

# A Computational Formal Model of the Invasiveness of Eastern Species in European Water Frog Populations

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**Abstract.** European water frog populations are mainly composed by two species: *Pelophylax lessonae* (pool frog) and *Pelophylax esculentus* (edible frog). These populations are called L-E complexes. Edible frogs are a hybrid form between *P. lessonae* and *Pelophylax ridibundus* (eastern lake frog) and they reproduce in a particular way, called hybridogenesis. These frog populations have been studied in the contexts of evolution and speciation. In order to have stability of L-E complexes (namely self-maintenance of the population structure) some conditions are necessary. We present a computational formal model of European water frog population based on a variant of P systems in which evolution rules are applied in a probabilistic maximally parallel manner. Probabilities of application of rules will be computed on the basis of parameters to be associated with each rule. By means of our model we show how the stabilization of L-E complexes can be obtained. In particular, we show how the introduction of translocated eastern lake frogs in such complexes can lead to the collapse of the populations. The study of conditions for population stability and of possible threats to endangered species is of particular importance for the maintenance of biodiversity, which is an aspect of sustainable development.

## 1 Introduction

Lake frog (*Pelophylax ridibundus* Pallas, 1771) and pool frog (*Pelophylax lessonae* Camerano, 1882) can mate producing the hybrid edible frog (*Pelophylax esculentus* Linneus, 1758). The edible frog can coexist with one or both of the parental species giving rise to mixed populations. Usually the genotypes of *P. ridibundus*, *P. lessonae* and *P. esculentus* are indicated by *RR*, *LL*, and *LR*, respectively. In Europe there are mainly mixed populations containing *P. lessonae* and *P. esculentus*, called L-E systems. Hybrids in these populations reproduce in a particular way, called *hybridogenesis* [6]. Hybridogenesis consists in a particular gametogenetic process in which the hybrids exclude one of their parental genomes premeiotically, and transmit the other one, clonally, to eggs and sperm. This particular way of reproduction requires that hybrids

**Table 1.** Reproductive pattern of water frogs

	<i>LL</i>	<i>LR</i>
<i>L<sub>y</sub>L</i>	<i>L<sub>y</sub>L</i> <i>LL</i>	<i>L<sub>y</sub>R</i> <i>LR</i>
<i>L<sub>y</sub>R</i>	<i>LR</i>	<i>RR</i> not viable

live sympatrically with the parental species the genome of which is eliminated. In this way hybrids in a L-E system eliminate the L genome thus producing *P. esculentus* when mating with *P. lessonae*, and generating *P. ridibundus* when mating with other hybrids. Usually *P. ridibundus* generated in L-E complexes are inviable due to deleterious mutations accumulated in the clonally transmitted R genome [10, 21, 24]. Because of inviability of *P. esculentus*  $\times$  *P. esculentus* offspring, edible frog populations cannot survive alone, but they must act as a sexual parasite of one of the parental species. In L-E complexes the reproductive pattern is the one in Table 1 where the subscribed Y indicates the male sexual chromosome.

Note that the Y chromosome, determining the sex of frog males, can occur only in the L genome, due to primary hybridization which involved, for size constraints, *P. lessonae* males and *P. ridibundus* females. Table 1 shows that only one of the three possible matings resulting in viable offspring produce *LL* genotypes. This would give an advantage to edible frogs which could outnumber *P. lessonae* and eventually eliminate them. This situation would result in an extinction also of *P. esculentus* which cannot survive without the parental species. In addition to their relative abundance which can be promoted by the above reproductive pattern, edible frogs show, by heterosis, a greater fitness than the parental species [2, 12, 23]. The sum of relative abundance and heterosis should out-compete *P. lessonae* in L-E complexes. The widespread distribution of L-E complexes reveals the existence of mechanisms which contribute to the stability of such complexes, namely to the ability of such populations to self-maintain their structure. Among such mechanisms sexual selection seems to be one of the most important: *P. esculentus* females prefer *P. lessonae* males with respect to males of their own species [1, 5, 9, 19, 20]. Many mathematical and computational models were devoted to the study of the influence of sexual selection in the evolution of populations, the models in [11, 22] show how female preference is able to stabilize L-E complexes by counterbalancing both heterosis and reproductive advantage of edible frogs.

In this paper we are interested in modelling and simulating the dynamics of L-E complexes. The study of conditions for population stability and of possible threats to endangered species is of particular importance for the maintainance of biodiversity, which is an aspect of sustainable development.

*P systems* are a model of computation that has recently found new applications as a notation for the modelling of biological systems. We define a minimal variant of *P systems* that allows the dynamics of such L-E complexes to be formally described. Although defined with a specific example in mind, our variant of *P systems* will include features that allow it to be used to describe many other kinds of populations. We choose to adopt a formal notation based on *P systems* for the modelling of L-E complexes rather than directly implementing a computational model by using a general purpose programming language. This allows us to unambiguously define and describe the model. Moreover, in general the use of formal modelling notations for the construction of population models can enable the application of formal analysis tools (such as model checkers and static analysis tools) for the verification of properties of the populations of interest.

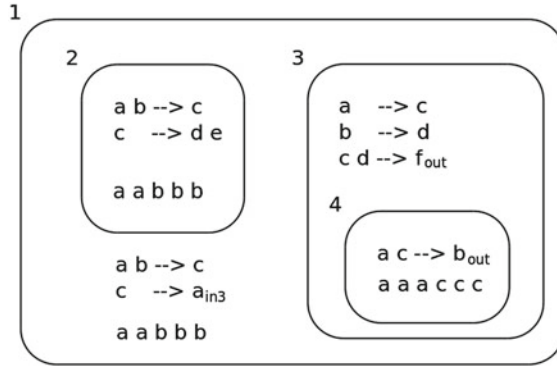
We analyze, by means of a *P systems* model, two aspects of L-E complexes. The first one is why L-E complexes generate almost all inviable *P. ridibundus* offspring. The second one is how female preference can contribute to stabilize the complexes. Finally, we show that the introduction of *P. ridibundus* can destabilize L-E populations. This is a real problem, as pointed out by Vorburger and Reyer in [25]. Their hypothesis is confirmed by our model.

## 2 A Variant of P Systems for Population Modelling

*P systems* (also known as *membrane systems*) are a bio-inspired model of computation proposed by G. Păun in [15] in the context of Natural Computing. *P systems* were originally aimed at investigating the computing capabilities of cells as new unconventional computing architectures. The motivation for such studies was that the extremely high (virtually unbounded) degree of parallelism in biochemical phenomena occurring within cells could have allowed the solution of computationally hard problems in short times. Many theoretical results have been achieved on *P systems* by considering many different variants of such a formalism (see [14, 16] for an overview).

The formalism of *P systems* falls in the category of rewriting systems, in which a structure with given characteristics evolves by means of application of some rewriting rules. In the case of *P systems*, the structure is inspired by the internal structure of cells, namely it consists of a hierarchy of *membranes*. Each membrane is identified by a unique label and in each membrane there can be a multiset of *objects* (representing molecules) that change over time by the application of rewriting rules (called *evolution rules* and representing chemical reactions). Each evolution rule consists of two multisets of objects (representing reactants and products of the described chemical reaction). A rule in a membrane can be applied only to objects in the same membrane. Some objects produced by the rule remain in the same membrane, others are sent *out* of the membrane, others are sent *into* the inner membranes (assumed to exist) which are identified by their labels.

Evolution rules in *P systems* are (usually) applied with *maximal parallelism*, namely at each step of evolution different rules can be applied at the same time



**Fig. 1.** An example of P system

(on different objects), the same rule can be applied more than once, and it cannot happen that a rule is not applied when the objects needed for its triggering are available (i.e. not used by any other rule). An example of P system is shown in Fig. 1, where membranes are depicted as boxes, objects as letters and evolution rules have the form  $u \rightarrow v$ , where  $u$  is a multiset of objects (reactants) and  $v$  is a multiset of object with target indication (products). Note that the target indication of products that remain in the same membrane is omitted.

In the last few years P systems found new applications as notations for the modelling of biological systems. In particular, quantitative extensions of P systems have been proposed that allow biochemical pathways to be suitably described and simulated [3, 13, 17, 18]. In addition, variants of P systems have been applied to the modelling and simulation of populations and ecosystems [7, 8].

The variant of P systems we define in this paper includes a minimal set of features necessary to model populations. We consider *flat P systems* [4], namely P systems consisting of a single membrane, since a membrane structure is not useful for our purposes. On the other hand, the key ingredients that we consider are (i) evolution rules with functional rates, (ii) probabilistic maximal parallelism and (iii) rule promoters. The aim of this new variant of P systems is to make modelling of populations easier, by avoiding in the modelling formalism unnecessary functionalities that are present in other similar variants of P systems.

In population models, evolution rules are used to describe events such as reproduction, death, growth, and so on. In general there may be several rules describing one of these events and involving the same individual. For instance, the same female individual may be involved in one of different reproduction rules, one rule for each possible kind of male it can mate with. Some of these rules may be more likely to be applied than others since the events they describe are more likely than others. (For instance, some females may have a sexual preference for some specific kinds of males.) Associating rates with rules allows the latter to be chosen in a probabilistic way, where probabilities are proportional to the

rates. Moreover, by allowing rates to be functions, rather than constant values, we have that the probability of applying a rule can depend on the current state of the system (for instance on the size of the population, or on the number of individuals of a specific kind).

Although a form of probabilistic choice for evolution rules has to be considered, maximal parallelism is still useful since it avoids starvation of individuals. Indeed, populations often evolve by stages (e.g. reproduction, selection, etc...) in which (almost) all of the individuals are involved. By combining maximal parallelism with probabilistic choice of reactions we allow the whole population to evolve in a coherent way and, at the same time, each individual to follow its own fate.

Finally, since in each stage of evolution of a population different kinds of event may happen, we need a way to enable different sets of rules depending on the current stage. For instance, during a reproduction stage only reproduction rules should be enabled, whereas during a selection stage only death/survival rules should be enabled. In order to obtain this result we exploit rule promoters, that can be used to enable/disable a set of rules by simply including/removing an object from the state of the system.

We are now ready to define the variant of P systems we use for population modelling. We call it *Minimal Probabilistic P systems (MPP systems)*.

**Definition 1 (MPP system).** *A Minimal Probabilistic P system is a tuple  $\langle V, w_0, R \rangle$  where:*

- *$V$  is a possibly infinite alphabet of objects, with  $V^*$  denoting the universe of all multisets having  $V$  as support.*
- *$w_0 \in V^*$  is a multiset describing the initial state of the system*
- *$R$  is a finite set of evolution rules having the form*

$$u \xrightarrow{f} v \mid_p$$

*where  $u, v, p \in V^*$  are multisets (often denoted without brackets) of reactants, products and promoters, respectively, and  $f : V^* \mapsto \mathbb{R}^{\geq 0}$  is a rate function.*

A state (or configuration) of a MPP system is a multiset of objects in  $V^*$ . By definition, the initial state is  $w_0$ . We denote a generic state of the system as  $w$ . Moreover, we denote with  $|w|$  the size (number of objects) of the multiset  $w$ , and with  $|w|_a$  the number of instances of object  $a$  contained in multiset  $w$ .

The evolution of a MPP system is given by a sequence of probabilistic maximally parallel steps. In each step a maximal multiset of evolution rule instances is selected and applied as described by Algorithm 1. Given  $w$  the current system state, the algorithm copies  $w$  into  $x$ , and then iteratively selects and applies applicable rules. At each iteration, one of the applicable rules (the set of which is denoted  $R'$ ) is probabilistically chosen. The probability of each rule to be chosen is proportional to the rate value obtained by applying its rate function to the current state  $w$ . Once a rule is selected, its application consists in removing its reactants from  $x$  and adding its products into  $y$ . The latter multiset will collect

**Algorithm 1.** Probabilistic maximally parallel evolution step

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function STEP( $w$ )
   $x = w$ 
   $y = \emptyset$ 
  while there exists  $u \xrightarrow{f} v \mid_p$  in  $R$  s.t.  $u \subseteq x$  and  $p \subseteq w$  do
     $R' = \{u \xrightarrow{f} v \mid_p \in R \mid u \subseteq x \text{ and } p \subseteq w\}$ 
    choose  $u' \xrightarrow{f'} v' \mid_{p'}$  from  $R'$  with a probability proportional to  $f'(w)$ 
     $x = x \setminus u'$ 
     $y = y \cup v'$ 
  end while
  return  $x \cup y$ 
end function

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all products of all applied rules. Such products are not immediately added to  $x$  to avoid the application of a rule at the  $i$ -th iteration to consume objects produced by a rule applied in a previous iteration. Indeed, this iterative procedure simulates a parallel application of rules in which the reactions are applied all at the same time (their products are available only at the next parallel step). Once objects in  $x$  are such that no further rule in  $R$  can be applied to them, the algorithm stops iterating and returns the new state of the system  $x \cup y$  (where  $x$  are the unused objects and  $y$  are the new products). Note that in order to determine (in the guard of the loop and in the definition of  $R'$ ) whether a rule is applicable reactants are checked to be contained in  $x$  (the remaining objects) while promoters are checked to be present in  $w$  (the system state at the beginning of the iteration).

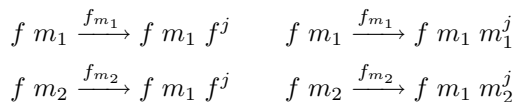
*Example 1.* We consider a MPP system representing a reproductive event in a sexual population with  $XY$  sex-determination system. In the initial population there are females ( $f$ ) and two types of males ( $m_1, m_2$ ). Suppose that females prefer  $m_1$  males with a preference value of 0.7, while they mate with  $m_2$  males with a preference value of 0.3. We consider that the different traits of  $m_1$  and  $m_2$  are coded on the  $Y$  sexual chromosome. Thus the males in the offspring produced by  $m_1$  and  $m_2$  males are of kind  $m_1$  and  $m_2$ , respectively. We consider also that each mating generates a single juvenile. The actual matings, in addition to female preferences depend on the availability of the two kinds of males.

The MPP system representing the described reproductive event is the triple  $\langle V_{fm}, w_{ofm}, R_{fm} \rangle$ . The alphabet  $V_{fm}$  is defined as follows:

$$V_{fm} = \{f, m_1, m_2, f^j, m_1^j, m_2^j\}$$

where the  $j$  superscript indicates juveniles.

The set of reproduction rules  $R_{fm}$  contains the following rules:



where  $f_{m_1}(w) = 0.7 \cdot |w|_{m_1} \cdot 0.5$  and  $f_{m_2}(w) = 0.3 \cdot |w|_{m_2} \cdot 0.5$ . Note that the result of  $f_{m_1}(w)$  is given by the preference of females for  $m_1$  males multiplied by the number of  $m_1$  males in the population and the probability of producing a male or a female (0.5).  $f_{m_2}(w)$  is analogous.

Given the following initial population:

$$w_{0fm} = m_1, m_1, m_1, m_2, m_2, m_2, f, f, f, f, f, f, f$$

we obtain the following rates:  $f_{m_1}(w_{0fm}) = 1.05$  and  $f_{m_2}(w_{0fm}) = 0.45$ . Note that two females cannot find a partner for reproduction in this event because there are not enough males.

### 3 Population Dynamics of L-E Complexes

In this section we study the dynamics of European water frog populations. In particular, we show that female preferences and the inviability of *P. ridibundus* offspring can stabilize L-E complexes. Moreover, we show how the introduction of translocated *P. ridibundus* in stable L-E complexes can lead to the collapse of the systems.

#### 3.1 Deleterious Mutations and Female Preferences are Necessary for the Stability of L-E Complexes

**The MPP systems model.** We model a L-E complex by means of a MPP system  $\langle V_{LE}, w_{0LE}, R_{LE} \rangle$  in which each individual of the population is represented by an object in the state of the system. Hence, the alphabet  $V_{LE}$  contains one object for each possible genotype of an individual. We use different objects for juveniles (immature individuals) and adults. Moreover, the alphabet includes some control objects used to realize alternation of reproduction and selection stages. As a consequence, we define  $V_{LE} = V_{LEa} \cup V_{LEj} \cup V_{ctrl}$ , where  $V_{LEa}$  represents adults,  $V_{LEj}$  represents juveniles and  $V_{ctrl}$  are control objects.

Since the *R* genome may contain a deleterious mutation or not, we use different objects for representing *P. esculentus* and *P. ridibundus* individuals carrying or not a mutation in their genotype. Thus, the alphabet representing adults is

$$V_{LEa} = \{ LL, L_yL, LR_*, L_yR_*, LR_\circ, L_yR_\circ, R_*R_\circ, R_\circR_\circ \}$$

where *y* represents the *Y* chromosome, and  $*$  and  $\circ$  represent the presence and the absence of a deleterious mutation, respectively. Note that according to the reproductive pattern of L-E complexes in Table 1 males with *RR* genotypes cannot be produced in a L-E complex. Moreover, note that object  $R_\circR_*$  is not present in  $V_{LEa}$  since the individual it represents is indistinguishable from the one represented by  $R_*R_\circ$ , and hence we use only one object to represent it.

The alphabet representing juveniles is

$$V_{LEj} = \{ LL^j, L_yL^j, LR_*^j, L_yR_*^j, LR_\circ^j, L_yR_\circ^j, R_*R_*^j, R_*R_\circ^j, R_\circR_\circ^j \}$$

where  $j$  denotes that the individual is a juvenile, and the other notations are as before. Note that  $R_*R_*^j$  is allowed although it represents non viable genotype since in our model individuals with such a genotype will be allowed to be born, but they will not be allowed to become adults.

Finally, the alphabet of control objects is

$$V_{ctrl} = \mathbb{N} \cup \{ REPR, SEL \}$$

where  $REPR$  and  $SEL$  represent reproduction and selection stages, respectively, and natural numbers will be used as objects regulating the alternance of the two considered stages.

The set of evolution rules  $R_{LE}$  contains reproduction, selection and control rules. Hence, we have  $R_{LE} = R_{LEr} \cup R_{LEs} \cup R_{ctrl}$ .

Reproduction rules  $R_{LEr}$  are of the following form:

$$x \ y \xrightarrow{f_{xy}} x \ y \ z \mid_{REPR}$$

where  $x \in V_{LEa}$  is any object representing a female and  $y \in V_{LEa}$  is any object representing a male. Function  $f_{xy}$  gives the rate of mating of females of type  $x$  with males of type  $y$  by taking into account the sexual preferences of  $x$  females and the quantities of individuals of types  $x$  and  $y$ . In particular, given a multiset of object  $w$  (a system state), we have

$$f_{xy}(w) = k_{mate}(x, y) \cdot |w|_x \cdot |w|_y \cdot 1/k_{o\_kind}(x, y)$$

where  $k_{mate}(x, y)$  is the preference of a female  $x$  for a male  $y$ , and  $k_{o\_kind}(x, y)$  is the number of possible offspring kinds that can be generated by the mating of  $x$  with  $y$ . Remark that  $1/k_{o\_kind}(x, y)$  distributes the rate of the mating event of  $x$  and  $y$  over the rules for this mating.

Finally,  $z \in V_{LEj}$  is an object representing the newborn, and it is related with  $x$  and  $y$  as described in Table 1. For example, for  $x = LL$  and  $y = L_yL$  there are two rules, one with  $z = L_yL^j$  and the other with  $z = LL^j$ . On the other hand, for  $x = LR_*$  and  $y = L_yR_o$  there is one single rule with  $z = R_*R_o^j$ . As a consequence,  $k_{o\_kind}(LL, L_yL) = 2$  whereas  $k_{o\_kind}(LR_*, L_yR_o) = 1$ . The other combinations of  $x$  and  $y$  are analogous. The full list of reproduction rules is in the pre-proceedings version of this paper.

As regards selection rules  $R_{LEs}$ , they contain two rules for each individual of the population describing its survival and its death during the selection stage, respectively. The presence of these two rules for each type of individual together with maximal parallelism ensure that during a selection stage each individual will be faced with the two fates.

Survival and death rules are of the forms that follow. For each object  $x \in V_{LEa}$  representing an adult individual we have:

$$x \xrightarrow{g_x} x \mid_{SEL} \quad x \xrightarrow{g'_x} \epsilon \mid_{SEL}$$

where  $\epsilon$  represent the empty multiset and  $g_x$  and  $g'_x$  give the probability of survival and death, respectively, of an individual of type  $x$ . Function  $g_x$  takes



into account the size of the population, the carrying capacity of the environment and the fitness of the individual. More precisely, given  $w \in V^*$  representing a system state, parameter  $cc$  representing the carrying capacity of the environment and parameter  $k_{fit}(x)$  representing the fitness of individuals of type  $x$ , we have:

$$g_x(w) = \frac{1}{1 + \frac{|w|}{k_{fit}(x) \cdot cc}}$$

Function  $g'_x$  is such that for all  $w \in V^*$  it holds  $g'_x(w) = 1 - g_x(w)$ .

For each object  $x^j \in (V_{LEj} \setminus \{R_*R_*^j\})$  representing a juvenile (but not  $R_*R_*^j$ ) we have:

$$x^j \xrightarrow{g_{x^j}} x \mid_{SEL} \quad x^j \xrightarrow{g'_{x^j}} \epsilon \mid_{SEL}$$

where  $x \in V_{LE}$  is the object representing the adult of the same type of  $x^j$ , and  $\epsilon$ ,  $g_{x^j}$  and  $g'_{x^j}$  are as before. In the case of  $R_*R_*^j$  we consider only the death rule, since such a kind of juvenile is considered too unfit to be able to grow up. Hence, we have only

$$R_*R_*^j \xrightarrow{f_1} \epsilon \mid_{SEL}$$

where for all  $w \in V^*$  it holds  $f_1(w) = 1$ .

Finally, as regards control rules  $R_{ctrl}$ , they are responsible for the appearance and disappearance of objects  $REPR$  and  $SEL$  in order to activate alternatively reproduction and selection rules. For the sake of simplicity, we assume that the offspring of each female in each reproduction stage are exactly  $n$ . We also assume that each of the offspring is the result of a different mating (this is a very rough simplification that however should not change significantly the global population dynamics). Hence, the object  $REPR$  has to be present for  $n$  subsequent steps, then it has to be replaced by  $SEL$  for one step, and these  $n + 1$  steps should be iterated forever. This result is obtained by ensuring that  $REPR$  is in the initial state of the system and by using the following control rules:

$$\begin{array}{ccccccc} 1 & \xrightarrow{f_1} & 2 & & 2 & \xrightarrow{f_1} & 3 & & \dots & & (n-1) & \xrightarrow{f_1} & n \\ n & REPR & \xrightarrow{f_1} & SEL & & SEL & \xrightarrow{f_1} & 1 & REPR \end{array}$$

where, as before, for all  $w \in V^*$  it holds  $f_1(w) = 1$ .

The initial state  $w_{0LE}$  of the MPP system will change in different simulations. In general, it will contain the control objects 1 and  $REPR$ , and one object for each individual present in the considered initial population.

**Parameters.** In order to perform simulations we consider the following initial parameters (some of them will be changed later on).

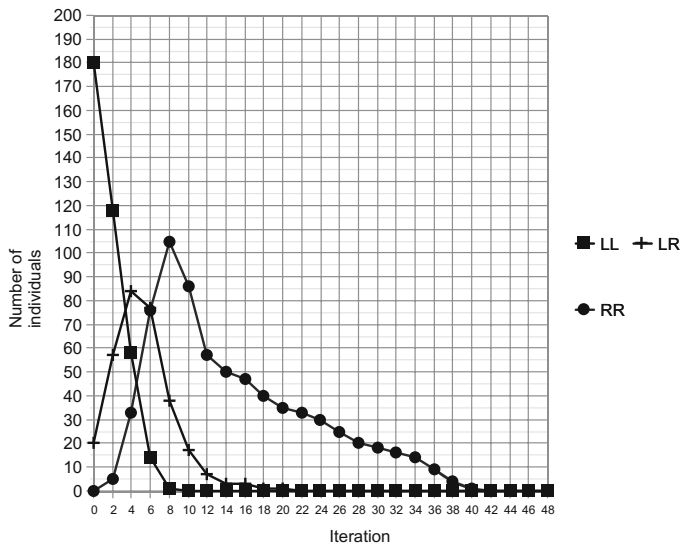
- No sexual preference: for every female  $x$  and male  $y$  we have  $k_{mate}(x, y) = 1$ .
- 10 % higher fitness for hybrids (heterosis effect), namely

$$k_{fit}(x) = \begin{cases} 0.55 & \text{if } x \in \{LyR_* LyR_\circ LyR_*^j LyR_\circ^j\} \\ 0.5 & \text{if } x \in V_{LEa} \setminus \{LyR_*^j LyR_\circ^j\}. \end{cases}$$

- The carrying capacity  $cc$  is set to 400.
- The number of reproduction stages  $n$  is set to 3.

**Results.** We study the stability of L-E complexes by considering populations without deleterious mutations in the  $R$  genome of *P. esculentus*. We performed 1000 simulations with initial populations composed by *P. lessonae* frogs and a percentages of 10% of mutation-free edible frogs. The initial state of the system is hence described by the multiset  $w_{0LE}$  consisting of 90 instances of  $LL$ , 90 of  $L_yL$ , 10 of  $LR_o$ , 10 of  $L_yR_o$  and of the control objects 1 and  $REPR$ .

We observe that, in all the simulations, the population evolves towards a mono-specific population of viable all-females *P. ridibundus* which eventually collapses for the absence of males (recall that the  $Y$  chromosome can occur only on the  $L$  genome). Figure 2 shows the outcome of a typical simulation. If viable *P. ridibundus* females are produced, the reproductive pattern becomes the



**Fig. 2.** Result of a simulation of a L-E complex without deleterious mutations.

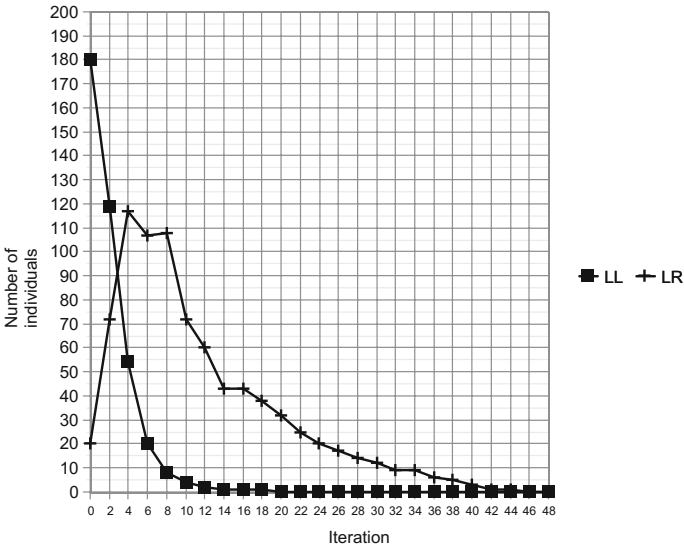
**Table 2.** Reproductive pattern of water frogs without deleterious mutations.

	$LL$		$LR$		$RR$	
$L_yL$	$L_yL$	$LL$	$L_yR$	$L_R$	$L_yR$	$L_R$
$L_yR$	$LR$		$RR$		$RR$	

one depicted in Table 2. Edible frogs are numerically advantaged from possible mating between *P. ridibundus* females and *P. lessonae* males. It is clear from the table that this reproductive pattern generates a numerical disadvantage for pool frogs, the population of which decreases. The decrease in the *P. lessonae* population has, as a consequence, a decrease of produced  $L$  gametes, which, in turn, results in a bigger production of lake frogs. Thus the population of *P. ridibundus* females grows and eventually they out-compete the other species.

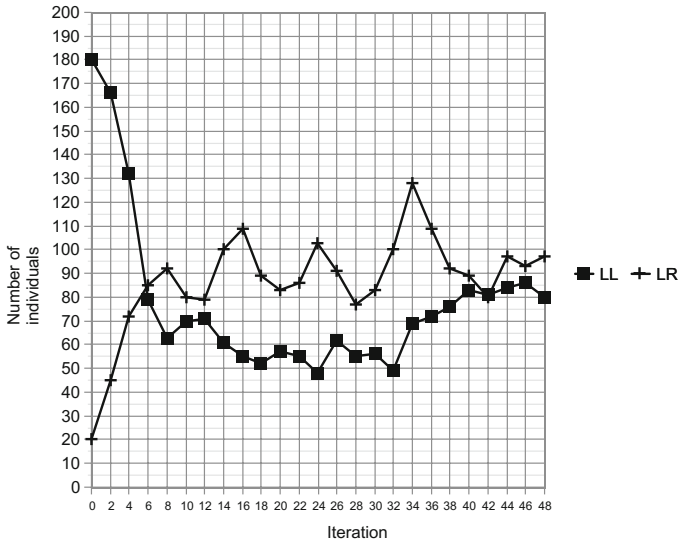
Let us now consider an initial population with the same percentages of edible frogs (10%), but in which all the *P. esculentus* individuals carry the deleterious mutations on the  $R$  genome, that is *P. ridibundus* females are not viable and they do not appear in the population. The initial state of the system is hence described by the multiset  $w_{0LE}$  consisting of 90 instances of  $LL$ , 90 of  $L_yL$ , 10 of  $LR_o$ , 10 of  $L_yR_*$  and of the control objects 1 and  $REPR$ .

We performed 1000 simulations. We observe that also in this case the population collapses in all simulations. The cause of the collapse is due to the fact that both the reproductive pattern of Table 1 and the greater fitness of edible frogs give an advantage to *P. esculentus* frogs forcing the complex towards a mono-specific population. A population with *P. esculantus* alone cannot survive. Figure 3 shows the outcome of a typical simulation in this case.



**Fig. 3.** Result of a simulation of a L-E complex with deleterious mutations.

Finally we introduce in the population a female preference towards  $L_yL$  males (observed experimentally in [1, 9, 20]). In particular, we set  $k_{mate}(LL, L_yL) = 6$  and  $k_{mate}(LR, L_yL) = 2$ . Also in this case we performed 1000 simulations with the same initial state as before.



**Fig. 4.** Result of a simulation of a L-E complex with deleterious mutations and sexual selection.

We observe that in all simulation the complex evolves towards a stable L-E complex. Figure 4 shows the outcome of a typical simulation in this case.

Note that we do not show the outcome of simulations in a population with female preferences but without deleterious mutations in the R genome. Actually, also in this case the population evolves towards a all-females *P. ridibundus* population.

### 3.2 Invasion of Translocated *P. Ridibundus*

The main point that we study with our model is the consequence of the introduction of *P. ridibundus* in stable L-E complexes. *P. ridibundus* can mate both with *P. esculentus*, producing *P. ridibundus*, and with *P. lessonae* (primary hybridization), producing *P. esculentus*.

**The MPP Systems Model.** In order to study the dynamics of a L-E complex in which *P. ridibundus* can be introduced we need to extend our previous model (defined in Sect. 3.1). Indeed, we need to include in the model objects and rules describing the behaviour of *P. ridibundus* males.

Consequently, we define a MPP system  $\langle V_{LER}, w_{0LER}, R_{LER} \rangle$  where  $V_{LER} = V_{LERa} \cup V_{LERj} \cup V_{ctrl}$  and  $R_{LER} = R_{LERr} \cup R_{LERs} \cup R_{ctrl}$ , where, in turn, we have:

- $V_{LERa} = \{LL, L_yL, LR_*, L_yR_*, LR_o, L_yR_o, R_*R_o, R_yR_o, R_yR_*, R_oR_o, R_yR_o\}$

- $V_{LERj} = \{LL^j, L_yL^j, LR_*^j, L_yR_*^j, LR_o^j, L_yR_o^j, R_*R_*^j, R_{y*}R_*^j, R_*R_o^j, R_{y*}R_o^j, R_{y_o}R_*^j, R_oR_o^j, R_{y_o}R_o^j\}$
- $R_{LERr}$  and  $R_{LErs}$  extend  $R_{LEr}$  and  $R_{LEs}$ , respectively, with analogous rules for *P. ridibundus* males
- $V_{ctrl}$  and  $R_{ctrl}$  are as before

Note that, given the impossibility of mating between *P. ridibundus* male with *P. lessonae* females (for size reasons),  $L_*R_{y_o}$  individuals cannot be produced. Note also that in reproduction rules involving *P. ridibundus* males with one mutation, namely  $R_*R_{y_o}$  we have to consider more possibilities for the genotype of the offspring than in the previous cases. Indeed, by means of recombination a male of this type can produce four kinds of gametes:  $R_*$ ,  $R_o$ ,  $R_{y*}$  and  $R_{y_o}$ .

The full list of reproduction rules is in the pre-proceedings version of this paper.

**Parameters.** In order to perform simulations we consider the following initial parameters (some of them will be changed later on) that we know, for the previous model, could lead to a stable L-E complex if deleterious mutations are present.

- Sexual preference:

$$k_{mate}(x, y) = \begin{cases} 6 & \text{if } x = LL \text{ and } y = L_yL \\ 2 & \text{if } x \in \{LR_*, LR_o\} \text{ and } y = L_yL \\ 0 & \text{if } x = LL \text{ and } y \in \{R_{y*}R_o, R_{y_o}R_*, R_{y_o}R_o\} \\ 1 & \text{otherwise} \end{cases}$$

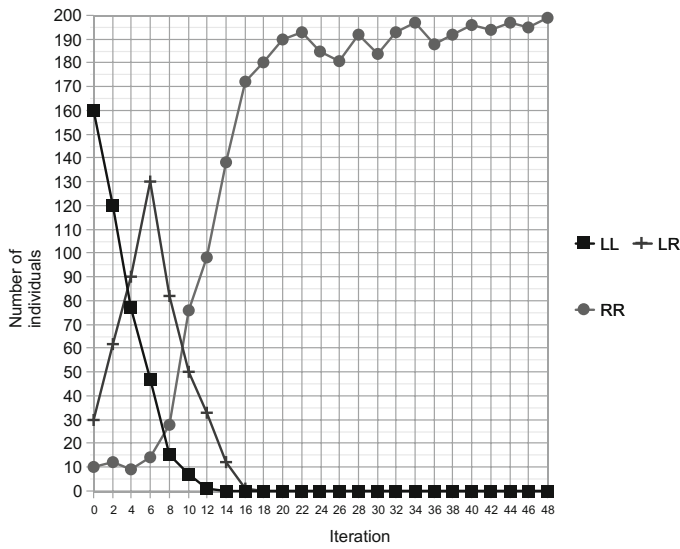
- 10 % higher fitness for hybrids (heterosis effect), namely

$$k_{fit}(x) = \begin{cases} 0.55 & \text{if } x \in \{L_yR_*L_yR_oL_yR_*^jL_yR_o^j\} \\ 0.5 & \text{if } x \in V_{LEa} \setminus \{L_yR_*^jL_yR_o^j\}. \end{cases}$$

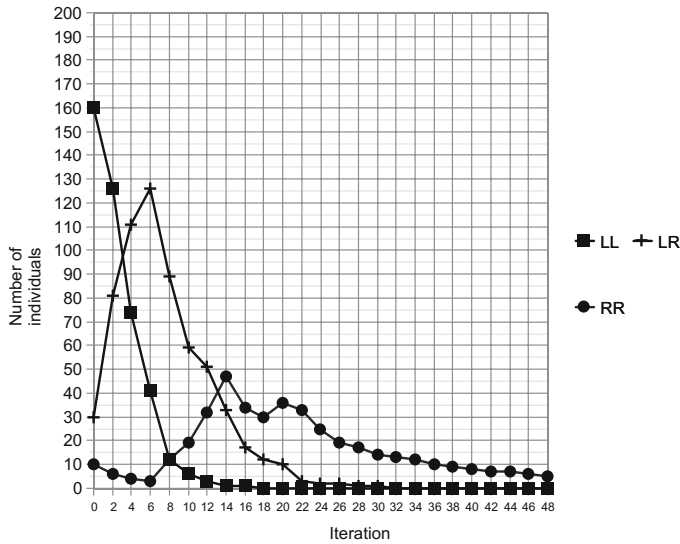
- The carrying capacity  $cc$  is set to 400.
- The number of reproduction stages  $n$  is set to 3.

**Results.** We performed 1000 simulations with initial populations composed by 80 % of *P. lessonae* frogs, 15 % of mutation-free edible frogs and 5 % of *P. ridibundus* frogs. The initial state of the system is hence described by the multiset  $w_{0LER}$  consisting of 80 instances of  $LL$ , 80 of  $L_yL$ , 15 of  $LR_*$ , 15 of  $L_yR_*$ , 5 of  $R_oR_o$ , 5 of  $R_{y_o}R_o$ , and of the control objects 1 and  $REPR$ .

The results in this case are of two kinds: 73 % of simulations result in a mono-specific *P. ridibundus* population while 27 % of simulations result in a collapse of the whole population. Figure 5 and 6 show typical population dynamics. Because the introduced lake frogs are mutation-free and because they can mate with *P.*



**Fig. 5.** Simulation of invasion leading to replacement of the population by lake *P. ridibundus* frogs.



**Fig. 6.** Simulation of invasion leading to replacement of the population by lake *P. ridibundus* frogs.

*esculentus* frogs, deleterious mutations are gradually purged. Thus, the population evolves towards a mono-specific *P. ridibundus* system. In this situation, if males are present, the *P. ridibundus* population can survive, otherwise it will collapse. The survival of *P. ridibundus* males is threatened by female preferences towards *LL* males and the advantage of *P. esculentus* for their heterosis. In all cases, the initial L-E complex is destroyed, as predicted in [25].

## 4 Conclusions

In this paper we have faced the ecological problem of stability European water frog populations. We have shown how female preferences and deleterious mutations stabilize L-E complexes and also how the introduction of translocated *P. ridibundus* frogs can destroy such complexes. For modelling this phenomena we have used a variant of P systems and we have shown their suitability for describing real macroscopic ecological systems.

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