

## A Case of Sympatric Speciation?

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### Snail Models

The shells of snails exhibit either dextral or sinistral coiling. This chirality affects reproduction: in many cases animals of opposite coil cannot copulate. Edmund Gittenberger proposed in *Evolution* that this form of reproductive isolation could explain the sympatric populations of opposite chirality.

The additional facts are simple: snails move short distances (so inbreeding is common); the genotype of the mother determines the direction in the shell coiling of the offspring (maternal inheritance); the coiling seems to depend on a single genetic locus; and some hermaphroditic gastropods are capable of self-fertilization. Gittenberger concludes that “[t]he population-genetic processes involved ... deserve to be studied mathematically”.

In response, M. Johnson, B. Clark and J. Murray developed a simulation model based on a specific species (*Partula Suturalis*) which is polymorphic. The results from their simulations led them to conclude that the reproductive isolation imposed by chirality is a “negligible barrier to gene exchange”.

They carried out a second series of simulations with a stepping stone model of migration between 51 demes that included frequency-dependent selection. Their overall conclusion is that “chirality ... is particularly unlikely to serve as a basis for sympatric speciation”.

A model with the opposite conclusion was developed by H.A. Orr. His key idea was to recognize that local snail populations are often subdivided, leading to the founding of colonies by a small number of invaders. He carried out numerous Monte Carlo simulations introducing a single recessive or dominant mutation into a small population, and compared the results with simulations with neutral mutations. His conclusions are that “... maternal-effect mutations are fixed at a frequency somewhat below, but of the same order of magnitude as neutral mutations” ( $1/2N_e$ ), and that fixation occurs much more rapidly than neutral mutations and is independent of dominance.

This is a unique situation: a single gene is responsible for creating reproductive isolation and maternal inheritance reduces the selective disadvantage of the mutant allele, so there is a small probability of fixation of a mutation. Inbreeding, due to the low vagility of snails, could also favor speciation. My explorations of

this topic follow.

### Mathematical Models

Let  $D$  and  $d$  denote respectively the alleles for dextral (dominant) and sinistral (recessive) shell coiling for a snail population. Let  $+$  (dextral) and  $-$  (sinistral) denote the individual's phenotype. With this notation the population will have five possible types of individuals:  $DD^+$ ,  $Dd^+$ ,  $dd^+$ ,  $Dd^-$ , and  $dd^-$ , whose relative frequencies are indicated by  $x_1, x_2, x_3, x_4$ , and  $x_5$  respectively. Maternal inheritance explains the counter-intuitive types  $dd^+$  and  $Dd^-$ ; reproductive isolation by coiling chirality makes certain crosses impossible.

For an infinite (i.e., large enough) diploid population, with males and females equally divided among the population types, the result of random mating is summarized in the following table (mother's type horizontally and father's vertically):

	$DD^+$	$Dd^+$	$dd^+$	$Dd^-$	$dd^-$
$DD^+$	$4DD^+$	$2DD^+/2Dd^+$	$4Dd^-$	$\emptyset$	$\emptyset$
$Dd^+$	$2DD^+/2Dd^+$	$DD^+/2Dd^+/dd^+$	$2Dd^-/2dd^-$	$\emptyset$	$\emptyset$
$dd^+$	$4Dd^+$	$2Dd^+/2dd^+$	$4dd^-$	$\emptyset$	$\emptyset$
$Dd^-$	$\emptyset$	$\emptyset$	$\emptyset$	$DD^+/2Dd^+/dd^+$	$2Dd^-/2dd^-$
$dd^-$	$\emptyset$	$\emptyset$	$\emptyset$	$2Dd^+/2dd^+$	$4dd^-$

Assuming discrete generations and indicating the next generation frequencies as  $x'_i$  leads to the following system of nonlinear difference equations:

$$\begin{aligned}
 x'_1 &= (4x_1^2 + x_2^2 + x_4^2 + 4x_1x_2)/\hat{\mathbf{x}} \\
 x'_2 &= (2x_2^2 + 2x_4^2 + 4x_1x_2 + 4x_1x_3 + 2x_2x_3 + 2x_4x_5)/\hat{\mathbf{x}} \\
 x'_3 &= (x_2^2 + x_4^2 + 2x_2x_3 + 2x_4x_5)/\hat{\mathbf{x}} \\
 x'_4 &= (4x_1x_3 + 2x_2x_3 + 2x_4x_5)/\hat{\mathbf{x}} \\
 x'_5 &= (4x_3^2 + 4x_5^2 + 2x_2x_3 + 2x_4x_5)/\hat{\mathbf{x}},
 \end{aligned}$$

where  $\hat{\mathbf{x}}$  is the sum of the numerators ( $\hat{\mathbf{x}} = 4 \sum x_i^2 + 8(x_1x_2 + x_1x_3 + x_2x_3 + x_4x_5)$ ) so that the variables are relative frequencies ( $\sum x_i = 1$ ); thus any four  $x_i$ 's are independent. Vector notation can be used for simplicity of notation:  $\mathbf{x} = (x_1, x_2, x_3, x_4, x_5)$ .

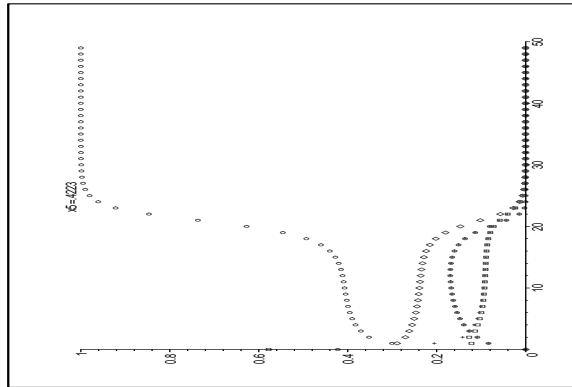
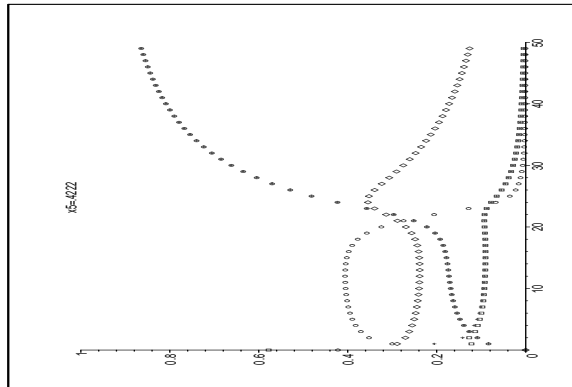
### Steady States

Under most circumstances the snail population will eliminate all but one of the two homozygous types  $DD^+$  and  $dd^-$ , i.e.,  $(1, 0, 0, 0, 0)$  and  $(0, 0, 0, 0, 1)$

are asymptotically stable steady states. I will call these two homozygous types 'coherent', since  $dd^+$  is homozygous but produces offspring with opposite coiling. No other population of a single type can be maintained, since heterozygous types produce, as offspring, some of the other types (for example, if  $x_2 > 0$  then both  $DD^+$  and  $dd^+$  appear in the next generation; an initial distribution - unlikely, of course! - of only  $dd^+$  snails leads to only  $dd^-$  snails in a single generation).

An unstable steady state occurs at  $(.5, 0, 0, 0, .5)$ . Coexistence of the coherent homozygotes  $DD^+$  and  $dd^-$  is not maintained for other proportions. An initial distribution of  $(a, 0, 0, 0, b)$ ,  $a \neq b$ , eventually reaches one of the two stable steady states; the population type which is initially most common prevails. This can be shown by studying, for instance,  $\Delta x_1 = x'_1 - x_1 = 4a^2/(4a^2 + 4b^2) - a = a(-2a^2 + 3a - 1)/(a^2 + b^2)$  whose sign is determined by the numerator of the last expression which is positive if  $a > .5$  and negative otherwise, indicating that  $x_1$  will tend to increase at each generation if its initial frequency is more than 0.5 and decrease if less than 0.5. If  $a = .5$  then  $\Delta x_1 = 0$ , which explains the unstable steady state. This can be stated in the language of Liapunov functions: let  $L = -x_1$  on the two-dimensional invariant subspace ('edge') of the state space given by frequencies of the form  $U_a = \{\mathbf{x} : \mathbf{x} = (a, 0, 0, 0, b), a > b\}$ , then  $\dot{L} \leq 0$  with equality at  $x_1 = 1$ , the asymptotically stable steady state. Similarly  $L = -x_4$  on the subspace given by  $U_b = \{\mathbf{x} : \mathbf{x} = (a, 0, 0, 0, b), a < b\}$ , shows the asymptotic stability of  $x_4 = 1$  for frequencies in the subspace. The unstable steady state follows from the boundary of the two positively invariant sets mentioned.

A particular interesting initial distribution consists of  $Dd^-$  and  $dd^-$  types (sinistrals). A critical value for  $x_5$  on the interval  $(.4222, .4223)$  determines the outcome of the system. If  $x_5$  is less than the critical value the population becomes exclusively homozygous dextral (slowly), otherwise it reaches the sinistral (recessive) steady state (see figures above). This suggests that a homozygous sinistral population would be sensitive to immigration of other population types, and that the region of attraction of  $(0, 0, 0, 0, 1)$  is smaller than the region for the homozygous dextral steady state. The figures show that the greatest change occurs between the 16th and the 26th generations; this behavior does not seem to be due to numerical roundoff errors.



## Mutation and Migration

Suppose migration or mutation introduces  $dd^-$  snails into a population at a constant rate. This requires the addition of a term  $m$  into the numerator of the equation for  $x'_5$ ,

$$x'_5 = (4x_3^2 + 4x_5^2 + 2x_2x_3 + 2x_4x_5 + m)/\hat{x}.$$

Suppose a homozygous  $DD^+$  population receives this migration. In this case the model predicts a stable polymorphism of the two coherent homozygous types with frequencies  $\hat{x}_1 = (3 + \sqrt{1 - 2m})/4$  and  $\hat{x}_5 = (1 - \sqrt{1 - 2m})/4$ , for example:  $m = .001$  results in  $\hat{x}_1 = .99975$  and  $\hat{x}_5 = .00025$ . A good approximation to  $\hat{x}_5$  is  $m/4$  for small  $m$  (the linearization of the expression for  $\hat{x}_5$ ). At the steady state the population frequencies will satisfy  $\hat{x}'_1 = \hat{x}_1$  and  $\hat{x}'_5 = \hat{x}_5$ . This condition, with all the other frequencies at zero, leads (after a bit of algebra) to  $4\hat{x}_1^2 + 4\hat{x}_5^2 + m = 4\hat{x}_1 = (4\hat{x}_5^2 + m)/\hat{x}_5$ ; the last equation then solves to  $\hat{x}_5 = 1 - \hat{x}_1 = (\hat{x}_1 \pm \sqrt{\hat{x}_1^2 - m})/2$  which in turn can be solved for  $\hat{x}_1$ .

Mutation or migration of  $dd^-$  types into other population distributions also lead, albeit slowly, to the same result. For example, an initial distribution with equal frequencies for the five types results in  $x_1$  with only 3 accurate digits after ten thousand generations (in particular,  $x_2$  decreases very slowly).

### **Selfing**

Gastropods are hermaphroditic, although selfing rates are low. To include selfing the equations can be modified by adding a term  $4sx_i$  to the numerator of the  $i$ -th equation in the system. No qualitative difference in behavior results from this change. The steady states mentioned do not change. The critical value for the initial distribution consisting of  $Dd^-$  and  $dd^-$  types dividing the regions of attraction on the 'edge' subspace mentioned in that section is shifted so that, for example with  $s = .05$  it occurs when  $x_5$  is on the interval (.4143, .4144) and the greatest changes occur a bit later than the 16th generation. The polymorphism obtained by mutation or migration is exactly as before (the selfing terms cancel in solving for  $\hat{x}_5$ ).

### **Conclusions**

This model does not include genetic drift caused by small population sizes. It does, however, support the notion that a small founder population of reverse coiling with respect to the main population, could be fixed if its composition happens to be in an appropriate proportion.