Dispersion Patterns of Ant Nests in a Cool-temperate Woodland of Northern Japan

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冷温帯森林内におけるアリ巣の分散様式

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Abstract

Dispersion patterns of ant nests were analysed by the $\mathring{m}-m$ regression method (IWAO. 1968) and the covariance method (KERSHAW, 1960) in a cool-temperate woodland of Tomakomai Experiment Forest of Hokkaido University. *Aphaenogaster smythiesi japonica* and *Myrmica ruginodis* seemed most territorial, since their nests were most dispersed and they were in negative association with some species. *Lasius niger* was negatively associated with some ants but their nests were a little more aggregated than those of the former two species, because they often formed polydomous colonies. Nests of *Myrmecina graminicola nipponica* were remarkably aggregated partly due to inhabiting microhabitats which were patchily distributed in the woods surveyed. Tiny ants *Leptothorax* sp. and *Pheidole fervida* showed nearly random or slightly aggregated distribution of conspecific nests and the nil association with other species.

Keywords: Ant, Dispersion pattern, Covariance, Tomakomai.

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Introduction

In general, nest sites of social bees and wasps are chosen by colony-founding queens and the colonies rarely move to other sites thereafter. Some ants continuously inhabit founder-chosen sites for many years, too. For example, the nest longevity of huge-mound building *Formica* ants sometimes reach several decades, e. g. 30 years in *Formica exectoides* (ANDREWS, 1926) or 20 to 25 years in *F. ulkei* (DREYER, 1942). Another mound builder *Pogonomyrmex* occasionally uses a nest for some years, too (VAN PELT, 1976). However, most ant species often abandon old uncomfortable nests and move to newly built ones (TALBOT, 1946; GENTRY, 1974; HIGASHI, 1976; MÖGLIGH, 1978; SMALLWOOD and CULVER, 1979; SMALLWOOD, 1982). For instance, SMALLWOOD (1982) observed scme ant species frequently relocating their nests at the rate of half lives 12.9 days (*Tapinomma sessile*) to 89.9 days (*Formica subsericea*). The frequent relocation creates the nest dispersion reflecting the intra- and interspecific relations in ants; that is, the analyses of nest dispersion undoubtedly provide the information on the presence or absence of intercolonial competition within a given community (LEVINGS and TRANIELLO, 1981).

We have made a comprehensive survey of ants in a cool-temperate woodland Tomakomai Experiment Forest of Hokkaido University since 1977 (YAMAMOTO et al., 1980; TODA et al., 1987). As a third report on the survey, we analyse the dispersion patterns of ant nests in relation to colony size, aggressiveness, body size and nesting system of each species.

Before going further, we wish to express our sincere thanks to Dr. Kenkichi ISHIGAKI and other staff members of Tomakomai Experiment Forest of Hokkaido University, for their kind assistance in the course of the present research.

Methods

In 1977 a survey of ant nests was conducted in a second-growth woods dominated by *Quercus mongolica* var. *grosseserrata* and *Acer mono*. In total five 5 m × 10 m quadrats were chosen in the woods: two in mid May (hereafter Q–Ma, Mb), two in early August (Q–Aa, Ab), one in early October (Q–O). In each quadrat ant nests were searched by digging ground surface about 5 cm deep with hand hoes. Whenever nests were discovered, their location was recorded, with the microhabitat description of nest sites.

Colony size of each species was examined by collecting many colonies mainly in and around this woods in 1982 and 1984 and additionally around Mt. Usu (about 60 km west of Tomakomai) in 1984. Small to medium colonies containing ca. 1,000 workers or less were entirely collected and all workers were counted in the laboratory. In large colonies containing thousands of workers, however, only a part of the colony was collected and whole colony size was roughly estimated from the number of workers in the partial colony collected. Aggressiveness of workers against foreigners from other colonies was examined in the course of collecting colonies, too.

Results

In the quadrat census in 1977, 185 nests of 10 species were obtained with the average density of 0.74 nests per square meter (Table 1). Fauna and nest density were little varied among the five quadrats, with the following dominant species: *Aphaenogaster smythiesi japonica* (hereafter As), *Myrmecina graminicola nipponica* (Mg), *Myrmica ruginodis* (Mr), *Lasius niger* (Ln), *Leptothorax* sp. (Ls), *Pheidole fervida* (Pf), *Ponera japonica*. Out of them, nest density of *P. japonica* might be underestimated, because this species was tiny and subterranean with small colonies (less than 15 workers), and the only 5 cm deep excavation might not be enough to find all of their nests within the quadrats.

Table 1. Number of ant nests collected in the quadrat census

Species \ Quadrat	Spring		Summer		Autumn	Total
	Ma	Mb	Aa	Ab	O	
Aphaenogaster smythiesi japonica (As)	7	9	12	6	12	46
Myrmecina graminicola nipponica (Mg)	15	5	4	10	2	36
Myrmica ruginodis (Mr)	2	6	6	5	7	26
Lasius niger (Ln)	4	2	10	4	3	23
Leptothorax sp. (Ls)	3	6	5	0	3	17
Pheidole fervida (Pf)	3	2	4	2	6	17
Ponera japonica	5	1	2	8	0	16
Paratrechina flavipes	0	0	2	0	0	2
Lasius hayashi	1	0	0	0	0	1
Myrmica lobicornis	1	0	0	0	0	1
Total	41	31	45	35	33	185
Density (/m^2)	0.82	0.62	0.90	0.70	0.66	0.74

Some traits of the dominant species other than *P. japonica* are given in Table 2. As and Mr often contained more than 1,000 workers which were aggressive against foreigners from other colonies. Ln was relatively aggressive and had large colonies, too. However, unlike As and Mr which were mainly monodomous, this species often formed polydomous colonies in which there were some queenless satellite nests around a queenright main nest. Mg was less aggressive and had small colonies containing less than 50 workers and multiple queens. For nesting, this species preferred mosses or grass roots which were patchily distributed in each quadrat. The tiny ant Ls was less aggressive and formed small colonies consisting of less than 100 workers always in small dead twigs which were abundant and homogeneously distributed on the forest floor surveyed. Colonies of another tiny ant Pf were sometimes composed of more than 1,000 workers which were

Table 2. Some traits of dominant ant species

	Head width (mm)	Colony size	Aggressiveness	Main nesting system	Main nest site
As	1.02 (0.79 −1.23)	ca. 1600 (250− ca. 3500)	+	monodomous	litters, with underground nest structure
Mg	0.82 (0.75 −0.95)	23 (11−47)	−	?	mosses, grass roots
Mr	1.03 (0.75 −1.19)	ca. 1100 (50− ca. 2300)	+	monodomous	litters, with underground nest structure
Ln	0.95 (0.79 −1.03)	ca. 2800 (620− ca. 7500)	+	polydomous	dead trees, with underground nest structure
Ls	0.51 (0.48 −0.6)	57 (25−85)	−	monodomous	small dead twigs
Pf*	0.60 (0.57 −0.63)	900 (340− ca. 1400)	+	?	dead trees, with underground nest structure

* tiny subcaste only.
In head width and colony size, an average is given with range. For ant species As to Pf, see Table 1.

aggressive against foreigners.

Dispersion patterns of ant nests were analysed with $\overset{*}{m}-m$ regression method of Iwao (1968), by counting all nests within blocks of $(5\,m/16)^2$, $(5\,m/8)^2$, $(5\,m/4)^2$, $(5\,m/2)^2$ and $(5\,m)^2$. The regression $\overset{*}{m}=1.02\,m-0.02$ obtained by pooling data over the year suggested an approximately random distribution of ant nests. However, the dispersion pattern showed seasonal variation as follows: $\overset{*}{m}=1.04\,m$ in the spring (Q-Ma, Mb), $\overset{*}{m}=0.97\,m-0.12$ in the summer (Q-Aa, Ab), $m^*=1.1\,m$ in the autumn (Q-O); that is, the nests were more dispersed in the summer than in the spring and autumn.

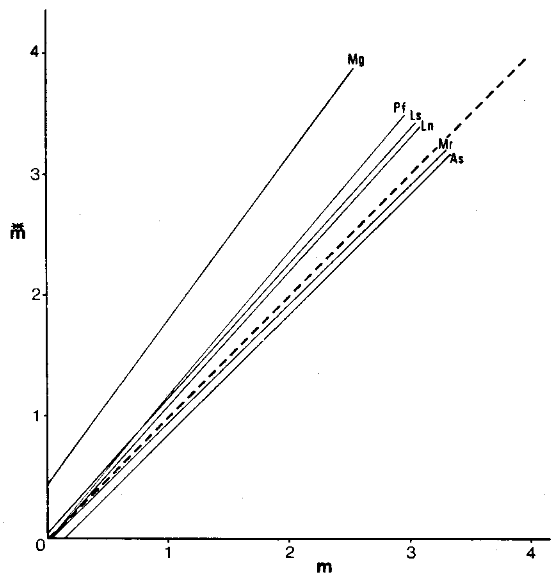

Fig. 1. $\overset{*}{M}-m$ regression lines of dominant species.

As: *Aphaenogaster smythiesi japonica*; Mr: *Myrmica ruginodis*; Ln: *Lasius niger*; Ls: *Leptothorax* sp.; Pf: *Pheidole fervida*; Mg: *Myrmecina graminicola nipponica.* A broken line means $\overset{*}{m}=m$.

The pattern of nest dispersion was species-dependent (Fig. 1). As and Mr showed nearly random or slightly overdispersed distribution: $\overset{*}{m}=0.99\,m-0.12$ in As, $\overset{*}{m}=0.96\,m$

-0.04 in Mr. Nests of Ln, Ls and Pf were also randomly distributed but a little more aggregated than those of As and Mr: $\mathring{m}=1.1\,m-0.04$ in Ln; $\mathring{m}=1.1\,m+0.04$ in Ls; $\mathring{m}=1.19\,m-0.04$ in Pf. On the contrary, Mg showed remarkably aggregated distribution with the regression $\mathring{m}=1.35\,m+0.41$.

Interspecific association was analysed with the following covariance method of KERSHAW (1960):

When nests of species A and B are not independently distributed,

$$\text{var.}(A+B) = \text{var.}\,A+\text{var.}\,B+2\,\text{covar.}\,AB$$

or

$$Va+b = Va+Vb+2Cab$$

$$Cab = (Va+b-Va-Vb)/2.$$

Now

$$r = Cab/\sqrt{VaVb}$$

i. e.

$$r = (Va+b-Va-Vb)/2\sqrt{VaVb}\,.$$

The statistical significance of r can be tested by the usual t test, i. e. $t=\sqrt{r^2(N-2)/(1-r^2)}$ (degree of freedom: $N-2$) where N is the number of blocks surveyed. Here, the size of block was $(5\,m/4)^2$, i. e. $N=(4^2\times 2$ blocks per quadrat) $\times(5$ quadrat$)=160$ blocks.

As shown in Fig. 2, As, Mr and Ln were negatively associated with each other, with $r=-0.198$ (As-Ln) to -0.155 (As-Mr) which were statistically significant at $p<0.05$. Mg was negatively associated with these species, especially with As ($r=-0.14$, $p<0.1$) and Mr ($r=-0.138$, $p<0.1$). However, tiny ants Ls and Pf showed nearly nil association with all species.

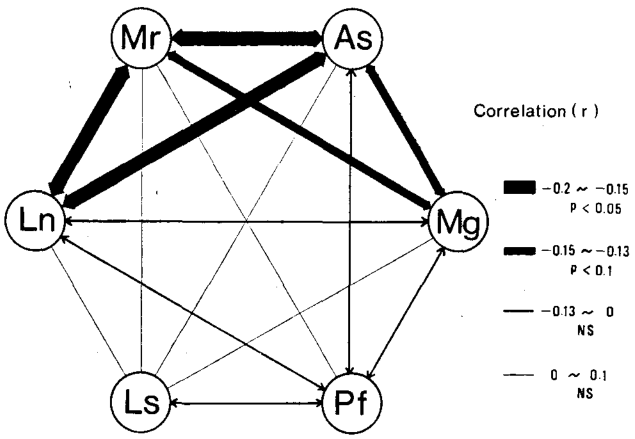

Fig. 2. Interspecific association patterns, given by covariance method of KERSHAW (1960).

For abbreviations of species name, see Fig. 1.

Discussion

Main factors regulating the dispersion of ant nests are the distribution of food and potential nest sites, intercolonial territoriality, escape from predators and parasites, and nesting system i. e. monodomous or polydomous (BRIAN, 1956; BRIAN, HIBBLE and STRADLING, 1965; BARONI-URBANI, 1979; SMALLWOOD and CULVER, 1979; HÖLLDOBLER and LUMDSDEN, 1980; HERBERS, 1985). Out of them intercolonial territoriality is a key factor primarily controlling the nest dispersion (LEVINGS and TRANIELLO, 1981). Although it is nearly impossible to confirm territorialities of all colonies on the forest floor covered by a thick litter layer, the aggressiveness and colony size of each species should be correlated with their territoriality. Actually, colonies of *Aphaenogaster smythiesi japonica* and *Myrmica ruginodis* which contained a great number of relatively aggressive workers appeared competitive against other colonies, since they showed the slightly overdispersed distribution of conspecific nests and the negative association with some species. Another large colony-sized species *Lasius niger* showed negative association with some species but their nests were a little more aggregated than those of *A. smythiesi japonica* and *M. ruginodis*, because this ant was often polydomous and the colony fragmentation could produce a dispersion pattern of nests situated more closely than random expectation. *Pheidole fervida* sometimes made large colonies but showed relatively aggregated nest distribution, partly because they preferred dead trunks and fallen trees which were heterogeneously distributed in the quadrats surveyed. The workers of this ant were aggressive against foreigners from other colonies but seemed too tiny to expel them from their territory; this may be why *Pheidole fervida* showed nearly nil association with other species. *Leptothorax* sp. appeared least competitive not only against other species (nil association with any other species) but also against conspecific colonies (nearly random distribution), doubtless because this tiny ant was less aggressive and made small colonies within small dead twigs which were abundant in all quadrats. *Myrmecina graminicola nipponica* was less aggressive and formed small colonies, but they showed negative association with territorial species such as *Aphaenogaster smythiesi japonica* and *Myrmica ruginodis*, seemingly because workers of this species were too large to avoid attack of other species. *M. graminicola nipponica* showed remarkably aggregated nest distribution partly due to nesting under mosses or at grass roots which were patchily distributed in the quadrats. Moreover, they may be polydomous, because they frequently showed polygyny which often induces polydomous colonies in various phyletic lines of ants (HIGASHI, 1983). Anyway, the nesting system of this species remains for further studies.

HERBERS (1985) reported that the dispersion of ant nests showed seasonal variation, i. e. contraction of the ant community in the spring, expansion in the summer and slight contraction by late summer, which is consistent with the present observation. According to HIGASHI (1976), *Formica yessensis* proliferates their nests by budding from the spring to early summer but, in prehibernation season, abandons many nests unsuitable for overwintering. In Hokkaido where air temperature often falls to $-20°C$ or less in the winter, most species hibernate underground to avoid freezing, which may drive different species to aggregate in microsites appropriate to overwintering.

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要　　約

北大苫小牧演習林の二次林内にて，アリ巣の分散様式を調査し，以下の結果を得た。

1. 5つの5 m×10 m コードラート内にて計185巣 (0.74巣/m²) を得た。優占種はヤマアシナガアリ，シワクシケアリ，カドフシアリ，トビイロケアリ，ムネボソアリ sp., アズマオオズアカアリ，ヒメハリアリである。

2. 巌 (1968) の $\mathring{m}-m$ 回帰法により，巣の集中傾向を求めたところ，カドフシアリは強度の集中分布を示した。他のアリ類の巣は比較的ランダムに分布するが，ヤマアシナガアリとシワクシケアリは，トビイロケアリ，ムネボソアリ sp., アズマオオズアカアリに比べ，より均等な分布を示した。

3. KERSHAW (1960) の共分散法により種間の分布相関を求めた。中型種のヤマアシナガアリ，シワクシケアリ，トビイロケアリは異種のアリに対し排他的であるが，小型種のムネボソアリ sp. やアズマオオズアカアリは他種アリの巣の近くでも比較的容易に営巣する。中型種のカドフシアリは他種に対し排他的ではないが，ヤマアシナガアリやシワクシケアリの巣の近くはさけて営巣する傾向が見られた。

4. 以上のような各アリ種の分散様式は，コロニーサイズ，ハタラキアリの体の大きさ，攻撃性，営巣地選好性，多巣性か単巣性かなどと関連している。

5. 全アリ巣の分散様式は，HERBERS (1985) が明らかにしたように季節により異り，春や秋は夏に比べやや集中分布を示す傾向がある。