

## **Genetic structure, morphological variation, and gametogenic peculiarities in water frogs (*Pelophylax*) from northeastern European Russia**

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### **Abstract**

The edible frog, *Pelophylax esculentus*, is a hybrid form that reproduces via clonal propagation of only one of the parental genomes through generations of hybrids while the genome of other parental species is eliminated during gametogenesis. Such reproductive ability requires hybrids to coexist with one of the parental species or rarely both parental species causing the formation of so-called population systems. Population systems and reproductive biology of water frogs from the east of the range remained partially unexplored. In this study, we investigated the distributions, population systems, genetic structure, types of gametes, and morphological variability of water frogs of the genus *Pelophylax* from the northeastern parts of their ranges (Mari El Republic and adjacent territories, Russia). We examined 1,337 individuals from 68 localities using morphological traits combined with DNA flow cytometry and a multilocus approach (fragments of a nuclear and two mitochondrial genes). We revealed five types of population systems: “pure” populations of the parental *P. ridibundus* (R) and *P. lessonae* (L), mixed populations of parental species (R-L) along and with their hybrids (R-E-L), as well as mixed populations of *P. lessonae* and *P. esculentus* (L-E). However, the “pure” hybrid (E) and the mixed *P. ridibundus* and *P. esculentus* (R-E) population systems were not found. All hybrids studied by DNA flow cytometry were diploid. Analysis of gametogenesis showed that the majority of hybrid males, as well as hybrid females from the L-E system, produced gametes with the *P. ridibundus* genome. However, in the R-E-L system, hybrid females were usually sterile. The reproduction of hybrids in such systems is primarily based on crosses of *P. esculentus* males with *P. lessonae* females. Molecular analysis showed the presence of mitochondrial and nuclear DNA introgression of the Anatolian marsh frog (*P. cf. bedriagae*) into both *P. ridibundus* and *P. esculentus*. The observations of alleles and haplotypes of *P. cf. bedriagae* in *P. ridibundus* and *P. esculentus* individuals from the same localities suggest de novo formation of local hybrids. However, the presence of the Balkan marsh frog (*P. kurtmuelleri*) haplotypes in local hybrids supports the hypothesis regarding the migration of old hemiclonal lineages from glacial refugia. Finally, the diagnostic value of various morphological characteristics was discussed.

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### **Keywords**

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