Correction

After publication of "Evolution in stage-structured populations" by M. Barfield et al. (*American Naturalist* 177:397–409), the authors found a typographical error that crept in during the final revision.

In the last expression of equation (6), $\bar{a}_{ij}^{-1}$ should have followed c_{ij}, giving $\bar{\mathbf{z}}'_i = \sum_j [c^t_{ij}\bar{\mathbf{z}}_j + c^f_{ij}\bar{\mathbf{g}}_j + c_{ij}\bar{a}_{ij}^{-1}(\mathbf{P}_j\nabla_{\bar{z}_j}\bar{t}_{ij} + \mathbf{G}_j\nabla_{\bar{z}_j}\bar{f}_{ij})]$, which can also be written as $\bar{\mathbf{z}}'_i = \sum_j (c^t_{ij}\bar{\mathbf{z}}_j + c^f_{ij}\bar{\mathbf{g}}_j) + \sum_j (c^t_{ij}\mathbf{P}_j\nabla_{\bar{z}_j}\ln\bar{t}_{ij} + c^f_{ij}\mathbf{G}_j\nabla_{\bar{z}_j}\ln\bar{f}_{ij})$. (Also, in the second line of eq. [6], $\phi(\mathbf{g}, \mathbf{z})$ should be $\phi_i(\mathbf{g}, \mathbf{z})$, and in the last paragraph of p. 399, $\bar{g}_j$, $\bar{z}_j$, G_j, and P_j should be $\bar{\mathbf{g}}_j$, $\bar{\mathbf{z}}_j$, $\mathbf{G}_j$, and $\mathbf{P}_j$, respectively.)

A correct form of equation (6) was used for the results in figures 1 and 2, so the only effect of this error on the rest of the article is that the expression for $\mathbf{b}_{zi}$ in appendix B should be $\mathbf{b}_{zi} = \sum_j (c^t_{ij}\mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\ln\bar{t}_{ij} + c^f_{ij}\mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\ln\bar{f}_{ij})$. This change has no effect on equations (B1)–(B7) provided the correct form of β is used. This also has no effect on the full derivation in appendix B because these terms are multiplied by 0 in equation (B7).

Since publication, requests have been made for the derivations of equations (5) and (6). These appear in the following appendix.

APPENDIX

Derivations of Equations (5) and (6) of Barfield, Holt, and Gomulkiewicz 2011 (BHG2011)

Assume

$$\begin{pmatrix}\mathbf{g}_i\\ \mathbf{z}_i\end{pmatrix}$$

is normally distributed with mean

$$\begin{pmatrix}\bar{\mathbf{g}}_i\\ \bar{\mathbf{z}}_i\end{pmatrix}$$

and variance-covariance matrix

$$\mathbf{M} = \begin{pmatrix}\mathbf{G}_i & \mathbf{G}_i\\ \mathbf{G}_i & \mathbf{P}_i\end{pmatrix},$$

where $\mathbf{g}_i$ is the vector of genotypes, $\mathbf{z}_i$ is the vector of phenotypes, $\mathbf{G}_i$ is the additive-genetic covariance matrix and $\mathbf{P}_i$ the phenotypic covariance matrix in stage i. With $\mathbf{z}_i = \mathbf{g}_i + \mathbf{e}_i$ this assumes only that $\mathbf{g}_i$ and $\mathbf{e}_i$ are independent. Let $p_i(\mathbf{g}, \mathbf{z})$ denote the probability density function of this distribution in the current generation, and quantities with primes denote those in the next generation.

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Derivation of BHG2011 Equation (5)

$$
\begin{aligned}
\bar{\mathbf{g}}_i' &= \int\int \mathbf{g}p_i'(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} = \frac{T_i'}{N_i'}\int\int \mathbf{g}\theta_i(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + \frac{F_i'}{N_i'}\int\int \mathbf{g}\phi_i(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} \\
&= \frac{T_i'}{N_i'}\int\int \mathbf{g}\frac{1}{T_i'}\sum_j N_j t_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + \frac{F_i'}{N_i'}\int \mathbf{g}\Phi_i(\mathbf{g})d\mathbf{g} \\
&= \frac{1}{N_i'}\sum_j N_j \int t_{ij}(\mathbf{z})\int \mathbf{g}p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} + \frac{1}{N_i'}\int \mathbf{g}\sum_j N_j\int f_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{z}d\mathbf{g} \\
&= \frac{1}{N_i'}\sum_j N_j \int a_{ij}(\mathbf{z})\int \mathbf{g}p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} = \frac{1}{N_i'}\sum_j N_j \int a_{ij}(\mathbf{z})\left[\int \mathbf{g}p_j(\mathbf{g}|\mathbf{z})d\mathbf{g}\right]p_j(\mathbf{z})d\mathbf{z} \\
&= \frac{1}{N_i'}\sum_j N_j \int a_{ij}(\mathbf{z})[\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}(\mathbf{z}-\bar{\mathbf{z}}_j)]p_j(\mathbf{z})d\mathbf{z} \\
&= \frac{1}{N_i'}\sum_j N_j\left\{\bar{a}_{ij}\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}\left[\int \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{z})d\mathbf{z} - \bar{a}_{ij}\bar{\mathbf{z}}_j\right]\right\},
\end{aligned}
\tag{A1}
$$

where $p_j(\mathbf{g}|\mathbf{z})$ is the conditional distribution of $\mathbf{g}$ given $\mathbf{z}$ and

$$p_j(\mathbf{z}) = \frac{1}{\sqrt{(2\pi)^m|\mathbf{P}_j|}}\exp\left\{-\frac{1}{2}(\mathbf{z}-\bar{\mathbf{z}}_j)^{\mathrm{T}}\mathbf{P}_j^{-1}(\mathbf{z}-\bar{\mathbf{z}}_j)\right\}$$

is the marginal distribution of $\mathbf{z}$, which means that

$$\nabla_{\bar{\mathbf{z}}_j}p_j(\mathbf{z}) = \mathbf{P}_j^{-1}(\mathbf{z}-\bar{\mathbf{z}}_j)p_j(\mathbf{z}) = -\nabla_{\mathbf{z}}p_j(\mathbf{z}),$$

where $\nabla_{\mathbf{x}}$ is the gradient operator with respect to the vector $\mathbf{x}$. The second line in equations (A1) uses the fact that the average genotype of stage-i offspring (the last double integral in the first line) is equal to the average genotype of their parents (the last integral in the second line).

Let

$$\mathbf{S}_{ij} = \bar{a}_{ij}^{-1}\int \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{z})d\mathbf{z} - \bar{\mathbf{z}}_j = \bar{a}_{ij}^{-1}\left[\int \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{z})d\mathbf{z} - \bar{a}_{ij}\bar{\mathbf{z}}_j\right].$$

This is the selection differential for individuals of stage j in terms of their contributions to stage i. We have

$$\bar{\mathbf{g}}_i' = \frac{1}{N_i'}\sum_j N_j\bar{a}_{ij}(\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}\mathbf{S}_{ij}).$$

Define $c_{ij} = \bar{a}_{ij}N_j/N_i'$, the fraction of stage-$i$ individuals contributed by stage j. Then

$$\bar{\mathbf{g}}_i' = \sum_j c_{ij}(\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}\mathbf{S}_{ij}). \tag{A2}$$

Now assume $a_{ij}(\mathbf{z})$ is independent of $\bar{\mathbf{z}}_j$ and consider

$$
\begin{aligned}
\nabla_{\bar{\mathbf{z}}_j}\ln\bar{a}_{ij} &= \bar{a}_{ij}^{-1}\int a_{ij}(\mathbf{z})\nabla_{\bar{\mathbf{z}}_j}p_j(\mathbf{z})d\mathbf{z} = \bar{a}_{ij}^{-1}\int a_{ij}(\mathbf{z})\mathbf{P}_j^{-1}(\mathbf{z}-\bar{\mathbf{z}}_j)p_j(\mathbf{z})d\mathbf{z} \\
&= \mathbf{P}_j^{-1}\left[\bar{a}_{ij}^{-1}\int \mathbf{z}a_{ij}(\mathbf{z})p_j(\mathbf{z})d\mathbf{z} - \bar{\mathbf{z}}_j\right] = \mathbf{P}_j^{-1}\mathbf{S}_{ij}.
\end{aligned}
$$

Thus, equation (A2) can also be written

$$\bar{\mathbf{g}}_i' = \sum_j c_{ij}(\bar{\mathbf{g}}_j + \mathbf{G}_j \nabla_{\bar{\mathbf{z}}_j} \ln \bar{a}_{ij}). \tag{A3}$$

Derivation of BHG2011 Equation (5) Using Integration by Parts (Univariate Trait Case)

The univariate version of equation (A1) above is

$$\bar{g}_i' = \frac{1}{N_i'} \sum N_j \left[\bar{a}_{ij}\bar{g}_j + G_j P_j^{-1} \int a_{ij}(z)(z - \bar{z}_j) p_j(z) dz \right].$$

For the integration by parts, let $u(z) = a_{ij}(z)$ and $dv = P_j^{-1}(z - \bar{z}_j)p_j(z)dz$, so $v(z) = -p_j(z)$. Then

$$\int a_{ij}(z) P_j^{-1}(z - \bar{z}_j) p_j(z) dz = [-a_{ij}(z)p_j(z)]_{-\infty}^{\infty} + \int \nabla_z a_{ij}(z) p_j(z) dz = \overline{\nabla_z a_{ij}},$$

assuming $a_{ij}(z)p_j(z) \to 0$ as $z \to \pm\infty$. (Note that $\nabla_x = d/dx$, i.e., differentiation with respect to x.) Thus,

$$\bar{g}_i' = \sum_j c_{ij}[\bar{g}_j + \bar{a}_{ij}^{-1} G_j \overline{\nabla_z a_{ij}(z)}]. \tag{A4}$$

As above, assume $a_{ij}(z)$ is independent of $\bar{z}_j$ and consider

$$\nabla_{\bar{z}_j}\bar{a}_{ij} = \nabla_{\bar{z}_j}\left[\int a_{ij}(z)p_j(z)dz \right] = \int a_{ij}(z)\nabla_{\bar{z}_j} p_j(z) dz = \int a_{ij}(z)[-\nabla_z p_j(z)]dz = -\int a_{ij}(z)\nabla_z p_j(z)dz.$$

Applying integration by parts to the last integral with $u(z) = a_{ij}(z)$ and $v(z) = p_j(z)$ shows that

$$\nabla_{\bar{z}_j}\bar{a}_{ij} = -[a_{ij}(z)p_j(z)]_{-\infty}^{\infty} + \int \nabla_z a_{ij}(z) p_j(z) dz = \overline{\nabla_z a_{ij}(z)}.$$

So equation (A4) is equivalent to

$$\bar{g}_j' = \sum_j c_{ij}[\bar{g}_j + \bar{a}_{ij}^{-1} G_j \nabla_{\bar{z}_j} \bar{a}_{ij}] = \sum_j c_{ij}[\bar{g}_j + G_j \nabla_{\bar{z}_j} \ln \bar{a}_{ij}].$$

Derivation of BHG2011 Equation (6)

$$\bar{\mathbf{z}}_i' = \int\int \mathbf{z} p_i'(\mathbf{g},\mathbf{z}) d\mathbf{g} d\mathbf{z} = \frac{T_i'}{N_i'} \int\int \mathbf{z}\theta_i(\mathbf{g},\mathbf{z}) d\mathbf{g} d\mathbf{z} + \frac{F_i'}{N_i'} \int\int \mathbf{z}\phi_i(\mathbf{g},\mathbf{z}) d\mathbf{g} d\mathbf{z}. \tag{A5}$$

We refer to the first term as A and the second as B. Consider term A:

$$A = \sum_j \frac{N_j}{N_i'} \int\int \mathbf{z} t_{ij}(\mathbf{z}) p_j(\mathbf{g},\mathbf{z}) d\mathbf{z} d\mathbf{g} = \sum_j \frac{N_j}{N_i'} \int \mathbf{z} t_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z}. \tag{A6}$$

Note that

$$\begin{aligned} \nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij} &= \int t_{ij}(\mathbf{z}) \nabla_{\bar{\mathbf{z}}_j} p_j(\mathbf{z}) d\mathbf{z} = \int t_{ij}(\mathbf{z}) \mathbf{P}_j^{-1}(\mathbf{z} - \bar{\mathbf{z}}_j) p_j(\mathbf{z}) d\mathbf{z} \\ &= \mathbf{P}_j^{-1}\left[\int \mathbf{z} t_{ij}(\mathbf{z}) p_j(\mathbf{z}) d\mathbf{z} - \bar{t}_{ij}\bar{\mathbf{z}}_j \right]. \end{aligned} \tag{A7}$$

Thus,

$$A = \sum_j \frac{N_j}{N_i'}(\bar{t}_{ij}\bar{\mathbf{z}}_j + \mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij}) = \sum_j (c_{ij}^t\bar{\mathbf{z}}_j + c_{ij}\bar{a}_{ij}^{-1}\mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij}) = \sum_j c_{ij}^t(\bar{\mathbf{z}}_j + \bar{t}_{ij}^{-1}\mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij}), \tag{A8}$$

where we have used the definitions $c_{ij}^t = N_j\bar{t}_{ij}/N_i'$ and $c_{ij} = N_j\bar{a}_{ij}/N_i'$.

Now consider the B term. Assuming that the mean phenotype of the offspring in each stage is equal to their mean genotype, and again using the assumption that the mean genotype of offspring is the same as their parents,

$$\begin{aligned} B &= \frac{F_i'}{N_i'}\int\int \mathbf{z}\phi_i(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} = \frac{F_i'}{N_i'}\int \mathbf{g}\Phi_i(\mathbf{g})d\mathbf{g} \\ &= \sum_j \frac{N_j}{N_i'}\int\int \mathbf{g}f_{ij}(\mathbf{z})p_j(\mathbf{g},\mathbf{z})d\mathbf{g}d\mathbf{z} = \sum_j \frac{N_j}{N_i'}\int\int \mathbf{g}f_{ij}(\mathbf{z})p_j(\mathbf{g}|\mathbf{z})p_j(\mathbf{z})d\mathbf{g}d\mathbf{z} \\ &= \sum_j \frac{N_j}{N_i'}\int f_{ij}(\mathbf{z})\left[\int\int \mathbf{g}p_j(\mathbf{g}|\mathbf{z})d\mathbf{g}\right]p_j(\mathbf{z})d\mathbf{z} = \sum_j \frac{N_j}{N_i'}\int f_{ij}(\mathbf{z})[\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}(\mathbf{z}-\bar{\mathbf{z}}_j)]p_j(\mathbf{z})d\mathbf{z} \\ &= \sum_j \frac{N_j}{N_i'}\left[\bar{f}_{ij}\bar{\mathbf{g}}_j + \mathbf{G}_j\mathbf{P}_j^{-1}\int f_{ij}(\mathbf{z})(\mathbf{z}-\bar{\mathbf{z}}_j)p_j(\mathbf{z})d\mathbf{z}\right]. \end{aligned} \tag{A9}$$

A calculation parallel to equation (A7) shows that

$$\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij} = \mathbf{P}_j^{-1}\left[\int\int (\mathbf{z}-\bar{\mathbf{z}}_j)f_{ij}(\mathbf{z})p_j(\mathbf{z})d\mathbf{z}\right]. \tag{A10}$$

Thus,

$$B = \sum_j \frac{N_j}{N_i'}[\bar{f}_{ij}\bar{\mathbf{g}}_j + \mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij}] = \sum_j (c_{ij}^f\bar{\mathbf{g}}_j + c_{ij}\bar{a}_{ij}^{-1}\mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij}) = \sum_j c_{ij}^f(\bar{\mathbf{g}}_j + \bar{f}_{ij}^{-1}\mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij}), \tag{A11}$$

where $c_{ij}^f = N_j\bar{f}_{ij}/N_i'$.

Combining equations (A8) and (A11) gives, finally, the correct form of equation (6) of BHG2011:

$$\bar{\mathbf{z}}_i' = \sum_j [c_{ij}^t\bar{\mathbf{z}}_j + c_{ij}^f\bar{\mathbf{g}}_j + c_{ij}\bar{a}_{ij}^{-1}(\mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij} + \mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij})]. \tag{A12}$$

Using the last expressions from equations (A8) and (A11) gives an alternative arrangement of equation (A12) that emphasizes parallels with BHG2011 equation (5):

$$\begin{aligned} \bar{\mathbf{z}}_i' &= \sum_j [c_{ij}^t(\bar{\mathbf{z}}_j + \mathbf{P}_j\bar{t}_{ij}^{-1}\nabla_{\bar{\mathbf{z}}_j}\bar{t}_{ij}) + c_{ij}^f(\bar{\mathbf{g}}_j + \mathbf{G}_j\bar{f}_{ij}^{-1}\nabla_{\bar{\mathbf{z}}_j}\bar{f}_{ij})] \\ &= \sum_j [c_{ij}^t(\bar{\mathbf{z}}_j + \mathbf{P}_j\nabla_{\bar{\mathbf{z}}_j}\ln\bar{t}_{ij}) + c_{ij}^f(\bar{\mathbf{g}}_j + \mathbf{G}_j\nabla_{\bar{\mathbf{z}}_j}\ln\bar{f}_{ij})] \\ &= \sum_j (c_{ij}^t\bar{\mathbf{z}}_j + c_{ij}^f\bar{\mathbf{g}}_j) + \sum_j (c_{ij}^t\mathbf{P}_j\nabla_{\bar{z}_j}\ln\bar{t}_{ij} + c_{ij}^f\mathbf{G}_j\nabla_{\bar{z}_j}\ln\bar{f}_{ij}). \end{aligned} \tag{A13}$$

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