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Wild Bee Survey at the Campus of Hokkaido University¹⁾

By

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(With 20 Text-figures and 9 Tables)

The present paper is an outcome of the periodical wild bee sampling made in 1959 at the campus of Hokkaido University. The survey was planned primarily to get information upon the annual cycles of various bee species as a basis for their comparative bionomics. After the completion of the survey, it was recognized that the data obtained can also be used to analyse the relative abundance and phenology of the local bee fauna, to some degree, quantitatively. The part concerning andrenid bees was already published (Sakagami and Matsumura 1967). Similar surveys were executed subsequently at some localities in Hokkaido (Matsumura and Munakata 1969, Sakagami and Fukuda 1972a, Munakata 1971, Fukuda *et al.* 1973). The same attempt was extended to study the bee fauna of Southern Brazil (Sakagami, Laroca and Moure 1967, Sakagami and Laroca 1971 a, b). Nevertheless, the analysis of the main body of the data taken in 1959 has been postponed because scientific names of many species have still not accurately been settled. But the extension of our surveys to other areas in Hokkaido has necessitated a compilation of the results in 1959 as a basis for further biofaunistic comparisons. This is the main reason why we publish here the results without awaiting for the taxonomic solution of all species collected.

Methods

1. *Areas surveyed:* The periodical sampling was made at the campus of Hokkaido University (UC) and the University Botanical Garden (BG) (Fig. 1). In and near Sapporo (43°N) the original vegetation, principally consisting of deciduous broad leaf forests, has mostly been replaced by rural and urban areas, leaving UC and BG as isolated refugial patches within a rapidly expanding city with one million inhabitants.

UC is about 1.0×1.5 km sq. in extent, but the sampling area in 1959 occupied only one third of the campus as shown in Fig. 1 which, though strongly secondary in vegetation, had still provided suitable feeding and nesting sites for bees. Thereafter, the favorable area has steadily been decreasing in size due to the continuous expansion of university buildings.

BG is about 0.3×0.3 km sq. The original deciduous forest is partly reserved but the

1) Wild bee biofaunistics and biocoenotics in Hokkaido VI.

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Fig. 1. Area surveyed. BG: University Botanical Garden, UC: University Campus. In UC, sampling areas are delimited with black wavy lines. Aerial photo was taken in 1970, so that some parts surveyed in 1959 are already replaced by buildings.

vegetation, particularly the lower strata, is strongly modified, enriched by the introduction of a variety of Japanese and exotic plants. The weather conditions in Sapporo, given in Fig. 5, A~C, are Dfb (Köppen) or A''₃ (Kira) in climatic formula, characterized by a short but relatively favorable summer. The bee season continues from late April to October without dearth.

2. *Sampling procedure:* As shown in the calendar given below, sampling was made weekly from late April to late September, each week four hours for both BG and UC, except for the first sampling at UC in April, which could be undertaken only one hour. These four hourly samplings were performed either continuously within one day or extending to two or rarely three days, mostly during 9:30~14:30, rarely to 15:30 and, as far as possible, in fine and calm weather.

Codes	Sampling periods in calendar dates	Codes	Sampling periods in calendar dates
IV-1	IV 19~25	VII-1	VII 5~11
IV-2	IV 26~V 2	VII-2	VII 12~18
V -1	V 3~9	VII-3	VII 19~25
V -2	V 10~16	VII-4	VII 26~VIII 1
V -3	V 17~23	VIII-1	VIII 2~8
V -4	V 24~30	VIII-2	VIII 9~15
VI-1	V 31~VI 6	VIII-3	VIII 16~22
VI-2	VI 7~13	VIII-4	VIII 23~29
VI-3	VI 14~20	IX-1	VIII 30~IX 5
VI-4	VI 21~27	IX-2	IX 6~12
VI-5	VI 28~VII 4	IX-3	IX 13~19
		IX-4	IX 20~26

Henceforth the sampling periods are cited with the code numbers. Before and after each hourly sampling, air temperature was measured with a shaded thermometer and intensity of isolation, cloud amount and wind classes were estimated by eye. At each hourly sampling any wild bees discovered on any kinds of flowers or in flight were captured without particular choice. The captured individuals were separately preserved according to the flower species visited. Care was taken to not stay too long at any particular spots. When one spot attracted numerous bees by the presence of many flowers in bloom, we collected as many specimens as possible at one time, then moved to other places, without waiting for further arrivals of other individuals.

The sampling was not made at the orchard within UC and places where some species, *Lasioglossum (Evyllaesus) duplex*, *Andrena valeriana*, etc., have formed nest aggregations.

3. *Possible sources of sampling biases:* The procedure given above is in many aspects defective to give an unbiased measure of relative abundance among bee species. Some possible sources of biases were enumerated in a previous paper (Sakagami, Laroca and Moure 1967): Influence of removal of individuals, adoption of individual collecting instead of random sweeping, relative ease of capture due to specific differences in size, agility and flower visiting habits, etc.

All these sources must have affected the results. Moreover, there are other sources of biases being inevitable by the spatiotemporal limitation at sampling: Each hourly sampling was made neither at the same hour in the same weather conditions nor at the same subarea. Another serious problem is the difficulty to catch bees visiting flowers of tall trees.

In spite of these difficulties, we believe that the execution of surveys along our procedure is better than the use of museum specimens to compare local faunal differences for the elimination of the preferences for rare species and particular seasons. Further, the surveys by our procedure could offer a basis for more precise sampling, either by improving collecting techniques or by developing less biased sampling designs.

4. *Citation of unnamed species:* The taxonomy of wild bees inhabiting Hokkaido is still not in a satisfactory state, with only five genera relatively well studied, *Osmia* (Yasumatsu and Hirashima 1950), *Andrena* (Hirashima 1962~'66), *Ceratina* (Yasumatsu and Hirashima 1969), *Bombus* (Sakagami and Ishikawa 1967, 1972), *Megachile* (Hirashima and Maeta in preparation). Consequently, scientific names of many species obtained in the present survey have still not accurately been determined, including numerous unnamed species. These species are henceforth cited with Arabic code numbers for each genus or, in Halictidae, for subgenus (the subgenus *Evyllaesus* is further subdivided into carinate and carinaless groups, cf. Table I and Appendix). These specific numbers were partly adopted in our previous studies (Sakagami and Fukuda 1972a, Fukuda *et al.* 1973) and will be used, fixed for each species, in the subsequent papers until the accurate names would be established. Some of these unsettled species, particularly those of carinaless *Evyllaesus*, are quite subtle in diagnostic characters so that their later lumping or splitting is possible. It is also likely that both sexes of one and the same species receive different code numbers due to difficulties in finding the correspondence between sexes. Therefore, some numerical data presented below may partly be modified, even though not seriously, after the solution of the taxonomic status of unsettled species.

Results and discussions

Results are divided into four parts, faunal makeup, phenology, life-cycle approach and flower visits. Some related discussions are given in each section.

1. Faunal makeup

The list of all species collected by the survey is given in the Appendix at the end of the paper. Table 1 summarizes at familial and generic levels the numbers of species and individuals sampled.

1.1. *Relative abundance at supraspecific levels*: A glance at the table the overwhelming predominance of Halictidae (all belonging Halictinae) is obvious, both areas combined occupying nearly the half of the total species number and nearly 60% of the total individuals. Among other groups, the Andrenidae takes the second rank both in species and individuals, followed by Anthophoridae, Colletidae, Megachilidae and Apidae in species number and Anthophoridae, Apidae, Megachilidae and Colletidae in individuals. Except Halictidae most groups are represented by only one genus or only one genus is predominant. At generic level, *Lasioglossum* s. lat. outnumbers all other groups in species number (35 spp, or 34.7 %), and its subgroup, carinaless *Evylaeus* (17 spp), is only exceeded by *Andrena*. Among other genera, only *Hylaeus* and *Nomada* have more than ten species. About 75% of total species number are occupied by these four genera. As to the relative abundance in terms of individual number, the predominance of *Lasioglossum* s. lat. is much more conspicuous, occupying nearly the half, 48.5%, of total individuals. Its predominant subgroup, carinate *Evylaeus*, occupies the top rank, followed by *Andrena*, *Lasioglossum* s.str., *Ceratina*, *Dialictus* and carinaless *Evylaeus*. The sum of these six predominant groups equals to about 75% of total individuals sampled. The individual/species ratio (Table 1, penultimate column) is the highest in *Ceratina*, followed by *Dialictus* and *Seladonia*, and, with a marked drop, by carinate *Evylaeus* and *Halictus* s.str. The higher value of the ratio in carinate *Evylaeus* indicates its harmonious predominance both in species and individual numbers, whereas that in other three groups the presence of a few successful species in spite of the small species number.

1.2. *Interfaunal comparisons*: The faunal makeup summarized in Table 1 reflects the structure of the assemblage from which the sample was extracted. As discussed in Sakagami, Laroca and Moure (1967), virtually several levels of assemblages must be considered in this type of data as given in the following ascending order, that is, wild bee assemblage characteristic to: 1) the area and year surveyed, 2) ditto, in average, 3) Sapporo and the vicinity, either as a whole or the lowland area with intensive human influence, 4) Hokkaido, reflecting insular and northern poverties as well as mixture of Eurosiberian and Manchurian elements, 5) The Holarctic region. For the lack of sufficient data to be compared, we can not, for

Table 1. Number of species and individuals of wild bees sampled

Family	Genus (Abbrev.)	Number of species			
		BG	UC	Total	Common
COLLETIDAE		9	7	12	4
	<i>Hylaeus (Hy)</i>	9	6	11	4
	<i>Colletes (Co)</i>	0	1	1	0
HALICTIDAE		36	36	43	29
	<i>Halictus (Ha)</i>	1	1	1	1
	<i>Seladonia (Sl)</i>	1	1	1	1
	<i>Lasioglossum (Lg)</i>	7	9	9	7
	<i>Dialictus (Dl)</i>	2	2	2	2
	Carinaless	12	14	17	9
	<i>Evylaeus (El)</i>				
	Carinate	7	4	7	4
	<i>Evylaeus (Et)</i>				
<i>Sphecodes (Sph)</i>	6	5	6	5	
ANDRENIDAE	<i>Andrena (Ad)</i>	16	12	18	10
MEGACHILIDAE		8	5	8	5
	<i>Megachile (Mg)</i>	3	3	3	3
	<i>Chalicodoma (Ch)</i>	1	0	1	0
	<i>Coelioxys (Cx)</i>	2	2	2	2
	<i>Osmia (Os)</i>	2	0	2	0
ANTHOPHORIDAE		11	12	15	8
Anthophorinae		2	2	2	2
	<i>Clisodon (Cl)</i>	1	1	1	1
	<i>Eucera (Eu)</i>	1	1	1	1
Nomadinae	<i>Nomada (Nm)</i>	7	8	11	4
Xylocopinae	<i>Ceratina (Ct)</i>	2	2	2	2
APIDAE	<i>Bombus (Bo)</i>	5	5	6	4
Total		85	77	102	60

the time being, to separate clearly which aspects of the result reflect these levels and sublevels derived.

As a tentative for such analysis, several available studies showing the relative abundance of various groups in numbers of both species and individual were compared in Fig. 2 in percentage ratios, adopting the following data; I. Sapporo: Result given in Table 1. II. HamaKoshimizu: Result of sampling made in HamaKoshimizu at littoral vegetation, Eastern Hokkaido, executed as an extension of the present survey using the same procedure, but with more spaced sampling intervals (Fukuda *et al.* 1973). III. Western Ukraina: Result of collecting for several years from various localities (Osychnyuk 1959). IV. Chicago: Result of two years' collecting in and near the city (Pearson 1933). V. São José dos Pinhais: Result of one year's sampling near Curitiba, the state capital of Paraná, Southern Brazil, using the procedure as in I, but with three times per month

in BG and UC, 1959, given at familial and generic levels

Number of individuals						Ratio Indiv./species
BG	%	UC	%	Total	%	
132	3.5	44	1.4	176	2.5	14.7
132	3.5	42	1.3	174	2.4	15.8
0	0.0	2	0.1	2	0.1	2.0
2,019	53.9	1,819	58.7	3,838	56.1	89.2
5	0.1	135	4.4	140	2.1	140.0
77	2.1	239	7.7	316	4.6	316.0
339	9.1	459	14.8	798	11.6	88.6
528	14.1	106	3.4	634	9.3	317.0
301	8.0	296	9.6	597	8.7	35.1
735	19.6	540	17.4	1,275	18.7	182.1
34	0.9	44	1.4	78	1.1	13.0
480	12.8	536	17.3	1,016	14.9	56.4
229	6.2	109	3.5	338	4.9	42.2
159	4.3	100	3.2	259	3.7	86.5
6	0.2	0	0.0	6	0.1	6.0
8	0.2	9	0.3	17	0.3	8.5
56	1.5	0	0.0	56	0.8	28.0
552	14.7	410	13.3	962	14.1	87.4
38	1.0	86	2.8	124	1.8	62.0
34	0.9	19	0.6	53	0.8	53.0
4	0.1	67	2.2	71	1.0	71.0
40	1.1	31	1.0	71	1.0	6.4
474	12.6	293	9.5	767	11.3	383.5
332	8.9	181	5.8	513	7.5	85.5
3,744	100.0	3,099	100.0	6,843	100.0	—

instead of weekly sampling (Sakagami, Laroca and Moure 1967). The data I, II and V were taken with the same procedure so that the results are directly comparable. As to III and IV, it is uncertain whether or not the sampling was made in the manner not overestimating individual numbers of rare species and not concentrated in favorable bee season. But the numerical data given in the papers were adopted as they may approximately reflect the real relative abundance. It is regrettable that numerous faunal lists so far published cannot be used for our purpose because they do not cite the number of individuals studied of each species, especially of the abundant ones. To facilitate the comparison, each family was subdivided into several predominant genera, regarding Sapporo as the standard, and "other ones", with indication of the number of genera involved. Further, the following arbitrary groupings were made: Halictidae, carinate and carinaless *Evylaeus* grouped together (=Ev), Megachilidae, *Chalicodoma* (I) included in *Megachile*, Anthophoridae: Exomalopsinae (V) included in Anthophorinae, *Tetralonia* (III

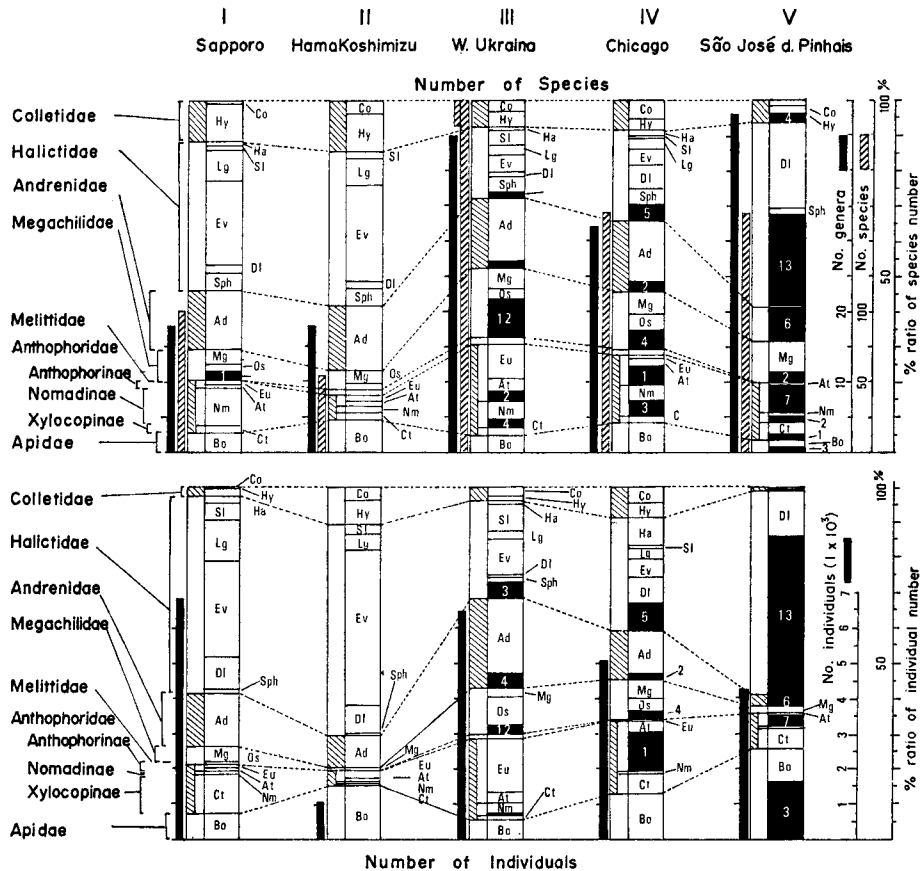


Fig. 2. Comparison of faunal makeup expressed in percentage species (above) and individual numbers (below) of major bee groups in five localities (I-V), accompanied with absolute numbers of genera, species and individuals collected (Scale at righthand). Predominant genera are shown with abbreviations (cf. Table 1). Other genera are shown with black blocks together with number of genera involved. Further explanations in text.

~IV) in *Eucera* and *Clisodon* and *Amegilla* (I~III) in *Anthophora* (=At). Other generic abbreviations are given in Table 1.

At family level, the results in Fig. 2 are summarized in the following two series of relative abundance (Apidae, Xylocopinae, Melittidae are abbreviated as AP, XY, MT, others comparable to the abbreviations of nominate genera):

Species:

- I: HA>>AD>CO>NM>MG>AP>AT, XY
- II: HA>>AD>CO>AP>MG>AT>NM, XY, MT

- III: AD \geq HA \geq MG \geq AT>NM>CO>AP>XY>MT
 IV: HA \gg AD>MG>AT, NM>CO, AP>XY \geq MT
 V: HA \gg MG>AD>AT>CO>XY>AP>NM

Individuals:

- I: HA \gg AD>XY>AP>MG>CO>AT>NM
 II: HA \gg AP>CO>AD>AT>XY, MG>NM>MT
 III: HA \geq AD>AT>MG>AP>CO>NM>MT>XY
 IV: HA \gg AT>AD>AP>MG>CO>XY>NM>MT
 V: HA \gg AP \gg XY>AT \geq AD>MG>CO>NM

Further, mean individuals per species (I/S) is arranged in the following series:

- I : XY (383.5) \gg HA (89.4) \geq AP (85.5)>AD (64.4) \geq AT (62.0)>MG (43.4) \gg CO (14.4) \gg NM (6.4)
 II: AP(32.4)>HA (26.0)>AT (16.5)>CO (13.9)>AD (9.6)>XY (7.0) \gg MG (2.5)>MT (1.0)
 III: MT (36.8)>HA, AD (31.8)>AT (30.9)>AP (26.1)>XY (16.1)>MG (14.4)>CO (12.1)>NM (7.9)
 IV: XY (76.3)>AP (62.4)>AT (49.5)>HA (36.8)>CO (30.0)>MG (20.9) \geq AD (20.6) \gg MT (9.0)>NM (5.8)
 V: AP (181.0) \gg XY (34.5)>HA (27.7) \gg AT (9.4) \geq AD (8.1)>MG, CO (4.4)>NM (3.7)

Some general trends and implications derived from the comparison of these data are enumerated below:

1) Overwhelming predominance of Halictidae both in species and individuals, only slightly exceeded (in species) or nearly rivalled by Andrenidae in W. Ukraine. This tendency may be common to most parts of the temperate Holarctis and Neotropics, but not always in other regions, especially in the Australian Region (Exceeded by Colletidae, Michener 1965, cf. Sakagami, Laroca and Moure 1967), and humid tropics (replaced by Apidae, Anthophoridae). Because of its rich speciation, the I/S value in Halictidae does not always occupy the first place but is never very low.

2) Predominance of Andrenidae in the Holarctis, usually occupying the second place in species and often in individuals, too.

3) Paucity of Melittidae both in species and individuals as a minor stenotrophic side branch, though occasionally abundant by a concentration to particular food plants (cf. I/S in W. Ukraine).

4) Numerical abundance of Apidae in individuals compared with species number. This is easily understood by their social mode of life, and the tendency may increase in two opposite directions, the High Arctic by Bombinae and humid tropics by Apinae.

5) Numerical paucity of Nomadinae in individuals, compared with species number, which is also easy to understand from their parasitic mode of life.

6) Minor importance of Xylocopinae in the Holarctis though I/S is often high by the presence of some successful *Ceratina* species.

7) Colletidae, Megachilidae and Anthophorinae as moderate to minor groups in the Holarctis. The Anthophorinae occasionally becomes moderately abundant

while the Megachilidae only rarely in individuals and I/S.

Besides these trends, being suggestive for further studies, some aspects particular to the areas compared are referred to:

8) The resemblance between Sapporo and HamaKoshimizu is obvious. The difference in species number is caused by the scarcity of Nomadinae in the latter, which is not difficult to understand from the smaller sample size taken more intermittently in combination with the peculiarity of this subfamily mentioned above (5). The difference in individual number is affected by the abundance of Colletidae and Apidae and relative scarcity of Xylocopinae and Andrenidae in HamaKoshimizu. The first three items are interpreted as northern tendencies while the last one is, for the time being, difficult to interpret.

9) The data in W. Ukraina are characterized by the relative scarcity of Halictidae, compensated by the increase in Megachilidae and Anthophorinae both in species and individuals. As to the species number this might be affected in part by sampling procedure. Collecting from diverse localities through several years may increase the number of rather sparsely distributed species as being frequent in two families cited. But, the fact that the same tendency is found in individual number indicates that the result might also represent the real faunal characteristic in this steppe area. Another characteristic, the scarcity of Xylocopinae in individuals compared with Sapporo, may rather reflect the particularity of the latter, caused by the excessive abundance of two *Ceratina* species.

10) The data in Chicago resembles those in Ukraina, and two interpretations given above may also be applied to here. But the general pattern in species number is intermediate between Sapporo and Ukraina by the increase of Halictidae and Apidae and decrease of Anthophorinae relative to Ukraina. This tendency is more or less repeated in individual number, too, but here the relative decrease of Andrenidae is noted.

Therefore, the patterns shown by I~IV are regarded various deviations from the general Holarctic pattern, caused by geographic and ecologic situations of the areas surveyed and collecting procedures employed.

11) Interestingly the sample from Southern Brazil does not deviate conspicuously from the Holarctic pattern at family level, showing a similarity to that of I and II, particularly in the predominance of Halictidae, though the increase of Apidae and decrease of Andrenidae in individual number are distinct. Apparently such pattern may not be expected in the Australian Region (Michener 1965). How the pattern may change in other areas of the Southern Hemisphere would be worthy to study. Finally some comments are added to the relative abundance at generic level.

12) The number of genera collected in I and II is equal (18), and mostly common (*Macropis*, collected in II but not in I, occurs in and near Sapporo. *Osmia* was not collected in II but from its environ), in spite of a marked scarcity in species and individuals in HamaKoshimizu. This reflects the homogenous wild bee fauna of Hokkaido at generic level. There are known only four genera so far

recorded from Hokkaido but not represented in I and II, two melittids (*Melitta*, *Dasyppoda*) and two anthophorids (*Epeolus*, *Tetralonia*). The first three genera are sporadically collected in and near Sapporo, only *Tetralonia* being confined to the southernmost part of Hokkaido.

13) The generic makeup in I and II shows the northern and depauperated bee fauna of Hokkaido. Only two southern groups reach Sapporo, *Chalicodoma* (*Eumegachilana*) and *Ceratina* (*Ceratinidia*). Most other genera and many subgenera are of the wide Holarctic or Palearctic distribution. This is clearly recognized by comparing I and II with III. Numerous genera collected in Ukraina do not reach Japan as indicated in Fig. 2 by the increase of black blocks (=other genera).

14) The same conclusion is derived from the comparison of I~II with IV. But here the faunal difference is affected by the Nearctic endemicity in the latter. The replacement in relative abundance between *Evyllaesus* and *Dialictus* (Knerer 1968) is suggested and a considerable part of Halictidae is represented by the species belonging to Augochlorini confined to the Western Hemisphere. In Anthophorinae, the part occupied by *Melissodes* is quite large.

15) The comparison of I~II with V demonstrates a completely different faunal makeup of the Neotropical sample at infra-familial level. In Halictidae, besides a rich speciation of *Dialictus*, more than a half of species and the majority of individuals are represented by Western genera. The poverty of Andrenidae accompanied with the omission of *Andrena*, differentiation of endemic anthophorine genera and the abundance of Apidae by the presence of stingless bees reflect the unusually rich Neotropical bee fauna, which is also indicated by the ratio of genera to species.

1.3. *Predominant species*: Fig. 3 shows the relative abundance of 20 predominant species in percentage ratio with the upper and lower fiducial limits ($p=0.95$), arranged in the descending order of individual number sampled at UC+BG. In all these species the lower fiducial limits exceed the value "100 x reciprocal of the total species number" (100/102) and their cumulative percentage ratio reaches 76.03, that is, involving about three fourth of total individuals. Reflecting the predominance of Halictidae, nine out of 20 belonging to this family, occupying 43.31%, followed by *Andrena* (11.67%), *Ceratina* (11.20%) and *Bombus* (6.15%). How these values and composition of predominant species vary in and near Hokkaido must be solved through further surveys. Here the result is tentatively compared with that obtained in HamaKoshimizu.

Between the two samples (102 spp, in Sapporo, 55 spp, in HamaKoshimizu), 40 species or 72.7% of the latter are common. Although the ratio may vary by more intense collecting, especially in HamaKoshimizu, it suggests the lack of conspicuous qualitative difference between two areas at species level. On the other hand, the makeup of predominant species is quite different. Comparing 20 predominant species in HamaKoshimizu (occupying 87.93% of total individuals)

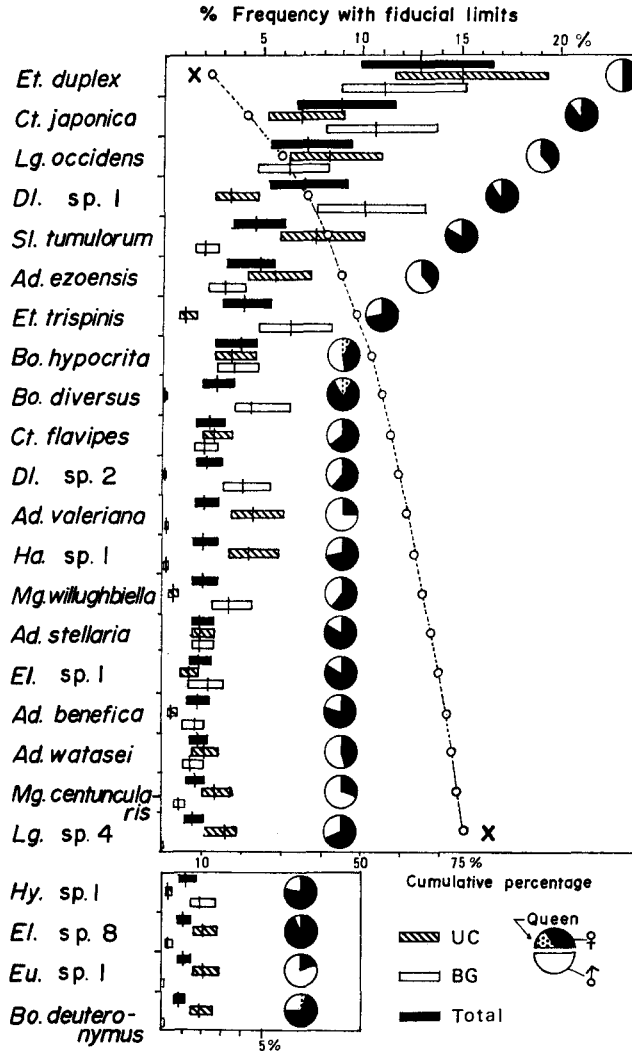


Fig. 3. Relative abundance of 20 predominant species shown by occurrence probability method. Percentage ratios of each species in BG, UC and both combined are given by a short vertical line on each horizontal bar indicating fiducial limits, accompanied with sex ratio in each species by pie graph (in bumblebees, queen and worker separated). Curve XX shows cumulative percentage (scale bottom). Four species at bottom are those predominant in one area but not in both areas combined.

with those in UC+BG, there are only three species common to both, *Dl.* sp. 1, *Bo. hypocrita* and *Sl. tumulorum*. Among 20 species in Sapporo, eight species (*Ct. japonica*, *Et. trispinis*, *Dl.* sp. 2, *Ha.* sp. 1, *Ad. stellaria*, *El.* sp. 1, *Ad. benefica*, *Lg.* sp. 4) are not collected and four (*Et. duplex*, *Bo. diversus*, *Ad. valeriana*, *Mg. willughbiella*) are represented by less than five specimens in HamaKoshimizu. On the contrary, five predominant species in HamaKoshimizu (*Et. albipes*, *El.* sp. 22, *El. ohei*, *Co.* sp. 2 and *Ad. kerriae*) are not collected in Sapporo. Certainly, further surveys may clarify the presence of these species in or near the other area. For instance, *Et. albipes* and *Ad. kerriae* are sporadically collected near Sapporo. However, a marked discrepancy in the makeup of predominant species between two areas is implicative to study the local differences of bee fauna in Hokkaido, which cannot necessarily be clarified through the comparison of species lists as was suggested elsewhere (Sakagami and Fukuda 1972a).

1.4. *Difference between two areas:* In connection with the last mentioned problem, the difference between two areas, BG and UC, is referred to. Table 1 shows some differences in faunal makeup at family level, for instance, Colletidae, Megachilidae and Apidae are more abundant in BG, while Andrenidae and Anthophorinae *vice versa*. Such differences would arise principally at familial level when two faunistically and ecologically different areas were compared, as seen in some examples in Fig. 2. In the present case, however, the two areas, separated only 300 m for each other, are apparently fragments derived from the common origin, so that most differences are explained at specific level.

Among 102 species collected (BG 85, UC 77), the species common to both areas are 60 or 58.8%. This ratio is not so high if the short distance of two areas is reminded. But many species are represented by so small number of individuals that the ratio mentioned may not indicate the real difference in faunal makeup. On the other hand, Fig. 3 shows many predominant species, 11 out of 20, are unevenly collected from two areas. To test the presence or not of such skewed distribution in other species, the fiducial limits of percentage ratio were calculated as in Fig. 3 for each species. The species were divided into the following five groups according to the unevenness of abundance between two areas:

- | | |
|-----------------------------------|-------------------|
| 1) $BG \gg UC$ and 5) $BG \ll UC$ | $P < 0.01$ |
| 2) $BG > UC$ and 4) $BG < UC$ | $0.01 < P < 0.05$ |
| 3) $BG \approx UC$ | $P > 0.05$ |

As given in Table 2, the difference in relative abundance between two areas is significant in 34 species (56.6%) and highly significant in 26 (43.3%) out of 60 species represented by ten or more specimens. This suggests that, in many if not all species, populations in two areas are now fairly isolated for one another.

Obviously this does not mean that the distance between two areas is out of the physiological flight capacity of bees. The return of a female of *Et. duplex* transplanted from BG to UC was once observed (Sakagami and Hayashida 1968). The captures of a few specimens of *Ad. valeriana* in BG probably means the dis-

Table 2. Difference in relative abundance of some predominant and abundant species between two areas (*=strong fliers)

Number of individuals collected	BG \gg UC	BG>UC	BG \approx UC	BG<UC	BG \ll UC
N \geq 200	<i>Et. trispinis</i>	<i>Dl. sp. 1</i>	<i>Et. duplex</i> <i>Ct. japonica</i> <i>Lg. occidentis</i> <i>Ad. ezoensis</i> * <i>Bo. hypocrita</i>		<i>Sl. tumulorum</i>
200>N \geq 100	* <i>Bo. diversus</i> <i>Dl. sp. 2</i> <i>Ad. benefica</i> * <i>Mg. willughbiella</i>		<i>Ct. flavipes</i> <i>Ad. stellaria</i> <i>El. sp. 1</i> <i>Ad. watasei</i>	* <i>Mg. centuncularis</i>	<i>Ad. valeriana</i> <i>Ha. sp. 1</i> <i>Lg. sp. 4</i>
100>N \geq 50	<i>Hy. sp. 1</i> <i>El. sp. 8</i>	<i>El. sp. 18</i>	<i>El. sp. 3</i> <i>Lg. esoense</i> <i>Et. sp. 2</i> <i>El. sp. 4</i> <i>Hy. paulus</i> * <i>Cl. sp. 1</i> <i>Lg. sp. 3</i>		* <i>Ev. sp. 1</i> * <i>Bo. deuteronymus</i>
50>N \geq 20	* <i>Os. cornifrons</i> <i>Et. apristus</i> <i>Ad. hikosana</i> <i>Nm. koebelei</i>	<i>Ad. sublaevigata</i>	<i>Ad. nawai</i> <i>Sph. easkii</i> <i>El. sp. 9</i> <i>El. sp. 5</i>	<i>Sph. scabricollis</i> <i>Lg. laeviventre</i>	<i>El. sp. 10</i> <i>El. sp. 16</i> <i>Ad. brassicae</i> <i>El. sp. 17</i>
20>N \geq 10	<i>Ad. kaguya</i>	* <i>Bo. ardens</i> * <i>Os. taurus</i>	<i>Ad. astragalina</i> <i>Ad. haemorrhoida</i> <i>Lg. discrepans</i> <i>Cx. sp. 2</i> <i>Hy. monticola</i> <i>Lg. mutilum</i>		<i>El. sp. 2</i> * <i>Bo. pseudo-baicalensis</i> <i>Nm. okamotonis</i> <i>Nm. sp. 3</i>
Number of species	12	5	26	3	14

persal from UC, because nest aggregation of this species, characterized by its crowding and conspicuousness, has never observed in BG during more than ten years (Sakagami and Matsumura 1967). However, these records could be regarded as showing the limit of economic flight distance. Bees are certainly agile fliers. But due to their attachment to nests, they, especially females, are much more sedentary than other actively flying insects in Diptera and Lepidoptera. This assumption is strengthened by the uneven distribution of the species belonging to Megachilidae, Anthophorinae and Apidae, all regarded as more agile fliers than other bees. Only two out of 11 species of these groups are distributed evenly in

both areas (*Bo. hypocrita* and *Cl. sp. 1*, cf. Table 2), indicating even these wide-roaming species confine their flight activities mainly to one area.

Finally, the relative abundance of the European honeybee workers between two areas are cited. In 1959, except five colonies of *Apis mellifera* Linné kept by us in UC, no colonies were placed in the area surrounding BG, at least within the radius of 1 km, probably 2 km, which was mostly occupied by urban zones (cf. Fig. 1). Therefore, most honeybees found in BG are guessed as foragers issued from UC colonies. During the survey the number of honeybees visiting flowers were simply counted for each hourly sampling, without capturing them. Therefore the figures obtained cannot directly be compared with the number of wild bees collected, but the comparison between two areas is possible as follows:

	IV		V		VI					VII					
Sampling period	1	2	1	2	3	4	1	2	3	4	5	1	2	3	4
Number counted															
UC	5	0	4	2	11	14	30	64	58	94	29	103	112	59	62
BG	25	1	0	0	0	0	1	2	1	0	36	2	20	0	0
	VIII				IX										
Sampling period	1	2	3	4	1	2	3	4							
Number counted															
UC	72	120	137	147	171	176	139	22							
BG	0	2	2	1	0	1	0	4							

The ratio BG/UC is larger than 1.0 only twice, IV-1 (visiting mostly *Galea lutea*) and VI-5 (mainly visiting white clover and *Salvia officinalis*). In other periods, the number counted in BG is incomparably less than in UC. The homing experiments previously made in UC shows that about one half of released workers return to the nest from the distances up to 2 km (Uchida and Kuwabara 1951). Therefore even such strong flier as honeybee tends to confine the foraging range to a relatively narrow area, provided sufficient food is available.

Consequently it is highly probable that bee assemblages in BG and UC are now fairly separately for each other. This must be kept in mind in biofaunistic surveys of a given area because the faunal makeup of two closely situated areas can be fairly different, which gives a warning to the premature generalization of the result obtained from a limited area to the whole region.

1.5. Estimation of the total number of species inhabiting the area surveyed: To estimate the total number of species inhabiting BG and UC, fitting trial of the truncated discrete log normal proposed by Preston (1948) was applied to the result obtained, adopting the procedure developed by Nagasawa (1969). A linear relation occurs between cumulative capture percentage expressed in probits and number of individuals per species, expressed by the upper class limits of grouping intervals in logarithms (Fig. 4). The fitness to the Preston's log normal is confirmed by χ^2 -test in BG, UC and both combined.

The estimates for the number of total species and of uncollected ones are

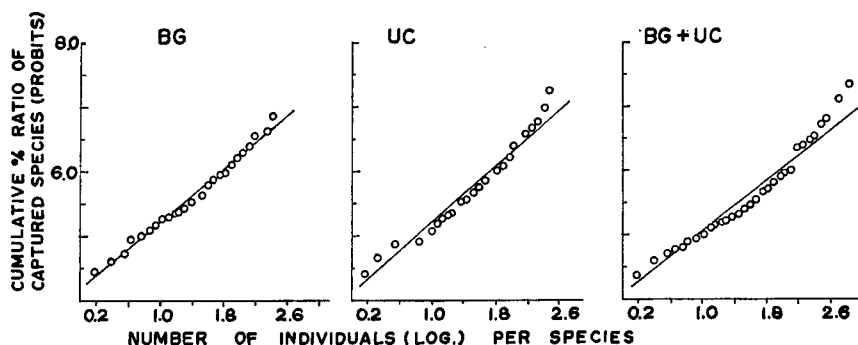


Fig. 4. Relation between number of species and individuals in BG, UC and both combined.

Table 3. Estimates for the number of total species inhabiting and of those not collected in the areas surveyed, together with those in São José dos Pinhais (SJP, cf. Nagasawa 1969). Calculated figures rounded to 0.01.

	BG	UC	BG+UC	SJP
Total number of species collected	85	77	102	163
Number of species represented by a single specimen	14	13	17	53
Estimate for total number of species inhabiting	98.29	86.85	115.32	266.42
Estimate for number of species not collected	13.30	9.85	13.33	103.42
Ditto, in percentage	13.53	11.34	21.56	38.82

given in Table 3, together with those estimated by Nagasawa (1969) for the result obtained in São José dos Pinhais, Southern Brazil, by using the same sampling procedure (Sakagami and Laroca and Moure 1967).

The results in BG and UC are more or less similar. The estimated percentage ratios of uncollected species are about 10%, sharply contrasting to that in São José dos Pinhais, where the ratio reaches 40%, as also suggested by a higher number of species represented by a single specimen. The difference is not difficult to understand when the conditions of the areas surveyed are compared. Our survey was made in the region characterized by the poverty of bee species, being quite different from the conditions in São José dos Pinhais as already explained in 1.2. (15).

Although the total number of bee species inhabited Hokkaido is still not precisely known, it certainly does not exceed 200 spp. The presence of 100 odd species in the small areas studied indicates its fairly rich faunal makeup, in spite of the small extent and isolation within a big city. At the same time, it suggests the relatively homogenous bee fauna of Hokkaido, as far as the species composition is concerned (cf. 1.2. item 12).

2. Phenology

Fig. 5 illustrates the seasonal change of the numbers of species and individuals in total and in each major group, together with the changes of climatic and floral conditions. Explanations are given as follows:

A. Air temperature: S. Mean at sampling; Mx, M and Mn, maximum, mean and minimum, means from records of Sapporo Meteorological Observatory, scale at lefthand; Dv. Deviation of monthly means in 1959 from M, scale at righthand.

B. Mean cloud amount (Cl, scale at lefthand) and wind class (Wd, scale at righthand) at sampling.

C. Weekly pluviometric and floral conditions in 1959: Rf. Rainfall, scale at lefthand (mm); Rd, Number of rainy days, each block represents one day; Ft and Fr. species numbers of flowering plants in bloom, total and those visited by bees, scale at righthand.

D. Species number of bees sampled, each family separately given (scale at lefthand) and the summed percentage ratio of individuals of five predominant species to total individual sampled (Dm) with scale at righthand.

E. Individual number sampled of each family, females and males separately given above and below base line, scale at lefthand.

Symbols: CO (Colletidae), AP (Apidae), AD (Andrenidae), MG (Megachilidae), AT (Anthophoridae), NM (Nomadinae), XY (Xylocopinae, N, newly emerged females), HA (Halictidae, ET, carinate *Evylaeus* excluding new females, N, newly emerged females), TO (Total individuals, scale at lefthand. ET, N, cf. HA, HM, Halictid males).

2.1. Seasonal change of species and individual number: As referred to in "Areas surveyed", the climate of Sapporo is divided into two major seasons from the viewpoint of wild bee activities: long and severe winter and relatively short but favorable bee season. The influence of climatic conditions upon bee phenology is obvious when the data taken in different years are compared as demonstrated in a previous paper (Sakagami and Matsumura 1967). But no particular relations are observed as far as only the data in 1959 are considered. In this year the air temperature was higher in early spring, but thereafter did not much deviate from the average, with the maximum in July to August (Fig. 5, A). Drops in early May and early June and rather erratic insolation and rainfalls (Fig. 5, B, C) do not correlate with any remarkable change in species and individual numbers. The number of flower species in bloom and those visited by bees (Fig. 5, C) gradually increase in spring and are more or less stable from June to early September, again not distinctly correlated with bee activities. Summarizing, the short bee season in Sapporo seems in general relatively stable except for the start and the end, without involving the periods with inhibition of bee activities by heavy rains, drought, high temperature, etc., as often recognized in southern regions, where the summer dearth is conspicuous in insect activities.

The number of species (Fig. 5, D) steadily increases in spring until reaching the peak in early June, with a corresponding decrease of the percentage ratio occupied by predominant species (Dm). Thereafter, the species number does not fluctuate much until mid September, followed by a rapid decline. This pattern is

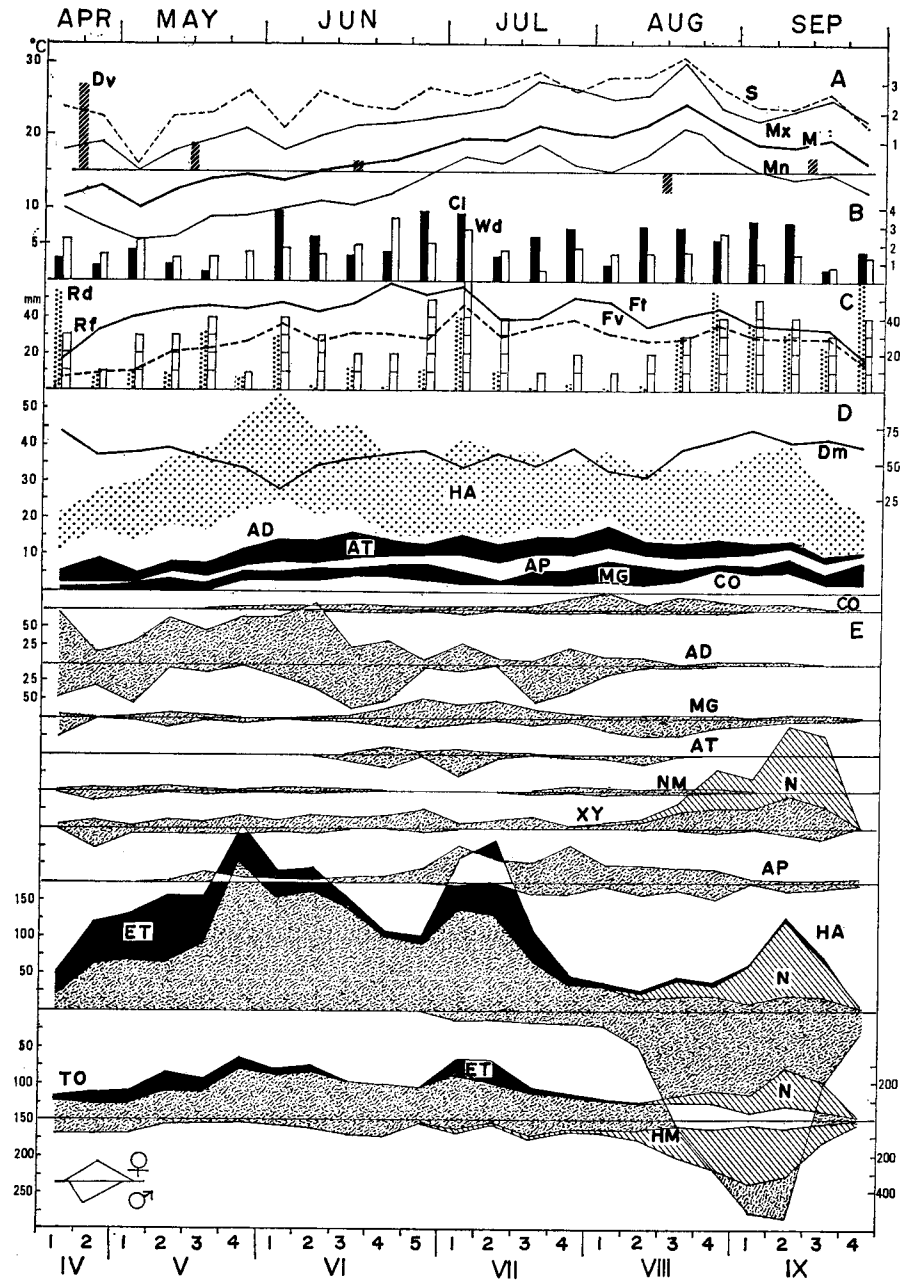


Fig. 5. Seasonal changes of environmental factors and species as well as individuals. Further explanations in text.

determined mostly by Halictidae, occupying the half of the total species in most periods. This family reaches the peak in June, then keeps more or less the same level until the second peak in mid September when the other groups begin to decline, caused by its peculiar life cycle explained in 3. 3. Among other groups, Andrenidae is decidedly vernal (cf. Sakagami and Matsumura 1967), whereas others do not show conspicuous change, though Colletidae is more abundant in later periods.

Concerning the total individual number, males have a single conspicuous peak in mid September, nearly exclusively caused by a burst of Halictidae (Fig. 5, E, TO and HA). The number of females fluctuates more mildly with three peaks each in late May to early June, early July and mid September. As seen from the figure, these peaks do not distinctly correlate with the change of climatic and floral conditions. The second peak seems to show a weak correlation with rainfall but the correspondence is not decisive. Comparing the curve TO (females) with that of each group, it is obvious that TO is strongly affected by the phenology of Halictidae, though the last peak is caused by both Halictidae and Xylocopinae. Even a single group of Halictidae, carinate *Evyllaesus*, plays an important role in fluctuation of total individual number (ET in TO and HA).

To show the seasonal relative abundance of various groups obscured by Halictidae, the phenology of the percentage ratios in individuals of the first and second ranked groups are given in Fig. 6, together with the ratios of other groups combined. Ignoring Halictidae, which occupies always the first rank except the first period (IV-I), the bee season is approximately divided into three periods mainly from the abundance of the second group: 1) *Andrena* Period: From late April (IV-I) to June (VI-3). Andrenidae occupies the second rank. The ratio of minor groups

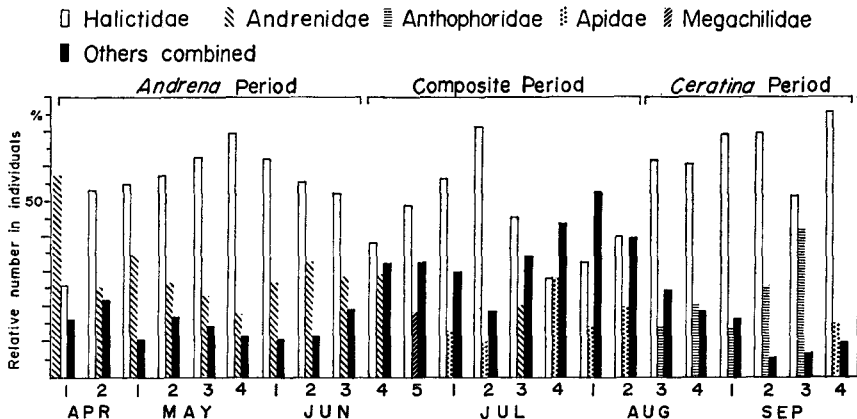


Fig. 6. Seasonal change of predominant groups. Groups occupying first and second ranks are shown together with other groups combined with percentage ratios of individual number in each sampling period.

is small. This period corresponds to the period of gradual increase of bees both in species and individuals, until reaching the first peak. 2) Composite Period: From late June (VI-4) to early August (VIII-2). The second group is variable, though Apidae (*Bombus*) is prevailing. The ratio of minor groups combined becomes higher, exceeding the second group, indicating the activities of diverse suprageneric groups other than Halictidae and Andrenidae. This period includes the second peak in TO (females, Fig. 5). The ratio of Halictidae fluctuates considerably. 3) *Ceratina* Period: From mid August (VIII-3) to late September. Anthophoridae occupies the second rank, nearly exclusively by the appearance of numerous newly emerged *Ceratina* (cf. 3.2). The ratio of Halictidae is constantly high by the appearance of newly emerged adults, especially males. The ratio of minor groups again decreases. This period, including the final female peak and the male peak, is different from the other two in the biotic status of constituents in life cycles, because only a fraction of females sampled on flowers participate in brood rearing, mostly being newly emerged halictid and *Ceratina* species before entering hibernation. Although the survey was stopped at the end of September, some halictine bees and bumblebees are collected on flowers in October.

2.2. *Seasonal change of predominant species*: The phenology of 20 predominant species (cf. Fig. 3) and 16 relatively abundant species is given in Fig. 7, the results in BG and UC combined. In these species, if the lower fiducial limit of the percentage ratio of relative abundance in each period exceeded the reciprocal of the number of species collected in respective period (multiplied by 100), they were regarded as predominants in the period and expressed with black blocks.

A glance at the figure reveals that many predominant species occur throughout the bee season, without exhibiting a clear seasonal succession. Apparently this causes in part the absence of sharp seasonal differentiation of bee fauna under the local climate, possibly being different from the southern regions. A closer inspection shows that most of these seasonally unlimited species belong to three groups, Halictidae, Xylocopinae and Apidae. In these groups, the records of occurrence given in Fig. 7 demonstrate only one side of their lives. Because of their particular life cycles, individuals collected in different seasons are different in the biotic status as explained in the next section (3.2.~3.4.). On the other hand, the change of predominant species is more clear in other groups, especially in Andrenidae (cf. also Sakagami and Matsumura 1967). Thus the seasonal differentiation of bee phenology is principally delimited by these groups. Even in this case, the succession is not gradual because many species appear rather synchronously due to the short length of favorable season.

2.3. *Relation between sampling interval and number of species sampled*: Any faunistic surveys seek to collect as many as possible number of species. In our survey the faunal makeup was sought not only in the species number but also in the relative abundance among species. But to complete the local faunal list is also

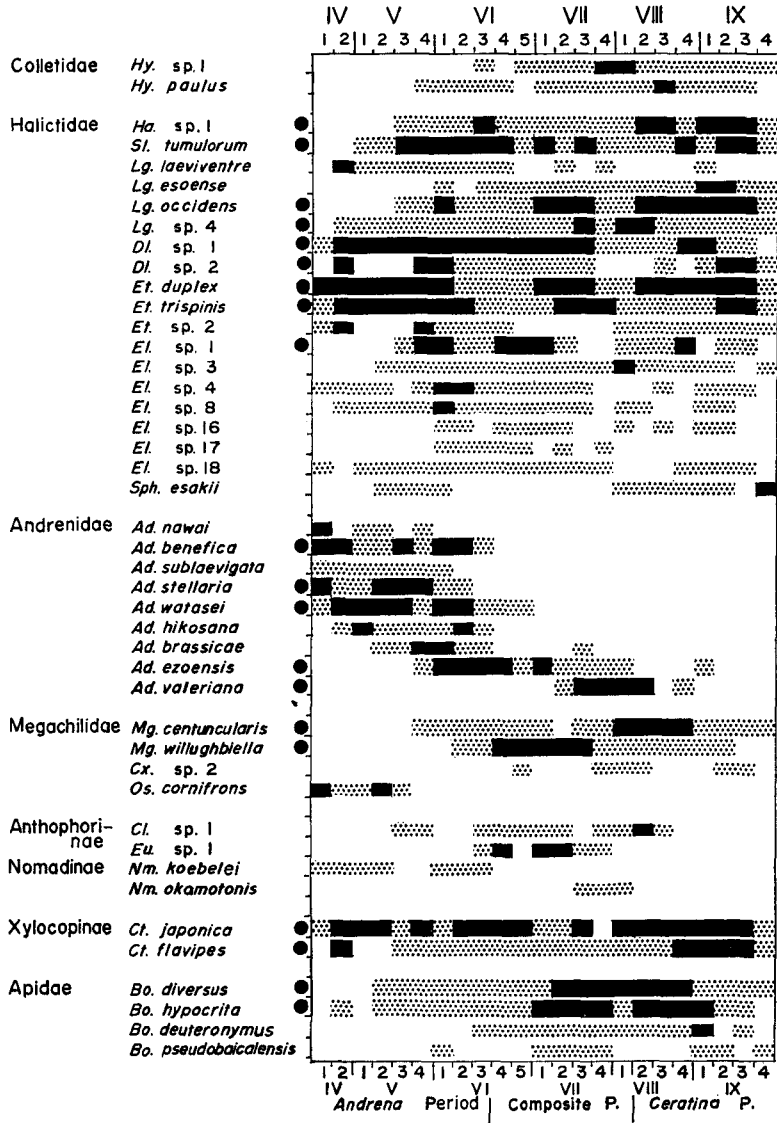


Fig. 7. Phenology of 20 predominant species (cf. Fig. 3, thick bars and marked with black circles) and 16 relatively abundant species (thin bars). Dotted, with capture records; Black block, predominant in the respective period.

one of the important aims in the biofaunistic survey. Because of the seasonal succession of various species, it is impossible to clarify the faunal makeup by a single sampling per year even in the area with a brief bee season as ours. On the other hand, it is difficult to make periodical sampling frequently, for instance, weekly as in the present work at the area remote from the laboratory. In this subsection a compromise between these contradictory conditions is sought on the basis of the results obtained.

The total number of species inhabiting two areas was estimated in 1. 5. Here the discussion is given based upon the actually collected number of species alone. As seen in Fig. 5, D, there are three peaks in the number of species in BG, UC and both combined (early June, early July and early September). The highest peak is found in early June (VI-1) in all BG+UC, UC and BG, with the number of species collected as follow:

No. species (%)	Rank in individual number
BG 35 (41.2)	15
UC 42 (53.8)	5
BG+UC 55 (53.9)	10

From the rank in the number of individuals among 23 sampling periods, it is certain that the high species number in VI-1 is not affected by the high individual number but reflects a real specific diversity at the transition from spring to early summer bee assemblages. Therefore this period could be regarded as the best season to collect as many as possible species under the local climate, though it involves only about a half of total bee species actually collected. To seek the other periods for the best complementary sampling, from the species collected in each period, those not collected in VI-1 was counted and the number was plotted in Fig. 8, together with the percentage in individual number occupied by these species. While the species curves do not show definite trends, the percentage curves show a clear trend, with the peak in IV-1, V-2, VII-4, which are regarded as the periods with the species not abundant in VI-1 are predominant. It is interesting that the curves show lower values in September, nevertheless a mild peak in species number is recognized in IX-2 (cf. Fig. 5, D). This indicates that the increase in this period is mostly brought by the species which are also active in VI-1, as more precisely explained in the next section.

From the trend in Fig. 8, we arbitrarily chose some sampling schedules which may yield as many as possible number of species from our survey as follows:

- A (one sampling per year). Early June (UC, BG VI-1)
- B (2). Early June (cf. A), Late July (UC, BG VII-4)
- C (3). Mid May (UC, BG V-2), Mid June (UC, BG VI-2), Late July (cf. B)
- D (4). Mid May, Mid June, Late July (cf. C), Early September (UC IX-1, BG IX-2)
- E (5). One per month. E_1 (Early part of each month, V-1, VI-1, VII-1, VIII-1 in UC and BG, IX-1 in UC, IX-2 in BG), E_2 (Middle part, V-2, VI-2, VII-2, VIII-2, IX-3 in UC; V-2, VI-3, VII-3, VIII-2, IX-3 in BG), E_3 (Late part, IV-1, V-4, VI-4, VII-4, VIII-4, IX-4 in UC; IV-2, V-3, VI-5, VII-4, VIII-4, IX-4 in BG)

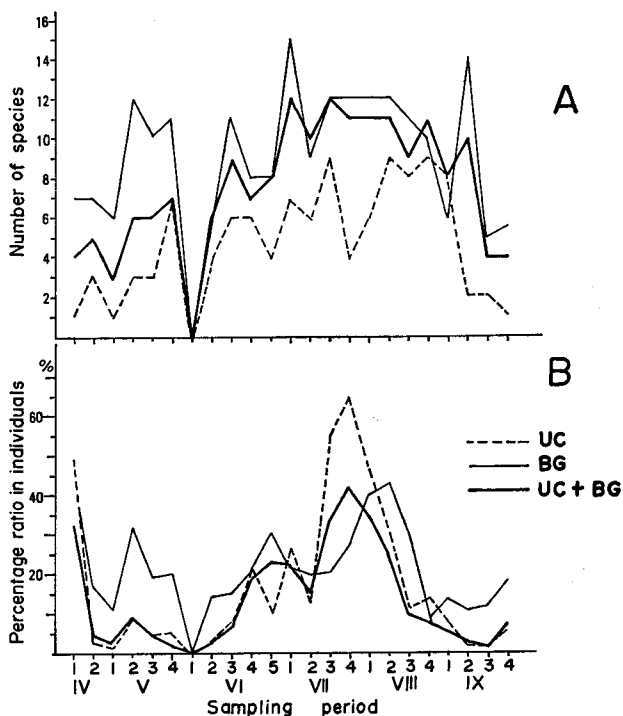


Fig. 8. Seasonal distribution of the number of species not collected in early June (VI-1) (A) and the percentage ratio in individuals of these uncollected species to total catch (B).

F (two sampling per month). F_1 (first and third periods in each month, for instance, V-1 and V-3), F_2 (second and fourth periods, for instance, V-2 and V-4)
 G (three sampling per month). Excluding April, three periods were chosen as $E_1 + E_2 + E_3$

Applying these schedules to our results, the corresponding numbers of species involved are calculated as in Table 4. Monthly sampling covers about 75% of total species without losing the predominant ones, being recommended to apprehend the outline of faunal makeup in the areas with climate similar to that in the surveyed area. Two samplings per month cover about 85% of the total species with the percentage ratio of the individuals of escaped species less than 1%, being favorable to yield a satisfactory conclusion. The inference given above was made purely on the empirical basis, being not immune to theoretical criticisms. Nevertheless, the result may help to find a convenient compromise between sampling efficiency and circumstantial limitations.

Table 4. Number of species covered by various sampling schedules based upon actual results in 1959. T: Total number of species (actually collected). N: Number of species covered, N%: Ditto, in percentage. U: Individual number of uncollected species U%: Ditto, in percentage.

Sampling schedule	UC+BG (T=102)				UC (T=78)				BG (T=85)				Number of uncollected predominant species (to 25th rank)		
	N	N%	U	U%	N	N%	U	U%	N	N%	U	U%	BG+UC	UC	BG
A	55	53.9	702	10.3	42	53.9	460	14.8	35	41.2	739	19.7	2	4	6
B	66	64.7	198	3.0	46	59.0	224	7.2	47	55.3	432	11.5	0	2	4
C	63	61.8	166	2.4	44	56.4	208	6.7	53	62.4	221	5.9	0	1	2
D	74	72.5	57	0.8	47	60.3	204	6.6	63	74.1	97	2.6	0	1	0
E ₁	85	83.3	42	0.6	59	75.6	39	1.3	68	80.0	82	2.2	0	0	0
E ₂	73	71.6	86	1.3	53	67.9	88	2.8	57	67.1	88	2.4	0	0	0
E ₃	78	76.5	71	1.0	56	71.8	46	1.5	64	75.3	88	2.4	0	0	0
F ₁	87	85.3	24	0.4	65	83.3	27	0.9	71	83.5	34	0.9	0	0	0
F ₂	94	92.2	8	0.1	66	84.6	42	1.4	78	91.8	7	0.2	0	0	0
G	95	93.1	9	0.1	70	89.7	8	0.3	82	96.5	5	0.1	0	0	0

3. Life cycle approach

Up to the present the faunal structure was described and discussed entirely based upon the numbers of species and individuals sampled. Certainly such approach is convenient and often inevitable to apprehend quantitatively the assemblage structure. However, if such way would be followed carelessly, there can appear a fallacy of interpreting the assemblage structure only based upon the mere numerical data, ignoring the lives of the assemblage members, each of which must have a particular mode of life. The same number of individuals collected in two species does not necessarily mean that they are at the same level in relative abundance, when their life mode is so different that the same sampling procedure is not always similarly effective to both. This is particularly true for bees, the life modes of which are quite variable among groups. We have still no reliable sampling procedure which takes diverse life modes in consideration. In the present section, some differences of life cycles in various bee groups are explained in connection with the result in the present survey. This may enlighten some aspects which are important for the understanding of wild bee assemblage structure but can not be clarified from the sampling data alone.

The life mode of bees is fairly variable and classified from diverse points of view, habitat preference, nesting site, nest structure and construction, flower visiting habits, life cycle (Malyshev 1935, Linsley 1958, Stephen, Bohart and Torchio 1969) and social structure (Michener 1969). In the present paper we only deal with some aspects of life cycle which directly affect the number represented in samples. On this account the bee groups collected in the area are divided in

the following four types, which are separately discussed below: 1) Typical solitary bees, 2) Xylocopinae (*Ceratina*), 3) Halictine bees, and 4) Apidae (*Bombus*).

3.1. Life cycle of typical solitary bees: This group involves all bee groups other than Xylocopinae, Halictidae and Apidae. In spite of diverse life modes exhibited by these bees, there is a biological character common to them: They all hibernate as immatures or adults in their natal cells. Consequently, there is no burst of newly emerged adults in autumn as seen in the other three groups, which is the main cause of the peaks of species and individual numbers in September in our result. The life cycle of the species belonging to the type concerned here is schematized as given in Fig. 9 below.

In this type, phenological difference is determined by three items: Number of generations per year, season of appearance and length of flight period in each generation which is determined by the length of life-span of each individual and/or the degree of synchronization at emergence. If there are more than one generation per year and/or the length of flight period prolongs, such species may appear for a lasting period throughout the bee season. By the relative scarcity of such species, the seasonal succession is more pronounced in typical solitary bees. The phenological differentiation of bee season is thus qualitatively determined mainly by this type of bees. As to the number of generations many bees seem univoltine even in warmer regions. Therefore it is likely that most bees concerned here possess only one generation per year. Nevertheless, some species are assumed as having a second generation at least partially from their prolonged activity. To confirm the number of generations in bees is not easy, ultimately necessitating the discovery of nests and the examination of the gradual shift of immature stages involved.

This is, however, a bottle neck in bionomic studies in bees, because nests of most species are only hazardly discovered and nearly always insufficient to make a closer life cycle analysis. In the present study, the relative age of the specimens sampled of some representative species was estimated by wear of some body parts. The life cycle assumed by this method is described and discussed each major group separately. In many species, some specimens were previously dispatched for exchange or donation, so that the number of specimens studied as to age structure differs slightly, but not considerably, from that used in sections I and II.

1) Colletidae: Most species appear during a short period, but the specimens examined are too scarce to determine the life cycle. Phenology of two species, *Hy. paulus* and *Hy. sp. 1* is given in Fig. 9, top. The relative age in females was divided into three classes based upon the wear in mandibles (1, intact, 2, slightly worn, 3, heavily worn). In *Hy. paulus* many specimens were dispatched before age determination, which were included in the curve. *Hy. paulus* seems to be bivoltine, but curiously no heavily worn females were obtained. *Hy. sp. 1* may have a partial second generation but further evidence is required. Beside these species, *Hy. monticola* might have a second generation at least partially, judging

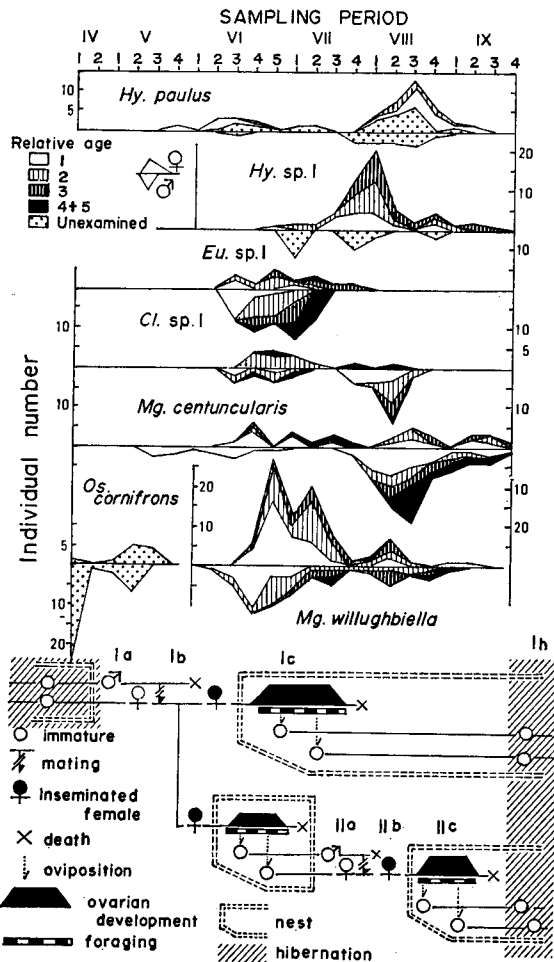


Fig. 9. Phenology of some predominant typical solitary bees. Estimation of relative age is given in text. Bottom, schematized life cycles of univoltine and bivoltine species, Ia-Ic, Ih and IIa-IIc, IIh show corresponding phases of two generations.

from capture records (cf. Appendix).

2) Andrenidae: This is the best group to trace the seasonal succession of various species as already described (Sakagami and Matsumura 1967). Most species appear in spring and early summer, possessing relatively short flight periods, though relatively long in *Ad. watasei* and *Ad. ezoensis* (cf. also Matsumura 1970). In Sakagami and Matsumura (1967), all species were regarded as univoltine. Later, a second generation, at least partially, was confirmed in *Ad. ezoensis* (Matsumura unpub., from nest excavation), and suggested in *Ad. brassicae* (from male activities cf. later).

3) Megachilidae: This family involves two groups with different phenology,

Osmia being active in early spring (Fig. 9, middle) and other genera of mainly summer bees. Phenology of two species of the second group is cited in Fig. 9. In females wing and mandiblar wear were classified in five classes of ascending order, and the relative age was expressed as combinations of these two indices (Mandible-Wing): 1 (1-1, 1-2), 2 (1-3, 2-1, 2-2, 2-3), 3 (1-4, 1-5, 2-4, 2-5, 3-1, 3-2, 3-3), 4 (3-4, 3-5, 4-1, 4-2), 5 (4-3, 4-4, 4-5, 5-1, 5-2, 5-3, 5-4, 5-5). In males wing wear alone was adopted. In both sexes, two oldest classes, 4 and 5, are grouped in Fig. 9. Two species exhibit very different life-cycle patterns. *Mg. willughbiella* may possess a single generation, whereas *Mg. centuncularis* certainly two per year. Predominance of males in the second generation is remarkable but it is unknown whether this represents a real imbalance in sex ratio or the different behavior of males as to flower visits.

4) Anthophorinae: In two species of this subfamily, females were collected not abundantly, and examination of mandibles was difficult to make. Therefore, the relative age was determined in *Eu.* sp. 1 by wing wear alone while in *Cl.* sp. 1 both by wing wear and coloration of hairs, which changed from bright fulvotestaceous to grayish. As shown in Fig. 9, *Eu.* sp. 1 is a typical univoltine summer species with a brief flight period. On the other hand, *Cl.* sp. 1 seems to have two generations, judging from the occurrence of worn males in late June to early July and fresh ones in late July to early August, though further evidence is required.

5) Nomadinae: It is difficult to trace the life cycle in this subfamily, because of the scarce number of individuals sampled, being characteristic to most parasitic bees. Probably most species are univoltine with a relatively short flight period. The seasonal succession of various species seems to occur corresponding to that of Andrenidae, the principal hosts. But *Nm.* aff. *fulva* could be bivoltine judging from capture records (cf. Appendix).

Number of generations per year and length of flight period offer a difficult problem in estimating the relative abundance among the species. For instance, suppose two species which start their flight activities approximately at the same time and with the same population size but the flight period is $A > B$. In such instance, the periodical sampling may bring much more specimens of A or A may be regarded as more abundant than B, in spite of the population density is equal between two species. Or, if A is univoltine and B bivoltine, it is not easy to judge which species is really more abundant. In this case, the interpretation may differ according to the usage of "abundance", whether it signifies the total individuals produced per year, or of a particular generation, or rather a product of individual number and mean life span as a measure of the influence of each species upon flowers. The relative abundance treated in the present work could be regarded as closest to the last mentioned meaning.

Another aspect worth to mention is a remarkable imbalance of sex ratio in some species (cf. Fig. 3). In some halictid and apid bees, such imbalance indicates a real deviation from the ratio 1:1 because of their complicated social patterns. In typical solitary bees, however, the real sex ratio must not deviate much from 1.0 or may show only a slight preponderance of males produced by telytokous

parthenogenesis.

From the samples obtained, 25 species of typical solitary bees represented by ten or more specimens were chosen and the deviation of sex ratio from the null hypothesis of 1:1 was tested. The result is given in Table 5, using the following categories, $\delta \gg \text{♀}$ or $\text{♀} \gg \delta$ ($P < 0.01$), $\delta > \text{♀}$ or $\delta < \text{♀}$ ($0.01 < P < 0.05$), $\delta \approx \text{♀}$ ($P > 0.05$), in the descending order of the male preponderance. The table shows the deviation from the ratio 1:1 in more than the half of the species, sometimes to extreme degrees, as in the species given at the top and bottom.

The appearance of such remarkable deviation is interpreted as a combined outcome of specific male behavior and our sampling procedure. The female behavior in bees are as a whole indubitably much more differentiated than in males. As to the sexual behavior, however, females are usually the passive sex not showing marked interspecific differentiation, with a probable exception of Apinae (honeybees and stingless bees). On the contrary, males exhibit various types of nuptial behavior as classified by Haas (1960): 1) Simple swarming course type, 2) Feeding

Table 5. Sex ratio in some predominant species of typical solitary bees

Sex ratio type	Species	Total number of specimens	Sex ratio $\delta/\text{♀}$
$\delta \gg \text{♀}$	<i>Eu. sp.1</i>	71	3.73
	<i>Os. cornifrons</i>	46	3.18
	<i>Cl. sp.1</i>	53	3.08
	<i>Ad. valeriana</i>	144	2.79
	<i>Mg. centuncularis</i>	113	2.53
	<i>Ad. ezoensis</i>	287	1.54
$\delta > \text{♀}$	<i>Os. taurus</i>	10	9.00
$\delta \approx \text{♀}$	<i>Cx. sp.2</i>	11	2.66
	<i>Ad. watasei</i>	116	1.23
	<i>Nm. koebeli</i>	24	1.00
	<i>Ad. hikosana</i>	36	0.64
	<i>Ad. haemorrhoea</i>	13	0.62
	<i>Ad. kaguya</i>	16	0.60
	<i>Nm. sp.3</i>	11	0.57
	<i>Nm. okamotonis</i>	12	0.33
	<i>Hy. monticola</i>	10	0.25
$\delta < \text{♀}$	<i>Mg. willughbiella</i>	140	0.65
	<i>Ad. astragalina</i>	19	0.27
$\delta \ll \text{♀}$	<i>Hy. paulus</i>	53	0.43
	<i>Ad. nawai</i>	43	0.30
	<i>Hy sp.1</i>	83	0.28
	<i>Ad. benefica</i>	120	0.26
	<i>Ad. stellaria</i>	132	0.20
	<i>Ad. sublaevigata</i>	42	0.20
	<i>Ad. brassicae</i>	30	0.03

course type, 3) Type with swarming courses correlated to feeding localities, 4) Territorial type. Such diverse behavior types may lead to the uneven distribution of males throughout the area surveyed. In our survey, any bee individuals were captured when discovered but it is evident that sampling was mainly undertaken at the places provided with flowers in bloom. Through this procedure, it is probable that the small areas where males were concentrated were ignored at sampling. Or, in other words, our sampling was more biased as to males than females.

This is explained best by some *Andrena* species, most species of which seemingly belong to the first type by Haas. The male predominance is seen in two species, *Ad. valeriana* and *Ad. ezoensis*, both summer species being exceptional for Andrenidae. In these species, males fly around with zigzag fashion on the area covered with white clover. Because this weed occupied a vast extent within the area surveyed, numerous males were noticed and collected during sampling. On the other hand, the female preponderance is noted in six *Andrena* species (Table 5). In three out of these six species, *Ad. nawai*, *Ad. sublevigata* and *Ad. brassicae*, one of us (S.F.S.) once observed in other occasions a concentration of numerous males within a narrow place not provided with flowers, where each male repeated zig-zag flights. The case of *Ad. brassicae* is cited here:

Okusawa, Otaru (June 30 '70, Fig. 10): An area of 5×5 m. sq. along the road passing the forested hill. The area was surrounded by forest but was free from tree and insolated, covered with white clover, sorrels and some grasses. Amid the area was a small elliptical heap of packed soil 150×70 cm, h. 40 cm, probably made artificially. The heap was sparsely covered with white clovers and about ten males of *Ad. brassicae* flew about 2~3 cm above the ground, taking a zig-zag course and following several definite routes as shown in the figure. Although individual recognition was not made, each male seemingly repeated go and return along the routes.

In our survey, *Ad. brassicae* is represented by 38 females and only one male. In a recent survey made at the foot of Mt. Moiwa suburb of Sapporo, the result was 243 females and no male (Kawano unpub.). The observation given above partly explain such imbalance of sex ratio in sampling mainly made on flowers. Considering the date of observation and the proterandric tendency common in *Andrena*, it also suggests the presence of a second generation in this species at least partially.

Therefore, it is inferred that the real relative

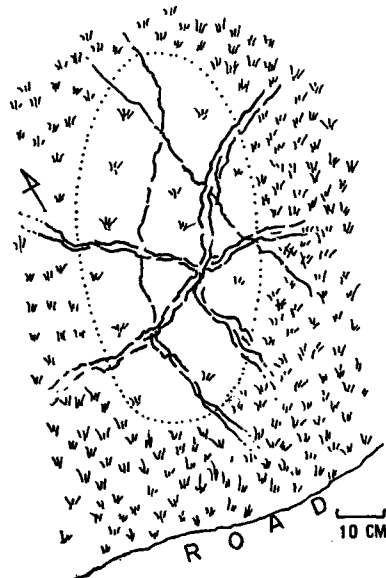


Fig. 10. Swarming flight courses found in *Andrena brassicae* males.

abundance is better reflected in the number of females captured than males, as far as our sampling procedure is concerned.

3.2. Life cycle of *Ceratina* species: Except *Allodape* and related genera, Xylocopine bees are basically solitary, but differ from typical solitary bees in several bionomic characters as pointed out by one of us (Sakagami and Laroca 1971 b). From the sociological point of view the beginning of contact between mother and offspring, either as immatures or as adults, is of the utmost importance. As to the wild bee biofaunistics, the following two characters are noteworthy: 1) Unusually long adult life span and resulting long flight activities, and 2) Hibernation by adults of both sexes once performed flight and feeding activities. These two features are reflected in phenology of two *Ceratina* species sampled in the present survey (Figs. 5~7). A closer analysis of seasonal trend was made by sorting the specimens collected into age classes (cf. 3.1., Megachilidae. Exception: Females with mandibular wear 2 and wing wear 1 was put into age class 1, not in 2). The results are shown in Fig. 11, together with schematized life cycle. Some important outcomes and derived findings are enumerated:

- 1) Gradual increase of worn individuals clearly shows one generation per year.
- 2) Flight period of females is very long as shown by the presence of heavily worn individuals in autumn which corresponds to the phenology given in Fig. 7. 3) Male flight period seems also longer than in typical solitary bees, as suggested by several worn individuals collected in September, especially in *Ct. flavipes*.
- 4) Reflecting the group character, newly emerged adults of both sexes are collected in autumn.
- 5) The number of new females in autumn is extremely high, being nearly equal to all other females combined as shown by the curves given in Fig. 11. 6) From the results of surveys in other areas this high number was seemingly caused by some special conditions in the areas surveyed. Anyhow, this is one of the main causes of the autumnal peak in curve XY and partly TO in Fig. 5, and as well as increased percentage ratio of Anthophoridae in Fig. 6.
- 7) Curiously the number of new males is much lower in autumn, especially in *Ct. japonica*, and higher in early spring than females, nevertheless the sex ratio judging from immatures in nests (Shiokawa unpub.) does not deviate much from 1:1.
- 8) This skewed sex ratio must reflect the different behavior between sexes in reference to flower visits. But, the scarcity of males in autumn does not relate to the mating behavior, because, in contrast to halictine bees and bumblebees, mating takes place in Xylocopinae in the next spring, not in autumn.
- 9) Among 255 new females (age class 1) of *Ct. japonica* and *Ct. flavipes* collected during VIII-4 ~ IX-4, some ones carried pollen loads on legs, 21 (8.3%) with trace and 14 (5.5%) with distinct loads in *Ct. japonica* and 2 (5.4%) and 1 (2.7%) in *Ct. flavipes*. Pollen foraging by females not participating in brood rearing is rare in other solitary bees but known in *Ct. asuncionis* in Southern Brazil (Sakagami and Laroca 1971b), suggesting temporary storage of food. It is possible that scarcity of new males in autumn relates to this trait, because communal hibernation of both sexes in the same hibernaculum is recorded

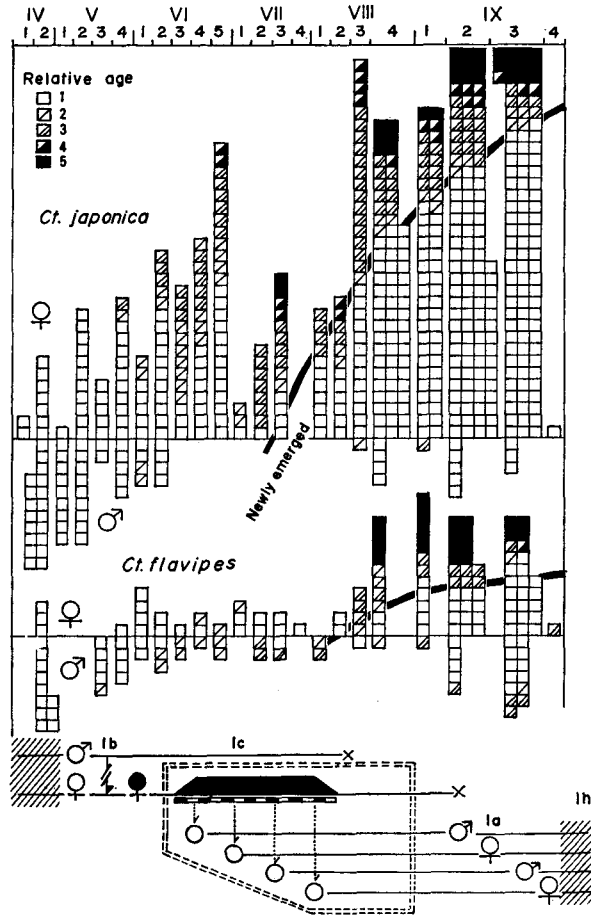


Fig. 11. Phenology of two *Ceratina* species. Each individual shown by a square with age indication, and their schematized life cycle at bottom (legends cf. Fig. 9).

in both species (Shiokawa 1966, and unpub.). 10) Old females alive to autumn seem to behave differently from brood rearing females at flower visits. As seen in Fig. 11 the number of such females is quite high compared with earlier seasons, not exhibiting gradual decrease from spring to autumn, which is logically expected if there is no difference in flower visiting activity. 11) Some of these old females (those collected during VIII-4 ~ IX-4, with mandibular wear 3 ~ 5), carried pollen loads on legs, nevertheless brood rearing already ceased: *Ct. japonica*: 10 (11.6%) trace and 10 (11.6%) distinct among 86 females; *Ct. flavipes*: 1 (4.2%) trace and 6 (25%) distinct among 24 females. 12) Survival of these old females to the next spring, confirmed in] *Ct. asuncionis* and some halictine bees (cf. 3.3.), was not revealed as shown by the absence of such females in early spring.

Thus, there are still many unsolved problems in life mode of two *Ceratina* species, but it was proved that their high ranks in relative abundance, the second and tenth respectively (Fig. 3), was partly caused by the emergence of new adults in autumn, which did not occur in typical solitary bees.

3.3. Life cycle of Halictine bees: Probably the halictine bees are one of the most fascinating groups for the study of social structure in bees, or in invertebrates in general, by the presence of diverse social patterns side by side in the same genus or subgenus (Sakagami and Michener 1962, Michener 1969, Sakagami in press). Just by this reason, however, it is most difficult to give a meaningful conclusion about the relative abundance of various species. In the case of eusocial species (cf. Michener 1969), the unit of life is apparently the association of individuals living in the same nest, not each individual. But the clarification of social structure, which may vary among species, is not an easy task. This ultimately necessitates the examination of gradual shift of inhabitants, both adults and immatures, in many nests. But the discovery of nest is very difficult in many species. One example may suffice to demonstrate it: *Lg. occidentis* is the third ranked species in our survey, yet one of us (S.F.S.) has discovered only four to five nests during more than fifteen years in the areas surveyed.

Even if we would succeed to clarify the social structure of each species, which varies often between two closely allied species, through painstaking field surveys, yet it is difficult to have a reliable index upon the relative abundance of nests. Therefore, we are obliged, for the time being, to consider the individuals captured out of nests as the units to measure the relative abundance, in the sense that given in 3.1., that is, regarding the relative abundance as a measure of the influence upon flowers.

Even under such limitation, it must be cautious to conclude the life cycles of diverse halictine species from capture records alone. Since 1958 one of us (S.F.S.) has been participating in bionomic studies of various species inhabiting the areas surveyed. The results on one species, *Et. duplex*, were serially published (Sakagami and Hayashida 1958~'68, Sakagami and Fukuda 1972b), and those on other species will be described elsewhere. In the present paper, the life cycles of some representative species are traced through age class analysis, using the criteria given in 3.1. (Megachilidae), but the data taken from nest excavation and examination of ovaries, spermatheca, etc. of adult females are incorporated to complement the interpretations.

Life cycles of some abundant species are given in Fig. 12, together with the relative abundance of females, males, and newly emerged females in percentage ratios. Schematized life cycles of *Et. duplex* and *Lg. occidentis* were presented in Sakagami and Hayashida 1968. Fig. 13 shows the phenology of four major groups involving many species. The synoptic inspection of two figures may give a perspective of diversified life cycles in this group.

Before dealing with each group, some traits general to halictine bees are briefly summarized: 1) Flight period of females are considerably long in many

species, caused partly by the next item, but partly by the diversity in life cycle, resulting in the lasting occurrence throughout the bee season (Fig. 7). 2) As in *Ceratina* newly emerged adults appear in autumn, causing the peaks in September in HA and TO (Fig. 5, E), especially in males. 3) In contrast to *Ceratina*, mating takes place in autumn, thereafter males die (with a few exceptions, for instance, *Lg. xanthopum* in Palaearctics and *Paraxystoglossa jocasta* in Neotropics, cf. Sakagami in press), leaving females which hibernate and start nesting activities in the next year. 4) Reflecting this characteristic, males appear only in the later half of the bee season, usually giving a skewed sequence in phenologic curves. In some species, a few old females survive to their second spring. This fact was confirmed in *Et. duplex* (Sakagami and Fukuda 1972b) and *Et. calceatus* (Sakagami and Munakata 1972), by the presence of heavily worn females in early spring. Regarding the females collected in early spring of age classes 3~5 as such, these two years old females are found in other species, too: *Dl.* sp. 1, *Et.* sp. 2, *Sl. tumulorum* and especially *Dl.* sp. 2 (Fig. 12).

Life cycles of each group are outlined based upon the results given in Figs. 12 and 13. Obviously some conclusions given below are affected by the conditions particular to the areas surveyed. It must be mentioned that autumnal burst of new adults was far inconspicuous in some surveys subsequently made in other areas. Often only a limited number of males and new females were collected. A similar result was also obtained in *Ceratina*. The cause of such difference is still unknown but environmental conditions, especially floristic makeup in autumn, may be important. Nevertheless, the results in the present survey may be useful for further researches.

1) *Halictus* s. str.: Phenology of *Ha.* sp. 1 shows a single generation per year, by the gradual shift of age classes in females. A few nest excavations and the length of flight period, as well as age class shift indicate that the species is solitary. The percentage ratio occupied by adults emerged in autumn is enormous, especially the ratio of new females is the highest among all species sampled.

2) *Seladonia*: The female curve shows a gradual decrease and corresponding shift of age classes, but intact females appear in July and August, causing the permanence of this class throughout the season. Only recently it was confirmed that this species is rudimentarily eusocial under local climate. Intact females in July and partly August are thus regarded as workers in matrifilial phase, though no conspicuous size difference is noticed between spring and summer females. The appearance of new autumn adults is distinct in both sexes, but not so conspicuously as in *Ha.* sp. 1.

3) *Lasioglossum* s.str.: Based upon phenology and nest excavation, all *Lasioglossum* species are regarded as solitary and univoltine. This group is divided into three subgroups by phenology, which correlate to some degree with morphological characters. 3a) *Laeviventre*-group: *Lg. laeviventre*, *Lg. discrepans* and *Lg.* sp.1, 3b) *Scitulum*-group: *Lg.* sp.4 and probably *Lg. scitulum*, and 3c) *Occidens*-group: All other species. The species of the first subgroup are typical

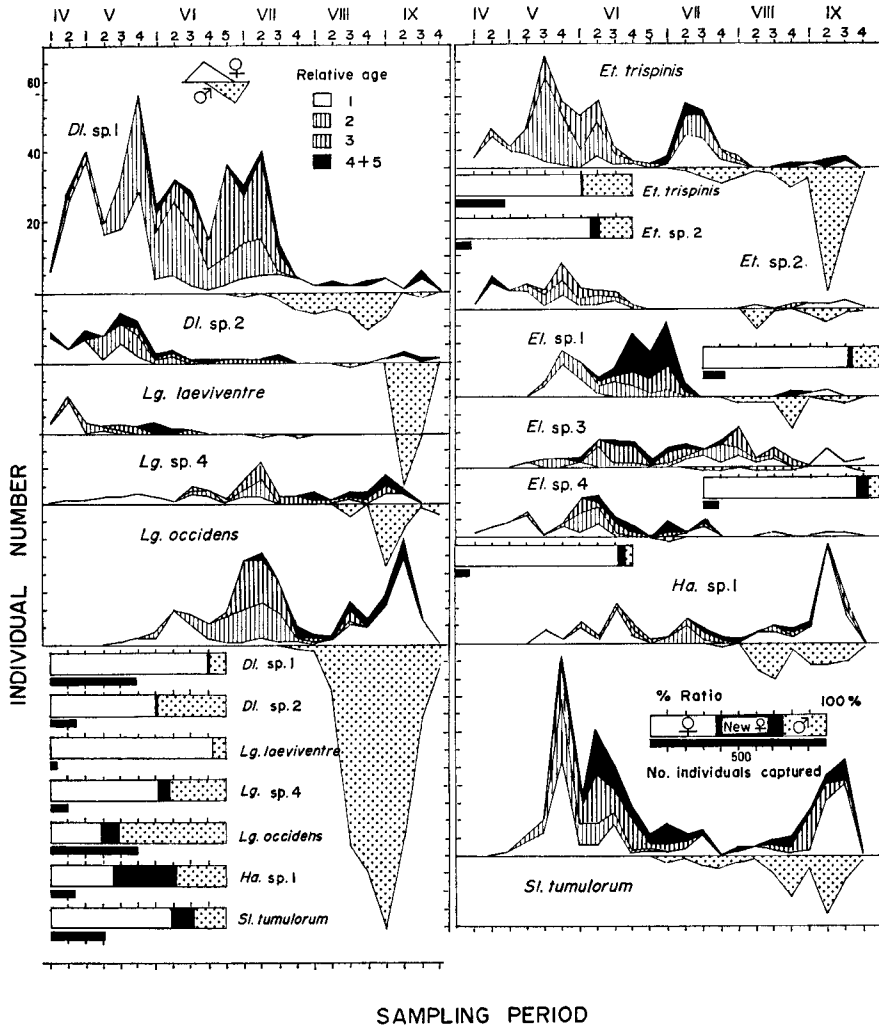


Fig. 12. Phenology of some representative halictine species with age succession, together with relative abundance of females, males and newly emerged females.

early spring bees, rapidly disappearing in late spring as shown by the curve of *Lg. laeviventre*. New autumn adults are scarce in all species. On the contrary, *occidentis* subgroup is characterized by the later appearance and burst of new autumn adults, as shown by the curve of *Lg. occidentis*. Phenology of *scitulum* subgroup, at least of *Lg. sp.4*, is basically same to *occidentis* subgroup, but it appears relatively earlier in spring. The relation among three subgroups is clear from the phenologic curve of *Lasioglossum* s.str. given in Fig. 13.

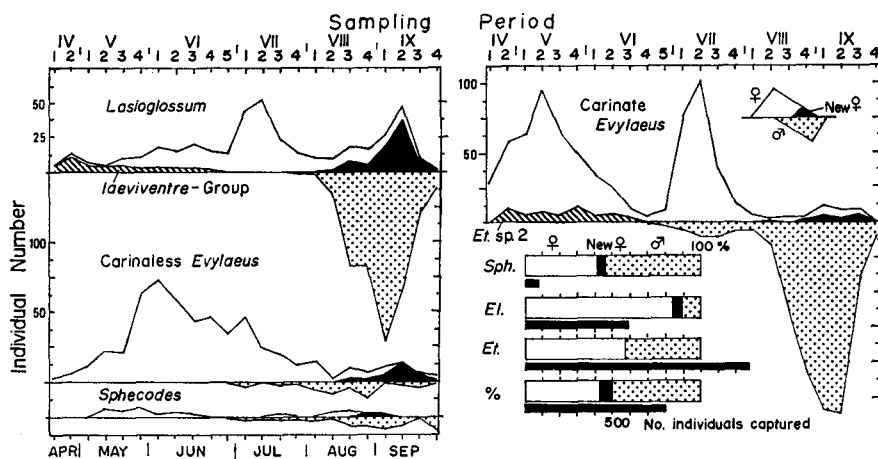


Fig. 13. Phenology of some major halictine groups, showing relative abundance of females, newly emerged females and males. Legends partly given in Fig. 12.

Lasioglossum (mainly the last two subgroups) is characterized by the burst of new adults, especially males, in autumn (cf. Fig. 13). As seen in Fig. 12 and Fig. 3 (cf. sex ratio), the high rank in relative abundance occupied by *Lg. occidentis* is distinctly affected by the preponderance of males.

4) *Dialictus*: The phenologic curves of two species are quite different. While *Dl. sp.2* rapidly decreases after early June, *Dl. sp.1* is abundant until mid July. It has long been known to one of us (S.F.S.) that polygynic association is common in this species, and the abundance in June and July was regarded as caused by unusually long flight activities of auxiliary females. But recently it was confirmed that a rudimentary eusociality appeared in summer. Thus, a small quantity of unworn females captured in June and July could be workers and the phenology of social structure requires further analysis. It is possible that *Dl. sp. 2* also possesses a rudimentary eusocial stage but again a closer analysis is required. In both species, autumn females are less abundant than in *Lasioglossum* (excluding *laeviventre* group) and *Halictus* s. lat. Males are more abundant than new females but less than in two groups mentioned.

5) *Carinate Evylaeus*: This group includes both solitary and eusocial species. Among the species sampled, *Et. duplex*, *Et. trispinis*, *Et. sp. 1* (from other data) and probably *Et. apristus* belong to the latter. *Et. sp. 2* is apparently solitary as seen in Fig. 12. Although only two specimens were captured, *Et. pallidulus* is also solitary (Sakagami and Munakata 1966). It has well been known that eusocial species of this group is characterized by an advanced caste differentiation and appearance of an inactive phase between solitary and matrifilial phases (Knerer and Plateaux-Quénu 1967, Sakagami and Hayashida 1968, Sakagami unpub.), causing a typically bimodal phenologic curve of females. Two peaks represent respectively solitary and matrifilial phase of a single generation, never two succes-

sive ones. A third low peak usually appears in autumn, composed of heavily worn females and newly emerged ones. This characteristic curve is best expressed in *Et. duplex*, the top ranked species in the present survey (Sakagami and Hayashida 1968). The phenology of another predominant species, *Et. trispinis*, given in Fig. 12, is similar to that of *Et. duplex*. The phenologic curve of total females of this group is given in Fig. 13. Excluding *Et. sp. 2*, which is separately presented, the majority of females are occupied by three eusocial species mentioned above so that the bimodality is clearly demonstrated. The female curve of Halictidae in Fig. 5 (E-HA) shows a distinct drop in June. It is now clear that this is mostly brought by the peculiar social and phenologic pattern in eusocial carinate *Evylaeus*. This drop is recognized in the curve of total females (Fig. 5, E-TO) though obviously less acutely. By the separate presentation of ET in the curve, it is clear that the drop of total female number is conditioned primarily by the phenology of carinate *Evylaeus* as the most predominant bee group than by environmental conditions.

In a previous paper (Sakagami and Fukuda 1972b), it was commented that few newly emerged autumn females of *Et. duplex* were captured on flowers contrasting to the burst of males, nevertheless the sex ratio was about 1:1 from nest examinations and all females excavated from hibernacula had fully loaded crops, proving their flower visits before hibernation. This curious imbalance, the reason of which is still unknown, is also seen in *Et. trispinis*, and less markedly in *Et. sp. 2* (Fig. 12). Consequently, the phenologic curve of total carinate *Evylaeus* exhibits an extremely skewed form as to autumn males and females (Fig. 13).

6) Carinaless *Evylaeus*: This group is represented by the highest number of species among all bee groups sampled. But the individual number of each species is so small than in other halictine groups that it is not easy to assume their life cycles. In this group, no eusocial species has so far been recorded from Hokkaido. Instead, the communal life, the presence of more than one female, each possessing her particular section, in the same nest, is known in *El. ohei* Hirashima and Sakagami (Sakagami, Hirashima and Ohé 1966, not represented in the present survey) and *El. sp. 16* (Sakagami unpub.). Many species seem univoltine as is shown by phenologic curve of *El. sp. 1* in Fig. 12, in which the number of heavily worn females is remarkably high in late June to early July for an unknown reason. Besides it *El. sp. 8, 10, 16, 17* are certainly univoltine. On the other hand, there are some species with a prolonged flight period. Two examples, *El. sp. 3* and *sp. 4* are cited in Fig. 12. The phenologic curve of *El. sp. 4* might hardly be interpreted as bivoltine. Yet the presence of a second generation, at least partially, is confirmed through nest excavations. The curve of *El. sp. 3* is much prolonged and their bivoltinism seems probable.

In most species, newly emerged autumn individuals, both females and males, are very few, as seen in *El. sp. 3* and *4*, though males of *El. sp. 1* are relatively abundant. This tendency is reflected in the phenologic curve of total carinaless *Evylaeus* given in Fig. 13.

7) *Sphecodes*: The total phenologic curve of this parasitic genus is presented

in Fig. 13 merely to complete the picture. Most species seem univoltine. *Sph. esakii* and *Sph. scabricollis* could be bivoltine. It is difficult to determine the number of generations in some species with a prolonged flight period, because due to their parasitic mode of life the number of specimens captured is small and mandibular wear cannot be used to estimate relative age.

Summarizing, the halictine bees, the most predominant group, are most diversified in life cycles. This peculiarity, offering in itself a fascinating problem, must be kept in mind in the biofaunistic survey of wild bees to avoid false conclusions upon the relative abundance and phenology.

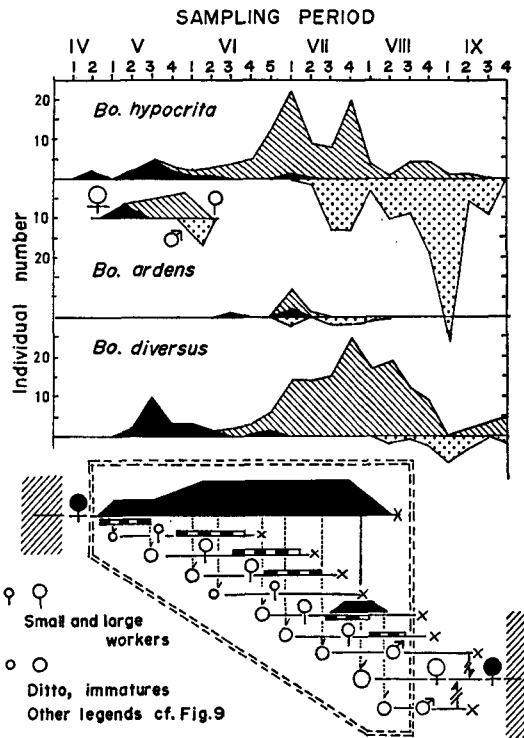


Fig. 14. Phenology of three bumblebee species and their schematized life cycle at bottom. Legends cf. Fig. 9.

3.4. Life cycle of Bumblebees: As the Japanese honeybee, *Apis cerana cerana* Fabricius, does not inhabit Hokkaido, the Family Apidae is represented there only by bumblebees. Being an exclusively eusocial group, its social pattern is much more complicated than in any other bees. But from the view point of relative abundance and phenology, it presents less difficulties than halictine bees, because the social pattern and life cycle in temperate regions are more stable among species, as schematized in Fig. 13 below, starting from solitary nest foundation by the queen through gradual growth of nest by worker production and culminating in the

issue of sexuals. Mating takes place in autumn. Males die and only fertilized queens hibernate. Phenologic curves of three species given in Fig. 14 show this general pattern, with the sequence of appearance from queens to workers and males. The newly emerged queens make flight activities but are seldom captured on flowers. The appearance of males is quite different between *Bo. ardens* and the other two species. *Bo. ardens* produces males already in early July. Certainly its colony is short-lived as in some other species of *Pyrobombus*, sharply contrasting to *Bo. diversus*, males of which appear only in August and September. *Bo. hypocrita* shows an intermediate type, with a prolonged male activity. Further, the abundant male production in this species is noteworthy, which is often observed in and near Sapporo. This may depend either on the specific difference in mating behavior as studied in the European species by Frank (1941) and Haas (1949), or on the appearance of laying workers by earlier deaths of queens. Although this species is certainly one of the predominant bumblebees in Hokkaido, this high male production must be reminded in discussing its relative abundance.

Finally the fact mentioned in halictine bees that the unit of life is nest, not each individual, is far more important in bumblebees because of its larger colony size, but how to incorporate this peculiarity in wild bee survey remains, for the time being, as an unsolved problem.

3.5. Relative abundance corrected with respect to life cycle types: In the preceding subsections we described various life cycles in wild bees, with special reference to the aspects being important as to surveys on relative abundance and phenology. Unfortunately we are still not in the position to develop an improved sampling procedure which eliminates the difference in life cycle patterns. Instead we give here the relative abundance of various bee groups obtained in our survey corrected on two aspects. As given in 3.1. the sex ratio of various species often considerably deviates from the theoretical ratio of 1:1. It was interpreted there that this deviation might be caused by male mating behavior particular to each group or species, and that our procedure was less biased as to females than males. In eusocial halictine bees and bumblebees, the real sex ratio itself varies from 1:1 because of their particular mode of life. To eliminate this variability, we calculated the relative abundance only based upon females. Nextly it was explained in 3.2. ~3.4. that in Xylocopinae, Halictidae and Apidae newly emerged adults appear, often abundantly, in autumn, which does not occur in typical solitary bees. To eliminate this difference, we calculated the relative abundance of various groups based upon the materials excluding males and autumn new females. The separation of the latter from other females is relatively easy because in autumn old females are more or less heavily worn. Fig. 15 compares these two corrected relative abundance, B and C, with the uncorrected one, A, given in Fig. 2 below.

The figure demonstrates no remarkable difference in the relative abundance calculated by three procedures at suprageneric level. This is fortunate because the use of total individuals, which would be often inevitable in small samples,

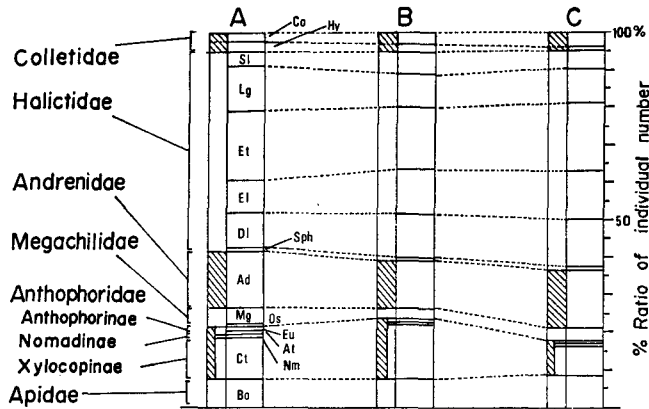


Fig. 15. Relative abundance of various bee groups obtained in the survey BG+UC, shown with percentage ratios in individual number. A. All individuals, B. Females alone, C. Ditto, excluding autumn new females.

could be allowed to estimate the relative abundance at least in and near the areas surveyed.

Some changes in relative abundance are pointed out. Halictidae continues to remain as the top group in all procedures, slightly increasing the ratio from A (56.1%) via B (58.0%) to C (60.2%). The same tendency is seen in Apidae (A, 7.5, B, 7.6, C, 8.6) and Colletidae (2.5, 3.0, 3.4). Andrenidae decreases in B, but slightly recovers in C (14.9, 12.7, 14.5), Megachilidae (4.9, 3.0, 3.5), Nomadinae (1.0, 0.8, 1.0) and Anthophorinae (1.8, 0.6, 0.7) behave similarly. The most conspicuous change is observed in Xylocopinae which increases from A (11.2%) to B (14.3%), but remarkably drops in C (8.3%). Within Halictidae, *Lasioglossum* (11.7, 8.9, 8.6) and *Halictus* (2.1, 2.2, 1.2) decrease, while carinaless *Erylaeus* (8.7, 12.2, 13.0) and *Dialictus* (9.3, 11.8, 13.0) increase, all reflecting life cycle patterns explained in 3.3.

Fig. 16 shows the relative abundance of 20 predominant species shown by the occurrence probability method as in Fig. 3. The ratios by three procedures are given in each species, which are arranged in the descending order in procedure C (given by black bars). Rank changes due to three procedures are given in right hand below. In general, highly ranked species are relatively stable in their predominance. Among ten top species by procedure A, only *Lg. occidentis* and *Ct. flavipes* show marked translocations, though the change of percentage ratio is conspicuous in *Ct. japonica* and *Dl. sp.1*. Rank changes are more frequent in less abundant species with drops of four species out of 20 predominants. In spite of these changes, the curve of cumulative percentage ratios is fairly similar between A (cf. Fig. 3) and C, in both, reaching ca. 55% at the 10th species and ca. 75% at the 20th.

In conclusion, the correction of relative abundance of various groups and of predominant species by life cycle peculiarities do not considerably modify the

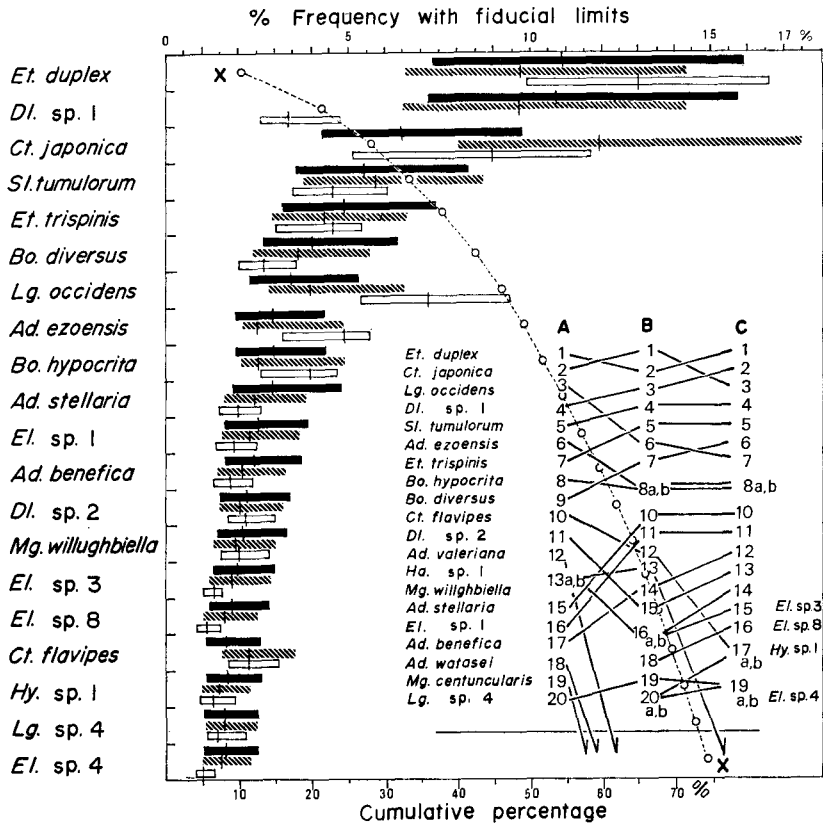


Fig. 16. Relative abundance of 20 predominant species obtained in the survey, BG and UC combined, shown by occurrence probability method. The species arranged in the descending order of individuals in procedure C. Black bars: All individuals (=Fig. 3). Hatched bars: Females alone. White bars: Ditto, excluding autumn new females. Curve XX shows cumulative percentage ratio by procedure C (scale at bottom). Rank changes due to three procedures given at righthand.

picture. Therefore, the calculation of relative abundance based upon all individuals sampled could be adopted as a convenient device to compare faunal makeup of two different assemblages, especially when the sample size is small, provided two necessary conditions are fulfilled: 1) Sampling without particular choice of certain species, especially rare ones, 2) Sampling throughout the bee season. Nevertheless, the reflections upon life cycle characteristics in various bee groups and species must be kept in mind to avoid the superficial interpretations of the results. This is especially important because only limited aspects of life cycle were adopted for the corrections described above.

4. Flower visits

Among all bee specimens sampled, 71 (1.03%) were captured in flight or on flowers unidentified. Excluding them the flower visits by bees in the areas surveyed are described and discussed here. The relations between bees and flower plants are complex. Here the descriptions are confined to some numerical results, leaving further analyses after the completion of wild bee surveys in and near Sapporo.

As mentioned in Methods, collecting bees from tall trees was difficult and often impossible, and sampling was not made in the orchard in UC with many fruit trees, mainly apples and pears. Another possible source of error is that bees were regarded as visiting particular flowers, even if they merely alighted on them. The flower visit by bees is a composite behavior, including both innate tendency and trial-and-error exercise in variable portions. Therefore the frequency of visits by some bee species to particular plants may vary from that of successful visits with nectar and/or pollen intake. Thus the results given below may deviate to some extent from real preference and visits.

4.1. Composition of flowers visited: The number of bee species and individuals visiting various plant families are presented in Tables 6 (UC) and 7 (BG), in the descending order of total bees captured. The composition of flowering plants visited by bees is evidently more complicated in BG, involving 36 families and 156 species against 24 families and 70 species in UC.

The number of visiting bee species is 77 in UC and 82 in BG. The percentage of visits to Compositae is overwhelming in both areas, covering more than 80% of visiting bee species. Visits to other plant families in terms of bee species slightly vary between two areas, probably reflecting the difference of floral makeup. For instance, Cruciferae and Leguminosae occupy the higher ranks in UC, by the abundance of open areas with rape and clovers, while the predominance of Rosaceae in BG is caused by the presence of numerous shrubs of this family there.

As to the number of visiting bee individuals, too, the first rank is occupied by Compositae, exceeding the half of total visits in UC and one third in BG, in both areas much more in male visits. In UC Compositae and the second ranked Leguminosae combined occupy about 75% of total visits, while in BG this level is reached by the sum of six predominantly visited plant families. Plant families occupying higher than the 10th rank in both areas are: Compositae, Leguminosae, Rosaceae, Cruciferae, Liliaceae, Scrophulariaceae and Labiatae. Among them Rosaceae and Cruciferae are remarkable by poor visits by males. (cf. also Fig. 17, Table 9). Certainly these plants are, together with Ranunculaceae and Saxifragaceae, mainly visited by brood rearing females for pollen foraging (Exception in Rosaceae, *Cimicifuga yezoensis*, cf. Tab. 9 and Fig. 20, *Dialictus* sp. 2). A discrepancy is observed in Ranunculaceae, occupying the fifth rank in UC with only two species but far inferior in BG in spite of involving ten species. Similarly Polygonaceae and Geraniaceae are less frequently visited in BG while Saxifragaceae being important in BG with numerous cultivated plants but not in UC.

The plant species visited are classified into four groups according to their

Table 6. Species and individual numbers of bees visiting various plant families in UC

Plant family	Species number		Number of bee individuals captured						Sex ratio ♂/♀
	plants	bees	Number			Percentage			
			♀	♂	♀♂	♀	♂	♀♂	
Compositae	15	63	905	795	1,700	46.2	69.9	54.9	0.88
Leguminosae	7	34	338	241	579	17.2	21.2	18.7	0.71
Cruciferae	9	38	288	20	308	14.7	1.8	9.9	0.07
Liliaceae	4	33	114	23	137	5.8	2.0	4.4	0.20
Ranunculaceae	2	27	116	13	129	5.9	1.1	4.2	0.11
Rosaceae	7	26	75	3	78	3.8	0.3	2.5	0.04
Geraniaceae	1	19	51	11	62	2.6	1.0	2.0	0.22
Labiatae	2	7	5	12	17	0.3	1.1	0.6	2.40
Scrophulariaceae	3	9	11	3	14	0.6	0.3	0.5	0.27
Polygonaceae	2	4	7	2	9	0.4	0.2	0.3	0.29
Caryophyllaceae	2	10	7	1	8	0.4	0.1	0.3	0.14
Onagraceae	1	5	6	2	8	0.3	0.2	0.3	0.33
Lythraceae	1	4	7	1	8	0.4	0.1	0.3	0.14
Umbelliferae	2	6	7	1	8	0.4	0.1	0.3	0.14
Oleaceae	3	6	4	3	7	0.2	0.3	0.2	0.75
Cucurbitaceae	1	4	3	1	4	0.2	0.1	0.1	0.33
Berberidaceae	1	3	3	0	3	0.2	-	0.1	-
Ericaceae	1	2	1	1	2	0.1	0.1	0.1	0.50
Malvaceae	1	2	2	0	2	0.1	-	0.1	-
Caprifoliaceae	1	1	1	0	1	0.1	-	0.0	-
Saxifragaceae	1	1	1	0	1	0.1	-	0.0	-
Oxalidaceae	1	1	1	0	1	0.1	-	0.0	-
Iridaceae	1	1	1	0	1	0.1	-	0.0	-
Linaceae	1	1	1	0	1	0.1	-	0.0	-
Total	70	77	1,955	1,133	3,088				

provenance: A. Escaped exotic weeds. B. Cultivated species including crops, ornamentals and those planted as specimens in BG, even though native in Japan including other areas in Hokkaido. C. Natives. Those regarded as the members of the primary vegetation in and near Sapporo. D. Native weeds. Native in Hokkaido but becoming abundant in secondary vegetation (Table 8)¹⁾. The species number of escaped exotic weeds is small in both areas but they are the principal food sources of bees in UC, where the ratio of bee visits to primary plants is only 9%. On the other hand, the ratios occupied by cultivated and native plants are evidently higher in BG. But even there exotic weeds receive a considerable visits. In a previous paper (Sakagami and Matsumura 1967) the percentage ratios of andrenid bees captured on A+B were given as 59.6% in BG and 87.8% in UC. The corresponding ratios in total wild bees are nearly identical, 58.1 and 87.0 respectively. This indicates that the whole wild bee assemblage in the areas studied are now strongly dependent on secondary vegetation. This condition

1) Some of these plants may be the prehistoric immigrants to Japan.

Table 7. Species and individual numbers of bees visiting various plant families in BG

Plant family	Species number		Number of bee individuals captured						Sex ratio ♀/♂
	plants	bees	Number			Percentage			
			♀	♂	♀♂	♀	♂	♀♂	
Compositae	25	64	728	598	1,326	28.6	49.8	35.4	0.82
Rosaceae	23	50	403	72	475	15.9	6.0	12.7	0.18
Liliaceae	9	32	195	95	295	7.7	7.9	7.8	0.49
Saxifragaceae	10	31	216	22	238	8.5	1.8	6.4	0.12
Labiatae	8	29	129	56	185	5.1	4.7	4.9	0.43
Leguminosae	7	28	78	105	183	3.1	8.7	4.9	1.35
Cruciferae	4	29	143	23	166	5.6	1.9	4.4	0.16
Scrophulariaceae	3	21	101	47	148	4.0	3.9	4.0	0.47
Malvaceae	3	17	82	38	120	3.2	3.2	3.2	0.46
Campanulaceae	2	13	75	21	96	3.0	1.8	2.6	0.28
Umbelliferae	6	22	57	3	60	2.2	0.3	1.6	0.05
Ericaceae	8	16	47	12	59	1.9	1.0	1.6	0.26
Ranunculaceae	10	18	34	16	50	1.3	1.3	1.3	0.47
Polygonaceae	5	17	22	28	50	0.9	2.3	1.3	1.27
Geraniaceae	2	15	40	8	48	1.6	0.7	1.3	0.20
Caprifoliaceae	4	17	28	7	35	1.1	0.6	0.9	0.25
Hypericaceae	1	9	24	2	26	0.9	0.2	0.7	0.08
Araliaceae	1	11	11	13	24	0.4	1.1	0.6	1.18
Lythraceae	1	3	15	2	17	0.6	0.2	0.5	0.13
Oleaceae	3	6	12	3	15	0.5	0.3	0.4	0.25
Caryophyllaceae	2	7	4	8	12	0.2	0.7	0.3	2.00
Berberidaceae	2	5	9	0	9	0.4	-	0.2	-
Staphyleaceae	1	6	6	2	8	0.2	0.2	0.2	0.33
Commelinaceae	1	7	5	3	8	0.2	0.3	0.2	0.60
Balsaminaceae	1	1	5	1	6	0.2	0.1	0.2	0.20
Crassulaceae	3	6	6	0	6	0.2	-	0.2	-
Valerianaceae	2	4	3	3	6	0.1	0.3	0.2	-
Others combined*	9	14	14	4	18	0.6	0.4	0.6	
Total	156	82	2,492	1,192	3,684				

* Number of plant species, bee species and bee individuals in parentheses. Cucurbitaceae (1, 3, 3), Papaveraceae (1, 2, 3), Rubiaceae (1, 3, 3), Violaceae (1, 1, 2) Iridaceae (1, 1, 2), Solanaceae (1, 1, 2), Primulaceae (1, 1, 1), Hamamelidaceae (1, 1, 1), Styracaceae (1, 1, 1).

must be common to the most parts of lowlands areas in Hokkaido transformed to rural or suburb zones.

Table 9 shows the predominantly visited plant species in UC and BG down to the 25th rank. Reflecting the floristic difference two areas are quite different in major bee plants. Moreover, the predominance is distinct in UC. The first two species, *Rudbeckia laciniata* and *Taraxacum officinale*, occupy in combination 42% and the 75% level is attained by the cumulative ratio to the 7th species. In BG, however, numerous plant species respectively attract a small portion of bees, which is recognized by the different rate of decrease of percentage ratios occupied by

various plants between BG and UC as well as the higher percentage of "others combined" in BG (Table 9), where even the cumulative ratio down to the 25th species only slightly exceeds the 72% level. Notwithstanding, the predominance

Table 8. Grouping of plants visited by bees according to provenance

Provenance	Number of plant species visited				Number of bee individuals visiting			
	UC	%	BG	%	UC	%	BG	%
A. Exotic	12	16.7	19	5.5	2,217	71.8	968	26.2
B. Cultivated	28	38.9	87	53.0	471	15.2	1,295	35.0
C. Natives	17	23.6	39	23.8	277	9.0	909	24.8
D. Native weeds	15	20.8	29	17.7	123	4.0	512	14.0

Table 9. Plants predominantly visited by bees in UC and BG (25 species). Family

Rank	Plant species (Family)	Prove- nance	UC			
			♀	♂	♂♀	♂♀ %
1	<i>Rudbeckia laciniata</i> (COM)	A	308	578	886	28.59
2	<i>Taraxacum officinale</i> (COM)	A	354	86	440	14.20
3	<i>Trifolium repens</i> (LEG)	A	215	176	391	12.62
4	<i>Brassica chinensis</i> var. <i>oleifera</i> (CRU)	B	243	5	248	8.00
5	<i>Erigeron annuus</i> (COM)	A	133	45	178	5.74
6	<i>Ranunculus</i> sp. (RAN)	A	115	12	127	4.10
7	<i>Allium festulosum</i> (LIL)	B	91	3	94	3.03
8	<i>Vicia cracca</i> (LEG)	C	42	43	85	2.78
9	<i>Geranium thunbergi</i> (GER)	C	51	11	62	2.00
10	<i>Arctium lappa</i> (COM)	A	25	27	52	1.68
11	<i>Trifolium pratense</i> (LEG)	A	35	16	51	1.65
12	<i>Sonchus brachyotis</i> (COM)	D	28	14	42	1.36
13	<i>Rosa multiflora</i> (ROS)	C	39	0	39	1.26
14	<i>Solidago canadensis</i> (COM)	A	14	24	38	1.23
15	<i>Petasites japonicus</i> var. <i>giganteus</i> (COM)	C	22	13	35	1.13
16	<i>Allium tuberosum</i> (LIL)	A	19	16	35	1.13
17	<i>Laburnum anagyroides</i> (LEG)	B	25	0	25	0.81
18	<i>Rorippa</i> sp. (CRU)	D	13	10	23	0.74
19	<i>Malus asiatica</i> (ROS)	B	15	3	18	0.58
20	<i>Brunella vulgaris</i> (LAB)	C	4	12	16	0.52
21	<i>Medicago sativa</i> (LEG)	A	11	5	16	0.52
22	<i>Rosa rugosa</i> (ROS)	B	15	0	15	0.48
23	<i>Brassica chinensis</i> (CRU)	B	13	2	15	0.48
24	<i>Coreopsis lanceolata</i> (COM)	B	10	3	13	0.42
25	<i>Rorippa islandica</i> (CRU)	D	12	0	12	0.39
	Others combined		103	29	132	4.27
	Total		1,955	1,133	3,088	

of exotic weeds is evident in both areas. Especially in UC the primary native plants are represented only by five out of 25 species and the total percentage by them are only ca. 7% compared with the overwhelming predominance of exotic weeds, that is, seven top species occupying 75% of total visits are all not natives. It is interesting that even in BG the cultivated species are not found within the first 10 predominants with two exceptions at lower ranks, whereas three exotic weeds, *Tx. officinale*, *Rd. laciniata* and *Erigeron annuus* combined, attain ca. 20%. These three species are apparently the important food sources of wild bees in the areas surveyed, respectively in spring, autumn and summer as described in the next subsection.

4.2. *Phenology of flower visits by bees:* Figs. 17 and 18 present the phenology

names are abbreviated by first three letters of scientific names (cf. Tables 6 and 7).

Plant species (Family)	Prove- nance	BG			
		♀	♂	♀♂	♀♂ %
<i>Taraxacum officinale</i> (COM)	A	320	73	393	10.50
<i>Rudbeckia laciniata</i> (COM)	A	89	164	253	6.76
<i>Gagea lutea</i> (LIL)	C	141	87	228	6.09
<i>Erigeron annuus</i> (COM)	A	83	63	146	3.90
<i>Rorippa indica</i> (CRU)	D	107	20	127	3.39
<i>Scrophularia grayana</i> (SCR)	D	88	33	121	3.23
<i>Aster ageratoides</i> var. <i>yezoensis</i> (COM)	C	41	80	121	3.23
<i>Cirsium aomorense</i> (COM)	B	98	19	117	3.13
<i>Salvia officinalis</i> (LAB)	B	88	28	116	3.10
<i>Anaphalis margaritacea</i> (COM)	C	31	66	97	2.59
<i>Rosa centifolia</i> , climber (ROS)	B	88	4	92	2.46
<i>Campanula</i> sp. (CAM)	B	72	19	91	2.43
<i>Spiraea betulifolia</i> var <i>grandifolia</i> (ROS)	B	84	2	86	2.30
<i>Hibiscus mutabilis</i> (MAL)	B	60	26	86	2.30
<i>Lathyrus maritimus</i> (LEG)	B	33	41	74	1.98
<i>Hydrangea macrophylla</i> (SAX)	B	63	1	64	1.71
<i>Trifolium repens</i> (LEG)	A	18	43	61	1.63
<i>Potentilla fruticosa</i> (ROS)	B	52	8	60	1.60
<i>Cimicifuga yezoensis</i> (ROS)	C	7	49	56	1.50
<i>Deutzia crenata</i> (SAX)	B	50	5	55	1.47
<i>Crataegus cuneata</i> (ROS)	B	50	1	51	1.36
<i>Eupatorium chinense</i> (COM)	A	6	41	47	1.26
<i>Hydrangea paniculata</i> (SAX)	C	39	6	45	1.20
<i>Deutzia gracilis</i> (SAX)	D	29	10	39	1.04
<i>Solidago canadensis</i> (COM)	A	7	31	38	1.01
Others combined		748	272	1,020	27.69
Total		2,492	1,192	3,684	

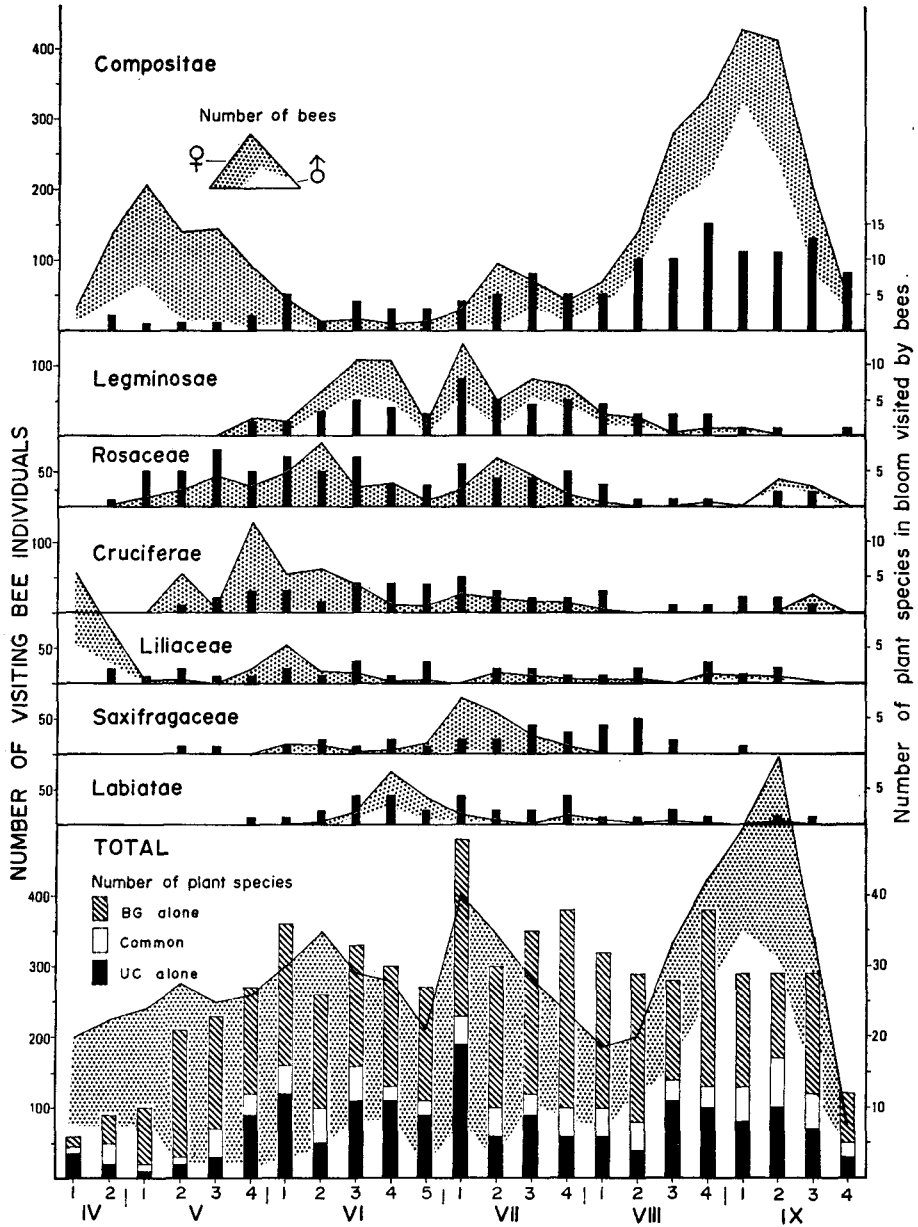


Fig. 17. Phenology of plant families predominantly visited by bees (UC+BG). Total visits at bottom, together with the ratios of plant species in bloom found only in BG or UC and those common to both areas shown with histograms.

of predominantly visited plants at familial and specific levels both BG and UC combined. The most conspicuous feature is the seasonal complementarity between Compositae and other plants. The former exhibits a distinct bimodality. The spring peak is started by *Petasites* and rapidly replaced by *Taraxacum*, which virtually monopolizes the visits to Compositae as shown by the scarce species number. The late peak is divided into two subpeaks, the first lower one is represented by *Erigeron* and the last highest one by *Rudbeckia*, which attracts numerous individuals of large halictine bees, *Ceratina*, *Bo. hypocrita*, *Mg. centuncularis*, etc. Moreover, many other composite plants, *Anaphalis*, *Arctium*, *Aster*, *Cirsium*, *Eupatorium*, *Solidago*, *Sonchus*, *Taraxacum* (Second bloom), etc. are in bloom. Thus the finale of the bee season in the areas is virtually determined by Compositae, as recognized by the comparison of two curves, top and bottom, in Fig. 17. The period between these two composite peaks is occupied by a variety of plants, especially by Leguminosae and Rosaceae followed by Saxifragaceae and Labiatae. While the legumes are mainly represented by clovers, especially the white clover in UC followed by *Vicia cracca*, the rosaceous plants involve numerous species, each of which attracts a small portion of bees. On the other hand, Cruciferae is more predominant in late spring, mostly represented by the rape in UC, though some other species, *Rorippa* spp., etc. bloom in summer. A most discrete phenology is exhibited by Liliaceae, in which, beside the peak in early spring by *Gagea lutea*, several species of rather different biotypes succeed, i.e. *Allium festulosum* in late spring and *A. tuberosum* in late summer to autumn. From these phenological trends the bee season in the areas surveyed is divided into the following four floral periods:

- I. *Gagea-Petasites* period: Late April to early May, short but well defined, being poor both in flower and bee species.
- II. Dandelion-rape period: May to early June. Early part nearly monopolized by *Tr. officinale*, later shared with rape and some rosaceous flowers. Although not surveyed fruit trees may be another important food source in this period. I+II approximately corresponding to *Andrena* period given in 2.1.
- III. White clover-*Erigeron* period: June to July. Characterized by a variety of flowers but two mentioned species are predominant. Approximately corresponding to the composite period given in 2.1.
- IV. *Rudbeckia* period: August to September. Beside *Rd. laciniata* with the overwhelming predominance, many autumnal composite flowers are in bloom. Approximately corresponding to *Ceratina* period in 2.1.

Except I, all other periods possess exotic weeds as indicator species, again showing a strong modification of the primary vegetation and adaptation of bees to the secondary vegetation. Histograms at the bottom of Fig. 17 show low ratios of plant species in bloom common to BG and UC in each sampling period. These 31 species are enumerated below in the order of blooming, with family abbreviations (cf. Tables 6 and 7) and provenance (cf. Table 8) in parentheses. The symbols b, u and c indicate the species are ranked within 25 predominantly

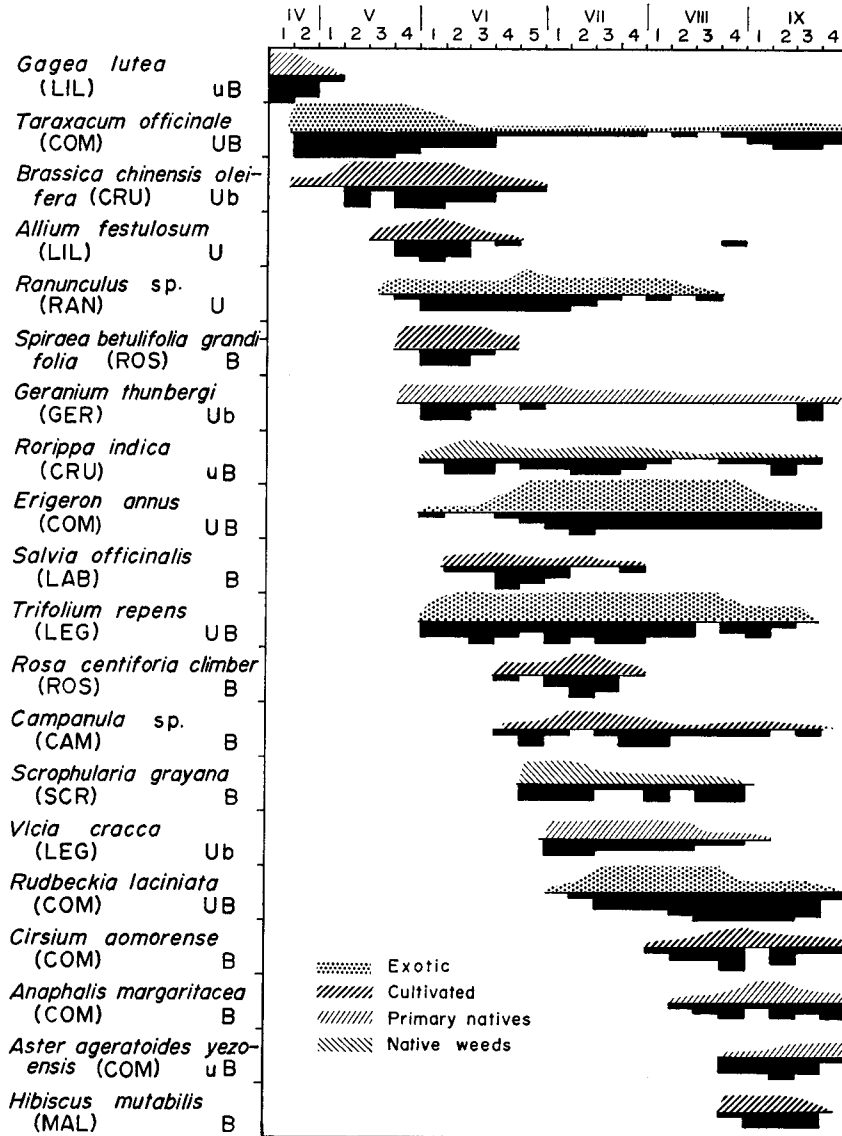


Fig. 18. Phenology of plant species predominantly visited by bees (=Those absorbed more than 2% of total visits either in BG or UC). Amount of flowers in bloom (above base line) divided in five arbitrary degrees. Amount of bee visits (below) divided in five degrees, 1~5, 6~10, 11~50, 51~100, 100~. Plant families are shown with first three letters of scientific names (cf. Tabs. 6,7,9). UB, uB, Ub, U and B: Relative abundance between UC and BG.

visited ones in BG, UC and BG+UC:

Gagea lutea (LIL, C)^b, *Forsythia suspensa* (OLE, B), *Taraxacum officinale* (COM, A)^c, *Stellaria media* (CAR, D), *Enkyanthus perulatus* (ERI, B), *Syringa vulgaris* (OLE, B), *Anthriscus nemorosa* (UMB, C), *Brassica chinensis* var. *oleifera* (CRU, B)^u, *Berberis amurensis* var. *japonica* (BER, C), *Trifolium repens* (LEG, A)^c, *Ranunculus chinensis* (RAN, C), *Heracleum dulce* (UMB, C), *Hydrangea macrophylla* (SAX, B)^b, *Rorippa indica* (CRU, D)^b, *Rosa rugosa* (ROS, B)^u, *Trifolium pratense* (LEG, A)^u, *Robinia pseudoacacia* (LEG, A), *Erigeron annuus* (COM, A)^c, *Ligustrum obtusifolium* (OLE, B), *Vicia cracca* (LEG, C)^u, *Rudbeckia laciniata* (COM, A)^c, *Althaea rosea* (MAL, B), *Arctium lappa* (COM, A)^u, *Solidago canadensis* (COM, A)^c, *Lythrum salicaria* (LYT, C), *Aster ageratoides* var. *yezoensis* (COM, C)^u, *Polygonum longisetum* (POL, D), *P. thunbergi* (POL, D), *Geranium thunbergi* (GER, C)^u, *Allium tuberosum* (LIL, A)^u, *Brassica chinensis* (CRU, B)^u.

Among these species, those predominantly visited in both areas are only five, *Tx. officinale*, *Tr. repens*, *Er. annuus*, *Rd. laciniata* and *So. canadensis*, all being exotic weeds belonging, except the second species, to Compositae. These four composite species alone attract 50% of total bee species and 90% of those visiting composite plants in UC and correspondingly 32 and 63% in BG, resulting in the phenological pattern of plants visited common to both areas as far as composite flowers are concerned, expressed, *Taraxacum-Erigeron-Rudbeckia-Solidago*. In other families, some imbalance is observed concerning bee-plant relations, either in the relative predominance (cf. 4.1.) or in phenology, for instance, in Liliaceae, Cruciferae and Rosaceae. The same tendency is recognized in the relation between plants and number of bee individuals, too.

4.3. Bee-flower relations at familial and specific levels of bees: In this final subsection, bee-flower relations are described with reference to particular bee families and species. Fig. 19 presents the numerical relation of visits of various bee families to certain predominantly visited plant families with percentage ratios. Some remarkable discrepancies between total visits (polygons) and visits to particular families (histograms) are recognized: 1) Lower visits of Halictidae to Leguminosae, compensated by higher visits to other families except for Liliaceae (BG). 2) Higher visits of Andrenidae to Leguminosae and Liliaceae (BG), compensated by lower visits to Compositae, Rosaceae (BG) and others. 3) Some minor deviations found in relations, Anthophoridae-Compositae, Rosaceae (UC), Cruciferae (BG), Megachilidae-Cruciferae and Liliaceae, and Apidae-Cruciferae, Liliaceae and others.

However, particular flower-bee relations are often concealed by such general presentation, because the percentage ratios are strongly affected by predominant groups, both bees (e.g. Halictidae) and plants (e.g. Compositae), which are in general devoid of specialized mutual relations at group level. Further, the grouping at higher levels ignores some conspicuous tendencies exhibited at specific or generic levels. For instance, a well known relation between long-tongued bees and deep or tubular flowers exists in the areas surveyed, too, but is not recognized

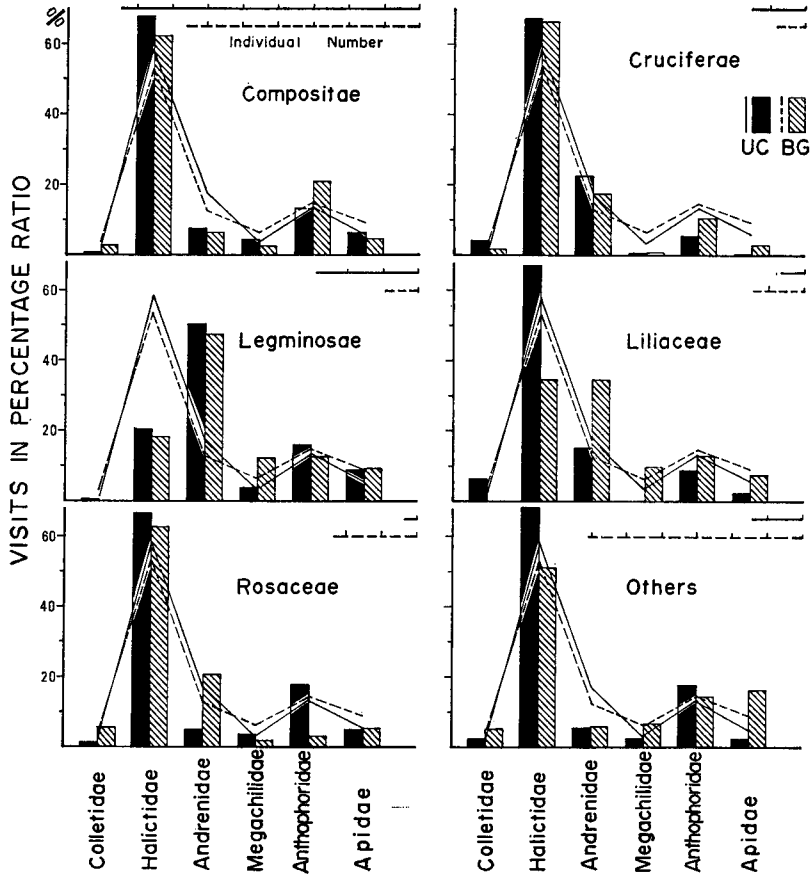


Fig. 19. Flower visiting tendency of various bee families to predominantly visited plant families in UC and BG, shown with percentage ratios of visiting bee individuals sampled on all plants (polygons) and on six plant groups (histograms). Total numbers sampled given by horizontal bars (one unit scale=200 individuals).

from Fig. 19. Higher visits of Andrenidae to Leguminosae do not indicate a trait general to this bee family, but is mainly caused by the presence of two predominant species intimately linked with legumes, *Ad. exoensis* and *Ad. valeriana* (Sakagami and Matsumura 1967). Therefore, the flower visits in some representative species were presented in Fig. 20.

The species represented by numerous individuals were arbitrarily chosen to cover various predominant genera. *Hy. paulus*, *Eu. sp. 1* and *Cl. sp. 1* were cited in spite of insufficient numbers. Andrenidae, already worked in Sakagami and Matsumura (1967)

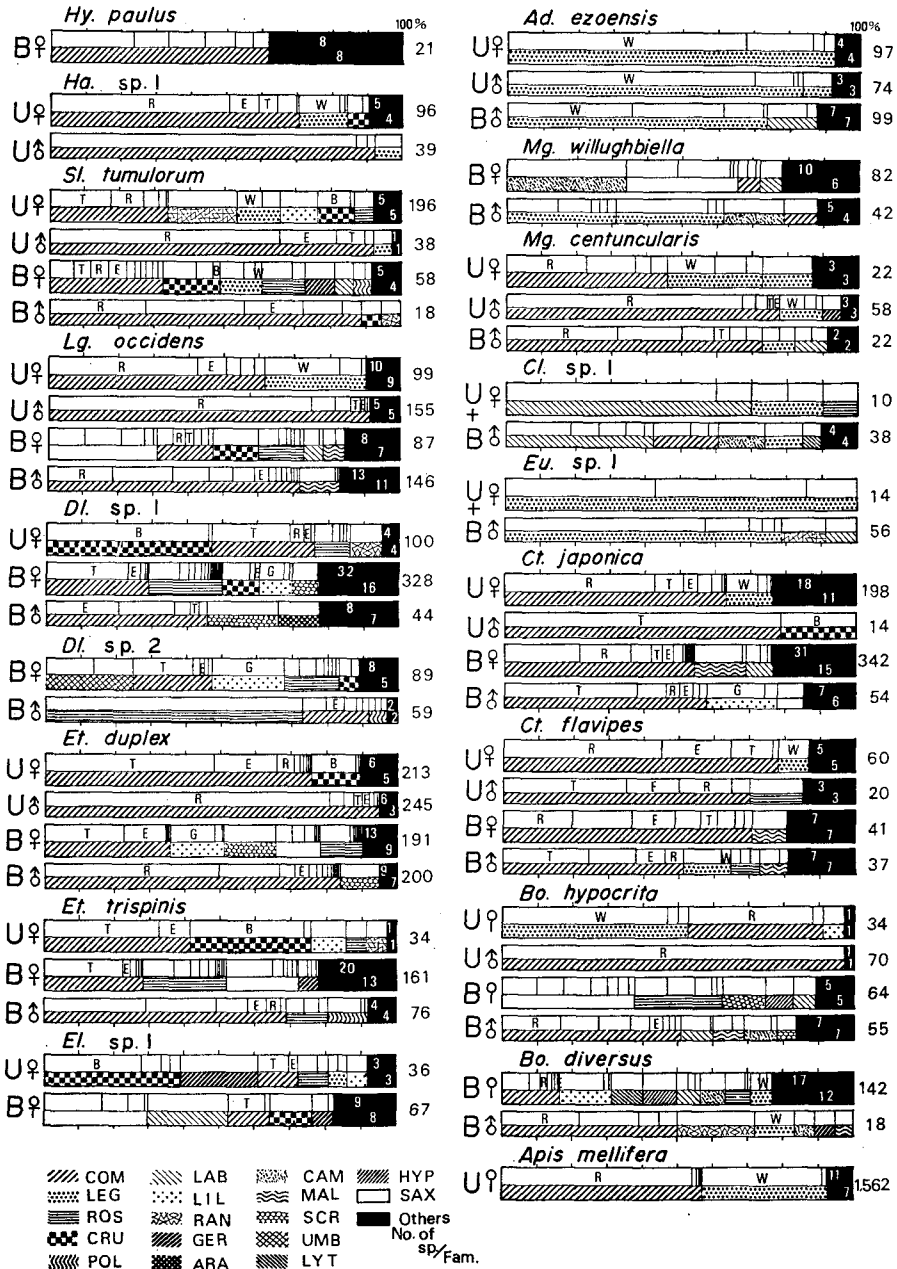
was discarded leaving one species. In each species sexes and areas were separately given, except for *Eu.* sp. 1 and *Cl.* sp. 1, and only those represented by more than ca. 15 specimens were illustrated. The graph of the honeybee (right-bottom) were prepared based upon the data by counting, not by collecting (cf. 1.4.). The pollen foragers were sorted by the presence of pollen loads but this information is not dealt herewith.

A glance at the figure it is noticed that flower visit spectra are richer in BG than in UC in most species cited and in both sexes. This coincides with the rich floral makeup in BG. Bees have a tendency to concentrate upon the plants growing in a large extent with a large amount of flowers (Free 1970). Unfortunately, we have still no measure on the relative amount of flowers of various plants visited by bees. But the situation mentioned, realized in UC by *Tx. officinale*, *Tr. repens*, *Ranunculus* sp. and *Rd. laciniata*, is less conspicuous in BG, except for *Gagea lutea* in early spring. Apparently this must cause an alternative situation, the attraction of a small portion of bees by numerous plant species, giving a richer flower spectra in Fig. 9.

The range of flower choice is quite variable among species. Most halictine species are more or less polytrophic, together with *Ceratina*, *Bo. hypocrita* (BG) and *Bo. diversus*. Among these species, those being abundant both in BG and UC show richer spectra in BG as mentioned above, which in turn proves the plasticity of flower visits in these species. Another extreme is exhibited by *Ad. ezoensis*, *Eu.* sp. 1, *Cl.* sp. 1 and, interestingly, by *Apis mellifera*. The first three species are apparently oligotrophic, attached either to legumes (*Ad. ezoensis*) or to deep viz. tubular flowers (*Eucera* and *Clisodon*). On the other hand, the oligotrophic tendency of the honeybee is superficial. This indubitably highly polytrophic species has a strong tendency to concentrate its foraging activities to favorable food sources at a given area or time, which is reinforced by a well developed foraging dance within the hive. The monotonous spectrum in Fig. 9 is an outcome of such particular trait, never reflecting the specific innate oligotrophy.

In other species, too, the flower spectra do not always reflect the visiting range at a given time. Most polytrophic species in Fig. 20 do not belong to typical solitary bees (cf. 3.1.), having a long active period. Obviously the strong oligotrophy does not favor this life cycle type and may be rare in these bees. But it is also true that the number of plant species flowering during their long active period is higher than in case of short-lived typical solitary bees. Therefore the comparison of flower spectra obtained during a limited period is also necessary to know the flower preference accurately. Another aspect of life cycle type affecting the spectra is the appearance of new adults in autumn in non typical solitary bees. This is distinctly correlated with the large ratio occupied by *Rd. laciniata* in UC in *Ha.* sp. 1 (♀ ♂), *Sl. tumulorum* (♂), *Lg. occidentis* (♀ ♂), *Et. duplex* (♂), *Ct. japonica* (♀), *Ct. flavipes* (♀) and *Bo. hypocrita* (♂), all exhibiting the autumnal burst of new adults (cf. 3.2 ~ 3.4)

Nevertheless, Fig. 20 shows some differences among species, which are regarded as particular to groups or species. This is demonstrated by the comparison of closely



allied ones. In Halictidae, the preference for legumes, especially *Tr. repens*, best recognized in females in UC, is distinct in *Ha.* sp.1, *Sl. tumulorum*, *Lg. occidentis* and in other species of *Lasioglossum* s. str., but virtually absent in *Dl.* sp.1 and 2, *Et. duplex* and *Et. trispinis*. The latter tendency also exists in *Et. calceatus* (Sakagami and Munakata 1972), probably widespread in some carinate *Evylaeus*. Further differences are recognized within the same subgenus. In *Dialictus* the higher preference for Umbelliferae in *Dl.* 2 is remarkable, and in carinate *Evylaeus* *Et. trispinis* shows a more diversified visiting tendency compared with the stronger attachment of *Et. duplex* to Compositae. The latter case is noteworthy because both species possess nearly identical life cycle and phenology (3.3.).

Two *Megachile* species differ in relative abundance in two areas and phenology (cf. 1.4. and 3.1). But these differences alone could not explain the difference in flower spectra. *Mg. centuncularis* shows a strong preference for Compositae while *Mg. willughbiella* prefers for *Campanula* sp. and Saxifragaceae (mostly *Hydrangea* for pollen foraging). On the other hand, two *Ceratina* species are similar in flower visits as in phenology (3.2.) as well as nesting habits (Shiokawa 1966), offering an interesting problem on the mechanism of their co-existence in the same habitat. Finally two bumblebee species are briefly referred to. They differ markedly in tongue length and correspondingly in flower visiting habits. The short-tongued *Bo. hypocrita* visits rather a variety of flowers while *Bo. diversus* is long-tongued and more oligotrophic. The specific difference in flower visits is evident in BG. Further, *Bo. hypocrita* is rather polytrophic in BG while visiting predominantly two plants alone, *Tr. repens* and *Rd. laciniata*, in UC. *Bo. diversus* is interestingly very few in UC (cf. 1.4), nevertheless *Tr. pratense*, the plant most preferred by this species at secondary vegetations in and near Sapporo, is relatively abundant in UC (Table 9) and visits to UC from BG is certainly not difficult by its flight capacity.

Up to the present the flower preference of bees were mainly studied with special attention to strongly oligotrophic species (cf. Linsley 1958). The above examples suggest the necessity and possibility of studying the same aspect in mildly oligotrophic to moderately polytrophic bees, too, either to clarify their ecological niches or to estimate their pollinating efficiency. The change of their flower preference according to floristic difference is of special interest in relation to their plasticity.

Fig. 20. Flower visiting spectra of some representative bee species, shown sexes and, in most species, areas (expressed with U and B) separately. Lower half: Plant families visited. Names given at bottom with abbreviations as in Fig. 18. Upper half: Species visited, each separated with vertical bars. Only six predominantly visited species shown with symbols, R (*Rudbeckia laciniata*) T, (*Taraxacum officinale*), W (*Trifolium repens*), E (*Erigeron annuus*), B (*Brassica chinensis* var. *oleifera*), G (*Gagea lutea*). Black blocks at righthand indicate minor families with species and family numbers. Number of visiting bees given at righthand of each spectrum.

Summary

Wild bee fauna of the campus of Hokkaido University (UC) including the Botanical Garden (BG) was surveyed by sampling bees four hours per week for each area from April to September, 1959.

1) The total sample, consisting of 102 species and 6,843 individuals, shows the predominance of Halictidae, followed by Andrenidae, both in species and individuals. At generic level, *Lasioglossum*, s. lat. and *Andrena* are most predominant, followed by *Hylaeus* and *Nomada* in species while *Ceratina* in individuals. The faunal makeup exhibits a basic resemblance with certain other Holarctic data.

2) The faunal makeup between BG and UC is considerably different, in spite of the short distance (300 m), suggesting that most bee populations in both areas are now fairly isolated one another. By the fitting trial of the Preston's log-normal to the data obtained, the total species inhabiting the areas surveyed was estimated as 115 spp.

3) The wild bee phenology in the areas shows a poor seasonal differentiation and absence of distinctly unfavorable period during the bee season, covering late April to September. Halictid species are predominant throughout the bee season, which is divided into three periods mainly on the basis of the second ranked groups: *Andrena* period (late April — mid June), Composite period (late June — early August), *Ceratina* period (mid August — late September). The last period is not self-sustaining as far as the brood rearing activity is regarded as the core of bee lives.

4) Phenology of predominant species reveals that seasonal differentiation is determined mainly by the groups other than Xylocopinae, Halictidae and Apidae. Based upon the data obtained a compromise was sought to match the catch of as many as possible species by limited samplings.

5) To avoid the superficial interpretations of numerical data, life cycle peculiarities of various bee groups were described and discussed, classifying them into four life cycle types, typical solitary bees, Xylocopinae, Halictidae and bumblebees. A tentative correction of the relative abundance was made by incorporating the life cycle peculiarities.

6) The analysis of flower visiting records reveals the overwhelming importance of Compositae, followed by Rosaceae, Leguminosae, Cruciferae, Liliaceae, Scrophulariaceae and Labiatae. The floral composition of visited plants markedly differs between BG and UC. In UC about 70% of bees were captured on exotic weeds and only 9% on primary native plants. The ratio is ca. 26 and 24% in BG, showing the adaptation of bee species to secondary vegetation in UC. The bee season is divided into four periods, *Gagea-Petasites* period (late April — early May), Dandelion-rape period (May — early June), White clover-*Erigeron* period (June — July) and *Rudbeckia* period (August — September). Flower visiting spectra of some representative species were presented and discussed.

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Appendix

List of wild bee species collected in 1959 at the campus of Hokkaido University (UC) and University Botanical Garden (BG).

- 1) Italic letters parenthetically given for each genus are abbreviated generic names used throughout our serial studies.
- 2) In text the species names of halictine bees are cited with abbreviated subgeneric names, in some groups (*Evylaeus*, *Dialictus*), with corresponding changes of terminations of specific names.
- 3) In each taxon, the number of sampled individuals is given after the scientific name, with a series of three figures: total number (in Gothic)=♀♀+♂♂ (in *Bombus*, =♀♀+♀♀+♂♂), followed by the numbers sampled at two areas, BG and UC, given parenthetically.
- 4) Letters B or U given before the specific names signify the species collected only at BG or UC.
- 5) Following the total number sampled, phenology of each species is shown, both sexes separately, with code numbers of sampling periods (cf. Methods) in which the species concerned was collected.

Family COLLETIDAE 176=133♀♀+43♂ (BG 132=107+25, UC 44=26+18)

Genus *Colletes* Latreille (*Co.*). UC 2=0♀♀+2♂

U 1. *Co.* sp.1. 2=0+2; VIII-4, IX-1.

Genus *Hylaeus* Fabricius (*Hy.*). 174=133♀♀+41♂
(BG 132=107+25, UC 42=26+16)

- B 2. *Hy. floralis* Smith. 4=4+0. IX-1, 3, 4.
3. *Hy. monticola* Bridwell. 10=8+2 (BG 9=7+2, UC 1=1+0). ♀ VI-1, 3~5, IX-1; ♂ V-4, VI-3.
- U 4. *Hy. nipponicus* Bridwell. 3=2+1. ♀ VI-3, 4; ♂ VI-5.
5. *Hy. paulus* Bridwell. 53=37+16 (BG 30=21+9, UC 23=16+7). ♀ V-4, VI-1~4, VII-1, 2, VIII-1~4, IX-1, 2; ♂ VI-3, VII-1, 4, VIII-1~4.
6. *Hy.* sp.1. 83=65+18 (BG 74=61+13, UC 9=4+5). ♀ VI-3, 5, VII-1~4,

VIII-1~4, IX-1~3; ♂ VI-3, VII-1~4, VIII-4.

7. *Hy. sp.4.* 7=4+3 (BG 4=3+1, UC 3=1+2). ♀ VI-1, 2, VII-3; ♂ V-4, VIII-1.
 B 8. *Hy. sp.5.* 5=5+0. VIII-4, IX-2.
 U 9. *Hy. sp.7.* 3=2+1. ♀ VI-4, 5; ♂ VI-2.
 B 10. *Hy. sp.10.* 3=3+0. VIII-3, 4, IX-4.
 B 11. *Hy. sp.11.* 1=1+0. IX-2.
 B 12. *Hy. sp.12.* 2=2+0. VIII-4, IX-2.

Family HALICTIDAE 3,838=2,610♀+1,228♂ (BG 2,019=1,377+642, UC 1,819=1,233+586)

Genus *Halictus* Latreille - Subgenus *Halictus* Latreille (*Ha.*).

140=101+39♂ (BG 5=5+0, UC 135=96+39)

13. *Ha. (Ha.) sp.1.* 140=101+39 (5=5+0, UC 135=96+39).
 ♀ V-3,4, VI-1~5, VII-1~4, VIII-1~4, IX-1~3; ♂ VII-4, VIII-2~4, IX-2~4.

Genus *Halictus* Latreille - Subgenus *Seladonia* Robertson (*Sl.*).

316=259♀+57♂ (BG 77=58+19, UC=239=201+38)

14. *Ha. (Sl.) tumulorum* Linné. 316=259+57 (BG 77=58+19, UC 239=201+38).
 ♀ V-1~4, VI-1~5, VII-1~3, VIII-1~4, IX-1~4; ♂ VI-2, VII-1~4, VIII-1~4, IX-1~4.

Genus *Lasioglossum* Curtis - Subgenus *Lasioglossum* Curtis (*Lg.*).

798=399♀+399♂ (BG 339=156+183, UC 459=243+216)

15. *Lg. (Lg.) discrepans* (Pérez). 11=8+3 (BG 10=7+3, UC 1=1+0). ♀ IV-1, V-1,3,4, VI-1~3, VII-1; ♂ IX-1~3.
 16. *Lg. (Lg.) esoense* Hirashima et Sakagami. 85=49+36 (BG 38=23+15, UC 47=26+21). ♀ VI-1,3~5, VII-1~4, VIII-1~4, IX-1~3; ♂ VIII-2~4, IX-1~4.
 17. *Lg. (Lg.) laeiventre* (Pérez). 36=33+3 (BG 8=6+2, UC 28=27+1). ♀ IV-1, 2, V-1~4, VI-1~4; ♂ VII-2, 4, IX-1.
 18. *Lg. (Lg.) mutilum* (Vachal). 10=8+2 (BG 7=5+2, UC 3=3+0). ♀ VI-1, VII-1,2,4, VIII-1; ♂ IX-2.
 19. *Lg. (Lg.) occidentens* (Smith). 492=192+300 (BG 234=88+146, UC 259=104+155).
 ♀ V-3,4, VI-1~5, VII-1~4, VIII-1~4, IX-1~3; ♂ VII-4, VIII-1~4, IX-1~4.
 U 20. *Lg. (Lg.) scitulum* (Smith). 1=0+1. VIII-3.
 21. *Lg. (Lg.) sp.1.* 6=5+1 (BG 4=4+0, UC 2=1+1). ♀ V-2,3, VI-2,3, VII-1; ♂ VIII-4.
 22. *Lg. (Lg.) sp.3.* 52=33+19 (BG 38=23+15, UC 14=10+4). ♀ V-3,4, VI-1~5, VII-1~3, VIII-1,2,4, IX-2,3; ♂ VIII-2,3, IX-1~3.
 U 23. *Lg. (Lg.) sp. 4.* 104=71+33. ♀ IV-2, V-1~4, VI-1~5, VII-1~4, VIII-1~4, IX-1,2; ♂ VIII-3, IX-1~4.

Genus *Lasioglossum* Curtis - Subgenus *Dialictus* Robertson (*Dl.*).

634=530♀+104♂ (BG 528=427+101, UC 106=103+3)

24. *Lg. (Dl.)* sp.1. **483**=438+45 (BG **378**=336+42, UC **105**=102+3). ♀ IV-1,2, V-1~4, VI-1~5, VII-1~4, VIII-1~4, IX-1~3; ♂ VII-1,3,4, VIII-1~4, IX-1,3.
25. *Lg. (Dl.)* sp.2. **151**=92+59 (BG **150**=91+59, UC **1**=1+0). ♀ IV-1,2, V-1~4, VI-1~5, VII-1~3, IX-1~4; ♂ VII-3, VIII-3, IX-2~4.

Genus *Lasioglossum* Curtis - Subgenus *Evyllaesus* Robertson, Carinate group (*Et.*).

1,275=734♀+541♂ (BG **735**=447+288, UC **540**=287+253)

26. *Lg. (Et.) apristum* (Vachal). **42**=32+10 (BG **40**=30+10, UC **2**=2+0). ♀ V-4, VI-1,4,5, VII-1~3, VIII-1; ♂ VIII-4, IX-2,3.
27. *Lg. (Et.) duplex* (Dalla Torre). **880**=439+441 (BG **414**=225+189, UC **446**=214+252). ♀ IV-1,2, V-1~4, VI-1~5, VII-1~4, VIII-1~4, IX-1~3; ♂ VI-5, VII-1~3, VIII-1~4, IX-1~4.
- B 28. *Lg. (Et.) pallidulum* (Matsumura). **2**=1+1. ♀ V-4; ♂ IX-2.
29. *Lg. (Et.) trispine* (Vachal). **275**=197+78 (BG **240**=164+76, UC **35**=33+2). ♀ IV-1,2, V-1~4, VI-1~5, VII-1~4, VIII-1,4, IX-1~3; ♂ VII-2~4, VIII-1~4, IX-1~4.
- B 30. *Lg. (Et.)* sp.1. **1**=0+1. IX-4.
31. *Lg. (Et.)* sp.2. **80**=65+15 (BG **36**=27+9, UC **44**=38+6). ♀ IV-1,2, V-1~4, VI-1~4, VIII-2,4, IX-1~3; ♂ VIII-1~3, IX-1~4.
- B 32. *Lg. (Et.)* sp.4. **2**=0+2. VII-1,2.

Genus *Lasioglossum* Curtis - Subgenus *Evyllaesus* Robertson, Carinaless group (*El.*).

597=551♀+46♂ (BG **301**=267+34, UC **296**=284+12)

33. *Lg. (El.)* sp.1. **124**=104+20 (BG **86**=68+18, UC **38**=36+2). ♀ V-3,4, VI-1~5, VII-1,2, VIII-4, IX-2,3; ♂ VIII-1~4, IX=2,3.
34. *Lg. (El.)* sp.2. **14**=10+4 (BG **1**=1+0, UC **13**=9+4). ♀ V-2, VI-1, VIII-3, IX-1~3; ♂ VIII-1,2.
35. *Lg. (El.)* sp.3. **92**=85+7 (BG **62**=56+6, UC **30**=29+1). ♀ V-2~4, VI-1~5, VII-1~4, VIII-1~4, IX-1,2,4; ♂ VII-3,4, VIII-2~4, IX-4.
36. *Lg. (El.)* sp.4. **69**=67+2 (BG **46**=45+1, UC **23**=22+1). ♀ IV-1,2, V-1~4, VI-1~5, VII-1~3, VIII-3, IX-2,3; ♂ VII-1, IX-1.
37. *Lg. (El.)* sp.5. **23**=21+2 (BG **13**=11+2, UC **10**=10+0). ♀ IV-2, V-1~4, VI-1~5, VII-1,3, VIII-3; ♂ VIII-3,4.
- U 38. *Lg. (El.)* sp.6. **2**=2+0. VI-5, IX-2.
39. *Lg. (El.)* sp.8. **76**=72+4 (BG **12**=9+3, UC **64**=63+1). ♀ IV-2, V-1~4, VI-1~5, VII-1~3, VIII-1, IX-1,2; ♂ VIII-1,2.
40. *Lg. (El.)* sp.9. **31**=29+2 (BG **21**=19+2, UC **10**=10+0). ♀ IV-1, V-1,3,4, VI-1~4; ♂ VII-1,4.
41. *Lg. (El.)* sp.10. **49**=49+0 (BG **6**=6+0, UC **43**=43+0). V-1,3,4, VI-1~5, VII-1~4, IX-1.
- B 42. *Lg. (El.)* sp.12. **1**=1+0. V-3.
- U 43. *Lg. (El.)* sp.14. **1**=0+1. VII-3.
- U 44. *Lg. (El.)* sp.16. **26**=25+1. ♀ VI-1,2,4,5, VII-1,2, VIII-1,3, IX-1,2,4; ♂ IX-2.
- U 45. *Lg. (El.)* sp.17. **25**=25+0. VI-1~5, VII-2,4.

46. *Lg. (El.)* sp.18. 61=60+1 (BG 51=50+1, UC 10=10+0). ♀ IV-1, V-1~4, VI-1~5, VII-1~4, VIII-4, IX-1~3; ♂ IX-3.
 B 47. *Lg. (El.)* sp.19. 1=1+0. VI-1.
 B 48. *Lg. (El.)* sp.A. 1=0+1. VII-1.
 U 49. *Lg. (El.)* sp.B. 1=0+1. VIII-2.

Genus *Sphecodes* Latreille (*Sph.*). 78=36♀+42♂
 (BG 34=17+17, UC 44=19+25)

50. *Sph. esakii* Strand et Yasumatsu. 33=16+17 (BG 19=7+12, UC 14=9+5). ♀ V-2~4, VI-1, VIII-2,3, IX-4; ♂ VIII-1,4, IX-1,2,4.
 51. *Sph. scabricollis* Wesmael ssp. 32=11+21 (BG 8=4+4, UC 24=7+17). ♀ VI-2,4, VII-3, VIII-2~4, IX-1; ♂ VII-4, VIII-2~4, IX-1,2,4.
 52. *Sph.* sp.1. 7=6+1 (BG 4=4+0, UC 3=2+1). ♀ V-2~4, VI-2, VIII-2; ♀ IX-1.
 53. *Sph.* sp.2. 2=2+0 (BG 1=1+0, UC 1=1+0). V-2, VI-1.
 B 54. *Sph.* sp.3. 1=1+0. V-4.
 55. *Sph.* sp.5. 3=0+3 (BG 1=0+1, UC 2=0+2). VII-1~3.

Family ANDRENIDAE 1,016=573♀+443♂ (BG 480=286+194, UC 536=287+249)

Genus *Andrena* Fabricius (*Ad.*)

The number of individuals in some species slightly differs from that reported in Sakagami and Matsumura (1967), due to the errors in the course of sorting and calculation, which were corrected in the following data.

56. *Ad. (Andrena) benefica* Hirashima. 120=95+25 (BG 105=85+20, UC 15=10+5). ♀ IV-1,2, V-1~4, VI-1~3; ♂ IV-1,2, V-1.
 57. *Ad. (Ad.) nawai* Cockerell. 43=33+10 (BG 22=20+2, UC 21=13+8). ♀ IV-1, V-1,2,4; ♂ IV-1.
 U 58. *Ad. (Cnemidandrena) seneciorum* Hirashima. 1=1+0. IX-1.
 59. *Ad. (Euandrena) stellaria* Hirashima (= *Euandrena hebes* Perez in Sakagami and Matsumura 1967). 132=110+22 (BG 72=58+14, UC 60=52+8). ♀ IV-1,2, V-1~4, VI-1,2; ♂ VI-1,2, V-1.
 B 60. *Ad. (E.) takachihoi* Hirashima (= *Euandrena* sp. 1 in Sakagami and Matsumura 1967). 1=1+0. IX-2.
 61. *Ad. (Gymnandrena) watasei* Cockerell. 116=52+64 (BG 53=28+25, UC 63=24+39). ♀ IV-1,2, V-1~4, VI-1~5; ♂ IV-1,2, V-1~4, VI-1~3.
 62. *Ad. (Holandrena) valeriana* Hirashima. 144=38+106 (BG 4=3+1, UC 140=35+105). ♀ VII-4, VIII-1,2,4; ♂ VII-2~4, VIII-1,2,4.
 B 63. *Ad. (Hoplendrena) dentata* Smith. 1=0+1. VI-1.
 64. *Ad. (Micrandrena) brassicae* Hirashima. 39=38+1 (BG 7=7+0, UC 32=31+1). ♀ V-2,4, VI-1~3; ♂ VII-3.
 B 65. *Ad. (M.) hikosana* Hirashima. 36=22+14. ♀ V-1~4, VI-1; ♂ IV-2, V-1.
 B 66. *Ad. (M.) kaguya* Hirashima. 16=10+6. ♀ IV-1,2, V-1~4, VI-1; ♂ IV-1, V-1,2.
 U 67. *Ad. (M.) komachi* Hirashima. 1=1+0. V-1.
 68. *Ad. (M.) sublevigata* Hirashima. 42=35+7 (BG 31=25+6, UC 11=10+1). ♀ IV-1, 2, V-1~4, VI-1; ♂ IV-1,2.
 B 69. *Ad. (M.)* sp.1. 3=0+3. VII-4, VIII-1,3.
 70. *Ad. (Plastandrena) astragalina* Hirashima. 19=15+4 (BG 10=8+2, UC 9=7+2).

- ♀ V-1~4, VI-1,3; ♂ V-1,3.
- B 71. *Ad. (Stenomelissa) halictoides* Smith. 2=1+1. ♀ V-4; ♂ V-3.
72. *Ad. (Taeniandrena) ezoensis* Hirashima. 287=113+174 (BG 114=15+99, UC 173=98+75). ♀ VI-1~5, VII-1~4, VIII-1, IX-1; ♂ V-4, VI-1~5, VII-1.
73. *Ad. (Trachandrena) haemorrhoea japonibia* Hirashima. 13=8+5 (BG 3=3+0, UC 10=5+5). ♀ IV-1, V-1,2, VI-1,2; ♂ IV-2, V-1,2.
- Family MEGACHILIDAE 338=137♀+201♂ (BG 229=108+121, UC 109=29+80)
- Genus *Chalicodoma* Lapeletier (*Ch.*). 6=0♀+6♂ (BG 6=0+6)
- B 74. *Ch. (Eumegachilana) sculpturalis* Smith. 6=0+6. VII-3, VIII-1,2.
- Genus *Megachile* Latreille (*Mg.*). 259=119♀+140♂ (BG 159=93+66, UC 100=26+74)
75. *Mg. centuncularis* ssp.¹⁾ 113=32+81 (BG 31=9+22, UC 82=23+59). ♀ VI-3,4, VII-1,3,4, VIII-1~4, IX-2~4; ♂ V-4, VI-1~5, VII-3,4, VIII-1~4, IX-1~3.
76. *Mg. willughbiella* ssp.¹⁾ 140=85+55 (BG 125=83+42, UC 15=2+13). ♀ VI-4,5, VII-1~4, VIII-1~3, IX-2; ♂ VI-2~5, VII-1~4, VIII-1~4, IX-1.
77. *Mg. tsurugensis* Cockerell. 3. 6=2+4 (BG 3=1+2, UC 3=1+2). ♀ VII-4, IX-3; ♂ VIII-1~3.
- Genus *Osmia* Panzer (*Os.*). 56=12♀+44♂ (BG 56=12+44).
- B 78. *Os. cornifrons* (Radoszkowski). 46=11+35. ♀ IV-1, V-1~3; ♂ IV-1,2, V-1,2.
- B 79. *Os. taurus* Smith. 10=1+9. ♀ V-2, ♂ V-1~4.
- Genus *Coelioxys* Latreille (*Cx.*). 17=6♀+11♂ (BG 8=3+5, UC 9=3+6)
80. *Cx.* sp.1. 6=3+3 (BG 4=2+2, UC 2=1+1). ♀ VI-4, VII-1; ♂ VI-5, VII-3, IX-2.
81. *Cx.* sp.2. 11=3+8 (BG 4=1+3, UC 7=2+5). ♀ VII-4, VIII-1, IX-3; ♂ VI-1,2,5, VII-4, VIII-1,2, IX-2.
- Family ANTHOPHORIDAE 962=708♀+254♂ (BG 552=413+139, UC 410=295+115)-Subfamily Anthophorinae 124=28+96 (BG 38=11+27, UC 86=17+69)
- Genus *Eucera* Scopoli (*Eu.*). 71=15♀+56♂ (BG 4=2+2, UC 67=13+54)
82. *Eu.* sp.1. 71=15+56 (BG 4=2+2, UC 67=13+54). ♀ VI-4, VII-1~4; ♂ VI-3,4, VII-1,2.
- Genus *Clisodon* Patton (*Cl.*). 53=13♀+40♂ (BG 34=9+25, UC 19=4+15)
83. *Cl.* sp.1. 53=13+40 (BG 34=9+25, UC 19=4+15). ♀ VI-4,5, VII-1,2,4; ♂ V-3, VI-3~5, VII-1,4, VIII-1~3.
- Family ANTHOPHORIDAE - Subfamily Nomadinae 71=38♀+33♂ (BG 40

1) Hirashima and Maeta, MS.

=19+21, UC 31=19+12)

Genus *Nomada* Scopoli (*Nm.*)

- U 84. *Nm. comparata* Cockerell. 1=1+0. VI-2.
 B 85. *Nm. hakonensis* Cockerell. 8=1+7. ♀ V-2, ♂ IV-1,2.
 86. *Nm. koebeli* Cockerell. 24=12+12 (BG 23=11+12, UC 1=1+0). ♀ IV-2, V-1,2, VI-1~3; ♂ IV-1,2, V-1.
 U 87. *Nm. okamotonis* Matsumura. 12=9+3. ♀ VII-4, VIII-1; ♂ VII-3, VIII-1.
 88. *Nm. sp.* (aff. *calloptera*). 2=1+1 (BG 1=1+0, UC 1=0+1). ♀ VI-1; ♂ IV-2.
 89. *Nm. sp.* (aff. *fulva*). 5=3+2 (BG 4=3+1, UC 1=0+1). ♀ VI-1,2, VIII-1; ♂ V-4, VI-3.
 U 90. *Nm. sp.*1. 1=0+1. VII-2.
 B 91. *Nm. sp.*2. 1=1+0. IV-2.
 U 92. *Nm. sp.*3. 11=7+4. ♀ VIII-1~4; ♂ VIII-1~3.
 93. *Nm. sp.*4. 5=3+2 (BG 2=2+0, UC 3=1+2). ♀ V-2,3, VI-1; ♂ V-1.
 B 94. *Nm. sp.*5. 1=0+1. IV-2.

Family ANTHOPHORIDAE - Subfamily Xylocopinae 767=642♀+125♂
 (BG 474=383+91, UC 293=259+34)

Genus *Ceratina* Latreille (*Ct.*)

95. *Ct. (Ceratinidia) flavipes* Smith. 159=102+57 (BG 78=41+37, UC 81=61+20). ♀ IV-2, V-3,4, VI-1,3~5, VII-1~4, VIII-2~4, IX-1~4; ♂ IV-2, V-3,4, VI-1~5, VII-2, 3, VIII-1, 3, 4, IX-1~3.
 96. *Ct. (C.) japonica* Cockerell. 608=540+68 (BG 396=342+54, UC 212=198+14). ♀ IV-1, 2, V-1~4, VI-1~5, VII-1~3, VIII-1~4, IX-1~4; ♂ IV-1, 2, V-1~4, VI-1, 2, VIII-3, 4, IX-1~3.

Family APIDAE 513=42♀+299♀+172♂ (BG 332=34+217+81, UC 181=8+82+91)

Genus *Bombus* Latreille (*Bo.*)

97. *Bo. (Bombus) hypocrita sapporoensis* Cockerell. 238=14+99+125 (BG 133=13+65+55, UC 105=1+34+70). ♀ IV-2, V-2~4, VI-1,2, VII-1; ♀ V-4, VI-1~5, VII-1~4, VIII-1~4, IX-1,2; ♂ VII-2~4, VIII-1~4, IX-1~3.
 98. *Bo. (Diversobombus) diversus tersatus* Smith. 183=20+145+18 (BG 181=20+143+18, UC 2=0+2+0). ♀ V-2~4, VI-1, 2, 5; ♀ VI-3~5, VII-1~4, VIII-1~4, IX-2~4; + VIII-2~4, IX-1~4.
 99. *Bo. (Pyrobombus) ardens sakagami* Tkalec. 17=3+7+7 (BG 15=1+7+7, UC 2=2+0+0). ♀ IV-1, VII-1; ♀ VI-3, VII-1,2; ♂ VII-1,3,4.
 B 100. *Bo. (P.) hyponorum koropokkrus* Sakagami et Ishikawa. 1=0+0+1. VII-1.
 101. *Bo. (Thoracobombus) deuteronymus deuteronymus* Schulz. 62=4+42+16 (BG 2=0+2+0, UC 60=4=40+16). ♀ VI-3, 4, VII-1, IX-1; ♀ VI-4, 5, VII-1~4, VIII-1~4, IX-1,3; ♂ VIII-2~4, IX-1.
 U 102. *Bo. (T.) pseudobaicalensis* Vogt. 12=1+6+5. ♀ V-1; ♀ VII-1~4, IX-1, 2; ♂ IX-1,2.