Biology and Philosophy **17:** 551–565, 2002.

Article

On Price's Equation and Average Fitness

BENJAMIN KERR*
Department of Biological Sciences
Stanford University
Stanford, CA 94305
USA

PETER GODFREY-SMITH
Philosophy Department
Stanford University
Stanford, CA 94305-2155
USA

Abstract. A number of recent discussions have argued that George Price's equation for representing evolutionary change is a powerful and illuminating tool, especially in the context of debates about multiple levels of selection. Our paper dissects Price's equation in detail, and compares it to another statistical tool: the calculation and comparison of average fitnesses. The relations between Price's equation and equations for evolutionary change using average fitness are closer than is sometimes supposed. The two approaches achieve a similar kind of statistical summary of one generation of change, and they achieve this via a similar loss of information about the underlying fitness structure.

Key words: altruism, average fitness, clumping, group selection, individual selection, marginal fitness, multi-level selection, Price's equation, statistics

1. Introduction

In the study of selection in structured populations, several researchers have suggested that Price's (1970, 1972, 1995) famous equation is a powerful and illuminating statistical tool (Frank 1995; Hamilton 1975; Sober and Wilson 1998). What exactly is the Price equation and what does it really do? In this paper we try to answer this question by drawing on our companion paper (this volume). In addition, we discuss another well-known statistical approach – that involving average (or "marginal") individual fitnesses. We will argue

---

* Current address: Ecology, Evolution and Behavior Department, University of Minnesota, 100 Ecology, 1987 Buford Circle, St. Paul, MN 55108, USA

that Price's approach and the average fitness approach actually have some deep underlying similarities.

Discussion of these statistical approaches is aided by reference to different ways of representing the selective process. In our companion paper in this volume we develop two alternative perspectives, the individualist perspective and the multi-level perspective. We will provide a summary of some results from our other paper before diving into the statistics.

Consider the following life-cycle for two types of organisms, ***A*** and ***B***, in an infinite population. Each generation, the individuals form an infinite number of size n groups (either randomly or non-randomly). Let $f_i(t)$ be the frequency of groups with i ***A*** types in generation t. The collection of these $f_i(t)$'s is the *group frequency distribution*, $f(t)$. Individuals reproduce asexually and fitness (the number of copies an individual can expect) depends both on its own type and on the composition of types within its group. Groups then break up, the parent individuals expire, and the cycle begins again with the offspring individuals forming the next set of groups.

There are different ways to describe "fitness" in this structured population. The *individualist perspective* assigns fitness-like properties only to individuals, using the following parameters:

$$\alpha_i = \begin{cases} \text{the expected number of copies of an } \boldsymbol{A} \text{ type} \\ \text{in a group with } i\,\boldsymbol{A} \text{ types and } (n-i)\,\boldsymbol{B} \text{ types} \end{cases},$$

$$\beta_i = \begin{cases} \text{the expected number of copies of a } \boldsymbol{B} \text{ type} \\ \text{in a group with } i\,\boldsymbol{A} \text{ types and } (n-i)\,\boldsymbol{B} \text{ types} \end{cases}.$$

Note the α_0 and β_n are undefined. The *multi-level perspective* recognizes groups as fitness-bearing entities, while simultaneously tracking how a group's productivity is shared between types within the group. The following parameters are used within the multi-level perspective:

$$\pi_i = \text{total number of copies from a group with } i\,\boldsymbol{A} \text{ types},$$

$$\phi_i = \frac{\text{number of } \boldsymbol{A} \text{ copies in a group with } i\,\boldsymbol{A} \text{ types}}{\text{total number of copies in a group with } i\,\boldsymbol{A} \text{ types}}.$$

Thus, π_i represents group productivity, and ϕ_i the fraction of this productivity claimed by ***A*** types, in a group with i ***A*** types.

Each set of parameters can be defined in terms of the other:[1]

$$\pi_i = i\alpha_i + (n-i)\beta_i, \quad \phi_i = \frac{i\alpha_i}{i\alpha_i + (n-i)\beta_i}, \tag{1}$$

$$\alpha_i = \frac{\phi_i \pi_i}{i}, \quad \beta_i = \frac{(1-\phi_i)\pi_i}{n-i}. \tag{2}$$

Thus, there is mathematical interchangeability between the individualist framework and the multi-level framework. The list of α_i's and β_i's and the list of π_i's and ϕ_i's comprise two interchangeable parameterizations of the *fitness structure* of the system.

Consider the population at generation t, where $\bar{p}(t)$ and $\bar{q}(t)$ are the population-wide frequencies of ***A*** and ***B***, respectively. Given the group frequency distribution and the fitness structure, we can compute the frequency of ***A*** and ***B*** in the next generation ($\bar{p}(t+1)$ and $\bar{q}(t+1)$). For example, using the individualist perspective we find:

$$\bar{w}\bar{p}(t+1) = \sum_{i=1}^{n} f_i(t)\frac{i}{n}\alpha_i, \tag{3}$$

$$\bar{w}\bar{q}(t+1) = \sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}\beta_i, \tag{4}$$

with mean individual fitness given by

$$\bar{w} = \sum_{i=1}^{n} f_i(t)\frac{i}{n}\alpha_i + \sum_{i=0}^{n-1} f_i(t)\frac{n-i}{n}\beta_i.$$

The same equations can also be written from the multi-level perspective:

$$\bar{\pi}\bar{p}(t+1) = \sum_{i=1}^{n} f_i(t)\phi_i\pi_i, \tag{5}$$

$$\bar{\pi}\bar{q}(t+1) = \sum_{i=0}^{n-1} f_i(t)(1-\phi_i)\pi_i, \tag{6}$$

with mean group productivity given by

$$\bar{\pi} = \sum_{i=0}^{n} f_i(t)\pi_i.$$

2. Averaging[2]

The first statistical tool we will examine uses average or "marginal" individual fitnesses. The status of these fitnesses has been a topic of dispute in several parts of the "units of selection" debates (Sober and Lewontin 1982; Sober and Wilson 1998). It is easiest to approach these statistics from the individualist perspective, but in principle they can be employed within either.

We begin by deriving the statistics. In the derivations, the following relations will be handy:

$$\bar{p}(t) = \sum_{i=0}^{n} f_i(t)\frac{i}{n}, \quad \bar{q}(t) = \sum_{i=0}^{n} f_i(t)\frac{(n-i)}{n}. \tag{7}$$

We can then rewrite equations (3) and (4) as follows:

$$\bar{w}\bar{p}(t+1) = \frac{\sum_{i=1}^{n} f_i(t)\frac{i}{n}\alpha_i}{\sum_{i=1}^{n} f_i(t)\frac{i}{n}}\bar{p}(t), \tag{8}$$

$$\bar{w}\bar{q}(t+1) = \frac{\sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}\beta_i}{\sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}}\bar{q}(t). \tag{9}$$

Equations (8) and (9) give formulas for the frequency of ***A*** and ***B*** in the next generation by multiplying the current frequencies by a "fitness factor" in each case. These fitness factors are, in fact, the average (or marginal) fitnesses of the two types – $w_A(t)$ and $w_B(t)$. They can be represented as follows:

$$w_A(t) = \frac{\sum_{i=1}^{n} f_i(t)\frac{i}{n}\alpha_i}{\sum_{i=1}^{n} f_i(t)\frac{i}{n}}, \tag{10}$$

and

$$w_B(t) = \frac{\sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}\beta_i}{\sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}}. \tag{11}$$

Up to this point we have used the group frequency distribution $f(t)$ as the basis for claims about averages. It is also possible to introduce a more explicit probabilistic framework, and there are advantages from doing so. We introduce the concept of a focal individual's "neighborhood," which is defined to be the collection of all other individuals in the focal's group besides the focal individual (see Nunney 1985). Given a group frequency distribution, these neighborhoods can be described statistically. If we let X be the number of ***A*** types in a neighborhood of a randomly selected ***A*** type, then X will be a discrete random variable. The same can be done for Y, the number of ***A*** types in a neighborhood of a randomly selected ***B*** type. In Appendix 1 we give the distributions for these random variables. If group formation is random, it is possible to show that both X and Y will be identically binomially distributed.[3] Whether group formation is random or not, the random variables describing neighborhoods can be used to give a compact and useful representation of average fitnesses. These representations treat average fitnesses as *expected values* – the fitness of a given type in each possible neighborhood is multiplied by the probability of its encountering that particular neighborhood. These results for each neighborhood are then summed to yield the expected fitness of that type for generation t. More formally, in the case of the $\boldsymbol{A}$ type,

$$w_A(t) = \sum_{x=0}^{n-1} \Pr\{X = x\}\alpha_{x+1}, \tag{12}$$

which in equivalent to

$$w_A(t) = E[\alpha_{X+1}]. \tag{13}$$

Similarly, the marginal fitness of $\boldsymbol{B}$ can be written as

$$w_B(t) = \sum_{y=0}^{n-1} \Pr\{Y = y\}\beta_y, \tag{14}$$

or

$$w_B(t) = E[\beta_Y]. \tag{15}$$

These fitnesses can be used to give an equation for evolutionary change. For instance, the change in frequency of $\boldsymbol{A}$, $\Delta\bar{p}$, can be given as:

$$\Delta\bar{p} = \frac{\bar{p}\bar{q}(E[\alpha_{X+1}] - E[\beta_Y])}{\bar{w}}. \tag{16}$$

From this we can give a criterion for the increase in the frequency of $\boldsymbol{A}$:

$$E[\alpha_{X+1}] > E[\beta_Y]. \tag{17}$$

Dugatkin and Reeve (1994) and Sterelny (1996) discuss how the composition of a type's group (or neighborhood) might be considered part of its *selective environment* (see also Alexander and Borgia 1978; Nunney 1985; Sterelny and Kitcher 1988; Waters 1991). So, in a way, equations (12) and (14) express the following sentiment: Given fitnesses (α_i or β_i) over a series of "environments," the increase of a type will depend both on how well it does in various "environments," and on the probability of encountering "environments" that are favorable to it.

Up to now, we have been using the individualist perspective to discuss the average fitness approach. However, the statistics associated with this approach can be obtained within the multi-level perspective as well.

3. The Price equation

Condition (17) is a statistical criterion for increase in type ***A***. However, it is certainly not the only statistical criterion. In this section we will show, as simply as possible, how to derive and use the Price equation to represent systems of this kind.

We will do this from the multi-level perspective. We start by writing a formula for the change in ***A*** frequency. If we subtract $\bar{\pi}\bar{p}(t)$ from both sides of (5), we have

$$\bar{\pi}(\bar{p}(t+1) - \bar{p}(t)) = \left\{\sum_{i=1}^{n} f_i(t)\phi_i\pi_i\right\} - \bar{\pi}\bar{p}(t).$$

Using identities (7), we have

$$\bar{\pi}(\Delta\bar{p}_{t\to t+1}) = \sum_{i=1}^{n} f_i(t)\left[\phi_i\pi_i - \bar{\pi}\left(\frac{i}{n}\right)\right].$$

We let $p_i = i/n$ be the frequency of ***A*** in a group with *i* ***A*** types. Rearranging the above expression gives

$$\bar{\pi}(\Delta\bar{p}_{t\to t+1}) = \sum_{i=1}^{n} f_i(t)[p_i(\pi_i - \bar{\pi}) + \pi_i(\phi_i - p_i)],$$

or

$$\bar{\pi}(\Delta\bar{p}_{t\to t+1}) = \sum_{i=1}^{n} f_i(t)(\pi_i - \bar{\pi})p_i - \sum_{i=1}^{n} f_i(t)\pi_i(p_i - \phi_i).$$

However, since $\sum_{i=1}^{n} f_i(t)(\pi_i - \bar{\pi})p_i = \sum_{i=1}^{n} f_i(t)(\pi_i - \bar{\pi})(p_i - \bar{p}(t))$, we have

$$\bar{\pi}(\Delta\bar{p}_{t\to t+1}) = \sum_{i=1}^{n} f_i(t)(\pi_i - \bar{\pi})(p_i - \bar{p}(t)) - \sum_{i=1}^{n} f_i(t)\pi_i(p_i - \phi_i).$$

Dropping the subscripts, we can rewrite the above as

$$\Delta\bar{p} = \frac{\mathrm{cov}(\pi, p) - E[\pi(p-\phi)]}{\bar{\pi}}. \tag{18}$$

Equation (18) is the famous Price equation (Price 1970, 1972, 1995) in a slightly altered form.[4]

The Price equation is useful in discussions of altruism. For our purposes here, we will define altruism as follows; the $\boldsymbol{A}$ type is an altruist if and only if $\pi_{i+1} > \pi_i$ for all $i \in \{0, 1, 2, \ldots n-1\}$, and $\phi_i < i/n$ for all mixed groups. That is, group productivity increases with the frequency of $\boldsymbol{A}$, but $\boldsymbol{A}$ types get less than their fair share within any mixed group. By this definition, $\mathrm{cov}(\pi, p)$ and $E[\pi(p - \phi)]$ must both be positive and the condition for altruist ($\boldsymbol{A}$) increase in frequency is

$$\mathrm{cov}(\pi, p) > E[\pi(p - \phi)]. \tag{19}$$

The covariance term in (19) measures the relationship between group productivity and the frequency of $\boldsymbol{A}$ within the group. The expectation term monitors average change in $\boldsymbol{A}$'s frequency within groups. These two terms have been interpreted as between-group and within-group components of selective processes, respectively (Price 1972; Hamilton 1975; Sober and Wilson 1998). Both "components" combine information about fitness structure weighted by the group frequency distribution; thus both are statistical abstractions.

While we have developed Price's approach within a multi-level perspective, there is no reason the exercise cannot be repeated within the individualist framework.

4. The role of statistical summaries within each perspective

Any evolutionary model of a structured population includes a "summarizing" step in which the outcomes of different processes are collected together. Statistical quantities, such as means, variances and covariances, can be used to compute these summaries. For any particular model, there will be different summary statistics available.

Two statistical frameworks that have been used in evolutionary models with population structure are the average fitness approach and Price's approach. Both of these statistical approaches can be used under either the individualist or multi-level perspective. However, each perspective is naturally associated with a particular way of summarizing the selective process.

To see this, we take a closer look at the inequalities that summarize the direction of evolutionary change. For the average fitness approach, this is inequality (17) and for the Price approach it is (19). In the case of (17) we see that this marginal criterion *separates out* the fitnesses of $\boldsymbol{A}$ and of $\boldsymbol{B}$ – the LHS term uses α's only and the RHS terms uses β's only. In the case of (19), the Price approach does not separate out the roles of $\boldsymbol{A}$ and $\boldsymbol{B}$, but instead compares π's and ϕ's, the group productivities and the within-group change. (Here the separation is not complete, as the RHS includes both terms.)

In some sense, averaging does for the individualist perspective what Price's equation does for the multi-level perspective. Both the average fitness formulae and Price's equation give statistical criteria for increase of a type and both break down the fitness structure in a way that is convenient for the associated perspective. The average fitness formulae can be written within the multi-level view, and the Price criterion can be expressed in individualist terms, but in both case we then find no useful "separation" of pieces of the fitness structure.

In a sense, the individualist perspective reveals averaging as a statistical summary that distinguishes the roles of different *individual types* in the population. The multi-level perspective, on the other hand, reveals Price's equation as a statistical summary that distinguishes changes at different *levels* within the structured population hierarchy. When using an individualist perspective, the average fitness approach is a natural summary of a parameterization centered on individual productivities. When using the multi-level perspective, Price's equation is a natural summary of a parameterization distinguishing group productivities from within group change. Given these observations, it is not surprising that Price, who used a multi-level perspective, summarized evolutionary change in terms of covariance; while others employing the individualist perspective, including Matessi and Jayakar (1976) and Cohen and Eshel (1976), summarized evolutionary change using the expectations of the average fitness approach.

While each perspective is naturally associated with a specific statistical approach, both statistical approaches share several common features. First, since average fitnesses and Price's statistics are summaries, there is inherent *loss of information* under either statistical approach. Details of the selective process are lost when using any descriptive statistic in lieu of a full description of the fitness structure and group frequency distribution. Second, in order to compute the relevant statistics in either approach, both the fitness structure (which could be represented using either one of the described perspectives) and the group frequency distribution are needed. Third, since the group frequency distribution can change generation to generation, the statistics from either approach must be recomputed every generation.

It is important to separate statistical summaries from the full description of the fitness structure and group frequency distribution. Our individualist perspective is simply one way to parameterize a fitness structure (with α's and β's). Our individualist perspective, in and of itself, does not make any claims or assumptions about averages. Average fitnesses are simply one available form of summary – one that is natural, but not essential to the perspective.

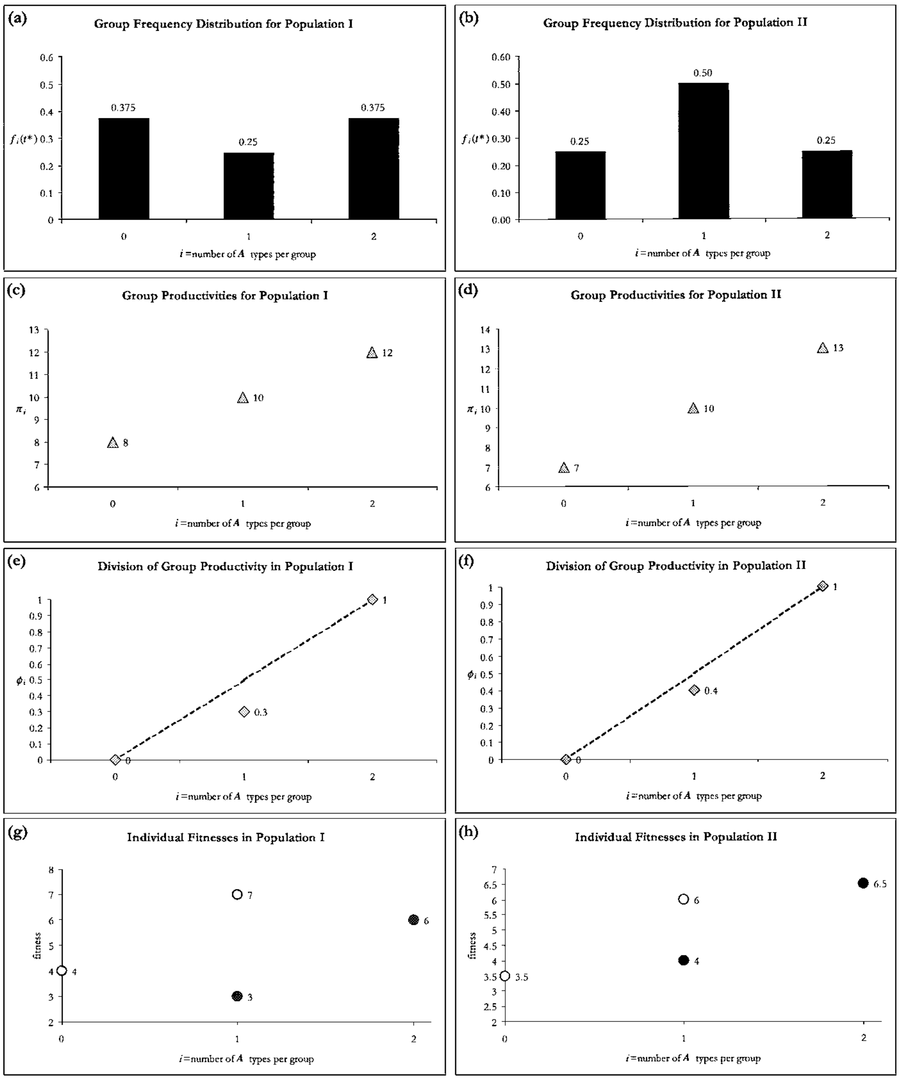

Figure 1. (a) The group frequency distribution for Population I (this distribution is clumped). (b) The group frequency distribution for Population II (this distribution is binomial with parameters $n = 2$ and $p = 1/2$). (c) The group productivities (π values) in Population I and (d) Population II. (e) The within group split of the group productivity (ϕ values) in Population I and (f) Population II. (g) The fitness structure for Population I (α and β values) represented within the individualist perspective (note that this structure is Class I using the terminology in our companion paper). (h) Individual fitnesses for Population II (note that this fitness structure is Class II).

We might think of an α/β parameterization plus average fitness statistics as a "package." And we could think of a π/ϕ parameterization plus Price's statistics as another package. There is a type of equivalence between these packages. However, it is a mistake to compare part of one package with a different part of the other package. In particular, it is a mistake to compare average fitnesses within an individualist package with the full fitness parameterization of the multi-level package. Similarly, it would not make sense to compare Price's statistics to a full fitness description within the individualist perspective.

If we are comparing the two statistical approaches themselves, we should not expect the components of the Price equation to avoid the type of information loss that comes with average fitnesses. This information loss is illustrated in Figure 1. In the figure we have two populations (I and II). Each population differs from the other in both its fitness structure (we show the fitness structures from both the multi-level perspective and the individualist perspective) and its group frequency distribution. When the covariance and expectation terms from Price's equation are computed, we see that they are *identical* across the two populations! Thus, the "between group" terms in the two populations are the same and the "within group" terms in the two populations are the same. However, we would surely not want to claim that the same selective event took place in both populations.

In population I, we have a fitness structure that is rather hostile to the evolution of altruism (a Class I structure, in the terminology of our companion paper). But a clumped group frequency distribution overcomes this problem for the altruist type. In population II, we have a fitness structure that is more favorable to altruism. This structure is one that allows altruism to do well even under random group formation (a Class II structure, in the terminology of the companion paper). The group frequency distribution for population II here is binomial. In essence, the change in the fitness structure when we move from population I to population II is compensated by the change in group frequency distribution, such that Price's statistics remain unchanged.

The same point applies to average fitnesses; it is possible to describe two populations differing in both their fitness structures and group frequency distributions that have the same average fitness statistics. Indeed, the two populations in Figure 1 have the same average fitness statistics as well as the same Price statistics.[5] Note that this is not necessarily the case; if two populations have the same statistics according to one of the two approaches, that does not imply they have the same statistics from the other approach.[6]

In sum, we have argued that Price's statistics and average individual fitnesses play similar roles within two alternative perspectives. Both statistics take the same kind of inputs – a fitness structure and a group frequency distribution – and both issue the same kind of output – a statistical summary of the action of selection over one generation. Each statistical approach organizes information differently, in a way that complements a particular parametization of the fitness structure (average fitnesses with individualism, Price with the multi-level perspective). Both approaches summarize a more complete representation of the selective process, and are hence subject to a similar kind of loss of information.

Appendix 1: Last member analysis

In our companion paper, we argue that the M-J proposition can be intuitively understood using "last member analysis." Suppose you are the last member to join a group with $n - 1$ members, with k ***A*** types among them ($k \in \{0, 1, 2, \dots n - 1\}$). These $n - 1$ individuals constitute your *neighborhood*. If $\alpha_{k+1} < \beta_k$, we say that you should choose to be a ***B*** type, whereas if $\alpha_{k+1} > \beta_k$, choosing to be an ***A*** type is superior. Now, if $\alpha_{k+1} < \beta_k$ for *all* $k \in \{0, 1, 2, \dots n - 1\}$ (a Class I structure), the last member to join any group should always decide to be a ***B*** type. Similarly, if $\alpha_{k+1} > \beta_k$ for *all* $k \in \{0, 1, 2, \dots n - 1\}$ (a Class II structure), the last member to join any group should always decide to be an ***A*** type. The M–J proposition states that if groups form randomly and the fitness structure is Class I, then ***B*** always increases in frequency, whereas ***A*** always increases when the fitness structure in Class II. Why does the last member heuristic agree with the evolutionary predictions of the M–J proposition?

We answer this question by returning to the random variables X and Y, which give the number of ***A*** types in the neighborhood of a randomly picked ***A*** type and ***B*** type, respectively.

X is a random variable with following distribution:

$$\Pr\{X = x\} = \frac{f_{x+1}(t)\frac{(x+1)}{n}}{\sum_{i=1}^{n} f_i(t)\frac{i}{n}},$$

Analogously, if Y is the number of ***A*** types in a neighborhood of a randomly selected ***B*** type, then it has the following distribution:

$$\Pr\{Y = y\} = \frac{f_y(t)\frac{(n-y)}{n}}{\sum_{i=0}^{n-1} f_i(t)\frac{(n-i)}{n}}.$$

Random formation of groups implies that the group frequency distribution is binomial (i.e. $f_i(t) = \binom{n}{i}(\bar{p}(t))^i(\bar{q}(t))^{n-i}$). Using this fact, and equations (7), we can rewrite the probability distribution for X and simplify to obtain the following:

$$\Pr\{X = x\} \; = \; \binom{n-1}{x} \bar{p}^x \bar{q}^{n-1-x}.$$

Similarly, it can be shown that:

$$\Pr\{Y = y\} \ = \ \binom{n-1}{y} \bar{p}^{y} \bar{q}^{n-1-y}.$$

That is, if groups are formed randomly, both X and Y are *identically* binomially distributed (with parameters $\bar{p}(t)$ and $n - 1$). Thus, a randomly selected ***A*** or ***B*** individual encounters k ***A*** types with the same probability.

This shows us why the last member heuristic works. The inequality $\alpha_{k+1} > \beta_k$ for all $k \in \{0, 1, 2, \ldots n - 1\}$ entails that $E[\alpha_{X+1}] > E[\beta_Y]$. And the inequality $\alpha_{k+1} < \beta_k$ for all $k \in \{0, 1, 2, \ldots n - 1\}$ entails that $E[\alpha_{X+1}] < E[\beta_Y]$. Thus, if the last member should always choose to be an ***A*** type, then random group formation implies that an ***A*** type will evolve to fixation. The same applies to ***B***. In cases of random group formation, information about the fitness structure (which is all that is used in last member analysis) alone can suffice to predict evolutionary outcomes.

Appendix 2: Statistical descriptions of clumping

It is widely recognized that a "clumped" frequency distribution can be important to the evolution of altruism. If altruists tend to interact more with altruists, while selfish types more often encounter selfish types, the evolution of altruism becomes more likely. The statistical frameworks we've discussed in this paper can be used to aid in understanding this role of clumping.

It is useful to define a measure of how far the group frequency distribution differs from a binomial distribution (which corresponds to random group formation). Here is one such "clumping index," C:

$$C = \frac{\sigma_p^2 - v^2}{v^2},$$

where σ_p^2 is the variance in ***A***'s frequency across groups, and $v^2 = \frac{\bar{p}(t)\bar{q}(t)}{n}$ is the variance in the frequency of the ***A*** type given random formation of groups. Thus, C is a measure of how dispersed the distribution $f(t)$ is relative to a binomial distribution. Positive values of C translate to "heavy-tail" frequency distributions, in which ***A*** individuals frequently encounter ***A*** types and ***B*** individuals encounter ***B*** types. Negative values of C translate to "heavy-center" distributions, in which the majority of groups tend to contain even mixes of ***A*** and ***B*** types. When $C = 0, f(t)$ is binomial; that is, groups form randomly.

So, if we consider the ***A*** type as an altruist, clumping allows ***A*** types to find themselves in environments in which they interact largely with other ***A***'s, while ***B*** types are encountering less favorable environments (the company of fellow selfish types). To develop this notion more rigorously, we employ a technique used in Charnov and Krebs (1975) (see also Wilson 1977, 1980). The number of altruists an average altruist possesses in its neighborhood is given by $E[X]$ and the expected number of altruists in a selfish type's neighborhood is given by $E[Y]$. Then it can be shown that

$$E[X] - E[Y] = C \tag{A2.1}$$

That is, our clumping index measures the difference in the number of altruists that a randomly picked altruist can expect to see and the number of altruists that a randomly picked selfish type can expect to see.

In order to examine the effects of clumping, as measured by C, we will use the additive fitness scheme studied in detail by Wilson (1977, 1980, 1990), where $\alpha_i = z + d + r(i - 1)$ and $\beta_i = z + ri$ (see also Wade 1985). Here, z is the "base" fitness, d represents the altruist's effect on its own fitness (the *d*onor of the altruism) and r represents the effect of the altruism on the fitness of a *r*ecipient individual (either an altruist or a selfish type). In order to satisfy the definition of altruism used here, we must have $d < r$ and $d + (n - 1)r > 0$. As Wilson (1977, 1980) shows, in the case of this additive model, we have:

$$\begin{aligned} E[\alpha_{X+1}] &= z + d - r + rn\left(\bar{p} + \frac{\sigma_p^2}{\bar{p}}\right), \\ E[\beta_Y] &= z + rn\left(\bar{p} - \frac{\sigma_p^2}{\bar{q}}\right). \end{aligned}$$

Thus, as the variance in frequency increases, we see $E[\alpha_{X+1}]$ increases and $E[\beta_Y]$ decreases. Another way to see the effect of variance is to focus on the difference $E[X] - E[Y]$. Condition (17) can be written as follows:

$$\begin{aligned} E[\alpha_{X+1}] &> E[\beta_Y] \\ E[z + d + rX] &> E[z + rY] \\ z + d + rE[X] &> z + rE[Y] \\ d &> r(E[Y] - E[X]) \\ -d &< Cr \end{aligned} \tag{A2.2}$$

Condition (A2.2) is given in a different form by Wilson (1977, 1980, 1990). High values of σ_p^2 produced by clumping make it more likely that condition (A2.2) will hold (i.e., by increasing C). The reader may note a similarity between (A2.2) and Hamilton's rule, with d as the "cost," r as the "benefit," and C as something akin to the "coefficient of relatedness."[7]

Clumping results in more groups with mostly ***A*** or mostly **B** and the variance in ***A*** frequency across groups increases. Within Price's framework, this can have the effect of increasing $\mathrm{cov}(\pi, p)$ and decreasing $E[\pi(p - \phi)]$ from equation (18), which makes condition (19) more likely. Again, we consider the linear model from above. Within the multi-level perspective, we have $\pi_i = nz + (d + (n - 1)r)i$ and $\phi_i = \frac{iz+(d+(i-1)r)i}{nz+(d+(n-1)r)i}$. We consider each term from Price's equation, starting with the covariance term:

$$\mathrm{cov}(\pi, p) = (d + (n - 1)r)n\sigma_p^2.$$

The other term from Price is:

$$E[\pi(p-\phi)] = (r-d)(n^2v^2 - n\sigma_p^2).$$

If we plug the above values for $\mathrm{cov}(\pi, p)$ and $E[\pi(p - \phi)]$ into condition (19) and simplify, we get condition (A2.2). As the variance in frequency σ_p^2 increases, $\mathrm{cov}(\pi, p)$ increases (note that we assume $d + (n - 1)r > 0$) and $E[\pi(p - \phi)]$ decreases (note that we assume $r > d$), making (19) more likely. Thus, we can investigate the role of clumping within either statistical perspective; in both cases, clumping tends to favor the ***A*** type.

Notes

[1] Since α_0 and β_n are undefined, we cannot use equations (1) for pure groups. However, we must have $\pi_0 = n\beta_0$, $\pi_n = n\alpha_n$, $\phi_0 = 0$, and $\phi_n = 1$.

[2] Many of the mathematical results in this section can be found in other papers (Matessi and Jayakar 1976; Cohen and Eshel 1976; Uyenoyama and Feldman 1980; Nunney 1985; Wilson 1990).

[3] This can be used to give a justification for some of the methods used in our companion paper; see Appendix 1.

[4] See also Wade (1985) and Frank (1995) for a general discussion of Price's work.

[5] For both populations $E[\alpha_{X+1}] = 5.25$, $E[\beta_Y] = 4.75$, $\mathrm{cov}(\pi, p) = 0.75$, and $E[\pi(p - \phi)] = 0.5$. Note that $E[\alpha_{X+1}] > E[\beta_Y]$ and $\mathrm{cov}(\pi, p) > E[\pi(p - \phi)]$ and so ***A*** increases in frequency according to relations (17) and (19).

[6] However, since the change in ***A***'s frequency will be the same regardless of the statistical framework we use, we can show that the following must be true (using (16) and (18)):

$$\mathrm{cov}(\pi, p) - E[\pi(p-\phi)] = n\bar{p}\bar{q}(E[\alpha_{X+1}] - E[\beta_Y]).$$

This equality connects the two statistical frameworks. However, it is possible that two populations may have equivalent Price statistics, while differing in their average fitness statistics, such that the above equality is still satisfied, or *vice versa*.

[7] Equation (A2.2) also relates to Nunney's (1985) equation (7). He calls d the "individual effect" on selection (d is the change in fitness a selfish individual can expect if it were to convert to altruism). Since Nunney requires a Class I structure in his definition of altruism, in his case, $d < 0$. For Nunney, the force of group selection would be given by Cr. In order for group selection for altruism to occur, this "group component" must be positive. Consequently, a necessary condition for group selection is that $C > 0$ or $\sigma_p^2 > v^2$. Thus, Nunney's definition of group selection requires clumping.

References

Alexander, R.D. and Borgia, G.: 1978, 'Group Selection, Altruism, and the Levels of Organization of Life', *Annual Review of Ecology and Systematics* **9**, 449–474.

Charnov, E.L. and Krebs, J.R.: 1975, 'The Evolution of Alarm Calls: Altruism or Manipulation?', *American Naturalist* **109**, 107–112.

Cohen, D. and Eshel, I.: 1976, 'On the Founder Effect and the Evolution of Altruistic Traits', *Theoretical Population Biology* **10**, 276–302.

Dugatkin, L.A. and Reeve, H.K.: 1994, 'Behavioral Ecology and Level of Selection: Dissolving the Group Selection Controversy', *Advances in the Study of Behavior* **23**, 101–133.

Frank, S.A.: 1995, 'George Price's Contributions to Evolutionary Genetics', *Journal of Theoretical Biology* **175**, 373–388.

Hamilton, W.D.: 1975, 'Innate Social Aptitudes in Man: An Approach from Evolutionary Genetics', in R. Fox (ed.), *Biosocial Anthropology*, Wiley, New York, pp. 133–155.

Matessi, C. and Jayakar, S.D.: 1976, 'Conditions for the Evolution of Altruism under Darwinian Selection', *Theoretical Population Biology* **9**, 360–387.

Nunney, L.: 1985, 'Group Selection, Altruism, and Structured-deme Models', *American Naturalist* **126**, 212–230.

Price, G.R.: 1970, 'Selection and Covariance', *Nature* **227**, 520–521.

Price, G.R.: 1972, 'Extension of Covariance Selection Mathematics', *Annuals of Human Genetics* **35**, 485–490.

Price, G.R.: 1995, 'The Nature of Selection', *Journal of Theoretical Biology* **175**, 389–396.

Sober, E. and Lewontin, R.C.: 1982, 'Artifact, Cause and Genic Selection', *Philosophy of Science* **49**, 157–180.

Sober, E. and Wilson, D.S.: 1998, *Unto Others: The Evolution and Psychology of Unselfish Behavior*, Harvard University Press, Cambridge.

Sterelny, K.: 1996, 'The Return of the Group', *Philosophy of Science* **63**, 562–584.

Sterelny, K. and Kitcher, P.: 1988, 'The Return of the Gene', *Journal of Philosophy* **85**.

Uyenoyama, M. and Feldman, M.W.: 1980, 'Theories of Kin and Group Selection: A Population Genetics Perspective', *Theoretical Population Biology* **17**, 380–414.

Wade, M.J.: 1985, 'Soft Selection, Hard Selection, Kin Selection, and Group Selection', *American Naturalist* **125**, 61–73.

Waters, C.K.: 1991, 'Tempered Realism About the Force of Selection', *Philosophy of Science* **58**, 553–573.

Wilson, D.S.: 1977, 'Structured Demes and the Evolution of Group-advantageous Traits', *American Naturalist* **111**, 157–185.

Wilson, D.S.: 1980, *The Natural Selection of Populations and Communities*, Benjamin/Cummings, Menlo Park.

Wilson, D.S.: 1990, 'Weak Altruism, Strong Group Selection', *Oikos* **59**, 135–140.