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Red Wood Ants *Formica* s. str. in Switzerland

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スイスのアカヤマアリ類 (*Formica* 亜属)

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Introduction

The red wood ants subgenus *Formica* which make huge conical mounds are the most familiar ants in Europe. Since the 18th century the pupae of these ants have been used to feed fishes and caged birds, and the collection of pupae was a common part-time occupation among farmers and woodcutters (Wuorenrinne 1978). For instance, in the area of Poprowsk in the 1800s, the inhabitants of seven villages earned 25,000 Rbl. by collecting the pupae during one summer (Gösswald 1951). Since 1 kg of dry pupae cost about 17 Rbl. at that time, this means about 1,500 kg of dry pupae (Wuorenrinne 1978). Therefore, the nest density of these ants has gradually decreased.

In this century, however, the importance of the protection of red wood ants has been claimed because of their utility for the biotic control of harmful insects in the forests. According to Gösswald (1958), for instance, the oaks near the ant nests grow better and put forth more leaves than those apart from the nests. This is also the case in coniferous forests (Gösswald 1978). It is due to the euryphagous ants preying upon the insects harmful for the trees. They hunt mostly the caterpillars of Lepidoptera and occassionally the sawflies and beetles (Gösswald, pers. com.). In recent years, the mounds of red wood ants are legally protected from the human impacts in many European countries. Since the Swiss government also gives strict protection to them, the ant colonies are plentiful in this mountainous country. Accordingly, the author surveyed red wood ants in Switzerland in 1978 to make an interspecific comparison of their distribution, size and shape of mounds, mating, and so on.

Moreover, the red wood ants have sociobiologically interesting traits, polygyny

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and polycalism, which are important in ant evolution (Hölldobler and Wilson 1977). For instance, in the South Jura of Switzerland *Formica lugubris* Zett. makes a huge polydomous colony consisting of 1,200 nests (Gris and Cherix 1977). Another purpose of this study is to disclose the ecological differences between the polydomous colonies of *F. lugubris* in the South Jura and of *F. yessensis* Forel in Ishikari Coast, Japan (Higashi and Yamauchi 1979).

Taxonomy of subgenus *Formica* in Europe

Since Linné described *Formica rufa* as early as 1758, the complex of red wood

Table 1. Taxonomic history of *Formica* s. str. in Europe (based on Yarrow 1955, Betrem 1960, Dlussky 1967, Kutter 1977).

Form\Author	Linné 1758	Retzius 1783	Fabricius 1804	Zetterstadt 1840	Nylander 1846	Förster 1850
I	*rufa*					
II		*pratensis*				
III			*truncorum*		*truncicola*	
IV				*lugubris*		
V						*polyctena*
VI						
VII						
VIII						

Form\Author	Schenck 1852	Mayr 1855	Forel 1874	Ruzsky 1895	Emery 1909	Bondroit 1918
I	*piniphila*		*rufa rufa*			*piniphila*
II		*ongerens*	*rufa pratensis*			*pratensis*
III		*truncorum*	*rufa truncicola*			*truncorum*
IV			*rufa rufopratensis*			*rufa*
V			*rufa rufa*			*polyctena*
VI				*uralensis*		
VII			*rufa rufopratensis*			*rufa*
VIII					*nigricans*	*cordieri*

Form\Author	Gösswald 1941	Yarrow 1955	Betrem 1960	Dlussky 1967	Kutter 1977
I	*rufa rufa+rufa rufopratensis major*	*rufa*	—	—	—
II	*rufa pratensis=minor pratenoides* (1951)	*nigricans*	—	*pratensis*	—
III		*truncorum*	—	—	—
IV		*lugubris*	—	—	—
V	*rufa rufopratensis minor +rufa r. p. major*		*polyctena*	—	—
VI			*uralensis*	(*Servi.*) *uralensis*	(*Form.*) *uralensis*
VII		*aquilonia*	—	—	—
VIII			*cordieri*		*pratensis* (or *nigricans*?)

ants has been split into several sibling species (Table 1). At present the following species are identified in Europe (Kutter 1977) : *rufa, pratensis, truncorum, lugubris, polyctena, uralensis, aquilonia* and a doubtful species *nigricans*. Out of them *F. pratensis* and *F. nigricans* are distinguished from each other by queens but not by worker caste, though the calssification of other species is possible even by workers. To be more precise, the queens of *F. nigricans* are more hairy than those of *F. pratensis*. But Kutter (1964, 1977) suggests that these two forms are probably conspecific because intermediate forms are often discovered. Adopting his opinion, *F. nigricans* is not distinguished from *F. pratensis* in the present study.

Geography of Switzerland

Switzerland occupies about 41,300 km^2 (slightly smaller than the Kyushu Island in Japan) between latitudes of 47°48′36″N and 45°49′09″N in central Europe. It

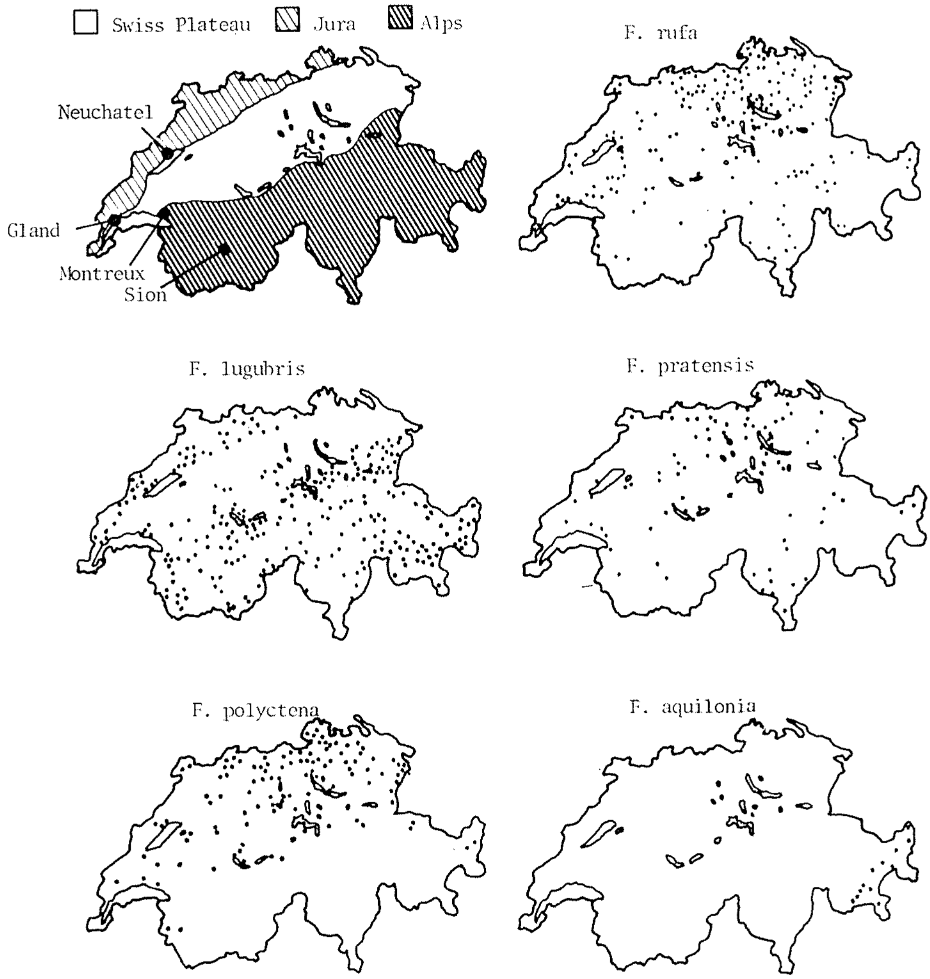

Fig. 1. Geography of Switzerland and distribution of *Formica* s. str. (cited from Kutter 1977).

is divided into three natural regions, the Swiss Plateau, the Alps and the Jura (Fig. 1). The Swiss Plateau which involves crop fields, pastures and many big cities is a basin between the Jura and the Alps, filled with glacial deposits in the Ice Age and now eroded by many rivers. Since the climate of this region is mild (mean annual temperature 8 to 9°C, annual precipitation about 1,100 mm), the temperate-zonal *Formica* such as *F. rufa*, *F. pratensis* and *F. polyctena* are abundant. The Alps consisting of granites and gneisses comprises roughly the southern half of Switzerland. High snow-covered mountains are separated by deeply eroded valleys. The climate is quite different between the valley and the top of mountains or between the north and south slopes. Around the timberline the subarctic *Formica* such as *F. lugubris* and *F. aquilonia* are distributed. The Jura is a boundary zone between Switzerland and France. It consists of regular limestone folds which form longitudinal valleys, long stretched ranges and narrow gaps giving outlet for the rivers. Since the climate is more severe than in the Swiss plateau but milder than in the Alps, *F. rufa*, *F. pratensis* and *F. polyctena* dominate the foot and *F. lugubris* nearly monopolizes the top of mountains.

The census of *Formica* nests was carried out mainly at the South Jura, with additional surveys at Sion (Alps), Montreux (Alps) and Neuchatel (Jura). The highest point of the South Jura is about 1,500 m above the sea, i. e. lower than the average timberline in Switzerland (1,800 to 2,000 m above the sea). Consequently, the area is covered with various trees from the foot to the top. The dominant trees are *Fagus sylvatica* below 800 m ; *Fagus sylvatica* at 800 to 1,100 m ; *Abies alba*, *Fagus sylvatica* and *Picea abies* at 1,100 to 1,300 m ; *Acer pseudoplatanus*, *Fagus sylvatica* and *Picea abies* around the top. According to the records of Weather Agency of Switzerland, the mean temperature of the ant active season, April to October, is about 15°C at 500 m, 12°C at 1,000 m and 8°C near the top. The precipitation during the same period is 650 mm, 800 mm and 1,100 mm respectively.

Results

1. *Distribution, size and shape of nests*

In the South Jura 84 colonies were found (Fig. 2), along the ways from Gland (400 m above the sea) to Chalet a Roch (1,450 m) and from Arzier (900 m) to Cerque (1,100 m). *F. pratensis* which inhabited the lowland preferred banks of farms and roadsides. *F. polyctena* was scarce in this region compared with other areas of the Swiss Jura (Kutter 1977). This species was distributed up to ca. 1,000 m, preferring the forest and its margin. The nests of *F. rufa* which were distributed from the foot to ca. 1,200 m were more abundant than those of the previous two species. It preferred the forest margin in the lowland but the grassland at 1,000 m or more. The most dominant species *F. lugubris* was found at any altitude, nearly monopolizing the highland.

A trip was made from Neuchatel (450 m) to Mont Racine (1,439 m), through Valangin (650 m) and Les Geneveys (850 m) (Fig. 3). According to Kutter (1977), in this region of the Swiss Jura *F. polyctena* is more abundant than in the South

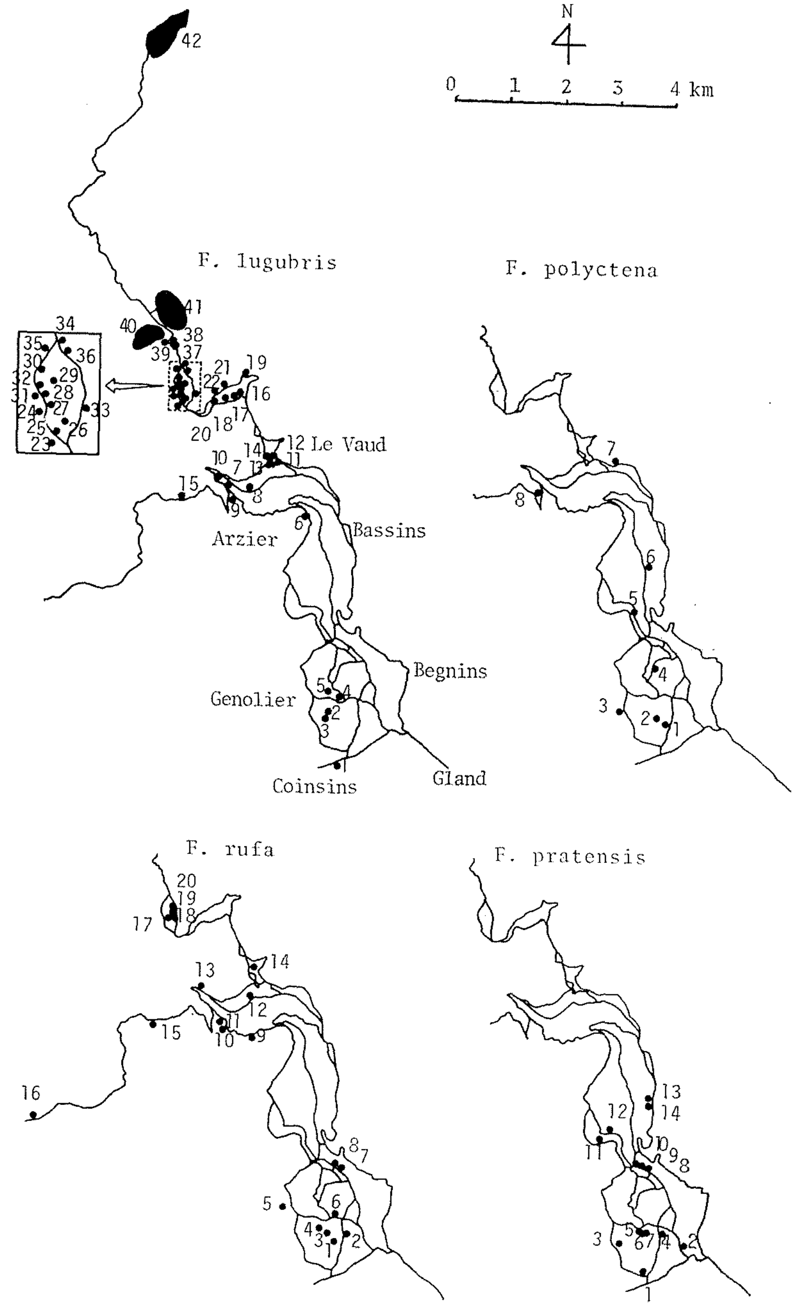

Fig. 2. Distribution of colonies in the South Jura. The code number for each colony corresponds to that in Appendix I.

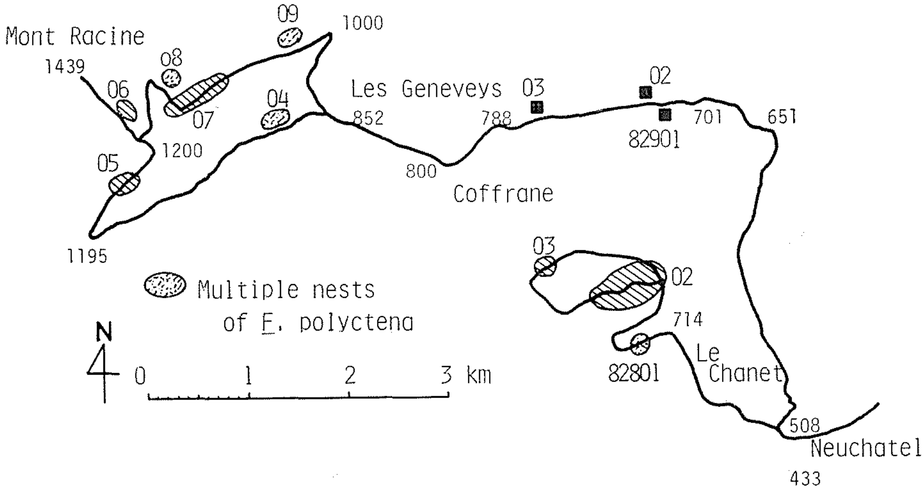

Fig. 3. Census route in Neuchatel area. The code number corresponds to that in Appendix III.

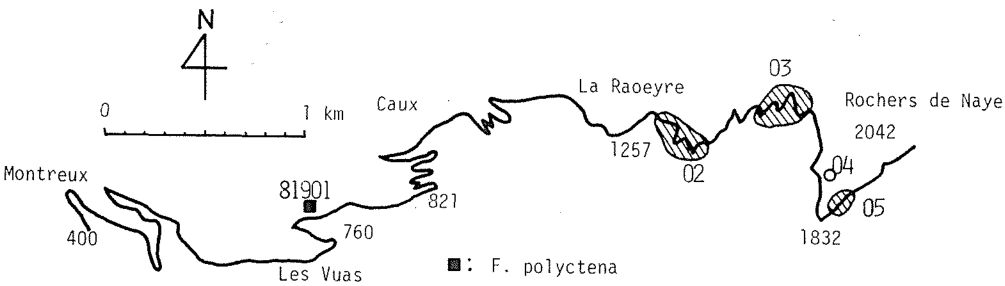

Fig. 4. Census route in Montreux area. The code number, cf. Appendix II B.

Jura. In the present trip 15 nests of this species were discovered from ca. 700 m to 1,250 m. *F. lugubris* was also dominant, making many oligo- or polydomous colonies as in the South Jura. At Montreu the census was carried out along the way from Montreu City (400 m) to the top of Mt. Rochers de Naye (2,042 m, Fig. 4). In this course one nest of *F. polyctena* and the countless nests of *F. lugubris* were found. Most colonies of *F. lugubris* distributed from 1,220 to 1,820 m were oligo- or polydomous. A further trip was made along the way from Sion City (500 m) to Lac de Tseuxier (1,777 m) through Drone (850 m), Mayens de la Dxou (1,400 m), Tsalan d'Ayent (2,115 m), Anzere (1,600 m), Plan des Conches (2,100 m), Lac des Audannes (2,500 m, Fig. 5). The area upper than ca. 1,200 m was nearly monopolized by many oligo- and polydomous colonies of *F. lugubris,* and only three nests of other species were discovered at 1,360 m or less. In the area upper than 1,700 m, many oligodomous colonies of *F.* (*Coptoformica*) *pressilabris* were also distributed.

The habitats of the nests could be divided into six : I, in the forest with dense trees ; II, in the forest with sparse trees ; III, the forest margin ; IV, the grassland

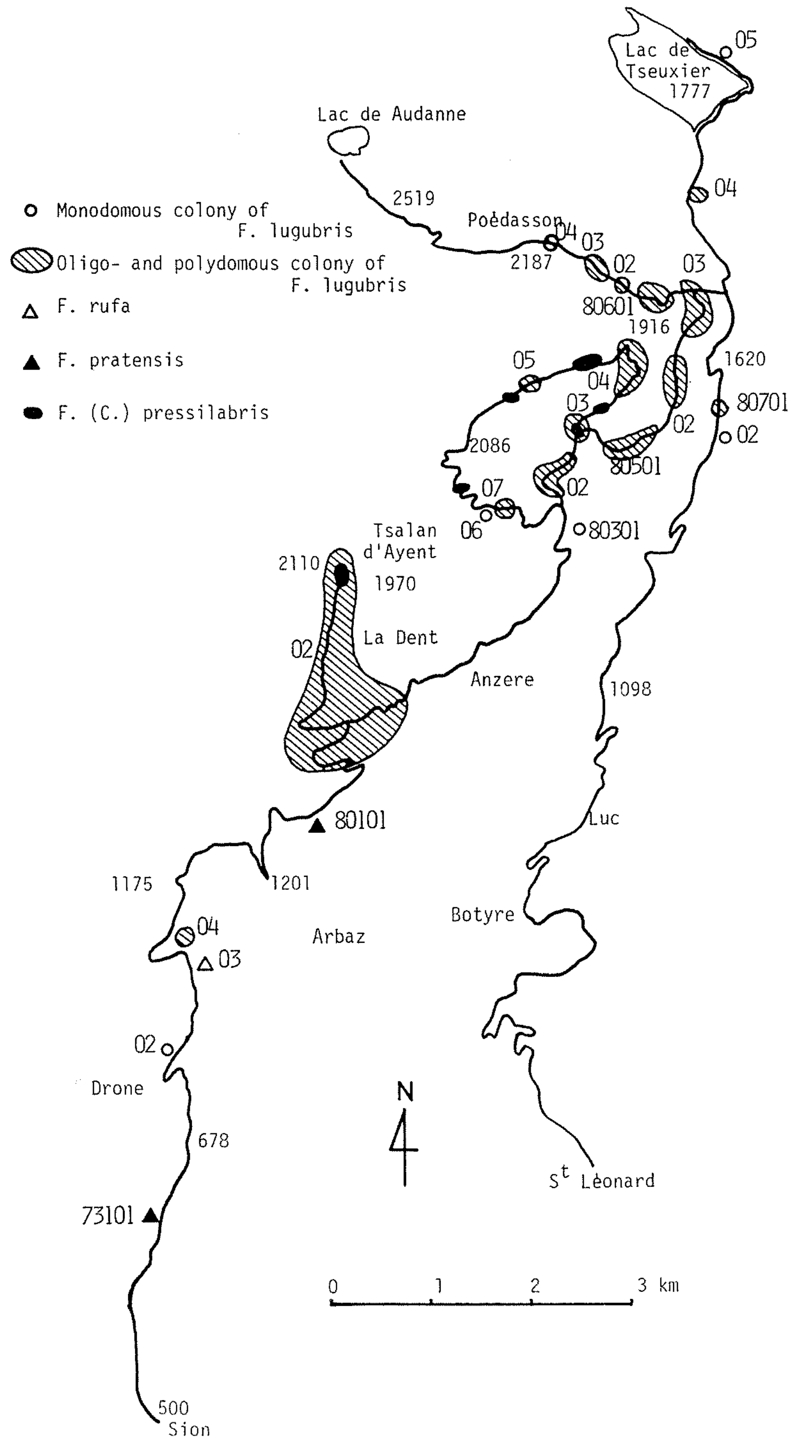

Fig. 5. Census route in Sion area. The code number, cf. Appendix II A.

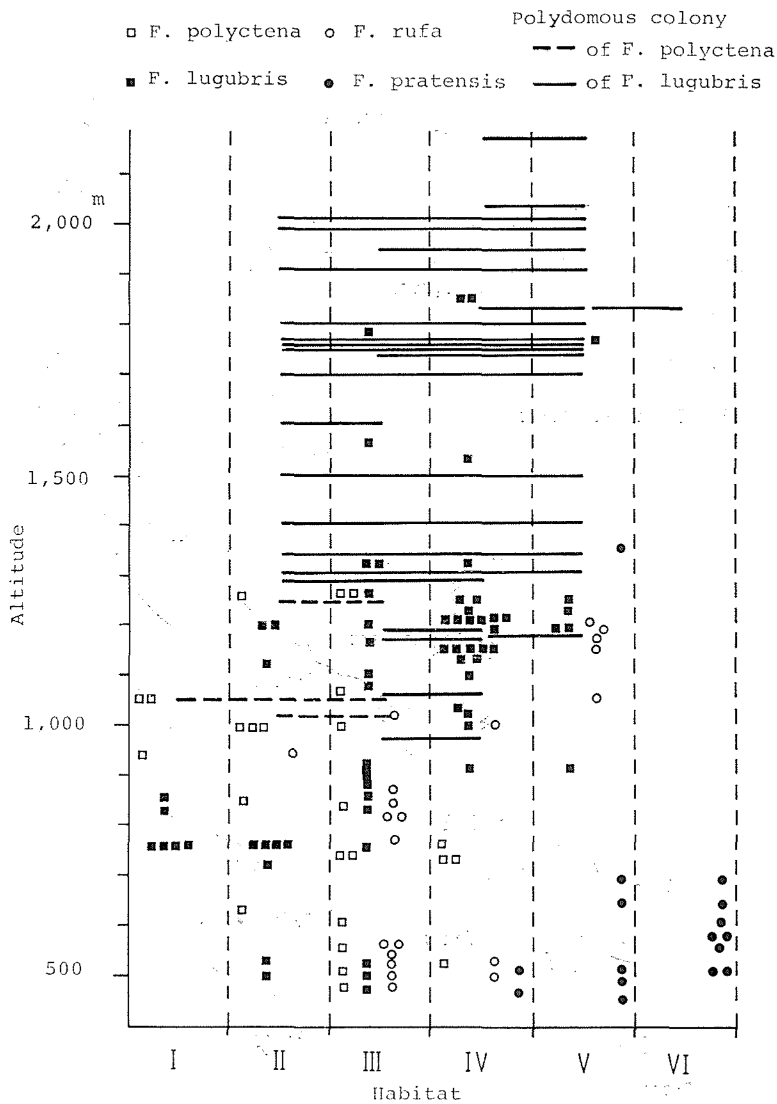

Fig. 6. Altitudinal distribution and habitat preference of each colony. Habitat I, the forest with dense trees; II, the forest with sparse trees; III, margin of the forest; IV, the grassland near the forest margin; V, the roots of a tree growing in the grassland; VI, open grassland.

near the forest margin; V, the roots of a tree growing in the grassland; VI, open grassland. Fig. 6 gives the habitat and altitudinal distribution of the nests found in all censuses. *F. pratensis* which preferred the habitats IV to VI was distributed from 460 to 1,360 m, mostly lower than 800 m. *F. rufa* was distributed from 490 to 1,200 m, inhabiting II to V. This species was apt to occupy closed habitats in the lowland but open habitats in the highland. *F. polyctena* which preferred I to IV, mainly II and III, was distributed from 489 to 1,250 m. The most dominant

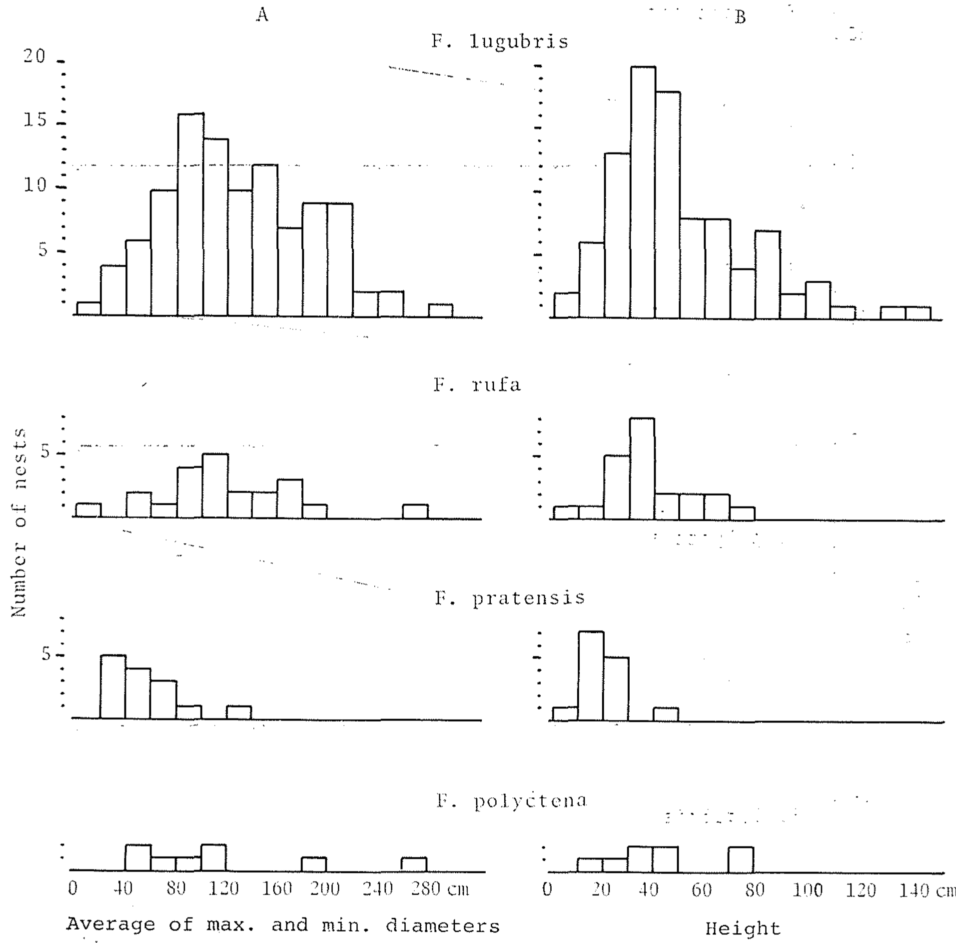

Fig. 7. Frequency distribution of mound size, by the average of maximum and minimum diameters (A) and by height (B).

species *F. lugubris* was discovered at any altitude below the timberline, prefering I to VI, mostly II to V. In the highlands this species frequently made oligo- or polydomous colonies up to 2,180 m.

Fig. 7 gives the frequency distribution of the mound size. The mean diameter and height of mounds were respectively 103±S.D. 41 cm and 45±20 cm in *F. lugubris*; 119±56 cm and 35±16 cm in *F. rufa*; 55±27 cm and 18±8 cm in *F. pratensis* ; 115±69 cm and 40±19 cm in *F. polyctena*. The relation between the diameter and the height of nests is shown in Fig. 8. Many mounds of *F. lugubris, rufa* and *polyctena* were elevated, but those of *F. pratensis* preferring open habitats were small and flat, probably because of less materials of nests or due to exposure to wind in the open habitats.

Most mounds were asymmetric. Fig. 9 gives the frequency of nests which have the longest slope to each direction. In *F. lugubris*, for instance, the percentage of the mounds facing each direction was as follows : 0%/N, 1.9/NE, 14.6/E, 19.4/SE,

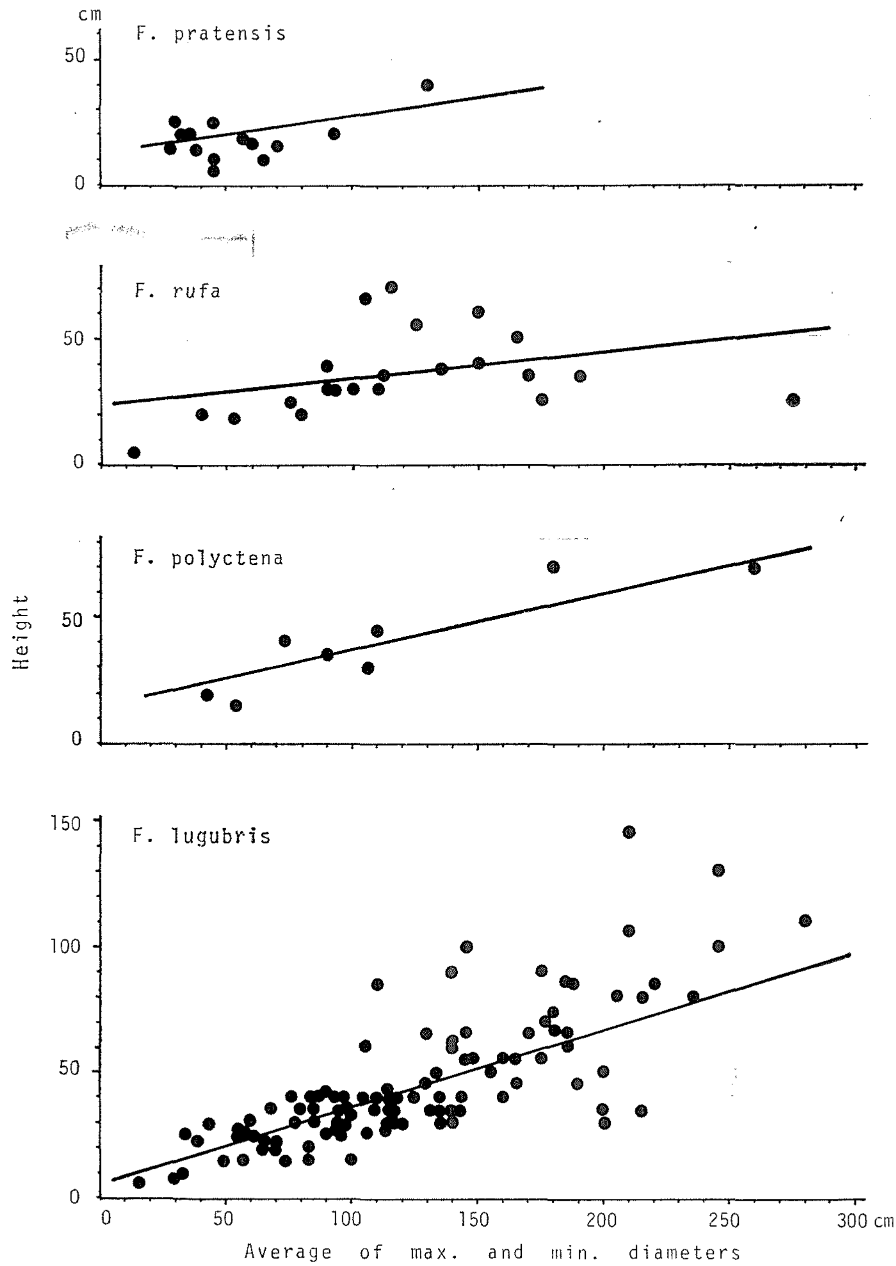

Fig. 8. Relation between diameter and height of mounds.
The regression line is given for each species.

34.0/S, 12.6/SW, 5.8/W, 0/NW, 11.7/symmetry. Thus, 80.6% mounds were well developed to east to southwest, that is, the direction of sun. This tendency was also observed in other species.

2. *Examples of three colony types, mono-, oligo- and polydomous colonies*

2.1. *Monodomous colony* (Fig. 10): *F. pratensis, rufa, polyctena, lugubris*

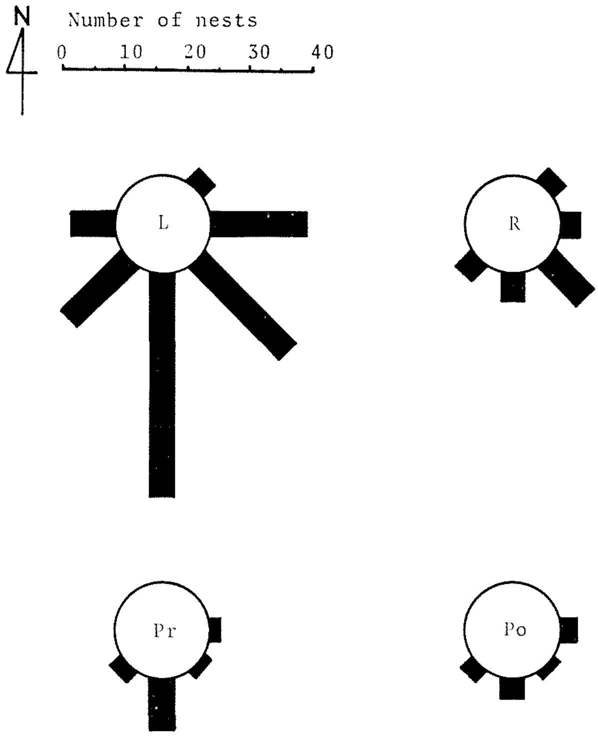

Fig. 9. Direction of the longest slope of mound. The length of black belt shows the nest abundance. L, *F. lugubris*; R, *F. rufa*; Pr, *F. pratensis*; Po, *F. polyctena*.

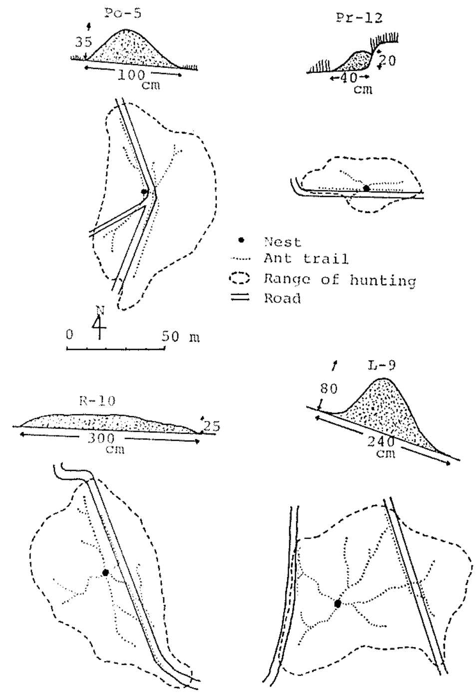

Fig. 10. Monodomous colonies.

Pr-12 (650 m above the sea): The nest of this colony was surrounded with dense weeds at the roots of an oak tree (habitat V). The size of mound was 40 cm (maximum diameter)-30 cm (minimum diameter)-20 cm (height). Four ant trails were developed along the road or into the grassland. The longest trail (23 m) reached another oak tree on which the workers were milking aphids. The maximum hunting distance, i. e. the distance of the remotest hunting point, was 33 m from the nest.

In late June when the weeds grew well and thickly covered the mound, this colony moved to an 8 m apart new nest which was nearly moundless with the size of 35-30-3 cm. On June 25 to 29 many adult workers, alates, pupae and larvae were carried by transporters from the old to the new nest. The daily count of the transportees is given in Table 2. From these figures the number of transportees during four days were estimated at ca. 15,000 workers, 160 males, 1,100 larvae, 2,000 worker pupae and 100 sexual pupae. Since no queen was observed, this colony should be mono- or oligogynous. After this movement the old nest was deserted.

R-10 (830 m): This colony occupied the edge of about 15 m high precipice (habitat III). Unlike typical nests of *F. rufa*, the mound was flat with the size of 300-250-25 cm. Five ant trails expanded from the nest, all ramifying near

Table 2. Number of transportees carried from an old to a new nest of a colony *Pr-12* in late June. L, larvae; WP and SP, pupae of workers and sexuals respectively; W, workers; M, males.

	Time			
	9:00–9:15	12:00–12:15	15:00–15:15	18:00–18:15
Jun. 25				
L	6	10	11	0
WP	8	29	31	11
SP	0	6	0	0
W	104	185	44	13
M	3	3	0	0
Jun. 26				
L	8	13	14	0
WP	8	7	33	7
SP	9	1	2	1
W	162	147	54	22
M	2	5	0	0
Jun. 28				
L	13	7	9	12
WP	5	11	7	3
SP	0	0	0	0
W	173	123	46	20
M	0	0	0	0
Jun. 29				
L	0			0
WP	10			0
SP	0	?	?	0
W	57			9
M	0			0

pine trees or at roadside. The longest trail reached 50 m long, and the maximum hunting distance was 70 m.

Po-5 (610 m): Nest size, 100-80-35 cm; habitat, roadside in the forest (III). Four ant trails expanded from the nest, each ramifying near the trees on which the workers were milking aphids. The longest trail was 50 m long, and the maximum hunting distance was 60 m from the nest.

L-9 (840 m): Nest size, 240-230-80 cm; habitat, a loose slope in a shady forest (I). Four ant trails expanded from the mound, each ramifying near the trees or along the forest margin. Most trees near the nest were visited by many hunters and aphid milkers. The longest ant trail reached 50 m and the most distant hunters were foraging 70 m apart from the nest. On fine days in July to August, may bivouacs where a lot of pupae were stored were made under stones along the roadside.

2. 2. *Oligodomous colonies* (Fig. 11): *F. rufa, lugubris, polyctena*

R-14 (940 m above the sea): Three nests in a forest (habitat II). The sizes of three mounds located within 6 m from each other were 220-160-35 cm, 180-160-35 cm and 150-120-40 cm. Ant trails which reached 40 m long in the maximum combined these nests to each other or to neighboring trees. The maximum hunting distance was 90 m from the colony.

About 50 m apart from the colony, there was a huge abandoned mound with the size of 360-330-30 cm. The oligodomous colony might be made by the fission of the nest which should have been deserted for too shady habitat (habitat I).

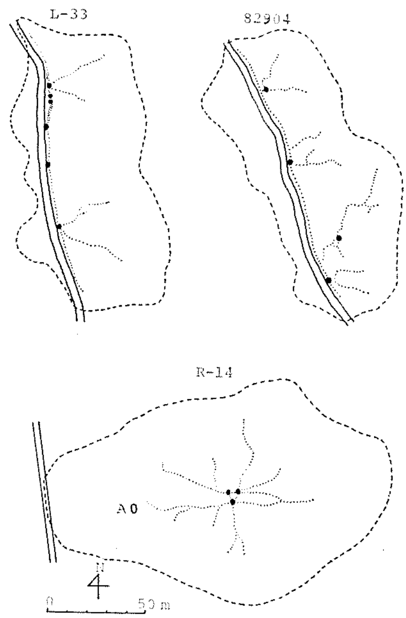

Fig. 11. Oligodomous colonies. Patterns are the same as in Fig. 10. A, a huge abandoned nest.

L-33 (1,180 m): Six nests in habitats III and IV. The sizes of six mounds were 150-130-30 cm, 230-200-35 cm, 150-115-35 cm, 120-110-30 cm, 100-90-35 cm, 80-60-20 cm. The maximum distance among these mounds was 71 m long. These nests were combined with each other by ant trails ramifying at many trees.

82904 (a colony of *F. polyctena* discovered at the altitude of 1,000 m in Mont Racine, cf. Fig. 3): Four nests in the habitats II and III. The sizes of four mounds were 200-200-50 cm, 200-180-40 cm, 160-130-50 cm, 210-200-45 cm. The internest distance was 130 m in the maximum. Ant trails were well developed.

2. 3. *Polydomous colonies of F. lugubris*

L-42 (1,400 m above the sea): This colony consisting of about 1,200 nests within 0.7 km² range was found by Gris and Cherix (1977). This area was wholly covered with thick snow until mid May. It thawed from late May and disappeared before late June. Even in early June when some exposed spots of ground appeared some ant trails were observed. Eggs and many larvae were already observed in early June when most mounds were covered with snow yet. On June 11 some pupae were also observed and first new adults, mostly sexuals, emerged shortly before late June. However, the fullscale extranidal activities of workers began from early July, because it was rainy and cold in June. After the most active season, early July to late August, the extranidal functions declined and nearly ceased before early October.

The author set following three quadrats, each 50×100 m, within this polydomous colony: QI on southwestern margin of the colony, QII in the center, QIII on northern margin (Fig. 12). In total 24 inhabited and 17 abandoned nests were contained in mid June (Table 3): 6 and 5 respectively in QI, 13 and 11 in QII, 5 and 1 in QIII. The mean size of the inhabited mounds in QI was 112±S.D. 31 cm in diameter and 46±25 cm in height; 117±43 cm and 77±26 cm respectively in QII; 159±13 cm and 58±4 cm in QIII. Thus, the mounds were more abundant and bigger in the center of the colony than those on the margin. During the budding season, from late June to late July, 14 abandoned nests were reused: 3/QI, 10/QII, 1/QIII, that is, budding was more frequent in the center. However, these nests were abandoned in autumn and only the nests having been adopted for previous hibernation were used for the next winter again.

In order to clarify the influence of this colony on the distribution of other ant species, the ant fauna was surveyed at four habitats (forest, its margin, grassland, bare land) in two areas, outside (A) and inside (B) the range of the polydomous colony (Fig. 12). Each habitat was surveyed for 30 minutes, therefore, in total 120 minutes in each area. As Table 4 gives, the polydomous colony is not the main cause of the faunal poorness in the forest of B, because the forest in A was also nearly defaunated. However, in the grassland and on the forest margin the polydomous colony seemed to expel some species such as *F. lemani*, *My. ruginodis* and *Ma. rubida*.

L-40 (1,300 m): This polydomous colony inhabited the forest of *P. abies* near Bois de Peney. The mean size of 25 mounds chosen voluntarily was 153±S.D. 53 cm in diameter and 58±28 cm in height. In this colony a quadrat of 100×100 m area was set to study the internest drifting of workers. This quadrat contained 33 inhabited nests which were combined with each other by many ant trails (Fig. 13). Through these trails the workers drifted among nests and the transporters frequently carried broods and seemingly young workers. Foreign workers transferred artificially from other colonies which were not combined with this colony by the ant trails were aggressively bitten by the resident workers of this colony. To examine the frequency of internest drifting 1,000 workers were marked in mass on each of two nests (Nest No. 1 with red dye and 2 with blue dye, cf. Fig. 13) on June 24 to 27, i. e. in total 2,000 marked workers. After the marking finished, all nests were patted to lure out the intranidal workers. Although the discovery ratio of marked workers decreased day by day, the percentage of drifters increaspe as follows (Fig. 14): <14%/2 days after marking, <15%/4 days, <20%/6 days, <21%/9 days, 26%/12 days, 28%/16 days, 30%/20 days, 28%/26 days. Twenty days after marking the maximum distance of drifting was 49 m from the original nest where they were marked. To see how many workers on a given nest were visitors, the baiting test was carried out for 50 workers on the nest 1. Consequently, forty-eight workers brought the baits into the nest 1 but two workers to a neighboring nest 2. This means that only 4% workers were visitors and other 96% ones were resident to the nest.

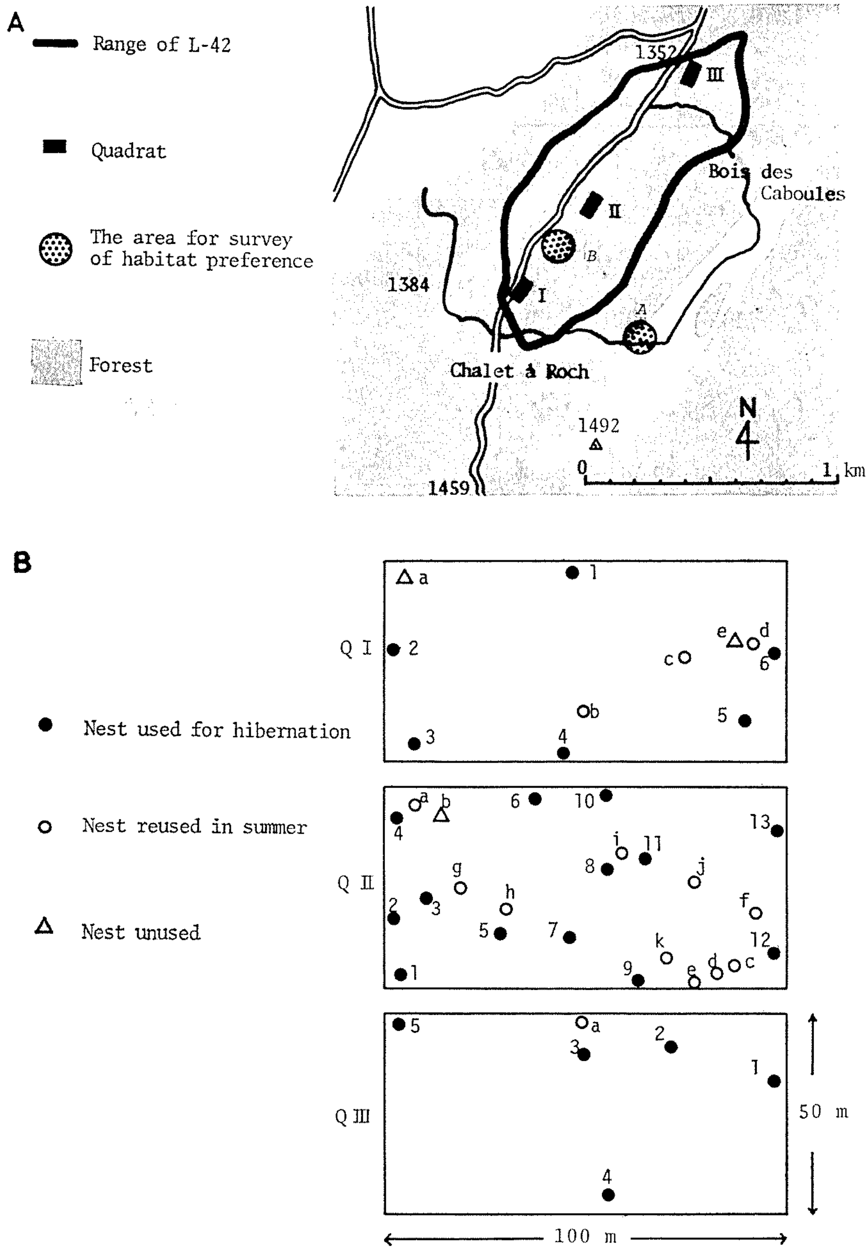

Fig. 12. Range of a polydomous colony *L-42* (A) and three quadrats set within the range (B). In A, I to III, quadrats of 50×100 m area; *A* and *B*, where the ant fauna was surveyed. The nest codes in B correspond to those in Table 3.

Table 3. Nests in three quadrats. MAD, maximum diameter of the mound; MID, minimum diameter; H, height. ++, inhabited by many workers; +, inhabited by a few workers; −, deserted. Grades of habitat, cf. Fig. 6.

Nest code	MAD-MID-H (cm)	Habitat	Jun. 15	Jun. 22	Jul. 5	Aug. 17	Oct. 1
I-1	155-130-40	III	++	++	++	++	++
2	130-110-30	III	++	++	++	++	++
3	90- 85-40	IV	++	++	++	++	++
4	125-100-35	V	++	++	++	++	++
5	150-140-100	VI	++	++	++	++	++
6	60- 60-30	II	++	++	++	++	++
a	80- 70-20	III	−	−	−	−	−
b	130-100-55	II	−	−	+	++	−
c	45- 40- 8	III	−	−	++	++	−
d	25- 20- 1	II	−	−	−	++	−
e	50- 50- 8	VI	−	−	−	−	−
II-1	210-200-80	II	++	++	++	++	++
2	170-160-55	III	++	++	++	++	++
3	160-120-90	V	++	++	++	++	++
4	120-110-35	IV	++	++	++	++	++
5	180-170-90	II	++	++	++	++	++
6	220-210-80	II	++	++	++	++	++
7	200-170-85	III	++	++	++	++	++
8	135-130-50	IV	++	++	++	++	++
9	220-200-105	IV	++	++	++	++	++
10	140-120-45	V	++	++	++	++	++
11	160-120-60	IV	++	++	++	++	++
12	260-230-130	IV	++	++	++	++	++
13	250-240-100	II	++	++	++	++	++
a	140-130-40	V	−	−	−	++	−
b	220-200-80	II	−	−	−	−	−
c	80- 70-20	IV	−	−	++	++	−
d	65- 60-15	III	−	−	+	++	−
e	65- 60-10	III	−	−	−	++	−
f	30- 25- 5	IV	−	−	−	++	−
g	20- 15- 5	IV	−	−	−	++	−
h	25- 20- 5	III	−	−	−	++	−
i	10- 10- 3	III	−	−	−	++	−
j	10- 10- 3	III	−	−	−	++	−
k	20- 15- 5	IV	−	−	−	++	−
III-1	190-150-65	III	++	++	++	++	++
2	150-145-55	III	++	++	++	++	++
3	180-170-55	III	++	++	++	++	++
4	160-120-60	III	++	++	++	++	++
5	160-160-55	II	++	++	++	++	++
a	80- 60-15	II	−	−	−	++	−

Table 4. Comparison of ant fauna between outside and inside the supercolony *L-42*. B, bare land; G, grassland; M, forest margin; F, forest; w, only workers without nests.

Habitat	Number of nests by 30 min. survey							
	Outside				Inside			
	B	G	M	F	B	G	M	F
Species								
F. lugubris	0	0	0	0	w	w	2	4
F. lemani	w	3	1	0	w	0	0	0
My. scabrinodis	0	1	0	0	0	0	0	0
My. ruginodis	w	1	2	0	0	0	0	0
Le. muscorum	0	2	0	0	0	1	0	0
Le. nigriceps	0	1	0	0	0	3	0	0
Ma. rubida	0	7	1	0	0	2	0	0
T. caespitum	0	1	0	0	0	2	0	0
Total	0	16	4	0	0	8	2	4

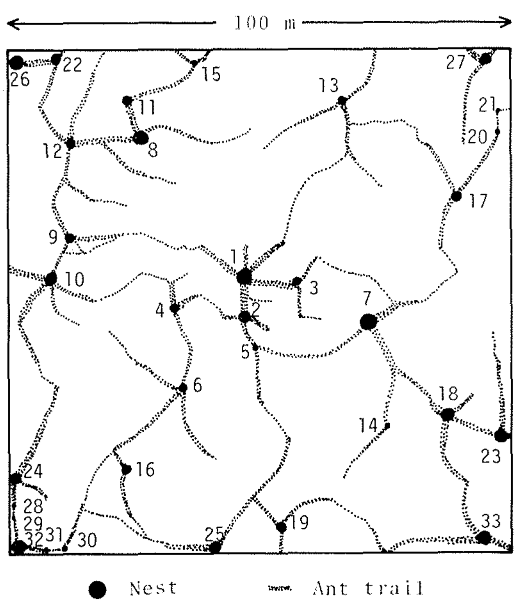

Fig. 13. Quadrat in a polydomous colony *L-40*, where the internest drifting of marked workers was studied.

3. *Nuptial flight and alate production*

The season of nuptial flight was altitudinally different: early to late June at Vich and the vicinity (500 m above the sea), late June to mid July at Chalet a Dessous (1,400 m), early August at Tsalan d'Ayent (2,000 m). The daily activity of flight was synchronized in the morning in open habitats (III to VI). For instance,

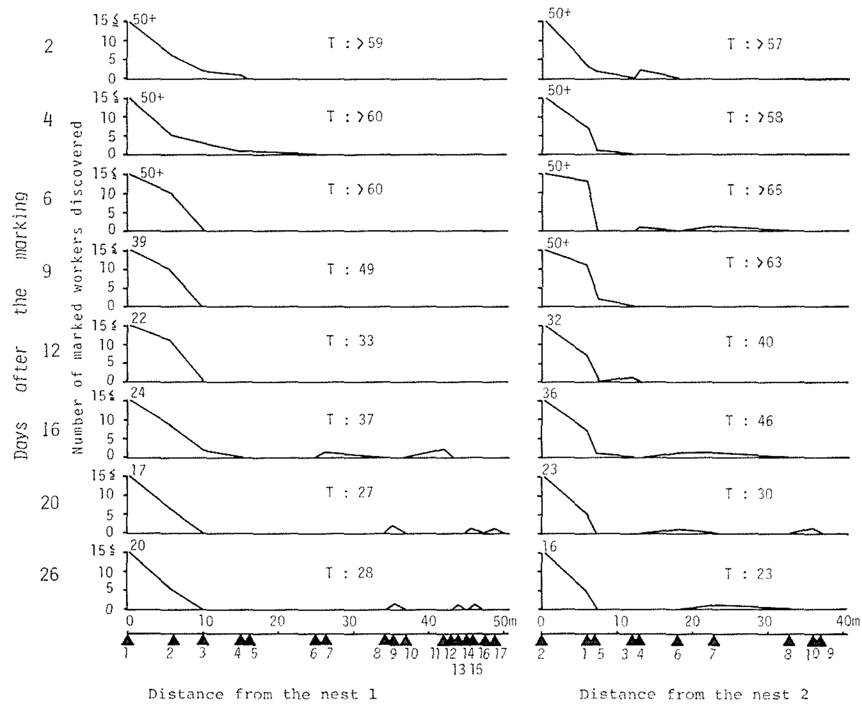

Fig. 14. Dispersal of marked workers in the 100×100 m quadrat in *L-40*. The nest codes correspond to those in Fig. 13. On June 24 to 27, 1,000 workers were marked on each of two nests, *1* and *2*. T, total of marked workers discovered in each survey.

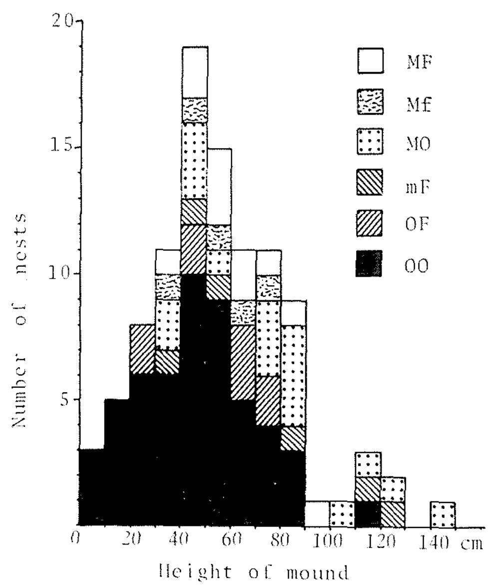

Fig. 15. Frequency of each type nest in a polydomous colony *L-40*, in relation to the nest size. MF, nests producing males and females evenly; Mf, both sexes but predominantly males; MO, only males; mF, predominantly females; OF, only females; OO, no sexual individual.

at *Pr-4* which was in a grassland near forest (habitat VI), the alates flied up at 10 : 35 to 11 : 50 a. m., June 13, mostly 11 : 00 to 11 : 30 when the mound was exposed to sunbeams. The alates which did not fly up before 11 : 50 went back into the nest to wait for next chance. Such a well synchronized flight was also observed at *Pr-11* (habitat VI), *R-6* (IV), *Po-5* (III), *L-33* (IV). However, in the colonies inhabiting the closed habitats I and II (e. g. *R-14*, *Po-8*, *L-9*), the alates stay on the mound throughout the daytime and flied up whenever the mound was exposed to sunbeams shining through foliage.

In a polydomous colony *L-40* 100 nests were examined to disclose the ratio among following six types of alate production : MO, producing only males ; Mf, both sexes but predominantly males ; OF, only females ; mF, predominantly females ; MF, both sexes evenly ; OO, no sexual. The number of nests for each type was as follows : 18/MO, 4/Mf, 9/OF, 5/mF, 12/MF, 52/OO. Thus, about a half of examined nests were fertile and the nests biasing to males (types MO, Mf) were 1.6 times more than those biasing to females (OF, mF). The mounds of fertile nests were apt to be more elevated than those of sterile nests (Fig. 15).

Discussion

The importance of mounds for thermoregulation has been stressed by many authors (Kato 1939, Steiner 1947, Scherba 1959, 1962, Kneitz 1969, Ceusters 1977). According to Raignier (1947), the temperature in the mound of *F. polyctena* is different from part to part of the mound but fairly stable (23-30°C in the daytime) at about 30 cm below the mound surface through ant active season. The temperature falls 3 to 4°C at night but more slowly than air temperature. The optimum temperature recovers in the next morning within only one hour after being beaten by sun beams. As the source of heat, the direct insolation and physiological heat generation are supposed, but the former factor may be prevailing in ants unlike winged social Aculeata in which the latter is more important (Steiner 1947). The mound shape facing the direction of sun should be adaptive to catch sufficient solar radiation.

McClusky (1958, 1965) suggests an endogenous circadian rhythm in the flight activities of labo-cultured *Iridomyrmex* and *Veromessor* males. But in *Formica* the climatic factors such as light intensity and temperature profoundly affect their flight activities (Wellenstein 1928, Scherba 1958, 1961, Kannowski 1959, 1963, Talbot 1959, 1964, Anderson and Kannowski 1960). Therefore, the flight time of the day is not always rigid if the species prefers different habitats. As the present study disclosed, the synchronism of the flight activity should be more advanced in *F. pratensis* and *F. rufa* preferring open habitats than in *F. polyctena* and *F. lugubris* frequently inhabiting even the closed forests.

The polydomous colony of *F. lugubris* in the South Jura has the following characteristics different from that of *F. yessensis* in Ishikari Coast : 1. *F. lugubris* more prefers the forests of rocky mountains, while *F. yessensis* occupies the coastal sandy grassland (Higashi and Yamauchi 1979). 2. The ant fauna is poor in both colonies. However, in the South Jura it should not be due to the elimination by *F. lugubris* but due to the cold temperature which inhibits the colonization of other ant species, though in Ishikari Coast many ant species are expelled by the aggressive workers of *F. yessensis* (Higashi and Yamauchi 1979). 3. Each nest of *F. lugubris* is big and solid, attaining the population size of ca. 50,000 adult individuals (Breen 1977). In *F. yessensis* the nest is nearly moundless and the population size per nest is 6,800 on the average (Ito 1973). Consequently, many nests of *F. yessensis* are frequently built by budding in spring but abandoned in autumn every year (Higashi 1976). 4. Although the snow remains until later season in the South Jura, the life cycle elapses so earlier that the first callows emerge in late June. In Ishikari Coast the snow disappears before early May but the new adults emerge after mid July. The early emergence of *F. lugubris* should be due to the developed mounds which well regulate nest temperature. 5. The ratio of fertile nests among well established nests is about 0.48 in *F. lugubris*, which is fairly higher than 0.14 in *F. yessensis* (Ito and Imamura 1974). 6. Ant trails are well developed in the colony of *F. lugubris*. In Ishikari Coast the trails are indistinct (Higashi 1978). 7. In *F. lugubris* the workers of a given colony are aggressively hostile against the foreign individuals artificially transferred from other colonies. The colony in Ishikari Coast also refuses foreign queens but sometimes friendly accepts foreign workers (Higashi, unpub.).

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Summary

In 1978, the census of red wood ants *Formica* s. str. was made in Switzerland. The main results are:

1. Four species were discovered. *F. pratensis* which preferred open habitats such as grasslands and roadsides was distributed from 460 to 1,360 m above the sea, mostly at 800 m or less. *F. rufa* was distributed from 490 to 1,200 m, inhabiting forest margin in the lowland but grassland in the highland. *F. polyctena* preferring forest and its margin was distributed from 480 to 1,250 m. *F. lugubris* which was the most dominant in any area occupied any altitude below the timberline (ca. 2,000 m), mostly inhabiting forest and its margin.
2. The daily flight activity in nuptial season was well synchronized in open habitats. Therefore, the synchronism developed well in *F. pratensis* and *F. rufa*.
3. Each nest of *F. rufa*, *F. polyctena* and *F. lugubris* had a huge mound, mean size of which was ca. 110 cm in diameter and ca. 50 cm in height. However, the mounds of *F. pratensis* were small (mean diameter 55 cm) and flat (mean height 18 cm), probably due to less materials of nests or due to being exposed to wind in the open habitats.
4. The mounds of any species faced east to southwest, i. e. the direction of sun.
5. The colony of *F. pratensis* was always monodomous, but *F. lugubris* frequently made oligo- and polydomous colonies. *F. rufa* and *F. polyctena* were mostly mono- but occasionally oligodomous.
6. The polydomous colony of *F. lugubris* had characteristics quite different from that of *F. yessensis* in Ishikari Coast.

Appendix I. Nests discovered in the South Jura. D, direction of the longest slope of mound. H, habitats divided into six grades (cf. Fig. 6). Mx, Mn and H are maximum and minimum diameters and height of each mound respectively.

Nest Code	Altitude (m)	Size of mound (cm) (Mx–Mn–H)	D	H
	F. pratensis			
Pr– 1	460	70– 70– 15	S	V
2	470	80– 50– 10	S	VI
3	500	60– 50– 15	S	V
4	510	50– 40– 25	SW	VI
5	510	50– 40– 10	S	VI
6	510	150–110– 40	S	V
7	510	95– 90– 20	S	VI
8	560	30– 30– 25	S	VI
9	560	30– 25– 15	—	VI
10	560	45– 30– 15	SW	VI
11	640	70– 45– 15	SE	VI
12	650	40– 30– 20	S	V
13	690	40– 25– 20	E	V
14	690	50– 40– 5	—	VI
	F. rufa			
R– 1	490	60– 45– 17	SW	III
2	500	13– 13– 5	—	VI
3	500	160–140– 60	SE	III
4	500	90– 90– 30	S	III
5	510	100– 85– 30	SE	III
6	516	40– 40– 20	S	VI
7	550	80– 70– 25	SW	III
8	560	120–100– 30	E	III
9	770	120–110– 70	NE	III
10	830	300–250– 25	E	III
11	830	200–130– 50	NE	III
12	830	180–170– 25	—	III
13	860	190–110– 40	S	III
14–1	940	220–160– 35	SE	II
2	940	180–160– 35	SE	II
3	940	150–120– 40	SE	II
15	1,000	90– 70– 20	S	VI
16	1,050	100– 80– 35	SE	V
17	1,160	140– 90– 35	S	V
18	1,180	100–100– 30	SE	V
19	1,190	130–120– 55	SE	V
20	1,200	120– 90– 65	SW	V
	F. polyctena			
Po– 1	480	60– 50– 15	S	III

Appendix I. (Continued)

Nest Code	Altitude (m)	Size of mound (cm) (Mx-Mn-H)	D	H
Po- 2	500	80- 65- 40	S	III
3	520	100-100- 30	E	IV
4	560	40- 40- 20	SW	III
5	610	100- 80- 35	E	III
6	630	120-100- 40	SW	II
7	840	200-160- 70	S	III
8	940	270-250- 70	SE	I
		F. lugubris		
L- 1	470	120-110- 40	E	III
2	500	35- 30- 25	S	III
3	500	70- 65- 35	S	II
4	510	80- 80- 35	S	III
5	520	130-100- 40	S	II
6	720	150-120- 40	E	II
7	830	220-180- 30	S	III
8	830	30- 30- 8	SW	III
9	840	240-230- 80	NE	I
10	840	200-180- 45	S	I
11	880	95- 70- 20	E	III
12	880	80- 60- 15	NE	III
13-1	910	60- 50- 25	S	III
2	910	60- 55- 15	SE	III
14	910	35- 30- 10	S	IV
15-1	980	110- 80- 40	SE	IV
2	980	70- 60- 20	SE	III
3	980	70- 70- 20	S	IV
16	1,010	60- 55- 25	E	IV
17	1,020	100- 90- 30	E	IV
18-1	1,050	110-110- 40	E	IV
2	1,050	90- 80- 35	S	III
19	1,080	200-120- 40	E	III
20	1,100	150-120- 35	E	IV
21	1,100	110- 90- 30	SE	III
22	1,120	70- 50- 25	SE	II
23	1,150	210-190- 35	SE	IV
24	1,150	60- 40- 15	SW	IV
25	1,160	160-110- 30	SE	IV
26	1,160	120-110- 35	S	IV
27-1	1,160	100- 85- 40	S	IV
2	1,160	80- 75- 30	SE	IV
28	1,160	110-100- 30	S	IV
29	1,160	15- 15- 6	—	IV
30	1,160	110-100- 60	SW	III
31-1	1,160	80- 70- 40	S	IV

Appendix I. (Continued)

Nest Code	Altitude (m)	Size of mound (cm) (Mx-Mn-H)	D	H
L- 31-2	1,160	70- 60- 20	S	IV
3	1,160	100- 80- 25	S	IV
32-1	1,170	100- 85- 30	S	IV
2	1,180	170-110- 35	S	III
33-1	1,180	150-130- 30	S E	IV
2	1,180	230-200- 35	S E	III
3	1,180	150-115- 35	S W	IV
4	1,180	120-110- 30	S W	IV
5	1,180	100- 90- 35	W	III
6	1,180	80- 60- 20	W	III
34-1	1,190	100- 95- 30	S	V
2	1,190	100-100- 15	W	V
3	1,190	110-100- 40	S	IV
35	1,190	120-110- 30	S W	IV
36	1,200	55- 55- 25	S W	IV
37	1,220	45- 30- 20	W	IV
38	1,230	90- 80- 30	S	IV
39	1,240	120-110- 40	S W	IV
40-1	1,300	190-170- 70	—	II
2	1,300	220-200-145	—	II
3	1,300	130-120- 40	S W	IV
4	1,300	150-130- 35	S	III
5	1,300	290-270-110	S	III
6	1,300	110- 80- 25	S W	III
7	1,300	90- 80- 40	—	IV
8	1,300	45- 40- 25	S E	V
9	1,300	200-170- 85	S	III
10	1,300	210-190- 50	S	III
11	1,300	150-140- 65	S	IV
12	1,300	90- 75- 15	S	IV
13	1,300	110- 80- 40	—	III
14	1,300	120-110- 30	E	III
15	1,300	200-170- 60	S W	III
16	1,300	190-170- 70	S E	III
17	1,300	140-120- 65	E	III
18	1,300	170-160- 45	—	III
19	1,300	95- 90- 35	S	IV
20	1,300	180-130- 50	S E	III
21	1,300	150-140- 55	S E	IV
22	1,300	230-190- 85	S	II
23	1,300	190-180- 65	S E	II
24	1,300	210-150- 70	S W	IV
25	1,300	230-210- 85	S	IV

Appendix II. Colonies in the Alps, Sion (A) and Montreux (B) areas. Pr, *F. pratensis*; R, *rufa*; Po, *polyctena*; L, *lugubris*. M, O and P mean mono-, oligo- and polydomous colonies respectively.

Colony Code		Species	Altitude	Structure	Direction	Habitat
A.	*73101*	Pr	620	M	S	VI
	2	L	930	M	SE	V
	3	R	1,010	M	SW	III
	4	L	1,050	O	S	VI
	80101	Pr	1,360	M	S	V
	2	L	1,050–2,100	P		II–V
	80301	L	1,520	M	S	VI
	2	L	1,700	P		II–V
	3	L	1,700	P		VI–V
	4	L	1,950–2,000	P		II–V
	5	L	2,050	P		VI–V
	6	L	1,850	M		IV
	7	L	1,850	O		IV
	80501	L	1,750	P		II–V
	2	L	1,750	P		II–V
	3	L	1,750	P		II–V
	4	L	1,750	P		III–V
	5	L	1,780	M	SW	III
	80601	L	1,900	P		II–V
	2	L	1,950	O		III–V
	3	L	2,000	P		II–V
	4	L	2,150	O		VI–V
	80701	L	1,600	O		II–III
	2	L	1,550	M	SE	III
B.	*81901*	Po	840	M	S	II
	2	L	1,220–1,300	P		II–IV
	3	L	1,450–1,600	P		II–V
	4	L	1,760	M	S	V
	5	L	1,820	O		V–VI

Appendix III. Nests in Neuchatel area. Symbols, cf. Appendices I and II.

Nest Code	Species	Altitude (m)	Size of mound (cm) (Mx–Mn–H)	D	H
82801-1	Po	740	190–180– 40	S	III
2	Po	740	210–190– 55	S	III
2-1	L	770	140–100– 30	S	II
2	L	770	160–160– 50	SW	I
3	L	770	120–110– 45	S	I
4	L	770	25– 25– 13	S	I
5	L	770	25– 25– 8	S	I
6	L	770	60– 50– 30	S	II

Appendix III. (Continued)

Nest Code	Species	Altitude (m)	Size of mound (cm) (Mx-Mn-H)	D	H
2-7	L	770	130-120- 35	E	II
3-1	L	770	150-140- 35	S E	III
2	L	770	70- 60- 35	S E	III
82901	Po	720	140- 80- 25	S E	II
2	Po	720	130-110- 30	S	IV
3	Po	770	170-110- 40	S	IV
4-1	Po	1,000	200-200- 50	S E	II
2	Po	1,000	200-180- 40	S E	III
3	Po	1,000	160-130- 50	S E	II
4	Po	1,000	210-200- 45	S	II
5-1	L	1,200	160-140- 40	S	II
2	L	1,200	50- 30- 20	S E	III
3	L	1,200	130-120- 45	S E	IV
4	L	1,200	180-170- 40	S	II
6-1	L	1,300	60- 50- 25	S W	IV
2	L	1,300	90- 80- 40	S W	III
3	L	1,300	160-140- 50	S W	III
7-1	L	1,180	110- 90- 30	S E	V
2	L	1,180	130-100- 50	S E	V
3	L	1,190	100- 90- 30	E	IV
4	L	1,200	120-110- 40	S E	IV
5	L	1,200	200-180- 40	S E	IV
6	L	1,220	80- 80- 35	S	V
7	L	1,220	120- 80- 35	S	V
8	L	1,220	220-200- 50	S E	III
8-1	Po	1,050	230-200- 60	E	III
2	Po	1,050	210-200- 50	S E	I
3	Po	1,050	200-180- 50	E	I
9-1	Po	1,250	150-130- 40	S E	II
2	Po	1,250	170-120- 45	S E	III
3	Po	1,250	210-200- 60	S E	III

Photo 1. Nest of *Formica pratensis* (arrowed).

Photo 2. Mound of *Formica rufa*.

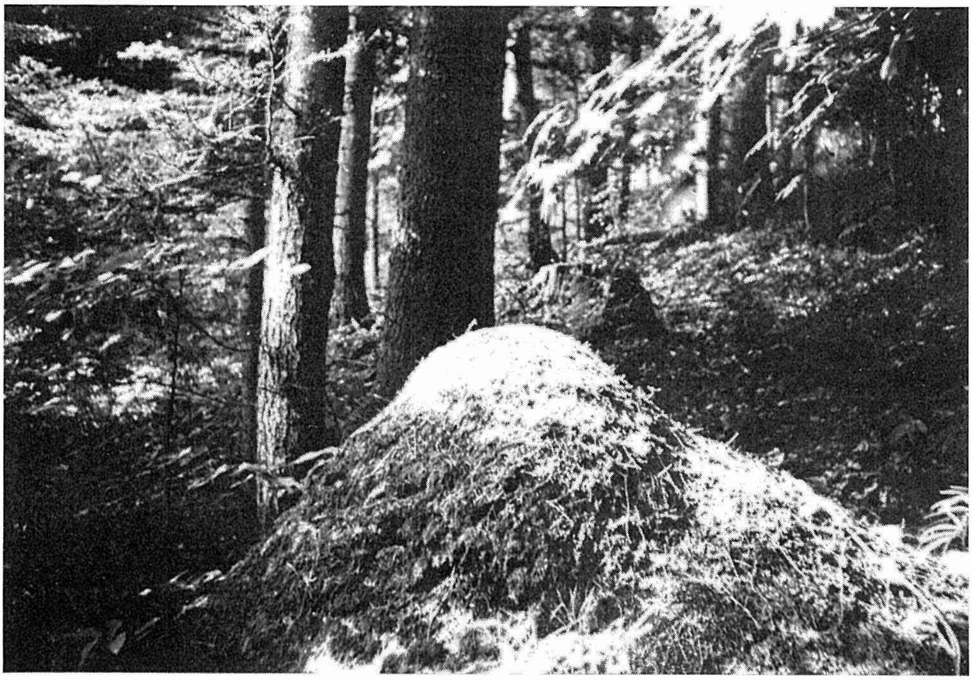

Photo 3. Mound of *Formica lugubris*.

Photo 4. Mound of *Formica polyctena*, netted to protect from the disturbance by birds (in Würzburg, West-Germany).

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Photo 5. Forest of *Picea abies* in the range of a polydomous colony of *Formica lugubris.*

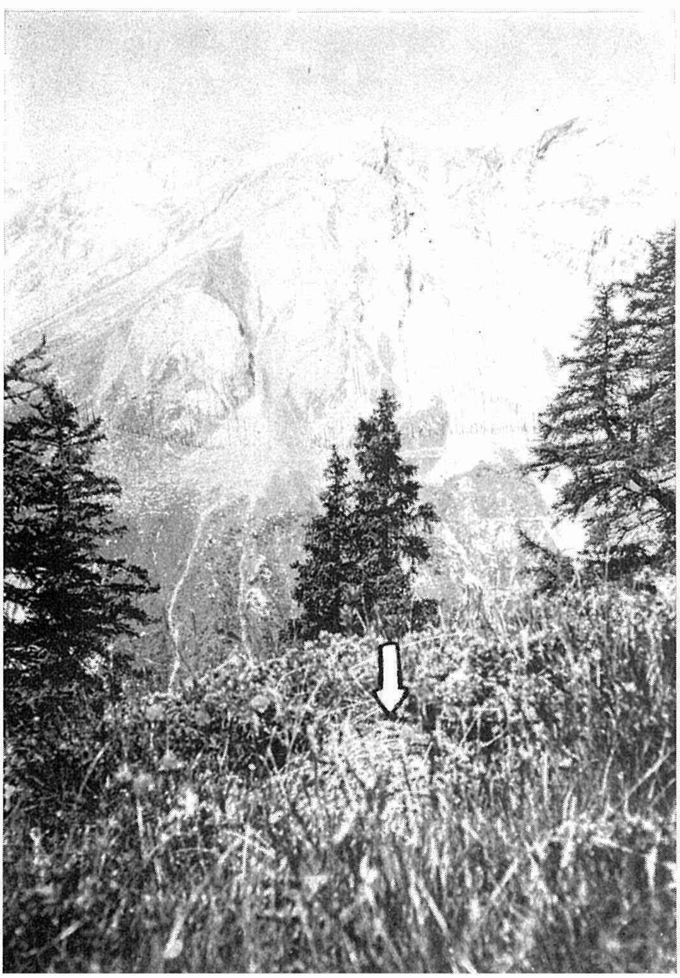

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Photo 6. Small nest of *Formica lugubris* (arrowed), at ca. 2,000 m above the sea.

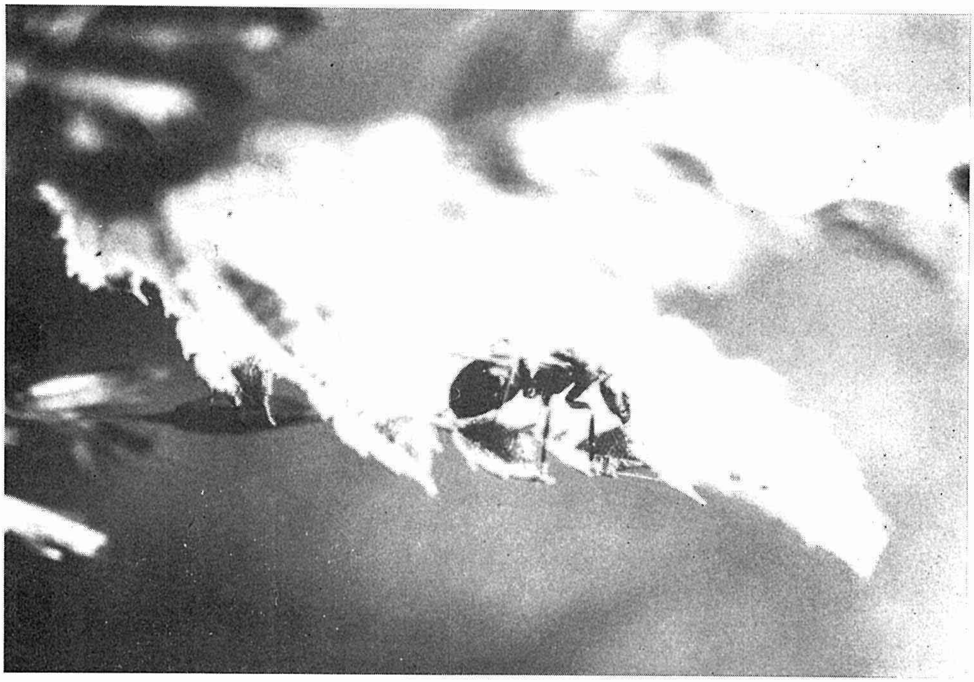

Photo 7. Alate queen of *Formica rufa* shortly before flying up.

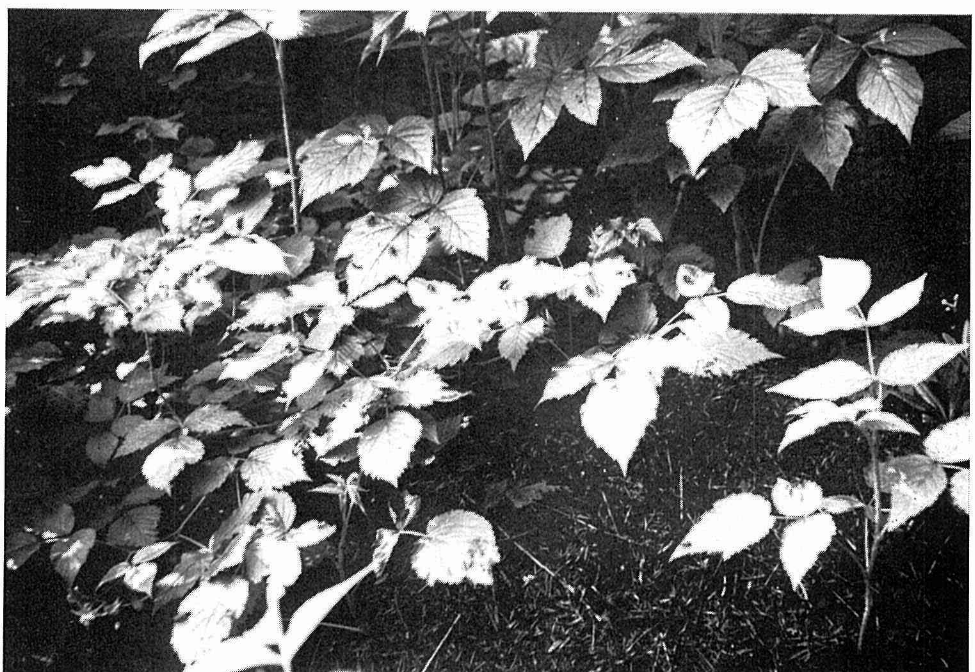

Photo 8. Some alates of *Formica lugubris* on the leaves, waiting for the chance to fly up.