Developmental selection and self-organization

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Abstract

Developmental selection is the differential survival and proliferation of developmental units, such as cellular lineages. This type of internal selection has been proposed as an explanation for diverse examples of self-organization, from the wiring of brains to the formation of pores on leaf surfaces. A general understanding of developmental selection has been slowed by failure to understand its relationship to familiar forms of genetical selection and evolution. I show the formal analogies between models of developmental selection and genetical selection. The general method I outline for the analysis of selective systems partitions self-organizing selective systems into generative rules that create variation and selective filters that move the population toward a target design. The method also emphasizes aggregate statistical measures of evolving systems, such as the covariance between particular traits and fitness. The identification of useful aggregate measures is a crucial step in the analysis of selective systems. I apply these concepts to a model of self-organization in ant colonies. Copyright © 1997 Elsevier Science Ireland Ltd

Keywords: Natural selection theory; Ant societies; Qualitative dynamics

1. Introduction

How do multicellular organisms develop complex form and purposeful, coordinated behavior from a single zygote? How do ant colonies build and defend nests as coordinated, superorganismal units? In each case the group of cells, or individuals, functions as an integrated unit without an explicit master plan or centralized, controlling agent. Individuals or colonies are said to 'self-organize' because large-scale group organization emerges from small-scale processes among the individual units.

Several candidate processes have been proposed for the development of pattern and the ontogeny of behavior. Network models emphasize pathways of stimulation and repression between pairs of units (Kauffman, 1993). Simple rules for pairwise interactions create an internal environment in which structure inevitably develops toward particular form. Gradient models emphasize changing concentrations of chemical signals in which local

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reaction centers interact with spatial diffusion (Meinhardt, 1995). Each reaction and diffusion process is itself simple, but the cascade of events organizes pattern on a large scale.

In this paper I analyze developmental selection as a self-organizing process (Changeux and Danchin, 1976; Edelman, 1987; Michaelson, 1987; Sachs, 1988). Developmental selection organizes by a two-step algorithm. Generative mechanisms create a population of alternative trajectories. Selective filters choose, from an excess of possibilities, those trajectories that satisfy particular design criteria. Large-scale pattern and behavior emerge from local rules for variation and selection.

In the next section I discuss the defining features of selective systems. I present a model for the development of ant colonies in the second part of the paper. Ants provide one of the most interesting and empirically tractable examples of self-organization.

2. What are the defining characteristics of selective systems?

2.1. Generative rules and selective filters

Generative rules and selective filters provide a reasonable description of selective systems. But the boundaries are not sharp among alternative descriptions for dynamical systems and self-organizing principles. Consider the following example from population genetics

$$dq_i/dt = (1 - \mu)q_i(w_i/\bar{w} - 1) - \mu(q_i - \bar{q}) \qquad (1)$$

where, in this model of haploid genetics, q_i is the frequency of the ith allele, w_i is the fitness of the ith allele, μ is the mutation rate from the ith allele to another allele (including i), and overbars specify average values. If there are, for example, two alleles, then the fitnesses might be $w_1 = 1 + s$ and $w_2 = 1 - s$. The dynamics are easily described, with the equilibrium determined by a balance between the relative strength of mutation, μ, and selection, s.

There is nothing inherent in Eq. (1) to suggest that it forms a system of variation and selection.

The system is simple, standard dynamics in which the interpretation of selection arises from a widely shared understanding about how to describe the underlying biology. For example, I referred to the term $-\mu(q_i - \bar{q})$ as random mutation. But with regard to the dynamics it might just as well be a frequency dependent Lamarckian process by which common types are induced by their neighbors to switch to rare types. A system is usually called Lamarckian when new variants arise in a manner that matches environmental stimuli. But Lamarckian systems also have dynamics determined by fitness differences among variants, that is, by an interaction between variation and selection.

The distinction between Lamarckian systems and genetical selection concerns the key process that leads to a good fit between the system and environmental challenge. In the Lamarckian scheme, good fit arises when the environment induces a matching change in a member of the population. Good fit arises in a genetical system when a random variant happens to match the environment; the beneficial variant is then deterministically increased by selective filters.

Selective enhancement in population genetics occurs because of differential reproductive success. Differential productivity is, in any system, a *description* of frequency change, but it may sometimes be appropriate to assign the *cause* of differential productivity to a selective filter designed specifically for that purpose. I illustrate this point about designed selective filters by interpreting Eq. (1) in terms of self-organization of ant colonies.

Suppose each worker works at a single task. The frequency of workers on task i is q_i. Workers signal the need for additional help to complete their task in proportion to the amount of uncompleted work. Signalling of need follows a purely 'local' rule, by which each individual signals according to the rate at which it encounters cues that indicate work to be done. For example, a worker signals in proportion to the rate at which it encounters untended larvae.

These recruitment signals cause workers to shift from tasks with low need to tasks with high priority. The changes in task distribution caused by these shifts can be described by $q_i' = q_i w_i/\bar{w}$.

This is identical to selection in a model of haploid genetics, where there is a population of entities labeled with the subscript i, with differential productivity measured by w_i. The set $\{w_i\}$ forms a selective filter that determines the colony dynamics of task allocation and self-organization. The selective filter is itself subject to evolutionary modification by natural selection of genetic variants, that is, the selective filter may be designed by adaptive processes.

As with any selective system, selective changes in task allocation within colonies depend on sufficient variation in task distribution. In Eq. (1), variation is generated by 'mutational' processes in the μ term. One interpretation for ant colonies is that individuals randomly change their task to another task with probability μ. Mutational variation is crucial for self-organization in this model because an important task can only be enhanced by selection (recruitment) after it has been discovered by at least one worker who can signal further need.

Signalling, recruitment, search and discovery are well-known attributes of task allocation in ant colonies (reviewed by Wilson, 1971; Bourke and Franks, 1995; Gordon, 1996). These processes have been understood without the need to describe dynamics in terms of selective language. What is gained by analyzing task dynamics in terms of selection?

Selective analysis emphasizes one path to self-organization: a clear division and synergy between generative mechanisms and selective filters. As noted above, selective analysis is usually reserved for dynamics in which the direction of search is partly uncoupled from the ultimate target defined by the selective filter (fitness). This kind of system is sometimes called blind variation and selection to emphasize that discovery arises by random search (Campbell, 1974). The idea that development and self-organization proceed by blind variation of developmental trajectories coupled with innately designed selective filters remains a minority view, although it has been discussed independently by many authors (e.g., Changeux and Danchin, 1976; Edelman, 1987; Michaelson, 1987; Sachs, 1988; Seeley et al., 1991; Wagner and Misof, 1993; Frank, 1996a; Frank, 1996b).

My analysis below will also highlight the separation between generative mechanisms and selective filters. But my main point is to emphasize that selective analysis calls attention to important aggregate properties in the dynamics of self-organization.

2.2. Aggregate quantities of selective systems

Useful analysis of complex dynamics usually depends on finding crucial aggregate properties. For example, the behavior of gases follows simple laws when one analyzes the aggregate quantities of the individual molecules, such as pressure and temperature. At a finer scale, the dynamics of individual particles are unpredictable and, with respect to practical problems, unimportant.

Many important phenotypes of organisms depend on the interaction of several genes. Useful theory has been almost impossible when studying dynamics at the level of the individual genes, and measurement of changing gene frequencies in the context of phenotypic evolution is often beyond hope. Yet considerable theoretical and empirical success has been achieved by studying aggregate properties of populations. Fisher (1918) was the first to show the logical relationship between the individual particles (genes) and the dynamics of aggregate properties such as the mean and variance of quantitative traits. The resulting field of quantitative genetics has been highly successful in the analysis of natural populations and in practical applications to plant and animal breeding (Falconer, 1989).

The Price equation is a powerful method for analyzing aggregate quantities of selective systems. I review the Price equation in the next section and, in the following section, summarize a standard application to the problem of mutation and selection.

2.3. The Price Equation

The Price equation is an exact, complete description of evolutionary change under all conditions (Price, 1970; Price, 1972; Frank, 1995). The equation adds considerable insight into many evolutionary problems by partitioning change into meaningful components.

Here is the derivation. Let there be a population (set) where each element is labeled by an index i. The frequency of elements with index i is q_i, and each element with index i has some character, z_i. One can think of elements with a common index as forming a subpopulation that makes up a fraction q_i of the total population. No restrictions are placed on how elements may be grouped.

A second (descendant) population has frequencies q_i' and characters z_i'. The change in the average character value, $\bar{z}$, between the two populations is

$$\Delta\bar{z} = \sum q_i' z_i' - \sum q_i z_i \tag{2}$$

Note that this equation applies to anything that evolves, since z may be defined in any way. For example, z_i may be the gene frequency of entities i, and thus $\bar{z}$ is the average gene frequency in the population, or z_i may be the square of a quantitative character, so that one can study the evolution of variances of traits. Applications are not limited to population genetics. For example, z_i may be the value of resources collected by bees foraging in the ith flower patch in a region (Frank, 1996a).

Both the power and the difficulty of the Price equation come from the unusual way it associates entities from two populations, which are typically called the ancestral and descendant populations. The value of q_i' is not obtained from the frequency of elements with index i in the descendant population, but from the proportion of the descendant population that is derived from the elements with index i in the parent population. If we define the fitness of element i as w_i, the contribution to the descendant population from type i in the parent population is $q_i' = q_i w_i / \bar{w}$, where $\bar{w}$ is the mean fitness of the parent population.

The assignment of character values z_i' also uses indices of the parent population. The value of z_i' is the average character value of the descendants of index i. Specifically, for an index i in the parent population, z_i' is obtained by weighting the character value of each entity in the descendant population by the fraction of the total fitness of i that it represents (see examples in later sections). The change in character value for descendants of i is defined as $\Delta z_i = z_i' - z_i$.

Eq. (2) is true with these definitions for q_i' and z_i'. We can proceed with the derivation by a few substitutions and rearrangements:

$$\Delta\bar{z} = \sum q_i(w_i/\bar{w})(z_i + \Delta z_i) - \sum q_i z_i$$

$$= \sum q_i(w_i/\bar{w} - 1)z_i + \sum q_i(w_i/\bar{w})\Delta z_i$$

which, using standard definitions from statistics for covariance (Cov) and expectation (E), yields the Price equation

$$\bar{w}\Delta\bar{z} = \mathrm{Cov}(w, z) + E(w\Delta z). \tag{3}$$

The two terms may be thought of as changes due to selection and transmission, respectively. The covariance between fitness and character value gives the change in the character caused by differential reproductive success. The expectation term is a fitness weighted measure of the change in character values between ancestor and descendant.

2.4. Aggregate quantities in a genetic model of mutation and selection

The Price equation can be applied to genetic models of mutation and selection (Frank and Slatkin, 1990). Assume a model of haploid genetics with a variety of alleles, i, each with frequency q_i and phenotype z_i. For a simple model of directional selection, we can set $w_i = 1 + sz_i$. The mutation process is such that the descendants of i have phenotype $z_i' = (1 - \mu)z_i + (\mu/2)(z_{i+1}) + (\mu/2)(z_{i-1})$, with the difference between successive pairs of alleles $z_{i+1} - z_i = 1$. With these assumptions $\Delta z_i = 0$, and substituting into the Price equation yields

$$\bar{w}\Delta\bar{z} = s\,\mathrm{Var}(z),$$

showing that the trait increases at a rate proportional to the selection coefficient s multiplied by the variance in z. We might also be interested in how $\mathrm{Var}(z) = \overline{z^2} - \bar{z}^2$ changes. The change in $\bar{z}$ is given in the previous equation, so we need the change in $\overline{z^2}$. We first calculate that $\Delta z_i^2 = \mu$ and then substitute, yielding

$$\bar{w}\overline{z^2} = s\,\mathrm{Cov}(z^2, z) + \mu$$

ignoring terms of order μs.

There is an extensive theory of quantitative genetics (Barton and Turelli, 1987; Falconer, 1989). My only purpose here is to show that such models highlight in a natural way the properties of generative mechanisms, μ, the selective filter, w_i, and natural summary statistics on the population such as variances and covariances of trait values.

In the following section I use this approach to study a simple model of self-organization in ant colonies.

3. Recruitment signals and selection among tasks

Eq. (1) describes the dynamics of a recruitment model for task distribution. Each worker works at a single task. She signals need for additional workers to help her according to the rate at which she locally encounters unfinished work. Signal strength per worker in task i, w_i, is in proportion to the amount of unfinished work in that task. Frequency changes caused by differential recruitment are $q_i' = q_i w_i / \bar{w}$. Random task switching occurs at rate μ, which allows discovery of tasks at which no workers are currently employed. These assumptions lead to the dynamics given by Eq. (1).

The recruitment signal (fitness) of each task depends on the amount of unfinished work, δ_i. Uncompleted work is determined by the difference between the colony's need for a task and the current allocation of workers to that task. The relative signal intensity for each task is defined as $\delta_i = p_i - q_i$ for the ith task, where p is the need for work and q is the current allocation. The p's and q's are given as frequencies such that $\Sigma p_i = \Sigma q_i = 1$. The strength of the recruitment signal for the ith task is $w_i = 1 + s\delta_i$. The colony-level measurement of unfinished work, δ_i, arises solely from the local rules that determine individual signalling strength, that is, the workers signal according to local need rather than the colony-level measures p_i and q_i. Local need is determined by the environment formed by the aggregate properties p and q. These aggregate properties subsequently change in response to individual behavior, completing the complex loop that determines the dynamics of colony-level behavior.

The need for work at a particular task depends on what other tasks are currently being performed. For example, the need for foraging and brood care increases as additional eggs are laid. The need for work also depends on factors extrinsic to the colony, for example, new food sources, weather changes, or attack by another colony. Thus, the need for work can be defined as

$$p_i = \sum_j b_{ij} q_j + \sum_k c_{ik} e_k$$

where b_{ij} is the need for the ith task created by work at the jth task, and c_{ik} is the need for the ith task created by the environmental variable e_k. The environmental variables e and the coefficients b and c are normalized so that $\Sigma p_i = 1$.

The next step is to find a useful aggregate quantity of colony task distribution. For example, a weighted average of the deviations between need and current allocation is $\bar{\delta} = \Sigma_i \alpha_i \delta_i$. One choice is to weight each deviation, δ_i, by current colony allocation to that task, $\alpha_i = q_i$. Analyzing that measure does provide some useful insight, but here I will focus on squared deviations, δ_i^2, with equal weights for each task, $\alpha_i = 1/n$, where n is the number of tasks. This is a distance measure between optimal and current allocation. The change in this distance measure in each time step is

$$\Delta \overline{\delta^2} = \sum \alpha_i' \delta_i'^2 - \sum \alpha_i \delta_i^2 = (1/n) \sum (\delta_i'^2 - \delta_i^2)$$

$$= E(\delta'^2) - \overline{\delta^2}.$$

Following the Price equation conventions discussed above, primed variables denote expected values in the subsequent time period for descendants of index i variables in the previous period. In particular,

$$\delta_i'^2 = (1 - \xi)\hat{\delta}_i^2 + \xi \overline{\delta^2},$$

where $\hat{\delta}_i^2$ is the value of the squared deviation for index i in the subsequent time period, and ξ is the rate at which tasks change from one index to another. In this case, tasks do not change between generations, $\xi = 0$, but it is important to maintain

the distinction between hat and prime measures of descendants.

To calculate the distance measure, we need

$$E(\delta'^2) = E(\hat{\delta}^2) = E(\hat{p} - \hat{q})^2.$$

Colony task allocations change according to

$$\hat{q} = (1 - \mu)q' + \mu\bar{q} = (1 - \mu)q w/\bar{w} + \mu\bar{q},$$

where, as before, $w_i = 1 + s\delta_i$ and μ is the rate at which individuals randomly switch tasks. To keep the model simple, for the purposes of illustration, I assume that the need for tasks, p, depends only on extrinsic, environmental factors, e, and is independent of colony task distribution, q. Random changes in the environment change the need for tasks according to

$$\hat{p} = p + \beta,$$

where β is a random variable with average value of zero and is bounded such that $\bar{p}$ is a probability (p tends to increase when near zero and decline when near one). Thus

$$E(p + \beta - q)^2 - \overline{\delta^2} = E(\delta + \beta)^2 - \overline{\delta^2}$$
$$= \text{Var}(\beta) + 2\text{Cov}(\delta, \beta),$$

where $\text{Var}(\beta)$ is the environmental variance. When $\overline{\delta^2}$ is large, p will tend to be near zero or one, thus environmental fluctuations will tend to reduce the variation in p through a negative value for $\text{Cov}(\delta, \beta)$ and therefore lower $\overline{\delta^2}$. When $\overline{\delta^2}$ is small, the $\text{Cov}(\delta, \beta)$ will be low. Environmental variation will therefore tend to increase $\overline{\delta^2}$.

Putting all terms together yields an approximate change in the distance measure

$$\Delta\overline{\delta^2} \approx \text{Var}(\beta) + 2\text{Cov}(\delta, \beta)$$
$$+ 2\mu[\text{Cov}(p, q) - \text{Var}(q)]$$
$$- 2s[\text{Cov}(q, \delta^2) + \bar{q}\overline{\delta^2}]. \tag{4}$$

where I have assumed that the magnitudes of s, μ and β are small relative to one. The effect of random changes in task, μ, can be understood by noting that

$$\overline{\delta^2} = \text{Var}(p) + \text{Var}(q) - 2\text{Cov}(p, q).$$

Random task switching will decrease the covariance, the match between p and q, raising $\overline{\delta^2}$.

Random task switching narrows the distribution of q because, on average, individuals will move from common to rare tasks. This reduces $\text{Var}(q)$, which reduces $\overline{\delta^2}$.

For the selection term, $\text{Cov}(q, \delta^2) + \bar{q}\overline{\delta^2} = E(q\delta^2)$, which is always positive. This term describes the rate at which selection steadily reduces the distance between optimal colony allocation, p, and current allocation, q, measured by $\overline{\delta^2}$.

4. Conclusion

This analysis demonstrates a rational method for dissecting the complex processes involved in colony development. The resulting description clearly separates the generative mechanism and the selective filter. The effects are all expressed in simple statistical quantities that provide natural aggregate descriptions of colony state.

This approach is not a substitute for standard dynamical analysis. Rather, it is a formal tool that allows comparison among different partitions of complex systems. For example, I prefer the split between generative mechanisms and selective filters, but perhaps an alternative view would provide a better description. The method also suggests a natural level for aggregation and the associated statistical quantities that measure crucial properties of the system. Again, alternative aggregations are possible. Each partition-aggregation pair provides a metaphor that suggests natural extensions in conceptual and empirical domains. The method outlined here provides a rational way to translate competing metaphors into formal analysis.

Acknowledgements

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