

In what follows, we provide derivations for some of the conditions in the chapter *The Evolution of Altruism* by Glenney & Kerr.

Derivation of condition [10]

Before the first round of reproduction, let the frequency of groups with i altruists be g_i :

$$g_i = \binom{n^*}{i} \bar{p}^i (1 - \bar{p})^{n^* - i}, \quad [\text{D1}]$$

where \bar{p} is the global frequency of altruists and n^* is the group size. After the first round of reproduction, let the frequency of groups with j altruists be given by f_j :

$$f_j = \sum_{i=0}^{n^*} \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^* - i}{n^*} \right)^{n - j} g_i, \quad [\text{D2}]$$

where n is the group size. Assuming a linear fitness structure (equations [6] and [7]), the average fitness of an altruist is:

$$\bar{\alpha} = \frac{1}{n\bar{p}} \sum_{j=0}^n f_j j(z + b(j-1) - c).$$

The average fitness of a defector is:

$$\bar{\delta} = \frac{1}{n(1 - \bar{p})} \sum_{j=0}^n f_j (n - j)(z + bj).$$

An increase in altruist frequency requires (by condition [13]):

$$\bar{\alpha} > \bar{\delta},$$

or

$$\sum_{j=0}^n f_j \left\{ \frac{j(z + b(j-1) - c)}{n\bar{p}} - \frac{(n-j)(z + bj)}{n(1 - \bar{p})} \right\} > 0,$$

$$\sum_{j=0}^n f_j \{ j(z + b(j-1) - c)(1 - \bar{p}) - (n-j)(z + bj)\bar{p} \} > 0,$$

$$\sum_{j=0}^n f_j \left\{ [zj(1-\bar{p}) - (n-j)z\bar{p}] + [bj(j-1)(1-\bar{p}) - (n-j)b_j\bar{p}] - cj(1-\bar{p}) \right\} > 0,$$

$$\sum_{j=0}^n f_j \left\{ [zj - nz\bar{p}] + [(bj^2 - bj)(1-\bar{p}) - nb_j\bar{p} + bj^2\bar{p}] - cj(1-\bar{p}) \right\} > 0,$$

$$\sum_{j=0}^n f_j \left\{ [zj - nz\bar{p}] + [bj^2 - bj + b_j\bar{p} - nb_j\bar{p}] - cj(1-\bar{p}) \right\} > 0,$$

$$\sum_{j=0}^n f_j \left\{ zj - nz\bar{p} + bj^2 - b(1+(n-1)\bar{p})j - c(1-\bar{p})j \right\} > 0,$$

$$\sum_{j=0}^n f_j \left\{ [z - b(1+(n-1)\bar{p}) - c(1-\bar{p})]j + bj^2 - nz\bar{p} \right\} > 0.$$

Using equation [D2], this condition becomes:

$$\sum_{j=0}^n \sum_{i=0}^{n^*} \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} g_i \left\{ [z - b(1+(n-1)\bar{p}) - c(1-\bar{p})]j + bj^2 - nz\bar{p} \right\} > 0.$$

Using equation [D1], this condition becomes:

$$\sum_{j=0}^n \sum_{i=0}^{n^*} \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} \left\{ [z - b(1+(n-1)\bar{p}) - c(1-\bar{p})]j + bj^2 - nz\bar{p} \right\} > 0,$$

or

$$\sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} \sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} \left\{ [z - b(1+(n-1)\bar{p}) - c(1-\bar{p})]j + bj^2 - nz\bar{p} \right\} > 0,$$

$$\sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} \left[\begin{aligned} & (z - b(1+(n-1)\bar{p}) - c(1-\bar{p})) \left\{ \sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} j \right\} \\ & + b \left\{ \sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} j^2 \right\} - nz\bar{p} \end{aligned} \right] > 0. \quad [\text{D3}]$$

To simplify [D3], we first simplify some of the sums in brackets. Consider the sum:

$$\sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} j.$$

This can be reworked as follows:

$$\sum_{j=1}^n \frac{n!}{j!(n-j)!} \left(\frac{i}{n^*}\right)^j \left(\frac{n^*-i}{n^*}\right)^{n-j} j,$$

$$n \left(\frac{i}{n^*}\right) \sum_{j=1}^n \frac{(n-1)!}{(j-1)!((n-1)-(j-1))!} \left(\frac{i}{n^*}\right)^{j-1} \left(\frac{n^*-i}{n^*}\right)^{(n-1)-(j-1)}.$$

Rewriting the index of the sum as $k = j-1$, we have:

$$n \left(\frac{i}{n^*}\right) \sum_{k=0}^{n-1} \frac{(n-1)!}{k!((n-1)-k)!} \left(\frac{i}{n^*}\right)^k \left(\frac{n^*-i}{n^*}\right)^{(n-1)-k},$$

However, the sum is simply all the terms of a binomial distribution (with parameters $n-1$ and i/n^*). Thus, this sum is simply unity, such that:

$$\sum_{j=1}^n \frac{n!}{j!(n-j)!} \left(\frac{i}{n^*}\right)^j \left(\frac{n^*-i}{n^*}\right)^{n-j} j = n \left(\frac{i}{n^*}\right). \quad [\text{D4}]$$

This is simply the expectation of a binomially distributed variable (with parameters n and (i/n^*)). Now consider the sum:

$$\sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*}\right)^j \left(\frac{n^*-i}{n^*}\right)^{n-j} j^2.$$

This can be reworked as follows:

$$\sum_{j=1}^n \frac{n!}{j!(n-j)!} \left(\frac{i}{n^*}\right)^j \left(\frac{n^*-i}{n^*}\right)^{n-j} j^2,$$

$$n \left(\frac{i}{n^*}\right) \sum_{j=1}^n \frac{(n-1)!}{(j-1)!((n-1)-(j-1))!} \left(\frac{i}{n^*}\right)^{j-1} \left(\frac{n^*-i}{n^*}\right)^{(n-1)-(j-1)} j,$$

$$n \left(\frac{i}{n^*}\right) \sum_{k=0}^{n-1} \frac{(n-1)!}{k!((n-1)-k)!} \left(\frac{i}{n^*}\right)^k \left(\frac{n^*-i}{n^*}\right)^{(n-1)-k} (k+1),$$

$$n \left(\frac{i}{n^*}\right) \left\{ \left[\sum_{k=0}^{n-1} \frac{(n-1)!}{k!((n-1)-k)!} \left(\frac{i}{n^*}\right)^k \left(\frac{n^*-i}{n^*}\right)^{(n-1)-k} k \right] + \left[\sum_{k=0}^{n-1} \frac{(n-1)!}{k!((n-1)-k)!} \left(\frac{i}{n^*}\right)^k \left(\frac{n^*-i}{n^*}\right)^{(n-1)-k} \right] \right\}.$$

Using equation [D4], we can simplify the above quantity:

$$n \binom{i}{n^*} \left\{ \left[(n-1) \binom{i}{n^*} \right] + 1 \right\}.$$

Thus,

$$\sum_{j=0}^n \binom{n}{j} \left(\frac{i}{n^*} \right)^j \left(\frac{n^*-i}{n^*} \right)^{n-j} j^2 = \frac{n(n-1)i^2 + n^*ni}{(n^*)^2}. \quad [\text{D5}]$$

We note that equations [D4] and [D5] can be derived much more quickly using a moment generating function approach. Using equations [D4] and [D5], we can simplify equation [D3]:

$$\sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} \left[(z - b(1+(n-1)\bar{p}) - c(1-\bar{p})) \left\{ n \binom{i}{n^*} \right\} + b \left\{ \frac{n(n-1)i^2 + n^*ni}{(n^*)^2} \right\} - nz\bar{p} \right] > 0,$$

or

$$\begin{aligned} & \sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} \left[\left\{ (z - b(1+(n-1)\bar{p}) - c(1-\bar{p})) + b \right\} \left(\frac{n}{n^*} \right) i + b \left\{ \frac{n(n-1)}{(n^*)^2} \right\} i^2 - nz\bar{p} \right] > 0, \\ & \left[\left\{ (z - b(1+(n-1)\bar{p}) - c(1-\bar{p})) + b \right\} \left(\frac{n}{n^*} \right) \left\{ \sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} i \right\} \right. \\ & \left. + b \left(\frac{n(n-1)}{(n^*)^2} \right) \left\{ \sum_{i=0}^{n^*} \binom{n^*}{i} \bar{p}^i (1-\bar{p})^{n^*-i} i^2 \right\} - nz\bar{p} \right] > 0, \quad [\text{D6}] \end{aligned}$$

Using simplifications nearly identical to those used to produce equations [D4] and [D5], we can simplify [D6]:

$$\left[\left\{ (z - b(1+(n-1)\bar{p}) - c(1-\bar{p})) + b \right\} \left(\frac{n}{n^*} \right) \{n^* \bar{p}\} \right. \\ \left. + b \left(\frac{n(n-1)}{(n^*)^2} \right) \{n^* \bar{p} [(n^*-1)\bar{p} + 1]\} - nz\bar{p} \right] > 0,$$

or

$$\begin{aligned} & \{-b(n-1)\bar{p} - c(1-\bar{p})\} n\bar{p} + b \left(\frac{n(n-1)}{n^*} \right) \{(n^*-1)\bar{p}^2 + \bar{p}\} > 0, \\ & -bn(n-1)\bar{p}^2 - c(1-\bar{p})n\bar{p} + bn(n-1) \left(\frac{(n^*-1)}{n^*} \right) \bar{p}^2 + bn(n-1) \left(\frac{1}{n^*} \right) \bar{p} > 0, \end{aligned}$$

$$-c(1-\bar{p})n\bar{p} - bn(n-1)\left(\frac{1}{n^*}\right)\bar{p}^2 + bn(n-1)\left(\frac{1}{n^*}\right)\bar{p} > 0,$$

$$bn(n-1)\left(\frac{1}{n^*}\right)\bar{p}(1-\bar{p}) > c(1-\bar{p})n\bar{p},$$

$$b(n-1)\left(\frac{1}{n^*}\right) > c.$$

With $B=b(n-1)$, the condition for the evolution of altruism is:

$$B\left(\frac{1}{n^*}\right) > c,$$

which completes the derivation.

Derivation of condition [12]

Here we consider the case where homogeneous groups of size n form with probability F and groups randomly form with probability $1-F$. Given these assumptions, the average fitness of an altruist and defector are:

$$\bar{\alpha} = F(z + b(n-1) - c) + (1-F)\frac{1}{n\bar{p}}\sum_{j=0}^n\binom{n}{j}\bar{p}^j(1-\bar{p})^{n-j}(z + b(j-1) - c)j,$$

$$\bar{\delta} = Fz + (1-F)\frac{1}{n(1-\bar{p})}\sum_{j=0}^n\binom{n}{j}\bar{p}^j(1-\bar{p})^{n-j}(z + bj)(n-j).$$

The average altruist fitness can be reworked as follows:

$$\bar{\alpha} = F(z + b(n-1) - c) + (1-F)\frac{1}{n\bar{p}}\sum_{j=0}^n\binom{n}{j}\bar{p}^j(1-\bar{p})^{n-j}((z - b - c)j + bj^2),$$

$$\bar{\alpha} = F(z + b(n-1) - c) + (1-F)\frac{(z - b - c)}{n\bar{p}}\left\{\sum_{j=0}^n\binom{n}{j}\bar{p}^j(1-\bar{p})^{n-j}j\right\} + (1-F)\frac{b}{n\bar{p}}\left\{\sum_{j=0}^n\binom{n}{j}\bar{p}^j(1-\bar{p})^{n-j}j^2\right\}.$$

Using simplifications nearly identical to those used to produce equations [D4] and [D5], we have

$$\bar{\alpha} = F(z + b(n-1) - c) + (1-F)\frac{(z - b - c)}{n\bar{p}}\{n\bar{p}\} + (1-F)\frac{b}{n\bar{p}}\{n\bar{p}[(n-1)\bar{p} + 1]\},$$

$$\bar{\alpha} = F(z + b(n-1) - c) + (1-F)(z - b - c) + (1-F)b[(n-1)\bar{p} + 1],$$

$$\bar{\alpha} = z - c + F(b(n-1)) + (1-F)b(n-1)\bar{p},$$

$$\bar{\alpha} = z + \{F + (1-F)\bar{p}\}(b(n-1)) - c.$$

The average defector fitness can be reworked as follows:

$$\bar{\delta} = Fz + (1-F) \frac{1}{n(1-\bar{p})} \sum_{j=0}^n \binom{n}{j} \bar{p}^j (1-\bar{p})^{n-j} (z + bj)(n-j),$$

$$\bar{\delta} = Fz + (1-F) \frac{1}{n(1-\bar{p})} \sum_{j=0}^n \binom{n}{j} \bar{p}^j (1-\bar{p})^{n-j} (zn + (bn-z)j - bj^2),$$

$$\bar{\delta} = Fz + (1-F) \frac{z}{(1-\bar{p})} + (1-F) \frac{bn-z}{n(1-\bar{p})} \left\{ \sum_{j=0}^n \binom{n}{j} \bar{p}^j (1-\bar{p})^{n-j} j \right\} - (1-F) \frac{b}{n(1-\bar{p})} \left\{ \sum_{j=0}^n \binom{n}{j} \bar{p}^j (1-\bar{p})^{n-j} j^2 \right\}.$$

$$\bar{\delta} = Fz + (1-F) \frac{z}{(1-\bar{p})} + (1-F) \frac{bn-z}{n(1-\bar{p})} \{n\bar{p}\} - (1-F) \frac{b}{n(1-\bar{p})} \{n\bar{p}[(n-1)\bar{p} + 1]\},$$

$$\bar{\delta} = Fz + (1-F) \frac{z}{(1-\bar{p})} + (1-F) \frac{(bn-z)\bar{p}}{(1-\bar{p})} - (1-F) \frac{(n-1)b\bar{p}^2}{(1-\bar{p})} - (1-F) \frac{b\bar{p}}{(1-\bar{p})},$$

$$\bar{\delta} = Fz + (1-F) \left\{ \frac{z(1-\bar{p}) + b(n-1)\bar{p} - (n-1)b\bar{p}^2}{(1-\bar{p})} \right\},$$

$$\bar{\delta} = Fz + (1-F) \left\{ \frac{z(1-\bar{p}) + b(n-1)\bar{p}(1-\bar{p})}{(1-\bar{p})} \right\},$$

$$\bar{\delta} = z + (1-F)\bar{p}(b(n-1)).$$

Condition [13] amounts to:

$$z + \{F + (1-F)\bar{p}\}(b(n-1)) - c > z + (1-F)\bar{p}(b(n-1)),$$

$$F(b(n-1)) - c > 0,$$

$$(b(n-1))F > c.$$

With $B=b(n-1)$, the condition for the evolution of altruism is:

$$BF > c,$$

which completes the derivation.

Derivation of condition [14]

Here we make no assumptions about the way groups form. Thus, we will let f_i be the frequency of groups with i altruists. In this general case, condition [13] is

$$\begin{aligned} \frac{1}{n\bar{p}} \sum_{i=0}^n f_i \alpha_{i-1} i &> \frac{1}{n(1-\bar{p})} \sum_{i=0}^n f_i \delta_i (n-i), \\ (1-\bar{p}) \sum_{i=0}^n f_i \alpha_{i-1} i &> \bar{p} \sum_{i=0}^n f_i \delta_i (n-i), \\ \sum_{i=0}^n f_i \alpha_{i-1} i - \bar{p} \sum_{i=0}^n f_i \{ \alpha_{i-1} i + \delta_i (n-i) \} &> 0. \end{aligned} \quad [\text{D7}]$$

In order to switch to a collective perspective, we note that:

$$\begin{aligned} \alpha_{i-1} i &= \pi_i \phi_i, \\ \alpha_{i-1} i + \delta_i (n-i) &= \pi_i. \end{aligned}$$

Thus, condition [D7] can be rewritten:

$$\begin{aligned} \sum_{i=0}^n f_i \pi_i \phi_i - \bar{p} \sum_{i=0}^n f_i \pi_i &> 0, \\ \sum_{i=0}^n f_i (\pi_i \phi_i - \pi_i \bar{p}) &> 0, \\ \sum_{i=0}^n f_i (\pi_i p_i - \pi_i \bar{p} + \pi_i \phi_i - \pi_i p_i) &> 0, \\ \sum_{i=0}^n f_i (\pi_i (p_i - \bar{p})) + \sum_{i=0}^n f_i \pi_i (\phi_i - p_i) &> 0, \\ \sum_{i=0}^n f_i ((\pi_i - \bar{\pi})(p_i - \bar{p})) + \sum_{i=0}^n f_i \pi_i (\phi_i - p_i) &> 0. \end{aligned} \quad [\text{D8}]$$

Thus, by standard statistical definitions, this condition becomes:

$$\text{cov}(\pi, p) + \text{ave}[\pi(\phi - p)] > 0,$$

which completes the derivation.

Derivation of condition [15]

We start by plugging equations [8] and [9] into condition [D8]:

$$\sum_{i=0}^n f_i ((nz + [B-c]i)(p_i - \bar{p})) + \sum_{i=0}^n f_i ([z - c + b(i-1)]i - (nz + [B-c]i)p_i) > 0.$$

Because $p_i = i/n$ and $B = (n-1)b$, we have:

$$\sum_{i=0}^n f_i ((z + [B-c]p_i)(p_i - \bar{p})) + \sum_{i=0}^n f_i ([z - c + b(i-1)]p_i - (z + [(n-1)b - c]p_i)p_i) > 0,$$

$$\sum_{i=0}^n f_i [B-c](p_i^2 - p_i\bar{p}) + \sum_{i=0}^n f_i ([bi - (b+c)]p_i - [(n-1)b - c]p_i^2) > 0,$$

$$\sum_{i=0}^n f_i [B-c](p_i^2 - p_i\bar{p}) > \sum_{i=0}^n f_i ((b+c) - nbp_i)p_i + [(n-1)b - c]p_i^2,$$

$$\sum_{i=0}^n f_i [B-c](p_i^2 - p_i\bar{p}) > \sum_{i=0}^n f_i ((b+c)p_i - nbp_i^2 + (n-1)bp_i^2 - cp_i^2),$$

$$\sum_{i=0}^n f_i [B-c](p_i^2 - p_i\bar{p}) > \sum_{i=0}^n f_i ((b+c)p_i - (b+c)p_i^2),$$

$$(B-c) \sum_{i=0}^n f_i (p_i^2 - p_i\bar{p}) > (b+c) \sum_{i=0}^n f_i (p_i - p_i^2),$$

$$(B-c) \sum_{i=0}^n f_i (p_i^2 - p_i\bar{p}) > (b+c) \sum_{i=0}^n f_i (p_i(1-\bar{p}) - (p_i^2 - p_i\bar{p})). \quad [\text{D9}]$$

The variance of altruistic frequency within groups is:

$$\sigma_p^2 = \left\{ \sum_{i=0}^n f_i p_i^2 \right\} - \bar{p}^2 = \sum_{i=0}^n f_i (p_i^2 - p_i\bar{p}).$$

Therefore, condition [D9] can be rephrased as follows:

$$(B-c)\sigma_p^2 > (b+c)(\bar{p}(1-\bar{p}) - \sigma_p^2),$$

which completes the derivation.
