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Evolutionarily stable strategies for stochastic processes

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Abstract

The classical definition of evolutionary stability assumes that the fitness of each phenotype is fully determined by the composition of phenotypes in the population and by the strategies of each of these phenotypes. In natural populations, however, stochasticity often plays a crucial role in determining the fitness of an individual and a deterministic fitness function is probably rather rare. For example, choices of a new host plant, prey or oviposition patch are completely stochastic processes. Here we introduce a new definition of ESS that takes into account the effect of stochasticity on individual fitness. Then we show an application of this definition in a realistic system.
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1. Introduction

Evolutionary stability of a phenotype (ESS) is defined as a property of the phenotype to defy the attacks of other phenotypes (Hofbauer and Sigmund, 1988). It is therefore assumed that fitness of each phenotype is fully determined by the composition of phenotypes in the population and by the strategies of each of these phenotypes. However, this is not always the case. Some examples are given below:

Each phenotype is characterised by a set of parameters, which in reality is so large that they cannot all be included into the definition of a phenotype fitness function, as verification of such a definition would not be possible. Therefore only a subset of important parameters is used and verified and the remainder is treated as random noise.

Certain external factors (e.g., temperature or wind) can substantially affect the immediate behaviour of a phenotype. We cannot ignore the evolutionary consequences of these factors, but their prediction is impossible. Thus even these processes are treated as if they acted at random.

When "redistributing" in the most general meaning of this word, organisms often choose a new host plant,

prey patch, oviposition patch, mating partner, etc. at random. The result of this choice—and consequently fitness of each individual—is therefore a realisation of a stochastic process.

In these three examples, which are common in nature, stochasticity plays a crucial role in determining the fitness of an individual and a deterministic fitness function is probably rather rare. Sometimes, as in the biologically most important example (example 3), it is even impossible to define fitness in a deterministic way.

Some definitions of ESS based on mathematical models of population dynamics do include stochastic effects as random perturbations of equilibria of such systems (Cressman, 1996). In others the stochastic effect is incorporated in the construction of a mathematical model of population dynamics or into the expression for the fitness function (Yoshimura and Clark, 1991; Sasaki and Ellner, 1995; Cressman, 1996; Yasuda and Ohnuma, 1999). The local character of the definition of ESS is then evident. Many authors (Ellner, 1985; Thomas, 1984; Yoshimura and Shields, 1987; Cressman, 1996) try to transform this fact to finding conditions for local stability of equilibria of stochastic differential equations. Their stochastic character is defined by a random set of input parameters. Properties of the solutions of stochastic differential equations are, however, strongly dependent on the shape of the random distribution of these parameters. These random distributions are usually

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supposed to be normal, which makes them less realistic, but the calculations are then relatively easy.

Here we introduce a new definition of ESS that takes into account the effect of stochasticity on individual fitness. Then we show how to apply this definition in a realistic system. We define the ESS for the predator oviposition strategy in a situation, where both the distribution of the prey on plants and subsequent immigration of the predator are supposed to be stochastic processes.

2. ESS definition in a stochastic situation

The original definition of ESS:

Definition 1. Let us denote by $W(I,Q)$, continuous in the second variable, the fitness function of an individual I-phenotype in a population, whose composition is Q and by $Q(\varepsilon) = \varepsilon J + (1-\varepsilon)I$, $\varepsilon \in [0,1]$, the mixed population, where ε is the frequency of J-phenotypes and $(1-\varepsilon)$ that of I-phenotypes.

A population of I-phenotypes is said to be evolutionary stable (ES), if there exists an $\varepsilon_0, 1 > \varepsilon_0 > 0$ such that for each $\varepsilon_0 > \varepsilon > 0$ and for each $J \neq I$

$$W(J, \varepsilon J + (1-\varepsilon)I) < W(I, \varepsilon J + (1-\varepsilon)I). \qquad (1)$$

(Here and in the following all fitness functions $W(I,.)$ are assumed to be nonnegative.)

When a metapopulation is considered, consisting of many populations living in n discrete patches (as for example a metapopulation of insects that consists of many populations, each living on one plant), then phenotype I is ES in n patches, if and only if it is ES in each patch.

In this definition, it is implicitly assumed that $W(.,.)$ is a deterministic function and therefore it can be decided, whether (1) holds, i.e., whether phenotype I is successful in competition with phenotype J, or not. This is not always the case. Fitness of an individual quite often depends on external factors with unknown underlying dynamics (e.g., weather) which have therefore to be considered as random noise.

To modify (1), so as to be applicable in a randomly fluctuating environment, we define a random "resolution function" $R(W(I,Q,),z)$, where z is a random variable representing the influence of randomly fluctuating environment. Function R can attain only two values: 1 if (1) holds and 0 otherwise. In addition, there are many possibilities for the population composition Q. In the classical approach, Eq. (1) must hold for any ε $(1 > \varepsilon_0 > \varepsilon > 0)$. If the population is composed at random, some of the compositions may be less probable than other ones. For example, in the classical ESS approach it is highly probable that a population consists

of a small number of mutants and of a large number of resident individuals. Therefore we define a random distribution $D_2[0;1]$ for the definition of the population composition, $Q(\varepsilon), \varepsilon \in D_2[0;1]$. These considerations lead us to the following modification of Definition 1:

Definition 2. Let $D_1[0;1]$, $D_2[0;1]$ be random distributions on the interval $[0;1]$, $z \in D_1[0;1]$, $\varepsilon \in D_2[0;1]$. Let I and J be phenotypes, $W(I,Q)$ the fitness function of phenotype I in a population, the composition of which is Q. Let $Q(\varepsilon) = \varepsilon J + (1-\varepsilon)I$. Let $0 \leqslant \varepsilon \leqslant 1$.

Define $R(.,.)$ as follows:

$$R(W(I,Q(\varepsilon)),z) = 1,$$
$$\text{if } \frac{W(I,Q(\varepsilon))}{W(I,Q(\varepsilon)) + W(J,Q(\varepsilon))} > z, \qquad (2)$$

$$R(W(I,Q(\varepsilon)),z) = 0,$$
$$\text{if } \frac{W(I,Q(\varepsilon))}{W(I,Q(\varepsilon)) + W(J,Q(\varepsilon))} \leqslant z.$$

Then *phenotype I is α-successful in competition with phenotype J*, if the probability that $R(W(I,Q(\varepsilon)),z) = 1$ in the set of $\varepsilon \in D_2[0;1]$ and $z \in D_1[0;1]$ is greater or equal to α:

$$P\{R(W(I,Q(\varepsilon)),z) = 1, \ \varepsilon \in D_2[0;1],$$
$$z \in D_1[0;1]\} \geqslant \alpha. \qquad (3)$$

Lemma 1. *Let there exist an ε_0, $1 > \varepsilon_0 > 0$ so that $P\{\varepsilon_0 \leqslant \varepsilon; \ \varepsilon \in D_2[0;1]\} = P\{z \geqslant \frac{1}{2}; \ z \in D_1[0;1]\} = 0$. Then if phenotype I is ESS according to definition 1, it is 1-successful in competition with all phenotypes $J \neq I$.*

Proof. If I is an ESS, then from (1), for all phenotypes $J \neq I$ and for all $\varepsilon < \varepsilon_0$, then it holds

$$\frac{W(I,Q(\varepsilon))}{W(I,Q(\varepsilon)) + W(J,Q(\varepsilon))} > \frac{1}{2}.$$

From (2) and $P\{z \geqslant \frac{1}{2}; \ z \in D_1[0;1]\} = 0$. it follows $P\{R(W(I,Q(\varepsilon)),z) = 1, \ \varepsilon \in D_2[0;1], z \in D_1\} = 1$. $\square$

Lemma 1 relates the classical definition of *ESS* to the condition of α-success. The local and non-random character of *ESS* is clearly seen from here: An *ESS* is α-successful only if the distributions of ε and z are of a special type. Definition (2) has the advantage that the criterion for I being α-successful (Eq. (3)) is probabilistic. This means that I can lose some contests with other phenotypes, but the measure of the set of such events (their probability) is smaller than $(1-\alpha)$. This becomes extremely important when one relates simulation results to ESS definition in a stochastic situation and thus bridges the local character of *ESS*.

Evolution can be seen—both temporally and spatially—as a very long (or infinite) sequence of

realisations of a stochastic process—for example, many generations of individuals living on many host plants. It may therefore happen that in a random situation there does not exist any phenotype satisfying conditions of Definition 1. How then is the evolutionary "stability" of a phenotype determined? In other words: How many other phenotypes has a certain phenotype to encounter and defeat in order to become "evolutionary stable" in a stochastic situation? We tackle this problem as follows: Assume that evolution is realised independently n times (in different instants and/or places).

Definition 3. Let n be a natural number. Let $D_1[0;1]$, $D_2[0;1]$ be random distributions on the interval $[0;1]$, $\varepsilon_k \in D_2[0;1]$, $z_k \in D_1[0;1]$, $k=1,2,\ldots,n$. Let $z=(z_1,\ldots,z_n)$, $\boldsymbol{\varepsilon}=(\varepsilon_1,\ldots,\varepsilon_n)$. Let I and J be phenotypes, let $Q_k(\varepsilon)=\varepsilon_k J+(1-\varepsilon_k)I$, $\varepsilon_k \in [0,1]$, $k=1,2,\ldots,n$ be compositions of the population. Let $\boldsymbol{Q}(\varepsilon)=(Q_1(\varepsilon_1),\ldots,Q_n(\varepsilon_n))$. Then we define a random fitness function of the phenotype I as follows:

$$WL(I,\boldsymbol{Q}(\varepsilon),z)=\sum_{i=1}^{n} W(I,Q_i(\varepsilon_i))R(W(I,Q_i(\varepsilon_i)),z_i)$$

(4)

Phenotype I is said to be α-n-successful in competition with phenotype J, if

$$P\{WL(I,\boldsymbol{Q}(\varepsilon),z)\geqslant WL(J,\boldsymbol{Q}(\varepsilon),z),$$
$$\varepsilon_k \in D_2[0,1], z_k \in D_1[0,1], k=1,2,\ldots,n\}\geqslant \alpha.$$

(5)

Remark 1. Definition 3 states that phenotype I is α-n-successful against phenotype J, if with probability $\geqslant \alpha$ phenotype I produces more progeny (i.e., has greater fitness) in the n independent realisations of the process than phenotype J.

Remark 2. Let there exist an ε_0, $1>\varepsilon_0>0$ so that $P\{\varepsilon_0\leqslant \varepsilon_k, \varepsilon_k \in D_2[0;1], k=1,2,\ldots,n\}=$ $P\{z_k\geqslant \frac{1}{2}; z_k \in D_1[0;1], k=1,2,\ldots,n\}=0$. Then if the phenotype I is ESS according to Definition 1, it is 1-n-successful in competition with all phenotypes $J\neq I$.

Let Ω be the set of all possible phenotypes. If J_1, $J_2 \in \Omega$, $J_1 \neq J_2$, then—in the general case—J_1 and J_2 may not occur with the same probability in the evolutionary process. Therefore we define another random distribution $D_3=D_3(\Omega)$. The ESS with probability (p-n-ESS) can now be defined as follows:

Definition 4. Let n be a natural number, $D_1[0;1]$, $D_2[0;1]$ random distributions on the interval $[0;1]$, $z_k \in D_1[0;1]$, $\varepsilon_k \in D_2(\Omega)$, $D_2[0;1]$, $k=1,2,\ldots,n$, $z(\varepsilon)=(z_1(\varepsilon_1),\ldots,z_n(\varepsilon_n))$, Ω the set of all phenotypes, $D_3=D_3(\Omega)$ a random distribution on Ω. Let for any I, $J \in D_3(\Omega)$: $Q_k(\varepsilon_k)=\varepsilon_k J+(1-\varepsilon_k)I$, $\varepsilon_k \in [0;1]$, $k=1,2,\ldots,n$ be

compositions of the population. Let $\boldsymbol{Q}(\varepsilon)=(Q_1(\varepsilon_1),\ldots,Q_n(\varepsilon_n))$. Let $WL(I,\boldsymbol{Q}(\varepsilon),z(\varepsilon))$ be defined by (4). Phenotype I is said to be evolutionary stable with probability p (abbreviated by p-n-ESS), if

$$P\{WL(I,\boldsymbol{Q}(\varepsilon),z)\geqslant WL(J,\boldsymbol{Q}(\varepsilon),z), \varepsilon_k \in D_2,$$
$$z_k \in D_1, J \in D_3, J\neq I, k=1,\ldots,n\}\geqslant p.$$

(6)

Remark 3. If phenotype I is α-n-successful in competition with any other phenotype J, then it is α-n-ESS.

Lemma 2. Let there exist ε_0, $1>\varepsilon_0>0$ so that $P\{\varepsilon_0\leqslant \varepsilon_k, \varepsilon_k \in D_2[0,1], k=1,2,\ldots,n\}=P\{z_k\geqslant \frac{1}{2}; z_k \in D_1[0;1], k=1,2,\ldots,n\}=0$. If phenotype I is ESS in all n patches, then I is 1-n-ESS.

Proof. According to the Remark 2, if I is an ESS, then it is 1-n-successful in competition with any $J\neq I$. According to the Remark 3 this implies that I is 1-n-ESS. □

3. Application of the concept of p-ESS to insect populations

Here we present a simple example of evolution of life history strategies of a hypothetical insect predator species in a realistic predator–prey system (motivated by ladybird–aphid systems). The illustrative situation described below typically requires a p-n-ESS concept, as in our model—although juvenile predators stay in one patch of prey during their development (one season)—adult predators redistribute themselves between patches at random after each season. The quality of any patch they find and assess for oviposition (patch is of a good quality, if it contains a large number of prey and a low number of conspecifics) can therefore be considered as realisation of a random variable. Thus the potential fitness of a predatory mother (number of her descendants at the end of the next season) is not a deterministic function of her strategy, but strongly depends on the quality of the random sequence of patches she visits during her reproductive period.

This example illustrates that the classical ESS approach is irrelevant in certain cases and the p-ESS concept must be used. However, it also demonstrates a biologically very interesting phenomenon: that evolution can lead to optimisation of predator oviposition strategies in the sense of reduction of intraspecific competition—avoidance of reproduction in sites already occupied by conspecifics, rather than to maximisation of its feeding rate.

3.1. Biological assumptions

Real insect predator–prey systems substantially differ from what is assumed by the classical (Lotka–Volterra,

Holling type, etc.) predator–prey models used by modellers (Dixon et al., 1997; Kindlmann and Dixon, 1999b). The main differences are (Dixon et al., 1995; Kindlmann and Dixon, 1999a): (i) Juveniles and adults have to be considered as two different entities, as the former stay within one patch and do not reproduce, while the latter move between patches of prey and reproduce there. (ii) Because of their high mobility, food availability seems to be much less restrictive for adults than juveniles, which are confined to one patch. Therefore, the functional response does not seem to be important for adults. (iii) Egg and larval cannibalism are common in insect predators (Osawa, 1989, 1991, 1992). Consequently, there is a strong selection pressure on adult predators to lay their eggs only in patches in the early stages of their development and avoid those containing conspecific larvae. This determines the strategies of predatory adults to a much greater extent than availability of food in one prey patch (Dixon et al., 1995, 1997; Kindlmann and Dixon, 1999a, b; Osawa, 1992).

Expressed in mathematical terms, in a realistic predator–prey metapopulation model one has to assume two thresholds for the population size in the patch: a lower threshold for the prey and an upper threshold for the predator. Below the lower threshold for prey population number, the predator offspring might starve, above the upper threshold for predator population number there is a large risk of predator offspring being cannibalised by conspecifics (Kindlmann and Dixon, 1999b).

Practical biological consequences of the above-mentioned assumptions for insect predator–prey systems will be published elsewhere. Here we concentrate on the algorithm that finds the p-n-ESS in this situation.

3.2. Model description

1. There are n patches ("plants"), m generations of predator–prey metapopulation, each generation consists of X prey individuals and of Y predator individuals.
2. In each generation, j, each possible predator phenotype I_j is characterised by two numbers:

   2.1. x_{Ij}—the lower threshold of population size of the prey in the patch, below which the predator will not lay eggs.

   2.2. y_{Ij}—the upper threshold of population size of predator in the patch, above which the predator will not lay eggs.

3. The pairs of phenotype characteristics are uniformly distributed in the set $[X_1, X_2] \times [Y_1, Y_2]$, X_1, X_2, Y_1, Y_2 are non-negative real numbers. According to Definition 4, $\Omega = [X_1, X_2] \times [Y_1, Y_2]$ and $D_3(\Omega)$ is a uniform distribution on Ω.
4. D_1 is a uniform distribution on $[0;1]$, $z \in D_1[0;1]$ is a random variable representing influence of randomly fluctuating environment *sensu* Definition 2.

5. $D_2[0;1]$ is a uniform distribution on the interval $[0;1]$, $\varepsilon \in D_2[0;1]$.
6. In each generation, j, we tested success of predator phenotype I_j in competition with phenotype J_j in a population, the composition of which is $Q(\varepsilon) = \varepsilon J_j + (1-\varepsilon)I_j$ in a randomly fluctuating environment defined by point 4 *sensu* Definition 2. The test consisted of the following steps:

   6.1. The total of n patches were sequentially colonised by the X prey individuals. In the model this was assured by sequential selection of X random numbers from a uniform distribution on the interval $[0,n]$. The total number of prey individuals in kth patch was increased by 1, whenever this random number was in the interval $[k-1,k]$.

   6.2. After that, the n patches were sequentially "colonised" by predators:

   6.2.1. In order to keep on average the above-mentioned proportion of phenotypes in offspring numbers, a random number was chosen from $[0,1]$. If this random number was smaller than ε, it was assumed that the predator searching for a patch in which to lay an egg was of phenotype J_j, otherwise it was assumed to be of phenotype I_j.

   6.2.2. A patch was chosen at random in the same manner as it was colonised by prey.

   6.2.3. If the total number of prey individuals was larger than x_{Ij} (or x_{Jj}, respectively) and if the total number of predator individuals was smaller than y_{Ij} (or y_{Jj}, respectively), the number of predators in this patch was increased by 1.

   6.2.4. If the total number of prey individuals was lower than x_{Ij} (or x_{Jj}, respectively) or if the total number of predator individuals was higher than y_{Ij} (or y_{Jj}, respectively) the predator was assumed not to reproduce and go to another patch—step 6.2.2. was repeated.

   6.2.5. Steps 6.2.2–6.2.4 were repeated until a suitable patch with more than x_{Ij} (x_{Jj}) prey individuals and less than y_{Ij} (x_{Jj}) predators was found, but not more than 10 times. If during the 10 trials the patch is not found, the predator is discarded.

   6.2.6. Procedure 6.2.2–6.2.5 was repeated Y times.

   6.2.7. Thus each of the patches was colonised by a mixture of I_j and J_j phenotypes. In each patch, k, denote by a_{jk} the number of prey individuals, by $p(I_j, k)$ the number of phenotype I_j predator individuals and by $p(J_j, k)$ the number of phenotype J_j predator individuals. If $p_{jk} = p(I_j, k) + p(J_j, k)$, then it is reasonable to assume (Kindlmann and Dixon, 1993) that the proportion of predatory larvae surviving to adulthood for each of the

phenotypes will be:

$$\text{pr}(I_j, k) = \frac{p(I_j, k) a_{jk} \eta}{a_{jk} \eta + p_{jk}} \quad \text{for phenotype } I_j,$$

$$\text{pr}(J_j, k) = \frac{p(J_j, k) a_{jk} \eta}{a_{jk} \eta + p_{jk}} \quad \text{for phenotype } J_j,$$

where η is the "preference for prey", common for both phenotypes and for all generations, is the relative likelihood of eating a prey compared to a conspecific.

6.2.8. Then a random number from the uniform [0,1] distribution was chosen. If this random number was smaller than $\text{pr}(I_j, k)/(\text{pr}(I_j, k) + \text{pr}(J_j, k))$, then the predator phenotype I_j was assumed to win and survive in patch k and *vice versa*.

6.2.9. Fitness of each of the phenotypes, was defined as FI_j, respectively FJ_j was defined as the sum of $\text{pr}(I_j, k)$, respectively $\text{pr}(J_j, k)$ of all patches, where the phenotype I_j, respectively J_j "won". If $FI_j \geqslant FJ_j$, then phenotype I_j was assumed to be more successful in this generation and tested against another J_j phenotype and vice versa.

7. Phenotype that won was then tested against another randomly chosen phenotype, J_{j+1}: see point 3.

3.3. Relation between p-m-ESS and the applied model

According to Definition 2 and to the way the model was built, fitness of phenotypes is calculated in each patch k and in each generation j as

$$W(I_j, Q_k(\varepsilon_k)) = \frac{p(I_j, k) a_{jk} \eta}{a_{jk} \eta + p_{jk}} \quad \text{for phenotype } I,$$

$$W(J_j, Q_k(\varepsilon_k)) = \frac{p(J_j, k) a_{jk} \eta}{a_{jk} \eta + p_{jk}} \quad \text{for phenotype } J$$

in step 6.2.7. of the algorithm described above. It strongly depends on the random way, how the individuals are distributed on plants in steps 6.1 and 6.2 of the algorithm. The resolution function R from Definition 2 is defined in 6.2.8 in our example. Thus the classical ESS approach cannot be used and the *p-m*-ESS theory is the only relevant one and Definitions 2–4 are to be applied.

In our example of an insect population both phenotypes and the external factors were chosen from a uniform distribution. Computer simulation of evolution during 50 000 generations was performed. Fig. 1 shows the frequencies of success of different phenotypes characterised by different combinations of x_I (minimum number of prey), y_I (maximum number of predators) during the generation cycle in our model run. Fig. 2

shows the probabilities described in (5) for different combinations of x_I (minimum number of prey), y_I (maximum number of predators) during the generation cycle. Fig. 3 then shows the relation between *p-m*-ESS (Fig. 2) and frequencies of occurrence of phenotypes (Fig. 1). It is evident from this figure that these two values are closely correlated.

The results shown in Figs. 1 and 2 have an important biological meaning. The frequencies of success of phenotypes decline quite steeply from the optimal values. Therefore there should be a strong selection pressure in insect predators for ovipositing only in patches, where there is more than a certain minimum number of prey and less than a certain maximum
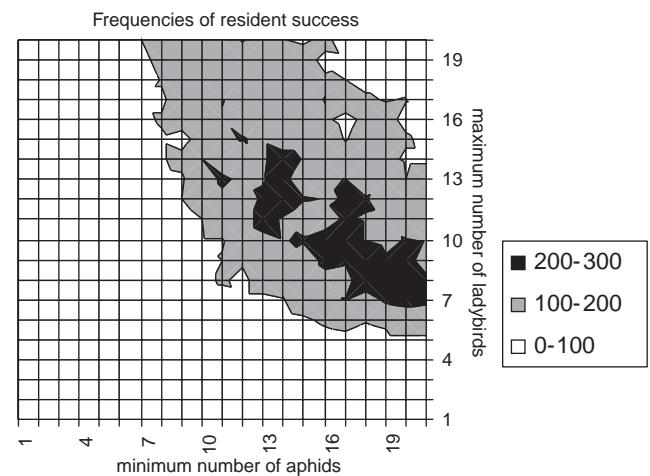

Fig. 1. Frequencies of resident success of phenotypes characterised by different combinations of x_I (minimum number of prey), y_I (maximum number of ladybirds) during the generation cycle in our model run.
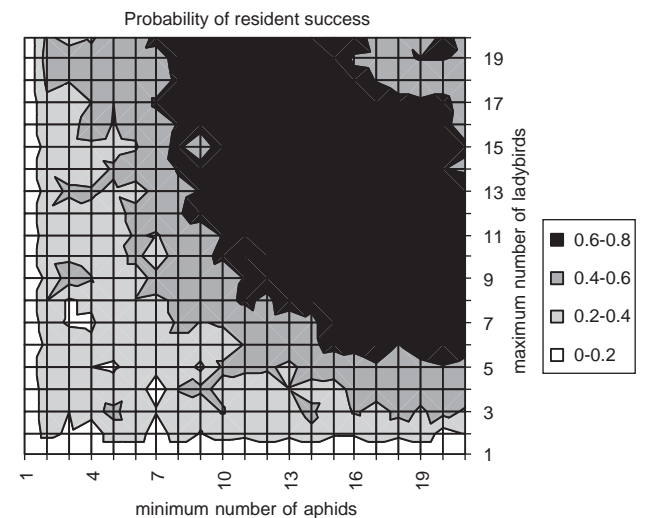

Fig. 2. Probabilities described in (6) of different combinations of x_I (minimum number of prey), y_I (maximum number of ladybirds) during the generation cycle.

Dependence of the probability of resident success on the resident frequency
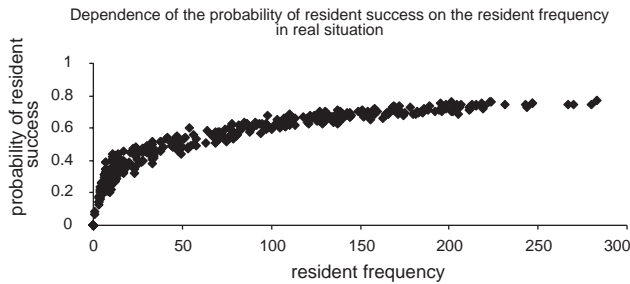in real situation

Fig. 3. Dependence of the probability p of resident success described in (6) on the frequency of resident success.

number of other predator offspring present. It was shown that insect predators do not reproduce in patches, where prey is scarce, but they also react to "oviposition deterring pheromone" released by conspecific larvae by ceasing oviposition and looking for another patch (Kindlmann and Dixon, 1999a). Thus empirical data confirm our model predictions.

4. Conclusions

The classical definition of ESS does not apply to many natural situations. Therefore, there is a need for a new definition of an evolutionary stable phenotype. The occurrence of phenotypes in the patch, composition of predator populations in the patch and variation of external factors are considered as stochastic factors. These stochastic effects are expressed by distribution functions. The new definition of ESS is not dependent on the form of these distribution functions. The uncertainties in the evolutionary process are reflected in the new definition of ESS, which is stochastic rather than deterministic. This concept makes it possible to distinguish between evolutionary stability with the a priori given probability p (p-m-ESS). This is a more general definition than that of classical ESS, as the relations are defined only with probability 1. Very important for practical purposes seems to be finding the explicit relation between p-m-ESS and frequencies of occurrence of phenotypes. The phenotypes, which are the most frequently successful in competition with other ones are p-m-ESS with a large p.

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