

Ethological Mechanisms of Population Density Control in Coadaptive Complexes of Ants

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Abstract—The data on the zonal and biotopical distribution of 70 ant species in the southern Western Siberian Plain and adjacent regions were analyzed. The results showed that, against the background of a considerable diversity of the ant fauna, multispecies communities dominated by *Formica pratensis* retain the constant species composition and the quantitative ratio of nests over the area from the northern forest steppe to the southern boundary of the steppe zone, and the basic features of their species composition remain unchanged up to the desert zone. In such coadaptive complexes, stable interspecies relationships and characteristic mechanisms of density regulation develop. Field experiments on artificially changing the size of ant families in communities with different dominants demonstrated that ants of dominant species actively regulate the level of dynamic density of subdominant species and exterminate “excess” individuals, estimating their number fairly accurately. Such a form of interspecies relationships is named interspecies social control.

INTRODUCTION

Multispecies communities of ants are formed due to similarity of biotopical distribution of different species. Ants belong to one of a few animal groups in which coexistence of many species with significantly overlapping ecological niches is possible. In communities of these insects, interspecies relationships are diverse and include both negative forms, such as predation, competition, and parasitism, and positive interrelations—mutualism and proto-cooperation. Multispecies associations populating the same biocenosis comprise a *coadaptive complex*, as named by Dlusskii (1981) to emphasize the constancy of close relationships between coexisting species. In most myrmecological studies, however, individual ant communities in certain landscapes were considered. Their results indicate that dominant ants usually occur in combinations with the same sets of other species (Brian, 1965; Galle, 1975), and such communities are characterized by hierarchical relationships between dominant, subdominant, and subordinate species (Kaczmarek, 1953; Reznikova, 1980; Savoläinen and Vepsäläinen, 1988).

Our experimental studies demonstrated for the first time that the interspecies hierarchy is directly related to trophic competition, on the one hand, and to characteristic mutualistic relationships, on the other. The latter mean that dominant ants use subdominants as guides while searching for prey, and ants belonging to non-dominant species steal prey from dominants and use their homopteran colonies to obtain honeydew (Reznikova, 1975, 1982; Novgorodova and Reznikova, 1996). Such a balance between the competitive and mutualistic relationships is based on the quantitative ratio of dynamic densities of different species in a community

(Reznikova, 1996). As dominant species usually have a wide zonal distribution, it may well be that such multispecies ant complexes maintain the integrity of their system as a whole in different natural zones and landscapes. In this context, the question arises as to what are the mechanisms regulating the abundance of different species.

The present paper summarizes the results of more than 20-year investigations on the fauna and ecology of ants. The main objects were communities with dominance of *Formica pratensis*, which were studied along the meridional transect through the southern Western Siberian Plain and adjacent territories. Ecological experiments in the field were performed on ant communities with different dominants (*F. pratensis*, *F. uralensis*, *F. polycтена*, and *F. sanguinea*) in the steppe, forest-steppe, and forest landscapes of western Siberia and Tuva. A new form of interspecies relationships was revealed in ant communities. This form, characteristic of stable coadaptive complexes, was named interspecies social control, and the corresponding hypothesis was discussed at the VI International Congress of Ecology (Reznikova, 1994).

THE CONSTANCY OF STRUCTURE IN COADAPTIVE COMPLEXES WITH DOMINANCE OF *FORMICA PRATENSIS*

Studies on the ant fauna were performed from 1972 to 1979 in valleys and interfluvies of the Irtysh River and some of its tributaries (the Ishim, Ui, Tui, Tara, and Char rivers), the Ayaguz, Kurchum, Kolguty, Chernyi Irtysh, and Ili rivers flowing into lakes Zaisan and Balkhash, and in the Alakol' and Balkhash depressions

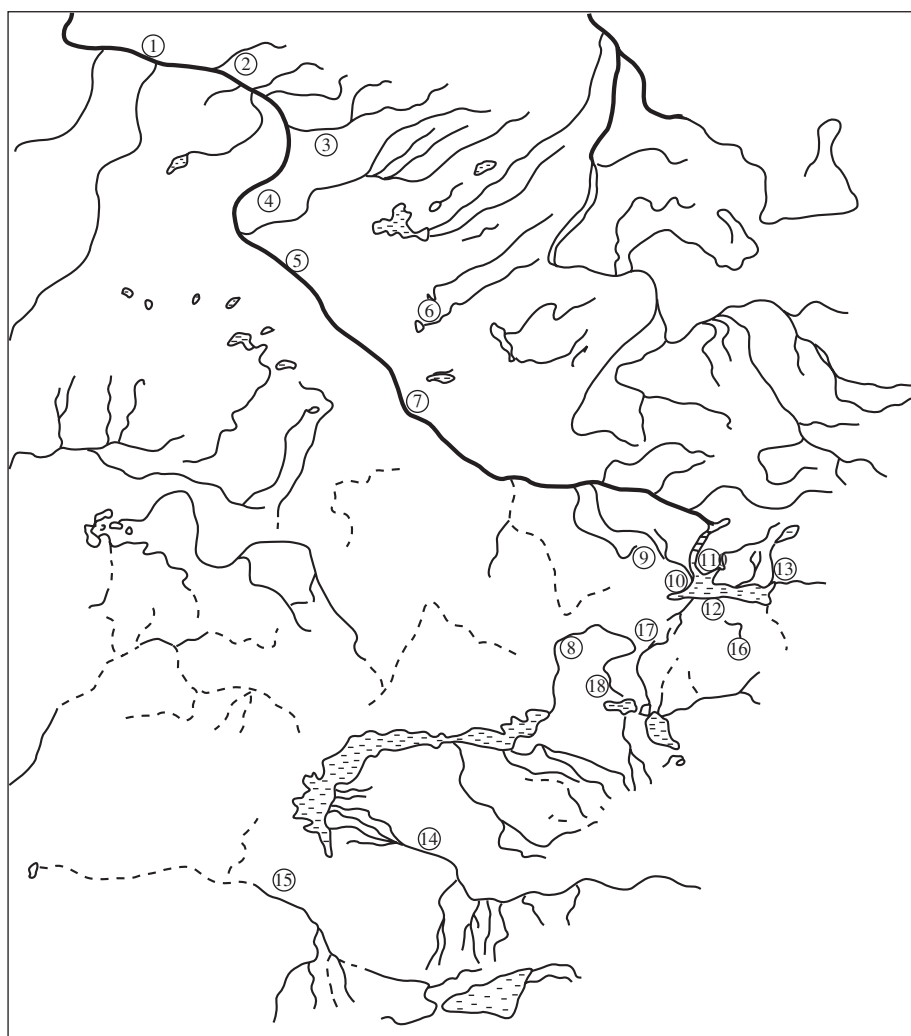
(figure). In each of these 18 transects, five geomorphological levels were distinguished: low and high floodplains, low and medium floodplain terraces, and flat interfluvies. On each level, 15 test plots 5×5 m in size were laid.

Large nests of *Formica* and *Camponotus* were recorded during route censuses. A total of 70 ant species were found (Reznikova, 1983).

To describe multispecies communities with *F. pratensis* dominance, 60 plots 1200–1800 m² in size were analyzed in 12 transects. The structure of different associations was compared with respect to a relative parameter, namely, the number of nests of each species on the territory controlled by one *F. pratensis* family, recalculated per reference area. Table 1 shows the average maximum numbers of nests of different ants (per *F. pratensis* feeding territory) in communities typical of the steppe landscapes of each natural zone.

Ant species having wide ranges with centers in the forest–steppe and steppe belonged to the same commu-

nities not only in these zones, but also in the subtaiga and in more southerly regions, up to deserts. This concerns *F. cunicularia*, *F. rufibarbis*, *L. alienus*, *M. scabrinodis*, *M. salina*, *M. deplanata*, and *T. caespitum*. On the other hand, *F. pratensis* at the periphery of its range proved to be a member of other coadaptive complexes. In the northern part of the range, this species was included into the impoverished community of forest ants because forest–steppe and steppe species (*F. cunicularia*, *F. rufibarbis*, and *T. caespitum*) do not reach the taiga zone, and species characteristic of the subtaiga and taiga (*Myrmica ruginodis*, *M. rubra*, *M. rugulosa*, *F. fusca*, and *L. niger*) are abundant only in zonal landscapes proper, where *F. pratensis* is rare. On the contrary, associations with *F. pratensis* in the desert zone included not only forest–steppe and deserts ants, but also the species that, like *F. pratensis*, live there in the intrazonal landscapes: *Myrmica bergi*, *Tetramorium inerme*, *T. indocile*, *Plagiolepis* sp., and *Leptothorax balhashensis*. Thus, in associations with *F. pratensis*



Location of valley transects (1–18).

Table 1. Number of nests of different ant species per feeding territory of *Formica pratensis* in different natural zones (average maximum values recalculated per reference area)

Species	Number of transect									
	1	2	4	5	6	7	9	10	13	14
<i>Formica fusca</i>	1	2								
<i>F. cunicularia</i>			4	5	5	7	8		5	
<i>F. rufibarbis</i>								6		5
<i>Lasius niger</i>	1	2								
<i>L. alienus</i>			4	11	12	10	12	7	8	
<i>Myrmica ruginodis</i>	5	8								
<i>M. scabrinodis</i>		10	8	6	8	7				
<i>M. schenki</i>		8	3	6	5	6				
<i>M. salina</i>				10	12	8	5	6		4
<i>M. deplanata</i>			4	5	10	8	5	5	13	
<i>M. bergi</i>										3
<i>Tetramorium caespitum</i>			4	6	5	15	11	6	7	3
<i>T. inerme</i>										4
<i>T. indocile</i>										6
<i>T. schneideri</i>										1
<i>Camponotus turcestanicus</i>										2
<i>Plagiolepis</i> sp.										2

Note: Numbers of transects correspond to those in the figure.

dominance, the number of species increased from 4 in the north to 8–10 in the south.

In the central part of the *F. pratensis* range (forest steppe and steppe), both the species composition and the numerical ratio of nests of nondominant ants per feeding area of the dominant proved to be constant: 5–7 *F. cunicularia* or *F. rufibarbis* nests, 10–12 nests of *Myrmica* species (*M. scabrinodis*, *M. salina*, and *M. deplanata*), approximately the same number of *Lasius alienus* nests, and 8–15 *T. caespitum* nests. In the semi-desert and desert zones, the ratio of nests was somewhat different due to the absence of *L. alienus* and lower abundance of *T. caespitum*, but the community remained essentially the same. In such coadaptive ant complexes with a constant structure, consistent forms of interaction between families of different species could be expected.

EXPERIMENTAL ANALYSIS OF ETHOLOGICAL MECHANISMS OF POPULATION DENSITY CONTROL IN MULTISPECIES ANT COMMUNITIES

This part of the work was based on the system of original field experiments involving artificial changes in the abundance of individuals of different species in ant communities.

Materials and Methods

Experiments were performed on three model multi-species associations of ants in different regions of southern Siberia (Table 2). In all the associations, dominant ants belonged to the species that build their dome-shaped nests of plant debris and protect their feeding territories, which contain a network of feeding paths. The size of their families varied from several tens to several hundreds of thousands of individuals. Subdominant and subordinate ants belonged to species constructing underground nests with the population ranging from several hundreds to several thousands of individuals. A few large families of subdominants occurred only in biotopes unsuitable for the dominant species. Prey of subordinate species consisted of smaller invertebrates than that of dominants, but food spectra of all the ant species generally overlapped (Reznikova, 1983).

Association I was located on the western slope of the Tannu–Ola ridge, in the wormwood–shrub steppe. The average density of nests (number per hectare) was 5–7 in dominant *F. uralensis*, about 50 in subdominant *F. picea*, and 120 in subordinate *M. lobicornis*. Association II inhabited the southeastern Baraba steppe with grass–wormwood vegetation. The average number of nests per ha was 4–5 in dominant *F. pratensis* and 12 in subdominant *F. cunicularia*. Association III was located in the park forest of the Novosibirsk Akademgorodok

Table 2. Results of field experiments on artificially changing the size of ant families

Date	Com-munity	Plot number	Interacting species	Number of accepted pupae	Dynamic density of ants on feeding territory, ind./m ² /min		Response of dominant species
					average	after increase in family size	
July–August 1978	I	1	<i>Formica uralensis</i> – <i>F. picea</i>	300	0.3 ± 0.01	1.5 ± 0.12	250 <i>F. picea</i> killed
		2	<i>F. uralensis</i> – <i>F. picea</i>	350	0.3 ± 0.02	1.8 ± 0.17	350 <i>F. picea</i> killed
		3	<i>F. picea</i> – <i>Myrmica lobicornis</i>	100	1.3 ± 0.15	2.1 ± 0.20	Nest of <i>M. lobicornis</i> blocked
June–July 1986	II	4	<i>F. pratensis</i> – <i>F. cunicularia</i>	2000	0.5 ± 0.03	2.2 ± 0.20	1500 <i>F. cunicularia</i> killed and 200 pupae transported to dominant's nest
		5	<i>F. pratensis</i> – <i>F. cunicularia</i>	2000	0.5 ± 0.06	2.2 ± 0.19	1000 subdominant ants killed and 3000 pupae transported to dominant's nest
		6	<i>F. pratensis</i> – <i>F. cunicularia</i>	2000	0.5 ± 0.04	2.4 ± 0.18	1000 subdominant ants killed and 500 pupae transported to dominant's nest
June–July 1989	III	7	<i>F. sanguinea</i> – <i>F. cunicularia</i>	3500	0.7 ± 0.08	2.5 ± 0.23	Nest of <i>F. cunicularia</i> is occupied by <i>F. sanguinea</i>
		8	<i>F. sanguinea</i> – <i>F. cunicularia</i>	3500	0.7 ± 0.01	2.3 ± 0.31	Nest of <i>F. cunicularia</i> is occupied by <i>F. sanguinea</i>
July–August 1993		9	<i>F. cunicularia</i> – <i>M. scabrinodis</i>	200	2.2 ± 0.45	3.6 ± 0.26	Nest of <i>M. scabrinodis</i> blocked

(campus), in a mixed stand. In this association, three pairs of interacting species were studied: *Formica sanguinea*–*F. cunicularia*, *F. sanguinea*–*F. fusca* (dominant–subdominant), and *F. cunicularia*–*M. scabrinodis* (subdominant–subordinate).

The purpose was to determine the upper limit to which the family size in subordinate ants can increase in the presence of dominant species. To this end, we performed two experiments on three 1200–1600-m² plots in association I (July–August 1978), three experiments in association II (June–July 1978 and June–August 1988), and two experiments in association III (June–July 1989 and July–August 1993). In association I, a sharp increase in the size of three *F. picea* families was caused by adding conspecific pupae. On plot 1, for example, 300 pupae were added to one family during three days (Table 2). To avoid direct competition for food between this species and dominant *F. uralensis*, *F. picea* ants received additional food from feeders with narrow entrances, which were too small for *F. uralensis*. Thus, the dominant species directly responded to an increase in the abundance of the subordinate species on the territory, rather than to the depletion of food resources. Continuous observations on the behavior of ants during the periods of their daytime activity were performed beginning from day 8 after the onset of experiments. Changes in the dynamic density of ants on

the territory were revealed by means of censuses taken on 36 plots (25 × 25 cm, three minutes on each plot) from 8 to 9 a.m. on days 8–14 of the experiment. The experiment in association II was performed by the same scheme. During seven days, each of three *F. cunicularia* families received 2000 additional pupae and was fed from feeders inaccessible for *F. pratensis*. In association III, additional nests of subdominants were transferred in wooden containers (40 × 40 × 50 cm) on the territory of the dominant species. Thus, on plot 7, a family of *F. cunicularia* (1300 ants) was placed on the territory controlled by *F. sanguinea* ants 7 m away from their nest; on plot 8, a family of 1000 *F. fusca* ants was placed at a distance of 9 m from the nest of *F. sanguinea*. After two weeks, when transplanted families settled in a new place, they were gradually supplemented with additional conspecific pupae (3500 pupae during 20 days). The dynamic density of ants on the territory in this period was recorded every three days, according to the same scheme as in association II.

To assess the response of ants to the increased density of nondominant species at a lower hierarchical level, several experiments on increasing the numbers of subordinate species in associations I (*M. lobicornis*) and III (*M. scabrinodis*) were performed. The nests of these species situated on the territory of subdominants

were supplemented with 25 conspecific pupae per day, with continuous observations on the behavior of ants.

Response of Dominants to the Growth of Families of Nondominant Species

When the size of a family in *F. picea* was increased by adding excess pupae, the territorial behavior of dominant *F. uralensis* ants changed in a similar way in all the three experiments (Table 2). On plot 1 of association I, for example, one of *F. picea* families received 300 pupae. After eight days, when ants emerged from cocoons, this family constructed two new underground sections during two days. On experimental day 11, the dynamic density of *F. picea* ants on the plot near these sections (about 4 m²) increased from 0.3 to 1.5 ind./m²/min. At the same time, the dynamic density of *F. uralensis* on the same plot increased from 4 to 40 ind./m²/min. During the next two days, *F. uralensis* killed and brought into their nest about 250 *F. picea* ants. They not only killed subdominants in the feeding territory, but also entered their nest (I observed *F. uralensis* ants carrying dead *F. picea* along their feeding paths). These ants subsequently occupied the new sections of the *F. picea* nest, using them as their temporary nest, and controlled the adjacent territory until the end of summer. Marking the ants on this territory, I revealed the permanent group of individuals controlling this area. After this conflict, *F. uralensis* did not manifest any aggressiveness toward *F. picea*.

In association II, three *F. cunicularia* families, each having the nest of three sections, were used in three experiments which yielded similar results. Thus, the first family received 2000 pupae during seven days. On day 10, the ants began active construction works, and by day 15 they had built the new aboveground capsule nest in the place of the former underground sectional nest. By this time, the average dynamic density of ants on their territory had increased from 0.5 to 2.0 ind./m²/min. However, as in the case with the family not exposed to the impact of dominant species, the permanent flow of feeding individuals on this territory was not formed because *F. pratensis* ants destroyed the new nest of the subdominant. During one day, they killed about 1000 *F. cunicularia* ants and carried them to their nest, together with approximately 500 pupae of this species. In contrast to *F. uralensis*, however, *F. pratensis* ants did not occupy the nest and the territory of *F. cunicularia* but allowed their activities on the feeding territory after essentially reducing their dynamic density.

In association III, *F. sanguinea* tolerated the families of subordinate species introduced to their territory, until their dynamic density exceeded the critical level (Table 2). When the family size of *F. cunicularia* increased, dominant ants occupied artificial nests and carried away both pupae and workers. In one case, *F. sanguinea* transferred their female into the artificial nest and established a permanent exchange path between both nests.

At the lower hierarchical level, interspecies interactions in the community were somewhat different. Thus, in the experiment carried out in association I, the abundance of *M. lobicornis* was increased by adding excess pupae. The ants accepted pupae during four days. Thereafter, the number of *F. picea* ants commonly present near the nest of the subordinate species increased from 3–4 to 15–20. They blocked the *M. lobicornis* nest and did not allow these ants to bring in pupae or food. The results of marking showed that a permanent group of *F. picea* workers operated there, notwithstanding the resistance of nest owners. If members of this group perished, new ants took their place, and this continued until the end of the season. Dominant *F. uralensis* ants visited this area but did not participate in the conflict. In one month, the number of *M. lobicornis* ants leaving the nest decreased threefold, and all their family perished by the end of summer. A similar blockade of the subordinate species nest by subdominant ants was observed in the experiment on increasing the size of *M. scabrinodis* family, performed in association II (Table 2).

The results of field experiments demonstrated the existence of a surprisingly fragile equilibrium between the competitive and mutualistic relationships (see Reznikova, 1982, 1983) in multispecies ant communities and revealed the threshold values of the dynamic density of nondominant species at which their coexistence with dominants is still possible. The existence of ethological mechanisms regulating population density of ants in communities appears to be based on the constancy of structure of coadaptive ant complexes.

The data obtained in our recent studies suggest that fine regulation of biotic relationships in ants is based on flexibility of individual behavior and learning processes. Experiments showed that ants of dominant species are characterized by an intricate system of communication based on distant guidance and the ability to estimate the number of objects (Reznikova and Ryabko, 1990, 1995). Ants apparently use these abilities for estimating the frequency of encounters with individuals of other species on their territory.

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