FUNCTIONAL MONOGYNY OF *LEPTOTHORAX ACERVORUM* IN NORTHERN JAPAN*

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Introduction

In the ant tribe Leptothoraciine, the number of queens per colony is greatly varied among species. For instance, *Leptothorax curvispinosus* (Wilson 1974) and *L. longispinosus* (Herbers 1986) often show polygyny in which multiple queens are inseminated and actually lay eggs, while *L. congruus* (Ito, unpublished) is always monogynous. *L. gredleri* (Buschinger 1968) and *Leptothorax* sp. A (Heinze 1990) establish more complex colonies in which multiple queens are involved but oviposition is almost monopolized by only one queen. Buschinger (1968) called the polygyny with one egg-layer "functional monogyny".

Leptothorax acervorum is widespread over boreal or subalpine areas of Eurasia and North America and, based on the observation conducted in Europe by Buschinger (1968 and pers. commu.), their social structure has been regarded as facultative polygyny in which 29% of the colonies are polygynous and most of the queens are inseminated egg-layers. To confirm whether the facultative polygyny is the common rule of this circumpolar species or not, I observed the social structure of *L. acervorum* collected in northern Japan.

Study Area and Methods

Sampling of wild colonies was carried out in the Experiment Forest of Tokyo University, Furano, northern Japan. As a rule 10 to 12 nests were collected every two weeks from late May to early October, 1989. Dealated queens contained in each colony were immediately dissected in the laboratory to examine ovarian development, insemination and, in post-flight season (late September), decomposition level of wing muscles. Workers, alates and imma-

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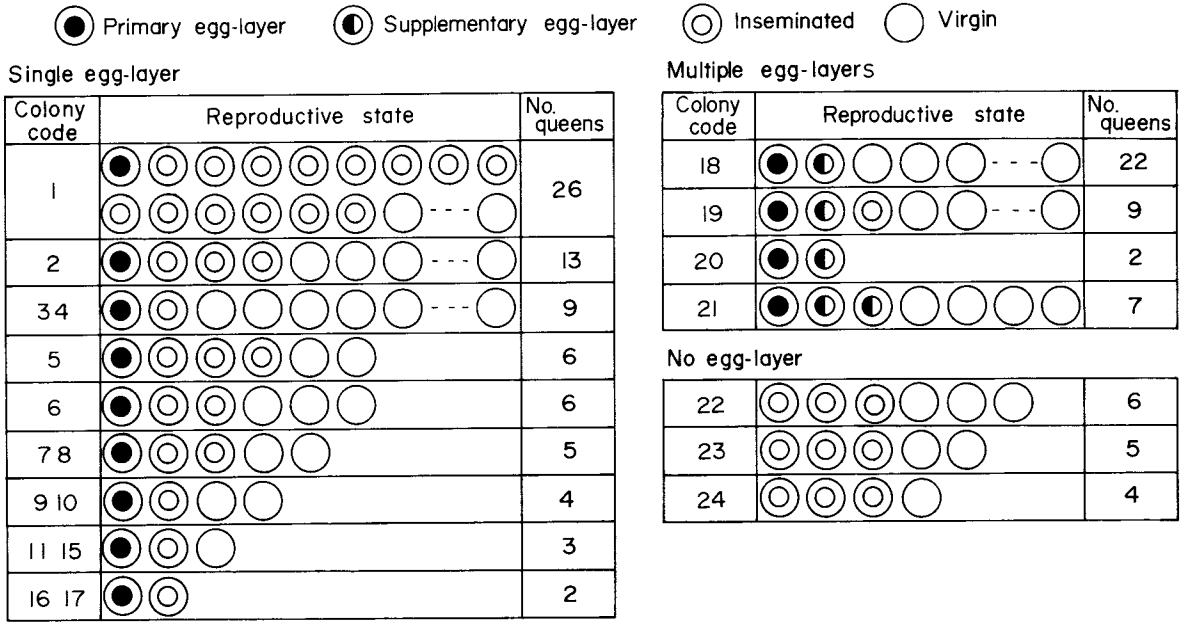

Fig. 1. Reproductive condition of queens in 24 colonies containing two or more inseminated queens.

tures were preserved in 80% ethanol and then counted in off-season of fieldwork. The head width of workers was measured in 19 colonies of different colony size to determine the queen-founded incipient colonies in which the workers are smaller than in developed colonies or than in colonies established by colonial budding.

Results

Number of queens.

In the regular samplng, the colonies were rarely discovered in the soil but frequently in dead birch twigs fallen on sunny gaps or paths of the forest. Of 105 colonies collected, 12 contained no queen; 36 single queen; 57 multiple up to 27 queens. The mean number of queens per colony was 3.6 ± SD 5.6.

Reproductive condition of queens in multi-queen colonies.

In 33 of 57 multi-queen colonies, only one queen bore a sperm-filled spermatheca and a developed ovary and the other queens were virgin and sterile. The other 24 colonies contained two or more inseminated queens (Fig. 1); however, the number of egg-layers was as small as one in 17 colonies, two in 3 colonies (Colony Nos. 18, 19, 20) and three in No. 21. Even in these 4 multi-layer colonies, only one queen bore well-developed ovarioles and dense accumulation of yellow bodies and the other egg-layers were supplementary with short ovarioles and tiny yellow bodies (Fig. 2). Although Nos. 22, 23 and 24 contained no egg-layers, there were many immatures, suggesting that these were new colonies established by colonial budding prior to the ovarian development in one of the inseminated queens. Overall, the colonies of Japanese *L. acervorum* often contain multiple queens but should be regarded as functional monogyny according to the definition of Buschinger (1968).

In the colonies collected soon after the nuptial season (colonies No. 25, 26, 28), some queens had fresh wing muscles as intact as those of alate females (Table 1). This means that multiple-queen colonies occur by adopting queens newly produced.

Seasonal fluctuation of queen number per colony.

Although about 70% of colonies had multiple queens in spring and autumn, the ratio of single-queen colonies slightly exceeded that of multi-queen colonies in mid summer (Fig. 3A). The summer

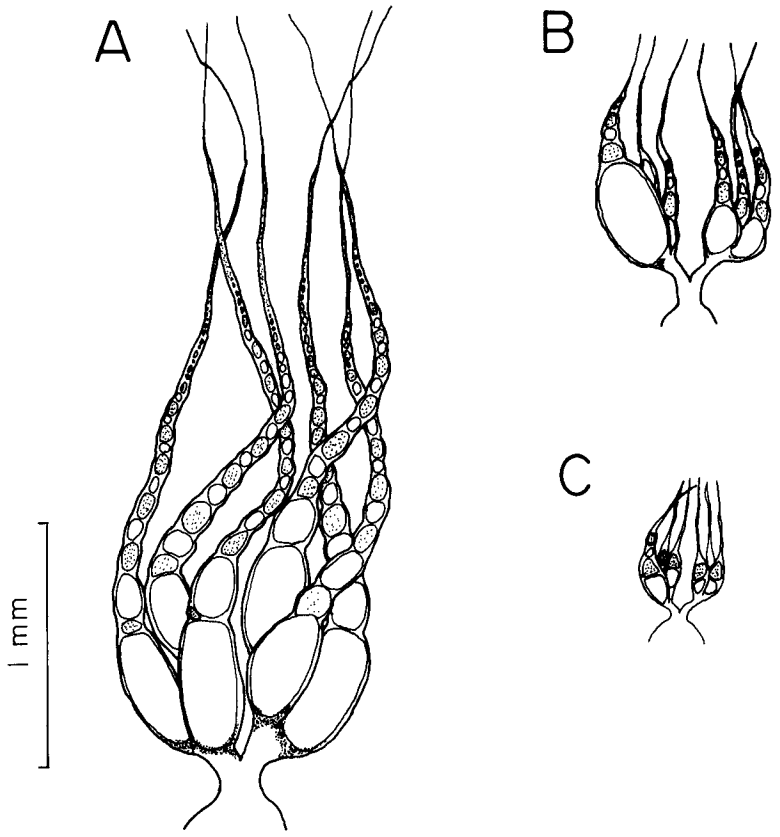

Fig. 2. Ovaries of *L. acervorum* queens. A. prime egg-layer; B. supplementary egg-layer; C. sterile.

decrease of the queens per colony was further supported by the seasonal trend of mean queen number in multi-queen colonies (Fig. 3B). These results indicate that the summer is the season of colonial budding, in many cases of which one inseminated queen and many workers leave mother colony containing multiple queens. The recovery of the queen number in autumn is probably due to the adoption of newly produced queens as suggested by the presence of dealated queens bearing fresh wing muscles.

Table 1. Wing muscles of queens in multi-queen colonies collected in late September. I. almost intact, II. partly decomposed, III. completely decomposed.

Colony code	*I*	*II*	*III*	*Total*
9	0	3	1	4
11	0	1	2	3
12	0	2	1	3
25	1	0	1	2
26	1	0	1	2
27	0	6	3	9
28	6	4	6	16

Likelihood of the independent colony foundation by a queen.

The mean colony size was smaller in single-queen colonies (38.0 ± 32.0) than in multi-queen colonies (65.5 ± 34.0), the difference being statistically significant at $p < 0.05$ in G-test. In particular, most of the extremely small colonies containing 0 to 20 workers were single-queen colonies (Fig. 4A), suggesting that the queen can start their

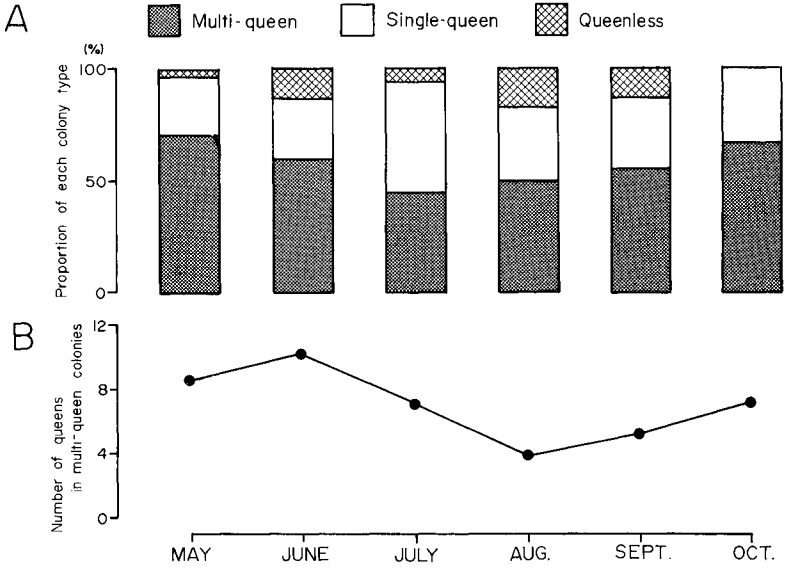

Fig. 3. Seasonal fluctuation of colony type composition (A) and queen number in multi-queen colonies (B).

Table 2. Comparison of social structure between European population and present population.

	*Europe**	*Furano*
Monogyny		
queen inseminated	30.5%	32.3%
queen virgin	0.5%	1.9%
Polygyny		
functional monogyny with		
single inseminated queen	27.0%	28.7%
multiple inseminated queens	2.5%	16.0%
functional polygyny	29.0%	3.8%
all queens sterile	1.5%	5.7%
Queenless	10.0%	11.4%

*Buschinger (1968, pers. commun.)

colonies by independent colony foundation. This suggestion was supported by the presence of remarkably small workers in the small-sized colonies containing only one queen (Fig. 4B). The small-sized colonies consisting of larger workers appeared to be established by the budding of colonies.

Discussion

The definition of queen or gyne is presently controversial (Buschinger 1987, Peeters and Crozier 1988). As a rule, I support Peeters and Crozier (1988) who defined "queen" in a strict morphological sense regardless of her function. However, I herein use "functional monogyny" for the polygyny with single inseminated egg-layer and "functional polygyny" for the polygyny with multiple inseminated egg-layers.

As shown in Table 2, the number of egg-layers is only one in most colonies of Furano while the functionally polygynous colonies constitute 29% of all colonies in Europe. Consequently, the mean number of workers per colony is significantly smaller in Furano population (55.8) than in European population (111.3).

As comprehensively discussed by Holldobler and Wilson (1977), elementary properties in the organization of insect societies generally bias toward monogyny in the course of evolution by natural

selection, and the polygyny is adopted only when special ecological constraints are imposed on the population. Frequent raiding and usurpation by parasitic species appear one of the most serious constraints to host species. In this case, the counter selection will favor functionally polygynous colonies of host species to avoid the risk of colonial collapse by adopting multiple egg-layers which will produce more workers than single egg-layer. In fact, the European colonies of *L. acervorum* are frequently raided by the social parasite *Harpagoxenus sublaevis* while the social parasites of *L. acervorum* are absent or, even if exist, very rare in Japan, suggesting that the frequent occurrence of functional polygyny in European *L. acervorum* is partly due to social parasites.

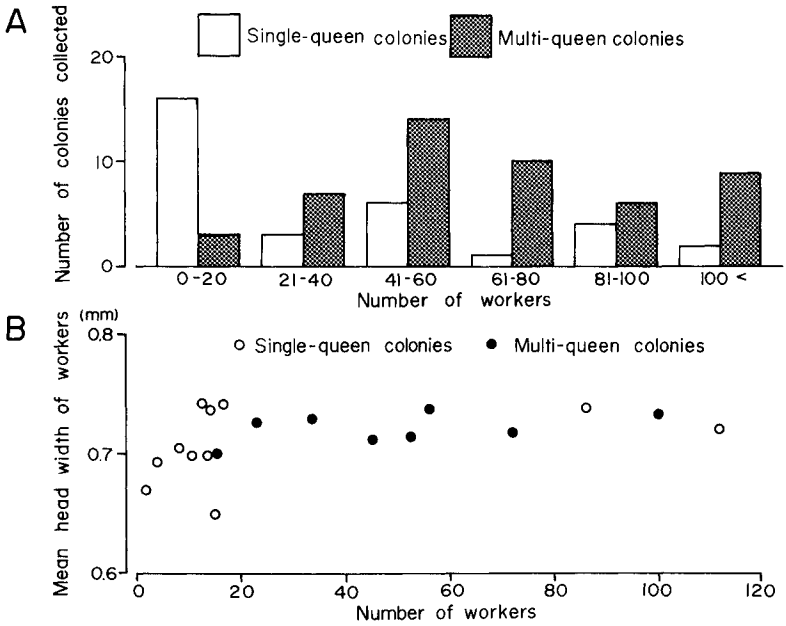

Fig. 4. Frequency distribution of colony size (A) and mean head width of workers (B).

SUMMARY

Social structure of the circumpolar ant species *Leptothorax acervorum* was studied in northern Japan. Main results were: 1. Polygynous colonies constituted 54.4% of 105 colonies collected. 2. Unlike European population in which many of the polygynous colonies contained multiple egg-layers, most of the polygynous colonies of the present population showed functional monogyny comprising only one egg-layer. 3. Although a few colonies contained two or three egg-layers, the number of prime egg-layers bearing well-developed ovaries was always one. 4. This polygyny appeared to occur by adopting new queens into their mother colonies, i.e. secondary polygyny. 5. Most of the new colonies seemed to be established by colonial budding; however, the presence of some colonies consisting of remarkably small workers suggested the likelihood of independent colony foundation by a queen as well.

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