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USING THE HETEROCENTRIC MODEL IN POPULATION-CONSORTIUM ANALYSIS OF THE NEST-DWELLING ARTHROPODS OF THE SAND MARTIN (*RIPARIA RIPARIA* (LINNAEUS, 1758)) IN SARATOV REGION

E.N. Kondratev[1], A.S. Sazhnev[2], V.V. Anikin[3], A.A. Mironova[4]

[1, 3, 4] *Saratov State University, Saratov, Russia*
[2] *Papanin Institute for Biology of Inland Waters Russian Academy of Sciences, Borok vill., Yaroslavl Region, Russia*
[2] *Joint Directorate of the Mordovia State Nature Reserve and National Park "Smolny", Saransk, Russia*
[1] *eugene.n.kondratyev@gmail.com*

Abstract. *Background*. The composition of the nest-dwelling fauna is highly diverse. When examining the population of arthropods (Arthropoda) in the nests of the sand martin *Riparia riparia* (Linnaeus, 1758) as a heterogeneous consortium, a heterocentric model was constructed for the first time, allowing for the assessment of the qualitative structure of the consortium taking into account various groups of connections between its members. *Materials and methods.* The materials were collected in 7 districts of Saratov Region during 2019–2021 by excavating nests of *Riparia riparia*. The Tullgren funnel was used for collecting arthropods, and the nesting material was additionally manually sifted. After laboratory processing and identifying the arthropods, their number was counted to construct the model. *Results.* Constructing a heterocentric model enabled demonstrating different types of consortial connections between the determinant (sand martin and its nest) and consorts (arthropods) to assess the qualitative structure of this model. *Conclusions*. During population and consortium analysis of invertebrates inhabiting the nests of *Riparia riparia*, three groups of consortial connections (topical, trophic, fensive) and nine variants (substrate-stational, hematophages, zoophages, phytophages, polyphages, saprophages, keratophages, aphages, fensive) of connections were identified. Insects participate in all nine variants of connections, mites have five variants of connections, while pseudoscorpions, spiders, centipedes, millipedes, and woodlice have two variants of connections.

Keywords: heteroconcentric model, *Riparia riparia*, sand martin, nest-dwelling fauna, fauna, Saratov Region, Russia

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ПОСТРОЕНИЕ ГЕТЕРОКОНЦЕНТРОВОЙ МОДЕЛИ ЧЛЕНИСТОНОГИХ В ГНЕЗДАХ БЕРЕГОВОЙ ЛАСТОЧКИ (*RIPARIA RIPARIA* (LINNAEUS, 1758)) НА ТЕРРИТОРИИ САРАТОВСКОЙ ОБЛАСТИ С ИСПОЛЬЗОВАНИЕМ ПОПУЛЯЦИОННО-КОНСОРТИВНОГО АНАЛИЗА

Е. Н. Кондратьев[1], А. С. Сажнев[2], В. В. Аникин[3], А. А. Миронова[4]

[1, 3, 4] *Саратовский государственный университет имени Н. Г. Чернышевского, Саратов, Россия*
[2] *Институт биологии внутренних вод им. И. Д. Папанина Российской академии наук, пос. Борок, Россия*
[2] *Объединенная дирекция Мордовского государственного природного заповедника имени П. Г. Смидовича и национального парка «Смольный», Саранск, Россия*
[1] *eugene.n.kondratyev@gmail.com*

Аннотация. *Актуальность и цели.* Состав нидикольной фауны очень разнообразен. Рассматривая население членистоногих (Arthropoda) гнезд ласточки береговушки *Riparia riparia* (Linnaeus, 1758), как гетерогенную консорцию, при ее анализе впервые была построена гетероконцентровая модель, позволяющая оценить качественную структуру консорции с учетом различных групп связей между ее участниками. *Материалы и методы.* Материал собирали в 7 районах Саратовской области в течении 2019–2021 гг., выкапывая гнезда *Riparia riparia*. Для сбора членистоногих применяли термофотоэклоектор Туллгрена, дополнительно перебирая гнездовой материал вручную. После камеральной обработки и определения членистоногих подсчитывали их количество для построения модели. *Результаты.* С помощью построения гетероконцентровой модели удалось показать разные типы консортивных связей между детерминантом (береговая ласточка и ее гнездо) и консортами (членистоногие), дать оценку качественной структуры данной модели. *Выводы.* В ходе популяционно-консортивного анализа населения беспозвоночных в гнездах *Riparia riparia* было выделено три группы консортивных связей (топические, трофические и форические) и девять вариантов связей (субстратно-стациальные, гематофагия, зоофагия, фитофагия, полифагия, сапрофагия, кератофагия, афагния и форические). Насекомые участвуют во всех девяти вариантах связей, клещи имеют пять вариантов связей, ложноскорпионы, пауки, хилоподы, диплоподы и мокрицы имеют по два варианта связи.

Ключевые слова: гетероконцентровая модель, *Riparia riparia*, береговая ласточка, нидиколы, фауна, Саратовская область, Россия

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Introduction

Bird nests are microbiocenoses that provide special conditions for the habitat of Acariformes, Parasitiformes, Heteroptera, Lepidoptera, Coleoptera, Diptera and Siphonaptera [1–10]. The specificity of the nest fauna, its differentiation according to topical and trophic relationships with the nest of the host, allows considering the nest as a consortium [11, 12]. Where arthropods serve as associates, they concentrate around the determinant (the nest and its host). Unlike the classical definition of a consortium [13, 14], there is no autotrophic producer here, so nests are considered a heterotrophic consortium [15, 16]. There are different representations of consortium organization [13, 14, 17, 18], but one of the most informative is the heterocentric model. It includes all variants of consortial relationships between the determinant (and its nest) and each individual associate, which enables the most complete reflection of the qualitative structure of the consortium in its population-consortium analysis. In addition, the model perfectly illustrates the existing types of relationships in the considered consortium at the level of potential and real concentrations. The aim of the study is to analyze the qualitative organization of arthropod consortia in the nests of the sand martin (*Riparia riparia*) in different areas of the Saratov Region.

Materials and methods

The description of the structure of the burrow and nest of the sand martin is as follows. The nesting habitat of the sand martin is represented by a subterranean (burrows in shores) complex of a multi-year type [19]. The entrance to the burrow is oval-shaped, with the larger diameter usually located in the horizontal plane, and the smaller diameter in the vertical one. The burrow ends in an expansion where a simple nest is constructed. Due to the nest location deep inside the burrow, unique temperature conditions are created (during the study, the temperature varied from 16.5–17.5 °C), which are more constant throughout the day than the air temperature [20]. When colonies form on river banks, periodic water erosion often partially destroys the cliff during spring floods, forcing most martins to build new nests each year, although sometimes they occupy old nests by extending the burrow [21]. The nest is usually lined with plant material, feathers, stems of herbaceous plants, and their roots. During egg-laying, the martins continue to supply building material to the nest, gradually increasing its size. Feathers are brought by the birds usually during the period when the hatchlings are completely featherless. The completion of construction coincides with the hatching of the first nestlings [22]. Thus, specific conditions are created for the existence of consortium elements [4].

Description of the location of the sand martin colonies

The entomological material from the sand martin nests was collected in the following areas of the Saratov Region (Table 1).

Table 1

Sampling locations and number of collected nests

Date	Locality	Latitude, N	Longitude, E	$n^1(s^2)$
2019				
23–24.VI; 5–7.VII	Khvalynsky distr., vicinity of Ivanovka vill., shore of the Volga River	52.4002	48.0906	52(25)
20.VII	Krasnoarmeysky discr., vicinity of Mordovo vill., shore of the Volga River	51.1242	45.8160	19(8)
25.VII	Saratov, Gagarinsky distr., vicinity of Sand Umet vill., abandoned sand quarry	51.5219	45.6280	13(9)
2020				
25.VI; 29.VII; 7.XI	Khvalynsky distr., vicinity of Ivanovka vill., shore of the Volga River	52.4002	48.0906	53(31)
25.VI; 30.VII	Khvalynsky distr., vicinity of Demkino vill., sand quarry	52.2670	47.7965	22(11)
26.VI; 30.VII; 7.XI	Khvalynsky distr., vicinity of Elshanka vill., pond shore	52.6043	47.9766	23(16)
26.VII	Lysogorsky distr., vicinity of Simonovka vill., shore of the Medveditsa River	51.3569	44.8001	25(1)
	Lysogorsky distr., vicinity of Ataevka vill., shore of the Medveditsa River	51.3100	44.8205	13(4)
27.VII	Saratov, Gagarinsky distr., vicinity of Sand Umet vill., abandoned sand quarry	51.5219	45.6280	12(3)
2021				
8.V; 27.VI	Khvalynsky distr., vicinity of Elshanka vill., pond shore	52.6043	47.9766	16(5)
27.VI; 8.VII; 11.VII; 5.XI	Khvalynsky distr., vicinity of Ivanovka vill., shore of the Volga River	52.4002	48.0906	49(24)
8.VII; 4.XI	Khvalynsky distr., vicinity of Apalikha vill., sand quarry	52.3171	47.6780	24(7)
	Khvalynsky distr., vicinity of Demkino vill., sand quarry	52.2670	47.7965	19(9)
27.VIII	Rovensky distr., vicinity of Beregovoe vill., shore of the Volga River	50.7565	46.0117	16(4)
3.XI	Engelssky distr., vicinity of Malaya Topolevka vill., sand quarry	51.5566	46.2827	22(8)
6.XI	Voskresensky distr., vicinity of Komarovka vill., shore of the Tereshka River	51.9667	46.6604	9(2)

N o t e s: [1]n – total number of burrows examined in the colony, [2]s – number of nests collected.

The studied colonies can be divided into three groups.

1. Colonies in sand quarries. The burrows of these colonies are located in a sand cliff at a height of 0.5–3.5 m. The length of such colonies varies from 1.2 to 25 m. The entrance holes of the burrows are elongated in a chain of 2–6 tiers in the upper third of the cliff. In the Sand Umet village quarry, the birds were last recorded in 2019. In the Demkino village, the birds were recorded in both 2020 and 2021. The colonies in the Apalikha and Malaya Topolevka villages were already abandoned in 2021. Ruderal vegetation grows around all colonies.

2. Colonies in the territory of the Saratov Region and Volgograd Region. Colonies are located in a soil, sand, and soil-sand coastal cliff at a height of 1.2–7 m. The length of such colonies varies from 3 to 40 m. Colonies are long-lasting, but in different years the location of the burrows and the number of nesting birds varies significantly due to the collapse of the shore and changes in nesting conditions. The entrance holes of the burrows are elongated in a chain of 1–5 tiers in the middle or upper third of the cliff. The birds in the colony in the vicinity of the Ivanovka village were recorded all three years, but due to strong shore collapse, burrows are always built from scratch. The colony in the Mordovo village was last inhabited by the birds in 2019. The colony in the Beregovoe village was abandoned in 2021. Ruderal vegetation grows around all colonies.

3. Colonies on small rivers. Colonies are located in a soil cliff at a height of 1.5–2.5 m. The length of the colonies varies from 2 to 4 m. The entrance holes of burrows are elongated in a chain of 1–4 tiers in the middle or upper third of the cliff. Often, the burrows are located very sparsely. The colonies are unstable due to the collapse of the shore and changes in nesting conditions. The colony in the Elshanka village was inhabited in 2020, but the birds were not recorded in 2021, and ruderal vegetation

grows there. The colonies in the vicinity of the Simonovka and Ataevka villages were abandoned in 2020, and they are located near meadow edges in the floodplain forest. The colony in the Komarovka village was abandoned in 2021, and ruderal vegetation grows there.

Research Methodology

The nest material was extracted during the excavation of burrows and individually placed in numbered zip-lock bags. Samples were dissected using a Tullgren funnel (extraction for 2–3 hours), followed by manual examination for arthropods that did not pass through the funnel [23]. The material was fixed in 70 % ethanol solution.

The following sources were used to identify the material. The identification of ticks [24–29], pseudoscorpions [30], hay mites [31], thrips [31], dipterans [32–34], and fleas [33] were conducted by the first author using standard methods. The identification of beetles was carried out according to Die Käfer Europas [35] and performed by A.S. Sazhnev (Borok). The identification of Lepidoptera was carried out using modern keys [36–41]. All identifications of microlepidoptera were made using genital structures of species according to the standard method [42] and performed by V.V. Anikin (Saratov). Hemipterans and ants were identified by K.A. Grebenikov (Balashikha). The identification of Trombidiformes was carried out by A.A. Khaustov (Tyumen). Collembolans were identified by A.B. Babenko (Moscow) and R.A. Sayfutdinov (Moscow).

After identifying and counting the material, 2 heterocentric models of consortium were constructed, including 8 types of concentrations, based on consortial relationships [17,18, 43]. The potential sizes of the concentrations in the first model correspond to the number of consortia species included in it, while in the second model, they correspond to the number of individual consortia included. The largest concentration in the model determines the potential size of all others (dotted line). The real sizes of the concentrations (dark circles) correspond to the actual number of species/individuals included in them [43]. The construction of the heterocentric model was carried out using Adobe Photoshop CC 2019.

Results and discussion

In the presented consortium, the dominant (system-forming) groups of relationships are trophic and topical (Fig. 1, 2 and Table 2). At the trophic level (by number), six types of relationships are distinguished, corresponding to hematophages, zoophages, phytophages, saprophages, polyphages, and aphages.

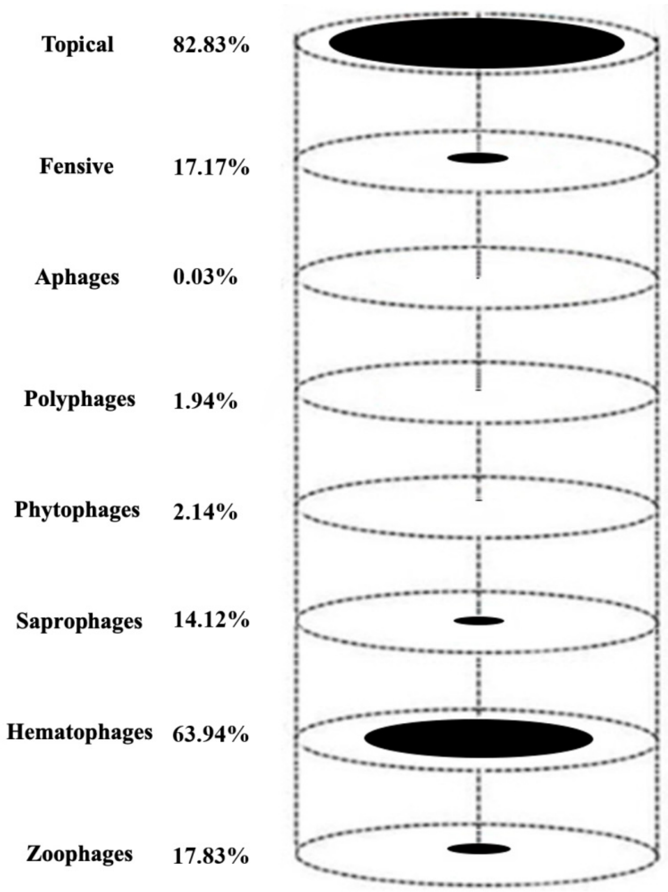

Fig. 1. Heterocentric model of consortium "sand martin and its nest" by abundance

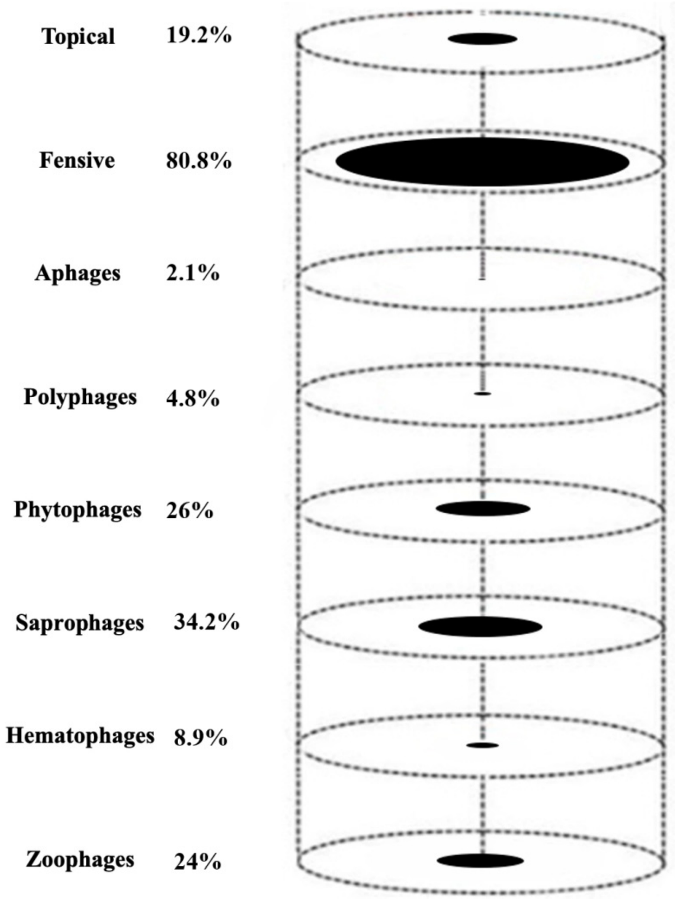

Fig. 2. Heterocentric model of consortium "sand martin and its nest" by amount of species

Table 2

Classification of consortial connections of the sand martin nest-dwelling fauna

Group of connections	Type of connection	Variant of connection	Connection with the determinant
Topical	Substrate-stational	Substrate-stational	Bird and nest
Trophic	Biotrophic	Hematophages	Bird
		Zoophages	Nest
		Phytophages	Nest
		Polyphages	Nest
	Saprotrophic	Saprophages	Nest
		Keratophages (Scavenger)	Bird
		Aphages	Absent
Fensive	Fensive	Fensive	Burrow

In the consortial model by abundance (Fig. 1), hematophages (*Ixodes lividus* (Koch, 1844), *Rhipicephalus sanguineus* (Latreille, 1806), *Haemogamasus horridus* (Michael, 1892), *H. liponyssoides* (Ewing, 1925), *Dermanyssus hirundinis* (Hermann, 1804), *Androlaelaps casalis* (Berlese, 1887), *Oeciacus hirundinis* (Lamarck, 1816), *Platygastroidea* sp., *Leptoconops* aff. *borealis* (Gutsevich, 1945), *Ceratophyllus styx* (Rothschild, 1900)), feeding on the nest host – *Riparia riparia*, are the most represented (63.94 %).

Additionally, zoophages dominate in the consortium – 17.83 % (*Cheiridium museorum* (Leach, 1817), *Chernes cimicoides* (Fabricius, 1793), *Cyrtolaelas* sp., *Rhodacarellus* sp., *Euryparasitus tori* (Davydova, 1970), *Geholaspis mandibularis* (Berlse, 1904), *Lasioseius muricatus* (Koch, 1839), *Protogamasellus mica* (Athias-Henriot, 1961), *Melichares* sp., *Geolaelapsa culeifer* (Canestrini, 1884), *G. expolitus* (Berlese, 1904), *Stratiolaelaps miles* (Berlese, 1892), *Sphaerolichus* sp., *Spinibdella subrufa* (Rack, 1961), *Cunaxa setirostris* (Hermann, 1804), *Lupaeus subterraneus* (Berlese, 1916), *Anystis* sp., *Neognathus terrestris* (Summers and Schinger, 1955), *Caeculus* sp., *Haploglossa nidicola* (Fairmare, 1853), *H. picipennis* (Gyllenhal, 1827), *Falagrioma thoracica* (Stephens, 1832), *Leptacinus sulcifrons* (Stephens, 1833), *Sepedophilus obtusus* (Luze, 1902), *Saprinus rugifer* (Paykull, 1809), *Lampyris noctiluca* (Linnaeus, 1758), *Syntormon* sp., *Xanthochlorus* sp., *Crossopalpus* sp., order Araneae, class Chilopoda, larvae of families *Carabidae* spp., *Cecidomyiidae* spp., Empididae spp., and larvae of *Haploglossa* sp.) that primarily use hematophages, but also feed on other arthropods from the nest.

Saprophages are also quite diverse (*Nenteria* sp., *Pachylaelaps perlucidus* (Mašán, 2007), *Pneumolaelaps lubrica* (Voigts & Oudemans, 1904), *Siteroptres* sp., *Belba* sp., *Oppia* sp., *Achipteria* sp., *Ceratozetes* sp., *Acarus siro* (Linnaeus, 1758), *Bakerdania* sp., *Scutovertex* aff. *sculptus* (Michael, 1879), *Damaeus* sp., Diplopoda class, Oniscidea suborder, *Campodeaplus iochaeta* (Silvestri, 1912), *Proisotoma minuta* (Tullberg, 1871), *Desoria* sp., *Tomocerus vulgaris* (Yosii, 1954), *Pseudosinellas exoculata* (Schött, 1902), *Entomobrya* sp., *Lepidocyrtus* sp., *Arrhopalites* sp., *Mesaphoru rayosii* (Rusek, 1967), *Hemisotomather mophila* (Axelson, 1900), *Seira* aff. *squamoornata* (Scherbakov, 1898), *Liposcelis divinatoria* (Müller, 1776), *Lepinotus reticulatus* (Enderlein, 1904), *Pleurophorus caesus* (Panzer, 1796), *Plagiogonus arenarius* (Olivier, 1789), *Dermestes laniarius* (Illiger, 1801), *Sericoderus lateralis* (Gyllenhal, 1827), *Xyleborinus saxeseni* (Reitter, 1913), *Anthicus flavipes* (Panzer, 1796), *Corticaria* sp., *Corticaria crenulata* (Gyllenhal, 1827), *Blaps lethifera* (Marsham, 1802), *Niditinea fuscella* (Linnaeus, 1758), *Infurcitinea rumelicella* (Rebel, 1903), *Epicypta scatophora* (Edwards, 1913), *Trichonta* sp., *Platypezidae*, larvae of *Lagria* sp., *Ceratopogon* sp., *Fannia* sp., Scarabaeidae, Elateridae, Tenebrionidae, Infurcitinea, Syrphidae, Panorpidae), feeding on decomposing residues of both plant and animal origin.

Phytophagous species are significantly less represented – 2.14 % (*Ameroseius delicatus* Berlese, 1918, *Gaeolaelaps brevipilis* (Bernhard, 1969), *Laelaspis heselhausi* (Oudemans, 1912), *Cosmolaelaps zachvatkini* (Buyakova & Goncharova, 1972), *Aptinothrips stylifer* (Trybom, 1894), *Chirothrips manicatus* (Haliday, 1836), *Thrips* sp., *Haplothrips tritici* (Kurdjumov, 1912), *Berytinus clavipes* (Fabricius, 1775), *Agrilus hyperici* (Creutzer, 1799), *Cytilus sericeus* (Forster, 1771), *Chaetocnema hortensis* (Geoffroy, 1785), *Acompsia cinerella* (Clerck, 1759), *Brachmia dimidiella* (Denis & Schiffermüller, 1775), *Rhyacia simulans* (Hufnagel, 1766), *Epermenia ochreomaculella* (Millière, 1854), *Acleris forsskaleana* (Linnaeus, 1758), *Cochylidia implicitana* (Wocke, 1856), *Borkhausenia fuscescens* Haworth, 1829, *Caloptilia fidella* (Reutti, 1853), *Laodamia faecella* (Zeller, 1839), *Loxostege sticticalis* (Linnaeus, 1761), *Polypogon tentacularia* (Linnaeus, 1758), *Ctenosciara* aff. *hyalipennis* (Meigen, 1804), *Lycoriella* sp., *Phytosciara* sp., *Gitona* sp., *Agathomyia* sp., *Megaselia* aff. *flavicoxa* (Zetterstedt, 1848), *M.* aff. *elongata* (Wood, 1914), *Metopin*a aff. *galeata* (Haliday, 1833), the family Tachinidae and Parasitengona, larvae of the families Chrysomelidae, Phoridae, Sarcophagidae, larvae of the orders Thysanoptera and Hemiptera), feeding on plant parts of the nest. Polyphagous species constitute 1.94 % (*Tetramorium* sp., *Solenopsis fugax* (Latreille, 1798), *Lasius flavus* (Fabricius, 1782), *Lasius* cf. *alienus* (Forester, 1850), *Myrmica rubra* (Linnaeus, 1758), *Formica rufa* Linnaeus, 1761, *Camponotusa ethiops* (Latreille, 1798)), feeding on a variety of plant and animal food. A few aphagous species were found in the collected material (0.03 %) (*Sycorax silacea* (Haliday, 1839), *Kiefferulus tendipediformis* (Goetghebuer, 1921), *Schwenckfeldina carbonaria* (Meigen, 1830)).

In the consortium model based on topical connections (Fig. 2), the niche represents an isolated part, where only a group of substrate-substrate connections is distinguished (82.83 %).

The substrate-station connection is mainly performed by hematophagous species – 63.69 % (*Ixodes lividus* (Koch, 1844), *Haemogamasus horridus* (Michael, 1892), *H. liponyssoides* (Ewing, 1925), *Dermanyssus hirundinis* (Hermann, 1804), *Androlaelaps casalis* (Berlese, 1887), *Oeciacus hirundinis* (Lamarck, 1816), *Ceratophyllus styx* (Rothschild, 1900)); zoophagous species – 15.5 % (*Cyrtolaelaps* sp., *Euryparasitus tori* (Davydova, 1970), *Stratiolaelaps miles* (Berlese, 1892), *Haploglossa nidicola* (Fairmare, 1853), *H. picipennis* (Gyllenhal, 1827), *Falagrio mathoracica* (Stephens, 1832), *Saprinus rugifer* (Paykull, 1809), as well as larvae of *Haploglossa* sp.) and saprophagous species – 3.64 % (*Pneumolaelaps lubrica* (Voigts & Oudemans, 1904), *Acarus siro* (Linnaeus, 1758), *Liposcelis divinatoria* (Müller, 1776), *Dermestes laniarius* (Illiger, 1801), *Niditinea fuscella* (Linnaeus, 1758), *Infurcitinea rumelicella* (Rebel, 1903), larvae of *Lagria* sp., larvae of the families Scarabaeidae, Elateridae, Tenebrionidae, Infurcitinea), which use determinant environmental preferences as topical and trophic resources.

Regarding the number of species at the trophic level, saprophages (50 species), zoophages (35 species), and phytophages (39 species) dominate. Hematophages (13 species), polyphages (7 species), and aphages (3 species) are significantly fewer. At the topical level, there are few species that implement substrate-station connections in this consortium (28 species). There are significantly more species (118 species) that have fensive connections (use burrows as a place for temporary protection).

Using the heteroconcentric model of the consortium, it was possible to visually demonstrate the relationships between the determinant (sand martin and its nest) and consortium (arthropods).

Conclusion

Functional analysis of heterotrophic consortia of the sand martin nest (*Riparia riparia*) in the Saratov Region using the heterocentric model showed the presence of three groups of consortial relationships and nine variants of connections. Among the analyzed systematic groups of invertebrates, insects had the highest number of types of connections. Insects occur in all types and species of connections: substrate-stational, bio- and saprotrophic, and fensive. Ticks have six types of connections (phytophages, hematophages, zoophages, substrate-stational saprotrophs, and fensive). Pseudoscorpions, spiders, millipedes, centipedes, and mites have two types of connections each. Pseudoscorpions, spiders, and centipedes are represented by zoophages, while millipedes and mites are saprotrophs. Additionally, pseudoscorpions, spiders, millipedes, centipedes, and mites are connected with the determinant, burrow, and nest through fensive connections, realizing themselves as topocanosters. Thus, insects, with their high ecological plasticity, are able to form the greatest number of functional types of connections within the consortium "sand martin and its nest".

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