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Biology of the Primitive Social Bee, *Halictus duplex* Dalla Torre, III. Activities in Spring Solitary Phase[1)2)]

By

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(With 15 Text-figures)

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1) Contribution No. 540 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

2) This species belongs to the genus *Lasioglossum* Curtis (Subgenus *Evylaeus* Robertson) in the classification by Michener (1944). But the genus *Halictus* Latraille will conveniently be used in this and subsequent papers of the series, in order to avoid the change of title. In future the subgeneric name might be altered according to the infrageneric revision of *Lasioglossum* now being attempted by Prof. Michener.

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In the two previous papers the life history of *Halictus duplex* Dalla Torre was outlined and nest structure and immature stages were described (Sakagami & Hayashida, 1958, 1960). As shown in those papers, this species possesses two distinct active periods in Sapporo, separated by a pre-summer inactive period lasting about a month, that is, the spring solitary phase during late April to late May and the summer matrifilial phase (Cf. Sakagami & Michener, in press) during July. In the spring phase, each nest contains in most cases only one female, which further survives in the same nest and forms, together with her daughters, the summer matifilial association. The activities in spring solitary phase essentially differ but little from those observed in other solitary bees. Nevertheless, a closer investigation of this phase is indispensable to understand the much complicated summer phase. The present paper deals with spring activities such as spatiotemporal distribution of nests, behaviour at nest sites, ovary development, sex ratio in spring broods and other miscellaneous observations.

The writers are much indebted to Prof. Tohru Uchida, Zoological Institute, Hokkaido University, under whose direction the study was carried out, to Prof. Charles D. Michener, Department of Entomology, University of Kansas, who kindly gave them invaluable suggestions, and to Prof. Misao Tatewaki, the Director, and all other members of the staff of the University Botanical Garden, where most parts of observations were undertaken, for their generosity in allowing them a free use of nest sites.

I. Spatiotemporal distribution of nests

H. duplex is one of the earliest spring bees in Sapporo and its vicinity. The nest tumuli appear soon after the disappearance of snow cover and rapidly increase in number subsequently. Further, this species has a strong tendency to form nest aggregations (or villages, colonies, pseudocolonies etc. as called by other writers) within a limited area. This section concerns such spatiotemporal distribution of nests in spring phase.

1. 1. Spatial nest distribution of a whole aggregation

Occasionally small aggregations each consisting of a dozen to a few, or even single nest are found separated more than 1 km from neighbouring aggregations. But the tendency to congregate within a limited area is one of the traits characteristic to the species. One of such large aggregations was fully mapped in 1959 spring.

The nest site studied is the beds of medicinal plants in the University Botanical Garden. As seen in Fig. 1, left, the area is rectangular, longer in NS direction, approximately 18×42 m^2 in extent and made up of 21 beds margined by tiles. (12 beds are rectangular, 1 central one circular, 2 southernmost ones of quartercircle, and the other 6 of deformed-rectangular). Within each bed six to ten species of medicinal plants were grown, each quadrately surrounded by inner tile margins. These double tile margins offered an ideal

coordinate system for mapping each nest. The whole area is surrounded by deciduous trees on the N,E, and W sides, while continuous to the open flowering beds on the S side. All nests with conspicuous tumuli were recorded on April 22, 1959, that is, at a rather earlier stage in the spring nesting activities. The increase and decrease of nests were of course considerable after that day, but the map sufficiently illustrates a nest aggregation typical to the species, which consisted of about 1960 nests in total.

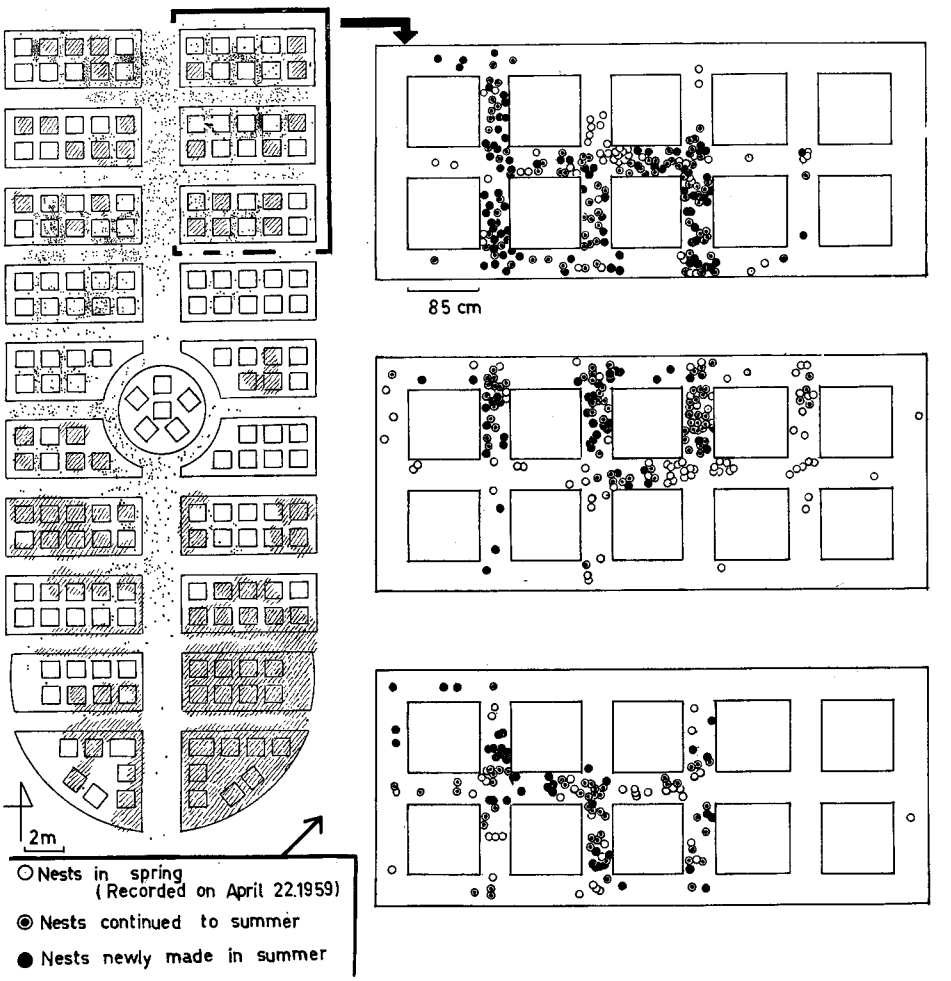


Fig. 1. A nest aggregation in the beds of medicinal plants, Hokkaido University Botanical Garden (1959). Left: Distribution of the whole aggregation (Dots: single nests, Hatching: Accumulation of vegetable covers), Right: Dotto, North-eastern sections showing only nests located between inner and outer tile margins.

In the figure, the areas indicated by hatching show the accumulations of dead foliage and other vegetable debris, of which the amounts locally differed according to the kinds of plants on or near each area. The fact that no single nest was discovered on these covered area clearly illustrates the avoidance of surface cover by the species. Further there was a local difference of shading by surrounding trees. The V-shaped zone demarcated by lines connecting NE and NW corners to the southernmost point of the whole area studied was relatively well insolated throughout the daytime, where majority of nests were discovered. The local difference within this V-shaped zone may partly depend on differences in microclimate, especially on shade according to the different kinds of medicinal plants. For instance, the fourth bed (from the north) is poorly occupied in the eastern half, apparently caused by the dense shade covering this bed.

However, the minute local differences in environmental factors cannot fully explain the apparently patched distribution, especially in the northern areas. Moreover, the flowering beds and paths between them, which are to the south of the beds of medicinal plants surveyed, were occupied by only several dozens of nests. This tendency was consistently maintained throughout five years' surreys. Nevertheless there was no remarkable difference in extent, microclimate and edaphic conditions between these two areas. This strong suggests conservatism in nest site preference (Michener *et al.*, 1958).

One important fact must be mentioned: Only a fraction of these spring nests could successfully be maintained to the summer matrifilial phase. To determine the ratio of survived nests, all areas between outer and inner tile margins of eight northern rectangular beds were reexamined in summer and the numbers of nests which had disappeared, survived, or were newly observed in summer were recorded. Fig. 1 right shows the survivalship of nests in the northern three beds in the eastern half, in expressing three kinds of nests by white, double and black circles respectively. Of course the circles do not represent the actual sizes of nests. The result will be referred to below in Section 1. 4.

1. 2. Spatial distribution and environmental factors

A closer survey of nest aggregation in a more limited area was carried out in 1958, in the shrubbery of the Botanical Garden, where a nest aggregation was residental at least since 1956.

The area contains two rows of beds each running in NS direction. The western row is composed of five beds of approximately 13.6×3.5 m^2, while the eastern longer one consisted of 10 beds of each 20.0×3.5 m^2, of which northern parts are shown in Fig. 2,A. The majority of nests were found on the four northern beds (K_1-K_4) of the eastern row and the paths separating these beds. The survey was made only with these four beds excluding paths. In each bed the shrubs were planted so sparsely that there were ample spaces to be utilized by *H. duplex* as nest sites (Cf. Fig. 2, B). During April 15–17 before appearance of nest tumuli, all weeds were removed from the beds. Each bed was accurately mapped with land marks made by piercing wooden rods every 50 cm along the tile margins. Following the first discovery of nests on Aprill 22, the beds were visited every 2–4 days

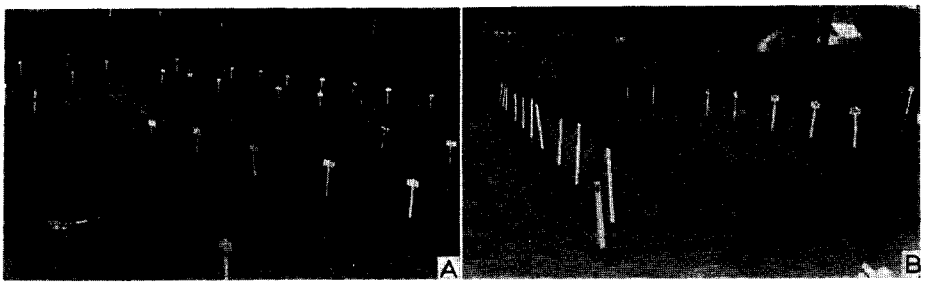


Fig. 2. Shrubbery, Hokkaido University Botanical Garden. A : Northern half of shrubbery, B : Beds K_1 (left) and K_2 (right) close-uped (Photo. in 1960).

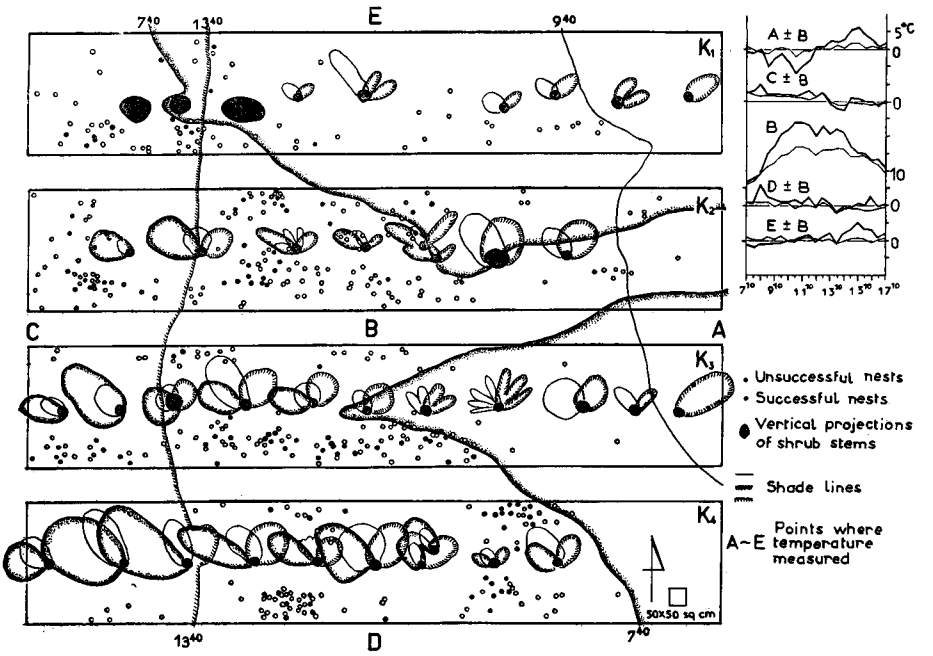


Fig. 3. Distribution of nests in the shrubbery (1958), in relation to the extent of shades at three different hours (7^{40}, 9^{40} 13^{40} on Apirl 30). Right : Local difference of diurnal changes of temperatures at air (thick line) and soil surface (thin line) at four points (A,C,D & E), expressed by deviations from those measured at the center of the area (B). (Arrangement of shrubs is not same between Figs. 2 & 3, for it was changed in 1960).

until June 10 excluding rainy days. In each visit newly discovered nests were plotted on the scaled chart and given particular numbers. Simultaneously the conditions of previously plotted nests such as *open, close, with or without tumulus* etc. were recorded.

Fig. 3 gives distribution of all 465 nests, either successful (that is, continued to the summer phase, 118 in total and expressed by black circles) or not (white circles) in these four beds. The total number in each bed and the relative abundance in northern (N), southern (S), western (W) and eastern (E) halves in each bed are (data on the successful nests in parentheses) :

Beds	K_1	K_2	K_3	K_4
Total number of nests	68(12)	169(36)	129(38)	99(32)
% in E to total number in each bed	20.5(0.0)	27.2(11.1)	33.0(21.0)	49.5(62.5)
% in N to total number in each bed	20.5(2.9)	35.0(47.7)	20.0(7.9)	37.4(46.6)

The relative abundance was $K_2>K_3>K_4>K_1$, and W>E and S>N in all four beds. These relative orders are seen in the distribution of successful nests, too, except in K_4 where E>W was observed. Therefore the successful nests were abundant where the nest population was itself sufficiently high. Some environmental factors were analysed in order to detect the causes of such non-random distribution.

1. 2. 1. Edaphic factors

In a previous paper (S-H, II, p. 95)[1], the conditions of grounds to be preferred by *H. duplex* as nest sites were enumerated : well insolated, flat or occasionally slightly inclined, rather hard ground, with moderate humidity, without or with only sparse plant and other surface covers. Although the shrubbery beds had so well fulfiled such conditions that further pedological analyses seemed to be unnecessary, some conditions were measured during April.

Soil samples were taken from E and W halves of each bed at the depth of 10 cm below surface and analysed as follows :

pH : Determined by pH comparator using mixtures of half water and half sample soil allowed to stand for 24 hours.

Amount of humus : Determined by reweighing soil samples after 24 hours desiccation at 110°C in an oven.

Constitution of soil particles : One hundred gr well desiccated soil was carefully washed with water. Larger vegetable particles were picked out (A), clay and silt including fine humus particles were washed out (B). The remainder was divided into fine (C) and coarse sand (D) by sieving through 0.5 sq mm mesh cloth. Parts, A,C,D were weighed after desiccation and the weight of part B was obtained by subtracting A+C+D from 100 gr.

The results are :

Section sampled	pH	Amount of humus (gr/100gr)	Clay	Fine sand	Coarse sand	Vegetable matter
K_1 E	5.6	7.5	78.5	19.1	2.2	0.2

1) The writer' second paper (Sakagami & Hayashida, 1960) is henceforth abbreviated S-H, II.

K_1	W	5.6	7.6	81.3	16.8	1.8	0.1
K_2	E	5.6	7.5	83.5	15.0	1.5	0.1
K_2	W	5.6	6.5	83.9	15.1	1.0	0.0
K_3	E	5.6	7.5	80.8	17.1	1.9	0.2
K_3	W	5.6	7.0	86.1	12.7	1.0	0.2
K_4	E	5.6	7.1	81.3	16.9	1.5	0.3
K_4	W	5.7	7.4	83.1	15.5	1.3	0.1
Mean		5.61	7.26	82.3	16.0	1.5	0.15
S.d.		0.035	0.374	2.323	1.898	0.414	0.093

As seen in the table, the area was very homogeneous in the three conditions determined. A slightly less amount of humus in K_2W, K_3W and K_4E seems to be insufficient to explain the occurrence of numerous nests in these sections. The amount of surface cover was relatively large in K_1E, K_3E and W, which also cannot explain the distribution pattern. The soil profile was not systematically observed, but the depth of the boundary between A and B horizones was variable, with no close relation to the definite sections. In many excavated nests, the spring cell-clusters were mostly found within A-horizon, simply because the range of this horizon was usually deeper than 15 cm. Occasionally cell-clusters made in B-horizon, or even mosaic cell-clusters made by black soil above and red soil below were found when the depth of A-horizon was less than 10 cm.

Consequently, the edaphic factors cannot sufficiently explain the patched distribution of nests in the area studied. It has also been reported that many halictine bees show no particular preference to the definite minute pedological properties in the nesting ground (Sakagami & Michener, in press).

1. 2. 2. Climatic factors

In order to analyse the microclimatic difference within the area studied, air and surface temperature were measured on April 30, 1958 from 7^{10} to 17^{10} every 30' at five points : B at the center of the area, A,C,D,E at the middle of the four sides surrounding the area (Fig. 3). On that day the cloud amount gradually increased in the afternoon, but the cloud was relatively thin, so that did not markedly affect the insolation. The diurnal change of air and surface temperatures at B, chosen arbitrarily as the standard, is indicated in the middle of the graph presented at the right side of Fig, 3 together with the ± deviations of the values in points A,C,D,E from those simultaneously measured at B.

By using abbreviations *C* and *c* (distinctly or slightly cooler than at the center), *W* and *w* (distinctly or slightly warmer than at the center), *C-w* (distinctly cooler in morning and slightly warmer in afternoon) etc., the results are summarized :

Northern side (E)	*c-W*	Eastern side (A)	*C-W*
Southern side (D)	*W-cw*	Western side (C)	*W-cw*

As already mentioned, the nests were more scarce in eastern than western halves in all beds. Furthermore, the northernmost bed, K_1, was provided with few nests except for the western quarter (Fig. 3). This fact coincides with, and

is perhaps partly caused by the relatively cooler morning in the north-eastern section mentioned above.

A more precise picture concerning the relation between nest distribution and microclimatic gradient was obtained from the diurnal change of the extent of shaded area which was mapped on the same day every 30′ simultaneously with the measurement of temperatures.

There were two sorts of shade projecting over the ground. The area was surrounded by deciduous trees of about 10–20 m in height on the northern, eastern and western sides. The shade given by these trees covered a large extent but was relatively faint. On the other hand, the shade given by the shrubs planted on the beds was relatively small in area but dense. These two types of shade may affect differently the nest distribution, but were not separately treated. The mapping was undertaken on April 30, that is, at the very incipient stage of the spring active phase. On that day all trees and most shrubs which provided shade were still without dense foliage, which resulted in only very faint shade. Later, the shade became gradually denser, and the distribution of shade at a given time varied slightly from that on April 30, according to the change in foliage and height of the sun. Moreover, the comparison of nest and shade distributions, not only the nests already found on April 30,but all nests recorded throughout the spring phase was considered. In spite of probable errors evoked by such lack of temporal accordance between two measurements, the results were remarkable as given below.

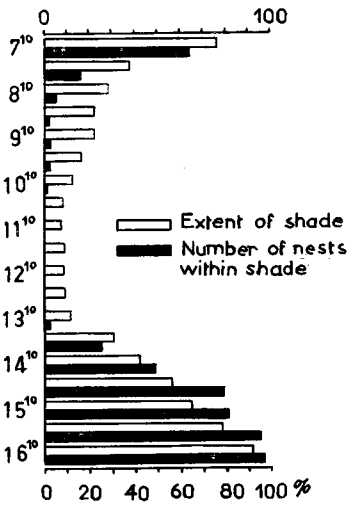


Fig. 4. Correlation between extent of shaded area and number of nests within shade in the diurnal course.

Fig 4 illustrates a distinct correlation between the diurnal change of the extent of shaded area (% of the whole area) and the number of nests within the shade (% of the total number of nests). The extent of shade occupied 77.3% of

the whole area at 7^{10}, at which time nearly 65% of nests were within the shade. Later both values rapidly decreased; during the period 9^{40}–13^{10}, in which most flight activities were observed, the shade occupied nearly or less than 10% of the whole area, mostly given by the shrubs planted in the beds, and there were no nests within the shade. Thereafter, both extent of shade and number of nests within shade again rapidly increased up to 92.2% and 97% respectively at 16^{10}.

Further the correlation of nest distribution and the pattern of diurnal change of shaded time was sought as in Fig. 5. The whole area was divided into diverse types according to the patterns of diurnal change of shading. The number of nests within each type was given as histogram. From the figure it is clear that the distribution of nests is affected not by the total duration but the distribution of shaded time. The nests were, either in total number or in number of successful ones alone, more abundant in the areas well insolated since early morning, even if shaded in the afternoon, the fact fairly well corresponding to the spatial difference in air and soil temperatures given above (See also Fig. 4, The number of nests within shade is larger in afternoon than in morning).

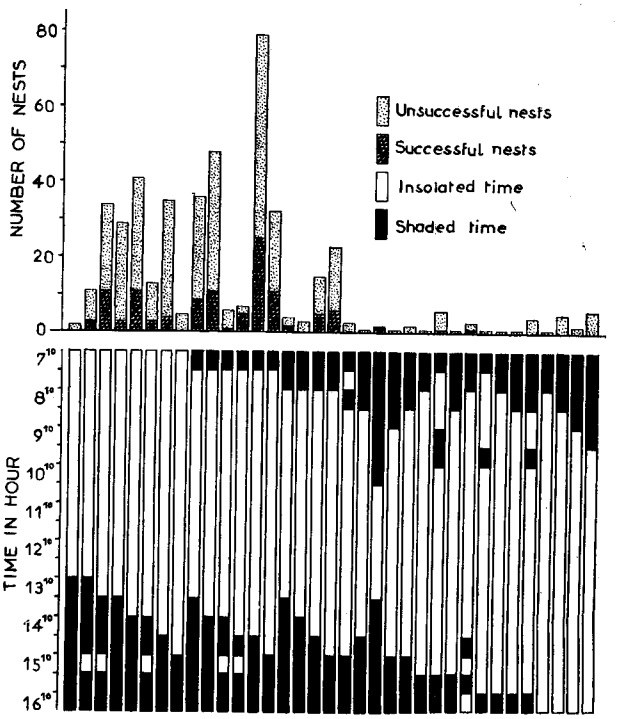


Fig. 5. Relation between patterns of diurnal change of shade and number of nests in differently shaded places.

In Fig. 3 three shade lines at 7^{40}, 9^{40} and 13^{40} are respectively given. The distribution of nests well accorded to the shade line at 7^{40}. The nests were very scarce in the area eastwards of this line. Moreover, the figure illustrates the differential effects of large but faint shade given by surrounding trees and small but dense shade by shrubs : Nests were extremely scarce within the shade given by the latter. (See also Fig. 4. There were no nests within the shade during 10^{40}–12^{40} when the shade was given solely by shrubs). It was previously mentioned that the nests were less abundant in the northern than in the southern halves in all beds. This might be explained by the shade line at 7^{40} in the case of bed K_1, while the shade given by shrubs may be responsible in three other beds.

In conclusion, the unbalance of nest distribution within the area can, at least partly, be explained by the microclimatic gradient : The warmer the area in the morning, the more the nests found there.

1.2.3. Spatial distribution pattern

The importance of microclimatic gradient has been established. Nevertheless, it is difficult to explain the nest distribution adequately as due to this factor alone. Even within the central area limited by three shade lines at 7^{40}, 9^{40} and 13^{40} (Fig. 3), the distribution of nests is clearly patchy. Although a closer mathematical analysis is out of the scope of the present study, an attempt was made in order to objectively establish such patchiness.

From the central area limited by the three shade lines, a number of 50×50 cm^2 quadrates were selected from Fig. 3. After discarding the quadrates which were partly overlapped by the shaded area, irrespective of whether shade was caused by trees or shrubs, in total 252 quadrates were selected. In Fig. 6 the actual frequency distribution of nests in these selected quadrates is given. Further the fitness of the observed values to the theoretical values of Poisson's distribution and of Pólya-Eggenberger's contagious distribution was tested.

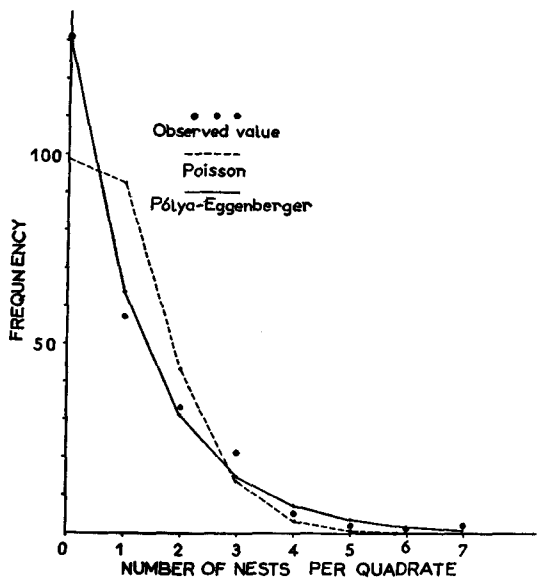
As seen in the figure, the values observed considerably deviate from the Poisson's values. The coefficient of diversity $\sum(x-\bar{x})^2/[\bar{x}(n-1)]$ was about 1.913, hence significantly higher than 1 at 1% level of probability, suggesting an excessive patchiness. On the other hand, the observed values relatively well coincided with the theoretical values of Pólya-Eggenberger's ($\chi^2 \fallingdotseq 4.09$, $n=6$, $0.75 > pr > 0.50$).

The excessive patchiness proved above may be caused either by the environmental heterogeneity or by the gregarious tendency of the species concerned. In the present case, however, the heterogeneity in the environmental factors is not too great, because the influence of shade was mostly removed before the observations. Therefore, the apparent patchiness seen in Fig. 3 is probably an outcome of a specific trait, in this case, the tendency of young females to remain at the places where they had emerged in their parental nests, as known in many solitary bees (Michener *et al.*, 1958, Cf. also Sakagami & Michener, in press).

1. 3. Temporal nest distribution

As mentioned above in Section 1. 2. the nest census was taken every 2–4

days between April 22 and June 10. From these continuous records of individual nests, five cumulative curves and one ratio curve were prepared as shown in Fig.



No. nest per quadrate	Values observed	Values expected from	
		Poisson	P.-E.
0	131	98.83	129.78
1	57	92.83	63.55
2	33	43.29	3.186
3	21	13.51	14.82
4	5	3.162	7.12
5	2	0.592	3.43
6	1	0.093	1.63
7	2	0.012	0.79
	252	252.000	252.00

Fig. 6. Frequency distribution of nests in 50×50 cm^2 quadrates.

7, together with daily weather records cited from the data supplied by the Sapporo Meteorological Observatory. A few remarks may be necessary to each curve:

T: Cumulation of all nests newly discovered on each census day.

A: Cumulation of abandoned nests. Some nests remained in open condition in successive records. Further absence of owner's activities were apparently by diverse symptoms such as 1) gradual collapsing and diminishing of initial tumuli, 2) lack of newly deposited soil around entrances, 3) gradual ruin of entrances, 4) occurrence of other animals at entrances, etc. When these symptoms were observed in more than two successive recordings, the nests were regarded as abondoned (Y). Further, some nests were observed in closed condition in successive recordings. In this instance (X), the nests are considered either as being actually abandoned (Xu) or as entered into inactive stage (Xs). Separation of Xu and Xs is not always easy, although cases of Xu are indubitably more frequent in earlier half, while Xs cases are in the latter half of the spring solitary phase. Xs was obtained from individual records of nests which survived to summer, then, Xu from $X-Xs$. The curve A represents the cumulation of $Y+Xu$.

T-A: Daily change of differences between curves T and A.

S: Of 465 nests in total recorded, some nests were excavated during the inactive phase in June for diverse purpose (P), while others were untouched to summer (R). In the case of R, separation of successful (Rs) and unsuccessful nests (Ru) was easy from the observations made at summer phase. In excavated nests, the nests were regarded as

successful (Ps) when containing both mother and intact progeny. The curve S represents the cumulation of $Ps+Rs$.

Q : The cessation of spring active phase in each successful nest was determined from the individual records. The nests were regarded as entered into the inactive phase, when the entrances were seen in closed condition at the time of more than 2 successive recordings, of which the cumulation is presented in cruve Q.

S/T : Daily change of ratio S/T.

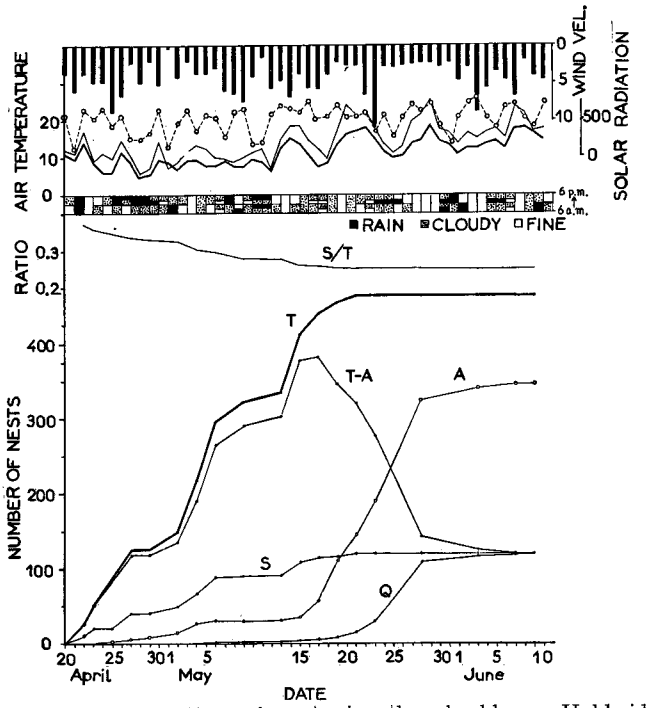


Fig. 7. Temporal distribution of nests in the shrubbery, Hokkaido University Botanical Garden (1958), accompanied with weather records taken by Sapporo Meteorological Observatory (Above) : Daily change of air temperatures at 10^{00} (thin line) and daily mean (thick line), solar radiation (cal/cm^2) on soil surface (broken line), mean wind velosity (m/sec) (bar-histogram) and general weather from 6^{00} (below) to 18^{00} (above). Concerning population curves S/T, T, T-A, A, S, Q, see in text.

From the figure, similar trends are observed between T and S, as well as A and Q. In the curve T, the cumulation of all nests observed, the rate of increase is linear until the upper asymptote is reached on May 21 (approximately 15–20/day). In a closer inspection, there are found three periods in which the rate is relatively low : April 27-May 2, May 6–13 and May 15–21. The final period represents the cessation of nesting activities in this aggregation. On the other

hand, the two lag periods may suggest the influence of adverse weather. As seen in the figure above, these periods were relatively rainy and the mean air temperature and air temperature at 10^{00} were often less than 10°C and 15°C respectively. Though not so conspicuous as in the other factors mentioned, the amount of solar radiation and wind velosity also seem to be correlated in some degree to the nest increase. The curve differs from the logistic curve by the absence of initial lag period. Actually the synchronous appearance of a relatively large number of new nests at the commencement of the spring phase is characteristic to this species perhaps caused by the synchronous response of many individuals to the favorable weather conditions. The curve S, the cumulation of successful nests, shows a similar trend but the rate of increase is distinctly low and the ratio S/T monotonously decreases from 0.37 on April 22 to 0.25 on May 21, indicating a gradual decrease of the relative abundance of successful nests.

On the other hand, the curve Q, the cumulation of nests which entered into inactive phase, increases up to about May 21 more conspicuously than S within a relatively short period, which suggests rather synchronous cessation of the solitary phase in comparison with its commencement. However, the prolonged growth of T is apparently partly caused by a false-increase, that is, by the excavation of a second or even a third nest by some home-lost individuals (Cf. Section 2.3.2.). The trend of A, the cumulation of abandoned nests, is similar to that of Q but the rate of increase is higher, just comparable to the relation of T to S. The curve T-A shows the number of nests which were regarded as *active* in each census. The difference between T-A and S indicates, together with a rapid increase of A in late May, that a fairly large number of nests could not survive to summer ; nevertheless they were active during a considerable time, in other words, there was an occurrence of numerous nests which were damaged during the inactive phase in June. From these results it was clearly established that the spring solitary phase is a well defined period in the annual cycle of this species, lying between the hibernating phase and pre-summer inactive phase.

The duration of the spring phase in each nest, whether successful or not, was obtained from the individual nest records. The frequency distribution of various lengths of that phase is presented in Fig. 8 in relation to the date of foundation. The duration is widely variable not only in unsuccessful nests but also in successful ones. Even excluding apparently erroneous records such as the successful nests which were recorded as active during only 3–7 days in the spring phase (Cf. Fig. 8, May 17–20), the range of the duration extend from 9 to 38 days with mean 18.4 and standard deviation ± 8.09 ($n=118$). Moreover, the duration linearly decreases in the course of the spring solitary phase, indicating the shortening of active phase in the nests commenced later[1]. However, the number of days

1) A rather clear linearity was partly brought about by an artefact : an interruption of census from May 23 to 28 (see, Fig. 7), during which most nests entered into the inactive phase.

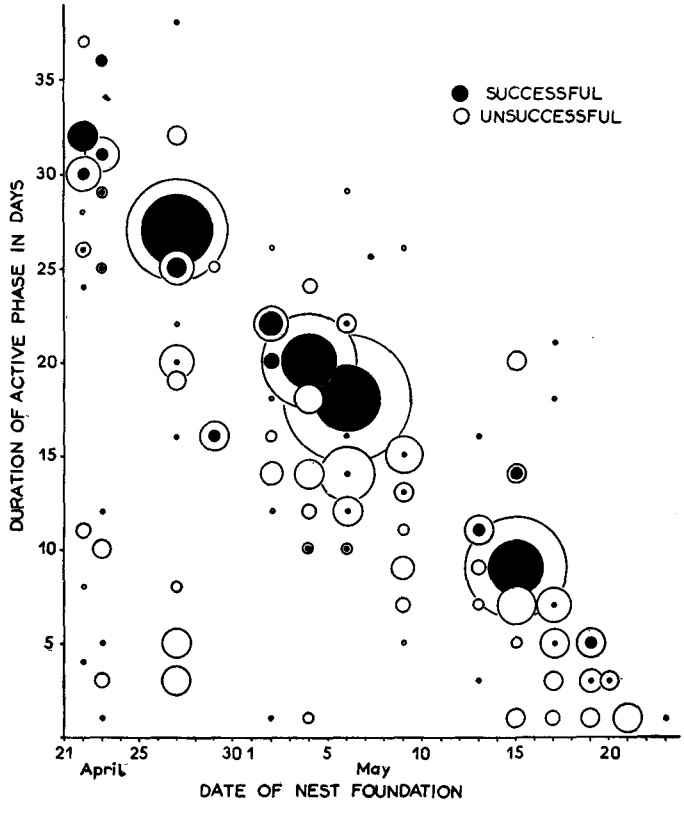


Fig. 8. Relation between date of foundation and duration of active period in spring phase. Total (white circles) and Successful nests (black circles) in given combinations of date and duration. Diameters of circles approximately represent the frequency of cases.

necessary to complete the provisioning for broods seems to be less than the mean, because in the nests founded at earlier dates, many days might be spent without foraging due to adverse weather. There is no clear correlation between duration of spring phase and survivality. Of course most nests of which the active period was very short must be unsuccessful. But there is a large number of unsuccessful nests, of which the activities continued as long as successful ones founded on the same days. The similar tendency was already noted in the difference between *T-A* and *S* in Fig. 7. A wide range of variability may be a rule in the duration of spring phase in this species.

Insufficient but interesting data were obtained on the local difference of the

developmental course probably caused by microclimatic conditions. In 1959, the immature stages were sampled for another purpose not only from the aggregation in the University Botanical Garden but also subsidiarily from another aggregation located in the University Campus as follows :

Date	Location	Developmental stage						
		Larvae			Pupae with			
		with pollen ball	without pollen ball	defecadte	white eyes	pink to violet eyes	black eyes	body more or less pigmented
June 9	Bot. Garden		18	9	10			
〃	*Univ. Campus*	*20*	*10*	*12*				
12	B. G.		14	48	63			
17	〃			1	1	23	3	1
19	〃				2	10	15	
20	*U. C.*			*6*	*7*	*4*		
23	B. G.						4	6

The delayed development in the University Campus is obvious when the data on June 9, and on June 19-23 are compared. While the aggregation in the Botanical Garden had been exposed under full insolation from 9^{30} to 13^{00}, that in the University Campus received only a little insolation in morning, inhibited by a thick wood standing eastwards to the nest site. The delayed development in the latter place was probably caused by the retarded daily activities of females, especially in the early spring, due to the microclimatic difference conditioned topographically.

1. 4. Survival rate of spring nests

As mentioned in the previous section, only a fraction of the nests started in the spring active phase can be maintained to the summer active phase. This appears to be important concerning the population dynamics of the species concerned, so that some results obtained in 1957, 1958 and 1960 are summarized in this section.

Because all surveys were not primarily attempted to determine the survival rate, the procedures employed differed in each year. In 1957, three 1 m^2 quadrates were plotted in the relatively densely occupied areas on beds K_2 and K_3 in the shrubbery (Cf. Section 1.2.). All nests found within the quadrates were marked from May 1 and excavated during May 30-July 3. The nests containing both mother and intact progeny were regarded as successful nests, while others as unsuccessful ones. In 1958 the survival rate was obtained as an outcome of the studies on the spatiotemporal distribution mentioned in Section 1.2. and 1.3. The successful nests are given by $Ps+Rs$ in Section 1.3. in 1960, 150 nests were marked on June 1, and partly excavated and examined during July 8–28.

As seen from the results summarized in Table 1, the survival rate fluctuates from 14.7 to 28.9% (mean 22.5). The lower rate in 1960 is understood from

Table 1. Survival rate of spring nests

			1957 mother		1958 certified by			1960 mother		Total (%)
					excavation, mother		summer reacti-			
			survived	lost	survived	lost	vation	survived	lost	
Unsuccessful	Cavity and cell-cluster undetected	No trace		37		97	187*		2	323(47.8)
		Occupied by *Formica fusca japonica*		5		1	3		1	10(1.6)
		Perforated by earthworm		4		1				5(0.8)
		Main burrow alone	3	14		2		1	28	48(7.1)
		Total	3	60		101	190	1	31	386(57.3)
	Cavity or cell-cluster detected	Cavity ruined	1	12		1			32	46(6.8)
		Cavity intact								
		cell-cluster ruined		4		9	1**		6	20(3.0)
		occupied by ants		2		33		1	20	56(8.3)
		Parasitized by Diptera	no records		1	11		1	1	14(2.0)
		Total	1	18	1	54	1	2	59	136(20.1)
Successful			18		40		78	16		156(22.6)
Total nests			22	78	41	155	269	19	90	674
Survival rate (%)			18.0		20.4		28.9	14.7		22.5

* In this case "no trace" does not mean the complete disappearance of nest structure as in other cases, but merely the absence of summer reactivation.

** Occasionally examined by excavation in summer.

adverse weather condition in this year. Difference in 1958 between the nests examined by excavation and by affirmation in summer cannot sufficiently be explained, but is perhaps partly caused by the fact that seemingly more active assemblages in K_3 and K_4 (Cf. 1. 2.) were left for summer observations. The causes of unsucessful nests are mostly unknown. Some known cases are shown in the table.

Some remarks must be added as to replacement by ants. When the nests are replaced by the nests of *Formica fusca japonica* Motschulsky, the whole architectural plan is completely damaged. It is certain that this relatively large and populous ant can drive away the bees by a gradual extension of the nest. On the other hand, smaller ants,

mainly *Paratrechina flavipes* (F. Smith), occasionally, *Pheidole fervida* Smith, occupy the nests of *H. duplex* but usually adopt cavities, or often even cell-clusters without destruction. In these cases, it is uncertain whether the invasion of ants in the cause or the result of nest abandonment. Among other nests abandoned for unknown causes, the infection by mold was frequent. In this case again whether proliferation of mold signifies the cause or the result of abandonment is difficult to determine. But the latter possibility is greater, because the cell-clusters are usually free from mold if the mother bees survive within.

A difficulty arises when one attempts to estimate the survival rate of the spring *females* based upon that of the spring *nests* mentioned above. As later seen in 2.3.2. the memory of females for their nests is still weak at the initial stage of nest foundation, which results in the abandonment of nests once started and leads to the excavation of a second nest. Consequently, the total number of nests obtained by periodical census does not mean the actual number of inhabitants in the aggregation at the beginning of the spring solitary phase. It is assumed that the difference is not too great, because the increase of abandoned nests is relatively inconspicuous at the early stage of spring solitary phase, that is, at the stage at which the nest memory of many females appears to be still less firm than in later stages (Cf. Fig. 7, Curve A). Nevertheless, the difference cannot be objectively determined at present.

In Section 1.3., the lack of clear correlation between date of nest foundation and survivality was mentioned. The same can be said as to the relation between date of nest foundation and number of cells per cluster. In 40 successful nests examined by excavation in 1958 (Cf. Table 1), the relation is as follows :

Number of cells per cluster	1	2	3	4	5	6	7	8	9	10
Founded during										
April 22–30	1	1	1	2	3	1	2	3	1	
May 1–10		2	2	5	2	4		1		
May 11–20	1				3	3	1			1
Total	2	3	3	7	8	8	3	4	1	1

Small cell clusters are slightly frequent in early May, but without significant difference. The mean cell number per cluster is 5.1, which is approximately the same as the value given in previous paper (S-H, II, pp 64–65).

The data are still insufficient to make an estimation of the seasonal population trend, but a preliminary approximation is tentatively given as follows : As seen in Table 1, the survival rate of nests fluctuates from 14.7 to 28.9% with the mean at 22.5%. Even if the excavation of more than one nest by home-lost bees is considered, the survival rate of spring females may not much deviate from 20%, because a considerable portion of re-founded nests by such bees again must be unsuccessful. When the mothers of successful nests (about 20% of the total population in early spring) rear each five daughters in average as given above[1)],

1) The number of males produced in the spring solitary phase is so small compared to that of females (Cf. 3.1) that it can be neglected in the population estimation, however important in the formal sociology.

the total population of the next generation becomes approximately the same as that in early spring, with the decrease of nest population to one-fifty, while the increase of inhabitants per each nest to five times. However, following this stage, the mode of population growth deviates from that in solitary animals, taking the way particular to many social insects, i.e., characterized by the co-existence of a long living mother as the reproductive core with daughters mostly devoid of the reproductive role except for the parthenogenetic production of males in one and the same nest. (The increase of inhabitants in each nest is, therefore, six times instead of five, though this value cannot be evaluated as in solitary animals). Hence, the increased population in each successful nest is not equivalent to the increase at the same rate in other solitary animals. Whether or not this peculiar composition in the summer matrifilial association is more efficient compared to the spring solitary phase is a very interesting aspect, but still open to question.

Table 2. Activities of some spring

	Nest No.	Founded on	Activities on May									No. of flights without pollen	
			15	17	19	20	21	24	26	27	28	15	17
Nests continued to summer	1	≧ April 23	⊕	⊕	⊕	−		⊕	−	−	⊕	3+1	0+1
	8	April 23	⊕	⊕	⊕	−		⊕	−	⊕	⊕	0+2	0+1
	14	〃 〃	⊕	○	⊕	−		⊕	−	⊕	−	2+7	0
	10	April 27	⊕	⊕	⊕	−		−	−	⊕	⊕	4+1	0
	3	May 4	⊕	○	⊕	⊕			−	⊕	⊕	**4+1**	0
	4	〃 〃	⊕	○	⊕	−	⊕	⊕	−	⊕	⊕	1+1	0
	11	May 6	⊕	○	⊕	−	⊕	⊕	−	⊕	⊕	1+1	0
	6	May 13	⊕	⊕	⊕	−	⊕	⊕	−	○	⊕	**0+2**	0+1
									Mean			2+2.25	
Nests not continued to summer	12	April 23	⊕	○	⊕	+			−	+	−	0+3	0
	2	May 6	⊕	⊕	⊕	−			⊕	−	−	4+4	0+2
	13	〃 〃	⊕	⊕	⊕	−			−	+	−	4+4	0+2
	15	〃 〃	⊕	⊕	⊕	−			−		○	3+1	0+2
	5	May 13	⊕	⊕	⊕	−	⊕		−	?	?	**4+4**	1+0
	7	May 14	⊕	⊕	⊕	+			−	+	−	0+1	0+1
	9	May 15	⊕	○	⊕	−			−	?	−	0+1	0+1
	16	〃 〃	⊕	○	⊕	−			−	?	−	0+1	0
	17	〃 〃	○	○	⊕	−			−	−	−	0	0

⊕ : With flight activities
○ : With some activities other than flights
\+ : Entrance opened
− : Entrance closed
? : Entrance opened, presumably abandoned judging from the entry and exit of *Formica fusca japonica* Motschulsky
Underlined : Cases in which the number of actual flights might be more than, or the duration much than the figures given.

Anyhow, a quite high mortality (more or less 80%) in the spring phase must be considered in further studies as to the population trend of this species.

In the studies of wild bees, it is well known that the nests once discovered at an active state are often abandoned later. In spite of its importance to the population dynamics of the wild bees, there has hitherto been published only a little quantitative information about this aspect (Cf. Linsley, 1958). The result given in the present section is indubitably still very incomplete, but may be suggestive for further researches along this line.

II. Behaviour at nest site

Diverse behaviour at nest site, especially behaviour concerning foraging activities, was observed mainly in 1958 at the nests of the shrubbery, University Botanical Garden. Among them 17 nests were more or less continuously subjected

nests individually observed

with and loads on May		Ratio of duration spent by flights to *daytime open period* (both in minute) on May					
19	28	17		19		28	
6+1	4+1	11/210	4.75%	131/195	67.2%	76/238	31.9%
1+0	1+0	5/ 82	6.1	33/ 78	42.5	?/229	–
*(4−1	–	0/162	0.0	*(77/164	47.0	–	–
*(1−2				139/164	85.0		
4+1	**2+4**	2/261	0.75	181/224	80.8	**55/236**	23.3
5+0	6+1	0/185	0.0	91/193	41.2	63/207	30.3
5+1	**3+0**	0/300	0.0	164/225	73.0	**40/120**	33.3
2+0	**4+1**	0/**120**	0.0	188/273	68.7	**76**/153	49.7
6+1	4+3	2/204	1.0	**102/301**	33.8	49/**169**	29.1
4.9+0.8	3.4+1.4			122.9/	60.5	59.8/	32.9
?**1+0**	–	0/**180**	0.0	**307/394**	78.0	–	
3+0	–	8/175	4.8	108/171	63.2	–	
*(3+2	–	12/175	6.9	*(**122**/230	48.8	–	
*(0+2				**50**/230	21.7		
*(7+0	–	24/210	11.4	*(206/287	72.0	–	
*(1+0				?/287			
1+0	–	18/ 92	19.6	39/186	20.6	–	
2+0	–	4/204	1.95	189/222	85.2	–	
3+1	–	0/ 95	0.0	**187/283**	66.0	–	
1+1	–	0/ 26	0.0	72/29	73.0	–	
1+1	–	0/ 40	0.0	76/98	78.5	–	

Periods of observations
May 15, 9^{30}–14^{00}
May 17, 19, see in Fig. 9
May 20, 12^{05-30}
May 21, 9^{00}–12^{00}
May 26, 9^{30}–11^{60} (Adverse weather)
May 27, 10^{00}–13^{00}
May 28, 8^{30}–14^{00}
* Polyginial nests

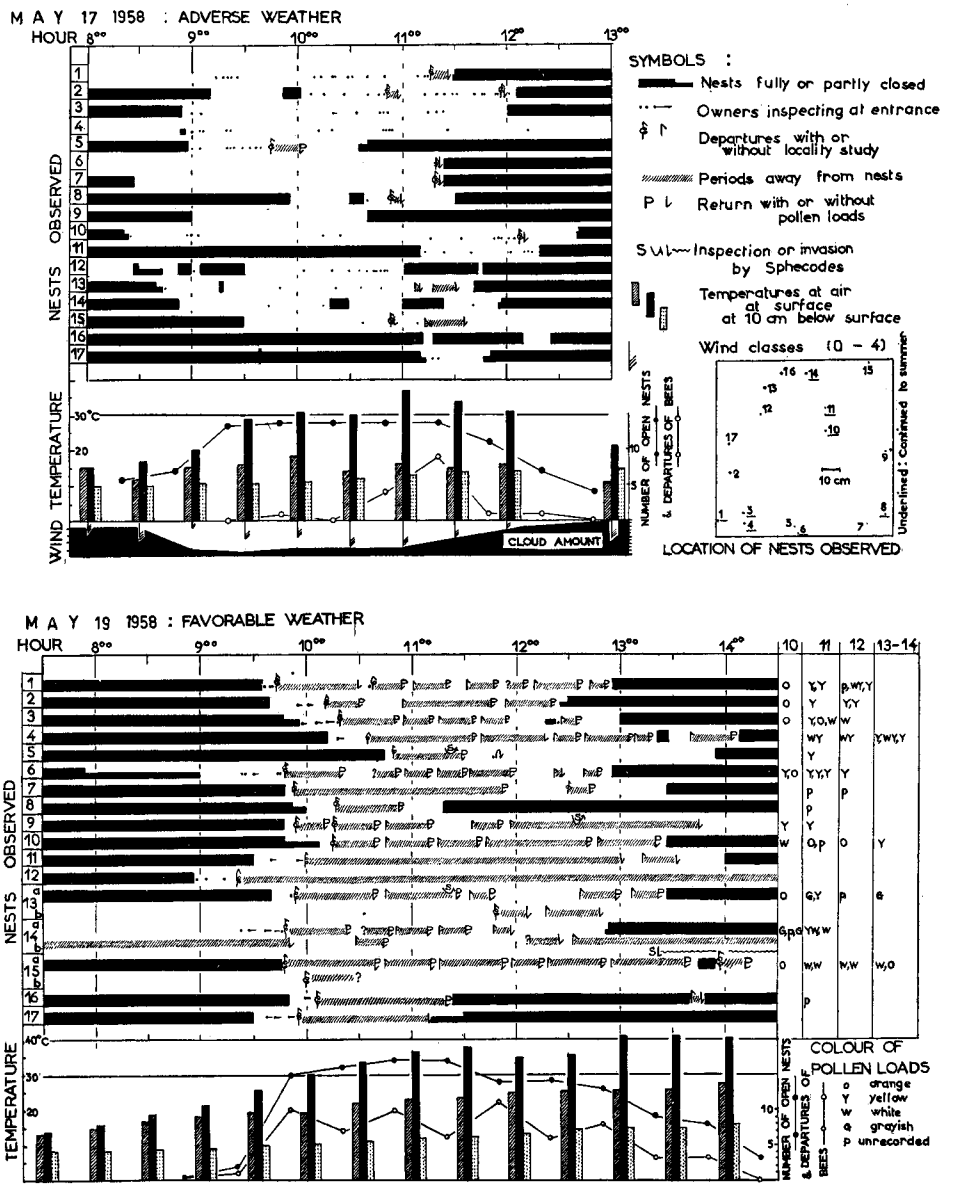


Fig. 9. Activities of some individually observed nests on two days of different weather conditions.

to observation from May 15 to 28, of which results are seen in Table 2. Further, the recrods of continuous observations in two days are illustrated in Fig. 9. As weather conditions in these two days were diametrically opposed to each other, the figures show the behavioural difference under adverse (May 17) and favorable (May 19) conditions.

2. 1. Opening and closing of nest entrances

As reported previously (S-H, II), the nest entrances are opened at daytime and closed at evening and night or occasionally even in the daytime under adverse conditions. When the entrance is closed, the soil particles seem to be brought up from the lower section of the burrow. At first a loose soil mass appears (half-closed). The mass is piled up and becomes compact as a result of further inside additions of soil. At opening of nests, the soil plug seems to be pushed down from the inside. The entrance is either gradually or abruptly opened, appearently according to the strength of the energy exerted upon the plug.

The entrance is opened quite early in the morning. The records obtained on May 15, 17 and 19, 1958, on which the observations were made from relatively early hours, were as follows :

Hour	$>7^{29}$	7^{30-59}	8^{00-29}	8^{30-59}	9^{00-29}	9^{30-59}	10^{00-29}	10^{30-59}	$11^{00}<$
May 15	|——	——	11	——	——	——	5	0	2	0
May 17	|—	4 —|	2	4	2	1	1	0	2
May 19	3	1	0	1	2	9	0	1	0

The individual difference is considerable, but most nests were opened before 10^{00}. It is interesting that nests were opened on May 17 at earlier hours than on May 19, although the daytime weather was decidedly better on May 19. This reversed relation is explained by the following measurements of soil temperature on the two days :

Temperature below surface	Date	7^{30}	8^{00}	8^{30}	9^{00}	9^{30}	10^{00}
5 cm	May 17	—	10.3	10.6	11.6	13.2	15.0
	19	8.0	8.4	9.5	10.7	12.5	13.5
10 cm	May 17	—	10.0	10.0	10.5	10.8	11.2
	19	8.7	8.7	9.0	9.2	10.0	10.5

In contrast to the air temperature given in Fig. 9, the soil temperature at two depths during period 8^{00}–10^{00} was always higher on May 17. This relation may be responsible for the difference in the morning openings between the two days, for the adult bees within the nests are seemingly hardly affected directly by the weather condition above soil surface, but mainly by that below the surface.

The time elasped between opening of a nest in morning and first flight seems to be affected by the microlimate immediately above the soil surface. On May 17, most nests had been opened since comparatively early hours. As shown in Fig. 9 by black dots, the nest owners repeatedly appeared at the nest entrances, slightly

stretched out of the nests, turning their heads and antennae to and fro as if examining atmospheric conditions, but retreated within nests. Before 10^{00}, only one flight was made by No. 5, 48′ after the opening of the nest. On May 19, most individuals engaged in flight activities. The duration between opening of nest and first flight was: 1) in 4 nests opened before 9^{00}; 27,'112′, 138′+,144′+, 2) in 11 nests opened between 9^{00}–9^{59}; 6′,6′,7′,9′,16′,16′,24′,25′,31′,33′,47′, 3) in 2 nests opened after 10^{00}; 4′, 23′. The shortening of the duration between opening and first flight in the nests opened later may be explained by the influence of wind velocity and temperature immediately below the soil surface.

Although the nests are often closed temporarily during the foraging time, here are given some records of the final closure in the evening:

Date	Weather	10^{00-29}	10^{30-59}	11^{00-29}	11^{30-59}	12^{00-29}	12^{30-59}	13^{00-29}	13^{30-59}	14^{00-29}	14^{30-59}	15^{00-}
May15	Variable					1	9	1	3			1
17	Cloudy-windy		2	2	5	4	1		3	.....		
19	Fine, calm			2		1	3	4	3	1	2	
27	Fine, calm		2	2	1	2	1	1	.....			
28	Fine, calm	1	2			5	1		.....			
Total		1	6	6	6	13	15	6	(9)	(1)	(2)	(1)

Many nests were already closed at about 12^{00}–13^{00}, but with a marked daily fluctuation: later on May 15 and 19, while earlier on other days. The earlier closing on May 17 may partly have been affected by the adverse weather, while that on May 27 and 28 was perhaps caused either by the progress of maternal work in parallel to the development of broods, or by the higher air temperature in afternoon (air temperature at noon 28.5°C on May 28, while it was 25°C on May 19). But it is difficult to determine the principal factor to induce the final closing. There were found a few nests which remained open until the next day, in spite of the presence of the foraging females (Nests, No. 9, 12, on May 19, Cf. Fig. 9).

The following tabulation indicates that the entrances are often closed quickly after the final return:

Duration of time between final reutrn and closing (in min.)	0–2	3–5	6–10	11–20	21-30	31–60	61–
No. cases observed	12	7	6	6	5	9	3

As seen in Fig. 9, the nests are often closed during daytime. Such temporary closures were more frequent on May 17 than on May 19, perhaps as a response to the adverse weather. The duration of these temporary closures was measured as follows: Less than 5′ (5 cases), 6–10′ (1), 11–20′ (1) 21–30′ (3) 31–40′ (2), 41–50′ (2), more than 60′ (3). Most were of short duration, but there were some prolonged closings No. 16 was closed on May 19 after a single foraging trip from 11^{23} to 13^{40} (137′), followed by a very short flight without bringing pollen loads (Fig. 9). The temporary closings are not concentrated in definite hours. Often some individuals temporarily closed their nests, nevertheless others were fully active

in foraging.

From the records of opening and closing, the duration of *daytime open period* was calculated in each nest on each day:

	Duration in hours (d)					
	$0<d<1$	$1<d<2$	$2<d<3$	$3<d<4$	$4<d<5$	$5<d$
Duration between first opening and final closing of nest	1	5	2(5)	14(14)	1(9)	1(1)
Ditto, excluding duration of daytime temporary closing	2	5	7(5)	10(7)	2(3)	1(1)

The cases in which opening and closing were not exactly recorded are shown in parentheses, in which the actual durations of time were longer than the estimations given above. Most nests were opened about 3–4 hours per day. In contrast to the total duration of flight period shown in Table 2, weather condition does not markedly affect the duration of *daytime open period*, unless too the latter is severe.

2. 2. Foraging statistics

The duration of foraging trips was measured in 17 more or less continuosuly observed nests as listed in Table 2, and further in other occasionally observed nests. The distribution of the trip and intertrip durations (in minutes) are shown as histograms in Fig. 10. The means, standard deviations and sample size are respectively: Trips with loads, 18.95′, 13.35, 88; Trips without loads, 21.49′, 16.95, 57; Intertrips after with loads, 9.80′, 8.34, 66; Intertrips after trips without loads, 15.00′, 15.18, 27. Although the ranges of trip duration are considerably wide, most were, either with or without loads, accomplished within 30 minutes. The significance of trips without loads is often obscure. Lack of load may represent either nectar foraging or trips with poor crop. The duration of intertrip periods after such trips without loads was frequently far less than that between trips with loads as shown in the sample size. This depends on the fact that such *unsuccessful* trips were often executed isolately, not repeated subsequently, suggesting the abandonment of further affected by adverse conditions (Cf. Fig. 9).

As seen in Fig. 9 right hand, each female often works on more than one pollen source within one and the same day. This partly depends on the different diurnal rhythms of pollen yielding plants. For instance, orange coloured loads were prevailing on May 19 during 10^{00}–11^{00}, then replaced by yellow or white ones. The intertrip duration also varied from case to case but was in general distinctly shorter than trip duration, especially when the trips with loads were executed successively. This indicates that the bees under such circumstance depart immediately after depositing their previous loads. There is no clear correlation between length of trip and intertrip duration measured successively.

The number of foraging trips per day is also variable. The numbers of trips with and without loads on May 15, 17, 19 and 28 in the 17 nests are shown in Table 2, together with the durations of total flight times and of *daytime open period* on May 17, 19 and 28. The means in 8 successful nests were 2.00–2.25 (trips

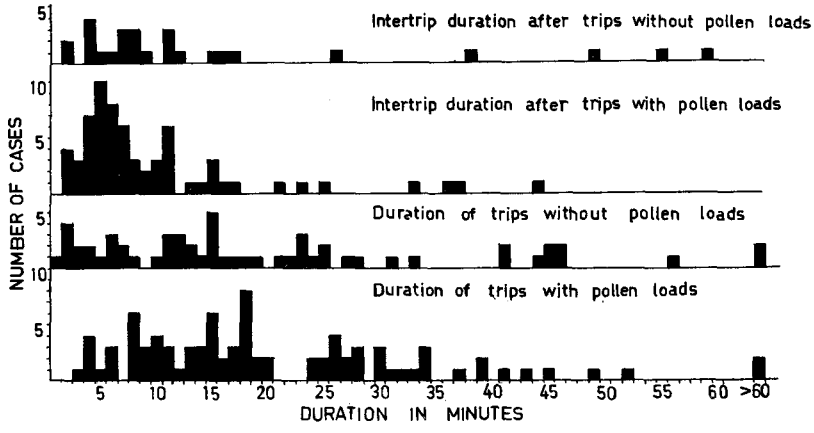


Fig. 10. Distribution of flight trip and intertrip durations.

with and without loads), 4.9–0.8, 3.4–1.4 on May 15, 19 and 28 respectively. Correspondingly, the mean total flight duration and its ratio to the *daytime open period* were 122.9′ (60.5%) on May 19 and 59.8′ (32.9%) on May 28 respectively. Although it is still premature to offer any definite conclusions from these meagre data, the daily flight number may be estimated at 3–4 in average, and 4–5 at the peak of foraging, as far as the weather conditions are favorable. In these continuously observed nests, the foraging trips were more or less observed in all successful nests except No. 14 until May 28, while most unsuccessful ones showed scarcely such activities from much earlier periods. But as seen in Section 1.3., this does not always mean the absence of successful nests, of which the active period was shorter than one month.

That the weather conditions strongly affect the foraging activities is obvious when the data in Fig. 9 and Table 2 gathered on May 17 and other days are compared.

The relations between weather conditions and foraging activities are seen in Fig. 11. A return flights do not primarily depend on the weather condition, only the departure from the nests was considered. The weather conditions at each departure were obtained from the linear interpolation of half-hourly successive measurements of temperature, wind class etc. The distribution of the absolute number of departures in each *weather class* (with intervals of 1°C in air, soil surface and soil temperatures ; of 1 class in wind classes (0–6) and cloud amounts (1–10) are shown in Fig. 11 as frequency polygons of thin lines (ordinate left). However, the observed duration of time for each weather class varied widely. For instance, the duration of the range 35.0-35.9°C in air temperature (expressed as 35°C in Fig. 11 (abscissa) was 390′, while that of the range 17.0–17.9°C was only 60′ in the total observation duration. Therefore the absolute number of departures in each weather class was divided by the total observed duration in which such weather condition was realiz-

ed. This corrected distribution of *departures per minute* is illustrated by polygons of thick lines (ordinate). Similarly, absolute numbers of departures and departures per hour in each daytime hour are shown in Fig. 11. The horizontal line in each graph shows the mean number of departures per minute or per hour.

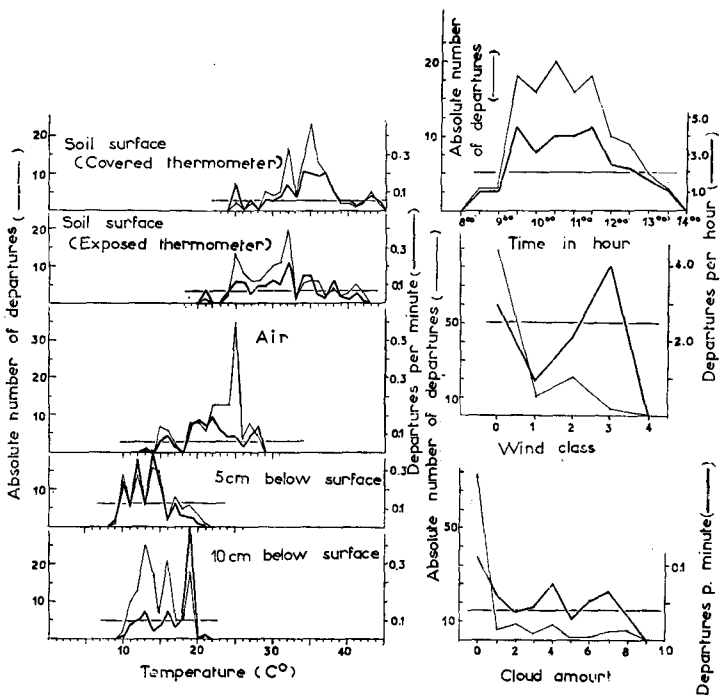


Fig. 11. Relations between flight and weather conditions.

In general both thin and thick lines show a similar tendency in each graph, but there are several marked deviations, notably in air temperature at 25°C, in which the departures were frequent (35) in absolute number, but scarce if the long observed duration (390′) was considered, and at wind class 3, in which the opposite relation was observed. It is difficult to ascertain the favorable range as to each weather condition, but the ranges exceeding the horizontal mean line, and moreover *only in the middle peak of each distribution*, were arbitrarily regarded as the optimal range as follows :

Soil temperature 10 cm below surface : 12–19°C
Soil temperature 5 cm below surface : 10–14
Surface temperature (exposed thermometer) : 25–32
Surface temperature (covered thermometer) : 31–38
Air temperature : 19–25

Wind class : 0
Cloud amount : 0–1
Daytime hours : 9^{30}–12^{30}

Among them wind class and cloud amount were subjectively corrected by considering the absolute number. The high peak in wind class 3 was caused by 4 departures followed by quick retunrs which occured within only 30′ of total observation time, whereas wind classes 0–2 were existent when there was least duration more than 300′.

What is then the principal and immediate factor to induce departures from the entrances ? Although it is not easy to reply correctly to this question, the soil surface temperature measured both by exposed and covered thermometers and cloud amount as an indicator of insolation may be most important. The soil temperature below surface may, if favorable, stimulate each female and enforce her to ascend the burrow to the entrance. At the entrance she stays for a little time to examine the outer environ. Except at the peak of daily foraging activity, she takes flight only after such examination. Under adverse condition, she disappears into the burrow without taking flight. Soon she reappears, examines and again disappears. Such examination is repeatedly performed but she seldom leaves her nest. In such situation, the air temperature and wind velocity do not directly interfere in the flight drive. Only the surface temperature and cloud amount may directly be perceived.

After departure, however, these two last mentioned factors may be highly influential. As seen in Fig. 9 (May 17), the females once departed often soon returned under adverse conditions. All 4 departures at wind class 3, which resulted in the high peak in the departure per minute in graph (Fig. 11), were followed but such immediate returns. As to the diurnal rhythm of foraging activity, this species decidedly shows the peak in the afternoon, like as in many solitary bees in the temperate regions.

2. 3. Miscellaneous observations at nest site

2. 3. 1. Orientation flight

Each female performs an orientation flight at the first departure on each day. After inspecting by antennae for a while at the entrance, and occasionally after crawling about 1 cm from the entrance, she makes circular flights of about 3–5 cm in diameter 3–4 times. Then the circular flights are repeated always with her head directed to the nest entrance 3–5 times with enlarged diameters of 30–50 cm, often to 1 m before disappearing to the presumable foraging area (Fig. 12. A). In the second and subsequent departures, the orientation flight is either discarded or simplified if it rarely occurs (Fig. 12, B), except for 1) the instances in which a considerable time has elasped between two departures (Fig. 12, C) and 2) the initial stage of the spring phase in which the orientation flight was often performed in full expression even in the second and subsequent departures. The

occurrence of orientation flight in 55 first to third departures observed during May 15–28 were : 29/30 in the first flight departures, 3/15 in the second departures and 0/10 in the third departures.

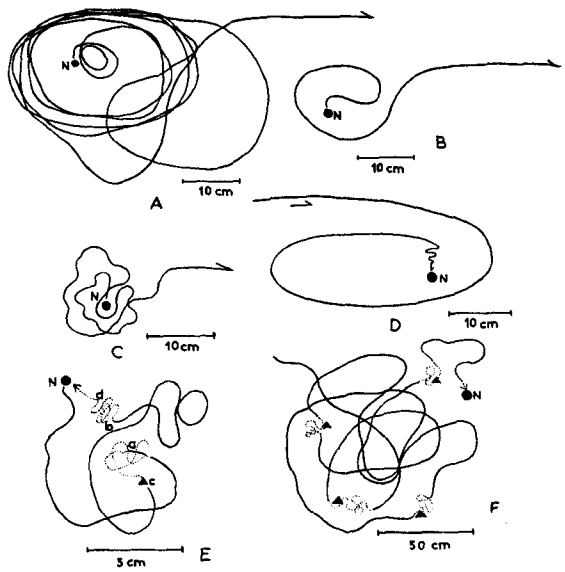


Fig. 12. Some examples of orientation flight and temporary disorientation (solid line : flight course, dotted line : crawling course, triangle : attempts of digging, N : nest). A : Typical orientation flight at first trip, B : Orientation flight at later trips, C : Orientation flight at the later trips after a considerable time of indoor works, D : Typical return course, E & F : Temporal disorientations around the nests (see in text).

At the peak of foraging activities from 11^{00} to 12^{00}, each female used to start directly and suddenly from the nest entrance, so that the accurate recording of departure was occasionally difficult. In the way back, the flight speed decreased near the entrance, usually accompanied with some horizontal swingings (Fig. 12, D). Occasionally some conspicuous landmarks were utilized in the orientation. One female used to return to the distinctive foliage of a shrub before entering her nest situated about 2 cm eastward of the shrub.

2. 3. 2. Memory of nest location

Once the foraging activities commences, the memory of nest location is firmly established. The drifting to neighbouring nests is rather rare even in a dense aggregation with internidal distance often nearly 1 cm. On the other hand, the memory of nest location is relatively weak in the pre-foraging period as shown by the following observations :

Observation 1 : One female just started from her nest, (Nest 1) was captured at

11^{00}, April 30, 1957, marked with yellow paint and released. The individual flew away and never returned thereafter. At 12^{15} a further female taken from another nest was marked with red paint and introduced to Nest 1. At first for a while she resisted this enforcement, but soon disappeared within the nest. About 5′ later, she was seen at the entrance and behaved as if the proper nest owner. She was seen in the same nest on the next day but left the nest after a mild stimulation by a rod never returned thereafter. Such artificial introduction was tested in two further nests, with similar results.

There are several observations in which the temporary loss of nest memory was noticed. Two instances are cited herewith :

Observation 2 : April 24, 1958 (Fig. 12, E). A female started from her nest and landed at *a*, about 5 cm distant from the nest entrance, crawled there about as if searching for the nest entrance, and dug at *c* for about 2′. Then she again flew around and landed at *b*. After crawling around for a while, she arrived at *d* about 2 cm from the entrance, then ran straight to the entrance and entered within.

Observation 3 : May 13, 1958 (Fig. 12, F). A female appeared in wing in the nest site, landed on and crawled to and fro searching for her nest, which was *discovered* at 11^{32}. During 5′ before discovery, she eagerly examined soil crevices and attempted to dig at four points noted in the figure with triangles.

As seen in these instances, the females whose memory of nest location was temporarily confused often started to dig anew in the vicinity of the proper nests. Such attempts are usually temporary, but occasionally resulted in the formation of a second nest by abandonment of the former one. As already touched upon in 1.4., this is indubitably one of the causes of the frequent nest abandonment, notably at the early stage of the spring phase.

The orientation of a returning bee is often remarkably confused by artificially closing the entrance during their absence. Even females at the peak of foraging activities, with firmly established nest memory, were often confused in such a way, searching to and fro on the ground and repeatedly digging anew at various points. Or the female flew away and returned frequently after a considerable time (to 30′). This indicates the importance of sight, probably of scototactic nature (v. Buddenbrock, 1952, p. 60) in the orientation. The importance of the nest entrance as a cue is well known in other solitary wasps and bees (in *Halictus malachurus* Kirby, see Legewie, 1925). On the other hand, the role of the olfactory sense, too, seems to be important in the immediate environs of the entrance. The temporarily disoriented bees often ran straight to the proper nest when she accidentally came about 1–2 cm near the entrance during her random crawling (Cf. Observation 2 mentioned above).

On May 28, 1958, a female showed a distinct shock reaction at the entrance and flew away when she returned from her foraging trip, nevertheless her nest memory was very firm either seasonally (the later period of the spring phase) or as to the daytime (10^{05}, after three foraging trips). After a few minutes, an ant worker (*Formica fusca japonica* Motschulsky) crawled out from the entrance, which it had entered for foraging food.

2. 3. 3. Behaviour at nest entrance

The spring nests possess no specialized junitor even temporarily, for the nests are principally headed by a single female. However, the nest owners often stay at the entrance for considerable time, especially under adverse weather (Fig. 9), occasionally broken by a brief flight followed by immediate return. The behaviour of such bees seldom differs from that of the junitors in the summer matrifilial associations. They often exposed their fore-bodies to the second metasomal tergum and stay in this position with heads and antennae continuously inspecting the environment. They are very sensitive to approaching objects and immediately retreat when some objects such as a finger, a pencil etc. are shaken in front of the entrances. Blocking by the metasoma under stronger stimulations was never observed either in spring or summer phases, in spite of repeated attempts to induce it by stimulating in diverse ways and intensities. Therefore, this species appears to lack this defensive attitude, which was repeatedly informed regarding other halictine bees (for instance, *H. malachurus* Kirby, Legewie, 1925 ; *Lasioglossum stultum* (Cresson) and *Chloralictus rhytidiphorum* Moure, Michener & Lange, 1958a)[1]. Judging from the behaviour of spring females at the entrance, the differentiated junitor behaviour characteristic to halictine bees is likely to be deviated from the conflict between the drive to leave nest and environmental resistance perceived, as already suggested by Goetsch & Eisner (1930) in ants.

2. 3. 4. Pollen foraging for self-utilization

The homing bees with large pollen loads in the hind legs are usually the females who have already commenced their maternal care. But there are some instances in which such is not the case.

On April 24, 1958, a nest was excavated at 12^{00} after the female with large pollen loads entered. The nest was still devoid of brood cells ; it consisted of only a simple burrow of 9 cm depth, without deposition of pollen in any parts. On May 2, 1959, a female with large pollen loads entered the nest at 8^{55}. The nest was excavated after her departure at 9^{10}, but no pollen deposition was found in the simple vertical burrow of 16 cm depth. At 9^{30} the bee returned to the nest site with full loads. The examination of the crops of both specimens revealed abundant pollen masses.

Observations show that the pollen taken by the adults as nutriment to develop their ovaries is ingested not only on the flowers, but in the nest after being transported.

2. 3. 5. Occurrence of two females in the same nest

Although the summer nests of *H. duplex* are inhabited by several females, the spring female and her daughters, the spring nests contain in most cases a single female. This is one of the most important features of this species in the com-

1) The generic names follow the original paper. In Michener's classification they are *Lasioglossum* (*Evylaeus*) *malachurum*, L. (*Chloralictus*) *stultum* and *L.* (*C.*) *rhytidiphorum* respectively.

parative sociology of halictine bees. Leaving its full discussion for elsewhere, the writers would give a few exceptions to such monogyny:

Observation 1: May 13, 1958. A female returning at about 12^{00} was artificially inhibited to enter her nest by blocking the nest entrance. After a confused flights of 15′, with interesting crawlings and diggings in the vicinity, a further example of temporary disorientation, she entered when the entrance was re-opened by the observer. Simultaneously a female, which was, in all the probability, another individual, appeared at the entrance and inspected around, suggesting the occurrence of two females in the nest.

Observation 2: May 15, 1958. Nest No. Q-4-2 had been closed at 12^{05}, with the still moist soil mass, which indicates the occurrence of a female within. A female with abundant pollen loads arrived, opened the entrance without hesitation, and disappeared within. Immediately, another female appeared at the entrance, took the air after a gentle simultation offered, and returned to the entrance after a brief flight. Her legs were provided with no pollen loads, proving that the two females were different individuals.

Observation 3: May 19, 1958. Fig. 9 shows that nests Nos. 13, 14 and 15 contained at least two females on this day, or to speak truely, the records cannot satisfactorily be explained unless the occurrence of two females is postulated. Moreover, it is dubious whether or not the females which finally entered Nest No. 9 was its proper owner. This female landed at first 5 cm south of No. 10 (Cf. Fig. 3 map), crawled and dug there for a while, then took the air and landed between Nos. 2 and 17. After a short crawling she approached No. 9, the only open nest nearby at that time, and disappeared therein with very *unsettled* attitude.

Observation 4: During May 21–24, 1958, the nest owners were marked with coloured paints in some nests. In five nests, the fidelity nest was confirmed until May 28. But in one nest the owner transferred to another, seemingly, recently abandoned nest. In the third nest, two females were captured and marked with different colour paints. One remained in the nest during May 21–27, but the other was seen in a different nest from May 27–28.

Although the above observations suggest occasional polygyny and drifting, such are rather exceptional in the spring phase. It is very conceivable that such polygyny is only temporary even if does occur. Among nearly one thousand nests excavated before the emergence of daughter females, the occurrence of more than one female per nest was never observed. Consequently, it can be said in safety that the spring phase is principally *solitary-monogynous*.

The spring females often express a marked aggressiveness when confined within the same container. In such instance, often one female was killed by stinging. This severe aggressiveness may be responsible to explain the scarcity of spring polygyny. At flighting, each female often turns upside down and retains this posture for a while, bending her metasomal tip to sting the opponent. Or, the body posture is normal and middle and hind legs of one side are raised against the approaching opponent. Both postures are taken by bumblebees in a more exaggerated manner. Stöckhert (1932) reported occasional polygyny (2–3 females per nest) in the spring solitary phase of *H. malachurus* Kirby, a species possessing a typical matrifilial life mode with discrete reproductive periods like as

in *H. duplex*. But he considered that such spring polygyny differed from the friendly co-existence in summer matrifilial association. Although his assumption is not supported by ample evidence, such seems to be valid on the occasional spring polygyny in *H. duplex*, too.

III. Sex ratio and additional notes on nest architecture

In this section some items of information obtained from the results of nest excavation are given, which are additional to items presented the previous paper (S-H, II).

3. 1. Sex ratio in spring broods

The decreased production of males, either decrease in the absolute number, or decrease due to the limitation of the period producting males, is one of the important aspects in the gradual elaboration of social organization in Hymenoptera. Such tendency is also seen halictine bees. For instance, the spring broods of *H. malachurus* are composed of females alone (Stöckhert, 1923, Noll, 1930, Bonelli, 1948). *H. marginatus* Brullé completely lacks males until the time of the final stage of its perennial nest (Plateaux-Quénu, 1959). Further, some species are intermediate in this aspect, that is, spring males are produced but in a distinctly (less amount) than females, as in *H. sexcinctus* Fabricius, *H. maculatus* Smith and *H. immarginatus* Schck. (Stöckhert, 1923) like as in *duplex*. Such decreased production of males in spring broods is regarded as an indication of incipient social evolution. Nevertheless no numerical data have hitherto been given in any of the species mentioned above.[1)]

It is not always easy to ascertain accurately the sex ratio of offspring in each nest. In earlier nests, most broods are still young, and it is difficult to identify their sexes by dissection or by rearing them until pupation. On the other hand, the sex ratio in later stage nests cannot accurately be determined, because some emerged bees, notably males, leave their cradels. The following data show the sex ratio in the all the broods obtained through excavation, of which the sexes were accurately determined. In the late spring nests the newly emerged daughter bees are found in the nests together with their mothers. Such nests were excluded from the data, for the males after emergence do not remain in the nests.

Year	Females	Males	Ratio
1957	41	4	10.25 : 1
1958	97	10(3)	9.7 : 1 (32.6 : 1)
1959	578	19	30.4 : 1
1960	60	1	60.0 : 1
Total	776	34(27)	22.8 (28.7) : 1

1) The generic names of the species cited follow the original papers. In the recent system, all belonging to *Lasioglossum* except *sexcinctus* which to *Halictus* (*Halictus*).

In two nests obtained in 1958, all broods were males (6 males in one nest, Fig. 13, B, one male in the other, Fig. 13, A), and the mothers were unfertilized in both nests, apparently due to the failure of mating in the preceding autumn. The ratio excluding these two cases is given in parentheses. It is recognized that the ratio of males to females is considerably variable from year to year but decidedly low.

The arrangment of sex in each nest cluster was determined in a few nests alone. The results are illustrated in Fig. 13 A-H. The presumptive relative order

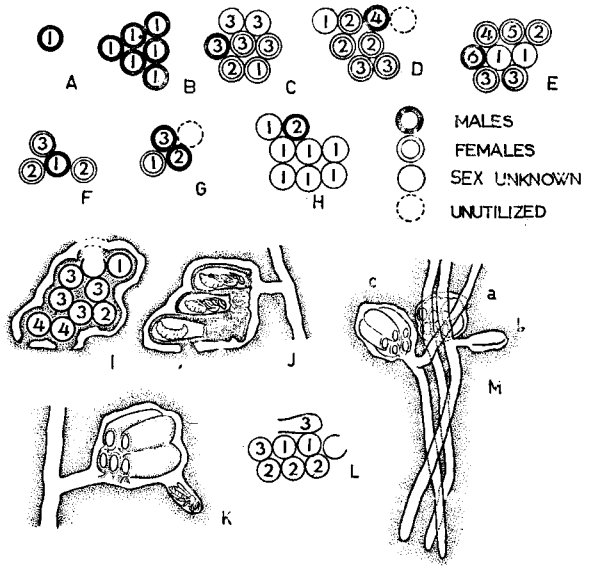


Fig. 13. Distribution of sexes within a cell cluster (A-H) and some abnormal architecture (I-M). Numerals indicate the relative ages of broods.

of oviposition is numerically given in the figures. Excluding two nests with unfertilized mothers and male broods alone, the males are supposed to be produced later, except for one instance, in which a male was clearly oviposited at first (Fig. 13 F). Correlation of cell number in each nest and occurrence of male offspring is given below. The data are supplementary to Table 6 of S-H, II, p. 65, but only partly so, because only those nests in which the sexes of all broods are relatively well known were selected.

No. cells per nest (1958–1960)	1	2	3	4	5	6	7	8	9	* Unisexual nests
Total frequency	1	1	4	7	12	9	8	10	3	headed by un-
Frequency of nests containing male	1*		1	2	1	1*	1	4		fertilized females

As shown above, the nests containing males are the relatively larger ones,

but without distinct correlation. The cause of such occasional production of male is unknown. The spermatecae of mothers of Nests E and H (Fig. 13) possessed abundant sperm, indicating, together with the arrangement in F (Fig. 13), that the production of males was not caused by the exhaustion of sperm reserve.

Although the production of males is very sporadic in spring broods, such accidentally produced males play a remarkable role in the social organization of this species, by fertilizing some daughter bees produced in the same season.

3. 2. Additional notes on nest architecture

Since the publication of the previous paper (S-H, II), some additional information has been gained as to the nest architecture, mostly rather of abnormal nature as described below:

a) Complete cavity surrounding a single cell: A nest excavated on June 25, 1958 contained only one cell with male pupa, and the mother was unfertilized as stated above in Section 3.1. (Fig. 13 A). The cavity surrounding the cell had been completely excavated, leaving a thin pillar which connected the walls of the cavity and the bottom of the cell near the entrance of the latter. As stated previously (S-H, II, Section 2. 4.), a cavity is usually not found in younger nests containing still only 1–2 cells. The completion of a cavity around a single cell may suggest that female, being very small in body size, was abnormal in reproductive vigor, too.

b) Extreme proximity among nests: The dense aggregation of this species was sufficiently mentioned in Section I. Caused by such high density, the nests are often found closely contiguous to one another. An extreme case of such proximity was found among three nests excavated on June 17, 1958 (Fig. 13 M). Among them, the distance between cluster cavities of nests *a* and *b* was 5 mm, of *a* and *c* was only 0.8 mm. The distance between the lower shafts was 1–5 mm. In such instance, it is very probably that the nests once communicated occasionally but are soon barricaded from one another.

c) Nest with additional lower shaft: A nest already closed was excavated on June 23, 1959. The female was captured at the rear bottom of the cell cavity, where she had been actively digging. A short blind shaft about 1 cm in length had already been constructed, while the proper lower shaft was normal. This explains the formation of a second blind shaft recorded in the previous paper (S-H, II, Section 1.5.2, Fig. 46).

d) Cell-clusters of abnormal arrangement: In the previous paper, the developmental gradient within a cell-cluster of this species was confirmed *upwards* in general (Section 2.3., Table 11, Figs. 80–98). In two nests illustrated in Fig. 13, I-J and L of the present paper, both excavated on June 20, 1959, the developmental gradient was rather *downwards* (judging from the relative stages of brood contained given numerically in the figures). In one nest (L) the uppermost cell was perpendicular to the direction of cluster (Cf. S-H, II, Section 1.3.2., d), apparently being an addition. The arrangement in the other cluster (I and J) was more remarkable. The plane given by the openings of cells was the type of *forward construction of upper cell layers* (S-H, II, Section 1.3.2.,c), which had previously never been discovered. Moreover, a large soil mass was deposited at the front of the lower cell layers, so that the front of the cluster was itself vertical. This abnormal architecture, in combination with the downward developmental gradient and the position of a horizontal lateral (or lateroid, Sakagami & Michener, in press), which opened at the middle of the cavity, can not reasonably be explained unless the application of some *building technique*

is assumed, which seems to be not performed in this species under normal conditions (Cf. S-H, II : p. 79, foot note, Cf. also Sakagami & Michener, in press).

IV. Ovary development and related problems

The change of ovarian state and related internal features during the spring phase and post-spring inactive phase were studied in 1957, with females taken from excavated nests, in 1958 with those taken both from nests and on flowers, and in 1960 with those taken on flowers, except for some individuals from nests in late June and early July. The ovarian state was classified into the following six stages :

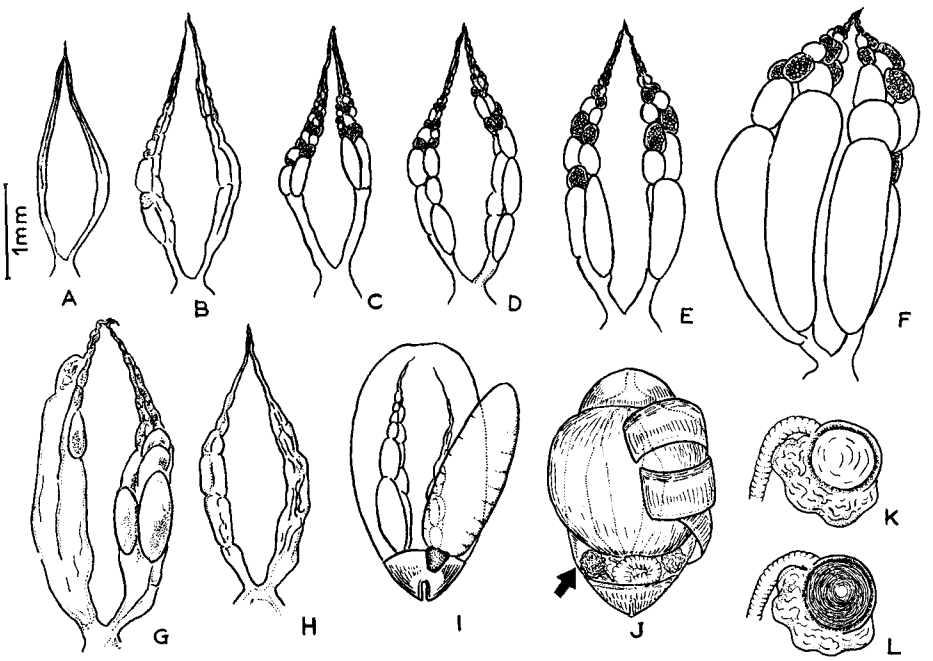


Fig. 14. Ovarian development and related features. Ovarian state I(A), II(B, C), III(D), IV(E, F), V(G), VI(H), ovaries in a stylopatized female (I), Greatly extended crop filled with nectar (J), Spermatheca without (K) or with sperm mass (L).

I. Undeveloped to appearance of incipient constrictions in ovarioles (Fig. 14 A).
II. Distinct constrictions to appearance of oocytes (Fig. 14, B ,C).
III. With abundant oocytes and nurse cells (Fig. 14, D).
IV. Peak of activity with submature of fully mature oocytes (Fig. 14, E,F). Fig. 14 F shows the maximum development. Usually each ovary possesses only one fully mature oocyte.

V. Commencement of degeneration (Fig. 14, G). When the oocytes are still large, distinguished from IV by the occurrence of yellowish spots in some parts of ovarioles.

VI. Further advance of degeneration (Fig. 14, H). Distinguished from II and III by the irregular and relaxed condition, with enlarged ovarian calyces.

Of course these stages can not be sharply distinguished from one another. Distinction is especially difficult between II-III, V-IV, VI-II or III, and VI-I (in the later stage of VI). In the unilateral development, the more developed side alone was considered. Further the following features were recorded in each female : 1) Nectar content in crop (abundant (Fig. 14, J) or not) ; 2) Pollen content in crop and mesenteron plus rectum (present or not) ; 3) Fertilized (Fig. 14, L) or not (Fig. 14, K) ; 4) Stylopatized or not. Body size and wear of wings and mandibles were also noted, but these points will be described elsewhere in connection with the caste problem.

The results are presented in Fig. 15, in which each female examined is represented either by circle (fertilized) or quadrate (unfertilized), together with ovarian state and

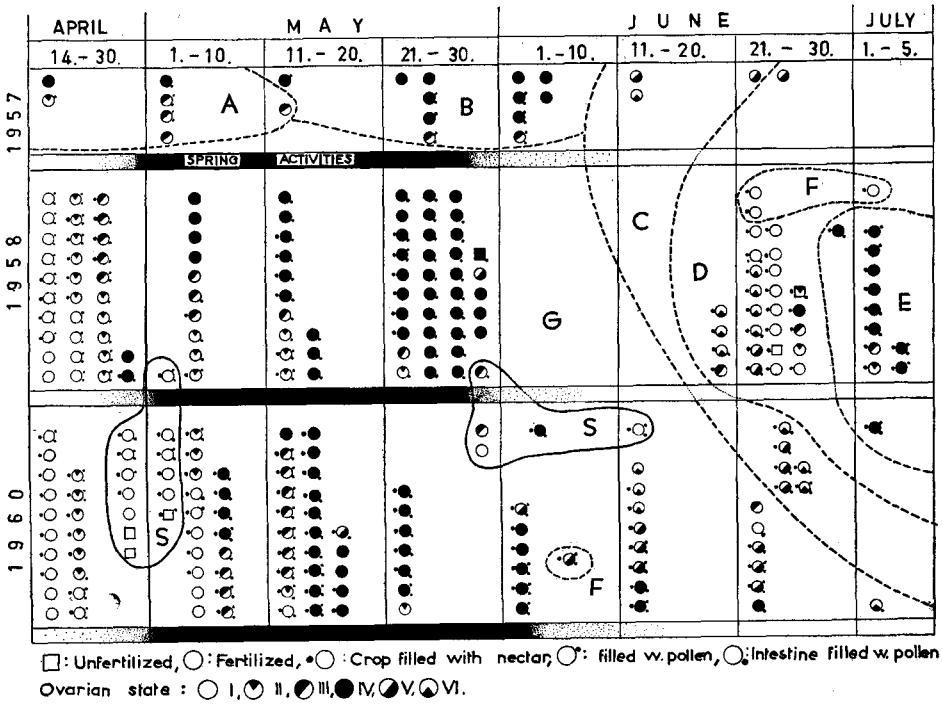


Fig. 15. Seasonal change of ovarian state and related features. Specimens taken from nests still without broods (A), from nests with eggs (B), from nests already without eggs (C), from nests already without larvae, still without emerged daughters (D), from nests of some daughters emerged (E), from nests containing mother but the development disturbed in midway (F), G : on flowers, S : Ditto, stylopatized.

related features indicated by appropriate symbols. The whole material was divided into the following eight classes according to the condition of capture :

A : Those taken from nests still without brood cells.
B : Those taken from nests with eggs.
C : Those taken from nests without eggs.
D : Those taken from nests without larvae, but still without emerged daughters.
E : Those taken from nests with some emerged daughters.
F : Those taken from nests of which the development has been disturbed midway, although containing mothers.
G : Those taken on flowers.
S : Ditto, stylopatized.

4. 1. Ovary development

Concerning the females captures on flowers, the ovaries of those taken in late April were mostly still before or at the incipient stage of development. The females with a fully developed ovary increased in early to middle May, attained the peak in late May, and were gradually replaced by ovary-degenerated females. In 1960, seven females were captured on flowers in late June to early July (Cf. Fig. 15). In this stage, most nests were already firmly closed, so that some of these females seemed to have lost their nests for unknown causes. In this year, 1960, the weather conditions were very irregular, which affected the spring activities and delayed the general course of life as clearly seen by comparing the data taken in 1958 and 1960.

As to the females taken from the nests, the ovaries were already fully developed or nearly so in nests still devoid of brood cells (A), mostly well developed in nests with eggs (B), more or less in degeneration in nests already devoid of eggs (C), mostly degenerated with some females in the incipient regeneration in nests without larvae but before the emergence of daughters (D) and mostly re-developed in nests in which the daughters began to emerge (E). The delay in 1960 is rendered more notable by comparison of the data obtained in 1958 and 1960.

4. 2. Occurrence of unfertilized females

Although the majority of females examined were fertilized, some unfertilized females were captured (0/23 in 1957, 3/131 in 1958, 3/113 in 1960), apparently caused by the unsuccessful mating in the preceding autumn. In 1960, all three unfertilized females were captured on flowers at the earlier stage and stylopatized ; those in 1958 were captured from the nests and their ovarian state approximately corresponded to that of fertilized females captured in the same period. Two unfertilized females shown in the figure (in the period June 21–30, 1958) are those already referred to in Section 3.1., that is, the mothers of two nests with six and one male brood respectively. All these data suggest that unfertilized females *can* develop their ovaries and construct their nests as can the fertilized ones. The supposed weak reproductive drive (expressed by the female which produced only one male brood) may be the outcome of some abnormality in the reproductive ability

rather than the non-occurrence of fertilization.

4. 3. Contents of alimentary canal

There was found a parallelism between the state of the ovaries and contents of the alimentary canal. In the early females still without developed ovaries, the crop was usually empty. In such females the odour characteristic to the species which persists even in the pinned specimens was often still very noticeable. Later, the females with fully loaded alimentary canal gradually increased parallel with the development of ovaries. Such individuals emit a strong specific odour when captured. Therefore, the spring intake indubitably activities the metabolism in general as well as the development of ovaries. However, the ovary development is complicated matter consisting of several sub-processes. In some early spring females (Cf. data in 1958, 1960, Fig. 15) the constriction of ovarioles was seen in spite of the lack of pollen masses in crops as well as in the mesenteron. This suggests that at least some subprocesses can be commenced without activation by pollen ingestion.

At the peak of foraging activities, the crops are either filled with nectar or empty, apparently caused by the condition of capture. In 1960, 10 females were respectively captured at the entrance, either at departure for or at return from a foraging trip. While the crops were virtually empty in 10 departing bees, they were filled abundant nectar in 10 returning bees. In the females taken during the middle to late May at the peak of the ovarian development, the pollen mass was either found or not in the mesenteron and rectum, but mostly not in the crop. Consequently, it seems that the pollen is taken, as the nutriment to develop ovaries, only in the early spring.

In the females taken from the closed nests (classes, C,D,E,) after the cessation of foraging activities, the crops were fully loaded with nectar, often occupying the majority of the metasoma (Fig. 14, J), but the pollen mass was at most found only in rectum and mesenteron and very rarely in the crop (4/39 in 1958, 1/7 in 1960). Therefore, the pollen ingestion at the later stage of spring phase appears to be unnecessary to induce the second development of ovaries in the summer matrifilial association. In such females self-confined in nests, a pair of conspicuous fat body messes are seen near the metasomal tips laterally, approximately above the last sternum (Fig. 14, J, shown with arrow). These masses exist in the females in any periods but usually whitish to pale-yellowish, while deep yellow and very compact in the females of the period concerned. Microscopically the masses show no structural difference to other fat bodies : each cell contains abundant oil drop-lets and cell boundaries are very inconspicuous. Perhaps the nutriment required for the second ovary development is concentrated and reserved in these masses. Two females captured on flowers in June 25 (the last records of captures on flowers) possessed no such conspicuous fat body masses.

4. 4. Stylopatization

The stylopatized females were formed to the number of 2 out of 131 spring

female bees in 1958, and 16 out of 113 in 1960, all on flowers, The number of per host is mostly 1, rarely 2 ; the heads of parasites projected mostly between 5– and 6–, rarely between 4– and 5–metasomal tergum. In these bees, the ovaries were generally rudimentary but occasionally attained to stage III, and in one individual even to IV. In this host collected on June 6, 1960, the ovary of unparasitized side was fully, and of the parasitized side, considerably developed (Fig. 14 I). In the parasitized specimens, there were found the following symptoms, of which the intensities varied from host to host : 1) Comparatively smaller body size, 2) Inconspicuous tergal hair bands, 3) Paler tint of tergal sclerites. No tendency of distinct sexreversal was confirmed in any character examined in the infested bees.

V Summary and concluding remarks

5. 1. Summary of results obtained

The results described in the preceding section are summarized :

I. Spatiotemporal distribution of nests

Nests of this species tend to form large aggregations within a limited area. The lack of vegetation and other surface cover is essential in the nest site preference (1.1.–1.2.). Minute pedological factors such as amount of humus, pH, and constitution of soil particles seem to play no important role (1.2.1.), whereas the microclimate markedly affects the distribution. Nests are abundant in the areas well insolated from early morning (1.2.2.). However, an excessive patchiness fitting to Pólya-Eggenberger's contagious distribution was proved even after the microclimatic influence was removed as far as possible. This may be explained by a gregarious trait characteristic to the species (1.2.3.).

The spring solitary phase is a sharply defined period in the annual cycle of this species. The increase of newly founded nests is rather gradual, while the cessation of the spring phase in each nest is more synchronous. The active period varies considerably, but in general becomes shortened in the nests founded comparatively late. There is no clear correlation between duration of active period and continuation of nest till the summer matrifilial phase (1. 3.).

Among the nests founded in the spring solitary phase, about 80% were abandoned without reactivation in the summer matrifilial stage. In more than half of such unsuccessful nests, the causes of abandonment are unknown, but it is certain that it was partly caused by the loss of nest memory in the incipient stage of nest foundation. While the mean cell number in successful nests is about five, the daughter population at the beginning of the summer matrifilial phase appears to be equal to the mother population at the beginning of spring solitary phase. This numerical equivalency never means biological equivalency, because of the difference of the social pattern between two active phase. At least, a remarkably high mortality in the spring solitary phase must be considered in further researches about population dynamics of this species (1. 4.).

II. Behaviour at nest site.

During the spring phase, each nest is, proved the weather conditions are not too severe, opened in morning, usually earlier than 10^{00} and closed mostly before 13^{00}. Total duration of the *daytime open period* is therefore about 2–4 hours. But within this period nests are often temporarily closed for variable durations of time, even if at the peak of foraging activities. Within 4–44′ after opening nests in morning, the nest owners make their first flight, again as far as weather conditions are favorable. This duration is longer in the nests opened later. In diverse weather, the bees repeatedly inspect the outer environment at the nest entrances but do not make actual flights. The time elasped between return from the final flight and closing of nest is variable, but usually less than 1 hour, mostly within 10′ (2.1.).

Mean lengths of the trip (with or without pollen loads) and length of inter-trip (after trips with or without pollen loads) are 18.95′, 21.49′, 9.80′ and 15.0′, respectively. At the peak of foraging activities, bees depart from nests immediately after depositing their pollen loads. Each bee can work on more than two sorts of pollen sources within one and the same day. Under favorable weather, time consumed in trips occupies 30–60% of the daytime open period, and the number of trips per day is estimated 3–4 in average and 4–5 at the peak of foraging activities (2.2).

The optimum range of weather conditions to elicit the departures from nests are approximately: 12–19°C and 10–14°C in soil temperatures 10 and 5 cm below surface respectively, 25–32°C and 31–38°C in surface temperatures measured by exposed and covered thermometers respectively, 19–25°C in air temperature, 0 in wind class, 0–1 cloud amount. The relative importance of these conditions is difficult to determine, but soil surface temperature and cloud amount may be principally responsible. Most flights are made during the period 9^{30}–12^{30} (2.2.).

Each female makes an elaborate orientation flight at the first departure on each day. At the second and subsequent flights, the orientation flight is either simplified or omitted. At the peak of foraging activities, each female is accustomed to start directly from the nest entrance (2.3.1.). The memory of nest location is firmly established after the foraging activities have commenced. In the pre-foraging period, however, the memory is so poor that the nests are often abandoned. Even in the foraging period, some femals occasionally lose their nest memory and being to dig new burrows. Such disorientation is indubitably one of the main causes of frequent nest abandonment (2.3.2.).

Although spring nests possess no specialized junitor, the inspecting behaviour of owners at the entrances is the same as that observed in the junitors of the summer matrifilial association (2.3.3.). At the commencement of the foraging period, the females themselves consume pollen particles not only on the flowers but also in the nests after transporting pollen loads (2. 3. 4.). Occasionally two females can co-exist within the same nest. But such is rather rare and seems to be temporary. The spring phase of this species is decidedly solitary and monogynous in general

(2.3.5.).

III. Sex ratio and additional notes on nest structure

The spring broods mostly consist of females alone, but males appear in the ratio of 1 : 10–60. The male eggs are produced in either the earlier or the later stage of the ovipositing sequence of each female. There is no clear correlation between appearance of males and size of spring batch (3.1.).

Some additional data, being supplementary to the previous records, were obtained concerning the nest architecture, mostly of abnormal natures such as: Occurrence of a complete cavity surrounding a single cell, extreme proximity among nests, nests with an additional lower shaft, cell-cluster of abnormal arrangement. In one nest, evidence was observed of the application of a building technique, which is absent in the usual nesting procedure of this species (3.2.).

IV. Ovary development and related problems

The ovaries are still not developed at the beginning of the spring phase (late April to early May), but begin to develop in parallel to the commencement of foraging and brood rearing activities, to attain the peak in middle to late May. Thereafter the ovaries gradually degenerate in the pre-summer inactive phase, during which the females confine themselves within the closed nests, and reach the minimum size in late June. Then, regeneration commences and the full development is attained in early July, when the daughter bees begin to emerge (4.1.).

Six unfertilized females were obtained among 168 females examined. Three of them taken on floweres were stylopatized, while two taken from nests had reared male broods (4.2.). At the beginning of the spring phase, each female consumes pollen which activates the development of eggs. In the pre-summer inactive phase, the females self-confined in the nests possess a large amount of nectar stored in the crops but they are without pollen stores. This suggests that the pollen ingestion is unnecessary to induce the second development of ovaries in the summer matrifilial phase. Such females possess a pair of conspicuous yellow fat bodies near the metasomal tip, which are seemingly the reservoir for the nutriment used to induce the second reproductive activities (4.3.). In 16 stylopatized females examined, the ovaries were mostly atrophied, but in a few individuals slightly developed. Some symptoms of stylopatization were observed but no tendency of sex-reversal was detected (4.4.).

5. 2. Some remarks concerning the spring solitary phase

The primary purpose of the present third report is to give an accurate picture of the spring solitary phase. The activities in this phase are virtually similar to those of numerous solitary bees. The possible significance of descriptions in this report may be precisely realized only after comparison with the activities in the summer phase of this species as well as with the life history of other halictine bees. Here are merely offered several remarks, which appear to be important and suggestive for further studies of this and related species.

First of all, the spring phase was clearly confirmed as a definite period.

Accordingly, the life cycle of this species can be divided into the following six phases: 1) Winter hibernating phase, 2) Spring solitary active phase, 3) Pre-summer inactive phase, 4) Summer matrifilial active phase, 5) Post-summer inactive phase, 6) Autumn pre-hibernating phase. While the post-summer inactive phase is relatively short and can not always be clearly recognized as a distinct phase, the pre-summer inactive phase is a very distinct one, which sharply separates the two active phase immediately before and after it.

The occurrence of such a discrete productive cycle is also found in *H. malachurus* Kirby and some other European species mentioned in Section 3. 1. and in *H. trispinis* Vachal in Japan (Sakagami, unpub.)[1]. In such species each reproductive phase appears as if to represent a distinct generation, nevertheless the spring female continues to survive within the same nest throughout these phases. The stated occurrence of thelytokous parthenogenesis erroneously asserted by Fabre (1903), Armbruster (1923) and Legewie (1925) ,which was adopted by Claude-Joseph (1927) and Rayment (many papers, for instance 1955), but throughly criticized by Noll (1931) is apparently an outcome of failure to observe the discrete reproduction by such long-lived mothers.

From the standpoint of social evolution, discrete reproduction offers an interesting transitional link. Since Wheeler (1923) the prolongation of adult stage of nest founding mothers has been regarded one of the important moments in the commencement of social evolution in insects. The discrete reproduction in some halictine bees may be regarded as a discrepancy between the longevity and reproductivity: Longevity could be extended but reproductivity could not be continuously maintained in the same level, resulting in the alternation of active and inactive phases. Concerning this relation it is interesting to cite two other types of social patterns in halictine bees. In *Lasioglossum* (*Chloralictus*) *rhytidiphorum* (Moure), the longevity of the mother is short but following her, her position is occupied by one of her daughters, so that the reproductive activities are continuous in the nest as a whole. In *L.* (*C.*) *stultum* (Cresson) the mother is long-lived and her reproductive activity is continuous throughout season, that is, continuous either by herself or in the nest as a whole (Michener, 1958, Michener & Lange, 1958b).

Using abbreviations *C* and *D* for continuous and discrete reproductions of the nest as a whole, *c* and *d* for those of the mother and her successor, and *L* and *l* for the long and short life of mothers, three types may be distinguished: *DdL* (*duplex*), *Cdl* (*rhytidiphorum*) and *CcL* (*stultum*). In the evolution of social patterns Type *CcL* is apparently the most advanced type, while the relative antiquity between *DdL* and *Cdl* is still an open question. the writers' opinion inclines to the assumption that the two latter types evolved independently of each other as follows: based upon a limited biotic potential and energy sources, the

1) In Michener's system, *Lasioglossum* (*Evylaeus*) *trispine* (Vachal).

prolongation of life $l \rightarrow L$ and continuity of reproductivity $r \rightarrow R$ during a given time interval may stand in a competitive situation. In Type *Cdl C* might be achieved by the advancement of $r \rightarrow R$ rather than $l \rightarrow L$, whereas in Type *Ddl*, $l \rightarrow L$ might be promoted at the sacrifice of $r \rightarrow R$. It is unknown whether Type *CcL* evolved from *DdL* or *Cdl*. But the course *Cdl*$\rightarrow$*CcL* is more plausible than *DdL*$\rightarrow$*CcL*. Once the daughter bees start to assist their mother when the latter is still active by laying, the mother may be discharged from various activities and be specialized to oviposition. This may in turn increase her reproductivity and ultimately her longevity, through a reciprocal feed-back process amplified by the production of worker castes. The summit attained in this way may be shown by the honeybee.

On the other hand, once Type *DdL* is established, it may rather be difficult to develop the process $D \rightarrow C$, because the assistance by daughters cannot continuously be available. Of course this type may evolve up to a considerable degree. The perennial nests of *H. marginatus* Brulle (Plateaux-Quénu, 1959) may represent the summit of this course. But it is never as a direct outcome of *H. duplex-H. malachurus* type, even in the sense of social evolution instead of phylogeny. However, the social refinement might not to be attained as in the course *Cdl*$\rightarrow$*CcL*, and the course *DdL* may be regarded as a small side branch in social evolution.

Although the hypothesis cited above is admittedly still premature, requiring further qualification in both theory and concrete data, it must be pointed out that the assumption is held concerning two processes, $l \rightarrow L$ and $r \rightarrow R$ alone, excluding other important aspects such as caste differentiation. For instance, *H. marginatus* does not belong to the course of *H. duplex* in the last mentioned aspect. Morphological caste differentiation is slightly and distinctly evolved in *H. duplex* and *H. malachurus* respectively, but it is practically absent in *H. marginatus*.

Further, the limits of present knowledge, it is dangerous or even often meaningless to assert the relative height of social evolution among diverse species *in general*. A species might be more differentiated in population size, social pattern etc. than another species, but the relation might be reversed in caste differentiation, either morphological or functional, nest architecture, communication etc. These particular aspects of social evolution might intimately correlated with one another, but never *a priori*, especially in halictine bees (Sakagami and Fukushima, 1961). Until further knowledge is accumulated, it is recommended to discuss the relative height among species only in each particular aspect independently, without too hurriedly making a vague generalization by uncritically combining different aspects.

Among the species with discrete reproduction, the reproductive phase is once per year in the perennial species, *H. marginatus*. In other species there occur three (*malachurus*) or two (*duplex* and other species cited) reproductive phases within one year. In such instances, the alternation of inactive and active phases does not correspond to the rapid change in seasonal climatic trend, so the alterna-

tion is considered as a phenomenon governed by some innate process. Such occurrence of more than one distinctly limited reproductive period of the same individual within one year is relatively rare in the insects, offering an interesting problem in the study of diapause.

The second problem is the monogyny in the spring phase. In all species cited above, the initial active phase is usually monogynous, although occasional polygyny is reported in most species and is rather more frequent than in many solitary species other than halictine bees[1]. Recently Michener (1957, Cf. also Michener & Lange, 1958) published a new interpretation on the evolution of social bees other than Xylocopinae (*Allodape-Exoneura* Complex) through a process called *semisocial* instead of the *subsocial* process followed by wasps, ants, termites and bees of *Allodape-Exoneura* Complex (Sakagami, 1960).

According to Michener, the semisocial process is marked by steps 1) nest aggregations, 2) use of a common nest by several females, each of which constructs and provisions her own cells, 3) initiation of division of labor and cooperation among such females, and 4) differentiation of the females into queens and workers and establishment of a numerical preponderance of females over males.

Considering the life history of *duplex* and other species cited above, the above steps 2) and 3) are difficult to find or to guess in the course of the social evolution of this species, neverthelss step 1) has well been confirmed. It may be true that the process assumed by Michener is realized some groups, as seen in certain Neotropical bees studied by himself. But his hypothesis, which underestimates the role of monogynous foundation, cannot satisfactorily explain the occurrence of social halictine bees, of which the nests are started monogynously and then develop into matrifilial associations. Consequently, it is suggested that at least two types of social patterns, monogynous-matrifilial association and aggregation, evolved independently within the subfamily (Sakagami & Michener, in press).

Finally, a few words must be given as to the appearance of males in the spring broods, which occurrence however scanty, offers an interesting problem. As the role of these males will be fully described in a subsequent paper of this series, here it is only mentioned that these males occasionally fertilized some summer daughter bees, which consequently produce female progeny. Therefore the autumnal females are of compound origins, mostly the daughters, but partly the granddaughters of the spring mother. Such complication is, however, of a transitional nature in the evolution of social patterns, eliminated in more advanced species such as *malachurus*, of which the spring broods are composed of females alone.

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1) *H. trispinis* is exceptional ; the nests contain usually more than one fertilized female in the spring phase.

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