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THE DISTRIBUTION OF GREEN FROGS (*Rana esculenta* COMPLEX) IN NIZHNY NOVGOROD PROVINCE, CENTRAL EUROPEAN RUSSIA

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The occurrence of three green frog taxa [*Rana lessonae* (L), *R. ridibunda* (R), and *R. esculenta* (E)] in Nizhny Novgorod Province was evidenced by DNA flow cytometry analysis. Our data are the first reliable record of the hybrid *R. esculenta* for the province (the Middle Volga River basin). All hybrids were diploid. *Rana lessonae* is spread throughout the province, except its extreme north-east. The distribution of *Rana ridibunda* is wider and covers the northernmost area. *Rana esculenta* is quite sparse. In the province, all three species, probably, reach the northern limits of their ranges. Six population systems were revealed; both with a single species (R, L, and, probably, E) and with mixed species populations (LE, REL and RL). The geographic trends in occurrences of hybrids and various kinds of population systems in eastern Europe are discussed.

Key words: Ranidae, *Rana esculenta* complex, DNA flow cytometry, genome size, hybrids, population systems, Nizhny Novgorod Province, central European Russia.

INTRODUCTION

In eastern Europe, green frogs (the *Rana esculenta* complex) comprise three taxa. These are two "normal" Mendelian species — *Rana ridibunda* Pallas, 1771, and *R. lessonae* Camerano, 1882, as well as *R. esculenta* Linnaeus, 1758 of the hybrid origin. The latter exhibits an unusual mode of speciation, characterized by complicated genetic mechanisms, namely: hybridization, so-called hemiclonal (or meroclonal) inheritance, polyploidy, unisexual and bisexual population systems (e.g., Borkin et al., 1987; Graff and Polls Pelaz, 1989; Berger, 1990; Günther, 1990; Vinogradov et al., 1988, 1990, 1991; Caune and Borkin, 1993; Lada, 1995). As yet, the distribution of hybrid *R. esculenta* in the vast territory of European Russia is obscure.

In the previous century, many authors have published a lot of data assigned to "*R. esculenta*." However, under this name, perhaps, they have worked mostly with *R. lessonae* or *R. lessonae* and *R. esculenta*, as well as, rarely, with *R. ridibunda*. For instance, after the Second World War, Soviet authors followed the classic guide book by Terentjev and Chernov (1949) who recognized two species (*R. ridibunda* and "*R. esculenta*") only.

The distributional records of *R. esculenta* in the European part of Russia are quite scarce. Using an albumin electrophoretical approach and nuclear DNA flow cytometry, we recorded hybrids in the western part (Kaliningrad and Pskov Provinces — Borkin et al., 1986, 1999; our unpublished data), in the middle-southern part (the Central Chernozem Region — Lada et al., 1995), and in central part (Ivanovo Province— Okulova et al., 1997; Udmurt Republic — Borissovsky et al., 2000, 2001) of European Russia. In the central latitudes of European Russia, both parental species, *R. lessonae* and *R. ridibunda*, are distributed largely sympatrically (e.g., Borkin et al., 1979; Borkin, 1998), and, sometimes, both species

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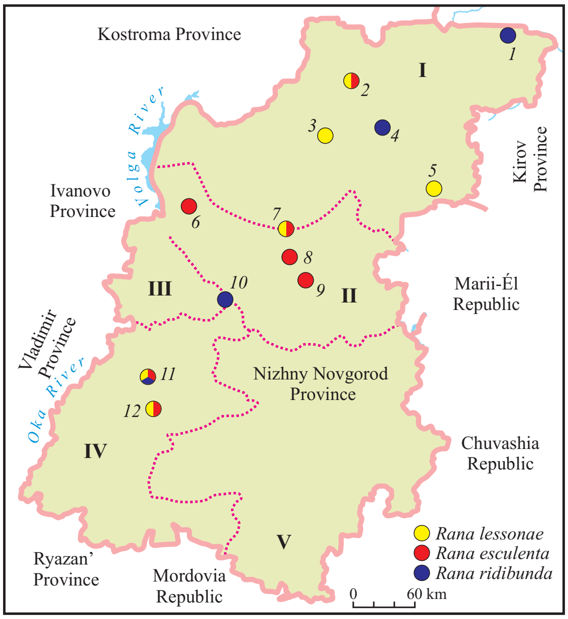

Fig. 1. The distribution of green frogs, which were used for DNA flow cytometry, in Nizhny Novgorod Province. The localities are listed in Table 1. I – V, Geographic areas (see text).

co-exist in the same localities (e.g., Lada et al., 1995; Okulova et al., 1997). Nevertheless, V. I. Garanin (Borkin et al., 1979; Garanin, 1983) failed to identify the hybrid *R. esculenta* in the Volga – Kama rivers basin. Moreover, Alexandrovskaya and Bykov (1979) suggested that the rareness or lacking of hybrids in the central and eastern parts of European Russia might be associated with the change in climatic zones. Indeed, in the west of the former Soviet Union, the zone of suboceanic climate is replaced by the zone with subcontinental climate. In the latter, the habitat isolation between two parental species should be increased (Alexandrovskaya and Bykov, 1979).

Nizhny Novgorod Province or Nizhegorodskaya oblast' [*russian*] is situated in the central part of East European Plain. The province covers the northern part of the Middle Volga River basin between 58°06′ N and 54°27′ N from the north to the south (i.e., about 400 km), and between 41°48′ E and 47°46′ E from the west to the east (approximately 300 km). Its territory is equal to 76,900 km^2 (e.g., Pestov et al., 2001). For comparison, that is larger than the double area of the Netherlands and somewhat smaller than the territory of Austria. Recently, Pestov with associates (2001) summarized all available data concerning the amphibian (12 species) and reptilian (7 species) fauna of Nizhny Novgorod Province.

From the north to the south, the territory of Nizhny Novgorod Province is covered by the coniferous forests (the southern taiga), by the northern broad-leaved forests with predominance of lime-trees (*Tilia cordata*) and oaks (*Quercus robur*) as well as even by the grasslands (the steppes). Gribova et al. (1980) provided a more detailed description of these types of vegetation.

In our opinion, Nizhny Novgorod Province is a key area to elucidate possible trends in the geographic distribution of *R. esculenta* in central European Russia.

In this paper we examine the patterns of geographic distribution of green frogs of Nizhny Novgorod Province as well as the composition of population systems.

MATERIAL AND METHODS

Forty four specimens were collected from twelve localities situated in various regions of Nizhny Novgorod Province (Fig. 1, Table 1). It is important to underline that in the course of the field trips a frog sampling was focused on localities with presumed hybrids [*R. esculenta* (Fig. 2)], with markedly less attention to parental species, *R. ridibunda* in particular. The small size of samples, ranging from 1 to 14, has been limited by strong biodiversity conservation policy performed by the staff of "Dront" Ecological Center. Although green frogs are not included to the provincial list of protected animals, the samples were taken under the permission of the "Dront" Center. They are deposited in the collection of the Zoological Institute, Russian Academy of Sciences, St. Petersburg.

The amount of DNA per nucleus (genome size) was measured by DNA flow cytometry. The details of the technique have been published previously (e.g., Vinogradov et al., 1990; Rosanov and Vinogradov, 1998; Borkin et al., 2001).

RESULTS

According to the nuclear DNA content, three green frog species were identified in Nizhny Novgorod Province (Fig. 3). Among 44 specimens from twelve localities, eight individuals were allocated to

Fig. 2. A female *Rana esculenta* from Golubikha Village, Vetluga District, August 1, 2000. Photo by Mark Pestov.

TABLE 1. The List of Green Frogs (*Rana esculenta* complex) Used for DNA Flow Cytometry Analysis

No.	Species	*n*	Latitude	Longitude	Locality
1	*R. ridibunda*	1	57°50′ N	47°01′ E	Yangarka Village [12], Tonshaevo District, June 14, 1999
2	*R. lessonae*	2	57°42′ N	45°10′ E	Golubikha Village [15], Vetluga District, August 1, 2000
	R. esculenta	2			
3	*R. lessonae*	3	57°26′ N	45°04′ E	Mikhalenino Village [18], Varnavino District, July 3 – 10, 2000
4	*R. ridibunda*	1	57°26′ N	45°43′ E	Zalivnaya Usad'ba Village [21], Uren' District, June 15, 1999
5	*R. lessonae*	2	57°02′ N	46°23′ E	Malye Kilemary Village [56], Sharanga District, July 24, 2000
6	*R. esculenta*	2	56°52′ N	43°34′ E	Burkovo Village [60], Gorodets District, August 19, 2000
7	*R. lessonae*	4	56°46′ N	44°33′ E	Zhuzhelka Village [72], Semenov District, July 28, 2001
	R. esculenta	10			
8	*R. esculenta*	3	56°40′ N	44°39′ E	Khakhaly Village [74], Semenov District, July 26, 2000
9	*R. esculenta*	1	56°30′ N	44°49′ E	Rustai Village [79], Bor District, Jule 15, 2002
10	*R. ridibunda*	5	56°19′ N	44°04′ E	Nizhny Novgorod City [104], October 6, 2002
11	*R. lessonae*	1	55°51′ N	43°04′ E	Cherneevo Village [134], Pavlovo District, June 16, 1999
	R. esculenta	4			
	R. ridibunda	1			
12	*R. lessonae*	1	55°40′ N	43°07′ E	Lesunovo Village [158], Sosnovo District, August 20, 2000
	R. esculenta	1			

Note. The locality numbers listed by Pestov et al. (2001) are given in square brackets.

R. ridibunda, 13 to *R. lessonae*, and 23 to *R. esculenta* (Tables 2 and 3). *Rana lessonae* was characterized by the smallest values of genome size, *R. ridibunda* by the largest ones, while *R. esculenta* had intermediate values (Fig. 3). This is in agreement with the hybrid origin of the latter species. Importantly, the value ranges of species did not overlap (Table 3), and this allowed us to identify each specimen with the 100% confidence.

All frogs under the study were diploid. The values of genome size displayed no correlation with sex or locality.

Among the samples from twelve localities, eight ones contained a single species only — three cases were with *R. ridibunda*, two with *R. lessonae*, and three with *R. esculenta*. Four other samples were mixed and consisted of two species (*R. lessonae* and *R. esculenta* — three cases) or of all three species (*R. ridibunda*, *R. esculenta*, and *R. lessonae* — one case).

DISCUSSION

Historical and Taxonomic Considerations

Nikolai Varpakhovsky (1888a, 1888b) has published the first data about green frogs of the modern Nizhny Novgorod Province territory. Among seven species of amphibians, "*Rana viridis*" was mentioned to be quite abundant. His collection taken in 1887 in the territory of the former Nizhny Novgorod Government (guberniya [*russian*]) is still kept at the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZISP), and at the Zoological Museum of the Nizhny Novgorod University (ZMNNU). According to the famous Russian herpetologist A. M. Nikolsky (1918), a specimen collected by "Warpachowsky, 1887" from "Barnukowo" (Bornukovo, ZISP 1628) belonged to "*Rana esculenta*" (p. 17), and, by the implication, to the "subsp. *ridibunda*" (p. 21). Later, this specimen was ascribed to "*Rana esculenta lessonae*" by P. V. Terentjev (1927a, p. 88), and to *R. lessonae* by V. I. Garanin (2000). Recently (Pestov et al., 2001), the examination of Varpakhovsky's green frogs demonstrated that his "*R. viridis*" contained, in fact, two currently recognized species, namely, *R. esculenta* from Bornukovo Village (ZISP), and *R. ridibunda* (four specimens, without exact localities, ZMNNU). However, based on current examination, the ZISP specimen should be as-

TABLE 2. The Amount of Nuclear DNA in Green Frogs from Twelve Localities of Nizhny Novgorod Province

No.	Species	Locality	*n*	Mean	SD	Min	Max
1	*R. ridibunda*	Yangarka	1♂	1.536			
2	*R. lessonae*	Golubikha	2♂	1.301		1.300	1.301
	R. esculenta		2♂	1.407		1.406	1.408
3	*R. lessonae*	Mikhalenino	1♂ + 2♀	1.296	0.002	1.294	1.298
4	*R. ridibunda*	Zalivnaya Usad'ba	1♀	1.535			
5	*R. lessonae*	Malye Kilemary	1♂ + 1♀	1.293		1.292	1.294
6	*R. esculenta*	Burkovo	2♂	1.425		1.424	1.426
7	*R. lessonae*	Zhuzhelka	2♂ + 2juv	1.303	0.004	1.299	1.309
	R. esculenta		1♂ + 9juv	1.412	0.005	1.399	1.416
8	*R. esculenta*	Khakhaly	2♂ + 1♀	1.406	0.004	1.402	1.409
9	*R. esculenta*	Rustay	1♀	1.413			
10	*R. ridibunda*	Nizhny Novgorod	2♀ + 1♀ + 2juv	1.529	0.003	1.526	1.533
11	*R. lessonae*	Cherneevo	1♀	1.302			
	R. esculenta		1♂ + 3♀	1.416	0.005	1.409	1.421
	R. ridibunda		1♀	1.538			
12	*R. lessonae*	Lesunovo	1♂	1.309			
	R. esculenta		1♂	1.408			

Note. The values of genome size are expressed in arbitrary units in relation to that of *Rana temporaria*.

TABLE 3. The Variation of Genome Size in Green Frogs of Nizhny Novgorod Province (arbitrary units expressed in relation to genome size of *Rana temporaria*)

Species	*n*	Mean	SD	Range
R. lessonae	13	1.300	0.005	1.292 – 1.309
R. esculenta	23	1.412	0.006	1.399 – 1.426
R. ridibunda	8	1.532	0.005	1.526 – 1.538

signed to *R. lessonae* (L. J. Borkin and G. A. Lada, unpublished data). Therefore, we confirmed the identification by Garanin (2000).

Prof. Mikhail Rouzsky, a well-known zoologist of the Imperial Kazan University (Russian Empire), has applied the name "*Rana esculenta*" to green frogs of the former Kazan Government and adjacent southern areas of recent Nizhny Novgorod Province (Rouzsky, 1894). He recognized two main color patterns among frogs, namely: 1) with light vertebral stripe along bright green dorsum; and 2) without such a stripe and with dull (gray or brown) dorsum. However, some animals with bright green dorsal coloration had no vertebral stripe. Interestingly, a few frogs had brown temporal mask, like *R. temporaria*. Rouzsky (1894) suggested that the variation in coloration of *R. esculenta* was influenced by habitat, sex, age, and, partially, season.

In 1927, Pavel Terentjev has published a paper about the herpetofauna of the Central Industrial area (Tsentral'no-Promyshlennaya oblast' [*russian*]), which then included Nizhny Novgorod Province. He has recognized two species of green frogs: *R. ridibunda ridibunda* and *R. esculenta lessonae* (Terentjev, 1927b). In the same year, in a taxonomic paper, Terentjev (1927a) already introduced the two-species concept for green frogs of European part of the former Soviet Union (*R. ridibunda* and "*R. esculenta*").

Since Terentjev's papers, the previous single-species concept of Nikolsky (1918) has been replaced by the two-species scheme. The latter was widely accepted by Soviet zoologists, especially after the publication of the famous guide book on the herpetofauna of the USSR (Terentjev and Chernov, 1949). For instance, Prof. Ivan Pusanov from the former Gorky State University (Pusanov et al., 1942, 1955) has applied Terentjev's taxonomic treatment to green frogs of Gorky Province [the former name of Nizhny Novgorod Province in the Soviet time]. Curiously, A. N. Formozov (1935, p. 178), a well-known Soviet vertebrate zoologist and ecologist, mentioned two kinds of green frogs in Nizhny Novgorod Province: "Green and river frogs are common near rivers and lakes of the province." Krassavtsev (1935) published a paper about feeding of "*R. ridibunda ridibunda*" in the environs of Nizhny Novgorod.

The exciting discovery of the hybrid origin of *R. esculenta* by Polish herpetologist Leszek Berger (1967, 1978) stimulated recognizing three species among green frogs of eastern Europe. However, in

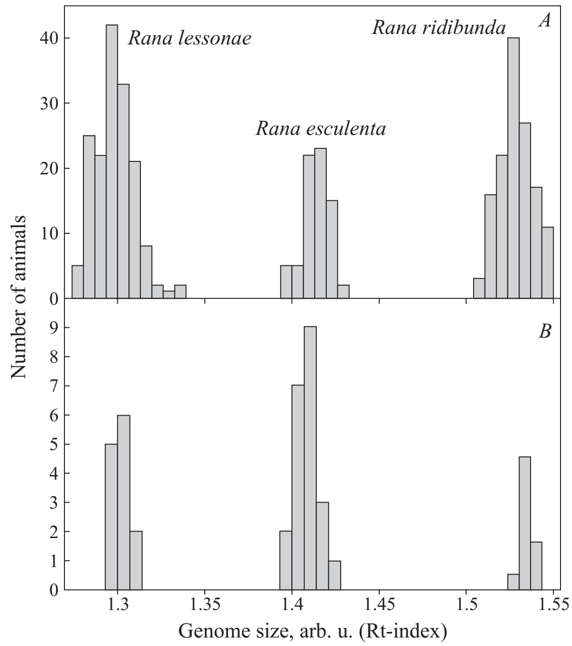

Fig. 3. Genome size in three taxa of green frogs expressed in arbitrary units in relation to genome size of *Rana temporaria* (Rt-index). *A*, Summarized data for frogs of the East European Plain; *B*, data for frogs from Nizhny Novgorod Province.

his book Garanin (1983) has arranged green frogs of the vast territory of Volga – Kama rivers region to *R. ridibunda* and *R. lessonae* only, with no record of hybrid *R. esculenta*.

Our cytometric analysis provided the first precise data on the occurrence of three taxa of green frogs of Nizhny Novgorod Province. Moreover, this is the first reliable evidence of existence of hybrid *R. esculenta* in the province, and for the Middle Volga River area as a whole.

Geographic Distribution

Geographically, three life zones (biomes) pass over the territory of Nizhny Novgorod Province (e.g., Pestov et al., 2001). Moreover, this area is divided in five areas in terms of physical geography (Fig. 1: I – V). The area I (Severnoe Zavolzh'e [*russian*]) is situated within the taiga zone (the southern taiga subzone), with quite dense fir forests and relatively severe climate. The areas II (Yuzhnoe Zavolzh'e [*russian*]), III (Volzhsko-Okskoe Mezhdurech'e [*russian*]), and IV (Zapadnoe Predvolzh'e [*russian*]) are arranged to the mixed (coniferous and deciduous) forest zone. Finally, the area V is a part of the deciduous (broad-leaved) forest zone, with a large area of grass steppes. However, the majority of primary forests has been cut down and replaced by the secondary forests and grasslands significantly modified by agriculture.

The field survey demonstrates that green frogs are distributed in all five areas of the region (Fig. 4). Among 200 herpetological localities listed by Pestov et al. (2001), green frogs were recorded in 123 (61.5%). Table 4 provides some data about the occurrence of green frog species among these localities. We calculated the frequencies based on the list of field records published by Pestov et al. (2001). In Nizhny Novgorod Province, *R. lessonae* was found in 84 localities (68%), and *R. ridibunda* in 71 (58%), whereas *R. esculenta* in 7 localities (6%) only. However, it should be mentioned that the species allocation has been made in the field conditions by various collectors, using the external characters only, and, sometimes, might be incorrect. For instance, formerly Pestov et al. (2000) listed 14 localities of *R. esculenta*.

Geographically, in Nizhny Novgorod Province *R. ridibunda* is distributed wider (Fig. 5) than *R. lessonae* because the latter species is not found in the extreme north-east of the region (Fig. 6). Pestov et al. (2001) suggested that there *R. lessonae* might reach the northern limit of its range. Indeed, this species is characteristic of the mixed and deciduous forest zones. *Rana lessonae* is a typical inhabitant of various permanent forest water reservoirs. However, the species avoids the fir forest of the taiga zone, with the predominance of *Picea abies* and *P. obovata*.

TABLE 4. The Distribution of Green Frogs (the *Rana esculenta* complex) Among 123 Localities of Nizhny Novgorod Province

Species	Localities	
	n	%
Localities with a single species		
R. lessonae (L)	49	40
R. esculenta (E)	1	1
R. ridibunda (R)	38	31
Localities with coexisting species		
L + R	30	24
L + E	2	2
L + E + R	3	2
Total		
R. lessonae	84	68
R. esculenta	6	5
R. ridibunda	71	58

Note. Data based on the field records listed by Pestov et al. (2001).

The Golubikha Village, Vetluga District [57°43′ N, 45°09′ E] seems to be the northernmost locality of *R. lessonae* in Nizhny Novgorod Province (Fig. 5; Pestov et al., 2001). This point, together with Russkie Krai Village [57°23′ N, 46°50′ E], the settlement Kiknur [57°18′ N, 47°11′ E], and Nolinsk Town [57°33′ N, 49°57′ E] in the Kirov Province (Garanin, 1983, 2000), and Russkaya Bab'ya Village [57°05′ N, 51°32′ E] in the Udmurt Republic (Borissovsky et al., 2001), are the northernmost records of the species in the Volga – Kama rivers basin in general.

We observed similar distribution in the northwest of European Russia, where the northern limit of the main range of *R. lessonae* coincides with the transition from the mixed forest zone to the taiga zone (Borkin and Tikhenko, 1979; Borkin et al., 1979; our data). However, some isolated populations, perhaps, of relict origin, occur in the southern taiga. We suggest that such an island-like pattern of the distribution of *R. lessonae* may take place in the northern part of Nizhny Novgorod Province as well.

Unlike *R. lessonae*, *R. ridibunda* is a species which, as a rule, avoids any forest, and which prefers to inhabit various open landscapes, although, sometimes, *R. ridibunda* can penetrate into forest areas using river beds (Garanin, 1983; Lada et al., 1995).

This species displays a paradoxical pattern of the geographic distribution in relation to *R. lessonae* (Borkin et al., 1979). In the northwest of eastern Europe, the northern limit of the native range of *R. ridibunda* is markedly shifted to the south in comparison with that of *R. lessonae*. Some isolated populations of *R. ridibunda*, which exist far beyond the main range, were introduced, accidentally or deliberately, by humans, for instance, in the environs of Riga (Latvia) or in St. Petersburg (Russia).

Another situation is in the north-east of European distribution of green frogs. In this area, *R. ridibunda* is spread obviously northward beyond the northern range limit of *R. lessonae*. Thus, in Nizhny Novgorod Province *R. ridibunda* was recorded in the northernmost part of the area I, including the Pizhma River area (Fig. 5). The species was found in Shakhun'ya District (the settlement Syava, 58°01′ N, 46°19′ E, and Vakhtan Town, 57°58′ N, 46°40′ E), as well as in Tonshaevo District (Berezinsky Point, 57°57′ N, 46°59′ E, and Yangarka Village, 57°50′ N, 47°00′ E).

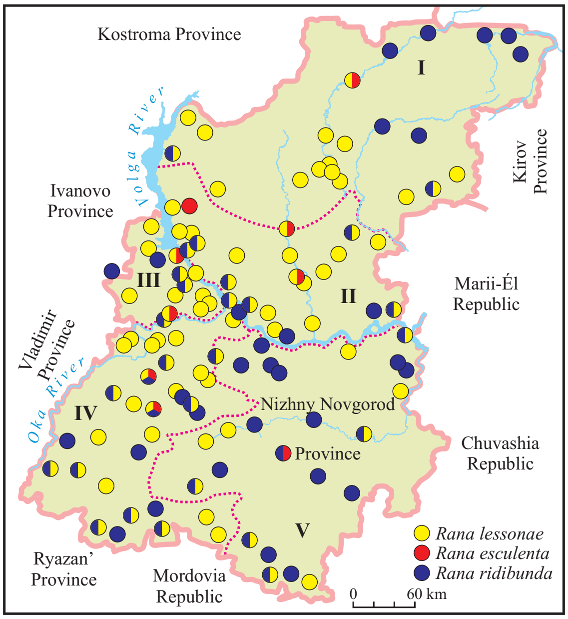

Fig. 4. The overall distribution of green frogs (records of three taxa summarized) in Nizhny Novgorod Province across the geographic regions (I – V), according to Pestov et al. (2001).

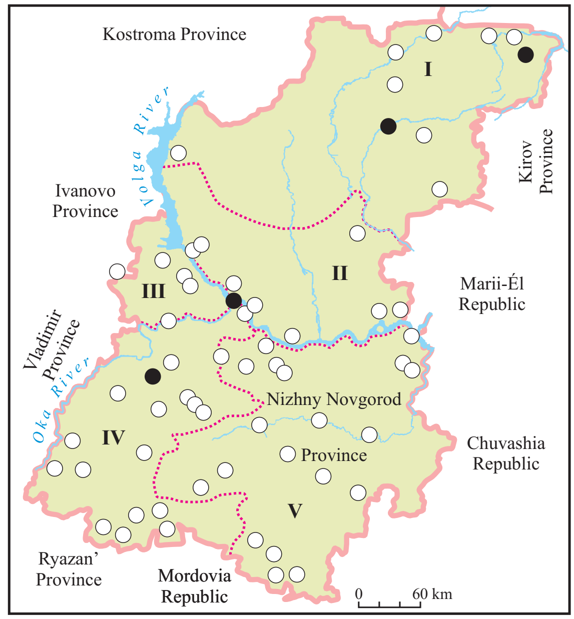

Fig. 5. The distribution of *Rana ridibunda* in Nizhny Novgorod Province (Pestov et al., 2001; our data). I – V, Geographic areas. The localities with frogs examined by DNA flow cytometry are marked by solid circles.

Such a pattern of the distribution of both species is supported by the comparison of maps with green frogs records known for the Volga – Kama territory (Garanin, 1983, 2000). For instance, in the adjacent Kirov Province, *R. ridibunda* reaches the Murygino settlement, Yuriya District [58°44′ N, 49°27′ E], and Klimkovka Village, Belaya Kholunitsa District [58°53′ N, 51°14′ E]. These are the northernmost localities for the species in Russia in general. In Udmurt Republic, which is situated to the east from Nizhny Novgorod Province as well, *R. ridibunda* was also recorded in more northern latitudes than *R. lessonae* (Borissovsky et al., 2001).

Two scenarios might be proposed to explain the origin of such "northern gap" between the distributional limits of the two species. The first scenario is associated with human activity. In the past, dense fir forests might be a barrier to prevent any movement of both species to the north, because *R. lessonae*, being a forest species, as a rule, avoids such a kind of coniferous forests, while *R. ridibunda*, being a species of open landscapes, avoids any dense forests. After the extensive deforestation in historical time, especially between late 18th century and early 20th century (Garanin, 1983), new open landscapes may have established another barrier for *R. lessonae*, on the one hand, and become an "ecological corridor" for the distribution of *R. ridibunda*, on the other hand. If this suggestion is correct, the northernmost populations of *R. ridibunda* should be considered relatively recent colonists of the area.

An alternative explanation is based on native changes in life zones. Approximately 5000 years ago, in the so-called xerothermic subboreal epoch, local forests have been replaced by the steppes, which have spread northwards to Vologda City (Stankov, 1951), even beyond the current northern border of the region. Later, the climate has been more and more moist and colder. The grasslands have stepped back southward, and the taiga has covered the northern part of Nizhny Novgorod Province, again (Pusanov et al., 1942, 1955). In this scenario, the northern isolated populations of *R. ridibunda* should be considered a relic of the xerothermic time. Although we incline to support the relict origin of those populations, one should keep in mind that, at least, in the 20th century, the anthropogenic impact obviously predominated over the natural factors that caused the evolution in the local ecosystems.

Thus, in eastern Europe, the northernmost parts of green frog range are inhabited by allopatric popu-

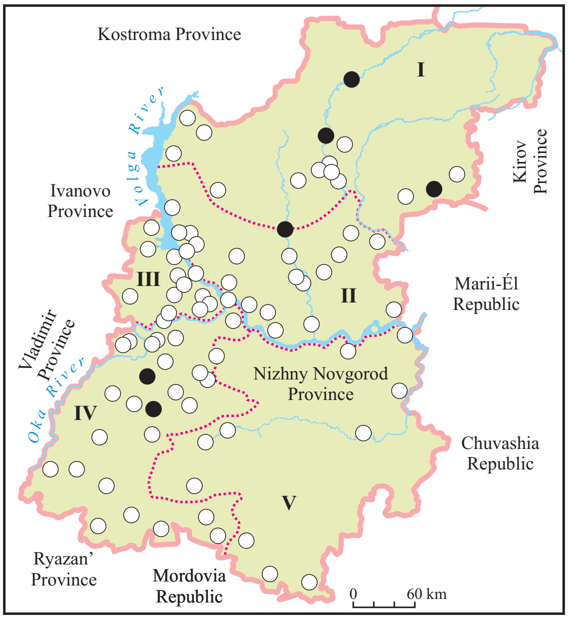

Fig. 6. The distribution of *Rana lessonae* in Nizhny Novgorod Province (Pestov et al., 2001; our data). I – V, Geographic areas. The localities with frogs examined by DNA flow cytometry are marked by solid circles.

lations of *R. lessonae* in the northwest, and by allopatric populations of *R. ridibunda* in the northeast. In the latter area the abundance of the species is very low (our field observations).

In Nizhny Novgorod Province, *R. esculenta* occurs quite rare in comparison with its both parental species. Recently, Pestov et al. (2001) reported five presumed localities, based on preliminary unpublished data (Burkovo, Khakhaly, Cherneevo, Lesunovo, and Rustay), and two more questionable localities (the environs of Zavolzh'e Town, 56°38′ N, 43°24′ E). In this paper we confirmed the existence of diploid hybrids in seven localities (Table 1 and 2; Fig. 7), including the first four records listed above, and two additional records, namely Golubikha and Zhuzhelka villages. Importantly, Golubikha (57° 43′ N, 45°09′ E) is the northernmost record of *R. esculenta* in general. In addition, in the course of field trip in June 17, 1999, S. N. Litvinchuk identified *R. esculenta* at the environs of Dzerzhinsk Town, 56°14′ N, 43°26′ E; however, this sample was not examined by flow DNA cytometry.

Formerly, we already mentioned a specimen of "*R. esculenta*" collected by Varpakhovsky near Bornukovo Village (55°22′ N, 44°48′ E). In June 26, 1999, we (Litvinchuk and Pestov) visited this locality; we failed to find any hybrids (and *R. lessonae*) here, and all captured frogs (21 individuals) belonged to *R. ridibunda*, according to external characters.

Thus, the cytologically confirmed distribution of *R. esculenta* is confined to three geographic regions only (I, II, and IV). All these localities are situated in the zone of mixed forests (the areas II and IV), and in the transition zone to the southern taiga (I). However, perhaps, *R. esculenta* exists in the area III as well. No reliable records are known for the grasslands (steppes). Therefore, geographically, hybrid frogs seem to be distributed in the area shared with *R. lessonae*. Indeed, the northernmost records of both species coincide (Golubikha Village, 57°43′ N, 45°09′ E). However, within the geographic range, *R. esculenta* occurs markedly rarer in comparison with its parental species. The further more comprehensive studies, combined more careful field search with biochemical or cytological confirmation should elucidate whether that rarity is natural phenomenon or sample deficiency.

Population Systems

The first classification of the population systems, according to the taxa, was made by Uzzell and Berger (1975). German authors (Günther, 1975, 1983, 1991; Plötner et al., 1994) proposed a more detailed scheme in terms of genotypic structure, sex ratio and relative frequencies of species in mixed populations. However, a detailed subdivision of population systems into discrete types should be based on clear and constant characters as well as on solid data basis. Otherwise, it creates more confusion than a real increase in knowledge (Plötner and Schmeller, 2001). Therefore, we used the simpler approach of Uzzell and Berger because our samples were small and not supported with long-time field observations.

In the territory of the former Soviet Union, eight types of population systems of green frogs are known (Borkin et al., 1986, 1987; Caune and Borkin, 1993; Lada et al., 1995). In Nizhny Novgorod Province, the field survey (Pestov et al., 2001; our data) and DNA flow cytometry analysis allowed us to identify six types only. Three of them were the cases with single-species systems, and other three cases were associated with more complicated population systems with coexisting species.

1. L-system: "pure" populations of *R. lessonae* only seem to be widely distributed over the region

(Table 4). The frogs from Mikhalenino Village, used for DNA cytometric analysis (Tables 1 and 2) supported the existence such populations evidenced by the field examination (Pestov et al., 2001).

2. R-system: "pure" populations of *R. ridibunda* only are the most wide-spread type of population systems (Table 4). Allopatric populations of the species are distributed in the northern part of the region (Fig. 6).

3. E-system: "pure" populations should consist of hybrid frogs (*R. esculenta*) only. In August 1999, Pestov and Katunov have recorded such a population near Burkovo Village, Gorodets District (Pestov et al., 2001). The identity of two specimens, taken at the locality, with *R. esculenta* has been confirmed by our DNA flow cytometry analysis (Table 2). However, the Burkovo population needs further comprehensive field examination and laboratory analysis based on larger sample size. The locality is situated in the area II of the zone of mixed forests.

4. RL-system: mixed populations in which *R. ridibunda* co-exists with *R. lessonae*, and no hybrids are found. According to the field data (Table 4; Pestov et al., 2001), the occurrence of such systems should be quite often in Nizhny Novgorod Province because both species were recorded in 23 percent of localities with green frogs. However, their co-existence in the same water reservoirs needs further confirmation.

5. LE-system: mixed populations consisting of *R. lessonae* and *R. esculenta*. Pestov et al. (2001) suspected two neighbor localities with such population systems. These were in the environs of Rustai and Khakhaly villages. Like a presumed single population of *R. esculenta* (E-system) mentioned above, both localities are situated in the area II. Our cytometric analysis supported the existence of *R. esculenta* at Rustai and Khakhaly. Moreover, both species were also revealed from Golubikha, Zhuzhelka, and Lesunovo localities (Table 2). Pestov with associates (2001) mentioned *R. ridibunda* (perhaps, erroneously) and *R. lessonae* for the former locality, only *R. lessonae* for the second locality, and three species for the latter locality. Therefore, at least, four populations (Rustai, Khakhaly, Golubikha, and Zhuzhelka), probably, belong to the LE-system.

6. REL-system: mixed populations comprise all three taxa of green frogs. Based on the field records, Pestov et al. (2001) listed three localities, which were inhabited by three species (Table 4). These were

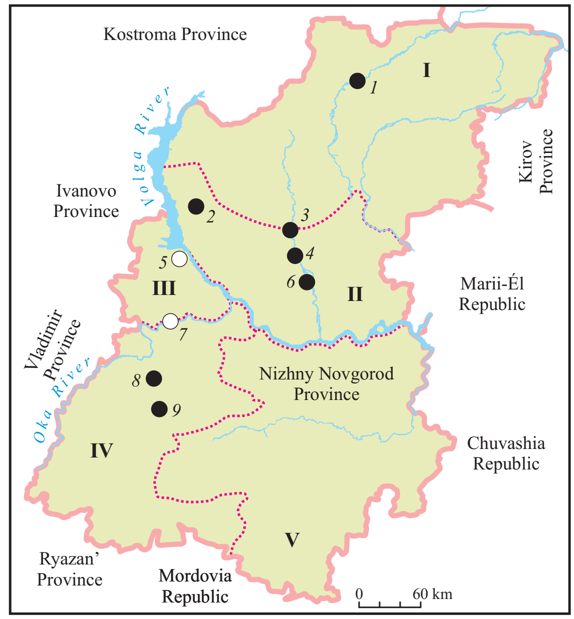

Fig. 7. The distribution of hybrid *Rana esculenta* in Nizhny Novgorod Province (Pestov et al., 2001; our data). I – V, Geographic regions. The localities with frogs examined by DNA flow cytometry are marked by solid circles. *1*, Golubikha; *2*, Burkovo; *3*, Zhuzhelka; *4*, Khakhaly; *5*, Zavolzh'e; *6*, Rustai; *7*, Dzerzhinsk; *8*, Cherneevo; *9*, Lesunovo.

Cherneevo (Fig. 8) and Lesunovo villages, and Zavolzh'e Town. Cytometrically, we examined quite small samples from the two latter localities. In the Cherneevo sample, we identified all three species, whereas in the Lesunovo sample *R. lessonae* and *R. esculenta* only. However, sampling was focused on presumed hybrids. In June 1999, S. N. Litvinchuk found syntopic populations of *R. lessonae* and *R. esculenta* in the environs of Dzerzhinsk Town (previously, individuals of *R. ridibunda* were found by Pestov et al., 2001). Thus, in Nizhny Novgorod Province there are two obvious cases and two more presumed cases with the REL population systems.

The Northern vs. Southern Comparisons

Apart from Nizhny Novgorod Province, we have also studied the green frog composition in Ivanovo Province, a neighboring region to the west (Okulova et al., 1997), and in Udmurt Republic, lying to the east (Borissovsky et al., 2000, 2001). These three administrative units of European Russia belong to the Volga River Basin and are situated roughly between 59°N and 54°N. Formerly, we have also published

Fig. 8. The syntopic habitat of *R. ridibunda*, *R. esculenta*, and *R. lessonae* (the REL population system) in Cherneevo Village, Nizhny Novgorod Province. Photo by Spartak Litvinchuk, June 1999.

detailed data about the distribution of green frogs in a more southern area, named the Central Chernozem Region (Tsentral'no-chernozemnyi raion [*russian*]) (Lada et al., 1995). This region, united five provinces, is located to the south-west from the Volga provinces mentioned above, approximately between 54°N and 51°N.

The comparison of record frequencies in these regions (Table 5) demonstrates obviously increased occurrence of *R. esculenta* in more southern latitudes. Parallel, perhaps, the Central Chernozem Region is characterized by more diverse set of population systems (Table 6). Interestingly, the localities with coexisting *R. lessonae* and *R. ridibunda* in more northern latitudes seem to occur higher than in more southern area. For instance, such localities in the Central Chernozem Region comprise about two percent only (Lada et al., 1995) instead of above 20% in Nizhny Novgorod Province (Table 4).

Thus, our data do not support the hypothesis (Alexandrovskaya and Bykov, 1979) about the lack of hybrid *R. esculenta* in areas of eastern Europe with the subcontinental climate. Indeed, current field survey and DNA flow cytometry analysis revealed some

TABLE 5. The Occurrence of Localities with Hybrids (*Rana esculenta*) in Various Regions of European Russia

Region	Localities with			References
	green frogs	*R. esculenta*		
	n	*n*	%	
Udmurt Republic	75	6	8	Borissovsky et al., 2001
Nizhny Novgorod Province	123	9	7	Pestov et al., 2001; our data
Ivanovo Province	41	2	5	Okulova et al., 1997
Central Chernozem Region	101	21	21	Lada et al., 1995

localities with diploid hybrids in Ivanovo Province, Nizhny Novgorod Province, and Udmurt Republic, i.e., in the northern part of the Middle Volga River Basin. The confirmed distribution of *R. esculenta* in these regions also conflicts with previous Garanin's idea (Borkin et al., 1979; Garanin, 1983) about the lack of hybrids in the Volga – Kama territory, despite numerous cases of the co-existence of parental species (*R. lessonae* and *R. ridibunda*) in the same localities. However, recently, he suggested an occasional occurrence of *R. esculenta* in this region (Korchagina and Garanin, 1996; Garanin, 2000). Interestingly, in the Raif forest area, a portion of Volzhsko-Kamsky Nature Reserve, situated near Kazan (Tatarstan Republic), the habitat differences were found between *R. ridibunda* (large lakes), *R. lessonae* (forest water reservoirs), and presumed *R. esculenta*, which was revealed in open water reservoirs near the forest outskirts (Korchagina and Garanin, 1996).

On the other hand, an increased number of localities with presumed RL population system might be characteristic of the Volga – Kama area. The occurrence of REL population systems seems to be another important feature of the East European Plain. For instance, in the Central Chernozem Region, such populations were found more frequently than any other type of mixed populations (Lada et al., 1995). Two localities with REL systems were recorded in Ivanovo Province (Okulova et al., 1997), six — in Udmurt Republic (Borissovsky et al., 2001), and two or, probably, three ones in Nizhny Novgorod Province. Moreover, for Tatarstan Republic, Garanin (2000) listed three localities with presumed hybrids; both parental species were recorded as well. The Tatarstan cases, of course, need the further examination by flow DNA cytometry.

Pusanov et al. (1955) suggested that in the postglacial epoch green frogs might have spread to Nizhny Novgorod Province from the south-west, i.e., from the Central Chernozem Region. That may explain the origin and distribution of REL mixed populations in Nizhny Novgorod Province and adjacent regions.

The quite high occurrence of the REL type of population systems, certainly, is of much interest. Curiously, only occasional records of such a system are known for the remaining vast portion of the sympatric distribution of three green frog taxa in Europe. The syntopic co-existence of *R. ridibunda*, *R. esculenta*, and *R. lessonae* has been evidenced from central and north-western Ukraine (Mezhzherin and Morozov-Leonov, 1993, 1996; our unpublished data), from the Danube Delta (Günther et al., 1991), from Hungary (Gubányi, 1992), from northern Serbia (Spasić-Bošković et al., 1999), from Czech Republic (Kotlik and Šůlová, 1994), and from western Germany (Schröer and Greven, 1998; also, probably, Eikhorst, 1981, p. 107). However, one should keep in mind that, sometimes, the REL population systems may be not native. For instance, Borkin et al. (1986) have reported a case of such mixed populations for the environs of Riga, Latvia. Certainly, the origin of the system was caused by an introduction of *R. ridibunda* in the 1920s (Caune, 1987).

We suggest that some regional differences in terms of the occurrence of hybrids, polyploidy, and various population systems may exist in various parts of Europe, where *R. lessonae*, *R. ridibunda*, and *R. esculenta* are largely sympatric.

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TABLE 6. The Occurrence of Various Population Systems in the Northern and the Southern Parts of the Sympatry Zone of Green Frogs

Population system	Northern part			Southern part Chernozem Region (5 provinces)
	Ivanovo Province	Nizhny Novgorod Province	Udmurt Republic	
L	+	+	+	+
R	+	+	+	+
E	–	+?	–	+
LR	+	+	+	+
LE	–	+	+	+
RE	–	–	–	+
LER	+	+	+	+
Total	**4**	**5 (or 6)**	**5**	**7**

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