Structure of Saprophagous Invertebrate Community on a Steppe Catena in the Trans-Volga Region

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Received January 13, 1998

Abstract—The saprophagous ground-surface invertebrate community was studied on a steppe catena in Samara Province during 2 years. Nine species of darkling beetles (Coleoptera, Tenebrionidae), millipede *Megaphyllum rossicum* (Diplopoda), cockroach *Ectobius duskei* (Blattodea), and one species of woodlice (Isopoda) were found. The tenebrionid species had the highest density in early June, the millipedes, in early July, *Ectobius duskei*, in August, and the Isopoda species, in September. The maximum densities of these invertebrates were usually registered in different catenary positions. So, woodlice and millipedes were the most abundant in various positions of the upper part of the catena (dry steppe), and cockroaches and darkling beetles, on the flat interfluve and in the lower part of the catena (steppe meadow). Common tenebrionid species also have the maximum abundance in different positions on the catena. By linear sizes, species of darkling beetles can be divided into four groups with a intergroup length ratio of 1.32–1.40, which is higher than the well-known Hutchinsonian ratio (1.26–1.28). In each group, there is only one abundant species (*Crypticus quisquilius, Opatrum sabulosum, Tentyria nomas, Blaps lethifera*), with the sizes of these species differing even greater (1.35–1.75).

Invertebrate plant-litter consumers destroy plant debris in the initial stage of the detrital trophic chain (Striganova, 1980). In their absence, the decomposition of litter considerably decelerates, affecting among other things the fertility of soil (Begon *et al.*, 1989). In this paper, an attempt is undertaken to analyze the structure of a community of saprophages belonging to the mesofauna, i.e. large and medium-sized arthropods, primary crushers of plant debris in steppe ecosystems. The paper deals with arthropods of a drainage series (catena), which is a chain of ecosystems integrated by soil and surface drainage into a landscape unity (Stebaev, 1963) and a natural subdivision of the steppe landscape (Mordkovich *et al.*, 1985). A brief characteristic of the population of soil-surface inhabiting arthropods was given by Lyubechanskii *et al.* (1997). The structure of the community of ants on the catena was considered separately by Dorosheva *et al.* (1998, 1998a).

PHYSIOGRAPHICAL CHARACTERISTICS OF THE CATENA

The territory studied belongs to the area of Obshchii Syrt Hills of the physiographical province Vozvyshennyi Syrt of the Trans-Volga Region (Zakharov, 1971; Gerasimov and Doskach, 1937). The catena is situated 4 km south-west of Fitali, Bol'shechernigovskii District, Samara Province, about 52°03′N, 51°20′E, being a slope of the valley Kirilov Dol situated at the watershed of the river Bol'shoi Irgiz and its tributary Rostash. This watershed is a part of Sinii Syrt, a large flat-topped hill system separating the basins of Volga and Ural.

The slope is of southern exposition and has a weakly convex profile of unequal steepness, with height gradient of 31.75 m and length of about 440 m. The catena is arrow-shaped, lying between the main valley of Kirilov Dol (valley of a stream) and its right "tributary" valley. As a result of such a position in the relief, the area of watershed slope in the profile studied is represented by a narrow (about 1-m-wide) crest sloping toward both valleys.

According to geobotanical regionalization, the territory studied is referred to the Ergeni-Transvolga steppe subprovince of the Transvolga-Kazakhstan steppe province in the Prichernomorsk-Kazakhstan infraregion of the Eurasian steppe region (Steppes of Eurasia, 1991). The local flat interfluve is occupied by dry steppe on southern chernozems with dominating *Stipa capillata, Stipa lessingiana*, and xerophytic steppe forbs (*Artemisia austriaca* and *Galatella villosa*). This association is replaced downwards by a wormwood-fescue steppe of even more xerophytic appearance and low projecting coverage with abundant

Table 1. Characteristics of registration plots of the pitfall-trap line on the Kirilov Dol catena

Position	Altitude (m)*	Interval (m)**	Comments
1	0.300	–	Flood plain meadows
2	1.352	21.4	
3	2.614	26.2	
4	3.605	9.6	Forb-fescue-feathergrass steppe
5	5.925	58.9	
6	8.298	42.3	Reed steppe of valley slope
7	16.494	44.0	
8	22.949	42.2	Dry steppe on crest
9	27.021	23.7	
10	31.753	110.1	Dry steppe on flat interfluve

* Elevation above level of the stream bottom at the foot of the catena.
** Distance from the previous point along the slope.

dwarf semishrubs (*Kochia prostrata, Atraphaxis frutescens, Salsola laricina*). Such a steppe occupies the crest of the watershed slope. In the place of transition of the crest into the valley slope, it gives way to a forb-reed-feathergrass steppe (with high participation of *Stipa tirsa, Phragmites australis, Glycyrrhiza glabra*, and *Amygdalus nana*) on eroded soils with shortened profile. In passing to the alluvial fan, it is replaced by a true forbs-fescue-feathergrass steppe on alluvial chernozem-like soils. The flood-land is occupied by meadows, varying from a steppe meadow in the upper part of the flood-land to a hygrophytic meadow bordering the river-bed like a narrow stripe.

In the immediate vicinity, in the upper reaches of Kirilov Dol, lies a ravine aspen grove. A wide edge of this grove is formed by shrubs with *Frangula alnus, Rhamnus cathartica, Crataegus* sp., *Cerasus fruticosa*, and *Prunus spinosa*.

MATERIAL AND METHODS

Ground-dwelling invertebrates on the catena were counted from 7.VII.1993 to 5.X.1993 and from 31.V.1994 to 25.VIII.1994. The invertebrates were collected into pitfall traps (0.5-1 glass pots) one-third filled with a 4% solution of formaldehyde, examined every 10 days. The traps were placed along a transect through the catena in 10 plots: 2 traps in each registration plot in 1993 or 3 traps arranged in a triangle with side length of 5–6 m in 1994. The position of plots remained unchanged over the whole working period. The catena was gauged with a level, and for all plots

their relative elevations above the stream-bed and distances between them were calculated. Characteristics of registration plots in each position along the profile are given in Table 1. Plots 1–3 were situated in different variants of flood-plain meadows; plots 4 and 5, in forbs-fescue-feathergrass steppe on the alluvial fan; plots 6 and 7, in a "reed" steppe on the valley slope; plots 8 and 9, in a dry steppe on the crest; and plot 10, in a dry steppe on the flat interfluve (Table 1).

The number of invertebrates entrapped in each plot during each registration period was expressed as number of specimens per 100 trap-days (hereafter spm. per 100 trap-days). This recalculation made the obtained data comparable. The standard method of trap collecting seems to be adequate for studying this community because of the rather large sizes of saprophagous species under study (with body length of 6-7 mm in the smallest species, *Crypticus quisquilius*), their comparable mobility, and mainly crepuscular or nocturnal activity. It was suggested that, with the unified counting technique, the probability of entrapping for specimens of one species mainly depends on their number per unit area, i.e. density. In this way the relative abundance and relative dynamic density of species under study were estimated.

As a part of the study, the total body length and also length and width of mandibles in some species of darkling beetles were measured. The measurements were done with the help of an eyepiece micrometer on a MBS–9 binocular magnifier. The body length was measured from apices of mandibles to apices of elytra.

The length of mandibles was measured from their anterior margin to the center of the posterior articulatory tubercle, and their width, in the widest place.

Four groups of saprophages are considered: Tenebrionidae [9 species: *Tentyria nomas* Pall., *Blaps lethifera* Marsh., *B. halophyla* F.-W., *Platyscelis hypolithos* Pall., *Oodescelis polita* (Sturm), *O. melas* F.-W., *Pedinus femoralis* (L.), *Opatrum sabulosum* (L.), *Crypticus quisquilius* (L.)], Blattodea (*Ectobius duskei* Ad.), Diplopoda [*Megaphyllum rossicum* (Timotheev)], and a species of Isopoda. Of all saprophagous specimens entrapped on the catena, representatives of these species comprised about 80% in number and 90–95% in biomass. The material is deposited in the collection of Siberian Zoological Museum (Institute of Animal Systematics and Ecology, Siberian Division, Russian Academy of Sciences, Novosibirsk).

RESULTS AND DISCUSSION

Seasonal Dynamics of Saprophage Abundance (Fig. 1)

In darkling beetles, the highest total dynamic density (hereafter density) is 76 spm. per 100 trap-days; however, this maximum was reached only in early summer for a short time and only because of *Opatrum sabulosum* which became the most abundant species in the first 10 days of June 1994. During the rest of the season, the density of darkling beetles ranged from 1 to 5 spm. per 100 trap-days, without substantial peaks or falls.

In 1993, the density of *Ectobius duskei* Ad. was in some positions almost an order of magnitude higher than that of other saprophagous insects (darkling beetles and small weevils of the genus *Trachyphloeus*). Unlike all other ground-dwelling insects, *E. duskei* had density increasing in the second half of June (from 7 to 60 spm. per 100 trap-days) and then gradually decreasing, to attain the previous values in late September. The density of *E. duskei* was much lower in 1994 than in 1993, and even in the August peak it was half that of 1993. Nevertheless, the coincidence of peaks of this parameter in both years (in August) is obvious.

The density of *Megaphyllum rossicum* in 1993 was the highest in the first half of July (about 20 spm. per 100 trap-days in a position), then it decreased gradually to zero, and then somewhat increased in Septem-
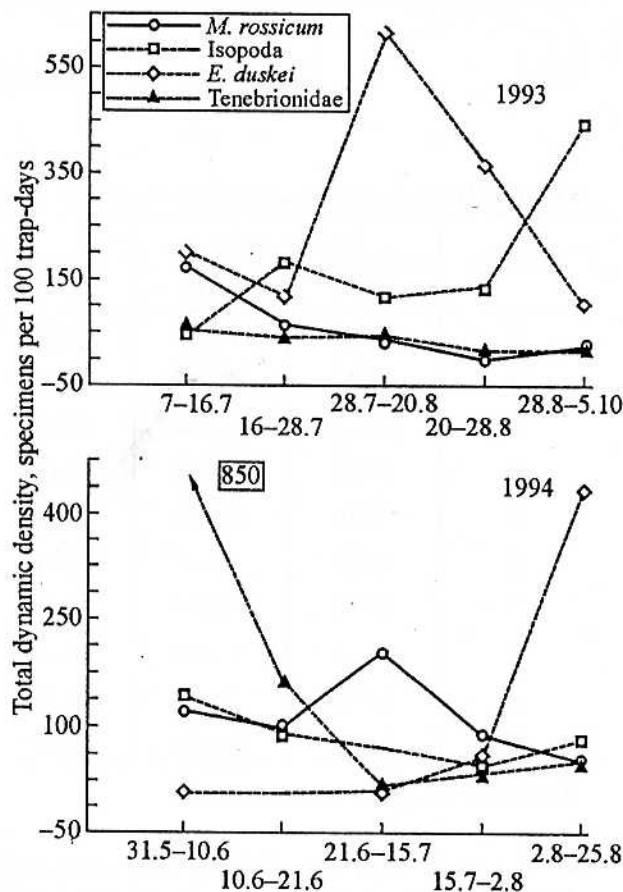

Fig. 1. Seasonal dynamics of saprophage abundance on the Kirilov Dol catena in 1993 and 1994.

ber. In 1994, the maximum density of *M. rossicum* was observed in the end of June–1st half of July (i.e. in the same period as in 1993), with about the same values. However, it did not decrease to zero by the end of August, remaining at the level of 4 spm. per 100 trap-days in a position.

The number of Isopoda in traps was the highest in September in 1993, and in early June in 1994. It is believed that their seasonal dynamics has two peaks, but one of these (the spring-time peak in 1993 and the autumnal in 1994) was not embraced by the registration period. The density of Isopoda reached 11 spm. per 100 trap-days in a position in spring and 45 in autumn. It was on average higher in 1993.

Hence, consumers of large plant litter (Tenebrionidae, *Megaphyllum rossicum*, *Ectobius duskei*, and Isopoda) reach the maximum density successively at different times during the summer season (early June, 1st half of July, August, and September, respectively). Isopoda are exceptional, having reached peak density

Table 2. Total number of saprophages (specimens per 100 trap-days) on the Kirilov Dol catena in 1993 and 1994

Position	Tenebrionidae		E. duskei		Isopoda		M. rossicum	
	1993	1994	1993	1994	1993	1994	1993	1994
1	0.000	1.638	0.000	0.000	0.000	0.000	0.000	3.180
2	2.934	**47.386**	0.000	0.000	0.000	0.000	0.000	4.550
3	2.712	39.204	0.790	4.560	0.000	1.520	0.000	12.410
4	3.342	21.566	13.430	21.280	5.280	0.000	0.000	0.000
5	**7.916**	13.132	68.160	**106.060**	0.000	5.220	4.170	32.320
6	1.702	1.504	59.914	45.600	· 0.000	3.330	6.250	49.220
7	3.750	14.554	23.218	4.100	32.440	44.120	12.730	93.370
8	2.000	2.310	28.808	25.650	**801.950**	**376.640**	65.870	109.740
9	5.316	13.520	21.248	22.800	85.910	6.370	**200.370**	**148.780**
10	**5.618**	**40.400**	47.700	**181.150**	2.900	0.000	0.000	0.000

Note. Maxima are printed in bold face.

in the early summer of 1994 simultaneously with Tenebrionidae. Presumably, such a distribution in time is unrelated to features of their life cycle, since specimens of different stages were found at density peaks in each group studied (with exception of darkling beetles, which is due to collecting with pitfall traps).

Distribution of Saprophage Densities over Catenary Positions

All the four main groups of saprophages inhabit most of the catena, but their densities differ markedly in different positions.

The dynamic density of darkling beetles in 1993 was extremely high in positions 5, and also 9 and 10, on the catena (8 and 6 spm. per 100 trap-days, respectively). In 1994, the distribution changed: the highest densities of darkling beetles (due to *Opatrum sabulosum*) were observed in low positions (the 2nd and 3rd with 40 and 50 spm. per 100 trap-days, respectively) and again in the uppermost position (10th), but not in the middle ones. Excluding the first third of June with predominance of *Opatrum sabulosum*, we have a threefold decrease of the maximum density, but the pattern did not change significantly: as before, the low positions (2nd and 3rd) appear to be the richest in darkling beetles, with a minor peak also observed in position 10.

The average density of *Ectobius duskei* in the season of 1993 was extremely high in the middle of the catena (positions 5 and 6, with 68 and 60 spm. per 100

trap-days, respectively). It was also high in position 10 (on the flat interfluve), reaching there a value of 48 spm. per 100 trap-days. *E. duskei* did not occur in positions 1 and 2, and only few specimens were registered in position 3 (average density less than 1). It may be assumed that *E. duskei* avoids humid habitats with meadow vegetation and tends toward habitats with medium humidity (local flat interfluve and transitional parts of the catena). In 1994, the distribution remained the same as in 1993, with minor modifications. Peaks in positions 5 and 10 became even more pronounced.

Hence, insects tend toward middle catenary positions in 1993 (damp year), instead of upper and low positions, inhabited in the droughty 1994 year.

Millipedes undeniably peaked in position 9 in 1993, and in positions 8 and 9 in 1994. Woodlice peaked in position 8 in both 1993 and 1994. Thus, millipedes and woodlice, on the one hand, and darkling beetles and cockroaches, on the other, form two groups between which the space of the catena is divided. Cockroaches and darkling beetles prefer more humid (transitional and flat interfluve) positions, millipedes and woodlice, drier (eluvial) positions (Table 2).

It is noteworthy that, while the maximum density of darkling beetles was an order of magnitude lower than that of *Ectobius duskei* and two orders of magnitude lower than the densities of woodlice and millepedes in 1993, it was between one third and half the maximum densities of *Ectobius duskei* and millipedes in 1994.

Table 3. Distribution of abundant species of darkling beetles over positions of the Kirilov Dol catena (total number for two years, specimens per 100 trap-days)

Position	Opatrum sabulosum	Crypticus quisquilius	Blaps lethifera	Tentyria nomas	Pedinus femoralis	Oodescelis melas	Sum without O. sabulosum	Sum
1	8.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00
2	**210.81**	22.73	5.56	12.50	1.32	0.00	42.11	**252.92**
3	147.50	21.95	4.00	0.00	1.32	**31.62**	**58.89**	206.39
4	89.00	16.39	5.87	0.00	0.00	1.32	23.58	112.58
5	68.58	**27.08**	6.25	0.00	3.33	0.00	36.66	105.24
6	64.83	7.86	0.00	0.00	0.00	0.00	7.86	72.69
7	0.00	0.00	12.50	0.00	2.77	0.00	15.27	15.27
8	56.66	0.00	12.87	17.67	4.34	0.00	34.88	91.54
9	4.54	5.17	**20.57**	**43.59**	10.79	0.00	**80.12**	84.66
10	**174.66**	**14.83**	14.17	0.00	**17.36**	0.00	46.36	**221.02**

Note: Maxima are printed in bold face.

The peaks of the total densities of all the dominant groups in each year did not coincide and fell on different positions of the catena. In 1993, this was observed for 3 abundant groups, the peaks of the tenebrionid density coinciding with those for the rest of the saprophages. However, in 1994, when the ratio of densities became somewhat more equable, the lower peak of darkling beetles shifted even lower over the slope, into meadow positions. As for the second peak (on the flat interfluve), it still coincided with the maximum density of *Ectobius duskei.*

Position 10 was one of the few positions where the other two groups of saprophages were almost or completely absent, especially in 1994. In the season of 1993, the total density of all saprophages in position 10 was 0.11 and 0.06 times those in positions 9 and 8, respectively. In July and August 1993 and in June 1994, the projecting coverage of vegetation and litter was estimated on areas of 1 square meter in positions 9 and 10; that of vegetation constituted less than 20% and 50–60% and that of litter no more than 10% and 90–95%, respectively. Thus, the distribution of saprophage density appeared to be opposite to the that of the potential food resources (plant litter) and the protective properties of the habitat.

Hence, it may be suggested that the low density of saprophages in position 10 in 1993 was caused not by deficiency of available resources, but by some other factors. The increase in densities of both *Ectobius duskei* and Tenebrionidae on the flat interfluve in 1994 can be interpreted as resulting from their penetration into the "ecological rarefaction" zone where the amount of food resources exceeded the possibility of their assimilation by the species. Note that in 1994 the total density of saprophages in position 10 was already somewhat greater than that in position 9 and only 2.3 times lower than that in position 8.

It should also be noted that the distribution of density peaks along the catena in the three groups dominating in 1993 was preserved in 1994, although weather conditions were strongly different in the two years: 1993 was extremely humid, whereas 1994 was moderately arid and hot. Darkling beetles were the only group whose spatial distribution changed. This change may be due to a direct influence of the climate, which also agrees with the direction of the shift (toward more humid habitat). However, in this case, the absence of reaction in the other groups calls for explanation. A non-contradictory explanation can be provided under the assumption that the distribution of the saprophages along the catena is controlled by the potential interspecific competition. Two phenomena can be understood in the light of this assumption: (1) the relative independence of the distribution from direct impact of abiotic factors and (2) the shift of the density peak just for darkling beetles (as a group whose abundance increased sharply in lower positions during the period from 1993 to 1994) and just in that direction along the catena where the total density of saprophages becomes lower.

A reservation should be made that actual competition is not assumed here for this community. The available facts are not sufficient for that. It can be suggested that the spatial (and, as indicated above, also temporal) structure of the saprophage community had been formed under the influence of the "ghost of the competition past" (Connell, 1980) and/or under the threat of "competition future." In the latter case, the observed spatial-temporal distribution is meant to correspond to the minimum level of the interspecific competition and any change of this distribution will lead to stronger competition. To escape the competition, the species return to the previous boundaries, and, thus, the whole system is in a potential well. In this case, the peak of darkling beetles in meadow positions may reflect the preferences fixed in the course of evolution, and the small peak in position 5 becomes possible simply owing to the low total density of darkling beetles in 1993.

Structure of the Assemblage of Darkling Beetles

Above, tenebrionids are considered an indivisible group. This is justified by their low total density, with the density of each species (with, possibly, exception of Opatrum sabulosum) negligibly low as compared to that in the other groups of saprophages. Yet, the coexistence of species within the given group is of certain interest.

We recorded 9 of the 13 species of Tenebrionidae reported from Samara Province east of Volga in the previous studies (Aleinikova and Utrobina, 1964; Busheva, 1969). One of the species, Opatrum sabulosum, was sharply dominant on the catena; the density of Crypticus quisquilius was also high. These two species are characteristic of a wide variety of habitats, from humid meadows to dry steppes (Mordkovich, 1978), tending toward mesic habitats. Pedinus femoralis is also a forest-steppe mesophilous species; the catena studied is situated at the southern boundary of its distribution. Oodescelis melas is confined to outskirts of small ravine forests and bushes. Of the species listed above, only Blaps lethifera and Tentyria nomas inhabit flat interfluve steppes.

In general, the tenebrionid fauna of the catena is of forest-steppe rather than steppe character, probably because of the proximity of the transect to the insular aspen grove and mesic lateral valley. The darkling beetle species are distributed along the catena in accordance with their environmental preferences

(Table 3). The lower half of the catena is inhabited by the most abundant Opatrum sabulosum and Crypticus quisquilius. The first species shows a distinct peak in position 2, while the maximum density of Crypticus quisquilius is "spread" among positions 2 to 5. It is characteristic that the density of both the species increases again on the flat interfluve and they have a second peak in position 10. The density of the mesophilous Pedinus femoralis increases from the bottom to top of the catena, also peaking on the flat interfluve. Oodescelis melas is met practically only in position ·3. The other two species, Blaps lethifera and Tentyria nomas, are the most abundant in position 9, the most arid within the catena.

The total abundance distribution of tenebrionid species (all positions over all periods) is sharply uneven. Opatrum sabulosum is absolutely dominant in their assemblage, its density being 1–2 orders of magnitude higher than that of any other darkling beetle species. The maximum density of darkling beetles is determined by the presence of this species and falls on positions 2 and 10. When this species is not taken into account, the maximum density is observed in positions 3 and 9 (Table 3).

It is evident that density peaks of various species are grouped in positions 2, 3 and 9, 10. Does this mean that darkling beetles are not segregated here with respect to consumption of common resources? The relative size of the coexisting species may offer indirect confirmation of such a segregation. In many cases, the difference in mouthpart sizes in related species correlates with the difference in sizes of their feeding objects. In particular, such a correlation between sizes of mandibles and sizes of prey was recorded in tiger beetles (Coleoptera, Carabidae, Cicindelinae) (Pearson and Mury, 1979). If sizes of mouthparts are proportinal to the total sizes of animals, the sizes of feeding objects also correlate with the latter. The correlation was recorded (Fenchel, 1975) for such saprophages as mud snails (Hydrobiidae). Furthermore, the distinctions in body sizes of closely related species may find reflection in their different ways to use the physical space of a biotope (Walter and Norton, 1984). Under certain conditions, it would be expected that the coexisting potential competitors differ in linear size by no less than a factor of 1.26–1.28. This value is named the Hutchinsonian ratio or Santa Rosalia index. A voluminous literature is devoted to its interpretation and its fulfillment or failure in real communities (Sim-
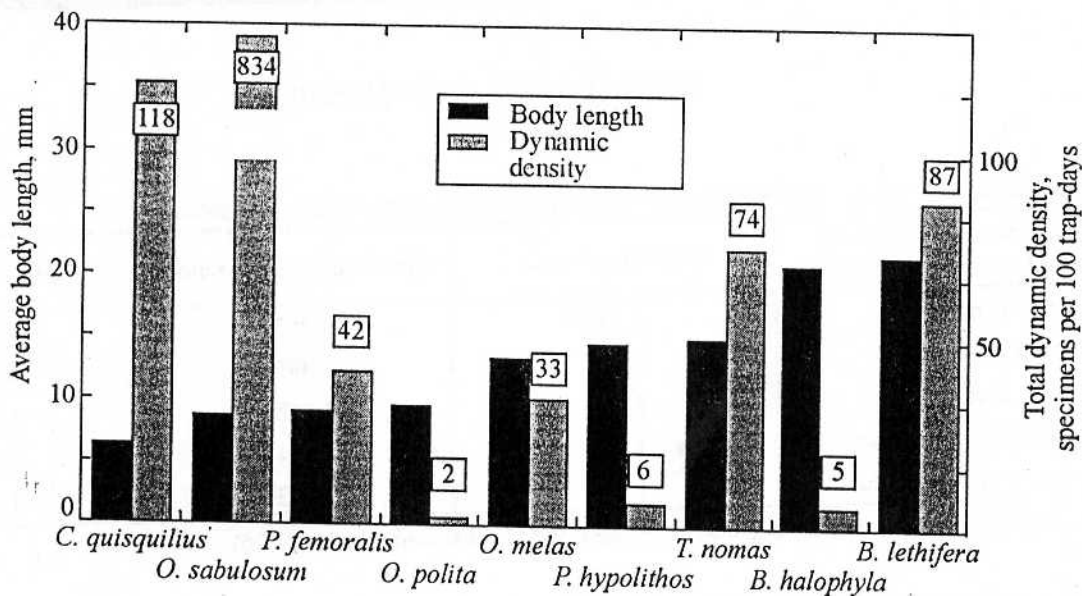
Fig. 2. Length of mandibles in the abundant species of darkling beetles in the Kirilov Dol catena.

berloff and Boecklen, 1981; Wiens, 1982; Rogovin, 1986; Giller, 1988; Azovskii, 1990; Basset, 1995). Although this rule is debatable, its fulfillment in a community of coexisting closely related species clearly indicates their divergence in utilization of trophic or some other resources (Giller, 1988). In this case, the usually discussed question as to whether the segregation is caused by competition, or random selection of species, or some other reason is not important. Previously the fulfillment of the Hutchinsonian rule has been recorded for the size structure of communities of predacious tiger beetles (Pearson and Mury, 1979) and ground beetles *Pterostichus* (Coleoptera, Carabidae) (Brandl and Topp, 1985), and, among saprophages, for Hydrobiidae (Fenchel, 1975).

An analysis of the linear sizes of darkling beetles in the present community indicated that they form 4 groups of species with interspecies ratio (1.32–1.40) exceeding the theoretically required value. Each group contains only one abundant species (*Crypticus quisquilius, Opatrum sabulosum, Tentyria nomas, Blaps lethifera*) with even greater interspecies ratio (1.35–1.75) (Fig. 2). The remaining species of darkling beetles were met as single specimens only and can be probably regarded as strangers from neighboring, more mesic habitats, which agrees with the characteristics of these species known from the literature.

Mandibles (as the most important of the food-obtaining structures in the beetles) were measured in 6 most abundant species. Mandibles in all the species

studied are robust, have similar triangular shape with an acuminate anterior end somewhat bent interiorly and ventrad, and differ in proportions: in small-sized species the mandible bases are somewhat wider. The mandible length is reliably proportional to their width ($r = 1.00$, $P < 0.05$), and both these indices are reliably proportional to the body length of the beetle ($r = 0.97-0.98$, $P < 0.05$). The mandible length distributions in different species and within each species differ from the normal one, possibly because of the small sample sizes (no more than 15 specimens of each species were measured).

Body length ratios differ from those of the mouthpart sizes, although the order of the species remains the same (Fig. 3). For the pair of the species *Tentyria*
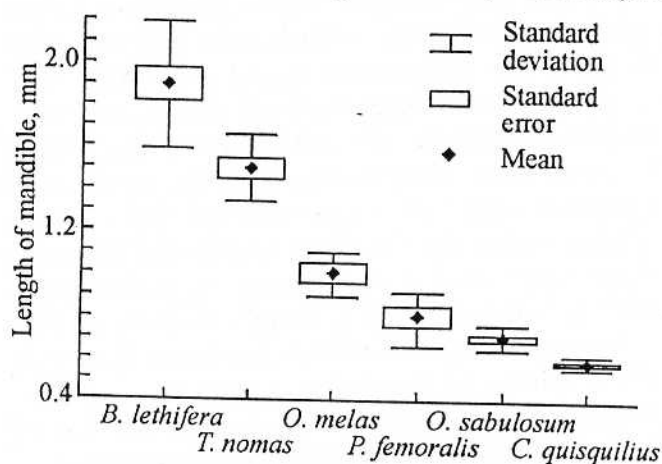

Fig. 3. Length of mandibles in the abundant species of darkling beetles in the Kirilov Dol catena.

Table 4. Linear size ratio in the dominant species of darkling beetles in the Kirilov Dol catena

Pairs of species darkling beetles ranged in order of decreasing sizes	Body length ratio	Mandibular length ratio	Mandibular width ratio
B. lethifera / T. nomas	**1.442**	**1.263**	1.221
T. nomas / O. melas	1.131	**1.495**	**1.525**
O. melas / P. femoralis	**1.490**	1.258	**1.260**
P. femoralis / O. sabulosum	1.040	1.124	1.068
O. sabulosum / C. quiquilius	**1.354**	1.213	1.153

Note: Ratios printed in bold face are equal to, or exceed, the Hutchinsonian ratios (1.26).

nomas/Oodescelis melas the ratio of mouthpart sizes corresponds to the Hutchinsonian ratio and that of the body lengths does not. In the pair Opatrum sabulosum/Crypticus quisquilius (the most abundant species), the situation is the opposite. The last two species differ in how they use the biotope space: O. sabulosum is a ground-surface species, and C. quisquilius inhabits litter. Pedinus femoralis and O. sabulosum practically do not differ in body length and in mandible size ratios. However, the dynamic densities of these species differ by almost three orders of magnitude, including a difference by an order of magnitude on the flat interfluve preferred by both species.

Hence, in the given assemblage, the Hutchinsonian ratio is fulfilled at least for one character (length of body or mandibles) in all common species of darkling beetles, with the exception of sharply differing ones (Table 4).

The low total density of darkling beetles and their highly uneven abundance distributions give no reason to assume any considerable role of competitive relations either within the given group or with other saprophages inhabiting the catena (possibly, except O. sabulosum). Nevertheless, a rather pronounced segregation of species is observed within the group of darkling beetles. Some of them are dispersed along the catena as described above, with density peaks not coinciding. In the cases when several species have coinciding peaks, they either reach maximum density at different times, as O. sabulosum and Crypticus quisquilius, or strongly differ in size, as the same pair of species and the pair Blaps lethifera–Tentyria nomas.

CONCLUSION

The investigated soil-surface saprophage community occupies the Kirilov Dol catena along its whole length. Hence, the chosen spatial scale appears to be adequate for analysis of the community structure. Four basic groups of saprophages inhabiting the catena practically from top to bottom have density maxima not coinciding in space and time. In the most species-rich group (assemblage of darkling beetles), the species only partly differentiate the use of space and time on the same scale, but the size structure of the group corresponds to finer segregation of species regarding the utilization of some local resources, such as food or space, on the scale of a phytogenous pattern and microrelief. The dynamics of the whole community in 1993–1994 can be interpreted, with some reservations, as governed by the potential competition for trophic resources.

REFERENCES

1. Azovskii, A.I., Taxonomic Relationship, Morphological Similarity and Ecological Proximity of Species in the Community of Marine Psammophilous Ciliates, Zool. Zh., 1990, vol. 69, no. 5, pp. 5–16.
2. Aleinikova, M.M. and Utrobina, N.M., The Fauna of Tenebrionidae and Their Distribution in Middle Trans-Volga, Pochvennaya fauna Srednego Povolzh'ya (Soil

Fauna of Middle Trans-Volga), Moscow: Nauka, 1964, pp. 52–66.

3. Basset, A., Body Size-related Coexistence: an Approach through Allometric Constraints on Home-range Use, *Ecology*, 1995, vol. 76, no. 4, pp. 1027–1035.

4. Begon, M., Harper, J.L., and Townsend, K., *Ecology. Individuals, Populations and Communities*, in 2 vols., Oxford, etc.: Blackwell Scientific Publications, 1986. Translated under the Title: *Ekologiya. Osobi, populyatsii i soobshchestva*, Moscow: Mir, 1989.

5. Brandl, R. and Topp, R., Size Structure of *Pterostichus* spp. (Carabidae): Aspects of Competition, *Oikos*, 1985, vol. 44, no. 2, pp. 234–238.

6. Busheva, A.V., Soil-dwelling Invertebrates of Solonetz Complex in Kuibyshev Province, *Cand. Sci. (Biol.) Dissertation*, Kuibyshev, 1969.

7. Connell, J.H., Diversity and the Coevolution of Competitors, or the Ghost of Competition Past, *Oikos*, 1980, vol. 35, no. 1, pp. 131–138.

8. Dorosheva, E.A., Smelyanskii, I.E., Lyubechanskii, I.I., and Reznikova, Zh.I., The Structure of Ant Community in Steppe Catena on Evidence of Accounting with Pitfall Traps, *Murav'i i zashzhita lesa, Materialy X Vseros. Mirmekolog. Simp.* (Ants and Forest Protection, Proceedings of the X All-Russian Myrmecological Symposium), Moscow: Inst. Probl. Ekologii i Evolyutsii, Ross. Akad. Nauk, 1998, pp. 58–63.

9. Dorosheva, E.A., Smelyanskii, I.E., Lyubechanskii, I.I., and Reznikova, Zh.I., The Spatial-Temporal Distribution of Ants within a Drainage-Geochemical Series of Landscapes in Transvolga Steppes, *Biologicheskoe raznoobrazie zhivotnykh Sibiri, Materialy Dokl. Simp. "110 let sibirskoi zoologii"* (Biological Diversity of Animals in Siberia, Proceedings of the Symposium "110 Years of Siberian Zoology"), Tomsk: Tomsk. Gos. Univ., 1998a, pp. 132–134.

10. Fenchel, T., Character Displacement and Coexistence in Mud Snails (Hydrobiidae), *Oecologia*, 1975, vol. 20, no. 1, pp. 367–376.

11. Gerasimov, I.P. and Doskach, A.G., Geomorphological Description of the Watershed Upland of Lower Trans-Volga, *Trudy Komissii po Irrigatsii, Vyp: 7, Pochvenno-geographicheskie issledovaniya v tselyakh irrigatsii* (Transactions of Irrigation Commission, no. 7, Soil-Geographical Studies Aimed at Irrigation, Prasolov, L.I., Ed.), Moscow-Leningrad: Akad. Nauk SSSR, 1937, pp. 9–62.

12. Giller, P.S., *Community Structure and Niche*, London

and New York: Chapman and Hall, 1984, Translated under the Title: *Struktura soobshchestv i ekologicheskaya nisha*, Moscow: Mir, 1988.

13. Lyubechanskii, I.I., Smelyanskii, I.E., Legalov, A.A., and Dudko, R.Yu., Population of Ground-dwelling Invertebrates on a Steppe Catena in Trans-Volga, *Stepi Evrazii: sokhranenie prirodnogo raznoobraziya i monitoring sostoyaniya ekosistem, Materialy Mezhdunar. Simp.* (Steppes of Eurasia: Preservation of the Nature Diversity and Monitoring of Ecosystem Condition, Proceedings of International Symposium), Orenburg, 1997, pp. 109–110.

14. Mordkovich, V.G., *Zoologicheskaya diagnostika pochv lesostepnoi i stepnoi zon Sibiri* (Zoological Diagnostics of Soils in Forest-steppe and Steppe Zones of Siberia), Novosibirsk: Nauka, 1978.

15. Mordkovich, V.G., Shatokhina, N.G., and Titlyanova, A.A., *Stepnye kateny* (Steppe Catenas), Novosibirsk: Nauka, 1985.

16. Pearson, D.L. and Mury, E.J., Character Divergence and Convergence among Tiger Beetles (Coleoptera: Cicindelidae), *Ecology*, 1979, vol. 60, pp. 557–566.

17. Rogovin, K.A., Morphological Divergence and the Structure of Communities in Terrestrial Vertebrates, *Itogi nauki i tekhniki, Zoologiya pozvonochnykh* (Achievements in Science and Technology, Zoology of Vertebrates), 1986, vol. 14, pp. 71–126.

18. Simberloff, D.S. and Boecklen, W., Santa Rosalia Reconsidered: Size Ratios and Competition, *Evolution*, 1981, vol. 35, no. 6, pp. 1206–1228.

19. Stebaev, I.V., Changes in the Animal Population of Soils in the Course of their Development on Rocks and on Weathering Products in Forest-Steppe Landscapes of the South Urals, *Pedobiologia*, 1963, vol. 2, pp. 265–309.

20. *Stepi Evrazii* (Steppes of Eurasia), Lavrenko, E.M., Ed., Leningrad: Nauka, 1991.

21. Striganova, B.R., *Pitanie pochvennykh saprofagov* (Feeding of Soil Saprophages), Moscow: Nauka, 1980.

22. Walter, D.E. and Norton, R.A., Body Size Distribution in Sympatric Oribatid Mites (Acariformes: Sarcoptiformes) from California Pine Litter, *Pedobiologia*, 1984, vol. 27, no. 2, pp. 99–106.

23. Wiens, J.A., On Size Ratios and Sequences in Ecological Communities: are there no Rule?, *Ann. Zool. Fenn.*, 1982, vol. 19, no. 2, pp. 297–308.

24. Zakharov, A.S., *Rel'ef Kuibyshevskoi oblasti* (Relief of Kuibyshev Province), Kuibyshev: Kuibyshevskoe Knizhnoe Izd., 1971.