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**Distribution and Bionomics of a Transpalaeartic Eusocial
Halictine Bee, *Lasioglossum (Evyllaesus) calceatum*,
in Northern Japan, with Reference to Its
Solitary Life Cycle at High Altitude¹⁾**

By

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(With 9 Text-figures and 2 Tables)

In the course of bionomic studies on a eusocial halictine bee, *Lasioglossum (Evyllaesus) duplex* Dalla Torre, by one of us (S.F.S., Sakagami and Hayashida 1958-'68, Sakagami and Fukuda 1972b), we have noticed the presence of another closely similar species in Hokkaido, generally more confined to hilly or mountaneous areas. Consulting the key by Blüthgen (1924) the species went straight to *Halictus calceatus* Scopoli 1763, one of the commonest and most wide-spread species in Europe. The identification was confirmed by the comparison with some European specimens and the species was recorded as new to Japan (Sakagami and Fukuda 1972a). Some bionomic aspects of this species have already been studied in Europe (Bonelli 1965, '68 Knerer and Plateaux-Quénu 1966, '67 a~c, Plateaux-Quénu 1963, '64, '67, Vleugel 1961). Considering its enormous distribution range, the observations made in Eastern Asia must contribute to a better understanding of its bionomics. In the present paper, special reference is given to its distribution in Hokkaido in comparison with *L. duplex* and the appearance of a solitary life cycle at the top of Mt. Yokotsu, 1,167 m, in Southern Hokkaido, nevertheless the species is eusoical with a summer matrifilial phase in the lowlands, as in Central and Southern Europe.

1. Taxonomy

L. calceatum is closely similar to *L. duplex*, both indubitably belonging to the same species group. Their separation is possible in females by surface sculpture as follows:

1) Contribution No. 929 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan

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Characters (cf. Fig. 1)	<i>calceatum</i>	<i>duplex</i>
I. Supraclypeus and clypeus (1c vs. 1d)	Interspaces as wide as to wider than punctures, slightly coriaceous and moderately shining	Interspaces as wide as to narrower than punctures, distinctly coriaceous or microscopically finely reticulate and dimly shining
II. Mesoscutum posteriorly and mesoscutellum (2c vs. 2d)	Interspaces as on supraclypeus	Interspaces as on supraclypeus
III. Metasomal terga (3c vs. 3d)	Punctures sparser, small but distinct, interspaces less coriaceous with rather a stronger enamel-like luster	Punctures denser, minute and ill-defined, giving a rough and dimly shining appearance together with distinctly coriaceous interspaces
IV. Marginal areas of metasomal terga (3c vs. 3d)	Distinctly depigmented, often semitransparent	Virtually not depigmented, only at extremity narrowly brownish

Among these characters I and II show considerable variation, occasionally with intermediate conditions, while III and IV are fairly constant. As in most halictine bees, males possess coarser sculpture and more shiny interspaces in both species, but all characters given above are applicable to males, though III is the most useful (Genitalia still not precisely compared). Although the differences are slight, the separation is, once understood, not difficult. Most specimens listed in Table 1 could be identified without much difficulty with *L. calceatum* or *L. duplex*, even if collected at the same localities, with a single exception, one female from Onnebetsu (KA-12 in Fig. 2 and Table 1), which was identified with *L. duplex* but showed intermediate conditions in all characters mentioned. This suggests the rarity of hybridization even though both species live in same areas.

As shown in Fig. 5, A, B, body size of the two species overlaps in both sexes, though larger individuals are relatively more numerous in *L. calceatum*. No appreciable difference was detected between specimens of *L. calceatum* from Hokkaido and Europe (from France, Belgique and Bohemia). But all males in Hokkaido possessed black metasomas, with no reddish tint as is seemingly not rare in European populations. For a comment on nest architecture, see Section 5.3.

2. Distribution

The distribution of *L. calceatum* is enormous. Previous records have been compiled by Hirashima (1957) as follows:

Europe, E. and C. Asia (Blüthgen 1924), S. Manchuria (Hedicke 1940), Ussuri (Gussakovskij 1932), Siberia (Cockerell 1924, Blüthgen 1924, Cockerell 1925, *Halictus calceatus ulterior* Cockerell 1929 from Smolenschina, Tibeitye, Okeanskaja), North Africa (Blüthgen 1924).

The specimens examined of *L. calceatum* and *L. duplex* collected from diverse

localities in Hokkaido and the Shimokita Peninsula, the northernmost extremity of Honshu, are listed in Table 1 and the distribution of both species is mapped in Fig. 2 with indications of relative sample sizes and altitude of each locality. Approximate pie graphs show relative abundance when both species were collected at the same localities. The distinction of three altitudinal divisions is sometimes arbitrary. Localities higher than 200 and 800 m were respectively classified as hilly or mountaneous, but certain localities were designated as plains, even though higher than 200 m, when situated in the midst of a flat highland.

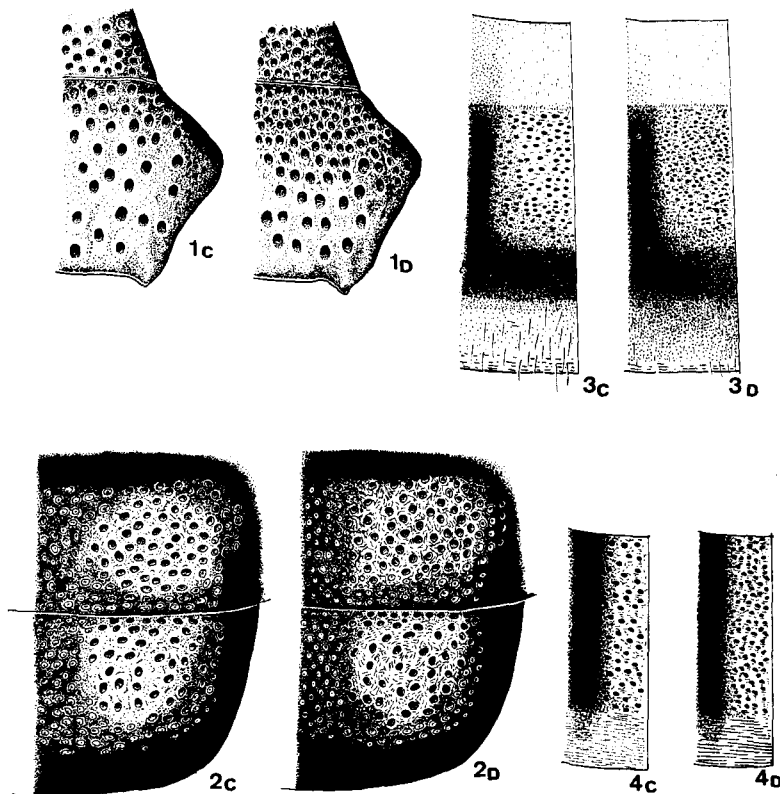


Fig. 1. Difference in surface sculpture between *L. calceatum* (c) and *L. duplex* (d). 1. Supraclypeus and clypeus (female); 2. Mesoscutum and mesoscutellum (female); 3. and 4. Metasomal tergum III (female and male).

Except for two areas, Sapporo and Hakodate with their environs, given separately in Fig. 2, P and Q, the capture records are still sparse throughout the area concerned and no specimens have yet been collected in Provinces Rumoi (RM)

Table 1. Capture records of *Lasioglossum calceatum* and *L. duplex* from northernmost Honshu (Aomori Prefecture) and Hokkaido.

Remarks: 1. Relative altitude. M. Mountains, H. Hills and mountain outskirts, P. Plains.

2. Males are still not sorted in collections from AO, HI, OS and TO-2.

Province (Abbrev.)	Locality		Number of specimens examined			
	Name (code no.)	relative altitude	<i>calceatum</i> (♀♀-♂♂)	<i>duplex</i> (♀♀-♂♂)	Total	%- <i>calceatum</i>
Aomori (AO) Shimokita peninsula	Sai (1)	P		7-	7	0.0
	Zaimoku (2)	P		9-	9	0.0
	Ikokuma (3)	P		8-	8	0.0
Hiyama (HI)	Okushiri Is., Eastern coast (1)	P		111-	111	0.0
	Okushiri Is., Northcape (2)	P	112-	1-	113	99.1
	Okushiri Is., Minouta (3)	P	12-		12	100.0
	Okushiri Is., Horanai~ Kamiwaki (4)	P	2-		2	100.0
	Okushiri Is., Hoyaishi (5)	P	18-	75-	93	19.4
	Esashi (6)	P	1-	71-	72	1.4
	Kenichi spa (7)	H	1-	1-	2	50.0
	Mt. Daisengen (1,072 m) (8)	M	2-		2	100.0
Oshima (OS)	Kojima Is. (1)	H	4-		4	100.0
	Era, Matsumae (2)	P		1-	1	0.0
	Yoshioka (3)	P		1-	1	0.0
	Fukushima (4)	P		32-	32	0.0
	Kikonai (5)	P		4-	4	0.0
	Mt. Hakodateyama, Hakodate (6)	H		75-	75	0.0
	Hachimanchô, Hakodate (7)	P		13-	13	0.0
	Yunokawa, Hakodate (8)	P		20-	20	0.0
	Masukawa, Hakodate (9)	P		1-	1	0.0
	Akagawa, Hakodate (10)	H	17-	155-	172	9.9
	Narukawa, Nanae (11)	H	14-	10-	24	58.4
	Niyama, Nanae (12)	H		58-	58	0.0
	Mt. Yokotsudake (1,167 m) (13)	M	58-		58	100.0
	Toyoura, Shirikishinai (14)	H	12-	13-	25	48.0
	Esan, Shirikishinai (15)	P	5-	2-	7	71.7
	Ônuma Park (16)	H		41-	41	0.0
	Oshironai, Kayabe (17)	P		1-	1	0.0
	Yakumo (18)	P		88-	88	0.0
Iburi (IB)	Ohkishi (1)	P		3-0	3	0.0
	Tôya (2)	P		1-0	1	0.0
	DateMombetsu (3)	P		24-0	24	0.0
	Gozensui, Muroran (4)	H	20-0	1-0	21	95.2
	Horobetsu (5)	H		46-0	46	0.0
	Numanohata (6)	P		2-0	2	0.0

Table 1. *continued*

Shiribeshi (SB)	Kuromatsunai (1)	P		3-0	3	0.0
	Kyôgoku (2)	H		17-0	17	0.0
	Kutchan (3)	P		1-0	1	0.0
	Iwanai (4)	P		1-0	1	0.0
	Bikuni, Shakotan Penins. (5)	P	1-0		1	100.0
	Okusawa, Otaru (6)	H	88-31	3-0	122	97.8
	Asarigawa spa (7)	H	6-0		6	100.0
Ishikari (IK)	Okuteine (1)	M		7-0	7	100.0
	Mt. Teine (950 m) (2)	M		0-4	4	100.0
	Teine, Sapporo (3)	P		1-0	1	0.0
	Bankei, Sapporo (4)	H	52-4		56	100.0
	Jyôzankei, Sapporo (5)	H	1-1	1-0	3	66.6
	Maruyama, Sapporo (6)	H		8-0	8	0.0
	Misumai, Sapporo (7)	H		57-1	58	0.0
	Fujinosawa, Sapporo (8)	P		8-0	8	0.0
	Hyakumatsuzawa, Sapporo (9)	H	1-0		1	100.0
	Mt. Soranuma, foot (10)	H		20-3	23	0.0
	Eniwa valley (11)	H		1-0	1	0.0
	University Campus, Sapporo (12)	P		456-427	883	0.0
	Tsukisappu, Sapporo (13)	P		289-47	336	0.0
	Shikotsu-Kohan (14)	P		4-0	4	0.0
	Shimamatsu (15)	P		3-0	3	0.0
	Chitose (16)	P		1-0	1	0.0
	Ebetsu (17)	P		5-0	5	0.0
	Tarukawa (18)	P		2-0	2	0.0
	Ishikari (19)	P		28-0	28	0.0
Sorachi (SR)	Naganuma (1)	P		1-0	1	0.0
	Satteki, Urausu (2)	P		15-0	15	0.0
	KitaMoshiri (3)	P	0-1		1	100.0
Tokachi (TO)	Obihiro (1)	P		10-0	10	0.0
	Atsunai (2)	P		71-	71	0.0
	Tomuraushi (3)	H	0-1			100.0
Kamikawa (KA)	Furano (1)	P		3-0	3	0.0
	Takanegahara (2)	M	5-0		5	100.0
	Kôgen spa (3)	M	4-0		4	100.0
	Jigokudani (4)	M	2-1		3	100.0
	Sôunkyo (5)	H	3-0		3	100.0
	Yukomanbetsu (6)	M	4-0		4	0.0
	Nokanan (7)	H		188-162	350	0.0
	Higashikawa (8)	P		1-0	1	0.0
	Asahiyama, Asahigawa (9)	H	0-1	67-4	72	1.4
	Inosawa, Asahigawa (10)	H	1-0	9-1	11	9.0
	Shibetsu (11)	H	2-0	1-0	3	66.6
	Onnebetsu (12)	H	7-0	4-0	11	63.7
	KamiOtoineppu (13)	P	7-28		35	100.0
	Nakagawa (14)	P	2-1		3	100.0

Table 1. *continued*

Abashiri (AS)	HamaKoshimizu (1)	P		4-0	4	0.0
	Abashiri (2)	P		1-0	1	0.0
	Kitami (3)	P		6-0	6	0.0
	Oketo (4)	H	1-0	1-0	2	50.0
Kurshiro (KU)	Nibushi spa (1)	H		25-0	25	0.0
	Tenneru, Kushiro (2)	P	18-13	5-0	36	86.2
	Akkeshi (3)	P	9-0		9	100.0
Nemuro (NE)	Onnetô (1)	P	5-1		6	100.0
	Yoroushi (2)	H	0-11		11	100.0
Sôya (SO)	Toyotomi (1)	P		1-0	1	0.0
	Wakkanai (2)	P	4-0		4	100.0
	Rishiri Is., Oniwaki (3)	P	3-0		3	100.0
	Rishiri Is., Mt. Rishiri (4)	M	2-0		2	100.0
	Rebun Is., Kafuka (5)	P	4-0		4	100.0
Kurile Is.,	Etorofu Is., Shana	P	1-0		1	100.0

and Hitaka (HT). Nevertheless there are some geographic trends perceptible in the relative abundance of the species.

Although not mutually exclusive in the strict sense, segregation of the two species is relatively clear on the mainland of Hokkaido east of the Ishikari depression, that is, *L. calceatum* is confined to northern, eastern and central mountaneous areas while *L. duplex* is prevalent in warmer areas. The presence of *L. calceatum* in SR-3, KA-3 and KA-12, all located in a relatively warm zone as suggested by isotherm, could be judged as exceptions, this zone is characterized by very cold winter.

In the rest of Hokkaido, *L. duplex* monopolizes the Ishikari depression and is prevalent in the southern provinces, where *L. calceatum* is found rather sporadically and usually confined to hilly and mountaneous areas as shown in the two relatively well explored areas (Fig. 2, P.Q). However, it is remarkable that this species is recorded from the coastal areas, not only from hilly parts (HI-7, OS-14, IB-4), but also from narrow coastal plains (SB-5, OS-15). Finally *L. calceatum* is recorded from Kojima, a small islet at southernmost Hokkaido (OS-1) and quite abundant in Okushiri Island (HI-1~5) which is characterized by invasion of southern faunal elements. The segregation of the species along the thermal gradient is obvious but it alone cannot explain the present distribution of *L. calceatum*. Segregation and isolation of local populations through glacial and postglacial eras should in part play a role for the realization of such pattern. Up to the present, this species is not recorded from Honshu (cf. AO in Fig. 2).

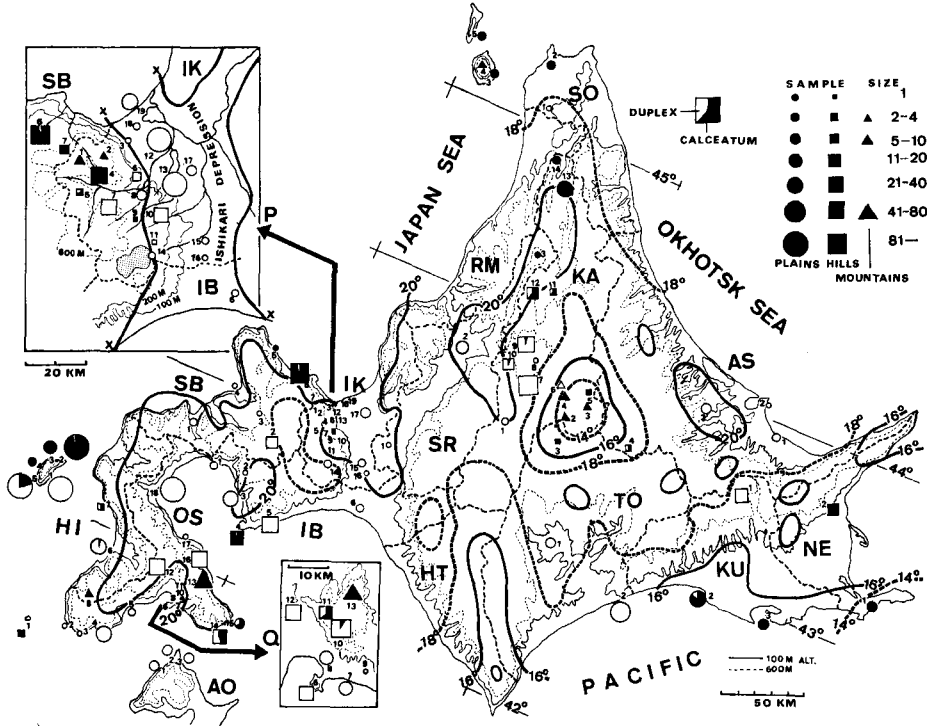


Fig. 2. Distribution of *L. calceatum* (black) and *L. duplex* (white) in Hokkaido and northernmost Honshu. Abbreviations of provinces and code numbers for localities are listed in Table 1. Isotherms show mean air temperature in July. Lines X-X in P indicate beach lines in early to middle Pleistocene.

3. Phenology and annual cycle

The annual cycle of *L. calceatum* was studied through phenological observations at two localities which are quite different in altitude, hence in climatic conditions.

One is Mt. Yokotsu in the Oshima Peninsula (Fig. 2, OS-13), southern Hokkaido. From two nest aggregations at the top (1,167 m), several nests were periodically excavated in 1968 and '69. The immatures involved were examined and adults were studied with respect to mandibular wear, ovarian condition, spermathecal content, etc. Some females captured on flowers were studied in the same way. Another locality is Okusawa, the hilly hinterland of Otaru City (Fig. 2, SB-6). Here no nest was discovered but both sexes were periodically captured in 1970 on flowers along roadsides at altitudes varying 150 to 200 m. The survey was made as a part of a periodical wild bee sampling based upon the

procedure developed by Sakagami, Laroca and Moure (1967). The area was visited three times per month. In each visit any wild bees on flowers were collected during four hours, which more or less corresponded to an excursion of about 4~5 km each time. Most bees were preserved as dry specimens but *L. calceatum* and some other halictines were put in Kahle's solution in the field. After returning to the laboratory, ovarian development and other features were examined as in the specimens from Mt. Yokotsu. An extraroutine collection was made on July 21 for *L. calceatum* alone.

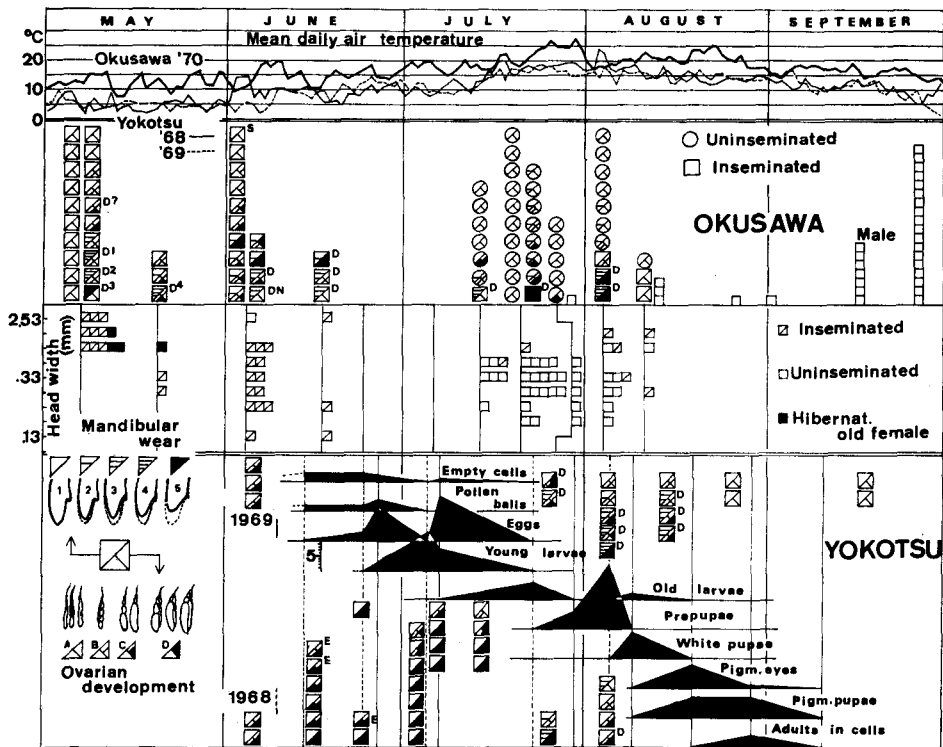


Fig. 3. Phenology of *L. calceatum* in Okusawa and Mt. Yokotsu. Daily fluctuation of mean air temperature at top. In both localities each female captured is expressed by a square (inseminated) or a circle (unseminated) showing mandibular wear and ovarian development (cf. bottom left). For Okusawa, periodical samples are given on days of collection and distribution of head widths is added. For Yokotsu, samples are clustered for each 10 days period and given approximately in corresponding period (1969 above and 1968 below), together with phenology of immatures (1969 on solid line, 1968 on broken line). Further symbols: D. Ovaries degenerated; S and N. Parasitized by stylops and nematodes; E. Spermatheca not examined; 1~4. Old mothers passed through their second winter.

The results of these surveys are summarized in Fig. 3, fluctuation of mean air temperatures at the top, results in Okusawa in the middle and those in Mt. Yokotsu at the bottom. The air temperature at the top of Mt. Yokotsu was calculated from continuous records taken at Hokkaido Prefectural Forest Nursery in Nanae (40 m alt.), applying the rate of decrease 0.6°C per 100 m alt. Similarly the air temperature in Okusawa was obtained by calibrating the records taken at Otaru Meteorological observatory.

3.1. Annual cycle in Okusawa: In Okusawa, *L. calceatum* was not an abundant species so that the number of specimens captured was insufficient to express the phenological sequence quantitatively, but enough to outline the pattern of annual cycle. First females were captured on May 7 '70 when snow patches still remained in shady places. Thereafter some females, all inseminated, were sporadically collected until June 17. The number is insufficient to trace the change of ovarian development precisely. But the data can be interpreted, in part by inference from results on the European populations (op. cit.) and on *L. duplex* (Sakagami and Hayashida 1961, '68), as indicating gradual development followed by degeneration in solitary nesting females. The record of few females with fully developed ovaries may be an outcome of small sample size caused by irregular weather conditions characteristic of the spring in Hokkaido, conditions which often affect the phenological sampling of wild bees.

The absence of specimens in two successive samplings, on May 24 and June 6, apparently corresponds to the presummer inactive phase characteristic of many eusocial *Evylaeus* species (op. cit., especially Knerer and Plateaux-Quénu 1967a, Sakagami and Hayashida 1968). Females reappeared by mid July and were captured until early August. Most of them were uninseminated, relatively small and with undeveloped ovaries. Indubitably these bees represent daughters produced by spring females and foraging as workers in summer matrifilial association (op. cit.). Some inseminated females collected in this period are either old mothers or newly emerged females which hibernate and found the nests the next spring. The scarcity of these new females on flowers, only three taken in early August, accords with observations on *L. duplex* (Sakagami and Fukuda, 1972b). The first male was captured in late July and thereafter a few males were collected in August and more in mid to late September, the phenology being similar to that of *L. duplex* (Sakagami and Hayashida 1968). The appearance of some males produced by spring females during solitary phase, recorded by Knerer and Plateaux-Quénu (1967b) in the European population of the same species and in *L. duplex* (Sakagami and Hayashida 1961, '68), is probable but could not be confirmed in our survey.

Summarizing, the annual cycle in Okusawa does not essentially differ from that recorded in European populations, consisting of the spring solitary phase, presummer inactive phase and summer matrifilial phase. Bonelli (1965) described the annual cycle of *L. calceatum* in Piazzol (950 m alt.), Prov. Trento, Italy, as

follows: A. Start of spring activity (late March~early April), B. Feeding on flowers (mid~late April), C. Foraging and cell construction (late April~early May), D. First inactive phase (mid May~early June), E. Start of summer reactivation (mid June~early July), F. Start of second inactive phase (early~late July), G. Start of autumn reactivation (early August~early September), H. End of activities (mid September). Our results are insufficient to make a precise comparison with this annual cycle in an Italian population, but are characterized by a delay of about one month in A, D, E, and obscurity of the second inactive phase, apparently caused by a compression of the annual cycle due to severer climatic conditions. A similar but less marked delay is recognized when the results are compared with the annual cycle of *L. duplex* in Sapporo (op. cit.), a delay of 10~15 days in A, D, E, and omission of F. Although Sapporo and Okusawa are not remote from each other (Fig. 2, P, IK-12 and SB-6), the climatic difference in spring due to altitudes is obvious in phenologies of many plants and insects.

3.2. Annual cycle in Mt. Yokotsu: A remarkable difference is noted in the annual cycle in Mt. Yokotsu, where the mean daily air temperature is 5~10°C lower than in Okusawa (Fig. 3, top). Because of strong winds throughout the year, the top is covered with snow only from mid November to mid April; nevertheless the snow remains to mid May at the level of 1,100 m. This earlier surface exposure must profoundly affect the hibernating females and their activity starts only in early June. It is interesting that most females captured in this period, either from nests or flowers, already possessed more or less developed ovaries. From this time onward all females, except possibly some whose spermathecae we failed to examine (shown by E), were inseminated with well developed ovaries until gradually replaced by ovarially degenerated or fresh females in early August. Thus, no uninseminated females with atrophied ovaries (workers) were found, giving clear evidence of the absence of a summer matrifilial phase.

The seasonal shift of immature stages in nests accords well with this single brood rearing activity by solitary females. Each stage gradually shifts to the subsequent one and the whole sequence indicates the presence of only one brood, not followed by a second one as in *L. duplex* in Sapporo (Sakagami and Hayashida 1958). Consequently, *L. calceatum* behaves as a solitary species under severe climate at the top of Mt. Yokotsu. This solitary brood produces males and hibernating females. The latter, after mating, repeat the same simple life cycle the next year. Males collected on flowers are still not sorted. From immatures reared in laboratory we obtained 23 male and 21 female adults during August, a sex ratio ca. 1:1 as in autumn sexuals of *L. duplex* (Sakagami and Hayashida 1968). No size difference between newborn females and those taken from nests or on flowers was confirmed.

3.3. Comparison of two annual cycles: Annual cycles in Okusawa and Mt. Yokotsu are schematically compared in Fig. 4, together with differences in thermal conditions in terms of accumulated day-dgrees, taking 5°C arbitrarily as the

physiological zero. Schematic cycles follow the system adopted in Sakagami and Hayashida (1968) but are given in a simplified manner. The ovarian development of some summer daughters is added to but other subsidiary data such as polygynic association and survival of old mothers described below are omitted.

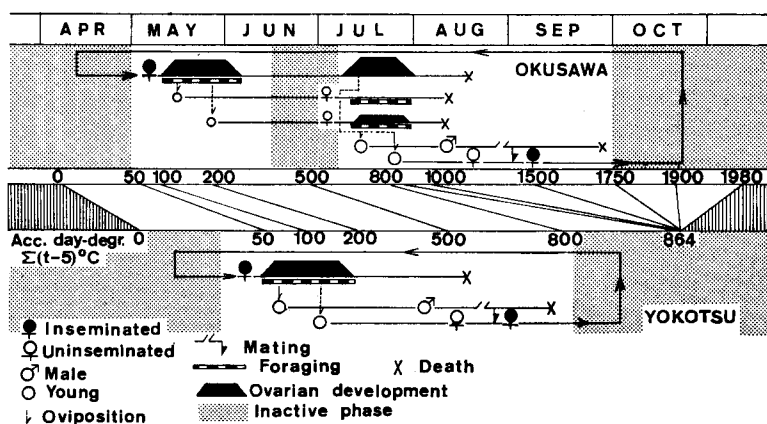


Fig. 4. Annual cycle of *L. calceatum* in Okusawa with presummer inactivation and summer matrifilial phase and in Mt. Yokotsu without such phases, given together with summation of day-degrees above 5°C.

We do not know precisely the thermal response of *L. calceatum* so that the relation between the annual cycle and thermal conditions can be inferred only crudely. The difference in accumulated day-degrees shows a delay of about 1.5 months at levels of 50~800°C. The spring nesting activity starts in both populations as $\pm 50^\circ\text{C}$, and the appearance of new females, summer daughters in Okusawa and autumn daughters in Yokotsu, at $\pm 500^\circ\text{C}$. While accumulated day-degrees still increase in Okusawa, allowing the insertion of the matrifilial phase more or less at the level of 800°C, the same level is already near the end of the season in Yokotsu, the maximum level attaining only 864°C against 1,980°C in Okusawa.

This comparison still cannot causally explain the occurrence of different cycles but delimits the environmental conditions necessary for a given cycle and the prediction of the annual cycle at given localities becomes possible. For instance, most populations recorded from the lowlands of central and southern Hokkaido must have a summer matrifilial phase, whereas those from high altitudes (Fig. 2, HI-8, IK-1, 2, KA-2~4, SO-4) may have the solitary cycle. It is still open to the question whether or not the same cycle appears in northern and eastern Hokkaido, but it is inferred that such is possible under the severe condition of some localities, for instance, NE-1.

3.4. *Survival of some old mothers to next spring*; In a previous paper (Sakagami and Fukuda 1972b), the casual survival of old mothers to their second spring was confirmed in *L. duplex* and some females with heavily worn mandibles captured in early spring were regarded as such old mothers. Among spring females of *L. calceatum* collected in Okusawa, we found similarly worn females and four of them, shown with numerals 1~4 in Fig. 3, were regarded with certainty as old mothers surviving 20~21 months, not only because of worn mandibles and early capture dates but also because their ovaries showed previous activity (presence of corpora lutea). Three of them, Nos. 1~3 captured on May 7, carried pollen loads on legs. The other, No. 4, taken on May 20, had no load but one of her ovaries contained an egg ready to lay, suggesting possible brood production in the second year, though such would obviously be quite exceptional. A fifth female marked with "?" in Fig. 3 also had the mark of previous ovarian activity but her mandibles were intact. It is difficult to interpret her status correctly, but she might be an overwintered daughter born in the late summer. Bonelli (1965) once assumed the survival of old mothers to the next spring but later (1968) abandoned the idea. The present result shows that such is circumstantially possible even though not frequent.

4. Size distribution and caste differentiation

Fig. 5 presents frequency distributions of head widths of *L. calceatum* and *L. duplex*. The comparison of the two species is given in A and B. As to females, only those captured from April to early June and newly emerged autumn females were used to avoid the wider variation that would be introduced by including summer females. Samples of *L. duplex* taken from various localities did not show marked difference except for the population from Nokanan (Table 1, Fig. 2, KA-7), which consisted of smaller individuals as given in A. In both sexes, the body size of the two species overlaps widely. Larger individuals are relatively more frequent in *L. calceatum*, but the mean head widths give no significant difference ($P>0.05$).

Fig. 5, C shows the size distribution of females from Okusawa and Mt. Yokotsu described in the previous section. Although there are more large females in Yokotsu, the difference is statistically insignificant ($P>0.30$). The size distributions of males from Yokotsu (using those emerged in laboratory) and Okusawa given in E are also not significantly different for one other ($P>0.05$).

Finally, Fig. 5, D, shows the size distribution of summer females in Okusawa and Hokkaido in total. The latter involves females captured during July in central and southern Hokkaido excluding mountains (M in Table 1). The difference between spring and summer females in Okusawa (C-O and D-O) is significant ($P<0.001$) while that between spring and summer females in total (A, *calceatum* and D-T) is not ($P>0.05$). The mean difference between spring and summer females is 3.5% in Okusawa and 5.5% in total. Both are less than the percentage caste difference in *L. duplex* (6.7%, Sakagami and Hayashida 1968) and interesting-

ly far less than in *L. calceatum* in France (13%, Knerer and Plateaux-Quénu 1967 b). The lack of marked difference between spring and summer females in Okusawa is also evident from the distribution of head widths given in Fig. 3 middle. The conspicuous difference in relative caste size between Northern Japan and Europe may express either a wide variation within the species or more plausibly a climate-conditioned variation such as a greater caste difference in southern areas. The fact mentioned shows the necessity of comparison of various populations to give a clearer picture of specific caste difference and its amplitude, especially in groups such as halictine bees, whose annual cycle and social pattern are considerably affected by climatic conditions.

Bonelli (1965) mentioned that spring females of *L. calceatum* are macrocephalic, without giving quantitative expression. Such an allometric difference between large and small individuals is widespread among halictine bees and occasionally results in conspicuous polymorphism (Sakagami and Moure 1967, Sakagami and Wain 1966). Sakagami and Hayashida (1968) found the presence of a cryptic allometry in superficially isometric *L. duplex*. However, this was not primarily linked with caste

differentiation; that is, larger summer daughters are more macrocephalic with wider metasomas than smaller ones, as well as smaller spring females being less macrocephalic with narrower metasomas than larger ones or even than extremely large summer ones. The body parts studied in *L. duplex* were measured in both sexes of *L. calceatum*, spring and summer females being left separate. The results presented in Fig. 6 show nothing other than repetition of those obtained for *L. duplex*. Without going much into a detailed analysis of relative growth, the ratios of two body parts (y) to head width (x) are given by the following linear regressions: A. $y=0.448x$, B. $y=0.479x$, C. $y=0.345x$, D. $y=0.413x$. In females, there is no different trend between spring and summer females, and similar trends

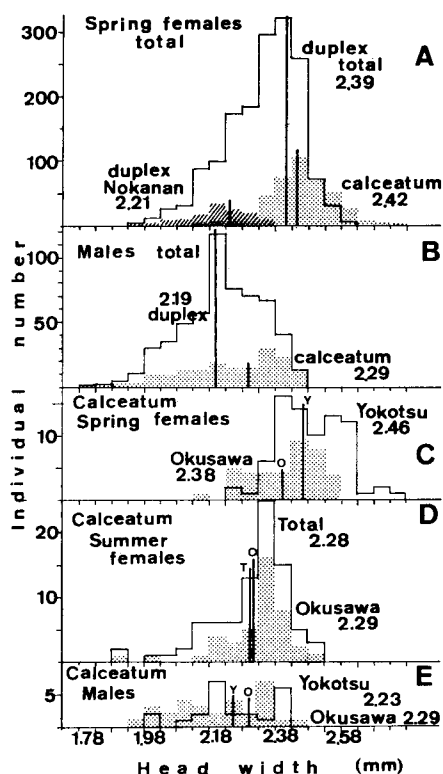


Fig. 5. Frequency distribution of head widths in *L. duplex* and *L. calceatum* (mean width given in each assemblage).

appear in males, too, though less conspicuously for the head. Therefore, the allometric trend may be regarded as basic to most halictine bees. In some social species the trend may coincide with caste differentiation, but exaggerated allometry does not necessarily indicate a higher social level. This is exhibited by the frequent appearance of conspicuous allometry in *Halictus* s. lat., which is socially relatively less evolved than *Eurylaeus* and *Dialictus* which include many socially advanced species (Sakagami 1972). The allometric difference between spring and summer females, or queens and workers, may obviously become greater in populations with greater size difference, possibly such as studied by Bonelli (op. cit.).

Percentage ovarian development of summer daughters in Okusawa is 14.3% when all workers with at least one ovary reaching degree C are regarded as ovarially developed (five out of 35 cf. Fig. 3, July to early August). The ratio is

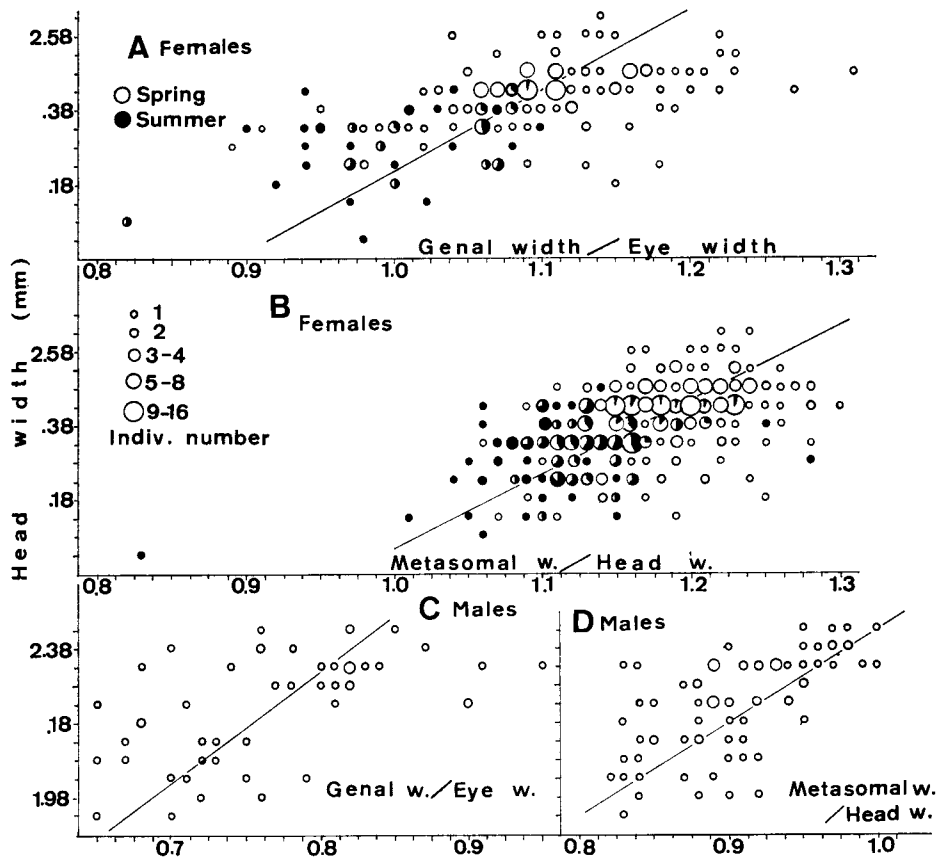


Fig. 6. Relative proportion of certain body parts in relation to body size (head width) in *L. calceatum*. Regression lines drawn from equations given in text.

less than for foragers (30.2%) or total summer females (20.2%) of *L. duplex* (Sakagami and Hayashida 1968, pp. 427 and 498). Only two individuals showed more or less bilaterally developed ovaries.

One problem concerning caste differentiation remains unsolved. How solitary females in Mt. Yokotsu can produce female offspring, whose average size equals that of mothers, and how they can produce the progeny with the sex ratio of about 1:1, whereas in Okusawa and certainly in other lowland areas the first brood of spring females produces smaller daughters and few males. The first problem is easily understood when the average body size in Mt. Yokotsu is smaller than in lowlands. Actually, however, the body size of Yokotsu population is larger than spring females of Okusawa and slightly larger than the average size of *L. calceatum* in Hokkaido, though both without significant difference. We know little of the mechanisms of caste determination in halictine bees, but quantitative difference of food seem to be important (cf. Sakagami 1972). Hence there must be a factor or factors which cause preparation of large pollen balls to produce the females equal to mothers in body size, at the top of Mt. Yokotsu. These factors might be of general nature, operating anywhere when a eusocial halictine species adopts a solitary annual cycle without dwarfism, due to severer climatic conditions. Prolonged photoperiod and resulting longer daily extranidal activities may explain the event when the solitary cycle appears at northern latitudes, but not at higher altitudes, especially when enough foraging time is often unavailable because of unstable mountain climates. The nearly synchronous and concentrated blooming at high altitudes might facilitate the foraging of plenty of food during a relatively short time. Further, unfavorable thermal condition might result in delayed maturation of eggs and furnish time sufficient to collect food to prepare larger pollen balls. But we have still no adequate explanation of this problem.

5. Nesting habits and related observations

As we could not find any nests in Okusawa and other localities, the following descriptions and observations were made exclusively from nests excavated on Mt. Yokotsu.

5.1. Nesting site: Mt. Yokotsu is the second highest peak on the Oshima Peninsula, located about 20 km NW of Hakodate. The top area is a flat tableland (Fig. 7, left-above) about 150×200 m. sq., forming a mosaic of bare pebbly ground and sparse low vegetation (Fig. 7, right). The nest aggregations have been known to one of us (M.M.) since 1960 but no detailed survey was made until 1967. Formerly nests were scattered along the trail for a considerable distance. Later the nesting site gradually dwindled with increasing human impact, installation of a radio relay station, horse grazing and trampling by increasing hikers. In 1968 only two aggregations remained, confined to narrow belts of 2×300 m. sq. and 5×30 m. sq., both mostly consisting of bare surface. Thereafter, the



Fig. 7. Nest site of *L. calceatum*. Left-above. Mt. Yokotsu seen from Hakodate. The top indicated with arrow. Left-below. Two nests with tumuli; Right. Nest site near the top (indicated with arrow).

number of nests rapidly decreased and no nest was found in 1971. Hence our survey was contemporaneous with the extinction of a local population.

5.2. Nest structure: In total 54 nests were excavated during 1968~'70. Nests illustrated in Fig. 8 are those regarded as representing normal pattern, those in Fig. 9 showing deviations from the normal pattern. The nest pattern belongs to type Vb of Sakagami and Michener (1962), characterized by the formation of a horizontal unilateral comb surrounded with a cavity, the comb-cavity system communicating with the main burrow by means of a short horizontal burrow or *lateroid*, named to distinguish it from genuine laterals in halictines, which are narrower than the main burrow and filled with soil after the closure of cells. Constriction of the entrance hole and presence of a lower blind burrow agree with the majority of halictine nests so far described (op. cit.).

Tumulus distinct in early stage nests (Fig. 7, left below), radial and central; inner wall occasionally smooth but without salivary consolidation. Entrance constricted to 3.2 to 3.5 mm, without turret. No special chamber or enlargement below entrance. Depth to bottom of blind burrow 5~17, mostly 7~14 cm, burrow 4~5 mm wide, without special enlargement; inner wall smooth but not polished; general direction vertical, often irregularly bending, without differentiated section but occasionally ramified. Lateroid mostly horizontal, 4 to 10 mm long,

as wide as main burrow, opening to upper or middle part of comb-cavity, inner wall as in main burrow.

Cells forming a unilateral horizontal comb, slightly divergent at back. Surface of comb smooth, being so elaborated that shape of each cell externally detectable. After completion, comb supported within cavity only at lower part by one to several pillars. Interspace between comb and cavity wall narrow. Cells elongate oval and bilaterally symmetric, with undersides flatter, 11~13 mm long, 5~6 mm in maximum diameter and 3~4 mm in neck diameter; inner wall smooth and polished.

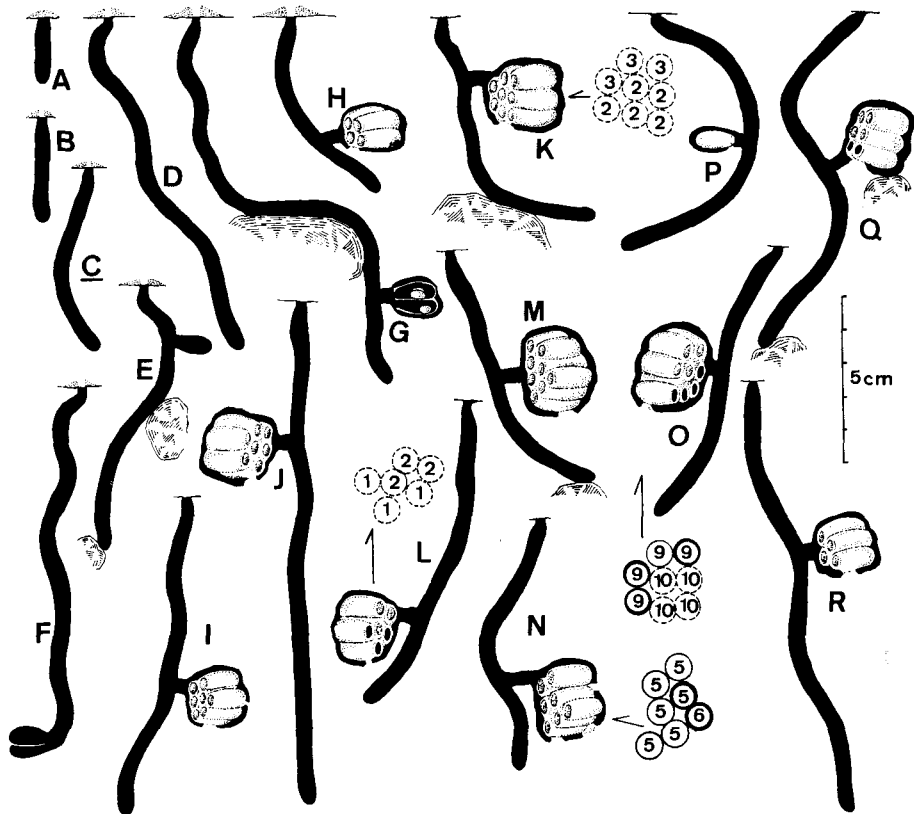


Fig. 8. Nests of *L. calceatum*, with normal nest pattern (Underlined, C, polygynic). A~D. Early nests with no cells; E, F. Nests with cells not surrounded with cavity; G~R. Nests with comb-cavity system. Immature stages in some nests shown with numerals: 1. Pollen ball alone; 2. Egg; 3~4. Young and old larvae; 5. Pre- and post-defecating larvae; 6. White pupa; 7. Colored eyed pupa; 8. Pigmented pupa; 9. Black pupa; 10. Cell after emergence. Thick and thin circles. Male and female. Broken circle, sex unknown.

Summarizing, the nest structure is virtually identical with that of *L. duplex* (Sakagami and Hayashida 1960), except for the position of the lateroid as noted to below.

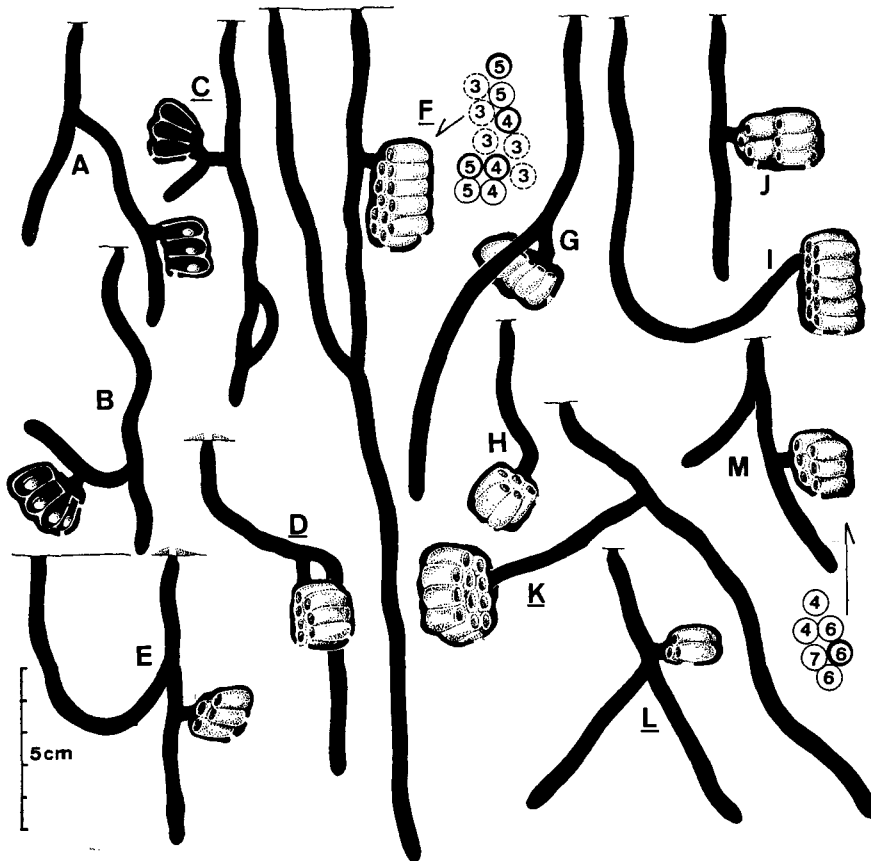


Fig. 9. Nests of *L. calceatum* with some deviations from normal pattern (Underlined, polygynic). Immatures shown in F and M as in Fig. 8. Explanations in text.

5.3. *Notes on lateroid*: Although there were some nests, the combs of which were located at the end of the main burrow (Fig. 9, H, I), most nests were provided with a lateroid connecting the main burrow and the comb. While lateroids mostly opened at the middle to lower part of the comb cavity in *L. duplex*, the position was contrary in *L. calceatum*, mostly opening at the middle to the upper part as shown by the following comparison (Data for *L. duplex* from Sakagami and Hayashida 1960, Table 5):

Species	Position of lateroid in relation to comb cavity				
	Opening at				
	Lower part	Middle part	Upper part	Top	
<i>calceatum</i>	1	13	17	1	
<i>duplex</i>	spring	25	17	0	0
	summer	48	13	6	0

Corresponding to the position of lateroids, the developmental gradient within the comb was distinctly upwards in 54.4% and more or less upwards in 77.2% in *L. duplex* (cf. op. cit. Table 11), *i.e.*, in most combs, lower cells contained younger immatures, following the progressive cell construction (Malyshev 1936) predominant in halictine nests (Sakagami and Michener 1962). In *L. calceatum* the prevalence of upper lateroids must relate to the downward gradient if the progressive pattern is kept here, too. Actually this point was difficult to trace because age differences among immatures within each comb were small in most nests. But some relevant cases seem to indicate a downward gradient in combs receiving lateroids about at the upper part but lateral or upward gradient in those receiving lateroids at the middle, thus:

Position of Lateroid	Developmental gradient					
	Down	Down+lateral	Lateral	Lateral+up	Up	Up+down
Upper	4	1	1		1	1
Middle			2	1	4	
Examples in figures	8, L, K			8, O	8, N	9, M

Fig. 9, F, showing a nest containing two adult females with presumably two different gradients, will be referred to 5.5.

The length of the lateroid is recorded in *L. duplex* as 8~14 mm in spring nests and 4~10 mm in summer nests, the latter being comparable to *L. calceatum*. An abnormally long lateroid (6 cm) was recorded in one nest (Fig. 9, K), but it is difficult to ascertain whether this was a true lateroid or to be interpreted as a combination of burrow ramification (cf. Fig. 9, A,L) and comb formation at the end of the main burrow (cf. Fig. 9, H,I).

The presence of lateroids in a Japanese population is noteworthy because there is a discrepancy in records of the nest pattern of *L. calceatum* in Europe. Ignoring old unreliable records, Malyshev (1936, Russia) gave a photograph showing a nest with a lateroid. Bonelli (1965, Italy) illustrated a spring nest with a very long lateroid and a very short blind burrow, whereas in the figure of a summer nest the comb cavity is drawn as if at the end of the main burrow, being comparable to Fig. 9, H. Finally the lateroid is distinctly absent in the figures given by Knerer (1969), Knerer and Plateaux-Quénu (1967b) and Plateaux-Quénu (1963, '64), all in France. Presumably the halictine nests with lateroids developed from the pattern with a comb cavity system along the main burrow, polyphyletically, in at least three groups, the Holarctic *Evylaeus* and the Neotropical *Augochloropsis* and *Megomma-*

tion (Sakagami and Michener 1962). The fact that nearly all comb-making *Erylaeus* species are devoid of this structure also suggests its derivative nature. Consequently the facultative lateroid formation in *L. calceatum* is interpreted either as an ethological differentiation within the enormous distribution range, or, if different nest patterns shown by Bonelli and in the present paper (Fig. 9, especially B, D, H, G, I, K) would appear rather frequently, as an instability of nest structure within some local populations.

5.4. *Nest development*: Spring nest founding was not directly observed. The foundation through subterranean dispersal, recently described in *L. duplex* by Sakagami and Fukuda (1972b) is possible judging from the unstable and often hostile spring weather in the nesting site. On the other hand, some of shallow incipient nests (Fig. 8, A~D) may have been excavated from the outside.

Cells not surrounded by the cavity were found in two early nests (Fig. 8, E and F, with only 1 and 2 empty cells each), indicating direct excavation in the substrate. All other nests possessed combs surrounded with cavities, even those relatively young ones with only two cells (2 cases, cf. Fig. 8, G) or three (2 cases, Fig. 9, A, C). Sakagami and Hayshida (1960) assumed the formation of comb-cavity system in *L. duplex* through direct excavation, not by building. But further observations of numerous nests revealed many combs with a few cells but completely surrounded with cavities. Possibly some techniques other than simple excavation in raw substrate is adopted both by *L. duplex* and *L. calceatum*, judging from the plasticity of nest building in some other halictines, notably *Augethorax pura* (Say) (Stockhammer 1966). Bonelli (1965) writes of the formation of the cavity before cell construction. In agreement with Plateaux-Quénu (1964), no such technique was traced in our observations.

The depth of the cavity bottom is distributed thus:

Depth (cm)	3~	4~	5~	6~	7~	8~	9~	10~	11~	12~
Frequency	5	8	6	6	3	0	5	1	2	1

The mean depth, 7.4 cm, is distinctly shallower than in *L. duplex* observed in Sapporo (op. cit., spring nests, 9.6 cm), reflecting the severer climate. Depth of the bottom of the blind burrow was measured as follows (nests with cells alone):

Depth (cm)	5~	6~	7~	8~	9~	10~	11~	12~	13~	14~	15~	16~	17~	26.6
Nests with young larvae	1	1		1	7	1	2	1	1	1	1			1
Nests with all older				4	2	1	2	1	2	1	2	1		

From the frequency distribution a gradual deepening of burrows is possible but not distinct. The bottom depth is more or less comparable to spring nests (6~12 cm) but shallower than summer nests (15 cm or more) of *L. duplex* (op. cit.).

The number of cells per nest is distributed as follows (Nests still with young

larvae and unsuccessful ones, for instance, Fig. 9, C, L, and those with two females excluded):

No. cells	1	3	4	5	6	7	8	10
Frequency	1	2	2	3	5	3	4	1

The mean, 5.8, is comparable to that in *L. duplex* (Sakagami and Hayashida 1968, 5~6 cells) and the maximum approximates that of *L. calceatum* in France (Plateaux-Quénu, 8 cells).

The differences in stages among immatures involved in each nest was quite low. Adopting stages given in Fig. 3, the difference was observed as follows: No difference (11 nests), 1-stage difference (9), 2 (4), 3 (4), 4 (2). Probably this reflects concentrated foraging during a short brood rearing period. Probable discontinuous activities were assumed in some nests with the following contents: A. Four colored eyed pupae and four cells after emergence, B. Two old larvae, three white pupae and one colored eyed pupa (Fig. 9, M), C. Six young larvae and one pollen ball (Fig. 8, I). Further, synchronous work at more than one cell, a trait fairly common in halictine bees (Sakagami and Michener 1962) is traced in the following nests: With 2 empty cells (2 nests, cf. Fig. 8, F), with 3 pollen balls before laying (1, cf. Fig. 9, A), with 2 pollen balls and 4 eggs (1), with 3 pollen balls and 3 eggs (1).

Except for those referred to lateroid (5.3.), some abnormal dispositions of nest elements were observed: Ramified main burrow (7 cases, Fig. 9, A, B, K, L, M. B with an ascending burrow), looped main burrow and additional burrow issuing from lateroid (C), vertical lateroid (D, G), obliquely located comb (B, G, H), two entrances (E, F), absence of blind burrow (H, I with abnormal course of burrow), irregular cell arrangement (J, similar to comb shown by Bonelli 1965). Some of these anomalies relate to the polygynic association described below, but others are difficult to interpret adequately.

5.5. *Presence of polygynic association:* Among 54 nests observed, six were inhabited by two females. Because of the importance of such polygynic association in halictine sociology, the cases are tabulated as follows:

Nest number	Date of excavation	Figure accompanied	Number of cells and contents	Ovarian conditions (Mandibular wear) of adults (cf. Fig. 3)
6802	VI 14	8, C	0	DC(1), DB(1)
6811	VII 5	9, C	3 all empty	DD(1), DD(1)
6812	" "	9, D	7 all young larvae	DD(1), DC(1)
6910	" 19	9, F	12 cf. Fig. 9, F	DD(2), DD(1)
6911	" "	9, K	11 1 pollen ball, 10 young larvae	CD(2), BA(1)
6915	VIII 9	-	3 infested by mold	C'C'(2), B'B'(1) (ovaries degenerating)

In most cases both females had similarly developed ovaries, showing no semi-social caste differentiation (Michener 1969, Sakagami 1972). The exception is No.

6911 in which one female had virtually atrophied ovaries with no sign of previous activity, presumably working as an auxiliary for foraging. It is noteworthy that most of these nests show some anomaly in nest structure, ramified burrows being especially frequent. This may indicate that these females kept, in spite of living together, their tendency to solitary life, partly behaving as if communal (Michener, Sakagami op. cit.). No 6911 is of special interest. By the unusual depth of the main burrow this case is inferred to represent reuse of the previous nest. Two females each could have made the entrance separately and worked rather independently within the same cavity. The curious centripetal developmental gradient in the comb suggests later fusion of their activities.

The appearance of polygynic associations in *L. calceatum* is also recorded by Bonelli (1965). Vleugel (1961) found it in five out of 16 spring nests in a Dutch population. Our result, about 11%, is distinctly higher than in *L. duplex*, in which only four dubious cases were noted among more than 500 spring nests. It is interesting if the frequencies differs between two species so closely related as these.

6. Flower visits

Flower visits so far recorded by us from various areas in Hokkaido are compiled in Table 2, seasons and sexes being given separately. Females with and without pollen loads are shown separately but differential visits for pollen and nectar are not recognizable from our results. The predominant visits to composite flowers are obvious, shown by the number of composite species visited, 16, against 22 non-composite ones. This becomes clearer when the number of specimens is compared, i.e., 335 out of 399 or 84% were captured on composites. But this does not necessarily mean a particular preference for this plant group. It may merely be caused by the overwhelming abundance of composites throughout the areas surveyed. *L. calceatum* is fairly polytrophic and polylectic, except for its probable avoidance of white clover, *Trifolium repens*, one of the predominant flowering weeds in Hokkaido. In Okusawa, *T. repens* was very abundant but no visit has so far been recorded. In this trait, *L. calceatum* agrees with *L. duplex*, in sharp contrast to some other halictines common in Hokkaido, for example, *L. (L.) occidentens* Smith and their relatives and *Halictus (Seladonia) tumulorum* Linné.

Another result is the role played by introduced plants, 236 out of 399 specimens or 60% being collected on them. This indicates the adaptation of *L. calceatum* to secondary vegetations as well as the drastic change of primary vegetation in Hokkaido (cf. Sakagami and Matsumura 1967). The percentages of specimens captured on the six predominantly visited plants are: *Taraxacum* 33.8%, *Belis* 18%, *Erigeron* 11.3%, *Petasites* 8.8%, *Picris* 8.0%, *Aster* 7.7%. These captured on *Belis* were more concentrated on Okushiri Island because of intensive local escape of this plant there. On the other hand, two introduced plants, *Taraxacum* in spring and *Erigeron* in summer, are now each principal food sources not only

Table 2. Records of flower visits by *Lasioglossum calceatum* in Hokkaido.

P: With pollen loads, N: Without pollen loads, T: Total

§: Introduced plants, +: Mountaneous or alpine plants

Plant (Family)	Bees collected on		
	Females: May - mid June		
	P	N	T
§ <i>Taraxacum officinale</i> (Compositae)	59	47	106
§ <i>Belis perennis</i> (")	53	8	61
<i>Petasites japonicus</i> var. <i>giganteus</i> (")	25	5	30
<i>Cerastium holosteoides</i> (Caryophyllaceae)	3	7	10
<i>Ixeris stolorifera</i> (Compositae)	1	3	4
<i>Potentilla stolorifera</i> (Rosaceae)	3		3
§ <i>Brassica campestris</i> (Cruciferae)	2		2
<i>Angelica ursina</i> (Umbelliferae)	2		2
<i>Potentilla fragarioides</i> (Rosaceae)	1		1
<i>Plantago camtschatica</i> (Plantaginaceae)	1		1
<i>Thermopsis rupinoides</i> (Leguminosae)	1		1
<i>Anemone pseudo-altica</i> (Rhanunculaceae)		1	1
<i>Rhanunculus francheti</i> (")	1		1
Total	152	71	223
Females: late June - mid August			
	P	N	T
§ <i>Erigeron annuus</i> (Compositae)	39	5	44
§ <i>Trifolium pratense</i> (Leguminosae)	6	4	10
<i>Picris hieracioides</i> (Compositae)	7	2	9
<i>Ixeris dentata</i> (")	6		6
<i>Eupatorium japonicum</i> var. <i>sachalinense</i> (")		5	5
+ <i>Hypericum yezoense</i> (Guttiferae)	4		4
<i>Geranium yezoense</i> (Geraniaceae)	3		3
§ <i>Oenothera</i> sp. (Oenotheraceae)	1	1	2
<i>Geranium thunbergi</i> (Geraniaceae)	1	1	2
<i>Dianthus superbis</i> var. <i>longicalycinus</i> (Caryophyllaceae)	1	1	2
<i>Ixeris stolorifera</i> (Compositae)	2		2
+ <i>Geum pentapetalum</i> (Rosaceae)	2		2
<i>Inula salicina</i> var. <i>asiatica</i> (Compositae)	1		1
§ <i>Aster</i> sp. (")	1		1
<i>Breca setosa</i> (")	1		1
<i>Aster ageratoides</i> var. <i>yezoensis</i> (")	1		1
§ <i>Taraxacum officinale</i> (")	1		1
<i>Iris</i> sp. (Iridaceae)	1		1
+ <i>Pentstemon frutescens</i> (Scrophulariaceae)	1		1
<i>Trollius riederianus</i> (Rhanunculaceae)	1		1
Total	80	19	99

Table 2. *continued*

Females (F, all N) and males (M): late August - October			
	F	M	T
<i>Aster ageratoides</i> var. <i>yezoensis</i> (Compositae)	2	24	26
<i>Picris hieracoides</i> (")	8	10	18
<i>Geranium thunbergi</i> (Geraniaceae)	3	7	10
§ <i>Taraxacum officinale</i> (Compositae)	6	2	8
<i>Senecio cannabifolium</i> (")		4	4
§ <i>Rudbeckia laciniata</i> (")		2	2
<i>Polygonum thunbergi</i> (Polygonaceae)		2	2
<i>Geranium yezoense</i> (Geraniaceae)		2	2
<i>Oxalis corniculata</i> (Oxalidaceae)		1	1
§ <i>Erigeron annuus</i> (Compositae)	1		1
<i>Sonchus brachyotus</i> (")		1	1
<i>Eupatorium japonicum</i> var. <i>sachalinense</i> (")		1	1
<i>Cirsium kamschaticum</i> (")	1		1
Total	21	56	77

for *L. calceatum* but also for many polytrophic bees in Hokkaido. Use of these escaped plants as food sources is still higher for other mainly lowland species such as *L. duplex*. Native plants visited by *L. calceatum* with relatively high frequencies, *Petasites*, *Picris*, *Aster*, *Geranium thunbergi*, etc., are mostly weeds common and widespread in Hokkaido, usually more abundant in secondary vegetation. These facts show that *L. calceatum* in Hokkaido is now sustaining its life in an environment strongly modified from the original biotope, as is true for most lowland and hilly district bees.

Concluding remarks

Taxonomic and chorologic studies on *L. calceatum* inhabiting Hokkaido revealed two facts: virtual absence of morphological difference from European specimens and distribution biased to northern or colder areas. These facts indicate the relatively recent arrival of *L. calceatum* at Hokkaido from the northern part of the continent. The most probable interpretation would be its arrival during glacial periods, as is assumed for many other animal groups with northward biased distribution. As to bumblebees, the descent of most Japanese forms can be explained in the same way (Sakagami and Ishikawa 1969). Compared to them, the range of *L. calceatum* is enormous, in the West not only covering North and Central Europe but occupying most of the Mediterranean subregion. However, it is conceivable that local populations within its range differ from one another in their response to climatic conditions. There are many animals which are widely distributed in the western Palaearctics but confined to northern areas in Eastern Asia. *L. calceatum* is regarded as such a Eurosiberian element in Japan, in

contrast to numerous representatives of the Manchurian subregion, which constitute the faunal skeleton of the Japanese Archipelago. Among halictine bees *L. (E.) albipes* (Fabricius) and *Halictus (Seladonia) tumulorum* Linné exhibit similar distribution patterns.

In the absence of palaeontological evidence, the time of the arrival of *L. calceatum* in Hokkaido is only indirectly inferred. Certainly it arrived before the final formation of the straits now separating Japan from the continent, which occurred 20,000~12,000 years ago. As seen in Fig. 2 (P, XX), the palaeolittoral lines show the segregation of western Hokkaido from the rest of the island during early to middle Pleistocene (from "Materials for Geology in Hokkaido", 1967). The arrival of *L. calceatum* in western Hokkaido must have been after the fusion of these two land masses, about 110,000~150,000 years ago, at the end of the Riss ice-age. Arrival in eastern Hokkaido could be a little but not too much earlier than the period mentioned, judging from the absence of morphological differentiation between Japanese and continental specimens. For the same reason, arrival in Hokkaido before early Pleistocene is far less probable. Further, the discrete distribution given in Fig. 2 suggests the probable shift of distribution within Hokkaido. In parallel with the appearance of a warmer climate, the populations in the mainland would retreat to cooler areas, but such was probably difficult for those inhabiting western Hokkaido, because the Ishikari depression would act as a climatic barrier preventing northward migration. Geographical isolation should also play a role for the population of Okushiri Island. As to the populations in the mainland, even an complete retreat to the continent followed by a recolonization is not always excluded.

These speculations, still imperfect, throw a dim light on the origin of *L. duplex*. Although our knowledge on the halictine fauna of Eastern Asia is still insufficient, *L. duplex* seems endemic to Japan (Hirashima 1957). Further, *L. duplex* and *L. calceatum* are closely similar and certainly derived from the nearest common ancestor. Considering the wide range of *L. calceatum*, it is not improbable that *L. duplex* is a descendant of an earlier colonization of *L. calceatum* in Japan, becoming an independent species and insular vicariant by isolation, now partially overlapped by the later invasion of *L. calceatum*. At any rate, it is probable that *L. duplex* has lived much longer than *L. calceatum* in Japan. An ethological finding also favors the close relationship of these species. The presence of lateroids in nests of both species was described in 5.3. That the lateroid is a derived feature is quite plausible, both from the assumed evolution of halictine nest architecture (Sakagami and Michener 1962) and the fact that *L. duplex* is the only carinate *Evylaeus* with this feature as a stable characteristic. The facultative presence of a lateroid in *L. calceatum* implies the following alternatives: either *L. duplex* was derived from the population of *L. calceatum* already with lateroid formation or this trait appeared independently in both species. Even if the latter would be the case, it still favors a close relation between two species. Further information on the presence or absence of lateroids in various local

populations of *L. calceatum* may help in understanding the speciation in the *L. calceatum* group.

Finally, the solitary life cycle of *L. calceatum* on Mt. Yokotsu is briefly considered. The change of life cycle according to climate is suggested for some halictine species. The famous eusocial life of *L. (Evyllaes) malachurum* (Kirby) in Central and South Europe seems to be replaced by the solitary life in northern Germany (Alfken, cf. Legewie 1925). In *L. (Dialictus) imitatum* (Smith) the size difference between queens and workers and percentage male production are respectively 7~8% and 4% in Kansas (Michener 1969) while 5 and 45% in Ontario (Knerer and Plateaux-Quénu 1967 b). All these records suggest the tendency to shorten or to omit the matrifilial phase in colder climates. But so far no authentic record has been published which shows the presence of different life cycles according to climate in the same species, whereas both mono- and polygynic nests were found synchronously in the same place in some semisocial halictine species (Michener and Lange 1958, Michener and Kerfoot 1967). The present study on the life cycle of *L. calceatum* in the lowlands and at a high altitude demonstrates that this species can behave either eusocially or solitarily according to climatic conditions.

Up to the present, however, we explained the result without referring to the genealogical direction of two annual cycles, either from solitary to eusocial or *vice versa*. Obviously the former direction predominates when the social evolution of halictine bees is considered in general. But with respect to each eusocial species, the atavism to solitary life would not be impossible. Even in other insects in which the eusocial cycle is firmly established as the life pattern, the tendency to shorten the matrifilial phase is discernable at the colder margins of their distributions. The decreased number of workers is famous in some high Arctic bumblebees (cf. Richards 1931, Milliron and Oliver 1966). Yamane (1969) verified in *Polistes* wasps a marked abbreviation of the matrifilial phase in northern climates. In these groups, however, complete return to the solitary cycle may be difficult or impossible. On the other hand, such would be possible in halictine bees because of their weak caste differentiation (Sakagami 1972). The matrifilial phase, being surely the summit of their social evolution, could be omitted without breaking the succession of generations if two conditions are fulfilled: the production of the progeny with the sex ration of ca. 1:1 and of daughters as large as mothers (cf. Section 4), both realized in the population of Mt. Yokotsu. We cannot conclude with certainty whether solitary life on Mt. Yokotsu was autochthonous or atavistic, but the latter possibility is not excluded, assuming a possible swinging between solitary and eusocial cycles at the northern edge of distribution throughout glacial eras, as an adaptation to the changing climatic conditions.

We still do not know whether the different life cycles seen in *L. calceatum* are genetically controlled in each population, forming different ecotypes, or are reversible according to conditions, without modification of genetic structure. Further, because of the discrete brood production characteristic of eusocial *Evyllaes*

species (Knerer and Plateaux-Quénu 1967b, Sakagami and Hayashida 1968), the behavior of populations living in intermediate climates is of particular interest, the question being whether the matrifilial phase gradually changes or appears facultatively among different nests within the same population. These problems could be tested circumstantially through reciprocal transplantations of two populations living in different climates.

Summary

The distribution and bionomics of a Transpalaeartic halictine species, *Lasioglossum (Evyllaesus) calceatum* (Scopoli) in Hokkaido, northern Japan, were studied in comparison with those of a closely related species, *L. (E.) duplex* (Dalla Torre), endemic to Japan.

In the main part of Hokkaido *L. calceatum* occupies colder areas than *L. duplex* but this regularity is less distinct in western Hokkaido where *L. calceatum* occurs in some warmer localities, suggesting isolation during past ages.

The life cycle was studied in two localities. In Okusawa, a lowland area, it followed the pattern common to eusocial *Evyllaesus* species, consisting of spring solitary, presummer inactive and summer matrifilial phases. On the top of Mt. Yokotsu, 1,167 m, however, *L. calceatum* behaved as a solitary species. The nest structure studied in Mt. Yokotsu did not differ from that described from Europe, with a remarkable exception, the possession of the lateroid connecting main burrow and comb-cavity, found in *L. duplex* but not in some European populations of *L. calceatum*. In addition, survival of old mothers to their second spring, presence of spring polygynic association, polytrophic flower visits, adaptation to introduced plants, etc. were observed.

Based upon these facts, the possible course of its arrival at Japan, its relation to *L. duplex*, and the relation between solitary and eusocial cycles were considered.

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