



Assortative mating and the cost of inbreeding – A simulation approach

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ABSTRACT

Assortative mating is an important factor in the process of speciation. Models of speciation frequently deal with small founder populations often with mating preferences based on ecological traits or habitat preferences. Small populations, on the other hand might suffer from inbreeding. However, few studies have explored the combined effects of assortative mating and inbreeding in such populations. Can they speciate, or are they doomed to eventually go extinct? With this simulation we show that assortative mating based on similarities increases the possibility for change in a population, as long as the population does not suffer from inbreeding depression. Inbred populations seem not to be able to cope with strong assortative mating, as this is likely to elevate the level of inbreeding, increasing the risks of inbreeding depression and as a result decreasing population mean fitness. This in turn hinders the possibility of change, and instead might drive the population to extinction.

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1. Introduction

Assortative mating, i.e. the tendency of individuals to select mates more phenotypically similar to themselves than expected under random mating, has in many models been described as a possible driving force in sympatric and parapatric speciation (e.g. Dieckmann and Doebeli, 1999; Gavrillets, 2004). One set of such models are those that combine the process of divergent selection for resource use with the evolution of assortative mating. These models assume that if there is selection leading to a disparity in resource use, then this may promote selection for assortative mating between individuals that uses the same resource, as random mating would result in unfit hybrids (Felsenstein, 1981; Maynard Smith, 1966; Udovic, 1980). For this to come about, linkage disequilibrium is required to build up between the loci that determine resource use and those that determine preference for mates. Alternatively, the mechanism could involve a ‘magic trait’ (Gavrillets, 2004), i.e. a set of loci that pleiotropically determine both mating and resource preference (Hawthorn and Via, 2001; McKinnon and Rundle, 2002). One possible scenario where the above mentioned models might apply is when a host shift occurs in phytophagous insects (Berlocher and Feder, 2002; Dres and Mallet, 2002; Via, 2001). However, this form of mating system, where assortative mating is operating, brings with it a well-known cost when individuals spend time and effort searching for the right mates (Verzijden et al., 2005), but also a cost not often discussed earlier in the literature, namely the risk of inbreeding. There is an understandable reason for the obvious lack of attention to this important effect of assortative mating, and it is the fact that most models

assume that populations are very large when assortative mating initiates, an assumption not quite biologically reasonable. Examples that have been used are those where assortative mating starts on an island on the basis of an ecological trait (Kirkpatrick and Servedio, 1999), or within a group of phytophagous insects encountering and utilizing a new host plant (Berlocher and Feder, 2002; Dres and Mallet, 2002; Via, 2001). In both of these cases assortative mating should be adaptive, or even crucial for adaptive divergence to take place, but the population sizes are most likely fairly small given the ecological settings of the model.

The model of assortative mating most favourable to speciation is the one with phenotype matching (Verzijden et al., 2005), i.e. when assortative mating is based on phenotypic similarity. Assortative mating then occurs, according to the now classic models of sympatric speciation, among the most extreme individuals, who have a high probability of being closely related if in a small population, thus increasing the probability of expressing recessive deleterious mutations in homozygotes, and concomitant inbreeding depression i.e. reduced fitness due to the act of breeding between related individuals.

Although the literature on inbreeding and assortative mating per se is rich, assortative mating and inbreeding in conjunction is basically absent in the literature on speciation, and thus there is a fundamental lack of knowledge of the interaction of the two in the speciation process, even though the interaction has been studied in other contexts (e.g. Epinat and Lenormand, 2009). One empirical study experimentally explored the interaction of inbreeding and assortative mating, and found evidence for such an interaction that needs to be considered in further work on speciation (Rova and Björklund ms).

The possible outcomes of inbreeding are difficult to predict since they ultimately depend on the actual deleterious mutations accumulated in each population, and of population history (Theodorou and Couvet, 2006). In small populations it also depends on the stochastic

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effects of drift, and the effectiveness of purging (Crnokrak and Barrett, 2002). It has indeed been shown that purging can quite effectively cleanse a population from its genetic load, and thus, at least temporarily, increase its fitness (Crnokrak and Barrett, 2002; Theodorou and Couvet, 2006). Earlier empirical evidence of the positive effects of purging stems from the studies done by Barret and Charlesworth (1991), Fowler and Whitlock (1999), and Crnokrak and Barrett (2002).

Since the effects of inbreeding are highly stochastic, experiments can only capture a small part of the potential problem. An alternative approach is to use computer simulations, and in this study we will contrast two sets of populations selected to move to a new adaptive peak through a change in an ecological trait. The first set of populations are without any deleterious mutations, while in the other set of populations deleterious mutations are allowed to accumulate randomly with regard to phenotypic effects and the ecological trait. We will add assortative mating of different strengths and also analyse the effect of a cost in terms of mate search. The populations will be kept fairly small ($N=100$) to mimic cases such as founder effects, and host shifts, where population sizes are likely to be low at the start.

2. Methods

The simulation consists of sexually reproducing, diploid individuals with non-overlapping generations, thus being an individual-based model. The ecological trait underlying the mating system was determined by 20 diallelic loci with additive effects, such that the trait mean is the sum of the allelic effects of the separate loci (i.e. Falconer, 1989), resulting in a normal distribution of the trait. We assumed that each diploid individual had 100 loci (i.e. 200 alleles) that could be affected by mutations. Each locus was assigned a value of zero initially, while mutations were given a negative value. Mutations were taken from a gamma-distribution with parameters 0.5 and 3.0 based on Martin and Lenormand (2006). Allelic effects were multiplicative within each locus, meaning that for small mutational effects (<5), the effects were for all practical purposes close to additive in homozygous state, while mutations of large effects had a very large impact on fitness in homozygous state. This means that a single mutation of strength -1.0 impose a fitness cost of $-(1/200) = -0.5\%$. A single mutation of strength -14 impose a fitness cost of $-(14/200) = -7\%$, i.e. not entirely recessive but with a fitness cost that is not very strong. A homozygote for a mutation of the same strength suffer a fitness reduction of $-(14*14)/200 = -98\%$, i.e. basically lethal. The probability of getting one mutation of strength -14 is 0.0034 using this gamma distribution, and getting two independent mutations at the same locus of this strength is therefore $(0.0034*1/100)*(0.0034*1/100) \approx 10^{-9}$. This means that in a population of limited size (in the order of 1000s or less), homozygotes for mutations of a strong negative effect is almost exclusively caused by inbreeding, rather than multiple hits of the same mutation. Mutations were additive across loci, which means that the effects of one mutation is related to all other mutations that might be present in each individual. Before the run, mutations were allowed to accumulate for 20 generations.

The fitness (w) of individual i with trait z was calculated as:

$$w(i) = 1 - \frac{(z(i) - \theta)^2}{\omega}$$

where θ is the optimal trait value and ω the strength of stabilizing selection around the optimum (based on Lynch and Lande, 1993). In the simulations ω was set to 5, which indicates a rather strong stabilizing selection, i.e. a narrow fitness peak.

The total fitness of an individual was the sum of the fitness determined by the ecological trait, i.e. how close the individual was to the

ecological optimum, and the total effect of deleterious mutations. In the simulations where there were no deleterious mutations, total fitness equaled ecological fitness. The fitness of a breeding pair was determined by the sum of the two pair-members. The mean fitness of individuals was scaled to a mean of 1.0, implying that the expected number of offspring of a given pair was two in an equilibrium situation. In other words individuals were replacing themselves. In reality, we fed the pair-fitness value into a Poisson-distribution with the mean equal to the pair-fitness value. This introduces a certain degree of demographic stochasticity, which adds realism to the model.

Since we introduce demographic stochasticity, populations will fluctuate. To keep the fluctuations low we introduced density-compensation (d) using the Ricker function;

$$d = e^{r(1 - N_t/K)}$$

where r is the degree of density-compensation, here set to 1.0, N_t is population size a time t , and K is the carrying capacity, always set to 100. This gives a value of 1.0 if the population is at carrying capacity, below 1.0, and thus damping the reproductive output, when $N > K$, and larger than 1.0, and thus boosting the reproductive output, if $N < K$. The low level of r ensures that this density-compensation keeps the population roughly at a constant size under equilibrium conditions (e.g. Ranta et al., 2006).

Assortative mating was implemented as the probability (p) of a female (F) with size z_F to mate with a male (M) of a size z_M similar to herself according to the function;

$$p_{\text{mate}} = e^{\left(-C \frac{(z_F - z_M)^2}{\gamma}\right)}$$

where C determines the degree of assortative mating (Gavrilets and Vose, 2009). If $C = 0$ there is random mating, while if $C > 0$ the degree of assortative mating increases. γ determines the degree of choosiness, i.e. how close a mate must be to the choosing female before he is chosen. The mating function gives the probability of a mating given the difference in size between the mates, where $P_{\text{mate}} = 1$ if they are of equal size, and then the probability levels off at a rate determined by C (Fig. 1). In the simulations we used $C = 1.5, 2.0$, and 3.0 , and γ was set to be 10 in all runs.

We introduced a cost to assortative mating by limiting the number of males a female was allowed to visit. In the first case, a female was allowed to assess one male only, and if he was within her limits they mated with probability p_{mate} , otherwise a random male was chosen, in the second case a female was allowed to search among 10 males, and in the last run among all males. At reproduction, offspring inherited their genes from each parent with an equal chance of getting either of the two parental alleles.

We started the simulation by moving the optimum one standard deviation above the mean value, i.e. we introduced directional selection for a larger size. If the population at the end of the simulation, which lasted for 500 generations, had a mean size < 0.2 SD from the new optimum, we scored this as a peak shift. After each run we noted the mean distance to the new optimum, the change in mean fitness, and the change in population mean, population size, and the lowest population size during the time period. Each parameter combination (three values of C , three levels of cost, and with and without deleterious mutations), was run 500 times. To differentiate between the two major sets of populations we call the runs with populations without any deleterious mutations for the Clean populations, and the runs with populations with deleterious mutations for the Mutation populations. All simulations were done in MatLab.

3. Results

The probability of a peak shift was higher in the Mutation populations compared to the Clean ones (mean percentage of population

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