Studies on the Ecological Distribution of Ants in Kutchan and its Adjacent Area¹⁾²⁾

By Kazuo Hayashida

(Biological Laboratory, Sapporo Otani Junior College and Zoological Institute, Faculty of Science, Hokkaido University)

In previous works (Hayashida 1960, Hayashida and Maeda 1960), the ecological distribution of ants in two districts, Sapporo and Akkeshi was reported. As the third report on the ecological distribution of ants in Hokkaido, the present paper deals with the results of survey made in the northern part of Southwestern Hokkaido, where the Oshima peninsula joins to the mainland. Hitherto there has been given no record on the myrmecofauna of this district. The results given in the present poper are mainly outcome of quantitative analyses of ant distribution, made in Kutchan, Kozawa, Iwanai and Mt. Yôtei in 1958 and 1959.

Before going further the writer wishes to express his cordial thanks to Prof. Tohru Uchida and Dr. Shôichi F. Sakagami, under whose guidance the present study was carried out.

The district studied and method employed

As shown in Fig. 1 (A), the district is located in the northern part of Southwestern Hokkaido, forming the Shiribeshi Mountainous Area belonging to the Nasu Volcanic Zone. The district is situated between two important demarcation lines emphasized by Tatewaki (1958): Kuromatsunai- and Ishikari-Depressions (cf. Fig. 1, B). According to his monograph of Forest Ecology of Hokkaido, the phytogeographical characteristics of these depressions are summarized as follows: Kuromatsunai Depression forms the northern limit of many important Japanese or Japanese-Chinese elements of the typical temperate zone. The representaive forests of temperate Japan are restricted to the parts southward of this depression, for instance, those of Fagus crenata, Thulopsis dolabrate var. Hondai. Pinus pariflora var. pentaphylla, Pterocarya rhoifolia, Aesculus turbinata etc. Picea jezoensis as the important element of coniferous forest in Hokkaido and Sakhalin, does not go southward beyond the

¹⁾ Contribution No. 661 from Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

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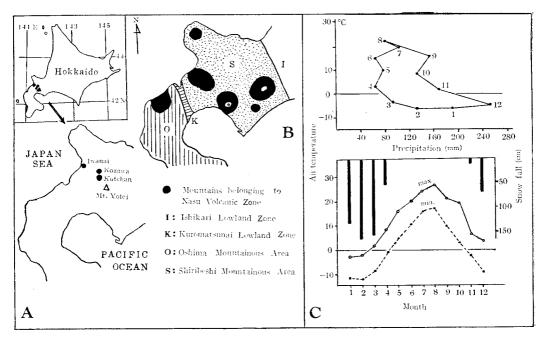


Fig. 1. Maps and climatic conditions of the district studied. A: Location of the district witgin Hokkaido, B: Topography of the Southwestern Hokkaido, C: Annual changes of moutbly air temperature, snow-fall and clmograph of Lutchan (From "Climate of Hokkaido" published by Sapporo Region al Meterological Observatory, 1952).

depression, *Picea Glehni* behaves also more or less in a similar way. Ishikari Depression is known as the line dividing Hokkaido into two distinct parts, Southwestern- and Eastern Hokkaido. The former is phytogeographically only an extension of Northern Honshu, the main island of Japan, while in the latter, occupying the main part of Hokkaido, occur some Japanese derivatives belonging to the circumpolar elements as alpine plants, the Eurasian and the Northern Pacific elements in the most of middle part, and some relics of the Eastern Asian elements as well as developed oak and birch forests in the eastern district affected by the volcanic activity of the Mashû group.

Therefore, geobotanical features of the district studied indicate that it represents the northern limit of cold temperate zone in Japan. For instance, the Japanese-beach (Fagus crenata) forms as association with Sasa, but the birches (Betula) and oaks (Quercus), well developed in Eastern Hokkaido, do not occur here except in high mountains.

Concerning to climatic features, the district is characterized by relatively low temperature and high winter precipitation caused by the heavy snow-fall, being one of the areas in Japan famous by the deep snow cover. For instance, the precipitation in February exceeds in Kutchan 150 cm (mean depth: 166.6; maximum depth: 188.7 cm during seven years from 1944 to 1950) (cf. Fig. 1, C). The local air mass and various topographical conditions including the occurrence of high mountains such as Mt. Yôtei and Mts. Nisekos with more than 1,000 m high above sea level, may be responsible to such snowy winter.

In this study, quantitative sampling was undertaken, that is, the number of colonies

discovered within 0.5 hour was counted in each habitat (cf. Hayashida 1960). Such unit-interval sampling was repeated five times, consisting half number of quantitative sampling formerly employed by the writer, for each habitat type shown in the next section. Occasionally, qulitative sampling was also made in order to obtain a perspective of faunal make-up, especially, in the survey of the vertical distribution in Mt. Yôtei.

Distribution in various habitats

As in previous papers (Hayashida 1960, Hayashida and Maeda 1960), habitats were distinguished into five types in the district studied, namely, BA (bare or sparsely vegetated place such as cropfield, road side etc.), HG (grassy or herby land on soil ground as meadow and pasture-like areas). SH (grassy or herby land on mainly sand dune near the sea-shore), WM (wood margins scrub) and WL (woods). The characters of each habitat were given in a previous paper (Hayashida 1960, p. 129). Although the relative extent of each habitat could not be measured, habitats WM and HG are more extensive, WL and BA moderately extensive, while SH is confined to the seashore in Iwanai as far as the localities studied are concerned. The quantitative sampling was carried out in each locality as follows:

T 11.	Number of sampling in various habitats								
Locality	BA	SH	HG	WM	WL				
Kutchan	2	0	2	2	2				
Kozawa	2	0	2	2	2				
Iwanai	1	5	1	1	1				

There was no remarkable difference among these localities not only in general distribution, but also in habitat and nest site preference etc. Therefore, the results from these localities will subsequently be treated as a whole without in separation.

In these habitats and Mt. Yôtei, as listed in Table 1, 24 forms of ants, including subspecies and varieties, were collected, being about a half of ant species so far recorded from Hokkaido. Most of these 24 forms belong to the Subfamily *Formicinae*, mainly to the genera *Paratrechina*, *Lasius*, *Camponotus* and *Formica*.

Three species, Myrmica kurokii, Formica fusca and Leptothorax acervorum, were never discovered in the areas below 500 m above the sea level, apparently because they were typical alpine or subalpine species in Hokkaido. Except these forms, there is no particular aspect to be mentioned concerning the faunal make-up, being more or less common to that in two districts studied in the previous works. But the number of forms seems to be scarce when compared with 28 forms in Sapporo, probably depending on the limited number of samplings.

Judging from relative abundance, Formica fusca japonica, Lasius niger and Myrmica ruginodis, all being the commonest ants in Hokkaido, are obviously the most dominant species in the district studied, too, occupying, when combined, 59, of the total number of colonies discovered by quantitative sampling. Abundance of the number of species and as

Table 1. Species collected in Kutchan, Kozawa, Iwanai and Mt. Yôtei, together with their relative abundance in various habitats. Relative abundance indicates the number of colonies discovered by the unit-interval sampling, while species collected by qualitative sampling also are shown with cross.

Order of abundance	Specific name (Abbrev.)			n var	ious	undan habita WM	ıts	Total (Ratio,%)	In Mt. Yôtei
3	Myrmica ruginodis Nylander	(M)			21	17	30	68 (19.0)	+
4	M. lobicornis var. jessensis Forel	(Ml)	7	17	2			26 (7.2)	
	M. kurokii Forel	(Mk)							+
6	Aphaenogaster famerica Smith	(A)				16	3	19 (5.3)	+
7	Leptothorax spinosior Forel	(Lt)	9	4	3			16 (4.4)	
16	Lept. congruus F. Smith	(Lc)		1				1 (0.3)	
	Lept, acervorum Fabricius	(Lr)							+
14	Pheidole fervida (F. Smith)	(Ph)				2	1	3 (0.9)	
5	Tetramorium caespitum Wheeler	(T)	7	8	5			20 (5.5)	
16	Dolichoderus sibiricus Emery	(D)				1		1 (0.3)	
8	Paratrechina flavipes (F. Smith)	(Pa)	3		4	3	2	12 (3.3)	
2	Lasius niger Linné	(L)	2	1	13	45	12	73 (20.3)	+
13	L. alienus (Foerster)	(La)			3	1	1	5 (1.5)	
12	L. flavus (Fabricius)	(Lf)				1	5	6 (1.8)	
10	L. fuliginosus (Latreille)	(Lg)			1	7	2	10 (2.7)	
	L. spathepus Wheeler	(Ls)			+		+		
15	Camponotus obscripes Mayr	(<i>C</i>)				1	1	2 (0.6)	+
8	Camp. herculeanus japonicus Mayr	(Cj)	6		5	1		12 (3.3)	
16	Camp. caryae var. nawaii Ito	(Cn)				1		1 (0.3)	
	Farmica fusca Linné	(Ff)							+
1	F. fusca japonica Motschulsky	(F)	44	8	21	1		74 (20.6)	+
11	F. exsecta fukaii Wheeler	(Fe)	3		5	1		9 (2.5)	+
16	F. sanguinea fusciceps Emery	(Fs)	1					1 (0.3)	+
	F. truncorum yessensis Forel	(Fy)		+					
	Number of species (19 spp. in total)*	9	6	11	14	9		
	Number of colonies		82	39	83	98	57	359	

^{*} The number of species collected by qualitative sampling is excluded from the calculation.

well as of colonies in various habitats seems to correlate to the extent of each habitat, in general the highest in habitat WM while the lowest in SH. Such tendency was also recognized in Sapporo and its vicinity, but not so remarkable as in the district studied. These facts will partly be explained by the difference in the nesting conditions as discussed in the section dealing with nest site preference.

Another aspect of the distribution in various habitats is considered by the tolerance range of each species. As seen in Table 1, dominant and abundant species occur in three or five habitats except *Aphaenogaster famelica* in two. The widest tolerance covering all habitats, is represented by *Lasius niger*, nextly four habitats by *Formica fusca japonica*, both being definitely dominant species in Hokkaido.

From the richest number of species, the general habitat preference given in Table 1, which will be analyzed in more detail in the next section, and the occupation by dominant species and others, it is assumed that habitats WM and HG are the most favorable environment by most species, preferred not only by the dominant species but also by other ones.

Habitat preference

The distribution of colonies in various habitats was analyzed to clarify the habitat preference of each species as well as the distribution pattern and characterization of each habitat as in previous works.

(1) Habitat preference and distribution pattern of each species

Habitat preference is measured by the following two procedures: comparison of habitat preference derived from the frequency and number of colonies in each species (cf. Hayashida 1963) and of the correlation indicies between species and habitat. In the former case, the frequency of discovery and number of all species excluding scarce or rare ones in various habitats were plotted in a rectangular co-ordinate. The results of ten species illustrated in Fig. 2, show that the wider its dimension, so the higher the habitat preference of the species concerned. The highly exclusive habitat preference is represented by *Aphaenogaster famelica* (A) and *Lasius fuliginosus* (Lg) to habitat WM, high preference of two habitats by *Myrmica lobicornis* var. *jessensis* (Ml) (BA, SH), Formica exsecta fukaii (Fe) (HG, BA), Camponotus herculeanus japonicus (Cj) (BA, HG), preference of three habitats by Myrmica ruginodis (M), Lasius niger (L) (HG, WM, WL), Formica fusca japonica (F) (BA, SH, HG). In Paratrechina flavipes (Pa), though the number of colonies is not so abundant as the frequency of discovery, the preference seems to be not too specialized, occurring in various habitats.

Nextly, the correlation indices between frequency of the species and habitat such as Nf/(nFH), c/C and c/f were used as in the writer's previous paper (cf. Hayashida 1960). The values of these indices in relatively abundant ten species are presented in Table 2. Frequency-colony number indices, c/f and C/F, are important to estimate quantitatively the distribution of colonies both in each habitat and the whole district. The higher values indicate the more

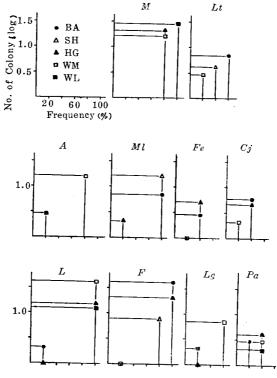


Fig. 2. Habitat preference derived from the frequency of discovery and the number of colonies in ten dominant or abundant species.

Table 2. Correlation indices between relatively abundant species and habitat.

C: Total numbr of colonies found in the whole district

c: Number of colonies found in each habitat

F: Total number of samples in which the species was found

f: Number of samles of each habitat in which the species was found

H: Number of habitats

N: Total number of samples made in the whole district

n: Number of samples made in each habitat.

		N f/(n FH)					c/f			c/C						The whole	
_	BA	SH	HG	WM	WL	BA	SH	HG	WM	WL	BA	SH	HG	WM	WL	F	area C/F_
\boldsymbol{F}	0.33	0.27	0.33	0.77	0.00	8.80	2.00	4.20	1.00	_	0.59	0.11	0.28	0.02	0.00	15	4.93
L	0.06	0.06	0.26	0.31	0.31	2.00	1.00	3.25	8.60	2.40	0.03	0.01	0.18	0.61	0.17	16	4.56
M	0.00	0.00	0.31	0.31	0.38	_	-	5.25	4.25	6.00	0.00	0.00	0.31	0.25	0.44	13	5.23
Ml	0.44	0.44	0.12	0.00	0.00	1.75	4.25	2.00	_	-	0.23	0.65	0.12	0.00	0.00	9	2.88
T	0.33	0.33	0.33	0.00	0.00	7.00	8.00	5.00	-	-	0.35	0.40	0.25	0.00	0.00	3	6.66
\boldsymbol{A}	0.00	0.00	0.00	0.80	0.20		-	_	4.00	3.00	0.00	0.00	0.00	0.74	0.26	5	3.80
Lt	0.50	0.33	0.17	0.00	0.00	3.00	2.00	3.00	_	_	0.56	0.25	0.19	0.00	0.00	6	2.66
Pa	0.25	0.00	0.33	0.25	0.17	3.00	-	2.00	1.50	1.00	0.25	0.00	0.33	0.25	0.17	7	1.00
Cj	0.40	0.00	0.40	0.20	0.00	3.00	-	2.50	1.00	-	0.50	0.00	0.41	0.09	0.00	5	2.40
Lg	0.00	0.00	0.20	0.60	0.20	-	-	1.00	2.33	2.00	0.00	0.00	0.10	0.70	0.20	5	2.00

aggregate or patched distribution of colonies. For instance, c/f value 8.80 of F (Formica fusca japonica) in habitat BA is the highest, indicating the abundant occurrence of colonies in the most suitable habitat for this dominant species, while value 1.00 in WM means the unsuitable condition to establish. In case of T (Tetramorium caespitum), another example is given, that is, this species was discovered 7, 8, 5 colonies in BA, SH and HG respectively by only a single sampling in each habitat. The corresponding values of c/f, 7.00, 8.00, 5.00 show a highly aggregate distribution in limited areas. The ecological consideration is, however, not accurately derived from the values of c/f alone. For instance in Lt (Leptothorax spinosior), the value 3.00 of c/f in BA is just high as the value in HG. But nine colonies of this species were discovered in three samplings in BA and three in one sampling in HG. Therefore, the quantitative distribution of this species is different in habitat BA and HG, namely, more uniform and relatively abundant in BA, while rather patched in HG. A similar example is also seen in A (Aphaenogaster famelica), c/f is 16/4 = 4.00 in WM and 3/1 = 3.00 in WL. Such peculiarity was less conspicuous in other species.

The value of C/F is the mean number of colonies discovered per one sampling. Values of dominant species range from 4.56 to 5.25, and those of abundant ones are less than 4.00 except 6.66 in *Tetramorium caespitum*. In scarce or rare species, the values of C/F do not exceed 3.00, usually 1.00 in the district studied, though the data are not shown in Table 2.

The distribution pattern of each species is characterized also by the values of correlation indices, Nf/(nFH) and c/C as illustrated in Fig. 3. By the comparing histograms of each species, the following three main types of distribution pattern are recognized.

- (1) Patched distribution pattern ---- Typical pattern is shown by Leptothorax congruus, Dolichoderus sibiricus, Lasius alienus, Formica sanguinea fusciceps and Camponotus caryae var. nawaii, and modified pattern in Lasius flavus, Aphaenogaster famelica, Pheidole fervida and Camponotus obscripes.
- (2) Sparse distribution pattern ---- Myrmica lobicornis var. jessensis, Leptothorax spinosior, Tetramorium caespitum, Lasius fuliginosus, Formica exsecta fukaii and Camponotus herculeanus japonicus.
- (3) Uniform distribution pattern - Formica fusca japonica, Lasius niger, Myrmica ruginodis and Paratrechina flavipes.

As seen in Fig. 3, about half of the species discovered in quantitative samplings belong to the patched distribution pattern, in which the ratio of species number is more than in Sapporo, but not so high as in Akkeshi, where the ratio attains to 2/3, reflecting its poor myrmecofauna (Hayashida and Maeda 1960). On the other hand, the species belonging to the sparse distribution pattern are more numerous than both in Akkeshi and Sapporo, occupying the majority of the abundant species in the district studied. Three dominant species and *Paratrechina flavipes*, the species characterized by the lack of special preference as already shown, are classified into the uniform distribution pattern.

Therefore, the make-up of myrmecofauna in the district studied seems to be a little different from two other districts already surveyd. The core of the myrmecofauna is occupied by the dominant species (227 in number of colonies, 63.2%), with a little contribution by

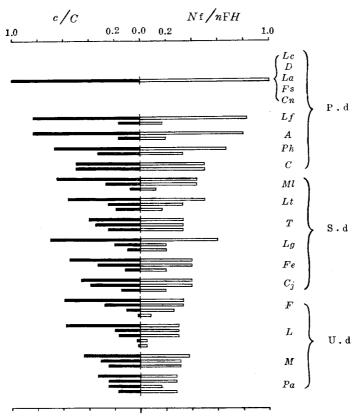


Fig. 3. Histograms corresponding to the values of two correlative indices, c/C and Nf/(nFH) of quantitatively collected species in the district. P. d: Patched distribution pattern, S. d: Sparse distribution pattern, U. d: Uniform distribution pattern.

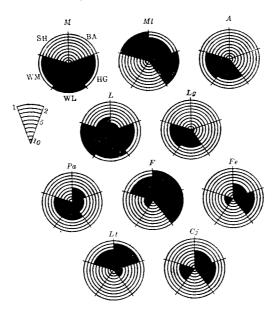


Fig. 4. The order of habitat preference by modified pie graphs, in which preference of ten dominant and abundant species is shown by the descending order from periphery to center of each graph.

the abundant species belonged to the sparse distribution pattern (93, 25.9%), those (39, 10.9%) sporadically distribute over the whole district. In Sapporo and Akkeshi, the parts occupied by these three groups are 980 (67.23%), 67 (4.61%), 444 (28.16%) and 354 (81.00%), 26 (5.95%), 57 (13.05%) respectively.

The range in the habitat preference of each species was also analyzed. The order of relative habitat preference among ten dominant and abundant species discovered in each habitat is represented by modified pie graphs in Fig. 4. For instance, *L* (*Lasius niger*) was 8th in BA, 6th in SH, 3rd in HG, 1st in WM and 2nd in WL. Some aspects of peculiarity of preference in each species and resemblance among various species are seen: *Lasius niger* possesses rather wide habitat preference, especially, in WM, WL and HG as similar to that in *Myrmica ruginodis*. Another example of widely distributed species is *Paratrechina flavipes* which distributes in all habitats except sand dune, though always occupying relatively low ranks.

From the comparison of pie graphs, similarity of habitat preference among the species is obtained as follows:

Type of habitat preferred*	Species					
BA, HG, SH BA, HG, WM BA, HG, WM, WL HG, WM, WL WM, WL	Formica fusca japonica, Myrmica lobicorns var. jessensis Formica exsecta fukaii, Camponotus herculeanus japonicus Paratrechina flavipes Lasius niger, Myrmica ruginodis Aphaenogaster famelica, Lasius fuliginosus					

^{(*} The habitats are arranged by the descending order)

Most of species assemblages classified in each type of habitat preference accord to the results of field observation as well to that in Sapporo except Camponotus herculeanus japonicus (BA. BS, HG in Sapporo). In Akkeshi, however, the habitat preference of the dominant or abundant species such as Lasius niger, Myrmica ruginodis and Lasius flavus differed from that in Sapporo and Kutchan Districts, distributing in habitats BS and BA, too. Probably specific difference in tolerance range to some environmental, notably microclimatic conditions is responsible for the occurrence of such local difference. It was recognized that the strong predominant species in BA and BS such as Formica fusca japonica and Myrmica lobicornis var. jessensis were rare or scarce in Akkeshi.

(2) The characterization of habitat

Nextly, the other aspect of habitat preference, differential utilization of habitats by various species, is considered. According to the occurrence probability method by Kato (1952), the ratio of number of colonies occupied by each species was calculated in each habitat, together, with its confidence interval within 95% reliability. The confidence interval of each species is shown in Fig. 5. As described in the previous papers, when the low confidence limit of the colony ratio of the species exceeds the mean colony number, such species are regarded as dominant species in each habitat. The results are arranged as follows:

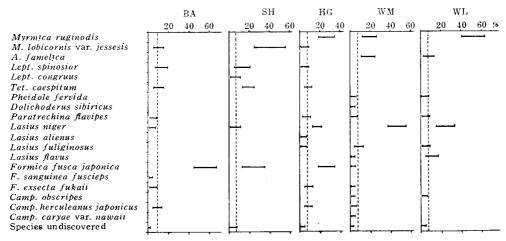


Fig. 5. The ratio of colony number of each species in various habitats, given by bars representing the confidence interval in 95% reliability (Vertical broken line: the upper confidence limit of mean colony number).

Habitat	Dominant species	Abundant species
BA	Fromica fusca japonica	Leptothorax spinosior
SH	Myrmica lobicornis var. jessensis, Formica fusca japonica, Tetramorium caespitum	Leptothorax spinosior
HG	Myrmica ruginodis, Formica fusca japonica, Lasius niger	
WM	Lasius niger, Myrmica ruginodis, Aphaenogaster famelica	
WL	Myrmica ruginodis, Lasius niger	Lasius flavus

Three species, Formica fusca japonica, Lasius niger and Myrmica ruginodis, being dominant in the district as a whole, are also dominant in three habitats. Some differences are found between the obtained results and those in Sapporo and Akkeshi. For instance, in Sapporo, Myrmica lobicornis var. jessensis is a typical dominant species in habitat BA but not so in SH, whereas it is dominant in SH in the district studied. Formica fusca japonica is dominant in HG in the district studied but not in Sapporo. One of the dominant species of WL in the district studied, Lasius niger, is only abundant in Sapporo in the same habitat, not in Akkeshi. These examples seem to indicate the occurrence of some local difference in ecological conditions among three districts studied, even in the same habitats.

Further characterization of habitats was made by using Motomura's law of geometric series, by the formula $\log y + ax = b$ (Motomura 1932, abbreviations as in the previous paper). From the values illustrated in Fig. 6, the degree of complexity series was obtained as follow: HG>WM>BA>WL>SH. Comparing this to that in Sapporo and Akkeshi, it is remarkable that HG is at the top in the complexity order in the district studied while the last in the other two. No conspicuous difference was found among three districts as to other habitats. Corresponding to the decrease of woodland and increase of grassy and herby lands the species preferred woods or sparsely vegetated areas in other districts are probably obliged to distribute in wood margin or cultivated land in the district studied, within the range of

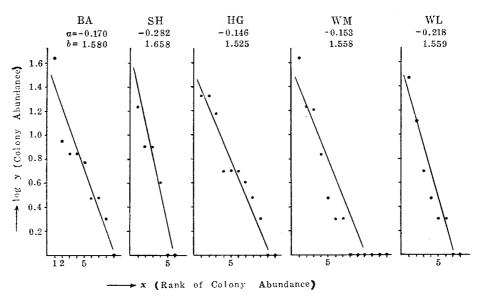


Fig. 6. Comparison of assemblage complexity in various habitats. Each regression line was derived from the law of geometric series.

ecological tolerance. In parallel to advanced reclamation, the species preferred sparsely vegetated habitats will be obliged to invade cultivated lands in this district.

The values of b as an index of the population density of the assemblage showed the following series: SH>BA>WM=WL>HG. Contrary to the complexity of assemblage mentioned above in the district studied, an opposite result was obtained from the series of population density, that is, the highest in SH and the lowest in HG. This is difficult to explained. As seen in Fig. 6, each of the 1st rank of colony abundance in SH and in HG is certainly similar, but the number of species discovered in the latter habitat is nearly double in the former. From the result of calculation, the regression line of habitat SH is steeper than that of HG, but the relative abundance of HG passably surpasses in that of SH. High density of population derived from the calculation of index in SH may probably be understood by the relative abundance of colonies against scarse occurrence of the species when the frequency of discovery does not be considered.

Nest site preference

Analysis of nest site preference is useful not only for the recognition of microhabitats preferred by each species, but also for comparison of utilization of nest sites in various habitats. The diversity in habitat preference may fundamentally be explained from the relative availability of various sites and rather fixed tendency to prefer definite sites. The nest sites distinguished in the district and their abbreviations are as follows (The frequent occurrence in various habitats in gothic):

1: in exposed loam or clay surface (BA, HG)

1: in shaded loam or clay soil (HG, WM, WL)

s: in shaded sandy surface (SH)

u: under stones (BA, SH, HG, WM, WL)

m: under accumulations of humus and other debris (BA, SH, HG, WM, WL)

r: around the roots of grasses and herbs (BA, SH, HG, WM, WL)

n: around the roots of living trees (HG, WM, WL)

w: in trunks of living trees (WM, WL)

d: in decayed stumps or fallen logs (SH, HG, WM, WL)

In order to study the relation between nest sites and habitats, number of nest sites sampled and those of species and colonies in various nest sites in each habitat are presented in Table 3.

	Number of samples in which utilization of each nest site was confirmed					Number of species					Number of colonies				
	BA	SH	HG	WM	WL	BA	SH	HG	WM	WL	BA	SH	HG	WM	WL
1	5		2			6		3			46		6		
ī			2	3	1			4	4	1			7	11	2
s		2					2					2			
u	3		3	3	1	6		4	3	1	17		5	5	1
m	3	3	5	5	5	4	2	5	5	7	8	4	14	32	28
r	4	5	5	3	2	5	5	9	5	1	11	32	42	17	4
n			1	3	5			1	3	4			1	18	7
w				1					1					1	
d		-1	3	4	4		1	4	4	4		1	6	13	14

Table 3. Utilization of nest sites in each habitat.

(1) Degree of utilization

As seen in Table 3, nest sites, m and r, are well utilized in all types of habitat. The total number of samplings was 25 in five habitats of the district studied, in which the frequency of utilization of m and r was 21 and 19 respectively. The occurrence of diverse nest sites was high in HG and WM where the preferred nest sites were m, r, u and d. Besides, these sites were also frequently used in WL, probably caused by the rich environmental diversity to allow the occurrence of various nest sites, contrasting to other habitats, especially such as SH. The higher preference of m and r was confirmed in the number of species and colonies, too. Even in habitat BA, in which these sites are not common, m and r are relatively highly utilized by four or five species. Consequently, in the district studied, number of colonies was the largest in r and firly large in m. In BA, the predominant nest site, l. was extremely well preferred by the dominant species, Formica fusca japonica, while r in HG by numerous species. On the other hand, in WM, in which the largest number of colonies was discovered, the utilization of very diverse nest sites such as m, n, r and d, and even l was confirmed. It was already confirmed in Akkeshi District that woodland habitats, WM and WL, tended to show the utilization of diverse nest sites with a more or less similar degree of preference. This appears to be valid in the district in the present study, too. The number of species in a given habitat is thus affected by the availability of various nest sites within it.

(2) Nest site preference of each species

As seen in Table 4, most of the species tend to prefer certain nest sites. Species possessing strong preference tendency are *Myrmica ruginodis* (m or r), *Myrmica lobicornis* var. *jessensis* (r), *Aphaenogaster famelica* (\bar{l} or m), *Leptothorax spinosior* (u), *Tetramorium caespitum* (r or m), *Paratrechina flavipes* (m), *Lasius niger* (m, n, r and d), *Camponotus herculeanus japonicus* (\bar{l} or \bar{l}), *Formica fusca japonica* (\bar{l} or r), and *Formica exsecta fukaii* (r), especically, nest sites, m and r were highly preferred by many species (\bar{l} and \bar{l} 3 spp. respectively) as well colonies (\bar{l} 6 and \bar{l} 25 respectively), suggesting the favorable sites for numerous species in this district. On the other hand, nest sites \bar{s} and w seem to be unsuitable judging from its scarcity to be utilized: \bar{s} was utilized only by *Leptothorax congruus* (\bar{l} colony) and *Formica fusca japonica* (\bar{l} 1), and w by *Dolichoderus sibiricus* (\bar{l} 1) alone. As these two nest sites are not scarce in the district studied, it is certain that few species utilizing them occurred. Futhermore, the strong habitat preference by various species in HG and WM is supposedly explained by the abundance of various suitable nest sites.

Table 4. Number of colonies of each species found at various nest sites in the district studied.

				Types of	nest sit	e prefere	ence		
		(sl)		(m	nu)	(1	nr)	(d	w)
	1	Ĩ	s	m	u	n	r	d	w
Myrmica ruginodis				38		2	20	8	
M. lobicornis var. jessensis	2			4	2		18		
Aphanogaster famelica		9		7	3				
Lept. spinosior	2	1	1	E	7		3	2	
Lept. congruus								1	
Pheidole fervida				1			1	1	
Tetramorium caespitum	3			6	2		9		
Dolichoderus sibiricus									1
Paratrechina flavipes	2			6	3		1		
Lasius niger		3		17	5	17	16	- 15	
L. alienus				1					
L. flavus				2		2	1	1	
L. fuliginosus				1		. 3	2	4	
Camp. obscripes	1					2			
Camp, herculeanus japonicus	6	3			1		2		
Camp. caryae var. nawaii								1	
F. fusca japonica	37	4	1	2	5		24	1	
F. exsecta fukaii				1			8		
F. sanguinea fusciceps							1		
Number of colonies (c)	52	20	2	86	28	26	125	34	1
Number of species (s)	6	5	2	12	8	5	13	9	1
Ratio c/s in each type		74/8		114	4/14	15	1/14	35	/10
Order of preference		-		n	r>mu>:	sl≫dw			

Table 5.	Types of nest site preference distinguished from the relative occupation
	of preferred nest site in relatively abundant species.
	1

Species	Preference order	Preference type*	
F. fusca japonica Camp. herculeanus japonicus	sl-nr-mu-dw sl-nr-mu	sl-nr II	
F. exsecta fukaii	nr-mu	nr-mu I	
T. caespitum, M. lobicornis var. jessensis	nr-mu-sl	nr-mu II	
L. niger	nr-mu-dw-sl	nr-mu III	
L. fuliginosus	nr-dw-mu	nr-dw III	
A. fameilca	mu-sl	mu-sl I	
Para, flavipes Lept, spinosior	mu-sl-nr mu-sl-nr-dw	mu-sl II	
M. ruginodis	mu-nr-dw	mu-nr III	

^{*} Classification of preference types was represented in the writer's paper (1963), which was distinguished into 40.

The various sites are classified into four major types from the nest site preference of all species as follows: Type sl (including s, l and l), mu (m and u), nr (n and r) and dw (d and w) (cf. the ecological characteristics of each type in the previous paper, 1960). The order of relative preference among four types is shown by the following series: nr>mu>sl>dw, which suggests that the highly utilized sites are occupied by those abundant in grassy or herby land and woodland habitats.

The relative preference of these types by various species was also analyzed. As given previously (Hayashida 1963), the nest site preference is further reclassified into ten by the combinations of two major types. In Table 5, relatively abundant eleven species in the district studied are arranged according to eight preference types confirmed. Most of them belonged to three subtypes of nr-mu and two of mu-sl.

A few words will be given on the relationship between habitat preference and nest site preference. Relative preference of nest site in each of habitat type depends on the difference of habitat nature and the relative abundance of nest sites. Relative preference order of nest sites in each habitat type was shown in Table 6. From the table, three series of preference order are distinguished which differed in another, though the series in habitat type H rather resembes to that of W, where the order of mu and nr is reverse to that in H. These sites are relatively preferred even in B in spite of their relatively small availability. The occurrence of relatively large number of species and colonies in habitat BA may be explained by

Table 6. Relative preference of nest site represented by the ratio, c/s, where c and s are the number of colonies and species respectively in each habitat type.

Habitat type	Ту	pe of nest	D-1-4:		
	sl	mu	nr	$d\mathbf{w}$	Relative preference order
B (BA)	46/6	25/6	11/5	_	sl>mu>nr
H (SH, HG)	11/5	23/8	75/10	7/5	nr > mu > sl > dw
W (WM, WL)	13/4	66/9	4 6/6	28/7	mu > nr > dw > sl

the dense occupation by dominant species together with effective utilization of nest sites, m, r and u, nevertheless these are not highly available ones, by relatively abundant species. The series of relative preference order of nest sites in each habitat type in the district studied fairly accords to that in Sapporo, but the position of habitat B in the district studied is very different from that in Akkeshi. The similarity of relative preference order of nest sites seems to correspond to resemblance of ecological conditions for distribution of ants. If this assumption would be valid, the ecological conditions of the district studied probably resembles to that of Sapporo, while quite different to Akkeshi.

Degree of co-existence

In order to understand the general make-up of ant community in the district studied, degree of co-existence was analyzed as to the district as a whole and also as to each habitat, by using co-existence index $Ed = 100 \cdot h/a$, where h and a are respectively the number of samples in which both species, A and B were, or A alone was discovered.

(1) Co-existence over the district as a whole

The degree of co-existence of three dominant and three abundant species to all discovered ones was illustrated in Fig. 7. High degree of co-existence of Lasius niger and Formica fusca japonica with the other five species seems to indicate the large number of colonies and the wide tolerance in habitat preference of these species. The resemblance of habitat prefence and distribution pattern between two species is given high degree each other, for instance, Lasius niger and Myrmica ruginodis ($M\rightarrow L$: 80% more, $L\rightarrow M$: 60–79), Formica fusca japonica and Leptothorax spinosior ($Lt\rightarrow F$: 80% more, $F\rightarrow Lt$: 60–79), Myrmica lobicornis var. jessensis and Formica fusca japonica ($Ml\rightarrow F$: 80% more, $F\rightarrow Ml$: 40–59). While an opposite example is given by Paratrechina flavipes, which possesses high degree of co-existence to Lasius niger (80% more), Myrmica ruginodis (60–79), Formica fusca japonica and Aphaenogaster famelica, but the values to other species are lower than 40%, because of relatively

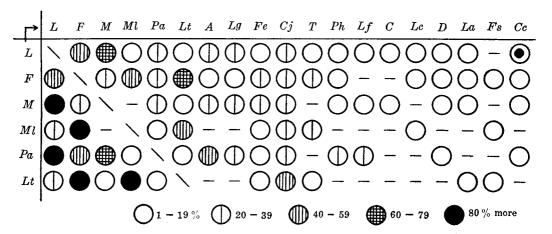


Fig. 7. The degree of co-existence of dominant or abundant species (vertically arranged) over the whole district to all species discovered.

low frequency of discovery and of small number of colonies in various habitats inspite of possessing unspecialized habitat preference and rather uniform distribution pattern.

(2) Co-existence in each habitat

The degree of co-existence among various species collected in more than 40% out of five samples in each habitat, is illustrated in Fig. 8, by using co-existence indices, the smaller value of either Ed_1 or Ed_2 (cf. Hayashida 1960). From these results, the interspecific relation in each habitat may briefly be described as follows:

In habitat BA: High degrees of co-existence are seen among three dominant species, all effectively utilized the suitable places. Although *Camponotus herculeanus japonicus* is rather less abundant, its co-existence is relatively high with *Leptothorax spinosior*, but is not with the other two dominant species. This fact suggests the similarity of micro-distribution between *Camponotus herculeanus japonicus* and *Leptothorax spinosior*. Contrary to this example, the degree of co-existence of *Formica exsecta fukaii* with other four species is less than 59% or zero, apparently not caused by any differences in micro-distribution.

In habitat SH: Co-existence is very high between two dominant species, *Formica fusca japonica* and *Myrmica lobicornis* var. *jessensis*, while that of *Leptothorax spinosior* with others is low, probably because of simple faunal make-up.

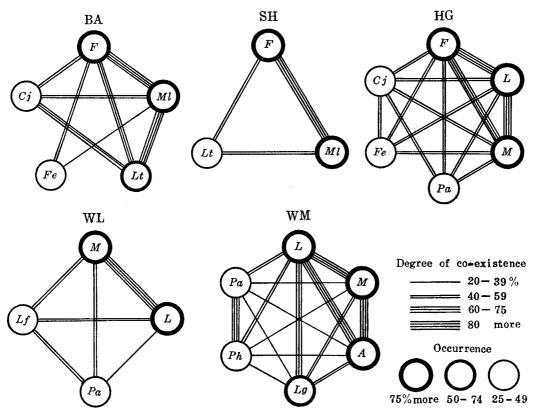


Fig. 8. The degree of co-existence among the species occurred in more than 25% of total sampling in each habitat. The descending order of frequency of occurrence is given in clockwise, with the most frequent species at the top.

In habitat HG: The degree of co-existence with each other are very high among three dominant species, Formica fusca japonica, Lasius niger and Myrmica ruginodis, because of their frequent occurrence. Other values of co-existence of the species in this habitat also show relatively high degree, at least, more than 40%, except for the case between Paratrechina flavipes and Formica exsecta fukaii, where the degree of co-existence is zero. Such high degree of co-existence among the species may result, together with the complicate faunal make-up, in the realization of strong preference of habitat by various species and the similar pattern of nest site of utilization.

In habitat WM: The high degree of co-existence among dominant species are similar as in other habitats. But there are some different features: the high values are also seen between relatively less frequent species, for instance, a very high degree of co-existence is recognized between *Pheidole fervida* and *Paratrechina flavipes* probably by limited microdistribution in this habitat. The degree of co-existence of *Lasius fuliginosus* offers another particular example, the value with *Lasius niger* is the highest, but is generally low with other species, mainly because of the different nest site preference (cf. Table 5). Hence, certain similar preference to habitat or nest site under diverse ecological conditions results in the high degree of co-existence among the species mentioned above in this habitat.

In habitat WL: Co-existence is surely the highest between two dominant species. Myrmica ruginodis and Lasius niger, but low among others. Therefore, the quantitative distribution of ants in this habitat is given by a relatively simple figure chiefly made by two dominant species. Such tendency, derived from the low population density, is remarkably different from that of Sapporo, where the interrelation is very complicate in woodland type habitats. WM and WL. As far as the writer's field observations go, however, the number of species and colonies tends to decrease in mountainous areas and interior of woods. Therefore, the habitat WL in the district studied, may still keep natural conditions for habitation of ants, because the district studied belongs mostly to mountainous outskirts covered by woods within the Shiribeshi Mountainous Area.

Vertical distribution in Mt. Yôtei

Studies on the vertical distribution of Japanese ants have been reported from Central Honshu (Morisita 1945) and Central Hokkaido (Kogure 1953). In Colorado, Gregg (1947) gave a report on the vertical distribution of ants in Mts. Rocky with respect to altitudinal indicators. The qualitative collection of ants of Mt. Yôtei by the writer was made mainly in the northwest slopes and at the top with sparsely vegetated rocky area in 1959 summer. Mt. Yôtei is a typical dormant conical volcano belonging to the Nasu Volcanic Zone (cf. Fig. 1, A and B). Hasegawa (1962) divided the altitudinal zones of the vegetation on Mt. Yôtei as follows: *Pinus pumila* zone (generally corresponding to Alpine zone), *Betula Ermani* zone (Subalpine zone) and montane broad-leaf forest zone (Montane zone). Futhermore, following plants are frequently listed as abundant species on the slope investigated: *Sasa* (from the

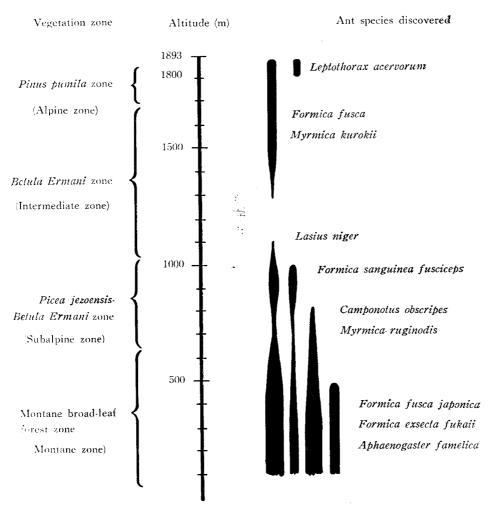


Fig. 9. The vertical distribution of antsin Mt. Yôtei together with altitubes and vegetatin zones.

foothills to about 1700 m, abundant), billbery (*Vaccinium Vitis-Idaea*, 1700–1850 m, relatively abundant), mountain-ash (*Sorbus Matsumurana*, 1400–1850 m, less abundant; *S. commixta*, 650–1400 m, less abundant), maple (*Acer ukurunduense*, *A. Tshonoskii*, 950–1300 m, less abundant) etc.

The vertical distribution of ten forms including subspecies and varieties of ants collected is given in Fig. 9 together with vegetation zones at corresponding to altitudes. There are three typical alpine species, Formica fusca, Myrmica kurokii and Leptothorax acervorum which distribute higher than about 1300 m, while seven species which commonly occurred in foothills and plains were discovered below about 1100 m. It was impossible to find any ants between altitudes of 1100 to 1300 m, more or less corresponding to Betula Ermani zone, and the ants were scarce in Picea jezoensis-Betula Ermani zone (Subalpine zone), especially rare in the spruce woods. Such a definite vertical segregation between alpine and low altitude species and scarcity of ants in spruce and birch forests are common to Mt. Taisetsu and

Mt. Rishiri(Hayashida, unpublished). Leptothorax acervorum was only found from the dead trunks of Pinus pumila at the sparsely vegetated area of the top of mountain. The nests of Formica fusca and Myrmica kurokii were discovered in decayed wood or under stones or accumulated vegetable matters from about 1300 m in altitude to near the rocky area of the top. The ants distributed in the Subalpine zone were not so much in numerous and mainly established their colonies along the mountain paths. At the Montane zone, most of the species collected are those found in lowlands, too.

Notes on the Zoogeography in Hokkaido

Besides the ecological distribution in each district and in each habitat, the zoogeographical perspective covering broader areas is necessary for the full understanding of myrmecofauna of Hokkaido. Closer considerations on this aspect will be given at the end of this serial

Table 7. Comparison of ant species discovered in Kutchan, Sapporo and Hakodate Districts, together with their occurrence in Honshu. +++: abundant, ++: less abundant, +: scarce; o: occurrence without relative abundance, m: occurrence only in high mountains.

	Hokkaido		2 16	Но	Honshu		
Sapporo	Kutchan	Hakodate	Specific name	Tôhoku	Other Areas		
+			Camponotus yessensis	0			
+		1	Camponotus kiusiuensis		o		
+			Crematogaster laboriosa	o	О		
+	+		Leptothorax congruus	o	0		
+	+		Camponotus caryae var. nawaii	О	0		
++	+		Formica sanguinea fusciceps	o	m		
+	+	+	Lasius alienus	o	o		
+	++	+	Formica exsecta fukaii	o	m		
++	+	+	Dolichoderus sibiricus	o			
++	+	+	Lasius spathepus	О	0		
+ $+$	++	++	Aphaenogaster famelica	o	О		
+	++	++	Tetramorium caespitum	o	o		
+	++	++	Leptothorax spinosior	. о	o		
+++	+	++	Camponotus obscripes	О	o		
++	+	++	Formica truncorum yessensis	0	m		
+++	+	++	Pheidole fervida	o	О		
+++	++	++	Camponotus herculeanus japonicus	О	o		
+++	++	. ++	Lasius fuliginosus	О	0		
+++	++	++	Lasius flavus	О	О		
+++	++	++	Paratrechina flavipes	О	o		
+++	+++	++	Myrmica lobicornis var. jessensis	О			
+++	+++	+++	Formica fusca japonica	О	О		
+++	+++	+++	Lasius niger	О	o		
+++	+++	+++	Myrmica ruginodis	o	m		
++		++	Lasius umbratus	О	0		
++		' +	Camponotus caryae quadrinotatus	o	О		
+	'	+	Vollenhovia emeryi	О	o		
+		+	Solenopsis fugax	o	0		
+		+	Ponera japonicus	o	0		
		+	Polyergus samurai	О	o		
		+	Aphaenogaster sp.	o			

work. Here is given a brief preliminary comparison of faunal make-up among the following three districts, all locating in the western half of Hokkaido.

Kutchan District: The area covered by the present study.

Sapporo District: The area studied in a previous survey (Hayashida 1960).

Hakodate District: The southernmost area of Oshima peninsula, including Hakodate, Matsumae and Esashi (From Morisita 1945 and the writer's unpublished data).

The number of species common to three districts are 18, occuping the majority of total species. Species common to only two districts are 3 between Sapporo and Kutchan, 5 between Sapporo and Hakodate, but none between Kutchan and Hakodate. Three species discovered only in Sapporo District are rare in Hokkaido throughout, but they are also collected from the northern part of Honshu, so that their occurrence in Southwestern Hokkaido, including Hakodate and Kutchan Districts is not always improbable. Among of two species only collected from Hakodate District, Polyergus samurai is the species very difficult to discovered, because of its obligatory dulotic mode of life, and another species, Aphaenogaster sp. is also found in Akkeshi, far remote from Hakodate District. Their occurrence in other districts of Hokkaido is not highly probable. Although the faunal make-up of the district studied is rather similar to that of Sapporo, no marked difference between Kutchan and Hakodate Districts was found. Probably, the district studied occupies the transitional zone between Hakodate and Sapporo Districts. The faunal make-up seems to gradually impoverish from Hakodate and Sapporo, but the gradient of such impoverishment is probably so weak that no conspicuous local particularity is found, except for some characteristic features caused by the ecological characteristics of the district studied, than by the local shift of fanual make-up.

Discussion

From the comparison of the ant fauna among Sapporo, Hakodate and Kutchan, the district studied, no clear, difference on local characteristics is detected as to the district studied. Consequently, the ant fauna of this district has no importance such as in phyto-geographical zonation characterized by the occurrence of two demarcation lines as reference to in the introduction (Tatewaki 1958). On the other hand, the analyses of habitat and nest site preference suggest the importance of some topographical conditions such as mountainous areas, foothills, plains, sand dunes etc. and the nature of vegetation for the distribution of ants in the district studied. Relationship between species discovered and climatic conditions, characterized by heavy snow-fall in winter and relatively low precipitation in summer, does not show any particular ecological relation within the limit of this study. The relatively abundant occurrence of *Formica exsecta fukaii* and *Tetramorium caespitum* than in Sapporo and Hakodate Districts may be assumed that these species distribute more abundantly in the Japan Sea coast of Hokkaido, but a definite conclusion will be given later.

Ant species discovered in the district studied include no very rare ones, and the dominant species, Formica fusca japonica, Lasius niger and Myrmica ruginodis are those fairly common in Hokkaido throughout. These facts also indicate that the district studied is not

under particular environmental conditions. The relatively poor occurrence both in number of species and colonies may partly be explained by the general poverty due to the large extent of mountainous areas. Apparently the district studied was primarily covered with the dense forests. After the beginning of the human settlement, forests and other natural conditions were gradually altered, resulting in the increase of grassy or herby lands and sparsely vegetated areas by reclamation. As stated by Gösswald (1932), the human interference, especially, destruction of primary vegetation and replacement by cultivated or urban areas, may result in a serious damage of habitats preferred by many species of ants. The original micro-habitat conditions are markedly changed and the fluctuation of physical conditions becomes severer. The consequent severer conditions such as strong insolation, rapid evaporation and violent diurnal change of temperature both above and below the soil surface, may induce the retreat of many ant species to better protected areas. In parallel to such retreat, those preferring sparsely vagetated habitats and grassy or herby lands may gradually increase, partly caused by the unintentional human activities. Some characteristics in the make-up of myrmecofauna may partly be explained in this way.

Judging from the analyses of habitat preference, the species preferring the woodland type habitats, Camponotus obscripes, Formica exsecta fukaii, Lasius fuliginosus and Dolichoderus sibiricus show relatively narrow range of distribution in the district, but the eurytopic species such as Lasius niger, Myrmica ruginodis and Paratrechina flavipes are predominant throughout the whole district, and Formica fusca japonica and Myrmica lobicornis var. jessensis, preferring bare or sparsely vegetated areas also frequent from such habitats in this district. Hence, it is assumed that the ant fauna of the district studied is laid in the process of gradual allogenic succession depending on the change of the environment from woodland to grassy or herby land. The other characteristics of the ant fauna in the district studied is rlatively low assemblage on the species in each habitat. Actually, the species possessing the uniform distribution pattern are three dominant species and Paratrechina flavipes, more than half of the species recorded have patched distribution pattern. Even in habitat HG (grassy or herby lands) which showed the highest degree of complexity series, the community structure is rather simple. Probably the natural enviroment of the district does not allow the high flourishment of the colonies caused by unsettled conditions due to the advanced human interference. Furthermore, the simple structure of community is also derived from the fact that the higher degrees of co-existence are obtained only between or among dominant species in each habitat. Some differences from Sapporo or Akkeshi Districts, are recognized even concerning one and the same habitat. For instance, the number of species and colonies in habitat BA (bare or sparsely vegetated place) is markedly different among Kutchan, Sapporo and Akkeshi Districts, probably caused by the influence of climatic conditions and the age of the habitat.

A few words are given on the nest site preference. The frequently utilized sites in various habitats are m (under accumulations of humus and other debries) and r (around the roots of grasses and herbs), both provide moderate physical conditions and convinience for establishment of colony. On the other hand, \bar{s} (in shaded sandy surface) and w (in trunks of living trees) are utilized in low degrees, indicating the severe physical conditions for nesting in the former and the poverty of species utilizing in the latter. These facts correspond to

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the high complexity of community in habitat HG, according to the richness of favorable nest sites. Although there is no clear correspondence between the faunal make-up of myrmecofauna and vegetational zonation, the nature of vegetation seemingly affect on the micro-distribution of ants, governing the conditions suitable for nest sites in each habitat. Talbot (1934) and Gregg (1944) obtained the positive correlation between succession of vegetation and ecological distribution of ants. This may be explained by the specific adaptability of such ant species for diverse environmental conditions offered by the vegetation. Correspondingly it is assumed that the ecological distribution of ants may change gradually untill reaching the final phase of open habitat community.

The vertical distribution of ants in Mt. Yôtei more or less accords to the vegetation zones arranged by Hasegawa (1962). Three species of alpine ants were found only from the Alpine zone, while seven others from the Subalpine and Montane zones. Therefore, habitat segregation was clearly recognized with regard to altitudinal as well vegetational zones. Such segregation was also seen in the Rocky Mountains in Colorado: only two species are at above timber line (11500 ft.) and ten species are indicative of the coniferous forests (8000 to 11500 ft.), but twenty-two ones may be taken as characteristic of basal plains (Gregg 1947). The specific difference in tolerance range to some environmental conditions such as temperature, wind force, vegetation cover, insolation, food supply etc. would be responsible for such habitat segregation in the higher mountain.

Another interesting fact is the scarcity of ants in the Intermediate zone between Alpine and Subalpine zones. The alpine species seem to prefer colder, windy and less shaded conditions offered by the severe environment. It is still unknown why these alpine species cannot distribute in the Intermediate zone, the environmental conditions of which are more favorable for most of ant species. The study of torelance range of these species to such conditions intervened or not by inter-specific competition is needed in further studies. The segregation of fauna between top areas and lower slope, separated by the Intermediate zone being scarce both in number of species and individuals is empirically frequently encountered in various mountainous areas, not only in ants but in many other animal groups. This may be considered one of the interesting problems in high altitude ecology.

Summary

The ecological distribution of ants was studied in Kutchan and its adjacent area, together with the vertical distribution in Mt. Yôtei. Twenty-four forms belonging to three subfamilies and ten genera were discovered from the district studied from both quantitative and qualitative samplings. The habitat preference was analysed quantitatively in five habitats. In the district studied, grassy or herby lands and wood margins are more preferred than woods and sand dune with sparse vegetation. Relatively scarce number of species and simple assemblage of ants in all habitats surveyed indicate that the district is unstable in natural conditions, probably due to the process of gradual destruction of primary vegetation by human activities and their replacement by monotonous, man-made environment.

The nest site preference and degree of co-existence were also analyzed. From the

utilization of each species in nine typical nest sites, preference was distinguished into eight types. The predominant preference of nest sites m (under accumulation of humus and other debries) and r (around the roots of grasses or herbs), reflects the trends in habitat preference mentioned above. Degree of co-existence was high among the dominant species, but not among less abundant ones both in the whole district and in each habitat, probably caused by the simple structure of ant community in the district studied.

From a survey of vertical distribution of ants in Mt. Yôtei, a certain definite habitate segregation was recognized with respect to the altitude and vegetation zone between alpine and montane species. The ant colonies were practically absent in the Intermediate zone as often seen in other mountains, as well as in other animal groups, suggesting the necessity of the causal analysis.

References

- Gösswald, K. 1932. Oekologische Studien über die Ameisen fauna des mittleren Maingebietes. Zeitsch. wiss. Zool., 142 (1): 1–156.
- Gregg, R. E. 1944. The auts of the Chicago region. Ann. Ent. Soc. Amer., 37: 447-480.
- 1947. Altitudinal indicators among the Formicidae. Univ. Colorado Studies, Ser. D, 2 (3): 385-403.
- Hasegawa, J. 1962. Altitudinal zones of the vegetation on Mt. Yôtei, Prov. Shiribeshi, Hokkaido. Jap. Jour. Ecol., 12 (2): 67-72 (In Japanese with English summary).
- Hayashida, K. 1960. Studies on the ecological distribution of ants in Sapporo and its vicinity. Ins. Soc., 7 (2): 125-162.
- 1963. Some analytical procedures on the ecological distribution of ants. Jour. Sapporo Otani Junior College, 1: 1-26 (In Japanese).
- & S. Maeda 1960. Studies on the ecological distribution of ants in Akkeshi. Jour. Fac. Sci. Hokkaido Univ. Ser. VI, 14 (3): 305-319.
- Kogure, T. 1953. Ants of Central Hokkaido. Shaishu to Shiiku, 15 (9): 203-206 (In Japanese).
- Kato, M. 1955. Analytical method of animal community. Ser. Exp. Biol., Nakayama, Tokyo, pp. 77 (In Japanese).
- Morisita, M. 1945 a. Natural history of Japan. 5. Insects II. Formicidae. Kenkyu Sha, Tokyo, 1-56 (In Japanese).
- ______ 1945 b. Ants in the Southernmost of Hokkaido. Mushi, 16 (6): 21-28 (In Japanese).
- Motomura, I. 1933. A statistical method in animal Synecology. Zool. Mag., Tokyo, 44: 379-398 (In Japanese). Sapporo Regional Meteorological Observatory 1952. Climate of Hokkaido. Sapporo, pp. 419 (In Japanese).
- Talbot, M. 1934. Distribution of ants in Chicago region with reference to ecological factors and physiological toleration. Ecol., 35 (4): 416-439.
- Tatewaki, M. 1958. Forest ecology of the island of the North Pacific Ocean. Jour, Fac. Agr. Hokkaido Univ. 50 (4): 71-486.