



Title	アカヤマアリ類(Formica亜属)における二次的多女王制の出現機構
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Citation	環境科学 : 北海道大学大学院環境科学研究科紀要, 6(1), 1-13
Issue Date	1983-12-20
Doc URL	http://hdl.handle.net/2115/37151
Type	bulletin (article)
File Information	6(1)_1-13.pdf



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Mechanism Underlying the Appearance of Secondary Polygyny in Subgenus *Formica* Ants

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アカヤマアリ類 (*Formica* 亜属) における
二次的多女王制の出現機構

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Introduction

Colonies of most ant species are founded by a single queen previously inseminated in a nuptial flight. The monogynous state is maintained even after the colony reaches maturity. Nevertheless, some ant species are often oligo- or polygynous. Most of these colonies are founded by pleometrosis, i. e. multiple queens found a colony together (primary polygyny, Wilson 1971), though in most cases all queens except one are gradually expelled (Hölldobler and Wilson 1977) or their ovaries become atrophic (Buschinger 1967). Since many normally monogynous species are facultatively pleometrotic, temporary polygyny via pleometrosis is not rare in ants (Baroni-Urbani 1968, Hölldobler and Wilson 1977).

In a minority of species secondary polygyny frequently occurs, where many alate queens abandon their nuptial flight and stay in the mother colony. Until now secondary polygyny has been observed in four subfamilies of ants that are phylogenetically distant from each other (Wilson 1971, Banks *et al.* 1973, Janzen 1973, Higashi 1976, Hölldobler and Wilson 1977, Kutter 1977) (Fig. 1). Polygynous colonies sometimes become supercolonies containing countless queens and nests. Up to date, supercolonies have been discovered in *Iridomyrmex humilis* (Markin 1968), *Pseudomyrmex venefica* (Janzen 1973), *Formica lugubris* (Gris and Cherix 1977), *Formica yessensis* (Higashi and Yamauchi 1979). Another important issue is the frequent existence of pairs of closely related sibling species, of which one is mostly monogynous but the other frequently polygynous (Wilson 1971, Hölldobler and Wilson 1977): for instance, *Myrmica ruginodis macrogyna* and *M. r. microgyna*

Received 23 Aug. 1982

1982年8月23日受理

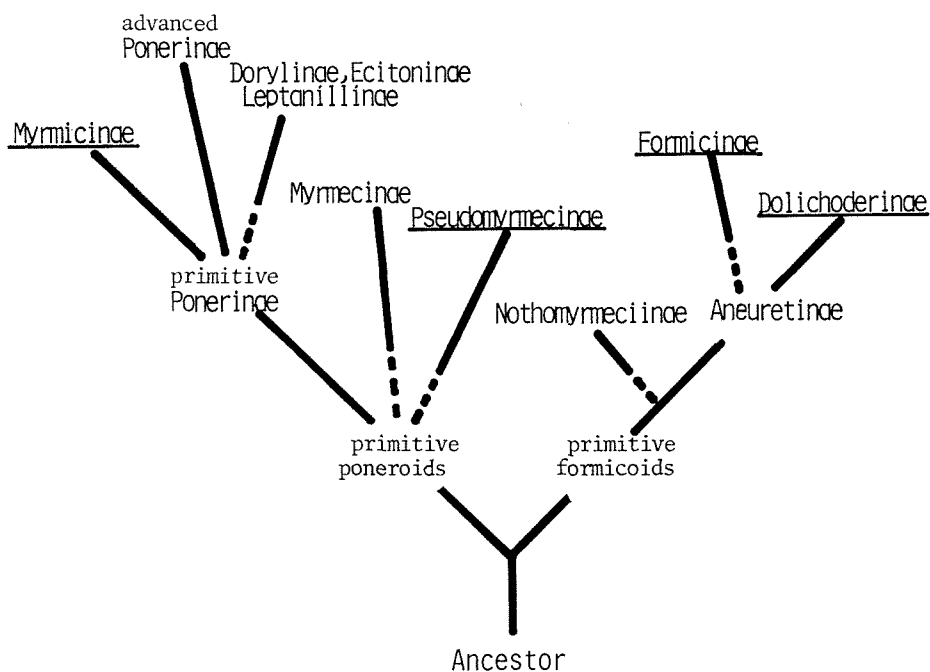


Fig. 1. Phylogenetic relationship of subfamilies (underlined) which produced the secondarily polygynous species. Dendrogram, cited from Taylor (1978).

Table 1. Geographic distribution and main gyny of *Formica* s. str. in Europe (Betrem 1960, Otto 1962, Marikovsky 1963, Gösswald *et al* 1965, Dlussky 1967, Rosengren 1969, Pisarski 1973, Bolton and Collingwood 1975, Breen 1977, Kutter 1977, etc.).

Species	Distribution	Main gyny
<i>F. rufa</i>	Euro-Siberian	Monogyny
<i>F. pratensis</i>	Palaearctic	Monogyny
<i>F. truncorum</i>	Euro-Siberian	Mono- or oligogyny
<i>F. lugubris</i>	Boreal and the Alps	Polygyny
<i>F. polyclena</i>	Euro-Siberian	Polygyny
<i>F. aquilonia</i>	Boreal and the Alps	Polygyny
<i>F. uralensis</i>	Boreal	Polygyny

(Brian and Brian 1955), *Pseudomyrmex flavidula* and *P. venefica* (Janzen 1973), *Lasius niger* and *L. sakagami* (Yamauchi, pers. com.). The *Formica rufa* group is also characterized by such sibling species (see Table 1). This phenomenon implies that the evolution of secondary polygyny is possible without long evolutionary time.

Secondary polygyny is one of the most important traits in the evolution of ants (Hölldobler and Wilson 1977). However, certain aspects of its ecology and probable evolution are not well explained yet :

1. How do queens of polygynous species abandon their nuptial flight (proximate factor)?
2. What are the selective factors that may result in the inhibition of the flight of many queens (ultimate factor)?
3. Why has it arisen independently in different phyletic lines?

One of the excellent means to solve these problems is the ecological comparison between mono- and polygynous sibling species. Particularly, it should be important to compare the production of sexuals and the mating behavior of alates in nuptial season. The author made the comparative studies of *Formica* s. str. in Switzerland in the mating season in 1978.

Study Area

Switzerland is divided into three natural regions: the Swiss Plateau, the Alps and the Jura. The present study was made mainly at the South Jura, with additional survey near Anzere in the Alps (Fig. 2). The highest point of the South Jura is about 1,500 m above the sea, i. e. slightly lower than the average timberline (1,800 to 2,000 m).

According to the records of Weather Agency of Switzerland, the mean temperature during the ant active season 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, 900 mm and 1,100 mm respectively.



Fig. 2. Sites surveyed in Switzerland.

Method

Colonies were surveyed along the way from Gland (400 m above the sea) to Chalet a Roch (1,450 m), by recording the habitat of each colony as follows: 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 standing in the grassland; VI, open grassland.

Some colonies discovered were inspected every five days whether the colonies contained alates or not, by excavating the mound surfaces. In flight season the mating behavior was also observed in several colonies.

Results

Distribution of colonies

In the South Jura 84 colonies were found: 14/*F. pratensis*, 20/*F. rufa*, 8/*F. polychaeta*, 42/*F. lugubris*. The altitudinal distribution and habitat of these colonies

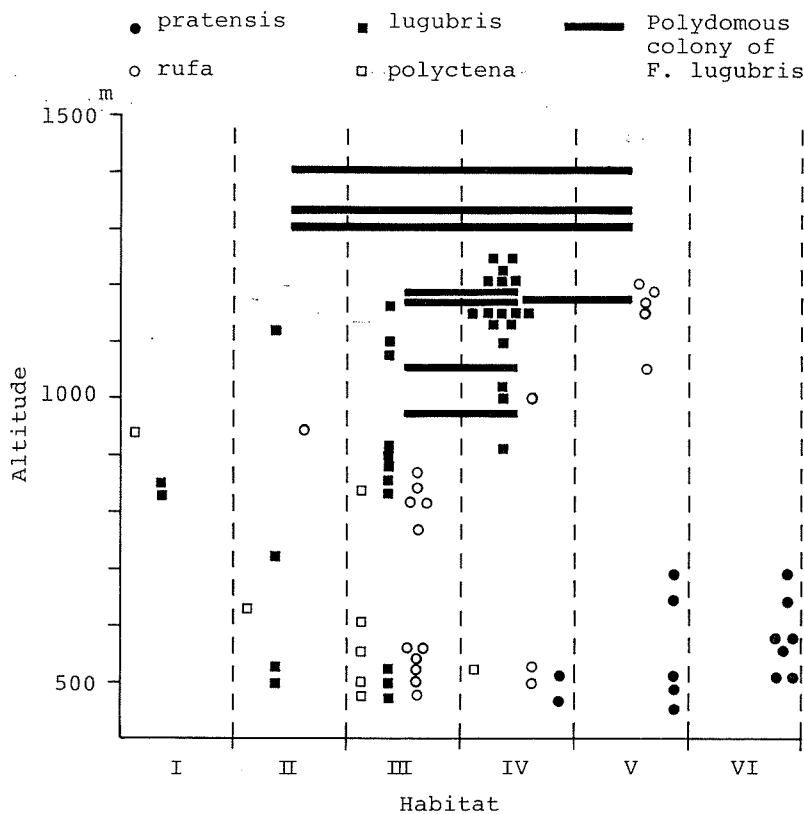


Fig. 3. Vertical distribution and habitat preference of each colony. Habitat I, the forest with dense trees; II, the forest with sparse trees; III, margin of the forest; IV, the grassland near the forest margin; V, the roots of a tree standing in the grassland; VI, open grassland.

are given in Fig. 3. *F. pratensis* inhabited the foot of mountain, preferring banks of farms and roadsides (habitats IV to VI). *F. rufa* was distributed up to 1,200 m. This species preferred forest margin (III, IV) at low altitude but the grassland (V) in the highland. Unlike these monogynous species, the polygynous species inhabited more closed habitats. *F. polychaeta* was distributed from the foot to ca. 1,000 m, preferring the inside and the margin of forest (I to IV). *F. lugubris* was also found in such habitats at low to middle altitude and even in the grassland around the top. This species often made oligo- and polydomous colonies.

Mating season

Out of 84 colonies discovered, 59 were frequently inspected whether they contained sexuals or not: 25 colonies/*F. lugubris*, 16/*F. rufa*, 10/*F. pratensis*, 8/*F. polychaeta*. Table 2 is a check list of the sexuals in each colony. Except for *F.*

Table 2. Check list of sexuals at each colony. MO, which produced only males; Mf, both sexes but mostly males; OF, only females; mF, mostly females; MF, both sexes evenly; OO, no sexuals. M and m, many and few adults of male respectively. F and f, those of alate females. —, no alate. ?, unknown.

Colony	Type	Jun.					Jul.					
		5-10	11-15	16-20	21-25	26-30	1-5	6-10	11-15	16-20	21-25	26-30
<i>F. pratensis</i>	Pr 1 Mf	—	m	m	M, f	—	—	—	—	—	—	—
	2 MO	m	m	m	—	—	—	—	—	—	—	—
	3 mF	m, F	m, F	f	—	—	—	—	—	—	—	—
	4 mF	?	m, F	f	—	—	—	—	—	—	—	—
	5 OF	?	?	f	—	—	—	—	—	—	—	—
	6 Mf	—	—	m	m	M, f	—	—	—	—	—	—
	7 Mf	?	?	?	M, f	M, f	M, f	—	—	—	—	—
	8 MO	—	—	—	M	M	M	—	—	—	—	—
	9 OO	?	—	—	—	—	—	—	—	—	—	—
	10 mF	—	—	—	f	m, F	F	—	—	—	—	—
<i>F. rufa</i>	R 1 OO	?	?	—	—	—	—	—	—	—	—	—
	2 OF	f	—	—	—	—	—	—	—	—	—	—
	3 mF	?	m, F	f	—	—	—	—	—	—	—	—
	4 MO	M	M	m	—	—	—	—	—	—	—	—
	5 mF	m, F	m, F	f	—	—	—	—	—	—	—	—
	6 MO	?	?	?	m	m	—	—	—	—	—	—
	7 MO	—	—	m	m	m	m	—	—	—	—	—
	8 MO	—	—	m	m	M	M	—	—	—	—	—
	9 MF	—	m	m, f	M, f	m, F	m, F	F	—	—	—	—
	10 OO	?	—	—	—	—	—	—	—	—	—	—
	11 OO	?	—	—	—	—	—	—	—	—	—	—
	12 mF	?	f	m, f	m, F	m, F	m, F	m, F	—	—	—	—
	13 Mf	?	?	?	m	M	M	m, f	—	—	—	—
	14 Mf	?	?	—	m, f	M, f	M, f	M, f	m, f	—	—	—
	15 MF	?	?	—	m, f	M, f	m, F	m, F	f	—	—	—
	16 OF	?	?	—	f	F	F	F	f	—	—	—

Table 2 (Continued).

Colony	Type	Jun.						Jul.					
		5-10	11-15	16-20	21-25	26-30	1-5	6-10	11-15	16-20	21-25	26-30	
<i>F. polycytena</i>	Po	1	OO	?	?	—	—	—	—	—	—	—	—
	2	OO	?	—	—	—	—	—	—	—	—	—	
	3	OO	?	—	—	—	—	—	—	—	—	—	
	4	OO	—	—	—	—	—	—	—	—	—	—	
	5	Mf	M, f	m	—	—	—	—	—	—	—	—	
	6	MO	m	—	—	—	—	—	—	—	—	—	
	7	OO	?	?	?	—	—	—	—	—	—	—	
	8	MO	—	m	M	M	m	—	—	—	—	—	
<i>F. lugubris</i>	L	1	mF	?	?	f	F	m, F	—	—	—	—	—
	2	OO	?	—	—	—	—	—	—	—	—	—	
	3	OO	—	—	—	—	—	—	—	—	—	—	
	4	OF	F	f	—	—	—	—	—	—	—	—	
	5	MF	—	—	m	M, f	M, f	m, F	—	—	—	—	
	6	OO	—	—	—	—	—	—	—	—	—	—	
	7	MO	?	?	?	m	—	—	—	—	—	—	
	8	MO	—	—	m	m	M	M	m	—	—	—	
	9	OO	?	—	—	—	—	—	—	—	—	—	
	10	MF	?	?	—	m	M	m, f	F	F	F	—	
	11	MO	?	—	m	M	M	M	M	M	—	—	
	12	MF	?	?	—	—	m	m, f	M, f	m, F	—	—	
	13	MF	?	?	—	m	m, f	M, F	M, F	m, f	—	—	
	14	MF	?	?	—	—	m	M	M, f	f	F	—	
	15	OO	?	?	?	—	—	—	—	—	—	—	
	16	MF	?	?	?	—	—	—	m, f	m, f	—	—	
	17	OO	?	?	?	—	—	—	—	—	—	—	
	18	OO	?	?	?	—	—	—	—	—	—	—	
	19	MF	?	?	—	m	m, f	M, F	M, F	m, F	—	—	
	20	MF	?	?	—	m	M	M	M, F	M, F	m, F	f	
	21	MO	?	?	—	—	m	m	M	M	—	—	
	22	OF	?	?	—	—	—	—	f	f	f	f	
	23	MF	?	?	—	—	m, f	M, F	M, F	M, F	M, F	m, f	
	24	MF	?	?	—	—	m, f	M, F	M, F	M, F	M, F	m, f	
	25	MF	—	—	—	—	m, f	M, F	M, F	M, F	m, f	—	

polycytena, the flight of which was slightly earlier than that of other species, the mating season at given altitude was nearly the same among the species. Thus, the alates were observed in early to late June around the foot of mountain, from mid June to mid July at 1,000 m and from late June to late July near the top of the Jura (Fig. 4). Near the timberline of the Alps they were found even in August.

Production of sexuals

In 16 colonies no alate was discovered. Other 43 fertile colonies which produced sexual individuals could be divided into five types: MO, which produced

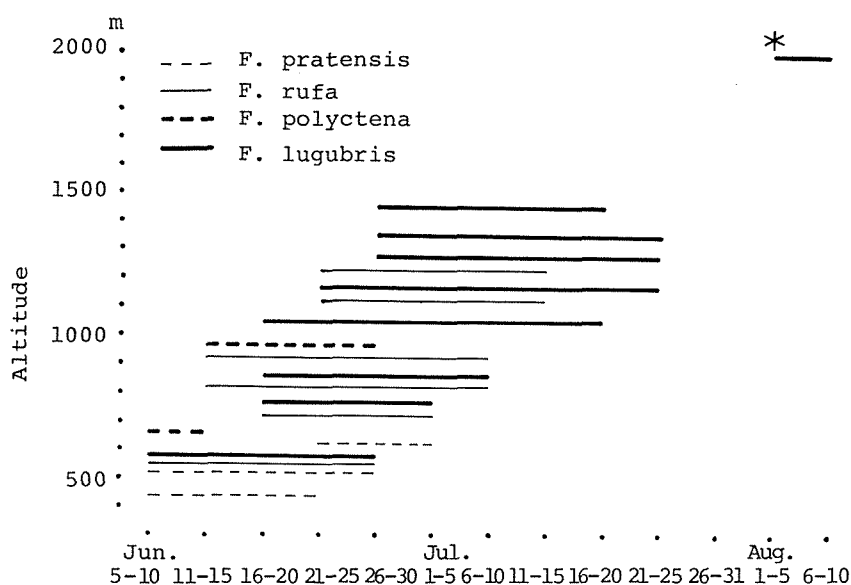


Fig. 4. Season when alates were observed at each altitude. *, near Anzere in the Alps.

Table 3. Number of five type fertile colonies in each species. Explanation of symbols, in Table 2.

Species \ Type	MO	Mf	OF	mF	MF	Total
<i>F. pratensis</i>	2	3	1	3	0	9
<i>F. rufa</i>	4	2	2	3	2	13
<i>F. lugubris</i>	4	0	2	1	11	18

only males; Mf, both sexes but mostly males; OF, only females; mF, mostly females; MF, both sexes evenly. The number of five type colonies in each species is given in Table 3. The colonies of monogynous species *F. pratensis* and *F. rufa* significantly inclined to either sex (MO, Mf, OF, mF), while in the polygynous species *F. lugubris* 11 out of 18 fertile colonies produced both sexes evenly. Even in the colonies which produced both sexes the duration of coexistence of males and females was short, because the males tended to emerge and fly up earlier than the females (e.g. R 9, L 10, L 14, L 20 in Table 2). The fertile colony of *F. polyctena* was too few to analyse.

Daily flight activity (Fig. 5)

Alates flew on sunny or, occasionally, cloudy days. The flight in the colony inhabiting forest margin or grassland was observed in the morning in all species. Therefore, the flights of the monogynous species *F. pratensis* and *F. rufa* which preferred open habitats were mostly concentrated in the morning. In the closed habitat often preferred by the polygynous species the flights were observed whenever

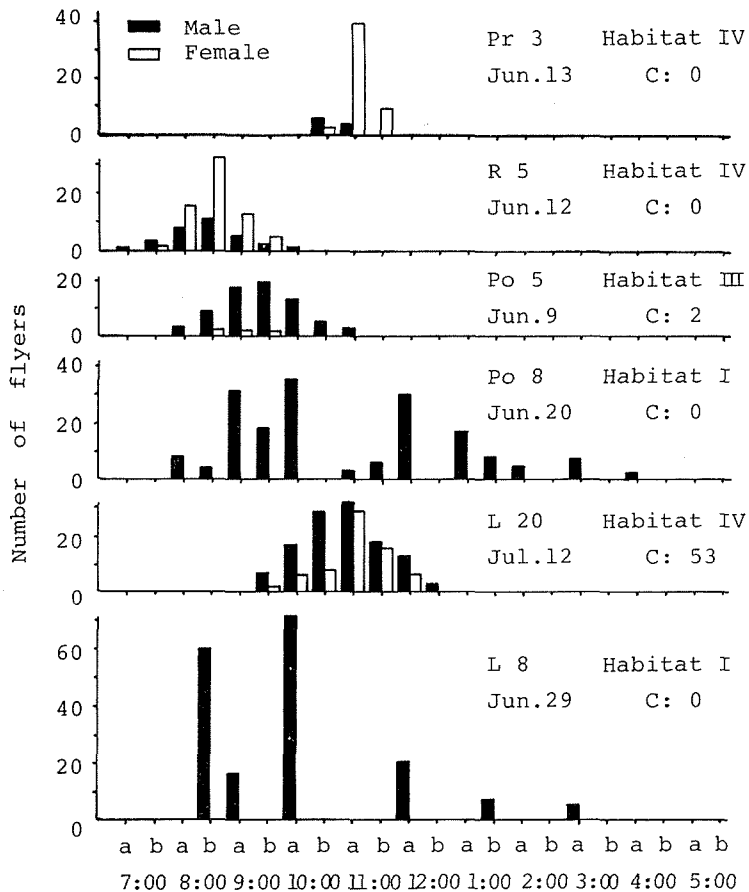


Fig. 5. Daily flight activity. C: number of intracolony copulations observed. a, i:00 to i:15. b, i:30 to i:45.

the sun beams struck the nest through the trees. For instance, the alates of forest colony L 8 always stayed on the mound throughout the daytime and excitedly flew whenever the nest was exposed to the sunshine. These observations mean that the flight activity is more synchronized in the monogynous species than in the polygynous ones.

Behavior of alates

In OF type colonies: The behavior of queens was not different between mono- and polygynous species. Typically a queen would first stay at a nest entrance. Several minutes later she would begin wandering on or around the mound alternately resting and antennating with other queens and workers. She would then climb up a grass blade or a tree twig and rest several minutes there. If weather conditions were not proper for the flight, she returned to the nest to wait for next chance. If they were acceptable, the queen would flutter her wings and fly up. However, some queens failed to fly and fell on the ground, probably due to their heavy bodies. After several trials they also flew away finally. The flight ability

of the queens was not different between mono- and polygynous species. This means that some queens of the polygynous species abandon their flight in spite of sufficient ability to fly.

In MO type colonies: After staying at a nest entrance, males would run to and climb up the grass blades and trees. When meeting with other males, they antennated but shortly became indifferent. If the weather conditions were optimal for the flight, they fluttered and flew up with rare failures. In the colonies having developed mounds, some males flew up from the top of the mound directly. The behavior mentioned was nearly the same among four species, unless they were excited. But a significant difference was observed when they were excited by sunbeams. In *F. pratensis* and *F. rufa* even the excited males rarely leapt at other individuals but only fluttered to fly. However, the excited males of *F. polyctena* and *F. lugubris* frequently ran and fluttered on the nest surface or the grass blades and leapt to other males. They undoubtedly showed mating behavior.

In the colonies where two sexes coexisted (types MF, Mf, mF): The females and males of *F. pratensis* and *rufa* behaved like those in previous two type colonies, being indifferent each other. On the other hand, many copulations between brother and sister, i. e. intracolony copulation, occurred on and around the nest of the polygynous species. The intracolony copulation was caused by the excited and fluttering males. For instance, in a colony L20 of *F. lugubris* at least 53 intracolony copulations occurred during three hours (Fig. 5).

In total 145 queens captured shortly before they were about to fly were dissected to see whether they contained sperms in seminal receptacles or not: 60 queens of *F. pratensis*, 50/*F. rufa*, 5/*F. polyctena*, 30/*F. lugubris*. Except for four queens of *F. lugubris*, they were not inseminated. Moreover, in total 20 queens of *F. lugubris* copulating on the grasses or trees were followed. Only 4 females flew up, but 13 returned into the nest and 3 began to wander on the ground. This suggests that virgin queens tend to fly but inseminated ones were apt to return to the mother colony.

Discussion

The mechanism underlying the appearance of secondary polygyny has not been explained up to the present. But the facts that it occurs in distant phyletic lines independently and that polygynous species often have monogynous sibling relatives suggest that the mechanism is not so complicated. The present study on *Formica* s. str. clarified that the virgin queens tend to fly with the same ability as those of monogynous species, but many queens that experience intracolony copulation stay at mother colony. The flight of virgin queens and the remaining of the inseminated ones at their nest of origin is also observed in *F. yessensis* (Higashi, unpub.). Gösswald (1962) also reported that the inseminated females of *F. polyctena* run to dark sites and removed their wings while the virgins preferred lightness and copulated with males. According to Schmidt and Cherix (pers. com.), some of dealated queens within a nest are virgin in *F. polyctena* and *F. lugubris*. This

suggests that a part of virgins also abandon their flight and can live for some years like the inseminated queens. But such a long survival of virgin queens is impossible in monogynous species, because they cannot produce workers which are generated only from fertilized eggs. Therefore, the flight abandonment of virgin queens may have evolved secondarily after the evolution of polygyny.

The flight of queens has two functions, dispersal and mating (Kannowski 1963). Since in the life of a queen of any ant species mortality is highest in nuptial flight, the natural selection should always favor the queen to accomplish the first function during virgin stage and, shortly after being inseminated, to remove own wings and hide somewhere. Consequently, when the intracolony mating occurred, it is natural for the inseminated queens of any phyletic line to abandon their flight and, unless being expelled by the mother or workers, stay at the mother colony.

The important problem is why the intracolony copulation occurs frequently in polygynous species. From Table 4 giving the ecological difference among four species, two causes are supposed: First, the chance of the coexistence of brother and sister is higher in polygynous species, since the colonies producing both sexes evenly are more than those of monogynous species (cf. also Talbot and Kenedy 1940, Talbot 1945, 1948). However, this is not a main cause, because even in the monogynous species the coexistence of two sexes occurs frequently in Mf and mF type colonies. Second, the continence inhibiting the intracolony copulation is broken in males of polygynous species. This should be the most definitive and direct cause inducing intracolony copulation.

Then, what is the natural selection favoring the intracolony mating? Unlike the proximate factor mentioned above, the ultimate factor inhibiting the flight of many queens seems quite different among the phyletic lines, because the distribution area of the polygynous species is diverse from the subtropics (e.g. *Iridomyrmex humilis*, *Pseudomyrmex venefica*) to the subarctic zone (e.g. *Formica uralensis*, *F. aquilonia*). For *Formica* s. str. it can be supposed as follows:

Table 4. Ecological comparison among four species. Habitats I to VI, cf. text.

	Monogynous species		Polygynous species	
	<i>pratensis</i>	<i>rufa</i>	<i>lugubris</i>	<i>polycтена</i>
Vertical distribution	400-700 m	400-1,200	400-1,400	400-950
Habitat	IV-VI	III-V	I-V	I-IV
Flight time				
Open habitat	Synchronized		Ditto	
Closed habitat	—		Whenever the sunbeams pour upon the mound	
Intracolony copulation	Rare		Frequent	
Coexistence of both sexes evenly	Rare		Frequent ?	
Emergence of alates	Male is earlier		Ditto ?	
Behaviour of virgin queens	No significant difference among four species			
and males	Continent to the concolony alates		Not continent	

After the nuptial flight, queens of subgenus *Formica* make incipient colonies by discovering the nests of *Serviformica* and usurping the position of host queens. Under the temporary social parasitism, the success of their colony founding always depends on the density and social structure of *Serviformica*. Under lower density of the host colonies the discovery of the host nest would be more difficult. Even when a queen finds a host colony, the social structure of the colony affects her success. Small incipient colonies would be taken over more easily. Even some developed monogynous colonies may also be taken over. But the conquest of oligo- and polygynous ones would be nearly impossible. Consequently, subgenus *Formica* would adopt the secondary polygyny under the condition where the colonies of *Serviformica* are sparse or some oligo- and polygynous host species are dominant. The following two facts seem to support this idea: 1. The boreal and alpine species of subgenus *Formica*, i.e. *F. lugubris*, *F. aquilonia*, *F. uralensis*, are all polygynous, often making polydomous colonies. This is probably due to the scarcity of *Serviformica* at alpine areas or due to the prevalence of the mostly oligo- and polygynous species *Formica* (*Serviformica*) *lemanii* in the boreal and alpine areas. Thus, although Pianka (1974) mentioned the frequent occurrence of r selections in the unstable and nondirected environment, in *Formica* s. str. the K selection can also occur in the unstable region through the biotic steps such as social parasitism. 2. *Coptoformica* which also adopts the temporary social parasitism is also frequently polygynous.

Acknowledgements

I wish to express my sincere thanks to Prof. S. F. Sakagami, Institute of Low Temperature Science, Hokkaido University, for his kind guidance to the present study, and to Prof. K. Gösswald, Ameisen Schützwarte, Würzburg, Dr. K. Horstmann, Institut Für Angewandte Zoologie, Würzburg, Dr. D. Cherix, Musée Zoologique, Lausanne, Dr. R. Rosengren, Department of Zoology, Helsinki University, for their useful advices during my stay in Europe. Particular appreciation is also due to Prof. G. H. Schmidt, Technische Universität, Hannover, for his useful information on the polygyny of *Formica* s. str.

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Summary

The comparative studies between monogynous (*F. pratensis*, *F. rufa*) and polygynous *Formica* (*F. polyctena*, *F. lugubris*) were made in mating season in Switzerland. The main results are:

1. The mating season was altitudinally different: early to late June in the lowland (400 to 500 m above the sea), mid June to mid July at ca. 1,000 m, even in August near the timberline

(1,800 to 2,000 m).

2. Compared with monogynous species, the polygynous ones had following characteristics:

i) Many colonies preferred more closed habitats. ii) In the colonies inhabiting the dense forest, the flight time was not so synchronized as in the open habitats. iii) The colony producing both sexes evenly was abundant. iv) Intracolony copulation frequently occurred.

3. Most of the queens who flew up were virgin. On the other hand, the queens inseminated by males before flying up were apt to return to the mother colony.

4. The intracolony copulation was caused by the males who lost the sexual continence to the concolony queens.

The natural selection inhibiting the flight of queens of polygynous *Formica* was considered in connection with their temporary social parasitism.