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POLYGYNY AND NUPTIAL FLIGHT OF *FORMICA (FORMICA) YESSENSIS* FOREL AT ISHIKARI COAST, HOKKAIDO, JAPAN *

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SUMMARY

Polygyny and nuptial flight were observed in a supercolony of a Japanese red wood ant *Formica (Formica) yessensis* Forel at Ishikari Coast, Hokkaido, Japan. The main results are:

1. The vertical distribution of queens in nests seasonally fluctuated, preferring deeper parts (mainly 40 to 60 cm below the ground surface) in hibernation season but shallower parts (10 to 40 cm) in summer. This fluctuation was significantly correlative with that of the vertical distribution of workers except mid July to prehibernation season.

2. In nests the queens tended to aggregate with each other at same chambers without hostility. They all had developed ovaries in egg laying season.

3. Abundant sexuals were produced in the average year, but occasional absence of such mass production was also possible.

4. The inseminated new queens tended to return to the mother colony, while most virgins tried to fly away.

RESUME

Polygynie et vol nuptial chez Formica (Formica) yessensis Forel **à Ishikari Coast, Hokkaido, Japon**

La polygynie et le vol nuptial ont été étudiés dans une super-colonie de fourmis rousses japonaises *Formica (Formica) yessensis* Forel à Ishikari Coast, Hokkaido, Japon. Les principaux résultats sont les suivants:

1. La distribution verticale des reines dans les nids varie en fonction de la saison: les reines préfèrent les zones profondes en hiver (40 à 60 cm sous la surface du sol) et

* Biological and ecological studies of a supercolonial ant *Formica yessensis* Forel, XI.

les zones peu profondes en été (10 à 40 cm). Cette distribution est positivement corrélée avec celle des ouvrières, excepté entre mi-juillet et la période de pré-hibernation.

2. Dans les nids, les reines tendent à s'agréger dans les mêmes chambres sans hostilité. Toutes ont des ovaires développés pendant la période de production du couvain.

3. La production des sexués est généralement abondante, mais peut parfois faire complètement défaut.

4. Les nouvelles reines « fécondées » tendent à retourner à la colonie-mère, alors que la plupart des femelles vierges essayent de voler plus loin.

INTRODUCTION

Formica (Formica) yessensis Forel forms a big colony at Ishikari Coast, Hokkaido, Japan, consisting of thousands of nests (ITO, 1971 ; HIGASHI and YAMAUCHI, 1979). As already reported by some authors, this colony shows some sociobiologically interesting characteristics such as the polyethism among workers (HIGASHI, 1974, 1976 ; IMAMURA, 1978), polycalism (ITO and IMAMURA, 1974 ; HIGASHI, 1978), frequent budding and abandonment of nests (HIGASHI, 1976), elimination of other ants (HIGASHI and YAMAUCHI, 1979), and so on. The present study was undertaken as a part of the comprehensive studies of this colony.

As HÖLLDOBLER and WILSON (1977) mentioned, the polycalism does not always correlate with polygyny. Thus, many monogynous ant species are polydomous and some polygynous species are monodomous. However, a big polydomous colony consisting of countless nests, i.e. supercolony, is always polygynous. This is also the case of the present colony (ITO, 1973 ; HIGASHI, 1976). This means that we must necessarily clarify how and why the polygyny could be developed, in order to solve the evolutionary significance of the supercolony. Therefore, the present study takes note on the structure of the polygyny and on the reason why some queens abandon their nuptial flight.

STUDY SITE

Ishikari Coast is located in the western part of Hokkaido, facing the Japan Sea. This sandy coast extends ca. 17 km along the seaside *(fig. 1)*. About 200 m apart from the shore line, a primary oak forest of about 150 m width continues parallel to the shore line. Since the warm Japan Current reaches offshore, the climate is less severe *(fig. 2)* than in northern or eastern Hokkaido.

On this coast thick snow covers the ground from December to March. Then it gradually thaws and disappears before late April. Plants grow since the ground is partially exposed, first gradually then speedily in late May to June. During the hot season, mid July to mid August, the plant zonation is most conspicuous : Zone A, the exposed beach with no grass cover. B, nearly monopolized by *Elymus mollis*. C, *El.*

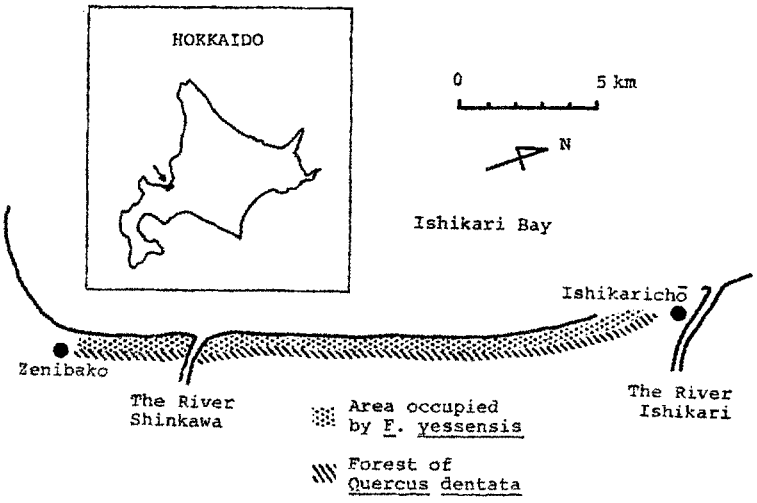

Fig. 1. — Ishikari Coast where a huge supercolony of *F. yessensis* is situated.

Fig. 1. — Côte d'Ishikari où se trouve une gigantesque super-colonie de *F. yessensis*.

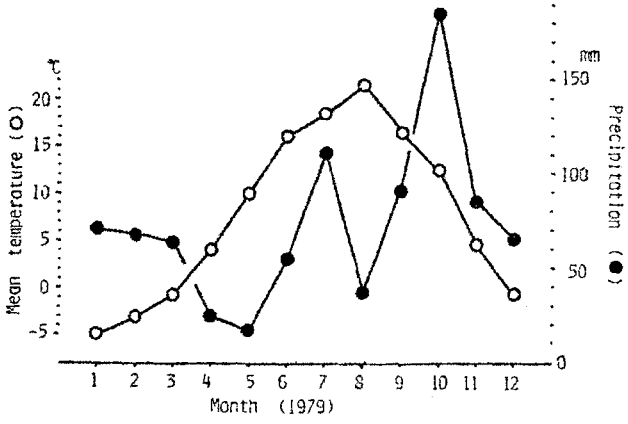

Fig. 2. — Monthly precipitation and average temperature in 1979 at Ishikari Coast.

Fig. 2. — Précipitations mensuelles et température moyenne en 1979 à Ishikari.

mollis with occasional admixture of *Calystegia soldanella, Carex kobomugi, Poa pratensis,* etc. D, frequent appearance of *Rosa rugosa, Ca. kobomugi, Equisetum hiemale,* etc. with occasional admixture of *Miscanthus sinensis.* E, dominated by crowds of *Mi. sinensis* with the plant density higher than in D. F, densely covered with *Mi. sinensis, Celastrus orbiculatus, Vitis coignetiæ, Lonicera morrowii,* etc. The nests of *F. yessensis* are abundant in zones D to F. From late August the plants gradually wither, and winter scene dominates the coast in November.

For a long time this coast was not disturbed by human activities. Recently the development of a big Ishikari New Port was started by the government of Hokkaido. Thus, most nests of this supercolony are destined for extinction in the near future.

METHOD

In total eight quadrats, each 10 × 10 m, were chosen in various seasons from the winter in 1974 to autumn in 1975 and all nests in each quadrat were excavated to see the vertical distribution of queens: quadrat I (henceforth Q I) with 10 inhabited and 11 abandoned nests, excavated in mid November to early December, 1974, i.e. hibernation season; Q II with 13 inhabited and 14 abandoned nests, May 7 to 12, 1975, post-hibernation; Q III with 13 inhabited and 2 abandoned nests, May 26 to 31, beginning of budding; Q IV with 18 inhabited and 1 abandoned nests, June 10 to 16, the midst of budding; Q V with 18 inhabited nests, June 30 to July 5, the end of budding season; Q VI with 16 inhabited nests, July 18 to 24, beginning of nuptial flight; Q VII with 21 inhabited nests, August 10 to 16, post-mating; Q VIII with 11 inhabited and 11 abandoned nests, September 21 to 25, prehibernation. At three nests in each quadrat the vertical distribution of workers was also checked to compare with that of queens.

Moreover, in the mating season some observations were also made to see why some queens abandon their nuptial flight.

RESULTS AND DISCUSSION

Seasonal fluctuation of queen distribution in the nests

The vertical distribution of queens and workers seasonally fluctuates *(fig. 3 and 4),* preferring deeper parts (mainly 40 to 60 cm) during hibernation but shallower parts (10 to 40 cm) in the summer. One of the causes of this tendency may be the seasonal fluctuation of soil temperature, being warmer at lower parts in winter but at upper parts in summer (*fig. 5*). Furthermore we can also suppose that the queens passively move with the workers. If so, the vertical distribution of queens should correlated with that of workers. In fact, the coefficient of correlation (r) is great from winter (QI) to early July (QV), i.e. $r = 0.8$. But from mid July (QVI) to prehibernation season (QVIII) it is 0.6 or less, in the minimum $r = 0.313$ in QVII surveyed in nuptial season. This may be at least due to the following two causes: First, the queens stop laying eggs before early August (Ito, 1973; Higashi, 1976), which may reduce the correlation between queens and workers. Second, alates and/or some newly dealated queens having returned after copulation may

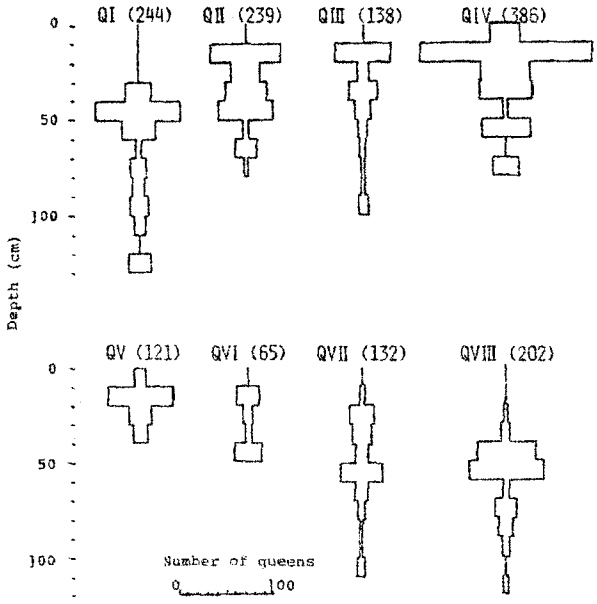

Fig. 3. — Vertical distribution of queens in each quadrat. The width of each belt shows the number of queens in each depth. In parentheses, total number of the queens.

Fig. 3. — Distribution verticale des reines dans chaque quadrat. La largeur de chaque bande indique le nombre de reines aux différentes hauteurs. Entre parenthèses, le nombre total de reines.

complicate the distribution of queens. If the queens are distributed randomly among nest chambers, the Poisson distribution of queen abundance per nest chamber should be expected, but this is not the case *(fig. 6)*. In any season the queens tend to aggregate with each other in the same chambers. Considering this phenomenon and that most, if not all, queens have well developed ovaries in the egg-laying season *(fig. 7)*, there seems to be no hostility among the cohabiting queens.

Mating

Since 1969 except for 1973 and 1978 the extent of nuptial flight has been recorded. The swarming of alates was observed in 1971 and 1974 to 1979 but not in 1969, 1970 and 1972. However, it is difficult to find alates in this coast for the following three reasons. First, as *figure 8* shows, the alates appear on the nest surface in early morning, and after about 8:00 they cannot

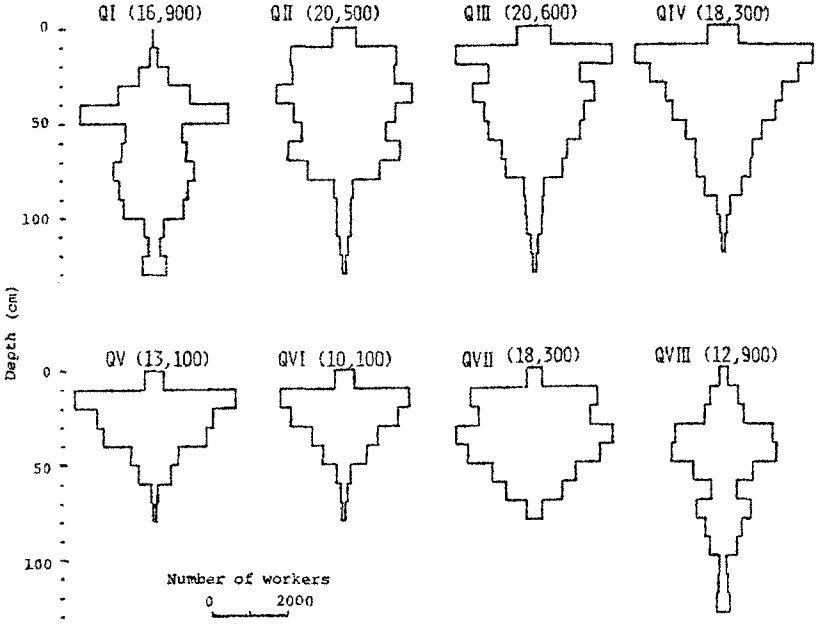

Fig. 4. — Vertical distribution of total workers within three nests.

Fig. 4. — Distribution verticale des ouvrières à l'intérieur du nid.

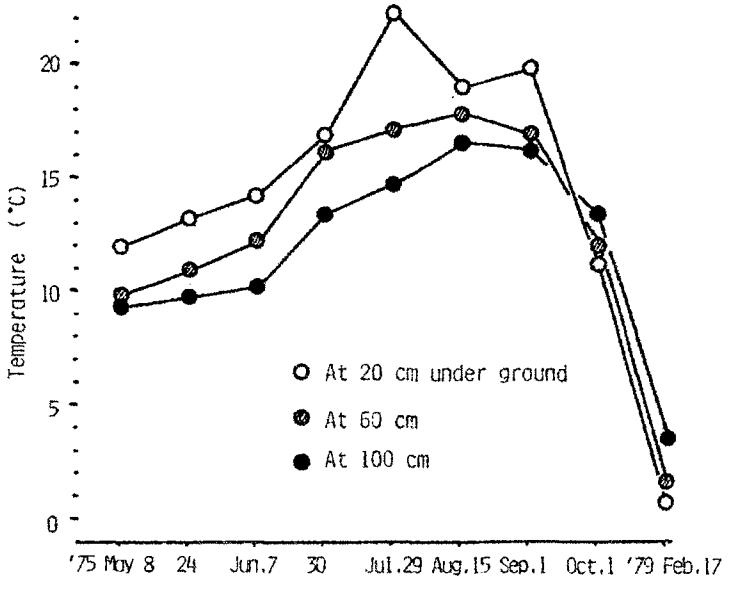

Fig. 5. — Underground temperature at Ishikari Coast. In late autumn to winter the deeper levels are warmer.

Fig. 5. — Température sous la surface du sol à Ishikari. De la fin de l'automne à l'hiver, les niveaux profonds sont plus chauds.

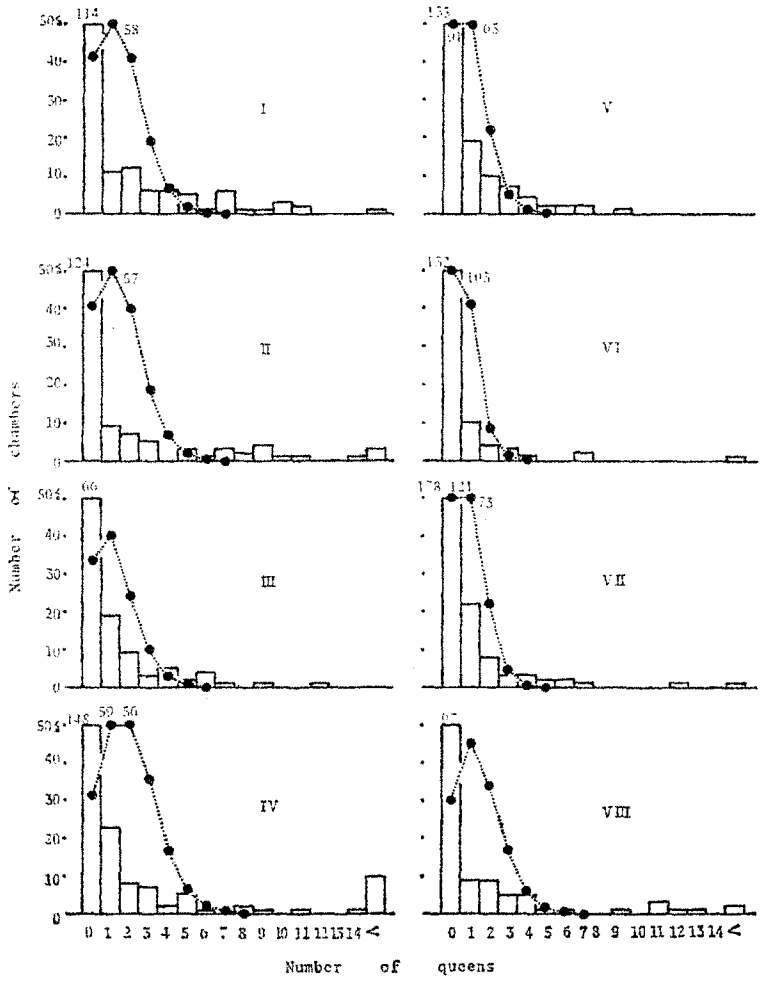

Fig. 6. — The frequency of queen abundance per chamber. The line graph shows the corresponding Poisson distribution.

Fig. 6. — Fréquence de l'abondance des reines par chambre. La ligne indique la distribution de Poisson correspondante.

be discovered without excavating the nests. Second, the period of full-scale flight is very short, only several days, when fine and calm days continue in late July. Third, the swarming of many alates is seen only at limited sites where the large nests with sexuals aggregate, and it is doubtful whether any sexuals were produced in 1969 and 1972. But in 1970 Ito (pers. com.) could

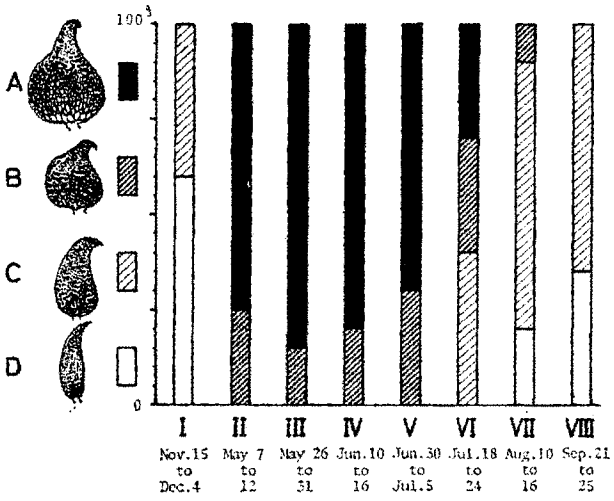

Fig. 7. — Annual trend of ovarian development of queens. In each season 20 queens were dissected. A. well developed ovary containing many mature eggs. B. developed with less mature eggs than in A. C. containing only immature. D. atrophic.

Fig. 7. — Variations annuelles du développement ovarien chez les reines. 20 reines sont disséquées à chaque saison. A. ovaire bien développé contenant de nombreux œufs mûrs. B. développé mais moins d'œufs mûrs que dans A. C. seulement des œufs immatures. D. atrophié.

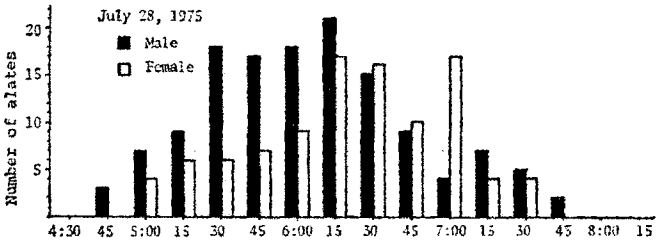

Fig. 8. — Fluctuation of alate abundance on and arround a nest on July 28, 1975.

Fig. 8. — Fluctuations de l'abondance des ailés sur et autour d'un nid le 28 juillet 1975.

not observe any sexuals in spite of frequent visits to the coast to see the swarming. Therefore, it is likely that *F. yessensis* on the coast usually produces abundant sexuals each year but occasional absence of such mass production is possible.

In order to discover the mechanism by which some new queens stop flying away, their behaviour should be observed in detail in the nuptial

season. Some aspects of flight activities in *F. yessensis* at Ishikari Coast have already been reported by ITO and IMAMURA (1974). In the present paper the results obtained since 1975 are described.

Alates fly early morning in late July to early August. For instance, on July 28, 1975, one male first appeared on a nest surface at 4:35, air temperature 19.1°C, just after the dawn *(fig. 8)*. Then males gradually increased, reaching the maximum (about 20) at 5:30 to 6:30. Many males climbed the grasses. After staying for several minutes on the grass blades, most of them flew away. Only a few ones flew up from the nest surface. An alate female first appeared at 4:54, 19.2°C, about 20 minutes later than the first male. The females also increased gradually, reaching a maximum (17) at 6:15 to 7:00. Many females climbed the grasses and some of them flew away. However, most flyers are blown by the morning wind which always blows from the land to the sea, and most, if not all, of them would fall on the sea and die there. First copulation was seen on the nest surface at 5:07, 19.2°C, continuing about 3 minutes. After the sun shine fell on the nest surface at 5:50, males were excited and frequently flew away or copulated with females staying on the grass blades. The copulation lasted about 3 to 5 minutes. After the sun shine became fierce at about 7:00, 22.2°C, the alates decreased and completely disappeared at about 8:00, 26.1°C. The alates were absent from all nests by August 2.

From 1975 to 1979, in total 50 alate females were pursued each for 20 minutes in the maximum. After the pursuit they were captured to see whether they had been inseminated or not. The flying females were caught by net and the returning ones picked up just before entering the nest. Seventeen females were captured in resting on the grass blades ; 16, just after flying up ; 5, wandering on the ground ; 12, entering the nest. Out of them, only 7 were inseminated : 0/resting, 0/flying, 2/wandering, 5/entering nest. Thus, the resting or flying females were virgin while some of returning or wandering ones were inseminated. In 1977 and 1979, in total 25 females copulating on the grass blades were also pursued. Out of them only 6 flew away but others entered neighboring nests (15) or wandered on the ground (4). These facts show that many inseminated females tend to return to the nest while most virgins try to fly away.

In 1975, 103 apterous queens were collected by excavating 10 nests in a swarming site in early August when the nuptial flight finished. Following interesting results were obtained. 1. Even in the nests from which males and females had emerged in the mating season (nest no. 1, 2, 3 in *table I)*, the contained queens were few, 9 to 18. This probably shows that the inseminated queens do not always return to their mother nest but often disperse to neighboring nests. 2. Queens captured were all inseminated. This should also mean that the females try to fly away if virgin in this coast. This is supported by the observation of GÖSSWALD (1962), in which the

Table I. — Nests excavated in early August, shortly after the nuptial flight finished.
+ : many alates emerged in flight season.
— : no alate emerged.

Tableau I. — Résultats de l'excavation des nids au début du mois d'août, juste après la fin du vol nuptial.
+ : beaucoup d'ailés ont quitté le nid durant la saison du vol.
— : aucun ailé n'est apparu.

Nest no.	1	2	3	4	5	6	7	8	9	10	Total
Alate	+	+	+	—	—	—	—	—	—	—	
Queen	18	13	9	31	17	13	2	0	—	0	103

inseminated females of *Formica polyctena* run to the dark site and abandon their wings while the virgins seek lightness.

However, some dealated queens are virgin in *F. polyctena* (SCHMIDT, 1971) and *F. lugubris* (CHERIX, pers. com.), which heavily contribute to male production (EHRHARDT, 1970). The long survival of virgin queens is uncommon in monogynous ants because they cannot produce workers which are generated only from the fertilized eggs. And the survival is possible only in polygynous colony. The scarcity of the dealated virgins in the polygynous ant *F. yessensis* may be due to the open habitat where alates can try to fly away. On the other hand the closed habitat forest and its margin more preferred by *F. polyctena* and *F. lugubris* may prevent the flight of some virgins. In any case, the exact reason why some virgin queens are contained in the colonies of *F. polyctena* and *F. lugubris* should be concluded by the further physiological and ethological studies of alates.

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