

UNIVERSITY OF GRONINGEN

Geographic parthenogenesis

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CONTENTS

1. Introduction	3
2. Hypothesis	
2.1. Mate limitation	5
2.2. Maladapted sexual migrants	5
2.3. Tangled bank hypothesis	6
2.4. Red Queen hypothesis	7
2.5. The metapopulation hypothesis	8
3. Discussion	
3.1. Experiment I	8
3.2. Experiment II	9
3.3. Experiment III	10
3.4. Experiment IV	11

Geographic parthenogenesis

The maintenance of both sexuality and asexuality is one of the oldest questions in the evolutionary ecology, also known as the paradox of sex. Insights into the maintenance of sex in natural populations may be gained from processes underlying different geographic distributions between sexuality and asexuality. While sexuality occurs generally in core habitats in contrast to marginal habitats like high latitudes and high altitudes, with asexuality it is the other way around. This is called geographic parthenogenesis. Although there are at least five main hypotheses which explain this pattern, they are all based on theoretical models. I stress the necessity testing these hypotheses rather than coming up with new ones. In this review I summarized the five main hypotheses to explain geographic parthenogenesis: Mate limitation, maladapted sexual migrants, the tangled bank hypothesis, a variant of the red queen hypothesis and the metapopulation hypothesis. Then I disentangled the hypotheses by looking at the differences in their predictions and, when it was possible, made an outline how they could be tested. The four hypotheses may all contribute to geographic parthenogenesis. None of them excludes another. The experiments can test the hypotheses of mate limitation, maladapted sexual migrants and the red queen hypothesis; however I was not able to disentangle the last from the tangled bank hypothesis. It is likely that one of the reproduction systems outcompetes the other but cannot maintain itself in certain condition which would explain the coexistence of sexuality and asexuality. It is important that we test the hypotheses because that is the best way to get insights into the advantages and disadvantage of sex in natural populations

Introduction

The vast majority of animals reproduce sexually, however many organisms reproduce asexually and some species do both. Why is there such a variety in reproduction styles? In other words, why does not one reproduction style outcompetes the other? This is one of the oldest and hardest questions in evolutionary ecology, called the paradox of sex . Biologists did large amounts of research on this topic but we still do not know the answer (Agrawal 2006, Becks and Agrawal 2012, Innes *et al* 2000, Jokela *et al* 2009, Scharnweber *et al* 2011)

Sex is associated with many costs. Unlike sexual individuals, asexual individuals do not need mates to reproduce. While sexual individuals spend energy on searching and competing for mates which makes them vulnerable for predators, asexual individuals can focus on their own health and reproduction (Agrawal 2006.

During sex, individuals can easily infect each other with diseases. However in a minority of species, mates can be beneficial because they provide parental care (Agrawal 2006). Sex brings other costs in the post zygotic stadium. First, sexual organisms produce males (Becks and Agrawal, 2012, Innes *et al* 2000, Jokela *et al* 2009, Scharnweber *et al* 2011) and second, sexual females pass only half of their genome to each of their young while asexual females produce clones of themselves. This theoretical model is also known as the two-fold cost of sex (Becks and Agrawal, 2012, Innes *et al* 2000, Scharnweber *et al* 2011). The consequence of sex is a redistribution of alleles and thus a shuffle of genotypes (Agrawal 2006) after which selection favors the best adapted individuals to reproduce. Hence, in a stable environment, organisms are well adapted to their environment. Sex would breakdown these good gene combinations so this is a disadvantage for

Geographic parthenogenesis

sexuality (Agrawal 2006, Becks and Agrawal 2012, Scharnweber *et al* 2011).

However, sex has also many benefits. Sexual species can adapt much quicker to changes in the environment than asexual species because their offspring has more variance in genotypes. Becks and Agrawal (2012) conclude that the rate of sex and recombination increases when there is selection for adaptation, which confirms the idea of sexual advantages in changing circumstances (Becks and Agrawal 2012). The Red Queen hypothesis describes that arms races, between parasites and hosts for example, create these changing circumstances. The Red Queen hypothesis is a very popular theory because of it describes short term benefits for sexuality whereas other theories like the Muller's ratchet come up with only long term advantages. The Muller's ratchet model explains that asexual populations suffer from mutation accumulation whereas sexual organisms can filter out the disadvantage mutations, therefore asexuality should be doomed on the long term (Agrawal 2006).

These processes may all provide an advantage to sexual reproduction. However, their relative importance to the maintenance of sex in natural populations remains an open question. We might find an answer this question when we look at the differences between sexual and asexual species in geographic distribution. While asexuality occurs generally in higher latitudes and altitudes, islands instead of mainland habitats, xeric rather than mesic conditions, continental as opposed to maritime regions and disturbed instead of undisturbed habitats, sexuality occurs in the opposed habitats (Glesener and Tilman 1978). This pattern is called geographic parthenogenesis (Gaggiotti 1994). It seems that asexuality is

favorable in other environments than sexuality (Gaggiotti 1994). Thus, depending on the environmental conditions either sexuality or asexuality would outcompete the alternative reproduction system.

There are five main hypotheses to explain geographic parthenogenesis (Haag and Ebert 2004). However, there are much variants of each hypothesis and most of them are based on the costs and benefits of sexuality described earlier. Some hypotheses contain new ideas while others only have elements of existing hypotheses. Hopefully these hypotheses lead to a better understanding of the advantages and disadvantages of sexual reproduction. I will discuss the following five hypotheses. First, the hypothesis of Peck *et al* (1998) argues that although sexuality normally has the advantage, sexual individuals which live in small populations mate with maladapted migrants, thus as a consequence they produce offspring with a lower fitness. Second, the theory of Gerritsen (1980) says that sexual individuals are normally favored but do not occur at low densities because then they do not encounter each other, which is necessary for reproduction. Thirdly, the Tangled Bank theory (Gaggiotti 1994) in which states that sexual organisms are in the advantage in environments with many niches. Due to their diversity in genotypes they can extract more resources from the environment and will suffer less from intraspecific competition compared to asexual organisms. Asexuality on the other hand has the advantages in non-changing habitats since adapted mothers produce only adapted daughters. Fourth, a variant of the Red Queen hypothesis by Glesener and Tilman (1978) which argues that sexuality is favored in 'unpredictable' habitats with greater biological accommodation because sexual population

Geographic parthenogenesis

adapt quicker to new circumstances. Asexuality is normally beneficial because they do not suffer from for example, the two-fold cost of sex. Fifth, the metapopulation hypothesis of Haag and Ebert (2004) argues that sexual populations in marginal habitats suffer from inbreeding depression which decreases their fitness; as a consequence asexual individuals will outcompete the sexual individuals. First, I will summarize a variant of each main hypothesis in this review. Then I disentangle them by looking at their predictions and when possible, I make an outline of the experiments with which the hypotheses could be tested.

Maladaptive migrants

Peck *et al* (1998) suggested that although sexuality normally has the advantage, sexual individuals which live in small populations mate with maladapted migrants, thus as a consequence they produce offspring with a lower fitness. In low latitudes there is a longer growing season than in high latitudes. Therefore populations living in the low latitudes would produce more offspring than populations in the high latitudes which results in smaller populations in high latitudes. Consequently, immigrants have a greater impact in high latitudes because the immigrants are a larger proportion of the population compared to low latitudes. Immigrants are adapted to the place they came from. As a consequence, they are often maladapted to their new habitat and have a lower fitness there. When these maladapted immigrants reproduce sexually with sexual natives, their offspring has a lower fitness than the offspring of two well adapted sexual natives. Thus because of geneflow from source populations to sink populations the fitness of the sexual sink populations would decrease. Well adapted asexual natives keep their high

fitness because they do not mix with the maladapted immigrants. This pattern would be expected in every population where the proportion of immigrants is high, for example populations which live in high altitudes and populations in marginal habitats where the population density is low compared to the central regions. Thus when the proportion of immigrants is high, an asexual population will outcompete a sexual population because sexual individuals produce offspring with a low fitness when they mate with maladapted migrants whereas asexual individuals avoid this mating (Peck *et al*, 1998).

Mate limitation

Gerritsen (1980) says that sexuality normally outcompetes asexuality, nevertheless in low densities sexual organisms suffer from mate limitation which favors asexuality. The individuals of a sexual species have to encounter mates otherwise the species will get extinct. When the encounter probability decreases the chance of extinction increases. The encounter probability is influenced by several parameters: the rate of movement, the detection radius, the length of the sexual period and the population density (Gerritsen, 1980). Together the parameters should reach a critical encounter probability to sustain a population. When one of the parameters is decreased the others have to compensate (Gerritsen, 1980). The minimum encounter probability to sustain a population I call the critical encounter probability. Gerritsen (1980) made a model which can calculate the critical population density (the minimum density to sustain a population). Noted that populations which live in patches the relevant population density is within the patch instead of the average density of the whole habitat. He concludes that sexual

Geographic parthenogenesis

reproduction is possible when the probability of a population to decline to the critical density is low. Asexuality on the other hand is favored when the probability of a population to decline to the critical density is high. Population density is restricted in habitats with low carrying capacities, during colonization of new habitats and due to biological interactions. Gerritsen (1980) expects that adaptations which increase the encounter probability, and thereby reduce the critical density, are favored in sexual populations. He gave three types of adaptations to decrease the critical density. First, adaptations that increase the probability of encountering a mate, like increase in moving speed and encounter radius, which is determined by the sensory systems of the animal like visual detection, mechanoreceptors and chemical senses. Second, thanks to seasonal breeding, discrete cohorts reach maturity at the same time. When an individual becomes mature later than the rest of the population, everybody has already mated. When an individual becomes mature too early on the other hand, the chance of mating before the rest of his or her cohort reach maturity is very small and it will cost energy. And finally, populations may reproduce via cyclic parthenogenesis, which means that parthenogenesis alternates with sexuality. Cyclic parthenogen combine the benefits of both reproduction systems, therefore the population can sustain itself when the population declines beneath critical densities. When the population density rises above the critical density they reproduce sexually and otherwise they reproduce parthenogenetically. Sexual populations, especially the ones which have to cope with mate limitation, should have developed at least one of these adaptations to increase the probability to encounter mates.

The density of individuals in sexual populations is always higher than the critical density, except for cyclic parthenogenetic species. On the other hand, asexual organisms live in habitats where the population density is below the critical density continuously or where periods of high and low densities frequently alternate each other. Thus, sexuality normally outcompetes asexuality. However, in habitats where population densities are low, sexual organisms have to cope with mate limitation which favors asexuality (Gerritsen, 1980).

The Tangled Bank Hypothesis

The tangled bank hypothesis predicts that due to the differences in variability of their offspring, asexuality is favored in habitats with a few niches whereas sexuality is favored in habitats with many niches. The 'Tangled Bank model' was invented by Gliselin in 1974 (Gaggiotti 1994). Since then several biologist developed the model in different ways. Gaggiotti (1994) reviewed these models and made a computer model to explain geographic parthenogenesis (Gaggiotti 1994). When I mentioned the Tangled Bank hypotheses I referred to the hypotheses of Gaggiotti (1994). The hypothesis argues that sexual organisms produce more diverse offspring than asexual organisms and that the fitness of an individual or genome differs between niches. Assuming that asexual mothers are well adapted to the niche they occupy, their offspring would be well adapted to that niche as well. On the other hand, because of the diversity in the sexual offspring a proportion of them would be well adapted to the same niche of their parents. The rest of the offspring would be better adapted to other niches. In a habitat with a low number of niches all the offspring of asexual organisms is well adapted compared to just a small

Geographic parthenogenesis

proportion of the sexual offspring, therefore asexuality would be favored. In habitats with many niches the sexual offspring can occupy several niches, consequently they will suffer less from intraspecific competition and the offspring can extract more food from the environment. The asexual offspring is just adapted to (and thus will occupy) one niche and as a result they will compete with their sisters for resources. The tangled bank hypothesis predicts that asexuality is favored in habitats with a few niches whereas sexuality is favored in habitats with many niches.

The Tangled Bank defined habitat heterogeneity as the “the existence of a large number of niches or different resource species to be consumed by different genotypes in any single habitat” (Gaggioti, 1994). The models which used this definition conclude that sexuality would only be maintained in the following conditions: significant niche differences among species, low environmental variability, severe resource depletion and low cost of sex. Even if these conditions are satisfied they expect that asexual clones will never be excluded completely. Gaggioti (1994) defines the habitats in those models as “fine grained” and made a computer model with “coarse grained” habitats. This means that a habitat is subdivided into different patches. He concludes that sexuality is more easily maintained (Gaggiotti, 1994).

Red Queen Hypothesis

Glesener and Tilman (1978) did a literature study on geographic parthenogenesis in terrestrial animals. They believe that asexuality is normally favored due to the two-fold cost of sex and that the arguments of the Red Queens hypothesis overrule this advantage in some environments. Like the tangled bank model

Glesener and Tilman (1978) explain that sexual offspring has a greater variance in genotypes than the asexual offspring, which are identical. Therefore asexuality would do better in a predictable non-changing environment because the genotypes of asexual organisms are predictable as well. However, because of the variance in the genotypes of their progeny sexual organisms produce a lot of less adapted offspring in a non-changing environment. The advantage of sexuality lies in the ability to adapt quickly. Hence the sexual species will do well in a changing and unpredictable environment. Sexual organisms would occur in habitats with greater “biological accommodation” (Sanders 1968). Glesener and Tilman (1978) argue that, compared to asexual organisms, sexual organisms can deal better with biological influences like predators, preys and parasites which are less predictable than physical influences (Glesener and Tilman 1978). Selection favors predators and parasites which are adapt to their prey the best, while the preys which have new adaptations against their predators and parasites will be favored by selection too. Thus these arms races will select for organisms who can quickly adapt which are sexual organisms in general.

Glesener and Tilman (1978) also suggest that the arms races contribute to environmental changes which are less predictable than climate fluctuations and occur more frequently than catastrophes. Sexuality contributes to unpredictability which in turn favors sexuality. Consequently he would expect simultaneous sexuality to occur. Thus sexuality is favored in ‘unpredictable’ habitats with greater biological accommodation because they adapt quicker to new circumstances whereas asexuality has the advantages in non-changing habitat since

Geographic parthenogenesis

adapted mothers produce only adapted daughters (Glesener and Tilman 1978).

The metapopulation hypothesis

The hypothesis of Haag and Ebert (2004) argue that sexual populations in marginal habitats suffer from inbreeding depression which decreases their fitness; as a consequence asexual individuals will outcompete the sexual individuals. Populations in marginal habitats often exist in metapopulations. In metapopulations, dynamics as subdivision, local extinction and recolonization occur more often. These metapopulation dynamics create genetic bottlenecks, which in turn cause genetic drift. In sexual populations, genetic drift increases inbreeding which might reduce their fitness. In asexual populations on the other hand, inbreeding does not occur and therefore they do not suffer from inbreeding depression (Haag and Ebert 2004). It is thought that metapopulations go through phases of extreme variation in fitness (Haag and Ebert 2004) and this hypothesis assumes that sexual organisms arise repeatedly from the sexual populations. Consequently, asexual individuals that arise during a period of a high fitness can outcompete their sexual relatives during periods of low fitnesses. Thereby Haag and Ebert (2004) argue that asexual populations have an advantage in recolonization of habitats because they may be more dispersive than inbred sexual populations.

Discussion

Since we know the principles of each hypothesis we can look at experiments which test them individually. I will give an outline for four experiments. They will disentangle all hypotheses except for the Tangled Bang hypothesis. The outcome of these experiments

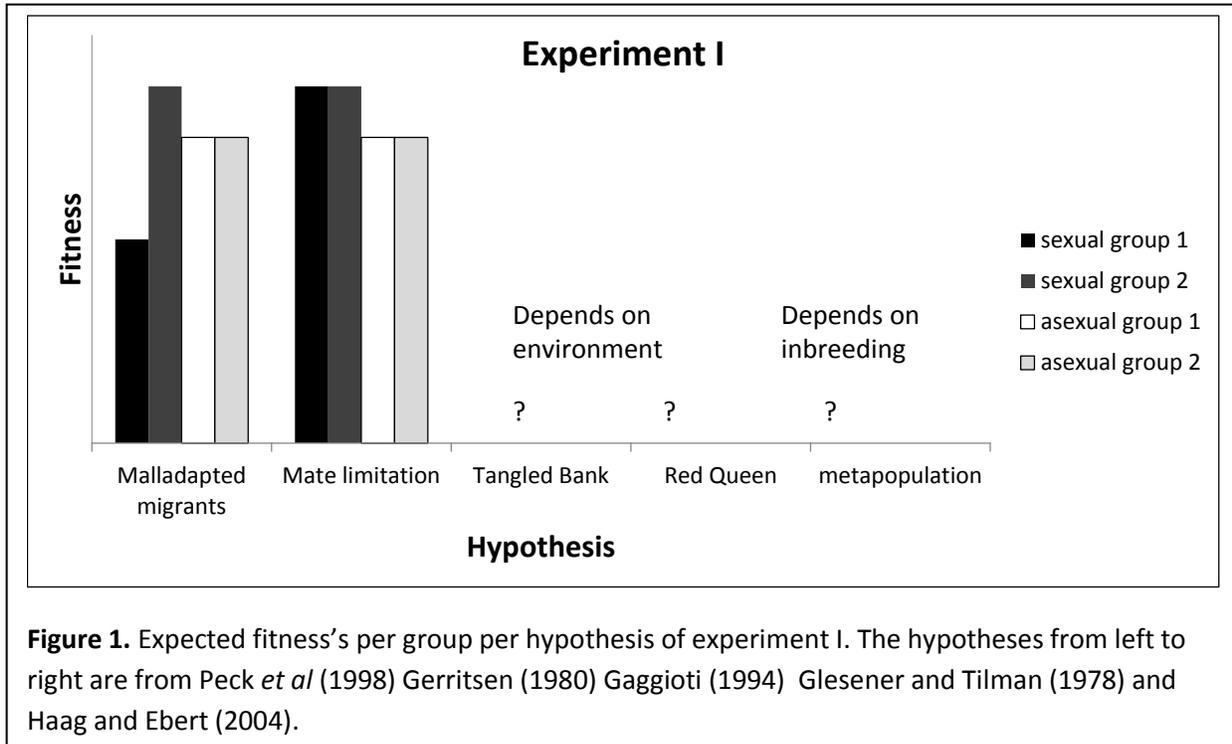
will give insights into the question why sex is maintained in natural populations.

Experiment I

The basic idea of the hypothesis of Peck *et al* (1998) is that maladaptive migrants decrease the fitness of small sexual populations. To test this we should take a sexual population and an asexual population which are closely relative from a core habitat. We transfer these populations to a marginal habitat where it usually does not occur. For example a habitat where a parthenogenetic another sister species lives so there is a high probability that the population survives. However, individuals from the core habitat should be able to migrate to the marginal habitat. Then we divide the populations in two groups. In the first group the sexual individuals will be able to mate with these migrants whereas the second group will not, everything else is equal. For example when we use a species where only the females are wingless. Then we can make two enclosures: one where mating with migrants is impossible and the other where mating is possible. Then flying migrants (males) can mate with just one of the groups. The problem here is that males of that group can feed outside the enclosure or may migrate to other habitats.

Another possibility would be that we put the groups in enclosures and add migrants to the first enclosure. The migrants can be collected from the habitat outside the enclosures. However, maybe it is very hard to collect these migrants. Thereby you can argue that it is unfair to add individuals to just one of the populations. Nevertheless we can solve this problem by dividing the original populations in three groups. The third group can be used as a stock. When a migrant is added to the first

Geographic parthenogenesis



enclosure we put an individual from the third group in the second enclosure.

The expected results are shown in figure 1. Peck *et al* (1998) expect in contrast to the other hypotheses that the offspring of sexual individuals which can mate with the migrants would have a lower fitness than the sexual offspring which parents were isolated from the migrants. All the other hypotheses do not expect a difference between these sexual individuals in the groups. None of the hypotheses expects a difference between the asexual individuals of the groups. Nevertheless, both Peck *et al* (1998) and Gerritsen (1980) expect that the asexual organism of both groups have a lower fitness than the sexual individuals of group. Peck *et al* (1998) say that sex is in the advantage when sexual individuals do not mate with maladapted individual whereas Gerritsen (1980) argues that sex is beneficial when there is no mate limitation (assuming that there is no mate limitation in

this experiment). The results that the hypotheses of Gaggioti (1994) and Glesener and Tilman (1978) expect depend on the number of niches and the biological accommodation in the marginal habitat. The expectations of Haag and Ebert (2004) depend on the level of inbreeding depression in the populations. Therefore the expected results of these hypotheses are not shown in figure 1.

Experiment II

I will give two experiments which are able to test the hypotheses of both Gerritsen (1980) and Haag and Ebert (2004). The basic idea of the hypothesis of Gerritsen (1980) is that lower population densities decrease the mate encounter probability. Therefore there should be setups which differ in population density or encounter probability. I suggest that we take many identical cages. In the first cage we put one sexual and one asexual individual, in the second cage we put two individuals of both

Geographic parthenogenesis

reproduction systems, in the third cage we put three etc. It is important that the cages are as big as possible so the differences in population density are large and the sexual individuals in lower density cages have trouble with encounter mates, noted that when using a smaller organism the cages are relatively bigger. In this experiment the amount of resources should not be a limiting factor. The experiment should be run a few generations and afterwards we look if the sexual and asexual populations between the cages differ in fitness. Another possibility is to do the same experiment but start with the same population size in every cage and differ the amount of resources. Then the population density will be formed on a more natural way which better represents the real situation.

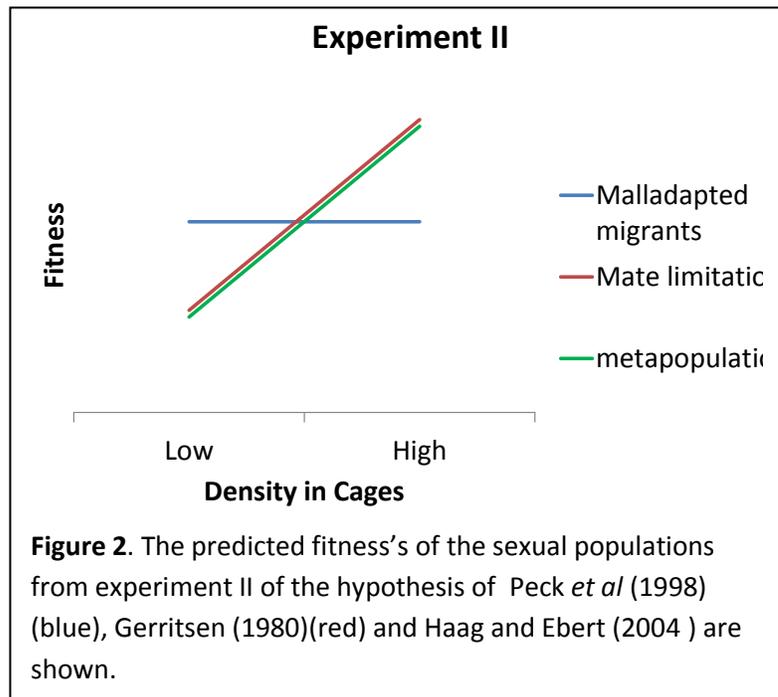
I will only discuss the results the first variant of the experiment. The results of the sexual populations are shown in figure 2. The hypothesis of Gerritsen *et al.* (1980) predicts that the sexual population in the lower density cages will become extinct whereas they will establish higher density cages. The individuals of the low density cages have an encounter probability which is too low to sustain the population. Haag and Ebert (2004) expect the same results however they argue that the low density cages contain smaller populations and therefore these populations suffer from inbreeding depression. Later I will explain how we can disentangle them. Peck *et al* (1998) predict that the sexual populations are in the advantage but there no differences between the cages, because the sexual individuals do not mate with maladapted

migrants. The predictions of Gaggioti (1994) Glesener and Tilman (1978) again depends on the on the number of niches and the biological accommodation in the cages.

Experiment III

The problem is that I expect that Gerritsen *et al.* (1980) and Haag and Ebert (2004) predict the same results. Nevertheless we can disentangle them with the following experiment. We will do the same as experiment II, however we make a duplicate of every cage. We will run the experiment but after each generation we exchange half of the individuals of each cage with the half of the individuals of the other cage which started with the same circumstances (figure 3). After a few generations we will look at the differences in fitness.

Every hypothesis will expect exactly the same as in experiment II except from the hypothesis of Haag and Ebert (2004). The level of inbreeding would be decreased because the sexual offspring mates less with brothers and sisters.



Geographic parthenogenesis

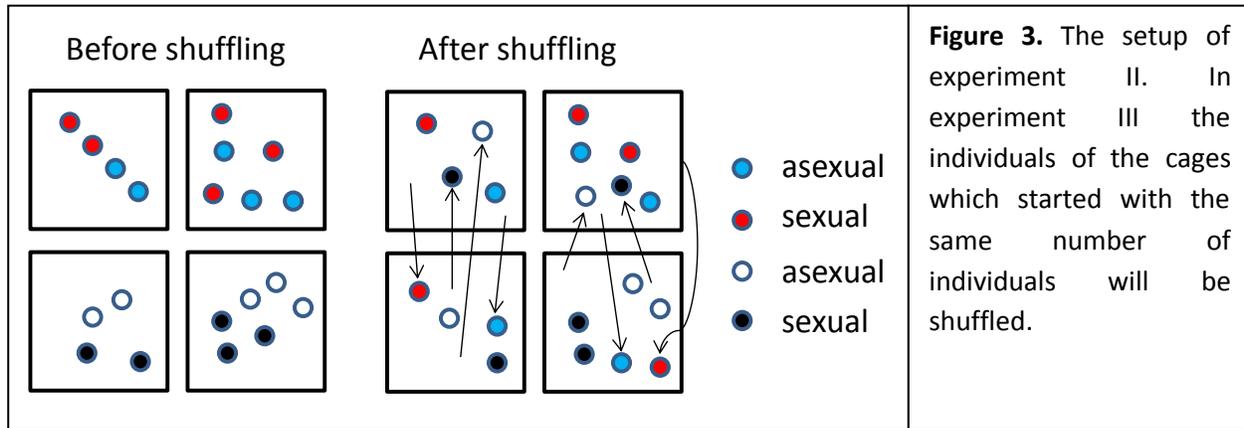


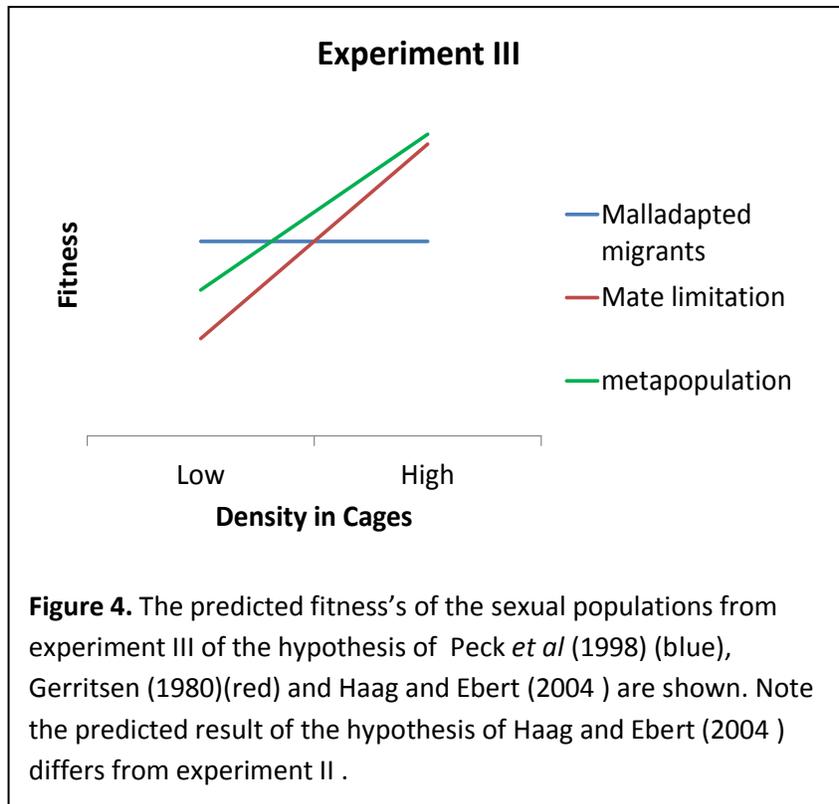
Figure 3. The setup of experiment II. In experiment III the individuals of the cages which started with the same number of individuals will be shuffled.

Therefore Haag and Ebert (2004) predict that the fitness in experiment III would be higher than in experiment II (figure 4).

Experiment IV

Although there are differences between the tangled bank hypothesis (Gaggioti 1994) and the hypothesis of Glesener and Tilman (1978), the predictions they make are very similar. Both predict that sexuality is in the advantage when the environment is more complex. That is the reason why I think that it is not possible to disentangle them and develop an experiment which can test the hypothesis individually. The number of niches where the tangled bank model (Gaggioti 1994) is based on correlates with biological accommodation, which is the fundament for Glesener and Tilman (1978) their theory. When we are able to create environments with the same number of niches and with different numbers of arms races or the other way around there might be a possibility. But for now I assume that this is not possible.

Although we cannot disentangle them from each other, we can create an experiment to test whether at least one of them is true. To test the hypotheses there should be an experiment where everything is equal except for the number of niches or the level of biological accommodation. Nevertheless, adding or removing a niche without changing the rest of the environment sounds very hard. However to disentangle these two hypothesis from the rest we only have to



Geographic parthenogenesis

make sure that there is the same level of inbreeding, encounter probability and the same number of maladapted migrants. We can take several enclosures which differ in the number of niches and number of interactions. For example one enclosure with 1 plant species, one enclosure with 10 plant species and 10 herbivore species and one enclosure with 30 plant species 30 herbivores and 5 predators. Then we add a large sexual population and a large population of an asexual sister species to each enclosure and measure their fitness. Large populations suffer less from inbreeding depression.

Unless the population density declines to a level beneath the critical density Gerritsen (1980) would predict no differences in fitness between the environments. Peck *et al* (1998) also expect no differences because migration is not possible. The hypothesis of Glesener and Tilman (1978) expects that the complexity would favor the sexual organisms, therefore the sexual populations in the second and third experiment would do relatively better than the asexual species compared with the first experiment. The Tangled Bank hypothesis of Gaggiotti (1994) argues that in the enclosures with more species there are more niches, so he expects the same as Glesener and Tilman (1978). Haag and Ebert (2004) only predict differences when there is inbreeding depression. However, when the populations are big enough inbreeding depression is negligible.

The basic idea of making hypotheses which predict geographic parthenogenesis is to get insights in the processes which influence the maintenance of sex. However, only when we test these hypotheses we can be sure that the factors on which the hypotheses are based on play a role in the maintenance of sex. Therefore

it is useless to make hypotheses, or make modifications existing hypothesis, which cannot be tested or be disentangled from the others, even if they explain the pattern of geographic parthenogenesis better. There are five main hypotheses and none of them is tested, so the next step is to test these hypothesis and look at the results and hopefully they will help to better understand the paradox of sex.

References

- Agrawal AF, 2006 Evolution of Sex: why do organisms shuffle their genotypes? – *Current Biology* 16, 696-704
- Becks L, Agrawal AF, 2012: The evolution of sex is favoured during adaptation to new environments. – *PLoS Biology* 10: e1001317
- Gaggiotti OE, 1994: An ecological model for the maintenance of sex and geographic parthenogenesis. – *Journal of theoretical Biology* 167: 201-221
- Gerritsen J, 1978: Sex and parthenogenesis in sparse populations. – *The American Naturalist* 115, 718-742
- Glesener and Tilman RR, Tilman D, 1978: Sexuality and the components of environmental uncertainty: clues from geographic parthenogenesis in terrestrial animals. – *The American Naturalist* 112, 659-673
- Haag CR, Ebert D, 2004: A new hypothesis to explain geographic parthenogenesis. – *Annales Zoologici Fennici* 41: 539-544
- Innes DJ, Fox CJ, Winsor GL, 2000: Avoiding the cost of males in obligately asexual *Daphnia pulex* (Leydig). – *The Royal Society* 267: 991-997
- Jokela J, Dybdahl MF, Lively CM, 2009: The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of

Geographic parthenogenesis

sexual and asexual Snails. – *The American Naturalist* 17: 43-53

Peck JR, Yearsley JM, Waxman D, 1998:
Explaining the geographic distributions of sexual
and asexual populations. – *Nature* 391: 889-
892.

Sanders HL, 1968: Marine benthic diversity: a
comparative study. – *The American Naturalist*
120: 243-282

Scharnweber K, Plath M, Tobler M, 2011:
Feeding efficiency and food competition in
coexisting sexual and asexual livebearing fishes
of the genus *Poecilia*. – *Environment Biology
Fish* 90: 197-205