Nest Proliferation by Budding and Nest Growth Pattern in *Formica* (*Formica*) *yessensis* in Ishikari Shore[1)]

By

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(*With 11 Text-figures and 2 Tables*)

The present study was undertaken as a part of the comprehensive studies on a red wood ant *Formica* (*Formica*) *yessensis* Forel inhabiting northern Japan (Ito 1971, '73, Imamura 1974, Ito and Imamura 1974, Higashi 1974). This species belongs to *Formica rufa*-group, some species of which are famous by the absence of internidal hostility, which results in the exchange of members among adjacent nests (Wheeler 1928, Scherba 1961, '64, Gösswald 1962). *Formica yessensis* also exhibits such polydomous system (Ito and Imamura 1974). Colony multiplication is often realized by budding in polydomous species e.g. *Monomorium pharaonis*, *M. floricola*, *Iridomyrmex humilis*, *Lasius minutes*, *Formica exsecta*-group, etc. (cf. Smith 1936 b, Creighton 1950, Kannowski 1959). The polydomous species of *F. rufa*-group also multiply their nests by budding (Gösswald 1951, Lange 1956, '58). Each new nest is established by the departure of a group of workers from one nest, or occasionally more, to the site nearby where queens are later carried in or alien queens just after nuptial flight are adopted, though the pioneer colony in a new habitat is possibly made by usurping some *Serviformica* nests as practiced by other species of *rufa*-group (cf. Wheeler 1910, Creighton 1950, Gösswald 1957). That this is relatively rare is suggested by the fact that only two records of such heterospecific nests have been recorded in and near Sapporo for more than 10 years (Imamura and Higashi unpubl.).

In order to clarify nest proliferation by budding in *F. yessensis*, the seasonal change of nest abundance throughout the entire annual cycle, including hibernation period, and the way of budding were observed in the present study.

Before going further I wish to express my sincere gratitude to Dr. Shôichi F. Sakagami for his pertinent guidance through the present study, and to Prof. Mayumi Yamada for his reading through the manuscript. Cordial thanks are also due to Messrs. Masao Ito and Shinji Imamura for their useful advices.

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1) Biological and Ecological Studies of a supercolonial ant *Formica yessensis* Forel. VI.

Methods

In late April to early May, 1974, eight quadrats of 10×10 m area (QI～VIII) and two additional ones of 5×5 m (QIX and X) were chosen. All nests in these quadrats were examined irrespective of either inhabited or not and a short pole bearing recognition mark was stood by each nest. Of these nests, those in QI～IV and QIX were used for the study of seasonal change of nest abundance, and the others for the study of nest growth.

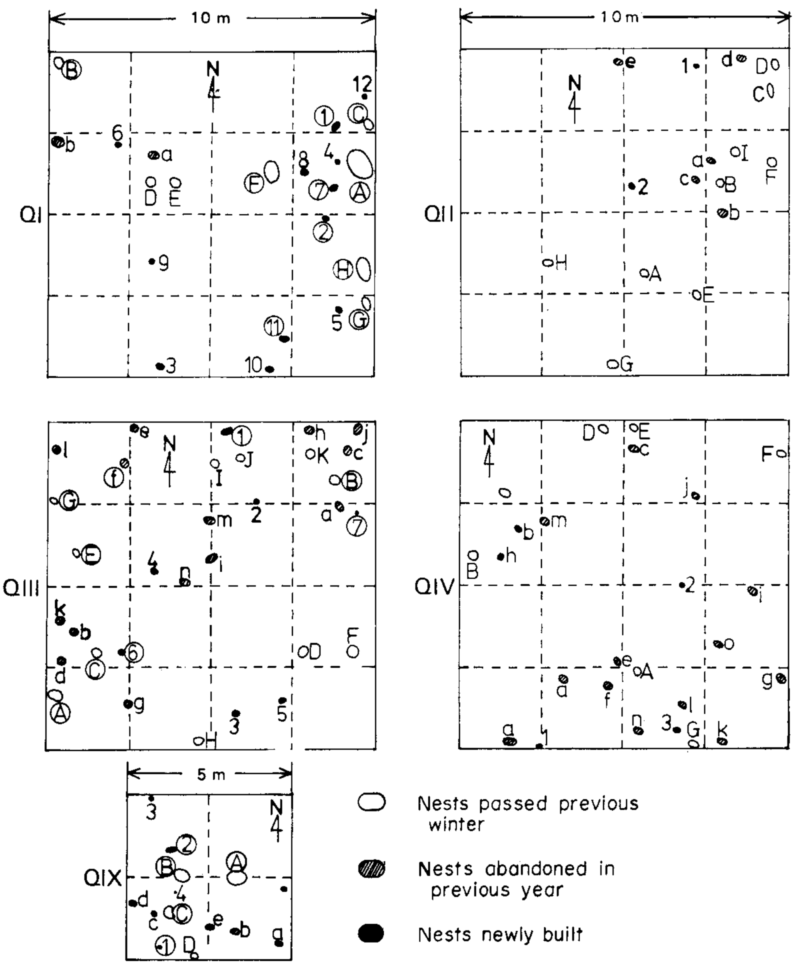


Fig. 1. Quadrats used for the study of seasonal nest abundance. Capitals, nests passed winter 1973～'74. Small letters, nests abandoned in '73 though the structure remained in spring '74. Arabic numerals, nests newly built in '74. Circles enclosing these symbols in QI, QIII, QIX, nests used for winter 1974～'75.

Seasonal change of nest abundance (QI~IV and QIX, Fig. 1)

The activity of each nest was examined by visiting each quadrat 2~5 times a month from early May to mid October (Fig. 2). At any census new nests were looked for and when discovered a pole with recognition mark was stood by. Although a few newly built nests might be overlooked at the first inspection due to their small size, most of them must have been detected at the second inspection.

All nests in QI, QIII and QIX were excavated in hibernation period i.e. mid November to early December when snow covered the shore, to examine the nest structure and the number of hibernation nests. In QI, ants were collected and counted in laboratory. QII and QIV were not excavated but left for further observations in the following year.

Growth of individual nest newly built or reoccupied (QV~VIII and QX).

Each quadrat was repeatedly visited and new nests were marked. Then the nests were excavated at various ages.

The excavation was carried out just after dawn in spring and autumn and in the daylight in summer when the extranidal activities of ant dropped to the minimum either by the coldness or by the hotness. Procedure of excavation is as follows: 1) Nest surface was sketched in detail. 2) Nest surface was divided by parallel lines running 5 cm apart from each other by means of putting short poles outside the nest periphery. 3) Nest was covered with sands to minimize the escape of ants. 4) A pit of about 1 m deep was dug by the nest. 5) Nest was gradually excavated with a small hand shovel starting from the lateral wall of the pit. In the course of excavation nest structure was sketched at every pole.

Measurement of body size and estimation of relative age

Measurement of body size and mandibular wear of workers were carried out as in a previous paper (Higashi 1974). The maximum outerorbital distance was chosen as the index for body size and mandibles were divided into four classes according to wear: I. Intact or nearly so, i.e. completely pointed, II. slightly worn, III. apparently worn and IV. heavily worn.

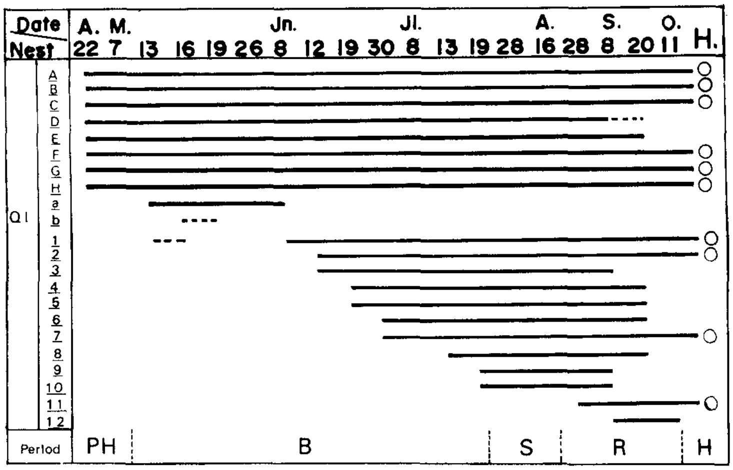
Results

1. *Seasonal changes of nest abundance* (Fig. 3)

From the relative abundance of inhabited nests, the annual life in Ishikari Shore can be divided into five periods: 1) Post-hibernation, 2) budding, 3) stable, 4) retraction (causing abandonment of some nests), 5) hibernation. A few buddings, however, could be seen in the periods 3 and 4, and some cases of nest abandonment in 2 and 3, too.

1.1. *Post-hibernation period, late April to early May*: Number of active nests was 8 nests/QI, 9/QII, 11/QIII, 7/QIV and 4/QIX, 39 in total, all certainly used for hibernation. Some unoccupied nests were also observed: 2 nests/QI, 5/QII, 14/QIII, 15/QI and 5/QIX, 41 in total.

1.2. *Budding period, mid May to mid July*: After the first detection on May 13 (QI–**1**), new nests increased gradually to early June and later more rapidly to mid July. During mid June to mid July 9/QI, 2/QII, 6/QIII, 3/QIV and 5/IX, in total 25 were newly recorded, reaching nearly 83% of all new nests built in



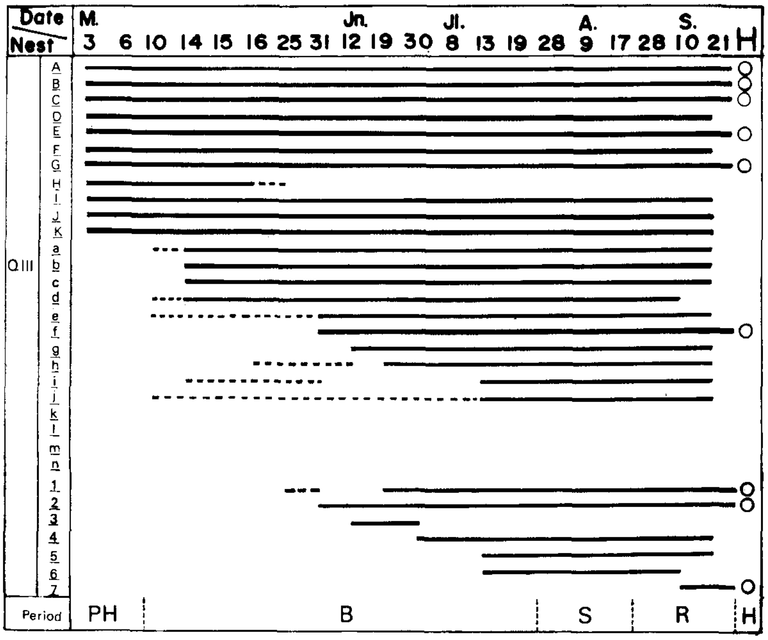
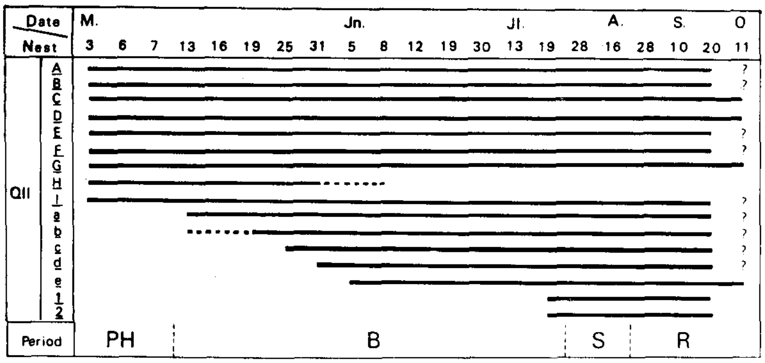
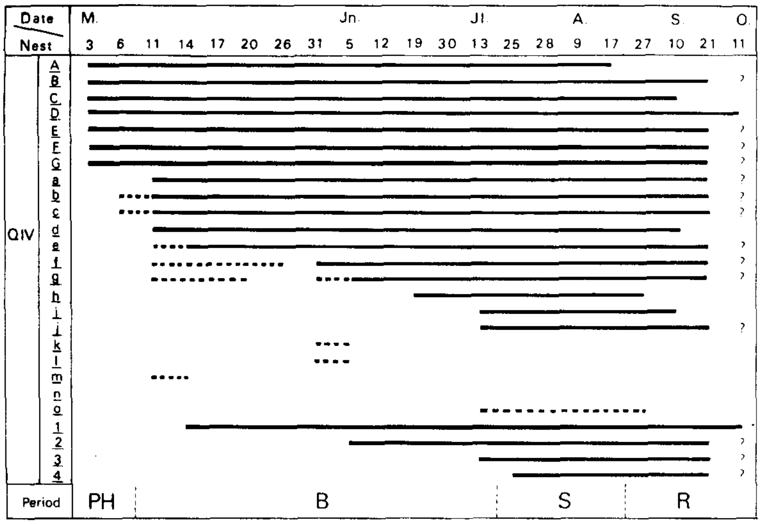
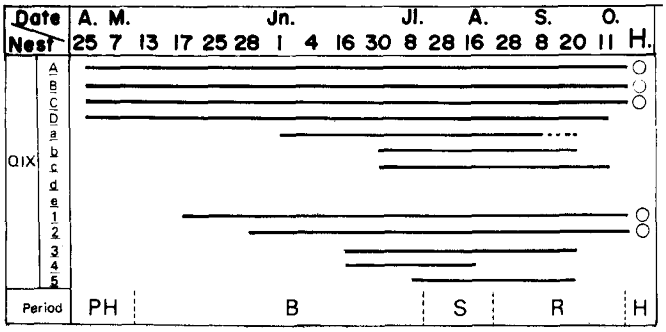


Fig. 2. Activity of each nest. Solid line, active. Broken line, sluggish or inactive. ○, used for hibernation. PH, post-hibernation period; B, budding period; S, stable period; R, retraction period; H, hibernation.


Date
Nest
M. Jn. Jl. A. S. O
3 6 7 13 16 19 25 31 5 8 12 19 30 13 19 28 16 28 10 20 11
QII
A B C D E F G H I a b c d e 1 2
Period
PH B S R


Date
Nest
M. Jn. Jl. A. S. O.
3 6 11 14 17 20 26 31 5 12 19 30 13 25 28 9 17 27 10 21 11
QIV
A B C D E F G a b c d e f g h i j k l m n o 1 2 3 4
Period
PH B S R


Date
Nest
A. M. Jn. Jl. A. S. O.
25 7 13 17 25 28 1 4 16 30 8 28 16 28 8 20 11 H.
QIX
A B C D a b c d e 1 2 3 4 5
Period
PH B S R H

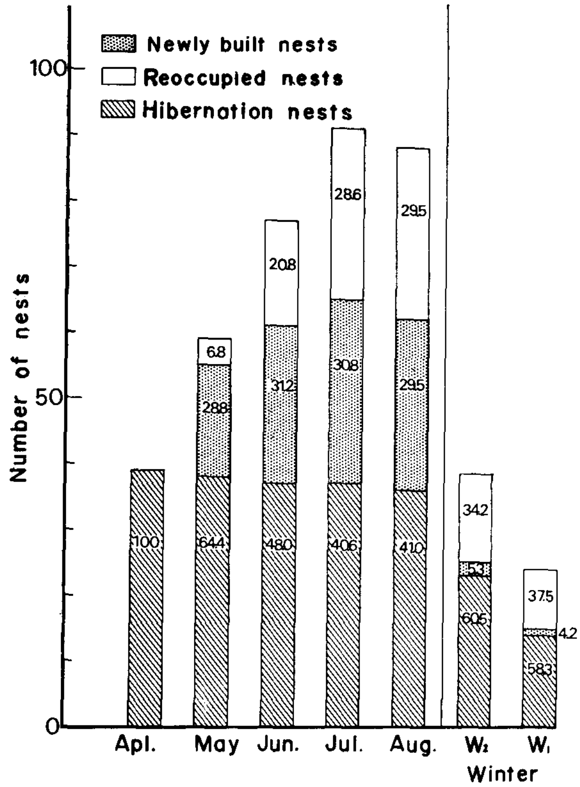


Fig. 3. Seasonal change of number of inhabited nests. Numerals added to each histogram show the percentage occupied by various nest types. W1, actual result in three excavated quadrats (QI, QIII, QIX); W2, estimation based upon the mortality in each type of nests in three excavated quadrats.

1974 (Fig. 4A).

Furthermore, many nests abandoned in the preceding autumn were reoccupied in mid May to mid July. It was difficult to decide the date of reoccupation accurately, because some workers, seemingly hunters, visited even inactive nests. Therefore, the beginning of active nest building was used as the criterion for reoccupation.

Reoccupied nests appeared in mid May and increased first rapidly from May to early June, then gradually until mid July, reaching 29 nests or nearly 71% of 41 nests abandoned in the last year (Fig. 4B). All 12 nests never completely reoccupied were decomposed by rain or wind before mid August.

1.3. *Stable period, mid July to mid August*: In mid summer the number of active nests was nearly stable in each quadrat, being nearly two to three times as many as that in post-hibernation period: 2.3 times/QI, 1.7/QII, 2.3/QIII, 3/QIV and 3/QIX. The percentage of relative abundance in all inhabited nests was respectively 41% (hibernated nests), 31% (reoccupied ones) and 28% (newly built ones).

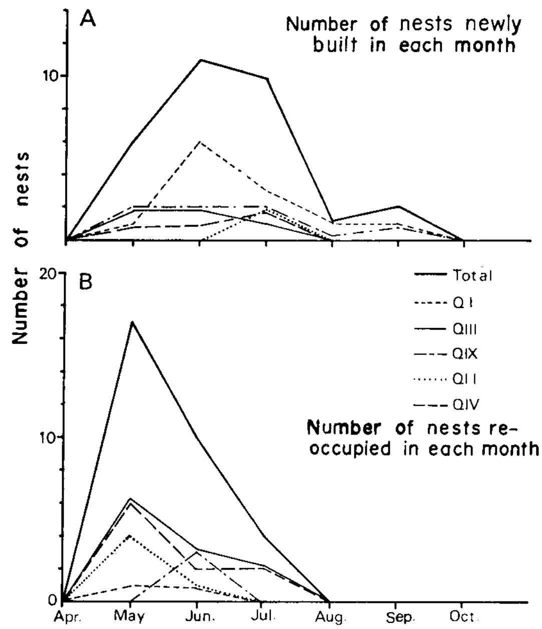


Fig. 4. Number of newly built (A) and reoccupied nests (B) in each month.

1.4.~1.5. *Retraction and hibernation periods*: In September to mid October many active nests were definitely abandoned. But it was difficult to distinguish accurately whether a given nest was really abandoned or not in late September to October, because extranidal activities of inhabited nests were also sluggish at that period and some abandoned nests were visited by hunters and used for bivouacs. Therefore, the nest mortality in this season was studied by excavating three quadrats, QI, III and IX in hibernation period.

Only 10 nests in QI, 9/QIII and 5/QIX were inhabited in winter, so that the nest mortality in autumn reached 50% (10/20), 65% (17/26) and 55% (6/11) respectively. Thus, more than a half of the nests active in summer to early autumn were abandoned in September to October. Interestingly, the number of these hibernating nests was nearly equal to that of the hibernating nests in the last winter, respectively 8 and 10 in QI, 11 and 9 in QIII and 4 and 5 in QIX (Fig. 5). New nests which entered in hibernation involved all those built in May (QI-**1**, QIII-**1**,**2**, QIX-**1**,**2**) and some ones built in June (QI—**2**, **7**) or early autumn (QI–**11**, QIII–**7**) but none of those built in mid summer (Fig. 2). Therefore, the abandonment of some nests used for hibernation in the last winter was compensated mainly by new nests built in spring or early autumn. Only one reoccupied nest (QIII–*f*) was used for hibernation.

Table 1. Relations among nest size, hibernation and nest types in QI, QIII, QIX. X: Number of nests entered in hibernation in 1974~75. Y: Number of nests abandoned during 1974. HN: Post-hibernating nests (passing winter 1973–'74). RN: Nests reoccupied in 1974. NN: Nests newly built in 1974.

Nest size	X				Y			
	HN	RN	NN	Total	HN	RN	NN	Total
~5 cm			1	1			2	2
~10			1	1			4	4
~15			1	1	2	1	3	6
~20	3		2	5	2	2	3	7
~25	3	1	2	6	1	2	1	4
~30	1			1	3	2		5
~35			1	1	1	4		5
~40	3		1	4		1		1
~50	1			1				
~60	2			2				
60~	1			1				
Total	14	1	9	24	9	12	13	34

Relation between nest size and hibernation is shown in Table 1. As an index of nest size, the mean of the longest and shortest axes of nest surface measured in September was adopted. Hibernation nests are generally larger than abandoned nests. Average size of the former was about 30 cm while that of the latter 20 cm. Most nests less than 15 cm were abandoned except for three new ones, one (QIX–1) built in May and two (QI–**11**, QIII–**7**) in early autumn. Of six abandoned nests larger than 30 cm, five were the reoccupied ones. The extent of nest entrance was generally larger in abandoned nests than in hibernation ones, and the mound seemed less developed in the former than in the latter.

While all hibernation nests had one or more shafts of about 1 m deep where most hibernating ants concentrated (Imamura 1974), most abandoned nests possessed shafts (QI-*D*, QIII-*I*, *K*), only 20 to 50 cm deep, seemingly too shallow for effective hibernation. All these shallow shafts were occupied by aggregations of *Porcellio* sp. In QIX–**2** with two shafts, one shaft was not occupied by any animals while the other filled with ants. The inhabited nests were provided with 2~8 hibernating shafts each filled with ants and 85~125 cm, in average 90 cm deep (Appendix I). Most abandoned nests were occupied by *Porcellio*. Even in QI–*A* with ants, some *Porcellio* individuals were discovered at the parts of the nest free from ants.

The numbers of workers and queens in each hibernating nest in QI are given in Appendix I. The number of workers ranged from 1,500 (*1*, *2*) to 17,800 (*A*), in average 5,300. Queens were involved in all nests, the number ranging 3 (1) to 61 (*G*). Even new nests involved some queens, in the maximum 31, together with 6,400 workers (*7*).

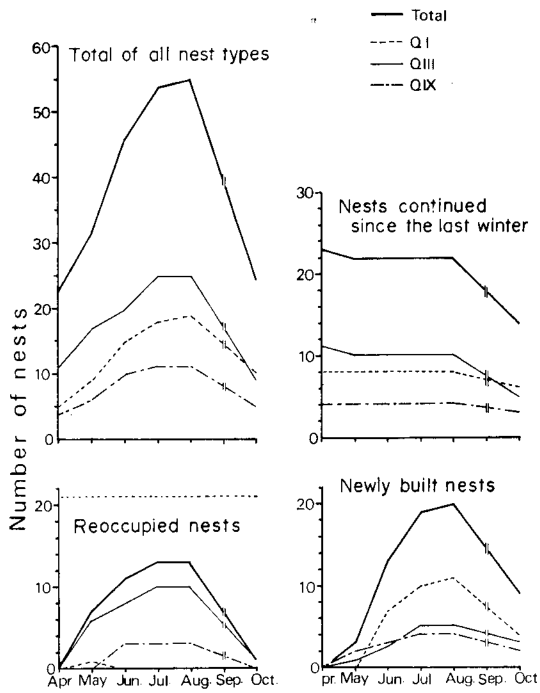


Fig. 5. Seasonal change of number of inhabited nests at the end of each month in three quadrats (QI, QIII, QIX) excavated in winter.

As seen in Fig. 1, hibernation nests were not distributed at random. Some nests clumped at particular areas are apt to be successful in hibernation. In QI, except for *B*, most hibernation nests were found in the eastern part, though some small abandoned nests were involved there. In QIX most hibernation nests were found at the middle. In QIII six out of nine hibernation nests were located in the western part while at the center even large nests such as *i* or *j* were abandoned. This suggests the interventions of some microtopographical conditions and internidal relations for the establishment of successful hibernation nests.

2. Growth and abandonment of nests newly founded by budding

As mentioned in 1.2, two types of budding are recognized, reoccupation of old nests and establishment at new sites. Nests of these two types showed different growth pattern from each other, especially in the early growth stage.

2.1. *Reoccupation of old nest sites* (Appendix II.1)

In post-hibernation period most nests deserted in the last year retained their chambers not decomposed but the long shafts were in decomposition (two exceptions, QV-*a*, *b*, both established side by side in a slope covered with a dense mat of withered *Miscanthus sinensis*). Unless reoccupied such nests gradually decompose. As mentioned in 1.2. all unoccupied nests were completely disintegrated by mid August.

Some nests, excavated when a few workers were carrying out sand particles from the inside, contained 30～100 workers (QV-*b*,*c*,*d*, QVI-*a*,*c*,*f*, QVII-*d*). All reoccupied nests necessarily pass this stage at the start of nest growth.

In nests with 150～300 workers (QX-*a*, QVI-*d*), extranidal building was so intense that small piles of withered grasses or twigs newly gathered, not being the remnant of the last year, were seen on the nest surface. Although it was virtually impossible to distinguish old and newly built parts of subterranean structures, the later expansion is certain, since numerous ants carrying out sand particles from the inside were seen on such nests. For instance, QVI-*e* with 370 workers had a shaft 28 cm deep probably newly dug, because intensive intranidal building was observed. In QVI no nests abandoned in the last year had shafts except for a single one with a short shaft (QVI-*h* with more than 7,000 workers).

Large mounds were seen in some nests with about 500 workers. For instance, the mound of QV-*a* was nearly 3.5 cm high and 15 cm in the maximum diameter, which was similar to that of new nests with the corresponding number of workers. Most reoccupied nests with about 500 workers were similar to the nests newly built or those continued since the last year, except for some large nests with the surface diameter over 30 cm. In such large nests, the old structures sometimes still remained without repairing.

Of the six nests containing 1,000 or more workers at excavation (QV-*e*, QVI-*b*, *h*, QVII-*e*, *f*, QVIII-*a*), two (QV-*e*, QVII-*e*) had shafts deeper than 25 cm. The worker number reached more than 7,000 in QVI-*h*, which was reoccupied in early June and excavated on September 11. This nest had a large mound and a seemingly incipient shaft.

2.2. *Growth of new nests*

Two types of new nests are recognized, those built under wooden boards or clods which have served as temporary shelters for ants, and those built without such shelters.

2.2.1. *Building of exposed new nests* (Appendix II.2)

The relation between worker number and estimated nest age shows no definite trend (Fig. 6). In the most quickly developed nests the number of workers exceeded 1,700 within a week (QVI–10), while some slowly made nests contained only less than 350 workers even two weeks after the first detection (QV–7). The others lie intermediate between these extremes. Even in the nests built in the same season the growth speed was different one another, e.g. QVIII-10 with more than 1,900 workers at nest age 8±4 days while QV–7 less than 350 at 14±2 days, though both were built in mid June. Further, new nests excavated within 10 days after the start are divided into two classes, those with less than 700 workers and those with more than 1,700 (Fig. 6).

The building of a new nest is generally started by a few small to medium sized workers. One instance is cited: About 13:00, May 15, 10 to 15 workers were digging an incipient nest in QVIII (nest surface temperature 23°C). Some medium to large workers wandering near the spot occasionally participated in the digging but soon left there. After 30 minutes, seven workers continuing to dig were captured and the maximum outerorbital distance and degree of mandibular wear were measured. Most of them were fairly small and middle aged (cf. Section 2.3.)

Such incipient or incomplete nests are sometimes detected throughout the active season, especially in May to mid July. But most are soon abandoned and only a few ones develop into complete nests.

Complete nests are divided into four growth stages according to worker number and nest structure (Fig. 7).

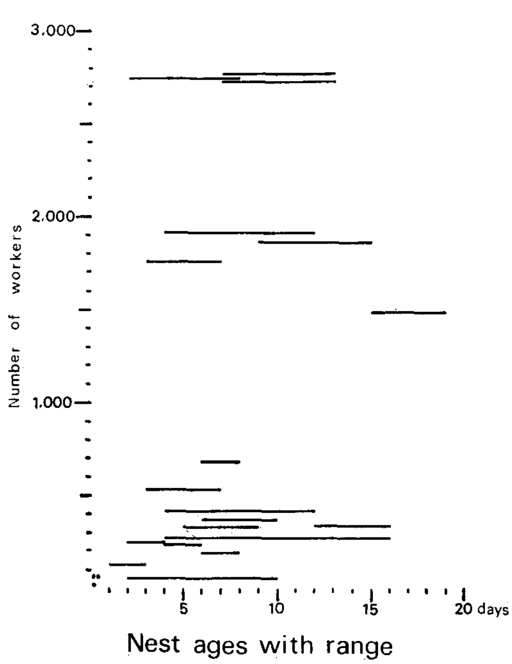


Fig. 6. Relationship between the number of workers and nest age in unprotected newly built nests (given with estimation).

The following terms are adopted. *Burrow*: a shallow vertical hole, about 5 cm deep in the maximum. *Gallery*: a narrow tunnel connecting chambers. *Chamber*: nearly round and flat subterranean cavity mostly concentrated within 10 cm deep. *Shaft*: a vertical burrow starting from chambers downward, reaching 180 cm deep in the maximum at Ishikari (cf. Ito 1973).

Stage I: A burrow with about 100 workers (QV–1, QVII–4, QVIII–1, QX–2). In most nests the burrow is dug along a subterranean stem of eulalia (*Miscanthus sinensis*), sweet brier (*Rosa rugosa*), etc.

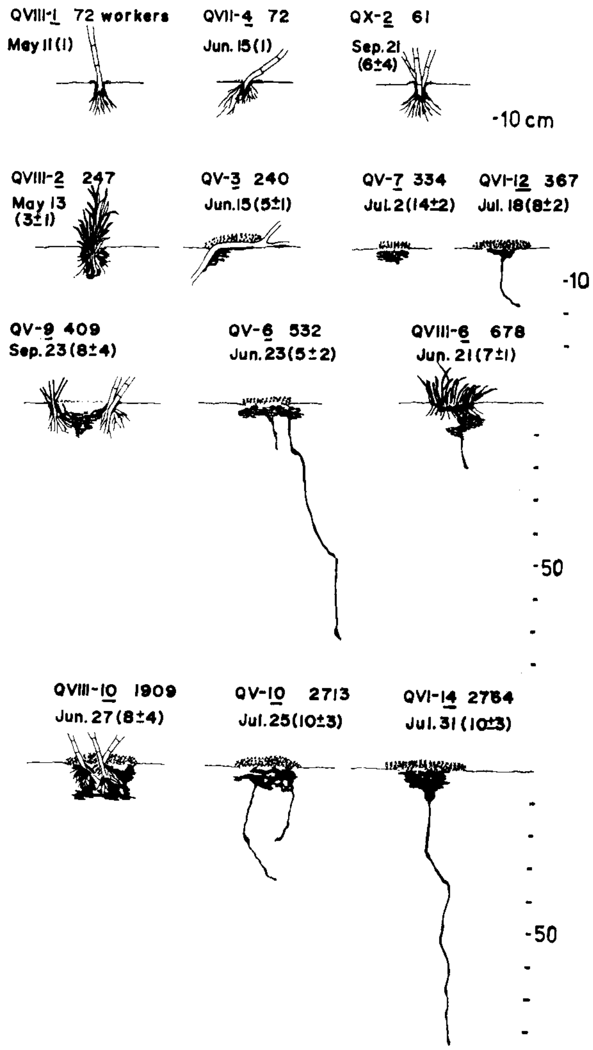


Fig. 7. Nest structures of exposed new nests.

Stage II: With horizontal galleries and 200 to 400 workers (QV-3, 7, QVI-11, 12, QVII-19, QVIII-2, 14). Some nests with mound composed of dead grasses or twigs (QV-3, 7) or with a shallow shaft, resembling Stage III. For instance, QVI-12 with 367 workers had a well developed mound and an incipient shaft reaching nearly 18 cm deep. As a whole the horizontal floor was a little deeper in the nests built in spring or autumn than in summer. Nest size given by the sum of longest and shortest axes divided by 2 was 7 (QVIII-14) to 17 (QV-3) cm. Nests with mound were larger than those without mound.

Stage III: Burrows and galleries making a labyrinth about 10 cm deep, with a developed mound, 400 to 700 workers (QV–6, 9, QVIII–6) and sometimes long shafts. For instance, QV–6 had a long shaft 70 cm deep, and QVIII–6 a shallow one 20 cm deep. Nest size was 13 (QV–6) to 20 cm (QVIII–6).

Stage IV: Galleries were anastomosed and in parts combined to make spherical cavities, 2 or 3 cm in diameter, with a well developed mound mostly 3 to 5 cm high and more than 1,000 workers (QV–10, QVI–9, 10, 14, 16, QVII–1, 21, QVIII–10, 12). Nest size was about 19 (QVI–10) to 33 cm (QVII–1). Three nests had shafts deeper than 25 cm (QV–10, QVI–14, QVII–21).

QVI–14 was started in mid July and excavated on July 31. It had a large mound and a long shaft (83 cm), involving more than 2,700 workers. Although the author could not see intense incoming transports of both adults and immatures, it was built probably by an abrupt immigration from a large hibernation nest (QVI-*D*) nearby, which was accidentally abandoned in late July, because the nest was unwillingly covered with sand by the author in excavating another neighboring nest.

QV-**10** was built in a thicket of eulalia in mid July and excavated on July 25. It had two shafts, 22 cm and 35 cm deep respectively.

QVII-**21** was also built in mid July and excavated on September 10. It had a ramified shaft and more than 4,000 workers.

2.2.2. *Nest building under a shelter* (Appendix II.3)

A few nests were made under wooden boards (QVIII–11, QVII–3). Furthermore, in five quadrats excavated in active seasons (QV ~ VIII and QX), some nests were made under the heap of sand produced from wrecks made by excavation. The growth of such nests was fairly different from that of exposed new nests.

At first many workers gathered under a shelter but digging was inactive. As they were large workers having fairly worn mandibles (cf. Appendix II. 3), most of them may be the hunters using the shelter only as a bivouac. Therefore, the worker number was related with the extent of the shelter.

Vertical burrows appeared in the nests with about 200 workers (QV–8, QVII–3, 9, 11, 13, 15, 18). QVII–13, for instance, had a shallow vertical burrow nearly 4 cm deep with some small to medium sized workers. In the nests with more than 500 workers, vertical burrows were lengthened and horizontal galleries developed. At this stage, many immatures and seemingly young adult workers were present in the subterranean section.

Generally the process of nest building under a shelter was more similar to that in reoccupation of old nest sites than that in exposed new nests.

2.3. *Mean body size and degree of mandibular wear of workers involved* (Appendix II)

The distribution of body size and degree of mandibular wear in workers randomly selected were measured in all 41 nests excavated in 1974: 14 (reoccupied nests), 15 (exposed new nests involving one incipient nest QVIII–3), 7 (sheltered new nests), 3 (nearly or completely abandoned nests) and 2 (post-hibernation nests).

2.3.1. *Mean body size*

In 13 cases containing more than 1,000 workers, the maximum outerorbital distance was measured with 100 workers randomly selected for each nest. In 10 out of 13 large nests body size distribution was statistically not different one another by *t*-test, having mean size about 1.32 mm and *SD* 0.15~0.18 mm. Thus, in most large nests size distribution did not differ among reoccupied nests, exposed new nests and post-hibernation nests.

But three other nests showed differences: 1.25±*SD* 0.161 (QVIII-10), 1.37±0.162 (QVI-8), 1.28±0.161 (QI-7). QVIII-10 was an exposed new nest built in mid June and involved about 1,900 workers when excavated on June 27. It had a large mound as usual in large nests but no shaft. QI-7 was built in late June and used for hibernation, involving 6,400 workers. The reason for the small mean size is unknown. QVI-8 was built under a large clod. Certainly the presence of effective shelters correlated to the larger mean body size.

Although no significant difference in mean body size was obtained among most large nests, a remarkable difference was recognized of mean body size of workers in early stages of nest growth between reoccupied old nests and exposed new nests. Sheltered new nests resembled the former in the mean body size.

In reoccupied and sheltered new nests, most workers were at first medium to large sized. In QVI-*f* with 61 workers, large workers were so numerous that mean size attained 1.42 mm. QVIII-**11** under a board had 48 workers, most of which were so large that the mean size attained 1.47 mm. As workers increased, mean size gradually decreased, approaching that of large nests mentioned above: 1.39 mm in QVI-*d* (223 workers), 1.36 in QVII-*b* (536 workers) and 1.32 in QV-*a* (590 workers). Statistically size distribution in QV-*a* was not different from large nests. From Fig. 8 mean body size in the nests reoccupied and those newly built under shelters seems to reach that in large nests at the stage with 500 to 700 workers, rarely 1,000 workers, except for a few nests such as QVI-8.

On the other hand, exposed new nests involved smaller workers.

In QVIII-3, an incipient nest (cf. Section 2.2.1), all workers were smaller than 1.3 mm with mean size only 1.13 mm. In Stage I mean size attained nearly 1.23 mm but was still smaller than in large nests: In QX-2 with 61 workers. about 24% of all workers were larger than 1.3 mm so that mean size increased to 1.24 mm, larger than in QVIII-3. In Stage II mean size was fairly different among three nests: 1.22 mm (QVIII-14), 1.29 (QVIII-2), 1.31 (QV-3). Thus, in QVIII-14 it was as small as that in Stage I but in QV-3 as large as in large nests. The former was built in September while the latter in June. In Stage III mean size was small in all three nests: 1.23 mm (QV-9), 1.24 (QV-6), 1.26 (QVIII-6). As in Stage II, the nest built in September (QV-9) showed the smallest mean size.

As a whole mean body size in most exposed nests was small until Stage III except for some nests such as QV-3 in which mean size attained that in large nests at stage II. Mean size seems to be smaller in nests built in September than those in other periods.

Fig. 8 shows a tendency of gradual increase of the mean size in accordance with population growth in exposed new nests, while mean size tends to decrease as the population becomes larger in nests reoccupied or newly built under shelters.

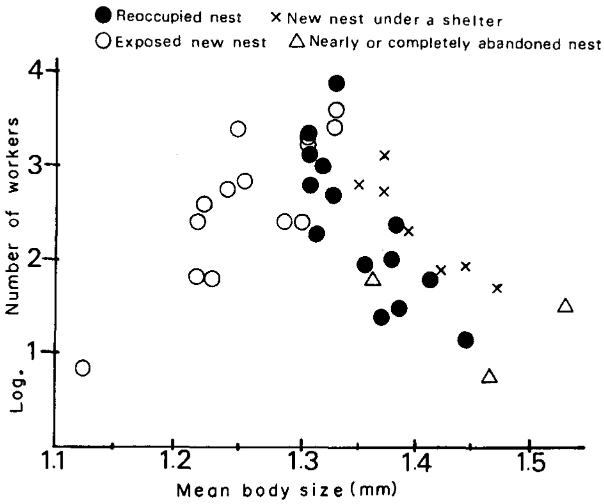


Fig. 8. Relationship between mean body size and number of workers in all types of nests.

In early growth stage, *SD* was small in exposed new nests, while similar to that of large nests in some nests reoccupied or built under shelters. For instance, QX-2 and QVI-*f* had the same number of workers (61 workers) but *SD* was 0.124 and 0.154 respectively. In exposed new nests *SD* reached that of large nests already in Stage II.

2.3.2. *Age structure estimated by mandibular wear*

In large nests with more than 1,000 workers, age structure estimated by mandibular wear is hardly different among the nests after hibernation, reoccupied and newly built if being excavated at same period. For instance, the percentage ratio of each wear class in the nests excavated in early August are 17% (Class I): 25 (II): 25 (III): 33 (IV) in a post-hibernation nest *Hib. B*, 14:31:27:28 in a reoccupied nest QV-*e*, 18:20:22:40 in QVI-16. In other periods, too, this tendency is seen from Fig. 9.

However, age structure is different between hibernation nests and those being active in summer. Some nests were excavated, in early March, 1974, and age structure by mandibular wear in 400 randomly selected workers was examined: 35% (Class I), 49 (II), 15 (III), 1(IV). Similar ratios were obtained in QI-7 excavated in the next hibernation period: 40% (I), 42 (II), 15 (III), 3 (IV). On

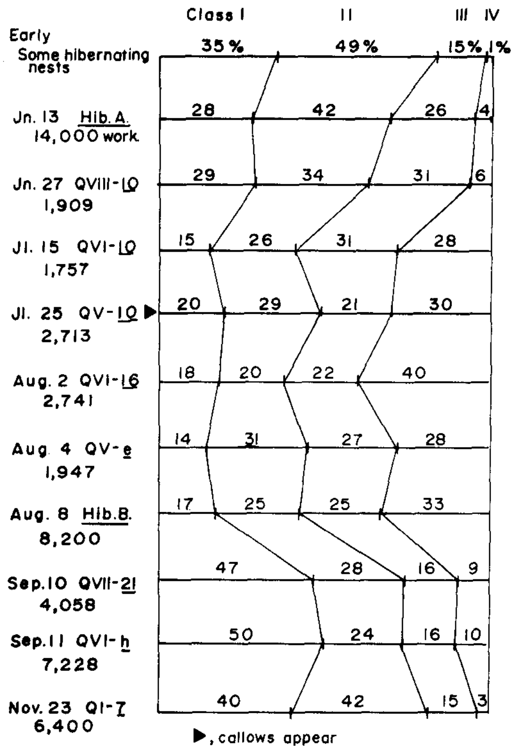


Fig. 9. Seasonal change in age structure estimated by mandibular wear. *Hib. A*, *Hib. B*: post-hibernating nests.

the other hand, the ratio of heavily worn mandibles fairly increase in all nests excavated in summer as *Hib. B*, QV-e or QVI--16 mentioned above. The nests excavated in other periods were intermediate between winter and mid summer nests. In Fig. 9 all nests with more than 1,500 workers are arranged in the order of excavation date. The figure possibly shows the seasonal change of age structure in the supercolony.

The quotient of the weighted mandibulr wear of a particular nest to that of the supercolony in the same season was adopted as an index of relative mean age (A) of the particular nest. Namely, $A \fallingdotseq 1$ means that the mean worker age of the concerned nest is the same to that of the supercolony, $A<1.0$ with more young workers, $1.0<A$ with more old workers. Some nests shown in Fig. 9 were adopted as the representative of the supercolony in each period. For instance, $A=3.71/2.06=1.80$ in QVII-*a* (3.71 and 2.06 are the weighted mandibular wear in QVII-*a* and *Hib. A* respectively. These two nests were excavated in the same period, mid June).

The relation between relative age index and worker number in each young nest is shown in Fig. 10. It is apparent that mean worker age is generally older in earlier stages in all nest types. As a whole, mean age is older in reoccupied nests or sheltered new nests than in exposed new nests. Many hunters with heavily worn mandibles (cf. Higashi 1974) may use the shelters or once abandoned nests only as temporary bivouacs.

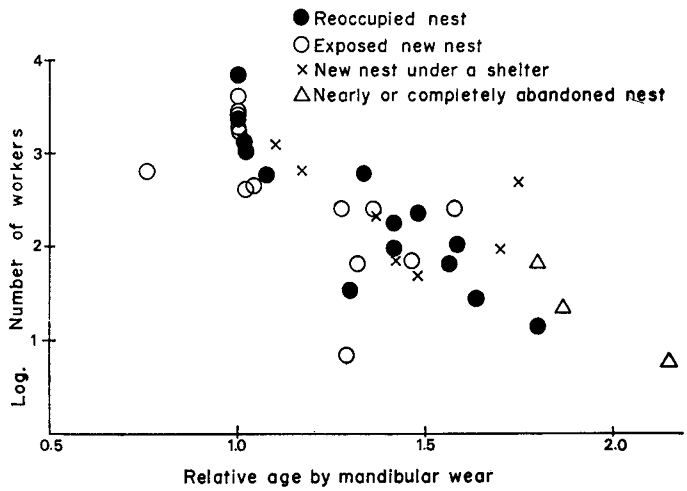


Fig. 10. Relationship between index of relative age and number of workers in all nest types.

In most exposed new nests mean age attained that in mature nests at Stage III, except QVIII–6 which had 678 workers involving numerous young ones for unknown reason. In nests reoccupied or built under shelters, mean age generally attains that in mature nests at stage with about 1,400 workers, later than in exposed nests, presumably because of the presence of many hunters as already mentioned.

2.4. *Appearance of queens and immatures* (Appendix II. 1,2,3)

Immatures are seen from early May to late September: Eggs, early May to early August; larvae, late May to late August; pupae, late June to late September (cf. also Ito 1973). The numbers of queens and immatures in each nest are shown in Appendix II. At nest excavation it was attempted to pick up all immatures as far as possible, though some ones, especially eggs and the youngest larvae mixed with sand might be overlooked.

2.4.1. *Reoccupied nests*

Immatures appeared at early stages of nest growth. Of reoccupied nests QV-*c* with 46 workers contained 13 larvae, though others with less than 100 workers were devoid of immatures. Except for the nests excavated at the beginning of brood production, all nests with more than 200 workers contained immatures. The maximal ratio of immatures to adult workers was about 1.5:1 in QVI-*b* with 977 workers. Queens were not seen in the nests involving less than 500 workers. QVII-*b* with 536 workers had five queens, QV-*a* with 590 workers two queens. But even in the nests with more than 1,000 workers, queens were often absent (QVIII-*a*, QVII-*f*). The maximal ratio of queens to adult workers was 1:122 in QVI-*b*.

2.4.2. *Sheltered new nests*

QVI–6 with 72 workers contained two larvae. The larvae were present in most nests with more than 100 workers. The ratio of immatures to adult workers reached 1.5:1 in QVI–7 with 599 workers. Queens were not seen in nests with less than 1,000 workers. Only QVI–8 with about 1,400 workers had nine queens.

2.4.3. *Exposed new nests*

In the course of growth in exposed new nests, immatures appeared as early as in nests reoccupied or built under shelters. QVII–4 with 72 workers contained two young larvae. Except for the nests excavated before mid June or after mid September when immatures were very scarce, they were seen in all nests with more than 100 workers. Generally the ratio of immatures to adult workers was larger than in the two nest types mentioned in 2.4.1. and 2.4.2.: 1.7: 1 (QVI–12 with 367 workers), 1.8:1 (QVI–9 with 1,482), 1.8: 1 (QV–10 with 2,713). On the other hand, queens were not seen in nests with less than 300 workers. They first appeared in QVI–12 with 367 workers and a shaft 18 cm deep but were often absent even in larger nests as in nests reoccupied or built under shelters. Queens were found in seven out of nine nests with more than 1,000 workers, in the maximum 18 in QVII–21. The ratio of queens to adult workers reached 1:165 in QVI–9.

2.5. *Role of intense transport of nest mates*

Transports of queens, immatures and adult workers by large workers were often observed throughout active season. Furthermore, intense transports were sometimes seen, especially in May to July. For instance, many immatures, adult workers and queens were carried from QIX-*A* to QIX–5 at 15:45 to 17:30 on July 14 (20.4°C on QIX-*A* at 16:45). QIX-5 had been detected on July 8. Since transports had never been seen before 15:30, it must have suddenly begun between 15:30 and 15:45, followed by intense transport for about one hour, until the cessation around 17:30. As the result 9/queens, 264 adult workers, 369 pupae, 87 larvae and 73 lumps of eggs were transported into QIX–5 (Table 2). Since a lump of eggs involves about 10 eggs, about 730 eggs might be carried in. It was certain that intense transports contributed to the abrupt development of QIX–5.

2.6. *Nest abandonment in autumn* (Appendix II. 2,3)

Of the nests excavated in September, QVI–19, QVIII–13, QVII–24 and QVII–23 were nearly abandoned and QVI–18, QVII–22 and QX–1 were completely

Table 2. Number of individuals transported from QIX-*A* to 5 during 15:45 to 17:30, July 14. Eggs are given by number of lumps with estimated number of eggs in brackets (20.4°C on *A* at 16:45).

Time	15:45~16:45~17:30		Total
Queens	4	5	9
Adult workers	186	78	264
Pupae	283	86	369
Larvae	68	19	87
Eggs	48 (480)	25 (250)	73 (730)
Total	589(1021)	213 (438)	802(1459)

abandoned. All workers involved in the last three nests must have been hunters using these nests as bivouac sites, because they were large and had heavily worn mandibles (Fig. 8, 10). Some workers in the former nests (QVI–19, QVIII–13, QVII–24 and QVII–23) might be hunters, but others might be the remainders before emigration, because some workers had intact or nearly unworn mandibles (cf. Higashi 1974). No queens or immatures were seen in these nests. No shaft was seen and most of the chambers were small, though it was unknown whether shafts had been decomposed after abandonment or never been dug from the beginning of nest establishment.

Discussion

Seasonal change of the abundance of inhabited nests

In *Formica ulkei* Emery, 8 to 14% of all nests were newly built in each year by budding, which exclusively occurred in late April to early June (Scherba 1958). In other mound building ants such as *F. exsectoides* (Andrews 1926), too, the ratio of nests built by budding is comparable to the case in *F. ulkei.* In *F. yessensis,* however, budding is so frequent that the number of inhabited nests in summer doubled or more, compared with that soon after hibernation as shown in Section 1 (cf. also Ito and Imamura 1974). Further, budding in *F. yessensis* is sometimes seen even in mid summer to early autumn, though mostly performed in spring to early summer. These differences may be partly due to the difference in nest structure between *F. yessensis* and the other species cited. Large nests with a well developed mound of *F. ulkei* would not be built so easily as small nests with less developed mounds in *F. yessensis.*

Reoccupied nests occupy more than 30% of all inhabited summer nests in *F. yessensis* while reoccupation is relatively rare in *F. opaciventris* (Scherba 1961) and *F. ulkei* (Scherba 1958). Most reoccupied nests in *F. yessensis* are abandoned in autumn (cf. also Ito 1973), even though some ones are quite large (cf. Table 1). Therefore, large nests are not necessarily used for hibernation.

Seasonal change of the abundance of inhabited nests have rarely been reported in *F. rufa*-group. But Klimetzek (1972) clarified that some species of *F. rufa*-group showed comparatively high mortality of nests during three years (from 1966 to '69) as following: 73% (119 abandoned nests in 1969/163 nests active in 1966) in *F. rufa* L., 45.3% (24/53) in *F. polyctena* Först., 53.3% (16/30) in *F. pratensis* Retz., 58.3% (7/12) in *F. lugubris* Zett, 100% (2/2) in *F. truncorum*, 64.6% (168/260) in total. This means that mean nest mortality per year in *F. rufa*-group is nearly 20% (64.6%/3 years), being fairly high compared with the figure 5 to 10% in *F. ulkei* (Scherba 1958). In *F. yessensis*, too, the nest mortality in autumn is fairly high. In newly built nests the mortality was about 63%.

These facts suggest the abandonment of many new nests within the year. Of the nests continued since the last winter, 25 to 55% are abandoned before the coming winter, so that even hibernated nests may last only 2 to 4 years without any temporary abandonment. The life span of nest in *F. yessensis* in Ishikari Shore is thus extremely short compared with the longevity of the nest of large mound building ant such as *F. exsectoides* (30 years, Andrews 1926) or *F. ulkei* (20 to 25 years, Dreyer 1942). Althoug large nests more than 1 m in nest diameter, 2 m in the maximum, are sometimes seen in *F. yessensis* in Ishikari Shore, these seem to be built as a result of fusion of two or more adjacent nests or partial translocation from the original nest site which has become inadequate to live (Ito 1973).

The number of nests passed the winter 1974–'75 was nearly equal to that in the last winter, suggesting a stability in number of hibernated nests in Ishikari Shore in spite of intense budding and nest abandonment performed each year. Summarizing, *F. yessensis* is characterized by the rapid turnover of nests.

Nest growth

In the present study it was confirmed that budding was mainly initiated by middle to old aged workers. In exposed new nests the initiators were significantly smaller than in nests reoccupied or newly founded under shelters. Most larger workers in the latter would be hunters, using the nests only as bivouac sites. These results are consistent with the size-age-task correlation in worker polyethism (Higashi 1974) in which it was shown that aged workers tend to perform extranidal activities, except for some fairly specialized aphid visitors. As to the size-task correlation, hunting is achieved by large workers while digging by small to medium ones though correlations are fairly plastic.

Although the releasing mechanism of budding and reoccupation of old nest sites has not been clarified, it seems suggestive to the problem that activities of a few smaller workers induce the performance of the same activity by others, resulting in incipient nest growth as in QVIII–3 (cf. Section 2.2.1), even though those atractees (larger workers) may soon abandon the work. Chen (1937 b) experimentally showed in *Camponotus japonicus* var. *aterrimus* Emery that some workers led others into nest building and the leaders were smaller than the followers in most cases. Such relationship might exist also in *F. yessensis*.

As these exposed new nests grow, the young workers seemingly adapted to intranidal activities (Higashi 1974) increase gradually. Although it was not clear whether they were mostly transported from large post-hibernation nests or immigrated into the nest by themselves, intense transports as mentioned in Section 2.5 seemed to be rare before the nest attained the level of 500 to 700 workers, because a leap in worker number did not happen before that level (Fig. 6). After attaining the level of 500 to 700 workers, many workers, mostly young ones, may be carried into new nests rather abruptly from post-hibernation nests, since a leap of worker number was seen between that stage and the stage with more than 1,500 workers. But intense transports in younger nests may sometimes occur. For instance, QVIII–6 (cf. Section 2.3.2) with small age index may have been developed by intense transports of many young workers at Stage II. Although the releasing mechanism of such intense transport is unknown, repeated transports by a limited number of active transporters are possibly responsible for rapid population increase (Higashi unpubl.).

In nests reoccupied or newly built under shelters, too, intense transports and abrupt development of nests were often seen, especially in May to June. But mean worker age in these nests is generally older than that in exposed nests. This may mean that many hunters are yet using these old nests only as bivouacs until the nests are filled with a sufficient number of household workers as in exposed nests.

Immatures were observed to be transported even into the nests with about 50 workers except for nearly abandoned nests. It means that immatures do not necessarily require a developed mound and chambers, provided with enough nursers and suitable environmental factors such as temperature and humidity.

In ant species practicing solitary nest foundation, the post-mating queens are nearly always discovered in nests except for very old orphan nests the queens of which had died. In polydomous species proliferating through budding, queens are not obligatory members of a nest. Ito (1973) reported that 12 out of 53 excavated nests of *F. yessensis* had no queens even in a nest containing about 13,000 workers. He also showed in other nests that the number of queens per nest was erratic, ranging from 1 to 213. In some other species in *F. rufa*-group, too, (*F. polyctena* Foerster, Gösswald 1951; *F. rufa* L., Gösswald 1951, Lange 1956) the queen number is unstable. In the present study no queens were found in nests with less than 300 workers (cf. also Ito 1973), which was presumably the minimum number of workers required to have the queens.

Ito and Imamura (1974) mentioned the fertile nests of *F. yessensis* containing sexual pupae occupied only 6.4% of all nests, which were usually provided with larger mounds than those without sexuals. Furthermore, they presumed that most new nests do not produce sexuals. In the present study, no sexual pupae or alates were found in new nests or even in some post-hibernating nests in late July. This favors the assumption mentioned, though further examination of new nests, especially large ones in July, are necessary to solve the problem.

Nest abandonment and hibernation

In laboratory colonies of *F.* (*Raptiformica*) *sanguinea* Latreille (Dobrzanska 1959), a few callows leave the nest only one or two days after emergence. But as to *F.* (*F.*) *polyctena* Förster (cited as *F. rufa rufo-pratensis minor*), Otto (1958) mentioned that date of the departure from the nest was different among individuals in laboratory but generallly 40 days after emergence so that the callows emerged after late August could not go out of their nests within the year. In *F. yessensis*, however, the callows in the abandoned nests must emigrate by themselves, because the transports were rare in autumn. Emigration may be gradual through the retraction period, as no intense drifting into hibernation nests was observed.

Many nests abandoned in autumn were occupied by *Porcellio* for hibernation, except a few nests seemingly abandoned in early to mid October. In such nests, the individual number of *Porcellio* in each nest was less in the nests abandoned later (Appendix I). These facts suggest that *Porcellio* invades in the sites for hibernation so earlier than nest abandonment by ants that the nests abandoned later are rarely occupied by them. *Porcellio* were sometimes found even in the nest used for hibernation by ants at ant free parts (QI–*A*). Therefore, *Porcellio* may hardly affect nest abandonment by ants, merely using ant free nests or their parts. Ants seem to be nearly indifferent to *Porcellio,* because co-existence of ants and some *Porcellio* without any attack by ants to living *Porcellio* was sometimes seen even in excavating the summer nests by the author. Some ants carrying dead *Porcellio* were occasionally observed but attack on living *Porcellio* has never been seen during three year survey in Ishikari Shore. Further observations are necessary to understand the relation between these two arthropods.

Although the types of nests used for hibernation are yet not definitely clarified, some related observations are enumerated:

1. No new nest built in July was used for hibernation, nevertheless three nests possessed long shafts enough for hibernation (QV–10, QVI–14, QVII–21). Since Ito (1973) observed some new nests built in July and used for hibernation, some of the three nests mentioned might be used for hibernation if not be excavated. From the present study, however, it is likely that some new nests may be abandoned in autumn, even provided with long shafts.

2. Most nests reoccupied in spring to summer were never used for hibernation, even though nest diameter was as large as that of hibernation nests (Table 1), and some of them contained a large number of workers, about 7,200 in the maximum (QVI-*h*), or had long shafts (QV-*e*), QVII-*e*). Ito (1973) also showed that most reoccupied nests were abandoned in autumn. Therefore, some reoccupied nests may be abandoned, even with long shafts.

3. In some new nests, shafts were already seen a few days after the first detection: about 5 days in QV–6, 10 days in QV–10 and QVI–14. Shafts may be dug within a few days also in autumn, if necessary.

4. Most shafts free from ants were occupied by *Porcellio.* Probably among

the shafts free from ants only those occupied by *Porcellio* were maintained while others decomposed mainly by rains and snow thawing. Only one exception was found: QIX–2 had two shafts, one being vacant, while the other used by ants for hibernation. The vacant shaft seemed to be abandoned by ants after completion of hibernation by *Porcellio.*

5. Most nests abandoned after successful hibernation had no shaft. Even in inhabited nests, shafts were generally shorter in summer nests than in winter nests. Therefore, shafts may be decomposed rapidly if unused.

6. Some clumps of nests were wholly abandoned, while other clumps were used for hibernation (Fig. 1).

7. Diameter of nest entrance was generally larger in abandoned nests than in hibernated ones. Mounds seemed less developed in deserted nests than in hibernated nests.

Ito (1973) and Imamura (1974) stressed the presence of shaft as a condition necessary for hibernation. In the present study, too, well mature nests with long shafts were predominantly used for hibernation. The presence of shafts may be a necessary, but not sufficient condition for hibernation, as some nests were abandoned in spite of possessing long shafts. Further, long shafts were made not

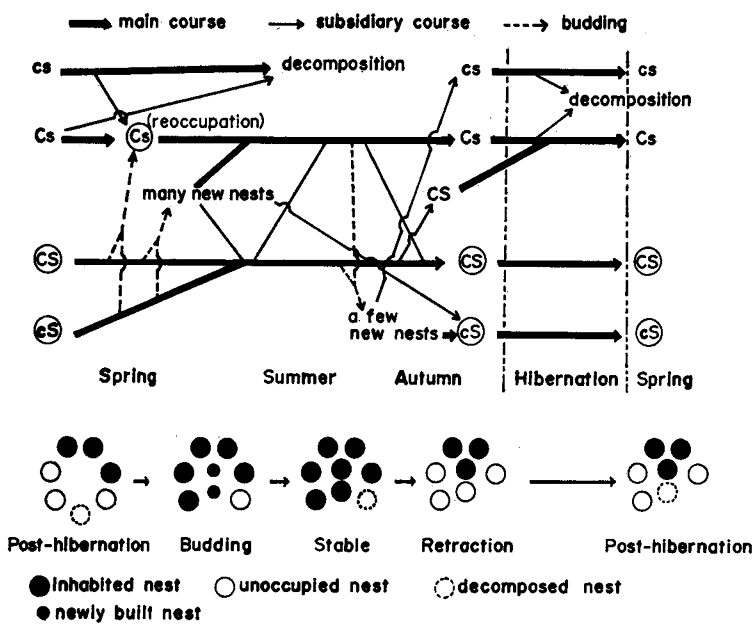


Fig. 11 Presumed change of nest types and nest abundance in the annual course. A: change of nest types. Encircled nest types inhabited and those not encircled are unoccupied. The explanations about the symbols of nest type are given in text. B: the approximate ratio between inhabited and unoccupied nests in each period.

only for hibernation but also in spring to summer, if necessary, and easily decomposed if unused.

Fig. 11 shows the presumable annual change of nest types schematically, according to the degree of development in chamber and shaft, which complements the schemes by Ito (1973) and Imamura (1947). Each nest type is defined as follows: CS: nest with large chambers and one or more long shafts. Cs: large chambers and no long shaft. cS: small chamber and long shaft. cs: small chamber and no long shaft.

Most post-hibernating cS soon change to CS in spring to early summer with some exceptions such as QIII-*H*, which was abandoned in spring. While many CS maintain long shafts until autumn and most of them are used for hibernation, some ones lose shafts in summer. Some Cs changed from CS may again have long shfats in autumn and be used for hibernation. About 39% of these posthibernating nests are abandoned by late autumn.

About 67% of Cs abandoned in the last autumn are reoccupied in spring to early summer. Most of reoccupied nests are inhabited until autumn, then abandoned except only a fraction, such as QIII-*f*, used for hibernation. Some Cs change to CS in summer. All unreoccupied Cs are completely decomposed by mid August. While some cs are reoccupied and change to Cs, others are decomposed earlier.

Some new nests built in spring to early summer change to Cs while others change to CS, with some exceptions, e.g. QIX-1 which was built in spring and used for hibernation though the surface diameter was less than 15 cm. New nests built in autumn tend to be used for hibernation. Most abandoned smaller nests seem to be decomposed, especially in snow thawing period, because the number of cs is less in spring than in autumn.

The author assumes heat conservation in nests as a more essential factor for hibernation than the occurrence of shaft. If heat conservation is unfavorable, even the ants in mature nests with long shafts may gradualy emigrate to other nests in the warm daytime in autumn. This assumption is supported by the facts that the diameter of nest entrance is generally larger and mound is more scanty in abandoned nests than in hibernated nests. The fact that new nests used for hibernation were built in cooler season, spring or autumn, also supports the assumption. The nests established in cooler season may be built at warmer sites to which even callows may easily be lead by thermotaxis. The fact that some particular clumps involved more hibernated nests than the others (Section 1.5.) favors this assumption.

However, it must be mentioned that some results obtained in Ishikari Shore may be fairly different from the life of *F. yessensis* in other environments such as forest edges or rocky mountains. The nests are so easily dug and decomposed in the sandy ground in Ishikari Shore that mean nest age may be generally shorter than nests dug in humus or rocky ground, where nests are probably difficult to build while not easily be decomposed. To obtain the whole picture of the life mode of *F. yessensis*, some comparative observations in other environment are required.

Estimation of life span in adult workers

In laboratory colonies ant workers of many species are said to live for more than a year (2 years in *Myrmica laevinodis*, Brian 1951, more than one year in *Aphaenogaster rudis*, Fielde 1904 b, etc.). But their mean life span in natural fields may be different from that in laboratory.

In the present study, seasonal change of worker composition according to body size distribution and degree of mandibular wear was clarified in large nests. Worker composition was nearly same among most types of nests. Fig. 9 probably shows seasonal change of worker age structure in the supercolony. Intact (Class I) and slightly worn (Class II) mandibles occupy only about 40% of all workers in mid July just before the appearance of callows, while more than 80% in the last winter. If the classes with intact or slightly worn mandibles decreased subsequently with similar rates, Classes I and II may change to III or partly IV by mid October except for some workers presumably specialized for aphid milking (cf. Higashi 1974). Therefore, the author assumes that most wintering workers with intact or slightly worn mandibles, occupying about 80%, are yearlings and only about 20% with apparently or heavily worn mandibles are older workers, probably emerged in the later phase of the last year.

According to Ito (1973), the ratio of immatures to adult workers reached 1.7∼4.2:1 in large nests involving about 2,000 or more workers in mid July. In the present study, the ratio reached about 1.5∼1.8:1 in large nests of all types. Even if egg mortality is fairly high, the number of pupae and larvae exceeded that of adult workers. This suggests that *F. yessensis* probably produces a vast number of callows exceeding the number of old workers every year. From these facts, life span of most workers probably does not exceed one year and only about 20% of the workers survive more than one year.

Summary

Budding pattern, nest proliferation and hibernation in *Formica (Formica) yessensis* Forel were studied in Ishikari Shore near Sapporo. The main results are:

1) Two types of budding are seen, new building and reoccupation of abandoned nests. 2). Budding is frequent in spring to early summer. In mid summer, the ratios of post-hibernation nests, reoccupied nests and new nests to all inhabited nests were 40.6, 30.8 and 28.6%, respectively. 3). Nest abandonment is especially frequent in autumn. The mortality of nests inhabited in summer reaches 36% in nests continued since the last year, 92% in reoccupied nests and 65% in new nests. 4). All new nests used for hibernation were built in spring or early autumn but not in summer. 5). Number of hibernating nests seems nearly stable from year to year. 6). Reoccupation of abandoned nests and building of

new nests under shelters are started mainly by old and large workers. On the other hand, new nests at exposed sites are started mainly by middle to old aged and small ones. 7). No definite correlation is found between the number of workers involved and estimated nest age. 8). Immatures first appear in the growth stage with ca. 50 adult workers. 9). Queens are never seen before the growth stage with ca. 300 workers and often absent even in large nests. 10). Intense immigration accelerated by transports seems to occur at the growth stage with ca. 500 to 700 workers, when nest had well developed nest structure. 11). Shafts are necessary for hibernation, but some nests having shafts in summer to autumn were abandoned before hibernation. Hibernation may be successful mainly in nests with sufficient heat conservation. 12). Mean life span of workers is estimated to be less than one year in most individuals, only 20% surviving to the next year under natural conditions.

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Appendix I.

Nests excavated in mid November to early December in QI. I: Date on which new nest was first detected (new nests) or building was first seen (reoccupied nests). II: Date on which nest abandonment was confirmed b.h., just before hibernation. III: Date of nest excavation. IV: Longest and shortest axes of the nest surface. V: Development of mound. ++, large; +, small. VI: Maximum depth of the chamber. VII: Depth of each shaft (lines connecting some numerals mean ramification of same shaft). VIII: Number of queens. IX: Number of workers. X: Amount of *Porcellio*. ++, plenty; +, scarce; –, absent.

Nest	I	II	III	IV	V	VI	VII	VIII	IX	X
B	—	—	Nov. 12	25×24	++	12	110 125 120	29	7400	–
b	—	—	13	20×18	–	-	-	-	-	++
6	Jun. 30	Sept. 20	13	7×6	+	7	-	-	-	++
a	May 13	Jun. 8	13	22×16	+	10	-	-	-	++
D	—	Sept. 8	15	28×24	++	10	25	-	-	++
E	—	Sept. 20	15	17×13	+	10	-	-	-	+
9	Jul. 19	Sept. 8	15	5×5	+	8	-	-	-	++
F	—	—	18	24×20	++	10	90-75	8	5700	–
8	Jul. 13	b.h.	19	15×13	+	5	-	-	-	–
1	May 13	—	19	25×16	++	11	94-90-70	3	1500	–
C	—	—	20	27×25	++	15	100 76 64-60	10	3100	–
12	Sept. 8	b.h.	20	10×8	+	7	-	-	-	–
A	—	—	22	120×90	++	15	125-70 100/85/80 120 120 90	51	17800	+
4	Jun. 19	b.h.	23	10×8	+	7	-	-	-	–
7	Jun. 30	—	23	32×30	++	10	95-75 80 50	31	6400	–
2	Jun. 12	—	23	20×20	++	8	110-35	13	1500	–
5	Jun. 19	Sept. 20	24	25×24	++	8	-	-	-	+
H	—	—	24	60×50	++	11	115 100 80	25	3700	–
G	—	—	Dec. 4	40×35	++	10	80 65 45	61	2600	–
11	Aug. 28	—	4	15×15	+	10	60-55 80	13	3100	–
10	Jul. 19	Sept. 8	5	15×15	++	10	-	-	-	++
3	Jun. 12	Sept. 8	5	19×16	++	10	-	-	-	++

Appendix II.

Newly built or reoccupied nests excavated during active season for the study of nest growth. II.1: reoccupied nests, II.2: newly built nests without any shelters (including hibernating nest QI-*7* and an incipient nest QVIII-*3*), II.3: nests newly built under the shelters e.g. boards or clods. Age in reoccupied nests was estimated according to the date of the start of nest building. D: date of excavation. A: estimated age in days. Columns IV~VII, cf. Appendix I. XI: mean body size with *SD*. XII: relative mean age index (cf. Section 2.3.2.). Two post-hibernating nests, *Hib. A* and *Hib. B*, were added to II.3.

II.1

Nest	D (A)	Workers	Queens	Pupae	Larvae	Eggs	Total
QVI-*a*	May 14(2±1)	101	-	-	-	-	101
QX-*a*	15(3±1)	179	-	-	-	-	179
QVIII-*a*	Jun. 7(10±2)	1283	-	-	-	-	1283
QV-*a*	14(12±2)	590	2	-	9	63	664
QVII-*a*	16(-)	14	-	-	-	-	14
QVII-*b*	16(6±3)	536	5	-	-	35	576
QVI-*b*	19(17±2)	977	8	-	83	1343	2411
QVI-*c*	21(15±2)	32	-	-	-	-	32
QV-*b*	21(24±3)	91	-	-	-	-	91
QVII-*c*	21(13±3)	444	-	-	4	-	448
QVII-*d*	21(13±3)	88	-	-	-	-	88
QVI-*d*	25(2±1)	223	-	1	4	-	228
QVI-*e*	26(18±3)	370	-	-	87	-	457
QVI-*f*	26(5±2)	61	-	-	-	-	61
QVI-*c*	Jul. 4(20±1)	46	-	-	13	-	59
QV-*d*	5(22±5)	44	-	-	-	-	44
QVII-*e*	14(27±1)	1207	8	85	206	508	2014
QVI-*g*	19(-)	27	-	-	-	-	27
QV-*e*	Aug. 4(68±2)	1947	10	4	238	131	2330
QVII-*f*	Sept. 8(92±3)	1234	-	5	-	-	1239
QVI-*h*	11(100±2)	7228	2	203	-	-	7433

Nest	IV	V	VI	VII	XI	XII
QVI-*a*	35×30	−	9	-	1.37±0.129	1.58
QX-*a*	15×15	−	10	-	1.36±0.141	1.41
QVIII-*a*	43×35	+	15	-	1.31±0.165	1.01
QV-*a*	25×18	+	14	60	1.32±0.156	1.07
QVII-*a*	9×7	−	6	-	1.45±0.134	1.80
QVII-*b*	15×8	++	7	-	1.36±0.143	1.34
QVI-*b*	50×30	−	10	-	-	-
QVI-*c*	17×8	−	4	-	1.37±0.159	1.64
QV-*b*	15×10	−	6	55	-	-
QVII-*c*	33×10	−	6	-	-	-
QVII-*d*	5×2	−	6	-	1.35±0.162	1.41
QVI-*d*	17×9	+	10	-	1.39±0.106	1.48
QVI-*e*	22×20	+	5	28	-	-
QVI-*f*	5×4	−	5	-	1.42±0.154	1.57
QV-*c*	6×5	−	7	-	-	-
QV-*d*	5×5	−	8	30	-	-
QVII-*e*	22×10	++	8	26	1.34±0.155	1.03
QVI-*g*	21×13	−	4	-	1.37±0.124	1.30
QV-*e*	20×15	++	11	38	1.32±0.156	1.00
QVII-*f*	25×18	+	15	-	-	-
QVI-*h*	46×27	+	12	22	1.33±0.161	1.00

II.2

Nest	D (A)	Workers	Queens	Pupae	Larvae	Eggs	Total
QVIII-*1*	May 11(2±1)	72	-	-	-	-	72
QVIII-*2*	13(3±1)	247	-	-	-	-	247
QVIII-*3*	15(-)	7	-	-	-	-	7
QVIII-*4*	16(1)	15	-	-	-	-	15
QV-*1*	19(2±1)	106	-	-	-	-	106
QVII-*4*	Jun. 15(2±1)	72	-	-	2	-	74
QV-*3*	15(5±1)	240	-	-	-	-	240
QVII-*6*	16(1)	18	-	-	-	-	18
QVIII-*6*	21(7±1)	678	-	-	209	247	1134
QV-*6*	23(5±2)	532	-	-	121	230	883
QVIII-*10*	27(8±4)	1909	2	-	51	43	1969
QV-*7*	Jul. 2(14±2)	334	-	41	62	122	559
QVI-*10*	15(5±2)	1757	3	650	148	363	2921
QVI-*11*	17(7±2)	314	-	57	2	-	373
QVI-*13*	17(2±1)	129	-	49	-	-	178
QVII-*19*	18(7±1)	192	-	1	-	56	249
QVI-*12*	18(8±2)	367	1	66	62	492	988
QV-*10*	25(10±3)	2713	5	9	2517	2483	7727
QVI-*9*	27(17±2)	1482	9	609	1085	984	4169
QVI-*14*	31(10±3)	2764	12	276	1128	706	4886
QVI-*16*	Aug. 2(5±3)	2741	1	2767	460	44	6013
QVIII-*12*	17(12±3)	1860	-	13	22	-	1895
QVIII-*13*	Sept. 8(27±4)	22	-	-	-	-	22
QVII-*21*	10(53±6)	4058	18	142	-	-	4218
QVII-*22*	10(43±2)	5	-	-	-	-	5
QVII-*24*	10(28±3)	60	-	-	-	-	60
QVIII-*14*	13(10±6)	273	-	-	-	-	273
QX-*1*	14(61±3)	6	-	-	-	-	6
QVII-*1*	18(108±2)	2353	-	28	-	-	2381
QVII-*23*	19(37±3)	34	-	-	-	-	34
QX-*2*	21(6±4)	61	-	-	-	-	61
QV-*9*	23(8±4)	409	-	-	-	-	409

Nest	IV	V	VI	VII	XI	XII
QVIII-*1*	3×3	–	5	-	1.22±0.123	1.46
QVIII-*2*	10×10	–	9	-	1.29±0.160	1.28
QVIII-*3*	-	–	-	-	1.13±0.074	1.29
QVIII-*4*	2×1	–	2	-	-	-
QV-*1*	3×3	–	5	-	-	-
QVII-*4*	3×3	–	4	-	-	-
QV-*3*	20×15	++	7	-	1.31±0.152	1.58
QVII-*6*	2×2	–	2	-	-	-
QVIII-*6*	25×15	–	10	20	1.26±0.171	0.76
QV-*6*	15×10	++	5	70, 13	1.24±0.144	1.04
QVIII-*10*	18×10	++	11	-	1.25±0.161	1.00
QV-*7*	10×10	+	5	-	-	-
QVI-*10*	20×18	++	10	-	1.31±0.151	1.00
QVI-*11*	10×10	+	5	-	-	-

QVI-*13*	17×16	+	4	-	-	-
QVII-*19*	15×15	+	5	-	-	-
QVI-*12*	19×13	++	4	18	-	-
QV-*10*	20×15	++	8	35, 22	1.31±0.161	1.00
QVI-*2*	25×17	++	7	-	-	-
QVI-*14*	25×10	++	7	83	-	-
QVI-*16*	30×18	++	11	-	1.33±0.171	1.00
QVIII-*12*	25×20	++	8	-	-	-
QVIII-*13*	25×20	–	3	-	-	-
QVII-*21*	35×26	++	8	46-35	1.33±0.149	1.00
QVII-*22*	10×10	+	4	-	-	-
QVII-*24*	5×5	–	10	-	1.36±0.147	1.80
QVIII-*14*	9×5	–	10	-	1.22±0.161	1.38
QX-*1*	13×5	–	5	-	1.46±0.123	2.14
QVII-*1*	38×27	+	9	-	-	-
QVII-*23*	10×5	+	4	-	1.38±0.137	1.86
QX-*2*	4×3	–	5	-	1.24±0.124	1.84
QV-*9*	25×10	–	10	-	1.23±0.127	1.02
QI-*7*	Shown in Appendix I.				1.28±0.161	1.00

II.3

Nest	D (A)	Workers	Queens	Pupae	Larvae	Eggs	XI	XII
QVIII-*7*	Jun. 23(2±1)	82	-	-	-	-	-	-
QVII-*7*	25(4±2)	100	-	-	-	-	-	-
QVII-*8*	25(4±2)	92	-	-	-	-	1.44±0.114	1.70
QVI-*2*	25(4±2)	512	-	-	16	-	1.37±0.131	1.55
QVII-*3*	Jul. 2(33±2)	298	-	-	2	-	-	-
QVII-*9*	2(11±2)	219	-	1	1	-	-	-
QV-*8*	4(8±2)	211	-	-	-	-	-	-
QVIII-*11*	8(2±1)	48	-	-	-	-	1.47±0.156	1.48
QVII-*10*	8(13±1)	18	-	-	-	-	-	-
QVII-*13*	8(2±1)	209	-	-	-	-	1.39±0.144	1.38
QVII-*17*	8(2±1)	85	-	-	-	-	1.42±0.123	1.42
QVI-*4*	8(8±1)	560	-	130	57	-	-	-
QVI-*6*	8(2±1)	72	-	-	2	-	-	-
QVI-*8*	9(3±1)	1372	9	260	162	897	1.37±0.162	1.10
QVII-*15*	9(3±1)	179	-	7	-	-	-	-
QVII-*12*	11(14±1)	73	-	-	-	-	-	-
QVII-*16*	11(5±1)	68	-	-	-	-	-	-
QVII-*18*	11(3±1)	298	-	2	23	-	-	-
QVI-*7*	Sept. 11(5±1)	599	-	101	231	556	1.35±0.153	1.17
QVII-*11*	14(17±1)	169	-	-	-	-	-	-
QVII-*14*	14(8±1)	38	-	-	-	-	-	-
QVI-*17*	13(29±3)	428	-	29	-	-	-	-
QVI-*19*	13(21±3)	24	-	-	-	-	-	-
QVI-*18*	13(39±3)	9	-	-	-	-	-	-
Hib. A.	-	14000	-	-	-	-	1.32±0.178	1.00
Hib. B.	-	8200	-	-	-	-	1.31±0.150	1.00