The Density-adjusted Approach

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Let us start with the following budget constraint.

\[ b_a p_a + c_a m_a + d_a z_a \leq \alpha \zeta_a w_a, \quad \forall a \]  \hspace{1cm} (1)

where \( b_a, c_a, d_a \) are constant coefficients, which express the rate at which energy can be used to achieve various levels of survival, fertility or growth. Term \( \alpha \zeta_a \) is a production coefficient linking body-size with the net production, or acquisition through foraging, of disposable energy. We add the coefficient \( \alpha \) to characterize the possible influence of density pressure. As we shall see, when the population size is larger, the foraging or hunting efficiency of all ages goes down, and hence \( \alpha \) reduces. The body size evolves according to

\[ w_{a+1} \equiv w_a + z_a. \]

Again, we assume determinate growth, with age \( r + 1 \) the mature age. So for ages \( a \leq r \), the individual is growing but not bearing. For ages \( a \geq r + 1 \), the individual is bearing but stops growing. We also consider a transfer from the adult age \( j \) to a premature age \( i \). Since we do not normalize \( \zeta_a \) to be 1 (as

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we did in the longevity paper), and we consider direct transfer of energies, we do not have the \( \eta_{ij} \) adjustment term. The transfer feasibility constraint is

\[
\lambda^{j-i} g(R_i) = p_i \cdots p_{j-1} T_j.
\]

Other identities include

\[
\begin{align*}
  z_s &= \alpha \zeta_s w_s - b_s p_s, \quad s \leq r, \ s \neq i, \\
  z_i &= \alpha \zeta_i w_i + R_i - b_i p_i, \\
  m_s &= \alpha \zeta_s w_s - b_s p_s, \quad s \geq r + 1, \ s \neq j, \\
  m_j &= \alpha \zeta_j w_j - T_j - b_j p_j.
\end{align*}
\]

Furthermore, we let

\[
K_i(\alpha) = \frac{1}{d_i} \left(1 + \frac{\alpha \zeta_i}{d_i+1}\right) \cdots \left(1 + \frac{\alpha \zeta_r}{d_r}\right).
\]

Term \( K_i(\alpha) \) is the compound effect of size accumulation from age \( i < r \) to maturity. It is easy to see that \( \partial K_i(\alpha) / \partial \alpha > 0 \).²

The problem of a selfish gene is to solve

\[
\lambda^t = \max_{\theta_s} p_1 \cdots p_r [p_{r+1} m_{r+1} \lambda^{t-r-1} + \cdots + p_{r+1} \cdots p_y m_y \lambda^{t-y}], \tag{2}
\]

subject to the above-mentioned identity constraints. Note that since

\[
\begin{align*}
w_{r+1} &= \left(1 + \frac{\alpha \zeta_r}{d_r}\right) w_r - \frac{b_r p_r}{d_r} \\
&= \left(1 + \frac{\alpha \zeta_r}{d_r}\right) \left[ \left(1 + \frac{\alpha \zeta_{r-1}}{d_{r-1}}\right) w_{r-1} - \frac{b_{r-1} p_{r-1}}{d_{r-1}} \right] - \frac{b_r p_r}{d_r} \\
&= \cdots
\end{align*}
\]

By iteration, it can be seen that \( \partial w_{r+1} / \partial \alpha > 0 \).

²If \( i = r \), then \( K_r = 1/d_r \) and \( \partial K_r / \partial \alpha = 0 \).
Suppose we are at time zero and originally at a stationary population with size $N_0$ and growth rate $\lambda = 1$. If a transfer is introduced and is selected, it will increase $\lambda$, and hence the population size grows according to $N_t = N_0 \lambda^t$. This in turn will cause density pressure and reduce the foraging efficiency $\alpha$ in the long run. To see how the transfer evolves in the long run, totally differentiating (2), we have

$$
\left\{ K_i(\alpha) \alpha \left[ \frac{\zeta r+1 p r+1 \lambda y-r}{c r+1} + \cdots + \frac{\zeta y p r+1 \cdots p y \lambda}{c y} \right] - p r+1 \cdots p j \frac{\lambda y-j+1}{c j} G_{i j} \right\} dR_i
+ \left[ \frac{\zeta r+1 p r+1 \lambda y-r-1}{c r+1} + \cdots + \frac{\zeta y p r+1 \cdots p y \lambda}{c y} \right] \left( w_{r+1} + \alpha \frac{\partial w_{r+1}}{\partial \alpha} \right) d\alpha + \Gamma d\lambda = 0,
$$

(3)

where $\Gamma < 0$ is the coefficient associated with $d\lambda$. In the above expression, the coefficient (terms in the curly brackets) of $dR_i$ should be positive if the increase in $R_i$ is to be selected. In the long run, $\lambda$ will go back to 1, hence $d\lambda = 0$. Given $dR_i > 0$ and that the coefficient in front of $d\alpha$ is positive, it implies that the corresponding change in $\alpha$ must be negative; that is, $\alpha$ should decrease, revealing a density pressure in the long run.

For $k \leq r$, differentiating the right hand side of (2) with respect to $p_k$ and using the envelope theorem, we see that its first order condition is proportional to the following expression:

$$
\Delta_{p_k} \equiv \left[ p r+1 m r+1 \lambda y-r + \cdots + p r+1 \cdots p y m y \lambda \right] - p k b_k K_k(\alpha) \alpha \left[ \frac{\zeta r+1 p r+1 \lambda y-r}{c r+1} + \cdots + \frac{\zeta y p r+1 \cdots p y \lambda}{c y} \right]
+ \frac{(p r+1 \cdots p j) \lambda y-i+1 g(R_i)}{c j (p i \cdots p j-1)} \cdot I(k) = 0, \quad k \leq r
$$

(4)

where $I(k) = 1$ if $r \geq k \geq i$, and $I(k) = 0$ otherwise. The term associated with $I(k)$ is from the differentiation of $dT_j/dR_i$, which is nonzero only if $k$ is in the range between $i$ and $j$. 

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Totally differentiating (4) we have

\[ \frac{\partial \Delta p_k}{\partial R_i} dR_i + \frac{\partial \Delta p_k}{\partial \alpha} d\alpha + \frac{\partial \Delta p_k}{\partial \lambda} d\lambda + \frac{\partial \Delta p_k}{\partial p_k} dp_k = 0. \]  

(5)

In the long run equilibrium, \( d\lambda = 0 \) and the relationship between \( d\alpha \) and \( dR_i \) must hold in accordance with (3). The second order condition of the maximization guarantees that \( \frac{\partial \Delta p_k}{\partial p_k} < 0 \). Thus, the sign of \( \frac{dp_k}{dR_i} \) in the long run hinges upon the sign of \( \frac{\partial \Delta p_k}{\partial R_i} dR_i + \frac{\partial \Delta p_k}{\partial \alpha} d\alpha \).

Let us first look at the case when \( i \leq k \leq r \). Differentiating \( \Delta p_k \) with respect to \( R_i \) and \( \alpha \) respectively, we have

\[ \frac{\partial \Delta p_k}{\partial R_i} = K_i(\alpha) \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right], \]

\[ \frac{\partial \Delta p_k}{\partial \alpha} = -p_k b_k \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right] \left( K_k(\alpha) + \alpha \frac{\partial K_k(\alpha)}{\partial \alpha} \right) \]

\[ + \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right] \left( \frac{\partial K_k(\alpha)}{\partial \alpha} \right). \]

Given the condition in (3) of a long run equilibrium with \( d\lambda = 0 \), we see that

\[ \frac{\partial \Delta p_k}{\partial R_i} dR_i + \frac{\partial \Delta p_k}{\partial \alpha} d\alpha = p_{r+1} \cdots p_j \frac{\lambda y - j + 1}{c_j} G_{ij} dR_i \]

\[ - p_k b_k \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right] \left( K_k(\alpha) + \alpha \frac{\partial K_k(\alpha)}{\partial \alpha} \right) d\alpha > 0. \]

The above expression is positive because \( dR_i > 0 \), the coefficient term in front of \( d\alpha \) is positive, and \( d\alpha < 0 \) because the of the increase in density pressure.

Next let us look at the case when \( k < i \). Now the differentiation of \( \Delta p_k \) with respect to \( R_i \) looks like

\[ \frac{\partial \Delta p_k}{\partial R_i} = K_i(\alpha) \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right] - p_{r+1} \cdots p_j \frac{\lambda y - j + 1}{c_j} G_{ij}, \]

\[ = - \left[ \frac{\zeta_{r+1} p_{r+1} \lambda y - r}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda^y}{c_y} \right] \left( K_k(\alpha) + \alpha \frac{\partial K_k(\alpha)}{\partial \alpha} \right) d\alpha > 0. \]
and the formula of $\frac{\partial \Delta p_k}{\partial \alpha}$ is the same as above because the term associated with $I(k)$ does not have $\alpha$. Again, using (3), one see that

$$\frac{\partial \Delta p_k}{\partial R_i} dR_i + \frac{\partial \Delta p_k}{\partial \alpha} d\alpha = -p_k b_k \left[ \frac{\zeta_{r+1} p_{r+1} \lambda^{y-r}}{c_{r+1}} + \cdots + \frac{\zeta_y p_{r+1} \cdots p_y \lambda}{c_y} \right] \left( K_k(\alpha) + \alpha \frac{\partial K_k(\alpha)}{\partial \alpha} \right) d\alpha > 0. \quad (7)$$

The above expression is positive because $d\alpha < 0$, also due to the fact of increasing density pressure.

Now we look at the case when $r+1 \leq k \leq j-1$, the ages after maturity but before transferring. The first order condition for $p_k$ is

$$\Delta p_k \equiv (m_k \lambda^{y-k+1} + p_{k+1} m_{k+1} \lambda^{y-k} + \cdots + p_{k+1} \cdots p_y m_y \lambda) - \frac{p_k b_k \lambda^{y-k+1}}{c_k} + \left( \frac{p_k \cdots p_j \lambda^{y-j+1} g(R_i)}{c_j p_k (p_i \cdots p_{j-1})} \right) I(k) = 0, \quad k \geq r+1 \quad (8)$$

where $I(k) = 1$ if $r+1 \leq k \leq j-1$, and $I(k) = 0$ otherwise. The differentiation of $\Delta p_k$ with respect to $R_i$ and $\alpha$ are respectively

$$\frac{\partial \Delta p_k}{\partial R_i} = K_i(\alpha) \left[ \frac{\zeta_k p_k \lambda^{y-k+1}}{c_k} + \cdots + \frac{\zeta_y p_k \cdots p_y \lambda}{c_y} \right]$$

$$\frac{\partial \Delta p_k}{\partial \alpha} = \left[ \frac{\zeta_k p_k \lambda^{y-k+1}}{c_k} + \cdots + \frac{\zeta_y p_k \cdots p_y \lambda}{c_y} \right] \left( w_{r+1} + \alpha \frac{\partial w_{r+1}}{\partial \alpha} \right).$$

Equation (3) tells us that the following expression must hold$^3$

$$\alpha K_i(\alpha) dR_i + \left( w_{r+1} + \alpha \frac{\partial w_{r+1}}{\partial \alpha} \right) d\alpha > 0$$

It can be seen that

$$\frac{\partial \Delta p_k}{\partial R_i} dR_i + \frac{\partial \Delta p_k}{\partial \alpha} d\alpha = \left[ \frac{\zeta_k p_k \lambda^{y-k+1}}{c_k} + \cdots + \frac{\zeta_y p_k \cdots p_y \lambda}{c_y} \right] \left[ \alpha K_i(\alpha) dR_i + \left( w_{r+1} + \alpha \frac{\partial w_{r+1}}{\partial \alpha} \right) d\alpha \right], \quad (9)$$

$^3$Otherwise (3) is impossible to hold, given that the term $p_{r+1} \cdots p_j \lambda^{y-j+1} G_{ij} dR_i > 0.$
which is still positive.

Finally, for \( k \geq j \), we can differentiate \( \Delta_{p_k} \) in (8), knowing that \( I(k) = 0 \). There is no term associated with \( g(R_i) \), and hence the differentiation is simple. The result is exactly the same as in (9), and is positive.

In sum, a selection-improving increase in the transfer from age \( j \) to age \( i \) increases the survival probability of all ages.

If all \( p_a \)’s increase in the new long run equilibrium after this transfer, given that \( \lambda \) remains the same (= 1) under the density pressure, we know from (2) that many \( m_a \)’s should decrease. It may be possible that fertility at some ages increase, due to the substitution from less efficient fertile ages (with larger \( c_a \)) to more efficient ages (with smaller \( c_a \)). But since \( p_1 \cdots p_r \) increases, we do know from (2) that the

\[
p_{r+1} m_{r+1} + \cdots + p_{r+1} \cdots p_y m_y
\]

must reduce.

\footnote{For all \( k > j \), \( I(k) = 0 \), and there is no \( m_k \) term for \( k > j \). Since \( R_i \) enters only in \( m_a \ \forall a \leq j \), no extra terms appear.}