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A MODEL OF SYMPATRIC SPECIATION THROUGH REINFORCEMENT

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Abstract. Sympatric speciation, i.e. the evolutionary split of one species into two in the same environment, has been a highly troublesome concept. It has been a questioned if it is actually possible. Even though there have been a number of reported results both in the wild and from controlled experiments in laboratories, those findings are both hard to get and hard to analyze, or even repeat. In the current study we propose a mathematical model which addresses the question of sympatric speciation and the evolution of reinforcement. Our aim has been to capture some of the essential features such as: phenotype, resources, competition, heritage, mutation, and reinforcement, in as simple a way as possible. Still, the resulting model is not too easy to grasp with purely analytical tools, so we have also complemented those studies with stochastic simulations. We present a few results that both illustrates the usefulness of such a model, but also rises new biological questions about sympatric speciation and reinforcement in particular.

1. Introduction.

In the year 1707 two boys were born who both turned out to ponder on the concept of species. Carl Nilsson was born in the spring in Sweden and Georges-Louis Leclerc was born in the fall in France. Later, they became known as Comte de Buffon and Linnaeus. They did not come to the same conclusion regarding the possibility for species to evolve and they did not came to respect each others work particularly high. Linnaeus created a hierarchical order of the different, by God given, species, while Buffon had a more dynamical view on species and defined that two animals — of different gender — belong to the same species if they can produce a fertile offspring. Buffon[2] turned out to be an important inspiration to Charles Darwin, who on the other hand obviously used the linnaean system in

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[2] Buffon is also known for his probabilistic works such as the so called Buffon's needle problem, see for example [26].

his studies. In “The Origins of Species” Darwin calls speciation “the mystery of mysteries”.

1.1. **Speciation.** In [2, p. 110] the question “How does speciation occur?” (with its underlying question: “Can organisms speciate in sympatry?”) is listed among the five “big questions” in evolutionary biology.

Good introductions to the speciation problem is given in van Dooren’s thesis [33] and in [25, Chapter 14].

Speciation is a delicate interplay between selection, mutations, genetic drift and environmental effects. All these processes are highly demanding to study separately. Together, the challenge is breathtaking. We have therefore chosen to study a mathematical model of a highly simplified situation. Even though we try to make the mathematical model as simple as possible, it turned out that including the ingredients of sexual selection with reinforcement, niched food sources and evolutionary dynamics, makes the model rather hard to analytically grasp, and we have therefore added a number of simulation results.

1.2. **Sympatric speciation.** It was long debated if sympatric speciation, i.e. the split of one species into two separate in the *same* environment, was possible at all, or in other words, was it necessary that two populations of the species be physically separated (allopatric), e.g. on two different islands, in order to evolve into two different species? However, since Bush’s experiment on flies [8], there is a more general acceptance for the possibility of sympatric speciation. The main barrier for splitting a species into two in a common environment is how to avoid hybrids.

1.3. **Reinforcement.** To obtain speciation in sympatry, one need reinforcement, i.e. enhancement of prezygotic[3] isolation. Reinforcement is also called “The Wallace effect” after the co-discoverer of evolution. However, the very term “reinforcement” was coined by Blair [7]. In [32] there is an interesting simulation on how plants can diverge from each other using separate flowering times as reinforcement. See also the simulations performed in [27]. Recent work on bird song as reinforcement mechanism for flycatchers are given in [24]. In [29] the so called gene flow was studied as a force behind reinforcement, and in [13] and [21] other models are presented to study reinforcement using PDE:s. In order to investigate the effect of reinforcement, besides observation from nature (e.g. the above mentioned [24]), a series of experiments have been set up starting from the Drosophila “Destroy-The-Hybrids” experiment by Koopman [20] which showed that reinforcement evolved so that instead of a hybrid rate around 50%, it decreased to 5% within only six generations. The intriguing history of reinforcement is described in [11, Chapter 10]. A short introduction to reinforcement can also be found in [28]. Here we would like to mention [3], [22], [34], and the books [16, especially Chapters 1,6, and 7], [18, especially Chapter 10 by R. Bürger and C. Krall], and [12, where Chapter 10 is devoted to reinforcement, see especially Figures 10.3 and 10.4] as inspiring sources. See also the many interesting articles in [1]. Another study that is highly relevant to our approach is Dieckmann and Doebelie’s [15]. However their approach is different in several aspects.

Let us point out the comparative study performed by Coyne and Orr, [10] which considered prezygotic isolation between species in both sympatry and allopatry. As expected, the reinforcement is stronger in the sympatric case.

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[3] before fertilization

1.4. **Introduction of the model.** This paper addresses the question of *sympatric speciation* in combination with *reinforcement dynamics*. By sympatric speciation we mean that a population of one species through mutations, competition, mating etc. may break up into two or more distinct species sharing the same habitat. A species can be defined in different ways, but here we mean a sub-population such that essentially all (sexual) reproduction takes place within that sub-population. *Reinforcement* is then defined as a process by which natural selection strengthens the separation of the sub-populations.

In our model, the population is described via a phenotype distribution $u = u(z,t)$, where z is the phenotype of an individual. The phenotype has several components, some of which are related to the adaptation to the environment (such as the beak length of a bird), and some have no connection with the environment, but are important for the way in which the individuals recognize each other. This could be for example the color of the bird, e.g. if an individual prefers mating partners of a certain color. Initially, we assume that all individuals in the species share a common such "color", but both those can evolve through mutations to form reinforcement, i.e. pre-zygotic barriers. It is this unguided process that we are mainly interested to study.

The environment is modeled as a function $f(x)$ or $f(x,t)$, which describes the availability of some resource, e.g. food, that limits the population size. In our examples, x is also one of the components of the phenotype z, and in this way it is possible to measure an individual's adaptation to the environment.

It is reasonable to assume that speciation occurs on a time scale that is very slow compared to variations in the population size, and therefore we assume that the population is constant at the carrying capacity of the habitat, and hence all the reproduction will achieve is a modification of the phenotype distribution. Since we are interested in sympatric speciation, each pair of individuals has potentially the same probability of meeting. However, the mating rate of a given couple is computed as a function of the attraction between the individuals in the couple (as given by their phenotype), and the number of offspring in the litter depends on the parents' adaption to the environment (expressed in terms of the phenotype value x).

The phenotype of the offspring is simply computed as the average of the parents' phenotype. This may be a good model for phenotypic traits such as body length or weight, but certainly in other cases a better model would be that the offspring chooses the phenotype of one of the parents. In either case we add a random component to the phenotype of the offspring. And although this is a model for sexual reproduction, gender is not taken into account here. The real biological process behind the result of the mixing of the parents' genotypes is highly complex.

Since our focus is to study the evolution of reinforcement leading to a decreased number of "hybrids", we are interested in laws on phenotypic trait that is hybrid-prone. The law we picked – taking the average of the parents – is indeed such a law. Another possibility is to randomly pick the genotype from one of the parents, plus a possible mutation, as the offspring's genotype. See for example [17, 15], where a model of multilocus genetics is considered: for each locus there are two possible alleles, 0 and 1, and the phenotype is determined by the number of 1-alleles. Our model could be obtained as a scaling limit when the number of loci becomes infinitely large: the offspring would get the average of the parents' phenotype as a result of the law of large numbers, and the central limit theorem could justify the normally distributed variation around the mean. Note that Figure 5 in[15] shows that an increase in the number of loci gives longer time until branching, which is an indication that our average model, is indeed hybrid-prone.

The dynamics can then be modeled as a (time discrete) Markov process, which will be described in detail in Section 2. The model is first described for a population with a finite number of individuals, and all simulations are carried out for that case. We then rescale the problem by letting the number of individuals approach infinity, to obtain a limiting Markov process (still time discrete).

Finally, we will need a mathematical definition of speciation: we say that speciation has occurred if when fitting a bimodal distribution to the phenotype distribution, the two means are significantly different.

There are many mathematical questions that need to be addressed, and these are only touched on in this paper; the mathematical theory is work in progression, and will be the topic of a future paper.

The question of speciation has been addressed also from a more mathematical point of view by several authors. Typically then competition is a driving force for speciation, and modeled by variations of logistic equations. This is the case of [15] where results similar to ours are presented, although the basic models are different. Two papers where a more complete mathematical analysis is given are [14], and [23] (see also [31]).

The rest of the paper is organized as follows:

- First, the basics of the time-discrete model is introduced.
- In Section 2.3 we analyze the asymptotic situation when the population size increases to infinity.
- In Section 2.4 we compare our evolutionary dynamical model with earlier results from a few different fields where an averaging principle governs the updating dynamics. The examples are taken from aligning rods and schools of fish.
- Results are presented with graphs of simulations in Section 3 both for the discrete and continuous food source cases.
- The question on time to speciation is illustrated in Section 3.1.4.
- In Section 4 we discuss the model, its results and possible future work.

2. **The model.**

2.1. **A time discrete model.**

We think of a population living in an environment, where some essential resource (which will be called "food") whose distribution in a space $\mathcal{X}$ is given by a (positive) measure f.

In the population, an individual is characterized by its phenotype $z = (x, y, y^*)$. The first component x tells where in the space $\mathcal{X}$ an individual is best adapted to gather food. The beak length of a bird and the distribution of different size flowers in an environment could be one example. In our model $\mathcal{X}$ is $\mathbb{R}$ or some subset thereof.

The remaining components of the phenotype, $y, y^* \in \mathcal{Y}$, are related to the mating of individuals: y describes the appearance (looks) of an individual, and y^* is the appearance it prefers to see in a potential mating partner. One could have $\mathcal{X} = \mathcal{Y}$, but here we think of a phenotype independent of the adaptation to the food resources. With birds, y could be the pitch of an individual's song, and y^* the pitch it likes its partner to sing.

In the dynamic model time is discrete, and the whole population is replaced from one generation to the next. The population phenotype at a given time t is then given by $Z^N \equiv (z_1, ..., z_N) \in (\mathcal{X} \times \mathcal{Y} \times \mathcal{Y}^*)^N \equiv \mathcal{Z}^N$, whose evolution is modeled as a Markov chain, $\{Z_t^N\}_{t\in\mathbb{N}}$. The size of the population $N = N_t$ is itself time dependent, and we write $Z_t = Z_t^{N_t}$ for the configuration of the population at time t.

These individuals are polygamous, because there is no absolute limit as to with how many other individuals they may produce offspring. Each individual chooses one mating partner in the population, but it can itself be chosen many times, and hence the number of mating partners for a given individual depends on how often it is chosen by another individual. Once a pair is formed, the number of their offspring depends on their joint ability to collect food.

More precisely, a population that at generation t has $N = N_t$ individuals, produces a population at generation $t+1$ according to the following description:

- The population at generation t is given as $Z_t = \{z_j\}_{j=1}^{N_t} = \{(x_j, y_j, y_j^*)\}_{j=1}^{N_t}$. The status of an individual is determined by its phenotype, but also by $c_j = c_j(Z_t)$, which is the fraction of the total food resource, $\|f\| = \int_{\mathcal{X}} f(dx)$, it is able to collect. The value of c_j depends on the resource distribution $f(x)$, and on the population phenotype, and is given as

$$c_j(Z_t) = \int_{\mathcal{X}} \frac{e^{-(x_j-x)^2/2\gamma_x^2}}{\sum_{k=1}^{N_t} e^{-(x_k-x)^2/2\gamma_x^2}} \frac{f(dx)}{\|f\|}. \tag{1}$$

  The interpretation is that each individual succeeds in collecting a fraction of the food at position x according to its relative competitive strength at that point; the food source is depleted by the population. The parameter γ_x is constant, the same for all individuals in the population. It determines how the competitive strength of an individual decreases away from the optimal point x of its phenotype.
- Each individual, j, chooses a mating partner $k = k_j \neq j$ according to a probability distribution $P_j(k) = P_j(k\,; Z^N)$ which is determined by the appearance parameter y_j, and the preference parameters y_k^* of the other individuals:

$$P_j(k; Z^N) = \begin{cases} \dfrac{e^{-(|y_k - y_j^*|^2 + |y_j^* - y_k|^2)/2\gamma_m^2}}{\sum_{i\neq k} e^{-(|y_k^* - y_i|^2 + |y_i^* - y_k|^2)/2\gamma_m^2}} & (j \neq k) \\ 0 & (k = j)\,. \end{cases} \tag{2}$$

  Here γ_m is an additional parameter, the same for the entire population, that determines how selective individuals are about choosing their partners.
- The couple (j, k_j) then produces an offspring of size $n_j = n_{j,k_j}$ which is a Poisson distribution with a parameter $\lambda_{j,k} = \lambda_{j,k}(Z^N)$ that is determined by the two parents' common ability to find sources to provide for the children:

$$\lambda_{j,k} = \frac{c_j + c_k}{2} \int_{\mathcal{X}} f(dx)\,. \tag{3}$$

  The new population size $N_{t+1} = \sum_j^{N_t} n_j$ is therefore a Poisson distributed random variable.
- The phenotype of each child is given as an average of the phenotypes of the parents plus a random perturbation. In our simulations, we assume that the phenotype belongs to a (convex) subset of $\mathbb{R}^m$, and the random perturbations

are independent and normally distributed. The phenotype of a child is then

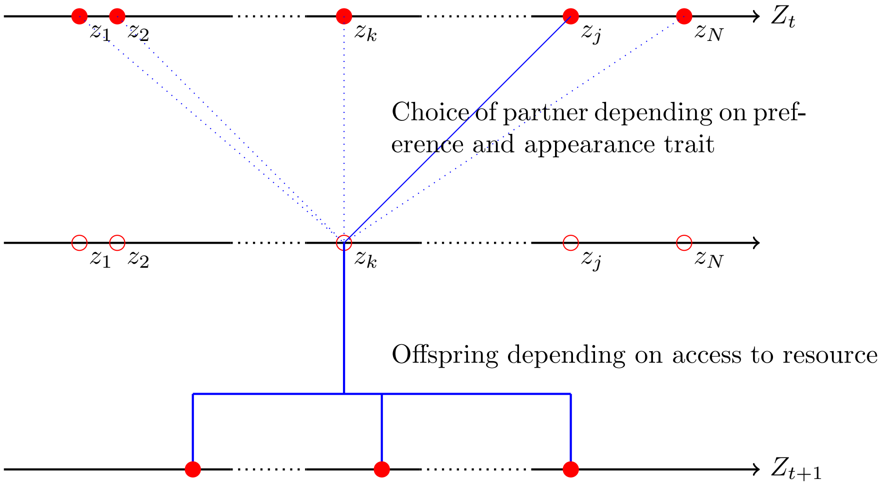
$$(x,y,y^*)_{\text{child}} = \frac{(x_j,y_j,y_j^*)+(x_k,y_k,y_k^*)}{2} + (\xi,\eta,\eta^*)\,, \tag{4}$$

where ξ, η and η^* are normally distributed with mean zero and variance σ_x^2, σ_y^2 and $\sigma_{y^*}^2$ respectively. With shorter notation

$$(x,y,y^*)_{\text{child}} = z_{\text{child}} = \frac{z_j+z_k}{2} + \zeta\,, \tag{5}$$

where the law of ζ is given by a Gaussian function $M(\zeta)$.

The process is described in the following diagram:



Note that the precise form of c_j, $P_j(k)$ and $\lambda_{j,k}$ depends on N_t, but this dependence is suppressed from the notation. When needed, the argument Z_t is written out.

The reproduction procedure is repeated for each individual in every generation. This means that the whole population is replaced, and that every individual gets one choice of a partner for mating. By the way the model is constructed, the reproduction of an individual is independent of the other individuals in a generation, in the sense that all random variables involved in the reproduction of one individual are independent of the random variables that determine the reproduction of the other individuals. The competition between the individuals, which determines the variables c_j, is deterministic, and expressed uniquely in terms of the population phenotype at time t.

This also means that the total size of the population at time $t+1$ is the sum of N independent Poisson distributed random variables, and therefore is also Poisson distributed. Hence it may happen that none of the individuals produce an offspring, and in fact, there is always a positive probability that the population will die out from one generation to the next, and with probability one, the population will die out in finite time; however, the expected time for this to happen will at least grow exponentially with $\|f\|$.

Even though there is competition, there is no absolute limitation of the number of individuals, and although this does not generally happen, it is possible to construct situations where the population grows exponentially fast; this will be discussed later.

The input parameters to the model are the initial distribution of the population, the measure $f(dx)$ which defines the distribution of the resource $\mathcal{X}$, the variance parameters σ_x^2, σ_y^2 and $\sigma_{y^*}^2$ that give the variance of the random mutations, and γ_m and γ_x, where γ_m^{-1} and γ_x^{-1} measure the choosiness with mating partner and food respectively.

Remark 1. In *e.g.* [31] and [23] competition is modeled as a binary interaction and acts on the mortality rate; here competition is mediated via the food resource, and influences the number of children.

2.2. **A time discrete master equation.** In this section we give a more precise mathematical definition of the model. The notation is similar to the one used e.g. in [19, 23].

A population with N individuals, $Z_t = \{z_1, ..., z_N\}$ can be identified with a finite point measure,

$$Z_t = \sum_{j=1}^{\langle Z_t,1\rangle} \delta_{z_j} \,. \tag{6}$$

Here $\langle Z_t, \phi\rangle = \int_{\mathcal{Z}} \phi(z) Z_t(dz)$, so $\langle Z_t, 1\rangle = N_t$ just counts the size of the population at time t. A direct advantage of this is that there is no need for explicitly stating that the numbering of the individuals is arbitrary (so that all formulas should be invariant under permutations of the indices).

The next generation, Z_{t+1} then consists of the children of all individuals in the population:

$$Z_{t+1} = \sum_{j=1}^{\langle Z_t,1\rangle} \Gamma(\cdot, z_j) = \int_{\mathcal{Z}} \Gamma(\cdot, z) Z_t(dz), \tag{7}$$

where $\Gamma(\cdot, z_j)$ is a (random) point measure with one Dirac measure for each child of individual j (to avoid double counting, the children are said to belong to the parent that chooses its partner, not to the chosen partner). The distribution of the random measures $\Gamma(\cdot, z_j)$ depends on the whole population, Z_t, because of the random choice of partners, and the competition of food resources.

The function $c_j(Z_t)$ defined in (1) states how the total food resource, $\|f\| = \int_{\mathcal{X}} f(dx)$ is distributed over the population. In the new notation, this can conveniently be expressed as a point measure $c(z, Z_t)Z_t(dz)$, where $c(z, Z_t)$ is the continuous (with respect to z) function

$$c(z, Z_t) = \int_{\mathcal{X}} \frac{\exp(-|x' - x|^2/2\gamma_x^2)}{\int_{\mathcal{Z}} \exp(-|x' - x''|^2/2\gamma_x^2) Z_t(dz'')} \frac{f(dx')}{\|f\|} \,, \tag{8}$$

which is a probability density with respect to the measure Z_t (here and elsewhere x denotes the projection of $z = (x, y, y^*)$ on $\mathcal{X}$).

With $c(z, Z_t)$, we may now formulate the distribution of the offspring $\Gamma(\cdot, z_j) = \sum_{n=1}^{N_\Gamma} \delta_{z_n}$ of an individual z_j, conditioned on its choice of mating partner z_k, where $N_\Gamma = \langle \Gamma(\cdot, z_j|z_k), 1\rangle$ is a Poisson distributed random number with parameter $\lambda(z_j, z_k; Z_t) = \|f\|(c(z_j, Z_t) + c(z_k, Z_t))/2$, and the z_n are i.i.d. with density

$M(z-(z_j+z_k)/2)$. In other words,

$$\Gamma(\cdot, z_j \mid z_j \text{ chooses } z_k) \quad = \quad \int_{\mathcal{Z}} \delta_{z-(z_j+z_k)/2} N_\Gamma(dz)\,, \tag{9}$$

where $N_\Gamma(dz)$ is a Poisson point measure with intensity measure $\lambda(z_j, z_k; Z_t)M(z)$. Hence

$$\begin{aligned}
&\mathbb{E}\Big[\int_{\mathcal{Z}} \phi(z)\Gamma(dz, z_j|z_j \text{ chooses } z_k)\Big] \\
&\quad = \quad \sum_{m=0}^{\infty} \frac{\lambda(z_j, z_k; Z_t)^m e^{-\lambda(z_j,z_k;Z_t)}}{m!} m \int_{\mathcal{Z}} \phi(z) M(z-(z_j+z_k)/2)\,dz \\
&\quad = \quad \lambda(z_j, z_k; Z_t) \int_{\mathcal{Z}} \phi(z) M(z-(z_j+z_k)/2)\,dz\,.
\end{aligned} \tag{10}$$

Similarly, expressed in this notation, the probability that an individual with phenotype z_j chooses a partner with phenotype z_k is

$$P_{z_j}(z_k)Z_t(dz_k) = \frac{e^{-(|y_k^*-y_j|^2+|y_j^*-y_k|^2)/2\gamma_m^2}\mathbb{1}_{z_k\neq z_j}}{\displaystyle\int_{z'\neq z_j} e^{-(|y'^*-y_j|^2+|y_j^*-y'|^2)/2\gamma_m^2} Z_t(dz')} Z_t(dz_k)\,. \tag{11}$$

The function $P_{z_j}(z_k)$ is a continuous function $(z_j, z_k) \mapsto [0,1]$, but it is only evaluated on the support of Z_t.

To find the distribution of the offspring of an individual z_j it is now enough to multiply (10) with $P_{z_j}(z_k)Z_t(dz_k)$ and integrate over x_k. The full population at generation $t+1$ satisfies, for any $\phi \in C(\mathcal{Z})$,

$$\begin{aligned}
&\mathbb{E}\Big[\int_Z \phi(z) Z_{t+1}(dz)\Big] \\
&\quad = \int_Z \phi(z) \int\int_{\mathcal{Z}\times\mathcal{Z}} M(z-(z_j+z_k)/2)\lambda(z_k, z_j)P_{z_j}(z_k)Z_t(dz_j)Z_t(dz_k)dz\,.
\end{aligned} \tag{12}$$

This expression does not fully characterize the measure Z_{t+1}, but it gives some useful information. Taking $\phi \equiv 1$, and using that $\int_{\mathcal{Z}} \lambda(z_j, z_k)P_{z_j}(dz_k) \le \|f\| \max \frac{c_j+c_k}{2} \le \|f\|/2$ we find

$$\mathbb{E}\langle Z_{t+1}, 1\rangle \quad \le \quad \int_{\mathcal{Z}} \max_{z_k} \lambda(z_j, z_k)\, Z_t(dz_j) \le \frac{\|f\|}{2}\langle Z_t, 1\rangle\,, \tag{13}$$

which means that the population will at most grow exponentially fast. This could potentially happen if each individual has knowledge about the food distribution in the population and is able to choose the best possible partner, and in addition there are individuals who are able to collect a fraction of the food that is independent of $\langle Z_t, 1\rangle$. Of course exponential growth is not realistic over a longer time period, but the model could rather easily be modified to limit the population size. On the other hand $\lambda(z_j, z_k) \ge \|f\|\frac{c_j}{2}$ (i.e., the worst case is when the chosen partner does not bring any resources), and so

$$\begin{aligned}
\mathbb{E}\langle Z_{t+1}, 1\rangle \quad &\ge \quad \int_{\mathcal{Z}} \min_{z_k} \lambda(z_j, z_k)\, Z_t(dz_j) \\
&\ge \quad \frac{1}{2}\int_{\mathcal{X}} f(dx) \int_{\mathcal{Z}} c(z_j, Z_t)\, Z_t(dz_j) \ge \frac{1}{2}\int_{\mathcal{X}} f(dx),
\end{aligned} \tag{14}$$

and therefore the population is not expected to decrease below a fixed level, defined only by the amount of available food. The simulations indicate that in most reasonable cases, the population size stabilizes on $\int_{\mathcal{X}} f(dx)$. From equation (14) we may also deduce that the expected number of generations before the population dies out is at least $e^{\|f\|/2}$, so that for practical purposes, this never happens (in our simulations $\|f\| \geq 60$).

The simulations results that are presented in Section 3 show that in general we cannot expect a unique stationary state, even when the size of the population is stable. However, there may be quantities, functions of Z_t, that do converge to unique limits when $t \to \infty$. Two candidates are $\mathbb{E}\left[\int_{\mathcal{Z}} c(z) \log\left(\langle Z_t, 1\rangle c(z)\right) Z_t(dz)\right]$ and $\mathbb{E}[\langle Z_t, 1\rangle]$. The first of these is, of course, the expected population size, and the second is the relative entropy of the food distribution with respect to the probability measure $Z_t/|Z_t|$. We let

$$W_c(Z_t) \quad = \quad \int_{\mathcal{Z}} c(z) \log\left(\langle Z_t, 1\rangle c(z)\right) Z_t(dz). \tag{15}$$

Then $W_c(Z_t) \geq 0$ and equal to zero if and only if the food resource is equally distributed among the $\langle Z_t, 1\rangle$ individuals in the population.

2.3. The limit of infinitely many individuals.

The notation used here follows rather closely that of [19], and consider measures of the form

$$\nu^n \quad = \quad \frac{1}{n} \sum_{j=1}^{n\langle \nu^n, 1\rangle} \delta_{z_j}\,. \tag{16}$$

The set of all such measures is denoted $\mathcal{M}^n(\mathcal{Z})$. We now wish to move the process described in Section 2.2 to $\mathcal{M}^n$, by taking the initial data $Z_0^n \in \mathcal{M}^n(\mathcal{Z})$. To rescale the dynamics, note first that $c(\cdot, Z_t^n)$ from (8) and $P_{z_j}(\cdot)$ $(j = 1, ..., n\langle Z_t^n, 1\rangle)$ from (11) still are probability densities with respect to the measure Z_t^n (n.b. the number of individuals in the population will be $n\langle Z_t, 1\rangle$). The offspring measures $\Gamma(\cdot, z_j)$ conditioned on the choice of mating partner are still defined as in (9), where the Poisson measure is replaced by $n^{-1}N_\Gamma(dz)$ and the intensity measure for N_Γ is changed to $n\lambda(z_j, z_k; Z_t^n)M(z)$. The rest essentially remains unchanged, and in particular the estimates (13) and (14) hold. Therefore the process is still well defined for any $n \geq 1$.

Suppose now that $Z_t^n(dz) \rightharpoonup u_t(z)dz$ weakly as measures when $n \to \infty$. Then

$$c(z; Z_t^n) \quad \to \quad c(z; u) \;=\; \int_{\mathcal{X}} \frac{\exp(-|x' - x|^2/2\gamma_x^2)}{\int_{\mathcal{Z}} \exp(-|x' - x''|^2/2\gamma_x^2) u_t(z'') dz''} f(dx')\,, \tag{17}$$

pointwise in z, and similarly

$$P_{z_j}(z_k; Z_t^n) \quad \to \quad P_{z_j}(z_k; u_t) = \frac{e^{-(|y_k^* - y_j|^2 + |y_j^* - y_k|^2)/2\gamma_m^2}}{\displaystyle\int_{\mathcal{Z}} e^{-(|y'^* - y_j|^2 + |y_j^* - y'|^2)/2\gamma_m^2} u_t(z') dz'}. \tag{18}$$

In the limit, this expression is defined for almost all $(z_j, z_k) \in \mathcal{Z} \times \mathcal{Z}$, and because the set $\{z_j = z_k\}$ is a set of measure zero (with respect to $u_t(z_j)u_t(z_k)dz_j dz_k$), the diagonal may be included in the definition of P. Moreover, $c(\,\cdot\,; u)$ and $P_{z_j}(\,\cdot\,; u)$ are probability measures with respect to u.

And, at least formally, the random offspring measures converge to deterministic (absolutely continuous) measures:

$$\Gamma(\cdot, z_j \mid z_j \text{ chooses } z_k; Z_t^n) \quad \rightharpoonup \quad \lambda(z_j, z_k; u)M(z - (z_j + z_k)/2)dz\,, \tag{19}$$

where $\lambda(z_j, z_k; u) = \|f\| \left(c(z_j; u) + c(z_k; u)\right)/2$. In the limit, the right hand side is defined for (almost) all $z_j, z_k \in \mathcal{Z}$.

The total population is in this case represented by $\int_{\mathcal{Z}} u(z)\,dz$, and the resource entropy W_c by

$$W_c(u) \quad = \quad \int_{\mathcal{Z}} c(z) \log\left(\|u\| c(z)\right)\, u(z)\,dz\,, \tag{20}$$

and because u is the density of a deterministic measure, there is no need to evaluate the expectation W_c in this case.

Finally we may write the master equation for the limiting densities u_n, which corresponds to equation (12):

$$\begin{aligned} &\int_{\mathcal{Z}} \phi(z) u_{t+1}(z)\,dz \qquad\qquad (21)\\ &= \int_{\mathcal{Z}}\int_{\mathcal{Z}}\int_{\mathcal{Z}} u_t(z')u_t(z'')\lambda(z', z''; u)P_{z'}(z''; u)M(z)\phi\left(\frac{z'+z''}{2} + z\right) dz'dz''dz \\ &= \int_{\mathcal{Z}} \left[\int_{\mathcal{Z}}\int_{\mathcal{Z}} u_t(z')u_t(z'')\lambda(z', z''; u) \times \right.\\ &\qquad\qquad \left. P_{z'}(z''; u)M\left(z - \frac{z'+z''}{2}\right) dwdz''\right]\phi(z)\,dz\,. \end{aligned}$$

In the change of variables used to obtain the last line, it is assumed that $\mathcal{Z} = \mathbb{R}^d$. To conclude, u_{t+1} can be expressed in terms of u_t using the expression in brackets in the last member of (21).

This derivation is strictly formal, in that we have passed to the limit in each factor separately.

2.4. **Related models.**

The mechanism for reproduction in our model is very simple: choose two parents, compute the number of their offspring, and generate children with a phenotype that is the average of the parent's phenotype plus a random noise term. If all parent pairs are chosen with equal probability, and that each reproduction results in a pair of children, the model becomes much simpler, and indeed very similar to stochastic particle models that have been studied in other contexts.

One such example is a model for the alignment of rods [5]. It is a model in continuous time, where the basic state space is not $\mathbb{R}^d$ but the circle S^1. Their starting point is the limiting equation, which is similar to the Boltzmann equation:

$$\partial_t f(\theta, t) \quad = \quad D\partial^2_{\theta\theta} f(\theta, t) + \int_{-\pi}^{\pi} f(\theta + \phi, t) f(\theta - \phi, t)\,d\phi - f(\theta, t)\,. \tag{22}$$

The main results of their paper is a rather explicit expression of the stationary states, and a qualitative result: for large values of D the uniform distribution is the only stationary solution, but for smaller values of the diffusion there is (at least) a second stationary solution, and the uniform state becomes unstable.

An equation similar to (22) has been studied, first in [6], as a model for the collective motion of self-propelled particles (e.g. fish schools). This model is analyzed in further detail in [9], where the master equation for a finite system is taken as a starting point, and the aim is to make a rigorous derivation of a Boltzmann equations similar to (22), e.g.

$$\partial_t f(\theta,t) \quad = \quad \int_{-\pi}^{\pi}\int_{\theta'-\pi}^{\theta'+\pi} f(\theta',t)f(\theta'',t)M\left(\theta-\frac{\theta'+\theta''}{2}\right)\,d\theta' d\theta'' - f(\theta,t)\,.$$

A key issue is the question of propagation of chaos, which in this case essentially implies that the two particles that interact can be chosen independently: the joint pair distribution is given as a product, $f(\theta',t)f(\theta'',t)$. This is what Boltzmann called the *Stosszahlansatz*.

Note that the noise terms are introduced in different ways in (22) and (23), and this gives a different expression for the stationary states. The simplest case is where the state space is $\mathbb{R}$, and the added noise comes from a Gaussian distribution. The dynamics then consists in drawing two particles with states x_1 and x_2 independently, and modify the state of this pair according to

$$(x_1,x_2) \quad \mapsto \quad \left(\frac{x_1+x_2}{2}+\xi_1, \frac{x_1+x_2}{2}+\xi_2\right)\,. \tag{23}$$

where ξ_1, and ξ_2 are two independent Gaussian random variables. This is very similar to (4), but the dynamics is much simpler, and in this case it is possible to compute the stationary distribution of x (assuming the propagation of chaos). With a Gaussian noise term, also x has a Gaussian distribution, but with a variance that is twice that of ξ. The analysis is carried out in detail in [9] (see also [4]).

3. Results.

In this section we present results from computer simulations. These are carried out according to the explicit description in Section 2.1. There are many parameters in the model, but here we show some examples with different food distributions, noise in the offspring distribution, selectivity in the choice of partner and choice of food. The remaining parameters are left unchanged.

In all simulation results that are presented here, the population size remains very close to the total amount of food in the system. By particular methods of the selection of mating partner, the population may grow exponentially, as indicated in equation (13), but no such results are presented here. Thus, varying the amount of food is the same as varying the size of the population, and this has a strong impact on the long time behavior of the system.

In one series of simulations, the food resource is concentrated in two or three positions in the space $\mathcal{X}=\mathbb{R}$. This means that the state space is already prepared for a predetermined number of niches that can carry independent populations. This kind of extreme distribution is used to illustrate the importance of reinforcement. It turns out that even in the case where the food is distributed in two equal Dirac masses, speciation does not take place without the reinforcement mechanism. Furthermore, the speciation is realized more rapidly with a higher dimension d of the spaces available for reinforcement, $\mathcal{Y}=\mathbb{R}^d$ and $\mathcal{Y}^*=\mathbb{R}^d$.

The graphs that represent the simulations may show very distinctly when speciation takes place, i.e. when the population splits into two sub-populations. However, to really compare the time needed for speciation to take place in different situations, an unambiguous definition is needed. We do this by fitting the population to a sum of two Gaussian distributions, with different means and masses, but with the same variance, using a maximum likelihood method with

$$MLE = \prod [\frac{c}{\sigma} e^{-(x_i-\mu_1)^2/\sigma^2} + \frac{1-c}{\sigma} e^{-(x_i-\mu_2)^2/\sigma^2}] . \tag{24}$$

We have used only the x-component of the phenotype for this, but we might as well

have included the y and y^*-components. Then we say that speciation has taken place when the means of the two Gaussian are significantly different. We have only implemented this for the split into two sub-populations.

In a another series of experiments, the food distribution is Gaussian, and so there is no *a priori* defined positions where subspecies would be expected to appear. In this case the species may split into many different species, the number depending on the population size (or total amount of food), and on the size of the noise terms.

3.1. **A discrete food distribution.** Here the food distribution $f(dx)$ is a sum of Dirac measures:

$$f = \sum m_n \delta_{x_m} . \tag{25}$$

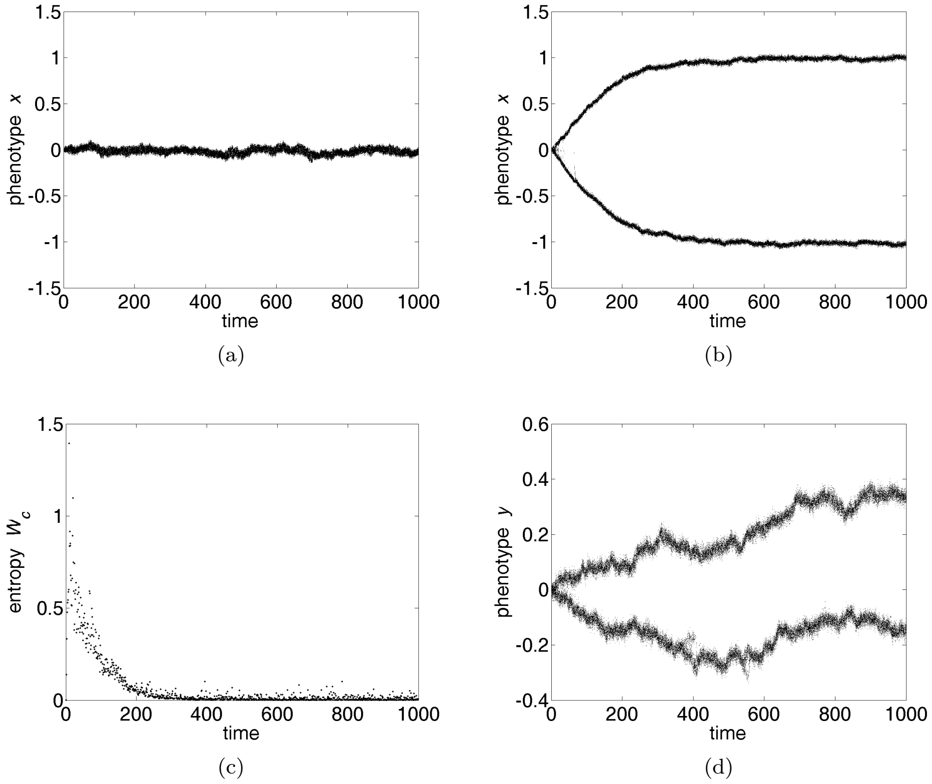
In the examples there are either two or three terms in this sum. In the case of only one term, $f = m\delta_{x_1}$, one would expect the population average of x in the phenotype $z = (x, y, y*)$ to approach x_0 as time increases; taking the average of the parents' phenotype tends to concentrate the distribution, but the part of the population phenotype distribution that is closest to x_0 is favored in the competition. This is indeed what happens. The case were f consists of several point masses is more interesting: depending on the parameters, the population will either keep together as one population, but with a population average of x that converges to some average optimum; or else the population may split in several sub populations with sub population averages of x that converge to the different point masses of f.

3.1.1. *Reinforcement.* The effect of reinforcement is seen in Figure 1(a), where reinforcement has been inhibited by setting the mutation rate for y and y^* to zero, compared to Figure 1(b), where y and y^* may change (in both cases the initial values are $y = y^* = 0$, so initially the there is no selection depending on appearance and preference). Without reinforcement the population will not branch but by mutations the population mean of x moves towards the center of mass of the food distribution.

In 1(d) we also show the distribution of the appearance trait, y. In this case the distribution of y^*, the preference trait, is almost identical to that of y, and is not shown. In this case the entropy W_c is decaying as expected (see fig 1(c)).

3.1.2. *Several food sites.* The case of three food sources starting off equilibrium phenotype is seen in figure 2. The main population moves towards the equilibrium which is the center. Eventually all three sources will have its own sub-population. The random evolution can take rather different paths, but the end result is the same. The figures 2(a) and 2(b) show the evolution of the distribution of the x and y trait for one simulation run, and 2(c) and 2(d) for another run, using identical simulation parameters.

To look at the trait distribution in this way is not quite enough to conclude that a speciation has taken place. One really needs to verify that mating takes place (almost) only within the sub-populations. One way of illustrating this is to make a

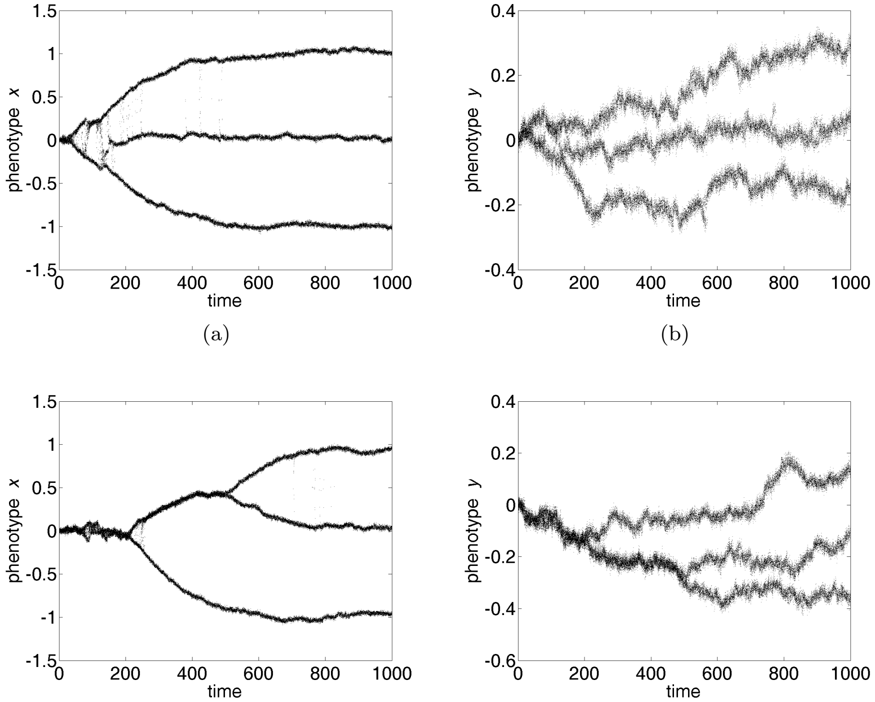


(a) (b) (c) (d)

Figure 1: (a) and (b) shows the evolution of the x-trait without and with reinforcement. (c) and (d) refer to the same simulation as (b), and show the decay of the c-entropy, W_c, and the evolution of the appearance trait y.

scatter plot of the x-trait of an individual against the x-trait of her mating partner. This has been done in figure 3 for four different times. The graphs support our claim that speciation has taken place.

3.1.3. *Concentrated food sources of different size.* When most of the food resource is concentrated at one point, with a smaller amount at another point, most of the population will have an x trait that is close to the large food resource. However, groups of individuals will try to exploit also the smaller sources. This is illustrated in figure 4, which also shows another result: In 4(a) the food resource has the form $53\delta_{-1} + 7\delta_1$, and in 4(b), the food resource is exactly twice as large as in 4(a) (see also table 1). In the first case, the groups of individuals that move towards the small food resource are not large enough to survive, whereas in 4(b) a strong subgroup of individuals move towards the smaller source, and forms a smaller group that uses the small food resource. In 4(c), the evolution of the y corresponding to the larger population is shown, and 4(d) shows the evolution of W_c, the c-entropy.



(a) (b)

(c) (d)

Figure 2: Two simulations with identical parameters. (a) and (c) show the evolution of the distribution of trait x in the population, and (b) and (d) show the evolution of trait y. Here the food distribution is 20.0 $(\delta_{-1} + \delta_0 + \delta_1)$. The remaining parameters can be found in Table 1.

3.1.4. *Effect of preference space dimensionality and population size:* The number of generations until the population splits into two species decreases when the dimension d of the appearance-preference space $\mathcal{Y} = \mathbb{R}^d$ increases (see figure 5(a)). In other words, when there are more traits to consider, specialization occurs faster. Although we have no precise mathematical argument to support this simulation result, it is plausible, because with more details to recognize in a partner, it is easier for individuals to identify a subgroup.

Another argument is that the y traits follow a random motion, and in a higher dimension it is less likely that the y traits of subgroups collide, and hence the subgroups are more stable. Comparing figure 4(a) and figure 4(b) we see that that speciation occurs faster and with greater stability when the amount of food (and hence the population) is larger. This is is further investigated in figure 5(b), where the time to the first speciation is plotted as a function of the total amount of food. A possible explanation for this is that a small isolated sub-population is likely to die out rather soon because the size of the offspring is Poisson distributed with a small rate in this case.

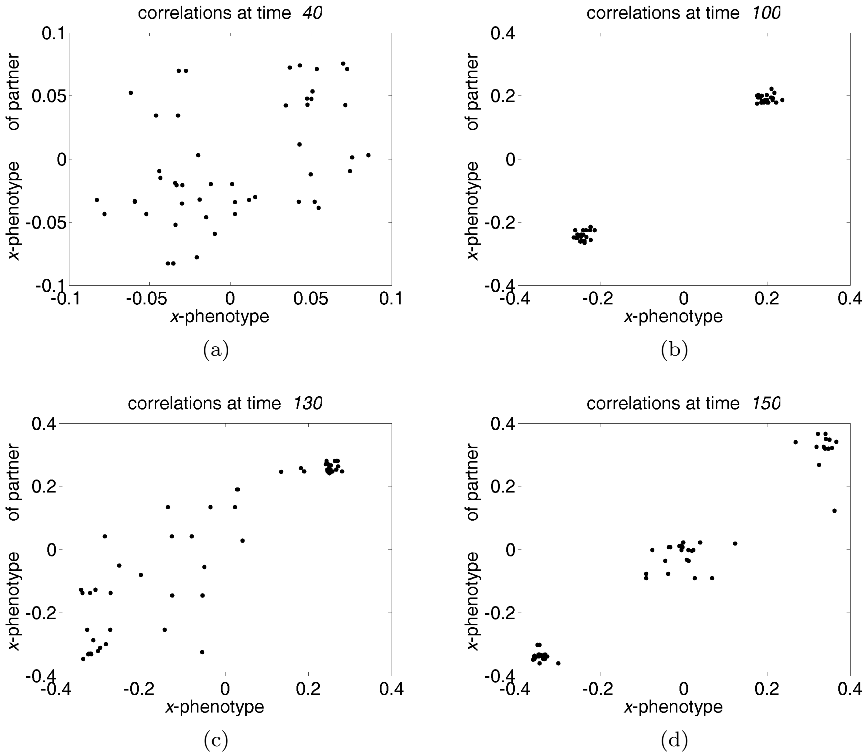


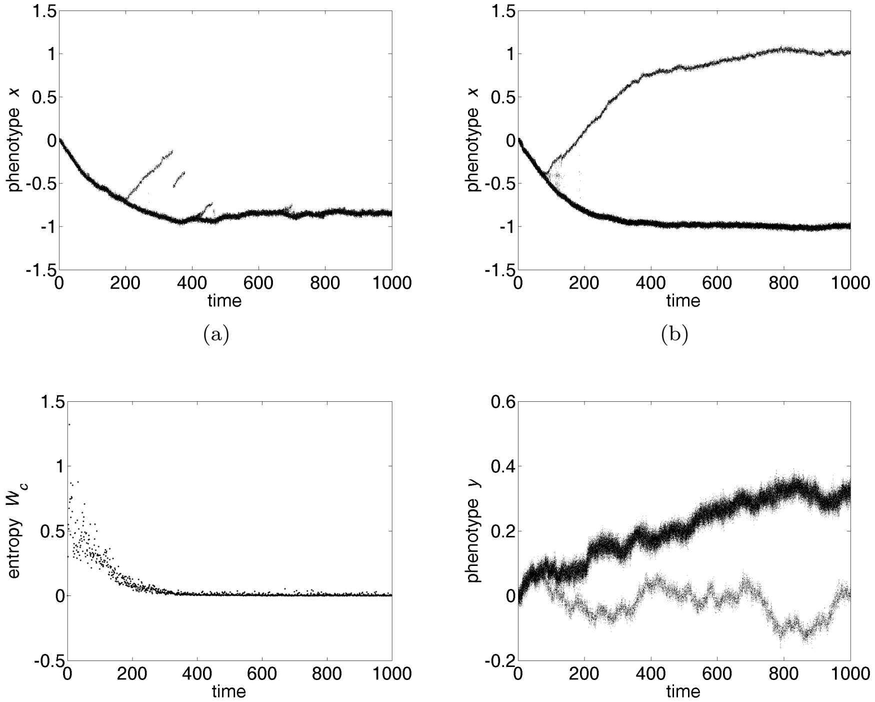
Figure 3: Each point is of the form (x_j, x_{k_j}), where x_j is the x-trait of individual number j, and x_{k_j} is the x-trait of the chosen partner. (a), (b), (c) and (d) represent the generations at time 40, 100, 130 and 160 in the same simulation as depicted in Fig. 2(a) and (b).

3.2. **A continuous food distribution.** With discrete food distributions as the ones used in Section 3.1, the environment is prepared for sub-populations specializing in the food located at one place. In this section the food distribution is continuous:

$$f(x) \quad = \quad Ce^{-x^2}, \tag{26}$$

where the constant C is changed to modify the total amount of food. Also in this case speciation takes place, as can be seen the graphs. In figure 8, the total amount of food is set to 100, and the total population stays around the same number, but split in four sub-populations. Because there are no *a priori* positions for the x-trait of the sub-populations, it is interesting to carry out the simulation over a very large number of generations, to evaluate the stability of the new species.

The next two graphs show how the behavior changes with increasing population size. Figure 7 shows a simulation where the total amount of food was 1000 (which was also approximately the size of the population), and in Figure 8, the amount of



(a) (b)

(c) (d)

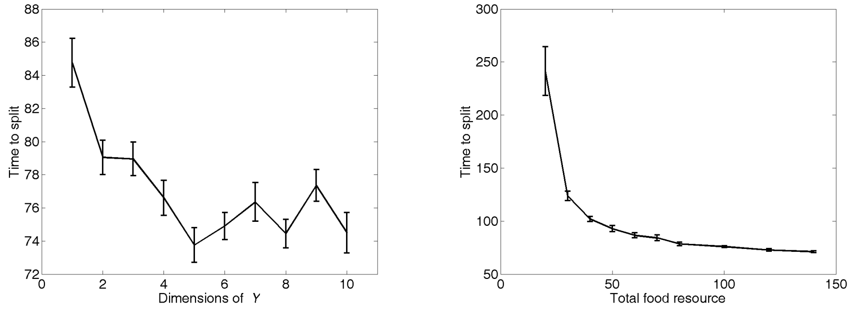
Figure 4: The food distribution is $53\delta_{-1}+7\delta_1$ in (a) and $106\delta_{-1}+14\delta_1$ in (b). With the smaller amount of food, the attempts to exploit the small source fail, whereas in (b) the one try succeeds. (c) shows the c entropy corresponding to (b), and (d) the evolution of the y-distribution.

food was 20000. In both cases, panel (a) shows the evolution of trait x, and panel (b) trait y.

4. **Discussion.** In the paper we have presented a mathematical model for *sympatric speciation* through *reinforcement*. The sexual reproduction is modeled at phenotypic level: the offspring of a couple inherits the average of the parents' phenotypes, but with some random variation. The size of the offspring depends on the parents' common *ability to compete for food*, which is given by one component of the phenotype. This ability, however, is not important in the selection of mating partners, which is done on the basis of *appearance* and *preference*, which are the remaining components of the phenotype in our model. This is then combined to construct a Markov chain.

From a mathematical point of view, much remains to be done, and in subsequent works, we hope to solve some of the following problems:

- to characterize the conditions under which speciation occurs;
- to characterize the long time behavior;
- to make the infinite population limit rigorous;



(a) (b)

Figure 5: In (a) the time needed for speciation is plotted as a function of the number of degrees of freedom in the y-trait. The instant of speciation is defined as the time when the fitting of a bimodal distribution is significantly better than the fitting of a unimodal distriubtion, as described in the text. In (b) the time needed for speciation is plotted as a function of the amount of food (and hence the size of the total population). We can see that the time required for speciation decreases with higher dimension of y, and with increasing population. All simulation parameters are given in Table 1.

- to give a mathematically solid argument to explain that the time to speciation decreases with increasing dimensionality of the appearance-preference space.

It would also be natural to make the model continuous in time.

The computer simulations show that, with this model, speciation typically will take place. The random variation in the offspring phenotype makes the population explore the food resources, and the reinforcement dynamics may help the population to split into sub-populations that reproduce essentially within the group.

And in our simulations, the reinforcement is essential, without it the population does not split. Even more so: when the reinforcement dynamics has more components, it evolves quicker and thus the speciation happens faster.

From a biological point of view, the model is simplified. For example, the competition for food resources only has an influence on the reproduction rate, and not on the survival. This means that under certain conditions, the population may grow exponentially (although we have only seen this in the simulations for very special kinds of selection models).

In Buffon's definition, two individuals belong to the same species if they are able to produce a fertile offspring[4]. In this sense we do not have speciation in our model, because all pairs of individuals can produce fertile offspring if they wish to. However, it is very plausible that in the real world, this separation of a population into sub-populations that prefer to mate within the sub-population,

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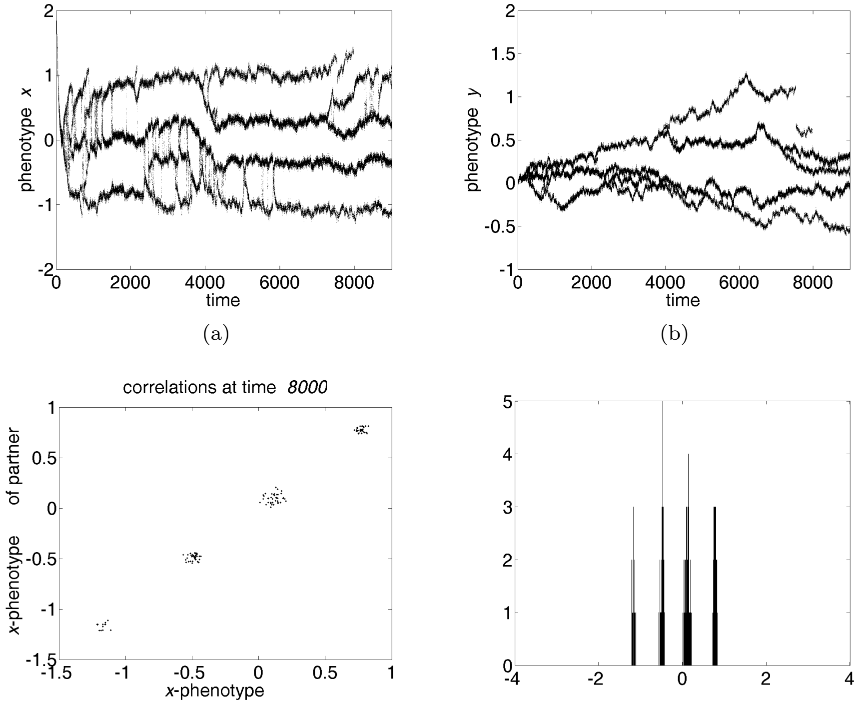
[4] Buffon's definition is today outdated, since it only makes sense if the relationship 'to have fertile offsprings' is a transitive relation. However, this is not always the case, see for example [30]. Furthermore, the situation is not always symmetric as the fertility of the offspring can vary considerable depending on in which of the two populations, the female is picked.



(a) (b)

(c) (d)

Figure 6: The food distribution is Ce^{-x^2} with C such that the total food amount is 100. In (a) and (b), the distribution of the x and y traits are shown, and (c) shows the correlation between the x-trait of an individual and its mating partner at generation 8000. The histogram in (c) shows the distribution of x at time 8000.

is what happens first. Then, after many generations, the phenotypes of the subpopulations are so different, including post-zygotic barriers, that they are different species even according to Buffon.

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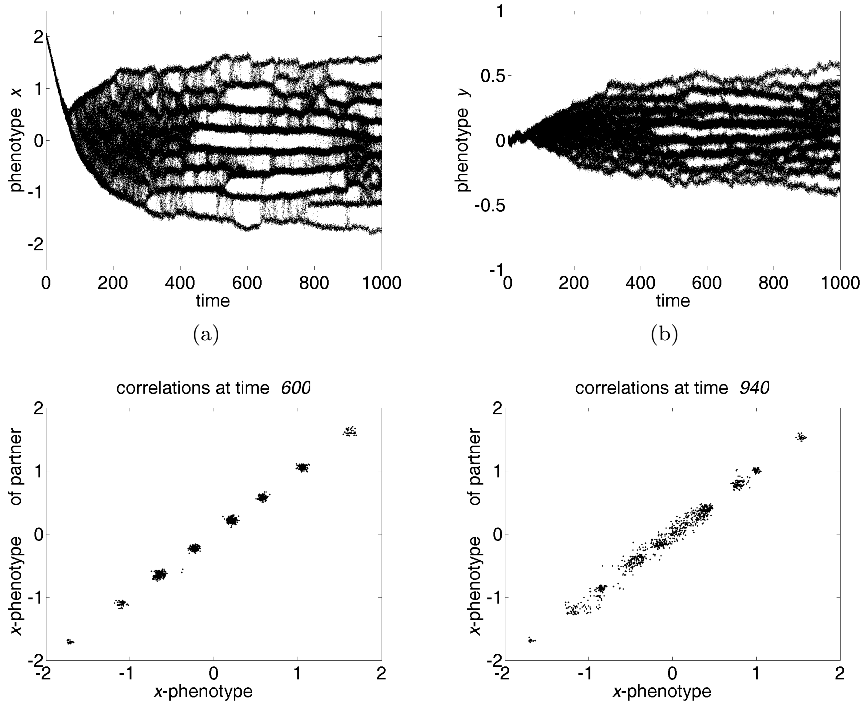

(a) (b)

(c) (d)

Figure 7: The food distribution here is Ce^{-x^2} with C such that the total amount of food is 1000. (a) and (b) show the distribution of the x and y traits, and (c) and (d) show the correlation between the x trait of an individual and of its mating partner at two different times.

figure	f	γ_x	γ_m	σ_x	σ_y	σ_{y*}	comment
1(a)	$30(\delta_{-1}+\delta_1)$	0.1	0.01	0.01	0.0	0.0	no reinforcement
1(b)	$30(\delta_{-1}+\delta_1)$	0.1	0.01	0.01	0.01	0.01	with reinforcement
2,3	$20(\delta_{-1}+\delta_0+\delta_1)$	0.1	0.01	0.01	0.01	0.01	
4(a)	$53\delta_{-1}+7\delta_1$	0.1	0.01	0.01	0.01	0.01	
4(b)	$106\delta_{-1}+14\delta_1$	0.1	0.01	0.01	0.01	0.01	
5(a)	$30(\delta_{-1}+\delta_1)$	0.1	0.01	0.01	0.01	0.01	$\mathcal{Y}=\mathbb{R}^d$, varying d
5(b)	$C(\delta_{-1}+\delta_1)$	0.1	0.01	0.01	0.01	0.01	varying C
6	$C\exp(-x^2)$	0.1	0.01	0.01	0.01	0.01	$\int f dx = 100$
7	$C\exp(-x^2)$	0.1	0.01	0.01	0.01	0.01	$\int f dx = 1000$
8	$C\exp(-x^2)$	0.1	0.01	0.01	0.01	0.01	$\int f dx = 20000$

Table 1: Simulation parameters used for producing the figures.

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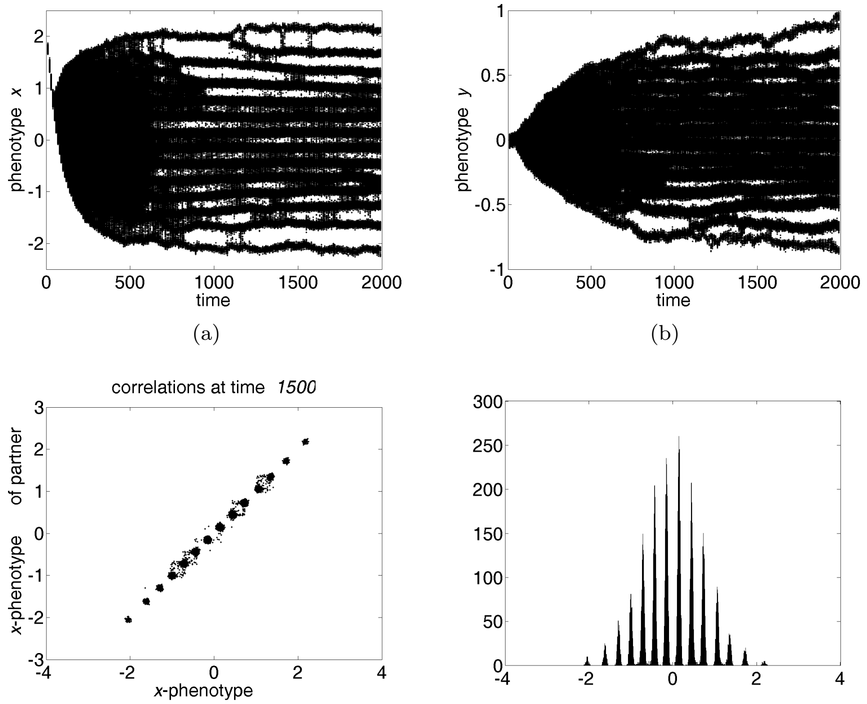

(a) (b)

(c) (d)

Figure 8: The food distribution here is Ce^{-x^2} with C such that the total amount of food is 20000. In (a) and (b), the distribution of the x and y traits are shown, and (c) shows a correlation plot of x in an individual and its partner at time 1500. (d) shows a histogram of x at time 1500. It is striking how well this follows the Gaussian food distribution.

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