

Computer Simulation #4: Genetic Drift *versus* Selection in *Cepaea nemoralis*

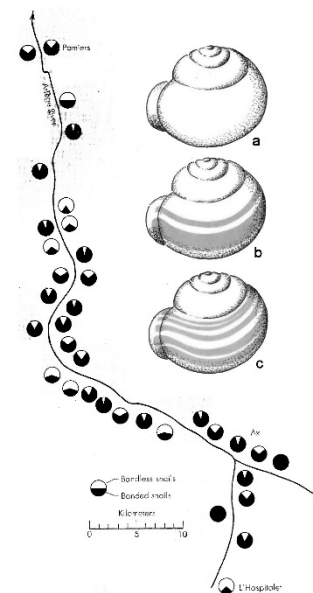
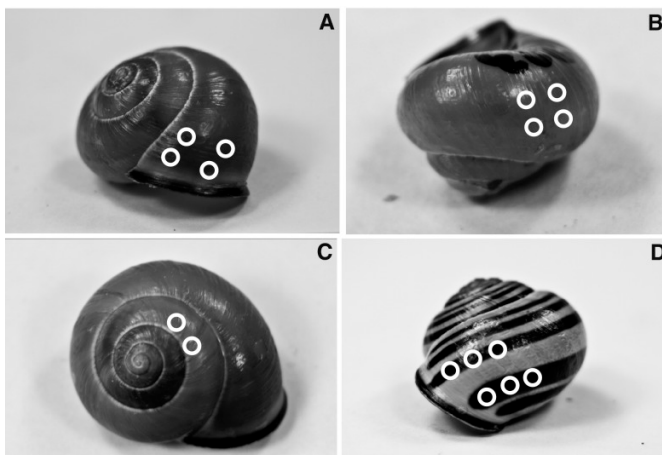
Cepaea nemoralis, the European land snail, is the classic example of the interplay of **deterministic** (natural selection) and **stochastic** (genetic drift) factors in evolution. EB Fords' studies on this species are the origin of Ecological Genetics.

Cepaea is widespread in western Europe and southern Great Britain; related species occur in North America, including Newfoundland. *C. nemoralis* is phenotypically polymorphic: individuals have dark or light shells, and from zero to five bands [below, left]. The polymorphism is controlled genetically: **dark** alleles are dominant to **light**, and **un-banded** alleles are dominant to **banded**.

Cepaea, like *Biston betularia*, is subject to differential visual predation by birds based on **crypsis**. The principle predators are song thrushes, which drop the snails on flat rocks ("thrush anvils"), which breaks the shells open so that the birds can eat the contents. Predation patterns can be measured by examination of the phenotypes of **broken** shells at the anvils. The incidence of the various shell types varies **inversely** according to habitat type. Broken **light-colored** shells are more common at anvils in **dark** "brown" backgrounds [e.g., bare soil], and less common in **light** "green" backgrounds [e.g., grasslands]. Broken **un-banded** shells are more common in "high contrast" habitats [e.g., short grass fields], and are less common on "low contrast" habitats [e.g., deep-shadow woodlands]. Much of the variation among colonies seems to be correlated with these two environmental variables. Snails that stand out visually are preferentially eaten by thrushes and show up more frequently as broken shells at the anvils: the more cryptic do not show up as frequently.

Genetic drift also plays a role. The snails occur in colonies of different sizes, from tens to thousands of individuals. Colonies are well-separated micro-geographically, and gene flow between colonies is severely limited by the creatures' sedentary habits. Different shell forms typically co-exist in most colonies, and the frequency of each type varies greatly over short distances [below, right], not always in accordance with predictions from crypsis. It has been shown that there is greater genetic variation (measured as variance) in shell patterns among **smaller** colonies than **larger**, consistent with the expectations of genetic drift. Some small colonies may even become '**fixed**' for '**lost**' for the '**wrong**', non-cryptic shell pattern.

This exercise compares the behavior of alleles in large and smaller populations, with greater or lesser degrees intensity of selection, and thus the interaction between **stochastic** Genetic Drift and **deterministic** Natural Selection in determining the degree of genetic polymorphism in natural populations.



1. Over time, in which size colony are allele frequencies more variable *among populations*? Why?
2. Is a species composed of *multiple small populations* 'more variable' than one composed of a *few large populations*? Explain.
3. Can **deleterious** alleles be **fixed** in a population? Under what circumstances? Explain.
4. What is the *ultimate fate* of alleles, even in 'large' populations? Explain.
5. For what values of s and N do the effects of selection and drift achieve an approximate equilibrium of Δq ?

$q = 0.1$ $N =$ / $S =$	0.100	0.010	0.001	0.0001	0.00001	0.000001	0.000
10							
100							
1,000							
10,000							

$q = 0.5$ $N =$ / $S =$	0.100	0.010	0.001	0.0001	0.00001	0.000
10						
100						
1,000						
10,000						

$q = 0.9$ $N =$ / $S =$	0.100	0.010	0.001	0.0001	0.00001	0.000
10						
100						
1,000						
10,000						