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Source: Zoological Science, 15(3) : 409-414

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.15.409

ZOOLOGICAL SCIENCE **15**: 409–414 (1998)


# Polygyny and Monoandry in the Ant *Formica japonica* (Hymenoptera: Formicidae)

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**ABSTRACT**—Queen number, mating frequency and nest kin-structure of the ant *Formica japonica* were studied in the field and the laboratory. Nest excavation in the study site, the east slope of Mt. Fuji, Gotenba, Japan, revealed that *F. japonica* is weakly polygynous all year round and the queen number increases after the nuptial flight season, suggesting the adoption of newly mated queens by established nests. Dissection and laboratory rearing demonstrated that nearly all queens in polygynous nests had mated and were fertile with mature oocytes in their ovaries. Multilocus DNA fingerprinting was used to examine kin relationships among ants found in the same nests. The fingerprint band patterns were apparently governed by a simple genetic rule and suggested monoandry (single mating per queen). The mean band sharing score of DNA fingerprints among full sisters was 0.90, and the mean value between queens and their daughters was 0.75. Comparison of DNA fingerprints of adult and pupal workers with pupal gynes suggested that multiple queens in a nest may contribute unequally to gyne (new queen) production.

## INTRODUCTION

The presence of multiple queens in a nest (polygyny) has significant consequences to many functions of ant colony, e.g. the growth rate, the number and distribution of nest sites, the colony longevity and survival rate, the sex ratio of offspring, and the kinship structure of nestmates (Hölldobler and Wilson, 1990). In some ant species with polygyny, reproductive output is shared equally among queens, but in some others they produce offspring differentially (Keller, 1988; Ross, 1988, 1993; Pamilo and Seppä, 1994). Since the offspring of ant colony contains both of fertile members (sexuals, i.e. gynes and males) and largely or absolutely sterile members (workers), the reproductive success of nestmate queens depends not only on their relative fecundity but also on the proportion of their eggs to develop into sexuals (Keller and Vargo, 1993).

*Formica* (*Serviformica*) *japonica* Motschulsky is one of the commonest ants in Japan, but its social structure has been controversial. Kondoh (1968) excavated nests of this species in Tokyo (35°35´N, 139°40´E), central part of Japan, and reported that all the nests he examined contained single queens (monogyny) in all the seasons except a short post-mating period, during which the nests became polygynous temporarily. To the contrary, Higashi (1979) studied the species at Ishikari Shore (44°15´N, 141°20´E) in more northern part of Japan, Hokkaido, and indicated that it is polygynous all year round. He also suggested the possibility of nest proliferation by budding and internest grouping before hibernation. There is another study on the population structure of *F. japonica*, in which Yamauchi and Suzuki (1987) reported polygynous and polydomous nature of this species in Gifu City (35°25´N, 136°45´E; c.270 km west to Tokyo). (Polydomy denotes use of several nests by single colonies while monodomy occurs when single colonies occupy single nests.) Genus *Formica* is known to contain species that show both monogynous and polygynous populations depending on the area of distribution. In some of these facultatively polygynous species, both population forms are observed even in the same geographical region (Rosengren *et al*., 1993). Thus, as for the social structure and its biogeographical variation of *Formica japonica*, more study is needed to know the details.

We report here the characteristics of polygyny of *F. japonica* studied on the east slope of Mt. Fuji, central Japan, and the kin structure of the nestmate ants revealed by multilocus DNA fingerprinting.

## MATERIALS AND METHODS

### Study site

The study site ($60 \times 100$ m$^2$) was established at the elevation of 1400 m on the east slope, Gotenba, of Mt. Fuji. This altitude is the highest limit of the vertical distribution of this species on Mt. Fuji (M. Kondoh, personal communication). The surface of this site, as well as the surroundings, was covered with a thick layer of scoria (breakable volcanic rock) and poorly vegetated (Inoue, 1982, for reference). As nest entrances of *F. japonica* are opened on the ground surface, a

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total of 207 nests were mapped based on this nest structure from May 1992 to October 1993. Analysis given below was done for the pooled data of both years.

Colonies of *F. japonica* in this area were apparently monodomous, drawing on the following observations. First, nest openings which supposedly belonged to a colony were aggregated well in a cluster, and such aggregations were spatially well separated from each other. Second, excavation in the active seasons indicated that nests of *F. japonica* extended vertically to the maximal depth of about 80 cm and nest chambers in the ground were located almost directly under the expanse of surface openings, suggesting that the underground horizontal connection between different nests is not plausible. Thus, in the following analysis, *F. japonica* nests, especially in active seasons, are considered independent units (but see below for the possibility of seasonal polydomy).

For marking each nest, a $15 \times 15$ cm$^2$ ceramic tile (Inax) was placed on the center of aggregation of nest openings and the number was given on the tile surface using a felt-tip pen. Of the nests marked in this way, 22 were fully excavated later and all or part of ants found were collected and brought to the laboratory depending on the study objectives. For the other nests, specimens were collected only from under the tiles, where adult ants (including queens) were coming up with immature individuals from the underground, especially, during daytime in fine weather.

**Laboratory treatment**

Part of queens collected in the field were dissected in the laboratory within 1 or 2 days after collection and their insemination and ovary development were examined. The other ants were reared in artificial nests placed in plastic trays at 20°C, or preserved in a freezer at –30°C.

**DNA fingerprinting**

To extract DNA from individual ants, we used a modification of the procedure described by Laird *et al.* (1991). A whole ant was minced in a 500 μl of cold 5% sodium citrate and the tissue was rinsed in another fresh volume of the same solution. Proteinase K (Wako) and lysis buffer (100 mM Tris-HCl, 5 mM EDTA, 0.2% SDS, 200 mM NaCl) were added, and the mixture was incubated at 55°C. Then RNase A (Böhringer Mannheim) was added to the mixture (100 μg/ml), and it was incubated at 37°C. Following a series of phenol-chloroform and chloroform extractions, DNA was precipitated using an equal volume of absolute isopropanol. Pellet was rinsed with 70% ethanol, dried under vacuum and dissolved in 100 μl of TE (10 mM Tris-HCl, 1 mM EDTA). Extracted DNA from a single individual amounted to 2 μg in adult and pupal workers and 10-15 μg in adult and pupal gynes.

2 μg of DNA from each specimen was digested with *Hae* III (Takara) under standard conditions. Digest was extracted by phenol-chloroform and chloroform, and then precipitated using two volumes of absolute ethanol at –80°C. Pellet was rinsed, dried and dissolved in 10 μl of TE and electrophoresed through an agarose gel (1%, 25 cm long, BRL) in TAE buffer (40 mM Tris-acetate pH 8.0, 2 mM EDTA). DNA size markers (*Hin*d III-digested λDNA) were run on each gel. The gel was depurinated in 0.5 M HCl, followed by denaturation in alkali solution (1.5 M NaCl, 0.5 M NaOH) and neutralization in 0.5 M Tris-HCl pH 6.7, 1.5 M NaCl. DNA was then transferred from the gel to a nylon membrane (Schleicher & Schuell) by vacuum blotting (Millipore) in 10xSSC buffer (1.5 M NaCl, 0.15 M sodium citrate). The DNA on the membrane was finally fixed by ultraviolet rays.

DNA clone pMY7, isolated from the ant *Manica yessensis* by K. M., was used as probes. The pMY7 is the genomic fragment containing T-rich regions (Satoh *et al.*, 1997). The probes were labeled with [α-$^{32}$P]dCTP by a multiprime labeling kit (Takara or Bio-Rad). Prehybridization and hybridization were carried out at 65°C in 263 mM $Na_2HPO_4$ pH 7.2, 1 mM EDTA pH 8.0, 7% SDS, 1% BSA (fraction V) (after Westneat *et al.*, 1988). After washing off the surplus probes, the membrane was exposed to Fuji RX film at –70°C, or to a BAS imaging plate (Fuji film).

**Evaluation of DNA fingerprints and statistical analysis**

Only DNA fragments from 2.0 kb to 23.1 kb were scored for analysis. To identify the fingerprint bands on the membranes, we made visual comparison on the band profile scans obtained with the BAS imaging analyzer.

Under arrhenotoky in Hymenoptera, if DNA fragments are inherited in a simple Mendelian fashion and also the queen mates with only one male, all her daughters (i.e. workers and gynes) should have a completely identical pattern as for the bands absent in the queen's profile. This is because such bands must originate from the haploid genome of the male parent. To examine this, DNA fingerprints of a queen and her laboratory-raised daughters were analyzed on 8 cultures.

To estimate the genetic relationships among nestmates, the mean band sharing score was used. Comparison were made only between the fingerprints run on the same gel. Bands were considered to be identical in two individuals if and only if the bands had similar mobility and intensity (Jeffreys *et al.*, 1985). Band sharing score, *s*, is given by $s = 2N_{ab} / (N_a + N_b)$, where $N_{ab}$ is the number of bands shared by two ants a and b, and $N_a$ and $N_b$ are total numbers of bands in a and b, respectively (Wetton *et al.*, 1987; Lynch, 1990).

Standard parametric procedures (basically, *t*-test) were used to test differences in mean *s* among groups. The mean *s* was calculated from all possible pair-wise comparisons within groups.

## RESULTS

### Number of queens and their fertility

Twenty-two nests of *F. japonica* were completely excavated during May-October and all of the queens discovered were collected. The queen number per nest ranged from 1 to 22 (mean = 5), but most nests (n = 18) had 2-9 queens (polygyny) and only 3 nests were monogynous (Fig. 1). There was a seasonal difference in the queen number. The mean of 11 nests excavated in May and June was 3.27 (SD = 1.56), whereas the mean of 7 nests excavated in July and August was 5.86 (SD = 2.27). The difference was significant ($t = 2.88$, $p < 0.05$, two-tailed). The increase of queen number in the summer period suggests that newly mated queens are adopted

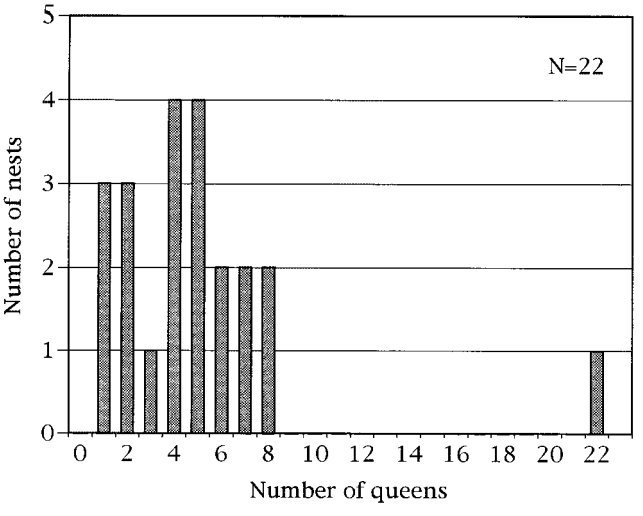


**Fig. 1.** Distribution of queen number of *F. japonica* nests on east slope of Mt. Fuji.

by established nests (see below).

In ten of the 22 nests, all inhabitants (adult workers and immature individuals, in addition to queens) were collected. The range of adult worker population was approximately 300 – 5300 (mean c.2000), but there was no significant correlation between the number of workers and that of queens ($r$ = 0.375, $p > 0.1$).

A total of 20 queens which were found in 3 nests excavated between late July and early September were dissected immediately after collection. Dissection showed that they were all inseminated and had active ovaries which were filled with mature oocytes. In addition, 33 queens from 4 nests excavated between late July and late October were reared separately in the laboratory. The purpose of this rearing was to obtain the confirmed matrilineal units for DNA fingerprinting (see below). During this culture, 25 of the 33 queens laid eggs, but 8 died without laying eggs. Eggs laid by 23 of the 25 queens finally gave rise to workers, indicating their insemination. Eggs of the other two queens always disappeared shortly after being deposited. These queens were supposed to be uninseminated, so that at least 23 of the 33 queens reared in the laboratory were confirmed to be mated. The results of dissection and laboratory rearing thus jointly demonstrated that most, if not all, of dealated queens present in nests were functional, i.e. inseminated and producing diploid progeny.

## Inheritance of DNA fragments and number of queen's matings

We analyzed DNA fingerprints of 8 laboratory cultures derived from 3 nests. Figure 2 shows an example of gel which contains two cultures: two *F. japonica* queens (a and b) and their daughters (worker pupae produced in the laboratory). These queens were collected from the same nest (no.92-11) but reared separately. In culture a (Fig. 2), a total of 37 bands were scored on a group of 6 fingerprints (the queen and her 5 daughter workers; see Table 1). Of the 37 bands, 9 were lacking in the queen's profile, but all of them were commonly present in the 5 workers (Table 1). This sharing pattern indicates that these 9 bands came from a single male that had mated with the queen. The same result was obtained also for the remaining 7 cultures (Table 2).

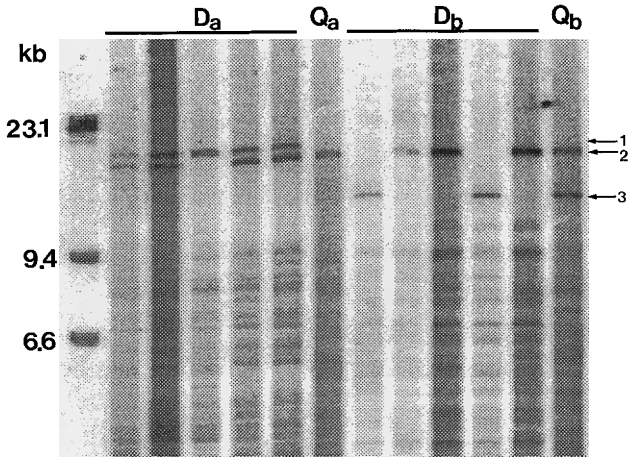


**Fig. 2.** DNA fingerprints of two laboratory cultures (families a and b) of *F. japonica*. Q and D denote queens and their daughters (workers), respectively. In family a, the band 1 is supposed to be of male (father)-origin. In family b, the bands 2 and 3 present in the queen show allelism. Molecular marker is λ-DNA digested with *Hin*d III.

## Band sharing score

For each of the 8 laboratory cultures mentioned above, we calculated the band sharing scores between the queen and her daughters, and those among daughters (Table 3). The mean queen-daughter scores ranged from 0.68 to 0.80 (global mean = 0.75), whereas the scores among daughters ranged from 0.85 to 0.94 (global mean = 0.90). In all 8 cultures, the queen-daughter scores were significantly lower than the scores among daughters ($p < 0.01$ in all $t$-tests). This result accords with the theoretically predicted difference in the relatedness between the mother-daughter kinship (0.5) and

**Table 1.** Genotypes of 6 ants (queen and 5 workers) of laboratory culture "a". Rows (1-37) are the bands scored on DNA fingerprints. Arrows indicate the bands supposed to be derived from a male parent.

| | Q | W1 | W2 | W3 | W4 | W5 | |
|---|---|---|---|---|---|---|---|
| 1 | − | + | + | + | + | + | ← |
| 2 | + | + | + | − | + | + | |
| 3 | − | + | + | + | + | + | ← |
| 4 | + | + | + | − | + | + | |
| 5 | + | + | + | + | + | + | |
| 6 | + | + | − | + | + | − | |
| 7 | + | + | + | + | + | + | |
| 8 | + | + | + | + | + | + | |
| 9 | + | − | − | − | − | − | |
| 10 | − | + | + | + | + | + | ← |
| 11 | + | + | + | + | + | + | |
| 12 | + | + | − | + | + | − | |
| 13 | + | + | + | + | + | + | |
| 14 | + | + | − | + | + | + | |
| 15 | − | + | + | + | + | + | ← |
| 16 | + | + | + | + | + | + | |
| 17 | + | + | − | + | − | − | |
| 18 | + | + | + | + | + | + | |
| 19 | + | + | + | + | + | + | |
| 20 | + | − | + | + | + | − | |
| 21 | − | + | + | + | + | + | ← |
| 22 | + | + | − | − | − | + | |
| 23 | + | − | − | − | + | − | |
| 24 | + | + | + | + | − | + | |
| 25 | + | + | + | + | + | + | |
| 26 | + | + | + | + | + | + | |
| 27 | − | + | + | + | + | + | ← |
| 28 | + | − | + | − | − | − | |
| 29 | + | + | + | + | + | + | |
| 30 | + | + | + | + | + | + | |
| 31 | + | − | + | − | − | + | |
| 32 | + | + | − | + | + | + | |
| 33 | + | + | + | + | + | − | |
| 34 | + | + | + | + | + | + | |
| 35 | − | + | + | + | + | + | ← |
| 36 | − | + | + | + | + | + | ← |
| 37 | − | + | + | + | + | + | ← |

**Table 2.** Number of bands of each category scored by DNA fingerprinting of 8 laboratory cultures (a-h) of *Formica japonica*. The queen and 5-7 workers were fingerprinted for each culture.

| Culture | Shared by queen and all workers | Shared by queen and part of workers | Present in queen but absent in all workers | Absent in queen but present in all workers | Total |
|---|---|---|---|---|---|
| a | 13 | 14 | 1 | 9 | 37 |
| b | 17 | 7 | 2 | 7 | 33 |
| c | 13 | 13 | 2 | 8 | 36 |
| d | 11 | 9 | 3 | 5 | 28 |
| e | 14 | 11 | 0 | 6 | 31 |
| f | 15 | 9 | 0 | 8 | 32 |
| g | 17 | 10 | 1 | 8 | 36 |
| h | 11 | 17 | 1 | 9 | 38 |

**Table 3.** Mean band sharing scores of DNA fingerprints of 8 laboratory cultures of *F. japonica*. N is nubmer of pair comparison.

| | Between queen and workers | | | Among workers | | |
|---|---|---|---|---|---|---|
| Culture | Mean | SD | N | Mean | SD | N |
| a | 0.72 | 0.03 | 5 | 0.88 | 0.03 | 10 |
| b | 0.79 | 0.03 | 5 | 0.94 | 0.03 | 10 |
| c | 0.74 | 0.02 | 5 | 0.93 | 0.04 | 10 |
| d | 0.75 | 0.03 | 5 | 0.89 | 0.02 | 10 |
| e | 0.80 | 0.03 | 5 | 0.89 | 0.03 | 10 |
| f | 0.78 | 0.03 | 5 | 0.92 | 0.03 | 10 |
| g | 0.79 | 0.03 | 5 | 0.93 | 0.02 | 10 |
| h | 0.68 | 0.10 | 7 | 0.85 | 0.05 | 21 |

the among-sister kinship (0.75), under the assumption of monogyny and the queen's single mating.

### Analysis of field-collected specimens

In the summer of 1993, adult workers and worker and gyne pupae were collected from under the tiles covering the nest entrances of three *F. japonica* nests (nos. 54, 174 and 198). Although these nests were not excavated and no queen was collected, DNA analysis of the collected specimens suggested some interesting points (Table 4). First, the mean band sharing score in adult workers varied in the 3 nests. The scores of nests 174 and 198 (0.59 and 0.69, respectively) were much lower than those obtained from the laboratory-reared workers (0.85-0.94), who were supposed to be full sisters (above). When compared with the laboratory-obtained lowest score (0.85 of culture h), the difference was statistically significant [$t'$ = 5.626, $p < 0.01$, approximate $t$-test (Sokal and Rohlf, 1981) for nest 174, and $t$ = 7.812, $p < 0.01$ for nest 198; two-tailed]. Worker pupae of nest 174 also showed a significant difference ($t'$ = 3.527, $p < 0.01$). On the other hand, the value of nest 54 (0.90) was within the range of laboratory scores. It is thus likely that the examined adult workers of nest 54 were full sisters which derived from the same queen, while the adult workers of nests 174 and 198 were the mixed progenies of more than one queen.

Second, in contrast to the results of workers, the scores of gyne pupae (0.84 – 0.91, Table 4) were concordant in the 3 nests and very close to or within the range of laboratory values (0.85 – 0.94). This suggests that the examined gyne pupae were mothered by a single queen in each nest. Further, the details of band sharing scores between worker pupae and gyne pupae (5 each) of nest 174 are given in Table 5. All 5 gyne pupae had a markedly larger number of common bands with worker pupa "o" than with the other 4 pupae ($p < 0.01$, T-method; Sokal and Rohlf, 1981). And the mean (0.81, SD = 0.04) was close to the laboratory lowest score (0.85; $t$ = 1.734, ns, two-tailed). This suggests that the gyne pupae and "o" share the mother whereas the other 4 worker pupae (l, m, n and p) were produced by other queen(s).

Finally, from the scores of all offspring groups of nest 54 (0.89 – 0.91) being at the full-sister level, it is also possible that this colony is monogynous.

## DISCUSSION

Multiple fertile queens were found in more than 80% nests of *F. japonica* excavated on the east slope of Mt. Fuji. Including the previous study (Higashi, 1979; Yamauchi and Suzuki, 1987), polygyny has been confirmed in the widely distant 3 localities, Ishikari, Mt. Fuji and Gifu, in Japan. Thus, currently, polygyny is more common in this species. Mean number of

**Table 4.** Band sharing scores (mean ± SD) in adult workers, worker pupae and gyne pupae of 3 field-collected nests. Figures in parentheses are number of pair comparison.

| | Adult worker | Worker pupa | Gyne pupa |
|---|---|---|---|
| Nest 54 | 0.90 ± 0.03 (10) | 0.89 ± 0.03 (10) | 0.91 ± 0.03 (10) |
| Nest 174 | 0.59 ± 0.11 (6) | 0.70 ± 0.13 (10) | 0.84 ± 0.04 (10) |
| Nest 198 | 0.69 ± 0.06 (10) | 0.87 ± 0.06 (10) | 0.91 ± 0.03 (3) |

**Table 5.** Band sharing scores between worker pupae (l-p) and gyne pupae (u-y) of nest 174

| | Worker pupa | | | | |
|---|---|---|---|---|---|
| Gyne pupa | l | m | n | o | p |
| u | 0.63 | 0.64 | 0.58 | 0.85 | 0.67 |
| v | 0.53 | 0.55 | 0.55 | 0.77 | 0.61 |
| w | 0.66 | 0.67 | 0.63 | 0.84 | 0.72 |
| x | 0.61 | 0.59 | 0.59 | 0.80 | 0.68 |
| y | 0.61 | 0.66 | 0.66 | 0.77 | 0.71 |
| Mean | 0.61 | 0.62 | 0.60 | 0.81 | 0.68 |
| SD | 0.05 | 0.05 | 0.04 | 0.04 | 0.04 |

queens per nest on Mt. Fuji was 5 and the degree of polygyny and the size of nest population are similar to those at Ishikari Shore (Higashi, 1979), where 15 nests excavated in May-November ranged in queen number from 1 to 15 (mean 6) and in worker number from about 500 to 12000 (mean c.4000) and again there was no significant correlation between them ($r$ = 0.331, ns; calculated from data on Table 1 in Higashi, 1979).

On the other hand, independent colony foundation by solitary *F. japonica* queens is a well known fact in lowlands of Japan (e.g. Kondoh, 1968; Kitamura, 1984). Although Yamauchi and Suzuki (1987) suggested adoption of new queens by established nests, they also discovered many *F. japonica* nests started by single foundresses in their study site. At Ishikari Shore, Higashi (1979) only supposed that nests proliferate by budding. In our study site, no obvious case of independent founding has been observed. Instead, we obtained only evidence suggesting the adoption of newly mated queens (above), which phenomenon is generally thought to be coupled with nest proliferation by budding (Hölldobler and Wilson, 1977). Further, Higashi (1979) found that nest population size in winter becomes four times larger than in summer (about 7000 and 1700, respectively). From this, he thought that at Ishikari Shore, summer nests group together into a smaller number of nests before hibernation. This nest system is seasonal polydomy. In our study, each nest was considered as an independent colony (monodomy) since aggregations of nest openings on the surface were well separated from each other in active seasons. However, the seasonal fragmentation and reunion of nests as observed at Ishikari Shore is also possible for the population of Mt. Fuji. Further study is needed to confirm this point.

DNA fingeprinting demonstrated single paternity in the worker offspring produced by *F. japonica* queens in the laboratory. However, single paternity in sampled worker offspring does not necessarily prove the queen's single mating (monoandry), because many factors are known to cause a biased representation of sperms from multiple males who copulated with the queen in her offspring (Boomsma and Ratnieks, 1996). In particular, errors caused by non-sampling of offspring sired by the other males become serious when the sample size is small. We analyzed only 5-7 workers for each culture, but no detection of offspring sired by the 2nd or other male in total 42 workers of 8 cultures would fairly support the queen's monoandry (but for effects of sperm bias on non-sampling errors, see Boomsma and Ratnieks, 1996).

Analysis of DNA profiles of ants found in the same nests suggested a complex kin-structure of *F. japonica*. Although no queen was collected and the number of offspring examined was limited (5 gyne pupae in 2 nests each and 3 gyne pupae in one nest), the band sharing scores of gyne pupae were as high as the full sister level in all 3 nests, while the scores among workers were variable. This may indicate that multiple queens contribute to worker production more or less equally, but their contribution to gyne production tends to be unequal. A similar unequal gyne production and more equal worker production among multiple queens was demonstrated with laboratory colonies of *Solenopsis invicta* (Ross, 1988). In this laboratory study, domination in gyne production by a queen was usually associated with a rapid weight loss followed by death of the queen (mostly within 80 days after she became dominated). Moreover, there was another type of queens, whose domination in gyne production continued over 400 days. The presence of such variants for domination length suggests that we need to collect queens and distinguish what factors are important in determining the reproductive variability among them.

The ecological factors associated with the adaptive significance of polygyny in ants have been argued frequently (see Hölldobler and Wilson, 1977; Keller, 1993; Bourke and Franks, 1995). Recently, based on their theoretical model analysis, Tsuji and Tsuji (1996) predict that, thanks to its early reproduction effect, dependent colony foundation coupled with polygyny would be adaptive in the habitat that subjects a population to a random density-independent fluctuation. In our study site, the ground features often change due to a snowslide occurring in early spring. (When it is large-scale, the ground is hollowed out deeply in a large area.) Hence, occurrence of polygynous *F. japonica* population in this habitat coincides with their prediction. However, it is unknown how the snowslides or other environmental disturbance affect this ant population.

A combination of weak polygyny, monodomy (or small-scale polydomy) and monoandry is likely common in species of *Serviformica* (Pamilo, 1982; Snyder, 1992; this study; for review, see Rosengren *et al*., 1993). Among other ecological factors promoting evolution of polygyny, interspecific social parasitism may be relevant properly to the members of *Serviformica*. As *Serviformica* species are hosts of slave-raiding ants (*Polyergus* and the subgenus *Raptiformica*) or temporary social parasites (the subgenus *Coptoformica*), some authors think that polygyny in *Serviformica* may be defense against queen killing by such social parasites (Rosengren and Pamilo, 1983). As concerns this, in polygynous nests of *F. japonica*, we found that multiple queens stay singly, or in a few, in separate chambers of a nest (Murakami, unpublished observation). Such living apart of queens inside a nest is called oligogyny (Hölldobler and Wilson, 1990) and oligogyny has been generally considered as a result of kin conflict, but this

system could be effective against extermination of host queens by intruding parasitic foundresses. We may thus expect a positive correlation between the intensity of social parasitism and the degree of polygyny across different local populations of *F. japonica* or some other host species. Therefore, combining this issue, we need a further survey of geographical variation in the social structure of *F. japonica*.

## ACKNOWLEDGMENTS

We wish to thank Mr. Norio Ikura, Mr. Taro Katsumata and Dr. Masaki Kondoh for their support and hospitality on Mt. Fuji. Appreciation is extended to Gotenba City Hall and Fuji School of the Ground Self-Defense Force for affording us facilities in the study site. We also thank two anonymous referees for their helpful comments. This study was supported in part by Grants-in-Aid for Scientific Research from the Ministry of Education, Science, Sports and Culture of Japan (No.05640716 to K.M. and No.07454211 to T.M.).

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(Received November 6, 1997 / Accepted March 18, 1998)