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The Structure of the Fauna and Life Cycles of Black Flies (Diptera, Simuliidae) in Streams of the Forest-Steppe in Central Russia

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Abstract—The paper deals with the species composition, life cycles, structure of the fauna, and biodiversity of black flies (Diptera, Simuliidae) in different types of streams in the central Russian forest-steppe. Complexes of black flies in different types of streams are rather similar but faunas differ in the dominance structure.

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Black flies (family Simuliidae) are well-known bloodsuckers and vectors of pathogens of transmissive diseases. Significant increases in the population density of bloodsucking black flies, accompanied by heavy damage to their hosts, are periodically observed in central European Russia, including forest-steppe regions (Khitsova and Budaeva, 2006). Black flies can be potentially dangerous vectors of onchocercosis, anaplasmosis, tularemia, and other diseases. Preimaginal stages of black flies form a significant component of zooperiphyton and zoophytos in streams of central Russia, frequently dominating in the number and biomass.

In the forest-steppe of Central Russia (the forest-steppe part of the Central Chernozem provinces), the family Simuliidae was examined in Voronezh Province, mainly in relation to the ecology of adults of mass bloodsucking species (Skufjin, 1949; Marchukova and Ryabykh, 1959; Kolycheva, 1966; Marchukova, 1971; Kamolov, 1976). Larvae and pupae developing in streams were not examined, which hampered revealing of species with low population density and species not attacking animals and humans in this territory (but retaining their potential danger). The present work is devoted to the species composition, life cycles, structure, and biodiversity of black flies in different streams of central Russian forest-steppe. Materials on faunistic and ecological investigations of black flies in Central Chernozem region are also available in other publications of the authors (Budaeva, 2006; Budaeva and Khitsova, 2006, 2007; Budaeva et al., 2006).

CHARACTERISTICS OF THE REGION EXAMINED

The material was collected in the forest-steppe in Voronezh, Lipetsk, and Belgorod Provinces. This is a plain territory with expressed valley-ravine relief. Forests occupy no more than 10 % of the territory and are represented by oak and pine forests, and also by mixed pine-forests with pines prevailing. The watershed regions are nearly entirely ploughed; the floodlands are represented by meadows or, less frequently, by forests. The climate of the region is temperately continental.

The majority of the streams examined belong to the Don River basin. The rivers are relatively shallow, typically plain, with gentle river inclination and slow water; the bottom is usually sandy, or, less frequently, clayey or stony. The rivers are fed mainly from melting snow; as a result, spring water is very high, covering floodlands with water. Due to unstable water supply, significant number of rivers is dry during low water periods; a large number of streams is characterized by the zero minimal discharge. The rivers are strongly influenced by anthropogenic factors; processes of river degradation are observed (Kurdov, 1995; Zherdev and Borodkin, 2003).

MATERIALS AND METHODS

The studies were performed in 1998–2007. We examined the preimaginal stages of black flies developing in streams and estimated the activity of attacks of adult black flies in terrestrial biotopes. A total of

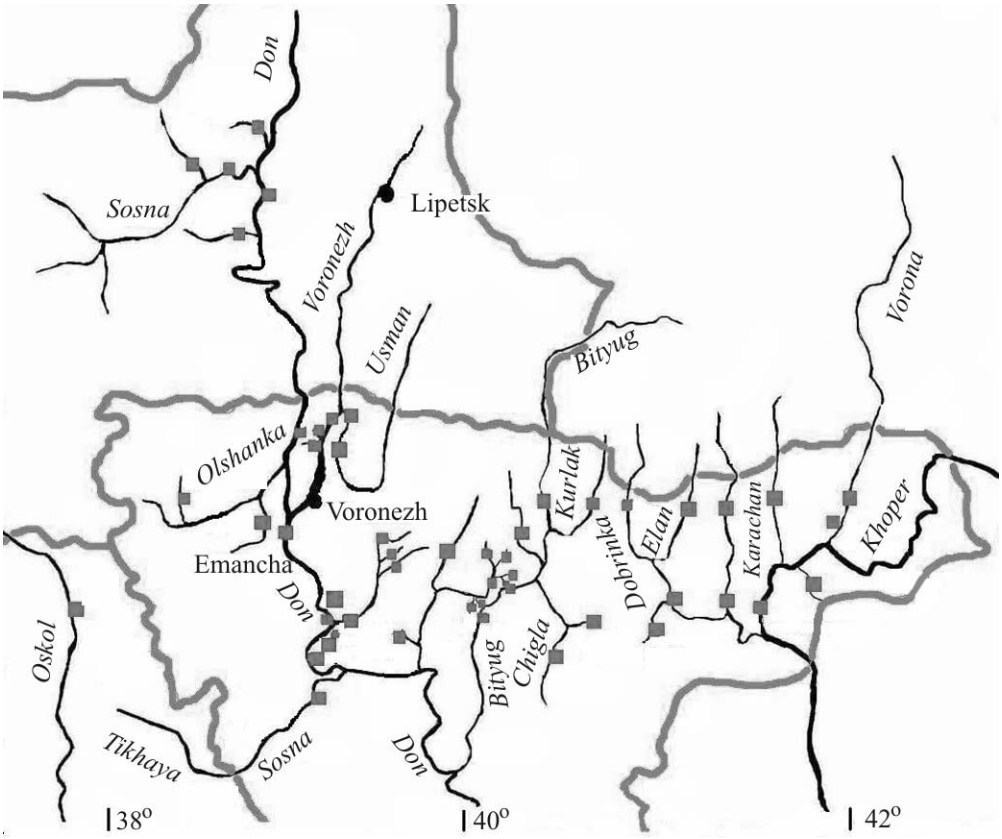

Fig. 1. Collecting sites of immature black fly species in the territory of central Russian forest-steppe.

44 streams of different types were observed in 61 registration sites; stationary observations were performed in four sites (Fig. 1). On the whole, 343 samples were collected; each sample included 1–5 testing samples and registrations; a total of 59583 and 14459 specimens of larvae and pupae and adult black flies, respectively, were collected.

Larvae and pupae were collected according to the method of Rubzov (1956). The population density of preimaginal stages was estimated as the density of larvae and pupae per 1 dm^2 of projective surface of the substrate.

Larvae, pupae, and adults were determined according to the keys of Yankovsky (2002) and Rubzov (1956). Correctness of determination was checked by specialists of the Zoological Institute RAS in St. Petersburg (ZIN).

Analysis of the structure of the black fly fauna was performed taking into account the relative population density of species (N_i) and their occurrence (P_i). Domination of species in streams was estimated by the Palii-Kovnatsky index (Palii, 1966; Bakanov, 1987; Shitikov et al., 2003).

A comparative analysis of black fly biodiversity was estimated by means of Margalef (D_{Mg}), Shannon (H'), Pielou (E), and Simpson indices (D_S) (Megarran, 1992; Shitikov et al., 2003). Chekanovsky-Sorensen (I_{CS}) index was used for determination of similarity between black fly faunas in singled out types of streams. The data was statistically treated with EXCEL and STATISTICA software.

RESULTS AND DISCUSSION

During the years of investigations, the following 26 black fly species belonging to 12 genera were revealed: *Greniera rivi* (Ivashchenko, 1970), *Cnephia pallipes* (Fries, 1824), *Wilhelmia balcanica* (Enderlein, 1924), *W. equina* (Linnaeus, 1758), *W. lineata* (Meigen, 1804), *Byssodon maculatus* (Meigen, 1804), *Cnetha lidiae* Semushin et Ussova, 1983, *C. verna* (Macquart, 1826), *Cnetha* sp., *Nevermannia angustitarsis* (Lundström, 1911), *N. latigonia* (Rubzov, 1956), *N. lundstromi* (Enderlein, 1921), *Eusimulium angustipes* (Edwards, 1915), *Schoenbaueria nigra* (Meigen, 1804), *Boophthora erythrocephala* (De Geer, 1776), *B. sericata* (Meigen, 1830), *Odagmia frigida* (Rubzov, 1940), *O. ornata* (Meigen, 1818), *O. pratora*

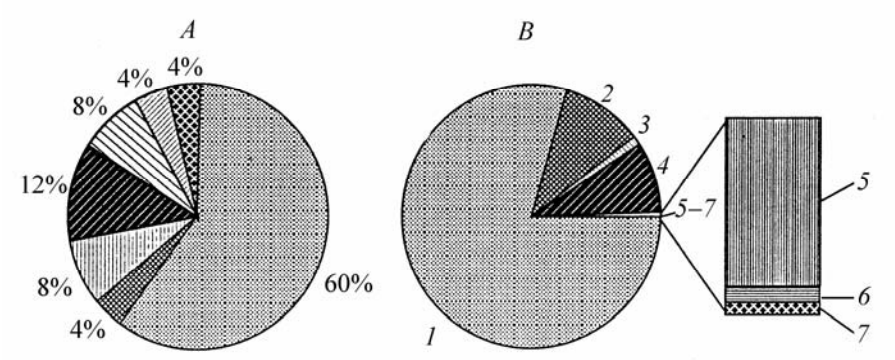

Fig. 2. The distribution of black fly species in the central Russian forest-steppe among ecological-faunistic complexes (%): (*A*) by the number of species; (*B*) by relative population density. Ecological-faunistic complexes: *1*, boreal-polyzonal; *2*, forest; *3*, mountain-plain steppe; *4*, boreal; *5*, boreal-forest; *6*, subarid; *7*, polyzonal.

(Friederichs, 1921), *Argentisimulium noelleri* (Friederichs, 1920), *Simulium longipalpae* (Beltukova, 1955), *S. morsitans* (Edwards, 1915), *S. paramorsitans* (Rubzov, 1956), *S. posticatum* (Meigen, 1838), *S. simulans* (Rubzov, 1956), *Simulium* sp. aff. *reptans* (Linnaeus, 1758). Two species, *Simulium reptans* (Linnaeus, 1758) and *Odagmia frigida* (Rubzov, 1940), revealed by Skufjin (1949) and Martchukova and Ryabykh (1959), are absent on our collections.

Ecological and faunistic analysis allowed us to reveal the prevalence of boreal-polyzonal species in streams of the forest-steppe in central Russia (Fig. 2)[1]; these species form the nucleus of the regional fauna; the most abundant species include *Boophthora erythrocephala* and *Odagmia ornata*. Relatively high population density is also characteristic of the forest species *Schoenbaueria nigra* and the boreal species *Byssodon maculatus*. The presence of the boreal and boreal-forest, and also mountain-plain steppe species and the subarid species in the black fly fauna of the central Russian forest-steppe testify to the diversity of the sources of its formation.

According to our observations, 12 species in the examined region are monovoltinic and develop in spring (Table 1). Ten species possess two or three generations per year. In the streams examined, 12 species overwinter at the egg stage; two species hibernate as eggs or larvae, depending on the environmental conditions; and 8 black fly species hibernate as larvae. Thus, black fly larvae in streams are observed all the year round, because some species are polyvoltinic and some species overwinter as larvae. The pupae develop in the streams of the region from the first 10 days of April till the beginning of October. Emergence of black flies lasts for more than 5 months, from the last ten days of April till early October.

The dependence of the species life cycles on the hydrological regime of streams was noted. In temporary rivers, freezing in winter, black flies hibernate as eggs, although in constant streams they hibernate as larvae (*Cnetha verna*, *Argentisimulium noelleri*). When rivers and brooks become dry in spring-summer, only a single generation frequently develops. In streams fed from springs, developmental periods are longer and borders between different generations are erased. In rivers with warmer water, black flies can develop more rapidly than in brooks; this fact was established by us for *Odagmia ornata*.

The examined rivers and brooks were subdivided into ecological types according to the principles of stream classification used during the analysis of the black fly fauna (Usova, 1961; Konurbaev, 1977). Taking into account the physical geographic, hydrological, and faunistic characteristics, all the streams were subdivided into five types.

The 1st type of streams included large (the Don) and middle-sized full-flowing rivers (Voronezh, Khoper, Vorona, and Oskol rivers) that are longer than 300 km, possess a large water stream area and a large number of tributaries. These rivers are 50 m wide or wider and up to 5 m long; their current is rather slow (0.2–0.5 m/sec), during the high water period reaching 0.6–0.8 m/sec. The bottom is sandy or, less frequently, clayey. According to our observations, the water temperature in winter and early spring constitutes about 1–2ºC. In May, the water warms up to 8–17ºC. In summer, the highest water temperature was recorded

[1] Distribution among the ecological-faunal complexes follows that by Panchenko (2003).

Table 1. Dates of pupation and the number of generation of black flies in the Central Russian forest-steppe

Species	Hibernating stage	Number of generations	Dates																	
			April			May			June			July			August			September		
			1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Wilhelmia equina	l	3		+	+	+		+	+	+	+	+	+	+	+		+	+		
Nevermannia latigonia	l	3		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
Odagmia ornata	l	3		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
O. pratora	l	1		+	+	+														
Boophthora erythrocephala	l	3			+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
B. sericata	l	1		+	+	+	+	+												
Eusimulium angustipes	l	3			+	+	+	+	+		+	+	+			+	+	+	+	+
Cnetha verna	e, l	2			+	+	+	+	+							+				
C. lidiae	e (l?)	1 (?)			+	+	+													
Greniera rivi	e	1			+	+	+													
Schoenbaueria nigra	e	1			+	+	+	+	+											
Cnetha sp.	l	2				+	+	+	+					+	+	+	+	+	+	+
Wilhelmia balcanica	e (l?)	2			+	+	+	+				+	+		+					
W. lineata	e (l?)	2				+	+	+				+								
Nevermannia lundstromi	?	?				+														
Argentisimulium noelleri	e, l	3				+	+	+	+		+	+	+		+	+				
Cnephia pallipes	e	1				+	+	+												
Simulium posticatum	e	1				+	+	+												
S. simulans	e	1				+	+	+												
S. morsitans	e	1					+	+	+											
S. paramorsitans	e	1					+	+	+											
Byssodon maculatus	e	1–2					+	+	+	+	+	+	+		+	+	+			
Simulium longipalpae	e	1						+												
Nevermannia angustitarsis	?	?						+												

Notes: (e) hibernating as egg; (l) hibernating as larva.

in July and the first half of August (25–27.4ºC). In September, the water slowly cools down (17–21ºC). The substrate for the attachment of immature black fly stages is mainly represented by narrow-leaved riverside aquatic and sunken plants, bridge deep foundations, and tree branches.

In streams of this type, 11 black fly species were found, including *Cnephia pallipes*, *Wilhelmia balcanica*, *W. equina*, *W. lineata*, *Byssodon maculatus*, *Nevermannia latigonia*, *Schoenbaueria nigra*, *Boophthora erythrocephala*, *B. sericata*, *Simulium morsitans*, and *S. paramorsitans*.

The 2nd type of streams includes middle-sized, shallow, and rapid rivers (Bityug, Savala, Tikhaya Sosna, Sosna, Yelan, Usman, and Ikorets rivers). They are 100–300 km long, 5–30 m wide, and down to 4 m deep. Their floodlands are exposed or forested. These rivers are meandering, segments with rapid current alternate with half-standing reaches. The rate of the current fluctuates between 0.3 and 0.6 m/sec and between 0.5 and 0.8 m/sec during high and low water periods, respectively. In winter and early spring, the water temperature constitutes about 0.5–1.0ºC. In May, the water warms up to 10–17ºC. In summer, the water temperature fluctuates from 19 to 25ºC; in September, from 15 to 20ºC. The bottom is sandy, in some places silty, with well-developed aquatic vegetation densely populated with black fly larvae.

Table 2. The scale of frequency of occurrence of black fly species in streams of the central Russian forest-steppe (immature stages)

P_i, %	Class of occurrence	Species characteristics
< 5	1	Rare
5–14.9	2	Infrequently found
15–49.9	3	Frequently found
50–100	4	Constantly found

Notes: (P_i) relative frequency of occurrence of the species.

The rivers of this type are populated with 14 black fly species, including *Cnephia pallipes*, *Wilhelmia balcanica*, *W. equina*, *W. lineata*, *Schoenbaueria nigra*, *Nevermannia latigonia*, *Eusimulium angustipes*, *Boophthora erythrocephala*, *B. sericata*, *Odagmia pratora*, *Argentisimulium noelleri*, *Simulium morsitans*, *S. paramorsitans*, and *S. posticatum*.

The 3rd type of streams includes small rivers with constant and episodic (during low water periods) current periods (Chigla, Karachan, Khvorostan, Tokai, Kurlak, Toida, Pal'na, Emancha, Dobrinka, Ol'shanka, Chichera, and Berezovka rivers). Their water resources are rather small. In the majority of these rivers, the basins are exposed, more than half of them are ploughed, crossed by ravines and gullies; their floodlands are of the meadow type. The riverbeds are meandering, silty, densely covered with aquatic vegetation, 1.5–30 m wide and 0.5–2.5 m deep. The water current is rapid during high water periods (0.4–0.9 m/sec) and low during low water periods. The bottom is sandy, clayey, or, in some places, stony. On the whole, yearly fluctuations of the water temperature in streams of this type constitute from 0.4°C to 27ºC. In spring-summer, these streams are rapidly and strongly warmed; in winter, they can freeze. Because of the small amount of water and shallow character, the water temperature in such rivers is subject to rapid changes depending on the weather, in comparison with full-water rivers. Black fly larvae and pupae attach to riverside aquatic and sunken plants and to stones.

A total of 16 black fly species (larvae and pupae) were revealed in streams of the type concerned: *Cnephia pallipes*, *Wilhelmia balcanica*, *W. equina*, *W. lineata*, *Schoenbaueria nigra*, *Nevermannia latigonia*, *N. lundstromi*, *Eusimulium angustipes*, *Boophthora erythrocephala*, *B. sericata*, *Odagmia ornata*, *O. pratora*, *Argentisimulium noelleri*, *Simulium paramorsitans*, *S. posticatum*, and *S. simulans*.

The 4th type of streams is represented by rivers that lost their status and turned into temporary streams with the zero minimal discharge: Topka, Krasnaya, Balka Talovaya, Kondrashkin Log, Sukhaya Berezovka rivers and numerous nameless streams (ravines, brooks, and drying rivers). The floodlands are exposed, covered with meadows and shrubs. In the majority of such rivers, the water stream is regulated by ponds, where the water current can be noticed only on concrete, metallic, or stony dam discharges. In winter, the discharge in the majority of dams is absent, and streams frequently freeze down to the bottom. The natural riverbeds are sandy or clayey. Fertilizers from adjacent fields frequently get into reservoirs. These streams are 0.3–2.0 m wide and 0.1–0.7 m deep; the current flow velocity is 0.15–0.40 m/sec. During the day, depending on the weather, the water temperature fluctuates stronger than in more full-water streams. In May, the water temperature fluctuates between 8ºC and 22ºC; in summer, between 16ºC and 28ºC; and in September, between 12ºC and 21ºC. Characteristic substrates for the attachment of larvae are represented by riverside and aquatic vegetation, concrete blocks, dam stones, and different garbage (plastic bags, broken glass, used tires, slate, etc.).

A total of 15 black fly species were found in streams of this type: *Greniera rivi*, *Cnephia pallipes*, Wilhelmia equina, *Nevermannia angustitarsis*, *N. latigonia*, *Eusimulium angustipes*, *Cnetha lidiae*, *C. verna*, *Boophthora erythrocephala*, *B. sericata*, *Odagmia ornata*, *O. pratora*, *Argentisimulium noelleri*, *Simulium paramorsitans*, and *S. simulans*.

The 5th type of streams is represented by spring brooks with constant current and low water temperature in summer (7–14ºC). Three brooks and a single river (Plyushchan') beginning as springs were examined. The brooks run in forests, their beds are sandy, with fallen leaves and branches. These streams are 20–50 cm wide and 5–15 cm deep. The current rate is 0.2–0.4 m/sec, the water temperature in spring-summer, 7–9ºC. Black fly larvae and pupae are attached to sandy bottom, leaves, twigs, and small aquatic-riverside plants.

The Plyushchan' River is about 7 km long, 3–5 m wide, and 0.1–0.5 m deep. The water temperature in summer constitutes 8–9ºC near the source (spring) and up to 14ºC downstream. The bottom is pebbly, with gravel and clay in some places. Larvae and pupae are localized on stones and submerged tree branches.

Table 3. The frequency of occurrence and domination of immature black fly stages in streams of the central Russian forest-steppe

Species	Type of stream										Total	
	1st		2nd		3rd		4th		5th			
	P_i	D_i	P_i	D_i	P_i	D_i	P_i	D_i	P_i	D_i	P_i	D_i
Greniera rivi							4.08	0.001			0.84	4.2×10^{-5}
Cnephia pallipes	1.54	0.011	2.33	0.006	6.45	0.021	816	1.940			4.20	0.179
Wilhelmia balcanica	8.93	0.009	4.65	0.012	9.68	0.048					5.46	0.011
W. equina	1.54	0.001	2.33	0.002	30.66	2.327	2.04	0.006			9.24	0.195
W. lineata	3.08	0.001	2.33	0.001	6.45	0.021					2.94	0.003
Schoenbaueria nigra	24.62	5.047	6.98	0.163	3.23	0.004					8.82	0.924
Byssodon maculatus	30.77	5.840									8.40	0.790
Cnetha verna							14.29	1.470	36.84	21.242	5.88	0.127
C. lidiae							6.12	0.007			1.26	2.5×10^{-4}
Cnetha sp.									63.16	25.131	5.04	0.018
Nevermannia angustitarsis							2.04	4.1×10^{-4}			0.42	1.7×10^{-5}
N. latigonia	1.54	0.001	25.58	0.120	37.10	1.124	22.45	0.299			19.33	0.211
N. lundstromi					1.61	3.2×10^{-4}					0.42	2.1×10^{-5}
Eusimulium angustipes			2.33	0.001	32.26	0.352	22.45	0.294			13.45	0.069
Boophthora erythrocephala	93.85	54.621	88	74.043	83.87	47.982	8.16	0.20			65.13	33.053
B. sericata	1.54	0.006	9.30	0.153	4.84	0.027	10.20	0.003			5.46	0.016
Odagmia ornata					35.48	3.924	57.14	31.330	5.26	0.084	21.43	2.537
O. pratora			11.63	0.053	4.84	0.085	8.16	0.048			5.04	0.031
Argentisimulium noelleri			2.33	0.001	6.45	0.024	10.20	0.521			4.20	0.039
Simulium longipalpae									5.26	0.034	0.42	2.5×10^{-5}
S. morsitans	4.62	0.002	11.63	0.107							3.36	0.003
S. paramorsitans	8.93	0.028	18.60	1.417	22.58	2.911	4.08	0.002			12.18	0.520
S. posticatum			11.63	0.193	12.90	0.353					5.46	0.048
S. simulans					1.61	0.007	2.04	2×10^{-4}	5.26	0.017	1.26	0.001

Notes: (P_i) relative frequency of occurrence of a species (%); (D_i) Palii-Kovnatsky index of domination (%).

In reservoirs of the 5th type, 5 black fly species were revealed: *Cnetha verna*, *Cnetha* sp., *Odagmia ornata*, *Simulium longipalpae*, and *S. simulans*.

According to the scale of occurrence of immature stages and adult black flies in the biocenoses examined, composed according to the method of Bakanova (1987), rare, infrequent, frequent, and constantly found (constant) species constitute up to 5%, 5.0–14.9%, 15–49.9%, and 50–100% of all the species (Table 2). The occurrence of a species (P_i) was determined as the ratio between the number of samples, in which this species was found, and the total number of samples taken from the given stream (Table 3).

The class of species constantly found in streams at immature stages (the 4th class in Table 2) includes *Boophthora erythrocephala*, prevailing in relation to

Table 4. The scale of domination of black fly species in streams of central Russian forest-steppe by Palii-Kovnatsky index

D_i (%)	log D_i	Degree of domination
$10 < D_i < 100$	$1 < \log D_i < 2$	Dominant
$1 < D_i < 10$	$0 < \log D_i < 1$	Subdominant
$0.1 < D_i < 1$	$-1 < \log D_i < 0$	Recedent
$0.01 < D_i < 0.1$	$-2 < \log D_i < -1$	Subrecedent of group A
$D_i < 0.01$	$\log D_i < -2$	Subrecedent of group B

Note: for designations, see Table 3.

occurrence and the population density in rivers of the first three types. It is a mass polycyclic species with larvae present in reservoirs all the year round. Frequently found species (the 3rd class) include *Odagmia ornata* and *Nevermannia latigonia*. *Odagmia ornata* is a polycyclic species; its larvae and pupae are most frequently found and possess the highest population density in small rivers and brooks of the 4th type. *Nevermannia latigonia* is an eurytopic polycyclic species; the immature stages of this species populate all the types of streams excluding spring brooks, but, unlike *O. ornata*, this species was low in number in all the water samples.

The 2nd class of occurrence in the rivers examined comprised 11 black fly species. The monocyclic species developing during a short period in spring are found in samples rather rarely; they include larvae and pupae of mass bloodsuckers *Schoenbaueria nigra* and *Byssodon maculatus*, the subdominant bloodsuckers *Simulium paramorsitans* and *S. morsitans*, and also *Boophthora sericata* and *Simulium posticatum*; the latter species demonstrate low bloodsucking activity. The 2nd class of occurrence also includes pupae and larvae of polycyclic species *Wilhelmia balcanica*, *W. equina*, *Cnetha verna*, *Cnetha* sp., and *Eusimulium angustipes*.

Rare species (the 1st class of occurrence) in forest-steppe streams comprised 10 black fly species. Some of them are rather rare in samples (*Cnephia pallipes*, *Wilhelmia lineata*, *Argentisimulium noelleri*, *Simulium morsitans*, and *S. simulans*); others are represented by solitary specimens (*Greniera rivi*, *Cnetha lidiae*, *Nevermannia angustitarsis*, *N. lundstromi*, and *Simulium longipalpae*).

Thus, the highest indices of occurrence are characteristic of polyvoltinic species with larvae and pupae present in streams all the year round. The low index of occurrence testifies not only to the rare occurrence of the species in the wild, but, more frequently, to the short period of its development; the latter statement is confirmed by the data on occurrence of larvae and pupae of mass bloodsuckers in rivers.

Domination of species in streams was estimated by means of the Palii-Kovnatsky index ($D_i = 100 \times P_i \times N_i$, with P_i designating relative occurrence and N_i, relative population density of species in fractions). We used a modified variant of the principle of gradation of domination by the value of this index, offered by Kovnatsky (from Bakanov, 1987) (Table 4).

Boophthora erythrocephala appeared to be the most dominating species among the immature stages of black flies in forest-steppe streams (Table 3, Fig. 3). This species demonstrates the highest values of indices of occurrence and the population density in streams of the 1st–3rd type. *Odagmia ornata* was included into the group of subdominating species; immature stages of this species are characterized by high values of indices of occurrence and population density in streams of the 3rd and 4th type.

The group of recedents included *Schoenbaueria nigra*, *Byssodon maculatus*, *Cnetha verna*, *Simulium paramorsitans*, *Cnephia pallipes*, *Wilhelmia equina*, and *Nevermannia latigonia*. The presence of species demonstrating a high degree of bloodsucking activity as adults (*Sch. nigra*, *B. maculatus*, *C. verna*, *S. paramorsitans*) is explained by the fact that these species demonstrate high values of population density only during short periods of larval development in spring.

The subrecedents of group A included *Wilhelmia balcanica*, *Cnetha* sp., *Eusimulium angustipes*, *Boophthora sericata*, *Odagmia pratora*, *Argentisimulium noelleri*, and *Simulium posticatum*; these species occur in streams in small numbers. The subrecedents of group B included *Greniera rivi*, *Wilhelmia lineata*, *Cnetha lidiae*, *Nevermannia angustitarsis*, *N. lundstromi*, *Simulium morsitans*, *S. longipalpae*, and *S. simulans* (Fig. 3).

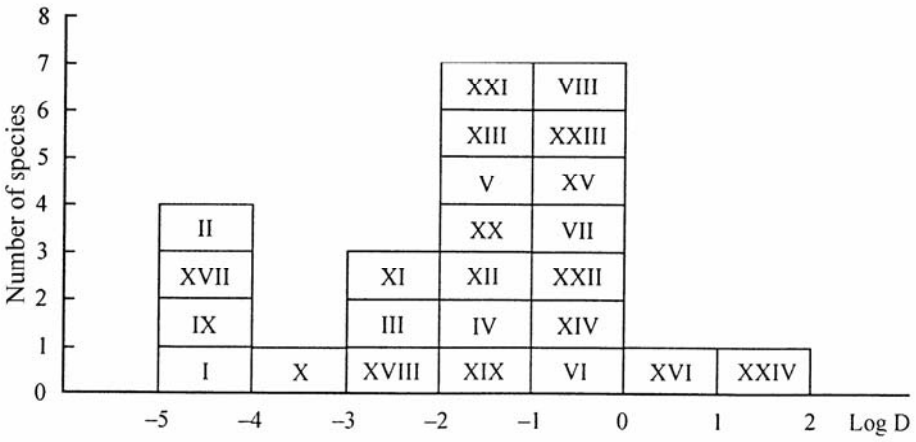

Fig. 3. The structure of domination of immature stages of black fly species (family Simuliidae) in streams of the central Russian forest-steppe. Abscissa: Palii-Kovnatsky index of domination, logarithmic value.

Comparison of the diversity of the black fly fauna at aquatic stages of development in streams was performed by means of Margalef (D_{Mg}), Shannon (H'), Pielou (E), and Simpson indices (D_S) (Table 5).

The species wealth of black flies (S) possesses similar values in streams of the 2nd, 3rd, and 4th type; the black fly population is poorer in full-water rivers (the 1st type); and the smallest number of species of the family Simuliidae was revealed in spring brooks (the 5th type), populated by several stenobiontic species. This is reflected in the approximately equal values of the Margalef index for preimaginal stages of black flies in streams of the 2nd, 3rd, and 4th type, a smaller value of D_{Mg} in the black fly population in streams of the 1st type, and the lowest value of this index in streams of the 5th type.

The value of the Shannon diversity index and distribution of relative abundance reflected in the Pielou index slightly decrease from the 3rd type of streams, where they are the highest, to the 4th type; these values are lower in streams of the 1st and 5th type; and the lowest, in the 2nd type of rivers; it reflects the decrease in evenness of the species abundance and the increase in the significance of the dominating species. The value of the Simpson index changes similarly; this index reflects the concentration of species domination more precisely in comparison with other indices. The value of the Simpson index is the lowest in streams of the 2nd type, where D_S value constitutes only a half of those in streams of the 3rd and the 5th type.

Thus, the fauna of black flies in medium-sized rivers of the 2nd type possesses the lowest degree of diversity. A large amount of black flies emerge in these streams, but domination of a single species (*Boophthora erythrocephala*) and the presence of other subrecedent species significantly decreases the diversity of the black fly fauna.

The rivers of the 3rd type are the most diverse; a single species (*B. erythrocephala*) also distinctly dominates there, but the evenness of the fauna significantly increases due to the larger role of subdominants and recedents.

The streams of the 4th type are closely related to those of the 3rd type; the increase in the population density of another dominant species (*Odagmia or-*

Table 5. Indices of diversity of black fly fauna in streams of the central Russian forest-steppe (immature stages)

Indices of diversity	Type of streams				
	1st	2nd	3rd	4th	5th
S	11	14	16	15	5
D_{Mg}	1.05	1.65	1.67	1.65	0.72
H'	1.03	0.70	1.66	1.32	0.80
E	0.43	0.27	0.60	0.49	0.50
D_S	2.38	1.27	2.75	2.70	2.04

Table 6. Indices of paired biocenotic similarity of black fly faunas in streams of the central Russian forest-steppe (Chekanovsky-Sorensen index)

Type of stream	1st	2nd	3rd	4th	5th
1st	1	0.61	0.58	0.03	0
2nd	0.8	1	0.69	0.04	0
3rd	0.67	0.87	1	0.18	0.02
4th	0.46	0.62	0.71	1	0.12
5th	0	0	0.19	0.3	1

Notes: Left bottom, analysis of qualitative data; right upward, analysis of quantitative data.

nata), however, results in the lower degree of evenness of the fauna in these streams.

The rivers of the 1st type are characterized by a low degree of species wealth, but possess a higher degree of evenness (*E*) in comparison with those of the 2nd type, which makes black fly fauna in these rivers more diverse than in medium-sized rivers of the 2nd type.

Estimation of species diversity in streams of the 5th type demonstrates a rather low degree of species richness in brooks and high indices of domination of some species.

Estimation of species diversity in the streams of the 5th type demonstrates a low degree of species wealth and high indices of the domination of separate species.

On the whole, the species complexes in different types of streams are characterized by high indices of similarity (Table 6). The highest degree of biocenotic similarity by Chekanovsky-Sorensen index (the analysis of qualitative data) was revealed for black fly faunas in rivers of the 2nd and 3rd type (0.87), the faunas of streams of the 1st and 4th type are similar to the abovementioned faunas to a lesser extent. The lowest degree of biocenotic similarity by the above index is characteristic of the streams of the 1st and 5th type.

Analysis of quantitative data by means of the Chekanovsky-Sorensen index demonstrates that differences in the black fly fauna in the examined rivers develop not as changes in species complexes, but as changes in the structure of domination (Table 6). Comparison of qualitative data also demonstrates the highest degree of similarity (0.69) between the black fly faunas of rivers of the 2nd and 3rd type; besides, the similarity of black fly faunas in brooks and temporary streams of the 4th type was also revealed.

CONCLUSIONS

The black fly fauna of the central Russian forest-steppe comprises 26 species belonging to 12 genera and is characterized by prevalence of boreal-polyzonal species.

In the central Russian forest-steppe, black flies possess 1–3 yearly generations. 12 species hibernate as eggs; 2 species, as eggs or larvae (depending on the weather conditions); 8 black fly species spend winter as larvae.

The highest degree of species diversity was revealed in small rivers and temporary streams; the lowest, in spring brooks.

Distinct domination of some polycyclic species is characteristic of the black fly faunas in different streams (*Boophthora erythrocephala* dominates in streams of the 1st, 2nd, and 3rd type; *Odagmia ornata*, in the streams of the 4th type); the species composition and the number of subdominant black flies in the rivers varies. As the result of evenness in the population density of species, the black fly fauna in the rivers of the 3rd type (constant and with a temporary stream) is the most diverse. The lowest degree of diversity was revealed in black flies of the medium-sized rivers of the 2nd type, which is stipulated by high indices of domination of *B. erythrocephala*. Monocyclic blood-sucking species (*Schoenbaueria nigra*, *Byssodon maculatus*, *Cnetha verna*, *Simulium paramorsitans*) whose role in terrestrial biocenoses is quite considerable, in streams possess high indices of population density only during a short period of larval development in spring, which determines their subsidiary position in the structure of black fly domination.

Some types of streams of the central Russian forest-steppe are characterized by similarity in black fly species complexes, which is determined by eurytopic nature of species developing in these streams and identity of some hydrological parameters in different rivers. Differences between black fly faunas in the examined streams are manifested in the structure of species domination. The black fly faunas in middle-sized and

small rivers (the 2nd and 3rd type of streams) are significantly similar; the faunas of spring brooks (the 5th type) and temporary streams (the 4th type) are the most original.

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