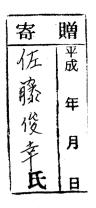
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ECOLOGICAL STUDIES ON THE ANTS, CAMPONOTUS NAWAI COMPLEX WITH SPECIAL REFERENCE TO THE POLYGYNY

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INTRODUCTION

Charles Darwin (1859) puzzled himself about the existence of sterile individuals (workers) in social insects (termites, ants, and some wasps and bees:
Recently, some aphids were found to be eusocial (Aoki 1984)). Why sterile workers could evolve without leaving their own offspring? His theory of natural selection based on the adaptation and differential reproduction of individuals could not give clear answer about this question. He noted, however, that those sterile castes helped their own mother (queen) and did not help unrelated individuals.

Later, Darwin's concept of "classical" fitness was extended by the concept of inclusive fitness and kin selection (Hamilton 1964). It predicts that if an individual leaves its genes more efficiently by helping reproduction of other individuals which are often related and share some portion of genes with him, then sterile and altruistic individuals, such as workers of social insects, could evolve.

Recently, it has been pointed out by many authors that the occurrence of polygyny, i.e., coexistence of multiple fertile queens in the colony, is an additional confusing problem for the ecology and sociobiology of social insects (Hoelldobler and Wilson 1977, etc.). From

the view point of inclusive fitness and kin selection, queens are intolerant of other egg-layers, and workers accept their mother queen only. Thus, colonies of social insects should incline to monogyny. When polygyny is observed, it is suspected that there are particular ecological circumstances favoring it (Hoelldobler and Wilson 1977; Pamilo and Rosengren 1984; Herbers 1986).

In ants, pairs of sibling species where one is monogynous and the other is polygynous, are known in several lineages (Hoelldobler and Wilson 1977; Brian 1983). Comparative studies on such species pairs should contribute to the better understanding of ecological factors leading to the coexistence of multiple fertile females in the colony.

Camponotus nawai complex is the most common arboreal ants in Japan and had been considered as single species for a long time. Recently, It was suggested that there were two population types in C. nawai: One is obligately monogynous and the other, facultatively polygynous (Yamaoka 1977, 1978; Satoh 1989). Subsequent ecological and morphological studies which were made during the course of this research revealed that those were two distinct species. The obligately monogynous species is C. nawai itself which has been described by Ito (1914), and the facultatively polygynous one is a new species, and described as C. yamaokai (Terayama and Satoh 1990).

They are considered as sibling species, very common in the arboreal community of Japan, and seem to share very similar ecological niches. Thus, *C. nawai* complex is desirable material to investigate what kind of ecological factors favors polygyny in ants.

This study primarily aimed to clarify the ecology and sociobiology of *C. nawai* complex through field surveys, observations, and experiments in the laboratory. Finally, ecological factors which affect the occurrence of polygyny in this species complex are discussed.

MATERIALS AND METHODS

1. Study materials

Camponotus nawai Ito complex is medium-sized, about 4-6 mm long in minor and major workers and about 8 mm in queens, black in color with two pairs of yellow spots in the first and second gastric tergites. This species complex distributes commonly from Honshu to Tokara Islands of Japan, and nests in hollow dead branches or bamboo grasses in evergreen broad-leaved forests.

This complex comprises from two sibling species: *C. nawai* is obligately monogynous and *C. yamaokai* is facultatively polygynous (Satoh 1989; Terayama and Satoh 1990). Those two species were morphologically very similar, but workers of *C. nawai* has larger body size, less prominent eyes, thicker and smaller petiole than workers of *C. yamaokai*, and male's paramea of *C. nawai* project more straightly than those of *C. yamaokai* (Terayama and Satoh 1990; see Fig. 1). Their distributions also separate parapatorically: Monogynous *C. nawai* ranges more southern or coastal regions than polygynous *C. yamaokai* (Fig. 2).

2. Study sites

Colonies of C. nawai complex were collected and

surveyed at various localities in Japan, from 1984 to 1990. Among them, following two sites were selected to study the colony seasonal cycles of *C. nawai* and *C. yamaokai*, and monthly collections were performed from 1985 to 1986: (1) *C. nawai* population - coastal forests at Shimoda, Shizuoka Pref., where *Quercus phillyraeoides* dominates and only monogynous or queenless nests are found; (2) *C. yamaokai* population - evergreen broadleaved forests at Mt. Tsukuba, Ibaraki Pref., where *Shiia sieboldii* dominates and polygynous nests are frequently found. Those were main study sites throughout this study.

3. Sampling procedures

In the forests, dead branches and stems of dead bamboo grasses encountered during a random search were broken by hands to examine for nesting of *C. nawai* complex. When the ants were discovered, the branch or bamboo grass was carried in a vinyl bag to the laboratory, where it was dissected and all of the ants inside were collected by insect aspirator into the vials. Although field collection was made in daytime, *C. nawai* complex is nocturnal (Satoh, unpubl. obs.), so that the entire nest population could be collected. Most of them were killed by ethyl acetate, the number of each caste was counted, and then they were fixed in a Kahle's or a

Carnoy solution followed by 70% alcohol. Others were maintained in the artificial nests for observations and experiments in the laboratory (see below).

4. Colony rearing

Colonies were maintained in the cylindrical plastic box (diameter, 12 cm; depth, 6 cm) or the plastic case (29 x 22 x 6 cm) in which glass tubes (inner diameter, 6.5 mm; length, 15 cm) were set on the floor as nest sites. The former was used in the aggression test between different nests, and the latter, in the behavioral observation. Inner sides of rearing boxes or cases were coated with fluon (I.C.I. United States, Inc.) to prevent ants from escaping. Those artificial nests were maintained at the room temperature (18-30°C), but observed nests were kept in the chambers of constant temperature (20-24°C) during observational period. Colonies were fed honey water and fresh carcasses of Drosophila, ad lib.

5. Aggression tests

Internest familiarity was tested by either of the following two methods. The first method was more sensitive but time-consuming than the second one and used only for polygynous *C. yamaokai* whose internest hostility was often very subtle.

Aggression tests I

In glass dishes (3.3 cm in diameter), workers of monogynous *C. nawai* attacked members of different colonies severely, but workers of *C. yamaokai* always avoided each other and aggressive behavior was never observed. Thus, for *C. yamaokai*, internest aggression was tested by the following method.

A worker from nest A was calmly introduced into the glass vial (4mm in inner-diameter, 3cm long) and confined in it. Another worker from nest B was also confined in another vial in the same way. Then, those two vials were connected at the opening, and the encounter between two workers was observed. Except when severe fighting began, at least five encounters were observed in each trial. The level of aggression was scored on an arbitrary scale (Table 1) which was slightly modified from Carlin and Hoelldobler (1983). Such trial was repeated ten times with different individuals and glass vials for each combination of the nest. This test was also performed within the same nest as control, and workers always accepted each other (aggression score is zero). All tests were performed within a few weeks after collection. Observed distributions of scores were compared by Mann-Whitney U-test to detect the statistical difference of aggressiveness.

Aggression tests II

During the study of population structure, all nests found in a quadrat or a block in the forests were mapped and collected thoroughly (details of sampling sites and nests collected are described later). Those nests were maintained in the plastic box (see above), and tested internest familiarity by following method.

A worker selected randomly from one nest was picked up lightly on the legs by forceps and transferred into another nest box, and the encounters between workers of different nests were observed at the room temperature (23-27°C, during observation). If severe fights occurred, ants concerned were immediately isolated from the nest box. If noticeable aggression did not happen, observations were continued until intruders encountered residents 10 times or more. Tests were repeated 3 to 5 times for each combination of the nest. When only aggressive encounters happened, those nests were judged to belong to different colonies. When only familiar (allogrooming or trophallaxis) or indifferent encounters happened, those nests were judged to belong to the same colony.

6. Queen and worker dissection

To evaluate the reproductive conditions of queens, they were dissected and examined with respect to: (1)

spermathecal contents; (2) presence or absence of corpora lutea; (3) number and length of ovarioles; (4) number of mature oocytes; (5) degree of wear of the mandibular teeth and the wing vestiges; (6) decomposition of wing muscles. Presence of corpora lutea indicates that the queen laid eggs actually. Degree of wear of wing vestiges and decomposition level of wing muscles give us some information on age of queens. Dissection of workers was also performed to examine their ovarian development under queenright or queenless conditions. Length of ovarioles was measured with an ocular micrometer accurate to 0.1 mm. Head width of queens and workers was also measured with an ocular micrometer accurate to 0.025 mm.

7. Allometric growth of colonies

To investigate colony development based on the allometric growth of workers, head and pronotum widths of workers were measured accurate to 0.025 mm by occular micrometer. Those measurement were performed for the colonies of various sizes which seemed to represent various developmental stages.

8. Behavioral observation

Observed colonies

Two colonies of *C. nawai* and three colonies of *C. yamaokai* were collected from Tokai-Kanto districts,

central Japan, during October 1985 and June 1986.

Details of those colonies are summarized in Table 2.

Queens of polygynous nests were marked individually with Mitsubishi Paint Marker. Colony SM contained three queens at the start of rearing, but one month later, large numbers of workers died from unknown causes and all but one queen were attacked and killed by workers, one each in two successive weeks.

Behavioral observation

Behavioral observations were made during September and October 1986, and additionary, during May to September 1987. Observation of queens and workers housed in the artificial observation nest (see above) was made under the tungsten light of adequate intensity with the aid of stereoscopic microscope. Observed colonies were habituated to the light and the room temperature (23-28°C) for one hour before observation. The light had no noticeable effects on the ants behavior. Time of observations fell between 10 and 24 hr., but behavior of ants did not change markedly with time. Instead, colonies seemed to be active periodically with much or less regular interval. Observations were made for a total of twenty hours for each colony. Positions of queens in the nest tube were recorded every five minutes by fitting the petiole of queens to the scale which was

put along the nest tube to the nearest 1mm.

Similarity analysis

Behavioral similarities among all queens observed were analyzed by cluster analysis based on the group average method, and were shown as a dendrogram.

Behavioral similarities between queens were calculated by the following formula (Odum 1950):

$$1 - \sum |N_{ai} - N_{bi}| / (N_a + N_b).$$

In above formula, N_{ai} and N_{bi} are the frequencies of i-th behavioral category observed in queens a and b, respectively: N_a is N_{ai} and N_b is N_{bi} . If the behavioral repertoire and the frequencies of each behavioral act of queens a and b are the same, the value becomes one. If the behavioral repertoire of queens is completely different, the value becomes zero. Details of observed behavioral categories are discribed later.

9. Development of eggs, larvae and pupae

To determine and compare developmental rate under various temperature conditions, immature stages of *C.*nawai and *C. yamaokai*, and of *C. tokioensis* and *C. itoi*which are monogynous and closely related to the *C. nawai*complex, were reared with workers in small glass vials (8 ml volume) at the constant temperature of 16, 19, 22 and 25°C. Those materials were collected from Shimoda (*C.*

nawai), Mt. Tsukuba (C. yamaokai) and Tokorozawa, Saitama Pref. (C. tokioensis and C. itoi). Eggs laid by queens in the stock colony were immediately transferred into vials. At the start of rearing, brood: worker ratio was controlled about 1:1 which was ordinary ratio in natural colonies. Typically, five or more workers and eggs were reared in the vial. More than ten vials were set at each temperature. Those small colonies were fed with honey water and fresh carcasses of Drosophila, ad lib. Those were observed once a day under dissecting microscope, and development of immature stages were recorded.

10. Interspecific aggression

To assess the competitive ability of *C. nawai* and *C. yamaokai*, interspecific aggression was tested as follows. A worker of each species was randomly selected from colonies of each species, and those two workers were introduced in small glass dishes (3 cm in diameter). Encounters of the workers were observed, and which species won the battle was recorded. In this tests, interaction between minor workers and between major workers was observed. Aggression between minor and major workers always resulted in the death or severe damage of minor workers irrespective of species.

11. Effects of queens on the production of reproductives

To examine effects of queens on alates production, a total of 16 colonies of *C. yamaokai* were collected from Mt. Tsukuba during December 1988 to February 1989. Then, queenless and heavily polygynous subcolonies were made by subdividing colonies into halves (two subcolonies) and adding all queens to one of the two subcolonies. Those subcolonies were reared in plastic cases (see above), and the production of reproductives was observed during subsequent reproductive seasons.

RESULTS

1. Colonies collected

From 1984 to 1990, a total of 427 and 570 nests of C. nawai and C. yamaokai, respectively were collected from various localities of Japan. In C. nawai, 274 nests (64.2%) were queenless, 151 (35.4%) were monogynous and 2 nests (0.4%) contained two queens which were both inseminated and had developed ovaries. In C. yamaokai, 66 nests (11.6%) were queenless, 105 (18.4%) were monogynous and 399 (70%) nests contained more than one Frequency distribution of queen numbers per nest is shown in Fig. 3. As described later, queenless nests were mostly a part of single polydomous (multi-nest) colonies in both species, and "queens" of polygynous nests of C. yamaokai were almost always inseminated. In many cases, population data will be analyzed after subdividing into egg-laying and non-egg-laying seasons (see below).

2. Seasonal life cycle

Of the 170 nests of *C. nawai* population collected at Shimoda between October 1985 and October 1986, 71 (42%) were monogynous and 99 (58%) were queenless. On the other hand, among a total of 136 nests of *C. yamaokai*

population collected at Mt. Tsukuba between December 1985 and November 1986, 88 nests (65%) were polygynous, 31 nests (23%) monogynous, and 17 nests (12%) queenless.

Except for the period when alate castes remained in the nests, the seasonal life cycles of both populations were similar (Fig. 4): Colonies hibernate with adults and larvae, eggs are laid from late spring to summer, new adults emerge in summer, and all eggs hatch by the end of However, alates were found only in summer at Shimoda whereas they appeared in late summer and remained in the nests through winter until the next spring at Mt. Tsukuba. In fact, nuptial flight of C. nawai population was observed in mid August from 1987 to 1989 at Shimoda. On the other hand, nuptial flights have never been observed in C. yamaokai. Alate females generally shed their wings within the nests and were found to be inseminated during late March to mid May at Mt. Tsukuba (Fig. 5). Population data from other localities were also consistent with above results. Thus it can be concluded that the mating season is summer in the obligately monogynous C. nawai, and spring in the facultatively polygynous C. yamaokai.

3. Mode of colony reproduction

Data for nest populations were treated by subdividing samples into those collected in the egg-

laying-season and those collected in the non-egg-laying season. For *C. nawai*, samples from May-August were used as the egg-laying-season, and for *C. yamaokai*, those from June-August. Samples from other months of the year for each species were used as the non-egg-laying season.

Figs. 6 and 7 show frequency distributions of the colony size (number of workers in a nest) in the egg-laying and the non-egg-laying seasons. In *C. nawai*, nest with single founding queen and incipient nests which contained a queen and a few minor but no major workers were collected throughout the year (Fig. 6). In *C. yamaokai*, however, there were no incipient nests, and only two founding queens were collected in spring (Fig. 7). In addition, the frequency of small nests increased in the egg-laying season in *C. yamaokai*, suggesting that colony splitting occurs in the active season in this species.

For *C. yamaokai*, the frequency distributions of the number of queens in a nest are shown in Fig. 3. In both egg-laying and non-egg-laying seasons except for mating season (May), frequency distributions were skewed similarly. In the mating season, however, nests tended to contain more queens than in the other seasons. This and the former results suggest that the colonies of *C. yamaokai* adopt newly mated queens in late spring and the number of queens in the nest decreases by colony fission

in summer. By contrast, new colonies of *C. nawai* seem to be always founded by single queen (haplometrosis).

Allometric growth of colonies

Representative examples of worker size (head width) distributions along with colony development of C. nawai were shown in Fig. 8. Incipient colonies contained a few minor workers whose size was very small (head width, 0.8 - 0.9 mm: Fig. 8.a). When colonies grew up to contain more than several individuals, major workers whose head width were around 1.5 mm emerged (Fig. 8.b-c). Further, intermediate-sized workers (media worker) whose head width were around 1.2 - 1.3 mm emerged when colonies became to contain more than several tens of individuals (Fig. 8.d-e). Colonies which contained a few hundreds of workers showed a complete set of polymorphism and a continuous worker size distribution (Fig. 8.f-g). Especially small workers disappeared during the colony development (Fig. 8.d-e).

Representative examples of worker size distributions of various sized colonies (nests) of *C. yamaokai* were shown in Fig. 9. In contrast to *C. nawai*, even the smallest colonies (nests) contained major workers (Fig. 9.a), and there were no incipient nests. Further, larger colonies (nests) of *C. yamaokai* showed more discretely dimorphic size distribution compared to *C. nawai*, and

medium sized workers were few (Fig. 9.b-e).

An alate female of *C. yamaokai* was caught by light trap at Mt. Tsukuba, in May 1989. She was reared in the laboratory and produced four minor workers. The distribution of worker head width of that incipient colony was shown in Fig. 9.f. Those workers were very small (head width, 0.75 - 0.85 m) compared to minor workers of natural colonies (Fig. 9.a-e). It was suggested that incipient colonies of *C. yamaokai*, if occurred, produced very small workers only like those of *C. nawai*.

4. Population structure

Population structure of *C. nawai* and *C. yamaokai* was studied by entire sampling within areas.

In Shimoda, for *C. nawai* population, two quadrates (10 x 10 m) were set, nests were collected entirely and internest familiarity was tested during May, 1988. Both in sites S1 and S2, it was revealed that colonies of *C. nawai* often possessed more than one nest site (Fig. 10). In August 1988, more extensive research was performed at site S3 (Fig. 11), and such a multi-colonial population structure was confirmed. In site S3, several founding queens and monodomous incipient colonies (No. 5, 16 and 21) were also found.

In Mt. Tsukuba, for C. yamaokai population,

population research within sites was made at five sites in December 1987 (site T1) and July 1988 (sites T2 to T5). Population structure of *C. yamaokai* was found variable. At one extreme, site T2 contained two monodomous and three polydomous colonies, and showed multicolonial population structure such as *C. nawai* (Fig. 12). At another extreme, site T1 contained only one polydomous colony, and showed unicolonial population structure, i.e., all nests in the site were familiar with each other (Fig. 13). Population structure of three other sites fell between those two extremes (Fig. 14). In *C. yamaokai*, founding queens and incipient nests were never collected in those sites.

5. Productivity of colonies, queens and workers

In this section, productive ability of *C. nawai* and *C. yamaokai* was examined from the view point of entire colonies, queens and workers. To compare productivity during egg-laying season, July and August samples were used, because the egg production of nests was at the peak in that period (see Fig. 4).

5.1 Productivity of colonies

Both species revealed positive correlation between the number of workers and brood (eggs, larvae, prepupae and pupae) in the nest in all seasons (Figs. 15 and 16). In Figs. 15 and 16, number of workers and brood in the nest was log-transformed to normalize the distribution of the data.

Table 3 shows numbers of brood per worker in the "nest" of C. nawai and C. yamaokai. As mentioned above, polydomous nesting habits of both species made it very difficult to collect entire "colonies" in every cases. The brood/worker ratio was not significantly (p>0.05) different in t-tests between queenless nests of C. nawai and C. yamaokai, and between queenright nests of them in both seasons. Queenless nests of C. nawai always had significantly smaller brood/worker ratio compared with queenright nests of both species. Queenless nests of C. yamaokai also had significantly smaller brood/worker ratio compared with queenright nests of both species in both seasons except for egg-laying season. As mentioned above, queenright nests of C. nawai often possess queenless satellite nests (64.2% of nests were queenless), so the brood/worker ratio of entire "colonies" of C. nawai may be smaller than those of C. yamaokai,

5.2 Productivity of queens

5.2.1 Number of brood and workers per queen

The brood/queen ratio of *C. nawai* was markedly higher than that of *C. yamaokai* (Table 4): All

comparisons were significant in t-tests in both seasons. The brood/queen ratio of *C. nawai* may be underestimates owing to the presence of queenless satellite nests (see above section), so the productivity of queens seems much greater in *C. nawai* than in *C. yamaokai*. In fact, the total length of queens' ovarioles was strikingly longer in *C. nawai* (see later section).

5.2.2 Reproductivity effects in C. yamaokai.

For the polygynous *C. yamaokai*, the relationships among the numbers of queens and workers and the quantity of brood in a nest were examined in further detail. In statistical analysis, numbers of individuals are normalized by log-transformation.

The number of queens was positively correlated with the number of workers (Fig. 17). Queen number was also correlated with the number of immature stages (Fig. 18).

However, a significant negative correlation was found between queen number and worker number per queen (Fig. 19). The number of immature stages per queen was also negatively correlated with the number of queens, although not significantly so in the egg-laying season (Fig. 20).

Therefore, the brood production at the colony level increases with the number of queens, but the per capita productivity of queens decreases with their number in the

colony.

5.3 Ovarian development of queens

In this section, reproductive condition of queens was examined based on dissection data concerning spermathecal contents, ovarian development and degeneration of wing muscles. Those data were presented in Appendix.

Queens whose spermathecal contents could be observed clearly were always (n=59) and almost always (97.3%; n=1120) inseminated in C. nawai and C. yamaokai, respectively. Ovarian size of queens was much larger in C. nawai (Table 5). Body size (represented by head width) of queens was also larger in C. nawai (Fig. 21), but the difference in ovarian size was disproportionately greater than the difference in body size. Of special interest is that the polygynous C. yamaokai shows bimodality in queen size distribution (Fig. 21). small-sized queens whose head widths were less than 1.275mm made up about 14% of all queens collected at Mt. Tsukuba and 20% at Mt. Kiyosumi. In addition, ovariole number of queens was also larger in C. nawai except for foundresses: in C. nawai, mean+SD=26.0+4.2, n=41, but for foundresses, 11.7 ± 1.5 , n=3; large queens of C. yamaokai, 12.1 ± 2.8 , n=953; small queens of *C. yamaokai*, 11.5 ± 2.6 , n=174.

To illustrate reproductive conditions of each queen in polygynous nests, the results of 9 nests which are considered as representative cases are shown in Table 6. In nests 85-270 to 86-263, 90-040 and 90-079, reproductive status of queens was not equal, and some queens had much longer ovaries and visible amount of corpora lutea which indicated active ovipositional activity. It seems that, however, such reproductive inequality is related to the age of queens: Older queens in which wing vestiges were more severely worn and wing muscles were more severely decomposed or replaced by fats tended to have more developed ovaries. For example, in nest 90-079, queens #4, #5 and #7 had corpora lutea and developed ovaries, but they seem far older than other queens of the nest, because their wing vestiges were completely worn and wing muscles were replaced by fats. Other queens of nest 90-079 had undeveloped ovaries, but their fresh wing vestiges and wing muscles indicate that they were recently dealated, very young queens. 90-002 to 90-036, most queens probably participated in the ovipositional activity more or less equally, and their worn wing vestiges and replaced wing muscles suggest that they were old ones. It is to be noted that small-sized queens did not necessarily have less developed ovaries than the larger one (see 85-270 #2, 86-263 # 2 and 90-002 # 4). In general, ovarian

development of queens in polygynous nests seems to correlate with age of queens, and there is no tendency that particular queens dominate over other queens in ovipositional activity throughout their lives.

5.4. Productivity of workers

5.4.1 Worker body size

There is no noticeable difference in worker morphology between *C. nawai* and *C. yamaokai*, but workers of *C. nawai* have significantly larger body size than workers of *C. yamaokai* (Table 7: Table 8, two-way ANOVA). In particular, major workers of *C. nawai* are markedly larger than those of *C. yamaokai*. Two-way ANOVA also revealed that intercolonial variation within species was significant in minor workers, but were not significant in major workers. In addition, worker size was not significantly different between single and multiple queen nests of *C. yamaokai*.

5.4.2. Ovarian development of workers

In *C. nawai*, workers of queenless nests had more developed ovaries than workers of queenright nests (Table 9(a): In minor workers, t=11.021, df=370, p<0.001; in major workers, t=4.879, df=210, P<0.001: Data of workers whose ovaries were completely atrophied were excluded). Some workers even had mature oocytes or corpola lutea. In *C. yamaokai*, workers of queenless nests didn't have

more developed ovaries than workers of queenright nests. Rather, workers of queenright nests tended to have more developed ovaries (Table 9(b): In minor workers, t=1.954, df=143, NS; in major workers, t=1.87, df=84, NS. In C. yamaokai, however, workers which had mature oocytes or corpola lutea were rarely observed. In queenless nests, minor workers of C. nawai had more developed ovaries than minor workers of C. yamaokai (t=4.459, df=292, p<0.001), but in queenright nests, the former had less developed ovaries than the latter (t=5.619, df=200, p<0.001). In queenless nests, major workers of C. nawai had equally developed ovaries compared to major workers of C. yamaokai (t=1.415, df=156, NS), but in queenright nests, the former had less developed ovaries than the latter (t=5.316, df=113, p<0.001).

Above results indicate that queens of *C. nawai* suppress ovarian development of workers more intensely than queens of *C. yamaokai*.

5.5. Production of reproductives and effects of queens
Production of reproductive castes (alate females and
males) was much lower in *C. yamaokai* (Table 10).

Queenless nests of *C. nawai* produced alates most
frequently and most abandantly (especially males). In *C.*nawai, numerical sex ratio was biased for males, but in

C. yamaokai, it was about 1:1.

In experimental colonies of *C. yamaokai*, heavily polygynous colonies never produced alate castes, but orphaned colonies produced alates as frequently as natural queenless nests (Table 11; also see Table 10).

6. Behavioral observation of queens and workers

6.1 Description of behavior

Observed behavior of queens is shown in Tables 12 to 12. Queens of *C. nawai* complex did not show any unique behaviors compared with queens of other polygynous ants (Wilson 1974a; Evesham 1984), but behavioral patterns which need more explanation are described below.

Solicit food from worker (or queen) - queen tapped on mandibles of worker (or queen) with antennae and forelegs persistently, but it was rarely followed by regurgitation.

Manipulate larva - queen manipulated larva with her mandibles, but didn't take any noticeable care.

Be carried by worker - worker pulled on mandibles or legs of queen with her mandibles.

Be attacked by worker - worker struck the body of queen continuously with her closed mandibles. Aggression by worker was observed once in queen P1d (Table 12). Queen P1d was found dead at the last observational bout, so was excluded in the following behavioral comparison.

Attack queen - when a queen (Table 13, queen P2c)

encountered other queens face to face, she trembled and tried to hit their bodies with her mandibles, but did not actually do so. The queens which received such aggression always ignored it.

6.2 Comparison of behavior among queens

Queens of polygynous colony P1 (except for P1d) were not significantly different in the frequency of each behavioral act which was observed frequently enough (expected frequency was more than five) to perform X²-tests (Table 12). For the queens of polygynous colony P2, there were significant differences among queens in the frequencies of self-grooming and allo-grooming by workers (Table 13): Queens of nest 1 more frequently groomed themselves than queens of nest 2, and queen P2b was more frequently groomed by workers than were other queens. In addition, only queen P2c showed hostility toward other queens, but actual fighting was not observed.

The queen of the secondarily monogynous colony, SM, was allo-groomed less frequently by workers but walked more frequently than queens of monogynous colonies, M1 and M2 (Table 14). Frequencies of self-grooming and regurgitation with workers, however, were not significantly different among those three queens.

Behavioral similarity among all queens observed is

shown as a dendrogram in Fig. 22. In light of the observations stated above, it can be generally concluded that queens from the monogynous population (cluster 1) were groomed and given food by workers more frequently, but walked inside the nest less frequently, than queens from the polygynous population (cluster 2). The queen of the secondarily monogynous colony, SM (cluster 2-ii), was donated food by workers as often as queens of the monogynous population, but was groomed by workers less frequently and walked more frequently, as was the case of queens from the polygynous population. Queens P2a, b and c (cluster 2-i), especially P2c (microgyne), self-groomed more frequently than other queens of the polygynous nest (cluster 2-iii).

6.3 Position of queens in the nest

Queen locations in the nest tube are shown as frequency distributions in Fig. 23. All distributions were significantly different each other by Kolmogorov-Smirnov tests (p<0.05). Except for Pld, the shape of frequency distributions was flatter and the value of coefficient of variation (CV) was higher in queens of monogynous nests than in those of polygynous nests. Queens of polygynous nests tended to aggregate around the center of nests, while queens of monogynous nests settled down more freely in the nests than those of polygynous

nests.

7. Development of eggs, larvae and pupae

Reared at less than 25°C, eggs of *C. nawai* complex and its allied species did not develop into pupae, and no adults emerged. In Table 15, developmental periods (days) of eggs, larvae, prepupae and pupae at 25°C are presented. In this experiment, all emerged adults were minor workers. Total developmental periods were based on the data of individuals whose development from eggs to adults were completely checked.

Developmental period of eggs was statistically longer in the following order (p>0.05): C. yamaokai > C. itoi > C. nawai = C. tokioensis. Larval period of C. yamaokai was significantly shorter than those of other species. Prepupal period was not significantly different between spcies except for C. tokioensis and C. nawai: Prepupal period of the former species was significantly shorter than that of the latter. Pupal and total developmental periods were not significantly different among species. For C. nawai complex and its allied species, it took about two months for eggs to emerge as adult minor workers at 25°C.

8. Aggression between different colonies

8.1. Intraspecific aggression

At Mt. Tsukuba, nests were collected at four sites during May, 1986: Site A was a small bush of bamboo grasses (about 2.4 m²) which was near to sites C and D but separated from them by a mountain path; site B was about 1 km apart from those three sites; sites C and D were adjacent but separated by a small stream. In this sampling, locations of the nests were not recorded, but the distance between nests was not beyond 5 m in each site.

Four polygynous nests (A1 to A4) and one polygynous nest (B1) were collected in site A and B, respectively (Table 16). All but nest A1 were constructed in the dead bamboo grass. Internest aggression was significant between all nest combinations compared to the control (p<0.001; Fig. 24.a). Further, pairwaise comparisons of the level of aggressions revealed that the levels of A1 x A3, A1 x A4, A2 x A3 and A3 x A4 (aggression score, 18 to 24), and of A1 x A2 and A2 x A4 (score 32 to 33) were not significantly different with each other (p>0.2), respectively, but the aggression level between those two groups was significantly different (p<0.05) except for A1 x A3. Aggression level of A1 x A3 (score 24) was not significantly different from that of all other

combinations (p>0.05), so intermediate among them. It was noteworthy that aggression levels of A1 x A2 and A2 x A4 were not significantly different from the level of A4 x B1 (score 38; Fig. 24.b), i.e., aggression level between nests of distant forest.

In the adjacent sites C and D, one monogynous (C2) and two polygynous nests (C1 and C3), and three polygynous nests (D1 to D3) were collected, respectively (Table 16). All nests were constructed in dead bamboo grass. Significant aggression (p<0.001) compared to the control was found between nests except for C2 x C3, D1 x D2 and C1 x D3 (Fig. 24.c.d.e). Aggression levels of C1 x C2, C1 x C3, D1 x D3, D2 x D3, C1 x D1 and C1 x D2 (score 15 to 23) were not significantly different (p>0.2) from each other, but were significantly (p<0.05) lower than that of distant forest nests (A4 x B1).

At Mt. Tsukuba (site E), and Tokorozawa (site F), nests within a defined area were mapped and collected entirely during October, 1986 (Fig. 25).

In site E, twelve nests were collected: E2 and E4 were queenless, E1, E9, E10 and E11 were monogynous, and other six nests were polygynous (Table 16; Fig. 25.a). All nests other than E12 were made in stems of dead bamboo grass. Three nests (E2, E3 and E12) which had enough number of workers to be tested with all other nests were chosen and the aggression tests were performed

(Table 17). E1 and E2 showed no significant aggression (p>0.2) with other nests except for E12. Nest E12 was significantly hostile toward all other nests tested (p<0.05).

In site F, eight nests were collected: F1 was queenless and others (F2 to F8) were polygynous (Table 16; Fig. 25.b). Except for F1, F2 and F7, nests were made in dead bamboo grass. F1 had too small population to test the internest familiarity by the method of aggression test I, so aggression tests were performed for all possible pairs of other nests (F2 to F8). None of the tests showed significant hostility compared to the control (p>0.2). On the other hand, significant internest aggression at the same level as in A4 x B1 was always observed between sites E and F.

8.2. Interspecific aggression

Interspecific aggression tests revealed that individual workers of *C. nawai* were superior to those of *C. yamaokai* in aggressive encounters (Table 18). Major workers were very aggressive compared to minor workers. When fights began, workers bit on the legs, antennae or mandibles of the opponents and often sprayed formic acids from the tip of abdomen.

9. Geographical distribution

9.1. Overall distributions in Japan

C. yamaokai distributed to more northern areas thanC. nawai in Japan (Figs. 2 and 26).

In the Pacific coast of Japan, especially in the Bousou Peninsula, the boundary line of both species closely corresponded with the isothermal line of the average of annual lowest temperature of -3.5°C. This line is known to correspond with the northern limit of several insects and plants which have subtropical origins.

9.2. Distribution in the contacting area

Moreover, in the Amatsu-Mt. Kiyosumi area in Chiba Pref. where both species were found, *C. nawai* was collected between the coastal forest and the mountain forest up to 200 m above sea level (Fig. 27, sites A-E), whereas only *C. yamaokai* was found in the forest above 250 m (sites F-H). Except for site C, two species were not collected at the same location. In Shimoda, Matsuzaki and Kawazu area in Izu Peninsula, ranges of *C. nawai* and *C. yamaokai* also did hardly overlap with each other, and the latter occupied inner or higher areas than the former (Fig. 28).

DISCUSSION

Obligately monogynous Camponotus nawai and facultatively polygynous C. yamaokai showed unique contrast in various ecological characteristics (summarized in Table 19). The differences found in the reproductive mode and productivity, and the parapatoric geographical distributions are common with other monogynous and polygynous sibling species such as Pseudomyrmex venefica group (Janzen 1973), "macrogyna" and "microgyna" of Mirmica ruginodis (Brian 1983), and monogynous and polygynous forms of Solenopsis invicta (Fletcher et al. 1980; Ross and Fletcher 1985). In the following sections, ecological and sociobiological features of C. nawai and C. yamaokai, and finally, ecological factors which favor polygyny in this species complex will be discussed.

1. Relatedness of queens in polygynous colony

Colonies of the facultatively polygynous *C. yamaokai* are functionary polygynous, and queens in the same nest are generally not hostile with each other (Tables 12 and 13). Collection, dissection and observation data suggest that the mating of *C. yamaokai* is performed within the nest and almost all alate females remain in their natal nest (Figs. 3, 5 and 7). In fact, the alate females

which had been marked with paint were found dealated in the same nest after the mating season (Satoh, unpubl. obs.). Although direct evidence has not yet been obtained for the degree of genetic relatedness among coexisting queens, the above results and observations suggest that they are genetically related with each other.

2. Queen polymorphism

Queen polymorphism as observed in C. yamaokai (Fig. 21) is also known in other polygynous ant species, such as Pseudomyrmex venefica (Janzen 1973) and Myrmica ruginodis (Brian 1983), and in the polygynous termite, Nasutitermes princeps (Roisin and Pasteels 1985). Smaller sized queens may be less advantageous than larger ones in the independent mode of colony founding, since they should have less energy reserves to rear the first brood by themselves. In colony reproduction by budding, however, smaller queens may not be necessarily less advantageous than larger ones, since they are attended by workers which supply food resources for rearing brood. Thus, it is suspected that mycrogynes of those polygynous species including C. yamaokai emerged with or after the evolution of polygyny and reproduction through nest budding.

3. Productivity of queens and colonies

The number of brood (including eggs, larvae, prepupae and pupae) per worker during egg-laying season tends to be larger in the polygynous *C. yamaokai* than in the monogynous *C. nawai* (Table 3). This is probably due to the participation of all or most queens in colony egg production, even though productivity of individual queens is lower in *C. yamaokai* than in *C. nawai* (Tables 4 and 5). A high brood/worker ratio could increase colony growth rate together with nest multiplication by budding but decrease food resources allocated to each immature and adult caste. Smaller adult body size (Fig. 21 and Table 7) and less developed ovaries of queens (Table 5) in *C. yamaokai* might be partly explained by per capita decrease of food resources.

The "reproductivity effect", that is, decrease in per capita productivity of females with increase in the number of females is a general rule in social insects (Michener 1964; Wilson 1974b; Yamauchi et al. 1982; Greenberg et al. 1985). *C. yamaokai* also showed this phenomenon (Fig. 20). The reproductivity effect might be viewed as a load of polygyny, which might be offset by particular ecological circumstances favoring polygyny. Nevertheless, if so, why polygyny is burdened with such a high cost is not evident. Queens of polygynous colonies,

however, may be genetically related with each other, so decrease in inclusive fitness could be relaxed by indirect effects of kin reproduction.

4. Production of reproductives

In *C. nawai*, queenless nests produced more reproductives (alate females and workers) than queenright nests (Table 10). Frequency of the nests which produced reproductives was also higher in queenless nests than in queenright nests (Table 10). It is generally said that queens of social insects inhibit the production of female reproductives (new queens) phelomonaly, and reproductives emerge when colonies become sufficiently large and queens' inhibition is weakened under the threshold level of caste differentiation (Wilson 1971).

In *C. yamaokai*, such a phenomenon was not found between queenless and queenright nests. Both kind of nests produced low number of reproductives at low frequencies (queenright nests, 39.4%; queenless nests, 33.3%) compared to *C. nawai* (Table 10).

The experimental nests of *C. yamaokai* which were added extra queens produced no reproductives during the two reproductive seasons, but queen-removed nests produced female and male reproductives in which females should be derived from eggs of previously existed queens (Table 11). This suggests that queen inhibition on the

alates production is also effective in *C. yamaokai*, and lower production of alates compared to *C. nawai* might be due to the higher level of inhibitory pheromon derived from multiple queens. The ecological significance of lower alates production in *C. yamaokai* will be discussed in the section of reproductive strategies.

5. Behavioral observation of queens and workers

Observations of the behavioral interactions between queens of polygynous societies are relatively scarce in ants. Some investigators found dominance hierarchies among queens in the same nest (Evesham 1984, in Myrmica rubra; Hoelldobler and Carlin 1985, in Iridomyrmex purpureus), but others found no evidence of such relationships (Wilson 1974a, in Leptothorax curvispinosus).

The polygynous *C. yamaokai* showed no evidence of dominance hierarchies among queens (Tables 12 and 13). Queens, except for a microgyne (P2c), did not show aggressive behavior towards other queens, and tended to aggregate around the center of the nest (Fig. 23). In the additional 20 hour observation which were made during the next summer, P2c showed no hostile behavior towards other queens. Thus, queens of polygynous nest seem to coexist without any antagonistic interaction.

Queens of C. nawai were groomed and fed by workers

more frequently but walked inside the nest less frequently than those of *C. yamaokai* (Table 14). In general, queens of polygynous nests were groomed and fed by workers equally. Queens of polygynous nests were also characterized by their frequent soliciting behavior, which was rarely observed in queens of monogynous nests. A queen of the secondarily monogynous nests, SM, is noteworthy in the following respect: She was fed by workers as frequently as queens of the monogynous form and rarely showed soliciting behavior. Thus, it seems that queens of polygynous nests share food resources equally and are short of food compared to queens of monogynous nests.

Some evidence indicates that queens of the polygynous form mate within their natal nest and remain in it (Fig. 5). Thus, a relatively high degree of relatedness is expected between coexisting queens. Such an ontogeny of queens makes them familiar with each other, and it becomes likely that peaceful relationships are realized between them.

6. Internest aggression in C. yamaokai

Polygynous ants generally show the reduced level of intercolonial hostility compared to monogynous and oligogynous species (Hoelldobler and Wilson 1977; Brian 1983). In the extreme case, intercolonial aggression is

completely lost, and even the fusion of different colonies could occur (*Pseudomyrmex venefica*, Janzen 1973; *Polyrhachis dives*, Yamauchi et al. 1987). It was revealed that queen discriminators were disproportionately important in nestmate recognition compared to worker discriminators and environmental odors (Carlin and Hoelldobler 1983, 1986, 1987). Presence of more than one queen, therefore, should complicate nestmate recognition cues or colony specific odor and reduce the efficiency of nestmate recognition.

In the polygynous *C. yamaokai*, considerable variations were observed in the internest aggression (Fig. 24). Individuals of adjacent nests often accepted each other completely, but sometimes mutual avoidance, alarm behavior, or weak to severe attack was observed between them. Nests from the distant sites always showed hostility toward each other.

Within site variation of aggressiveness is apparently confusing, but considering that *C. yamaokai*, as well as other polygynous ants, mainly reproduces by nest-budding, it can be explained. For example, if nest-budding was occurred in site A as shown in Fig. 29.a (the simplest case), mild aggression of A1 x A4, A4 x A3 and A3 x A2, and severe aggression of A1 x A3, A2 x A4 and A1 x A2 were plausible (see also Fig. 24.a). Similarly, in sites C and D, if nest-budding had occurred

as Fig. 29.b-d. observed variations are explained without contradiction.

Variation in aggressive responses was also observed within nests. For example, all levels of aggression were observed in A2 x A3 (Fig. 24.a). Why those intranest variation occurs is uncertain, but it is possible that non-aggressive workers had some direct or indirect experience of "odor" of non-nestmates, e.g., they had been in the same nest before budding, and it was also possible that aggressive workers had no experience of common odor, e.g., they emerged at different nests after budding, and there was no contact between those nests.

In site E, only nest E12 was significantly hostile toward other nests (Table 17), but the hostility was relatively weak against surrounding nests, E2, E8, E9 and E11 (Fig. 25.a). It is possible that E12 had previously been connected with those nests but the connection was lost. In site F, significant internest aggression was never observed (Fig 25.b). Such cases also suggest that C. yamaokai is able to form a super colony or to attain unicolonial population structure as is the case of other polygynous ants (see above section: Hoelldobler and Wilson 1977; Higashi 1978; Yamauchi et al. 1981). In fact, migration of workers and queens into different nests was observed by marking and recapture at Mt. Tsukuba, and was also ascertained in the artificially

introduced population at University of Tsukuba (Satoh, unpubl.).

Multiple queens and worker matrilines, and exchange of nest members, seem to enhance the variability of nestmate recognition cues, whether they are genetic or environmental, and polygynous colonies should become less discriminating against other colonies than monogynous one (Hoelldobler and Wilson 1977; Keller and Passera 1989; Morel et al. 1990). C. yamaokai workers do not exhibit clear aggression toward conspecifics in glass dishes, but do so toward the monogynous counterpart C. nawai. supports the above prediction, and coincides with the pattern of monogyne and polygyne Solenopsis invicta (Morel et al. 1990). There was, however, no remarkable difference in internest aggressiveness between queenless, monogynous and polygynous nests of C. yamaokai. stated above, those queenless or monogynous nests may mostly be a part of a polydomous colony and connected with other queenright nests, so they may not purely queenless or monogynous. Thus, the influence of queen numbers on nestmate recognition could not be verified in this case.

It was suggested that environmental odors, such as food and nest materials, could also affect nestmate recognition cues (Hoelldobler and Michener 1980; Carlin and Hoelldobler 1986). Nests of *C. yamaokai* were

collected in the forests of same vegetation, so food composition (insects carcasses and Homopteran secretions) was possibly similar within the sampling location. Further, nests of *C. yamaokai* were made in dead bamboo grasses or in dead branches of evergreen trees (mainly *Quercus* spp.), but kinds of nest materials did not affect nestmate recognition markedly. Such environmental odors possibly have only a minor role in nestmate recognition (Carlin and Hoelldobler 1986).

Finally, adjacent nests which might be derived from the same colony sometimes showed severe aggression each other, and the level of aggression was not significantly different from that of distant nests. This phenomenon indicates that, in C. yamaokai, nestmate recognition cues are transient as in Leptothorax curvispinosus (Stuart 1987), and could become distinct enough to reject unfamiliar conspecifics not like as Pseudomyrmex venefica (Janzen 1973) and Polyrhachis dives (Yamauchi et al. It seems that internest exchange of members is most important for the maintenance of unicolonial population structure compared to genetic resemblance, environmental odors (food composition and nest material), etc. If internest connections have been lost for a long enough time, whether it was intended or not, nestmate recognition cues may be altered to be distinguishable, and the nest may be segregated from the mother colony and

becomes an autonomous new colony.

7. Reproductive strategy of C. nawai and C. yamaokai

Obligately monogynous *C. nawai* performs nuptial flights in summer, and inseminated females found new colonies independently (haplometrosis). It is the typical mode of reproduction in ants (Wilson 1971; Hoelldobler and Bartz 1985). When colonies grow larger, they happen to occupy more than one nest sites, but colonies have a limitation on their size because they have only one propagator (queen). On the other hand, facultatively polygynous *C. yamaokai* never performs nuptial flights on a large scale, and colony reproduction is mostly attained through nest budding (colony fission). In the extreme case, a highly polydomous colony occupies single habitat entirely (Fig. 13) and the population becomes unicolonial in the sense of Hoelldobler and Wilson (1977).

Omitting nuptial flights and independent colony founding by single queen which seem most dangerous during the colony life history, colonies of *C. yamaokai* should have much higher colony founding success and colony growth rates than *C. nawai*. Production of reproductives was much lower in *C. yamaokai* than in *C. nawai* (Table 10). Because of the intranidal (within nest) mating and reproduction through nest budding, colonies of *C.*

yamaokai have no need to produce so many reproductives, and too many reproductives may rather burden the colony, because newly inseminated queens remain in the natal colony in most cases (Figs. 3, 5 and 7). In *C. yamaokai*, it seems more advantageous that colonies allocate more resource for production of workers instead of reproductives and inclease foraging and resource utilizing ability.

Life span of colonies is restricted by that of queens in monogynous *C. nawai*. On the other hand, colonies of *C. yamaokai* could continue to exist permanently by the renewal of functional reproductives. Without performing nuptial flights extensively, however, dispersal and colonization ability seem to be limited in *C. yamaokai* compared to *C. nawai*.

8. Ecological factors affecting evolution of polygyny

Reproductive strategy adopted by *C. yamaokai* and other polygynous ant species may be advantageous in the following two cases which are not mutually exclusive. In the first case, colony founding by single queen is extremely difficult because of the severe environment (for example, dried or fluctuating habitat or nest sites) or limitation of available nest sites, so remaining in her natal nest after mating and incidentally budding off with some workers is favored by newly inseminated queens

and also colonies. In the second case, colony founding by single queen is not necessarily difficult, but the "optimal" habitat is patchily distributed or restricted around the natal colonies. Therefore, dispersal for other places is less advantageous for newly inseminated queens than remaining in or near the natal colonies, even if availability of nest sites is not restricted.

Hoelldobler and Wilson (1977) point to two contrasting patterns of adaptation for polygyny in ants. The first is specialization on exceptionally short-lived, unstable nest sites, and the second is specialization on stable but patchily-distributed habitats. Pamilo and Rosengren (1984) consider the hypothesis of Koenig and Pitelka (1981) for cooperative breeding of birds as an extension of the latter category; the hypothesis indicates that resource localization, especially habitat localization, provides the selective background for cooperative breeding of birds (corresponding to polygyny in ants), and does not always require habitat specialists. They suggest that the localization of "optimal" habitats surrounded by marginal poorer habitats is the selective agent of polygyny in Formica execta in which polygynous nests are found in productive meadow habitats and monogynous nests are mainly found in less productive rocky forests. Recently, Herbers (1986) suggested that limitation of available nest sites was the most important selective factor favoring polygyny in Leptothorax longispinosus.

In the case of the C. nawai complex, however, on the author's general inspection, there is no remarkable differences in the habitats and nest sites between C. nawai and C. yamaokai except for geographical distributions (Figs. 2, 26, 27 and 28). Both forms inhabit evergreen broad-leaved forests, where hollow dead branches or bamboo grasses provide ample nest sites. Therefore, ecological factor(s) other than those indicated above might be responsible for the occurrence of polygyny in the C. nawai complex. One most responsible factor implied by their geographical distributions is the difficulty of independent colony founding in colder climates. If single foundress which mated in last summer or incipient colonies which contained a few minor workers can hardly endure the severe winter, adoption of newly inseminated females in the same nest and colony reproduction through nest budding might be favored rather than independent colony The polygynous C. yamaokai occurs in the most northern range among the related species (subgenus Myrmamblys), and is the most dominant species in the arboreal ant communities within its range. monogynous C. nawai did not distribute northward beyond the isothermal line of -3.5°C (the average of annual

lowest temperature) which corresponded with the northern limit of several insects and plants of subtropical origins (Fig. 26).

Why C. yamaokai cannot expand its range more southern areas? C. yamaokai is found in Miyajima Island, Hiroshima Pref. where has warm climate as other habitat of C. nawai, so C. yamaokai seems not physiologically inhabitable in more southern areas. It is suspected that C. nawai is superior to C. yamaokai in competitive ability for nesting sites owing to its aggressive dominance (Table 18), so C. yamaokai might be excluded from the distributional range of C. nawai. It seems that northern limit of C. nawai is determined by winter coldness in a physiological manner, while southern limit of C. yamaokai is settled as the result of competitive exclusion by C. nawai, so geographical distributions of those species should be separate parapatorically (Figs. 27 and 28).

SUMMARY

- 1. Life history, geographical distribution, population structure, and reproductive strategy of obligately monogynous Camponotus nawai and facultatively polygynous C. yamaokai were studied by field collection of colonies, dissection of queens and workers, aggression tests between nests, rearing experiments, and observation of laboratory colonies.
- 2. The seasonal changes of colony composition were similar in the two species except for the season in which alates (winged females and males) were found in nests. Colonies consisted of adults and larvae in winter. The wintered larvae developed to pupae and adults during summer. Eggs were laid during late spring and summer. All eggs hatched to larvae before late summer. C. nawai performed nuptial flight in August and never had alates in winter. In C. yamaokai, however, alates emerged in late summer and wintered in natal nests, mating probably occurred within the nest in spring and nuptial flight was not performed on a large scale.
- 3. Rearing at constant temperatures of 16, 19, 22 and 25°C revealed that larvae could not develop to pupae at less than 25°C, but could develop to adult workers in about two months at 25°C in both species.
- 4. In C. nawai, colonies were always founded by single

inseminated female independently, but in *C. yamaokai*, colonies were founded mainly by nest budding (colony fission) and a complete set of queen and worker castes was involved in colony founding.

- 5. *C. yamaokai* showed various degrees of internest hostility. Individuals from adjacent nests often accepted each other, but weak to severe aggression sometimes occurred between them. Individuals from nests far apart always fought severely. Observed variations of aggressiveness seem to be caused by colony reproduction through nest budding.
- 6. Aggression tests between workers of *C. nawai* and of *C. yamaokai* revealed that the former dominated over the latter in aggressive encounters.
- 7. Colonies of both species were often polydomous, i.e., occupied more than one nest sites. In *C. nawai* populations, there were many monodomous or polydomous colonies, thus population structure is considered as multicolonial. On the other hand, population structure of *C. yamaokai* was so variable that it ranged from multicolonial to unicolonial in which single colony had a huge number of nests and occupied single habitat entirely.
- 8. In both species, number of brood (eggs, larvae, prepupae and pupae) was positively correlated with number of workers in the nest. Number of brood per worker was

higher in *C. yamaokai* than in *C. nawai*, so productivity of colonies seems higher in *C. yamaokai*. However, number of brood per queen was significantly higher in *C. nawai*, so productivity of individual queen seems higher in *C. nawai*. In *C. yamaokai*, number of queens was positively correlated with number of workers and of brood, but negatively correlated with number of workers per queen and of brood per queen.

- 9. The body size and ovarian volume of queens were larger in *C. nawai*. Queens of *C. yamaokai* showed bimodal size distribution, though small queens were less frequent. Ovarian development of large and small queens was not significantly different. All or most queens in polygynous nests of *C. yamaokai* were fertile, thus polygyny is functional. In polygynous nests, ovarian development of queens seemed to correlate with age of queens and there was no tendency that particular queens dominated over other queens in oviposition activity throughout their lives.
- 10. In *C. nawai*, workers of queenless nests tended to have more developed ovaries than those of queenright nests, but in *C. yamaokai*, such a tendency was not observed.
- 11. Production of reproductive castes (winged females and males) was significantly higher in *C. nawai* than in *C. yamaokai*. In *C. yamaokai*, queen-removed nests

produced winged females and males, but queen-added nests did not produce them.

- 12. Queens of *C. nawai* were groomed by and received food from workers more frequently but walked about inside nests less frequently than queens of *C. yamaokai*. Hierarchical relationships were not observed among queens of polygynous nests. In general, those queens were equally cared for by workers, aggregated around the center of nests, and showed no hostility toward each other.
- 13. *C. nawai* distributed coastal and southern areas and not beyond the isothermal line of -3.5°C which was average of the annual lowest temperature. *C. yamaokai* distributed more northern and higher areas and the rangesof the two species contact parapatrically.
- 14. Reproductive strategy of *C. yamaokai* showed unique divergence from traditional one adopted by most ant species including *C. nawai*. *C. yamaokai* omits nuptial flights and independent colony founding by single queen, and reproduces by colony fission. Such reproductive strategy may be advantageous in northern areas which has severe winter climates for this arboreal ant group (subgenus *Myrmamblys*). It seems that polygyny of *C. yamaokai* evolved as adaptation to the colder winter climate and *C. yamaokai* became exceptionally dominant among arboreal ant communities in northern areas. The

reason why *C. yamaokai* cannot expand its range into southern areas might be that *C. nawai* dominates over *C. yamaokai* in aggressive encounters and excludes the latter from its range.

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APPENDIX. DISSECTION DATA OF QUEENS

HW: Head width. WV: Degree of wear in wing vestige; (0) not worn, (1) partly worn, (2) completely worn. WM: Degree of decomposition in wing muscle; (0) intact; (1) mildly, (2) hardly, and (3) completely decomposed; (4) replaced by fats. I: Insemination; inseminated (+) or not (-). CL: Corpora lutea; visible (+) or not (-). NO: Number of ovarioles. LO: Total length of ovarioles. NMO: Number of mature occytes.

1 Camponotus nawai

1-1 Shimoda (Nabeta), Shizuoka Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-378	11/19	1.53	2	4	/	/	/	/	/
85 - 405	12/23	1.58	2	3	+	/	/	/	/
85-407	12/23	1.60	2	3	/	/	/	/	/
86-001	1/19	1.60	2	4	+	+	23	115.0	0
86-002	1/19	1.50	2	3	/	/	/	/	/
86-022	1/20	1.53	1	3	+	- /	/	/	/
86-032	1/20	1.58	2	3	+	/	/	/	/
86-036	1/20	1.60	2	4	+	+	22	132.0	0
86-046	1/20	1.55	2	4	+	+	20	80.0	0
86-060	1/21	1.58	2	3	+		/	/	0
86-070	2/23	1.60	2	4	+	+	28	168.0	0
86-077	2/23	1.63	2	3	+	(omposed)
86-079	2/23	1.55	2	4	+	+	28	224.0	0
86-090	2/23	1.63	2	4	-/	/	. /	/	/
86-093	2/23	1.58	2	3	/	/	/	/	/
86-102	3/18	1.55	2	3	/	/	/	/	/
86-103	3/18	1.50	2	3	+	_	/	/	0
86-106	3/18	1.55	2	4	+	+	30	240.0	0
86-111	3/18	1.55	2	3	(decom	posed)
86-112	3/18	1.58	2	2	+	-	/	/	/
86-115	3/18	/	2	3	/	/	/	/	/
86-116	3/18	1.55	2	4	+	+	28	168.0	0
86-122	4/20	1.53	2	3	(decom	posed)
86-127	4/20	1.60	2	4	+	+	24	144.0	0
86-131	4/20	1.48	2	3	+	+	28	196.0	0
86-137	4/20	1.53	2	3	/	/	/	/	/
86-136	4/20	1.55	2	3	+	+	24	?	?
86-186	5/18	1.55	2	4	+	+	20	180.0	13
86-196	5/19	1.58	2	4	+	+	25	225.0	2
86-198	5/19	1.58	2	4	+	+	23	161.0	0
86-199	5/19	1.60	2	4	+	+	24	156.0	0
		1.58	2	4	+	+	16	96.0	1
86-244	6/15	1.63	2	2	+	+	20	40.0	0
86-248	6/15	1.48	2	4	+	+	30	210.0	11
86-249	6/15	,1.55	1	4	+	+	/	/	/
86-253	6/15	1.58	2	4	+	+	/	/	11
86-255	6/15	1.58	2	4	+	+	20	/	9
86-277	7/4	1.60	2	4	+	+	24	96.0	3
86-284	7/4	1.58	2	4	+	+	/	/	6

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-289	7/ 4	1.60	1	4	+	+	20	120.0	8
86-312	7/31	1.60	2	4	+	+	21	147.0	many
86-315	7/31	1.55	2	4	+	+	32	288.0	many
86-319	7/31	1.50	2	4	+	+	29	261.0	many
86-320	7/31	1.55	2	4	+	?	24	192.0	many
86-323	7/31	1.50	2	4	+	+	?	?	many
86-324	7/31	1.55	2	4	+	+	28	?	many
86-339	8/17	1.60	2	4	+	?	?	?	?
86-340	8/17	1.50	2	4	+	+	29	319.0	many
86-342	8/17	1.50	2	4	+	+	30	210.0	many
86-343	8/17	1.50	2	0	+	_	10	28.0	2
86-346	8/17	1.50	2	4	+	+	24	192.0	many
86-349	8/17	1.55	2	4	+	+	27	270.0	many
86-350	8/17	1.65	2	4	+	Ť	24	174.0	many
86-351	8/17	1.50	1	0	+		12	27.6	1
86-354	8/17	1.50	2	4	+	+	18	90.0	0
86-355	8/17	1.50	1	0	+	_	13	29.9	1
86-356	8/17	1.55	2	4	+	+	27	216.0	many

1-2 Amatsukominato, Chiba Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-158	7/27	1.50	2	4	+	+	28	246.8	many
85-160	7/27	1.55	0	0	?	?	?	?	?
85-166	7/27	1.55	2	4	+	+	27	205.5	2
85-169	7/27	1.60	2	4	+	+	32	280.0	many
85-175	7/28	1.55	2	4	+	+	29	239.3	many
85-181	7/28	1.50	2	4	+	+	32	312.0	many

1-3 Hayama, Miura Peninsura, Kanagawa Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-048	3/20	1.50	2	4	+	+	27	108.0	0

1-4 Matsuyama, Ehime Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO	
88-193 88-194		1.58 1.55		3				24.0 omposed	0	

1-5 Chyoushi, Chiba Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-013	1/14	1.65	2	4	+	+	28	154.0	0

1-6 Tateyama, Chiba Pref.

No.	Date	HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-028	1/15	1.70	0	4	+	+	30	105.0	0

1-7 Itou, Shizuoka Pref.

No.	Date	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-041	1/21		2	4	+	+	28	182.0	0
90-043	1/21	1.65	2	4	+	+	31	139.5	0
90-046	1/21	1.55	2	4	+	+	33	264.0	0

1-8 Mt. Takago, Chiba Pref.

No.	Date	HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-075	4/17	1.55	2	4	1	1	20	150.0	0

2 Camponotus yamaokai

#Q: Individual number of queens. "A" and "D" indicate alate and recently dealated females, respectively. "s" indicates microgyne whose head width is less than 1.28mm.

2-1 Tsukuba, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-384	12/ 2	1	1.35	1	1	+	_	6	10.2	0
		2	1.38	1	1	+		6	10.5	0
		3	1.35	1	1	+	_	6	10.2	0
		4	1.45	1	2	/	/	/	/	/
		5	1.35	1	2	?	_	8	14.0	0
		6	1.40	2	3	?	+	14	?	2
		7	1.35	1	2	(decom	posed)
		8	1.35	0	2	(decom	posed)
		9	1.35	0	1	(decom	posed)
		10	1.30	0	2	(decom	posed)
		11	1.35	0	1	?	_	6	9.6	0
		12	1.40	0	2	?	· . —	10	10.0	0
		13	1.35	1	2	+	. (dec	omposed)
		14	1.35	0	1	(decom	posed)
85-386	12/ 2	1	1.35	1	2	?	****	8	13.6	0
		2	1.35	1	2	(decom	posed)
		3	1.35	2	2	(decom	posed)
		4	/	1	2	(decom	posed)
		· 5	1.35	2	2	(decom	posed)
		6	1.33	2	3	(decom	posed)
		7	1.35	2	2	(decom	posed)
		8	1.35	2	2	(posed)
		9	1.33	2	2	(decom)

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-386	12/ 2	10 s11 s12 13 s14	1.35 1.20 1.15 1.33 1.25	2 0 0 1 0	2 2 1 3 2	((((decom decom	posed posed posed posed posed)
86-063	2/ 5	s1 2	$\begin{smallmatrix}1.25\\1.40\end{smallmatrix}$	2 2	3 3		-	14 decom	56.0 posed	0
86-066	2/ 5	1 s2	$\substack{1.30\\1.25}$	2 1	1 1	(?		decom	posed 5.6) 0
86-068	2/ 5	1	1.35	2	3	?	+	?	?	?
86-149	4/24	1 2 3 4	1.35 1.35 1.35 1.35	2 2 2 2	3 3 3	+ + +	 + 	8 12 14 12	12.8 27.6 46.2 40.8	0 0 4 3
86-150	4/24	1 2 3	1.30 1.30 1.30	2 2 2	3 3 3	+ + ?	- - ?	6 10 ?	? ? ?	? 4
86-151	4/24	1 2 s3	1.30 1.35 1.20	1 2 1	3 3 3	? + ?	? + ?	?	? ? ?	1 3 ?
86-153	4/24	1 2	1.35 1.35	2 1	3 1	?	?	? 14	? 42.0	?
86-154	4/24	1 2 3 4 5 6 7 8 9 10 11 12 13 14 s15 16 17 18 19 20 21 22 23 24	1.35 1.38 1.38 1.35 1.35 1.35 1.38 1.35 1.38 1.35 1.38 1.38 1.38 1.38 1.38 1.38 1.38	1 1 2 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1	2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2	++-++++++++++++++++++++++++++++++++++++		8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8 8	9.6 17.6 12.8 9.6 12.0 16.0 36.0 13.6 17.6 13.6 14.4 18.4 12.0 8.0 16.0 17.6 24.0 19.2 16.0 16.0 16.0	0 0 0 1 0 0 0 2 0 0 1 0 0 0 0 0 0 0 0 0

No.	Date	#Q	HW (mm)	WV	WM	· I	CL	NO	LO(mm)	NMO
86-154	4/24	27	1.40	1	3	+		8	24.0	2
		28	1.38	1	2	+	_	8	16.0	0
		29	1.38	1	2	+	_	12	20.4	1
		30	1.38	1	1	+		?	?	0
		31	1.38	1	2	+	-	8	16.0	1
		32	1.40	1	2	+	_	8	16.0	0
		33	1.38	1	2	+	_	8	16.0	0
		34	1.35	1	2					
		s35	1.18	1	2	+	-	16	48.0	0
		36	1.40	2	1	+	_	8	16.0	0
		37	1.40	1	3	+		12	36.0	4
		38	1.35	2	1	+	-	8	16.0	0
		39	1.38	1	1	+	_	8	12.0	0
		A 1	1.38	/	0	· <u> </u>	_	8	9.6	0
		A2	1.40	/	3			8	8.0	0
		A3	1.38	/	2	+	-	8	16.0	0
86-155	4/24	1	1.35	1	3	+	?	?	?	2
86-156	4/24	D1	1.35	0	0	_	·	4	6.4	0
		D2	1.35	2	0	_	-	4	4.4	0
		D3	1.30	1	0	-	-	4	5.2	0
		D4	1.35	0	0		. —	4	5.2	0
		D5	1.35	0	0		_	4	6.0	0
		D6	1.30	0	1		_	?	?	?
		A 1	1.38	/	2			8	16.0	0
		A2	1.33	1	0	-		8	12.0	0
86-157	4/24	1	1.35	2	3	?	?	10	?	?
	_	2	1.35	2	3	?	?	8	?	?
		3	1.35	2	3	(abd	omen	was lost)
86-158	4/24	s1	1.25	2	3	+	?	?	?	?
86-160	4/24	s1	1.15	1	1	+		8	8.0	1
		2	1.40	1	3	+	_	10	17.5	2
		3	1.35	1	3	+	-	10	11.3	2
		4	1.30	2	3	+	-	/		2
		5	1.35	1	2	?	?	?	?	?
		s6	1.23	1	1	+	_	10	15.0	2
		7	1.33	2	2	?	?	?	?	?
		8	1.33	2	2	+		10	20.0	2
		9	1.35	2	2	+	-	8	14.0	2
		10	1.38	2	2	+	_	?	?	1
		11	1.35	2	2	(deco	mposed)
86-161	4/24	1	1.35	2	3	?	?	8	?	2
		2	1.30	2	3	+	?	8	?	0
		As1	1.15	/	0			?	?	?
		As2	1.15	/	0	-		?	?	?
	4/30	1	1.28	1	2	+		8		/
86-162								_	•	-
86-162	1,00		1.35	1	O	-	_	4	8.0	1
86-162	., 00	D2 3	$\substack{1.35\\1.33}$	1 0	0	- +	_	4 10	$\begin{smallmatrix}8.0\\22.5\end{smallmatrix}$	1 0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-163	4/30	D1	1.33	1	0	+		8	16.0	0
		D2	1.35	0	0	+		8	17.6	4
		D3	1.35	1	0	+	_	8	13.6	0
		D4	1.35	0	0	+	_	8	17.6	0
		D5	1.38	0	0	+	-	8	16.0	0
		D6	1.38	0	0	+		8	18.4	1
		7	1.35	0	4	+	+	16	64.0	0
		8	1.33	1	2	+		10	20.0	1
		9	1.40	1	3	(decom	posed)
		10	1.43	1	4	`+	+	12	36.0	0
		11	1.38	1	1	+	· _	8	13.6	1
		D12	1.38	1	0	+		8	17.6	0
		13	1.38	ō	2	_		8	12.0	0
		14	1.35	1	1	+	_	8	16.0	0
		D15	1.38	1	0	+		12	24.0	1
		16	1.40	1	4	+	+	20	80.0	2
		D17	1.38	1	0	+	_	8	16.0	0
		18		1	2	+	_	8	17.6	2
			1.40		3			8	16.0	0
		19	1.38	0		+	·			
		20	1.40	2	2	+	_	$\begin{array}{c} 14 \\ 12 \end{array}$	70.0	0 0
		21	1.38	1	2	+	_		36.0	0
		22	1.35	2	3	(posed	<i>,</i>
		D23	1.38	1	0	+		8	16.0	2
		24	1.38	1	1	+	· -	12	24.0	0
		D25	1.38	1	0	+	_	12	24.0	0
		26	1.35	1	1	+		8	18.4	0
		27	1.35	1	2	+		8	13.6	0
		28	1.40	1	1	+		8	12.0	0
		29	1.38	1	1	+		10	22.0	0
		30	1.35	1	4	+	-	12	36.0	0
		31	1.38	1	1	+		8	16.0	0
		D32	1.35	1	0	+		8	16.0	0
		33	1.38	1	4	+	_	8	14.4	0
		34	1.38	1	1	+		8	16.0	0
		35	1.38	1	2	+	-	12	24.0	0
		36	1.38	1	1	+		8	16.0	1
		37	1.35	1	2	+	_	8	18.4	0
		38	1.38	2	4	+		8	16.0	2
		39	1.38	1	2	+		8	17.6	1
		40	1.35	1	2	+		8	16.0	1
		41	1.38	1	2	+	_	8	17.6	0
		42	1.38	1	2	+		8	17.6	1
		43	1.38	1	2	+	-	8	16.0	2
		44	1.38	1	2	+	_	8	16.0	0
		45	1.35	1	4	+	+	12	48.0	0
		46	1.38	1	2	+	-	8	16.0	1
		D47	1.38	0	ō	_	·	?	?	0
		48	1.35	1	2	+		10	20.0	1
		49	1.38	ī	2	+		8	12.0	ō
		50	1.38	1	1	+	_	10	15.0	ő
		s51	1.18	1	4	_		9	31.5	ő
		52	1.35	1	2	+		8	16.0	1
		D53	1.35 1.35	1	0	+	_	8	14.4	0
		54						10	18.0	0
		54 55	1.33	1	1	+		8		0
			1.38	2	2	+	_		16.0	
		D56	1.38	1	0	+		8	18.4	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMC
86-163	4/30	57	1.40	1	1	+	_	8	12.0	2
		58	1.38	1	2	_	_	10	20.0	0
86-164	4/30	1	1.33	1	2	+	_	4	5.0	0
		2	1.35	1	2	+	_	6	?	0
		3	1.33	0	2	+	-	14	70.0	0
		4	1.35	2	2	+	_	14	56.0	0
86-165	4/30	1	1.40	2	2	+		15	75.0	0
		2	1.43	2	2	+		16	?	0
86-166	4/30	1	1.35	2	1	+	_	5	8.8	0
		2	1.30	1	2	+	_	14	56.0	0
86-167	5/8	1	1.40	1	1	?		10	15.0	0
		2	1.38	2	4	+	+	12	48.0	0
		3	1.40	1	1	+	/	/	/	0
		4	1.40	1	1	+		12	18.0	0
		5	1.38	1	1	+	-	/	/	0
		6	1.40	1	1	+	_	/	/	0
		7	1,40	1	1	+	-	12	18.0	0
		8	1.40	1	1	+		12	18.0	0
		9	1.38	1	4	+	_	16	28.8	0
		10	1.38	2	1	+		/	/	0
		11	1.33	1	4	+	+	12	48.0	0
		12	1.33	1	1	+	-		/	0
		13	1.38	1	1	+			/	0
		A 1	1.40	/	0	+	-	/	/	0
		A 2	1.38	/	2	- ,		/,	/ /	2
	`	A3	1.38	_/_	1		_			0
		A4	1.40	/.	0	+	-	/	/ /	0
		A5	1.38	_/_	3		_			0
		A6	1.38		4	+				0
		A7	1.40	_/_	1	+	-	12	18.0	0
		A8	1.38	_/_	4	+	+	16	32.0	0
		A 9	1.43	/	4	-	/	/		/
36-168	5/8	s1	1.18	1	4	+		12	24.0	0
		D2	1.38	2	1	+	_	12	12.0	0
		3	1.35	1	2	+	-	12	18.0	2
		4	1.38	1	4	+	+	12	48.0	0
		5	1.40	1	2	+	_	12	21.6	1
		6	1.33	1	4	+	+	15	45.0	0
		7	1.40	2	4	+			/	/
		D8	1.40	1	1	+		12	18.0	0
		9	1.40	1	2	+	-	16	35.2	0
		10	1.40	1	2	+		12	26.4	1
		s11	1.23	2	4		-	. 12	15.6	0
		12	1.40	2	3	(decom)
		s13	1.20	1	3	(decom	posed)
		s14	1.20	1	2	+	_	/	10 0	/
		s15	1.23	1	2	+		12	18.0	0
		16	1.38	1	2	+		/	21.6	/
		17	1.38	2	2	+		12	21.6	0
	10	s18	1.18	1	2	+ -		/	/,	/,
	D	s19	1.18	1	1	+	_		/	/

No.	Date	#Q	HW(mm)	wv	WM	I	CL	NO	LO(mm)	NMO
86-168	5/8	D20 21 D22	1.38 1.40 1.40	2 1 1	1 2 1	+++++	- -	/ 12 12	/ 18.0 20.4	0
86-169	5/8	1 2 3	1.38 1.35 1.35	2 2 2	2 2 2	+++++	-	6 8 ?	6.0 ? ?	0 0 1
86-170	5/8	1 A1 A2 A3 A4 A5	1.38 1.40 1.35 1.35 1.33 1.35	2 2 / / / / /	2 2 0 0 0 0 0	+ +	- - - - - -	10 ? 8 8 8 8	7.5 ? 16.0 16.0 16.0 13.6 16.0	1 ? 0 1 0 0
86-171	5/8	1 2	1.35 1.30	1	2 4	++		12 12	12.0 15.0	0 0
86-172	5/ 8 5/ 8	1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17	1.35 1.35 1.35 1.38 1.38 1.35 1.38 1.40 1.40 1.40 1.38 1.33 1.38 1.35 1.38 1.35	1 1 2 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4	+++++++++++++++++++++++++++++++++++++++	+	15 14 16 11 11 13 11 14 12 11 12 14 10 14 12 14	30.0 28.0 35.2 33.0 32.5 44.0 42.0 36.0 30.0 22.0 42.0 25.0 28.0 30.0 28.0 39.0 48.0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
		3 s4 s5 6	1.45 1.20 1.20 1.38	1 2 2 1	2 4 2 4	+++++++++++++++++++++++++++++++++++++++	-	12 15 12 10	48.0 60.0 24.0 30.0	0 0 0
86-174	5/16	1 2 3 4 5 6 7 8 9 10 11 12	1.43 1.38 1.40 1.38 1.38 1.38 1.38 1.38 1.40 1.35 1.40	1 1 1 1 0 1 1 1 1 1	1 1 1 4 1 2 1 1 1 1 2	+ + + + + + + + + + + +		9 7 4 10 12 8 9 8 12 8	18.0 14.0 8.8 20.0 24.0 16.0 18.0 12.0 17.6 21.6 18.4 16.0	0 0 0 0 0 0 0 0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-174	5/16	13	1.35	1	4	+	?	16	?	0
		14	1.40	1	1	+	_	8	12.0	0
		15	1.38	1	1	+	_	8	16.0	0
		16	1.38	1	1	+		8	16.0	0
86-175	5/16	1	1.40	2	2	+	-	10	25.0	0
		D2	1.35	1	0	+	-	8	16.0	1
86-176	5/16	1	1.43	2	4	+		12	60.0	0
86-177	5/16	1	1.38	2	2	+	_	10	20.0	0
		s2	1.23	2	2	+	_	10	20.0	0
		s3	1.20	1	4	. +	-	9	22.5	0
		4	1.40	2	4	+		12	36.0	0
		s5	1.18	2	2	+	-	8	12.0	0
86-178	5/16	1	1.40	1	2	+	?	?	?	?
		2	1.40	2	2	+	?	?	?	?
		3	1.40	2	2	+	?	?	?	?
86-179	5/16	1	1.38	1	1	+	_	8	12.0	0
		2	1.35	1	1	+	-	10	16.0	0
		3	1.38	1	4	+		16	64.0	0
		D4	1.30	0	0	_		12	18.0	0
		5	1.43	1	4	+	_	12	36.0	0
		s6	1.15	1	4	+	-	8	12.0	0.
		D7	1.38	2	0	-	-	12	18.0	0
		D8	1.35	1	0	+	-	?	?	0
		9	1.33	1	3	+	_	8	12.0	0
		D10	1.33	1	0	+	_	12	16.8	0
		11	1.35	1	1	+	· <u>-</u>	12	18.0	0
		12	1.38	1	1	+		8	16.0	0
		13	1.33	1	1	?		8	16.0	0
		14	1.35	1	1	+	_	8	14.4	0
		15	1.35	1	4	+	-	14	63.0	0
		16	1.38	2	1	+		8	13.6	0
		17	1.35	1	1	+	_	8	16.0	0
		18	1.38	1	1	+		8	14.4	0
		19	1.38	1	4	+	-	?	?	1
		20	/	1	/	?	_	?	?	
		21	1.35	1	1	+	(omposed)
		22	1.33	1	1	+		8	16.0	0
86-180	5/16	1	1.43	2	4	+		14	84.0	0
		2	1.38	2	2	+	?	?	?	?
		3	1.33	2	2	+	?	8	?	?
		s4	1.25	2	2	+	?	?	. ?	?
		5	1.33	2	2	+		8	12.0	0
86-228	5/16	D1	1.38	0	0	+	<u>.</u>	6	10.2	0
		D2	1.33	0	0	-	-	6	10.8	0
		D3	1.38	0	0	+		6	12.0	0
		D4	1.38	0	0	+	_	6	10.8	0
		D5	1.35	0	0	+		8	17.6	0
		D6	1.35	0	0	+	_	8	16.0	0
		A 1	1.33	1	0			8	13.6	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-201	5/26	1	1.33	2	2	+		8	32.0	0
86-202	5/26	1	1.38	2	2	+	_	14	70.0	0
86-205	5/26	1	1.35	1	2	+	_	?	?	?
86-203	5/26	s1 s2 s3	1.18 1.25 1.20	1 2 2	2 4 2	+ + +	-	10 14 10	18.0 56.0 16.0	2 0 2
86-204	5/26	1 2	1.35 1.38	1 2	2 2	+ +	-	10	37.0 20.0	0
86-207	5/26	s 1 2 3	1.20 1.38 1.40	2 2 2	2 2 4	+++++	- - -	10 16 14	17.0 72.0 70.0	0 0 0
86-208	5/26	1	1.38	1	2	+		6	?	?
86-209	5/26	1 2 3	1.35 1.35 1.35	2 2 2	2 2 2	+++++++++++++++++++++++++++++++++++++++	- - -	14 12 12	49.0 48.0 36.0	0 0 0
86-210	5/26	1 2	1.35 1.35	2	2 2	+	_	12 12	54.0 48.0	2 2
86-211	5/26	\$1 2 \$3 4 5 6 7 8 \$9 10 \$11 12	1.25 1.33 1.20 1.35 1.35 1.40 1.38 1.23 1.38 1.23 1.38	1 1 1 1 1 1 1 1 1 1 1	4 3 4 4 2 4 4 2 4 4 2 4 4 4 2 4	+ + + + + + + + + +	+ - + - + -	8 9 13 15 17 13 12 10 15 10 12 16	16.0 12.0 18.0 32.5 45.0 85.0 26.0 24.0 15.0 75.0 20.0 60.0 40.0	0 0 0 0 1 0 1 1 0 0 2 0
86-212	5/26	1 s2	1.35 1.25	2 1	2 1	+	-	14 12	44.8 38.4	0 1
86-214	6/ 2	s1 2 3	1.18 1.30 1.33	2 2 2	2 2 2	+ + +	- - -	12 ? 12	36.0 ? 48.0	0 ? 0
86-215	6/ 2	s1	1.25	0	1	+	_	?	?	1
86-216	6/ 2	1	1.35	1	2	+	_	10	35.0	0
86-217	6/ 2	1 2 3 4 5	1.40 1.38 1.35 1.38 1.35	1 2 0 1 1	4 4 2 4 2	+ + + +	- - + -	12 12 8 16 13	36.0 48.0 16.0 80.0 26.0	0 0 1 0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-217	6/ 2	6	1.35	1	1	+	_	8	12.0	0
86-220	6/ 2	1	1.35	1	1	+	-	6	10.8	0
86-221	6/ 2	1 2 3 4 5 6	1.38 1.38 1.38 1.38 1.38	1 1 1 0 1	4 4 1 4 2 4	+ + + + +	+ - / + -	/ 12 12 / 12 12	27.6 18.0 / 30.0 30.0	0 1 0 0 0 1
86-222	6/ 2	1 2 3 4 5 6 7	1.40 1.35 1.40 1.38 1.38 1.40 1.38	1 1 0 0 1 1	4 4 4 4 4 4	+ + + + / + +	- + - / -	12 12 12 / / 12 /	36.0 24.0 48.0 / 36.0	2 2 1 0 / 1 0
86-223	6/ 2	1 2 3 4 5 6 7 8	1.40 1.40 1.38 1.40 1.35 1.38 1.38	2 2 1 1 1 1 1	4 4 4 4 3 4	+ + + + + + ?	? / + ?	12 15 13 12 10 / 13	36.0 30.0 32.5 36.0 25.0 78.0 36.0	4 0 0 0 0 0 0 0
86-226	6/ 2	1 2 s3 s4	1.35 1.38 1.20 1.18	1 2 1 1	4 4 1 1	+ + +	+ / - -	12 / 8 11	54.0 / 14.4 18.7	0 0 0 2
86-258	6/25	1 2 3	1.35 1.38 1.33	1 1 1	4 4 4	+ + +	+ ? -	10 12 12	80.0 79.2 60.0	6 8 2
86-260	6/25	1	1.35	2	2	+	-	6	15.0	0
86-261	6/25	1 2 3 4	1.35 1.38 1.33 1.38	2 2 2 2	4 4 2 1	+ + +	- - -	14 14 14	70.0 91.0 77.0 13.0	4 0 7 1
86-263	6/25	s1 s2 3	1.20 1.15 1.35	0 2 2	2 4 4	+++++++++++++++++++++++++++++++++++++++	+	12 12 12	30.0 54.0 66.0	2 2 1
86-264	6/25	1	1.38	2	4	+	_	14	91.0	19
86-270	6/25	1 2 3 4	1.40 1.43 1.40 1.38	1 1 1 1	2 2 2 2	+ + + +	- - -	12 12 10 12	26.4 50.4 35.0 45.6	0 4 3 3

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-272	6/25	s1	1.23	1	2	+		10	30.0	4
	•	2	1.33	1	2	+		12	48.0	2
		3	1.35	1	2	+		12	54.0	0
		4	1.38	$\overline{1}$	$\overline{2}$	(posed)
		5	1.35	1	$\overline{4}$	+	+	12	48.0	Ó
		6	1.35	1	2	+		12	60.0	0
		7	1.35	1	4	+	-	14	58.8	6
86-273	6/25	1	1.38	1	1	+	_	12	36.0	2
		2	1.38	1	4	+	+	12	48.0	1
		3	1.40	2	1	+	-	12	30.0	1
		4	1.33	1	4	+	+	14	70.0	3
		5	1.35	1	1	+	_	12	30.0	1
		6	1.40	1	1	+	_	12	30.0	0
		7	1.38	1	1	+	_	12	24.0	1
		8	1.38	1	$\overline{1}$	+		12	30.0	$\overline{2}$
		9	1.38	1	1	+		12	24.0	1
		10	1.38	1	1	+		12	24.0	0
		11	1.40	1	2	+		12	36.0	0
		12	1.38	1	1	+		12	30.0	3
		13	1.38		1			12	30.0	0
		14		1	4	+	-			0
			1.38	1		+	+	14	84.0	
		15	1.38	1	4	+	+	14	70.0	0
		16	1.40	1	1	+	-	12	24.0	1
		17	1.38	1	1	+		12	24.0	2
		18	1.38	1	1	+	-	12	24.0	0
		19	1.38	1	1	+		12	24.0	2
		20	1.38	1	1	+		14	28.0	0
		21	1.33	1	1	+	_	8	20.0	1
	_	22	1.35	1	1	+		12	24.0	2
		23	1.35	1	1	+	· 	12	24.0	1
		24	1.40	1	4	+	+	12	36.0	0
		25	1.38	1	4	+	/	/	/	1
86-275	6/25	1	1.28	1	4	+	_	10	52.0	0
		2	1.40	1	2	(posed)
		3	1.30	1	4	+	+	12	72.0	0
		4	1.38	1	4	+	+	12	60.0	0
86-292	7/23	1	1.35	2	4	+	+	14	98.0	many
86-293	7/23	1	1.30	1	2	+	+	?	?	4
		2	1.38	1	4	+	+	14	86.8	1
86-294	7/23	s1	1.18	1	3	(decom	posed)
86-296	7/23	1	1.33	0	4	+	+	14	72.8	11
	.,	2	1.35	1	4	+	+	12	72.0	6
86-298	7/23	1	1.35	2	2	+	-	10	30.0	2
86-299	7/23	1	1.35	1	1	+	_	12	31.2	3
		2	1.35	1	1	+		6	9.6	0
		3	1.35	1	2	+ ,		8	16.8	0

No.	Date	#Q	HW (mm)	WV	WM	1	CL	NO	LO(mm)	NMO
86-297	7/23	1	/	1	3	+		6	10.2	0
		2	1.38	0	2	+		10	20.0	0
86-295	7/23	1	1.35	2	4	+	+	14	56.0	1
		2	1.38	2	4	+	+	14	51.8	2
		3	1.38	2	4	+	+	10	30.0	0
		4	1.38	1	4	+	+	14	49.0	0
		5	1.35	2	4	+	+	10	30.0	0
		6	1.38	1	4	+	+	12	48.0	0
86-327	8/11	1	1.35	1	4	+	+	16	51.2	0
86-335	8/11	1	1.38	2	4	. +	+	12	48.0	0
86-333	8/11	1	1.38	0	4	+	+	16	96.0	8
86-336	8/11	1	1.33	0	4	+	+	14	93.8	14
86-332	8/11	1	1.38	2	4	+	+	10	27.0	0
		2	1.40	0	4	+	+	14	84.0	9
86-330	8/11	1	1.35	1	4	+	+	12	48.0	5
00 330	0/11	2	1.33	1	4	+	+	14	67.2	4
		3	1.35	1	4	+	+	12	48.0	4
86-334	8/11	1	1 25	1	4			12	60.0	10
00 334	0/11	2	1.35 1.38	1	4	+	++	14	72.8	6
		3	1.43	2	4	+	+	14	79.8	10
		4	1.38	2	4	+	+	14	77.0	12
86-329	8/11	1	1.35	2	4	+	+	12	42.0	5
00 020	0/11	2	1.35	1	4	+	+	10	41.0	0
		s3	1.18	2	4	+	+	10	50.0	5
		4	1.35	1	4	+	_	12	38.4	4
		5	1.35	2	4	+	+	11	55.0	3
86-328	8/11	1	1.35	1	2	_	_	10	25.0	3
00-326	0/11	2	1.33	1	2	+	+	10	20.0	2
		3	1.33	$\frac{1}{2}$	2	+	,	/	20.0	7
		4	1.28	2	4	+	+	14	53.2	3
		5	1.30	1	4	+	+	14	61.6	4
		6	1.33	$\overline{2}$	2	+	+	14	35.0	3
		7	1.33	2	2	+	-	12	22.8	0
86-337	8/11	1	1.35	1	4	+		12	30.0	0
	,	2	1.38	1	2	+	+	12	24.0	2
		3	1.35	1	4	+	_	12	24.0	2
		4	1.33	1	4	+		12	30.0	1
		5	1.38	0	4	+	-	12	24.0	0
		s6	1.23	1	4	+	+	12	48.0	6
		7	1.35	1	4	+		12	24.0	2
		s8	1.25	1	4	+	+	13	52.0	10
		′s9	$\frac{1.20}{1.25}$	1	4	+	+ /	14	56.0	3
		10 s11	$\begin{matrix}1.35\\1.25\end{matrix}$	$\frac{1}{0}$	4 4	?	+	16 12	32.0 66.0	7
		12	$1.25 \\ 1.40$	1	4	+	+	12	60.0	6

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-337	8/11	13	1.35	1	4	+		12	24.0	0
		14	1.33	1	4	+		14	28.0	1
		15	1.35	1	4	+	+	16	32.0	0
		16	1.38	1	4	+	_	12	24.0	2
		17	1.35	1	4	+		12	24.0	2
		18	1.33	1	4	+	_	12	24.0	0
		19	1.33	1	4 2	+	-	$\begin{array}{c} 12 \\ 12 \end{array}$	$24.0 \\ 24.0$	1 1
		A 1	1.35	/	.	+	_	12	24.0	1
86-358	9/9	1	1.38	2	4	+	+	14	28.0	0
		2	1.40	1	2	+	+	14	56.0	0
86-360	9/9	1	1.35	1	4	+	-	16	32.0	0
		2	1.38	1	4	+	+	16	36.8	. 0
		3	1.35	1	4	+	+	12	25.2	0
		4	1.35	0	4	+	+	12	24.0	0
		5	1.35	1	4	+	+	16	28.8	0
		6	1.35	0	4	+	+	14	35.0	0
		7	1.30	0	4	+	+.	16	27.2	0
		8	1.38	1	4	+	+	16	40.0	0
86-361	9/9	1	1,40	1	4	+	+	15	30.0	0
		2	1.38	0	4	+	+	12	36.0	0
86-424	10/13	1	1.35	1	4	+		13	58.5	0
		As1	1.23	/	0	?		8	8.0	0
		As2	1.20	/	1	_		8	8.0	0
		As3	1.25	./	0	_		8	8.0	0
		As4	1.23	/	0			8	8.0	0
	_	As5	1.20	1	0			8	8.0	0
		As6	1.25	/	0	_		8	8.0	0
86-425	10/13	1	1.35	1	4	+	_	12	24.0	0
		2	1.35	1	4	+	-	12	24.0	0
		3	1.38	2	4	+	+	13	52.0	0
		4	1.33	1	4	?	_	12	18.0	0
		D5	1.38	1	0	-	_	12	24.0	0
		6	1.35	1	4	+		10	20.0	0
		7	1.33	2	4	+	-	15	30.0	0
		D8	1.38	0	0		-	8	12.0	0
		9	1.33	1	4	+		14	21.0	0
		10	1.35	0	4	+	-	12	18.0	0
		11	1.35	2	4	+		12	24.0	0
		12	1.33	1	4	+	-	12	24.0	0
		13	1.38	1	4	+	-	12	24.0	0
		A 1	1.35	/	0	-	-	8	8.0	0
		A2	1.38	/	0			8	16.0	0
		A3	1.38	/	0	-	-	12	20.4	0
		A4	1.40	1	0	_	-	?	?	0
		A5	1.38	/	0	-		8	14.4	0
		A6	1.38	/	0		-	10	12.0	0
		A7	1.35	-/	0	-	_	8	13.6	0
		A8	1.35	/	0	-	-	8	16.0	0
		A9	1.35	/	0			12	25.2	0
		A10 A11	1.35 1.43	/	0	-	-	8 8	$\begin{smallmatrix}15.2\\12.0\end{smallmatrix}$	0
					0					0

No.	Date #Q	HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
	A12	1.38	/	0		***	8	13.6	0
	A13	1.40	/	0		-	10	15.0	0
	A14	1.40	/	0			10	20.0	0
	A15	1.38	/	0			8	12.0	0
	A16	1.40	/	0	-		8	14.4	0
	A17	1.35	/	0	_	-	10	20.0	0
	A18	1.38	/	0	-	-	12	18.0	0
	A19	1.40	/	0	-	_	10	15.0	0
	A20	1.35	/	0			8	14.4	0
	A21	1.35	/	0		-	8	13.6	0
	A22	1.40	/	0	-		8	16.0	0
	A23	1.38	/	0	-		10	15.0	0
88-028	3/10 s1	1.25	2	2	+	-	12	24.0	0
	s2	1.25	2	1			10	?	0
	s3	1.25	2	2	+	_	8	16.0	1
	s4	1.20	2	1	+	-	?	?	0
	Ds5	1.23	2	0	_		8	16.0	0
	6	1.35	2	4	+	+	14	70.0	0
	s7	1.25	2	1	+		8	16.0	0
	s8	1.23	2	2	+		8	12.0	0
	A1	1.30	/	0			8	12.0	0
	As2	1.20	1	0	-	_	/	/	0
	As3	1.20	/	0	_		/	/	0
38-030	3/10 1	1.35	2	1	+	_	8	14.4	0
	2	1.40	2	2	+	_	/	/-	
	3	1.30	2	4	+	+	15	45.0	0
	s4	1.18	2	1	+,	https	10	15.0	0
	` 5	1.28	2	4	+	+	14	63.0	0
	s6	1.18	1	1	+	. —	8	12.0	0
	s7	1.20	1	1	+		8	/	/
	8	1.38	2	4	+	+	16	64.0	0
	Ds9	1.20	2	0		_	8	12.0	0
	s10	1.20	1	1	+	_	8	12.0	0
	Ds11	1.25	0	0	_		8	12.0	0
	D12	1.43	0	0	+	_	18	39.6	0
	s13	1.23	0	3	. +		/	/	/
	s14	1.25	1	1	+	-	12	20.4	1
	Ds15	1.18	2	0	+		10	12.0	0
	D16	1.40	1	0	-	-	8	10.4	0
	17	1.35	0	1	+		12	24.0	0
	18	1.40	2	4	+	+	12	42.0	0
	s19	1.23	1	1	+	-	12	14.4	0
	s20	1.13	1	2	+	-	12	20.4	0
	s21	1.23	0	3	+		/	/	/
	22	1.28	1	4	+	+	16	48.0	0
	s23	1.13	0	/	/	/	/	/	/
	s24	1.25	1	1	+		/	/	/
	s25	1.20	1	1	?	+	12	36.0	0
	A1	1.40	/	0		_	8	12.0	0
	As2	1.18	/	0	_	_	/	/	/
	Ás3	1.18	/	0	-		/	/	/
	As4	1.20	1	0	_	_	/	/	/
	As5	1.25	/	3		_	/	/	/
	A6	1.40	/	0			16	32.0	0 .

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-030	3/10	A7 Asd	1.38 1.20	/	0	-	, -	16 8	$\begin{array}{c} 32.0 \\ 12.0 \end{array}$	0 0
88-031	3/10	1	1.40	1	2	+		12	20.4	0
		2	1.35	2	4	+	+	14	42.0	0
		3	1.38	1	4	+	-	12	24.0	0
		4	1.35	2	4	+	+	16	48.0	0
		5	1.35	2	4	+	+	14	35.0	0
		6	1.30	0	2	+	+	12	36.0	0
		7	1.30	1	4	+	+	13	58.5	0
		8	1.30	2	4	+	+	16	56.0	0
		9 ~ 1.0	1.38	2	4	,+	+	16	32.0	0
		s10 11	1.18	2	4	+	+	16 12	$64.0 \\ 24.0$	0 0
		12	$1.33 \\ 1.35$	0 2	2	+	+	14	56.0	0
		13	1.35	2	4	+	+	12	36.0	0
		14	1.35	2	4	+	+	12	42.0	0
		15	1.35	2	4	+	+	16	56.0	0
		16	1.33	2	2	+	+	16	48.0	ő
		17	1.35	0	2	+	+	12	30.0	ő
		18	1.38	2	3	+	+	12	48.0	0
		19	1.35	2	3	+	_	$\overline{14}$	30.8	0
		20	1.35	2	4	+	+	18	54.0	0
		21	1.35	2	4	+	+	13	52.0	0
		22	1.33	2	4	+	+	16	48.0	0
		23	1.35	0	4	+	+	12	36.0	0
		24	1.38	2	4	+		16	32.0	0
		25	1.35	2	4	+	+	16	56.0	0
		26	1.35	2	4	+	+	16	48.0	0
	`	27	1.38	2	4	+	+	13	45.5	0
		s28	1.15	2	4	+	+	16	48.0	0
		29	1.35	0	4	+	+	16	56.0	0
		s30 s31	$\begin{array}{c} 1.15 \\ 1.15 \end{array}$	2	3 4	+	+	/ 12	48.0	0
88-032	3/10	1	1.35	1	4	+	+	16	48.0	0
		2	1.33	0	1	+	+	12	36.0	0
		s3	1.13	1	1	+		12	24.0	1
		s 4	1.20	1	1	+		14	21.0	1
		5	1.40	1	4	+	+	14	42.0	0
88-033	3/10	1	1.35	1	4	+	+	16	40.0	0
		2	1.35	2	4	+	+	17	76.5	0
		s3	1.15	2	4	+	+	16	64.0	0
		4	1.30	2	4	+	+	16	64.0	0
		5	1.38	2	2	+	_	16	48.0	0
		6	1.35	0	4	+	+	16	72.0	0
		7	1.38	2	4	+	+	12	36.0	0
		8	1.35	2	3	+	/	/	/,	/
		9	1.38	2	3	+	_ /	1.4	/ /2 ^	/
		10 11	1.38	2	4	+	+	14 12	$\begin{array}{c} 42.0 \\ 36.0 \end{array}$	0 0
		12	$\begin{array}{c} 1.38 \\ 1.40 \end{array}$	2 2	4 4	+	+	$\frac{12}{14}$	49.0	0
		13	1.40	2	4	+	+	16	48.0	0
		14	1.33	1	4	+	+	16	72.0	0
		15	1.33	2	4	+	+	14	28.0	ŏ

No.	Date #6) HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-033	3/10 s16	1.25	2	4	+	+	12	48.0	0
89-115	1/14 1 A1		3						
89-121	1/17 1		3						
	2		4						
	s3		3						
	4	1.28	3						
	5		4						
	6		4						
	As1	1.18	2						
89-002	4/13 D1		0	0	· —	-	10	18.0	0
	D2		0	1		-	12	19.2	0
	D3 D4		0	0	-		10 10	$\begin{array}{c} 13.0 \\ 10.0 \end{array}$	0 0
	D4	1.33	0	U	_		10	10.0	U
89-014	4/14 1	1.38	1	2	+		12	36.0	0
	s2		2	4	+	-	10	20.0	0
	Ds3		0	0	+		8	8.8	0
	s4		2	2	+	+	11	33.0	0
	5		0	4	+	?	12	24.0	0
	s6 s7		1	3 4	+	?	? 12	? 24.0	0 0
	8		2 1	4	+	?	12	24.0 ?	0
	9		2	4	+	<u>.</u>	14	42.0	ő
	10		1	4	+	_	12	30.0	Ö
	11		1	4	+	_	16	48.0	0
	s12	1.13	2	2	+	(dec	omposed)
	Ds13		0	0	-		8	8.0	0
	s14		2	4	+		10	30.0	0
	As1	1.18	/	0	+		10	10.0	0
89-015	4/14 1		1	4	+	-	12	?	0
	s2		2	4	+	+	16	56.0	0
	3		1	4	+	+	14	42.0	0
	4 5		1 2	4 4	+	?	14 12	24.0	0 0
	6		1	4	+	+	12	42.0	0
	7		2	4	+	+	13	52.0	ő
	8a		1	4	?	?	12	30.0	0
	s9		1	4	+	,	13	39.0	0
	As1		/	0	-	-	8	13.6	0
89-145	4/14 1	1.33	2	4	+	?	8	40.0	0
	s2	1.25	1	3	+	?	14	42.0	0
	s3		2	4	+	?	13	45.5	0
	4		2	4	+	?	12	36.0	0
	5		2	1	?	?	13	45.5	0
	Ds6		1	0	+	_	8.	9.6	1
	s7	1.18	2	4	+		15	45.0	1
	Ds8	1.20	2	0	+		8	10.4	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
89-085	4/27	1	1.38	1	4	+		12	18.0	0
		Ds2	1.20	ō	Ō	+		14	22.4	Ŏ
		3	1.38	1	4	+		12	24.0	0
		4	1.38	2	4	+		15	33.0	Ō
		Ds5	1.20	0	0	+		8	12.0	0
		Ds6	1.25	0	0	+	_	8	14.4	0
		7	1.38	2	4	+	_	12	18.0	0
		8	1.35	1	4	+	?	12	60.0	0
		9	1.38	2	4	+	_	8	20.0	0
		s10	1.18	0	4	+	· _	12	18.0	0
		11	1.33	2	4	+		12	36.0	0
		12	1.38	2	4	+	?	12	36.0	0
		13	1.38	2	4	+		13	32.5	0
		14	1.38	2	4	+		8	20.0	0
		15	1.38	1	4	+	?	11	38.5	0
		16	1.38	2	4	+	_	12	15.0	0
		17	1.40	1	4	+	_	8	20.0	0
		18	1.40	2	4	+		12	24.0	0
		19	1.38	1	4	+	+	12	60.0	0
		20	1.38	1	4	+	+	12	26.4	0
	D	s21	1.20	0	0	+		8	13.6	0
		22	1.38	2	4	+	+	12	36.0	0
		A 1	1.38	1	4			12	14.4	0
89-102	5/15	1	1.38	1	4	+	+	12	36.0	0
		2	1.40	1	1	+	_	8	16.0	2
		3	1.35	1	4	+	_	10	20.0	0
		4	1.35	1	4	(,	decom	posed)
		5	1.35	2	4	`+	_	10	30.0	0
	~	s6	1.25	2	4	(posed)
		7	1.35	2	4	Ì			posed)
		8	1.38	2	4	Ì.			posed	·)
		A1	1.38	1	0	`	_	8	12.0	o´
		A2	1.38		0	_	_	8	20.0	0

2-2 Mt. Kiyosumi, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-165	7/28	s1	1.15	0	3	+	_	12	51.0	2
		s2	1.20	1	3	?	_	12	60.0	2
		3	1.30	1	3	-	+	15	67.5	0
		4	1.35	1	3			11	38.5	3
		5	1.35	2	3	+		13	48.8	0
		6	1.30	2	3	+	+	12	60.0	0
		7	1.35	1	3	+	+	15	52.5	0
		8	1.30	1	3	+	+	13	52.0	0
		9	1.30	1	2	+	+	11	39.8	0
		s 10	1.20	1	3		· ·	14	59.5	2
		11	1.35	1	2	+	_	16	60.0	1
		12	1.40	1	2		(de	ecomp	osed)	
		13	1.35	2	3	+	+	12	42.0	42
		14	1.35	2	3	+	-	16	64.0	1
		s15	1.15	2	3		+	13	52.0	0
		16	1.30	1	3	+	+	13	50.5	1

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-165	7/28	17	1.35	2	3	+	+	14	77.0	0
		18	1.35	2	. 3			11	49.5	0
		19	1.40	2	?	+	+	16	72.0	. 0
		20	1.35	2	?	+	_	14	42.0	0
		21	1.35	0	?	+	+	12	60.0	1
		22	1.35	2	?	+	-	16	56.0	2
		23	1.35	2	?	+		13	42.0	2
		24	1.30	2	?	+	-	12	27.0	0
		25	1.35	2	4	+		13	44.0	0
		26	1.40	2	2	+	_	14	42.0	0
		s27	1.10	2	2	+	+	12	39.0	0
		28	1.30	2	3	+	+	11	36.0	2
		29	1.35	2	4	+	+	13	47.0	0
		s30	1.20	2	3	+		15	37.5	0
		31								
85-265	9/21	1	1.35	1	2	+		14	20.3	0
		2	1.32	2	3	+	_	10	23.0	0
		3	1.30	2	2	+		7	15.0	0
		4	1.31	2	1	+		12	24.3	0
		5	1.35	1	1	+		14	24.2	0
		6	1.31	$\tilde{2}$	3	+	-	8	9.1	Ō
		7	1.34	0	$\ddot{2}$	+	_	12	18.9	Ö
		8	1.31	2	2	_		12	24.6	ŏ
		9	1.30	2	2	?	_	6	?	Ŏ
		10	1.35	2	4	+	+	16	78.2	ő
		11	1.35	2	2	+	_	9	14.0	ŏ
		12	1.34	2	2	+	_	12	24.6	0
		13	1.32	2	2	+		12	21.7	0
	_	14	1.35	2	2	+	_	10	24.0	Ő
		15	1.31	2	1	+		9	18.9	0
		16	1.32	2	2	+		10	19.5	0
		17	1.32	1	2	+	_	9	18.9	0
		18	1.35	2	2	+	_	12		0
		19	1.35		2			11	$\begin{smallmatrix}22.2\\17.4\end{smallmatrix}$	0
		19	1.33	2	2	+		11	17.4	U
85-270	9/21	1	1.35	2	3	+	_	12	27.6	0
		s2	1.25	2	4	+	+	11	83.6	0
85-268	9/21	1	1.30	1	4	+	+	14	49.0	0
	-	2	1.35	2	4	+	+	14	44.8	0
		3	1.31	2	4	+	+	16	73.6	0
		4	1.30	2	4	+	+	13	58.5	0
		5	1.30	2	4	+	+	15	42.0	0
		6	1.30	2	4	+	+	16	48.0	0
85-279	9/22	c 1	1 20	<u> </u>	1	1		12	18.0	0
00-218	3/44	s1 2	1.20	0	1	+	-			
			1.34	1	4	+	+	16	56.0	0
		s3	1.15	1	3	+	-	15	30.0	0
		s4	1.15	2	4	+	+	14	51.8	0
		s5	1.17	2	2	+	_	14	23.8	1
		s6	1.18	0	1	+		8	12.8	0
		s7	1.15	0	3	+	-	12	19.2	0
		8 8	1.16	0	1	+	-	12	21.6	0

2-3 Tokorozawa, Saitama Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
86-300	7/25	1 2 s3 4 5 6 7 8 s9 s10 11	1.35 1.38 1.20 1.35 1.40 1.38 1.38 1.38 1.23 1.23	1 1 2 2 2 2 1 2 2 2 2 2 2 1	4 4 3 4 4 4 4 4 4 4 4 4	///////////////////////////////////////	///////////////////////////////////////	/ 12 / / / / / / /	24.0 / / / / / /	4 1 1 2 1 / 2 / 2 1
86-301	7/25	1 2 3 4 5 6 7 8 8 9 10 11 s12 13 s14	1.43 1.40 1.43 1.38 1.28 1.30 1.48 1.43 1.25 1.43 1.23 1.43	2 1 2 1 2 1 2 2 1 1 1 1 1 1 2 2 1 1 1 1	4 4 1 2 4 4 4 4 4 4 4 4	+ + + + + + + + + + + + + + + + + + + +	+ + + + - / / / + /	12 12 16 decom 8 12 / 8 10 16 14 12 8 /	48.0 36.0 64.0 posed / 40.0 48.0 56.0 24.0 16.0	1 0 0) / / / 0 0 1 0 1 2
86-302	7/25	1 2 3 4 s5 6	1.40 1.43 1.40 1.43 1.23 1.38	1 2 2 1 1	4 4 4 4 4	+ / + + / +	/////	///////////////////////////////////////	/////	/ / / / 2
86-303	7/25	1	1.43	1	4	+	+	12	48.0	7
86-304	7/25	1 2 3 4	1.43 1.40 1.38 1.28	2 2 1 1	4 4 4	+++	//	/ / 8	16.0	2 1 2 3
86-305	7/25	1 2 3 4 s5	1.40 1.40 1.40 1.28 1.25	1 1 1 1	4 4 4 4	/////	////	////	/////	////
86-307	7/25	1 2	1.38 1.40	2 2	4 4	+	/	//	//	0 2
86-308	7/25	s1	1.15	0	4	/	/	/	/	4

2-4 Komikado, Chiba Pref.

No.	Date	#Q	HW(mm)	WV	WM	Ι	CL	NO	LO(mm)	NMO
88-021	3/ 7	s1	1.20	2	1	+	. –	10	?	0
		s2	1.23	2	1	+	_	14	56.0	0
		s3	1.18	1	1		_	10	?	0
		4	1.35	1	1	+	_	12	48.0	0
		s5	1.18	1	1	+	_	12	36.0	0

2-5 Totsuka, Kanagawa Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMC
88-038	3/15	1	1.40	2	4	+	+	15	64.0	0
		2	1.40	1	4	+	+	16	80.0	. 0
		3	1.38	2	4	+	+	12	48.0	0
88-039	3/15	. 1	1.40	1	. 1	_		12	12.0	0
		D2	1.35	1	0	****		12	18.0	0
		3	1.43	1	1	+	_	12	18.0	0
		4	1.40	1	1	_	-	16	40.0	0
		5	1.40	1	1	-		16	24.0	0
		6	1.40	- 1	4	+		12	18.0	0
		7	1.38	1	1	+	-	14	28.0	0
		8	1.38	1	1	+		14	28.0	0
		9	1.43	1	1	+		12	18.0	0
		10	1.45	1	1	+		12	24.0	0
		11	1.43	1	1	+		12	19.2	0
		12	1.40	1	1	+		14	28.0	0
		13	1.38	0	1	+		12	24.0	0
		14	1.38	1	1	+	-	16	28.8	0
		15	1.38	1	4	+	_	16	32.0	0
		16	1.38	1	1	+		12	18.0	0
		17	1.38	1	1	+		12	21.6	0
		18	1.35	1	1	. +		16	12.0	0
		A 1	1.38	1	0	-	-		/	/-
		A2	1.40	/	0	-		10	15.0	0
		A3	1.38	1	0	-	_	10	20.0	0
		A4	1.40	/	0	_	_	/.		/
		A5	1.35	/	0		-	12	27.0	0
		A6	1.43	/,	0	-		8	10.4	0
		A7	1.35	/,	0		-	16	/	/
		A8	1.33	/,	2	-	_	16	24.0	0
		A9	1.38	/,	0	_		8	12.0	0
		A10	1.40	/,	0			16	32.0	0
		A11	1.40	/,	0	_		/	/	/
		A12	1.43	/,	0	+		12	12.0	0
		A13	1.43	/,	0	+	_	12	19.2	0
		A14	1.38		0	+	_	/	100	/
		A15	1.35	/,	0	_	_	12	18.0	0
		A16	1.35	/	0			12	24.0	0
88-040	3/15	1	1.38	1	4	+	+	12	60.0	0
		2	1.35	2	3	+	+	13	45.5	0
		3	1.38	2	3	(posed	·)
		4	1.35	2	4	+	+	15	45.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-041	3/15	s1	1.23	0	4	+	+	16	32.0	0
		2	1.35	2	4	+	+	16	48.0	0
		3	1.33	2	4	+	+	14	42.0	0
		s4	1.23	2	4	+	+	14	42.0	0
88-042	3/15	1	1.38	2	4	+	+	12	30.0	0

2-6 Busann, Miura Peninsura, Kanagawa Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-057	3/20	1	1.35	1	4	+	+	20	50.0	0
		s2	1.23	0	3	(posed)
88-059	3/20	1	1.35	2	4	+	+	17	85.0	0
88-064	3/20	s1	1.25	2	4	+	+	14	28.0	0
		s2	1.20	2	4	+	_	14	21.0	0
		s3	1.23	2	4	+		17	34.0	0
		s4	1.20	1	4	+	+	16	32.0	0
88-066	3/20	D1	1.38	1	0	-	_	10	15.0	0
		D2	1.40	1	0	_	-	/	/	/
		3	1.43	1	1	+	_	12	24.0	0
		D4	1.40	0	0	-		12	24.0	0
		5	1.35	0	1	_		/	/	/
		6	1.35	0	1	+		12	24.0	0
		A1	1.40	/	0	_	-	12	20.4	0
		A2	1.40	/	0	_	_	13	22.1	0
		A3	1.35	/	0	_	-	16	24.0	0
		A4	1.43	/	0	_		6	9.0	0
		A5	1.38	/	0	_	_	6	6.0	0
		A6	1.38	/	0	_	_	/	/	/
		A7	1.43	/	0	_	_	11	19.8	0
		A8	1.35	1	0	_	_	12	18.0	0
		As9	1.23	/	0		-	12	18.0	0
		A10	1.38	/	0	-	-	6	9.0	0

2-7 Mt. Kano, Bousou Peninsura, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-070	3/21	s1	1.20	2	4	+	+	12	48.0	0
	•	2	1.33	2	4	+	+	12	60.0	0
88-073	3/21	1	1.43	1	4	+	+	14	49.0	0
	·	2	1.43	2	4	+	+	12	36.0	0
		3	1.35	2	4	+	+	15	67.5	0
		4	1.38	2	4	+	+	14	70.0	0
		, 5	1.33	1	4	+	+	14	35.0	0
88-075	3/21	1	1.33	2	4	+	+	12	30.0	0
	,	2	1.38	2	4	+	+	16	64.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-076	3/21	1	1.38	2	4	+	+	11	33.0	0
		2	1.38	2	4	+	+	12	36.0	0
		3	1.38	2	4	+	+	14	56.0	0
		4	1.38	2	4	+	+	14	56.0	0
		s5	1.20	2	3	?	_	8	?	. 0
		6	1.38	1	4	+	+	14	42.0	0
		s7	1.23	1	4	+	+	14	56.0	0
		s8	1.18	1	4	+	+	12	36.0	0
•		9	1.38	1	4	+	+	12	36.0	0
		10	1.38	1	4	+	+	12	54.0	0
		11	1.35	2	4	+	+	12	36.0	0
		12	1.35	1	4	+	+	14	49.0	0
		13	1.38	2	4	+	+	12	42.0	0
		s14	1.18	2	4	. +	+	14	35.0	0
		s15	1.15	1	4	+	+	12	36.0	0
		16	1.35	1	4	+	+	13	32.5	0
		s17	1.15	2	3	(posed)
		s18	1.18	2	4	÷	+	12	30.0	0

2-8 Kisarazu, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
		" Q		<u> </u>						
88-077	3/21	1	1.35	2	4	+	+	12	24.0	0
		2	1.38	2	4	+	+	13	45.5	0
		3	1.35	1	4	+	+	12	42.0	0
		s4	1.20	1	4	+	+	12	30.0	0
		5	1.33	1	4	+	+	12	36.0	0
88-078	3/21	1	1.38	1	4	+	+	16	72.0	0
	,	2	1.40	$\overline{2}$	4	+	?	?	?	0
88-079	3/21	1	1.40	1	4	+	+	16	56.0	0
	-,	$\overline{2}$	1.40	2	4	+	+	13	45.5	0
		3	1.38	1	4	+	+	16	48.0	0
		4	1.35	2	4	+	+	17	59.5	0
		s 5	1.15	1	4	+	+	16	48.0	0
		6	1.40	$\bar{2}$	4	+	+	13	39.0	0
		7	1.40	2 2	4	+	+	14	56.0	0
		8	1.38	2	4	+	+	13	52.0	0
		9	1.35	2	4	+	+	12	36.0	0
		10	1.38	2	3	+	(omposed)
		11	1.43	2	4	+	÷	16	72.0	Ó
		12	1.38	2	4	+	+	14	35.0	0
		13	1.38	2	4	+	+	16	48.0	0
		14	1.35	2	4	+	+	12	42.0	0
		15	1.43	1	4	+	+	15	52.5	0
		16	1.40	1	4	+	+	13	39.0	0
		s17	1.15	2	4	+	+	14	63.0	0
		18	1.33	$\overline{1}$	4	+	+	12	30.0	0
		19	1.35	2	4	+	+	14	42.0	0
		20	1.40	$\overline{2}$	4	+	+	12	42.0	0
		s21	1.18	1	4	+	+	12	36.0	0
		22	1.38	$\hat{2}$	4	+	+	15	45.0	0
		s23	1.18	1	$\dot{\overline{4}}$	+	+	15	37.5	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-079	3/21	24	1.35	2	4	+	+	16	48.0	0
		25	1.35	2	4	+	+	15	60.0	0
		26	1.38	2	4	+	+	14	49.0	0
		27	1.38	2	4	+	+	16	56.0	0
		28	1.38	2	4	+	+	15	52.5	0
		s29	1.18	0	/	(decom	posed)
		s30	1.18	1	4	+	+	14	35.0	0
		s31	1.23	1	4	+	+	13	39.0	0
		s32	1.15	1	4	+	+	13	45.5	0
88-081	3/21	1	1.40	1	4	+	+	14	56.0	0
		2	1.40	1	4	+	+	16	56.0	0
		3	1.35	1	4	+	+	15	52.5	0
		4	1.35	. 1	4	+	+	12	36.0	0
		5	1.35	1	4	+	+	12	36.0	0
		s6	1.18	0	4	+	+	12	42.0	0
		7	1.33	2	4	+	+	14	42.0	0
		s8	1.15	1	4	+	+	14	35.0	0
		s 9	1.23	2	4	+	+	15	52.5	0
		10	1.40	1	4	+	+	12	30.0	0
		s11	1.20	2	4	(decom	posed)
		s12	1.15	2	4	+	+	16	32.0	0
		s13	1.18	, 2	4	+ -	+	12	30.0	0
		s14	1.25	0	4	+	+	13	39.0	0
		s15	1.13	2	4	+	+	12	36.0	0
		s16	1.18	2	4	+	+	13	39.0	0
		17	1.38	2	4	+	+	15	52.5	0

2-9 Aobayama, Sendai, Miyagi Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-121	4/ 4	1	1.30	2	4	+	+	13	52.0	0
		2	1.30	2	4	(posed)
		3	1.35	2	4	+	+	12	24.0	0
		4	1.30	2	4	-		12	18.0	0
		5	1.30	1	4	+	, -	12	18.0	0
		6	1.30	2	4	+		16	28.8	0
		D7	1.35	0	0	+		16	32.0	0
		8	1.28	1	4	+		14	23.8	0
		9	1.33	2	4	+		14	35.0	0
		10	1.30	1	4	+		14	28.0	0
		11	1.35	2	4	+		11	22.0	0
		12	1.33	2	4	+		12	18.0	0
		D13	1.35	0	0	_		16	24.0	0
		14	1.33	0	4	-	_	16	27.2	0
		15	1.33	1	4	+	_	14	25.2	0
		16	1.30	2	4	_	-	12	20.4	0
		17	1.33	2	4	(decom	posed)
		18	1.33	- 1	4	+		14	28.0	0
		19	1.38	2	4	?	?	10	30.0	0
		20	1.30	2	4	+	-	12	24.0	0
		21	1.30	1	4	+	_	12	/	0
		A1	1.33	/	0		-	12	18.0	0
		A2	1.35	/	0	. —	-	14	21.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-121	4/4	А3	1.35		0	_	-	11	16.5	0
	-	A4	1.33		0	_	_	12	24.0	0
		A5	1.35	/	0			12	14.4	0
		A6	1.35	1	0	_	_	/	/	/
		A7	1.38	/	0			12	/	0
		A8	1.35	/	0	_	_	11	16.5	0
		Α9	1.35	/	0	-	_	/	/	0
		A10	1.33	/	0	+		12	18.0	0
		A11	1.35	/	0	-	_	11	16.5	0
		A12	1.35	/	0	-		12	18.0	0
		A13	1.35	1	0	_	_	16	35.2	0
		A14	1.33		0		_	12	18.0	0
		A15	1.33	/	0	_		12	18.0	0
		A16	1.35	/	0	· —		12	16.8	0
88-123	4/4	s1	1.23	2	4	+		16	24.0	0

2-10 Miyajima, Hiroshima Pref.

No.	Date	#Q	HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-182	8/27	1	1.35	2	4	+	+	14	42.0	0
		2	1.40	2	4	+	+	14	35.0	0
		3	1.38	2	4	+	+	17	42.5	0

2-11 Matsuyama, Ehime Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-198	8/29	s1	1.23	1	4	+	+	10	30.0	0
		2	1.35	2	4	+	+	12	30.0	0
		3	1.30	2	4	+		12	18.0	0
88-199	8/29	1	1.30	1	4	+	+	14	42.0	0
88-200	8/29	1	1.38	1	3	((decom	posed)
88-201	8/29	1	1.38	2	3	((decom	posed)
		2	1.40	2	3	+	(omposed)
88-202	8/29	s1	1.18	2	4	+	+	14	35.0	0
88-203	8/29	. 1	1.38	1	4	+	_	14	28.0	4
		2	1.33	1	4	+	+	17	51.0	0

2-12 Kouchi Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-204	8/30	1	1.38	1	2	(decom	posed)
		s2	1.20	1	3	Ì		decom	posed)
		3	1.35	1	2	(decom	posed)
		A1	1.38	/	0	_		12	18.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
88-204	8/30	A2	1.38	/	0	_	_	/	/	
		A3	1.38	/	0			-		
		A4	1.38	/	0					
		A5	1.43	/	0					
		A6	1.38	/	0					
		A7	1.38	1	0					
		A8	1.38	/	0					
		A9	1.40	/	0					

2-13 Kamiohsawa, Shimoda, Shizuoka Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
89-158	12/16	A1	1.38	/	0			15	27.0	0
		A2	1.35	/	0		-	14	28.0	0
		A3	1.38	/	0			16	40.0	0
		A4	1.40	/	0	_		16	40.0	0
		A5	1.38	/	0	-	_	12	24.0	0
90-035	1/20	1	1.38	2	4	+	. +	14	44.8	0
		2	1.38	1	4	+	+	14	42.0	0
		3	1.38	2	4	+	+	15	45.0	0
		4	1.38	2	4	+	+	15	60.0	0
		5	1.35	2	4	+	+	13	49.4	0
		6	1.38	2	4	+	+	14	49.0	0
		7	1.35	1	4	+	+	12	50.4	0
		8	1.38	2	4	+	+	14	44.8	0
		9	1.38	1	4	+	+	13	47.2	0
90-036	1/20	1	1.40	2	4	+	+	16	72.0	0
		2	1.43	2	4	+	+	16	72.0	0
		3	1.40	2	4	+	+	14	67.2	0
90-037	1/20	1	1.40	1	4	+	+	15	90.0	0
90-038	1/20	1	1.35	0	2	+	_	12	39.6	0
90-039	1/20	1	1.40	2	4	+	+	16	76.8	0
		2	1.35	2	4	+	+	16	83.2	0
		s3	1.15	2	4	+	+	13	49.4	0
90-040	1/20	1	1.35	2	1	+		14	42.0	0
		2	1.35	0	1	+		15	42.0	0
		D3	1.33	0	0	+		14	37.8	0
		s4	1.20	1	4	+	+	14	44.8	0
		5	1.33	2	1	+		15	45.0	0
		6	1.33	2	4	+	+	16	80.0	0
		A 1	1.33	/	0	_	-	13	39.0	0
		A2	1.33	/	0	-	_	12	24.0	0
		А3	1.35	/	0	_	_	16	38.4	0
		As4	1.20	/	0	_		13	39.0	0
		A5	1.35	/	0	-		14	36.4	0
		A6	1.33	/	0	-		15	39.0	0
		A7	1.35	/.	0			14	35.0	0
		As8	1.18	/_	0			16	32.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-040	1/20	A10		/			_	15	32.5 37.5 49.5	0 0 0

2-14 Ohnabegoe, Matsuzaki, Shizuoka Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
89-169	12/16	A1	1.40	/	0	_	_	13	27.3	0
09-109	12/10	A2	1.38	/	ŏ	_	·	12	26.4	. 0
		A3	1.40	1	0	_	-	12	26.4	0
		A4	1.40	/	0	, -	_	12	27.6	0
		As5	1.20	/	0	_	-	12	21.6	0
90-087	5/20	1	1.40	1	4	+	+	12	36.0	0
. 50 001	0,20	2	1.40	1	4	+	+	15	45.0	0
		3	1.40	1	4	+	+	14	35.0	0
		4	1.33	1	/	/	/	/	/	/

2-15 Hokota, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-001	1/ 7	1	1.35	1	4	+	+	11	44.0	0
00 001	1, '	$\tilde{2}$	1.38	2	4	+	+	12	48.0	0
		s3	1.25	2	4	+	+	13	58.5	0
90-002	1/ 7	1	1.38	2	4	+	+	14	63.0	0
00 002	-/ '	$\tilde{2}$	1.35	2	4	+	+	15	55.5	0
		3	1.38	1	4	+	_	12	48.0	0
		s4	1.23	2	4	+	+	14	64.4	0
		As1	1.18	/	0	+	_	12	21.6	0
90-003	1/ 7	1	1.35	2	4	+	+	15	49.5	0
30 003	1/	2	1.35	2	$\overline{4}$	+	+	16	64.0	0
		3	1.35	2	4	+	+	15	57.0	0
		4	1.38	2	$\tilde{4}$	+	+	15	64.5	0
		5	1.38	2	4	+	+	15	48.0	0
		6	1.35	2	4	+	+	15	60.0	0
		7	1.35	$\bar{2}$	4	+	+	14	56.0	0
		8	1.35	2	4	+	+	15	75.0	0
		9	1.33	$\overline{2}$	$\overline{4}$	+	+	15	67.5	0
		10	1.35	2	$\overline{4}$	+	+	15	52.5	0
		11	1.35	2	4	+	+	13	58.5	0
		12	1.33	2	4	+	+	18	81.0	0
		13	1.38	2	4	+	+	15	70.5	0
		14	1.35	2	4	+	+	16	64.0	0
		15	1.40	2	$\overline{4}$	+	+	15	60.0	0
		16	1.35	2	$\overline{4}$	+	+	16	48.0	0
		, 17	1.35	2	4	+	+	15	55.7	0
		18	1.40	2	4	+	+	16	56.0	0
		19	1.33	2	4	+	+	14	49.0	0

2-16 Taiyoh-mura, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-004	1/ 7	1	1.38	2	4	+	+	13	58.5	0
		2	1.35	2	4	+	+	12	72.0	0
		3	1.38	1	4	+	+	11	38.5	0
		4	1.38	1	4	+	+	10	62.0	0
		5	1.35	2	4	+	+	12	48.0	0
		6	1.38	1	4	+	+	13	52.0	0
		7	1.38	2	4	+	+	13	65.0	0
90-005	1/ 7	1	1.35	2	4	+	+	15	33.0	0
		2	1.35	2	4	+	+	13	39.0	0
		3	1.38	2	4	+	+	16	48.0	0
		4	1.38	2	4	+	+	14	37.8	0
		5	1.38	2	4	+	+	15	55.7	0
		6	1.38	2	4	+	+	16	48.0	0
		7	1.38	2	4	+	+	14	39.2	0
		8	1.33	2	4	+	+	16	36.8	0
		9	1.35	2	4	+	+	15	45.0	0
		10	1.40	2	4	+	+	16	48.0	0
		11	1.38	2	4	+	+	17	45.9	0
		12	1.35	2	1	+	+	14	37.8	0
		13	1.35	2	4			17	39.1	0
		14	1.35	1	4	+	-	17	51.0	0
		15	1.38	2	4	+	-	14	37.8	0
		16	1.38	1	4		-	15	45.0	0

2-17 Kashima, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-006	1/ 7	1	1.38	1	4	+	+	15	84.0	0
		2	1.40	2	4	+		8	24.0	0
		3	1.40	2	4	+	+	12	36.0	0
		4	1.43	2	4	+	-	12	36.0	0

2-18 Asahi-mura, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-009	1/ 7	s1	1.23	2	4	+	+	13	42.9	0

2-19 Azuma-mura, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-010	1/14	1	1.35	2	4	+	+	12	72.0	0
		2	1.33	2	4	+	+	16	72.0	0
		3	1.35	2	4	+	+	12	55.2	0
		· 4	1.33	2	4	+	+	16	80.0	0
		s5	1.20	1	4	+	+	12	54.0	0
		6	1.33	2	4	+	+	14	70.0	0
		7	1.33	2	4	+	+	15	75.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-010	1/14		1.23 1.15							0 0

2-20 Chyohshi, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-012	1/14	1	1.38	2	4	+	+	13	65.0	0
		2	1.33	1	4	+	+	15	60.0	0
		3	1.38	1	4	+ -	+	15	82.5	0
		4	1.38	1	4	+	+	15	72.0	0
		5	1.35	1	4	+	+	14	65.8	0
90-014	1/14	1	1.38	2	4	+	+	14	70.0	0
		2	1.38	2	4	+	+	16	80.0	0
		3	1.38	2	4	+	+	13	78.0	0
		4	1.43	2	4	+	+	13	52.0	0
		5	1.40	2	4	+	+	14	70.0	0
		6	1.38	2	4	+	+ -	13	65.0	0
		7	1.40	2	4	+	+	15	60.0	0
		8	1.35	2	4	+	+	13	52.0	0
		9	1.43	0	4	+	+	17	85.0	0
		10	1.35	2	4	+	+	13	52.0	0
		11	1.35	2	4	+	+	15	67.5	0
		12	1.38	2	4	+	+	16	80.0	0
		13	1.40	2	4	+	+	17	102.0	0
		14	1.35	2	4	+	+	12	54.0	0
		15	1.35	2	4	+	+	15	75.0	0
		16	1.38	2	4	+	+	16	59.2	0
		17	1.40	2	4	+	+	15	82.5	0
		18	1.40	2	4	+	+	14	70.0	0
		19	1.40	2	4	+	+	15	82.5	0
		20	1.43	2	4	+	+	13	84.5	0

2-21 Misaki-chou, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-021	1/15	s1	1.18	2	4	+	+	11	27.5	0
		s2	1.15	1	4	+	+	12	32.4	0
		s3	1.20	2	4	+	+	10	30.0	0
		s4	1.18	1	4	+	+	6	15.0	0
		s5	1.15	1	4	+	+	8	21.6	0
90-022	1/15	1	1.38	2	4	+	+	14	70.0	0
		2	1.38	2	4	+	+	12	48.0	0

2-22 Ohhara, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-023	1/15	1	1.40	2	4	+	+	13	58.5	0
		2	1.38	2	4	+	(dec	omposed)
		3	1.38	2	4	+	+	15	79.5	0

2-23 Tateyama, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-029	1/15	1	1.38	2	4	+	+	14	63.0	0
		2	1.35	2	4	+	+	12	48.0	0
		3	1.35	2	4	+	+	15	45.0	0
		4	1.33	2	4	+	+	14	65.8	0
		5	1.40	2	4	+	+	12	36.0	0
		6	1.38	2	4	+	+	15	52.5	0

2-24 Amagiyugashima, Shizuoka Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-069	3/22	1	1.38	2	4	+	+	15	52.5	0
		2	1.38	2	4	+	+	17	51.0	0
		3	1.40	2	4	+	+	17	85.0	0
		4	1.40	1	4	+	+	13	58.5	0
		5	1.38	1	4	+	+	16	48.0	0

2-25 Hitachiohta, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-07	3/26	1	1.38	0	4	+	+	15	56.0	0
	·	2	1.38	2	4	+	+	14	70.0	0
		3	1.40	1	4	+	+	14	42.0	0
		4	1.43	2	4	+	+	14	63.0	0
	_	5	1.43	2	4	+	+	14	49.0	0
		6	1.38	2	4	+	+	16	72.0	0
		7	1.35	1	4	+	+	17	42.5	0
		8	1.38	1	4	+	+	15	60.0	0
		9	1.40	2	4	+	+	14	56.0	.0
		10	1.38	1	4	+	+	15	52.5	0
		11	1.35	2	4	+	+	14	63.0	0
		12	1.38	2	4	+	+	15	52.5	0
		13	1.38	2	4	+	+	14	70.0	0
		14	1.38	1	4	+	+	14	77.0	0
		15	1.35	2	4	+	+	14	35.0	0
		16	1.40	2	4	+	+	15	52.5	0
		17	1.25	2	4	+	+	17	68.0	0
		18	1.40	1	4	+	+	13	32.5	0
		19	1.38	1	4	+	+	15	60.0	0
		20	1.33	2	4	+	+	14	70.0	0

2-26 Maruyama, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-072	4/17	1	1.40	1	4	+	+	14	56.0	0
		· 2	1.35	1	1	+	+	14	35.0	0

2-27 Tone, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-079	5/ 9	D1	1.33	0	0	+	_	12	24.0	1
		D2	1.38	0	0	+		12	32.4	0
		D3	1.35	0	0	+	-	10	20.0	2
		4	1.40	2	4	+	+	12	72.0	0
		5	1.38	2	4	+	+	12	60.0	0
		D6	1.33	0	0	+	_	11	25.3	1
		7	1.43	2	4	+	+	16	88.0	3
		D8	1.33	0	0	+	_	12	24.0	0
		D9	1.35	0	0	+	_	11	22.0	1
		D10	1.38	0	0	+		12	24.0	1
		D11	1.33	0	0	+	_	12	26.4	1
		A 1	1.33	/	0	-		12	24.0	0
		A2	1.38	1	0			12	24.0	0
		A3	1.33		0	_		11	22.0	0
		A4	1.38	1	0	-		12	24.0	0
		A5	1.33	/	0		-	12	21.6	0

2-28 Syounan, Chiba Pref.

No.	Date	#Q	HW(mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-082	5/ 9	1	1.35	1	1	+	+	12	36.0	1
		2	1.38	2	1	+	+	12	36.0	0
		D3	1.38	1	0	+	+	12	24.0	1

2-29 Teganuma, Chiba Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-083	5/ 9	D1	1.38	0	0	+		12	24.0	1
		D2	1.38	0	0	+	_	12	30.0	0
		D3	1.38	0	0	+	-	12	30.0	0
		D4	1.28	1	0	+	_	13	26.0	1
		D5	1.35	2	0	+	_	12	24.0	0
		D6	1.35	2	0	+	-	11	22.0	0
		D7	1.40	2	0	+		12	30.0	0
		D8	1.30	0	0	+	_	14	28.0	0
		D9	1.40	1	0	+	-	12	24.0	0
		D10	1.35	1	0	+	***	14	42.0	0
		D11	1.35	0	0	+	_	12	30.0	0
		D12	1.38	1	0	+	-	12	24.0	0
		D13	1.35	0	0	+	-	12	18.0	0
		D14	1.35	1	0	+		12	24.0	0
		D15	1.35	0	0	+	-	13	26.0	1
		16	1.40	0	/	/	/	/	/	/
		D17	1.40	1	0	+	_	14	28.0	0
		D18	1.28	0	0	+		12	24.0	0
		D19	1.33	0	0	+	-	12	24.0	0
		D20	1.38	0	0	+		12	30.0	0
		D21	1.38	0	0	+		12	42.0	0
		D22	1.38	0	0	+		12	30.0	0
		D23	1.38	0	0	+	. —	12	30.0	0

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-083	5/ 9	D24	1.35	0	0	+	_	12	27.6	0
	,	D25	1.38	1	0	+		12	30.0	0
		D26	1.38	0	0	+	-	14	32.2	0
		D27	1.28	0	0	+	_	12	30.0	0
		D28	1.33	1	0	+		12	24.0	0
		D29	1.23	0	0	+		12	24.0	0
		D30	1.38	0	0	+		12	26.4	1
		31	1.25	1	2	_	_	/	/	/
		D32	1.35	1	0	+	_	12	24.0	0

2-30 Ushihori, Ibaraki Pref.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
90-084	5/12	1	1.40	2	4	+	+	15	75.0	0
90-085	5/12	1	1.40	1	4	+	+	12	54.0	0
	•	2	1.38	1	4	+	+	14	42.0	0
		3	1.38	1	4	+	+	14	42.0	0
		4	1.40	1	4	+	+	14	63.0	0
		5	1.35	1	4	+	+	16	64.0	0
		6	1.40	1	4	+	+	16	64.0	1
		7	1.43	2	4	+	+	13	52.0	0
90-086	5/12	1	1.40	1	4	+	—	12	30.0	1
	. *	2	1.40	2	4	+	+	16	40.0	0
		3	1.38	2	4	+	+	16	40.0	0
		4	1.38	2	4	+	+	14	30.8	0
	<	5	1.43	2	4	+	+	11	60.5	0
		6	1.38	1	4	+	+	14	77.0	0
		7	1.35	$\overline{2}$	4	+	+	12	36.0	0
		8	1.35	2	4	+	+	14	77.0	0
		9	1.35	2	4	+	+	18	63.0	0
		10	1.40	2	4	+		12	27.6	0

Table 1. Aggression scale used in scoring the responses of workers from different nests in glass vials.

- 0) Acceptance: Mutual tolerance, grooming, trophallaxis
- 1) Avoidance: Retreat back, escape from the oponent
- 2) Alarm: Open-mandible threat, posture of spraying formic acid
- 3) Weak attack: Nipping, leg pulling, body jerking
- 4) Full attack: Locking together, biting, spraying formic acid

Table 2. Observed colonies of C. nawai and C. yamaokai.

Colony		Sp. No	. of queens	No. of workers	No. of brood
M1	C.	nawai	1	c.220	many
M2	C .	nawai	1	c.220	many
P1	C.	yamaokai	7	c.110	many
		yamaokai	5	c.220	many
		yamaokai	1*	c.60	many

^{*} Workers killed two other queens.

Table 3. Brood/worker ratio in nests of *C. nawai* and *C. yamaokai*. Percentage of brood in the populations instead of the ratio was used after angular transformation in the statistical analysis.

Season		of queens the nest	Mean	95% confidence limits	No. of nests
Non-egg	C. nawai	0	0.61	0.54 - 0.67	154
-laying		1	0.91	0.77 - 1.07	58
	C. yamaokai	0	0.56	0.40 - 0.77	35
	•	1	0.80	0.68 - 0.93	49
		>1	0.87	0.81 - 0.92	230
Egg-	C.nawai	0	1.21	0.98 - 1.49	71
laying (Jul-Aug)		1	1.96	1.57 - 2.45	33
(0 42	C. yamaokai	0	1.19	0.08 - 25.61	4
		1	2.05	1.40 - 3.07	18
		>1	2.22	1.65 - 3.04	38

Table 4. Brood/Queen ratio in nests of *C. nawai* and *C. yamaokai*. Number of brood per queen was used after log-transformation in the statistical analysis.

Season		of queens the nest	Mean	95% confidence limits	No. of nests
Non-egg -laying	C. nawai	1	164.6	121.8 -222.5	58
100, 1118	C. yamaokai	1	53.5	42.2 - 67.7	49
		>1	24.3	21.6 - 27.3	230
Egg- laying	C. nawai	1.	262.2	184.8 -371.8	33
	C. yamaokai	1	67.5	53.3 - 85.4	18
(1 2 2 2 2 2 2 3)		>1	34.0	25.7 - 50.4	38

Table 5. Queen ovarian size in C. nawai (a) and C. yamaokai (b).

	Time of collection	Total length of ovarioles*		No. of queens examined
		Mean(mm)	SD	
(a) C. nawai	Winter	160.6	50.6	16
	Summer	202.7	68.7	22
(b) C. yamaokai				
Macrogyne	Winter	35.2	19.7	767
	Summer	43.2	20.4	164
Microgyne	Winter	23.6	16.0	25
	Summer	40.6	15.8	25

^{*} length of ovarioles x number of ovarioles

Table 6. Reproductive conditions of queens in polygynous nests of *C. yamaokai*. #Q: Individual number of queens; "s" indicates small-sized queens. HW: Head width. WV: Degree of wear in wing vestige; (0) not worn, (1) partly worn, (2) completely worn. WM: Degree of decomposition in wing muscle; (0) intact; (1) mildly, (2) hardly, and (3) completely decomposed; (4) replaced by fats. I: Insemination; inseminated (+) or not (-). CL: Corpora lutea; visible (+) or not (-). NO: Number of ovarioles. LO: Total length of ovarioles. NMO: Number of mature oocytes.

No.	Date	#Q	HW (mm)	WV	WM	I	CL	NO	LO(mm)	NMO
85-270	9/21	1	1.35	2	3	+		12	27.6	0
00 2.0	0,21	s2	1.25	2	4	+	+	11	83.6	0
85-279	9/22	s1	1.20	0	1	+	_	12	18.0	0
	,	2	1.34	1	4	+	+	16	56.0	0
		s3	1.15	1	3	+		15	30.0	0
		s4	1.15	2	4	+	+	14	51.8	0
		s5	1.17	2	2	+	· <u>-</u>	14	23.8	1
		s6	1.18	0	1	+	_	8	12.8	0
		s7	1.15	0	3	+	-	12	19.2	0
		8a	1.16	0	1	+	-	12	21.6	0
86-261	6/25	1	1.35	2	4	+		14	70.0	4
	,	2	1.38	2	4	+		14	91.0	0
		3	1.33	2	2	+	_	14	77.0	7
		4	1.38	2	1	+	· 	10	13.0	1 1
86-263	6/25	s1	1.20	0	2	+	_	12	30.0	2
00 200	0, 20	s2	1.15	2	$\overline{4}$	+	+	12	54.0	2
		3	1.35	2	4	+	_	12	66.0	2 1
90-002	1/ 7	1	1.38	2	4	+	+	14	63.0	0
	-, '	2	1.35	2	$\overline{4}$	+	+	15	55.5	0
		3	1.38	1	4	+		12	48.0	0
		s4	1.23	2	4	+	+	14	64.4	0

Table 6. Continued.

No.	Date	#Q	HW(mm)	WV	WM	Ι	CL	NO	LO(mm)	NMO
90-003	1/ 7	1	1.35	2	4	+	+	15	49.5	0
		2	1.35	2	4	+	+	16	64.0	0
		3	1.35	2	4	+	+	15	57.0	0
		4	1.38	2	4	+	+	15	64.5	0
		5	1.38	2	4	+	+	15	48.0	0
		6	1.35	2	4	+	+	15	60.0	0
		7	1.35	2	4	+	+	14	56.0	0
		8	1.35	2	4	+	+	15	75.0	0
		9	1.33	2	4	+	+	15	67.5	0
		10	1.35	. 2	4	+	+	15	52.5	0
		11	1.35	2	4	+	+	13	58.5	0
		12	1.33	2	4	+	+	18	81.0	0
		13	1.38	2	4	+	+	15	70.5	0
		14	1.35	2	4	+	+	16	64.0	0
		15	1.40	2	4	+	+	15	60.0	0
		16	1.35	2	4	+	+	16	48.0	0
		17	1.35	2	4	+	+ .	15	55.7	0
		18	1.40	2	4	+	+	16	56.0	0
		19	1.33	2	4	+	+	14	49.0	U
90-036	1/20	1	1.40	2	4	+	+	16	72.0	0
		2	1.43	2	4	+	+	16	72.0	0
	~	3	1.40	2	4	+	+	14	67.2	0
90-040	1/20	1	1.35	2	1	+		14	42.0	0
	•	2	1.35	0	1	+		15	42.0	0
		3	1.33	0	0	+	_	14	37.8	0
		s4	1.20	1	4	+	+	14	44.8	0
		5	1.33	2	. 1	+		15	45.0	0
		6	1.33	2	4	+	+	16	80.0	0
90-079	5/ 9	.1	1.33	0	0	+		12	24.0	1
	-, -	2	1.38	0	0	+	_	12	32.4	0
		3	1.35	0	0	+	-	10	20.0	2
		4	1.40	2	4	+	+	12	72.0	0
		5	1.38	2	4	+	+	12	60.0	0
		6	1.33	ō	0	+	_	11	25.3	1
		7	1.43	2	4	+	+	16	88.0	3
		8	1.33	0	0	+	_	12	24.0	0
		9	1.35	0	0	+		11	22.0	1
		10	1.38	0	0	+	_	12	24.0	1
		11	1.33	0	0	+	_	12	26.4	- 1

Table 7. Head widths of workers collected from *C. nawai* and *C. yamaokai* populations. Means(mm) and SD (in parentheses) are based on 100 workers from 10 nests from each location.

	C.	nawai	C. yan	aokai
Locality	Shimoda	Amatsu	Kiyosumi	Tsukuba
Minor worker	0.99	0.99 (0.07)	0.94 (0.04)	0.94 (0.04)
Major worker	1.51 (0.08)	1.51 (0.08)	1.34 (0.05)	1.32 (0.05)

Table 8. Two way ANOVA for head width of workers collected from *C. nawai* population (Shimoda) and *C. yamaokai* population (Mt. Tsukuba).

ns, p>0.05; **, p<0.01.

(a) Minor worker

Source of variation	df	SS	MS	F
Species	1	204.02	204.02	28.57**
Colony	9	98.48	10.94	2.71**
Species x colony	9	64.28	7.14	1.77 ns
Within error	180	726.40	4.04	
Total	199	1093.18		

(b) Major worker

Source of variation	df	SS	MS	F
Species	1	3088.98	3088.98	168.88**
Colony	9	119.20	13.24	1.84 ns
Species x colony	9	164.62	18.29	2.54**
Within error	180	1295.20	7.20	
Total	199	4668.00		

Table 9. Total ovariole length (mm) of workers in the queenless and queenright nests of *C. nawai* complex. Mean ± SD and number of workers examined (in parentheses) are shown.

	Queenless	Queenright
(a) C. nawai		
Minor worker	$2.13 \pm 0.87 (205)$	$1.30 \pm 0.48 (167)$
Major worker	$3.52 \pm 1.49 (132)$	2.62 <u>+</u> 0.89 (80)
(b) C. yamaokai		
Minor worker	$1.69 \pm 0.54 (89)$	$1.87 \pm 0.54 $ (56)
Major worker	$3.10 \pm 0.75 (26)$	$3.79 \pm 1.81 (60)$

Table 10. Number of females and males per nest in natural nests of *C. nawai* (a) and *C. yamaokai* (b) in the pre-mating period. Means and standard deviations are presented (number of nests is indicated in parentheses). Frequency of the nest which produced reproductives is also shown.

Female			
remare	Male	Total	Frequency
and and a state of the state of			
16.5±18.1 (21)	35.0±38.7 (32)	41.9 <u>+</u> 44.9 (35)	35/56 (62.5%)
15.0 ± 13.5 (3)	26.4 <u>+</u> 39.2 (10)	30.9 <u>+</u> 45.2 (10)	10/27 (37.0%)
16.3 ± 17.4 (24)	32.9 ± 38.5 (42)	39.4 <u>+</u> 44.7 (45)	45/83 (54.2%)
ai			
$4.3 \pm 3.4 $ (4)	2.6 <u>+</u> 1.8 (12)	4.0 ± 3.1 (12)	12/35 (34.3%)
2.6 <u>+</u> 2.0 (9)	3.2 ± 2.7 (13)	3.4 <u>+</u> 2.8 (19)	19/49 (38.8%)
6.8 <u>+</u> 8.8 (45)	6.7 <u>+</u> 7.4 (90)	10.0 <u>+</u> 10.4 (91)	91/230 (39.6%)
6.0 <u>+</u> 8.0 (58)	5.9 <u>+</u> 6.8 (115)	8.4 ± 9.5 (122)	122/314 (38.9%)
	$(2\overline{1})$ 15.0 ± 13.5 (3) 16.3 ± 17.4 (24) ai 4.3 ± 3.4 (4) 2.6 ± 2.0 (9) 6.8 ± 8.8 (45) 6.0 ± 8.0	$(2\overline{1}) \qquad (3\overline{2})$ $15.0 \pm 13.5 \qquad 26.4 \pm 39.2 \qquad (10)$ $16.3 \pm 17.4 \qquad 32.9 \pm 38.5 \qquad (4\overline{2})$ ai $4.3 \pm 3.4 \qquad 2.6 \pm 1.8 \qquad (1\overline{2})$ $2.6 \pm 2.0 \qquad 3.2 \pm 2.7 \qquad (1\overline{3})$ $6.8 \pm 8.8 \qquad 6.7 \pm 7.4 \qquad (90)$ $6.0 \pm 8.0 \qquad 5.9 \pm 6.8$	$(2\overline{1}) \qquad (3\overline{2}) \qquad (3\overline{5})$ $15.0 \pm 13.5 \qquad (26.4 \pm 39.2 \qquad 30.9 \pm 45.2 \qquad (10)$ $16.3 \pm 17.4 \qquad 32.9 \pm 38.5 \qquad 39.4 \pm 44.7 \qquad (4\overline{5})$ $2.6 \pm 1.8 \qquad (4\overline{2}) \qquad (12)$ $2.6 \pm 2.0 \qquad (13) \qquad (12)$ $2.6 \pm 2.0 \qquad (9) \qquad (13) \qquad (19)$ $6.8 \pm 8.8 \qquad 6.7 \pm 7.4 \qquad 10.0 \pm 10.4 \qquad (91)$ $6.0 \pm 8.0 \qquad 5.9 \pm 6.8 \qquad 8.4 \pm 9.5$

Table 11. Production of reproductives in experimental nests of *C. yamaokai*. Mean numbers of females and males per nest are presented with standard deviations (number of nests is indicated in parentheses). Frequency of the nest which produced reproductives is also shown.

	Female	Male	Total	Frequency
Queen-added nest	0	0	0	0/26 (0%)
Queen-removed nest	1.5 <u>+</u> 0.7 (2)	4.0 ± 4.7 (8)	3.9 <u>+</u> 4.4 (9)	9/26 (34.6%)

Table 12. Observed numbers of each behavior performed by or directed towards the queens of polygynous colony P1 in a total of 20hr. observation.

Behavior	Queen						x ² - test	
	a	b	С	ď*	е	f	g	CESC
Self-groom	5	5	4	0	6	5	10	NS
Be groomed								
by worker	6	6	13	25	4	10	5	NS
Regurgitate								
with worker	11	3	3	3	4	6	3	NS
with queen	2	0	0	0	0	1	1	
Solicit food								
from worker	10	2	4	20	6	13	7	NS
from queen	0	0	0	1	0	1	1	
Be solicited for								
food by queen	1	1	0	0	1	0	0	
Defecate	0	0	0	0	0	0	1	
Be carried								
by worker	0	0	0	1	0	0	0	
Be attacked								
by worker	0	0	0	1	0	0	0	
Walk	29	27	30	24	24	36	53	NS

^{*} died at the last observation

Table 13. Observed numbers of each behavior performed by or directed towards the queens of polygynous colony P2 in a total of 20hr. observation. Queens a, b and c, and queens d and e inhabited different nest tubes, respectively.

Behavior	Queen					X ² -test	
	nest 1			nest 2			
	a	b	c*	d	e		
Self-groom	13	11	32	6	3	p<0.001	
Be groomed							
by worker	2	13	3	6	3	p<0.005	
Regurgitate`							
with worker	0	0	3	1	4		
with larva**	1	0	0	0	0		
Solicit food							
from worker	3	1	3	5	8	NS	
from queen	0	0	1	0	0		
Be solicited for							
food by queen	1	0	0	0	0		
Attack queen	0	0	9	0	0		
Be attacked							
by queen	6	3	0	0	0		
Walk	28	25	41	25	44	NS	

^{*} microgyne

^{**} Direction of food exchange was unknown.

Table 14. Observed numbers of each behavior performed by or directed towards the queens of monogynous colonies in a total of 20hr. observation per colony.

Behavior		X^2 -test		
-	M1	M2	SM	
Self-groom	8	7	13	NS
Be groomed by worker	46	43	6	p<0.001
Regurgitate				
with worker Solicit food	29	21	21	NS
from worker	1	0	1	
Manipulate larva Be carried	0	0	1	
by worker	2	0	0	
Walk	20	18	30	p<0.005

Table 15. Developmental periods (days) of immature stages of four Japanease species of subgenus *Myrmamblys* at the constant temperature of 25°C. Means and standard deviations are presented. Sample size are indicated in parentheses.

	C. nawai	C. yamaokai	C. tokioensis	C. itoi
Egg	19.4 <u>+</u> 1.0 (20)	24.9 <u>+</u> 2.9 (24)	19.0 <u>+</u> 1.8 (12)	20.7 <u>+</u> 1.3 (19)
Larva	23.8 <u>+</u> 6.8 (11)	13.4 <u>+</u> 2.0 (12)	20.6 ± 7.5 (5)	19.3 ± 4.0 (4)
Prepupa	6.0 ± 1.0 (22)	5.9 ± 1.0 (48)	5.2 <u>+</u> 0.7 (13)	5.6 <u>+</u> 0.9 (24)
Pupa	15.9 ± 1.1 (18)	16.0 ± 1.3 (47)	15.7 ± 1.1 (14)	15.6 <u>+</u> 1.1 (20)
Total	57.7 <u>+</u> 3.8 (3)	61.1 <u>+</u> 3.4 (12)	60.2 <u>+</u> 7.9 (5)	59.8 <u>+</u> 5.1

Table 16. Composition of members and materials of the nests used in aggression tests. Q: Queen. Mi and Ma: Minor and major workers. F: Alate female. M: Male. L: Larva. E: Egg.

						····		
Nest	Composition						Nest material	
	Q	Mi	Ma	F	М	L	Е	material
A 1	2	106	19	5	0	32	0	twig
A2	2	31	7	0	0	59	0	bamboo grass
A3	16	66	13	0	0	104	1	bamboo grass
A4	6	288	64	0	0	248	0	bamboo grass
B1	2	69	13	0	0	69	0	bamboo grass
C1	2	127	38	0	0	78	0	bamboo grass
C2	1	61	6	0	0	107	0	bamboo grass
C3	3	138	18	0	0	96	0	bamboo grass
D1	2	120	36	0	0	153	10	bamboo grass
D2	13	370	75	0	7	225	39	bamboo grass
D3	2	337	54	0	1	301	5	bamboo grass
E 1	1	143	18	0	2	91	0	bamboo grass
E2	0	155	16	0	3	146	2	bamboo grass
E3	2	188	38	0	7	341	1	bamboo grass
E4	0	40	4	0	0	3	0	bamboo grass
E5	3	357	44	0	0	304	0	bamboo grass
E6	2	183	20	0	0	200	0	bamboo grass
E7	5	223	18	0	0	115	0	bamboo grass
E8	9	339	41	0	0	418	16	bamboo grass
E9	1	87	5	0	0	108	0	bamboo grass
E10	1	74	10	0	0	31	0	bamboo grass
E11	1	258	27	0	5	180	13	bamboo grass
E12	5	64	10	0	0	79	2	twig
F1	0	8	2	0	0	8	0	twig
F2	7	189	35	0	0	273	0	twig
F3	15	388	72	1	7	436	2	bamboo grass
F4	19	751	124	0	8	585	5	bamboo grass
F5	2	188	24	10	5	130	0	bamboo grass
F6	6	204	21	0	0	188	2	bamboo grass
F7	5	126	26	0	1	225	1	twig
F8	19	983	173	2	14	487	4	bamboo grass

Only total scores of aggression are shown. In statistical tests, distributions of scores were compared with control by Mann-Whitney U-test. *: 0.05>p>0.01. Table 17. Internest aggression of C, yamaokai at site E, Mt.Tsukuba. **: 0.01>p>0.001. ***: p<0.001. -: Not tested.

:	E12	* * * o	18**	0
	E11	က	· 🗝 .	* * * 6
	E10	0	ᆏ	l
uo	E9	1	7	*9
aggression	E8	0,	, − −1	*9
of agg	E7	0	0	18**
ores	E6	0		22**
Total scores	E 5	0		× * * × * *
Η	E4	0	0	t
	E3	H	0	18**
	E2	0		* * * 6
	压1	0 0	0	, I
	Nest	E 2	E 3	E12

Table 18. Interspecific aggression tests between minor workers and between major workers of *C. nawai* (M) and *C. yamaokai* (P). Observed number of each category is shown.

	Minor workers	Major workers
(a) Draw		
Both avoided injured died	194 (73.5%) 6 (2.3) 4 (1.5)	7 (14.0%) 3 (6.0) 3 (6.0)
(b) P wins		
P intact, M injured M died P injured, M died	7 (2.7) 0 0	2 (4.0) 0 1 (2.0)
(c) M wins		
M intact, P injured P died M injured, P died	15 (5.7) 31 (11.7) 7 (2.7)	1 (2.0) 11 (22.0) 22 (44.0)
Total	264	50

Table 19. Comparison of ecological characteristics between C. nawai and C. yamaokai.

		C. nawai	C. yamaokai
1)	Mating season	August	Spring
2)	Mode of colony reproduction	Independent founding by single queens	Mainly nest budding
3)	Productivity of the nest (brood/worker ratio)	Low	High
4)	Productivity of queens	High	Low
5)	Production of alates	High	Low
6)	Population structure	Multicolonial	Multi- or uni- colonial
7)	Geographical distribution	More southern	More northern

Figure 1. Morphological differences of Camponotus yamaokai (a, c, e. and g) and C. nawai (b, d, f and h). Compound eyes of minor workers (a and b), major workers (c and d) and queens (e and f). Male genitalia, lateral view (g and h). (From Terayama and Satoh 1990)

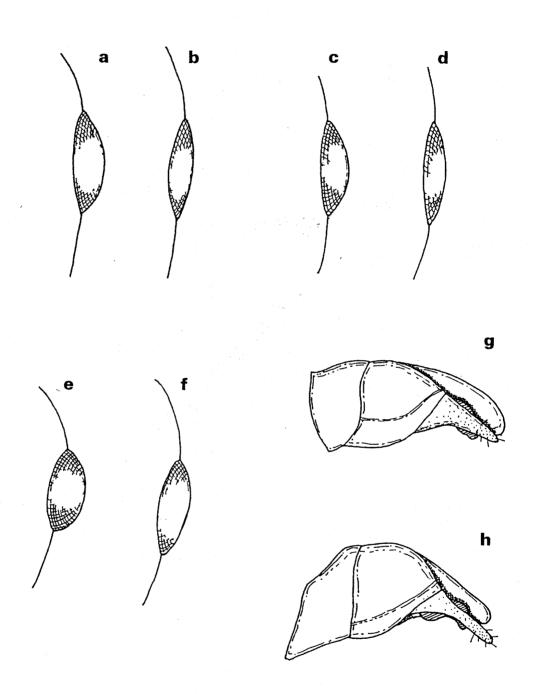


Figure 2. Distributions of *C. nawai* (closed circle) and *C. yamaokai* (open circle) in Japan.

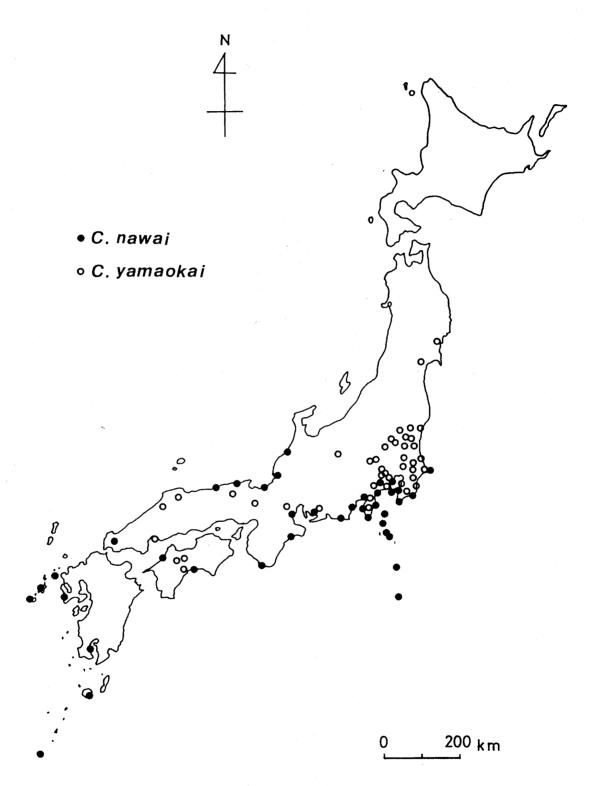
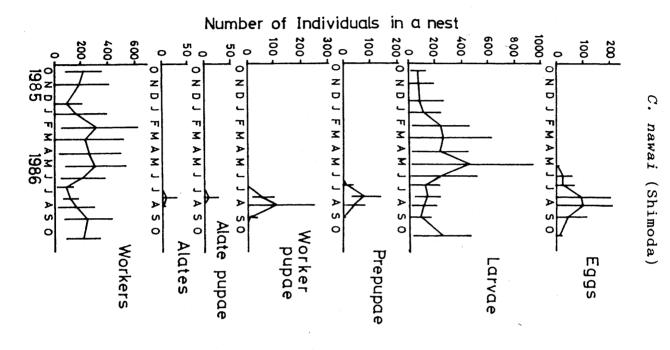
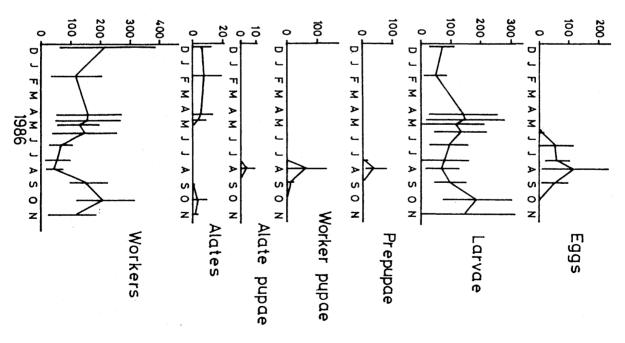


Figure 3. Frequency distributions of the number of queens per nest in polygynous *C. yamaokai*. (a) egglaying, (b) non-egg-laying, and (c) mating seasons.

shown with SD (vertical lines). Approximately 10 nests were Figure 4. Seasonal life cycles of (a) C. nawai population at Shimoda and (b) C. yamaokai population at Mt. Tsukuba. Mean number of each caste and immature stage per nest is collected in each case.







yamaokai (Mt. Tsukuba)

Figure 5. Frequency of alate and dealated females of C. yamaokai found in the nest from late summer to the next spring. Striped area indicates inseminated females.

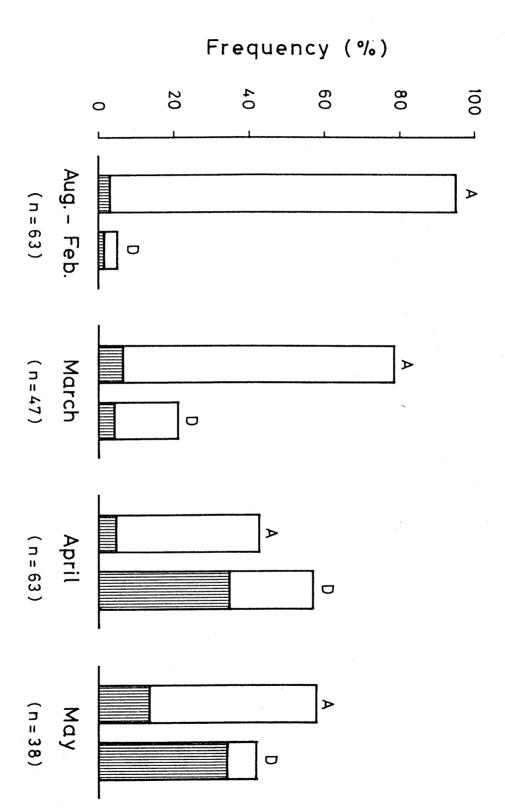


Figure 6. Frequency distributions of colony size (number of workers per nest) in C. nawai. Open bar: Egg-laying season. areas indicate single founding queen and incipient nests, Shaded bar: Non-egg-laying season. Stippled and striped respectively.

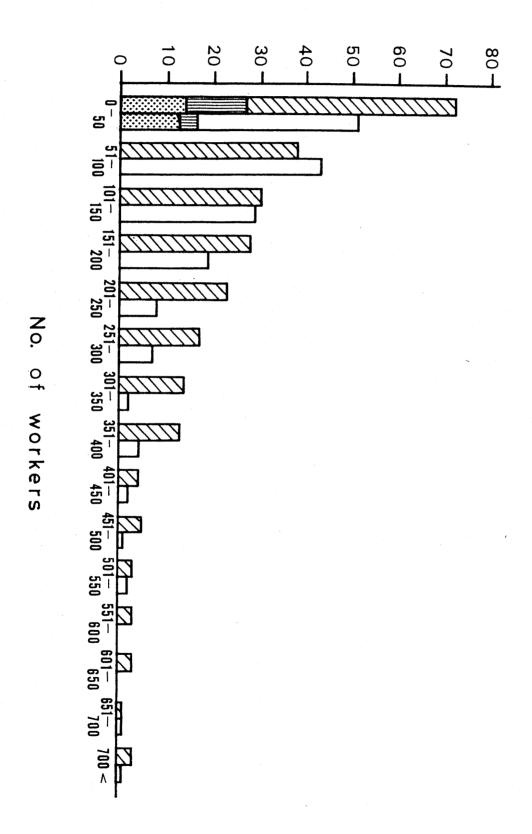


Figure 7. Frequency distributions of colony size (number of season. Shaded bar: Non-egg-laying season. Stippled area workers per nest) in C. yamaokai. Open bar: Egg-laying indicates single founding queen.

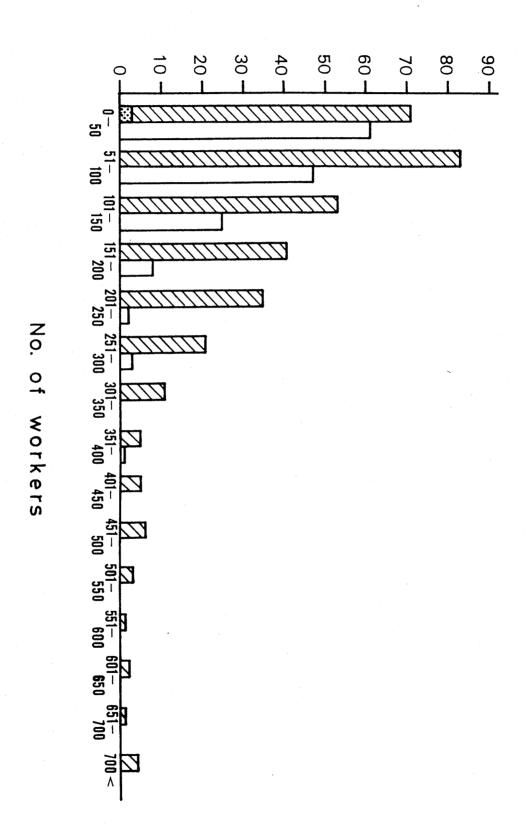
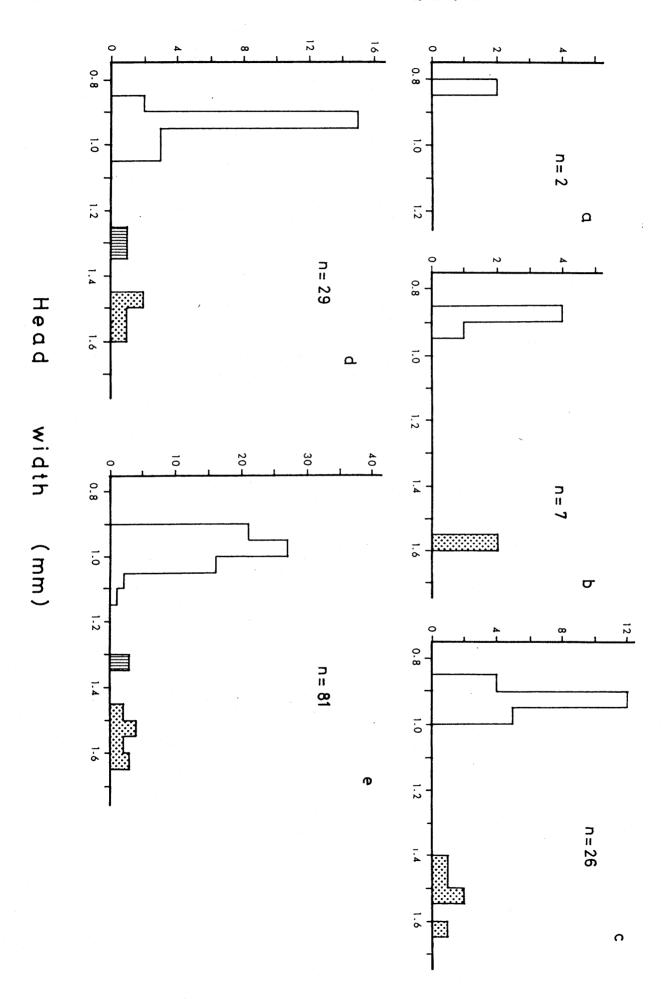


Figure 8. Worker size (head width) distributions along with areas indicate minor, major and media workers, respectively. colony development of C. nawai. Open, stippled and striped



Open, stippled and striped areas indicate minor, major and distributions along with colony development of C. nawai. Figure 8 (continued). Worker size (head width) media workers, respectively.

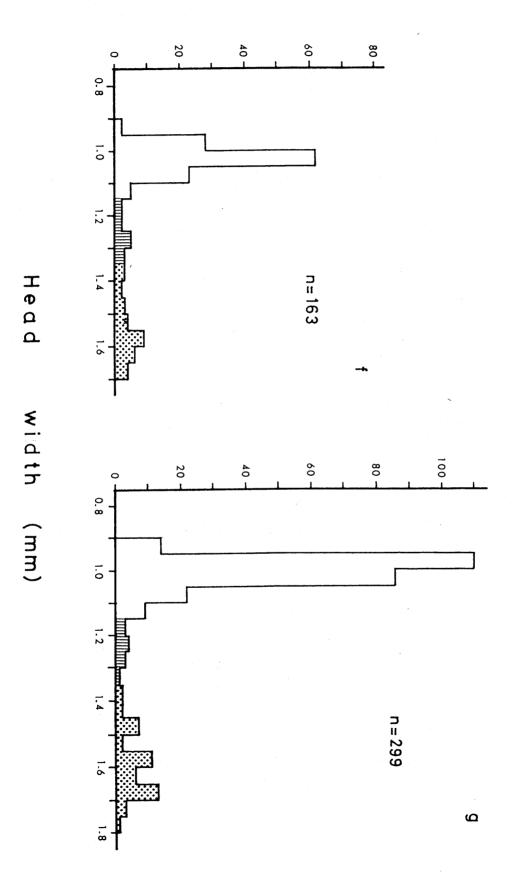


Figure 9. Worker size (head width) distributions in various sized colonies of *C. yamaokai*. Open and stippled areas indicate minor and major workers, respectively.

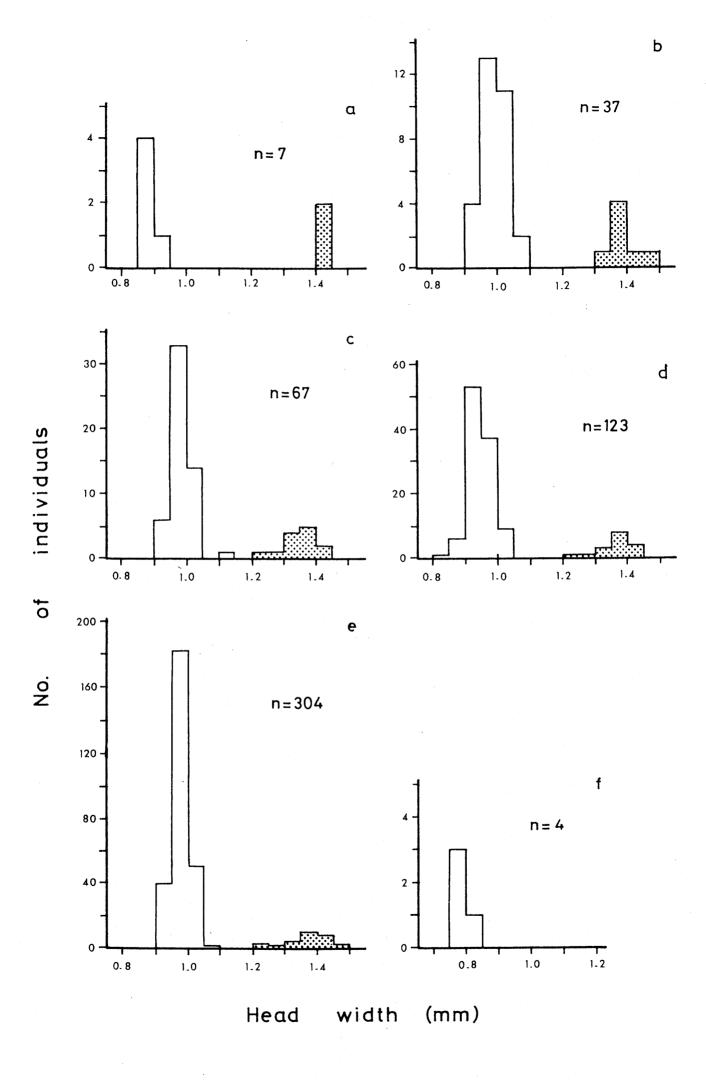
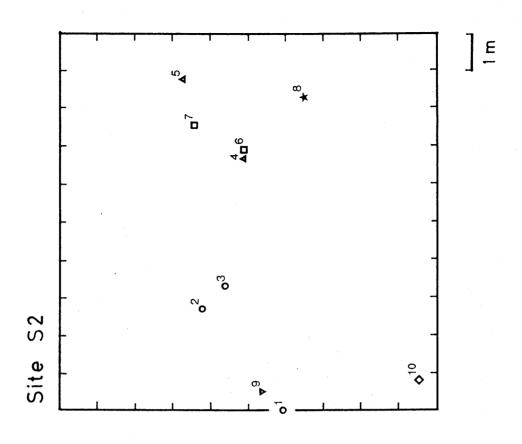


Figure 10. Horizontal distributions of nests at Shimoda, \mathcal{C} . Open and closed symbols indicate queenless and queenright nawai population (sites S1 and S2). Symbols of the same shape indicate the nests belonged to the same colony. (monogynous) nests, respectively.



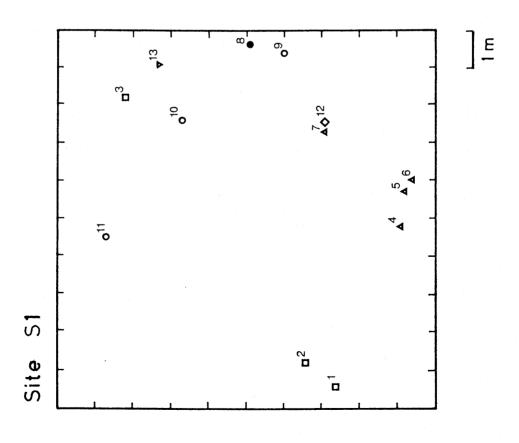
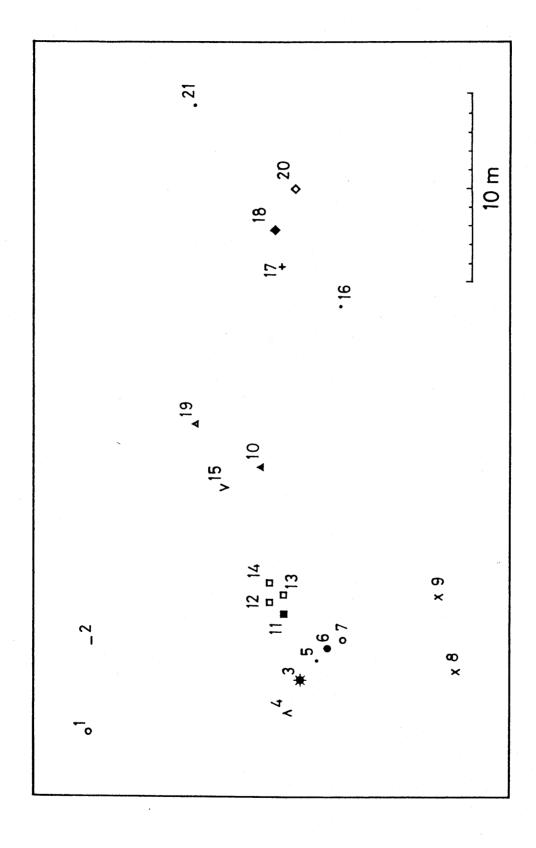
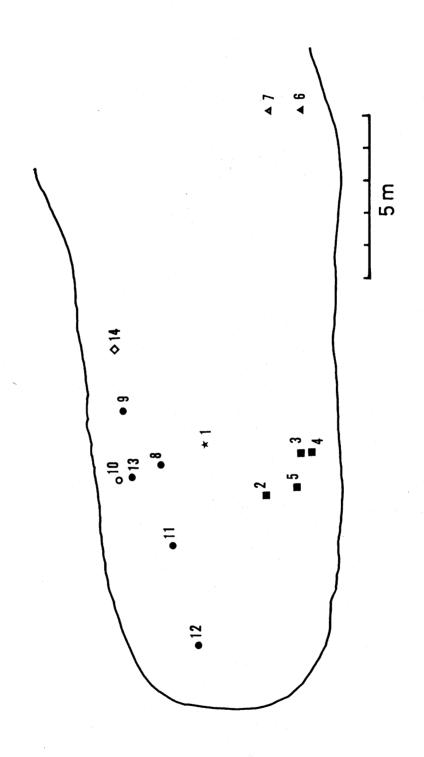


Figure 11. Horizontal distributions of nests at Shimoda, C. indicate the nests belonged to the same colony, but each dot represents a incipient monodomous colony. Open and nawai population (site S3). Symbols of the same shape closed symbols indicate queenless and queenright

(monogynous) nests, respectively.



Tsukuba, C. yamaokai population (site T2). Symbols of the colony. Open and closed symbols indicate queenless and Figure 12. Horizontal distributions of nests at Mt. same shape indicate the nests belonged to the same polygynous nests, respectively.



Tsukuba, C. yamaokai population (site T1). Symbols of the All nests found in this site were familiar with each other queenless, monogynous and polygynous nests, respectively. Figure 13. Horizontal distributions of nests at Mt. same shape indicate the nests belonged to the same colony. Open, dotted and closed circles represent (unicolonial population structure).

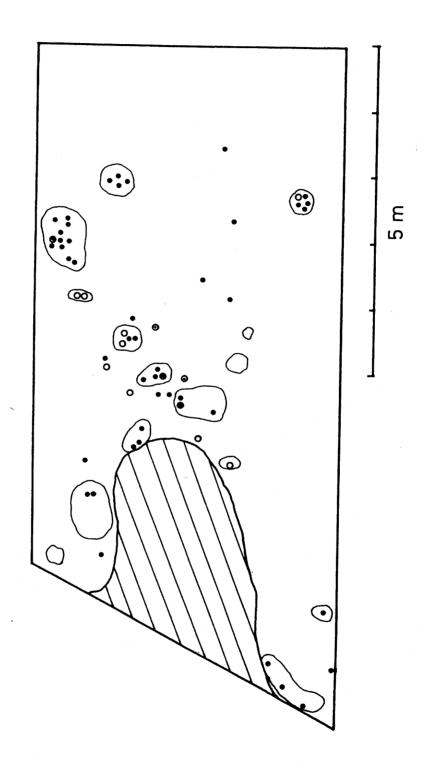


Figure 14. Horizontal distributions of nests at Mt. Tsukuba, *C. yamaokai* population (sites T3 to T5). Symbols of the same shape indicate the nests belonged to the same colony. Open, dotted and closed symbols represent queenless, monogynous and polygynous nests, respectively.

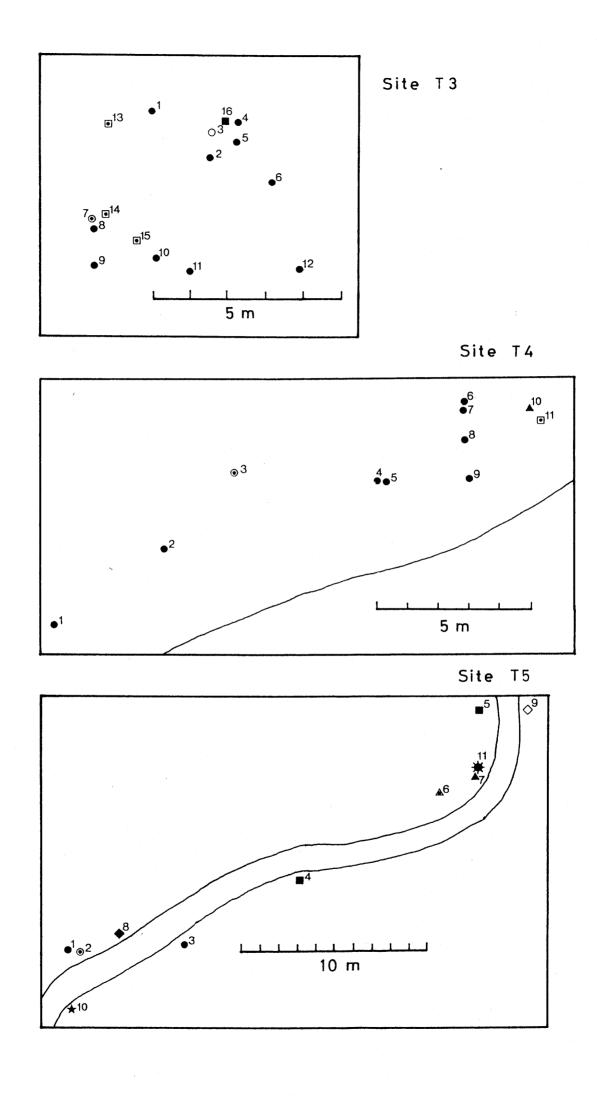


Figure 15. Correlation between the number of workers and number of brood in the nest in C. nawai.

- (a) Summer, queenright nests (r=0.774, df=31, p<0.01).
- (b) Summer, queenless nests (r=0.664, df=69, p<0.01).
- (c) Winter, queenright nests (r=0.841, df=56, p<0.01).
- (d) Winter, queenless nests (r=0.777, df=152, p<0.01).

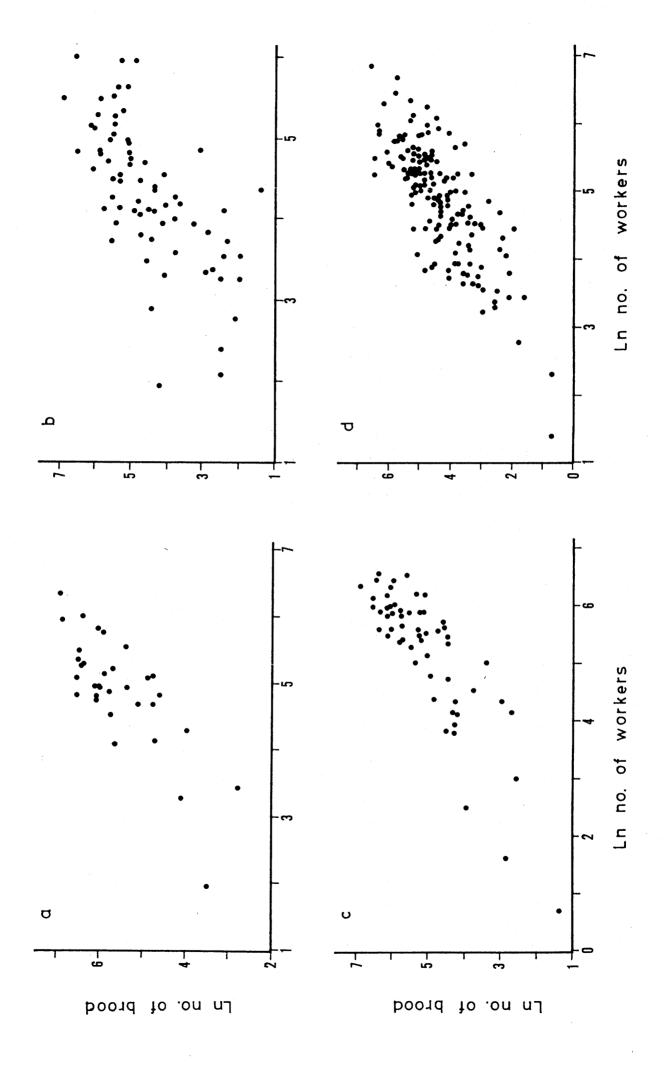
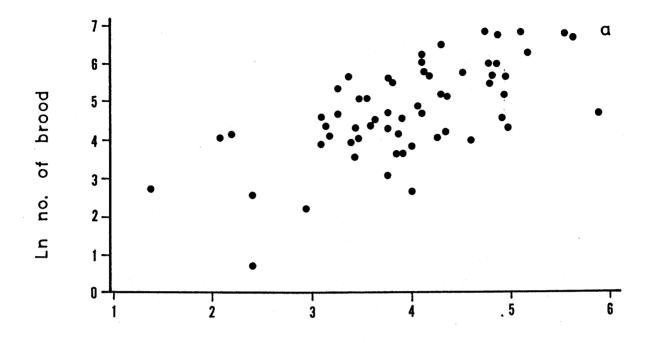
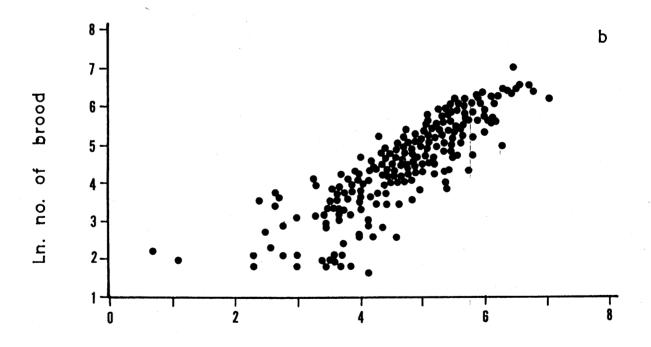


Figure 16. Correlation between the number of workers and number of broad in the nest in C. yamaokai.

- (a) Summer (r=0.643, df=58, p<0.01).
- (b) Winter (r=0.849, df=309, p<0.01).

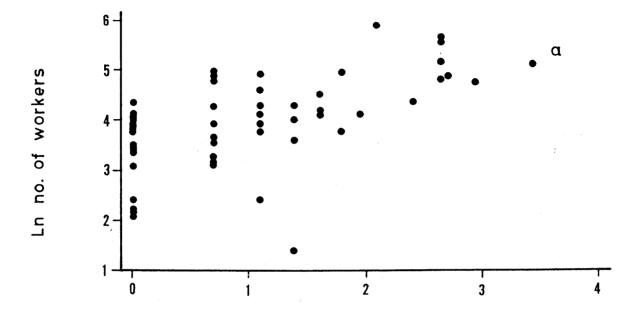


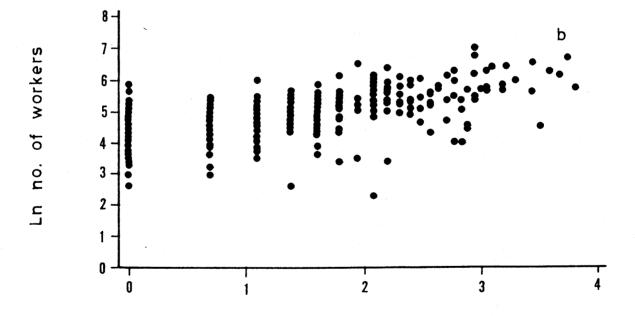


Ln no. of workers

Figure 17. Correlation between the number of queens and number of workers in the nest of *C. yamaokai*.

- (a) Summer (r=0.591, df=54, p<0.01).
- (b) Winter (r=0.567, df=277, p<0.01).

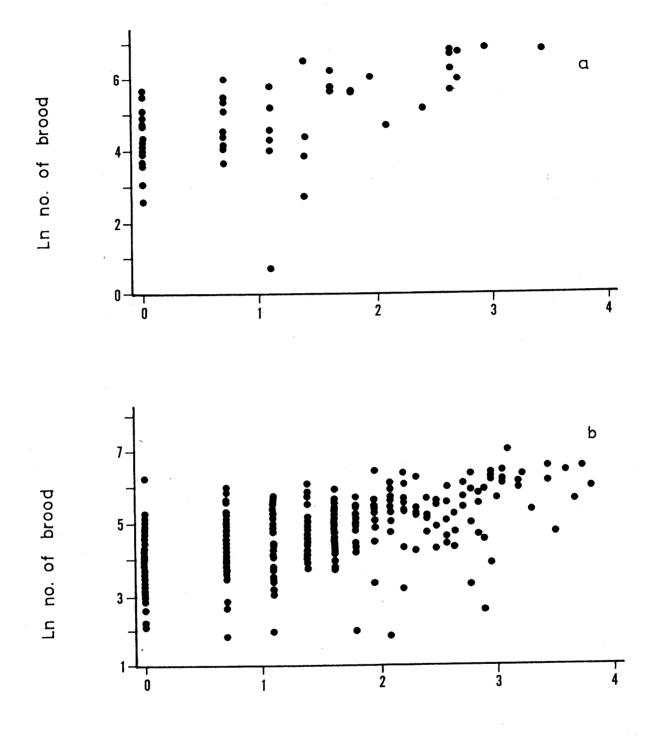




Ln no. of queens

Figure 18. Correlation between the number of queens and number of brood in the nest of C. yamaokai.

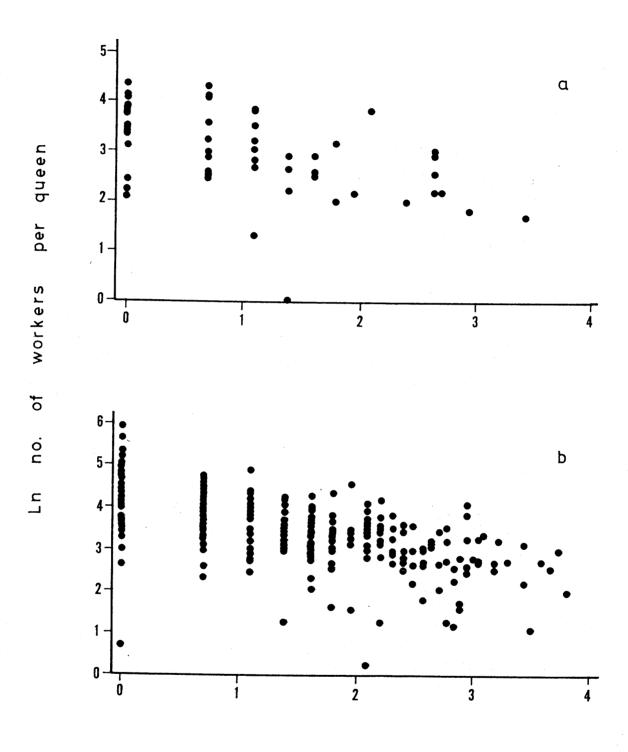
- (a) Summer (r=0.602, df=54, p<0.01).
- (b) Winter (r=0.530, df=277, p<0.01).



Ln no. of queens

Figure 19. Correlation between the number of queens and number of workers per queen in the nest of *C. yamaokai*.

- (a) Summer (r=-0.523, df=54, p<0.01).
- (b) Winter (r=-0.605, df=277, p<0.01).



Ln no. of queens

Figure 20. Correlation between the number of queens and number of brood per queen in the nest of C. yamaokai.

- (a) Summer (r=-0.256, df=54, p>0.05).
- (b) Winter (r=-0.499, df=277, p<0.01).

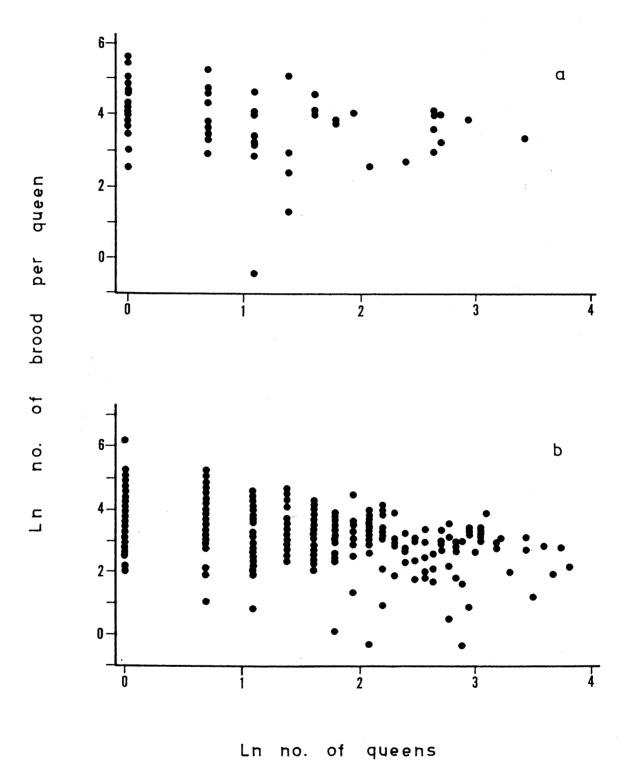
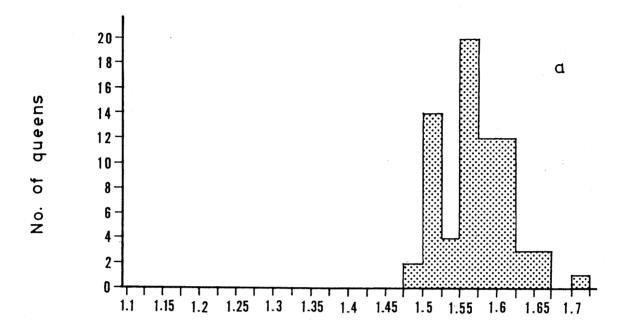


Figure 21. Size (head width) distributions of queens.

- (a) C. nawai (means \pm SD (mm): 1.559 \pm 0.045, n=70).
- (b) *C. yamaokai* (macrogyne, 1.365±0.03, n=1094; microgyne, 1.204±0.039, n=220). Queens whose head width are less than 1.275mm are defined as microgynes in *C. yamaokai*.



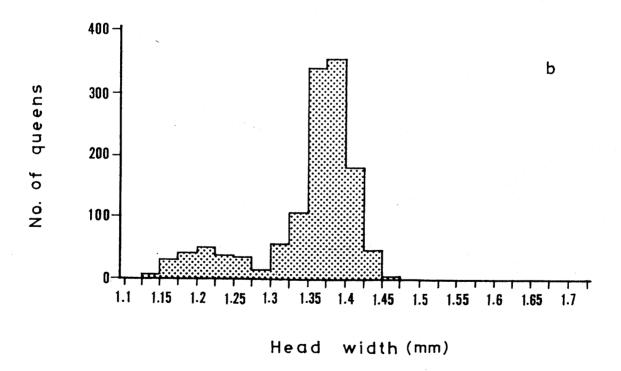
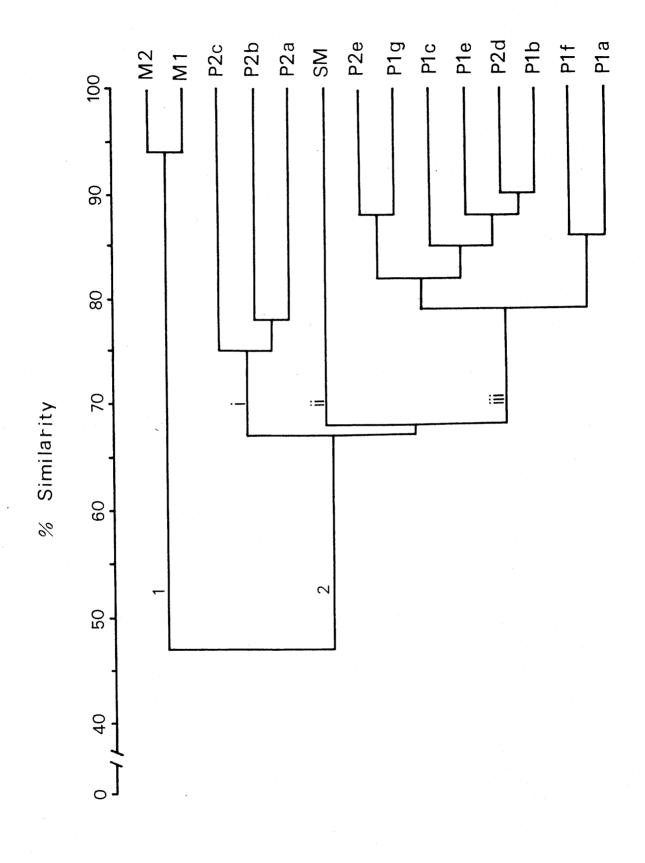


Figure 22. Behavioral similarities among queens. M1 and M2 are queens of *C. nawai*. SM is a secondarily monogynous queen of *C. yamaokai*. Pla-c, Ple-g and P2a-e were queens of *C. yamaokai*. P2c is a microgyne.



is also shown as a indicator of degree of concentration. A, of queens in the nest tube. Coefficient of variation (CV) Figure 23. Frequency distributions of observed positions B: Queens of C. nawai. C: A secondarily monogynous queen of C. yamaokai. D, E: Queens of polygynous colonies of C. yamaokai. P2c is a microgyne.

Frequency

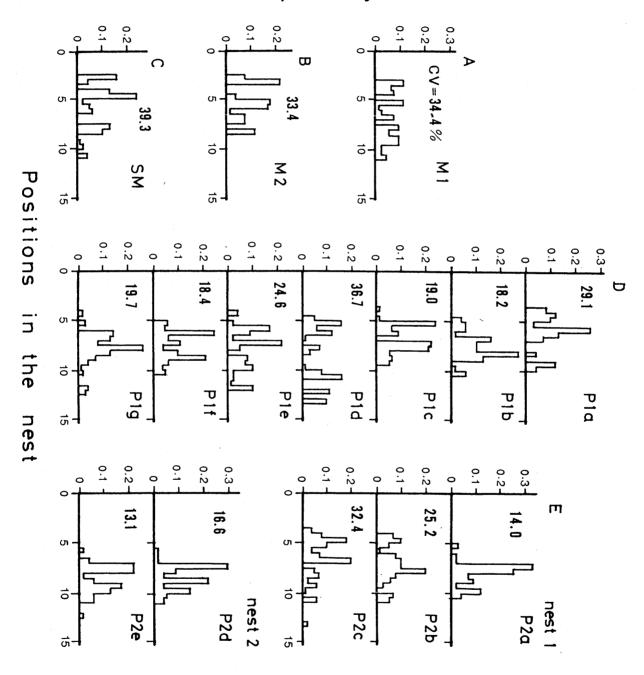
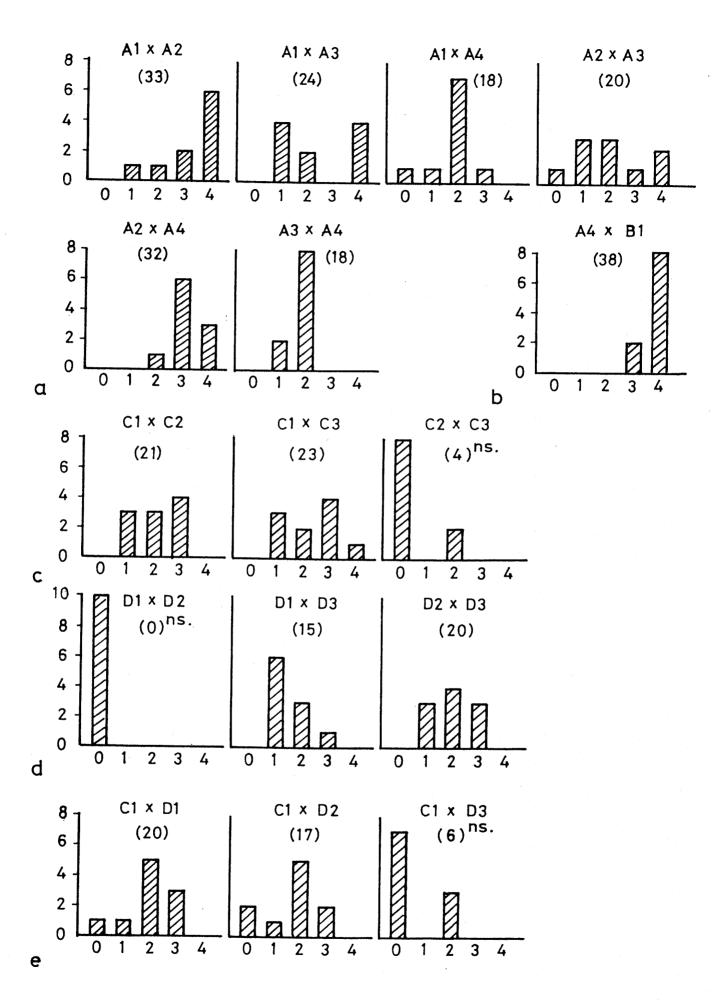
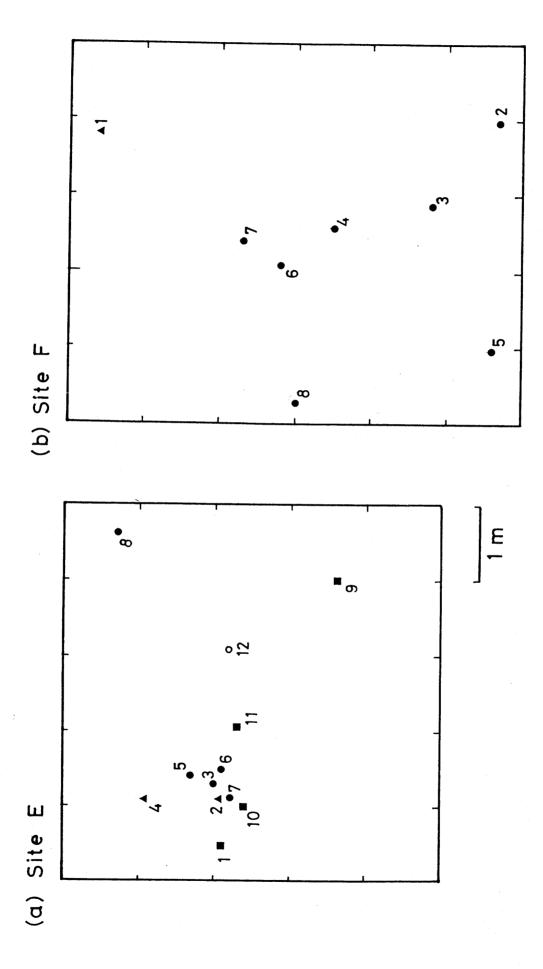


Figure 24. Frequency distributions of aggressive responses between the nests collected from sites A to D. Abscissa is score of aggression (see Table 1), and ordinate is observed number of responses. Total scores are shown in parentheses. Those distributions are significantly different (p<0.001 for each, Mann-Whitney U-test) from control (no aggression: total score is zero) except for C2 x C3, D1 x D2 and C1 x D3.



significant hostility toward other nests (see Table 17). At site F, there was no significant aggression (p>0.05) between Figure 25. Horizontal distributions of nests at site E (Mt. circles indicate queenless, monogynous and polygynous nests, Tsukuba) and site F (Tokorozawa). Triangles, squares and respectively. At site E, only E12 (open circle) showed nests.



of the average of annual lowest temperature of -3.5°C is shown. Kanto-Tokai districts, central Japan. The isothermal line Figure 26. Distributions of C. nawai and C. yamaokai in

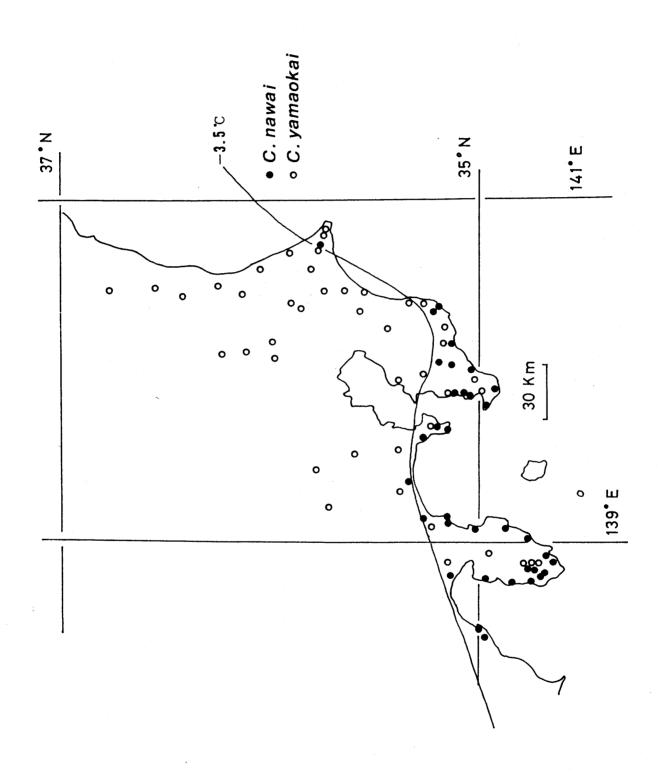


Figure 27. Vertical distribution of the *C. nawai* (solid bar) and *C. yamaokai* (open bar) in the Amatsu - Mt. Kiyosumi area (Chiba Pref.). Each circle represents the sample from more or less isolated forest.

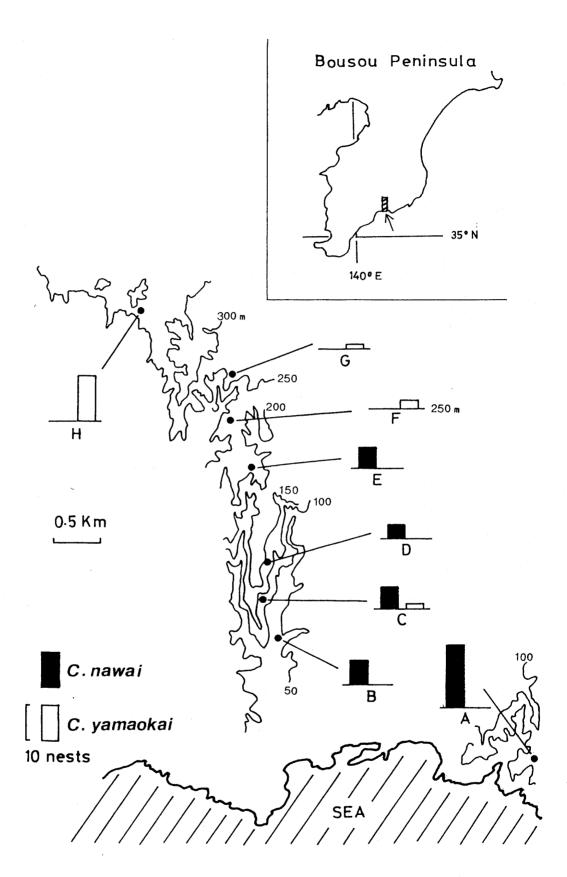
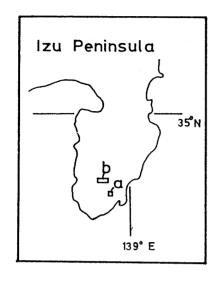
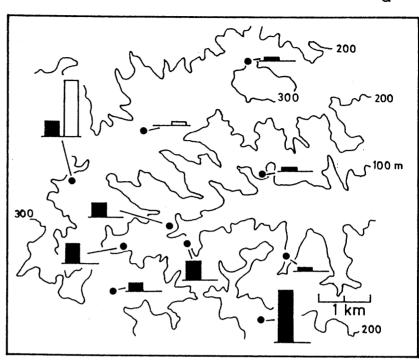


Figure 28. Distribution of *C. nawai* (solid bar) and *C. yamaokai* (open bar) in Izu Peninsula, central Japan. (a) Ohsawa, Shimoda-shi, Shizuoka Pref. (b) Ikeshiro, Matsuzaki-machi, Shizuoka Pref.





C. nawai 10 nests C. yamaokai

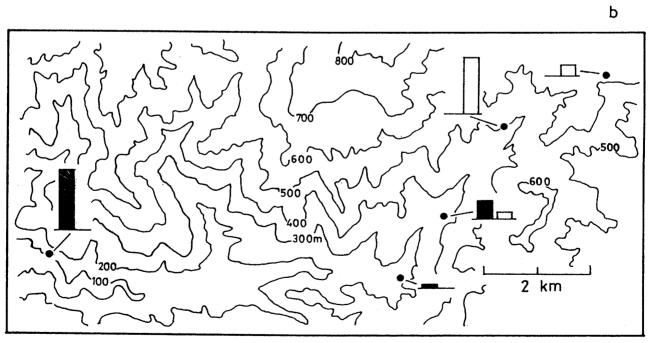


Figure 29. Possible patterns of nest budding at site A (a), site C (b), site D (c), and sites C and D (d) (see Fig. 24). Broken and solid lines indicate significant (p<0.05) and nonsignificant aggressions, respectively.

