Ecological Distribution of Ants in Mt. Atusanupuri, An Active Volcano in Akan National Park, Hokkaido[1)]

By

Kazuo Hayashida

(Zoological Institute, Hokkaido University)

(*With 3 Text figures*)

In order to clarify the ecological distribution of any animal group in a given area, it is needful to carry out standardized samplings covering numerous seemingly representative local diversities. Beside such an extensive study, it is often suggestive for further analysis to execute an intensive survey directed to certain localities provided with a peculiar physiography. With the purpose to study ecological distribution of ants in one particular situation, the present paper deals with the results of surveys in 1958 and 1959 made in Mt. Atusanupuri,[2)] an active volcano amid a homogeneous mixed forest.

Before going further, the writer wishes to express his sincere gratitude to Prof. Tohru Uchida and Dr. Shôichi F. Sakagami, under whose helpful guidance the present work has been carried out. His further thanks are also due to all members of the Teshikaga Forestry Office for their valuable information as to Mt. Atusanupuri, and especially to Prof. K. Yasumatsu, whose kindness in identifying some ant specimens was indispensable in the preparation of this paper.

1. The area studied and method employed

As illustrated in Figure 1, the topography of Akan National Park in Eastern Hokkaido comprises many volcanoes and caldera-lakes belonging to the southwest part of the Chishima Volcanic Zone. Recently, the original vegetation of the region has been gradually altered caused by the sightseening activities, but still remains as mixed or coniferous forests. Mt. Atusanupuri is a small active volcano situated near the east side of Lake Kutcharo (510 m at the top and about 200 m at the foot above sea level, *Cf.* Fig. 1). While there are numerous small craters still very active and deposits of sulphur and volcanic ash near the top, the most parts of the slopes are covered by some alpine plants such as *Pinus pumila*, *Ledum palustre* var. *yezoense*, *Empetrum nigrum*, *Sorbus sambucifolia* etc., in spite of the relatively low altitude. On the other hand, the vegetation surrounding the mountain consists of a mixed forest with *Picea jezoensis* Carr., *P. Glehni* Masters, *Tilia japonica* Simk., *Acer miyabei* Maxim., *Betula tauschii* Koidz, *Kalopanax ricinifolius* Miq.,

1) Contribution No. 467 from the Zoological Institute, Faculty of Science, Hokkaido University, Sapporo, Japan.

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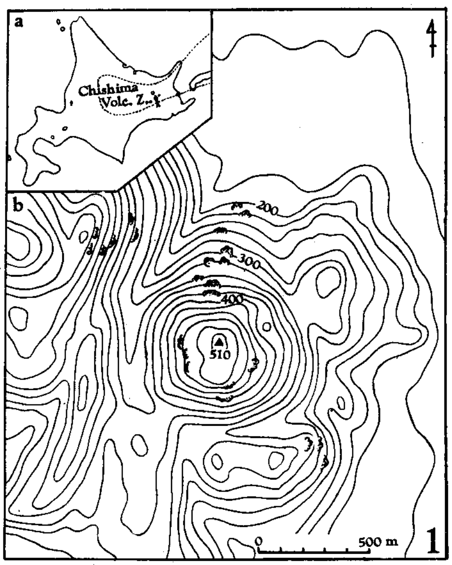

Fig. 1. Maps of area studied. (a) Location of Mt. Atusanupuri in Eastern Hokkaido. (b) General physiography of the mountain.

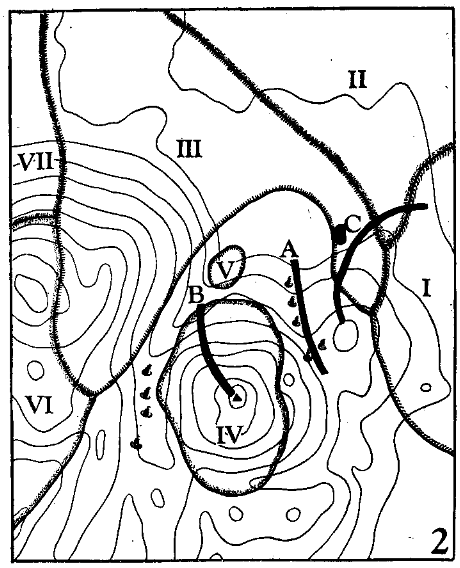

Fig. 2. Map of ecological conditions of area surveyed. Explanations of Roman Numerals are given in text.

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(Depth)	
0 – 10 cm	— Accumulation of humus and debris above loose, wet, and brown to pale brown sandy loam.
10 – 20	— Loose, wet and dark yellow to dark grey sandy loam.
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The writer employed a Belt Transect method and chose three prospecting courses: A, B and C (Fig. 2), according to the difference of vegetation. Each course was about 2 m wide. The samplings consisted of the discovery of nests: samplings were continuously carried out from the start to the end of the course accompanied with the making of records of the enviornmental condition where the nests were found. The characteristics of each course will briefly be given below:

Course A — Exposed stony or volcanic ash surface, including some small craters erupting sulphurous acid gas and other hotter gasses. Remarkably dry, exposed to insolation, almost without any plants.

Course B — Covered with the alpine plant association (*Cf.* Fig. 2. Association IV) from the foot to the top of the mountain.

Course C — Full course runs through exposed stony area, with alpine association (III), association of intermediate zone (II) and mountainous wood association (I), that is, the course passes through a spatial succession of vegetation.

2. Results

1) *Species collected*

From this area, the writer collected 11 forms as arranged in Table 1, according to the order of abundance of the colonies found. All species are typical palaearctic elements and as shown in Table 1, can further be subdivided into the following four groups from the stand point of the regional distribution (Teranishi 1929, 1933, Morisita 1945a, b, Kogure 1953, 1955, Hayashida 1957): G1: Those found exclusively in Hokkaido: *Formica truncorum*; G2: Those found in Southern Japan in the alpine zone: *F. fusca, Leptothorax acervorum, Camponotus herculeanus herculeanus* and *Myrmica ruginodis*; G3: Those found in Southern Japan in mountainous zone alone: *F. sanguinea* var. *fusciceps* and *M. lobicornis* var. *jessensis*; G4: Other species of wide distribution. The distribution of the most dominant species, F. *truncorum,* is limited to the Northern or Eastern Hokkaido alone, but *F. fusca* and *Leptothorax acervorum,* specific to the alpine zone, have been found even in the central district of Hokkaido from mountains higher than 1500 m above sea level. As variance with these facts, *Lasius niger, Myrmica lobicornis* var. *jessensis* and *Paratrechina flavipes* which are dominant or abundant species in Central, Western and Southern Hokkaido, were found as relatively rare species in the Eastern Hokkaido area surveyed. However, further study is required to determine whether the faunal make-up of Mt. Atusanupuri represents or not the Myrmecofauna of Eastern Hokkaido.

2) *Ecological distribution of ants in each course*

No ants were found from Course A, a completely bare area, indubitably due to the most unsuitable conditions for both colony establishment and growth of plants to be foraged. However, one individual of *F. truncorum* was seen wandering about the sulphur deposit only about 2 m distant from an active crater.

Table 1. Species and number of colonies found in various nest sites in Mt. Atusanupuri Nest sites u : under stones, l : in exposed loam surface (often mixed volcanic ash), m : under accumulation of fallen leaves and other debris, r : around the root of grasses and herbs, n : around the root of living tree, d : in fallen or decayed logs.

Specific name (*Abbrev.*)	Number of colonies in various nest sites						Total (Ratio, %)	Group*
	u	l	m	r	n	d		
Formica truncorum Fabricius (*Ft*)	1	3	27	8	22		61 (42.6)	G1
F. fusca Linné (*Ff*)	20	6	2			2	30 (21.0)	G2
Lasius flavus (Fabricius) (*Lf*)			14				14 (9.8)	G4
F. sanguinea var. *fusciceps* Emery (*Fs*)		1	2	7			10 (7.0)	G3
Myrmica ruginodis Nylander (*M*)	1		5			4	10 (7.0)	G2
Leptothorax acervorum Fabricius (*Lr*)			1			6	7 (4.9)	G2
Camponotus herculeanus herculeanus (Linné) (*Ch*)			1			3	4 (2.8)	G2
M. lobicornis var. *jessensis* Forel (*Ml*)			4				4 (2.8)	G3
Lasius niger Linné (*L*)					1		1 (0.7)	G4
L. alienus (Foerster) (*La*)						1	1 (0.7)	G4
Paratrechina flavipes (F. Smith) (*Pa*)				1			1 (0.7)	G4
Total (Ratio, %)	22 (15.4)	10 (7.7)	56 (39.1)	16 (11.2)	23 (16.1)	15 (10.5)	143	

* Explanation of each group is given in text

The nearest nest of this species was discovered about 80 m from the crater, hence *F. turncorum* may occupy the area of Course A as the outer limit of its home range.

As represented in Figure 3, 8 species were collected in Course B which is covered with alpine association. The higher part is dominated by an alpine species, *F. fusca*, but at most parts, any vertical segregation between alpine and plain species was scarcely to be seen.

Course C was provided with a succession of various vegetation types, from the exposed area at the top of the mountain, alpine plant association at the base to the broad-leaf woods. As seen in Table 2, 8 species were discovered. The distributional pattern clearly corresponding to the gradual vegetation change was obtained as follows :

Succession of habitat conditions (1) to (9) (*Cf.* Table 2)

Ff – Lf – Ft – Pa, M – Ml, Lr – Ft

F. truncorum and *F. fusca* were respectively dominant in woods and in exposed area, especially the dominancy of the latter species was approximately overwhelming along the paths through woods.

3) *Nest site preference*

The spatial segregation among species may depend on the difference of nest site preference among the similar habitat types. As shown on Table 1, nest sites within accumulations of fallen leaves and other debris were mostly preferred by 9 species, while those around the roots of living trees and under stones were also highly preferred, though the number of different species found was small.

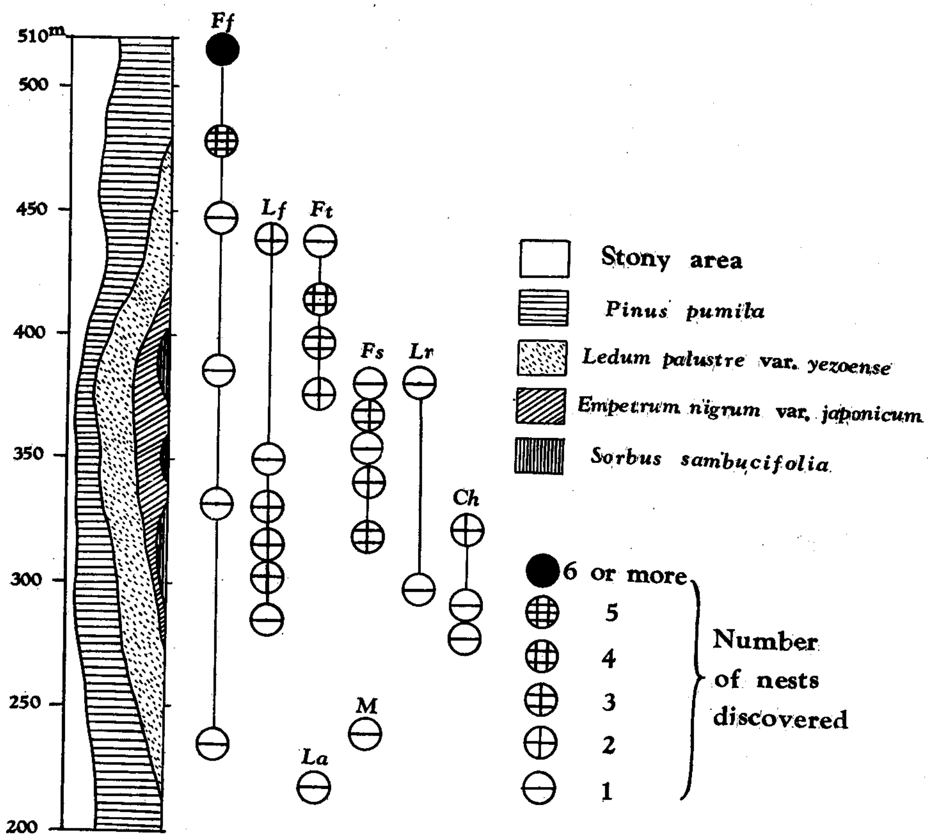

Fig. 3. Schema of succession of plant association and the vertical distribution of ant species with the relative abundance of nests at Course B.

The characteristic preference of some species are *F. fusca* mainly under stones, *F. truncorum* under accumulation of decaying matters or around the roots of trees, *L. flavus*, *Myrmica ruginodis* and *M. lobicornis* var. *jessensis* under accumulations of fallen leaves and other debris, *F. sanguinea* var. *fusciceps* around the roots of grasses or herbs and *Leptothorax acervorum* and *Camponotus herculeanus herculeanus* in fallen or deayed logs. The ecological conditions required for nest

Table 2. Relative abundance of nests discovered in various habitat conditions of Course C. ⧺ highly abundance, + abundance, ± less abundance, – rare.

Habitat conditions*	Relative abundance of nests discovered from various nest sites						Total sp. no. (Total col. no.)
	u	l	m	r	n	d	
(1) Exposed stony area (Mountain slope) +	⧺*Ff* (5)	+*Ff* (1)	±	–	–	±*Ff* (1)	1(7)
(2) Exposed stony area and *Pinus pumila* ⧺	⧺*Ff* (2)	+	+*Lf* (5)	–	⧺	+	2(7)
(3) *Pinus pumila* +	–	±	⧺	±	⧺*Ft* (7)	+	1(7)
(4) Exposed loam or volcanic ash surface and sparse grass or herb ±	+*Ff* (1)	+	±	*Ft* (2) ⧺*Pa* (1)	–	–	3(4)
(5) *Pinus pumila* and *Ledum palustre* var. *yezoense* +	±*Ft* (1) *M* (1)	±	⧺*M* (1)	–	⧺*Ft* (3)	+*M* (3)	2(9)
(6) *Ledum palustre* var. *yezoense* +	–	–	⧺*M* (1) *Ml* (2) *Ft* (2)	±	⧺	⧺*Lr* (1)	4(6)
(7) *Ledum palustre* var. *yezoense* and *Betula tauschii* ⧺	–	–	⧺*Ml* (1) *M* (1) *Ft* (3)	±	⧺	⧺*Lr* (2)	4(7)
(8) *Ledum palustre* var. *yezoense* and *Empetrum nigrum* var. *japonicum* +	–	–	⧺*Ml* (1) *Ft* (4)	±*Ft* (2)	⧺*Ft* (2)	⧺*Lr* (2)	3(11)
(9) *Quercus serrata*, *Hydrangea paniculata*, *Majanthemum bifolium* var. *dialatum* etc. (woods) ⧺	–	–*Ft* (1)	⧺*M* (1) *Ft* (12)	+*Ft* (2)	⧺*Ft* (9) *L* (1)	⧺*M* (1)	3(27)

* Arranged to the gradual change of surface condition from exposed areas to woods.

sites do not always agree to those for the home range which are generally more flexible. From the viewpoint of ecological conditions, nest site preference (NS) and home range (HR) of each species as to two serious environmental factors, light intensity and moisture, were arranged in Table 3. Some differences were recognized among species as in *F. truncorum* and *L. flavus*. Species with wide or narrow tolerance range are also distinguishable: the typical representatives of the eurytopic species are *F. fusca*, *F. truncorum*, *Camponotus herculeanus herculeanus* and *Myrmica lobicornis* var. *jessensis*, while those of the stenotopic ones *Leptothorax acervorum* and *Lasius flavus*.

Table 3. Nest site preference (NS) and Home range (HR) in relation to light intensity and moisture.

Light intensity	Moisture		
	low	moderate	high
high	*Ff*(HR) *Ft*(HR)	*Ff*(NS) *Ft*(HR) *Fs*(HR) *Ch*(HR) *Ml*(HR)	
moderate	*Ch*(NS)	*Ff*(NS) *Ft*(HR) *Fs*(NS) *M*(HR) *Lr*(NS) *Ml*(NS) *Ch*(NS)	*Lf*(HR)
low	*Ch*(HR) *Ml*(HR)	*Ch*(HR) *Ml*(HR) *M*(NS)	*Lf*(NS)

3. Discussion

Under the relatively severe environmental conditions such as sand dunes, peat beds, volcanic areas, the presence of plant covers seems to determine the relative abundance of ants. Talbot (1934) pointed out that the ant species strictly found in the sandy dune alone are so scarce in number, that sandy substrate is a strong barrier to many ant species. Likewise, Yasumatsu collected only three species from sandy areas in Fukuoka. On the other hand, in a highly damp area such as a peat bog near Sapporo, only two species were collected, suggesting the diametrically opposed extreme of the envrionmental hostility to ants. In the area mentioned above, Course A filled with blow off sulphurous acid gas and devoid of plant cover shows another extreme of sites unsuitable for ants as the peculiar surface state of an active volcano. In parallel to the increase of plant covers, which also corresponds to the distance from the area with craters, the ant colonies gradually increase in number. The dependance of the distribution of each species upon the features of plant associations can mostly clearly be seen in Course C, where the spatial succession of several associations is relatively obvious. The similar results are found in Europe (Gösswald 1932, Goetsch 1937) or in North America (Talbot 1943, Gregg 1944). On the other hand, such clear habitat segregation is less distinct in Course B, probably corresponding to the poor spatial differentiation of plant associations.

Furthermore, this course shows an interesting example of compressed vertical distribution. The typical alpine ants of Japan are *Formica fusca, Camponotus herculeanus sachalinensis, Myrmica kurokii* and *Leptohtorax acervorum* in Honshû (Morisita 1945a) and *F. fusca, F. picea, Myrmica kurokii* and *Leptothorax acervorum* in Hokkaido (reported in Mt. Taisetsu, Mt. Tokachi and Mt. Rishiri by

Kogure, 1953, 1955, and in Mt. Yôtei by Hayashida, unpubl.). Therefore, the typical alpine species in Mt. Atusanupuri are *F. fusca* and *Leptothorax acervorum*, although *Camponotus herculeanus herculeanus* has hitherto been recorded in boreal or subalpine regions in North America. Other species are rather common in both plain and hill areas, except *Lasius flavus* which is horizontally distributed throughout the Horlactic region (Wilson 1955) and vertically from the lowland in Southern Europe (Zimmermann 1934) to the mountainous areas in Switzerland (Forel). In Mt. Atusanupuri, especially in Course B, the higher levels are dominated by *F. fusca*, but in the lower parts, there is no vertical segregation between alpine and plain ant species, as seen in Fig. 3, consequently, no clear vertical differentiation in ants corresponding to the altitudinal and vegetational distribution as seen in other high mountains. In this low active volcano, the topographical and vegetational differentiations are compressed within a very small spatial area, which might result in the compression of ants distribution, too. In such a situation, each species may segregate its habitat from the others, according to the direct requirements for life, but never on a larger scale expressed by altitudinal segregation.

Summary

A survey on the ecological distribution of ants in a low active volcano, Mt. Atusanupuri was carried out. From the areas with plant covers, 11 forms of ants were collected, but no species were found from the exposed area near craters. Also habitat segregation was clearly seen according to the spatial succession of plant associations. There was found no vertical segregation between alpine and lowland species, suggesting a compressed vertical distribution within a relatively limited area.

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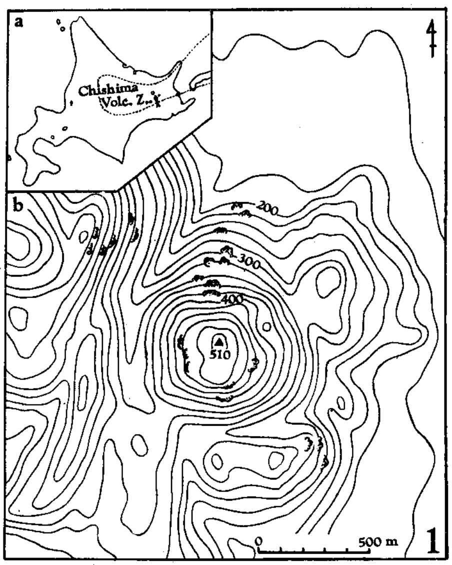

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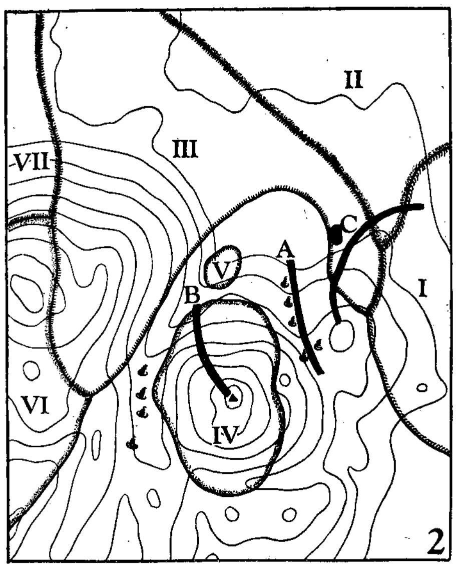

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Table 1. Species and number of colonies found in various nest sites in Mt. Atusanupuri
Nest sites u : under stones, l : in exposed loam surface (often mixed volcanic ash), m : under accumulation of fallen leaves and other debris, r : around the root of grasses and herbs, n : around the root of living tree, d : in fallen or decayed logs.

Specific name (*Abbrev.*)	Number of colonies in various nest sites						Total (Ratio, %)	Group*
	u	l	m	r	n	d		
Formica truncorum Fabricius (*Ft*)	1	3	27	8	22		61 (42.6)	G1
F. fusca Linné (*Ff*)	20	6	2			2	30 (21.0)	G2
Lasius flavus (Fabricius) (*Lf*)			14				14 (9.8)	G4
F. sanguinea var. *fusciceps* Emery (*Fs*)		1	2	7			10 (7.0)	G3
Myrmica ruginodis Nylander (*M*)	1		5			4	10 (7.0)	G2
Leptothorax acervorum Fabricius (*Lr*)			1			6	7 (4.9)	G2
Camponotus herculeanus herculeanus (Linné) (*Ch*)			1			3	4 (2.8)	G2
M. lobicornis var. *jessensis* Forel (*Ml*)			4				4 (2.8)	G3
Lasius niger Linné (*L*)					1		1 (0.7)	G4
L. alienus (Foerster) (*La*)						1	1 (0.7)	G4
Paratrechina flavipes (F. Smith) (*Pa*)				1			1 (0.7)	G4
Total (Ratio, %)	22 (15.4)	10 (7.7)	56 (39.1)	16 (11.2)	23 (16.1)	15 (10.5)	143	

* Explanation of each group is given in text

The nearest nest of this species was discovered about 80 m from the crater, hence *F. turncorum* may occupy the area of Course A as the outer limit of its home range.

As represented in Figure 3, 8 species were collected in Course B which is covered with alpine association. The higher part is dominated by an alpine species, *F. fusca*, but at most parts, any vertical segregation between alpine and plain species was scarcely to be seen.

Course C was provided with a succession of various vegetation types, from the exposed area at the top of the mountain, alpine plant association at the base to the broad-leaf woods. As seen in Table 2, 8 species were discovered. The distributional pattern clearly corresponding to the gradual vegetation change was obtained as follows :

Succession of habitat conditions (1) to (9) (*Cf.* Table 2)

Ff – Lf – Ft – Pa, M – Ml, Lr – Ft

F. truncorum and *F. fusca* were respectively dominant in woods and in exposed area, especially the dominancy of the latter species was approximately overwhelming along the paths through woods.

3) *Nest site preference*

The spatial segregation among species may depend on the difference of nest site preference among the similar habitat types. As shown on Table 1, nest sites within accumulations of fallen leaves and other debris were mostly preferred by 9 species, while those around the roots of living trees and under stones were also highly preferred, though the number of different species found was small.

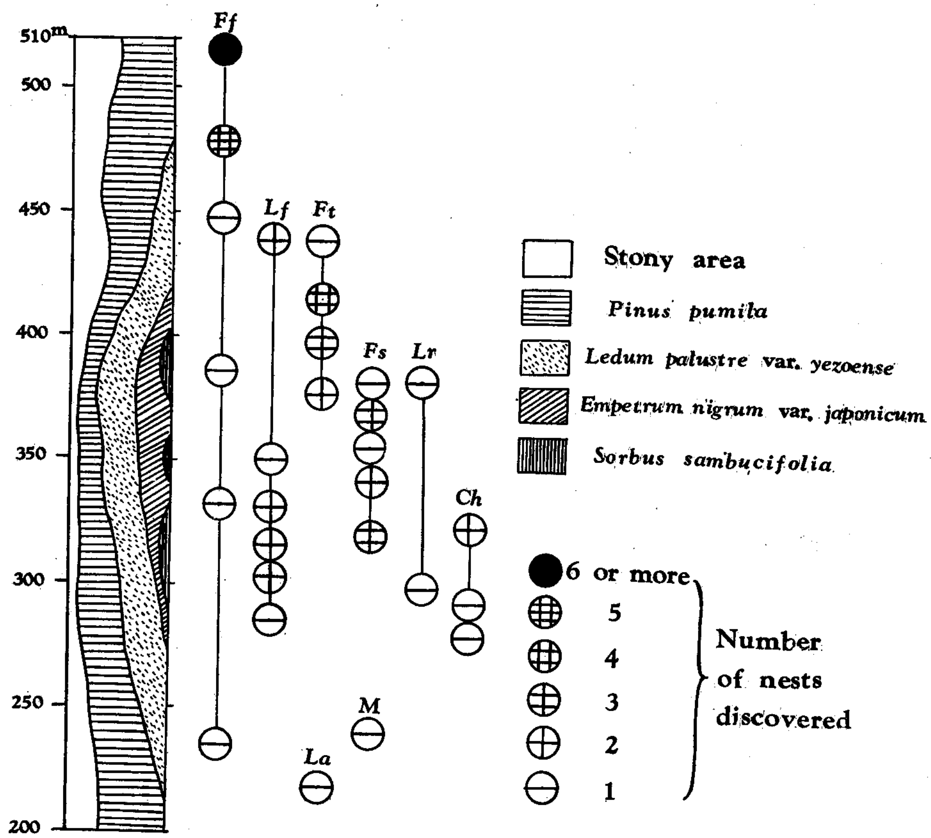

Fig. 3. Schema of succession of plant association and the vertical distribution of ant species with the relative abundance of nests at Course B.

The characteristic preference of some species are *F. fusca* mainly under stones, *F. truncorum* under accumulation of decaying matters or around the roots of trees, *L. flavus*, *Myrmica ruginodis* and *M. lobicornis* var. *jessensis* under accumulations of fallen leaves and other debris, *F. sanguinea* var. *fusciceps* around the roots of grasses or herbs and *Leptothorax acervorum* and *Camponotus herculeanus herculeanus* in fallen or deayed logs. The ecological conditions required for nest

Table 2. Relative abundance of nests discovered in various habitat conditions of Course C. ⧺ highly abundance, + abundance, ± less abundance, – rare.

Habitat conditions*	Relative abundance of nests discovered from various nest sites						Total sp. no. (Total col. no.)
	u	l	m	r	n	d	
(1) Exposed stony area (Mountain slope) +	⧺*Ff* (5)	+*Ff* (1)	±	–	–	±*Ff* (1)	1 (7)
(2) Exposed stony area and *Pinus pumila* ⧺	⧺*Ff* (2)	+	+*Lf* (5)	–	⧺	+	2 (7)
(3) *Pinus pumila* +	–	±	⧺	±	⧺*Ft* (7)	+	1 (7)
(4) Exposed loam or volcanic ash surface and sparse grass or herb ±	+*Ff* (1)	+	±	*Ft* (2) ⧺*Pa* (1)	–	–	3 (4)
(5) *Pinus pumila* and *Ledum palustre* var. *yezoense* +	±*Ft* (1) *M* (1)	±	⧺*M* (1)	–	⧺*Ft* (3)	+*M* (3)	2 (9)
(6) *Ledum palustre* var. *yezoense* +	–	–	⧺*M* (1) *Ml* (2) *Ft* (2)	±	⧺	⧺*Lr* (1)	4 (6)
(7) *Ledum palustre* var. *yezoense* and *Betula tauschii* ⧺	–	–	⧺*Ml* (1) *M* (1) *Ft* (3)	±	⧺	⧺*Lr* (2)	4 (7)
(8) *Ledum palustre* var. *yezoense* and *Empetrum nigrum* var. *japonicum* +	–	–	⧺*Ml* (1) *Ft* (4)	±*Ft* (2)	⧺*Ft* (2)	⧺*Lr* (2)	3 (11)
(9) *Quercus serrata*, *Hydrangea paniculata*, *Majanthemum bifolium* var. *dialatum* etc. (woods) ⧺	–	–*Ft* (1)	⧺*M* (1) *Ft* (12)	+*Ft* (2)	⧺*Ft* (9) *L* (1)	⧺*M* (1)	3 (27)

* Arranged to the gradual change of surface condition from exposed areas to woods.

sites do not always agree to those for the home range which are generally more flexible. From the viewpoint of ecological conditions, nest site preference (NS) and home range (HR) of each species as to two serious environmental factors, light intensity and moisture, were arranged in Table 3. Some differences were recognized among species as in *F. truncorum* and *L. flavus*. Species with wide or narrow tolerance range are also distinguishable: the typical representatives of the eurytopic species are *F. fusca*, *F. truncorum*, *Camponotus herculeanus herculeanus* and *Myrmica lobicornis* var. *jessensis*, while those of the stenotopic ones *Leptothorax acervorum* and *Lasius flavus*.

Table 3. Nest site preference (NS) and Home range (HR) in relation to light intensity and moisture.

Light intensity	Moisture		
	low	moderate	high
high	*Ff*(HR) *Ft*(HR)	*Ff*(NS) *Ft*(HR) *Fs*(HR) *Ch*(HR) *Ml*(HR)	
moderate	*Ch*(NS)	*Ff*(NS) *Ft*(HR) *Fs*(NS) *M*(HR) *Lr*(NS) *Ml*(NS) *Ch*(NS)	*Lf*(HR)
low	*Ch*(HR) *Ml*(HR)	*Ch*(HR) *Ml*(HR) *M*(NS)	*Lf*(NS)

3. Discussion

Under the relatively severe environmental conditions such as sand dunes, peat beds, volcanic areas, the presence of plant covers seems to determine the relative abundance of ants. Talbot (1934) pointed out that the ant species strictly found in the sandy dune alone are so scarce in number, that sandy substrate is a strong barrier to many ant species. Likewise, Yasumatsu collected only three species from sandy areas in Fukuoka. On the other hand, in a highly damp area such as a peat bog near Sapporo, only two species were collected, suggesting the diametrically opposed extreme of the envrionmental hostility to ants. In the area mentioned above, Course A filled with blow off sulphurous acid gas and devoid of plant cover shows another extreme of sites unsuitable for ants as the peculiar surface state of an active volcano. In parallel to the increase of plant covers, which also corresponds to the distance from the area with craters, the ant colonies gradually increase in number. The dependance of the distribution of each species upon the features of plant associations can mostly clearly be seen in Course C, where the spatial succession of several associations is relatively obvious. The similar results are found in Europe (Gösswald 1932, Goetsch 1937) or in North America (Talbot 1943, Gregg 1944). On the other hand, such clear habitat segregation is less distinct in Course B, probably corresponding to the poor spatial differentiation of plant associations.

Furthermore, this course shows an interesting example of compressed vertical distribution. The typical alpine ants of Japan are *Formica fusca*, *Camponotus herculeanus sachalinensis*, *Myrmica kurokii* and *Leptohtorax acervorum* in Honshû (Morisita 1945a) and *F. fusca*, *F. picea*, *Myrmica kurokii* and *Leptothorax acervorum* in Hokkaido (reported in Mt. Taisetsu, Mt. Tokachi and Mt. Rishiri by

Kogure, 1953, 1955, and in Mt. Yôtei by Hayashida, unpubl.). Therefore, the typical alpine species in Mt. Atusanupuri are *F. fusca* and *Leptothorax acervorum*, although *Camponotus herculeanus herculeanus* has hitherto been recorded in boreal or subalpine regions in North America. Other species are rather common in both plain and hill areas, except *Lasius flavus* which is horizontally distributed throughout the Horlactic region (Wilson 1955) and vertically from the lowland in Southern Europe (Zimmermann 1934) to the mountainous areas in Switzerland (Forel). In Mt. Atusanupuri, especially in Course B, the higher levels are dominated by *F. fusca*, but in the lower parts, there is no vertical segregation between alpine and plain ant species, as seen in Fig. 3, consequently, no clear vertical differentiation in ants corresponding to the altitudinal and vegetational distribution as seen in other high mountains. In this low active volcano, the topographical and vegetational differentiations are compressed within a very small spatial area, which might result in the compression of ants distribution, too. In such a situation, each species may segregate its habitat from the others, according to the direct requirements for life, but never on a larger scale expressed by altitudinal segregation.

Summary

A survey on the ecological distribution of ants in a low active volcano, Mt. Atusanupuri was carried out. From the areas with plant covers, 11 forms of ants were collected, but no species were found from the exposed area near craters. Also habitat segregation was clearly seen according to the spatial succession of plant associations. There was found no vertical segregation between alpine and lowland species, suggesting a compressed vertical distribution within a relatively limited area.

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