The Evolution of Dispersal in Random Environments and The Principle of Partial Control

Ecological Monographs, in press

Lee Altenberg
altenber@hawaii.edu
http://dynamics.org/Altenberg/PAPERS/

March 13, 2012
Outline

1. McNamara and Dall
4. $\text{Cov}_{\mathcal{FA}}$
   - Basic Results on the Fitness-Abundance Covariance
   - Generalization of The McNamara and Dall Model
   - The Conditional Dispersal Model
5. Summary of Results
   - Conclusions
'Stupid Strategies' Could Be Best for the Genes

*ScienceDaily* (Feb. 28, 2011) — Blindly copying what your parents did -- no matter how stupid it may seem -- could be the best strategy for the long-term success of your genes, according to research by the Universities of Exeter and Bristol.

The model of McNamara and Dall (2011) has the recursion:

\[ z(t + 1) = M(m) D z(t), \]

where \( D \) is a positive diagonal matrix, \( P \) is stochastic, \( P \pi = \pi \), \( e^\top = (1, 1, \ldots, 1) \), and

\[ M(m) := (1 - m)P + m \pi e^\top. \]

- \( z_i(t) \) is the number of individuals in environment \( i \) at time \( t \);
- \( z_i(t + 1) \) after one iteration of reproduction and dispersal.
Recursion eq: McD

\[ z_i(t + 1) = (1 - m) \sum_j P_{ij} D_j z_j(t) + m \pi_i \sum_j D_j z_j(t). \]
What the McNamara and Dall model represents is described as follows.

1. An individual is born into a site with environment type $i$;
2. The individual reproduces on the site, and produces an average of $D_i$ offspring when in environment $i$;
3. Each offspring disperses independently with probability $m$ to a random site;
4. There are an infinite number of sites, and each generation, sites of environment type $j$ change randomly and independently to type $i$ with probability $M_{ij}$;
5. The environments of the sites have reached a stationary distribution, so the probability that a random site will be in environment state $i$ is $\pi_i$. 
McNamara and Dall (2011) obtain analytical results for the case of $n = 2$ types of environment:

\[
\begin{bmatrix}
    z_1(t + 1) \\
    z_2(t + 1)
\end{bmatrix} = \mathbf{MD} \begin{bmatrix}
    z_1(t) \\
    z_2(t)
\end{bmatrix},
\]

where

\[
\mathbf{D} = \begin{bmatrix}
    D_1 & 0 \\
    0 & D_2
\end{bmatrix},
\]

and

\[
\mathbf{M} = (1 - m) \begin{bmatrix}
    1 - P_{21} & P_{12} \\
    P_{21} & 1 - P_{21}
\end{bmatrix} + m \begin{bmatrix}
    \pi_1 & \pi_1 \\
    1 - \pi_1 & 1 - \pi_1
\end{bmatrix}.
\]
Let $\rho(\text{MD})$ be the spectral radius of $\text{MD}$ — the asymptotic growth rate of the system.

Let $\mathbf{v} = (v_1, v_2)^\top$ be the stationary state of the system.

Let $\tau_i$ be the expected duration of environment $i$.

**Theorem (McNamara and Dall)**

1. If $\tau_1^{-1} + \tau_2^{-1} < 1$ then $\rho(\text{MD}) > \sum_{i=1}^{2} D_i \pi_i$ and
   1. $D_1 < D_2 \implies v_2 > \pi_2$
   2. $D_1 > D_2 \implies v_2 < \pi_2$. Philopatry favored.

2. If $\tau_1^{-1} + \tau_2^{-1} > 1$ then $\rho(\text{MD}) < \sum_{i=1}^{2} D_i \pi_i$ and
   1. $D_1 < D_2 \implies v_2 < \pi_2$
   2. $D_1 > D_2 \implies v_2 > \pi_2$. Dispersal favored.
To model conditional dispersal, augment the previous model with conditional dispersal probabilities $C_i =$ probability of dispersing when in environment $i$. Let $\mathbf{C}$ be the positive diagonal matrix of $C_i$.

$$
\mathbf{M}(\mathbf{C}) := \mathbf{P}[(\mathbf{I} - \mathbf{C}) + \pi \mathbf{e}^\top \mathbf{C}]
$$
Conditional Dispersal Model

Incorporate the possibility of imperfect information:

1. There is error in perceiving the correct environment, at rate $\epsilon_i$.

2. And there is always some dispersal, $C_{\text{min}}$.

3. This model produces the conditional dispersal rates

$$
\begin{bmatrix}
C_1 \\
C_2
\end{bmatrix} =
\begin{bmatrix}
1-\epsilon_1 & \epsilon_1 \\
\epsilon_2 & 1-\epsilon_2
\end{bmatrix}
\begin{bmatrix}
p_1 \\
p_2
\end{bmatrix} +
\begin{bmatrix}
C_{\text{min}} \\
C_{\text{min}}
\end{bmatrix}.
$$

4. Assuming that the species can vary $(p_1, p_2)$ over the range $[0,1] \times [0,1]$, the variation in $(C_1, C_2)$ falls within the parallelogram (shaded lighter) in next slide.
Gradient of the asymptotic growth rate, $\rho(M(C)D)$, over $(C_1, C_2) \in [0, 1]^2$

\[
slope = \frac{\pi_2 D_1 v_1(M(C)D)}{\pi_1 D_2 v_2(M(C)D)}
\]

\[
slope = \frac{1 - \epsilon_2}{\epsilon_1}
\]

\[
slope = \frac{\epsilon_2}{1 - \epsilon_1}
\]
1. Lighter means higher $\rho(M(C)D)$.

2. Model parameters used: $(D_1, D_2) = (1.0, 0.5)$, $(\rho_{12}, \rho_{21}) = (0.204, 0.107)$.

3. Diagonal dashed line $C_1 = C_2$ corresponds to variation in unconditional dispersal rates.

4. Perturbations are away from $(C_1, C_2) = (0.1, 0.1)$.

5. Perturbations into regions A+B+C increase $\rho(M(C)D)$, while perturbations into D+E decrease $\rho$.

6. Cue error rates $(\epsilon_1, \epsilon_2)$ constrain variation to fall within the parallelogram, with slope $\epsilon_2/(1-\epsilon_1)$ for the bottom, and $(1-\epsilon_2)/\epsilon_1$ for the side, where $\epsilon_i$ is the probability that environment $i$ gives the wrong cue.
1. To evolve conditional dispersal out of sink environment 2, $\epsilon_1$ must be small enough for the parallelogram to enter region C.

2. But the *unconstrained* ESS here is $(C_1, C_2) = (0, 1)$, and mutants anywhere in regions A+B+C are advantageous.
Karlin’s Theorems (1982)

Very important general theorems:

**Theorem (Karlin’s Theorem 5.1, 1982)**

Consider a family of stochastic matrices that commute and are symmetrizable to positive definite matrices:

\[ \mathcal{F} := \{ M_i = D_1 S_i D_2 : M_i M_j = M_j M_i \}, \]

where \( D_1 \) and \( D_2 \) are positive diagonal matrices, and each \( S_i \) is a positive definite symmetric real matrix. Let \( D \) be a positive diagonal matrix. Then for each \( M_i, M_j \in \mathcal{F} \), the spectral radius, \( \rho \), satisfies:

\[ \rho(M_i M_j D) \leq \rho(M_j D). \]
Theorem (Karlin’s Theorem 5.2, 1982)

Let $M$ be a non-negative irreducible stochastic matrix. Consider the family of matrices

$$M(\alpha) = (1-\alpha)I + \alpha M, \quad 0 \leq \alpha \leq 1.$$ 

Then for any positive diagonal matrix $D$, the spectral radius

$$\rho(\alpha) = \rho(M(\alpha)D)$$

is decreasing as $\alpha$ increases (strictly provided $D \neq dI$).

- Independently discovered with a novel proof by Kirkland, Li, and Schreiber (2006)
Karlin’s Theorem 5.2 was applied by Altenberg (1984) to generalize Feldman’s (1972) “Reduction Principle” in the evolution of genetic systems and dispersal.

Dynamics of invasion of a modifier allele:

\[ \epsilon_i(t + 1) = D_1 M D_2(i) \epsilon_i(t), \]

where \( M \) is the matrix of dispersal probabilities produced by the new modifier allele, and

\[
D_1 = \text{diag} \left[ \frac{1}{n^D(e)} \right]_{e=1}^N, \quad D_2(i) = \text{diag} \left[ \frac{n^S(e) \bar{w}(e, i)}{\bar{w}(e)} \right]_{e=1}^N.
\]
Results of Altenberg (1984)

where

\( n^S(e) \) is the population size in patch \( e \) after selection,

\( n^D(e) \) is the population size in patch \( e \) after dispersal,

\( \bar{w}(e) \) is the mean fitness in patch \( e \),

\( \bar{w}(e, i) \) is the mean fitness of the allele \( i \) under selection in patch \( e \),

\( n^S(e) = n(e) \bar{w}(e) \) under hard selection, and \( n^S(e) \) is fixed under soft selection.
Selection potential:

\[ V := \max_{e,i} \frac{n^S(e) \, w(e, i)}{n^D(e) \, w(e)} - 1, \]

\( V > 0 \) if there are differences among the terms

\[ \frac{n^S(e) \, w(e, i)}{n^D(e) \, w(e)}, \]

over the patches \( e \), and genotypes \( i \).
Result (Selection Potential Drives the Evolution)

The new modifier allele, a, can change frequency at a geometric rate, that is, $\rho(M_aD_1D_2(i)) \neq 1$, only if there is an equilibrium selection potential in the population, so that $D_1D_2(i) \neq 1$.

Result (Migration Eliminator)

A modifier allele which stops all migration will always increase when introduced to a population with an equilibrium selection potential, for any linkage to the locus under selection. There is always some deme in which the migration-stopping allele can increase.
If the modifier scales all dispersal probabilities by $\alpha$, then:

$$
\mathbf{M}(\alpha) := (1 - \alpha) \mathbf{I} + \alpha \overline{\mathbf{M}}.
$$

$$
\epsilon_i(t+1) = \mathbf{D}_1 \left[ (1-\alpha) \mathbf{I} + \alpha \overline{\mathbf{M}} \right] \mathbf{D}_2(i) \epsilon_i(t),
$$

where $\overline{\mathbf{M}}$ is the matrix of average dispersal probabilities produced by modifier alleles in the resident population. Karlin’s Theorem 5.2 provides:

**Result (Reduction Principle for Linear Variation)**

*When $V > 0$, the new modifier allele will invade if $\alpha < 1$, and it will be excluded if $\alpha > 1$.***
Departures from Reduction

There are four principal classes in which departures from reduction are found. The first three classes, which will not be further addressed here, are the

1. extinction-recolonization (metapopulation) models

2. discrete site-occupation models and

3. situations in which the population is kept in transient phases away from equilibrium, due to
   - genetic drift
   - directional selection
   - varying selection regimes
   - flux of beneficial mutations
   - cyclic or chaotic attractors.
The remaining class of departures from reduction: Variation in transmission departs from the form:

\[ M(\alpha) = (1 - \alpha) I + \alpha M \]

A principal source of these departures is the interaction of multiple transformation processes that change the transmissible information of the organism.
Studies of multiple transformation processes that exhibit departures from the reduction principle include the evolution of:

- recombination in the presence of mutation
- recombination in the presence of dispersal
- multiple mutation processes
- recombination in the presence of segregation and syngamy
- mutation in the presence of segregation and syngamy
- dispersal in the presence of mutation and recombination
- diffusion in the presence of advection, and vice versa
The pattern of departures from the reduction principle caused by multiple transformation processes was summarized by a simple heuristic:

**The principle of partial control:**

When the modifier gene has only partial control over the transformations occurring at loci under selection, then it may be possible for the *part which it controls* to evolve an increase in rates.
In several cases where multiple transformation processes produce departures from reduction, the stability matrix on the modifier gene has the form

$$M(m) = (1-m)A + mB,$$

where $A \neq I$ and $B \neq I$ are stochastic matrices, and $B - A \neq c(P - I)$ for any stochastic $P$ or $c \geq 0$. Here, Karlin’s Theorem 5.2 does not apply, leaving an entire class of models as an unsolved open problem.
The model of McNamara and Dall has the recursion:

\[
\mathbf{z}(t + 1) = \mathbf{M}(m) \mathbf{D} \mathbf{z}(t),
\]

where

\[
\mathbf{M}(m) := (1 - m)\mathbf{P} + m\pi \mathbf{e}^\top.
\]

1. This is an example of ‘partial control’, where we set \(\mathbf{A} = \mathbf{P}\) and \(\mathbf{B} = \pi \mathbf{e}^\top\), \(\pi\) being the stationary distribution for stochastic matrix \(\mathbf{P}\), i.e. \(\mathbf{P}\pi = \pi\).

2. The control exerted by \(m\) over the transformations occurring in the system is only ‘partial’ because the environment itself undergoes transformation, represented by \(\mathbf{P}\), and the organism cannot eliminate \(\mathbf{P}\), but only shift between \(\mathbf{P}\) and \(\pi \mathbf{e}^\top\).
Distinction Between *Forms of Dispersal* and *Forms of Variation* in Dispersal

1. Matrices of the form \((1 - m)A + mB\) appear in models of conditional dispersal where increased dispersal can evolve.

2. A distinction needs to be made, however, between
   1. the *form of dispersal* and
   2. the form of *variation* in dispersal.
Distinction Between *Forms of Dispersal* and *Forms of Variation* in Dispersal

In the dispersal literature,

1. the reduction principle is generally associated with ‘unconditional dispersal’, and

2. departures from reduction with ‘conditional dispersal’

This association, however, is not due to dispersal being conditional or unconditional, but is due to the *variation in dispersal* having the forms \((1 - m)A + mB\) vs. \((1 - m)I + mB\), respectively.

These two properties — the form of variation in dispersal, and whether dispersal is conditional or unconditional — are in fact separable.
Conditional dispersal (Kirkland, Li, and Schreiber (2006)):

\[ M = I - C + PC, \]

where \( C \) is the diagonal matrix of conditional dispersal rates, and \( P \) is the dispersal pattern.

- Let variation in dispersal be introduced via a parameter \( m \) that scales the dispersal probabilities, to give \( M(m) = I - mC + mPC \).

- In this case, \( M(m) \) is actually of the form \((1 - m)I + mB\), so the Reduction Principle holds:

\[
M(m) = I - mC + mPC \\
= (1-m)I + m[I + (P - I)C],
\]

and \( B = I + (P - I)C \) is a stochastic matrix.
An Illustration

Conversely, consider the model of variation that shifts dispersal between two *unconditional* dispersal strategies given by a Deakin Model:

\[ M(m) = (1-m)[(1-\alpha)I + \alpha q e^T] + m[(1-\beta)I + \beta p e^T].\]

- It has the form \((1 - m)A + mB\), and departures from reduction can occur.

- So we see that what determines whether the reduction principle applies is not whether dispersal is conditional or unconditional, but whether or not variation in dispersal is of the form \((1 - m)I + mB\).
Variation not of the form \((1 - m)I + mB\) allows many possibilities. In a survey of open problems in the spectral analysis of evolutionary dynamics (Altenberg, 2004) characterized the open question that stems from the reduction principle and its departures:

**Open Question**

Let \(A\) and \(B\) be irreducible stochastic matrices, and let \(D \neq cI\) be a positive diagonal matrix. Define

\[
M(m) = (1 - m)A + mB.
\]

For what conditions on \(A\), \(B\), and \(D\) is the spectral radius \(\rho(M(m)D)\) strictly decreasing in \(m\), for \(0 \leq m \leq 1\), [or]

\[
\frac{d}{dm}\rho(M(m)D) < 0?
\]
This brings us back to the McNamara and Dall Model

Original motivation for this paper:

1. to generalize the results of McNamara and Dall to an arbitrary number of environments, and

2. to gain insight into why their model produces departures from the reduction phenomenon.
Theorem (McNamara and Dall)

Let \( \mathbf{v} = (v_1, v_2) \) be the stationary state of the system.

1. If \( \tau_1^{-1} + \tau_2^{-1} < 1 \) then \( \rho(\text{MD}) > \sum_{i=1}^{2} D_i \pi_i \) and
   - \( D_1 < D_2 \implies v_2 > \pi_2 \)
   - \( D_1 > D_2 \implies v_2 < \pi_2 \).

2. If \( \tau_1^{-1} + \tau_2^{-1} = 1 \) then \( v_i = v_i(\mathbf{M}) = \pi_i, i = 1, 2 \), and
   \( \rho = \sum_{i=1}^{2} D_i \pi_i \).

3. If \( \tau_1^{-1} + \tau_2^{-1} > 1 \) then \( \rho < \sum_{i=1}^{2} D_i \pi_i \) and
   - \( D_1 < D_2 \implies v_2 < \pi_2 \)
   - \( D_1 > D_2 \implies v_2 > \pi_2 \).
Clues to the Generalization of the Results

A number of clues in their theorem all point to Karlin’s Theorem 5.1 as a means to generalize them:

1. The harmonic mean
2. The second eigenvalue
3. The limiting distribution: $\mathbf{P}\pi\mathbf{e}^\top = \pi\mathbf{e}^\top\mathbf{P}$
4. Symmetrizability

Time prevents exploring these in detail.
McNamara and Dall describe a “multiplier effect”:

- “One underappreciated consequence of the multiplier effect is that because individuals tend to be in locations to which they are well suited, its mere existence informs an organism that it is liable to be in favourable circumstances”;

- “individuals tend to be in locations to which they are well suited.”
Based on their mathematical results, however, a more accurate description of the ‘multiplier effect’ would be that:

- an organism is *more likely* to be in a favorable habitat than it *would be* if there were no growth advantage there, not that the organism is actually *liable to be there*.

This is the concept that I make precise as the *fitness-abundance covariance*. 
Illustration of Pulliam’s (1988) finding that any Fraction of stationary population may inhabit a sink.

Fraction in the sink habitat as a function of $m$ and $\pi_2$ in the Deakin model. Plotted for small, medium, and large fitness advantage of the source. Only sink fractions that are 50% and above are plotted. Census is just before dispersal.
When the majority of the population is in the sink, it means the distribution of organisms is negatively correlated with fitness (a negative growth–density covariance (Chesson, 2000).

However, the excess of the population above the settling rates \((\pi_1, \pi_2)\) is nevertheless positively correlated with fitness.

For example, with \(v_1 = 0.25\), some solutions include \((D_2/D_1, m, \pi_1) = (0.9, 0.2, 0.154)\), \((0.9, 0.8, 0.226)\), or \((0.1, 0.91, 0.01)\).

In each case, \(0.25 = v_1 > \pi_1 = 0.226, 0.154, \text{ or } 0.01\).
So, the covariance between fitness and this excess of the population in the source habitats is always positive.

This is what will be called the ‘fitness-abundance covariance’.

This is in fact what McNamara and Dall refer to when describing “when the multiplier effect works” — their Theorem A compares $v_1$ to $\pi_1$ rather than $v_1$ to $v_2$. 
Fitness-Abundance Covariance

An (apparently) new statistic: The covariance between something real and something imaginary!

**Definition (Fitness-Abundance Covariance)**

The *unweighted covariance between*

1. *the environment-specific growth rates, and*

2. *the excess of the stationary distribution above what the population would attain in the absence of heterogenous growth rates.*
Fitness-Abundance Covariance

- Let $v(\text{MD})$ be the stationary distribution of the system, censused just after dispersal ($M$)
- Let $v(\text{DM})$ be the stationary distribution of the system, censused just after selection ($D$)
- Let $v(\text{M})$ be the stationary distribution of the system in the imagined absence of selection
1 Post-dispersal:

\[
\text{Cov}_{FA}(\text{MD}) := \text{Cov}(D_i, v_i(\text{MD}) - v_i(\text{M}))
\]

\[
= \frac{1}{n} \sum_{i=1}^{n} D_i (v_i(\text{MD}) - v_i(\text{M}))
\]

\[
- \left[ \frac{1}{n} \sum_{i=1}^{n} D_i \right] \left[ \frac{1}{n} \sum_{j=1}^{n} (v_j(\text{MD}) - v_j(\text{M})) \right].
\]

2 Pre-dispersal:

\[
\text{Cov}_{FA}(\text{DM}) := \text{Cov}(D_i, v_i(\text{DM}) - v_i(\text{M}))
\]

\[
= \frac{1}{n} \sum_{i=1}^{n} D_i (v_i(\text{DM}) - v_i(\text{M}))
\]

\[
- \left[ \frac{1}{n} \sum_{i=1}^{n} D_i \right] \left[ \frac{1}{n} \sum_{j=1}^{n} (v_j(\text{DM}) - v_j(\text{M})) \right].
\]
Lemma

Set $\mathbf{v} \equiv \mathbf{v}(\text{MD})$, $\pi \equiv \mathbf{v}(\text{M})$, and $\rho \equiv \rho(\text{MD})$. Then

$$
\text{Cov}_{\mathcal{F}_A}(\text{MD}) = \frac{1}{n} \left( \rho - \sum_{i=1}^{n} D_i\pi_i \right), \quad \text{and}
$$

$$
\text{Cov}_{\mathcal{F}_A}(\text{DM}) = \frac{1}{n} \left( \frac{1}{\rho} \sum_{i=1}^{n} D_i^2 \pi_i - \sum_{i=1}^{n} D_i\pi_i \right).
$$
Theorem (Fitness-Abundance Covariance and Census Phases)

\[
\text{Cov}_{\mathcal{F},A}(\mathbf{D}_M) = \text{Cov}_{\mathcal{F},A}(\mathbf{M}_D) + \frac{1}{n\rho} \text{Var}_v(D_i),
\]

where \( \text{Var}_v(D_i) \) is the \( v(M_D) \)-weighted variance of \( D_i \),

\[
\text{Var}_v(D_i) := \sum_{i=1}^{n} v_i(M_D) D_i^2 - \left( \sum_{i=1}^{n} v_i(M_D) D_i \right)^2.
\]
Corollary

*If not all growth rates are equal within the stationary population, then* $\text{Cov}_{FA}(DM) > \text{Cov}_{FA}(MD)$.

This makes intuitive sense, because $\text{Cov}_{FA}(DM)$ measures the population while it is still in the states in which selection has just acted, while $\text{Cov}_{FA}(MD)$ measures the population after an intervening stage, $M$, of transformation in states has occurred.
Corollary (Derivatives of Fitness-Abundance Covariances and $\rho$)

Let $\mathbf{M}(m)$ be a family of irreducible stochastic matrices, differentiable in $m$, such that $\mathbf{v}(\mathbf{M}(m)) = \pi$ for all $m \in (0, 1]$. Let $\mathbf{D}$ be a positive diagonal matrix. Set $\rho \equiv \rho(\mathbf{M}(m)\mathbf{D})$.

Then

$$
\frac{d}{dm} \text{Cov}_{\mathcal{F}_A}(\mathbf{M}(m)\mathbf{D}) = \frac{1}{n} \frac{d\rho}{dm},
$$

and

$$
\frac{d}{dm} \text{Cov}_{\mathcal{F}_A}(\mathbf{D}\mathbf{M}(m)) = \frac{d}{dm} \text{Cov}_{\mathcal{F}_A}(\mathbf{M}(m)\mathbf{D}) + \frac{1}{n\rho} \left[ \frac{d}{dm} \text{Var}_{\mathbf{v}}(D_i) - \frac{1}{\rho} \text{Var}_{\mathbf{v}}(D_i) \right]. \tag{1}
$$
**Theorem (Sufficient Condition for Positive Fitness-Abundance Covariances)**

Let \( \mathbf{M} \) be the transition matrix of a reversible ergodic Markov chain, with only nonnegative eigenvalues. Let \( \mathbf{D} \neq c \mathbf{I} \) be a positive diagonal matrix.

Then

\[
\text{Cov}_{\mathcal{F_A}}(\mathbf{DM}) := \text{Cov}(D_i, v_i(\mathbf{DM}) - v_i(\mathbf{M})) >
\]

\[
\text{Cov}_{\mathcal{F_A}}(\mathbf{MD}) := \text{Cov}(D_i, v_i(\mathbf{MD}) - v_i(\mathbf{M})) \geq 0.
\]

If all the eigenvalues of \( \mathbf{M} \) are positive, the last inequality is strict.
Corollary (Cov_{FA} > 0 in the Deakin/House-of-Cards Model)

Let \( M(m) = (1 - m)I + m\pi e^T \), \( D \neq cI \), \( De > 0 \), and \( m \in (0, 1) \). Then \( \text{Cov}_{FA}(DM(m)) > \text{Cov}_{FA}(M(m)D) > 0 \).
Theorem (Sufficient Condition for Negative Post-Dispersal Fitness-Abundance Covariance)

Let $M$ be the transition matrix of a reversible ergodic Markov chain, with negative eigenvalues other than 1. Let $D \neq cI$ be a positive diagonal matrix. Then $\text{Cov}_{\mathcal{F}_A}(MD) < 0$. 
Let \( M \) be an irreducible aperiodic perturbation of an \( n \)-cycle matrix,

\[
M_{(c)} = \begin{bmatrix}
0 & 0 & 0 & \ldots & 0 & 1 \\
1 & 0 & 0 & \ldots & 0 & 0 \\
0 & 1 & 0 & \ldots & 0 & 0 \\
\vdots & 1 & \ddots & \ddots & \vdots & 0 \\
\vdots & \ddots & \ddots & \ddots & \vdots & \vdots \\
0 & 0 & 0 & \ldots & 1 & 0
\end{bmatrix}.
\]

Let \( D \neq cI \) be a positive diagonal matrix.
Theorem (Negative Post-Dispersal Fitness-Abundance Covariance from Cyclic Transformation)

For $\mathbf{M} \approx \mathbf{M}_C$, the post-dispersal fitness-abundance covariance is negative:

$$\text{Cov}_{\mathcal{F}_A}(\mathbf{MD}) \approx \text{Cov}_{\mathcal{F}_A}(\mathbf{M}_C \mathbf{D})$$

$$= \frac{1}{n} \left( \prod_{i=1}^{n} D_i^{1/n} - \frac{1}{n} \sum_{i=1}^{n} D_i \right) < 0.$$
Theorem (Negative Pre-Dispersal Fitness-Abundance Covariance from Cyclic Transformation)

When the states are transformed in a cycle, it is possible for the pre-dispersal fitness-abundance covariance to be negative.

An example is constructed. Let $M$ represent the period-3 cycle of states $1 \rightarrow 2 \rightarrow 3 \rightarrow 1 \ldots$

$$M = \begin{bmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{bmatrix},$$

and let $D = \text{diag}\left[ D_1, D_2, D_3 \right]$. 
Negative $\text{Cov}_{\mathcal{F}_A}(\text{DM})$ is produced by a situation in which individuals move from an optimal habitat to a source habitat with well under half the optimal growth rate, then to a near-lethal sink habitat, and then return to the optimal habitat.

One assumes a small amount of ‘leakage’ from cyclic dispersal pattern so the population can converge to the stationary distribution near $v(\text{MD})$.

Some examples, scaled so that $\rho(\text{MD}) = 1$, are:

- $\text{Cov}_{\mathcal{F}_A}(\text{DM}) = -0.14$ and $\text{Cov}_{\mathcal{F}_A}(\text{MD}) = -1.93$ at $(D_1, D_2, D_3) = (16.8, 3.53, 0.017)$, and
- $\text{Cov}_{\mathcal{F}_A}(\text{DM}) = -1.6$ and $\text{Cov}_{\mathcal{F}_A}(\text{MD}) = -4.92$ at $(D_1, D_2, D_3) = (41.5, 5.81, 0.0042)$. 
We shift now from general $\mathbf{M}$ to the specific model of dispersal in randomly changing environments of McNamara and Dall, $\mathbf{M}(m) := (1-m)\mathbf{P} + m \pi \mathbf{e}^\top$. First, we see how the direction of selection on unconditional dispersal corresponds to the sign of the post-dispersal fitness-abundance covariance.
Theorem (McNamara and Dall Model with an Arbitrary Number of Environments)

Let $\mathbf{M}(m) := (1-m)\mathbf{P} + m \pi \mathbf{e}^\top$, $m \in [0, 1]$, where $\mathbf{P}$ is an irreducible stochastic matrix, and $\mathbf{P}\pi = \pi$. Let $\mathbf{D} \neq c \mathbf{I}$ be a positive diagonal matrix. Set $\mathbf{v} \equiv \mathbf{v}(\mathbf{MD})$.

If $\rho(\mathbf{M}(m)\mathbf{D})$ strictly decreases with $m$ (the reduction phenomenon), then

$$\text{Cov}_{\mathcal{F}_A}(\mathbf{M}(m)\mathbf{D}) = \text{Cov}(D_i, v_i - \pi_i) > 0,$$

and if $\rho(\mathbf{M}(m)\mathbf{D})$ strictly increases with $m$ (departure from reduction), then

$$\text{Cov}_{\mathcal{F}_A}(\mathbf{M}(m)\mathbf{D}) = \text{Cov}(D_i, v_i - \pi_i) < 0.$$
Lemma (Harmonic Mean of Run Lengths, and the Trace of the Transition Matrix)

For a Markov chain with transition matrix $\mathbf{P}$, let $\tau_i(\mathbf{P})$ be the expected duration of state $i$, and let $E_H(\tau_i(\mathbf{P}))$ be the unweighted harmonic mean of $\{\tau_i(\mathbf{P})\}$. Let $\{\lambda_i(\mathbf{P})\}$ be the eigenvalues of $\mathbf{P}$. These are related by the following:

$$E_H(\tau_i(\mathbf{P})) := \frac{1}{\frac{1}{n} \sum_{i=1}^{n} \frac{1}{\tau_i(\mathbf{P})}} = \frac{1}{1 - \frac{1}{n} \sum_{i=1}^{n} \lambda_i(\mathbf{P})} \geq 1,$$

$$\iff E(\lambda_i(\mathbf{P})) := \frac{1}{n} \sum_{i=1}^{n} \lambda_i(\mathbf{P}) = 1 - \frac{1}{E_H(\tau_i(\mathbf{P}))} \geq 0.$$

$$\iff E(\lambda_i(\mathbf{P})) + \frac{1}{E_H(\tau_i(\mathbf{P}))} = 1.$$
The main result is now presented, which ties together:

- the eigenvalues of the environment transition matrix, $\mathbf{P}$,
- the effect of dispersal, $m$, on the population growth rate, $\rho$, and
- the harmonic mean of environment durations.

The result gives sufficient conditions in terms of the eigenvalues of $\mathbf{P}$ for departures from the reduction phenomenon.
Theorem (Eigenvalues, Reduction Phenomenon, and Harmonic Mean of Environment Durations)

Let $\mathbf{P}$ and $\mathbf{Q} \in \mathbb{R}^{n,n}$ be transition matrices of reversible ergodic Markov chains that commute with each other. Let $\tau_i(\mathbf{P}) = 1/(1 - P_{ii})$ be the expected length of runs of state $i$ under iteration of $\mathbf{P}$. Let $\mathbf{D} \neq c \mathbf{I}$ be a positive diagonal matrix, and

$$
\mathbf{M}(m) := \mathbf{P}[(1-m)\mathbf{I} + m\mathbf{Q}], \quad m \in [0,1].
$$
Theorem (continued)

1. If all eigenvalues of $P$ are positive, then

$$\frac{d}{dm}\rho(M(m)D) < 0,$$

(the reduction phenomenon) and

$$E_H(\tau_i(P)) > 1 + \frac{1}{n-1}.$$
Theorem (continued)

If all eigenvalues of $\mathbf{P}$ other than $\lambda_1(\mathbf{P}) = 1$ are negative, then

$$\frac{d}{dm} \rho(\mathbf{M}(m)\mathbf{D}) > 0,$$

(departure from the reduction phenomenon) and

$$1 \leq E_H(\tau_i(\mathbf{P})) < 1 + \frac{1}{n-1}.$$
Corollary

Special cases include $Q = P^t$ for $t \geq 1$, and $Q = P^\infty = \pi e^\top$, where $\pi = P\pi$ is the stationary distribution of $P$. 
Theorem (Memoryless Environmental Change)

Let $P$ and $Q \in \mathbb{R}^{n,n}$ be transition matrices of reversible ergodic Markov chains that commute with each other, $D \neq cI$ be a positive diagonal matrix, and $M(m) := P[(1-m)I + mQ]$, $m \in [0, 1]$. Let $P$ be the ‘House of Cards’ model:

$$P = (1-\alpha)I + \alpha \pi e^\top.$$

Then for $\alpha = 1$, $\frac{d}{dm} \rho(M(m)D) = 0$, and for $0 \leq \alpha < 1$, $\frac{d}{dm} \rho(M(m)D) < 0$. 
The result of McNamara and Dall that drew particular attention was their finding that, when organisms have slightly imperfect information about their environments, it may be better for the organism to ignore environmental cues and instead follow philopatry. Their model of cue-based conditional dispersal is a modification of eq:McDgeneral to:

\[
MD = P[(I - C) + \pi e^\top C]D,
\]

where \( C \) is a diagonal matrix of the conditional dispersal probabilities, \( C_i \), that an individual disperses given it is in environment \( i \).
Theorem (Conditional Dispersal)

Let \( \mathbf{D} \) and \( \mathbf{C} \) be positive diagonal matrices, with \( C_i \in (0, 1) \). Let \( \mathbf{M}(\mathbf{C}) := \mathbf{P}[(\mathbf{I} - \mathbf{C}) + \pi \mathbf{e}^\top \mathbf{C}] \), where \( \mathbf{P} \) is an irreducible stochastic matrix, and \( \pi = \mathbf{P} \pi \). Refer to the left and right Perron vectors as \( \mathbf{u} \equiv \mathbf{u}(\mathbf{M}(\mathbf{C})\mathbf{D}) \) and \( \mathbf{v} \equiv \mathbf{v}(\mathbf{M}(\mathbf{C})\mathbf{D}) \). Then:
Theorem (continued)

The derivative of the spectral radius with respect to each $C_\kappa$ is

$$
\frac{\partial}{\partial C_\kappa} \rho(P[(I - C) + \pi e^T C]D) = D_\kappa v_\kappa \sum_{i=1}^{n} u_i (\pi_i - P_{i\kappa}) = D_\kappa v_\kappa n [\text{Cov}(u_i, \pi_i) - \text{Cov}(u_i, P_{i\kappa})].
$$
Theorem (continued)

There is always at least one $\kappa$ for which

$$\frac{\partial}{\partial C_\kappa} \rho(P[(I - C) + \pi \, e^T C]D) > 0,$$

and at least one $\kappa$ for which

$$\frac{\partial}{\partial C_\kappa} \rho(P[(I - C) + \pi \, e^T C]D) < 0,$$

unless $D = cI$ or $P = \pi \, e^T$. 
Summary of Results

The ‘fitness-abundance covariance’ is introduced, $\text{Cov}_{\mathcal{FA}}$, which measures the association between growth rates and the excess in the stationary distribution above what it would be in the absence of heterogeneous growth.

Fisher’s Fundamental Theorem appears in the difference between pre- and post-dispersal values of $\text{Cov}_{\mathcal{FA}}$ in a stationary population.
Conditions are explored that produce negative or positive fitness-abundance covariance.

In McNamara and Dall’s model of unconditional dispersal in random environments, selection for greater philopatry implies a positive post-dispersal $\text{Cov}_{FA}$, and selection for lower philopatry implies a negative post-dispersal $\text{Cov}_{FA}$.

Whether philopatry is favored depends on the harmonic mean of the environment durations and the eigenvalues of the environment change matrix.
In the conditional dispersal model, there is always some environment where increased dispersal is advantageous, and some other environment where decreased dispersal is advantageous.

Phenotypic constraints upon the conditional dispersal probabilities can change the outcome so that philopatry is the ESS. In general, the ESS for conditional dispersal may depend very sensitively on the geometry of the space of accessible phenotypes.
Principle (Partial Control and Induced Directed Variation)

Undirected variation of a transformation process, i.e. equal scaling of all transition probabilities by a rate $m$, may act effectively like directed variation toward fitter types due to dynamics induced by other transformation processes and selection, so that increases in $m$ increase the population growth rate $\rho$. 
Directed Variation

- In conditional dispersal or directed mutation, it is obvious what direction the transition probabilities are being directed toward.

- In McNamara and Dall’s model, and examples of departures from reduction, directedness of the variation in transition probabilities with respect to fitness is an emergent property of the dynamics.

- Emergence of systemic directedness underlies e.g. the ‘deterministic mutation hypothesis’ for the evolution of sex (Kondrashov, 1982).
Directed Variation

Why a particular directedness with respect to selection emerges from the interaction of multiple transformation processes poses a central open question.
Andrewartha (1961) classically defined ecology as “the scientific study of the distribution and abundance of organisms.” In this respect, the fitness-abundance covariance statistic investigated here is a basic quantity.
The fitness-abundance covariance proves to have direct relationships with some ecological properties of populations.

- It captures the connection discovered by McNamara and Dall between the temporal properties of environmental change and selection for or against dispersal.

- A sampling of possible dispersal and environmental change processes reveals that the fitness-abundance covariance exhibits more complexity than intuition would perhaps suggest.
The goal here has been to pursue the mathematics underlying these relationships.

In so doing, these relationships are shown to connect to the body of work in the population genetics literature on the Reduction Principle for the evolution of genetic systems and dispersal, and provide new examples of departure from reduction.

The common mathematics underlying these models may lead to the eventual development of a theoretical treatment in which the different ecological and evolutionary phenomena are seen as different aspects of a single phenomenological structure.
Thank you for your attention.

dynamics.org/Altenberg/PAPERS/2011_DISPERSAL/