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| Author(s) | ITO, Masao |
| Citation | 北海道大學理學部紀要, 19(1), 270-293 |
| Issue Date | 1973-10 |
| Doc URL | https://hdl.handle.net/2115/27561 |
| Type | departmental bulletin paper |
| File Information | 19(1)_P270-293.pdf |

# Seasonal Population Trends and Nest Structure in a Polydomous Ant, *Formica* (*Formica*) *yessensis* Forel[1)]

By

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(*With 10 Text-figures and 2 Tables*)

Up to the present numerous studies have been published, mainly in Europe and North America, on the bionomics and ecology of the red wood ants or the subgenus *Formica* Linné, dealing with various aspects such as nest structure (Talbot 1963), nuptial flight (Talbot 1959, 1963), adult transport (Kneitz 1964), food habits (Ayre 1959), interspecific competition (Yasuno 1965), etc. However, our knowledge on this subgenus is mainly based upon the studies executed with only a few well known species, in particular *F. polyctena* Först. and *rufa* L. For the better understanding of the bionomics of this group, being important both from scientific and practical points of view for its peculiar mode of life (Gösswald 1951), further comparative studies with other, so far relatively ignored species are required.

Following the first report on the nest distribution (Ito 1971), this second paper deals with annual population trends and nest structure of *Formica yessensis* Forel, mainly observed at Ishikari Shore openland, the environmental conditions of which were described in the first report. The results presented below are still incomplete in many aspects but I believe they are useful to give a preliminary perspective on the bionomics of the species under local climate and to stimulate further analyses as well as comparative studies. In the present paper, the scientific names of other forms cited for comparison are those adopted by the original authors. The subsequent changes of names were conveniently ignored except for *F. polyctena* Förster, (frequently cited as *F. rufa rufopratensis minor* in previous papers).

Before going further, the annual cycle of *F. yessensis* is briefly sketched, together with the phenology of habitat. The littoral openland in Ishikari Shore is covered with thick snow from December to March, which starts to thaw in March and disappears in April. The plant growth is drastic in early to late June. The plant cover flourishes from July to early September, then decays in mid September

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1) Biological and Ecological Studies of *Formica yessensis* Forel. II.

*Jour. Fac. Sci. Hokkaido Univ. Ser. VI, Zool. 19 (1), 1973.*

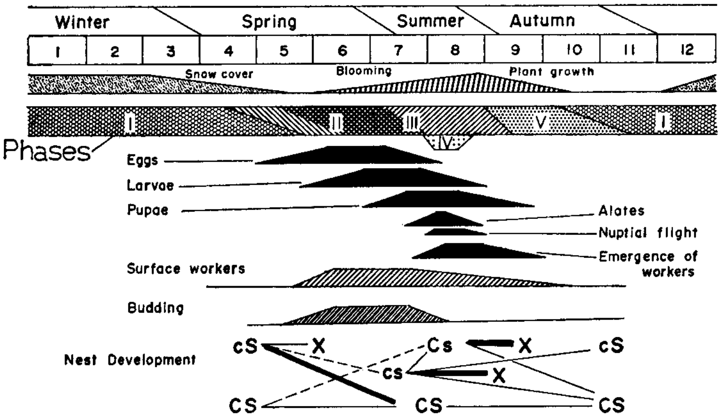

Fig. 1. Annual cycle of colony activities and development of nest structure with some environmental phenology in *F. yessensis* in Ishikari. Phases in annual cycle are as follow: I. Hibernating, II. Expansion, III. Breeding, IV. Mating (in a limited number of nests), V. Prehibernating phases. Duration given for each stage and caste means the existence in the colony, except for new workers showing the emergence. In nest development, the mark "x" means the nest abandoned, and the connecting line represents the developmental order, ascertained (thick solid line), probable (fine solid line) and doubtful case (broken line).

to October leaving a desolate winter scene in November, until covered with snow.

In correspondence to such environmental phenology, the annual cycle of *F. yessensis* proceeds as follows: Extranidal activities by post-hibernating workers begin in mid April just after thawing, though still at a low level. The fullscale activity starts approximately at late May, when the honey dew secreted by aphids on weeds and the oak, *Quercus dentata,* becomes available. The budding, the colony proliferation characteristic to this and other polydomous species, is practiced generally from May to July. The mound size as an index of high colony activities increases in some nests in June or July. New sexuals, produced in a limited number of nests, emerge in late July to early August and leave nest out for nuptial flights in early August. New workers emerge slightly after than sexuals, from early August to mid September. Extranidal activites abruptly drop in mid September to early October and virtually cease in November. The seasonal trends described above are summerized in Fig. 1.

## 1. Population trends

The population census of red wood ants at colony level involves some difficulties due to their peculier mode of life. At first the term *nest* is used here for each isolate subterranean domicile consisting of chambers and shafts, with or without a developed mound. These isolate domiciles or nests often stand closely nearby and interconnected by the drifting of inhabitants, forming a polydomous system developed in some ant groups (cf. Wilson 1971, Ch. 4), but rather exceptional in other social insects or even in most animals. Due to this peculiarity, the individuals sampled in a given nest are not necessarily those produced there. An extreme skepticism may conclude that the meaninglessness of population census in such open system with frequent member changes. In the present paper, however, the ants found in each nest are tentatively regarded as the proper inhabitants, for otherwise we cannot have a basis for further analysis.

Secondly, the census is obstacled by the subterranean nest system, often quite complicate and deep, enormous population size, and aggressive disposition of workers which gives a serious nuisance at excavation by biting and acid secretion. Consequently most previous papers dealing with this problem present the results either on the basis of only a few nests, or on crude estimation by sight. Thanks to the sandy soil in Ishikari Shore, being easy to excavate, I could examine in 1969 ~ 1971, 68 nests including 8 completely abandoned ones, and censused 53 of them with the procedures as follows:

1) Prior to the excavation, nest diameter, mound size and amount of decayed plant cover were recorded for each nest. The nest diameter was measured as follows: The outermost nest peripheries were determined by signs such as heaps of mound materials or brood chambers immediately below the ground surface, etc. The long and short nest axses were measured according to these peripheries and two figures were evened and adopted as the diameter. 2) Surface workers rushing out of nest were collected by repeatedly padding the nest surface until their virtual disappearance. They, given in Appendix I in parentheses, were preserved in 70% alcohol solution separately from those taken from nest inside for size comparison, though the result is not described in the present paper. 3) A pit was excavated at a nest side, about 30 cm apart from the nearest nest periphery, down to about 1.0 ~ 1.5 m. The exposed soil profile was carefully broken down little by little with a hand shovel, and nest structure, chambers and shafts, was sketched and measured. 4) In parallel with observations of nest structure, all inhabitants were successively collected and preserved in 70% alcohol for further stage and caste sorting in laboratory.

The crude results are presented in Appendix I at the end of the paper. As outside workers were collected only on the nest surface the actual number of adults belonging to each nest, at least at the time of excavation, would be higher than that given in the table, by ignoring those apart from nests for foraging or exploration, except for nests sampled in early May and late September or later, when extranidal activities were hardly observed. As no particular studies on oviposition rate and stage-specific mortalities were carried out, the results can not still be used for the analysis of population dynamics. Here some population statistics are preliminarily described and briefly discussed in reference to the results in related species.

**1.1.** *Number of adult inhabitants*: The number of adults was quite variable among nests, both in queens and workers. Except 12 orphan cases out of 53, the number of dealate queens ranged from 1 to 213, with the mean 24 and s.d. 44.6. As to workers, excluding four nests with less than 100 workers, which were regarded as virtually abandoned or just started, the number in 49 nests ranged from 260 to 51,000, with the mean 6,800 and s.d. 9,500. The result proves the polygyny in

Table 1. Population size in some species of the subgenus *Formica*.

| Species | Number of queens/nest | Authority | Number of workers/nest | Authority |
|---|---|---|---|---|
| *polyctena* Förster | ~5,000<br>~3,000 | Gösswald (1951)<br>Lange (1956) | 500,000~1,000,000 (maximum) | Gösswlad ('51) |
| *rufa* Linné | 1, partly polygyny | Lange (1958) | 100,000 (maximum) | Gösswald ('51) |
| *rufa rufopratensis major* Gösswald | ~ 100<br>~ 50 | Gösswald ('51)<br>Lange ('56) | intermediate between *rufa* and *polyctena* | Gösswald ('51) |
| *lugubris* Zetterstedt | polygyny | Lange ('58) | | |
| *nigricans* Emery (*pratensis* Retz.) | polygyny | Lange ('58) | | |
| *truncorum* Fabricius | 1? | Lange ('58) | 8,000~10,000 (maximum) | Stitz (1939) |
| *subnitens* Creighton | | | 20,118 in a average sized nest | Ayre (1957) |
| *yessensis* Forel | ~ 213,<br>24 (mean) | | 51,000 (maximum)<br>6,800 (mean) | Ito, in the present. |

this species, as shown in Table 1, approximately at the level comparable to *F. rufa rufopratensis major* with about 50 (Lange 1956) or 100 queens (Gösswald 1951) in the maximum, and possibly also to *F. nigricans* (=*pratensis*) and *F. lugbris*, while not so as in *F. polyctena* which has, in the maximum, 3,000 (Lange op. cit.) or 5,000 queens (Gösswald op. cit.). On the other hand, the number of workers per nest appears rather comparable to that in the monogynous species, *F. rufa* or *F. truncorum*, and also to an American species of *rufa* group, *F. subnitens*, though only one nest was examined in the species (the number of queens unknown), whereas apparently inferior to *F. polyctena* and probably to *F. r. r. major* (cf. Table 1). Therefore, nests of *F. yessensis* are assumed to be characterized by the relatively low worker population compared with the high number of queens.

**1.2.** *Queen worker ratio*: The queen worker ratio is 982 : 335,000 in total or 1: 340 (0.003), that is, about a half of, or less than in *F. polyctena*, in which the ratio is estimated at about 1: 100 ~200 from the data by Gösswald in Table 1. If the oviposition rate and life-span of queens in *F. polyctena* are equal to those in *F. yessensis*, 5,000 queens in *F. polyctena* must produce, in average, ca. 1,700,000 (=335,000×5,000/982), much higher than the maximum population reported. (Table 1). This suggests either higher oviposition rate or longer span of reproductive period in queens of *F. yessensis* than in *F. polyctena.*

The queen worker ratio in each nest is shown in Fig. 2. The lower number of workers per queen are relatively frequent in spring and autumn than in summer. A few extremely low number (that is, high queen ratio) obtained in spring, May and June, may be a condition just before nest proliferation (cf. Section **2.5.**). In

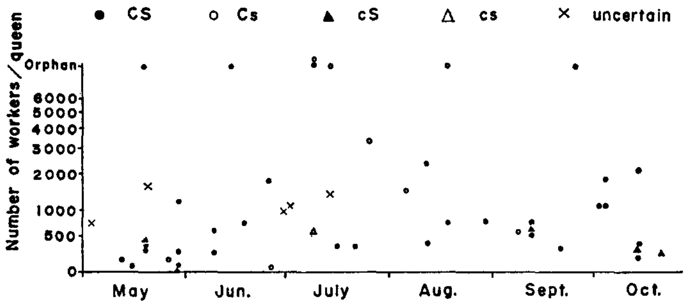

Fig. 2. Number of workers per queen in each nest examined in different seasons. Nests are shown by different symbols according to nest type (cf. 2.2.).

other cases, the result is still difficult to explain.

The number of sexuals per fertile nest, which was roughly 7% of total nests (Ito, unpub.), is in the maximum a few hundreds from the crude estimation by sight made at observation of nuptial flight or partial excavation of fertile nests in the course of nest census made on July 23~26 (cf. 2.1.). Even an accurately censused nest contained only 352 pupal sexuals as follows:

| Nest No. | dealate queen | alate queen | workers | sexual pupae | worker pupae | larvae | eggs | Total |
|---|---|---|---|---|---|---|---|---|
| 710726 | 2 | 1 | 6,700 | 352 | 2,700 | 2,000 | 550 | 5,300 |
| | | | 55% | 3% | 22% | 16% | 5% | |

**1.3.** *Immature stages*: The seasonal change of stage composition in each nest is shown in Fig. 3, giving the outline of annual breeding cycle.

*Eggs* (Fig. 3, A): Eggs rarely appear in early May, but mostly in late May. In June eggs are observed in every nest sampled, keeping a high level in percentage ratio. In July the ratio becomes lower and eggs disappear in some nests. In later months, they were not observed except in one case (early August, Nest 700806-a), suggesting the cessation of oviposition in late July. The precedence of eggs producing sexuals to those becoming workers known in some species, e.g. *F. polyctena* (Gösswald op. cit.) or *F. subnitens* (Ayre 1957), was not directly observed, but the earliest eggs observed on May 3 in Nest 690503 might be sexuals. The maximum number of eggs was obtained on June 9 in 1971 (Nest 710609), as follows:

| queens | workers | eggs | Total |
|---|---|---|---|
| 213 | 51,000 | 19,000 | 70,000 |
| | 73% | 27% | |

The maximum percentage ratio of eggs was obtained on May 29 in 1970 (Nest 700529), as follows:

| queens | workers | eggs | Total |
|---|---|---|---|
| 41 | 3,200 | 7,000 | 10,200 |
| | 31% | 69% | |

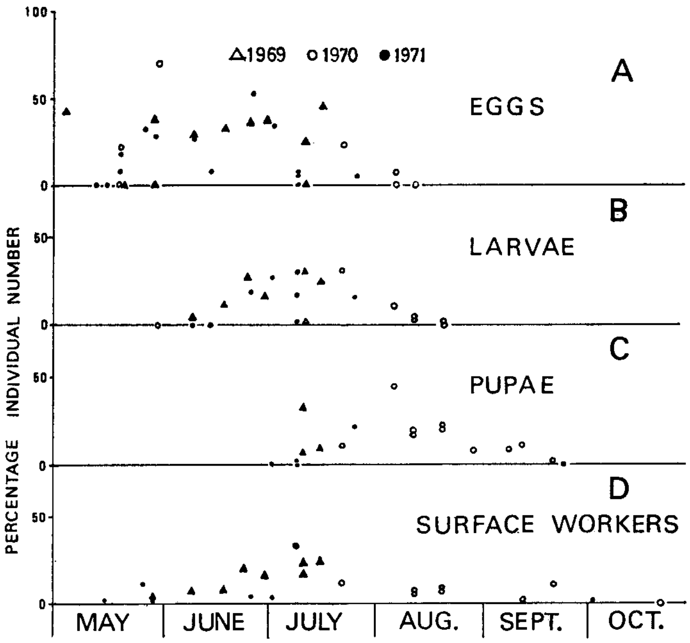

Fig. 3. Seasonal change of immatures and aggressive workers at nest surface, given by the percentage ratios to total nest inhabitants (in A~C) or to total workers (in D).

*Larvae* (Fig. 3, B): Larvae appear in June and are collected usually till late August. As an exceptional case, a larva was sampled in mid September (Nest 700912-d). The larvae are most abundant in mid June to mid July. The maximum number of larvae was obtained on July 2 in 1971 (Nest 710702):

| queens | workers | pupae | larvae | eggs | Total |
|---|---|---|---|---|---|
| 11 | 12,000 | 160 | 8,000 | 10,000 | 30,000 |
|  | 38% | 1% | 27% | 34% |  |

The maximum percentage ratio was obtained on July 22 in 1970 (Nest 700722):

| queens | workers | pupae | larvae | eggs | Total |
|---|---|---|---|---|---|
| 9 | 3,400 | 1,000 | 3,000 | 2,200 | 9,600 |
|  | 35% | 10% | 31% | 23% |  |

*Pupae* (Fig. 3, C): Pupae appear in early to mid July and usually remain till September, with the peak in early August. The maximum number of worker pupae was obtained on July 26 in 1971 as cited above (Nest 710726), and the maximum percentage ratio on Aug. 6 in 1970 (Nest 700806-a):

| queen | workers | pupae | larvae | eggs | Total |
|---|---|---|---|---|---|
| 1 | 1,600 | 1,600 | 380 | 300 | 3,900 |
|  | 41% | 41% | 10% | 8% |  |

Compared with the results in the European and New World relatives, the annual breeding cycle of *F. yessensis* in Ishikari Shore is characterized by the short span, apparently caused by the prolonged severe winter.

Aggressive workers rushing out at interference to nests occupy 0 to 33% of total worker population, showing a higher level in June and July (Fig. 3, D). Probably the proportion of such worker varies in relation to the breeding cycle, increasing in the season with numerous larvae in nests. Another instance of a high percentage was noticed in a small nest excavated on July 9 in 1971 (Nest 710709-a). This nest was apparently soon after the establishment so that must have extraordinarily numerous aggressive workers and few immatures. Caste and stage composition in the nest was as follows:

| queen | inside workers | outside workers | larvae | Total |
|---|---|---|---|---|
| 1 | 420 | 210 | 8 | 640 |
| | 67% | 33% | 1% | |

## 2. Nest structure

As mentioned in the previous section, nest structure was described and measured in many nests synchronously with population census. The crude data are presented in Appendix II at the end of the paper. A complete nest consists of three basic components: epigaeic mound, subterranean brood section and vertical shafts.

**2.1.** *Surface features and mound*: Nests are mostly made under the root-systems of weeds such as eulalia, *Miscanthus sinensis*, being predominant in the shore (Ito op. cit.). *F. yessensis* does not require cores such as decayed stumps for nest establishment as in *F. polyctena*, *F. rufa* and *F. truncorum* (Dlusskii 1967). The nest surface is characterized by the scarcity or absence of vegetation as well as accumulation of mound materials. The former is probably brought by the following three causes: 1) Plant buds are injured and removed as food by ants especially in spring. 2) Surface is covered with mound stuff gathered from the outside and margined by sand carried away from the nest. 3) Constant elaboration of soil in and around root systems inhibit the growth of plants. This exposed surface appearance is indistinct in young nests, gradually becoming conspicuous in accord with nest development, accompanied with the formation of a marginal sand grains demarcating the nest (Fig. 4, A, h). In older nests, the nest area slightly sinks into the ground (Fig. 4, A and B), probably caused by incessant mining activities by workers. Although the mound is characteristic to the species, it does not develop well in this open shore habitat, being moundless nests not rare. This may be explained in part because of the poverty of building materials and some local climatic conditions which may decrease mound building activity, and in part because this species is not a typical mound builder as *F.*

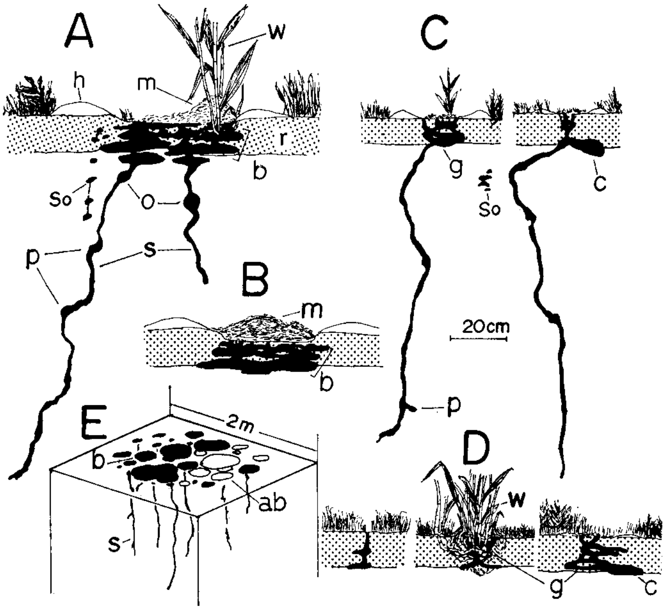

Fig. 4. Schematical presentation of nest structures of various nest types: A, All season nest (CS type). B, Summer nest (Cs). C, Winter nest (cS). D, Incipient or bivouac nest. ab, abandoned brood section. b, brood section. c, small brood chamber. g, looped or nestwork galleries. h, sand grains heaped and margining nesting area. m, mound. o, oval chamber. p, small chamber or partial enlargement of shaft. r, surficial zone with many fine root systems. s, vertical shaft. So: nest of *Solenopsis japonica.* w, weed. E, an instance of a compound nest (cf. **2.5**).

*polyctena* and allied species (Gösswald op. cit.), judging from the irregular shape of mounds often provided with a depression at the center unless supported by some cores. The mound consists of diverse finely broken vegetable matters such as decayed stalks, blades and hulls, mainly of eulalia, decayed leaves and twigs of sweet brier, *Rosa rugosa.* and oak, etc., all predominant in the area (Ito op. cit.). The inner structure of mound is complicated and easily broken so that I could not distinguish any fixed structure other than labyrinthine chamber and gallery system.

Previously the nest distribution in the shore was studied (Ito op. cit.). In the same census made on Sept. 24 ~Oct. 6, 1970, the relation between mound development and nest size as well as the ratio and size of abandoned nests were also recorded (Fig. 5, D). The census was repeated in 1971 three times, once to record both mound development and nest abandonment and twice to record the latter item alone (Fig. 5, A ~C). The results obtained are enumerated: 1) Well developed mounds are frequent in medium sized to large nests in the census made

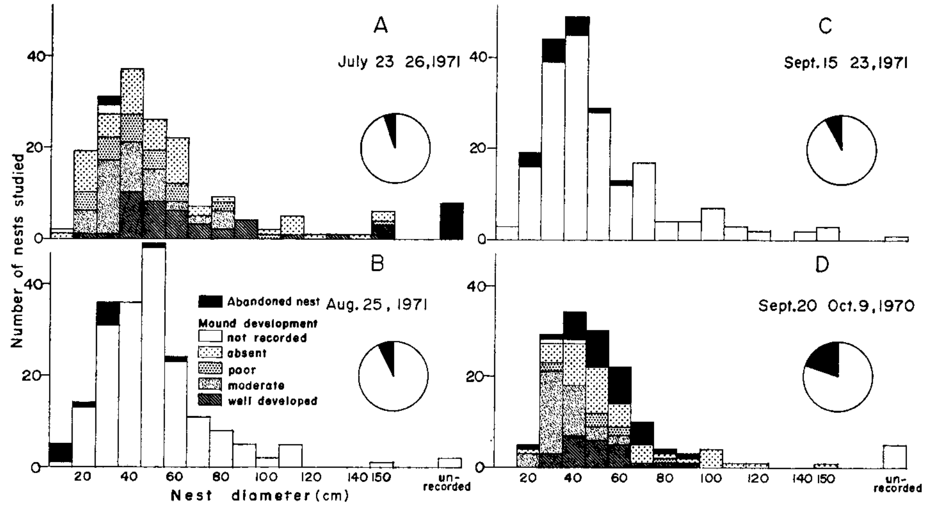

Fig. 5. Relation between nest diameter and mound development, and as well as nest abandonment. Percentage ratios of abandoned nests is shown by pie-graphs.

in July. 2) Moderately developed mounds are frequent in relatively small nests. 3) Poor mounds are observed in nests of diverse sizes with a rather constant ratio. 4) Moundless nests are variable in size, though the ratio is high in the nests larger than 90 cm (7/7 nests in autumn, 1970 and 9/16 in summer, 1971).

The higher number of nests with well developed mound in summer than in autumn is easily understood because the mound is certainly prepared to protect the brood by heat and moisture regulations. Positive correlation between nest size and mound development is also not difficult to explain because the mound would in general develop parallel to the nest growth. On the other hand, the absence of mound in some large nests is of interest, because it suggests an autogenic activity decline. The incesseant mining activities may accelerate plant decaying in and near the nest. The environmental pressure upon the nest must increase by the direct exposure to solar radiation, rain, wind, etc. and ultimately by the difficulty to obtain the food near the nest.

2.2. *Subterranean features*: All nests excavated were provided with a brood section made immediately beneath the ground level down to about 20 cm, mostly concentrated at the portion with fine root systems ranging from 0 ~10 cm deep (Fig. 4, A ~D, b, c). In the most cases, 44 out of 61 nests structurally observed, the brood section was an assembly of several lobular brood chambers with flat floor, usually 1 ~3 cm high and 3 ~20 cm wide. Some measurements on the size of chambers are given below:

| Nest No. | long axis | short axis | height | depth of the floor |
|---|---|---|---|---|
| 710709-a | 6 cm | 4 cm | 2 cm | 12cm |
| 710709-b | 8 | 3 | 3 | 6 |
| | 6 | 3 | 3 | 6 |
| 700806-a | 20 | 10 | 2 | 6 |
| 700806-b | 30 | 25 | 2 | 7 |
| 700812-a | 8 | 3 | 2 | 5 |
| | 9 | 9 | 2 | 9 |
| | 5 | 5 | 2 | 11 |
| | 5 | 3 | 1 | 5 |
| 700908 | 6 | 6 | 2 | 7 |
| | 7 | 6 | 3 | 11 |
| | 5 | 5 | 2 | 11 |
| | 15 | 9 | 3 | 9 |
| | 10 | 7 | 4 | 11 |
| | 5 | 4 | 2 | 8 |
| | 6 | 5 | 2 | 10 |
| | 5 | 5 | 3 | 13 |

These chambers are interconnected directly or by means of narrow galleries (ca. 1 cm wide) and arranged in one to three horizontal layers (Fig. 4. A and B, b). Brood section chambers sometimes fuse one another, forming a large flat cavity of 30×25 cm sq. as cited above (Nest 700806-b). In a nest excavated at montane rocky habitat in Misumai suburb of Sapporo, numerous ants with immatures were found within a cavity of 30×40 cm sq. made under a flat rock of ca. 50 cm in diameter, suggesting brood chambers as an essential part of more or less developed nests irrespective of nesting sites. However, in some nests (17/61) brood chambers did not develop well, represented only by one or a few small chambers (710709-a) or even by looped or anastomosing galleries (Fig. 4, C and D, c.g.). Thus, nests are classified into two types, those with developed brood section below ground surface and those without such, though two extremes are linked with various intermediate conditions.

Most nests (43/61) have one or more vertical shafts of 0.5 to 1.0 cm wide, descending down from the brood section, either directly from brood chambers or rarely from interconnecting galleries, (Fig. 4, A and C, s). Depth and number are variable (Fig. 6～7), ranging 25～180 cm (usually 30～120 cm), and 1～12 (usually 1～5) respectively. The ramification (6 cases) and fusion (4 cases) are exceptional (Appendix II, column IX). Partial enlargement or rarely floored chambers are sometimes made at the midway or bottom (Fig. 4, A and C, p), the size of which is relatively small and only in rare cases exceeds 5 cm in both height and width. At the uppermost part of shafts oval or bottle shaped chambers with or without flat floor are sometimes observed (cf. Appendix II, column VII). These oval chambers may be another basic structure adding to three nest components classified above. Some measurements on the size of oval chambers are given below:

| Nest No. | long axis | short axis | height | depth |
|---|---|---|---|---|
| 690529-a | 4 cm | 3 cm | 2 cm | 20 cm |
| 700912-c | 3 | 3 | 3 | 34 |
| 700921 | 3 | 3 | 2 | 13 |
|  | 2 | 2 | 1 | 19 |

In the nest made at slopes shafts are usually bent toward the hill side, probably due to the excavation along thermal and moisture gradients besides gravity. Some nests, 17 out of 61, had no such shafts. Thus, nests are also classified according to the presence or not of vertical shafts.

Nests of an inquiline ant, *Solenopsis japonica* Wheeler, are often encountered

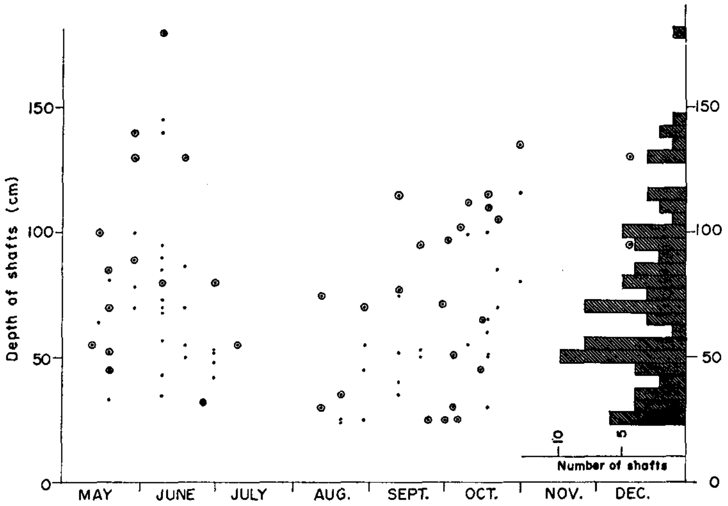

Fig. 6. Seasonal change of shaft depth. Ringed spot means the deepest shafts. Frequency distribution of depth in all nests at right hand.

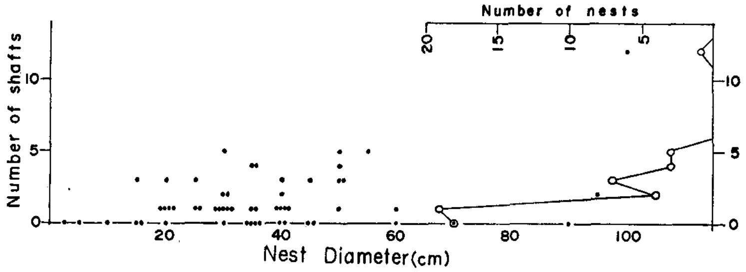

Fig. 7. Relation between number of shafts and nest diameter. Frequency distribution in all nests at right hand.

in the course of excavating nests of *F. yessensis*, 20 out of 44 nests particularly observed. They are found at diverse depth along both brood chambers and vertical shafts, usually at the zone shallower than 50 cm, as follows:

| Nest No. | Depth of *Solenopsis*' nest |
|---|---|
| 690529-a | 40 cm |
| 700820 | 4∼5, 7∼8, 7∼8, 8∼9 |
| 701002 | 8∼9, 9∼10, 11, 12∼14, 23∼30, 26∼30, 42 |
| 701016-b | 19 |
| 710512 | 18∼22, 45∼65. |
| 711010 | 7∼11, 20, 25∼41, 27∼35, 35∼65 |

But according to Yamauchi (pers. comm.), independent nests of this species are occasionally found in the places without nests of *F. yessensis*, so that this species could be regarded as a facultative inquiline.

2.3. *Nest types*: From the description given above various nests excavated are classified, according to the presence or not of distinct brood section (C, c) or of vertical shafts (S, s) into four types (number of nests observed in parentheses): CS (32), Cs (12), cS (11), cs (6). In this classification, nests with chambers, at least one of which exceeds 5×5 cm sq., are classified in C, and nests with at least one shaft deeper than 20 cm in S.

As seen from Fig. 2, CS nests are found throughout the year, though relatively scarce in summer. Cs are principally found in summer, cS mainly in spring and autumn, and all inhabited cs in summer (cf. Appendix III). From this seasonal trend it is assumed: 1) CS are all season nests, persistent through the year, 2) Type cs are incipient or bivouac nests and 3) Cs and cS are respectively summer and winter nests observed in the European relatives (Dlusskii op. cit.). The increased abandonment of medium sized nests toward autumn (cf. 2.5, Fig. 5), favors the assumption of Cs=summer nests given above, together with the following facts: Two of four abandoned medium nests excavated in autumn (Nests 711006-b and 711008 in Appendix II) had no shafts and the other two had each only one shallow shaft (Nests 711001 and 711006-a). On the other hand, abandonment of winter nests (cS) in spring has yet not been supported by excavation data, but it might occur, as mentioned in 2.5, (cf. Table 2). Judging from their small size, winter nests (cS) would be those newly made in autumn and a part of which would become all season nests in the next spring by the expansion of brood section. But, CS would be produced not only from cS but also from Cs or cs, judging from the occurrence of nests intermediate between CS and other types. (cf. Fig. 7).

Obviously, the explanation given above must be altered, if the pre-existing shafts can be eliminated by filling soil. If such would be the case, some Cs nests would be a later modification of CS, and cs of cS. Further, the later preparation of new shafts is also theoretically possible (CS→Cs→CS, or cs→cS→cs). Abandoned shafts are sometimes observed in active nests (cf. Appendix II, Nest 710609 etc.). But no direct evidence of the elimination of pre-existing shafts has hitherto been obtained. Shafts in nests excavated in summer are generally shallower (Fig. 6), against the expectation that deep-shafted nests frequent in spring and autumn must also be discovered in summer. This might serve as an indirect evidence for the later shortening of shafts by ants, but closer observations are required on this problem. The possible relations of various nest types explained above are summarized in Fig. 1, which may be suggestive for further critical studies.

2.4. *Relations between nest structure and population size*:

Some relations are recognized between population size and/or type of nests. Adult population per nest is generally proportional to the nest diameter which is an index of size of brood section (Fig. 8) and, excluding Cs nests, to the total length of all shafts combined (Fig. 9). Except the nests having population less than 100, the correlation coefficient in the former trend was 0.65. Except Cs, some nests highly deviated from the general trend in Fig. 8 do not show such deviation in Fig. 9. This result indicates that general coincidence between population size and the development of subterranean nest structure. Many students have hitherto denied the possibility to estimate the population by measuring nest size (Ayre op. cit., Dreyer 1942, and Young 1899, after Dlusslii op. cit). But the obtained result seem to require re-investigation on this problem. Such a tendency, I think, might be expected only for ants nests without or poor mound as this species, in which the diameter is directly an index of subterranean brood section. Populations of summer (Cs) nests usually deviated much from the trend, possibly because of incessant member exchange among surrounding nests. Therefore sampling in colder season would afford more precise coincidence, though even under this condition abandoned or obviously declining nests must be eliminated from the sampling.

2.5. *Nest proliferation*: In the polydomous species of *F. rufa* group, the queens cannot solitarily found colonies by themselves. The new colonies are established either by the departure of a group of workers from one nest to the site nearby, which later transport the queens from the mother nest or adopt new queens soon after nuptial flight (budding), or by the usurpation of the nests of appropriate species of the subgenus *Serviformica* by the dealated queen (temporal parasitism, Wheeler 1910).

In order to determine the budding or colony founding season of this species, a following procedure was adopted : A precise map of selected area (Fig. 10), 15× 15 m in extent, was made on May 29, 1970, and newly appeared nests were checked as to location, size, activity, etc., at irregular intervals of June 24, July 4, 10, 30 and October 15, 1970, and, May 26, July 8, August 25, September 18 and October 15, 1971. The sequence of results for each nest is shown in Appendix. III. for further analysis.

As shown in Table 2, nests identified with new were princpally detected in early season, July in 1970 and May to July in 1971, though some nests had already been initiated in 1970 preceding the first census. Only one new nest was recorded

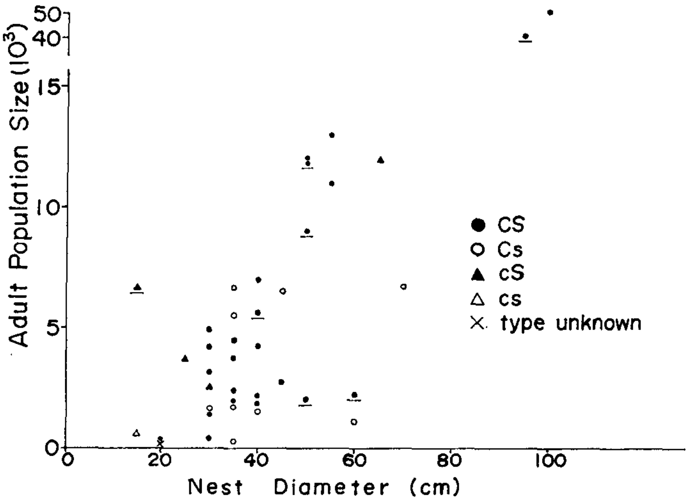

Fig. 8. Relation between adult population size and nest diameter. Each nest type are separately symbolized. Explanation on the nests underlined is given in text.

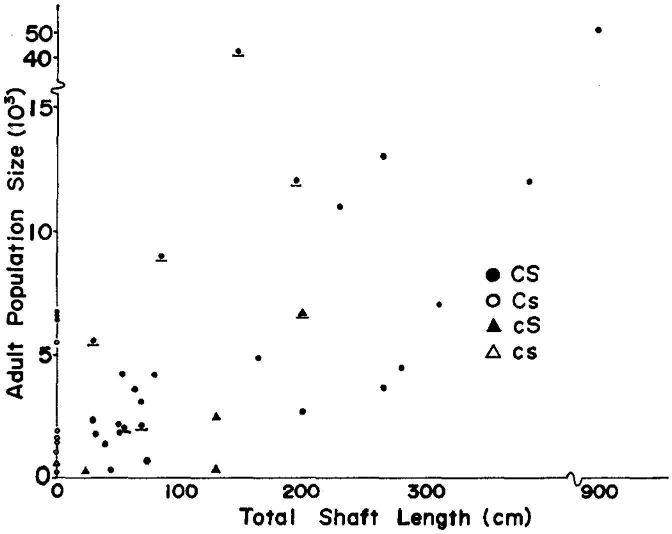

Fig. 9. Relation between adult population size and total shafts length in each nest (see also Fig. 8).

after July 31 in 1970 and no nest in 1971, indicating the colony foundation or budding carried out mostly in spring to early summer. This tendency is comparable with the case observed in *F.* (*Coptoformica*) *ulkei* Emery (Scherba 1958), nests

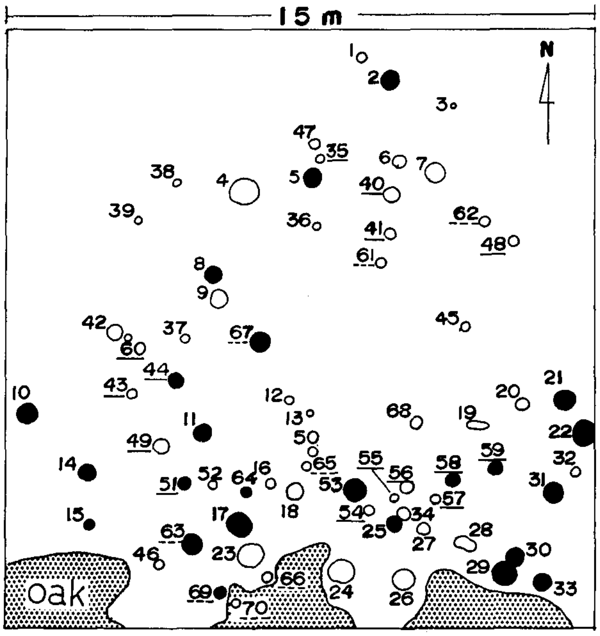

Fig. 10. The area selected for the periodical nest census. Solid black spots mean the locations of nests inhabited at the last census, and circles those once existed. Solid underline is given for nests newly made in 1970, and broken line for those in 1971.

Table 2. Number of nests periodically censused, presenting seasonal trend in occurrence of nest prolfieration, revival and abandonment.

| Date | May 29 | June 24 | July 4 | July 10 | July 30 | Oct. 20 | May 26 | July 8 | Aug. 25 | Sep. 8 | Oct. 15 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total number of nest inhabited | 33 | 29 | 30 | 42 | 51 | 42 | 38 | 37 | 34 | 30 | 24 |
| active | 23 | 23 | 26 | 37 | 46 | 39 | 34 | 37 | 29 | 26 | 24 |
| inactive | 10 | 6 | 4 | 5 | 5 | 3 | 4 | 0 | 5 | 4 | 0 |
| continued | / | 28 | 26 | 30 | 38 | 41 | 31 | 32 | 34 | 30 | 24 |
| initiated | / | 0 | 1 | 4 | 11 | 1 | 6 | 3 | 0 | 0 | 0 |
| revived | / | 1 | 3 | 8 | 2 | 0 | 0 | 2 | 0 | 0 | 0 |
| deserted | 23 | 5 | 3 | 0 | 4 | 10 | 10 | 6 | 3 | 4 | 6 |

of which bud in a limited period, namely in late April, May and early July.

The seasonal trend of nests either revived or deserted was simultaneously obtained by the same procedure (Table 2). The nest revival was observed exclusively in early summer, June or July, indicating the reoccupation of once deserted summer nests by migrant workers, probably followed by queen transport. On the other hand, abandonment of nests were relatively numerous in spring and autumn. On May 29, 1970, the size of them were generally small, with the mean 21 cm, ranging 5 ~50 cm in the diameter. Although a part of the number obtained might be of unsuccessful nests (cs) budded in the spring, the abandoned small nests might be winter nest (cS). On May 29, 1971, however, the size of abandoned nest was variable, ranging 10 ~75 cm in the diameter. Nests deserted in autumn were variable in size in both years, offering another evidence of abandonment of nests without deep shafts (Cs, cs, and a part of CS). Nests continued throughout two years were only 14 out of 70 nests detected through the censuses, indicating the short life span of nest in the shore. (cf. 2.1.).

Nests covering a large space, characterized by the continuous expansion of mound materials or decaying plant, 1.5×1.5 m sq. or more, are sometimes observed in Ishikari Shore. Such condition is regarded as compound nests produced by one or both of the following two ways: 1) Partial translocation from the original nesting site which has become inadequate. 2) Fusion of some neighbouring nests mostly issued from a common mother nest in parallel with the expansion of each one. Each way was actually observed at Nest 4 (the former) and Nest 29 *v.s.* 30 (the latter), (cf. Fig. 10 and Appendix III). These nests are usually composed of active and abandoned or unused parts, especially in the former case, the distinction of which is more or less possible from the surface conditions. In other words, a compound nest is structurally regarded as one being constructed of spatial combination among some nests. (Fig. 4, E).

## 3. Concluding remarks

Based upon the results described above, the life cycle of *F. yessensis* can tentatively be divided into five successive phases as following: 1) Hibernating phase, November to April, 2) Expansion phase, April to July, 3) Breeding phase, May to August, 4) Mating phase, July to August, 5) Prehibernating phase, September to November. (Fig. 1).

Among these five phases, the mating phase is facultative, appearing only in a limited number of nests. The breeding phase, which chronologically coincides largely with expansion and mating phases, is characteristic in various bionomic aspects. In this period, 1) The ratio of aggressive ants increases (Fig. 3, D), 2) The number of aphid visitors decreases (Ito unpub.), 3) Transports of both adults and immatures are carried out actively (Ito unpubl.), and 4) Reoccupation of abandoned nests becomes conspicuous. All these features relate with the existence and increase of immatures within nests, which may stimulate workers, intensify the activity level and ultimately modify the mode of activities.

Comparing the life cycle of *F. yessensis* in Ishikari to other related species, the deleyed start of breeding season governed by severe local climate is noteworthy. Breeding in March or April observed in other European species (Gösswald op. cit.) is never found at this habitat, where the snow cover remains till early April. Due to the delayed beginning of both extranidal activities and oviposition, the emergence of adult ants, sexuals as well as workers, does not occur till late July.

Nextly, some bionomic peculiarities of *F. yessensis* Forel are compared with other species based upon the discussions given in preceding sections.

1) This species is polygynous. The number of queens per nest is comparable to *F. rufa rufopratensis major*, and markedly less than in *F. polyctena.* The population size per nest is rather similar to that in monogynous species such as *F. rufa* and *F. truncorum.* On the other hand, the ratio queen/total adult population is probably not much inferior to *F. polyctena* and much more than monogynous species (cf. Section 1).

2) *F. yessensis* is not a good mound-builder such as *F. polyctena, rufa* and *rufa rufopratensis major* which produce enormous mounds, usually built around some cores such as decayed stubs (**2.1.**). Thus, *F. yessensis* resembles rather *F. pratensis,* though the mound does not contain sand particles as in the latter. (Dlusskii op. cit.).

3) In contrast to the poor mound formation, each nest has relatively well developed subterranean system composed of two components, brood section (C) and vertical shafts (S). The nests with both components, CS, are regarded as all season nests, while those with only one component developed as summer (Cs) and winter nests (cS), respectively. The presence of such two or three types are known at least in *F.* (*F.*) *polyctena* (Kneitz 1964), *F.* (*F.*) *rufa* L. (Oekland 1934, after Dlusskii op. cit.) and F. (*Raptiformica*) *sanguinea* Latereille (Atanasov 1952, after Dlusskii op. cit.). The former component, brood section, which can readily be detected from the outside especially in moundless nests, is probably present in all related species (cf. Dlusskii op. cit.), but it may be characteristic of *F. yessensis* that this section is generally confined within a limited vertical zone with fine root systems (cf. Fig. 4, A, r). On the other hand, the latter component, the shafts are reported in some other non-migratory ants belonging to other subgenera, *F.* (*Serviformica*) *cunicularia* Latereille, *F.* (*Coptoformica*) *pressilabris* Nylander (Dlusskii op. cit.), *F.* (*Serviformica*) *pallidefulva nitidiventris* Emery and *F.* (*Serviformica*) *pallidefulva schaufussi incerta* Emery (Talbot 1948). Deep shafts as observed in *F. yessensis* are known in nests of the former two species cited above. In *F. yessensis,* all season nests (CS) are more frequent than temporal ones. Therefore it is assumed that this species belongs to the migratory ants, but the tendency is weak, and the subterranean nest structure more or less resembles that reported of non-migratory ants belonging to other subgenera.

In conclusion, each bionomic feature of *F. yessensis* is basically similar to that in other species of the subgenus *Formica* Linné, but the integrated whole is different. In some aspects *F. yessensis* resembles *F. pratensis* (Gösswald op. cit.), for instance, in relatively small population size, polygyny, poor mound formation, habitat preference for openlands and forest margins (Ito op. cit.), and some other features described in a subsequent paper, indicate the occupation of the similar ecological niche by these two species. But, in some other aspects such as highly integrated nests and poorly developed mating flight (Ito unpub.) as well intensive internidal adults transports, etc., *F. yessensis* rather resembles *F. polyctena.*

Finally, it must be mentioned that my observations were mostly made in a shore openland, the soft substratum, poor vegetation and relatively uniform topographic conditions of which might affect the nest structure. Comparative observations of nests found at different habitats are indispensable to obtain reasonable conclusions.

### Acknowledgement

I wish to express my sincere thanks to Dr. Sh. F. Sakagami for his kind and pertinent guidance and to Prof. M. Yamada for his generous support and help throughout the work, further to Mr. K. Yamauchi who kindly allowed me the free use of his unpublished results on *F. yessensis* and to Dr. K. Hayashida, whose expert myrmecological suggestions were indispensable to the work. I am also indebted to many colleagues in the Zoological Institute, Faculty of Science, Hokkaido University, who helped me in various ways in the course of the present work, especially, Messrs. T. Okazawa, M. Yamamoto, and K. Yanase.

## Summary

As a part of the serial work on the bionomical and ecological studies of a Japanese red wood ant species, *Formica (Formica) yessensis* Forel, population census and nest structure were studied in Ishikari littoral openland, Hokkaido, Northern Japan, based upon excavations of 53 (for population) and 61 nests (for nest structure) with the following results:

1) Worker population per nest ranges from 260 to 51,000 with mean 6,800 and s.d. 9,500, while the number of queens per nest excluding orphan cases from 1 to 213, the mean 24 and s.d. 44.6 (Semiabandoned nests having less than one hundred population are eliminated from the calculation).

2) Oviposition begins in early May and larvae are observed from June to early August and pupae from July to September, showing the active season distinctly shorter than in the European relatives, reflecting severe climatic conditions.

3) Nests are divided into three basic components, mound, brood section (C) found down to 20 cm from the ground surface, and vertical shafts (S) descending down to 180 cm in the maximum.

4) Most nests possess well developed C and S, regarded as all season nests (CS), that is, nests persistent throughout the year, but some nests found mainly in summer have only developed C (Cs: summer nests), and others found principally in spring and autumn only developed S (cS: winter nest).

5) Foundation of new nests by budding is mainly carried out in spring (early May) to early summer (late July).

6) From these features and those described in a subsequent paper, it is

assumed that this species occupies the ecological niche similar to that possessed by *F.* (*F.*) *pratensis* Retzius in Europe.

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## Appendix I. Population size in nests examined.

Explanations: 1) First two numerals in nest No. indicate the year, and the other four the date of excavation. 2) The explanations about nest phases are given in text, and "aband." means nests abandoned, and those in parentheses show semi-abandoned nests with less than one hundred individuals. 3). Actual numbers are rounded to two significant figures. 4) Queen in parentheses is alate one. 5) Workers in parentheses are those captured outside of nests. 6) Pupae in parentheses are exposed ones. 7) Absence is expressed by the mark "—" in each item. 8) Colonies of *Solenopsis*, along nests examined are mentioned at the first column by+(presence), –(absence) and ×(uncertain).

| Nest No. | Nest Phase | Queens | Workers | Pupae | Larvae | Eggs | Total individual number |
|---|---|---|---|---|---|---|---|
| 690503$^{-}$ | II, III | 11 | 8,000 (—) | 0 | 0 | 6,000 | 14,000 |
| 710512$^{+}$ | I, II | 14 | 2,000 (—) | 0 | 0 | 0 | 2,000 |
| 710515$^{-}$ | I, II | 68 | 4,900 (—) | 0 | 0 | 0 | 5,000 |
| 700519-a$^{x}$ | I, II | 0 | 1,400 (—) | 0 | 0 | 0 | 1,400 |
| 700519-b$^{+}$ | II, III | 7 | 2,200 (—) | 0 | 0 | 500 | 2,700 |
| 710519-a$^{x}$ | II, III | 6 | 1,900 (—) | 0 | 0 | 400 | 2,300 |
| 710519-b$^{x}$ | II, III | 16 | 6,700 (36) | 0 | 0 | 600 | 7,300 |
| 690520$^{x}$ | I, II | 14 | 23,000 (—) | 0 | 0 | 0 | 22,000 |
| 710526$^{-}$ | II, III | 11 | 1,500 (160) | 0 | 0 | 700 | 2,200 |
| 690529-a | II, III | 6 | 7,000 (240) | 0 | 0 | 4,300 | 11,000 |
| 690529-b$^{-}$ | I, II | 11 | 310 (15) | 0 | 0 | 0 | 320 |
| 700529$^{x}$ | II, III | 41 | 3,200 (—) | 0 | 40 | 7,000 | 10,000 |
| 710529$^{+}$ | II, III | 147 | 41,000 (500) | 0 | 0 | 15,000 | 56,000 |
| 690609$^{-}$ | II, III | 7 | 4.200 (320) | 0 | 270 | 1,800 | 6,300 |
| 710609$^{-}$ | II, III | 213 | 51,000 (—) | 0 | 0 | 19,000 | 70,000 |
| 710614$^{x}$ | II, III | 0 | 5,500 (—) | 0 | 0 | 400 | 5,900 |
| 690618$^{x}$ | II, III | 16 | 12,000 (1,000) | 0 | 2,500 | 6,700 | 21,000 |
| 690625$^{-}$ | II, III | 1 | 1,800 (360) | 0 | 1,400 | 1,800 | 5,000 |
| 710626$^{+}$ | II, III | 114 | 6,600 (260) | 0 | 4,400 | 12,000 | 23,000 |
| 690630$^{x}$ | II, III | 11 | 11,000 (1,700) | 0 | 4,000 | 8,900 | 24,000 |
| 710702$^{+}$ | II, III | 11 | 12,000 (300) | 160( —) | 8,000 | 10,000 | 30,000 |
| 710709-a$^{+}$ | II, III | 1 | 630 (210) | 0 | 8 | 0 | 630 |
| 710709-b$^{-}$ | II, III | 0 | 4,200 (—) | 130( —) | 2,000 | 350 | 6,700 |
| 710709-c$^{+}$ | II, III | 0 | 1,900 (—) | 5( —) | 390 | 0 | 2,300 |
| 690711-a$^{-}$ | II, III | 0 | 260 (60) | 130( —) | 14 | 0 | 400 |
| 690711-b$^{+}$ | II, III | 6 | 8,400 (1,400) | 1,700( —) | 7,000 | 5,700 | 12,000 |
| 690716$^{+}$ | II, III | 5 | 1,800 (430) | 940( —) | 2,400 | 4,200 | 8,400 |
| 700722$^{+}$ | II, III | 9 | 3,400 (400) | 1,000(470) | 3,000 | 2,200 | 8,600 |
| 710726$^{-}$ | III, III | 2(+1) | 6,700 (—) | 352sexuals<br>2,700( —) | 2,000 | 550 | 21,000 |
| 700806-a$^{+}$ | III | 1 | 1,600 (—) | 1,600(230) | 30 | 300 | 3,500 |
| 700806-b$^{x}$ | (aband.) | 0 | 30 (—) | 0 | 0 | 0 | 30 |
| 700812-a$^{+}$ | III | 1 | 2,400 (140) | 610( —) | 110 | 0 | 3,300 |
| 700812-b$^{+}$ | III | 8 | 3,100 (220) | 650( 5) | 110 | 0 | 3,900 |
| 700820-a$^{+}$ | III | 0 | 1,100 (80) | 320( 20) | 0 | 0 | 1,400 |
| 700$^{8}$20-b$^{+}$ | III | 12 | 9.000 (800) | 2,400( 70) | 130 | 0 | 12,000 |
| 700820-a$^{-}$ | III | 15 | 12.000 (—) | 1,100(210) | 0 | 0 | 13,000 |
| 700829-b | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 700829-c | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 700908$^{-}$ | III, V | 11 | 6,500 (—) | 620( 20) | 0 | 0 | 7,200 |
| 700912-a$^{x}$ | (aband.) | 0 | 30 (—) | 0 | 0 | 0 | 30 |
| 700912-b$^{x}$ | (aband.) | 0 | 65 (15) | 0 | 0 | 0 | 65 |
| 700912-c$^{-}$ | III, V | 4 | 2,500 (20) | 10( —) | 0 | 0 | 2,500 |
| 700912-d$^{-}$ | III, V | 5 | 3,700 (80) | 440( 20) | 1 | 0 | 4,100 |
| 710912$^{+}$ | / | - | - | - | - | - | - |
| 700921$^{-}$ | III, V | 9 | 2,700 (300) | 50( —) | 0 | 0 | 2,800 |
| 710924-a$^{x}$ | (aband.) | 0 | 20 (—) | 0 | 0 | 0 | 20 |
| 710924-b$^{x}$ | V | 0 | 300 (—) | 0 | 0 | 0 | 300 |
| 710930$^{x}$ | / | - | - | - | - | - | - |

**Appendix I.** (*Continued*)

| Nest No. | Nest Phase | Queens | Workers | Pupae | Larvae | Eggs | Total individual number |
|---|---|---|---|---|---|---|---|
| 711001 | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 701002$^{+}$ | V | 4 | 4,500 (60) | 0 | 0 | 0 | 4,500 |
| 711004-a$^{x}$ | V | 3 | 5,600 (—) | 0 | 0 | 0 | 5,900 |
| 711004-b$^{x}$ | V | 2 | 2,100 (—) | 0 | 0 | 0 | 2,100 |
| 711006-a | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 711005-b | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 711006-c | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 711007$^{x}$ | / | - | - | - | - | - | - |
| 711008 | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| 711010$^{+}$ | III, V | 0 | 13,000 (680) | 80 | 0 | 0 | 13,000 |
| 701014-a$^{+}$ | V | 125 | 22,000 (—) | 0 | 0 | 0 | 22,000 |
| 701014-b$^{+}$ | V | 2 | 730 (—) | 0 | 0 | 0 | 730 |
| 701014-c$^{x}$ | V | 1 | 350 (—) | 0 | 0 | 0 | 350 |
| 701014-d$^{x}$ | V | 17 | 3,600 (—) | 0 | 0 | 0 | 3,600 |
| 701016-a$^{+}$ | / | / | / | / | / | / | / |
| 701016-b$^{+}$ | / | / | / | / | / | / | / |
| 701021$^{-}$ | V | 14 | 3,700 (0) | 0 | 0 | 0 | 0 |
| 701031$^{x}$ | V | - | - | - | - | - | - |
| 701214-a$^{x}$ | I | - | - | - | - | - | - |
| 701214-b | aband. | 0 | 0 | 0 | 0 | 0 | 0 |
| Total | | 982(+1) | 335,000 | | | | |

## Appendix II. Structure and type of nests examined.

Explanations: Each column represents following item: I. nest number, II. nest phase, III. nest type, IV. nest diameter V. mound development, VI. depth of brood section in the maximum, VII. depth of oval chamber, VIII. number of shafts, IX. depth of shafts. In mound development (V), ⧺ is given for well developed mound with the height more than 5 cm, + for relatively developed, ± for poor, and – for absence. Depth of brood section (IV) in parentheses means that of looped galleries. In VII, the mark "–" means absence. In VIII and IX, numbers in parentheses mean numbers and depth of abandoned shafts in inhabited nests. Ramification and fusion of shafts are shown in IX with connecting line and the asterisks, respectively.

| I | II | III | IV | V | VI | VII | VIII | IX |
|---|---|---|---|---|---|---|---|---|
| 690503 | II, III | / | / | / | / | / | / | / |
| 710512 | I, II | CS | 50cm | – | 10cm | - | 1 | 55cm |
| 710515 | I, II | CS | 30 | ± | 10 | 20, 37cm | 2 | 100, 64 |
| 700519-a | I, II | CS | 30 | – | 11 | - | 1 | 45 |
| 700519-b | II, III | CS | 60 | – | 11 | - | 1 | 70 |
| 710519-a | II, III | CS | 35 | + | / | 25, 40 | 1 | 52 |
| 710519-b | II, III | cS | 15 | / | 10 | / | 3 | 85, 81, 33 |
| 690520 | I, II | / | / | / | / | / | / | / |

**Appendix II.** (*Continued*)

| I | II | III | IV | V | VI | VII | VIII | IX |
|---|---|---|---|---|---|---|---|---|
| 710526 | II, III | Cs | 40 | + | 11 | - | 0 | |
| 690529-a | II, III | CS | 40 | ± | / | 20 | 3 | 140, 100, 70 |
| 690529-b | I, II | cS | 20 | ± | (15) | - | 1 | 130 |
| 700529 | II, III | / | / | / | / | / | / | / |
| 710529 | II, III | CS | 95 | ++ | / | / | 2 | 89-78 |
| 690609 | II, III | CS | 30 | ± | / | / | 1 | 80 |
| 710609 | II, III | CS | 100 | + | 30 | / | 12 | 180*, 145-97, 140, 90-68, 86*-57, 72, 65*, 46, 32 |
| 710614 | II, III | Cs | 35 | ++ | 18 | / | 0 | |
| 690618 | II, III | CS | 50 | − | 10 | - | 5(1) | 130, 87, 70, 55, 50, |
| 690625 | II, III | CS | 40 | − | 12 | - | 1 | 32 |
| 710626 | II, III | Cs | 35 | ++ | 10 | - | 0 | |
| 690630 | II, III | CS | 55 | ++ | 17 | 28, 40 | 5 | 80, 52-48, 52, 42 |
| 710702 | II, III | / | 65 | ± | / | / | / | / |
| 710709-a | II, III | cs | 15 | ± | 15 | - | 0 | |
| 710709-b | II, III | CS | 40 | ++ | 23 | - | 1 | 55 |
| 710709-c | II, III | Cs | 35 | ++ | (11) | - | 0 | |
| 690711-a | II, III | Cs | 35 | + | / | / | 0 | |
| 690711-b | II, III | CS | / | / | / | / | / | / |
| 690716 | II, III | CS | / | / | / | / | / | / |
| 700722 | II, III | CS | 50 | ± | / | / | / | / |
| 710726 | III, IV | Cs | 70 | ++ | 10 | - | 0 | |
| 700806-a | III | Cs | 30 | + | 10 | - | 0 | |
| 700806-b | (aband.) | / | 20 | / | / | / | / | / |
| 700812-a | III | CS | 35 | + | 7 | - | 1 | 30 |
| 700812-b | III | CS | 30 | + | 9 | - | 1 | 75 |
| 700820-a | III | Cs | 60 | ± | 11 | - | 0 | |
| 700820-b | III | CS | 50 | ± | / | / | 3 | 35, 25, 25 |
| 700829-a | III | CS | 50 | ++ | / | / | 4 | 70, 55, 45, 25 |
| 700829-b | aband. | / | 45 | / | / | / | / | / |
| 700829-c | aband. | cs | 20 | − | (15) | - | 0 | |
| 700908 | III, V | Cs | 45 | − | 13 | - | 0 | |
| 700912-a | (aband.) | cs | 10 | + | (5) | - | 0 | |
| 700912-b | (aband.) | cs | 5 | − | (10) | - | 0 | |
| 700912-c | III, IV | cS | 30 | ± | (5) | 34 | 3 | 75-68, 52 |
| 700912-d | III, V | CS | 35 | − | 10 | 12, 20 | 4(1) | 115, 75, 40, 35, (/) |
| 710912 | / | Cs | 90 | ++ | / | / | 0 | |
| 700921 | III, V | CS | 45 | + | 10 | 13, 19 | 3 | 95, 53, 50 |
| 710924-a | (aband.) | cs | 15 | ± | / | - | 0 | |
| 710924-b | V | cS | 20 | − | (11) | - | 1 | 25 |
| 710930 | / | cS | 20 | − | (8) | - | 1 | 71 |
| 711001 | aband. | CS | 25 | − | (12) | 20 | 1 | (25) |
| 701002 | V | CS | 35 | ± | (10) | 14, 20 | 4(1) | 97, 78, 78, 25, (/) |
| 711004-a | V | CS | 40 | − | 23 | / | 1 | 30 |
| 711004-b | V | CS | 40 | − | 15 | - | 1 | 51 |
| 711006-a | aband. | CS | 30 | − | 10 | 13 | 1 | 25 |
| 711006-b | aband. | Cs | 40 | − | 12 | - | 0 | |
| 711006-c | aband. | cs | 5 | − | (4) | - | 0 | |
| 711007 | / | CS | 40 | ± | 10 | 15 | 1 | 102* |

Apendex II. (*Continued*)

| I | II | III | IV | V | VI | VII | VIII | IX |
|---|---|---|---|---|---|---|---|---|
| 711008 | aband. | Cs | 45 | + | 12 | - | 0 | |
| 711010 | III, V | CS | 50 | + | / | / | 3 | 112, 99, 55 |
| 701014-a | V | / | / | / | / | / | / | / |
| 701014-b | V | CS | / | / | / | / | 1 | 75 |
| 701014-c | V | CS | 30 | − | 11 | / | 1 | 45 |
| 701014-d | V | CS | / | − | 15 | 13 | 1 | 65 |
| 701016-a | / | cS | 30 | ± | / | / | 5(1) | 110. 65. 50. 50, 30, (60) |
| 701016-b | / | cS | 25 | − | / | / | 2 | 115, 100 |
| 701021 | V | cS | 25 | − | 10 | 30 | 3 | 105, 85, 70 |
| 701031 | V | cS | 20 | − | 9 | 20, 35 | 3 | 135, 116, 80 |
| 701214-a | I | cS | 20 | − | 15 | - | 1 | 95 |
| 701214-b | aband. | cS | 25 | − | 15 | - | 1 | (130) |

## Appendix III. Activity of continuously observed nests.

Explanations: Nest conditions are represented with marks "+" (active), "±" (inactive), and – (deserted). Revival is shown with r and initiation with s, along the mark +. Asterisk is given for the nest continued throughout two years, along the nest number.

| Census Period<br>Nest | 1970 | | | | | | 1971 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | M. 29 | Jn. 24 | Jl. 4 | Jl. 10 | Jl. 30 | O. 20 | M. 26 | Jl. 8 | A. 25 | S. 8 | O. 15 |
| 1 | ± | − | | | | | | | | | |
| 2* | + | + | + | + | + | + | + | + | + | + | + |
| 3 | ± | − | | | | | | | | | |
| 4 | + | + | + | + | + | + | + | + | + | ± | − |
| 5* | + | + | + | + | + | + | + | + | + | + | + |
| 6 | + | ± | + | + | + | + | − | | | | |
| 7 | ± | + | + | + | + | + | + | + | + | − | |
| 8* | ± | + | + | + | + | + | + | + | + | + | + |
| 9 | ± | + | + | + | + | + | ± | + | + | + | − |
| 10* | + | + | + | + | + | + | + | + | + | + | + |
| 11* | + | + | + | + | + | + | + | + | + | + | + |
| 12 | ± | − | | | | | | | | | |
| 13 | ± | − | | | | | | | | | |
| 14* | ± | + | + | + | + | + | + | + | + | + | + |
| 15* | + | + | + | + | + | + | ± | + | + | + | + |
| 16 | + | + | + | + | + | + | + | − | | | |
| 17* | + | + | + | + | + | + | + | + | + | + | + |
| 18 | + | ± | + | + | + | + | − | | | | |
| 19 | ± | ± | − | $+^{r}$ | ± | − | | | | | |
| 20 | + | + | ± | ± | + | ± | − | | | | |
| 21* | + | + | + | + | + | + | + | + | + | + | + |
| 22 | + | + | + | + | + | + | + | | | | |
| 23 | + | + | + | + | + | + | − | $+^{r}$ | + | + | − |
| 24 | + | + | + | + | + | + | + | + | ± | ± | − |

**Appendix III.** (*Continued*)

| Census Period | 1970 | | | | | | 1971 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Nest | M. 29 | Jn. 24 | Jl. 4 | Jl. 10 | Jl. 30 | O. 20 | M. 26 | Jl. 8 | A. 20 | S. 8 | O. 15 |
| 25* | + | ± | ± | + | + | + | + | + | ± | + | + |
| 26 | + | + | + | + | + | + | + | + | ± | ± | − |
| 27 | + | ± | − | $+^{r}$ | + | + | ± | − | | | |
| 28 | + | − | $\pm^{r}$ | ± | − | | | | | | |
| 29* | + | + | + | + | + | +] | + | + | + | + | + |
| 30* | + | + | + | + | + | +] | | | | | |
| 31* | ± | + | + | + | + | + | + | + | + | + | + |
| 32 | + | ± | ± | ± | + | − | | | | | |
| 33* | + | + | + | + | + | + | + | + | + | + | + |
| 34 | …… | ..$+^{r}$ | − | $+^{r}$ | ± | − | | | | | |
| 35 | | | $+^{n}$ | + | + | + | + | + | ± | − | |
| 36 | …… | …… | $+^{r}$ | + | − | | | | | | |
| 37 | …… | …… | $+^{r}$ | ± | ± | − | | | | | |
| 38 | …… | …… | …… | $+^{r}$ | ± | ± | − | | | | |
| 39 | …… | …… | …… | $+^{r}$ | + | − | | | | | |
| 40 | | | | $+^{n}$ | ± | + | + | − | | | |
| 41 | | | | $+^{n}$ | − | | | | | | |
| 42 | …… | …… | …… | ..$+^{r}$ | + | + | + | − | | | |
| 43 | | | | $+^{n}$ | + | + | − | | | | |
| 44 | | | | $+^{n}$ | + | + | + | + | + | + | + |
| 45 | …… | …… | …… | ..$\pm^{r}$ | − | | | | | | |
| 46 | …… | …… | …… | ..$+^{r}$ | + | − | | | | | |
| 47 | …… | …… | …… | …… | $+^{r}$ | + | + | + | + | − | |
| 48 | | | | | $+^{n}$ | − | | | | | |
| 49 | | | | | $+^{n}$ | + | + | + | − | | |
| 50 | …… | …… | …… | …… | $+^{r}$ | − | | | | | |
| 51 | | | | | $+^{n}$ | + | + | + | + | + | + |
| 52 | | | | | $+^{n}$ | − | | | | | |
| 53 | | | | | $+^{n}$ | + | + | + | + | + | + |
| 54 | | | | | $+^{n}$ | ± | − | | | | |
| 55 | | | | | $+^{n}$ | − | | | | | |
| 56 | | | | | $+^{n}$ | + | − | | | | |
| 57 | | | | | $+^{n}$ | + | − | | | | |
| 58 | | | | | $+^{n}$ | + | + | + | + | + | + |
| 59 | | | | | $+^{n}$ | + | + | + | + | + | + |
| 60 | | | | | | $+^{n}$ | − | | | | |
| 61 | | | | | | | $\pm^{n}$ | + | − | | |
| 62 | | | | | | | $+^{n}$ | − | | | |
| 63 | | | | | | | $+^{n}$ | + | + | + | + |
| 64 | | | | | | | $+^{n}$ | + | + | + | + |
| 65 | | | | | | | $+^{n}$ | − | | | |
| 66 | | | | | | | $+^{n}$ | + | ± | ± | − |
| 67 | | | | | | | | $+^{n}$ | + | + | + |
| 68 | …… | …… | …… | …… | …… | …… | …… | $+^{r}$ | + | − | |
| 69 | | | | | | | | $+^{n}$ | + | + | + |
| 70 | | | | | | | | $+^{n}$ | − | | |