Russian Journal of Ecology, Vol. 27, No. 4, 1996, pp. 267–273. Translated from Ekologiya, Vol. 27, No. 4, 1996, pp. 275–281.

Organization of the Trophic Interrelations of Small Insectivora of the Taiga

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Received January 15, 1993

Abstract—On the basis of data collected in Karelia in 1984–1987, the application of the method of principal components is considered in detail for analysis of the food spectra of insectivorous mammals. This method permits consideration of the features of the trophic niches of different species and their distribution. Analysis of the food spectra reveals separation of the trophic zones of Insectivora by dwelling horizons.

Investigation of the functioning of ecosystems is impossible without considering trophic chains. Of particular interest in the understanding of the laws of ecosystem organization is analysis of the trophic relations in closely related species that share territory and have similar diets. Communities of insectivorous mammals may serve as a representative model for such study.

The purpose of the present study was to characterize the trophic organization of the small insectivorous complex as a whole and investigate the age-dependent feeding habits in background species of shrews.

There are two approaches to the assessment of food specialization in Insectivora. The first method is associated with investigation of the functional parts of the food-obtaining apparatus, but its application is limited to closely related species (Shvarts and Demin, 1986). The other, more traditional approach concerns the taxonomic spectra of the prey consumed by different species in terms of the nutritional role in the feeding of particular taxa (Yudin, 1962; Ivanter *et al.*, 1973; Vol'pert and Averenskii, 1983; Churchfield, 1984). However, information obtained in this way is so detailed that its analysis is difficult. The size of the prey of Insectivora has been considered less frequently (Pernetta, 1976).

We analyzed taxonomic spectra of prey consumed by Insectivora. To compare diets, the percent similarity and the Sjorensen index are occasionally used (Churchfield, 1984). Unfortunately, in this case, information in terms of the occurrence of certain types of food is lost, and only their availability or absence is taken into account. In the quantitative form (Mirkin *et al.*, 1989), these indices assess the differences in the absolute levels of food frequencies, reflecting their diet ratio to a lesser extent.

In searching for a statistical index of the similarity (difference) of food spectra that best takes into account the data obtained, we had to reject the Euclidian measure, whose value is affected by the number of parameters of the compared objects, and also the Mahalanobis and MacNaughton–Smith measures, based on the comparison of single-type objects.

After some time, we arrived at the linear correlation coefficient as an index of the similarity of animal diets reflecting the ratio of the food items represented in them. An evident advantage of the index is its relative independence of sample size: the more stomachs analyzed, the more precise the frequency of food items, but their ratio remains almost unchanged. Therefore, the index permits the comparison of bodies of data of different size.

In Karelia, seven species of small Insectivora coexist: *Sorex araneus, S. caecutiens, S. isodon, S. minutissimus, S. minutus, Neomys fodiens*, and *Sicista betulina*, i.e., six species of Insectivora proper (Soricidae) and one predominantly insectivorous rodent. The heterogeneous species composition of the population permits the consideration of trophic differences among both closely related species and distant taxa.

MATERIALS AND METHODS

The study was made in 1984–1987 on the territory of the Ladoga Theriological Station of the Laboratory of Zoology, Institute of Biology, Karelian Branch of the Academy of Sciences of the USSR (the neighborhood of the village Karku, Pitkyarantskii raion, Karelia). The animals were captured with snap-traps, trenches, and trapping jars with 4% formaldehyde in the majority of Insectivora habitats: in a bilberry pine forest, an *Oxalis* spruce forest, a mixed coniferous–broad-leaved forest, an alder grove, and overgrown clearings and on the edges of a sown meadow. The data were generalized in all habitats where captures were made.

The stomachs of the animals were preserved with 70% alcohol, and selection and determination of the contents were made under a binocular microscope. The stomach contents were analyzed in a total of 1420 *Sorex araneus*, 315 *S. minutus*, 140 *S. caecutiens*; 31 *S. isodon*; 8 *S. minutissimus*, 17 *N. fodiens*, and 104 *Sic. betulina*.

The frequency of each food item was calculated as the ratio of the number of stomachs containing this food to the total number of analyzed stomachs. Subsequently, all the main types of food of insectivorous diets (40 groups) were used; some primary materials were published previously (Makarov, 1986, 1988).

In different Insectivora, the lists of main prey proved to be similar, which permitted us to use the correlation coefficient for comparison. At the same time, this index is sensitive to the presence of zero values in the initial data and, thus, tends to be overestimated. To eliminate zero values, the frequency of the values of rare food items were sometimes added to other taxonomically or ecologically similar food items (in studies of the age variability of feeding).

The matrix of paired correlation coefficients served as a basis for component analysis (Jeffers, 1978). Calculations normally yielded two or three main components—sets of factor loads (eigenvectors) for each of the food items used in the analysis. According to the value of factor loads, groups of correlated food items were distinguished in the principal components. The first principal component distinguishes the largest groups and eliminates the greatest proportion of total variance. In this case, the maximal module values of the factor loads are characteristic of those food items that are most proportionally represented in the diets of different species, and, hence, are strongly correlated with one another. Conversely, food items with low load values are represented irregularly. Correspondingly, the interpretation of the principal components is determined by those food items that have maximal values of their factor loads. The second and third principal components are interpreted in a similar way in accordance with the value of the factor loads of the food items: to estimate their values, the proportion of variance that they eliminate should be taken into account.

Moreover, factor loads are coefficients in diagnostic equations that make it possible to estimate the affinity of each species spectra analyzed to a certain conventional food spectrum that has maximal values according to the given component. In this hypothetical ratio, the frequency of food items with large positive loads is high, whereas that of foods with large negative loads is small, and that of foods with small negative is random. Such estimates of correspondence (component values) are plotted on a graph. High values of the components imply strong affinity of the actual and hypothetical diets and vice versa.

The space organized by the axes of the principal components is a projection of trophic niches of the species and can be referred to as the "area of consumed resources." The centers of species niches in the multidimensional space of food resources are projected onto the plane of the principal components as points. In considering multispecific communities, the concept introduced makes it possible to analyze trophic niches and the possible competition proceeding from the assumption that change in trophic interrelations only occurs within the area of consumed resources.

In addition, correlation coefficients were used as a measure of distance ($1 - r$), which permitted cluster analysis of food spectra by the nearest neighbor method (Jeffers, 1978). To reveal the most specific diets, the inclusion measure was used as an exoticity index of food spectra (Andreev, 1980).

RESULTS AND DISCUSSION

The diet of Insectivora varied over years. Nevertheless, analysis of data generalized over several years is possible, because the specificity of the consumption of

Table 1. Component analysis of food spectra of different age groups of individuals of *Sorex araneus*, *S. caecutiens*, and *S. minutus*

No.	Food item	Eigenvectors ($E \times 100$)		
		1	2	3
1	Coleoptera: Carabidae, Staphylinidae (imagines, larvae)	55	–99	49
2	Coleoptera: weevils, click beetles, leaf beetles (imagines)	–99	32	–18
3	Coleoptera: click beetles (larvae)	–47	100	59
4	Diptera (imagines)	78	–75	–30
5	Lepidoptera; Hymenoptera, sawflies (larvae)	56	15	100
6	Hemiptera	100	–20	4
7	Spiders	84	54	26
8	Harvestmen	90	35	–45
9	Mollusks	–65	–99	22
10	Earthworms	–81	–75	24
Proportion of eliminated variance, %		57.7	26.0	13.4

different food items by species remained, as is seen from Fig. 1.

The main principles of the interpretation of the method of principal components should be preliminarily noted, for instance, in analysis of the age variability of the feeding of three background shrew species in terms of the ten leading food items. As can be seen from Fig. 2, in terms of the main component, *S. araneus* is placed on the left, *S. minutus* is on the right, and *S. caecutiens* is intermediate. Because the greatest factor loads in the first components are associated with food items nos. 2, 6–8, and 10 (Table 1), there are grounds to believe that their distribution in the diet determines the differentiation of the species–age classes on the axes of the components. Two groups are distinguished in terms of their frequency in stomachs of the species above (Fig. 3). The first group, comprising food items nos. 6–8, occurs rather often in stomachs of *S. minutus*, to a lesser extent in *S. caecutiens*, and occasionally in *S. araneus*. The factor loads of these food items are large and positive (see Table 1). The second class comprises food items nos. 2 and 10 with large negative indices. Correspondingly, their representation in stomachs is inverse to the first group. The diet of *S. araneus* tends to be similar to that of the overwintered individuals of *S. caecutiens*, whereas the diet of the current year's young of that species is more similar in terms of diet to *S. minutus*. Some substantial differences in the food spectra of *S. caecutiens* of different age are noted when they are maintained in captivity (Okhotina, 1974).

Food items 6–8 (Hemiptera, spiders, and harvestmen, respectively) are mobile dwellers of the herbaceous–dwarf shrub layer; item 10 (earthworms) comprises soil dwellers, and item 2 (leaf beetles, weevils, and click beetles) comprises phytophage beetles, largely associated with herbaceous vegetation. Proceeding from this distribution of food items, the first principle component can be interpreted as a ground-surface feeding type, which is the most characteristic of *S. minutus*.

The second principal component separates *S. araneus* from overwintered *S. caecutiens*. The highest factor loads are those of food items 3, 9, and 10 (soil larvae of click beetles, mollusks, and earthworms). Correspondingly, this main component can be classified as the "specificity of soil feeding," two different versions of which are displayed by *S. araneus* and overwintered individuals of *S. caecutiens*.

The proportion of variance of the third component is low (13.4%), but the distribution of animal groups in it shows common differences in the diets of different-age individuals, item 5 (caterpillars and sawfly larvae) being of particular importance. This component can be referred to as the "consumption of openly-dwelling phytophage larvae," which is less pronounced in individuals born in the current year, for example, in *S. minutus*, it is 30.3% versus 43.0% in adults.

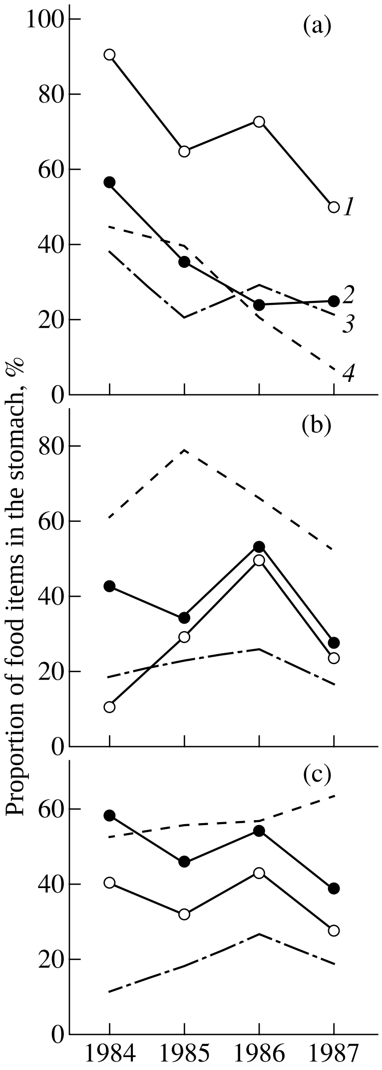

Fig. 1. Frequency of (a) lepidopteran larvae, (b) spiders, and (c) harvestmen in the stomachs of Insectivora: (*1*) *Sic. betulina*, (*2*) *Sorex caecutiens*, (*3*) *S. araneus*, (*4*) *S. minutus*.

Thus, analysis of the available data shows greater separation of food niches of different-age *S. caecutiens* in relation to the other two species (see Fig. 2). Data on the feeding pattern support the conclusion on the intermediate status of *S. caecutiens* between *S. araneus* and *S. minutus*, which stems from analysis of the dimensions of the food-obtaining apparatus (Shvarts and Demin, 1986), but they reveal more complex food specialization in the trophic system of closely related species. According to our data, there is partial spatial separation of the species: *S. araneus* is a litter–soil dweller, and *S. minutus* is a ground-surface dweller, whereas *S. caecutiens* is intermediate, i.e., it inhabits the ground surface and litter.

For a general characterization of the feeding of the insectivorous complex on the basis of a correlation matrix (for 38 items), a dendrogram of the similarity of the diets was plotted (Fig. 4). There are two two-species

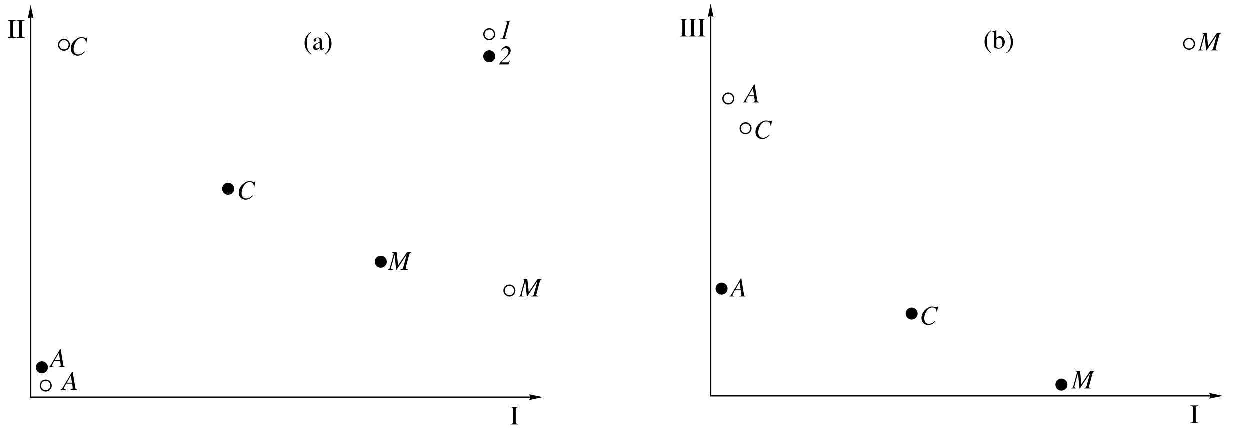

Fig. 2. Distribution of shrew diets on the planes (a) of the first and second and (b) first and third principal components: (*1*) overwintered individuals and (*2*) the current year's young; *A—Sorex araneus*; *C —S. caecutiens*, and *M—S. minutus*.

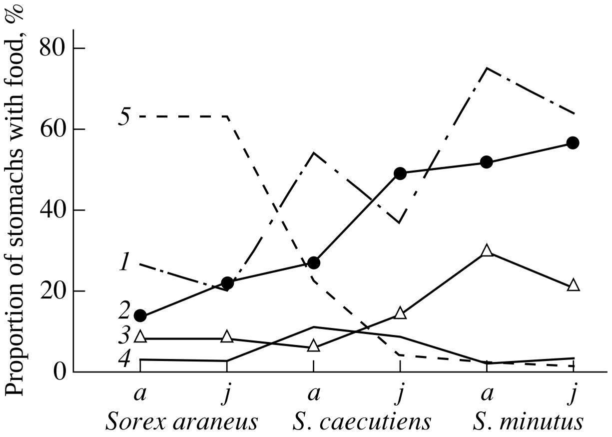

Fig. 3. Frequency of some food items in stomachs of shrews of different age: (*1*) spiders, (*2*) harvestmen, (*3*) bugs, (*4*) imagines of phytophage beetles (weevils, leaf beetles, and click beetles), and (*5*) earthworms.

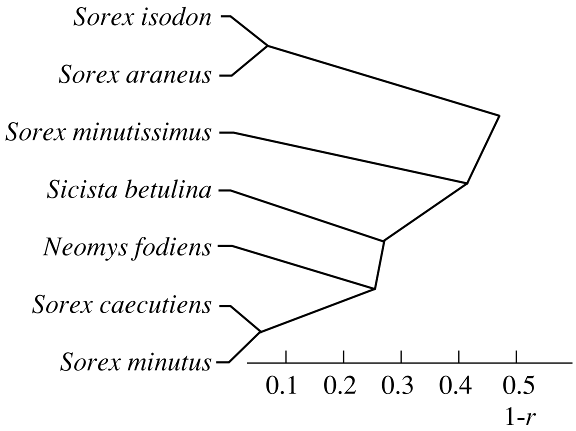

Fig. 4. Dendrogram of similarity of the diets of Insectivora for 38 food items.

classes on the graph: *S. minutus* and *S. caecutiens* in one, and *S. araneus* and *S. isodon* in the other. The other three species are intermediate, *Sic. betulina* and *N. fodiens* being close to the first pair of species.

We began component analysis of the trophic interrelations of the Insectivora complex by revealing specific and nonspecific groups of food items. To do so, the food spectra of all species for 39 food items were considered. The first component in this case reveals ground-surface dwellers, and the second, subterranean dwellers; the proportion of variance eliminated by these two groups amounted to 73.6%. Figure 5 shows an obvious separation of a group of 26 closely correlated food items and a group of 12 food items that did not fall into the first group. Analysis of the tables of the frequency of some individual food items in stomachs shows that the proportion of food items of the first class is only minor, and they are often absent altogether in the samples (zero values), which explains their high correlation.

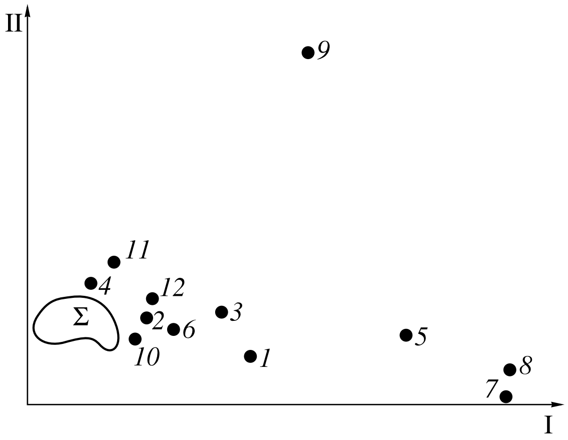

Fig. 5. Distribution of food items of Insectivora on the plane of the first and second principal components. Component I eliminates 59.5% of the variance; and component II, 18.3%. (*1*) Carabid imagines, (*2*) Staphylinid imagines; (*3*) dipteran imagines; (*4*) larvae of Sciaridae, (*5*) Lepidoptera larvae, (*6*) bugs, (*7*) spiders, (*8*) harvestmen, (*9*) earthworms, (*10*) plant food items, (*11*) unidentified dipteran larvae, (*12*) mites, and (Σ) 26 closely correlated food items.

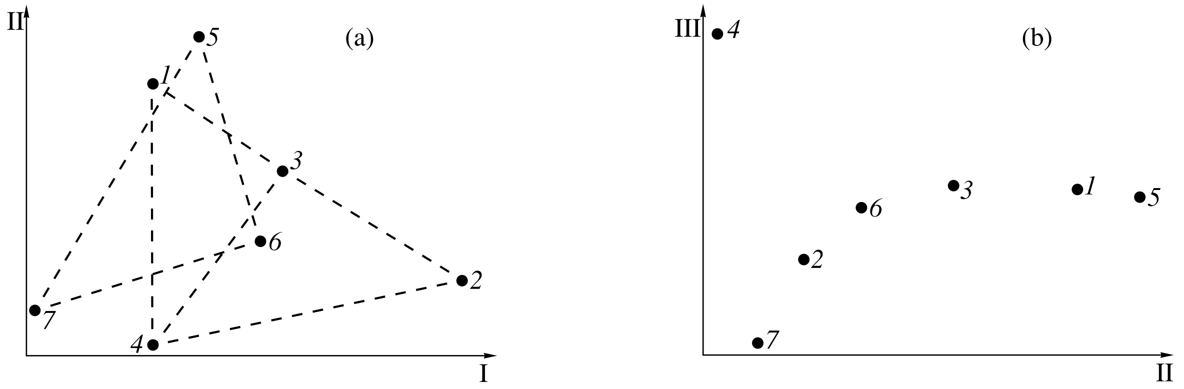

Fig. 6. Distribution of diets of Insectivora on planes of the (a) first and second and (b) second and third principal components (predominant and specific food items were considered). Lines connect species from the same center of origin: (*1–4*) European faunistic complex: (*1*) *Sorex araneus*, (*2*) *S. minutus*, (*3*) *N. fodiens*, (*4*) *Sic. betulina*; (*5–7*) Far-Eastern faunistic complex: (*5*) *S. isodon*, (*6*) *S. caecutiens*, and (*7*) *S. minutissimus*.

The food items of the second group account for 31% of the total food spectrum, whereas the total frequency of these items was 77%. Their frequency in the diets of different species, i.e., preference, varies, which causes a decrease in the levels of internal correlation and correlation with the first group. The second group are numerous food items responsible for the specificity of the feeding of insectivorous mammals.

Subsequently, two types of food items belonging to the second group were excluded from analysis. The first, mites, are of no importance in feeding due to their small size; the second are unidentified dipteran larvae, which strongly vary in terms of their ecology and size. The remaining ten food items were used in the investigation of trophic relations of the insectivorous-mammal complex by the principal component method.

The major contribution to the first component is made by ground-surface invertebrates: Staphylinidae imagines, Hemiptera, and spiders (Fig. 6 and Table 2); the second group is largely made up of soil dwellers: earthworms and Sciaridae larvae (Diptera). In the graph on the first component axis, opposite positions are occupied by *S. minutus* and *S. minutissimus*. These species are close in relation to the second component, whereas *S. isodon* and *Sic. betulina* are the most distant from each other. On the whole, the dispersion of species in the area of consumed resources shows no obvious aggregation, although some species neighbor fairly closely: the pairs *S. isodon* and *S. araneus* as well as *N. fodiens* and *S. caecutiens*.

To illustrate the specificity of species in terms of the inclusion index, an digraph of the “exoticity ratio” was plotted (Fig. 7). Here, *Sic. betulina* and *S. minutissiumus* are well defined. This demonstrates that their diets are the most specific.

The distribution of food spectra in the area of consumed resources is influenced by the origin of the species. The community of Insectivora in the area studied consists of representatives of two fauno–genetic complexes: the European complex includes *N. fodiens*, *S. araneus*, *S. minutus*, and *Sic. betulina*, while the Far-Eastern complex is represented by *S. isodon*, *S. caecutiens,* and *S. minutissimus*.

Table 2. Component analysis of food spectra of seven species of Insectivora in terms of specific mass food items

No.	Food item	Eigenvectors ($E \times 100$)		
		1	2	3
1	Coleoptera: Carabidae (imagines)	–52	–30	–94
2	Coleoptera: Staphylinidae (imagines)	86	51	19
3	Diptera (imagines)	61	37	44
4	Diptera: Sciaridae (larvae)	–10	84	6
5	Lepidoptera (larvae)	3	40	99
6	Hemiptera	100	21	–1
7	Spiders	90	–51	–8
8	Harvestmen	56	–55	–29
9	Earthworms	19	100	13
10	Plant food items	13	–20	100
Proportion of eliminated variance, %		33.2	26.9	23.6

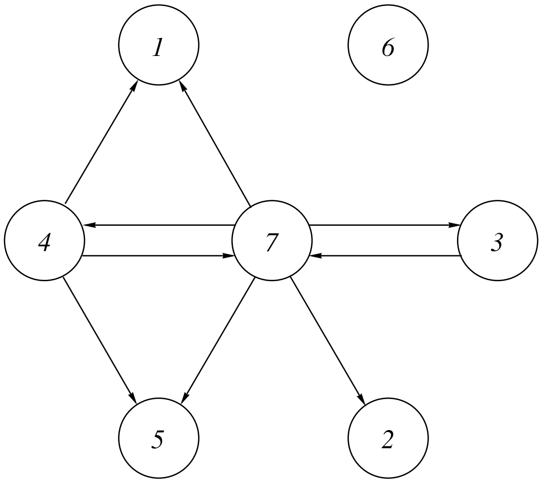

Fig. 7. Digraph of the exoticity ratio of the diets of Insectivora (at $P = 0.5$). Arrows are directed toward less exotic spectra; the other designations are as in Fig. 6.

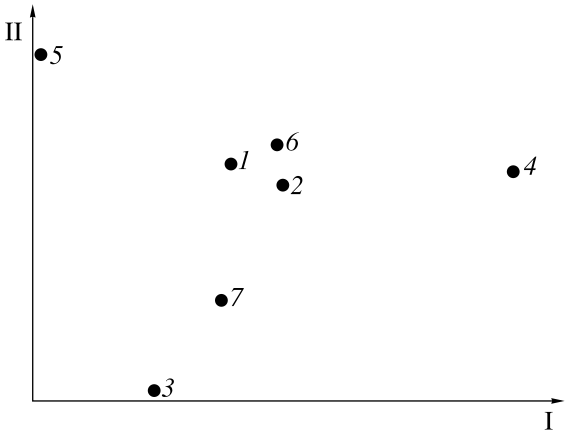

Fig. 8. Distribution of diets of Insectivora on the plane of the first and second principal components (rare food items were considered). Component I eliminates 36.9% of the variance, and component II eliminates 24.0%. See Fig. 6 for designations.

The distances between the species of each fauno–genetic complex in the space of the two main components are great and roughly equal.

In simultaneous considering both fauno–genetic complexes, the diets of some representatives of different fauno–genetic complexes prove to be located close to each other, which indicates possible competition between them. We can see that *S. caecutiens* is located in the middle of the area of consumed resources, rather far from the dominant indigenous species. Presumably this and the age-specific trophic specialization considered above determine the fact that *S. caecutiens* has the highest numbers of all the introduced species.

In the third main component (see Table 2), plant food items, caterpillars, and carabid imagines are well defined (the latter have a negative factor load). As can be seen from Fig. 6b, the third component sharply distinguishes *Sic. betulina*, whose important foods are plant items and caterpillars, the role of carabids being minimal (less than 1%). However, in captivity, we found that *Sic. betulina* willingly consumes carabids that are not big. The absence of these beetles in their natural diet indicates that, in nature, *Sic. betulina* does not encounter them, i.e., they feed not on the soil, but rather in the shrub and herbaceous–dwarf shrub layers.

The distribution of species in the space of the second and third components reflects the vertical dispersion of the feeding zones of the animals. The relationship with soil horizons weakens in the direction from *S. isodon* to *Sic. betulina*, *Sic. betulina*, and *S. minutissimus* being antipodes in terms of the consumption of carabids and plants. Shrews of different species are regularly distributed throughout the soil and ground-surface horizons.

Analysis of the comparison of food spectra of rare foods simply reflects patterns already noted. The first principal component can be determined as the ratio of the ground-surface and soil types of feeding. The rightmost position in terms of the first component is occupied by *Sic. betulina* (Fig. 8), which corresponds to the greater role of phytophages in its feeding (various beetles, aphids, and thrips). *S. isodon* proves to be a consumer of soil animals. The second component reflects some specificity of soil feeding, distinguishing between *S. isodon* and *N. fodiens*. Presumably, this is associated with the preferential consumption of insests dwelling under different moisture conditions.

In this version of analysis, the distribution of the food spectra of the species has some distinctive features compared with the preceding one. The lack of uniformity in the distribution of diets in the space of the principal components is well defined. The most numerous species form a closely aggregated class, whereas the others are sparsely distributed. This is caused by the fact that, in the stomachs of the background species, the frequency of rare food diets provides more accurate insight into their actual consumption compared with species that are few in number. This distinction is reflected in the graph. We can see that analysis of diets with rare food items fails to augment the conclusions obtained upon considering mass food items to determine the specificity of the feeding of the species.

CONCLUSION

(1) The specificity of the feeding of sympatric small Insectivora is manifested in the preference of particular food groups, the lists of the major food items consumed being almost completely overlapping. This is indicated by the dispersed distribution of specific features of feeding in the axes of the principal components.

(2) The specificity of food consumption is determined by the horizon in which the animals dwell. The relationship with soil invertebrates is weakens in the

direction from *S. isodon* and *S. araneus* to *S. minutissimus* and *Sic. betulina*.

(3) The feeding of shrews shows age-specific distinctions. The greatest differences in the diet was found in different-age individuals of *S. caecutiens*.

(4) The use of linear correlation indices and the principal component method in the analysis of food spectra of Insectivora provides informative results revealing factors of variability in their feeding.

(5) To conduct analysis of the trophic specialization of sympatric Insectivora, it is sufficient to take into account only the major items of their diets.

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