Drift in Quantitative Traits

The Math

There are several important facts to remember:

1. There is no tendency for allele frequencies to change in one direction versus another, i.e., $E(p') = p$.
2. The variance of allele frequencies in populations with the same starting allele frequencies is $Var(p') = p(1-p)/2N_e$.
3. The mean phenotype in a population is $\bar{x} = 2(p\alpha_1 + q\alpha_2)$, where α_1 and α_2 are the additive effects of allele A_1 and A_2, respectively.

To keep things simple, we'll assume that the trait in question is completely additive, i.e., the heterozygote is exactly intermediate in phenotype between the two homozygotes. Now

$$\begin{aligned} E(\bar{x})' &= E[2(p'\alpha_1 + q'\alpha_2)] \\ &= 2[E(p')\alpha_1 + E(q')\alpha_2] \\ &= 2(p\alpha_1 + q\alpha_2) \\ &= \bar{x} \end{aligned}$$

In other words, just as there is no tendency for allele frequencies to change in one direction or the other, there is no tendency for phenotypes to change in one direction or the other as a result of drift, i.e., $E(\bar{x})' = \bar{x}$.

Although there is no systematic tendency for phenotypes to change in one direction or another, phenotype frequencies will tend to change as allele frequencies change as a result of drift. Specifically,

$$\begin{aligned} Var(\bar{x}') &= Var[2(p'\alpha_1 + q'\alpha_2)] \\ &= 4[\alpha_1^2 Var(p') + 2\alpha_1\alpha_2 Cov(p', q') + \alpha_2^2 Var(q')] \\ &= 4Var(p')(\alpha_1^2 - 2\alpha_1\alpha_2 + \alpha_2^2) \\ &= 4\left(\frac{pq}{2N_e}\right)\alpha^2 \\ &= \frac{V_a}{N_e} \end{aligned}$$

Bulmer (*The Mathematical Theory of Quantitative Genetics*, Oxford University Press, 1980) show that the variance among populations diverging as a result of genetic drift increases linearly with time. Specifically,

$$Var(\bar{x}_t) = 2V_0 \left(1 - \left(1 - \frac{1}{2N_e}\right)^t\right)$$
$$\approx V_a \left(\frac{t}{N_e}\right) \quad ,$$

where V_0 is the initial additive genetic variance.

An application

Recall that Arnold found the following differences in number of tail and body vertebrae between coastal and inland populations of *Thamnophis elegans*:

Trait	Observed difference	V_a
body	16.21	35.4606
tail	9.69	37.2973

From the Central Limit Theorem and Bulmer's result, we would expect to find that 95% of populations diverging from one another differ from one another by no more than

$$4\sqrt{V_a\left(\frac{t}{N_e}\right)} \quad .$$

Thus, an observed difference of 16.12 body vertebrae is consistent with

$$\left(\frac{16.21}{4\sqrt{35.4606}}\right)^2 = 0.46 = \frac{t}{N_e} \quad ,$$

and an observed difference of 9.69 tail vertebrae is consistent with

$$\left(\frac{9.69}{4\sqrt{37.2973}}\right)^2 = 0.16 = \frac{t}{N_e} \quad .$$

If $N_e = 1000$ in these snakes, which seems likely to be an overestimate, the observed divergence could have occurred as a result of drift in as little as 160–460 generations. Similar caculations indicate that divergences among populations within the Coast Ranges could have occurred as a result of drift in as little as 1–10 generations.