## Homework April 21, 2015 (to be returned on April 28)

We want to determine mean and variance of the allele frequency variation $\Delta p$ in situations where the environment is fluctuating very rapidly. Viabilities are $w_{11}^{(t)}=1+Y_{1}^{(t)} ; w_{22}^{(t)}=1+Y_{2}^{(t)}$ and $w_{12}^{(t)}=1+\left(Y_{1}^{(t)}+Y_{2}^{(t)}\right) / 2$ for the homozygous $A_{1} A_{1}, A_{2} A_{2}$ and the heterozygous $A_{1} A_{2}$ or $A_{2} A_{1}$, respectively. The $Y$ 's are random variables supposed all independent and the index $t$ refers to the generations.

1) From the general formula that we derived during the lectures for the variation $\Delta p$ of the frequency $p$ of allele $A_{1}$ under random mating and selection with the previous viabilities, show that:

$$
\begin{equation*}
\Delta p^{(t)}=\frac{p^{(t)} q^{(t)}}{2} \frac{Y_{1}^{(t)}-Y_{2}^{(t)}}{1+p^{(t)} Y_{1}^{(t)}+q^{(t)} Y_{2}^{(t)}} . \tag{1}
\end{equation*}
$$

where $\Delta p^{(t)}$ indicates the difference between the values at the generations $t+1$ and $t$.
2) Suppose that the $Y$ 's are small and expand (1) to the second order.
3) Mean and variances of the $Y$ 's are: $\left\langle Y_{1}^{(t)}\right\rangle=\mu_{1} ;\left\langle Y_{2}^{(t)}\right\rangle=\mu_{2}$ and $\operatorname{Var} Y_{1}^{(t)}=\operatorname{Var} Y_{2}^{(t)}=\sigma^{2}$, with the means $\mu_{i}$ of the same order as the variance $\sigma^{2}$. Determine the expression of the mean $\left\langle\Delta p^{(t)}\right\rangle$ and $\operatorname{Var} \Delta p^{(t)}$.

The previous calculation was done under the hypothesis of additivity. To generalize to non-additive situations, one can suppose that viabilities are $w_{11}^{(t)}=W\left(1+Y_{1}^{(t)}\right) ; w_{22}^{(t)}=W\left(1+Y_{2}^{(t)}\right)$ and $w_{12}^{(t)}=W\left(1+\frac{Y_{1}^{(t)}+Y_{2}^{(t)}}{2}\right)$, where the $Y$ 's are again random variables, supposed all independent and the function $W(x)$ is a convex function, e.g. the Michaelis-Menten curve discussed during the course $W(x)=x(1+a) /(a+x)$.

1) Supposing the $Y$ 's small and having means and variances as above, calculate the geometric means, e.g. $w_{11}^{g}(t)=\left(\prod_{i=0}^{t-1} w_{11}^{i}\right)^{1 / t}$, and show that the condition for the heterozygote to be fitter than both homozygotes is

$$
\begin{equation*}
\left|\mu_{1}-\mu_{2}\right|<\frac{\sigma^{2}}{2 W^{\prime}(1)}\left(W^{\prime 2}(1)-W^{\prime \prime}(1)\right), \tag{2}
\end{equation*}
$$

where $W^{\prime}(1)$ and $W^{\prime \prime}(1)$ are the first and second derivatives of $W(x)$ at $x=1$.
2) Obtain the condition (2) of coexistence for the explicit form of $W$ given above, recover the additive limit and discuss whether the general case gives a range for coexistence larger or smaller than in the additive case.

