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Observations on the Nuptial Flight and Internidal Relationship in a Polydomous Ant, *Formica* (*Formica*) *yessensis* Forel[1]

By

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(*With 2 Text-figures and 5 Tables*)

Concerning the biology and ecology of a Japanese red wood ant, *Formica* (*Formica*) *yessensis* Forel, nest distribution (Ito 1971), seasonal population trends and nest structure (Ito 1973), and hibernation (Imamura 1974) have been described, mainly based upon observations made at the Ishikari Shore, Hokkaido, Japan. The present paper deals with some observations on the nuptial flight and internidal relationship in this species.

Numerous observations on nuptial flights of ants have been reported, but most of them are rather fragmentary, describing only the localities and times of incidence. Recent studies indicated the influence of climatic factors such as light intensity and temperature on the nuptial activity of many species of the genera, *Dolichoderus* (Kannowski 1959), *Formica* (Kannowski 1959, '63, Scherba 1958, '61, Talbot 1948, '59, '64), *Lasius* (Kannowski 1959), and *Myrmica* (Kannowski 1959). On the other hand, McClusky (1958, '65) suggested the endogenous time sense in *Iridomyrmex* and *Veromessor* males kept under laboratory conditions, showing a sharp increase in restlessness at just the hour at which nuptial flight occurs in the nature.

However, there are various types of nuptial flights in ants, differing in number and flight ability of the participating sexuals. In most species the queens start new colonies solitarily after the flights. But in some species the establishment of new nests is wholly accomplished by workers (budding), usually accompanying the reduction or ultimate omission of flight behavior.

In the present paper, the flight activity of *F. yessensis* which proliferates by budding is compared with other species of the genus *Formica* and the peculiarities of the present species are briefly discussed in reference to the polydomous system adopted by the species with frequent internidal drifting.

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[1] Biological and ecological studies of *Formica yessensis* Forel IV.

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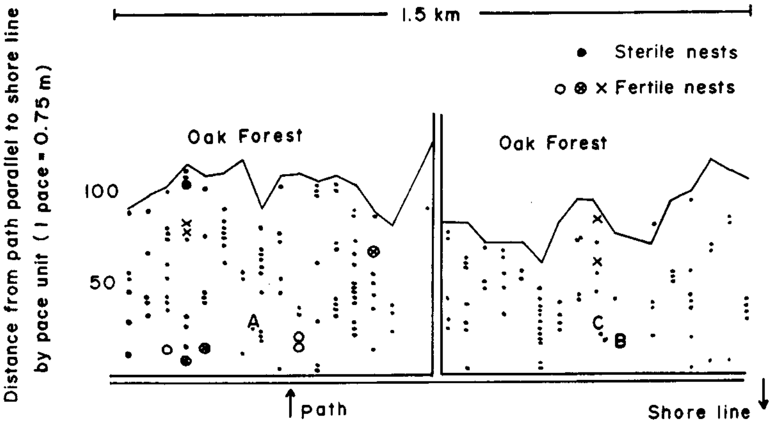

Fig. 1. Solid circles, sterile nests containing no sexual pupae. Open circles, fertile queen nests with more than 7 queen pupae within the 10 sexual pupae sampled. Crosses, fertile male nests involving more than 7 male pupae within the 10 sexual pupae sampled. Crossed open circles, fertile amphi-sexual nests containing more than 4 and less than 7 queen pupae within the 10 sexual pupae sampled.

Most observations related to the nuptial flight were executed by M.I., while those on internidal relationship by S.I.

Results and Discussions

The flight activity of *F. yessensis* was observed in Ishikari Shore in 1971. Intensive observations were made at three nests, A, B and C, respectively on August 8, 10 and 12∼15. Nest A was about 800 m remote from the other two which located 10 m apart for each other (Fig. 1). Beside them observations were casually carried out at other nests.

1. *Flight season*: The term 'flight season' is used here following the definition by Kannowski (1959), "the time interval during which flights of a species occur in a given area". *F. yessensis* hibernates only as adults (Imamura 1974) and post-hibernating queens start egg-laying in May (Ito 1973). The first sexual pupa was obtained on July 2, 1971, being the earliest record of pupa at Ishikari Shore. One alate was found within a nest on July 26, 1971, as the unique alate found within nests by excavation. The first flight was observed on August 8 and the last one on August 15, 1971. Although no systematic observations have been made, we roughly estimate the flight season of this species in Ishikari as late July to mid August. Table 1 presents the flight seasons of various *Formica* species, mostly cited from Kannowski (1963) except for *F. subnitens* (Ayre 1957) and the present species. Some European species, *F. rufibarbis*, *F. rufa* and *F. pratensis*, have flights in spring while all Nearctic species make flights only in summer.

Table 1. Flight seasons of various *Formica* species given by subgeneric names. Except *F. subnitens* (Ayre 1957) and *F. yessensis*, the information cited from Kannowski (1963). The subgeneric system follows Dlussky (1967). Some Nearctic species put in *Formica* s. str. by Creighton (1950) were placed in *Serviformica.*

Subgenus and species	Dates	Location
Formica		
pratensis Retzius	1) May 2, August 10. 2) June-October 3) May 13, 31	1) Switzerland 2) Germany 3) Germany
rufa Linnaeus	1) June 15 2) May 13, 31	1) England 2) Germany
obscuripes Forel	1) June 16–29 2) June	1) Michigan 2) North Dakota
subnitens Creighton	1) Late June-Early July	1) British Columbia
yessensis Forel	1) Late July-Mid August	1) Northern Japan
Serviformica		
rufibarbis Fabricius	1) April 18 2) July 1	1) England 2) Switzerland
cinerea Mayr	1) Late June-Mid July	1) Switzerland
fusca Linnaeus	1) August 2	1) Michigan
montana Emery	1) July 10-August 8	1) North Dakota
Coptoformica		
ulkei Emery	1) June 26-July 18 2) July 2–9	1) Michigan 2) Illinois
exsectoides Forel	1) August 6 2) July 9	1) Massachusetts 2) Tennessee
opaciventris Emery	1) August 10–24	1) Wyoming
Raptiformica		
sanguinea Latreille	1) July 3	1) Switzerland
subintegra Emery	1) July 6–27	1) Ohio
Neoformica		
pallidefulva nitidiventris Emery	1) July 12–24 2) July 15-August 4	1) Ohio 2) Michigan

Furthermore, the flight of *F. pratensis* is prolonged from May to October. This seems to be mainly due to the warmer local climate in England, Germany and Switzerland than in the areas of North America where the observations were made. Although no detailed climatic data are at hand, the average year temperatures in the localities given in Table 1 are roughly 10° to 15°C in Europe, 5° to 10°C in the United States and 7°C at Ishikari Shore, Hokkaido.

2. *Flight period*: Flight period is the time of the day at which flights take place (Kannowski 1959). The records in *F. yessensis* since the appearance to disappearance of alates on the nest surface and around it are shown in Table 2 with some climatic cues for the respective day of observation. Throughout the observation days, alates emerged from nests onto the nest surface between 5:00

Table 2. Time of mating activity of *F. yessensis*. The single asterisk means the occurence of the endogamous mating on the nest surface, and double ones those at nest entrance.

Date	Weather	Nest	Appearance	First copula
Aug. 8, 1971	fine, windy	A	5:20 a.m.	6:10 a.m.
10	cloudy, slightly windy	B	5:20	6:17
12	cloudy, slightly windy	C	?	?
13	overcast, windy	C*	5:00	5:30
14	fine but partly cloudy, calm	C**	5:10	6:04
15	cloudy, calm	C**	?	6:38

(*Continued*)

Date	Climax of mating	Disappearance	Ground surface temperature at appearance
Aug. 8	6:25—6:35 a.m.	8:10 a.m.	18.8°C
10	6:35—6:50	8:05	18.8°C
12	6:45—7:00	?	?
13	?	7:55	18.0°C
14	6:40—6:50	?	17.5°C
15	6:45—7:00	8:20	?

and 5:30, about 30 minutes after dawn, and disappeared between 7: 55 and 8:20. Table 3 gives the comparison of flight periods. But the start of flight would in part be affected by the time of sunrise which varies mostly by season and latitude, so that the data in the table may not be directly useful for precise comparison, unless measurements of light intensity and temperature, etc. are undertaken. At the present, it can only be said that flights of *Formica* tend to occur at early morning hours in various subgenera, with exceptions of two European species, *F. pratensis* and *F. rufa*, observed to fly much later. The Nearctic *F. montana* also flies in the evening. Although flights of *F. montana* in morning hours were confirmed, Kannowski (1963) presumed that they were the males left over from the previous afternoon.

3. *Mating activity*: Nuptial flight of *F. yessensis* is not so spectacular as in many other ants, with only up to 40 males emerging from one nest in a day to participate in the flight as far as observed. Queens have not been counted but apparently they do not largely outnumber males as the sex ratio of alates in this species is about 1:1 as described in section **6**. At about 5:00 alates of both sexes appear from nest exits, not interfered by workers. No modification of nest exits by workers prior to flight as reported in *F. rufa* by Marikovsky (1961) is detected. The alates ramble on the nest surface, repeating to enter and to come out of the exits for a half to one hour, then climb herbs and grasses nearby the nest with a slight precedence by males (Fig. 2-A, B). The alate queens also climb the same

Table 3. Flight periods of various *Formica* species. Asterisked species, the European, all others, the Nearctic, except *F. yessensis*. The sources of data given in Table 1.

Subgenus and species	Flight periods
Formica	
pratensis Retzius*	10:00 a.m., in morning, shortly after noon
rufa Linnaeus*	4:00 p.m., mid afternoon
obscuripes Forel	5.50–11:40 a.m., 7:08–11:20 a.m.
subnitens Creighton	8:00–10:00 a.m.
yessensis Forel	5:00–8.20 a.m.
Serviformica	
rufibarbis Fabricius*	7-00 a.m.
fusca Linnaeus	7:00–11:30 a.m., 8:50 a.m.
montana Emery	2:00–6:30 p.m., 5:30 a.m.-noon
Coptoformica	
ulkei Emery	5:20–9:05 a.m., 6:30–8:30 a.m.
opaciventris Emery	7:00–10:00 a.m.
Raptiformica	
sanguinea Latreille*	7:00–8:00 a.m.
subintegra Emery	7:00–10:00 a.m., 7:30–11:00 a.m.
subnuda Emery	early morning
Neoformica	
pallidefulva nitidiventris	6:10–11:40 a.m.

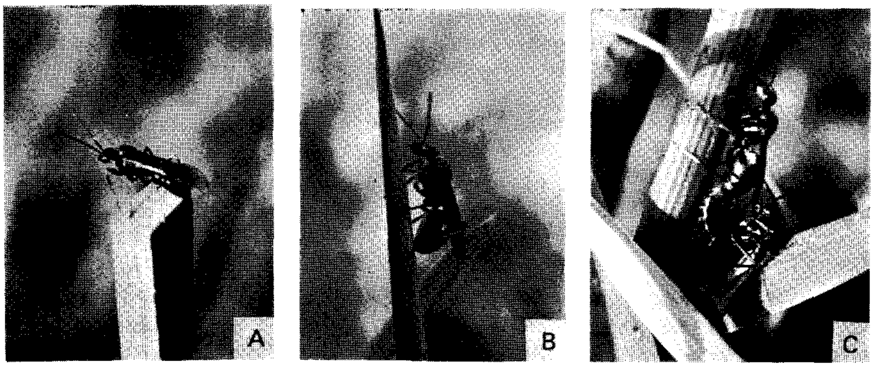

Fig. 2. Mating behavior: A. A male, just before flight, on a top of stick nearby the nest. B. A queen on a grass blade. C. Copulating posture.

posts but some of them continue to ramble without climbing.

In fine morning, males are activated and flutter as soon as the first sun beam strikes them. Some of them fly up to about 0.5 to 1 m high, slightly above the herbs, while others do not take off and continue to crawl on the plants. The low flight of males has been reported in *F. montana*, *F. subintegra* (Kannowski 1963) and *F. opaciventris* (Scherba 1961). Queen flight prior to copulation was not observed in the present species. In cloudy morning, flights are hardly seen but both sexes are apt to ramble on the nest surface. The lingering males are suddenly activated by accidental encounters with queens of their own nest and copulations take place among them. But such matings are apparently few and do not necessarily mean adelphogamy, the brother-sister mating, for frequent internidal transport of queens in spring (Imamura unpubl.) and for their entering nearby nests just after mating. As described in section **6**, both sexes tend to be produced in the same nest in this species.

The copulatory behavior seems almost similar to that of *F. subintegra*, *F. montana* (Kannowski 1963) and *F. opaciventris* (Scherba 1961): 1). Alighting at a spot about 20 to 30 cm remote from the queen on the plant, the male crawls in a slight zig-zag manner. 2). Once detecting a queen, the male approaches her straightly and tries to hold onto the dorsum of her thorax with the fore and mid legs and her gaster with the hind legs. Thereafter; if resistive, 3). The queen bends her gaster forward ventrally and moves away. If receptive, 4). The copulation is accomplished, and the male releases his hold on the thorax and extends posteriorly upsidedown from the queen gaster (Fig. 2-C). 5). Copulation lasts 30 seconds to 9 minutes (12 cases measured, mean 4.5 minutes).

The copulation time in *F. yessensis* seems longer than in *F. subintegra* where it was about 6 to 30 seconds and in *F. opaciventris*, 40 seconds to 2 minutes. The mating posture seems similar in *F. montana*, *F. subintegra* (Kannowski 1963), *F. pallidefulva schaufussi* var. *incerta* (Talbot 1948), *F. polyctena* (Gösswald 1957) and *F. yessensis*. Some agitated males rashly try to mate even with workers or fellow males. This suggests that the male of *F. yessensis* is unable to distinguish queens from other castes until the final phase, proposing an interesting problem for comparison.

Both sexes can mate more than once, though queens usually show the rejecting response cited above. Toward the end of mating period, males lose their energy and are usually caught by workers of their own species and dragged into nests as reported in *F. opaciventris* by Scherba (1961). The agitated phase of males lasts about a half to one hour.

The post-copulatory behavior of queens is variable. Three queens, Nos. 1～3, were found on herbs near the observed nest, A (cf. Fig. 1), on August 8, 1971, and their behavior was traced.

No. 1 was discovered on a blade at 5:50. Soon after the end of her first copulation taken place 6:10～6:19, she started to descend the blade to the ground and entered A where she emerged from.

No. 2 was discovered on a blade at 6:50. After the first copulation, 7:00～7:02, she took a rest on the blade several cm remote from the mating spot, grooming herself by licking the genital orifice and by cleaning antennae. Then she moved twice on the blade, in each passing several centimeters. About 40 minutes after her first copulation, a male approached her and mated with her in spite of her rejection. The second copulation lasted for 1.5 minutes. Soon after its completion, she suddenly became active and started to swiftly walk and to flutter and sometimes 'jumped' from a stalk to another. But she did not fly high so as to be lost from the sight. Finally at 7:45, after the rapid walking and 'jumping' over the distance of about 2 m straightly, she entered a nest next to the one she emerged from.

No. 3 was detected when she just mated on a blade at 7:30. As soon as the copulation terminated at 7: 32, she suddenly flew high and lost from the sight without showing any fluttering pause.

Generally speaking, most fertilized queens moved on foot and returned to the mother nests or entered some adjacent nests as in Nos. 1 and 2. Only a small fraction of them flew away.

Queens apparently unfertilized also return to the nests. The entering and returning of queens to nests are especially frequent at about 7:00 to 8:00, after the climax time of mating. Entering nests, queens are not carried by workers as sometimes done in *F. opaciventris* (Scherba 1961) or are rarely attacked by workers. Only five queens were observed to be attacked at A. One, a descendant from A, copulated with a nest mate on the surface of A and, while she was staying there, she was attacked and bitten off of her left wing. She stayed there until the observation was stopped. Two queens, probably not emerged from A were also attacked and one of them entered A in spite of the attack but the other walked away. The other two queens which came by air were rather violently attacked, one on a blade nearby A and the other just at an entrance of A. These two soon flew away elsewhere. The reason why some queens are attacked and others not is unknown and left for further clarification.

Besides, some interesting observations were gained: 1). When the daily mating activity was finished, an alate queen walked out of a nest at 7: 55, August 15, crawled about aimlessly and went into a long rest on a blade 3 m far from the nest, at least for two hours till the observation was stopped. This queen might be not fertilized. Kannowski (1963) described some secondary crawling of unfertilized queen of *F. subintegra*, "alate females from an all female nest....were observed to climb the stems on the mound early in the flight period and later, after no males had approached, to individually move down from the stems and out into the grass and up stems about 20–30 feet from the nest".

2). Prior to the start of daily mating activity, a dealated queen came from elsewhere and entered the observed nest, C, at 5: 07, August 14, 1971. The migration of dealated queens were observed in *F. rufa* by Marikovsky (1961), who speculated the function of this behavior as either to copulate for receiving sperm again or possibly to escape from nests "where producing females which do not participate in oviposition are in excess". But the present instance might be a mere emigration of an old queen irrespective of mating activity. At least these internidal movements of dealated queens present an information useful for the understanding of internidal relationship in these species.

3). When a male was trying to go out of the nest C at 6:00 on August 13, overcast and windy, a worker caught him by an antenna and took him back into the nest. In contrast to this case, several workers dragged a male out onto the nest surface at another nest at 8:00 on August 15, cloudy and calm, and the male soon flew away. These facts show that workers of *F. yessensis* control the activities of alates under some adequate conditions.

4. *Ratio of fertile nests in the nest population*: As in *F. opaciventris* observed by Scherba (1961), *F. yessensis* produces sexuals in only a fraction of nest population (cf. Fig. 1). In order to know the ratio of fertile nests producing sexuals, 178 nests were inspected during July 23 and 26, 1971, when the sexuals were in the pupal stage. At the census, only the superficial structure of nest was excavated and the pupae examined. Sexual pupae are distinctly larger than worker ones and the color of the cocoon is brown while yellowish white in the latter. As pupae are mostly stored in chambers, usually shallower than 10 cm, the determination of nest fertility by this method is regarded as reliable. Only 11 out of 178 nests or 6.4% contained sexual pupae. Occasional storage of sexual pupae in deeper chambers might have caused a slight underestimation, but it seems much lower than that in *F. opaciventris*, estimated as 20 to 25% by Scherba (1961). For a better estimation, however, the budding frequency should be considered together, because young nests recently formed by budding may not produce sexuals. As the detailed data on the relation between the age and fertility of nests have not been obtained, we simply present here the budding ratio of this species at Ishikari Shore, combining the results in 1970, '71 and '73. In these observations four quadrats were used, three of them are 10×10 m sq., each containing 10, 13 and 7 nests at the start of observation on April 22, 1973, and one 15×15 m sq. involving 33 nests at May 29, 1970. Some of these 33 nests may be those produced by budding in that year, but other cases are, in all probability, post-hibernation nests, though the age of each nest was unknown. In the first three 10×10 m sq. quadrats 39 nests in total were built by budding until June, 1973, and none of them perished. In the 15×15 m sq. quadrat 42 nests were produced by budding in active seasons of 1970 and '71, though 33 out of 42 buds and 18 of 33 preexisting nests were abandoned during the years (reoccupation of old nest sites is also regarded as budding). Therefore, almost a half of the 178 nests censused on July 23~26, 1971, for the estimation of the ratio of fertile nests were those newly produced in the same year and, the life span of nest is relatively short in the shore. Consequently, the real ratio of fertile nests among more or less established nests are estimated as $6.4\times(30+39)/30=13.7\%$, using only the data in 1973 and assuming that the buds newly formed the year do not produce sexuals.

5. *Structural characteristics of fertile nests*: *F. yessensis* does not build huge and compact mounds as those known in *F. polyctena* and *F. ulkei*, etc., distributed in Europe and North America. The mounds in *F. yessensis* is a mere loose thatch consisting of 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 plants in the shore (Ito 1973). The size of mound is small, covering only a part of flat nest surface, with the basal diameter less than 20 cm and height 5 cm in most cases. A considerable number of nests lack mounds.

Table 4. Relation between nest fertility and mound development. Further explanations in text.

Nest diameter (cm)	Number of fertile nest (with large mound)	Number of sterile nest (with large mound)
0-25	0(0)	31(1)
-35	0(0)	37(6)
-45	1(1)	31(7)
-55	3(3)	25(6)
-65	3(2)	13(2)
-75	2(1)	6(2)
-85	0(0)	6(1)
-95	0(0)	5(3)
-105	0(0)	2(0)
105-	2(2)	11(2)

It was found in the census that fertile nests had larger mounds than sterile ones. Nine out of the 11 fertile nests had relatively well-developed mounds exceeding 20 cm in basal diameter and 5 cm in height, while only 30 out of 167 sterile nests had such well-developed mounds (Table 4). This may or may not mean that the warmer intranidal climate provided by mounds facilitates the quick growth of sexual pupae larger than worker ones, or that sexual larvae spur the thatching behavior of the workers.

6. *Sex ratio*: At the excavation of fertile nests, ten sexual pupae were randomly collected from each nest and the sexes were determined by tearing the the cocoons. The result is as follows;

Nest No.	Nest diameter	Number of queen pupae	Nest No.	Nest diameter	Number of queen pupae
1	155(cm)	5	7	60	5
2	145	0	8	55	2
3	75	3	9	55	9
4	75	6	10	55	4
5	65	10	11	45	3
6	60	9			
				Mean 76(cm)	Total 56

The sex ratio was approximately 1:1 in total, although it was variable among nests. This result markedly contrasts with that reported in *F. opaciventris* by Scherba (1961), where male-female ratio was approximately 18:1. Also in some colonies of *F. obscuriventris* and *F. obscuripes* observed by Talbot (1964, '59 respectively), males outnumbered queens.

In many species of the genus *Formica* each fertile nest tends to produce either only males or queens in one nest but not both, as known in *F. polyctena* (Gösswald 1951) and *F. opaciventris* (Scherba 1961). In *F. yessensis*, however, nine out of 11 fertile nests contained both sexes despite that only 10 pupae were examined at

Table 5. Internidal movements in 320 recaptured workers. Further explanations in text.

Nest	Number of marked workers		
	residental in	visiting	
I	92	II 3	III 2
II	94	I 14	III 6
III	92	I 8	II 9
Total	278	42	

each nest. In *F. opaciventris* only 2 to 5% of fertile mounds produced both sexes and in the unisexual mounds the ratio of male-only: queen-only nests was approximately 30:1 (Scherba 1961).

7. *Internidal relationship*: Internidal movements of workers were studied in Ishikari Shore with three nests, (I, II and III) in August, 1972, when the nest proliferation by budding was completely passed over. At Ishikari budding occurs only in spring and early summer, from May to July (Ito 1973). Three observed nests were spaced, I–3m–II–5m–III–4m–I. Inhabitants at the nest surface of each nest were marked on the dorsum of gaster with lacquer paints of different colors on August 10, 22 and 29, and censused on August 14, 20, 27 and September 3. At the census the nest surface was repeatedly patted with a hand and marked workers rushing out of nests were captured and counted (Table 5). The procedure was continued for about 15 minutes in each case until no marked ants were seen on the nest surface. After counting they were released at the nest where they were captured. In total 2,250 individuals were marked and 320 of them were recaptured, including possible double recaptures or more. Among these 320 recaptured workers 42 were found in the nests where they were not marked, and the visits were reciprocal. Scherba (1964) invented 'the visting ratio' for *F. opaciventris* as (total number of visits counted/total individual number marked)×100. The ratio is useful for comparison among different species, provided the mark removal is checked in each case. The ratio for *F. opaciventris* was 1.99±0.70%. At the census he did not release recaptured marked workers in order to avoid double recaptures which would give a higher ratio. The 'visiting ratio' for *F. yessensis* could not be precisely calculated because the census method was different and the mark removal was not checked, but roughly lies between $2\sim4\%$.

However, recaptures of marked individuals, in general, can not be fully accomplished so that 'the visiting ratio' would be lower than the real ratio of visiting ants. For this reason, another ratio is introduced here, the 'drifting ratio' given as (total number of visits counted/total recapture number counted)×100. The 'drifting ratio' does not require to check the mark removal precisely for comparative purpose. But it may overestimate the real ratio, if visitors do not forage out of the nest in which they entered and the residental workers forage out of the nest where they were marked. For *F. yessensis* the 'drifting ratio' was much larger than the 'visiting ratio', that is $(42/320)\times 100=13\%$. But this value must have been apparently lower than the real ratio of internidal drifting, for a considerable number of marked individuals had visited other surrounding nests. On August 20, supplementary recaptures at eight other neighboring nests were made and three visits were confirmed. As eight visits were counted at the observed nests, I, II and III, on the same day, the compensated value is roughly $13\times(8+3)/8=18\%$.

On the other hand, in May 1973, Higashi (unpubl.) transferred 450 workers of *F. yessensis* from a nest found at roadside of Mt. Hakkenzan to a nest at Ishikari Shore which was perfectly surrounded by an iron plate preventing both incoming and outgoing of ants. He excavated the nest after a week and found that 413 were alive and 15 dead out of 450 which were marked on the dorsum of gaster. As Mt. Hakkenzan and Ishikari Shore are about 20 km apart each other and the habitat is very different, the former being a rocky south slope and the altitude about 300 m, it is certain that the internidal hostility in this species is almost absent.

Based upon these observations, *F. yessensis* is considered to form a polydomous system, though the species has no apparent internidal runways. Scherba (1964) considered *F. opaciventris* forms a discrete system, based upon the facts that nests are regularly spaced and no internidal runways are observed. But, as shown above, the absence of distinct runways may not necessarily mean that each nest is a discrete unit. It seems necessary to establish a clearer definition of polydomous system by testing the 'visiting ratio' as well as 'drifting ratio' and by studying the internidal hostility with many other ants.

Finally it must be mentioned that the exchange of nest members is practiced in *F. yessensis* by two methods; active drifting through own locomotion of adults and passive drifting of both adults and immatures transported by other workers. Although it is not excluded that some cases of drifting mentioned above realized by the second method, its ratio seems very low because the adults transported or transportees are mostly young individuals usually not rushing out from nests as those marked in the present study. The details on transports will be described elsewhere.

8. *Relation between reduced flight behavior and polydomous system*: Most species of the subgenus *Formica* found their nests by temporarily parasitizing the species of *Serviformica*. In *F. yessensis*, however, the heterospecific nests are so far recorded only twice in Hokkaido, one at Oshoro (cf. Ito 1971) and the other at

Kitamoshiri[1] (Imamura and Higashi unpubl.), both living with *F.* (*S.*) *japonica* Motchulsky. No such nests were discovered among innumrable nests occupying Ishikari Shore, nevertheless the nests of *F. japonica* were not scarce at the shoreside along the habitat of *F. yessensis*. This indicates the virtual dependance on budding as a colony proliferation method in the population at Ishikari.

It is probable that budding and degenerated nuptial flight are more or less correlated, as shown in the extreme cases in *Iridomyrmex humilis* (Skaife 1955) and *Monomorium pharaonis* (Peacock and Baxter 1950; Peacock et al. 1954; after Wilson 1971) in which the flights are absolutely abbreviated and the colonies multiply by fission. Further the latter two species are regarded as forming the polydomous system. In *F. polyctena* (Gösswald 1951) and *F. yessensis* the flight degeneration may not be so complete as in the above two species, but certainly more advanced than in most other ants. *F. polyctena* forms persistent internidal runways which facilitate the drifting of workers to neighboring mounds and *F. yessensis* exhibits frequent internidal drifting as described in the previous section, though without runways. Both these species proliferate through budding at least to some extent, and are assumed as polydomous ones.

Moreover the mating in these species would tend to be incestuous. In *F. yessensis* copulations among nest mates were confirmed under overcast and windy weather conditions which prevented flights, though they did not nesessarily mean adelphogamy, as the species is polygynous (Ito 1973), containing queens probably of various origins in one nest. It is also likely that the low ratio of fertile nests mentioned previously, together with the reduced flight behavior, accelerates inbreeding which may play a role in establishing the polydomous system by reducing the odor difference among nests.

In comparing the two forms of the *F. pallidefulva* complex, *F. pallidefulva schaufussi* var. *incerta* Wheeler and *F. pallidefulva nitidiventris* Emery, Talbot (1948) found that in *incerta* only 12 out of 21 colonies excavated contained alates while in *nitidiventris* 19 out of 21 colonies had winged forms. She showed that *incerta* was polygynous but *nitidiventris* monogynous, and the nest distribution of the former was clumpy while that of the latter sparse. She also observed in *incerta* one case of budding, and one copulation at the nest site followed by the entry of the post-copulatory queen into a nearby nest on foot. Although the nuptial flights in both species were not degenerated and most alates flew out of the sight, the descriptions suggest that *incerta* somewhat resembles polydomous species such as *F. yessensis*, while *nitidiventris* most other monodomous ones with discrete system, though internidal drifting in these species was not studied.

It seems probable that there are various degrees of flight degeneration and a parallelism between abbreviation of flight and dependance on budding. It is also possible that clumpy distribution of nest caused by budding tends to accelerate

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[1] The distinction between *F. yessensis* and '*F. truncorum* Fabricius' living in northern part of Hokkaido is difficult, but the colony observed was tentatively assumed as *F. yessensis*.

internidal drifting of workers. Further studies along this line are required with various ant groups, especially the genus *Formica.*

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Summary

The flight season of *F. yessensis* was estimated as late July to mid August and the flight period early morning. Under fine weather conditions most males and queens climbed herbs near nests after rambling on the nest surface, but some queens did not climb. Most males then flew up to about 0.5 to 1 m high, slightly above the herbs, but queens rarely flew. The sequence of mating was as follows: 1). Alighting at a spot about 20 to 30 cm remote from the queen on plants, the male crawls in a zig-zag manner. 2). Once detecting the queen, the male approaches her straightly and tries to hold onto the dorsum of her thorax with fore and mid legs and the gaster with the hind legs. If resistive, 3). The queen bends her gaster forward ventrally and moves away. If receptive, 4). A union is made, and the male releases his hold on the thorax and extends posteriorly upsidedown from queen gaster. 5). Copulation lasts 30 seconds to 9 minutes (12 cases measured, mean 4.5 minutes). Under overcast and windy weather conditions flights are hardly seen and copulations among nest mates are observed on the nest surface. Both sexes copulate more than once. After copulation males weakened and were dragged into nests by workers. Most queens returned to the mother nest or some adjacent ones on foot but a few flew away. Fertile nests occupied only 6.4% of all nests, usually with larger mounds than sterile ones. The sex ratio of alates was approximately 1:1. Internidal movement of workers was quite frequent with the drifting ratio approximately 18%. The relation between degenerated nuptial flight and polydomous system was briefly discussed.

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