observed between two areas in Sapporo (BG; 16.9%, UC; 16.7%), in spite of the difference of the absolute number of flower species. It is conceivable that many andrenid bees are more or less plastic as to the flower preference, adjusting their visits according to the relative richness of the floristic makeup. This plasticity is proven by their dependance on exotic plants, both in Sapporo and Hakodateyama. The rule is followed even by some oligotrophic species, such as *ezoensis*, which directs its innate preference for legumes to some imported species, white and red clovers.

Summary

Relative abundance, phenology and flower preference of andrenid bees were studied, based upon the periodical sampling of wild bees on flowers at a secondary field on Hakodateyama, a small hill in Southern Hokkaido, for 1960–1962.

Among in total 752 individuals belonging to 23 species sampled, most predom-

inant species is *Andrena komachi* (34% of total individuals) followed by *A. watasei*, *A. ezoensis* and *A. mitakensis* are next to the species. These dominant species occupy 70% of total individuals.

The flight season of adult andrenid bees in the area is about 170 days from middle April to late September. *A. dentata* and *A. kaguya* are probably digoneutric species, though most species are monogoneutric. The andrenid season in the area is divided into two distinct phases, the spring-summer phase consists of diverse activities of spring and summer species and the autumn phase monopolized by activity of *A. mitakensis*.

Among 54 flower species belonging to 21 families visited by andrenid bees, two exotic plants, European dandelion and white clover, and native *Potentilla fragarioides* are the most predominantly preferred flowers (58%). Compositae and Rosaceae are most important at family level. Most flower species mainly preferred are also important as pollen sources.

Comparing the faunal makeup between Sapporo and Hakodateyama, 13 out of 31 are the species common to both areas. There is no essential faunal difference, except for the abundance of autumn species *A. mitakensis*, and absence of *A. sublevigata* and *A. astragalina* in the latter area.

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