

STUDIES ON THE ECOLOGICAL DISTRIBUTION OF ANTS IN SAPPORO AND ITS VICINITY (1 et 2)

by

Kazuo HAYASHIDA

(*Zoological Institute, Hokkaido University.*)

Corresponding to the two major branches of biogeography, the distribution of any animal groups can be studied from two aspects, namely, regional and ecological, which are complementary to each other and different but not sharply distinguished. Up to present, the ecological distribution of ants in a given area has been studied by many investigators such as GÖSSWALD (1932), TALBOT (1934), GÖETSCH (1937), DENNIS (1938), GREGG (1944) and others. Their publications deal mostly, however, with European or Nearctic faunas. Concerning the ecological distribution of Far Eastern Myrmecofaunas, especially of Japan, there are no comprehensive studies for brief discussions by TERANISHI (1933), MORISITA (1945 *a, b*) and YASUMATSU (1948).

Since 1956, the writer has begun to study the ecological distribution of ants in Sapporo and its vicinity, with special reference to habitat or nest site preference by various species. Following a preliminary report (HAYASHIDA, 1957), quantitative sampling and further qualitative observations have been made, which form the main body of the present paper.

Before going further, the writer wishes to express his sincere gratitude to Prof. TOHRU UCHIDA and Dr. SHŌICHI F. SAKAGAMI under whose helpful guidance the present work has been carried out. His further thanks are also due to Mr. T. KOGURE, Dr. M. MORISITA, Prof. K. TSUNEKI, Dr. C. WATANABE and especially to Prof. K. YASUMATSU, whose kind advices and stimulation were indispensable in the preparation of the present paper.

I.—METHODS EMPLOYED

The distribution of various species was surveyed through two methods, qualitative and quantitative samplings. The former is a mere sampling of as many as possible species in a given habitat, without paying attention to the relative abundance of the species discovered. This was mainly carried out in 1956 to obtain a general perspective of the faunal make-up in the area studied as well the ecological characteristics of each species. The quantitative sampling consists of counting the number of colonies discovered in a given habitat during an interval of 0.5 hour. This unit-interval sampling was repeated twelve times for each seven habitat types as distinguished in the subsequent section. The relative abundance estimated by this method can be applied in safety only to the epigeic species, because the interval of 0.5 hour is not sufficient to examine the earth layers deeper than 10 cm below the surface. Consequently, the relative abundance of subterranean species must be solved in further studies using improved methods.

(1) Contribution No. 476 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

(2) Studies on the ecological distribution of ants in Hokkaido, I.

II.—DESCRIPTION OF THE AREA STUDIED

Topographically, Sapporo and its vicinity is mostly located on the Ishikari Lowland Zone, which exists between the two mountainous

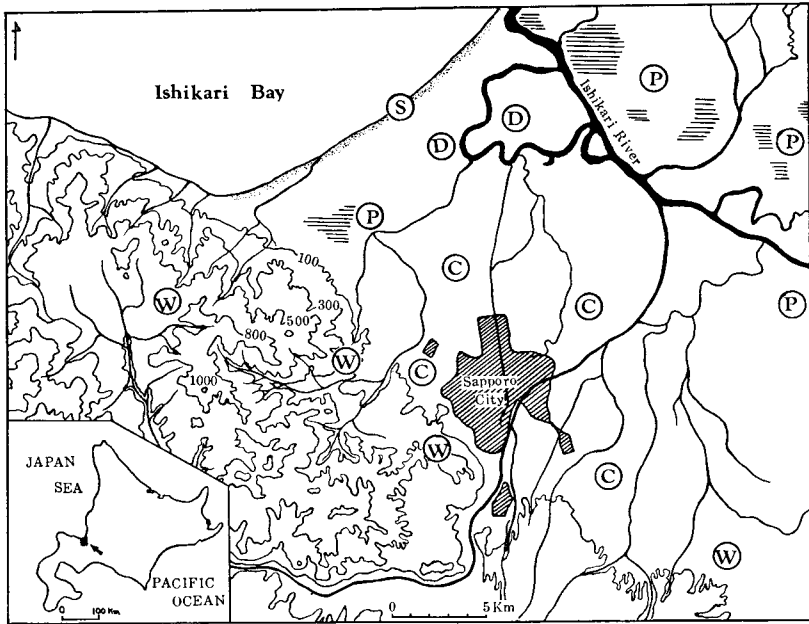


FIG. 1. — General topography of Sapporo and its vicinity. C : Crop field ; D : Damp ground ; P : Peat bog ; S : Sand dune ; W : Woodland.

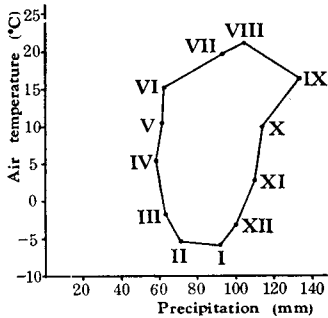


FIG. 2.

FIG. 2. — Climograph of Sapporo.

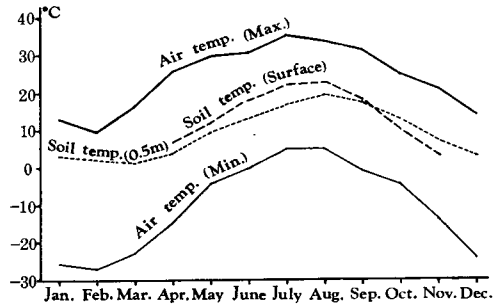


FIG. 3.

FIG. 3. — Annual changes of monthly air and soil temperature (From *Climate of Hokkaido*, published by Sapporo Region Meteor. Observatory (1952). Measured during last 60 years.

regions of Hokkaido, the mainbody of the island and the Oshima Peninsula; it faces the Japan Sea westwards with a narrow seashore belt, and is fringed by old volcanic zones in the south-western boundary. This

zone lies ecologically near the northernmost border of the Temperate Deciduous Forest Biom, possessing, in general, elms (*Ulmus propinqua*, *U. laciniata*), maples (*Acer Mono*, *A. Mayri*, *A. ornatum*) and lindens (*Tilia japonica*, *T. Maximowicziana*) as dominants (TATEWAKI, 1958). Through extensive cultivation, such original vegetation now has either retreated to the fringing mountainous zones or remains in the plain only in a few limited reserves. The greater part of area is being replaced by cropfield and urban districts as shown in Fig. 1. But considered *microscopically*, the area contains varieties of local diversities which enable numerous ant species to find habitats.

The main climatic features of the area are visualized from Figs. 2 and 3. Due to the long and severe winter and instable spring weather, the outer activities of ants are almost confined to the period from early May to late September, which means that both air and soil temperature exceed 10°C.

III.—SPECIES COLLECTED IN THE AREA

As listed in Table I, 28 forms, including subspecies and varieties, were collected from the area, all being typical palaeartic elements. Thanks to the kind advices by Prof. K. YASUMATSU, the specific names were partly revised from those cited in the preliminary paper, but there are still some species of which correct nomenclatorial solution remains for the future. For instance, the name *Camponotus caryae quadrinotatus* Forel and *Lasius niger* var. *alieno-niger* Forel repeatedly appeared in the earlier papers concerning Japanese ant fauna. But there occurs no Japanese species which corresponds to *Camp. caryae quadrinotatus*. The name *L. niger* var. *alieno-niger* was regarded as synonymous to *L. niger* (Linnaeus) by WILSON (1955), whose opinion is followed in the present paper. Moreover, the name *Lasius emarginatus* (OLIVIER) was adopted after WILSON, but the specific characters of the population in Sapporo do not always agree with those given in his description.

Ant species hitherto recorded from Hokkaido are about 50 (including infraspecific categories) (TERANISHI, 1929 *a, b*, 1932, KÔNO and SUGIHARA, 1939, MORISITA, 1945 *b*, KOGURE, 1953, 1955). More than half of them were discovered from the Ishikari Lowland Zone. Furthermore, the occurrence of several other species is likely to be found after earlier announcements.

IV.—DISTRIBUTION IN VARIOUS HABITATS

4.1 Classification of habitats.—The classification of habitats is a troublesome problem. Any systems inevitably savour of arbitrariness when it comes to considering the occurrence of transitional gradations

TABLE I.—SPECIES DISCOVERED IN SAPPORO AND ITS VICINITY, TOGETHER WITH THEIR RELATIVE ABUNDANCE IN VARIOUS HABITATS.

ORDER OF ABUNDANCE.	SPECIFIC NAME.	ABBREVIATION.	RELATIVE ABUNDANCE IN EACH HABITAT*.							TOTAL (%)					
			BS	BA	SH	PT	HG	WM	WL						
18	<i>Ponera scabra</i> Wheeler	(P)	9 (2)	1 (1)							4 (2)	18 (1.30)			
6	<i>Myrmica ruginodis</i> Nylander	(M)	5 (2)	12 (6)			4 (3)					4 (2)	103 (6.24)		
3	<i>M. lobicornis</i> var. <i>yessensis</i> Forel	(Mb)	27 (9)	67 (9)	25 (14)		55 (10)					13 (6)	160 (10.80)		
8	<i>Aphelegaster famelica</i> (F. Smith)	(A)	4 (3)	11 (4)			14 (6)					2 (2)	79 (5.45)		
7	<i>Pheidole fervida</i> Smith	(Ph)		11 (6)			2 (2)					33 (11)	81 (5.50)		
13	<i>Tetramorium caespitum</i> (Linné)	(T)	3 (1)	6 (3)			18 (6)					23 (5)	36 (2.16)		
16 a	<i>Leptothorax spinosior</i> Forel	(Ls)	15 (5)	9 (3)			2 (1)					1 (1)	28 (1.89)		
26 a	<i>Crematogaster laboriosa</i> Smith	(Cr)	2 (2)										1 (0.07)		
25	<i>Solenopsis fugax</i> Latreille	(S)											2 (0.15)		
23 b	<i>Vollenhovia emeryi</i> Wheeler	(V)		2 (2)									3 (3)	5 (0.35)	
23 a	<i>Dolichoderus quadripunctatus sibiricus</i> Emery	(D)													
4 a	<i>Paratrechina flavipes</i> (F. Smith)	(Pa)	16 (3)	35 (9)			30 (9)						2 (1)	5 (0.35)	
22	<i>Lasius umbratus</i> (Nylander)	(Lu)					2 (2)						8 (5)	144 (7.81)	
4 b	<i>L. flavus</i> (Fabricius)	(Lf)											4 (3)	7 (0.47)	
12	<i>L. brunneus</i> (Latreille)	(Lb)		3 (2)			7 (3)						6 (4)	114 (7.90)	
15	<i>L. emarginatus</i> (Olivier)	(Le)	29 (4)				21 (7)						11 (7)	35 (2.36)	
21	<i>L. alienus</i> (Foerster)	(La)											4 (3)	29 (1.86)	
2	<i>L. niger</i> (Linné)	(L)	33 (14)	45 (11)			10 (6)						26 (10)	8 (0.54)	
16 b	<i>L. fuliginosus</i> (Latreille)	(Lg)					1 (1)						13 (5)	210 (14.22)	
19	<i>L. spatheus</i> Wheeler	(Ls)		2 (1)									4 (3)	28 (1.89)	
11	<i>Camponotus obscuripes</i> Mayr	(C)					1 (1)						6 (2)	13 (0.88)	
9	<i>C. herculeanus japonicus</i> Mayr	(Cj)	16 (8)	9 (1)			11 (4)						7 (4)	36 (2.44)	
26 b	<i>C. yessensis</i> Teramishi	(Cy)											1 (1)	53 (3.49)	
26 c	<i>C. kiusiuensis</i> Santitschi	(Ck)											1 (1)	1 (0.07)	
20	<i>C. caryæ quadrinotatus</i> Forel	(Cc)	51 (12)	79 (12)			13 (5)						3 (2)	7 (4)	10 (0.68)
1	<i>Formica fusca japonica</i> Motschulsky	(F)	2 (1)	25 (8)			4 (3)						24 (8)	233 (15.58)	
14	<i>F. sanguinea</i> var. <i>jusciceps</i> Emery	(Fs)	8 (1)	17 (1)			2 (2)						14 (2)	31 (2.10)	
10	<i>F. truncorum yessensis</i> Forel	(Fy)											9 (3)	50 (3.38)	
Total number of species in each habitat (28 spp. in total)			14	17	15	2	15				20	16	1491		

* Number of colonies discovered by the unit-interval sampling and (in parentheses) number of samples in which the species was discovered. Species discovered only by the qualitative observation are indicated in italic letters.

TABLE II.—CHARACTERIZATION OF EACH HABITAT.

ABBREVIATED NAME.	SURFACE VEGETATION.	NONLIVING SURFACE COVERAGE.	SURFACE INSOLATION.	SOIL TYPE.	HUMIDITY.	RELATIVE SIZE WITHIN THE AREA STUDIED.	INTERFERENCE OF HUMAN ACTIVITIES.	EXAMPLES.
BS	very sparse	pebbles, stones and sparse decaying matter	large	sand	arid	small but relatively frequent as scattered areas	relatively weak	bare sand dunes, river-sides
BA	sparse	sparse pebbles and decaying matter	large	loam and clay with a slight mixture of humus	arid	large	generally large	crop fields, roadsides
SH	relatively dense	decaying matter and sparse pebbles	rather small but variable	sand	moderate to semi-arid	small but relatively frequent as scattered areas	moderate but variable	seashore
PT	dense	abundant decaying matter	weak	peat	very humid, exceptionally moderate	small	weak so far as not cultivated	peat bogs
HG	fairly dense	abundant decaying matter, rarely sparse pebbles and logs	weak	loam, clay and humus	rather humid	large	moderate to strong	pasture and meadows (herby or grassy land)
WM	dense both herbs and shrubs, exceptionally sparse	abundant decaying matter including logs	weak	loam, clay and humus	moderate to humid	large as many scattered areas	indistinct	wood margins and scrubs
WL	either dense tree sparse floor vegetation or sparse tree and dense floor	abundant decaying matter including logs	very weak	loam, clay and humus	humid	relatively small	weak	woods or forests

among major types. Some attempts made by earlier writers are briefly cited herewith:

GÖSSWALD (1932): *Central Main Region, Germany*. Ten major Facies (Laubwald, Mischwald, Nadelwald, Steinöden des Hauptmuschelkalkes, Steinöden des Wellenkalkes u. Anhydrites, (E)dgebiet des Plattensandsteins, Wiesen, Feldbaugebiete, Obst- u. Gartenbaugebiete und Weinberge) and nine undergrounds (Hauptmuschelkalk, Wellenkalk, Plattensandstein, Anhydrit, Sand, Waldboden, Lettenkole, Löss und Röt).

TALBOT (1934): *Chicago Region*. Ten ecological stages (beach, fore dunes, poplar dunes, pine dunes, black oak dunes, red-white oak dunes, mixed oak woods on clay, oak-maple woods on sand, beech-maple climax and prairie) based upon the substratal conditions and succession of plant community.

GÆTSCH (1937): *Islands Capri and Ischia, Gulf of Naples*. Four natural (Steinwüste, Strauchsteppe, Macchia und Sandwüste) and one artificial biotopes (Kulturlands) mainly based upon climatic conditions such as insolation, wind, moisture, etc.

GREGG (1944): *Chicago Region*. Thirteen ant-plant communities (Prairie-meadowpasture, Fore-dune-cottonwood, Coniferous dune, Black oak dune, Mesophytic dune ravine forest, Mixed oak forest, Oak-hickory forest, Beech-maple forest, Bog forest, Floodplain forest, Forest margin, Marsh, and Railway and Roadside).

MORLEY (1955): *Without reference to the particular area*. Six habitats (Bogs, swamps and rotted wood, Soil (neither extremely dry nor extremely damp), Very dry soil, Forest or woodland, Cosmopolitan (human habitations and countryside), and Mountains (over 6,500 feet) based upon the difference of nest sites.

In referring to these earlier contributions, the writer divided the area now under study into seven typical habitats as in Table II, mainly based upon the nature of vegetation and substratum.

4.2 General pattern of distribution.

—The number of colonies obtained by the unit-interval method in each habitat may reflect a general tendency of the distribution of various species. As seen in Table I, *Formica fusca japonica*, *Lasius*

niger and *Myrmica lobicornis* var. *jessensis* are obviously the most dominant species in the area studied, supplying 40.6 % of the total colonies discovered. Although less abundant, *Paratrechina flavipes*, *Lasius flavus*, *Myrmica ruginodis*, *Pheidole fervida*, *Aphaenogaster famelica* and much

Crematogaster laboriosa.

Lasius emarginatus.

Camponotus yessensis.

Formica sanguinea var. *fusciceps*.

Lasius alienus.

Myrmica ruginodis.

Lasius flavus.

Lasius fuliginosus.

Vollenhovia emeryi.

Formica fusca japonica.

Pheidole fervida.

Leptothorax spinosior.

Dolichoderus quadripunctatus sibiricus.

Aphaenogaster famelica.

Myrmica lobicornis var. *jessensis*.

Lasius spathepus.

Lasius umbratus.

Ponera scabra.

Paratrechina flavipes.

Formica truncorum yessensis.

Camponotus obscripes.

Lasius niger.

Tetramorium caespitum.

Lasius brunneus.

Camponotus herculeanus japonicus.

Camponotus caryæ quadrinotus.

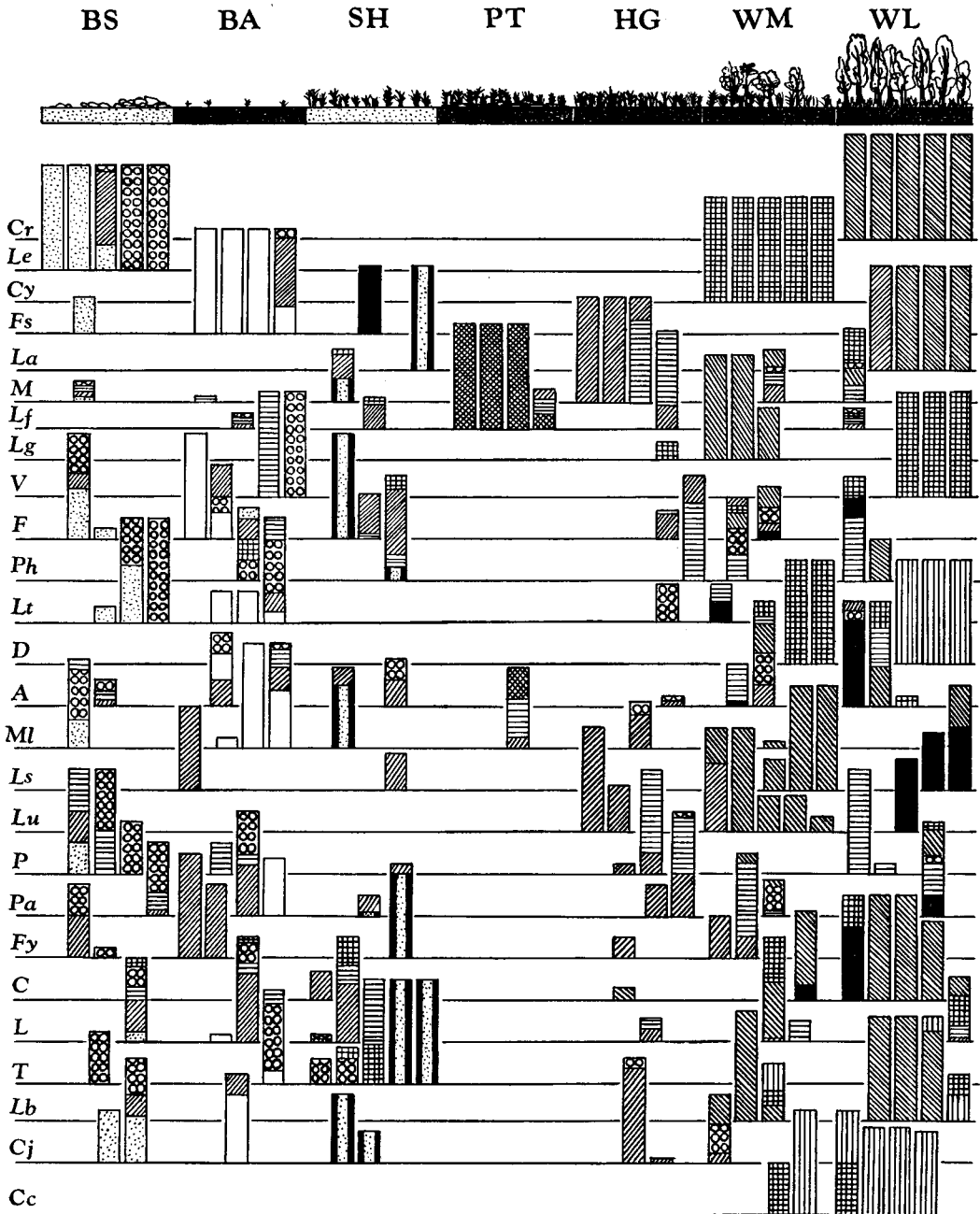


FIG. 4. — The distribution of various species in each habitat, together with preference of nest sits.

TABLE III. — CORRELATION INDICES BETWEEN RELATIVELY

SPECIES.	Nf/nFH						
	BS	BA	SH	PT	HG	WM	WL
<i>Ponera scabra</i>	0.25	0.13			0.37		0.25
<i>Myrmica ruginodis</i>	0.09	0.18	0.12		0.31	0.12	0.18
<i>M. lobicornis</i> var. <i>jessensis</i>	0.21	0.21	0.14	0.26	0.14	0.04	
<i>A. famelica</i>	0.09	0.12	0.12		0.08	0.25	0.34
<i>Pheidole fervida</i>		0.19	0.23		0.19	0.23	0.16
<i>Tetramorium cæspitum</i>	0.10	0.30	0.60				
<i>Leptothorax spinosior</i>	0.45	0.27			0.10	0.18	
<i>D. quadripunctatus sibiricus</i>						0.33	0.67
<i>Paratrechina flavipes</i>	0.08	0.24	0.07		0.24	0.13	0.24
<i>Lasius umbratus</i>					0.33	0.50	0.17
<i>L. flavus</i>		0.07	0.11	0.43	0.25	0.14	
<i>L. brunneus</i>						0.41	0.59
<i>L. emarginatus</i>	1.00						
<i>L. alienus</i>		0.30	0.20				0.50
<i>L. niger</i>	0.18	0.18	0.19		0.10	0.19	0.16
<i>L. fuliginosus</i>					0.09	0.54	0.37
<i>L. spathepus</i>		0.14	0.14			0.29	0.43
<i>Camponotus obscripes</i>			0.12		0.05	0.18	0.65
<i>C. herculeanus japonicus</i>	0.40	0.05	0.15		0.20	0.20	
<i>C. caryæ quadrinotatus</i>						0.33	0.67
<i>Formica fusca japonica</i>	0.25	0.25	0.23		0.10	0.17	
<i>F. sanguinea</i> var. <i>fusciceps</i>	0.08	0.67	0.25				
<i>F. truncorum yessensis</i>	0.11	0.11	0.34		0.22	0.22	

ABUNDANT SPECIES AND HABITAT (ABBREVIATIONS IN TEXT).

<i>c/f</i>							<i>c/C</i>							THE WHOLE AREA C/F
BS	BA	SH	PT	HG	WM	WL	BS	BA	SH	PT	HG	WM	WL	
4.5	1.0			1.3		2.0	0.50	0.06			0.22		0.22	2.4
2.5	2.0	2.3		5.5	2.2	2.2	0.04	0.12	0.09		0.53	0.09	0.13	3.2
			2.3	2.3	1.0		0.17	0.41	0.16	0.16	0.09	0.01		3.7
1.3	2.7	1.7		1.0	2.8	3.0	0.05	0.14	0.09		0.02	0.28	0.42	2.5
	1.8	2.3		3.0	1.9	4.6		0.14	0.20		0.22	0.16	0.28	2.6
3.0	2.0	3.9					0.08	0.19	0.75					3.3
3.0	3.0			2.0	1.0		0.54	0.32			0.07	0.07		2.5
					2.0	1.5						0.40	0.60	1.7
5.3	3.9	2.0		3.3	1.6	2.3	0.14	0.31	0.04		0.26	0.07	0.18	3.1
				1.0	1.3	1.0					0.28	0.57	0.15	1.2
	1.5	2.1	6.4	3.0	1.5			0.04	0.06	0.67	0.18	0.05		4.1
					1.6	2.4						0.31	0.69	2.1
7.2							1.00							7.2
	1.5	1.0				1.3		0.37	0.13				0.50	1.3
3.0	4.1	4.5		1.7	4.2	2.6	0.16	0.21	0.21		0.06	0.24	0.12	3.5
				1.0	2.0	2.6					0.04	0.50	0.46	2.2
	2.0	1.0			3.0	1.3		0.15	0.08			0.46	0.31	1.9
		1.0		1.0	2.0	2.5			0.05		0.03	0.17	0.75	2.1
2.0	9.0	3.3		2.7	1.7		0.30	0.17	0.19		0.21	0.13		2.7
					1.5	1.7						0.30	0.70	1.6
4.2	6.6	6.0		2.6	3.0		0.22	0.34	0.28		0.06	0.10		4.8
2.0	3.1	1.3					0.06	0.81	0.13					2.6
8.0	17.0	3.0		1.0	7.0		0.16	0.34	0.18		0.04	0.28		5.6

less frequent however, *Camponotus herculeanus japonicus* can be also regarded as a common species. The distribution of colonies in various habitats is illustrated in Fig. 4, together with the relative preference of nest sites discussed later. Among species presented in the figure, no definite conclusion can be reached concerning those such as *Vollenhovia emeryi*, *Crematogaster laboriosa*, and *Camponotus yessensis*, which were found only once or twice throughout the whole investigation. Excluding them, further analyses were developed to clarify three aspects: habitat preference and distribution pattern of each species, and characterization of each habitat.

4.3 Habitat preference and distribution pattern of each species.

Habitat preference is measured either by the numerical size of colony or frequency of discovery in each habitat. The correlation index between species and habitat is expressed by the following formula: $(Nf)/(nFH)$, where f is the numbers of samples of each habitat in which the species was found, F the total number of samples in which the species was found, N and n the number of total samples ($= 84$) and of samples in each habitat ($= 12$ in every case) respectively, and H the number of habitats ($= 7$) distinguished in the area studied. If the values of $(Nf)/(nFH)$ reaches the maximum (1.0), it means the highest degree of correlation, namely, the strong preference of the species concerned for a particular habitat. The more the value deviates from 1.0, the more the tolerance range of preference increases.

The colony ratio, c/C , and the patched degree of distribution of colonies in each habitat, c/f , also serve as correlation indices of the colony distribution, where c and C are the numbers of colonies found in each habitat and in the whole area respectively, and f as in above. The value of c/C signifies a ratio of relative abundance of colonies in each habitat, the maximum value (1.0) means that the colonies were discovered in one habitat alone. The values of these indices in relatively abundant species are presented in Table III.

From the values of the correlation index $(Nf)/(nFH)$ various species can be classified into the following three major categories, in which highly preferred habitats are shown by gothic letters:

I.—SPECIES FOUND MAINLY FROM ONE HABITAT ALONE.—1) Those not found from other habitats. *Lasius emarginatus* (**BS**). 2) Those only rarely found from other habitats. *Tetramorium cespitum* (BS, BA, **SH**), *Formica sanguinea* var. *fusciceps* (BS, **BA**, SH), *Myrmica ruginodis* (BS, BA, SH, **HG**, WM, WL).

II.—SPECIES FOUND MAINLY FROM TWO HABITATS.—1) Those not found from other habitats. *Dolichoderus quadripunctatus sibiricus* (**WM**, **WL**), *Lasius brunneus* (**WM**, **WL**), *Camponotus caryæ quadrinotatus* (**WM**, **WL**). 2) Those found also from other habitats. *Ponera scabra* (**BS**, BA, HG, WL), *Leptothorax spinosior* (**BS**, **BA**, HG, WM), *Lasius*

umbratus (HG, WM, WL), *L. flavus* (BA, SH, PT, HG, WM), *L. alienus* (BA, SH, WM, WL), *L. fuliginosus* (HG, SH, WM, WL), *Camp. obscripes* (SH, HG, WM, WL), *L. spathepus* (BA, SH, WM, WL).

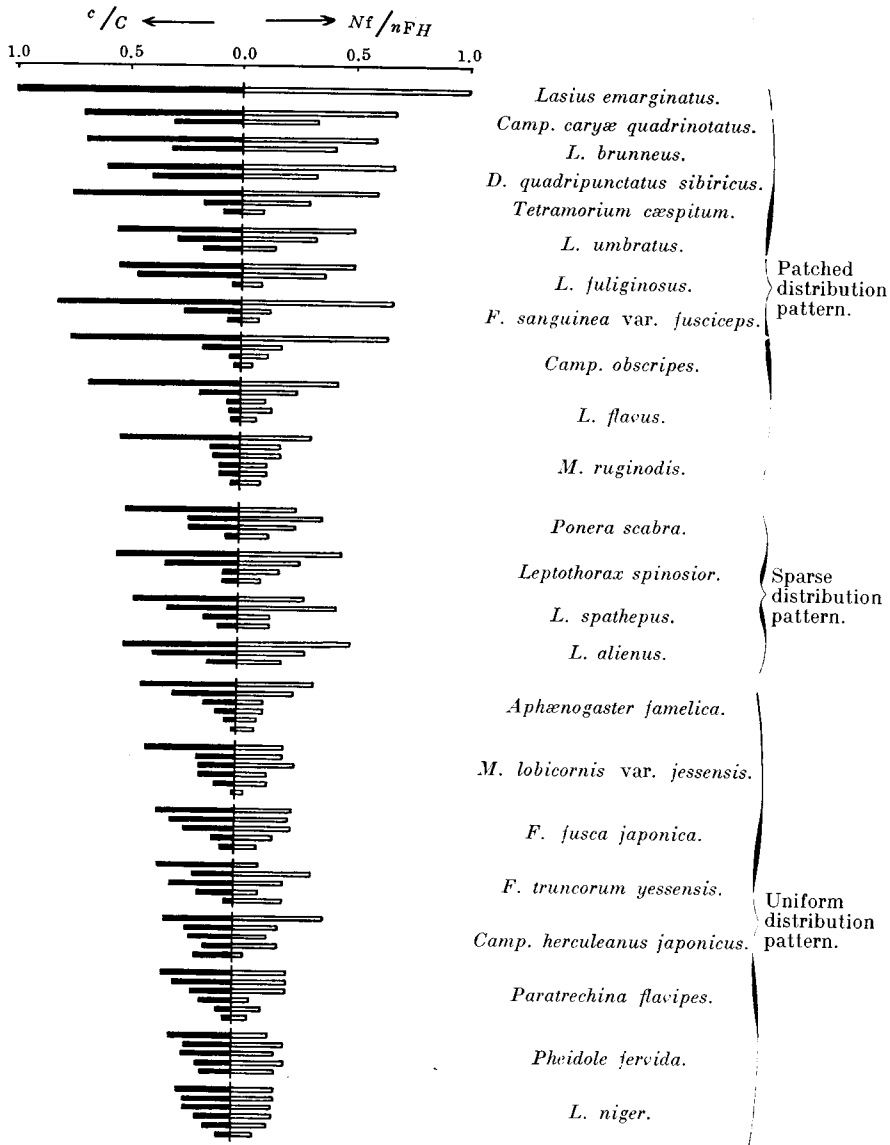


FIG. 5. — The values of indices c/C and Nf/nFH in various species. Each histogram corresponds to the value of two indices in the habitats.

III.—SPECIES FOUND FROM MORE THAN TWO HABITATS. 1) Those with a relatively definite habitat preference. *Aphænogaster famelica* (BS, BA, SH, HG, WM, WL), *Formica truncorum jessensis* (BA, BS, SH, HG, WM),

F. fusca japonica (BS, BA, SH, HG, WL), *Camp. herculeanus japonicus* (BS, BA, SH, HG, WM). 2) Those with a wide tolerance range of habitat preference. *Myrmica lobicornis* var. *jessensis* (BS, BA, SH, PT, HG, WM), *Pheidole fervida* (BA, SH, HG, WM, WL), *Paratrechina flavipes* (BS, BA, HG, WM, WL), *Lasius niger* (BS, BA, SH, HG, WM, WL).

The distribution pattern of each species is characterized also from the values of correlation indices in Table IV and Fig. 5; the following three main categories of distribution pattern are differentiated:

TABLE IV. — NUMBER OF HABITATS OF EACH SPECIES CONCERNED TO RANGE OF THE CORRELATION INDICES, *c/f* and *C/F*.

<i>c/f</i> ≥ <i>C/F</i>	<i>c/f</i> > <i>C/F</i>	<i>c/f</i> = <i>C/F</i>	<i>c/f</i> < <i>C/F</i>	SPECIES.
0	0	1	0	<i>L. emarginatus</i>
0	1	0	1	<i>D. quadripunctatus sibiricus</i> , <i>L. brunneus</i> , <i>Camp. caryæ quadri-notatus</i>
0	1	0	2	<i>L. umbratus</i> , <i>L. fuliginosus</i> , <i>F. sanguinea</i> var. <i>fusciceps</i>
0	1	0	3	<i>Camp. obscripes</i>
0	1	0	4	<i>L. flavus</i>
1	0	0	5	<i>M. ruginodis</i>
0	2	0	1	<i>T. cæspitum</i>
1	0	0	3	<i>Ponera scabra</i>
0	1	1	1	<i>L. alienus</i>
0	2	0	2	<i>L. spathepus</i> , <i>Leptothorax spinosior</i>
0	2	0	3	<i>F. fusca japonica</i>
1	1	0	3	<i>Pheidole fervida</i>
1	1	0	4	<i>M. lobicornis</i> var. <i>jessensis</i>
1	1	1	2	<i>Camp. herculeanus japonicus</i>
1	2	0	2	<i>F. truncorum jessensis</i>
0	3	0	3	<i>A. famelica</i> , <i>Para. flavipes</i> , <i>L. niger</i>

I.—PATCHED DISTRIBUTION PATTERN.—1) Species of typically patched distribution pattern *L. emarginatus*, *L. fuliginosus*, *L. umbratus*, *L. brunneus*, *D. quadripunctatus sibiricus*, *Camp. obscripes*, *Camp. caryæ quadri-notatus*, *T. cæspitum*, *F. sanguinea* var. *fusciceps*. 2) Species of modified patched distribution *M. ruginodis*, *L. flavus*.

II.—SPARSE DISTRIBUTION PATTERN.—*Ponera scabra*, *L. spathepus*, *L. alienus*, *Leptothorax spinosior*.

III.—UNIFORM DISTRIBUTION PATTERN.—1) Species of typically uniform distribution pattern *Pheidole fervida*, *Paratrechina flavipes*, *L. niger*. 2) Species of modified uniform distribution pattern *M. lobicornis* var. *jessensis*, *A. famelica*, *Camp. herculeanus japonicus*, *F. fusca japonica*, *F. truncorum jessensis*.

About half of the various species belong to the patched distribution

pattern, indicating a narrow tolerance range of habitat preference. The most typical example is *Lasius emarginatus*, of which all 29 colonies were found exclusively in BS, at the riverside of Monami Park near Sapporo, possessing the maximum values of two indices, $(Nf)/(nFH)$ and c/C . Although *Lasius flavus* and *Myrmica ruginodis* were found from various habitats, the fairly high values of $(Nf)/(nFH)$ and c/C were obtained in one particular habitat (0.43-0.67 and 0.31-0.53, respectively). On account of this fact, these two species were classified under the modified patched distribution. The sparse distribution pattern was applied to relatively scarce species, of which colonies were found in one or two habitats alone. As illustrated in Figure 5, *Leptothorax spinosior* and *Lasius alienus* are similar in the values of c/C and $(Nf)/(nFH)$ to the species of the patched distribution pattern, but not typical. On the other hand, *Ponera scabra* and *Lasius spathopus* exhibit a pattern rather resembling the uniform distribution pattern but the number of colonies is extremely less than that of species belonging to the latter category. Hence the sparse distribution pattern includes two subpatterns which are heterogeneous in their nature. The most species classified under the uniform distribution pattern possess a wide tolerance range of habitat preference and a large number of colonies in various habitats. These characters are typically presented by *Pheidole fervida*, *Paratrechina flavipes* and *Lasius niger*, while a modification of this characteristic pattern is seen in five other species, which show a tendency to group into the patched distribution on account of their slightly narrow tolerance range. The values of correlation indices c/C and Nf/nFH in the uniform pattern did not exceed 0.4 and mostly fluctuated between 0.1 and 0.2.

The distribution pattern can be also analysed from the comparison between c/f and C/F . If the number of habitats in which $c/f > C/F$, (h_1), is less than those being $c/f < C/F$, (h_2), this indicates a tendency toward patched distribution, while the reverse ratio suggests the uniform pattern. This index, (h_1/h_2) , can be applied, however, to the relatively abundant species alone. According to Table IV, three distribution patterns show the following range of h_1/h_2 : patched distribution pattern — 1/1—1/5, 2/1; sparse distribution pattern — 1/1, 1/3, 2/2; uniform distribution pattern — 2/2—2/4, 3/2—3/3.

Thus the various aspects of distribution patterns corresponding to the habitat types are given by these five indices, $(Nf)/(nFH)$, c/C , c/f , C/F and h_1/h_2 .

4.4 Characterization of habitats.—The characterization of habitats differently utilized among various species is the reciprocal approach of habitat preference analysis. According to the occurrence probability method of KATÔ, MATSUDA and YAMASITA (1952), the ratio of number of colonies occupied by various species was calculated in each habitat, together with its confidence interval within 95 % reliability.

In Fig. 6, the results are shown with the confidence interval in each

species. When the low confidence limit of the colony ratio of one species exceeds the upper confidence limit of the mean colony number (expressed in the figure as a vertical broken line), such species was regarded as dominant species in each habitat: BS - - - *F. fusca japonica*, *L. niger*; BA - - - *F. fusca japonica*, *M. lobicornis* var. *jessensis*, *L. niger*; SH - - - *F. fusca japonica*, *L. niger*; PT - - - *L. flavus*; HG - - - *M. ruginodis*, *Para. flavipes*; WM - - - *L. niger*; WL - - - *Aphænogaster famelica*.

The various habitats were arranged in the descending order of number of colonies and species (c , s respectively) and of the values of the ratio c/s , so the following three series were obtained:

c series - - - BA > SH > BS > WL > WM > HG > PT

s series - - - WM > BA > WL > SH = HG > BS > PT

c/s series - - - PT > BA > BS > SH > WL > HG > WM.

From these series, it is recognized that the richness in number of species does not always correspond to that of number of colonies. The ratio c/s is overwhelmingly large in PT, apparently caused by the peculiar environmental conditions, which permit only two species as the constant inhabitants. Excluding this peculiar case, the high value of c/s in BA is due to the abundance of dominant species, *Formica fusca japonica*, *Myrmica lobicornis* var. *jessensis* and *Lasius niger* in comparison with other relatively scarce species. A diametrically opposite case is shown by WM, where the dominance gradient is less steep and number of species was relatively large. From c -order mentioned above, the density of colonies is the highest in BA, the most suitable and flourishing habitat for both dominant and subordinate species, and very low in PT and HG, suggesting severe environmental resistance and lack of other nest sites. The further characterization of habitats, except PT, was made by using MOTOMURA's law of geometric series given by a formula: $\log y + ax = b$ (MOTOMURA, 1932), where y is the number of colonies, x the rank of the colony number among species and a and b are constants specific to each case; the results are illustrated in Fig. 7.

The value of $|a|$, the steepness of the regression line given in the figure, serves as an index of the complexity of each assemblage. Namely, the higher values of $|a|$ mean a simple composition with definite dominant species. Consequently, from the value of a given in Fig. 7, the following series of complexity degree is obtained: WM > WL > BA > BS > SH > HG. WM and WL contain the most complex assemblage with a relatively low colony density. Hence these woodland habitats are characterized by the diversity of environmental structure which attracts numerous species, rather than by the peculiar suitability to any particular species. The opposite picture is shown by HG and SH which are characterized by the general environmental severity for the most species. However, SH is preferred and well utilized by a few species, while HG possesses no marked dominant species. Hence two habitats occupy the intermediate position between WM, WL and BS, BA. The value of b approximately derived from the regression line in Fig. 7 can be

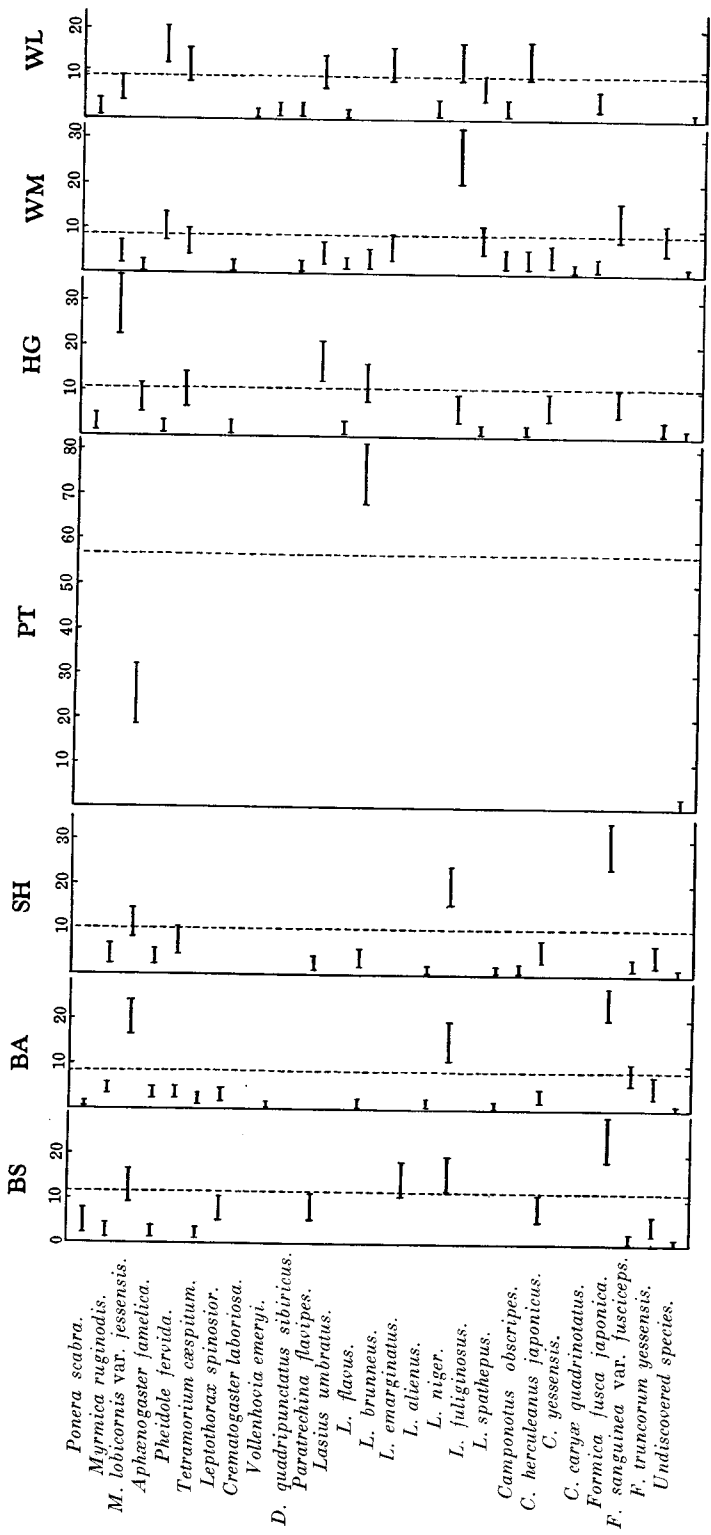


Fig. 6. — The colony ratio of each species in various habitats, shown by bar with the confidence range in 95 % reliability (*Abscissa*, the ratio expressed in %; *Vertical broken line*: the upper confidence limit of mean colony number).

accepted as the index of the population density of the assemblage as noticed by KATÔ and TORIUMI (1950). For instance, the series of b value, $BA > SH > BS > HG > WL > WM$, nearly resembles that of c/s

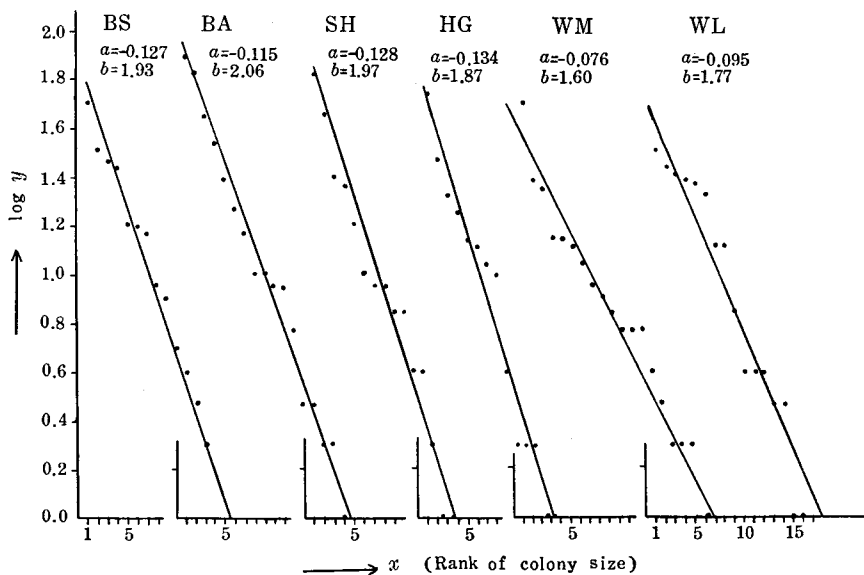


FIG. 7. — Comparison of assemblage complexity in various habitats. Each regression line was derived from the law of geometric series (See in text).

order except for two instances, SH-BS and HG-WL. Therefore, the colony density correlates to the abundance of vegetation, that is, the density is higher in sparsely vegetated habitats and lower in woodland ones.

V. — NEST SITE PREFERENCE

The distribution of various species in each habitat distinguished in the above section may indicate the general habitat preference by various species. On the other hand, the preference of nest site often deals with more confined microhabitats and occasionally shows a different tendency from that in the habitat preference. There is still no unitary classification of the nest sites of ants, although some writers have attempted to classify them: GÖSSWALD (1932), STEINNESTER, HOLZNESTER u. KUPPELBAUTEN; TALBOT (1934), log (L), soil (S), both log and soil (SL); DENNIS (1938), in weed and grass stems, in logs, stumps, in dead wood of standing trees, under stones, in ground, etc. In the present paper, the nest sites were distinguished and abbreviated as follows:

s: in exposed sandy surface; \bar{s} : in shaded sandy surface; l: in exposed loam or clay surface; \bar{l} : in shaded loam or clay surface; u: under stones;

m: under accumulations of humus and other debris; r: around the roots of grasses and herbs; p: in peat; n: around the roots of living trees; w: in trunks of living trees; d: in decayed stumps or fallen logs.

Many of these nest sites naturally have definite relations to each habitat respectively as presented in Table V.

5.1 Degree of utilization.—The availability of various nest sites differs within and among each separate habitat. As represented in Table V, s and u are practically inexhaustible and they are used rather indiscriminably by numerous species in habitat BS, while m and r sites are rather limited in number but distinctly preferred by several species. In BA, l is definitely preferred by two dominant species, *F. fusca japonica* and *M. lobicornis* var. *jessensis*, while r rather less abundant in this habitat, is also well utilized by dominant species, *L. niger* and *F. fusca japonica*. Other nest sites, u and m, lodge a relatively small number of colonies, but they act in BA as the cores to attract colonies of certain species which usually rather unsuitable to this habitat such as *M. ruginodis*, *A. famelica*, *Para. flavipes*, *F. truncorum yessensis*, etc., and consequently enrich the ant fauna of the habitat. In SH, the most available sites, r and \bar{s} , are preferred not only by the dominant species, *L. niger* and *F. fusca japonica*, but also by other less frequent inhabitants. A peculiar habitat, PT, provides a characteristic nest site, p, utilized by the two species, *L. flavus* and *M. lobicornis* var. *jessensis*. Owing to a relatively simple environmental structure in HG, both dominant species, *M. ruginodis* and *Para. flavipes*, and less numerous ones are obliged to use r and m, two representative nest sites in the habitat. On the other hand, the occurrence of diverse sites in WM and WL results in a marked increase of the number of species in proportion to the colony density of each species as shown by the small values of ratio *c/s* in the preceding section. *F. truncorum yessensis* is naturally an exception to this characteristic feature of woodland ant distribution, due to the peculiar life-mode characteristic of *F. rufa* group. The best nest site in WM and WL is n with its relatively shady and moist conditions, which is preferred by more than half of all wood-dwellers. But WL is one of the most unsuitable habitats for ants, especially in the darker innermost parts. Shaded bare loam or clay site, \bar{l} , mainly found by roadsides through woods is highly preferred by *A. famelica* and *Para. flavipes*, but their colonies were not always abundant in number.

From the facts mentioned above, it is suggested that the number of species in a given habitat is distinctly affected by the availability of diverse nest sites within that area.

5.2 Nest site preference of each species.—In contrast to the habitat preference, the nest site preference of each species is difficult to compare quantitatively because of the technical difficulty in measuring the frequency of nest sites within a given habitat. As seen in Table VI, however, most species tend to prefer certain characteristic nest sites. Species

TABLE VI. — COLONY NUMBER OF EACH SPECIES FOUND AT VARIOUS NEST SITES IN THE SUITABLE HABITAT.

SPECIES.	TYPE OF NEST SITE PREFERENCE.										
	ls				mu			nr		dw	
	s	\bar{s}	l	\bar{l}	p	u	m	r	n	w	d
<i>Ponera scabra</i>	1					4	11	2			
<i>M. ruginodis</i>	1	4				6	24	55	6		7
<i>M. lobicornis</i> var. <i>jessensis</i>	9	19	53		9	20	22	26	2		
<i>A. famelica</i>			4	14		13	15	14	10		9
<i>Pheidole ferdida</i>			2	3		7	31	18	12		6
<i>Tetramorium cæspitum</i>		13	1			10	5				3
<i>Leptothorax spinosior</i>	4		4	1		16	2	1			
<i>Crematogaster laboriosa</i>									1		
<i>Vollenhovia emeryi</i>						1	1				3
<i>D. quadripunctatus sibiricus</i>										3	2
<i>Para. flavipes</i>		1	12	4		30	26	32	7		2
<i>Lasius niger</i>	4	1	3			18	37	70	29		48
<i>L. alienus</i>								3	3		
<i>L. brunneus</i>									28	5	
<i>L. flavus</i>					72	3	22	15			2
<i>L. emarginatus</i>	13					12		4			
<i>L. fuliginosus</i>									26	1	1
<i>L. spathepus</i>				3				3	7		
<i>L. umbratus</i>				1				3	3		
<i>Camp. obscripes</i>				6				2	26		2
<i>C. herculeanus japonicus</i>	10	10	7			8		15	3		
<i>C. yessensis</i>											1
<i>C. caryæ quadrinotatus</i>										8	2
<i>F. fusca japonica</i>	27	47	58	4		33	3	52	8		1
<i>F. sanguinea</i> var. <i>fusciceps</i>	2	4	20			1		4			
<i>F. truncorum yessensis</i>		8				4	6	31	1		
<i>c</i>	71	110	165	36	81	186	205	350	172	17	81
<i>s</i>	9	11	11	8	2	16	13	18	16	4	15
Ratio <i>c/s</i> in each type	382/18				472/16			522/21		98/15	

showing a distinct preference are *D. quadripunctatus sibiricus* and *Camp. caryæ quadrinotatus* (w or d alone), *L. fuliginosus*, *L. spathepus*, *L. brunneus* and *Camp. obscripes* (mostly n), *M. lobicornis* var. *jessensis* and *F. sanguinea* var. *fusciceps* (mostly l). Especially, nest site r lodges such dwellers as *L. niger*, *M. ruginodis* and *F. truncorum yessensis*, when they are predominant. Also, many species tend to prefer u, n, especially m, suggesting the favorable nature of these shady and moist sites. Moreover, the preference of r and m by many species is significant even in the unsuitable habitats, as far as these sites exist in them (for instance, 5 colonies of *M. ruginodis* in BS and 12 colonies in BA). Contrary to these supposedly optimum sites, w seems to be an unsuitable site judging from its scarce utilization as seen in the table. The habitat PT, being highly damp and waste, is desperate in regard to the nesting conditions, which fact is substantiated by the occurrence of only two species in that relatively available situation.

From the nest site preference of 23, relatively frequent species summarized in Table VI, various nest sites are classified into four major categories: Type ls including s, \bar{s} , l and \bar{l} : characterized by excessive light intensity, low moisture relatively less food sources nearby.

Type mu including p, u, and m: characterized by remarkably weak light intensity, rather high moisture and probably adequate food sources nearby.

Type nr including n and r: characterized by weak light intensity, moderate moisture and sufficient food sources nearby.

Type dw including d and w: characterized by moderate or weak light intensity, moderate moisture and relatively much food in w but indistinct in d.

The relative preference of these types by various species is shown in Fig. 8, from which nine subtypes of nest site preference are obtained.

Finally, a few words will be offered with respect to the relationship between habitat preference and nest site preference. As seen in Table VII, the relative preference of nest sites in each habitat type is characteristic due to the differences of habitat nature and the presence of nest sites. Especially, this characteristic tendency is clearly shown in habitat types

Lasius emarginatus.

M. lobicornis var. *jessensis.*

Tetramorium cæspitum.

Camp. herculeanus japonicus.

F. fusca japonica.

F. sanguinea var. *fusciceps.*

L. flavus.

Ponera scabra.

Aphænogaster famelica.

Pheidole ferrida.

Para. flavipes.

Leptothorax spinosior.

Lasius alienus.

L. umbratus.

L. fuliginosus.

L. brunneus.

L. spathepus.

Camp. obscripes.

F. truncorum yessensis.

M. ruginodis.

L. niger.

D. quadripunctatus sibiricus.

Camp. caryæ quadrinotatus.

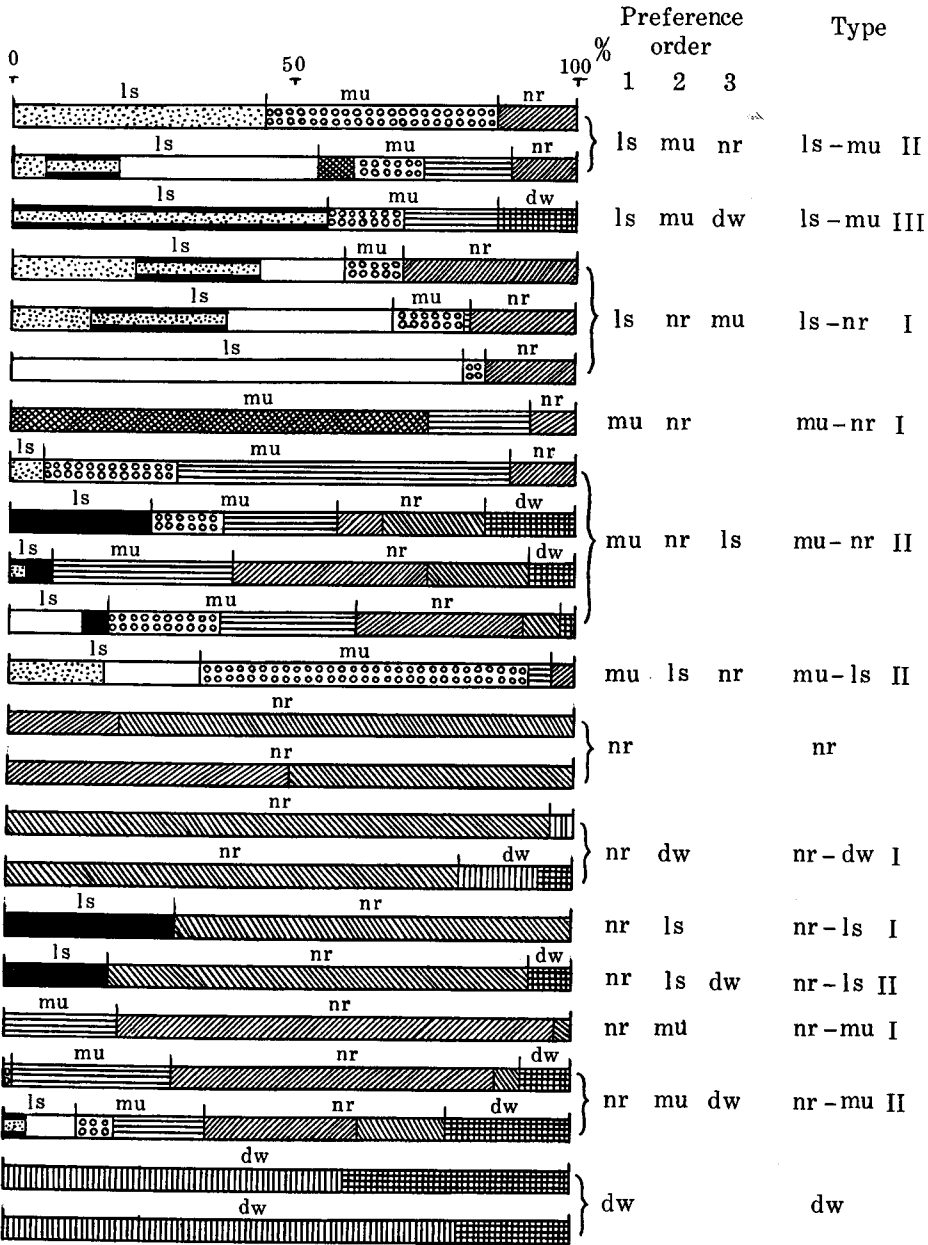


FIG. 8. — The relative occupation of preferred nest site in relatively abundant species and nine types of relative preference distinguished from the order of nest site preference.

B and P, and the correlation to habitat preference is in agreement with nest site preference. For instance, the species belonging to types ls-nr and ls-mu are characteristic of the habitat type B, except *Tetramorium*

TABLE VII. — RELATIVE PREFERENCE OF NEST SITE SHOWN BY A RATIO c/s , WHERE c AND s ARE THE NUMBER OF COLONIES AND SPECIES RESPECTIVELY IN EACH HABITAT TYPE.

HABITAT TYPE.	TYPE OF NEST SITE PREFERENCE.				RELATIVE PREFERENCE.
	ls	mu	nr	dw	
B (BS, BA)	236/13	177/15	147/15	5/1	ls — mu — nr — dw
H (SH, HG)	110/10	99/14	197/14	19/6	nr — ls — mu — dw
P (PT)	—	97/2	5/2	—	mu — nr
W (WM, WL)	36/7	99/11	197/14	84/11	nr — mu — dw — ls

caspitum which belongs to the latter type, while type mu-nr of *Lasius flavus*, the dominant species of habitat PT, offers the conditions similar to those of habitat type P. The species belonging to type dw, *Dolichoderus quadripunctatus sibiricus* and *Camp. caryæ quadrinotatus* are clearly those characteristically found in habitat type W. Although the relative preference in habitat types H and W is respectively characteristic in each feature, various other nest sites exist and the species belonging to these types nr and dw are found in both H and W. On the other hand, the lack of correlation between habitat and nest site preference was recognized in several species such as *Ponera scabra*, *Pheidole fervida*, *Aphæno-gaster famelica* and *Paratrechina flavipes*.

VI. — DEGREE OF CO-EXISTENCE AMONG SPECIES

Up to present, the relationship between the distribution of ants and the influence of various inorganic factors have been repeatedly discussed. But the distribution can also be considered from another aspect, viz., the interspecific relationship in a given environment. Although this approach was made by BRIAN (1952, 1955), TSUNEKI and ADACHI (1954), MORISITA (1939 *a, b*), etc., as a study of *inter-relation per se*, there is no comprehensive work in which the relation was studied from the standpoint of faunal make-up. The matter interspecific relations is, however, a very complicated problem, offering a dangerous pitfalls of false interpretations even to the experienced investigators. In the present paper, the problem was treated, as a preliminary approach, from a purely phenomenal standpoint by calculating the degree of co-existence in the whole area studied as in each habitat. There are numerous gradations in the degree of co-existence, from a distinctly positive relation to a diametrically opposite one. In certain cases, the causes evoking such diverse relations can be assumed as either differences in habitat preference or interference between

	F	L	MI	Pa	Lf	M	Ph	A	Cj	Fy	C	Lb	T	Fs	Lt	Lg	Le	P	Ls	Cc	La	Lu	V	D	Cr	Cy
<i>Formica fusca japonica.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Lasius niger.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Myrmica lobicornis</i> var. <i>jessensis</i> , MI	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Paratrechina flavipes.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Lasius flavus.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Myrmica ruginodis</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Pheidole levivida.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Aphaenogaster famelica.</i>	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Camponotus herculeanus japonicus.</i> Cj	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Formica truncorum yessensis.</i> Fy	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Camponotus obscripes.</i> C	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Lasius brunneus.</i> Lb	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Tetramorium caespitum.</i> T	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Formica sanguinea</i> var. <i>fusciiceps</i> . Fs	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Leptothorax spinosior.</i> Lt	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○
<i>Lasius fuliginosus.</i> Lg	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○	○

○ 1-19 % ⊕ 20-39 % ⊕ 40-59 % ⊕ 60-79 % ● 80 % more

FIG. 9. — The degree of co-existence of relatively frequent 16 species (vertically arranged) over the whole area to all species discovered.

species. Some of them are briefly touched upon in the subsequent sections, but thorough clarification of the causal relations must be solved by further analyses.

6.1 Co-existence over the whole area.—The degree of co-existence of one species (A) to another (B) in the whole area is simply calculated by the formula,

$$\text{Co-existence index } Ed = 100 \cdot h/a,$$

where h and a are respectively the number of samples in which both A and B or A was discovered. The degree of co-existence of relatively abundant 16 species in proportion to all species is illustrated in Fig. 9. The highest degree of co-existence of *L. niger* with the other 15 species agrees to the wide tolerance range of habitat preference and the large number of colonies of this species. The same tendency is, though less remarkable, seen also in *Para. flavipes*. On the other hand, the degree of co-existence of the most abundant species, *F. fusca japonica* varies from case to case, apparently due to the relatively limited range of habitat preference. The higher value of Ed in the other abundant species such as *M. ruginodis*, *M. lobicornis* var. *jessensis*, *A. famelica* and *Pheidole fervida* accords to the expectation from the larger chance to co-exist with others. The interesting cases are represented by *L. flavus*, *L. brunneus*, *L. fuliginosus*, *Camp. obsripes*, *C. herculeanus japonicus*, *F. sanguinea* var. *fusciceps* and *Leptothorax spinosior*, of which Ed values are generally not too high, but characterized by a considerable degree of co-existence with certain definite species. In *Tetramorium caespitum* and *F. truncorum yessensis*, the values of Ed were less than 50 % in every case, suggesting their ecological isolation.

From the above facts, it is clear that the degree of co-existence is not always high even between dominant species in the area studied, apparently because of the differences of adaptability to various environments. Consequently, further analysis of the problem must be separately undertaken for each habitat. The following list is tentative to further causal analyses. (Rare or cryptic species omitted from the consideration are: *Ponera scabra*, *Vollenhovia emeryi*, *Crematogaster laboriosa*, *Dolichoderus quadripunctatus sibiricus*, *Lasius emarginatus*, *L. alienus*, *L. spathepus*, *L. umbratus*, *Camp. caryæ quadrinotatus*, *C. yessensis*, *C. kiusiuensis* and *Solenopsis fugax*).

1. *Species-pairs of high Ed.* *F. fusca japonica* (F)-*L. niger* (L), *F-M. lobicornis* var. *jessensis* (Ml), L-Ml, L-Para. (Pa), L-M. *ruginodis* (M), Pa-M, Pa-A. *famelica* (A), A-Camp. *obsripes* (C), C-L. *brunneus* (Lb), C-L-*fuliginosus* (Lg), *fervida* (Ph), Ml-L. *flavus* (Lf), *C. herculeanus japonicus* (Cj)-*Leptothorax spinosior* (Lt).

2. *Species-pairs of moderate Ed.* F-Pa, F-F. *sanguinea* var. *fusciceps* (Fs), Pa-Ph, M-Ph, M-A, Ph-A, Lb-Lg.

3. *Species-pairs of low Ed.* F-Lf, F-A, F-M, F-C, F-Lb, L-Lf, Ml-Pa, Ml-M, Ml-Ph, Ml-A, Ml-C, Ml-Lb, Ml-Tetramorium (T), Ml-Fs, Ml-Lg, Pa-Lf, Lf-M, Lf-Ph, Lf-A, Lf-Lb, Lf-Lt, Lf-Lg, M-F. *truncorum yessensis*

(Fy), M-C, M-T, M-Lt, C-T, C-Lt, Lb-Lt, Fs-Lt, Lt-Lg, Ph-Fy, Ph-T, Ph-Lt, A-T, A-Fs, A-Lt, Cj-Fy, Cj-C, Cj-Lb, Cj-T, Cj-Lg, Fy-C, Fy-F, Fy-Fs, Fy-Lt, Fy-Lg.

4. *Species-pairs of generally moderate or low Ed, with partially high ones.* Pa-Cj, F-Cj, F-Fy, F-T, F-Lt, F-Lg, L-Ph, L-Cj, L-Fy, L-C, L-Lb, L-T, L-Fs, L-Lt, L-Lg, Mt-Cj, Mt-Lt, Pa-Fy, Pa-C, Pa-Lb, Pa-T, Pa-Fs, Pa-Lt, Pa-Lg, M-Cj, M-Lb, M-Fs, M-Lg, Ph-C, Ph-Lb, Ph-Fs, Ph-Lg, A-Cj, A-Fy, A-Lg, A-Lb, T-Fs, T-Lt.

6.2 Co-existence in each habitat.—With respect to the species discovered in more than 33.3 % out of 12 samples in each habitat, the degree of co-existence and coefficient of co-existence were calculated as follows (mainly after DICE, 1952): Degree of co-existence: $Ed_1 = B/A = 100 \cdot h/a$, $Ed_2 = A/B = 100 \cdot h/b$ where a , b , and h are respectively the number of samples in which either species A or B occurred, or in which both species were discovered together.

Coefficient of co-existence: $Ec = hn/ab$ where n is the total number of samples and a , b , h , are the same as above. The values of Ec larger or smaller than 1.0 indicate that the degree of co-existence positively or negatively deviates from the chance score, of which statistical significance is given by χ^2 test with YATES' correlation as follows:

	OBSERVED.	EXPECTED.
Species A alone	$a-h$	$a-ab/n$
Species B alone	$b-h$	$b-ab/n$
Neither A nor B	$n-h$	$(n-a)(n-b)/n$
Both species	h	ab/n

$\chi^2 = \sum D^2/E$ (d.f. = 1)
(D: Deviation from expectation, E: Expectation by chance)

The values of Ed and Ec are given in Table VIII, Ec of statistically significant values in fiducial limits of 5 and 1 % are shown by italics and gothic respectively. Furthermore, the degree of co-existence among various species in each habitat is illustrated in Fig. 10 by using the smaller value of either Ed_1 or Ed_2 . Based upon these results, the interspecific relation in each habitat is next briefly described.

1. *Habitat BS.*—The frequent species, *F. fusca japonica*, *Camp. herculeanus japonicus*, *L. niger* and *M. lobicornis* var. *jessensis* have distinct degrees of co-existence with each other, nevertheless some of them are not always abundantly found in many of the colonies (cf. Table I). Hence it is conceivable that the suitable places are effectively utilized as common nesting sites by these species. On the other hand, the low degree of

TABLE VIII. — THE VALUES OF *Ed* AND *Ec* AMONG VARIOUS SPECIES WHICH WERE DISCOVERED MORE THAN 33.3% OUT OF 42 SAMPLINGS IN EACH HABITAT. EACH *Ec* OF STATISTICALLY SIGNIFICANT VALUES IN FIDUCIAL LIMITS OF 5 AND 1% IS SHOWN BY ITALIC AND GOTHIC RESPECTIVELY.

(HABITAT BS.)						(HABITAT BA.)						(HABITAT WM.)												
F	L	Ml	Cj	Lt	Le	F	L	Ml	Pa	Fs	M	Ph	A	L	A	F	Ph	Lb	Lg	Pa	M	Lf	Cj	
F	91.7	75.0	66.7	41.7	33.3	F	91.7	75.0	75.0	66.7	50.0	50.0	33.3	L	66.7	66.7	58.3	58.3	41.7	33.3	33.3	33.3	33.3	
	1.92	1.75	1.66	1.42	1.33		1.92	1.75	1.67	1.67	1.50	1.50	1.33		1.67	1.67	1.58	1.58	1.42	1.33	1.33	1.33	1.33	
L	100	72.7	63.5	36.3	36.3	L	100	72.7	81.8	63.5	54.5	54.5	36.3	A	100	75.0	62.5	37.5	62.5	50.0	37.5	50.0	25.0	
	1.92	1.62	1.51	1.16	1.46		1.92	1.61	1.61	1.51	1.54	1.54	1.36		1.67	1.50	1.34	0.80	1.34	1.30	1.12	0.75	1.50	
Ml	100	88.9		44.5	33.3	Ml	100	88.9	66.7	66.7	33.3	44.5	44.5	F	100	75.0	62.5	50.0	62.5	50.0	37.5	50.0	37.5	
	1.75	1.62		1.24	1.08		1.75	1.61	1.33	1.41	0.83	1.11	1.44		1.67	1.50	1.34	1.07	1.34	1.30	1.12	0.75	1.12	
Cj	100	87.5	87.5	62.5	37.5	Pa	100	87.9	66.7	66.7	66.7	44.5	44.5	Ph	100	71.4	71.4	57.1	57.1	57.1	28.5	42.7	28.5	
	1.66	1.51	1.65	1.02	1.12		1.75	1.61	1.33	1.41	1.66	1.11	1.44		1.58	1.58	1.34	1.34	1.14	0.98	0.78	1.18	0.79	
Lt	100	80.0	80.0	100	20.0	Fs	100	87.5	75.0	75.0	62.5	37.5	25.0	Lb	100	42.7	57.1	57.1	42.7	42.7	28.5	42.7	28.5	
	1.42	1.16	1.24	1.62	0.45		1.67	1.51	1.41	1.41	1.46	0.88	0.75		1.58	0.80	1.07	1.14	0.86	1.02	0.79	0.79	1.18	
Le	100	100	75.0	75.0	25.0	M	100	100	50.0	100	83.3	50.0	33.3	Lg	100	71.4	71.4	57.1	42.7	57.1	42.7	42.7	42.7	
	1.33	1.46	1.08	1.12	0.45		1.50	1.54	0.83	1.66	1.46	0.67	0.83		1.58	1.34	1.34	1.44	0.86	1.37	1.18	1.18	1.18	
(HABITAT PT.)																								
						Ph	100	100	66.7	66.7	50.0	50.0	33.3	Pa	100	80.0	80.0	60.0	80.0	40.0	60.0	60.0	60.0	
							1.50	1.54	1.41	1.41	0.88	0.67	0.83		1.42	1.30	1.30	0.98	1.02	1.37	0.90	1.35	1.35	
Lf						A	100	100	100	100	50.0	50.0	50.0	M	100	75.0	75.0	50.0	50.0	75.0	50.0	75.0	50.0	
							1.33	1.36	1.44	1.44	0.57	0.83	0.83		1.33	1.12	1.12	0.79	0.79	1.18	1.18	1.50	1.00	
Lf						Lf	100	100	100	100	75.0	75.0	75.0	Lf	100	100	100	75.0	50.0	75.0	75.0	75.0	75.0	
							1.91								1.33	0.75	0.75	1.18	0.79	1.18	1.50	1.50	1.00	
Ml						Ml	100							Cj	100	50.0	75.0	50.0	75.0	75.0	75.0	50.0	50.0	
							1.91								1.33	1.50	1.12	0.79	1.18	1.18	1.35	1.00	1.00	

(HABITAT SH.)										(HABITAT HG.)										(HABITAT WL.)									
L	F	Ph	T	MU	M	A	M	Pa	Lf	L	MU	Ph	F	Cj	A	C	L	Lb	Pa	M	Ph	Lg	Cc						
L	91.7 1.92	58.3 1.58	50.0 1.50	50.0 1.50	33.3 1.33	33.3 1.33	M	90.0 1.90	60.0 1.45	50.0 1.33	40.0 1.06	60.0 1.60	30.0 0.90	40.0 1.40	A	90.9 1.82	90.9 1.90	81.8 1.71	81.1 1.82	54.5 1.54	36.3 1.16	36.3 1.16	27.2 1.02						
F	100 1.92	54.5 1.40	54.5 1.54	54.5 1.54	36.3 1.36	36.3 1.36	Pa	100 1.90	55.6 1.27	55.6 1.39	44.5 1.11	55.6 1.39	33.3 0.93	44.5 1.44	C	90.9 1.82	81.8 1.71	81.8 1.71	81.8 1.82	45.4 1.29	45.4 1.45	45.4 1.45	36.3 1.38						
Ph	100 1.58	85.9 1.40	14.7 0.31	42.7 0.93	28.5 0.78	42.7 1.18	Lf	85.9 1.45	71.4 1.55	28.5 1.55	71.4 1.55	71.4 1.55	28.5 0.69	0.0 0.00	L	100 1.90	90.0 1.71	80.0 1.60	80.0 1.68	50.0 1.33	50.0 1.20	30.0 1.20	30.0 1.05						
T	100 1.50	100 1.54	16.7 0.31	66.7 1.33	33.3 0.83	33.3 0.83	L	83.3 1.33	83.3 1.39	33.3 1.55	50.0 0.67	33.3 0.67	33.3 0.73	16.7 0.42	Lb	100 1.71	90.0 1.71	80.0 1.60	80.0 1.68	60.0 1.60	40.0 1.20	40.0 1.20	30.0 1.05						
MU	100 1.50	100 1.54	50.0 0.93	66.7 1.33	0.0 0.00	33.3 0.83	MU	66.7 1.06	66.7 1.11	33.3 0.62	33.3 0.67	33.3 0.67	66.7 1.46	50.0 1.25	Pa	100 1.82	100 1.82	88.9 1.68	88.9 1.68	55.6 1.39	44.5 1.24	33.3 0.93	32.2 0.72						
M	100 1.33	100 1.36	50.0 0.78	50.0 0.83	0.0 0.50	25.0 0.50	Ph	100 1.60	83.3 1.39	83.3 1.55	50.0 1.00	33.3 0.67	33.3 0.74	16.7 0.42	M	100 1.54	83.3 1.29	83.3 1.33	100 1.60	83.3 1.39	16.7 0.37	33.3 0.73	33.3 0.83						
A	100 1.33	100 1.36	75.0 1.18	50.0 0.83	50.0 0.83	25.0 0.50	F	60.0 0.90	60.0 0.93	40.0 0.69	40.0 0.73	40.0 1.46	40.0 0.90	40.0 0.90	Ph	80.0 1.16	100 1.45	80.0 1.20	80.0 1.24	20.0 0.37	60.0 1.20	40.0 1.20	40.0 0.90						
							Cj	100 1.40	100 1.44	0.0 0.00	25.0 0.42	25.0 0.42	50.0 0.90	50.0 0.90	Lg	80.0 1.16	100 1.45	80.0 1.20	80.0 0.93	40.0 0.73	60.0 0.73	40.0 1.20	40.0 0.90						
															Cc	75.0 1.02	100 1.38	75.0 1.05	50.0 0.72	50.0 0.83	50.0 0.90	50.0 0.90	50.0 0.90						

co-existence of other species, *A. famelica*, *Para. flavipes* and *L. emarginatus*, is apparently caused by the rarity of places of residence, especially *L. emarginatus* was discovered from one particular area which was almost devoid of other species.

2. *Habitat BA*.—High degree of co-existence exists among predominant species such as *F. fusca japonica*, *L. niger*, *M. lobicornis* var. *jessensis*, *Para. flavipes* and *F. sanguinea* var. *fusciceps*. *Ph. fervida* and *A. famelica* are not only less abundant but also have lower degree of co-existence with other species. This fact may indicate the absence of nest sites which are suitable to these species.

3. *Habitat SH*.—In general, the degree of co-existence is low except for two cases, namely, between *L. niger* and *F. fusca japonica*, and between *Tetramorium caespitum* and *M. lobicornis* var. *jessensis*. The former case is probably based upon their common habitat preference and the latter one on a similar preference of nest site (cf. Figs. 4 and 8).

4. *Habitat HG*.—Although the highest degree of co-existence is found only between dominant species, *M. ruginodis* and *Para. flavipes*, relatively high values are found also in the following species pairs: *M. ruginodis* and *L. flavus*, *M. ruginodis* and *Ph. fervida* and *L. niger*, *L. flavus* and *Pf. fervida* and *M. lobicornis* var. *jessensis* and *F. fusca japonica* with no clear correlation to the degree of abundance. It is natural that the species of habitat type B, *F. fusca japonica* and *Camp. herculeanus japonicus* scarcely exist in this habitat.

5. *Habitat PT*.—Caused by the unique environmental conditions, fairly high values of the *Ed* (91.7 %) and *Ec* (1.91) were obtained between two inhabitants, *L. flavus* and *M. lobicornis* var. *jessensis*.

6. *Habitat WM*.—Among dominant or abundant species, degrees of co-existence is relatively high, but the comparatively less abundant species such as *Para. flavipes* (*Pa*), *M. ruginodis* (*M*), *L. flavus* (*Lf*) and *Camp. herculeanus japonicus* (*Cj*) have lower values except in a few cases, for instance, *Pa-Lf*, *Pa-Cj* and *M-Lf*.

7. *Habitat WL*.—The degree of co-existence is characterized by remarkably high values among dominant species alone except between two comparatively less abundant species, *Ph. fervida* and *L. fuliginosus*. The degree of co-existence of less abundant species with dominant or abundant ones is fairly high (cf. Table VIII), therefore the low degree of co-existence may be related to the infrequent occurrence.

6.3 Relationship between degree of co-existence and habitat preference.—It is obvious that habitat preference markedly affects the degree of co-existence. If the degree of co-existence between two species decreases in parallel with the decrease of suitability of habitat, this may suggest that the co-existence, at least partly, is caused merely by a common tendency in the habitat preference. The opposite instances may be explained by the difference of habitat preference. The fluctuation of the values of $Ed = B/A$ when A occurred more frequently than B was exam-

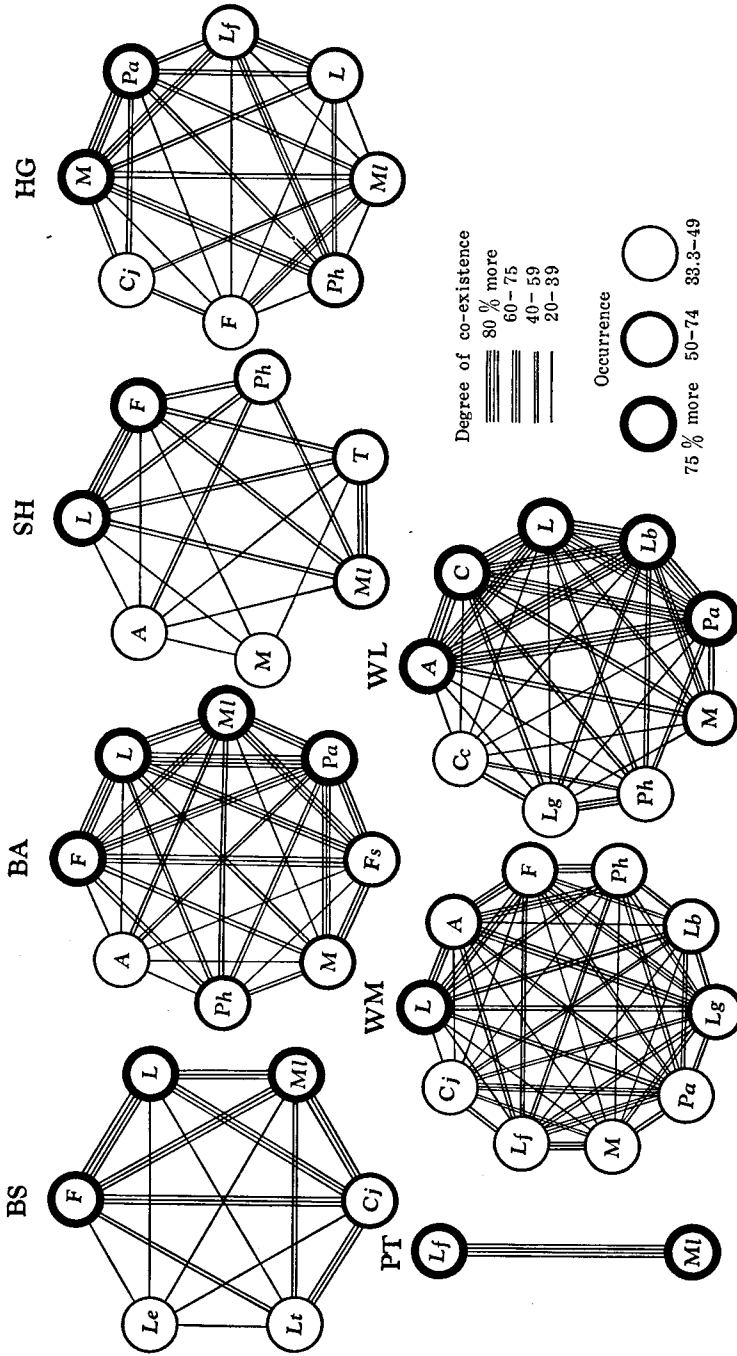


Fig. 10. — The degree of co-existence among various species occurred more than 33.3 % out of total samples in each habitat, while the descending order of occurrence of species was represented from the top, the most one, in clockwise (Abbreviations of specific name in Table 4).

ined in various habitats excluding PT (cf. Table VIII). From Tables I, VIII and Fig. 10, it is proved that the degree of co-existence with one another changes in parallel with the relative preference of habitat among three dominant species (*F. fusca japonica*, *L. niger* and *M. lobicornis* var. *jessensis*). The following species pairs may be included in this type, also: *L. niger* and *A. famelica*, *L. niger* and *M. ruginodis*, *Ph. fervida* and *M. ruginodis*, *Para. flavipes* and *A. famelica*. In this case, both species are more or less mutually tolerated in various habitats. Contrarily, a relatively low degree of co-existence is caused by the difference of habitat preference between *F. fusca japonica* and *Ph. fervida*, *F. fusca japonica* and *A. famelica*, *F. fusca japonica* and *M. ruginodis*, *M. ruginodis* and *M. lobicornis* var. *jessensis*, *A. famelica* and *M. lobicornis* var. *jessensis*, etc. Out of these two types where the relationship is relatively clear, the correspondance of abundance and co-existence is found between *L. niger* and *Para. flavipes*, *F. fusca japonica* and *Para. flavipes*, *Ph. fervida* and *A. famelica*, etc. In such instances, further analyses are required as to the difference of tolerance or preference for suitable sites between two species within one and the same habitat.

VII. — ADDITIONAL NOTES ON SOME ECOLOGICAL PROBLEMS

Besides habitat or nest site preference and interspecific co-existence described above, there are many further problems related to the ecological distribution of ants. A few of them are preliminarily discussed herewith.

7.1 Seasonal shift of outer activities.—Reflecting different sensitivities to the thermal gradient, the duration of field activities varies among species. In Fig. 11, there are presented mean climatic conditions (after 60 years of records taken at the Sapporo Meteorological Observatory) and the active period of 18 species (based upon the writer's field notes during 1956 to 1959). The species showing earliest appearance is *F. fusca japonica* of which the first record was taken on April 13, 1958, from a sunny situation in a crop field. Nextly, three species, *F. sanguinea* var. *fusciceps*, *F. truncorum yessensis* and *M. lobicornis* var. *jessensis*, appear synchronously about in late April. Activities of most other species begin in early May, leaving *M. ruginodis* which cannot be observed until middle May. *L. flavus* also begins to appear in this period. But it is difficult to determine the first appearance of this subterranean species. As to the relation to the habitat, it seems to be indicated that the appearance beings first at habitat BA, then gradually at WM, SH, BS, WL and finally HG. The species which are active up to late autumn are *F. fusca japonica*, *F. sanguinea* var. *fusciceps*, *M. lobicornis* var. *jessensis*, *L. fuliginosus* and *L. spathepus*, which can be found till early October. The last record of field activities was taken on October 27, 1959, in *F. fusca japonica* and *F. sanguinea* var. *fusciceps*, while the earliest disappearance was recognized

in the order *L. flavus*, *Leptothorax spinosior*, *Camp. caryæ quadrinotatus* and *D. quadripunctatus sibiricus*, in late September. Consequently, the gradation of disappearance in autumn corresponds conversely with that of appearance in spring.

As presented in Fig. 11, the full activities may already be observed in late May, but are never seen in early October, nevertheless, there is no marked difference of mean air temperature between the two periods. But a distinct difference between these seasons does exist in respect to the amount of solar radiation and frost falls, which may be partly responsible

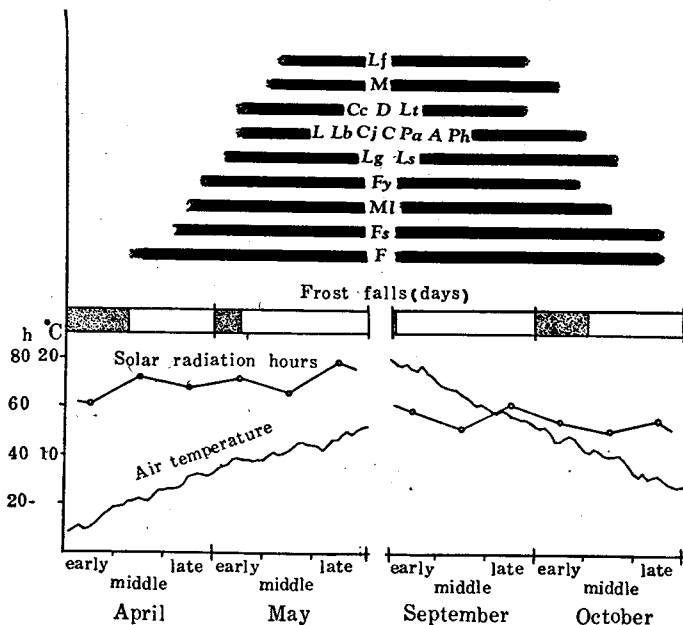


FIG. 11. — Mean climatic conditions in spring and autumn and active period of 18 species observed in Sapporo.

for the seasonal shift of ant activities. At any rate, it is obvious that the full activities of various ants are observed during middle May to late September, preceded by early May and followed by early October periods as the subactive seasons.

7.2 Relationship between distribution and habits.—The diverse habits expressed by various ant species have been one of the most attractive problems to many naturalists (WHEELER, 1910, etc.). It is clear that certain specific affect the patterns of ecological distribution through specific habitat or nest site preference. In this subsection, some miscellaneous instances of such things are briefly cited from the writer's observations.

Nest preference often correlates intimately with the feeding habits.

For instance, *L. fuliginosus* and *L. spathepus* depend mainly upon the honey dew of arboreal plant-lice. The nests of these species are characteristic to W type habitats and are always found around the roots or in the stems of living or decayed trees, from which the foraging individuals reach the plant-lice which inhabit the near-by trees. Another example of differentiated nest site preference is exhibited by *Dolichoderus quadripunctatus sibiricus*. As mentioned previously, this species together with *Camp. caryæ quadrinotatus* restricts the distribution, exclusively prefers holes or slits in standing tree, either dead or living. On a certain summer day of 1957, the writer observed a large foraging group of this species in a crop field usually not inhabited. After a little search, the nest was found in a pillaret of a shady hut standing in the field. It is doubtless that the colony was artificially brought to the new, strange habitat together with the tree containing the nest.

In some species possessing a wide tolerance range as to nest sites, there occurs occasionally an adaptive response corresponding to the nature of the nest site utilized. Below an open dry surface, *Para. flavipes* constructs a nest shaft often deeper than 20 cm, and the workers do not leave the nest during hot daytime; in the margins of woods, the colonies are discovered in such places as under stone, piled or fallen decayed matters, or rotting stumps, without deep burrowing.

Finally, the probable geographical variation of nest site preference may be treated concerning two widely distributed species. In Sapporo and its vicinity, *Lasius umbratus* never exists in open areas and the nests are always found around the roots of trees or herbs but never under stones, in the semi-humid zone of wood margins or grassy areas where the inhabitants may depend upon available plant-lice. However, in Europe, this species prefers rather dry areas avoiding humid conditions, and the nests are found in diverse sites: under stones, at roots of trees, in open surface, or in rotting wood (GÖSSWALD, 1932; ZIMMERMANN, 1934). In North America, the species is found in moist areas, but the nest sites are diversely preferred as in Europe (WILSON, 1955). A similar variability is seen in *Lasius flavus*. In Sapporo and its vicinity, this one of the typical subterranean species, prefers the roots of plants, underside of stones, or piled decaying matters as the nest sites. Similar preference was reported in North America. On the other hand, in Germany, the species is one of the very adaptable ones and prefers diverse sites such as hedgerows, grassy paths, wasteland with sparse vegetation, wood margin and forest floor (GÖSSWALD, 1932). In England, this species is fond of marshy ground, under stones, often raises the earth mounds in meadows (DONISTHORPE, 1927). Contrarily to the observations in Germany, in Ireland (O'ROURKE, 1934), it is found mostly in dry sunny localities with fine soil, never in marshes or rotting wood in the forest. There is no record of the flourishing of this species in the peat bog as previously mentioned by the present.

DISCUSSION

As mentioned in the introduction, the distribution of ants in a given area is studied from the standpoint either of regional or of ecological biogeography. There is no sharp boundary between these two approaches. The distinction is rather made by the inevitable difference of approach itself, while the healthy advancement of one approach depends upon the progress of the other. If regional studies were done without paying attention to the ecological characteristics of habitats and their inhabitants, they might not proceed beyond a mere catalogue-making. Conversely, the ecological approach may lead to false interpretation if it is advanced independently of regional observations, because the faunal make-up of a given area is adequately explained by the sum total of the previous history of habitats and their inhabitants, never by its contemporary ecological structure alone.

The regional studies were usually undertaken on areas of a relatively large extent in contrast to the ecological studies. But, theoretically, there is no reason to distinguish the two approaches according to the size of the area studied, at least so far as an area as large as Hokkaido is concerned. The writer's serial work on the distribution of ants in Hokkaido deals mainly with the ecological aspect, but the relationships between the two approaches will be considered in a future paper.

The ecological approach itself can also be made from various aspects, for example, causal analyses of limiting factors, comparative studies among diverse areas or habitats, case studies of representative species, inter- or intraspecific relation within the social organization, etc. As comparative considerations can be legitimately made only after the accumulation of further data as to other areas, here are offered only a few general remarks based upon the present study.

The distribution of any species is surely an outcome of the complicated interactions of diverse factors both external and internal, past and present, while it may also be explained in part by the interspecies adaptative differences such as different skills and methods for nesting and a dominance hierarchy has resulted from competition (BRIAN, 1958). The manifold influences of external factors are internally reflected by the preferences or avoidances characteristic to any species. Moreover, the mode of reproduction and colony foundation participate in the realization of various specific distribution patterns. The peculiarity of ant distribution in comparison with that of other animals lies in the creature's characteristic habit to form a more or less sedentary colony consisting of a considerable number of individuals even in such a species as *Ponera scabra*, of which the colonies are relatively less populous. As the biological unit of ants is the colony, instead of the individual, the mere counting of numbers of individuals within a unit area or interval is of little value. The population must be estimated upon the basis of the number of colonies.

Certain quantifications employed in the present paper are still insufficient, so that further improvement may be necessary. Perhaps, some procedures used in phytosociology may suggest procedures for future studies. In such instance, it must be remembered that any new technique should be so devised that the results obtained by earlier less accurate methods and those by improved ones can be objectively compared with each other to a certain extent. Further, it needs to be clarified whether or not the valid relative dominance can be obtained from a mere comparison of number of colonies. As an extreme instance, it may be ridiculous to compare the relative dominance of elephants and grasshoppers within the same area by the number of individuals alone. It may be necessary in the future to devise some *biological* measurements for comparison among diverse ant species.

Another difficulty exists in the specific difference of the chance by which colonies are discovered. The chance of discovery is always greater in the species possessing the characters described by the first items of the following pairs than in those possessing the alternative characters: active - sluggish, diurnal - nocturnal, colony populous - small, nest entrance exposed - concealed, and, epigaeic - subterranean. Furthermore, the counting of the number of colonies often becomes difficult in the species forming associated nests as in *Formica rufa* group, represented by *F. truncorum* and *F. truncorum jessensis* in Hokkaido. Although the number of colonies of the latter species in the present study was estimated from the observations of inter-colonial hostility, it was frequently not easy to obtain a real measure of the number of colonies.

After the ecological distribution of various species in diverse habitats had been surveyed by certain quantitative procedure, the results were analysed mainly from two aspects, habitat and species. As described above, certain habitats such as BA and WM are rich both in species and in number of colonies, while the opposite case is represented by PT. Between these extremes, there are numerous modes and degree of utilization by various species. Similarly, the habitat preference is fairly variable from species to species. For instance, such species as *L. niger*, *M. lobicornis* var. *jessensis*, *Para. flavides* exhibit a wide tolerance, while *L. emarginatus*, *Tetramorium caespitum*, *D. quadripunctatus sibiricus*, *L. brunneus*, *Camp. caryæ quadrinotatus* prefer certain definite habitats. The comparison of mode and degree of utilization of similar habitats in different areas is one of the most interesting problems forming a boundary field between regional and ecological approaches. The difference of habitat preference is probably an outcome of the species adaptability to diverse ecological factors. The preference by foundress queens obviously plays an essential role, but that by workers is not always less important, because the further exploration of foraging area must be developed by the latter within the available range. Moreover, there is often a migration of the whole colony initiated by workers. One example described by the writer in the preliminary report. Interesting cases are offered by *Lasius fuligi-*

nosus and *Formica truncorum yessensis*. The former species stands a colony dependently utilizing *Lasius umbratus* or *L. mixtus* as the host species; the same can be assumed as to the latter species, because its European relation, *Formica truncicola*, is parasitic on *F. fusca* groups (DONISTHORPE, 1927; GÖSSWALD, 1932, etc.). Nevertheless, the habitat and nest site preference between host and parasite species is the area studied differs distinctly in both instances, suggesting occurrence of migration in the course of nest replacement by parasites.

As to the external factors important to the distribution of ants, GÖSSWALD (1932) mentioned the following eight items: light, temperature, humidity, wind, substratum, vegetation, animal and human beings. Some important ones of them, notably, light, temperature, humidity and substratum, were unanimously accepted by many writers and discussed at length (GÖSSWALD, 1932; TALBOT, 1934; GÖETSCH, 1937; DENNIS, 1938, etc.), while others have been studied less extensively. The influence of wind seems to be considerable in the areas of sparse vegetation, mainly along the seashore and on the tops and slopes of mountains (GÖETSCH, 1937). The relationship between ant fauna and plant communities was analysed by TALBOT (1934) and GREGG (1944). GÖSSWALD concluded that the influence of various animal co-habitants is less than that of human beings. This opinion seems to the writer also to be valid, although no objective determination was carried out. The influence of human activities may be profound, rapid, and usually catastrophic to most species in comparison to the influence of other animals. This is clarified by the remarkably poor ant fauna of well cultivated crop fields; for example, in Sapporo and its vicinity, only two species, *Formica fusca japonica* and *Myrmica lobicornis* var. *yessensis*, were commonly found, usually as remnants. The role of other animals seems to be far less conspicuous than that of physical factors except for those, such as plant-lice, connected by an intimate bioeconomic relation. The rich ant fauna in the habitat WM may depend upon the constancy of external factors, diversity and abundance of both food ant nest sites, even though affected by human influences. The other ant species as co-habitants are of special interest from the standpoints of interspecific tolerance and isolation. It seems dangerous to magnify the importance of this relation over that of the physical factors. But to a relatively small extent, if the colony density is high enough to evoke diverse interference, the interspecific relationship perhaps regulates the distribution of colonies (BRIAN, 1952, 1955; TSUNEKI and ADACHI, 1954; HAYASHIDA, 1957). For the analysis of this problem, the degree of co-existence among various species in a given habitat must be accurately determined. In the present paper, some quantifications were undertaken for this purpose, leaving the causal analysis of the distribution patterns for future studies.

Finally it must be mentioned that the relative importance of various limiting factors is difficult of accurate determination, in respect to the

devising of some objective procedures to compare their influence acting in different modes.

Summary.

1. The ecological distribution of ants was studied in Sapporo and its vicinity.

2. From both quantitative and qualitative samplings, 28 forms belonging to 4 subfamilies and 14 genera were confirmed from the area studied.

3. Seven habitats were distinguished based upon diverse characters. The order of relative abundance of both numbers of colony and of species in these habitats was graded as follows: BA, WL, WM, SH, HG and PT (*cf.* Table I and in text). From the correlation index between species and habitat, the specific habitat preference was classified into three major categories, while the specific distribution pattern was characterized from both indices of colony ratio and of colony distribution into three main types: patched, sparse and uniform distribution pattern (*cf.* p. 136 in text). Concerning the relative abundance of both colonies and species, the dominant species and the population density were also recorded for each habitat.

4. The preference of nest sites by various species was similarly analysed from the frequency of occurrence of each species in 11 typical nest sites (*cf.* p. 140 in text). The preference was classified into four major categories: ls, mu, nr and dw (*cf.* p. 144 in text). Furthermore, the relationship between habitat and nest site preference was briefly discussed.

5. The co-existence among various species was analysed as to both the whole area and each particular habitat within it. The degree of co-existence seems to correspond, in the whole area throughout, to the tolerance range of habitat preference, while within each habitat, to the degree of habitat preference itself.

6. In connection with the results obtained, some general remarks on the ecological distribution of ants were presented. The duration of outer activity varied according to habitats, longest in those of BA, while shortest in HG. In comparison with the records in Europe and North America, the regional difference of nest site preference was pointed out in some pan-holarctic species.

Zusammenfassung.

1. Die ökologische Verbreitung der Ameisen wurde in Sapporo und Umgebung untersucht.

2. Durch sowohl quantitative als auch qualitative Sammlungen wurden 28, zu 4 Unterfamilien und 14 Gattungen gehörigen Formen aus dem untersuchten Gebiet bestätigt.

3. Begründet auf verschiedenen Eigenschaften wurden 7 Biotopen~~x~~ unterschieden. Die relative Abundanz wurde in den beiden Kolonien und Artenzahlen eingeordnet wie folgt: BA, WL, WM, SH, HG, BS und PT (siehe im Text und in Tabelle 1). Die eigenartige Biotopwahl wurde aus den Korrelationsindizes zwischen Art und Biotop in drei Hauptklassen, während die eigenartige Verbreitungstyp aus den beiden Indizes von Volksverhältnis und -verbreitung in drei Haupttypen, gefleckten, spärlichen und uniformen, eingeteilt. In Bezug auf die relative Häufigkeit der beiden Völken und Arten, wurden auch die übergelegten Arten und Bevölkerungsdichte in jedem Biotop hinzugefügt.

4. Aehnlichenweise wurde die Nistplatzwahl verschiedenen Arten durch die Häufigkeit des Vorhandenseins jeder Art in 11 typischen Nistplätzen analysiert (siehe im Text 140). Die Nistplatzwahl wurde in vier Hauptklassen ls, mu, nr und dw (siehe im Text 144) eingeteilt. Ueberdies, wurde die Beziehung zwischen Biotop- und Nistplatzwahl kurz erörtert.

5. Das Mitsein unter verschiedenen Arten wurde bezüglich des ganzen untersuchten Gebietes sowie als jedes besonderen Biotops analysiert. Es scheint, dass der Mitseinsgrad im ganzen Gebiete hindurch dem Toleranzbereiche der Biotopwahl, während innerhalb jedes Biotops dem Grad der biotopspezifischen Wahltenz entspricht.

6. Im Zusammenhang mit den gewonnenen Ergebnissen, wurden gewisse allgemeine Anmerkungen über die ökologische Verbreitung der Ameisen hinzugefügt. Die äussere Aktivitätsdauer wich dem Biotop entsprechend ab, am längsten in den Arten von Biotop BA, während am kürzesten in HG. Im Vergleich zu den Befunden in Europa und Nordamerika wurde die regionale Differenz der Nistplatzwahl in gewissen pan-holarktischen Arten hingewiesen.

LITERATURE CITED

1952. BRIAN (M. V.). — The structure of a dense ant population [*Jour. Anim. Ecol.*, **21** (1), 12-24]. — 1955. Food collection by a Scottish ant community [*Ibid.*, **24** (2), 336-351]. — 1956 (1958). Interaction between ant populations (*Proc. 10th Internat. Congr. Entom.*, **2**, 781-784).
1938. DENNIS (C. A.). — The distribution of ant species in Tennessee with reference to ecological factors [*Ann. Ent. Soc. Amer.*, **31** (2), 267-308].
1952. DICE (L. R.). — *Natural communities*, Univ. Michigan Press, Ann Arbor, 547 pages.
1927. DONISTHORPE (H.). — *British ants, their life-history and classification* (2nd edition, Routledge and Sons, London, 436 pages).
1937. GOETSCH (W.). — Formicidae Mediterraneae. Beiträge zur Kenntnis der Ameisen am Golfe von Neapel. II. Teil. Formicinen der Insel Capri und Ischia [*Pubb. Staz. Zool. Napoli*, **16** (2), 273-315].
1932. GÖSSWALD (K.). — Oekologische Studien über die Ameisenfauna des mittleren, Maingebietes [*Zeitsch. wiss. Zool.*, **142** (1), 1-156].
1944. GREGG (R. E.). — The ants of the Chicago region (*Ann. Ent. Soc. Amer.*, **37**, 447-480).
1957. HAYASHIDA (K.). — Ecological distribution of ants in Sapporo and vicinity (Preliminary report) [*Jour. Fac. Sci. Hokkaido Univ.*, ser. VI, **13** (1-4), 173-177].

1953. KOGURE (T.). — Ants of central Hokkaido [*Saishū to Shiiku*, **15** (9), 203-206 (in Japanese)]. — 1955. Additional notes on ants of central Hokkaido [*Ibid.*, **17** (3), 93 (in Japanese)].
1950. KATŌ (M.) and TORIUMI (M.). — Studies on the associative ecology of insects, II. Synecological investigation of the larval habitats of mosquitoes (*Sci. Rep. Tōhoku Univ.*, **18**, 473-476).
1952. KATŌ (M.), MATSUDA (T.) and YAMASITA (Z.). — Associative ecology of insects found in the paddy field cultivated by various planting forms (*Sci. Rep. Tōhoku Univ.*, **19**, 291-301).
1939. KŌNO (H.), SUGIHARA (Y.). — Die Formiciden im Tannen- und Fichtenwald in Japan [*Trans. Kansai Ent. Soc.*, **8**, 8-14 (in Japanese)].
- 1939 a. MORISITA (M.). — On the battles between *Tetramorium cæspitum jacoti* Wheeler and other species of ants [*Trans. Kansai Ent. Soc.*, **8**, 127-138 (in Japanese)]. — 1939 b. The interrelations of several species of ants on a tree [*Ibid.*, **9** (2), 22-42 (in Japanese)]. — 1945 a. Natural history of Japan. 5. Insects. II. Formicidæ [*Kenkyu Sha, Tokyo*, 1-56 (in Japanese)]. — 1945 b. Ants on the Southernmost of Hokkaido [*Mushi*, **16** (6), 21-28 (in Japanese)].
1955. MORLEY (D. W.). — *The ant world*, Penguin Books, London, 191 pages.
1935. MOTOMURA (I.). — A statistical method in animal Synecology [*Zool. Mag., Tokyo*, **44**, 379-398 (in Japanese)].
1950. O'ROURKE (F. J.). — The distribution and general ecology of the Irish Formicidæ (*Proc. Roy. Irish Acad.*, **52 B**, 383-410).
1952. *Sapporo Region Meteorological Observatory. Climate of Hokkaido* [Sapporo, 419 pages (in Japanese)].
1934. TALBOT (M.). — Distribution of ants in the Chicago region with reference to ecological factors and physiological toleration [*Ecol.*, **35** (4), 416-439].
1958. TATEWAKI (M.). — Forest ecology of the islands of the North Pacific Ocean [*Jour. Fac. Agr. Hokkaido Univ.*, **50** (4), 371-486].
- 1929 a. TERANISHI (C.). — Japanese ants, their behavior and distribution I [*Zool. Mag., Tokyo*, **41** (488), 239-251 (in Japanese)]. — 1929 b. Japanese ants, their behavior and distribution II [*Ibid.*, **41** (489), 312-332 (in Japanese)]. — 1932. A list of the ants of Sakhalin [*Trans. Kansai Ent. Soc.*, **3**, 39-54 (in Japanese)]. — 1933. A list of ants found at the sand dune of Tottori [*Ibid.*, **4**, 84-85 (in Japanese)].
1954. TSUNEKI (K.) and ADACHI (Y.). — The intra- and interspecific influence relations among nest populations of four species of ants [*Jap. Jour. Ecol.*, **7** (4), 166-171 (in Japanese with English summary)].
1910. WHEELER (W. M.). — *Ants, their structure, development and behavior*, Columbia Univ. Press, 663 pages.
1948. YASUMATSU (K.). — The distribution of ants [*Scientific Study in Native Country I*, Tokyo, 185-213 (in Japanese)].
1955. WILSON (E. O.). — A monographic revision of the ants genus *Lasius* [*Bull. Mus. Comp. Zool.*, **113** (1), 3-199].
1934. ZIMMERMANN (S.). — Beitrag zur Kenntnis der Ameisenfauna Süddalmatiens (*Verh. Zool.-bot. Ges. Wien*, **84**, 5-65).