Niche Construction in Quantitative Traits: Heritability and Response to Selection

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A $(N-1)$-individual indirect genetic effect

In order to isolate the effects of group size and ecological inheritance in the niche construction model, here we derive a more general indirect genetic effect model that can allow for group interactions between a focal individual and $N-1$ others. We start from the Moore et al. (1997) model, specifically with equations 4 and 5 from our main text. We note that the result below is also consistent with McGlothlin et al. (2010) eqn 18 and can be calculated from that starting point.

Phenotypes z_1 and z_2 are, as in the main text, defined as a linear combination of the direct additive genetic effects a_1 and a_2 respectively, and the environmental deviations e_1 and e_2 respectively. Phenotype z_1 is further affected by an interaction between an individual and, now, $N-1$ interaction partners. Assuming that the effects are linear and additive, this gives us a slightly modified version of equations 4 and 5 from the main text:

$$z_1 = a_1 + e_1 + \sum_{i=1}^{N-1} \Psi a'_{2i} + \Psi e'_{2i} \tag{A.1}$$

$$z_2 = a_2 + e_2 \tag{A.2}$$

We calculate the change in phenotypes z_j by taking the covariance of the breeding values A_j and the relevant phenotypes z_j and multiplying this by the relevant selection differential β_j. As for the IGE and niche ocnstruction models in the main text, the breeding value A_1 includes both the direct and indirect average effect of $A_1 = a_1 + \Psi(N-1)a_2$. We label the covariances (as in the main text) so that $\mathrm{cov}(a_1, a_1) = G_{11}$, $\mathrm{cov}(a_1, a_2) = G_{12}$. We further assume that there can be covariance between the genetic values of interactants (i.e. that they are related with relatedness parameter r). Thus we get

$$\Delta \bar{z} = G_{11} + \Psi(N-1)(1+r)G_{12} + \Psi^2(N-1)^2 r G_{22})\beta_1 + (G_{12} + \Psi(N-1)G_{22})\beta_2. \tag{A.3}$$

This value is plotted in the main text figure 2, black line. Figure A. 1. provides a more comprehensive comparison. This shows the effect of group interactions alone (black lines), and the effect of group interactions alongside ecological inheritance (red lines).
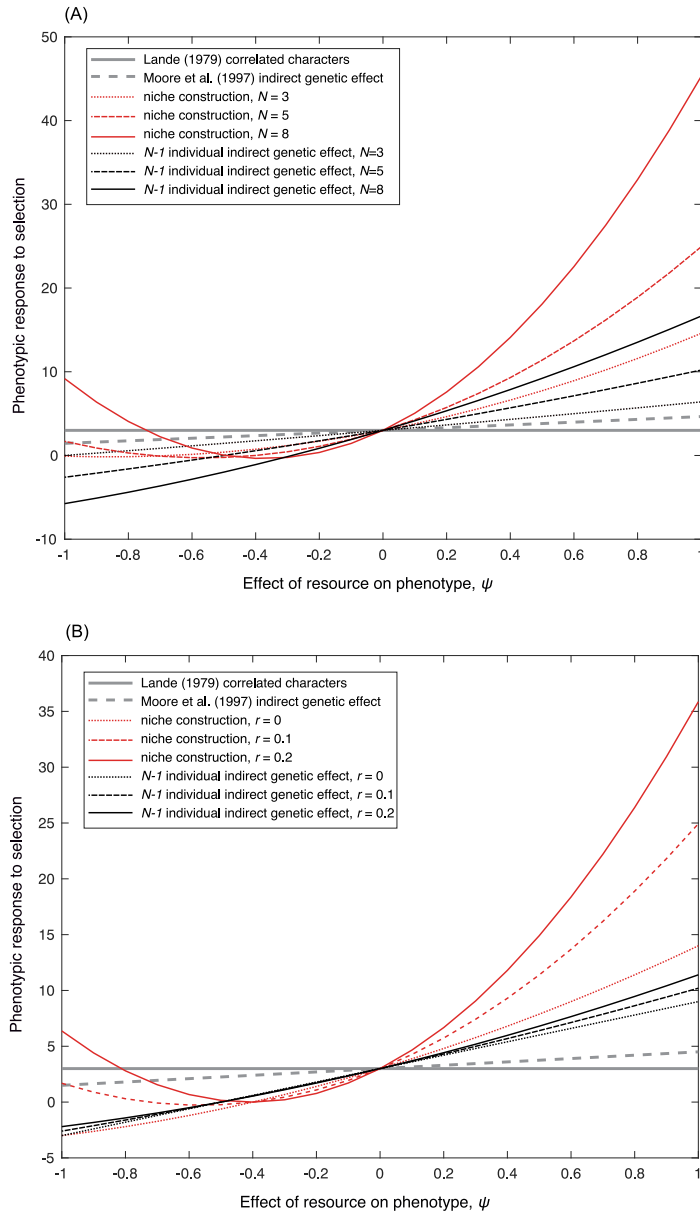
(A)

(B)

Figure A.1: Response of phenotype to selection ($\Delta\bar{z}$) in the presence (red) and absence (black and grey) of niche construction. The solid grey line shows the correlated characters model. This model shows the effect of correlated evolution in the absence of phenotypic interaction between traits. The dashed grey line shows the Moore et al. model of a pairwise indirect genetic effect, the indirect genetic effects model. Parameters are $\mu = 0.85, G_{11} = 4, G_{12} = 2, G_{22} = 1, \beta_1 = \beta_2 = 0.5, N = 5$ and $r = 0.1$. Note that all models give the same result when $\Psi = 0$ (i.e., when the interaction or resource has no effect on phenotype).

B   Phenotypic Variance

The phenotypic variance in the case of indirect genetic effects is given by

$$P_i = \text{cov}(z_1, z_1) \tag{B.1}$$

with

$$z_1 = a_1 + e_1 + \Psi a_2' + \Psi e_2' \tag{B.2}$$

we get

$$P_i = \text{cov}(a_1 + e_1 + \Psi a_2' + \Psi e_2', a_1 + e_1 + \Psi a_2' + \Psi e_2') \tag{B.3}$$

$$
\begin{aligned}
P_i = {} & \text{cov}(a_1, a_1) + \text{cov}(a_1, e_1) + \text{cov}(a_1, \Psi a_2') + \text{cov}(a_1, \Psi e_2') + \\
& \text{cov}(e_1, a_1) + \text{cov}(e_1, e_1) + \text{cov}(e_1, \Psi a_2') + \text{cov}(e_1, \Psi e_2') + \\
& \text{cov}(\Psi a_2', a_1) + \text{cov}(\Psi a_2', e_1) + \text{cov}(\Psi a_2', \Psi a_2') + \text{cov}(\Psi a_2', \Psi e_2') + \\
& \text{cov}(\Psi e_2', a_1) + \text{cov}(\Psi e_2', e_1) + \text{cov}(\Psi e_2', \Psi a_2') + \text{cov}(\Psi e_2', \Psi e_2')
\end{aligned} \tag{B.4}
$$

So we have

$$P_i = G_{11} + E_{11} + 2r\Psi G_{12} + \Psi^2 G_{22} + \Psi^2 E_{22} \tag{B.5}$$

where $\text{cov}(a_1, a_1) = G_{11}$, $\text{cov}(e_1, e_1) = E_{11}$, and $\text{cov}(a_2', a_2') = G_{22}$. We account for genetic covariance between individuals in the population by assuming some average relatedness in the population, r so that $\text{cov}(a_1, \Psi a_2')$, for example, is given by $r\Psi G_{12}$.

Similarly, in the case of niche construction we have

$$P_{nc} = \text{cov}(z_1, z_1) \tag{B.6}$$

$$z_1 = a_1 + e_1 + \Psi M_0 \sum_{i=1}^{N} (a_{2i} + e_{2i}) \tag{B.7}$$

where $M_0 = \sum_{\tau=0}^{n} \mu^\tau$. So we get

$$
P_{nc} = \text{cov}(a_1, a_1) + \text{cov}(a_1, e_1) + \text{cov}(a_1, \Psi M_0 \sum_{i=1}^{N}(a_{2i})) + \text{cov}(a_1, \Psi M_0 \sum_{i=1}^{N}(e_{2i})) +
$$

$$
\text{cov}(e_1, a_1) + \text{cov}(e_1, e_1) + \text{cov}(e_1, \Psi M_0 \sum_{i=1}^{N}(a_{2i})) + \text{cov}(e_1, \Psi M_0 \sum_{i=1}^{N}(e_{2i})) +
$$

$$
\text{cov}(\Psi M_0 \sum_{i=1}^{N}(a_{2i}), a_1) + \text{cov}(\Psi M_0 \sum_{i=1}^{N}(a_{2i}), e_1) +
$$

$$
\text{cov}(\Psi M_0 \sum_{i=1}^{N}(a_{2i}), \Psi M_0 \sum_{i=1}^{N}(a_{2i})) + \text{cov}(\Psi M_0 \sum_{i=1}^{N}(a_{2i}), \Psi M_0 \sum_{i=1}^{N}(e_{2i})) +
$$

$$
\text{cov}(\Psi M_0 \sum_{i=1}^{N}(e_{2i}), a_1) + \text{cov}(\Psi M_0 \sum_{i=1}^{N}(e_{2i}), e_1) +
$$

$$
\text{cov}(\Psi M_0 \sum_{i=1}^{N}(e_{2i}), \Psi M_0 \sum_{i=1}^{N}(a_{2i}) + \text{cov}(\Psi M_0 \sum_{i=1}^{N}(e_{2i}), \Psi M_0 \sum_{i=1}^{N}(e_{2i})) \quad \text{(B.8)}
$$

which, eventually, gives

$$
\begin{aligned}
P_{nc} = {}& G_{11} + E_{11} + 2\Psi(G_{12} + (N-1)rG_{12} + M_1 rN G_{12}) + \\
& \Psi^2(NG_{22} + N(N-1)rG_{22} + M_1^2(NG_{22} + N(N-1)rG_{22}) + \\
& NE_{22} + N(N-1)rE_{22} + M_1^2(NE_{22} + N(N-1)rE_{22})) \quad \text{(B.9)}
\end{aligned}
$$

where $M_1 = \sum_{\tau=1}^{n} \mu^\tau$.

C Heritability

C.1 Definition 1: the ratio of the additive genetic variance to the phenotypic variance

C.1.1 Indirect genetic effects

$$
h_i^2 = \frac{G_{11}}{P_i} \tag{C.1}
$$

C.1.2 Niche construction

$$
h_{nc}^2 = \frac{G_{11}}{P_{nc}} \tag{C.2}
$$

C.2 Definition 2: the ratio of the variance in the breeding values to the phenotypic variance

C.2.1 Indirect genetic effects

$$h_i^2 = \frac{G_{11} + \Psi 2 G_{12} + \Psi^2 G_{22}}{P_i} \tag{C.3}$$

C.2.2 Niche construction

$$h_{nc}^2 = \frac{G_{11} + 2N\Psi G_{12} + \Psi^2 N^2 G_{22}}{P_{nc}} \tag{C.4}$$

C.3 Definition 3: the ratio of the heritable (meaning genetic) component(s) of phenotypic variance to the total phenotypic variance

C.3.1 Indirect genetic effects

$$h_i^2 = \frac{G_{11} + 2r\Psi G_{12} + \Psi^2 G_{22}}{P_i} \tag{C.5}$$

C.3.2 Niche construction

$$h_{nc}^2 = \frac{G_{11} + 2\Psi(G_{12} + (N-1)rG_{12} + M_1 rNG_{12}) + \Psi^2 M_1^2(NG_{22} + N(N-1)rG_{22})}{P_{nc}} \tag{C.6}$$

D Family resemblance

In the niche construction model there are three potential sources of phenotypic similarity that must be considered (not including dominance deviations and non-heritable environmental similarities): additive genetics, the inherited social environment, and the social environment of the current generation. As is the case for maternal effects (discussed, for example, in Cheverud and Moore, 1994) the only way to pull these apart is by careful experimental design. Depending on the system this may or may not be possible.

The phenotypic covariance between family members can be calculated for this system. Following Falconer and Mackay (1996) p. 163. We assume that the phenotypic variance P has the following components:

$$P = V_A + V_E + V_S + V_{IE} \tag{D.1}$$

where V_A is additive genetic variance, V_E is the non-inherited environmental variance, V_S is the variance in the social environment or the contribution of the current population to the resource that affects the phenotype, and V_{IE} is the inherited environmental variance (this is a unique component of NC theory).

D.1 Offspring-Midparent covariance

Following Falconer and Mackay by not including the non-inherited environmental variance in parent-offspring covariance calculations we get:

$$cov(\text{midparent,offspring}) = \frac{1}{2}V_A + V_{IE} - V_{IE}(t - (n+1)) \tag{D.2}$$

where $V_{IE}(t - (n+1))$ is the variance in the parent generation's phenotypes that is attributable to the $t - (n+1)$th generation individuals, who no longer influence the phenotype of the t th generation but did influence their parents.

D.2 Offspring-Unrelated interacting adult

This covariance is interesting – there is an inheritance relationship between offspring and unrelated but interacting members of the parental generation. This is given by

$$cov(\text{unrelated interactor,offspring}) = V_{IE} - V_{IE}(t - (n+1)) \tag{D.3}$$

this can be tweaked to account for different levels of genetic relatedness.

D.3 Full siblings

The calculation in Falconer for the phenotypic correlation between full siblings does include the non-inherited environmental variance. Siblings are in the same generation and we assume they are part of one another's group of interacting individuals, so they share the current social environment, genetics, and an inherited environment

$$cov(\text{full sib,full sib}) = \frac{1}{2}V_A + V_E + V_{IE} + V_S. \tag{D.4}$$

Maybe the closest we have to an informative measure of heritability as we want to use it is something like

$$h_{NC}^2 = \frac{cov(\text{midparent,offspring})}{\text{phenotypic variance}} = \frac{\frac{1}{2}V_A + V_{IE} - V_{IE}(t - (n+1))}{V_A + V_{IE} + V_S + V_E} \tag{D.5}$$
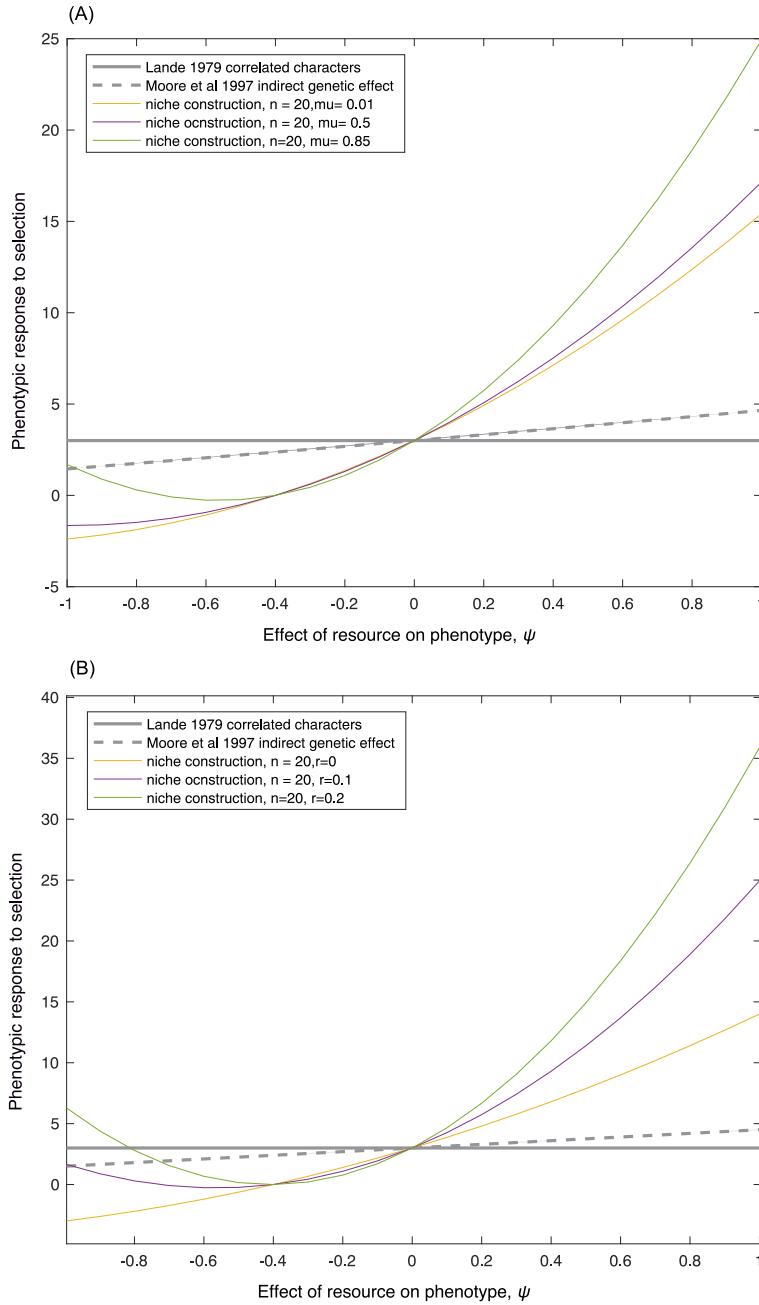
E   Parameter Sweeps

Figure E.1: Here we show in more detail the effect of the relatedness parameter, r and the rate of resource decay μ on the response to selection. Figure D.1 (a) shows the effect of the relatedness parameter r in the niche construction model where $r \in \{0, 0.1, 0.2\}$. Figure D.1 (b) shows the effect of the parameter $\mu \in \{0.01, 0.5, 0.85\}$. Other parameters are $\mu = 0.85, G_{11} = 4, G_{12} = 2, G_{22} = 1, \beta_1 = \beta_2 = 0.5, N = 5$ and $r = 0.1$. when not varied.