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Multilevel selection: the evolution of cooperation in non-kin groups

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Abstract Hamilton's (1964a, 1964b) landmark papers are rightly recognized as the formal basis for our understanding of the evolution of altruistic traits. However, Hamilton's equation as he originally expressed it is simplistic. A genetically oriented approach to studying multilevel selection can provide insights into how the terminology and assumptions used by Hamilton can be generalized. Using contextual analysis I demonstrated that Hamilton's rule actually embodies three distinct processes, group selection, individual selection, and transmission genetics or heritability. Whether an altruistic trait will evolve depends the balance of all of these factors. The genetical approach, and particularly, contextual analysis provides a means of separating these factors and examining them one at a time. Perhaps the greatest issue with Hamilton's equation is the interpretation of r . Hamilton (1964a) interpreted this as relatedness. In this paper I show that what Hamilton called relatedness is more generally interpreted as the proportion for variance among groups, and that many processes in addition to relatedness can increase the variance among groups. I also show that the evolution of an altruistic trait is driven by the ratio of the heritability at the group level to the heritability at the individual level. Under some circumstances this ratio can be greater than 1. In this situation altruism can evolve even if selection favoring selfish behavior is stronger than selection favoring altruism.

Keywords Multilevel selection · Kin selection · Group selection · Evolution of Altruism · Contextual analysis

Introduction

In this paper I will explore the relationship between kin selection and multilevel selection. The idea that kin selection is a form of multilevel selection is not new. Indeed, the term kin selection was introduced by Maynard-Smith (1964, 1976) as an alternative to group selection as a mechanism for the evolution of altruism. The relationship between kin and group selection, however, has often been difficult to understand. This difficulty has several sources. First, multilevel selection is often poorly understood, and mathematical formulations for multilevel selection are not widely appreciated. Second, as I shall show, kin selection is actually three distinct processes incorporated into a single concept. From a multilevel perspective these processes are individual selection against the altruistic trait, group selection in favor of the altruistic trait, and the heritable basis of the trait. Since multilevel selection theory typically separates these three processes direct comparisons between kin selection and multilevel selection can be difficult.

In this paper I will discuss three general topics. First, I will discuss multilevel selection, and contextual analysis, a statistical procedure for analyzing naturally occurring multilevel selection. Second, I will briefly review studies of group selection, and explore why studies of group selection are have always demonstrated greater responses to selection than predicted based upon classic theory. Finally, I will use these results to explore the relationship between kin selection and multilevel selection.

In discussing multilevel selection it is important to distinguish two distinct approaches to the study of this subject. I shall refer to these approaches as the adaptationist approach and the genetical approach (Goodnight and Stevens 1997). Students of the adaptationist approach seek to explain existing adaptations in terms of multilevel, and particularly group level selection, whereas students of the genetical approach focus on

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ongoing changes either by performing selection experiments, or by observing changes occurring in natural populations.

Kin selection and the adaptationist approach

The adaptationist approach has its origins in Darwin's (1859) efforts to explain the evolution of sterile castes eusocial insects, and has had both stunning successes, for example when used to explain biased sex ratios (Wilson and Colwell 1981), and dismal failures, for example when used to explain apparent self regulation of population size (Wynne-Edwards 1962).

The general method used in the adaptationist approach is to study the ecology, physiology, and other features of a trait or behavior in sufficient detail that a plausible explanation for how it evolved can be developed. The power of this approach lies in that it can be readily applied to nearly any trait or behavior, and has typically been applied to traits that are of great interest to biologists. The drawback to this approach is that there are necessarily many possible ways that a trait may have evolved. Choosing which is most plausible can be difficult, and there can be no guarantee that the evolution of the trait actually followed the most plausible path. Rules are needed to choose among possible explanations, and to decide which is most plausible. William's principle of parsimony provides an example of such a rule. This principle states that "In explaining adaptation, one should assume the adequacy of the simplest form of natural selection,..., unless the evidence clearly shows that this theory does not suffice." (Williams 1966). Using this principle explanations involving lower levels of selection are considered more plausible than those involving higher levels of selection. Thus, using this principle higher levels of selection, such as group selection are never used as an explanation for the evolution of a trait unless there are no possible explanations involving selection at a lower level.

Thus, central to using the adaptationist approach to study higher level selection is the focus on altruistic traits, that is traits that are opposed by individual selection, but favored by selection occurring at some higher level. It is this focus on the evolution of altruism that is central to the concept of kin selection. The term kin selection was first introduced by Maynard-Smith (1964) as an alternative to group selection, which was considered to be, at most, a minor force for evolutionary change. The core concepts of kin selection are embodied in Hamilton's equation (Hamilton 1964a, b):

$$\frac{\text{cost}}{\text{benefit}} < r, \quad (1)$$

where *cost* is the reduction in fitness an individual experiences by expressing a trait or performing a behavior, *benefit* is the increase in fitness that others receive as a result of this trait or behavior, and *r* is the degree of relatedness (between 0 and 1) between the

individual expressing the trait and the recipients of the benefit.

The genetical approach

The genetical approach comes from a very different, experimentally based tradition. It can most usefully be traced to the modern synthesis, and particularly Sewall Wright's shifting balance theory (Wright 1968, 1977). In contrast to the adaptationist approach it is the process of adaptation, rather than the resulting patterns of traits that are of interest.

As an example, consider experimental studies of group selection. There has been a growing number of such studies (Table 1). Table 1 also lists the traits that were the subjected to the group selection treatments. Notice that these traits cannot easily be related to the altruistic traits that are central to the adaptationist approach. Indeed the study of Goodnight (1985) is instructive. In this study populations consisted of 16 *Arabidopsis thaliana* growing in an array in sterile agar. Each treatment was a set of nine such populations, and the trait measured was leaf area. In this experiment there were three "group selection" treatments, group selection for high leaf area, group selection for low leaf area, and a "no group selection" treatment. In the group selection for high leaf area the mean leaf area for each of the nine populations was determined, and the three populations with the highest leaf area were selected to found the next generation. The remaining six populations were discarded. The group selection for low leaf area was identical, except that the three populations with the lowest mean leaf area were selected. In the no group selection treatments three populations were selected randomly to found the next generation. The individual selection treatments were similar in that within each population the eight individuals with the highest leaf area (individual selection for high leaf area), lowest leaf area (individual selection for low leaf area), or a randomly selected sample of eight individuals (no individual selection) were selected to serve as parents in the next generation. Each surviving population founded three offspring populations, and within each surviving population each surviving individual served as a parent for two offspring in each population. These group and individual selection treatments were combined in a factorial manner for a total of nine different selection treatments. In addition there was a series of environmental variation treatments; these will not be discussed in this paper.

The trait used in this study, leaf area, was chosen because it was easily measured, and of biological significance. In the context of the experiment there were certain treatment combinations that could be considered altruistic in the sense that group and individual selection were acting in opposite directions. An example of treatments in which leaf area was effectively altruistic trait are treatments in which there was group selection

Table 1 Laboratory studies of group selection. All studies detected a significant response to group selection

Study	Organism	Trait	Special features
Wade (1977)	<i>T. castaneum</i>	Population size	First experimental study of group selection
Wade (1980)	<i>T. castaneum</i>	Population size/cannibalism rate	Investigated the role of population structure in the response to selection
Wade and McCauley (1980)	<i>T. castaneum</i>	Population size	Effects of propagule size and random extinction on population differentiation
Craig (1982)	<i>T. castaneum</i>	Emigration rate	Replicated group selection treatments, explicit individual selection treatment
Wade (1982)	<i>T. castaneum</i>	Population size	Effects of migration on population differentiation
McClintock (1984)	Domestic rat	Male mating behavior	Documents probable group selection in male cooperation in mating
Goodnight (1985)	<i>A. thaliana</i>	Leaf area	First group selection in plants, factorially combined group and individual selection treatments
Wade (1987)	<i>T. castaneum</i>	Competitive ability	Interdemec selection for competitive ability
Goodnight (1990a, 1990b)	<i>T. castaneum</i> , <i>T. confusum</i>	Population size, emigration rate	Selection on two species communities, demonstration of contribution of genetic interactions among individuals
Wade and Goodnight (1991)	<i>T. castaneum</i>	Population size	Group selection by differential migration
Muir (1996)	Chickens	Egg production	Group selection in vertebrates, first commercial use of group selection in animals.
Swenson et al. (2000)	Microbial communities	Growth of a test plant, pH	Community selection in undefined species rich microbial communities

for low leaf area and individual selection for high leaf area. However, for other treatments no such categorization is possible. Because this was a manipulative study the effects of group selection could be detected even in treatment combinations where it was acting in concert with individual selection (e.g., group and individual selection for high leaf area). It is because of this focus on group selection as an applied treatment that altruism plays such a small role in the genetical approach to multilevel selection.

Group selection and interactions among individuals

One of the fascinating results of the group selection experiments listed in Table 1 is that without exception there was a significant response to group selection. Furthermore, although it is difficult to assign an expected response to group selection, the observed responses were always greater, and often far greater, than intuition based on classical models would suggest (Goodnight and Stevens 1997).

Several studies have examined potential reasons why group selection is so effective. In a review of models of group selection Wade (1978) listed a number of possible explanations, two of which stand out. First, early models of group selection assumed a migrant pool, whereas in his experiment Wade used a propagule pool. In a migrant pool model, after groups are selected to form the next generation the individuals are combined and randomly assigned to new groups, preventing multi-generation population differentiation. The propagule pool keeps groups intact, allowing multi-generation population differentiation to occur (Wade 1978). Second,

nearly all models of group selection assume additive effects. However, population size in *Tribolium* is determined by both additive and nonadditive components (Park 1948; Wade 1976, 1977; Goodnight and Stevens 1997). Although Wade did not examine the genetic basis of population size differences, it is likely that dominance, epistasis, and particularly genetically based ecological interactions among individuals contributed to the observed response. Wade (1978) suggested that propagule pool based group selection would be very effective when the genetic response involved nonadditive effects, whereas individual selection would be ineffective at selecting on gene interactions.

Empirical studies support Wade's (1978) suggestion. Goodnight (1990a, b) examined the response to community level selection in two species communities of *T. confusum* and *T. castaneum* (Fig. 2). Four traits were measured on each community, population size in *T. castaneum*, population size in *T. confusum*, emigration rate in *T. castaneum* and emigration rate in *T. confusum*. In each treatment selection for increased or decreased value for one trait was applied (e.g., selection for increased population size in *T. confusum*). There were a total of eight selection treatments (selection up or down for each of four traits), and there were two replicates of each treatment. As with all other multilevel selection experiments, Goodnight (1990a) observed a significant response to community level selection. An important feature of using a two species community, however, is that the communities can be experimentally broken up to examine the role of interspecies interactions. Goodnight (1990b) did this by applying three treatments. In the first treatment the intact communities were measured. In the second treatment the communities

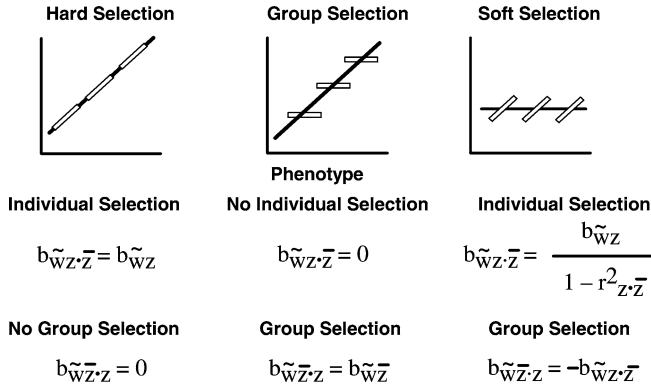


Fig. 1 The three models of selection examined by Goodnight et al. (1992). Each graph represents the relationship between relative fitness and phenotype within groups (*white lines*) and among group means (*black lines*). In the hard selection model fitness is determined solely by individual phenotype, however the relationship between group mean relative fitness and group mean phenotype will be parallel to the within group relationship. In the group selection model there is no relationship between relative fitness and phenotype within groups, but there is a positive relationship between group mean relative fitness and group mean phenotype. In the soft selection model there is a positive relationship between individual relative fitness and individual phenotype within groups. Among groups the relative fitness is constrained and there is no relationship between mean group relative fitness and mean group phenotype. Using contextual analysis it can be shown that for hard selection the partial regression of relative fitness on individual phenotype holding group phenotype constant ($b_{\tilde{W}Z \cdot Z}$) is equal to the simple regression of relative fitness on individual phenotype ($b_{\tilde{W}Z}$), indicating that individual selection is acting. Conversely the partial regression of relative fitness on group phenotype holding individual phenotype constant ($b_{\tilde{W}Z \cdot Z}$) is zero, indicating no group selection is acting. Similar logic can be used to show that in the group selection model there is no individual selection acting ($b_{\tilde{W}Z \cdot Z} = 0$), but there is group selection ($b_{\tilde{W}Z \cdot Z} = b_{\tilde{W}Z}$, where $b_{\tilde{W}Z}$ is the simple regression of relative fitness on group mean phenotype). Contextual analysis shows that the soft selection model has elements of both individual and group selection. Selection at the individual level is equal to the simple regression modified by the fraction of the total variance that is within groups ($1 - r_{Z \cdot Z}^2$), and group selection is equal and opposite in sign to individual selection

were separated into two single species populations, and the four traits measured on the single species populations. In the third treatment the communities were again broken up into single species populations, but a naive test strain of the opposite species was added. This third treatment was ecologically identical to the intact community—the same number of both species were added to found the community—however, the genetic structure was disrupted since one of the species was from the naive test strain.

The results of this study were dramatic. As expected there was a significant difference in the up and down selection lines for all four traits in the intact communities (first treatment). This confirmed that the communities did respond to community level selection. In the single species populations (second treatment), however, there were no significant differences between any of the selection lines, indicating that when the ecological

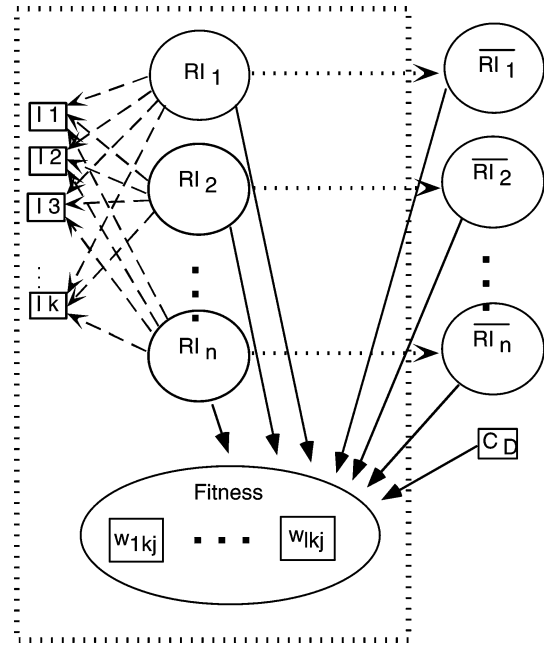


Fig. 2 In the study of Stevens et al. (1995) a large number of traits were measured, including number of leaves on different dates, plant height on several dates, internode length at different dates, date of emergence of the first true leaves, and measures of leaf senescence. Because of the large number of phenotypic traits measured a path analytic approach was deemed more appropriate than a standard regression approach (Crespie and Bookstein 1989). The path diagram used in this study is shown. CD is the contextual trait (density) and I1–Ik are the individual traits. Factors enclosed in *circles* are unmeasured (and unmeasurable) underlying factors. Factors enclosed in *boxes* are measured traits. Uncorrelated error terms (left out for clarity) should be included for all of the measured traits. The *solid arrows* indicate the regressions of the fitness components on the underlying factors. The *dashed lines* are the loadings of the measured traits in the rotated principal components analysis and were used to determine the underlying group and individual factors. The *dotted lines* indicate that the group factors are the group means of the individual factors (see Stevens et al. 1995 for a more complete description)

structure of the two species communities was disrupted the response to selection disappeared. In the reconstructed communities with one selected strain coupled with a test strain the results were more complex. For emigration rate in both species the response to selection was restored in the reconstructed communities indicating that for this trait the ecological structure, but not the genetic structure of the community was important. For population size in both species there were no differences between selection treatments. This indicates that the response to selection on population size was dependent on both the ecological and the genetic structure of the community. This is very strong evidence that genetically based interactions between species are contributing to the response to community selection. Since this is an interspecies interaction individual selection cannot act on this interaction, thus confirming Wade's (1978) suggestion that higher level selection can act on sources of genetic variance that is not available to lower levels.

Contextual analysis

The genetical approach has also been applied to observational field studies. In these studies the goal is to observe within generational change in mean phenotypes that are due to selection occurring at multiple levels. The basic approach is drawn from studies of individual selection in the field (e.g. Arnold and Wade 1984; Lande and Arnold 1982). Using the approach developed by Arnold and Wade, a series of morphological, behavioral and physiological traits of interest are measured on an individual. In addition, a measure of fitness is also measured. For example, in a study of sexual selection in bullfrogs Arnold and Wade (1984) used snout vent length as a morphological trait, and mating success as a fitness measure. A regression of the morphological trait on the fitness measure, and a significant regression is interpreted as individual selection acting on the trait. In the Arnold and Wade (1984) study a significant regression of body size on number of mates was interpreted to mean that there was significant sexual selection favoring larger males. Heisler and Damuth (1987) extended this idea by pointing out that ANY trait can be included in a selection analysis, and proposed that this logically includes traits measured on groups. This approach, termed contextual analysis was used by Goodnight et al. (1992) to examine several theoretical models of selection. For each model they examined they assumed a population structure of a set of groups each with the same number of individuals. Fitnesses were assigned based on the model of selection, and the relationship that that model implied to an arbitrary trait, Z . The particular models examined were hard selection, group selection, and soft selection (Fig. 1). In the hard selection model the fitness of an individual was solely determined by its phenotype independent of group membership. Intuition suggests that this should be solely individual selection, and Goodnight et al. (1992) showed that contextual analysis correctly identified this as individual selection with no group selection acting. In the group selection model fitness of an individual was assigned based solely on the mean phenotype of the group. The individual phenotype only affected fitness to the extent that it contributed to the group mean phenotype. In accordance with intuition, contextual analysis correctly identified the group selection model of fitness as group selection with no individual selection acting. Finally, in the soft selection model each group was assumed to produce the same number of offspring, that is, group productivity was constrained so that there was no variation in group mean fitness. Within groups, however, fitness was assigned based on the phenotype of the individual relative to other members of the same group. This is the interesting situation where the fitness of an individual is dependent on the mean phenotype of the group, suggesting that there should be group selection, however, because there is the lack of variation among groups in output suggests that no group selection is acting (Wade

1985). In this case contextual analysis detected both group and individual selection acting, but in equal and opposite directions. That is, the lack of variation in mean group fitness occurs because group selection is acting to constrain the increase in fitness due to individual selection.

Stevens et al. (1995) used contextual analysis in a field study of *Impatiens capensis*, and were able to show that group selection was occurring in this system. In this study a natural population of *I. capensis* was used. Unlike traditional models of group selection these populations were continuous with no clear boundaries between groups. Stevens et al. (1995) examined neighborhoods of increasing size around focal individuals and determined that plants further than 0.25 m away from an individual had little influence on fitness. For this reason contextual traits based on the individuals within 0.25 m an individual were used in the study. The important result from this aspect of the study is that groups need not be discrete entities. Rather, groups are defined by interactions and their effect on fitness. It is for this reason that Stevens et al. (1995) suggested that multilevel selection was preferable to the term group selection when using contextual analysis. Importantly, this aspect of the results demonstrates that from a mathematical perspective group selection in a system with discrete groups is no different than multilevel selection in a continuous population with overlapping neighborhoods of interaction.

In this study three measures of fitness were made, number of chasmogamous (open) flowers, number of cleistogamous (closed, self-pollinated) flowers, and survivorship. In addition to the fitness measures, a large number of morphological traits were measured and the number of plants within 0.25 m counted (see Stevens et al. 1995 for a full description). Because of the large number of traits measured, a path analytic approach similar to that proposed by Crespie and Bookstein (1989) was used (Fig. 2). This emphasizes that contextual analysis is a multilevel selection generalization of standard selection analysis theory, and that extensions of standard selection theory can be readily applied to contextual analysis. Fig. 3 shows the results of this analysis for the first factor, which appears to be a measure of size. The different fitness measures are considered separately since they do measure very different components of fitness. This analysis shows that there is strong individual selection on chasmogamous flowering, and for survivorship, larger plants produce more flowers and survive better, but no influence of the contextual traits, and therefore, no group selection. For survivorship there is a trend suggesting group selection, but this is not significant. For cleistogamous flowering there is a very different story in that there is both significant group and individual selection acting, and interestingly these are equal and approximately opposite in sign. This is an example of soft selection, as discussed above. Interestingly, it is also an example of the constant yield law in which over a wide range of planting densities many plants produce a constant yield per hectare (e.g., Harper

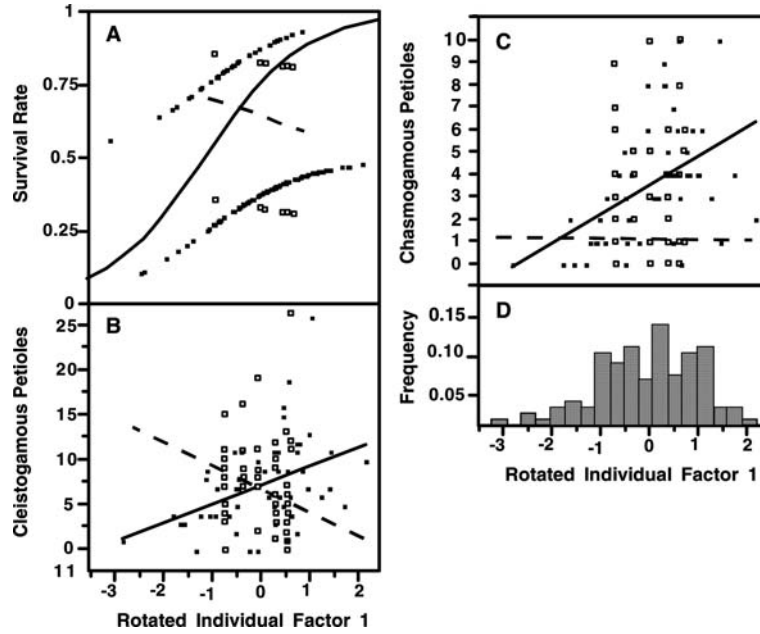


Fig. 3 The correlation of “size” (RF1, $\overline{\text{RF1}}$) with **a** probability of survival rate to first reproduction, **b** number of cleistogamous petals **c** number of chasmogamous petals in 1990. The *solid line* is the log linear regression of the fitness component on the individual trait (RF1). The *dashed line* is the regression of the fitness component on the group trait ($\overline{\text{RF1}}$). *Filled squares* are individual values and *open squares* are group values. The frequency distribution of the RF1 for all individuals in the study is shown in **(d)**. A significant regression indicates selection is acting; thus, individual selection favors large values of RF 1 (large size, see text) for all three traits and group selection favors small values of for both survival rate and cleistogamous petals

1977). Importantly, the results of this paper are consistent both with theoretical expectation (e.g., Goodnight et al. 1992) and the results of other work on *Impatiens* (e.g., Mitchell-Olds 1986; Mitchell-Olds and Bergelson 1990).

Although contextual analysis is a potentially powerful method of analyzing multilevel selection both from a theoretical and experimental perspective, it is important to recognize that as is generally true for regression based selection analysis methods it only measures within generation change. Thus, even if we detect significant selection acting on a contextual trait the trait may nevertheless not respond to selection for genetic reasons. That is, if the heritability of a trait is near zero than selection on that trait will not lead to a response. This issue potentially becomes a serious problem for multilevel selection because the expression of contextual traits frequently depends on interactions among individuals and the population structure, thus, they likely to be less stable than the Mendelian genetics of individual traits. On the other hand, as discussed above, contextual traits may be strongly influenced by interactions among individuals, which has the effect of potentially strongly increasing the heritability of contextual traits, provided the population structure is appropriate. Experimental studies have shown that higher-level selection is

very effective in the laboratory, and field experiments have shown that multilevel selection is acting within generations in nature. Whether the multilevel selection in nature is leading to a response to selection as predicted in the laboratory has yet to be experimentally addressed.

Contextual analysis and the evolution of altruism

Although contextual analysis is a statistical method firmly based within the genetical approach to the study of multilevel selection, it nevertheless can be applied to the discussion of kin selection and the evolution of altruism. To do this, recognize that an altruistic trait increases the fitness of other individuals in a group at the expense of the altruistic individual, as a consequence altruism is opposed by individual selection and favored by group selection. This means that the partial covariance between relative fitness and the individual trait, $\text{cov}(\tilde{w}, z \bullet \bar{z})$, and the partial covariance between relative fitness and the group trait, $\text{cov}(\tilde{w}, \bar{z} \bullet z)$, are of opposite sign. A partial covariance can be interpreted as the covariance between a trait and relative fitness holding the second trait constant, that is, the covariance independent of the effects of other trait. If z represents the degree of altruism, $\text{cov}(\tilde{w}, z \bullet \bar{z})$ will be negative and $\text{cov}(\tilde{w}, \bar{z} \bullet z)$ will be positive. Furthermore, $\text{cov}(\tilde{w}, z \bullet \bar{z})$ equals the within generation change in mean phenotype due to individual selection, and $\text{cov}(\tilde{w}, \bar{z} \bullet z)$ equals the within generation change in mean phenotype due to group selection (Arnold and Wade 1984; Goodnight et al. 1995). Using this logic, the average degree of altruism will increase within a generation when the absolute value of the partial covariance between the trait relative fitness is less than the partial covariance between the group mean of the trait and relative fitness:

$$|\text{cov}(w, \bar{z} \bullet z)| > |\text{cov}(w, z \bullet \bar{z})|. \quad (2)$$

Squaring both sides, and after some algebra this becomes:

$$\frac{(r_{wz} - r_{w\bar{z}}r_{z\bar{z}})^2}{(r_{w\bar{z}} - r_{wz}r_{z\bar{z}})^2} < r_{z\bar{z}}^2, \quad (3)$$

where r_{wz} and $r_{w\bar{z}}$ are the correlation between relative fitness and the individual and group level trait respectively and $r_{z\bar{z}}^2$ is the fraction of variance among groups. The squared correlation between fitness and the individual trait with the effects of the group trait removed, $(r_{wz} - r_{w\bar{z}}r_{z\bar{z}})^2$, is a measure of the strength of individual selection, and the equivalent to the cost in Hamilton's equation. Similarly, $(r_{w\bar{z}} - r_{wz}r_{z\bar{z}})^2$ is a measure of the strength of group selection and the equivalent of the benefit in Hamilton's equation. I have left this equation in the squared form because the squared correlations are equal to the fraction of the variance due to that effect. For example, $(r_{wz} - r_{w\bar{z}}r_{z\bar{z}})^2$ is the fraction of the variance in fitness that is due to individual selection, and $(r_{w\bar{z}} - r_{wz}r_{z\bar{z}})^2$ is the fraction of the variance in fitness due to group selection. Clearly the square root of the equation above would also hold, however, the relationships to variance components would no longer be as interpretable.

It is worth discussing $r_{z\bar{z}}^2$ in more detail. Although this is analogous to the relatedness in Hamilton's rule, the fraction of variance among populations is not necessary equal to relatedness. Relatedness is only one of many factors that can generate a variance among populations. Other factors that could potentially contribute to variance among groups are culture and behaviors enforcing conformity, shared diseases and symbionts, and changes in the local environment, such as depleting a food resource (Slobodkin 1974). Culture is probably most important in higher vertebrates, including humans, that are capable strong social structures and parental care, but is potentially important in any organism capable of learning. Behaviors enforcing conformity, such as policing behavior in bees (Ratnieks and Visscher 1989; Visscher 1996), are similar to culture in that they enforce within group conformity, and as a consequence increase the fraction of the total variance that is among groups. Shared diseases, symbionts, and environmental changes are interesting in that it is another species or external factor that is causing the members of a group to be similar. Nevertheless, if the members of the same group jointly modify their environment, or tend to preferentially infect each other this may be sufficient to magnify the differences among groups. Also, these factors may interact. For example, for many cockroaches and termites newly emerged adults obtain an infection of symbiotic protists by feeding on the hindgut fluids of a nestmate (Thorne 1997). Thus, a behavioral interaction results in members of the same colony sharing symbionts. Both the behavioral interaction of sharing and the resulting shared symbionts could act to enforce within group conformity and magnify among group differences.

Gene interactions such as epistasis and dominance can also increase the variance among populations. Goodnight (1987, 2000, Fig. 4) showed that all forms of gene interaction contribute to the variance among populations. This contribution to the variance among demes is particularly strong for additive by additive epistasis and additive by dominance epistasis. Dominance and dominance by dominance epistasis only contribute to the variance among demes at intermediate levels of inbreeding (see Goodnight 2000 for details). This is important in the context of Hamilton's rule because Hamilton's assumption that the important metric for comparing costs and benefits was relatedness. This works in an additive system because relatedness (measured by f), is linearly related to the variance among demes (Goodnight 2000). In the case of gene interaction this is not true. For example, additive by additive epistasis the relationship is concave upwards, and ultimately this component of genetic variance that does not contribute to evolution within groups can have a proportionately larger contribution than additive variance to the response to group selection.

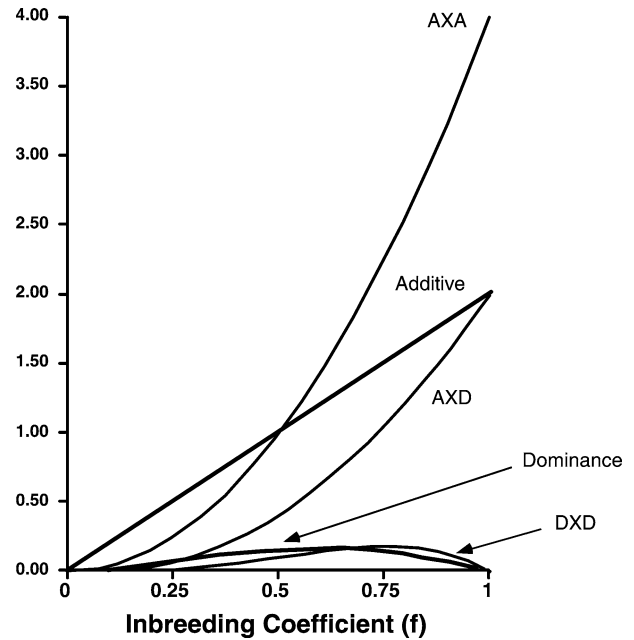


Fig. 4 The variance among groups due to different forms of one and two locus genetic interactions as a function of inbreeding coefficient. All variances are shown relative to the variance in the base population. For additive effects the relationship between inbreeding coefficient (analogous to relatedness) and variance among groups is linear. For other genetic effects it is non-linear. Dominance and Dominance \times Dominance epistasis contribute little to the variance among groups, whereas additive \times additive epistasis and additive \times dominance epistasis contribute strongly to the variance among groups, even though they do not contribute to a response to individual selection within groups. *Additive* additive genetic variance, *Dominance* dominance genetic variance, *A* \times *A* additive by additive epistasis; *A* \times *D* additive by dominance epistasis, *D* \times *D* dominance by dominance epistasis

Hamilton's rule and the response to selection

As discussed above, One limitation of contextual analysis and all regression based selection analysis methods in general is that they are designed to detect changes due to selection within generations. The detection of a significant selection pressure does not guarantee that a response to selection will occur. Hamilton's (1964a) original formulation of his model avoided this issue by assuming a direct relationship between genotype and phenotype. Thus, effectively in his models the heritability was 1.

The issue of heritabilities becomes particularly important for studies of multilevel selection and the analysis of Hamilton's rule. In the language of contextual analysis group level traits and individual level traits are considered to be different traits, even if they are as simple as the trait and the group mean of the trait. The view that they are separate traits is actually quite important, as the genetic basis of the traits at the two levels may be substantially different. For example, as discussed above, the group level trait may have genetically based interactions among individuals contributing to its heritability, something that will be environmental variation at the individual level. As a consequence, whether altruism evolves depends on whether or not the response to group selection is stronger than the response to individual selection, that is, it becomes a competing rates problem. The response to selection is a function of both the strength of selection and the heritability of the traits. That is, when considering the response to selection it is important to include not only the within generation selection but also the heritability and the possibility of correlated responses to selection. Thus, altruism will evolve if:

$$\left| \left(h_z^2 \left((\text{cov}(\tilde{w}, \bar{z} \bullet z)) + r_A \frac{\sigma_{A(\text{grp})}}{\sigma_{A(\text{ind})}} \text{cov}(\tilde{w}, z \bullet \bar{z}) \right) \right) \right| > \left| \left(h_z^2 \left((\text{cov}(\tilde{w}, z \bullet \bar{z})) + r_A \frac{\sigma_{A(\text{ind})}}{\sigma_{A(\text{grp})}} \text{cov}(\tilde{w}, \bar{z} \bullet z) \right) \right) \right|, \quad (4)$$

where r_A is the additive genetic correlation between the altruistic trait as measured at the group level and the altruistic trait as measured at the individual level, $\sigma_{A(\text{grp})}$ the additive genetic standard deviation for the group trait, and $\sigma_{A(\text{ind})}$ is the additive genetic standard deviation for the individual trait. Each side of this equation has two components. The first component, $(\text{cov}(\tilde{w}, \bar{z} \bullet z))$ and $(\text{cov}(\tilde{w}, z \bullet \bar{z}))$ represents the direct effects of group and individual selection respectively, and the second component, $(r_A (\sigma_{A(\text{grp})} / \sigma_{A(\text{ind})}) \text{cov}(\tilde{w}, z \bullet \bar{z}))$ and $(r_A (\sigma_{A(\text{ind})} / \sigma_{A(\text{grp})}) \text{cov}(\tilde{w}, \bar{z} \bullet z))$ represents the correlated effects of selection at the group level due to selection at the individual level and vice versa. This emphasizes that in the language of contextual analysis the altruistic trait expressed at the group level is considered to be a different trait, but correlated

than the trait expressed at the individual level. Also, for the type of trait normally modeled as altruistic the correlation between the group level trait and the individual level trait will be negative. That is, selection increasing the individual trait of selfishness will decrease the group trait of altruism. The correlated response portion of the equation will generally be negative, and thus act to decrease the overall response at that level.

In analogy to the equation for contextual analysis, and assuming that group and individual selection are acting in opposition this can be rearranged to become:

$$\frac{h_{\text{grp}}^2}{h_{\text{ind}}^2} > \frac{\text{cov}(\tilde{w}, z \bullet \bar{z}) + r_A (\sigma_{A(\text{grp})} / \sigma_{A(\text{ind})}) \text{cov}(\tilde{w}, \bar{z} \bullet z)}{\text{cov}(\tilde{w}, \bar{z} \bullet z) + r_A (\sigma_{A(\text{ind})} / \sigma_{A(\text{grp})}) \text{cov}(\tilde{w}, z \bullet \bar{z})}. \quad (5)$$

This is similar to the contextual analysis formulation, with the left hand side being the ratio of heritabilities rather than the variance among groups, and the right hand side being the ratio of the change in the trait at the individual level due to both direct and indirect selection to the change in the trait at the group level due to both direct and indirect selection.

Although this equation is structurally similar to the contextual analysis version of Hamilton's rule, it is not identical. Importantly the ratio of heritabilities on the left side of the equation is not the fraction of variance among demes, and can potentially become a ratio greater than 1. If there are only additive effects contributing the altruistic trait then $h_{\text{grp}}^2 / h_{\text{ind}}^2$ represents the correlated effects of selection at the group level due to selection at the individual level and vice versa. This emphasizes that in the language of contextual analysis the altruistic trait expressed at the group level is considered to be a different trait, but correlated than the trait expressed at the individual level. Also, for the type of trait normally modeled as altruistic the correlation between the group level trait and the individual level trait will be negative. That is, selection increasing the individual trait of selfishness will decrease the group trait of altruism. The correlated response portion of the equation will generally be negative, and thus act to decrease the overall response at that level.

This last point is critical. If $h_{\text{grp}}^2 / h_{\text{ind}}^2$ is greater than 1 then altruism can evolve even if selection in favor of the trait is weaker than selection opposing it. Thus, even if the advantages to cheating greatly outweigh the benefits of being an altruist this may not evolve if there are social behaviors such as policing behavior that enforce within group uniformity and therefore reduce the individual level heritability to near 0. Notice that interestingly in this case the policing behavior itself would contribute to increasing the group level heritability for the altruistic trait (among group variation in level of policing would be directly related to the mean level of altruism in the group). Epistasis or other forms of gene interaction could have the same effect. Additive by additive epistasis contributes disproportionately to the variance among groups, and therefore the group level heritabilities, but

in general it does not contribute to the heritabilities at the individual level (although it may through the process of conversion of epistasis into additive genetic variance (Goodnight 1995)).

Conclusions

Hamilton's (1964b, b) landmark papers are rightly recognized as the formal basis for our understanding of the evolution of altruistic traits that are advantageous to groups, but decrease individual fitness. This equation has served as the basis for the adaptationist approach to studying multilevel selection, and has provided huge insights into the evolution of social behavior. However, it must be recognized that Hamilton's equation as he originally expressed it, is simplistic.

The genetical approach provides insights into how the terminology and assumptions used by Hamilton can be relaxed to incorporate the results of experiments on multilevel selection. Using contextual analysis I demonstrated that Hamilton's rule actually embodies three distinct processes, group selection, individual selection, and transmission genetics or heritability. Whether an altruistic trait will evolve depends the balance of all of these factors. The genetical approach, and particularly, contextual analysis provides a means of separating these factors and examining them one at a time.

Perhaps the greatest issue with Hamilton's equation is the interpretation of r . Hamilton (1964a) interpreted this as relatedness. Contextual analysis shows that the r of Hamilton's equation is the proportion of variance among groups. In a system where group differentiation is determined entirely by additive gene action then the proportion of variance among groups is directly proportional to relatedness, and Hamilton's original formulation works. If there are complications such as interactions among individuals, or nonadditive gene action then the differentiation among populations will generally be greater than predicted by the relatedness. Perhaps more importantly, if the question is the evolution of altruism it is necessary to consider not only the strength of selection, but also the heritability of the group and individual level traits, and the genetic correlation between them. In Hamilton's original formulation he implicitly assumed that the heritability at both levels was 1. In extending the contextual analysis formulation to examine the response to selection the analogue to Hamilton's r becomes the ratio of heritabilities at the group and individual level. In an additive world with traits solely determined by genetics with no environmental effects this ratio will equal the relatedness. In systems with social interactions or nonadditive gene action this need not be true. Importantly, if there are strong interaction effects the ratio of group heritability to individual heritability may exceed 1. If this is the case than altruism can evolve even if selection at the group level is weaker than selection at the individual level.

Much remains to be done on this subject. For example, we really do not have a good understanding of what contributes to group heritability, how to measure it, or even how to define it. This is particularly true for the most interesting situations where selection is acting among contiguous neighborhoods, rather than among discrete groups. Nevertheless, although the genetical approach has not generally been concerned with the evolution of altruism, many of the insights from this approach to studying multilevel selection can provide insights into the interpretation of Hamilton's rule.

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