

# INTERSPECIFIC COMMUNICATION BETWEEN ANTS

by

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(With 3 Figures)  
(Acc. 15-VIII-1981)

## INTRODUCTION

The majority of investigations of interspecific ant relationships are devoted to competition (BRIAN, 1952; PONTIN, 1963; DLUSSKY, 1965, 1967; BRIAN, HIBBLE & KELLY, 1966; WILSON & TAYLOR, 1967; BARONI-URBANI, 1969a, b, 1974; GREENSLADE, 1971; LEVINS *et al.*, 1973; ELMES, 1974). Species with similar ecological niches usually seek maximum demarcation of their activity spheres (KACZMAREK, 1953; YASUNO, 1965; GALLE, 1972; STEBAEV & REZNIKOVA, 1974; DLUSSKY, 1975; LEVIEUX, 1977). At the same time due to mutual adaptation, the reduction of aggression and even interspecific trophallaxis in such ant species is observed (BHATKAR & KLOFT, 1977; REZNIKOVA, 1971; SEIMA, 1971, 1972). Mutual use of traces during foraging of some species has been observed (WILSON, 1965; WATKINS *et al.*, 1969; BARONI-URBANI, 1969). Such an interaction might be a precondition for interspecific communication. Previously, in the ecologically similar *F. picea* and *F. uralensis* we reported an unusual stimulation of searching activity of the dominant by the subdominant. The more agile *F. picea* in 90% of cases were the first to find bait hidden in labyrinths and involuntarily served as scouts for *F. uralensis* (STEBAEV & REZNIKOVA, 1972). The nature of the interaction enables us to assume the presence of exchange of information between ants of different species.

This report is devoted to the study of non-antagonistic relationships between ants and mechanisms of interspecific communication. It generalizes the results of several series of field experiments (REZNIKOVA, 1971, 1975; REZNIKOVA & KULIKOV, 1978).

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<sup>2)</sup> I wish to thank very much R. J. ANDREW for the editing of my paper and valuable remarks concerning the statistics.

## MATERIAL AND METHODS

We have chosen *F. pratensis* and *F. cunicularia* as the model pair of ecologically similar ant species. These, the most numerous species on the Siberian steppes, interact in a complex way (REZNIKOVA, 1971, 1975, 1976; STEBAEV & REZNIKOVA, 1974). The dominant *F. pratensis* determines to a great degree the character of the daily activity, the size of the feeding territory, the distribution between tiers, the quantity and composition of the prey taken by the subdominant species. At the same time *F. cunicularia* are ready at any moment to occupy the territory which is freed for any reason by *F. pratensis*. They often steal food from ants of the dominant species, making their way above them on the grass stalks and seizing the moment when the forager puts its prey on the ground.

The ecological peculiarities of the chosen ant species have previously been studied in detail (REZNIKOVA, 1974, 1979; REZNIKOVA & SHILLEROVA, 1978; REZNIKOVA & KULIKOV, 1978). *F. pratensis* and *F. cunicularia* are active predators, their prey including more than 130 species of invertebrates. The predominant part of *F. pratensis* food is composed of the inhabitants of the ground and soil (ants of their own and other species, beetles, spiders and bugs). *F. cunicularia* eats the herbage inhabitants (aphids, numerous species of cicada and bugs). However, the food spectrum of both species is quite similar.

The investigations were made in the South-West part of Barabinsk Steppe (Karasuk Research Station of Biology), in a cereals-*Artemisia*-grass association. Here the average number of *F. pratensis* nests amounts to 4-5 per hectare against 120 of *F. cunicularia*. Monocalic monogyne families (i.e. with one nest and one queen) of up to 100,000 individuals are characteristic for *F. pratensis*. They build nests of plant residues with domes up to 1.5 m in diameter. *F. cunicularia* also have monocalic monogyne families, but they build underground nests consisting of 1-4 sections with a population of 500-800 ants in each. The organisation of the feeding ground differs between the dominant and subdominant ants. A protected territory of about 700 m<sup>2</sup> with a network of depressed routes in the soil belongs to each family of *F. pratensis*. A distinct secondary division of the territory has been observed in families with a population of more than 7,000-8,000 individuals (DOBZANSKA, 1958). Every section of the route and feeding region belonging to it, is attended by a permanent group of foragers interacting with each other. The feeding territory of *F. cunicularia* has no exact boundaries and is not defended. Foragers act independently of each other, and during the day may change the hunting zones.

The experiments were carried out on three sections with an area of 1,200-1,800 m<sup>2</sup>. The interaction between ants during the search for food were studied by means of labyrinths containing meat bait. The simple labyrinths were made up of plastic boxes with a transparent cover and an outlet 10 mm in diameter. Entering the box, the ants came upon a non-transparent cylinder which they had to go around to reach the bait through a second entrance. The complicated labyrinths contained two vertical cylinders, one placed within the other. The bait was placed within the inner cylinder. Both cylinders had entrances, but from opposite sides. Ninety labyrinths of the same construction were used at one time. The labyrinths were placed on the ground 4 m apart. Records were taken every 10 minutes of the number of the original pieces of meat which remained in the labyrinths, and how many ants of each species had been there. Twenty counts were made during the day from 07 to 21 hr.

Trophic relations of each species were studied using counts of prey taken in a natural situation and during isolation of the dominant or subdominant nests. The counts were made visually during the whole period of foraging activity of ants for 30 minutes with 15 minute intervals (REZNIKOVA & KULIKOV, 1978). The isolation of the nests was carried out by means of plastic obstacles smeared with vaseline oil. During isolation ants got their food from troughs within the fences.



## RESULTS

## 1. Interactions between ants during the search for food.

Observation of ants acting in labyrinths showed that *F. cunicularia* coped with the task much better than *F. pratensis*. From the very beginning of the experiment they penetrated with equal ease into the simple and complicated labyrinths, dragging the bait all over the area of their feeding territory and on the feeding grounds of *F. pratensis*. The rate of dragging out the bait from the simple labyrinths averaged 2.3 portions per hour. In the complicated labyrinths the foragers dragged out the bait at an average rate of 3.8 portions per hour. Foragers of the dominant species succeeded in obtaining food from the simple labyrinths only on the third day of the experiment. They took food mainly from the labyrinths situated on the periphery of their feeding territory which were also frequented by *F. cunicularia*. Data confirming the recruiting of *F. pratensis* to visit labyrinths on the territory common with *F. cunicularia* are given in Table 1, the increased recruitment of *F. pratensis* on the secondary was significant ( $p < .02$ ,  $X^2$ ; KENDALL & STUART, 1966).

TABLE 1

*Searching activity of Formica pratensis in the different zones of the feeding territory*

The number of labyrinths visited by *F. pratensis*:

	In the centre of their feeding territory	On shared territory with <i>F. cunicularia</i>	
First day	11	4	15
Second day	2	10	12
	13	14	27

In spite of the small number of dominant foragers in the periphery zone, they dragged the bait at the same rate as the subdominants. In 70% of the instances *F. pratensis* were observed in the labyrinths together with *F. cunicularia* and in 78% of the instances the subdominants were the first to discover the bait. In the labyrinths where both species were acting, almost the entire bait was obtained by the dominant.

In this way the more enterprising subdominant interacting with the dominant plays the role of a scout. This makes us regard their trophic relations differently. On the one hand the partial common character of the ecologically similar species should cause competition between them. On the other hand, the presence of *F. cunicularia* appears to raise the effec-

tiveness of the search for food by *F. pratensis*. This can be demonstrated by alternately isolating the nests of both species. If the trophic relations involve only competition, then, in the absence of competitors, the foragers of each species should bring a greater amount of prey. In order to check this assumption 12 nests of *F. cunicularia* were isolated in an area where records of the prey of the ants had been kept during a whole summer (REZNIKOVA & KULIKOV, 1978). During a period of two days a record was made of the prey consumed by a family of *F. pratensis*. In the morning of the third day the enclosures were removed and in the evening of the same day the *F. pratensis* nest was isolated. On the next day an account was taken of the prey of the largest family of *F. cunicularia* and then the former situation on the section was restored. We compared the weight and the amount of the prey brought by ants at the time when each species was active alone (from 7 a.m. till 12 a.m.).

During the isolation of the dominant nest, the hunting activity of the subdominant was sharply increased. On this day the number of individuals of prey brought out increased about two times and the total weight of the prey more than three times (Fig. 1). The average weight of the prey was increased from 1.4 to 3.06 mg. Foragers brought larger insects such as usually taken by dominant species. However, when the subdominant nests were enclosed the *F. pratensis* family began to consume less protein food and its total weight was halved (Table 2). The reduction in intake in *F. pratensis* was significant ( $p < .036$ , one tailed, Mann-Whitney).

TABLE 2

*Total weight of prey carried into the nest (mg)*

Dates	<i>F. cunicularia</i>		<i>F. pratensis</i>	
5. VI	60	x <sub>3</sub>	800	B <sub>4</sub>
11. VI	65	x <sub>4</sub>	780	B <sub>2</sub>
15. VI	56	x <sub>2</sub>	720	B <sub>1</sub>
17. VI	70	x <sub>6</sub>	900	B <sub>6</sub>
20. VI	—		460	A <sub>2</sub>
21. VI	—		310	A <sub>1</sub>
22. VI	<b>380</b>	y <sub>1</sub>	—	
25. VI	48	x <sub>1</sub>	790	B <sub>3</sub>
30. VI	66	x <sub>5</sub>	820	B <sub>5</sub>

Bold type - time when neither type of nest was enclosed; ordinary print - time when the nest of the other species was enclosed.

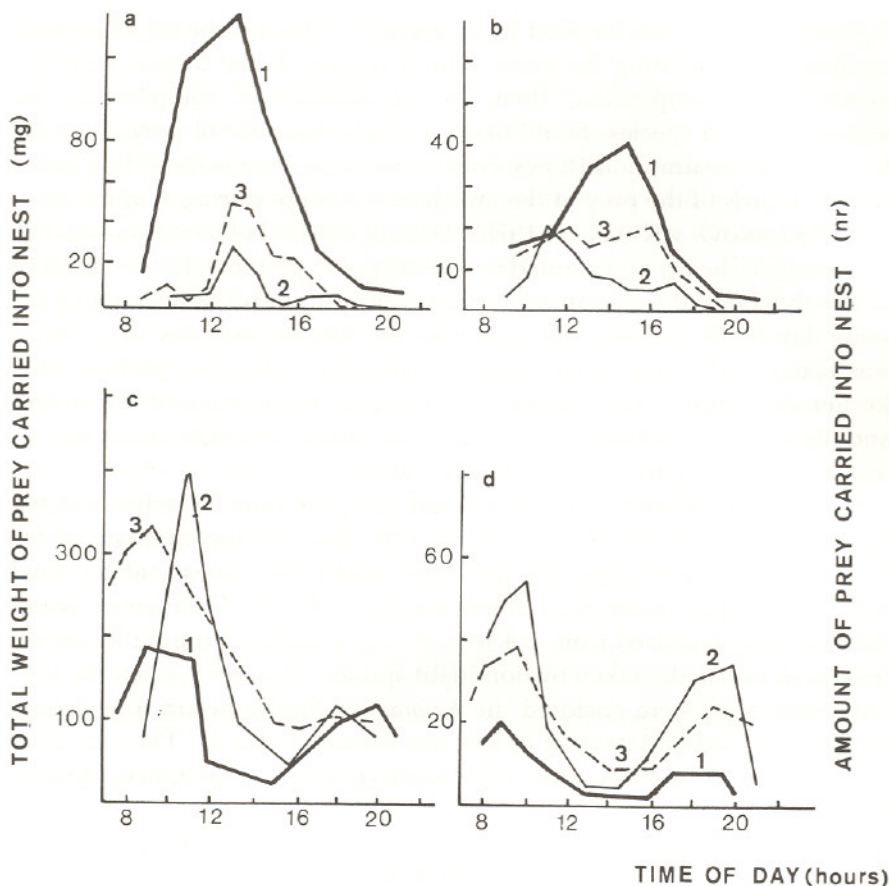


Fig. 1. Changes in hunting activity when the nests of the competitor species are isolated. Top: prey taken by *F. cunicularia* during the isolation of *F. pratensis* nests. Bottom: prey taken by *F. pratensis* during the isolation of *F. cunicularia* nests. 1: the hunting activity of ants when the nests of the competitor are closed; 2: the same before the experiment; 3: the same after the experiment. a, b, data on counting prey of *F. cunicularia* during isolation of *F. pratensis* nest. c, d, data on counting prey of *F. pratensis* during isolation of *F. cunicularia* nests.

Thus, the trophic relationships of *F. pratensis* and *F. cunicularia* are not limited by competition. The quantity of the subdominant prey is controlled by the presence of the dominant while the more active *F. cunicularia* at the same time increases the effectiveness of *F. pratensis* hunting activity.



## 2. Mechanisms of interspecific communication of ants.

### *Interspecific kinopsis.*

It is known that in joint hunting of foragers of one *Formica* genus an important role is played by kinopsis. The movements which are characteristic for this type of signalling are similar in ants belonging to the subgenus *Formica* s. str. and *Serviformica* as was shown for *Formica polyclena* and *F. fusca* (WALLIS, 1964). We assumed the existence of intraspecific kinopsis.

To verify this assumption, a stereotyped reaction of ants (the transporting of pupae to a light protected place) was used in a series of field experiments. Five or six individuals of *F. cunicularia* together with 10-12 pupae were put into a tightly closed U-shaped tube (100 × 100 × 12 mm). A black cap was put on one of its ends. The ants immediately began dragging the pupae to the darkened part of the tube. When all of them had been carried over, the cap was put on the other end of the tube. Thus the ants were forced to drag the pupae back again. Eleven of such tubes, with ants constantly running in them, were placed on the end parts of the *F. pratensis* routes.

An experimental plot was located on one side of the route, on the other a control with an empty tube. Fifty pieces of meat were placed in the centre of each of the plots bounded by tubes. A count was taken of the number of ants taking the bait during half an hour.

It turned out that within half an hour the ants had dragged away all of the bait from the test plots, but only 4-5 pieces of meat from the control plots. The number of foragers on the test plots were 2.5-4 more than on the control plots (Table 3). It is significant that the ants of nest 'C' and the ants of route 6 of nest 'A' did not react to the movement of *F. cunicularia* around the bait. There being no *F. cunicularia* nests near these routes, the *F. pratensis* foragers had in the past had no contact with them in these areas.

In order to find out whether *F. pratensis* were attracted only by the specific movements of the scout species, or by any moving object, tubes were offered with individuals of either their own family, or with *Formica exsecta*, which the given population of *F. pratensis* does not encounter in nature. It is seen from the Table 4 that *F. pratensis* were activated by the movements of their own species no less than by *F. cunicularia*. They did not respond at all, however, to the movement of the unknown *F. exsecta*. The coloration of the moving ants does not play a role. This was proved by an experiment (Table 4) in which *F. pratensis* which were inserted into the tube were marked with large spots of light coloured paint.

TABLE 3

*Display of interspecific kinopsis among ants*

<i>Formica pratensis</i> nests and routes		The number of <i>F. pratensis</i> ants taking the prey		
		Experimental plot	Control plot	X <sup>2</sup>
Nest A, route	1	26	8	< .01
	2	44	14	< .001
	3	30	10	< .01
	4	26	10	< .01
	5	221	3	< .001
Nest B, route	2	34	8	< .001
	3	54	16	< .001
	4	20	6	< .01
Nest C, route	1	20	34	NS
	2	50	42	NS
Nest A, route	6	16	20	NS

Experimental and control plots - the number of ants which took prey.

TABLE 4

*The reaction of F. pratensis to the movements of the ants of their own and other species*

U-shaped tubes contain	<i>F. pratensis</i> nests	The number of <i>F. pratensis</i> ants taking the prey		
		Experimental plot	Control plot	X <sup>2</sup>
<i>Formica</i> <i>exsecta</i>	A	34	48	NS
		25	35	NS
		12	8	NS
	B	24	16	NS
		44	46	NS
		40	34	NS
<i>F. pratensis</i>	A	58	66	NS
		20	4	< .01
		32	10	< .001
	B	44	16	< .001
		30	12	< .01
		34	10	< .001
Coloured <i>F. pratensis</i>	A	28	8	< .001

Thus it may be considered that *F. pratensis* are activated by the specific movements of the ants of their own and subdominant species, which they easily distinguished from other ants.

*The role of odour in the recognition of scout species.*

It is known that odour plays a basic role in the recognition of their slaves by slave-holding ants, as well as in suppression of aggression towards young individuals of another species (JAISON, 1975). The question arises, what role does odour play in the recognition of scout-species individuals by the foragers *F. pratensis*.

In our experiment three plots were chosen which contained equal numbers of individuals based on 15 counts of ant distribution. Twenty five boxes made of thin, dense netting were placed on each plot. In each box on one plot were 10 *F. cunicularia* taken from the nest situated on the same section; on another plot the boxes contained 10 *F. cunicularia* from a nest situated at a distance of 300 m. In the boxes of the third (control) plot, there were no ants at all. Troughs with syrup were placed on the surface of each box. During high daily activity periods of *F. pratensis* the number of foragers in all troughs was recorded 30 times. Maximum values obtained for every trough were compared and tested for significant differences using Student's t-test (Table 5).

TABLE 5

*The mean density of F. pratensis in the plots with boxes containing F. cunicularia*

<i>F. cunicularia</i> from the nest situated on the same section	<i>F. cunicularia</i> from the further nest	Control section with empty boxes
62.92 ± 6.32	40.08 ± 3.02	7.68 ± 1.17
p ≤ 0.01	p ≤ 0.001	p ≤ 0.001

It turned out that the boxes with ants in them attracted *F. pratensis* more than the empty ones. One and a half times more foragers were found in the boxes holding *F. cunicularia* from the nearest nest than in the boxes with *F. cunicularia* from the farthest one. It seems that *F. pratensis* distinguish *F. cunicularia* families with which they were previously in contact.

### 3. Interspecific interactions in locating bait.

Bait was offered in a central area, the approach to which was divided into ten equal sectors (Fig. 2). This apparatus was presented in plots visited by only one of two species, and in plots visited by both. Improvements in the ease with which the bait was found over a period of



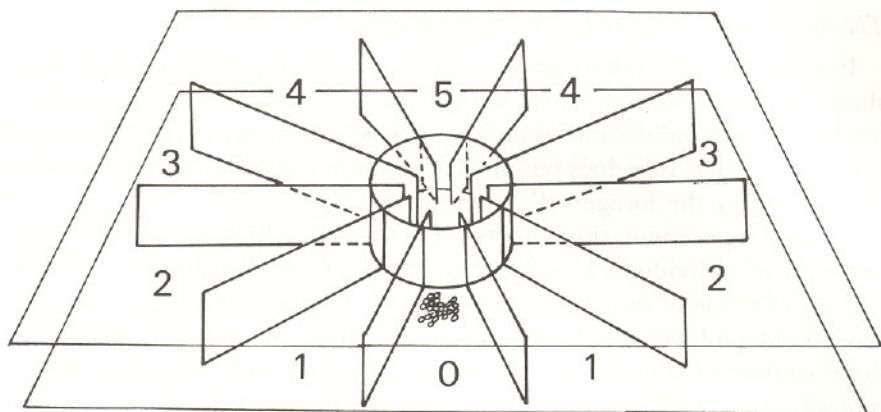


Fig. 2. Circular arrangement with the bait in one of the sectors. 0-5: numbers of the sectors.

three hours (Fig. 3), in which all visits were recorded, were assessed by assigning error points. Error points are the sum of the sector numbers entered before the bait was reached. Thus if an ant entered the sector opposite to the bait, and then visited all sectors in a half circuit of the apparatus on the way to the bait, it received  $5 + 4 + 3 + 2 + 1 = 15$  error points. Individual marking showed that on each plot where the species was active a constant group of about 10 *F. pratensis* and 2-3 *F. cunicularia* were working.

It turned out that within 10-15 minutes after the beginning of observation the bait was found by *F. cunicularia* ants and quickly dragged away.

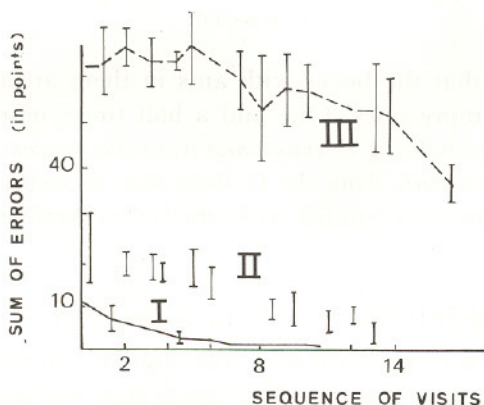


Fig. 3. The change of the number of errors during training: I: *F. cunicularia*; II: *F. pratensis* in contact with *F. cunicularia*; III: without contact. Each curve is the average of ten curves.

In the cases when mistakes were made they ran around and entered the correct sector. After the 3rd or the 4th visit the majority of the ants received no more than 3-5 points. *F. pratensis* on the contrary, roamed about the sectors for an hour, or even two, and found the bait only by chance. Later on, their searchings became orderly, but the sum of errors on average amounted to more than 30 points. If *F. pratensis* had the possibility of contact with *F. cunicularia* then they did not touch the bait at all for the first 40-50 minutes, allowing the subdominants to drag it away. During this time 3 or 4 *F. pratensis* foragers were near the sector watching the actions of the scout-species. Then they drove the *F. cunicularia* away and began dragging away the bait themselves. In this case improvement took place much faster (Fig. 3).

### CONCLUSION

Previously unknown types of interaction based on communication were found among ants of different species with widely overlapping ecological niches. Individuals of the subdominant species were better than the dominant species at discovering food when foraging by themselves on the feeding territory or when their hunting zones were changed. The dominant species was better able to mobilize groups to transport food. In complicated situations ants of the dominant species can learn the technique of getting food by imitating the actions of the subdominant species. In simple cases, interspecific kinopsis plays the main role. The ants of the dominant species distinguish the subdominants from other species by their specific actions and can recognize individuals by odour. Contact with scout-species greatly raises the effectiveness of the dominant's hunting activity; when deprived of such contact, only half as much prey is taken. Judging by analogous data obtained from the example of *F. uralensis* and *F. picea*, and also *F. pratensis* and *F. rufibarbis* (REZNIKOVA, 1980), it may be assumed that relations in ant communication of this type are in general characteristic of ecologically similar pairs of species playing the role of dominants and subdominants.

### SUMMARY

With the help of field experiments, the nonantagonistic relations and exchange of information among ants of various species occupying similar ecological niches were studied. *Formica pratensis* and *F. cunicularia glauca*, respectively dominant and subdominant in their associations, were chosen as the model pair. The dominant has a defended territory with a clearly defined secondary division. The feeding territory of the subdominant is organized to the type of individual foraging. The use of labyrinths with bait hidden in them showed that the subdominants are more enterprising foragers; when interacting with the domi-

nant they play the role of scouts. The amount of prey of *F. pratensis* is so dependent on the presence of *F. cunicularia* that when the nests of this species are isolated, the *F. pratensis* bring three times less prey. The basis for the interaction of the foragers of different species is interspecific kinopsis and distant training.

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# ZUSAMMENFASSUNG

Mit Hilfe von Feldversuchen wurden die gegenseitigen Beziehungen von zwei Ameisenarten, *Formica pratensis* und *F. cunicularia glauca* studiert, die im gleichen Biotop zusammenleben und sehr ähnliche oekologische Ansprüche haben. *F. pratensis* dominiert *F. cunicularia* und ist ihr beim Futtertransport überlegen. Letztere Art ist aber erfindischer bei der Nahrungssuche. Wenn *pratensis*-Nester künstlich von *cunicularia* isoliert wurden, trugen die *pratensis*-Arbeiterinnen dreimal weniger Beute ein.

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