



Simulation as a Method for Asymptotic System Behavior Identification (e.g. Water Frog Hemiclonal Population Systems)

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Abstract. Studying any system requires development of ways to describe the variety of its conditions. Such development includes three steps. The first one is to identify groups of similar systems (associative typology). The second one is to identify groups of objects which are similar in characteristics important for their description (analytic typology). The third one is to arrange systems into groups based on their predicted common future (dynamic typology).

We propose a method to build such a dynamic topology for a system. The first step is to build a simulation model of studied systems. The model must be undetermined and simulate stochastic processes. The model generates distribution of the studied systems output parameters with the same initial parameters. We prove the correctness of the model by aligning the parameters sets generated by the model with the set of the original systems conditions evaluated empirically. In case of a close match between the two, we can presume that the model is adequately describing the dynamics of the studied systems. On the next stage, we should determine the probability distribution of the systems transformation outcome. Such outcomes should be defined based on the simulation of the transformation of the systems during the time sufficient to determine its fate. If the systems demonstrate asymptotic behavior, its phase space can be divided into pools corresponding to its different future state prediction. A dynamic typology is determined by which of these pools each system falls into.

We implemented the pipeline described above to study water frog hemiclonal population systems. Water frogs (*Pelophylax esculentus* complex) is an animal group displaying interspecific hybridization and non-mendelian inheritance.

Keywords: Dynamic typology · Hemiclonal inheritance · *Pelophylax esculentus* complex · Simulation modelling

1 Introduction

1.1 Motivation

The processes of transformation of natural biological systems (populations, ecosystems etc.) are an important challenge for modern science. In many cases, these processes are not accessible for direct study (e.g. because of their long duration). In such cases, we have to build their transformation models based on (1) the observed diversity of their natural states, (2) our hypothesis about factors changing these states, and (3) empirical data available. Simulation models play a key role in such studies providing an opportunity to determine possible directions of the target systems' transformation and build their typology.

Generally, living nature can be divided into three domains. The first one is the oldest and includes bacteria and viruses. Here, genetic information can move relatively unrestrictedly from organism to organism via horizontal gene transfer. The second domain is the largest one composed of the majority of eukaryotic organisms. Genetic information is transmitted within individual species here. In each generation, genetic information is updated due to recombination during sexual reproduction. Some organisms occasionally reproduce clonally, i.e. without recombination. The third domain is the smallest and the least explored characterized by interspecific hybridization and hemiclonal inheritance. Biological systems in which reproduction of hemiclonal hybrids do occur have been described as Hemiclonal Population Systems (HPSs) [15].

This paper describes a computer simulation study of HPSs of water frogs which have been traditionally used as a model for studying this kind of biological systems. This is an extended version of our previous work [18]. First, we introduce the peculiar characteristics of these systems. In the next section, we describe the advantages of computer simulation as a modelling tool together with the specific characteristics of the model presented here. Computer simulation has been described as the collaboration between experimenting and modelling [7]. The empirical data available were used to set model parameters and to assess the performance of the model against real-world situations. We describe experiments conducted upon the model itself and the way in which these can complement fieldwork-based findings.

1.2 Reproduction within HPSs

Most life forms originated from sexual reproduction exhibit typical biosystem hierarchy in which organisms form populations that form species. In these populations, genetically unique individuals produce sex cells (gametes), which bear a unique genome (holistic unitary complex of hereditary information) resulting from recombination of two parental genomes. The consequence of this is the existence of a population gene pool (a common pool of genes).

Human is a good example of a species that reproduces through sexual recombination (Fig. 1A). There are two chromosome sets, two genomes in almost every cell of human body. One of these sets comes from the father, and the other from the mother. A woman produces several hundreds of eggs during her life, while a man can produce

several trillions of sperm. During the formation of eggs and sperm (germ cells), mother chromosomes must recognize the corresponding father chromosomes and vice versa. Then, recombination occurs when the pair of chromosomes exchange their sites. Recombination results in unique germ cells formation. Recognition and attachment of paired chromosomes occurs during the first stage of special type of cell division called meiosis. Interspecific hybrids (if they arise) are often sterile because chromosomes of different species cannot recognize each other during meiosis.

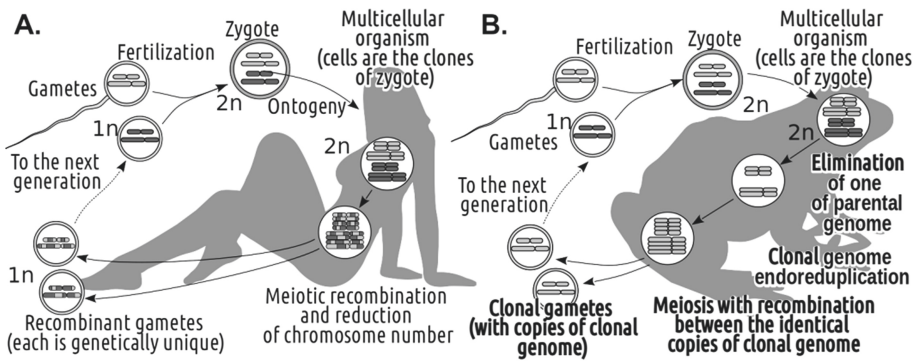


Fig. 1. Life cycle with fertilization and meiosis, which is a characteristic of organisms with sexual reproduction (A), compared to a modification of this cycle, which is a characteristic of interspecific hybrids with hemiclonal inheritance (B).

There are three ways to escape this hybrid incompatibility. The first way is clonality. The hybrids can reproduce without meiosis and recombination forming populations consisting of sets of genetically identical organisms, i.e. clones, (with accuracy limited by the error rate of copying during reproduction). These sets form relatively isolated lines consisting of genetically identical maternal and child individuals.

The second way is doubling of chromosome sets called polyploidy. As a result of the doubling, each chromosome has its own copy to pair with. Polyploidy plays crucial role in evolution, for example, it is an important pathway for emergence of new genes.

This work is focused on a relatively rare type of reproduction which differs from the two mentioned above. It is a characteristic of hybridogenic complexes of species such as so called *Pelophylax esculentus* complex formed by water frogs [11]. The complex consists of two parental species are *Pelophylax lessonae* (Camerano 1882) and *Pelophylax ridibundus* (Pallas 1771). They cross to produce hybrids named in a similar manner as species, e.g. *Pelophylax esculentus* (Linnaeus 1758).

The differences between the genomes of the parental species lead production of normal gametes through recombination becoming impossible. Breeding of the hybrids is rescued by specific changes in their life cycle (Fig. 1B). One parent genome of such hybrids is eliminated from the germline cells (i.e. the cells which develop into gametes). Thereafter, the second parental genome undergoes endoreduplication (i.e. doubles without cell division). As a result, the germline cells have two identical genomes (with accuracy limited by the errors of copying) and form genetically identical gametes.

Hemiclonal hybrids differ from both normal organisms with recombinant reproduction and clonal organisms. Accordingly, a HPS, where hemiclonal hybrids reproduce, differs from both normal recombinant and clonal populations. The following are the features of a HPS [15]:

- Cooperative reproduction of individuals that differ in species composition of their genomes (i.e. representatives of parental species and hybrids of various genome compositions);
- Vertical transmission of lines of clonal genomes, which can be combined with other recombinant or clonal genomes;
- In a HPS which includes individuals of the parental species, these individuals support the existence of a pool of recombining genes (gene pool), which corresponds to the gene pool of conventional monospecific populations;
- Limited interspecies recombination (i.e. transferring of fragments of genetic information from the genome of one parental species into the gene pool of another parental species) is occasionally observed.

The most common typology of a HPS is associated with identification which of the parental species, diploid and/or triploid hybrids (i.e. hybrids having two and three genomes, respectively) are present in the system. The presence of *P. esculentus* in the system is marked by the letter **E**, while letter **L** and **R** stand for *P. lessonae* and *P. ridibundus*, respectively. The presence of polyploid *P. esculentus* is denoted by the letter **p**. Thus, L-E-HPS label is used for HPS consisting of *P. lessonae* and diploid *P. esculentus*, and R-E-HPS is used for those consisting of *P. ridibundus* and diploid *P. esculentus*. Clonality of a genome is designated by putting its symbol in brackets. The sex determination system in water frogs is similar to that in humans, where the female genome includes the sex chromosome, and individuals with two female genomes are females (♀). The structure of the male genome includes the sex chromosome Y, and individuals with one female and one male genome are male (♂).

Consider the simplest example of a L-E-HPS (Fig. 2), which includes one parent species (*P. lessonae*) as well as hybrids which clonally transmit the female genome of *P. ridibundus* (^XR). Hybrids reproduce by crossing with the parental species: ♀^XL(^XR) × ♂^XL^YL → ♀^XL(^XR); ♂^YL(^XR); ♀^XL^XL × ♂^YL(^XR) → ♀^XL(^XR).

Different regions of the *P. esculentus* complex distribution have different compositions of HPSs [2, 10, 11]. In some regions, *P. esculentus* individuals simultaneously produce gametes (L) and (R). This phenomenon is called hybrid amphispermy. Such individuals are referred to as (L)(R).

By crossing hybrids which transmit genomes of the same parental species, representatives of these species may occur. Typically, these individuals die before reaching sexual maturity: ♀^XL(^XR) × ♂^YL(^XR) → ♀^XR^XR → †.

Genotypes of frogs in a HPS differ in their vitality and fertility. The composition of zygotes, tadpoles and frogs of the different ages may vary considerably within the same HPS. Another feature of the hybridogenic complexes of water frogs (not considered in this study) is that not only diploid but also triploid (LLR or LRR) and even tetraploid (e.g. LLRR) hybrids occur in some regions [2, 15].

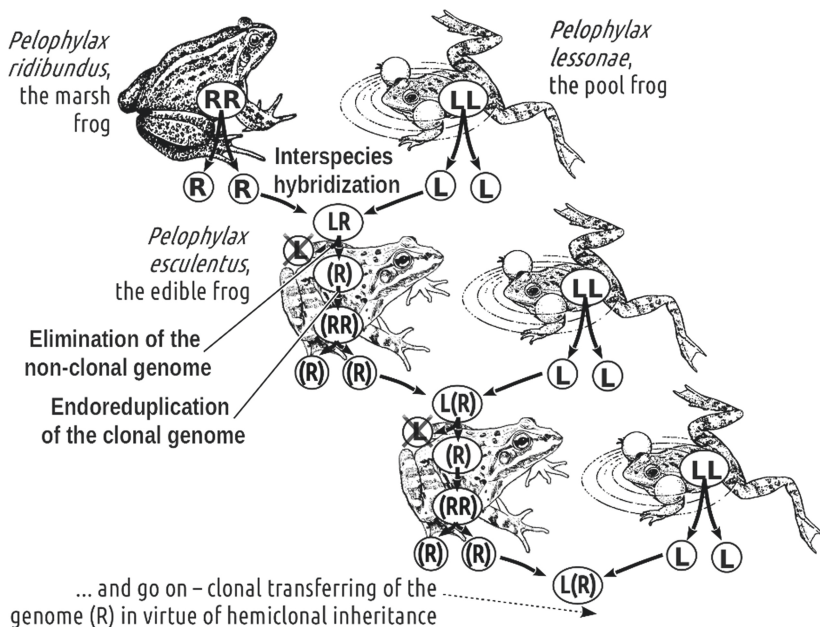


Fig. 2. The occurrence of *Pelophylax esculentus* is due to hybridization of *Pelophylax lessonae* with *Pelophylax ridibundus* and reproduction of *P. esculentus* with the parental species in L-E-HPS.

Hemiclinal hybridization, the consequence of which is the occurrence of a HPS, is observed not only in water frogs, but also in other species groups [1].

HPSs of hybridogenic species complexes are a little-known category of biosystems. Studying them, also by simulation of their transformations, should lead to important results. For example, understanding of the particular genome-selective elimination in interspecific hybrids may lead to development of new techniques for genome editing which would open new horizons in biotechnology and genetic medicine. Hemiclinal inheritance allows obtaining genetically identical offspring which inherit clonal genomes of two different parent species and may be useful in biotechnology and agriculture. Studies of origin of hemiclinal hybridization and its role in the evolution of hybridizing species are of considerable theoretical interest. Although studying HPS transformations per se cannot solve these problems, it provides better understanding of mechanisms of origin and maintenance of stability in biological systems where such amazing genetic phenomena are possible.

For further studies, it is necessary to describe the variety of possible states of HPSs, their dynamics, regularities and the conditions under which they are stable.

Direct studying of HPSs faces significant challenges. Determination of their composition and reproduction mechanisms is associated with a considerable amount of fieldwork. HPSs are relatively unusual and differ from well-known biosystems such as biocoenosis and sexually or clonally reproducing populations. Changes in HPS extend over time and may take decades. Composition of different HPSs is highly variable, and

some HPSs are unique systems whose occurrence is highly unlikely. Studying one unique HPS only may not be enough for understanding the patterns of their dynamics. Additionally, HPSs are complex systems containing many stochastically interacting components.

Several authors have used analytical modelling to describe the dynamics of a population system of water frogs [14 etc.]. Analytical models are suitable for studying separate aspects of the HPS' dynamics, however their usage faces considerable challenges since HPS is managed by interrelated sets of stochastic processes. We therefore consider simulation to be more useful to investigate the general properties of HPSs.

Christiansen [4] simulated reproduction of *P. esculentus* using deterministic model whereas our model allows modelling random events during animals' competition and breeding. The works of Bove et al. [3] and Quilodran et al. [12] are recent studies based on the simulation of water frogs' HPSs. These studies consider the stability of specific types of HPSs under certain conditions. In contrast, our work seeks to analyze all possible stable states of a certain category of HPSs.

There are several differences between our simulation and the published studies. (I) We consider demographic factors (non-competitive and competitive mortality, differences in the reproduction probability, changes in viability with age) typical for most populations simultaneously with unique features of HPS. (II) Our work explores the entire space of possible states of a certain category of HPS. (III) Finally, we estimated population parameters values using field studies of this category of HPS.

1.3 Scope of Modelling

We have previously built a deterministic discrete-time simulation model [5]. It enabled determination of the population composition for a specified number of simulation steps, commencing with the current HPS composition. The objective of the current work is to identify the set of stable states of a HPS (consisting solely of diploid water frog individuals) using a stochastic simulation.

The research was conducted in two steps. At first, a number of simulation experiments was performed for various initial compositions of the model HPS. The aim of this stage was to get an insight into the possible end states for the HPSs. At the second step, we analyzed and classified these end states. The dynamic typology of the system was constructed based on the various initial compositions of the HPSs, the observed final states, and the observed transitions from initial to final states.

Dynamic typology is based not only on analysis of the observed states of an object, but, above all, on a prediction of their future dynamics [9]. In this respect, dynamic typology differs from both associative typology (identification of groups of objects, related to one or more samples) and analytical typology (partitioning a set of objects into groups depending on the state of their observable characteristics) [15].

Hybrid frogs reproduce differently in different regions [10, 14]. In order to describe the dynamical typology for all possible types of HPSs and all known genetic forms of hybrids and their reproduction, it should first be solved for one selected region. We have previously described the Siverskyi Donetsk center of diversity of the *Pelophylax esculentus* complex located in the eastern Ukraine [15, 16] which is characterized by a high diversity of HPSs.

This center of diversity is divided into three subregions (Fig. 3). The R-E-subregion is located in the Mzha and the Udy river basins in Kharkiv Oblast. Here, HPSs consist of *P. ridibundus* and diploid *P. esculentus* and provide an opportunity to test our model. R-E-Ep-subregion is associated with the Siverskyi Donets river in Kharkiv Oblast. The HPSs in this subregion consist of *P. ridibundus*, diploid and polyploid (mostly triploid) *P. esculentus*. R-Epf-subregion is associated with the Siverskyi Donets river in Donetsk Oblast and Luhansk Oblast. The HPSs of this subregion consist of *P. ridibundus* and triploid females of *P. esculentus* with LLR genome composition.

We intend to describe the total variety of HPSs from the R-E-subregion of the Siverskyi Donets center of diversity of water frogs. As the first step, we consider a variety of HPSs located in the Mzha and the Udy river basins, which consist of the diploid individuals.

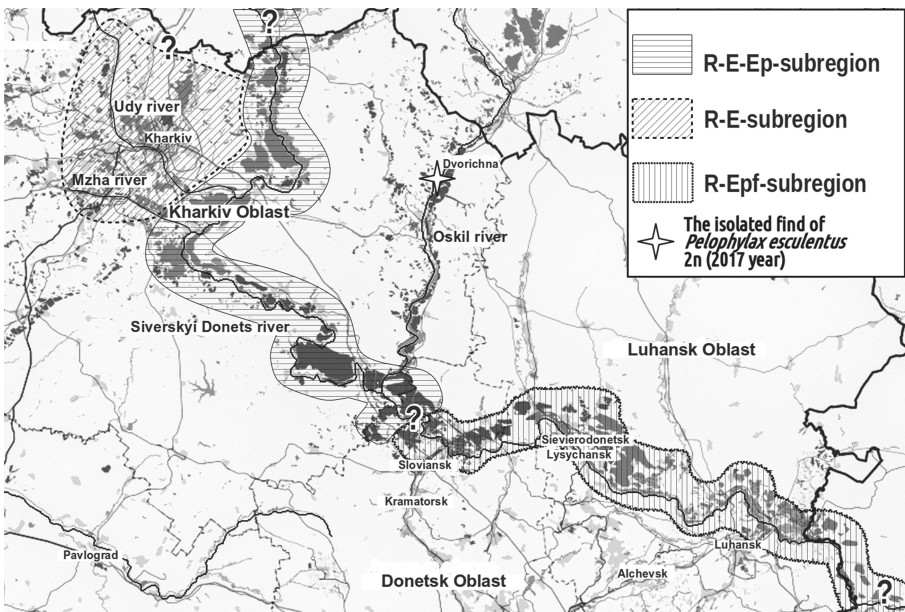


Fig. 3. The Siverskyi Donets center of diversity of *P. esculentus* complex (from [16], with modifications).

2 Model Description and Its Justification

2.1 The Cycle of the Model

A simulation model, as opposed to an analytical model, describes a process of the state transformations during time rather than the dependence of the future states of the system on the current one. Therefore, for model development it is sufficient to describe the algorithm of changes in the HPS sizes with time. In this model, time is divided into discrete steps through which the model cycles. The cycle of the model corresponds to

the calendar year. It sets the sequence of transformations: $\alpha \mathbf{n}_a^g \rightarrow \beta \mathbf{n}_a^g \rightarrow \gamma \mathbf{n}_a^g \rightarrow \delta \mathbf{n}_a^g \rightarrow \omega \mathbf{n}_a^g$. Here, $\alpha \mathbf{n}_a^g, \beta \mathbf{n}_a^g, \gamma \mathbf{n}_a^g, \delta \mathbf{n}_a^g$ and $\omega \mathbf{n}_a^g$ is a sequence of transformations of the individual's groups of the genotype (\mathbf{g}) and of the age (\mathbf{a}) which correspond to the different stages of the annual cycle (Table 1).

Of \mathbf{k} genotypes, \mathbf{x} is a female and \mathbf{y} is a male. At a certain stage, the females of genotype \mathbf{f}_a and males of genotypes \mathbf{m}_a form a pair followed by appearance of offspring. The other symbols are explained in the description of the input parameters of the model.

Table 1. A cycle of the model.

Symbol	Meaning	Transformation	Changing the number of individuals in the groups
$\alpha \mathbf{n}_a^g$	Initial number of individuals in group of certain genotype and age in each cycle	Start of cycle	$\alpha \mathbf{n}_a^g = \omega \mathbf{n}_a^g$
		Transition individuals to the next age	$\beta \mathbf{n}_a^g = \alpha \mathbf{n}_{a-1}^g$
$\beta \mathbf{n}_a^g$	Number of individuals in groups with allowance for their transition to the next age	Non-competitive death	$\gamma \mathbf{n}_a^g \approx \beta \mathbf{n}_a^g \times \mathbf{s}_a^g$
$\gamma \mathbf{n}_a^g$	Number of individuals in groups after non-competitive mortality		
$\delta \mathbf{n}_a^g$	Numbers of individuals in groups after joining immigrants	Immigration	$\delta \mathbf{n}_a^g = \gamma \mathbf{n}_a^g + \mathbf{i}_a^g$
		Competitive reduction in number of individuals	Algorithm of the calculation $\omega \mathbf{n}_a^g$ based on $\delta \mathbf{n}_a^g, \mathbf{c}_a^g, \mathbf{d}_a^g$ and \mathbf{V} (it is described below)
$\omega \mathbf{n}_a^g$	Numbers of individuals in groups after competitive mortality due to lack of resources	Parental pairs formation	Algorithm of the calculation $\mathbf{P}(\mathbf{f}_a^f, \mathbf{m}_a^m)$ based on $\omega \mathbf{n}_a^f, \mathbf{l}_a^f, \omega \mathbf{n}_a^m$ and \mathbf{e}_a^m (it is described separately below)
$\mathbf{P}(\mathbf{f}_a^f, \mathbf{m}_a^m)$	Number of pairs of a certain composition	Reproduction	$\omega \mathbf{n}_0^g = \sum (\mathbf{P}(\mathbf{f}_a^f, \mathbf{m}_a^m) \times \mathbf{o}^g(\mathbf{f}^f, \mathbf{m}^m) \times \mathbf{b}_a^f \times \mathbf{w}_a^m)$
$\omega \mathbf{n}_0^g$	Number of offspring ($\mathbf{a}=0$)		
End of cycle			

2.2 Input Parameters

Viability Parameters. $s_a^g \in [0, 1]$ —*survival*. This is proportion of individuals, which happens to survive the non-competitive death cycle. If $\mathbf{a} \geq \max \mathbf{a}_a^g$, then $s_a^g = 0$ where $\max \mathbf{a}_a^g$ is maximum life span, and \mathbf{a} is age of an individual.

$\mathbf{c}_a^g \in [0, 1]$ —*competitiveness factor*. Let's designate probability of an individual to survive over the competitive reduction as \mathbf{c}_a^g . Denote $\max \mathbf{c}^g$ as maximum value of this

probability that is a characteristic of the most competitive groups ($0 < \max \mathbf{c}' \leq 1$). According to the algorithm of the competitive reduction, the number of individuals in the entire HPC together with the value of competitiveness affects a probability to survive for each individual. The value of competitiveness factor $\mathbf{c}_a^g = \mathbf{c}_a^g / \max \mathbf{c}'$ can be defined as one of the input parameters of the model.

$\mathbf{d}_a^g, (\mathbf{d}_a^g \geq 0)$ —*demand*. This is the number of resources required for an individual of a certain group. It's magnitude is given for one cycle of the model.

$\mathbf{l}_a^f \in [0, 1]$ —*female loveliness*. This is the success rate of a female in her search for reproduction partner. this parameter is set in the same way as the competitiveness factor. Let's denote the maximum value of the probability to find a partner as $\max \mathbf{l}'$, $0 < \max \mathbf{l}' \leq 1$. This is a characteristic of the most successful groups of females. $\mathbf{l}_a^f = \mathbf{l}_a^f / \max \mathbf{l}'$. Denote the $\mathbf{mat} \mathbf{a}_a^g$ as the age of sexual maturity. For females with the age less than $\mathbf{mat} \mathbf{a}_a^g$ ($\mathbf{a} < \mathbf{mat} \mathbf{a}_a^g$), $\mathbf{l}_a^f = 0$.

Similarly, $\mathbf{e}_a^m \in [0, 1]$ —*male effectiveness*. This is the success rate of a male in his search for reproduction partner. Correspondingly, $\mathbf{e}_a^m = \mathbf{e}_a^m / \max \mathbf{e}'$. For males, the age of which ($\mathbf{a} < \mathbf{mat} \mathbf{a}_a^g$), $\mathbf{e}_a^m = 0$.

$\mathbf{b}_a^f \in \mathbb{N}$ —*breed*. This is the female fertility specified by the number of eggs produced by the females.

$\mathbf{w}_a^m \in [0, 1]$ —*wad*. This is the ability of males to fertilize measured by a fraction of eggs that should be fertilized by a given male.

$\mathbf{o}^g(\mathbf{f}^f, \mathbf{m}^m) \in [0, 1]$ —*offspring*. This is the proportion of the offspring of the g -th genotype of the female's f -genotype with the male's m -genotype. This parameter is set for all possible genotypes for entire pairs $\mathbf{P}(\mathbf{f}^f, \mathbf{m}^m)$.

Conditions for Experiment. The following global settings should be set to run an experiment or series of experiments.

$\mathbf{on}_a^g \in \mathbb{N}$ —*number*, which is the initial number of all groups.

$\mathbf{it}_a^g \in \mathbb{N}$ —*inbound*, which is the number of individual-immigrants at a certain cycle (\mathbf{t}) provided by the experiment script.

\mathbf{V} —*volume*—the availability of resources which is the amount of resources provided by a habitat measured in the number of resource units.

2.3 The Algorithm of the Model

A cycle of the model work is described in the Table 1. The table describes variations in the numbers of individual groups. In the model, however, calculations are first made for each individual and then summarized for the groups of individuals. For example, for a non-competitive reduction of quantities $\mathbf{t} \mathbf{n}_a^g \approx \mathbf{t} \mathbf{n}_a^g \times \mathbf{s}_a^g$. This process is implemented stochastically, thus sign \approx is used instead of $=$. A pseudo-random number generator defines the fate of each individual of each genotype and each age. An individual survives with the probability \mathbf{s}_a^g , and dies with the probability $1 - \mathbf{s}_a^g$.

Algorithm of the Competitive Mortality Rate. Denote the ${}^{\delta}D = \Sigma({}_t^{\delta}n_a^g \times d_a^g)$, ${}^{\varepsilon}n_a^g = {}^{\delta}n_a^g \times c_a^g$ and ${}^{\varepsilon}D = \Sigma({}_t^{\varepsilon}n_a^g \times d_a^g)$.

If ${}^{\delta}D \leq V$, then ${}_t^{\omega}n_a^g = {}^{\delta}n_a^g$.

If ${}^{\delta}D > V$ and ${}^{\varepsilon}D = V$, then ${}_t^{\omega}n_a^g \approx {}^{\varepsilon}n_a^g$.

If ${}^{\delta}D > V$ and ${}^{\varepsilon}D > V$, then ${}_t^{\omega}n_a^g \approx {}^{\varepsilon}n_a^g \times V/{}^{\varepsilon}D$.

If ${}^{\delta}D > V$ and ${}^{\varepsilon}D < V$, then ${}_t^{\omega}n_a^g \approx {}^{\delta}n_a^g - ({}^{\delta}n_a^g - {}^{\varepsilon}n_a^g) \times ({}^{\delta}D - V)/({}^{\delta}D - {}^{\varepsilon}D)$.

The fate of each individual of each genotype and each age is determined by a pseudo-random number generator. They survive with probability ${}_t^{\omega}n_a^g/{}^{\delta}n_a^g$ and die with probability $1 - {}^{\omega}n_a^g/{}^{\delta}n_a^g$.

Such a reduction in the number of individuals satisfies the following conditions:

- (1) Number of individuals before reduction is reduced up to the value that corresponds to resource availability.
- (2) Number of individuals in each group before the competitive reduction, ${}_t^{\delta}n_a^g$, is reduced to a number after competitive reduction, ${}_t^{\omega}n_a^g$, in such a way that percent of individuals in each group, which passed through the competitive reduction, is proportional to the competitiveness representatives in this group's: ${}_t^{\omega}n_a^g/{}^{\delta}n_a^g \sim c_a^g$.

Algorithm of the Parental Pairs Formation. Number of the female's f_a^f and the male's $m_{a'}^m$ pairs is determined in the following way:

$$P(f_a^f, m_{a'}^m) \approx {}^{\omega}n_a^f \times ({}^{\omega}n_a^f \times l_a^f / \Sigma({}^{\omega}n_a^f \times l_a^f)) \times ({}^{\omega}n_{a'}^m \times c_{a'}^m / \Sigma({}^{\omega}n_{a'}^m \times c_{a'}^m)).$$

The total number of females from the group f_a^f is multiplied by the probability of a female from the group to be selected by any male. This allows you to set the number of the females in the group who should find a partner in this iteration. The resulting number is multiplied by the probability of a male from the group $m_{a'}^m$ to be chosen by any female. In this way, one can identify the females from group f_a^f , which form a pair with the male from group $m_{a'}^m$.

The probability of the females from the group f_a^f to find a partner is determined by the ratio of the product of number of individuals in this group ${}^{\omega}n_a^f$ and the success factor of representatives from this group in finding a partner l_a^f , to the sum of such products for all groups of females.

The probability of the males from the group $m_{a'}^m$ to find a female is determined by the ratio of the product of number of individuals in this group ${}^{\omega}n_{a'}^m$ and the success factor of this group of representatives in finding a partner $c_{a'}^m$ to the sum of such products for all groups of males.

The fate of each particular female and male is determined by a random number generator according to the probabilities, given the expected number of pairs of $P(f_a^f, m_{a'}^m)$.

3 Selection of Parameters

The performance of the model was tested on processes observed in the all-diploid HPS from the Siverskyi Donets center of diversity of the *Pelophylax esculentus* complex. In total, eight different genomes can be transmitted in these HPS (Table 2).

There are no mature *P. lessonae* in the Siverskyi Donets center of diversity of the *Pelophylax esculentus* complex, and, thus, no genomes of ^XL and ^YL . In this paper, we have considered only diploid frogs. Therefore, only eight genotypes were considered in the simulation as shown in Table 3.

Table 2. The genomes considered in the model.

Genome	^XL	^YL	^XR	^YR	(^XL)	(^YL)	(^XR)	(^YR)
Type of inheritance	Recombinant				Clonal			
Species	<i>P. lessonae</i>		<i>P. ridibundus</i>		<i>P. lessonae</i>		<i>P. ridibundus</i>	
Sex	Female	Male	Female	Male	Female	Male	Female	Male

Table 3. The genotypes considered in this work.

	Females	Males
<i>P. ridibundus</i>	$^X\text{R}^X\text{R}$	$^X\text{R}^Y\text{R}$
<i>P. esculentus</i>	$^X\text{R}(^X\text{L}), (^X\text{L})(^X\text{R})$	$^X\text{R}(^Y\text{L}), ^Y\text{R}(^X\text{L}), (^X\text{L})(^Y\text{R}), (^Y\text{L})(^X\text{R}).$

A set of genomes is defined as $\mathbf{G} = [0, 1]^4 \times \{0, 1\}^2 \subset \mathbf{R}^4$. An individual is designated by three parameters: age $A \in \mathbf{N}$ and two genomes (g1 and g2). Thus, a set of individuals is $\mathbf{A} \times \mathbf{G} \subset \mathbf{R}^{13}$.

A set of HPS systems $\mathbf{HPS} = \Phi^{N+M} \subset \mathbf{R}^{13(N+M)}$ consists of $\mathbf{N} + \mathbf{M}$ frogs, where \mathbf{N} is the population size of the spawning HPS, and \mathbf{M} is the number of immature individuals.

The following data input is used in the model:

- A description of the initial composition of the model HPS, and a scenario of migrants entering it;
- A description of the parameters of the viabilities for all considered groups of individuals that differ by age and by genomic composition;
- A description of the results of all possible crossings in the model (probability distribution of occurrence of offspring with a specific genomic composition in crossings between different parents).

A detailed justification of the chosen default settings is based on empirical studies of natural HPSs, including, in the first place, determination of frogs lifespan and growth rates using skeletochronology, and estimation of population sizes and composition of the natural HPSs using the mark-and-recapture method [e.g., 8]. Assumptions about outcome of crossings (Table 4) were made based on the results of a study of gametogenesis in hybrid frogs from the Siverskyi Donets center of diversity of the

Pelophylax esculentus complex [2]. The model assumes that resource consumption is proportional to the biomass of an individual. Empty cells in the Table 4 correspond to the crossings which produce non-viable offspring. In cases when a cell, corresponding to a certain crossing, contains 2, 3 or 4 genotype, the descendants that correspond to these genotypes appear with equal probability (corresponding to 1/2, 1/3, or 1/4).

A preliminary research was carried out to determine the age structure of the model HPS in which we determined the equilibrium age structure of the HPS *P. ridibundus*. In next experiments, the age distribution of the initial composition of HPS corresponds to that age structure. In cases when we added new specimens into the HPS at a certain step, they were considered as 4 years old.

Table 4. The proposed crossings outcomes assumed for the modelling.

Genotypes	$\sigma\sigma$	$\text{}^{\text{X}}\text{R}\text{}^{\text{Y}}\text{R}$		$\text{}^{\text{X}}\text{R}(\text{}^{\text{Y}}\text{L})$	$\text{}^{\text{Y}}\text{R}(\text{}^{\text{X}}\text{L})$	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{Y}}\text{R})$		$(\text{}^{\text{Y}}\text{L})(\text{}^{\text{X}}\text{R})$	
$\text{}^{\text{Y}}\text{Y}$	Gametes	$\text{}^{\text{X}}\text{R}$	$\text{}^{\text{Y}}\text{R}$	$(\text{}^{\text{Y}}\text{L})$	$(\text{}^{\text{X}}\text{L})$	$(\text{}^{\text{X}}\text{L})$	$(\text{}^{\text{Y}}\text{R})$	$(\text{}^{\text{Y}}\text{L})$	$(\text{}^{\text{X}}\text{R})$
$\text{}^{\text{X}}\text{R}\text{}^{\text{X}}\text{R}$	$\text{}^{\text{X}}\text{R}$	$\text{}^{\text{X}}\text{R}\text{}^{\text{X}}\text{R}$	$\text{}^{\text{X}}\text{R}\text{}^{\text{Y}}\text{R}$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{Y}}\text{L})$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{X}}\text{R}\text{}^{\text{Y}}\text{R}$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{Y}}\text{L})$	$\text{}^{\text{X}}\text{R}\text{}^{\text{X}}\text{R}$
$\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$	$(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{Y}}\text{R}(\text{}^{\text{X}}\text{L})$	–	–	–	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{Y}}\text{R})$	–	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{X}}\text{R})$
$(\text{}^{\text{X}}\text{L})(\text{}^{\text{X}}\text{R})$	$(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$	$\text{}^{\text{Y}}\text{R}(\text{}^{\text{X}}\text{L})$	–	–	–	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{Y}}\text{R})$	–	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{X}}\text{R})$
	$(\text{}^{\text{X}}\text{R})$	$\text{}^{\text{X}}\text{R}\text{}^{\text{X}}\text{R}$	$\text{}^{\text{X}}\text{R}\text{}^{\text{Y}}\text{R}$	$(\text{}^{\text{Y}}\text{L})(\text{}^{\text{X}}\text{R})$	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{X}}\text{R})$	$(\text{}^{\text{X}}\text{L})(\text{}^{\text{X}}\text{R})$	$\text{}^{\text{X}}\text{R}\text{}^{\text{Y}}\text{R}$	$(\text{}^{\text{Y}}\text{L})(\text{}^{\text{X}}\text{R})$	$\text{}^{\text{X}}\text{R}\text{}^{\text{X}}\text{R}$

4 Case Studies

4.1 The Probabilistic Character of the Simulation Results

In the following case studies, we present two runs of the model, showing the effects of the introduction of particular hybrid individuals at different stages on the development of an HPS. Then we show the probabilities of different outcomes based on large numbers of replicated runs, with time of introduction of one exogenous individual systematically varying across the range of 300 simulated time steps.

Figure 4 shows dynamics of a model HPS formed from the population of the parent species (*P. ridibundus*) where hybrids that transmit female genomes form a different parent species were added ($\text{}^{\text{Y}}\text{Y}\text{}^{\text{X}}\text{R}(\text{}^{\text{X}}\text{L})$). As a result of crossing of hybrids with individuals of the parental species, all the progeny consists of hybrids as explained before. The progeny originated from crossing between the hybrids transmitting a clonal genome of the same species is non-viable Because of these, the number of hybrids in the model HPS increases which subsequently leads to extinction of the HPS.

Figure 5 shows a version in which genome $(\text{}^{\text{X}}\text{R})$ gets into the same HPS as in Fig. 4 where the number of carriers of the genome $(\text{}^{\text{X}}\text{L})$ increases in a way shown in Fig. 4. If the carriers of the genome $(\text{}^{\text{X}}\text{R})$ cross with individuals with genome $(\text{}^{\text{X}}\text{L})$, the offspring consists of individuals that simultaneously transmit both parental genomes: $(\text{}^{\text{X}}\text{L})$ and $(\text{}^{\text{X}}\text{R})$. In this case, the model HPS can move into a stable state.

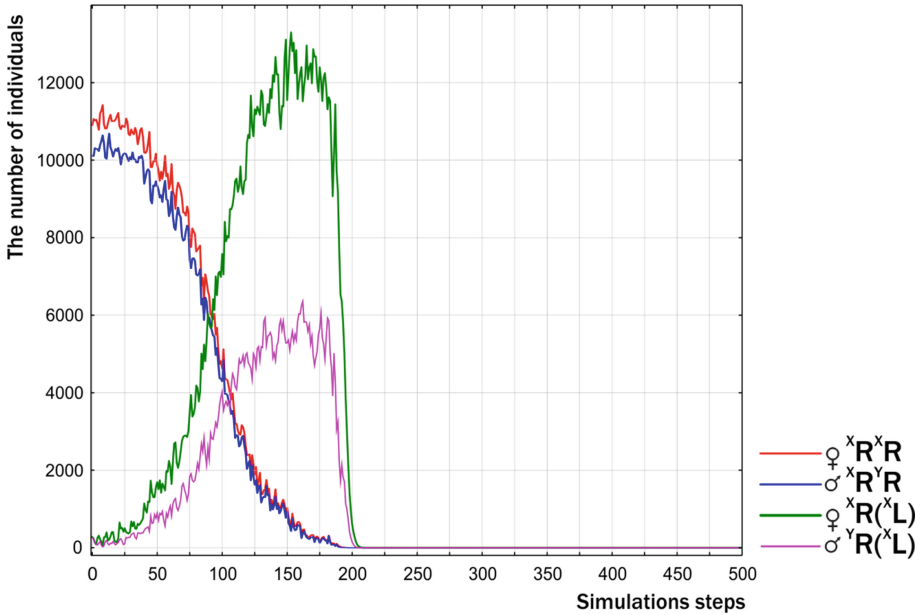


Fig. 4. Extinction of the R-E-HPS where genomes ($X L$) are transmitted. This process starts with one female *P. esculentus* $X R(X L)$ entering the population of *P. ridibundus* at the first simulation step.

A feature of the model is in its probabilistic character. Survival and reproduction of each individual are the casual processes. Their probabilities are determined by the viability parameters of each genotype and the age group. The probability distribution for the asymptotic states of a simulation can be determined for each of its possible initial conditions.

The simulation results are probabilistic in nature, and parameters of the initial state affect the probability of different outcomes. Figure 6 shows the probability distribution for the asymptotic states for a simulation of a HPS that initially started with 240 $♀ X R X R$, 250 $♂ X R Y R$ and 10 $♀ X R(X L)$. This initial composition leads to the HPS transformation that corresponds to the example shown in Fig. 4. Adding one individual $♀ X L(X R)$ at a certain stage can lead to movement of the HPS into a stable state similarly to the case shown in Fig. 5. We performed a series of simulations in which the initial composition was maintained unchanged but the time of adding $♀ X L(X R)$ varied between time step 1 up to time step 300. For each these time steps, 200 simulations were performed.

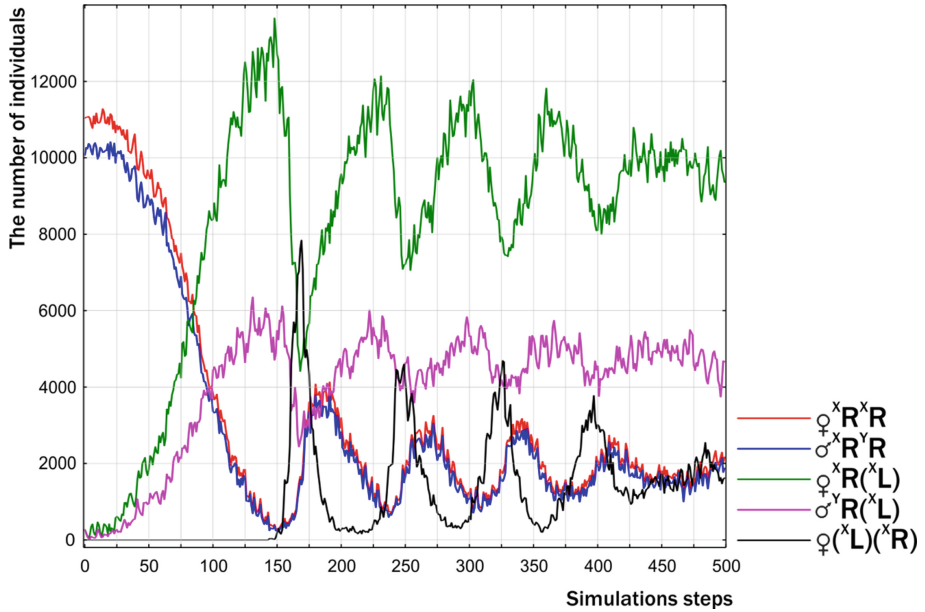


Fig. 5. Transition to a stable state of R-E-HPS, where genomes (X^R) and (X^L) are transmitted. We run the Fig. 4-model for 144 time steps, then stopped it and used the state at that moment as an input for this simulation. At the 145th step, one female *P. esculentus* (X^L)(X^R) was added in the HPS, that led to a transition of the HPS to a stable state.

There are three final states in the described above experiment:

- Genome (X^L) disappears from the model HPS which subsequently becomes a single population of *P. ridibundus*;
- The model HPS dies, as in Fig. 4;
- The model HPS reaches a stable state, as in Fig. 5.

As can be seen in Fig. 6, the maximum probability of reaching a stable state is more than 0.7, and this is achieved if a single female carrier (X^R) is added between time steps 140 and 150.

The unstable states were found during experiments with the model HPS. They change into other states over time under the influence of accidental causes. An example of transition from an unstable into a stable state is shown in Fig. 7.

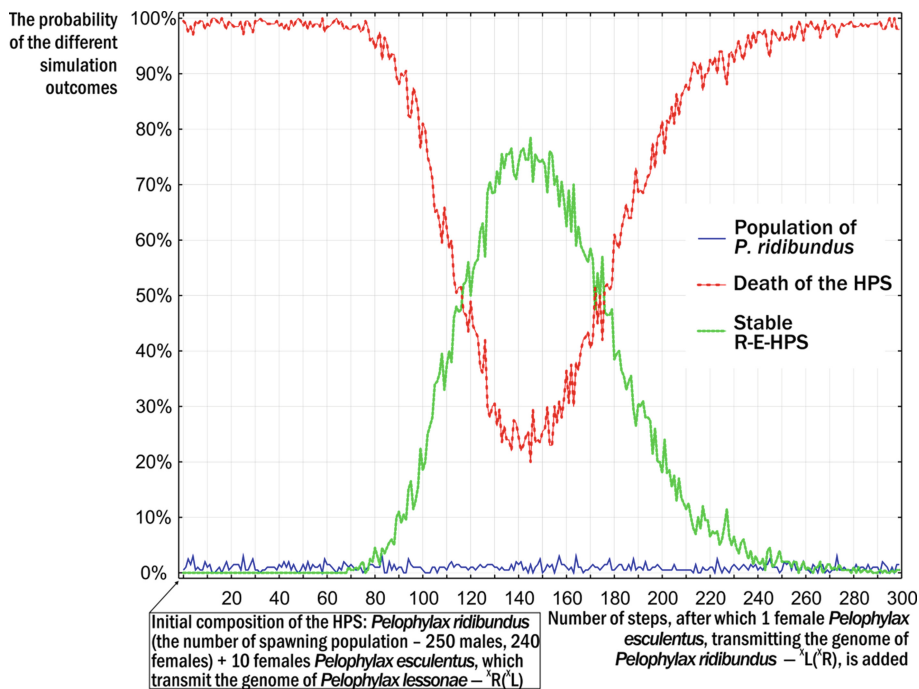


Fig. 6. Probability to reach one of three possible outcomes for the HPS depends on the time step when a single female *Pelophylax esculentus* transmitting genome of *Pelophylax ridibundus*, $L(R)$, is added to the system.

4.2 The Space of Possible Outcomes of the HPS Transformations

To determine the set of possible end states of the water frogs' HPS consisting of diploid representatives, we chose a set of initial states evenly distributed in the space of possible states. For eight examined genotypes, the proportion of each ($p\sigma^X R^X R$, $p\sigma^X R^Y R$ etc.) varied in increments of $1/8$ from 0 to $7/8$. Total $8! = 16,777,216$ such combinations are possible. Of these, the combinations that satisfy the following conditions were selected:

$$\begin{aligned} & p\sigma^X R^X R + p\sigma^X R^Y R + p\sigma^X R(XL) + p\sigma^X R(YL) + p\sigma^Y R(XL) + p\sigma(XL)(XR) + \\ & p\sigma(XL)(YR) + p\sigma(YL)(XR) = 1; \\ & p\sigma^X R^X R + p\sigma^X R(XL) + p\sigma(XL)(XR) > 0; \\ & p\sigma^X R^Y R + p\sigma^X R(YL) + p\sigma^Y R(XL) + p\sigma(XL)(YR) + p\sigma(YL)(XR) > 0. \end{aligned}$$

Naturally, it does not make sense to consider the combinations in which the total proportion of genotypes involving into the HPS is not equal to unity, as well as those in which there are no males or no females. The total number of genotypes that satisfy the above conditions equals 5895. Ten simulations of 500 steps were conducted for the 5895 starting points. The collection of all observed outcomes of the simulation was divided into types, depending on what kind of genotypes were presented in the model

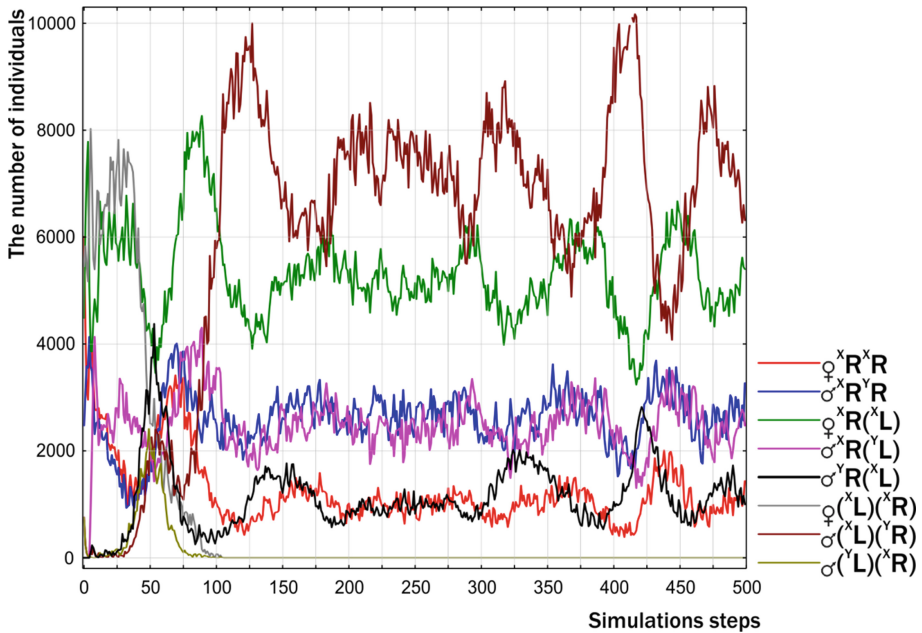


Fig. 7. The model HPS was in unstable state. After an accidental loss of genome ($^X R$) genotypes ($^X L$)($^X R$) and ($^Y L$)($^X R$) disappear, and the HPS moves into a stable state.

HPS over 500 steps. For 4778 initial states, all 10 iterations led to any one outcome. In 1117 cases, outcomes were variable. For these 1117 initial states 10 more runs were performed. The total number of simulations was 70,120.

To determine the states which the model HPS can move to, we examined the intervals between step 100 and 200, step 200 and 300, 300 and 400 as well as 400 and 500. The total number of intervals were 162,580 which is less than possible due to the model HPS, which dies at any stage of the simulation.

We used the method of principal components on the obtained set of 70,120 final states of individual simulations to assign them into groups. The first and the second principal components allow to divide the HPS into 6 groups (Fig. 8):

- Extinction—37,946 runs led to extinction of the HPS;
- R-E-HPS—22,204 runs resulted in different R-E-types of the HPSs;
- E-HPS-type I—5884 runs with the resulted HPSs include $\varphi(^X L)(^X R)$ and $\sigma(^X L)(^Y R)$;
- E-HPS-type II—3892 runs corresponding to another possible type of E-HPS, which include $\varphi(^X L)(^X R)$ and $\sigma(^Y L)(^X R)$;
- Extincting—124 runs with the results located close to the point of Extinction. They continue to end up in extinction. The structure of these outcomes can be further subdivided into 13 types;
- R-population—70 runs resulted in the model HPS becoming a population of *P. ridibundus*.

According to the results of the principal component analysis, the R-E-HPS group, which corresponds to 22,204 results, can be divided into three parts (Fig. 9):

- Stable R-E-HPS-type I—18,852 results corresponding to a stable state in Fig. 5;
- Stable R-E-HPS-type II—2,847 results corresponding to a stable state in Fig. 7;
- Indifferent R-E-HPS—505 results in which *P. ridibundus* is present together with *P. esculentus* transmitting both genome of *P. lessonae* and female genome of *P. ridibundus*.

To determine the dynamic types of the HPS, the 162 580 pairs of initial state and its outcome were analyzed. The observed states were classified by the types of stability as shown in Fig. 10.

The observed states are divided into three groups (Equilibrium states, Transient states and Attractive states) as shown in Fig. 10, though this division is rather subjective. The Indifferent equilibrium (II) can be considered as a transient state as well. Two versions of the transient states are associated with directed transitions to other states. The extinguishing state (IV) is associated with the transition to the extinction state (VI), whereas the transforming state (III) is associated with transition to the other states.

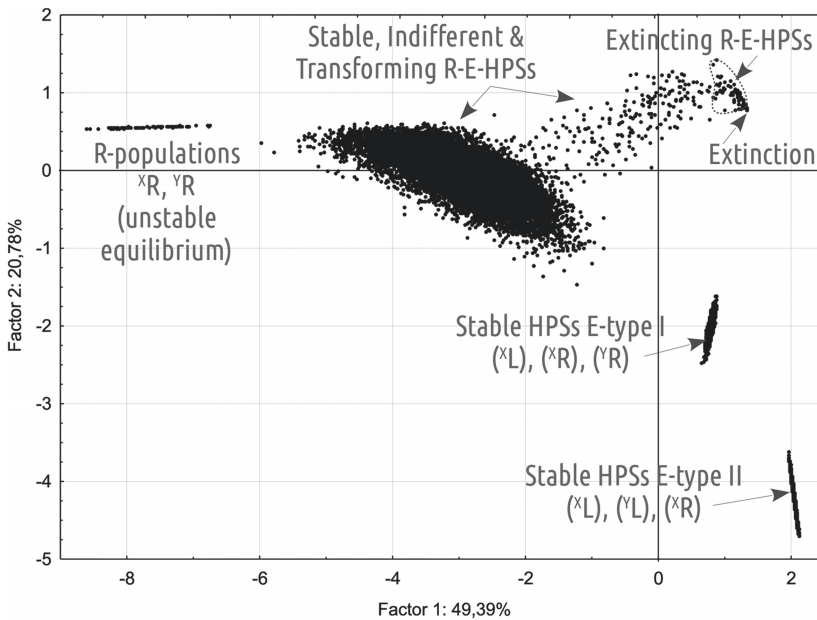


Fig. 8. Ordination of the results of 70,120 simulations on the plane of the first two principal components.

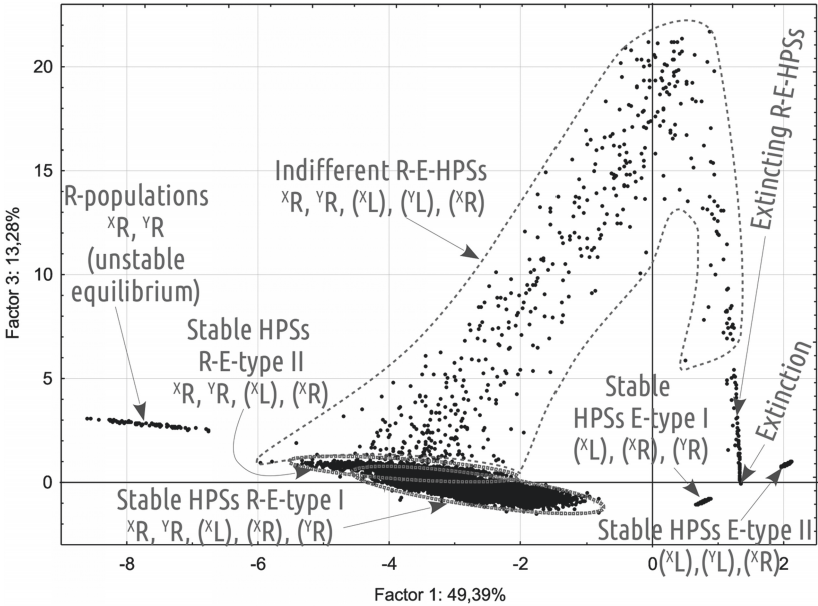


Fig. 9. Ordination of the results of the simulations as shown in Fig. 8 on the plane of the first and third principal components.

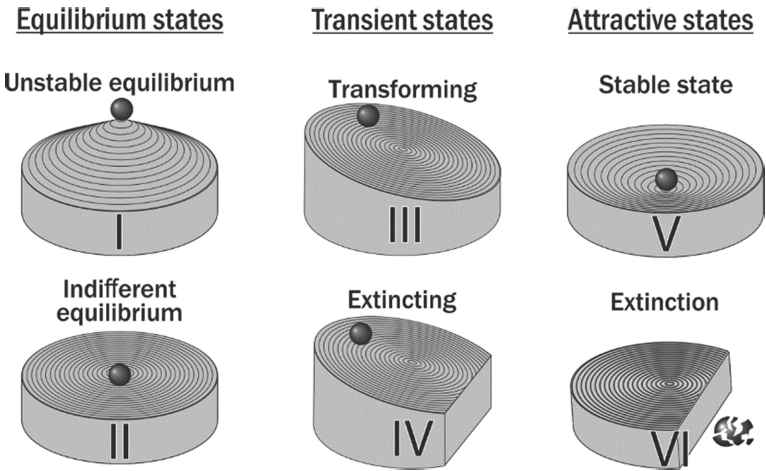


Fig. 10. The types of biosystems stability, observed in the experiments with the simulation model.

Six pools of sustainability exist in the space of possible states of a HPS consisting of diploid individuals, and this corresponds to the specific features of the Siverskyi Donetsk center of diversity of the *Pelophylax esculentus* complex concerning the character of the genome transmission. One of them complies with the population of

parental species. Two are E-HPS, i.e. spawning population of HPS consisting exclusively of *P. esculentus*. When crossing *P. esculentus* with the hybrid amphisperm, the offspring of parental species appearing in such systems dies before reaching the age of maturity.

E-HPS-type I:

$$\varphi(\mathbf{x}_L)(\mathbf{x}_R) \times \sigma(\mathbf{x}_L)(\mathbf{y}_R) \rightarrow \mathbf{x}_L \mathbf{x}_L: (\mathbf{x}_L)(\mathbf{x}_R): (\mathbf{x}_L)(\mathbf{y}_R): \mathbf{x}_R \mathbf{y}_R \rightarrow \varphi(\mathbf{x}_L)(\mathbf{x}_R): \sigma(\mathbf{x}_L)(\mathbf{y}_R);$$

E-HPS-type II:

$$\varphi(\mathbf{x}_L)(\mathbf{x}_R) \times \sigma(\mathbf{y}_L)(\mathbf{x}_R) \rightarrow \mathbf{x}_L \mathbf{y}_L: (\mathbf{x}_L)(\mathbf{x}_R): (\mathbf{y}_L)(\mathbf{x}_R): \mathbf{x}_R \mathbf{x}_R \rightarrow \varphi(\mathbf{x}_L)(\mathbf{x}_R): \sigma(\mathbf{y}_L)(\mathbf{x}_R).$$

There are two more basins of stability corresponding to the R-E-HPS containing *P. ridibundus* and *P. esculentus*, and the last basin is associated with extinction of the HPS.

5 Outcome Interpretation

When interpreting the results, one must be aware that results of a simulation is not a proof of the hypothesis. At the same time, using simulation models as an exploratory tool has a significant advantage over unformulated conceptual models. We do not have the sufficient empirical data to describe precisely the processes occurring in the natural HPSs. The lack of empirical data is compensated by a set of presumptions [13] and hypotheses. Simulation allows us to draw conclusions arising from the set of initial assumptions.

These sets of conclusions may or may not contradict the empirical patterns observed. A contradiction between the two is the basis for rejecting a set of the initial assumptions or adjustments. Despite an agreement between the two is not an evidence for accuracy of the initial assumptions, it can be considered as an argument in their favor, in other words it is a confirmation rather than a proof (Fig. 11).

Figure 11 shows how the simulation results can be used to select between different versions of the assumptions in the absence of empirical data. Model predictions regarding the expected diversity of HPS conditions depend on assumptions made during the development of the variant part of the model. The predicted (modeled) expected diversity of states of a HPS can be compared to the empirically observed diversity. The results of this comparison can be seen as the arguments in favor of such initial assumptions that led to patterns corresponding to the ones empirically observed.

We believe that this study is only a starting step in designing the dynamic typology of the water frogs' HPSs. The results of the simulation, among other findings, stimulate collection of empirical data. This can be seen in the example of E-HPSs, which was considered a stable E-HPS of type I. The possibility for this HPS to be the stable E-HPS of type II has been shown by our model. Comparison of the predictions obtained by the modelling and the available fragmented empirical data about the composition of the natural HPSs and the nature of gametogenesis in *P. esculentus* shows that E-type HPS is currently absent in the studied region despite that such a system likely was present in the region before [6]. The E-HPS was described in Is'kiv Pond, which is located in the

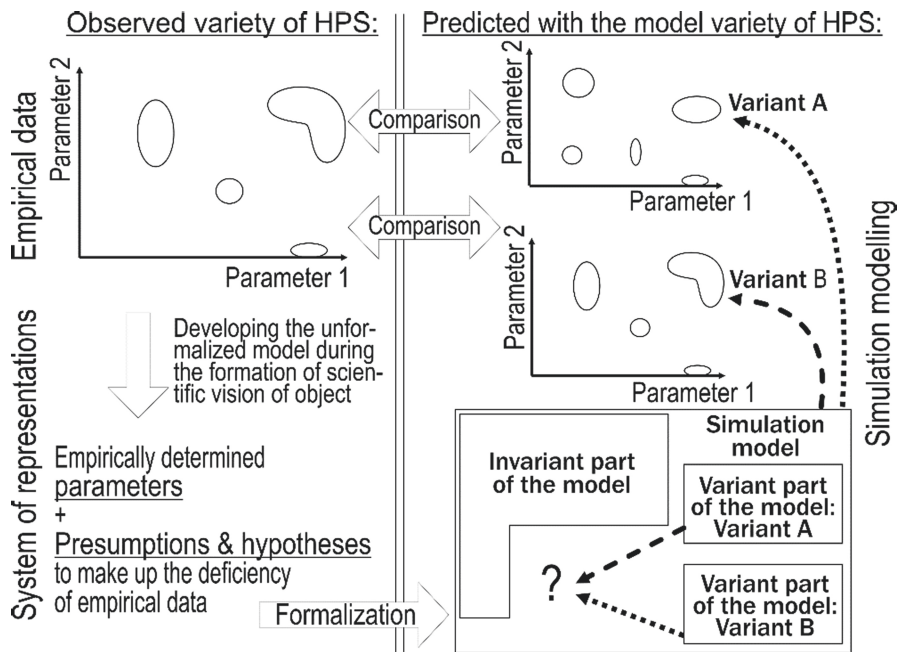


Fig. 11. Using a simulation model to test hypotheses about the mechanisms of a HPS functioning. The distribution of the outcomes of the model HPS is in agreement with the empirical data, and it is obtained when variant B of the variable part of the model is selected. It does not prove variant B to be true, but it allows to discard variant A in its favor.

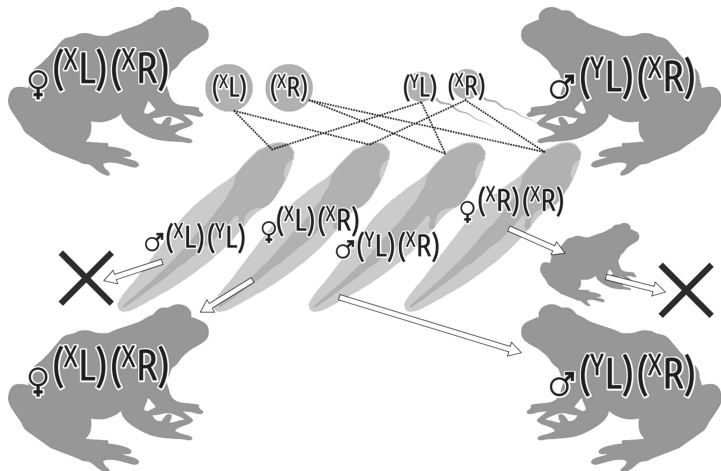


Fig. 12. Crossings occurring in E-HPSs of type II [8]. Crossings between the hybrids which transmit genomes of the same parental species produce representatives of this parental species which typically do not reach the age of sexual maturity. Such a HPS consists of male and female clones, each of them produces two types of gametes.

vicinity of the National Nature Park Gomilshanski Lisy. Since then, this HPS has undergone through considerable changes in composition. Our study shows that this system is in a transient state. However, the composition of tadpoles and yearlings in the Is'kiv pond closely corresponds to E-HPS of type II (Fig. 12) [8].

We have not observed individuals of genotype (LL) as it is likely that they die during the early stages of development. Individuals of genotype (RR) die after metamorphosis. We suggest that this difference is due to the fact that, in this system, genomes L are more strongly affected by clonal transmission during many generations. These observations were not taken into account in our model, but do not contradict the prediction it makes.

6 Discussion and Conclusion

We study an unusual category of biosystems, hemiclonal population systems, using the example of the hybridogenic complex of water frogs, the *Pelophylax esculentus* complex. The unusual method of reproduction of interspecific hybrids within HPSs results in their specific properties, which require in-depth investigation. A powerful method for studying such systems is a computer simulation.

A simulation model of the water frogs' HPS has been presented. As an input, the model uses parameters describing comparative vitality of various genotypes of frogs, the results of their possible crossings as well as the experimental conditions such as resource availability, initial composition of the model HPS, and a scenario for introduction of migrated frogs into the model HPS. Assumptions about the comparative vitality and the crossings results correspond to the results of population ecological studies of HPSs in the Siverskyi Donets center of diversity of the *Pelophylax esculentus* complex. Since empirical data were lacking, we approximated the values of the parameters supplied into the model based on a study of this region.

Replicated runs of the model provided a probability distribution of the outcomes of various transformations of the HPSs according to their initial states and experiment-determined parameters. We analyzed the processes in all-diploid HPSs from the Siverskyi Donets center of diversity of the *Pelophylax esculentus* complex, which is typical for the Mzha and the Uda river basins. A set of outcomes was obtained by sampling evenly among the starting points of runs in the space of possible states of a system. Only six stable states have been identified for such systems, one of which corresponds to the population of the parental species, two correspond to a HPS consisting of the parental species and hybrids, two correspond to a HPS only consisting hybrid individuals, and one state corresponds to the extinction of frogs in the simulated system.

The usefulness of the simulation is not limited by the fact that two stable previously unknown states can be identified: R-E-HPS-type II and E-HPS-type II. Results of simulations provide a baseline for further research and define a data collection strategy for testing the model performance. The currently available empirical data do not contradict the model findings. Future work will include studying unstable states of HPSs that are observed in nature [17], as well as development of the model through incorporating triploid hybrids, which are specific for the Siverskyi Donets center of diversity of the *Pelophylax esculentus* complex.

This work presents results of the joint work of a group of population ecologists and mathematical informaticians. From our the point of view, it should be of interest for both categories of scientists. Firstly, this work is a result of applying a simulation approach to determine the stability of the studied biosystems on the example of water frogs. Thus, this work is focused on batrachologists, population ecologists and researchers in hemiclinal hybridization.

Secondly, this paper is an attempt to develop a new approach for investigation of complex HPSs by simulation. From this point of view, the findings presented here may be of interest for scientists who work in diverse fields.

Like many other studies at the boundaries of two sciences, our work can be quite difficult to understand for both biologists and modelers. However, studies on the “interscience territory” have, in our opinion, the greatest potential for further development.

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