

Formation of Springtail (Collembola) Communities during Colonization of Ant-Hills

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Abstract—Formation of springtail assemblages in resettled nests of the ant *Formica aquilonia* was studied. The species composition and relative abundance of springtails was shown to depend on the age, hydrothermal regime, and condition of the ant nest. The abundance and species diversity of springtails increases during the initial period of the ant-hill growth. Old nests are characterized by the minimum species diversity, with one or two distinct dominants. High ecological plasticity, including resistance to high temperatures and low humidity, allows *Lepidocyrtus violaceus* to maintain its stable dominant position in the ant-hills. Species with relatively narrow hygro- and thermopreferenda quickly occupy temporal favorable niches, reach high abundance, and quickly disappear as the microclimatic conditions change.

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It is well known that the abundant bacteria, fungi, and algae in ant nests attract numerous small soil invertebrates, including springtails (Golubev and Bab'eva, 1972; Stebaeva et al., 1977; Zakharov, 1980; Pivovarov, 1987; Pokarzhevskij, 1981). In their dome nests built of plant debris, the ants maintain relatively stable and quite specific microclimatic conditions (Dlusskii, 1967; Galle, 1973; Stebaeva et al., 1977; Coenen-Stass et al., 1980; Horstmann and Schmid, 1986), which determine to a considerable extent the specific structure of a microarthropod community.

Our previous studies showed that springtail communities of ant-hills were characterized by distinct dominance of one or two species and, correspondingly, low species diversity and a low degree of evenness of the species structure. It was found that the springtail assemblages of *Formica* s. str. nests were not specific but composed of common litter- and soil-dwelling species. The composition and relative abundance of dominant species varied significantly even between neighboring nests (Reznikova and Sleptzova, 2003). Generally speaking, such a mosaic structure of springtail communities is typical of isle habitats (Chernova and Kuznetsova, 1990). This was demonstrated, in particular, by the examples of Arctic tussocks (Hertzberg et al., 2000) and isolated soil patches under solitary trees in urban areas (Kuznetsova, 2002). The factors determining the prevalence of a particular

species in a local community are still unknown. Wilson (1992) stated that random variations in colonization of habitats might be enhanced by deterministic interactions between species, resulting in different ways of their future development. This theoretical reasoning, however, was not tested by experimental studies of colonization of patchy habitats by microarthropods.

However, it is quite possible that initial stages of the colonization of such attractive “patches” as ant nests may involve dramatic interactions between different species of microarthropods. It would be important to reveal the particular advantages that allow the future dominant forms to colonize these specific “isle structures.” Ant-hills can be considered natural mesocosms which can be manipulated in order to study the pedobiontic communities under different conditions. In this work, we used the method of resettling *Formica aquilonia* nests to follow the initial stages of development of springtail assemblages in the nest domes and to reveal the possible factors affecting the dominance structure.

MATERIALS AND METHODS

Resettling the Nests of Formica aquilonia Yarr.

Within a recreational forest zone of Akademgorodok (Novosibirsk), there is an isolated forest patch of

18 ha, inhabited by *F. aquilonia*. Initially it comprised over 100 nests. In early June, 2000, Bugrova and co-authors (Bugrova et al., 2005, Sleptsova et al., 2005) carried out an experiment of relocating ant nests from a would-be construction site. A total of 24 nests, measuring 1 to 3 m in diameter, were relocated. The hill material of each nest was packed in sacks, transported on carts to a new territory, and placed on specially prepared wood fragments. Several days later, the remaining ants were collected and also transferred to a new place. The resettled nests were placed on the average 3 m apart. 30–35 days later, the resettled nests were on the average 65 cm in diameter and 15 cm in height, and the earth mounds started to form. About half of the resettled nests gave rise to 2–3 offshoots that were 40 cm in diameter and 20 cm high. In 2002, these resettled nests measured on the average 160 cm in diameter and 50 cm in height; the measurements of their offshoots were 90 cm and 30 cm, respectively.

Areas Studied

The nests of *F. aquilonia* were resettled in similar areas of birch-pine forest (density, 0.3–0.5). The undergrowth of the old area (no. 1) consisted of bird cherry and aspen, while the grass layer 30–100 cm high comprised goutweed, cocksfoot, wood bluegrass, everlasting pea, rough horsetail, and Solomon's seal; the projective cover was 70%. In the new area (no. 2), where the ant nests were resettled, the undergrowth consisted of bird cherry and Siberian spruce, and the grass layer (50–150 cm high), of bracken fern, rough horsetail, goutweed, cowparsnip, cocksfoot, and wood bluegrass; the projective cover was 80–90%. The illumination was similar in both areas (7–15% in late June). Area 2 was located farther away from buildings than area 1, and therefore experienced a lower anthropogenic load.

Characteristics of Nests of F. aquilonia

The red wood ant *F. aquilonia* is widely distributed in the forest areas of Siberia, where it usually forms large colonies (Dlusskii, 1967). The ants inhabit pine forests and lighter areas of larch stands. This species is more psychrophilic than other members of the red wood ant group (*F. polyctena* and *F. rufa*), and, if occurring sympatrically, occupies darker and more humid areas. Nests of all red wood ant species typically have a deep crater encircled by an earth mound.

The ant-hill proper consists mostly of small sprigs, conifer needles, birch aments, leaves, grass stems, and other elements. The ants regulate the thermal regime in the nest by changing the shape of the upper dome (Dmitrienko and Petrenko, 1976).

Study of the Springtail Community in the Ant-hills

In late May, 2000, samples were taken from eight *F. aquilonia* nests located in the old area. In early June, one month after resettling, samples were taken from four resettled nests and four offshoots in order to observe the initial stages of formation of the springtail assemblage. For comparison, we studied four nests located in the intact part of the original colony. In late May and late June, 2002, we examined two resettled nests, two well-developed offshoots of these nests, and two nests that had not been resettled. The studies of 2000 and 2002 used the same nests. In order to characterize the attractiveness of the nest domes for springtails, additional samples were taken in May 2002 from two relocated ant-hills that had been abandoned by the ants. The size structure of springtail assemblages was determined by counting juvenile forms, which differed from conspecific adults in size and body proportions.

Two samples (1/8 l, depth 5 cm) were taken from the central dome part of each nest. Ten control samples were taken from soil and forest litter within 10 m of the nest. Substrate temperature at the sampling sites was measured. Microarthropods were extracted using standard equipment. The springtails were counted and examined using a stereomicroscope. For identification, specimens were embedded in the standard For medium.

Data Processing

The dominance structure was analyzed using the scale proposed by Engelmann (1978), according to which eudominant forms comprise 40–100% of the total abundance, while dominant, subdominant, recedent, and subrecedent species comprise 12.5–39.9%, 4.0–12.4%, 1.3–3.9%, and less than 1.3%, respectively. We calculated the Shannon index of species diversity $H = -\sum [(N_i/N) \log_2(N_i/N)]$ and the evenness index of species abundance, derived from the Shannon index: $H/H_{\max} = H/\log_2 S$, where S is the number of species and N is abundance (Chernov, 1975; Magurran, 1988).

Table 1. Quantitative parameters of the springtail assemblages in *Formica aquilonia* nests and in the control

Parameter	Intact	Resettled	Offshoots	Abandoned	Control 1	Control 2
May 2000						
Abundance, ind./125 cm ³	4.5–100.6				4.5	14.6
Number of species	3–8				24	20
Shannon index <i>H</i>	1.3 ± 0.41				4	3.3
Evenness <i>H/H</i> _{max}	0.65 ± 0.18				0.88	0.76
July 2000						
Abundance, ind./125 cm ³	1.3–516.8	1.3–18.3	0–1		14.5	27.1
Number of species	2–3	1–9	0–2		19	25
Shannon index <i>H</i>	0.09 ± 0.06	1.29 ± 0.91	–		2.8	3.24
Evenness <i>H/H</i> _{max}	0.05 ± 0.04	0.6 ± 0.42	–		0.66	0.7
May 2002						
Abundance, ind./125 cm ³	99.5–421	95–166	66–96	45.5–60	18.5	24.4
Number of species	5–6	9–12	4–6	7–10	18	20
Shannon index <i>H</i>	1.49 ± 0.23	2.15 ± 0.08	1.3 ± 0.42	1.91 ± 0.33	3.3	3.64
Evenness <i>H/H</i> _{max}	0.61 ± 0.14	0.63 ± 0.04	0.59 ± 0.28	0.62 ± 0.03	0.75	0.93
June 2002						
Abundance, ind./125 cm ³	42–618	579.5–839.5	856–1979		65.1	81.7
Number of species	3–4	9–17	6–13		24	23
Shannon index <i>H</i>	0.28 ± 0.02	1.82 ± 0.62	0.76 ± 0.55		2.44	3.38
Evenness <i>H/H</i> _{max}	0.15 ± 0.01	0.5 ± 0.08	0.23 ± 0.12		0.53	0.75

Notes: control 1 refers to the original area of *Formica aquilonia* colony; control 2, to the area where the ant complex was relocated. The abundance and species number are shown as ranges from the minimum to the maximum value. The abundance is shown in the table as the number of individuals in a standard sample (125 cm³); whereas in the text it is expressed as the number of individuals per 1 m² (within a 5-cm layer).

RESULTS

Overall Springtail Community in the Areas Inhabited by F. aquilonia

In 2000, the overall springtail population of the territory originally occupied by the *F. aquilonia* colony was rather low: 1792 ind./m² in the soil horizon 0–5 cm in late May, and 5804 ind./m² in early June. The dominant forms in area 1 were *Protaphorura* sp. 1 (33%) and *Parisotoma notabilis* (19%) in spring, and *P. notabilis* (30%) and *Desoria* sp. (36%) in summer. A total of 29 springtail species were found in both the areas studied in 2000. However, the abundance of springtails in soil and forest litter was higher in the new area: 5812 ind./m² at the moment of resettling, and as many as 10796 ind./m² in summer. The dominant forms in area 2 in May were *Protaphorura* sp. 1 (17%) and *Desoria* sp. (30%); by mid-summer, *Desoria* sp. remained dominant (17%), while the relative abundance of *P. notabilis* (14%), *Lepidocyrtus violaceus* (17%), and *Tomocerus minutus* (24%) increased.

In 2002, the overall abundance of springtail community increased as compared to that of 2000 (Table 1). The species composition changed only insignificantly: in the old area, the fraction of *P. notabilis* increased to 58.5%, and in the new area, the fractions of *Isotomiella minor* and *T. minutus* increased to 23.7% and 20.4%, respectively.

Initial Stages of Formation of Springtail Community in Resettled Ant Nests

In the end of May, 2000 (before resettling), 15 springtail species were found in 8 nests of *F. aquilonia* (3–8 species in each dome). Though the abundance varied strongly (from 1800 to 42520 ind./m²), the dominant or eudominant position in all nests was occupied by the same species, namely *L. violaceus*. This upper litter-dweller comprised from 28 to 83% of the total abundance. In addition to this species, the following upper litter-dwelling forms reached the dominant status: *Entomobryoides myrmecophilus* (in

three nests), *Shoetella unungiculata* (in one nest), *Desoria* sp. n. (in one nest), and *Willowsia buski* (in one nest). The lower litter-dwellers were represented by the dominant *P. notabilis* (in two nests), and the upper soil-dwellers, by *Protaphorura* sp. 1 (in one nest). The Shannon index of species diversity was 1.3 ± 0.41 , and the evenness index was 0.65 ± 0.18 .

After resettling, the ants restored their nests and formed new ones (offshoots). In early July, one month after resettling, samples from 3 resettled nests yielded only occasional individuals of the litter-dwelling springtails *L. violaceus*, *E. myrmecophilus*, *P. notabilis*, *Drepanura quadrilineata*, and *W. buski*. In the most densely populated dome (9 species, 7320 ind./m²), euedaphic species were present as well. The most abundant species was the upper litter-dwelling *L. violaceus* (56.3%), which was present in all the four nests. Offshoots of the resettled nests, measuring up to 50 cm in diameter, either revealed no springtails at all, or contained occasional individuals of the upper litter-dwelling *L. violaceus*, *W. buski*, and *E. myrmecophilus*, and also the lower litter-dwelling *Pseudosinella* cf. *octopunctata*.

On the contrary, the abundance of springtails in the domes of three intact nests increased by mid-summer (53040–206720 ind./m²) as compared to that of spring. In one nest, only occasional individuals of *L. violaceus* and *E. myrmecophilus* were found. The index of species diversity and the evenness became much lower than in spring (0.09 ± 0.06 and 0.05 ± 0.04 , respectively), owing to the abruptly increasing fraction of *L. violaceus* (up to 96–99% of the total abundance). In all, six species of springtails were found in four control nests (2–3 species in each dome). These findings agree with our previous results, according to which the species diversity of springtails in the nest domes of red wood ants decreases in summer as the litter-dwelling forms increase their abundance while the soil-dwelling and soil-litter-dwelling ones disappear (Reznikova and Sleptsova, 2003).

Variability of Springtail Communities in *F. aquilonia* Nests

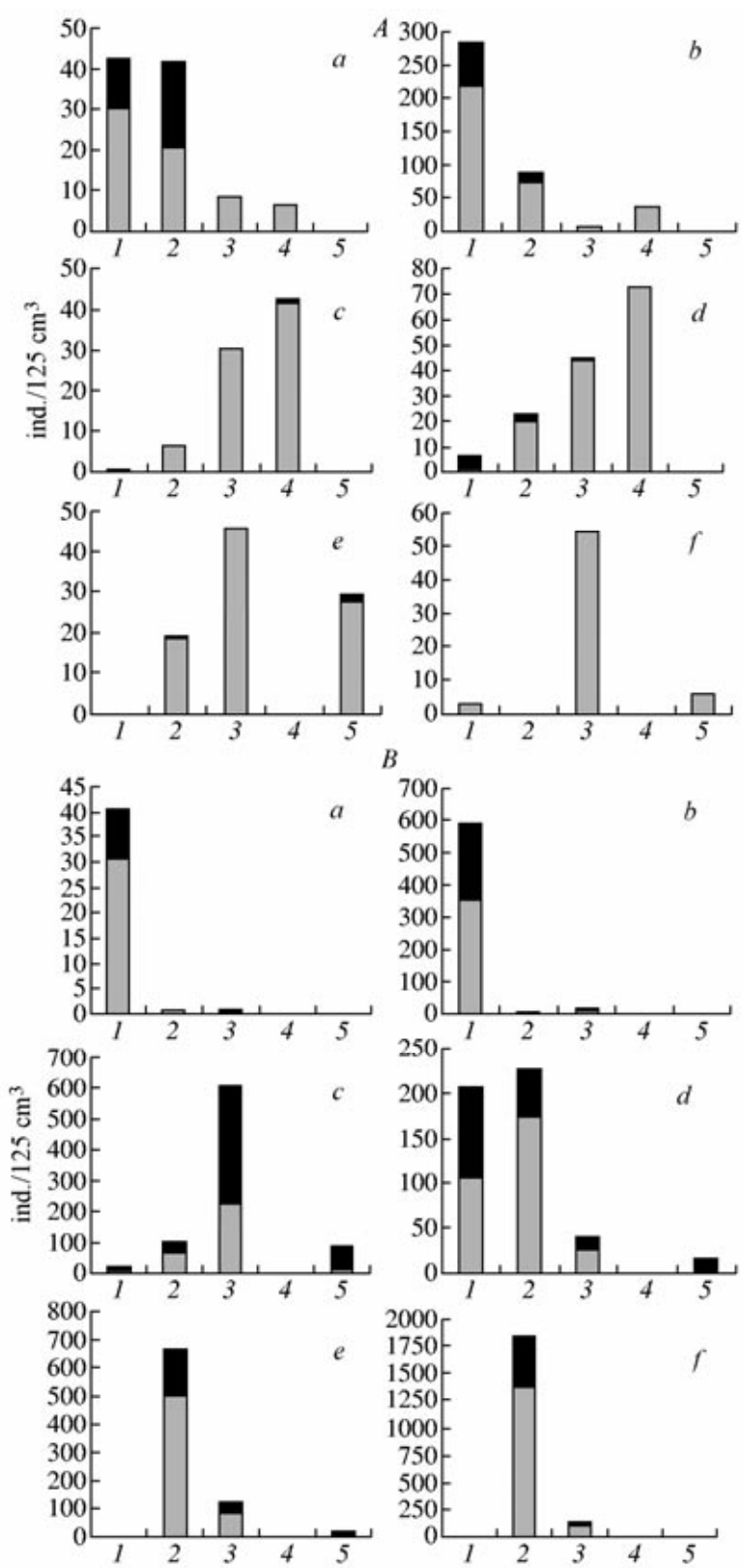
Two years after resettling, the domes and earth mounds of the nests were completely formed, while their offshoots grew to 90 cm in diameter and also developed earth mounds. The abundance and species diversity of springtails in these nests increased considerably as compared to 2000 (see Table 1). *L. violaceus* had the dominant status in all the nests located in the

new territory. However, the fraction of this species (32.1 and 27.1%) in resettled nests was lower than that of the eudominant *Pseudosinella* cf. *octopunctata* (44.7 and 44%). In the offshoots, the second position after *L. violaceus* (47.9 and 82.6%) was occupied by *E. myrmecophilus* (30.7 and 8.3%); in one nest, *P. notabilis* (19.8%) was also included in the dominant group.

In two intact nests, the composition of dominant species changed considerably as compared to that of 2000. The fraction of *L. violaceus* was only 8.5 and 1.8% of the total abundance of springtails, whereas *Friesea claviseta* (42.7 and 67.5%) and *P. notabilis* (41.7 and 21.1%) were dominant in both nests. The observed proportion of juveniles indicated active reproduction of these two species, which was, however, less evident in the resettled nests (figure, A).

In all the examined nests located within area 2, the abundance of springtails increased significantly in June 2002: it was 5–6 times as great as in spring in the resettled nests, and 13–20 times as great, in the offshoots (see Table 1). The dominance structure in the nests located in the new territory also changed. *Pseudosinella* cf. *octopunctata*, which in spring was dominant in the domes of resettled nests, was completely absent in June. The abundance of *L. violaceus* increased greatly (to 72%) in one of the resettled nests, the juveniles comprising 62% of this value (figure, B). In the dome of the other resettled nest, the dominant forms were *P. notabilis* (38%) and *F. claviseta* (35%); their populations included 48 and 23% of juvenile individuals, respectively. The abundance of *L. violaceus* in this nest increased insignificantly, its fraction comprising only 6.8%. In both offshoots, the fraction of *P. notabilis* increased greatly (to 77 and 93% of the total abundance). The fraction of juveniles in this species was much greater than in *L. violaceus*. The latter species comprised only 14.7 and 6.5%, respectively, of the total abundance of springtails in the offshoots.

The ant-hills located in the old territory yielded only four species of springtails. The Shannon index and the evenness of species abundance were much lower in the intact nests than in the resettled nests and their offshoots. In one dome, the abundance of springtails became 1.5 times as great (non-significant), while in the other nest, on the contrary, it decreased by the factor of 2 (see Table 1). The fraction of *F. claviseta* increased in both nests, reaching 95 and 96% of the



Abundance of adults and juveniles of the dominant springtail species in the nests of *Formica aquilonia* in late May (A) and early July (B), 2002. Intact nests (a, b), resettled nests (c, d), and offshoots (e, f); *Friesea claviveta* (1), *Parisotoma notabilis* (2), *Lepidocyrtus violaceus* (3), *Pseudosinella cf. octopunctata* (4), and *Entomobryoides myrmecophilus* (5). The dark portions of the columns correspond to the fractions of juveniles. The abundance is shown here as the number of individuals in a standard sample (125 cm³); whereas in the text it is expressed as the number of individuals per 1 m² (within a 5-cm layer).

total abundance, whereas the abundance of other species was reduced drastically. As in May, the population of *F. claviseta* comprised a large fraction of juveniles (figure, B).

Springtail Assemblages in Abandoned Ant-hills

In 2002, some of the resettled ant nests were abandoned. The former ant-hills were shapeless piles of plant debris. The temperature inside them did not rise above +10°C, whereas in the inhabited domes it reached 24.5–31°C. In May, the abundance of springtails in two abandoned nests was lower than in the inhabited ones, but higher than in the control (see Table 1). However, the number of *L. violaceus* in abandoned ant-hills was approximately the same as in inhabited nests. This species reached the eudominant status, comprising 67.5 and 54.9% of the total abundance of springtails in abandoned nests. This indicates a high degree of plasticity of this species, and in particular its tolerance to changes of the thermal regime. It should be noted that some springtail species which are common in the forest soil but rarely occur in living ant-hills were present in the abandoned domes and even reached a relatively high abundance. These species were the upper litter-dwelling *Desoria* sp. n. (16.5% in one dome), the lower litter-dwelling *T. minutus* (8.3%), the soil and litter-dwelling *Neanura muscorum* (9.2%), and the upper soil-dwelling *Supraptorura furcifera* (8.8%).

DISCUSSION

The use of “mesocosms” for studying biological processes in soil under natural conditions was proposed by Odum (1984) based on the notion that the processes observed in laboratory microcosms might differ from the real, natural ones (Kamplicher et al., 1995; Laakso et al., 1995). Ant nests, with their specific regulated microclimate and distinct boundaries, can be regarded as “natural mesocosms” and used for conducting experiments and studying interactions between species.

It is known that ant nest domes, built of plant debris, are mainly inhabited by litter-dwelling springtail species (Wisniewski, 1967; Stebaeva and Grishina, 1983). Ant-hills are usually characterized by a relatively low species diversity of springtails and a small set of interchanging dominant forms. This can be explained by the microclimatic conditions inside the domes. Owing to the specific shape of the nest, maintained by the ants, and metabolism of bacteria and the

ants themselves, the dome can be heated to +35°C and even more, with humidity changing from 30 to 100% (Dmitrienko and Petrenko, 1976; Coenen-Stass et al., 1980; Horstmann and Schmid, 1986; Frouz, 1996, 2000). The temperature in the examined ant-hills reached +31°C, whereas in the control it never exceeded +21°C. Such microclimatic conditions determine the prevalence of either thermo- and xeroresistant species, or the most flexible ones, which can quickly occupy the favorable niches and reproduce. We have tried to analyze the life strategies of the springtail species inhabiting ant-hill domes by studying their population dynamics.

The most abundant (comprising over 40% of the total number) and frequent species were the upper litter-dwelling *L. violaceus*, *E. myrmecophilus*, *F. claviseta* and the lower litter-dwelling *P. notabilis* and *Pseudosinella* cf. *octopunctata* (Table 2). *L. violaceus* and *P. notabilis* are often found in the litter of the surrounding biotope as well, though in considerably less numbers than in the ant-hills. *E. myrmecophilus* was rare in the forest litter; however, this species was recorded not in all ant-hills, and its abundance was lower than in other species.

Among the abundant species, the most stable population was that of *L. violaceus*, whereas other species were abundant only in certain periods. *L. violaceus* is one of the first species to colonize the developing nests, and remains in the abandoned nests for at least several years. Besides that, it may be assumed that *L. violaceus* is least affected by damage to the ant-hill. Decomposing plant remains in the domes appear to provide abundant food for this springtail. According to Berezina (1999), tissues of higher plants were found in guts of some representatives of *Lepidocyrtus*.

Outside the ant-hills, there may be other species with high ecological plasticity and a greater degree of xeroresistance, as well as the species that can be attracted by abundant food in the ant-hills (decomposing litter, microfauna). However, the particular combination of resources and conditions presents in the ant nests appears to be most favorable for *L. violaceus*.

The specific dominance structure and mosaic distribution of springtails in the ant nest domes suggest that complex interactions may exist between springtail species. In particular, analysis of the springtail population dynamics in all the studied nests of *F. aquilonia* in 2002 showed that the abundance of *Friesea clav-*

Table 2. Species composition of springtails in domes of *Formica aquilonia* nests and in the control

Species and life forms	2000				2002				
	intact	resettled	off-shoots	control	intact	resettled	offshoots	abandoned	control
Upper litter dwellers									
<i>Shoetella ununguiculata</i> (Tullb.)	dom.					subdom.			
<i>Hypogastrura</i> sp.				+					+
<i>Ceratophysella</i> sp.	subdom.								
<i>Friesea claviseta</i> Axels.	+	dom.		+	eudomin.	dom.	subdom.	+	+
<i>F. mirabilis</i> (Tullb.)									+
<i>Isotoma viridis</i> Bourl.	+	+		subdom.		+	+		+
<i>Desoria</i> sp.	dom.	+		dom.		+	+	dom.	+
<i>Proisotoma minuta</i> Tullb.						+			
<i>Vertagopus</i> sp. n. Potapov							+		
<i>Lepidocyrtus violaceus</i> (Geoffr.)	eudom.	eudom.	eudom.	dom.	subdom.	eudom.	eudom.	eudom.	subdom.
<i>Willowsia buski</i> (Lubb.)	dom.	eudom.	eudom.	+		subdom.			+
<i>Entomobrya obensis</i> Linn.		subdom.		+		+		+	
<i>E. lanuginosa</i> (Nic.)				+				+	
<i>Entomobryoides myrmecophilus</i> Reut.	eudom.	subdom.	eudom.	+	+	subdom.	dom.		+
<i>Drepanura quadrilineata</i> Steb.		subdom.		+					
<i>Sminthurinus niger</i> (Lubb.)	+			+					+
<i>Sminthurinus</i> sp.				+					+
<i>Sphaeridia pumilis</i> (Krausb.)				+					
<i>Deuterostminthurus pallipes</i> Börn. f. <i>repanda</i>				+					+
Lower litter dwellers									
<i>Anurida</i> sp.						+	+		+
<i>Parisotoma notabilis</i> Schaff.	eudom.	subdom.		dom.	eudom.	eudom.	eudom.	subdom.	eudom.
<i>Proisotoma minima</i> (Absol.)									+
<i>Pseudosinella</i> cf. <i>octopunctata</i> Börn.		subdom.	eudom.	+		eudom.		subdom.	
<i>Tomocerus minutus</i> Tullb.				dom.		subdom.	+	subdom.	dom.
<i>T. sibiricus</i> Reut.				+		+	+		subdom.
Litter and soil dwellers									
<i>Neanura muscorum</i> (Tempi.)				+	+	+		subdom.	+
<i>Micranurida pygmaea</i> Börn.							+		
<i>Folsomia rossica</i> Potapov & Dunger									+
<i>F. quadrioculata</i> (Tullb.)				+					
<i>Pseudosinella alba</i> (Pack.)	+			subdom.					
<i>P. sexoculata</i> Schött	+			+					
<i>Arrhopalites principalis</i> Stach									+
<i>Arrhopalites</i> sp.				+					

Table 2 (Contd.)

Species and life forms	2000				2002				
	intact	resettled	offshoots	control	intact	resettled	offshoots	abandoned	control
Upper soil dwellers									
<i>Protaphorura</i> cf. <i>octopunctata</i> (Tullb.)	dom.	+		eudom.		+	+		+
<i>Protaphorura</i> sp. 2				+				+	
<i>Protaphorura</i> sp. 3				dom.					
<i>Protaphorura</i> sp. 4				subdom.		+			
<i>Grananurida baicalica</i> Rusek				+			+		+
<i>Onychiurus</i> s. str. sp.				dom.	+	+			subdom.
<i>Supraphorura furcifera</i> (Börn.)				+		+	+	subdom.	subdom.
<i>Metaphorura affinis</i> (Börn.)				+					
<i>Isotomiella minor</i> (Schäff.)	+			subdom.		+			dom.
<i>Folsomia fimetaria</i> L.				+		+			
<i>F. inoculata</i> Stach				subdom.		+			+
Deep soil dwellers									
<i>Willemia intermedia</i> Mills				+					+
<i>W. anophthalma</i> Börn.									+
<i>Tantulonychiurus</i> sp.									+
<i>Mesaphorura macrochaeta</i> Rusek		subdom.		subdom.	+	+	+	+	subdom.
<i>M. krausbaueri</i> Börn.	subdom.			subdom.					+
<i>M. hylophila</i> Rusek				+		+			+
<i>M. critica</i> Ellis				+					+
<i>Megalothorax minimus</i> Will.									+
Total number of species	15	12	4	39	7	24	15	12	34

Notes: dom., dominant; subdom., subdominant; eudom., eudominant. The fraction of the total abundance is >40% for eudominants, >12.5% for dominants, and >4% for subdominants (Engelmann, 1978). The "+" sign marks recedent and subrecedent forms (no more than 3.9%). Each column (different variants of nests and the controls) presents united data from different surveys.

iseta increased greatly in a month's time, whereas that of *L. violaceus* remained almost stable. However, in one dome where the fraction of *F. claviseta* was low, the abundance of *L. violaceus* increased significantly due to a great number of juveniles (figure). Members of the genus *Friesea* have cutting-sucking mouthparts (Striganova, 1980). Unlike most springtail species, which are non-specialized saprophages feeding on litter, bacteria, and fungi, representatives of *Friesea* spp. consume animal food, such as small invertebrates, including springtails, and insect eggs (Singh, 1969). It may be assumed, with certain reservations, that the absence of population growth of *L. violaceus* is related to the high abundance of *F. claviseta* which feed on the eggs and juveniles of the former species. This hypothesis, however, must be experimentally tested.

In general, one may distinguish two types of the life strategies of springtails inhabiting ant-hills. The first type is exemplified by the upper litter-dwelling *L. violaceus*, which is one of the first to develop stable populations in the ant-hills because of its high ecological plasticity. A relatively high abundance of this species is preserved even after the nest is abandoned and its microclimate is maintained no more. The second strategy is used by the species with relatively narrow hygro- and thermopreferenda, which quickly occupy the favorable niches as they appear, reach a high abundance, and quickly disappear when the microclimate changes.

These strategies can be compared to the ecocentric strategies considered by MacArthur and Wilson (1967) and Ramenskii (1971). The first strategy corre-

sponds to the “patients,” or *L*-selection species, which are characterized by high tolerance to severe conditions, rather than by growth potentials. The second strategy corresponds to the “explerents,” or *r*-selection species, which have a low competitive power but are capable of very quick exploration of newly available territories, filling in the “gaps” among stronger competitors. The predatory *F. claviseta* may belong to “violents,” or *C*-selection species, which occupy the territory and keep it, suppressing the competitors by complete utilization of the available resources (Ramenskii, 1971).

CONCLUSION

Our study of the formation of springtail communities in resettled *F. aquilonia* nests has shown that at the initial stages of development the ant-hills are colonized by mobile litter-dwelling species, most resistant to arid conditions. The abundance and diversity of springtails increases as the nest grows and develops. The abundance of springtails in large old domes with relatively constant humidity may significantly exceed their abundance in the surrounding soil and litter.

The springtail communities formed in the nest domes of red wood ants are quite specific and differ from the initial zonal community. They are characterized by a relatively low species diversity and a high level of dominance of one or two litter-dwelling species. The total abundance and composition of dominant species can change drastically both from year to year and within a single season, owing to rapid reproduction of a particular species. It may be assumed that the activity of ants affects considerably the structure of the springtail community in a nest. This specificity is preserved at least two years after the nest is abandoned.

Springtails colonizing ant-hills use different life strategies. The forms best adapted to the conditions of the nest dome (such as *L. violaceus*) maintain a stable and high abundance. The species with relatively narrow hygro- and thermopreferenda, capable of quick exploration of the available favorable niches, reach a high abundance but decline quickly as the microclimate changes. Further experimental studies of the ecological features and behavior of springtail species inhabiting ant-hills, as well as their interaction, are needed to reveal the mechanisms of development of their local communities.

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