

EXPERIMENTAL STUDIES OF GROUP SELECTION: WHAT DO THEY TELL US ABOUT GROUP SELECTION IN NATURE?

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Abstract.—The study of group selection has developed along two autonomous lines. One approach, which we refer to as the adaptationist school, seeks to understand the evolution of existing traits by examining plausible mechanisms for their evolution and persistence. The other approach, which we refer to as the genetic school, seeks to examine how currently acting artificial or natural selection changes traits within populations and focuses on current evolutionary change. The levels of selection debate lies mainly within the adaptationist school, whereas the experimental studies of group selection lie within the genetic school. Because of the very different traditions and goals of these two schools, the experimental studies of group selection have not had a major impact on the group selection debate. We review the experimental results of the genetic school in the context of the group selection controversy and address the following questions: Under what conditions is group selection effective? What is the genetic basis of a response to group selection? How common is group selection in nature?

Experimental and theoretical studies of multilevel selection trace their origin to the work of Sewall Wright (1931, 1977) and his shifting balance theory. They actually antedate what is usually considered the origin of the modern and principally conceptual (Harrison and Hastings 1996a) thinking on group selection, namely, Wynne-Edwards's (1962) book *Animal Dispersion in Relation to Social Behavior* and the subsequent controversy that it generated. Why have the older theoretical and more recent experimentally oriented studies of multilevel selection had such a minor impact on the ongoing levels of selection controversy?

We suggest that there are two philosophies concerning multilevel selection: the adaptationist school and the genetic school. Differences in topics of interest, and consequently language, have kept the two schools distinct. Experimental studies from the genetic school may be overlooked because they address issues not typically of interest to the adaptationist school, which has housed the majority of the group selection debate. The experimental studies resolve some of the major controversies about group selection, provide insight about the importance of group selection in natural populations, and suggest novel evolutionary consequences of higher-level and multilevel selection. These contributions suggest

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that the synthesis of these two schools will further our understanding of organic evolution.

the adaptationist school

We refer to the more widely known tradition for studying group selection as the adaptationist school. The adaptationist school can be traced to Darwin's discussion of the evolution of sterile castes in insects, family selection (Darwin 1859), and cooperation in human societies (Darwin 1871). It was further developed by evolutionary biologists in the 1930s and 1940s (e.g., Allee et al. 1949). Wynne-Edwards (1962) advocated wholesale invocation of group selection as an explanation for apparently altruistic adaptations, that is, traits that benefit the group but reduce the fitness of the performer. The embrace of group selection was followed by a call to view group selection with suspicion (Maynard Smith 1964, 1976; Williams 1966) and subsequent rejection of group selection as an important evolutionary force. The adaptationist school focuses on observing existing phenotypes such as adaptive behaviors and hypothesizing plausible evolutionary mechanisms for their existence. For example, Wynne-Edwards (1962) was interested in population regulation and why many species are near what he considered an optimal density.

To explain the evolution of standing adaptations, one looks at patterns and attempts to infer process. Many potential evolutionary pathways for a particular trait exist. Some pathways involve individual selection, whereas others may involve higher levels of selection or selection acting simultaneously at multiple levels. Indeed, the possible pathways seem to be limited only by the biologist's imagination. The adaptationist school seeks to choose the most plausible pathway from all of the possible pathways, and rules are needed for deciding the most likely pathway. Many rules are implicit (e.g., explanations relying on divine intervention are dismissed in scientific discussions); however, others are explicit. One early rule for explaining adaptations was the principle of parsimony (Williams 1966): "In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations, unless the evidence clearly shows that this theory does not suffice" (p. 5). Parsimony is a valid rule and provides a clear ranking of the appropriateness of explanations. The principle of parsimony as described by Williams is primarily of interest because of its role in the group selection debate during the late 1960s and early 1970s. More recently, there has been a growing recognition of the limitations of this definition (e.g., Wilson 1983; Wilson and Sober 1989, 1994); nevertheless, Williams's principle serves as an example of the kinds of rules that are needed to explain adaptations *post hoc*.

As the adaptationist school has become more refined, Williams's principle of parsimony is no longer seen as the best guide for deciding among explanations for the evolution of a trait (Wilson 1983; Wilson and Sober 1989, 1994). This is particularly evident in discussions of sex ratio evolution (Wilson and Colwell 1981), but it can also be found in the discussion of the evolution of other traits.

Nevertheless, the adaptationist school remains focused on explaining the evolution of altruistic traits (Wilson 1983; Wilson and Sober 1989).

the genetic school

The genetic school traces its origins to the modern synthesis, particularly Wright's shifting balance theory (Wright 1931, 1977). Wright was interested in the general problem of evolution in structured populations, and group selection is an implicit element of these models (Wright 1945). The genetic school is experimentally oriented, with experiments derived from the field of quantitative genetics. It focuses on processes, such as changes in the distribution of phenotypes over generations, rather than the level of biological organization at which traits are adaptive (see also Griesemer and Wade 1988).

Unlike the central role it plays in the adaptationist school, the evolution of altruism is not explicitly considered by the genetic school. Because investigators often focus on the response to artificial selection, group selection and individual selection can be examined separately and together and acting in concert as well as in opposition. Traits are frequently chosen for particular properties, such as convenience or those that are likely to exhibit gene interaction, rather than any tendency to be altruistic. When group selection is artificially imposed as an experimental treatment, a statistically significant effect of the group selection treatments indicates that group selection is effective.

The genetic school investigates the quantitative genetic basis of the response to multilevel selection. Wright (1968, 1977) hypothesized that gene interaction (dominance and epistasis) were an integral and driving force behind the effectiveness of interdemographic selection. As a consequence, genetically based interactions both within and among individuals are considered in the response to higher levels of selection. The emphasis on gene interaction stands in contrast to that of the adaptationist school, which often assumes single gene additive effects when genetic mechanisms are even considered. The consideration of additive versus nonadditive gene effects in the response to selection contributes to the different conclusions about the relative importance of group selection in nature.

Finally, within the genetic school there has been a tendency to broaden the definition of group selection to include selection at any level above the individual. Many situations in which both population structure and individual fitness are influenced by neighbors are mathematically related to group selection.

Both schools are important avenues for investigating multilevel selection. The adaptationist school is oriented toward examining ecologically and evolutionarily important traits and explaining their evolution and persistence. It is the only approach available for studying the evolution of many important traits. However, it is difficult to eliminate alternative explanations for the evolution of a trait. The genetic school examines the process of selection and the (short-term) evolutionary change that results from selection. It is not restricted by the rules that govern the adaptationist school, and it allows examination of multilevel selection. Its weaknesses lie in the difficulty of applying experimental approaches to many ecologically important traits and organisms that do not lend themselves

to experimental manipulation. Traits that are no longer subject to the selection pressures that originally led to their evolution cannot be examined using this approach. Thus, the two schools are complementary and interdependent.

quantitative genetics and the genetic school

Experimental studies of group selection lie firmly within the genetic school. All of the researchers working on experimental group selection studies are trained as quantitative geneticists. As a consequence, quantitative genetic thinking has had a major influence on the genetic school. The influence can be elucidated by referring to an equation from quantitative genetics describing selection and its evolutionary consequences,

$$R = h^2 S, \quad (1)$$

where R is the response to selection, h^2 is heritability, and S is the selection differential (Falconer 1989). When selection acts on the individual, $h^2 = V_a/V_p$, the proportion of the phenotypic variance, V_p , that results from additive gene effects, V_a . Only additive gene effects contribute to the response to individual selection (Fisher 1958).

Equation (1) partitions evolution by natural selection into two components, S and R . Component S is the change in the mean phenotype of a population as a result of selection within a generation. Thus, S defines an ecological process by which, because of differences in phenotype, some individuals have higher fitness (produce more offspring) than do other individuals. Heritability (genetic effects) does not enter into S . The second component, R , the response to selection, is the change in the mean phenotype of a population between generations. Thus, R defines an evolutionary process by which the change within generations is translated into changes between generations. In standard quantitative genetics, the constant of proportionality is h^2 , a parameter between 0 and 1 describing the proportion of the phenotypic variance that contributes to the response to selection. Although equation (1) was developed for individual selection, it provides a conceptual framework that separates the ecological process of group selection from the evolutionary consequences of group selection.

The power of separating selection from the response to selection is that the difficult question of how often group selection in nature leads to evolutionary change can be divided into two more addressable questions. First, how effective is group selection at producing an evolutionary response? Second, is the ecological process of group selection common and strong in nature? Empirical answers to these questions require different approaches. The first question can be addressed in the laboratory. The second question can only be answered by measuring selection in nature.

how effective is group selection?

Group selection can be very effective (table 1). The first experiment to include group selection explicitly as a treatment was the pioneering work of Wade (1976, 1977). Wade used the trait population size in the red flour beetle

TABLE 1
Laboratory Studies of Group Selection

Study	Organism	Trait(s)	Special Features
Wade 1977	<i>Tribolium 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>Arabidopsis thaliana</i>	Leaf area	First group selection in plants; factorially combined group and individual selection treatments
Wade 1987	<i>T. castaneum</i>	Competitive ability	Interdemic selection for competitive ability
Goodnight 1990a, 1990b	<i>T. castaneum</i> , <i>Tribolium 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

Note. — All studies detected a significant response to group selection.

Tribolium castaneum. There is a long history of experimentation on competition and population regulation using *Tribolium* (e.g., Park 1948, 1954). An important finding from previous experiments was that population size in *Tribolium* is mainly governed by the cannibalism rate rather than differences in fertility or fecundity (Park et al. 1961, 1965; Stevens and Mertz 1985).

Wade hypothesized that group selection would be fairly ineffective and applied strong selection. In the treatment for group selection for large population size, after the populations were ranked by size (fig. 1), the largest population was used to set up as many populations as possible. For example, if it had 200 individuals, it was used to establish 12 populations (12 3 16 5 192), and the remaining eight individuals were discarded. Wade continued the process using the second largest population, and so forth, until he had set up the 48 populations that were in each treatment. A similar protocol was used in the treatment for selection for low population size; however, small populations can establish fewer populations with the consequence that more populations contributed to

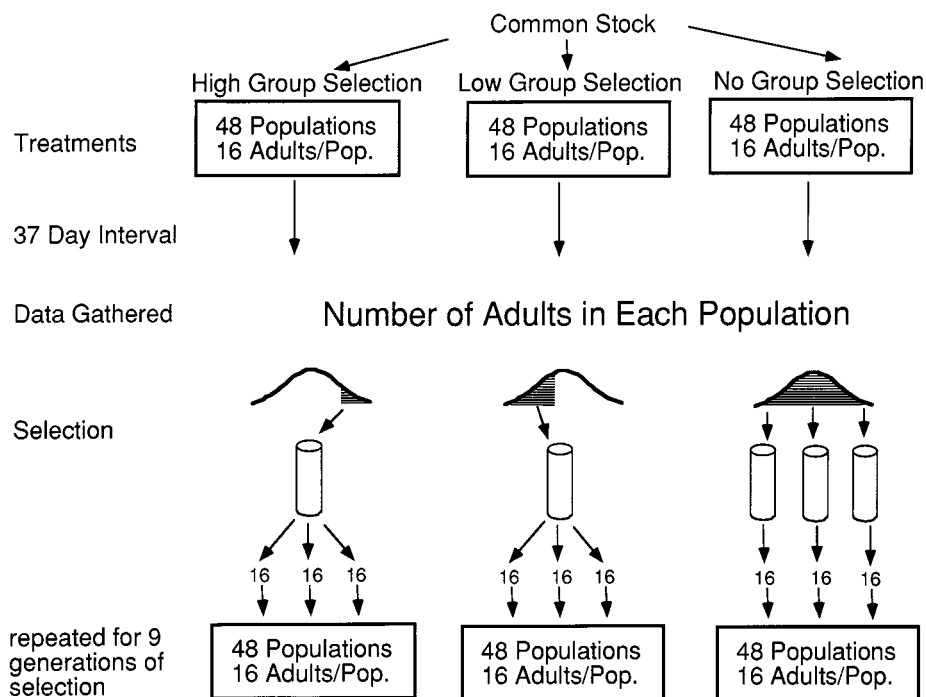


Fig. 1.—Schematic outline of Wade's (1977) experiment. Each selection treatment consisted of a metapopulation of 48 populations. Each population was started with 16 adults. After 37 d, the populations were censused, and group selection was performed based on the population size. In the no-group-selection control, all populations contributed one population to the next generation. (Redrawn from Wade 1977.)

each subsequent generation. Wade's design employed the largest selection differential possible, and the selection differential varied between generations and treatments. In addition to treatments for high and low group selection, Wade maintained a control of no group selection in which all populations contributed to the next generation and a random selection treatment in which populations were chosen at random to found the next generation. His random selection treatment was effectively a milder form of group selection for increased population size since larger populations established more populations than did small populations.

Wade's group selection was surprisingly effective (fig. 2). After nine generations of selection, the treatment for selection for high population size had a mean population size of 178 individuals, whereas the treatment for selection for low population size had a mean of 20 individuals. Furthermore, the response to selection was still detectable 3 yr after selection was relaxed (Wade 1984a, 1984b), which indicates that group selection had resulted in lasting evolutionary change.

Further studies examined why, contrary to expectation, group selection had

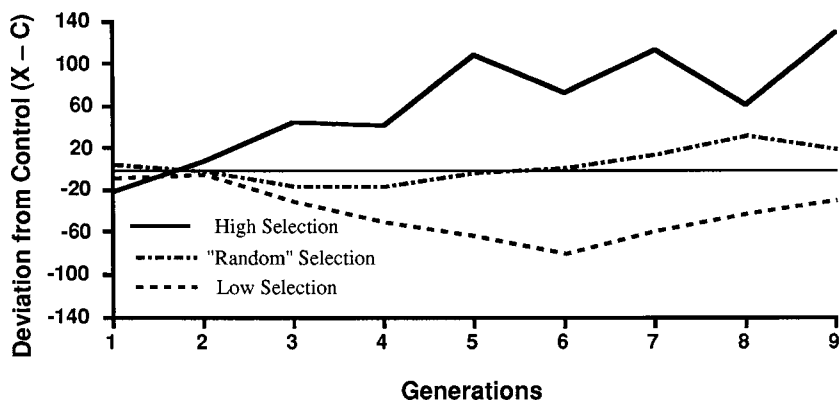


Fig. 2.—The response to selection in the Wade (1977) experiment. The response to group selection for high population size (*solid line*), group selection for low population size (*dashed line*), and random group selection line (*dashed-dotted line*) are plotted as a deviation from the no-group-selection control. The random selection line is effectively a milder form of group selection for high population size since larger populations founded more offspring populations than did small populations. In the final generation, the mean population size for the high selection line was 178, and mean population size for the low selection line was 20.

been so effective. In a review of models of group selection, Wade (1978) listed a number of possible explanations, two of which stand out. First, before 1977 nearly all models of group selection had assumed a migrant pool, whereas Wade used a propagule pool in his experiment. 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 multigeneration population differentiation. The propagule pool keeps groups intact, allowing multigeneration 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. 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 suggestion (Goodnight 1990b), and theoretical models with nonadditive genetic effects demonstrate that gene interaction greatly enhances the differentiation of populations (Griffing 1977, 1981a, 1981b, 1981c, 1981d, 1982a, 1982b, 1982c, 1982d, 1982e, 1982f; Goodnight 1987). Thus, early group selection models that consider only additive gene effects (e.g., Boorman and Levitt 1973; Levin and Kilmer 1974) ignore the major source of the unique genetic response to group selection.

Craig (1982) performed a group selection experiment building on Wade's results. He also used *T. castaneum*; however, the selected trait was emigration

rate. There was a constant and lower selection intensity, replication among group selection treatments, and three explicit individual selection treatments (no individual selection and weak [5%] or moderate [25%] individual selection against migration rate; the size of the experiment confined selection to one direction; D. M. Craig, personal communication). There was a significant response to group selection for migration rate but no response to individual selection.

Group and individual selection were performed on leaf area in *Arabidopsis thaliana* (Goodnight 1985), and the basic results of the *Tribolium* experiments were shown to be observable in plants. This experiment factorially combined three individual selection treatments (individual selection for high leaf area, no individual selection, and individual selection for low leaf area) with three group selection treatments (group selection for high leaf area, no group selection, and group selection for low leaf area). Because of the factorial design, it was possible to compare directly the effectiveness of group and individual selection and to factor out the effects of genetic drift. As with Craig's (1982) experiments, there was a highly significant response to group selection but no significant effect of the individual selection treatments. In fact, statistical analysis revealed a significant negative response to individual selection for high leaf area.

A recent study on group selection for egg production in chickens also warrants discussion (Craig and Muir 1996; Muir 1996). The advent of "egg factories" has resulted in housing chickens in multiple-hen cages rather than the more traditional open pens. The efficiency of maintaining a large number of chickens is improved, but the hens aggressively interact in the small cages, which increases mortality and reduces egg production. Muir selected among cages for increased egg production and observed a 160% increase in annual egg production per hen compared with that for unselected controls (Muir 1996). The selected line also showed fewer aggressive interactions and lower mortality. Aggressive interactions decreased to the point that beak trimming was not required, and mortality decreased 29%. The strains have an appraised value of at least \$3 million. With approximately 250 million laying hens in the United States, eliminating beak trimming at a nickel per bird and reducing mortality 29% for birds worth \$3.50 result in potential savings that greatly exceed the birds' appraised value (Craig and Muir 1996; W. M. Muir, personal communication). The first formal study of group selection in a vertebrate was both financially and intellectually significant.

A frequent criticism of group selection experiments is that the laboratory populations have extreme genetic isolation, whereas homogenizing forces in nature such as migration will lower among-population genetic variance, and group selection will not be effective (Harrison and Hastings 1996b). Empirical work invalidates this criticism. Most of the experiments cited earlier (table 1) were started from a single panmictic population, with no period of population differentiation. Indeed, Wade (1982) observed significant population differentiation and a significant response after a single generation of group selection even in the presence of migration as high as two migrants per generation (12.5% migration, $N = 16$) and population sizes as high as 48 individuals (Wade and McCauley 1980).

Population extinction is not required for group selection to be effective. In an experiment using *T. castaneum* (Wade and Goodnight 1991), group selection was applied by differential migration—that is, large populations contributing migrants to small populations rather than by differential extinction. Every generation, each of the 50 populations in each treatment were counted and assigned a relative fitness based on their population size divided by the mean population size for the treatment. If the relative fitness of a population was > 1 (larger than the treatment mean population size), the population sent out migrants. If the relative fitness of a population was < 1 (smaller than the treatment mean population size), it received migrants from a migrant pool. Group selection by differential migration resulted in a rapid response to selection even with little population differentiation ($f = 0.11$) and migration rates often thought to be sufficiently high to prevent population divergence ($N_m = 1.90$; Wright 1931).

why is group selection so effective?

A series of models by Griffing (1977, 1981a, 1981b, 1981c, 1981d, 1982a, 1982b, 1982c, 1982d, 1982e, 1982f) demonstrates how group selection can be so effective. Crop plants selected at the individual level for increased yield often show a negative response. On the other hand, group selection nearly always results in a positive response (Griffing 1977). A positive response to group selection was also observed in another study (Goodnight 1985), but also noted was a negative response to individual selection for increased leaf area. Griffing's models predict that individual selection for yield in a mixed-genotype stand favors aggressive individuals that acquire resources at the expense of their neighbors. These aggressive, high-yield individuals show a decreased yield when planted together. Individual selection with interacting individuals will result in a negative response in any trait that is genetically correlated with aggressiveness. On the other hand, group selection favors a balance between growth and aggression that maximizes group yield.

Additive genetic effects are genetic factors that directly contribute to the resemblance between parents and offspring (Falconer 1989) and are responsible for persistent responses to individual selection (Fisher 1958). Aggressive interactions, or any other form of genetically based interactions among individuals, are nonadditive genetic effects that cannot contribute to a response to individual selection but can contribute to a response to group selection. Nonadditive genetic effects within an individual (e.g., dominance and epistasis) also cannot contribute to a response to individual selection but can contribute to a response to group selection (Crow and Kimura 1970; Goodnight 1987).

All of the traits examined in group selection experiments are influenced by interactions among individuals. Population size in *Tribolium* is mainly determined by cannibalism rates (Park et al. 1961, 1965; McCauley and Wade 1980; Stevens and Mertz 1985), emigration rate in *Tribolium* is a function of population density with higher migration rates found in more dense populations (Craig 1982), leaf area in *Arabidopsis* varies dramatically as a function of planting density, and egg production in chickens is strongly influenced by aggressive interac-

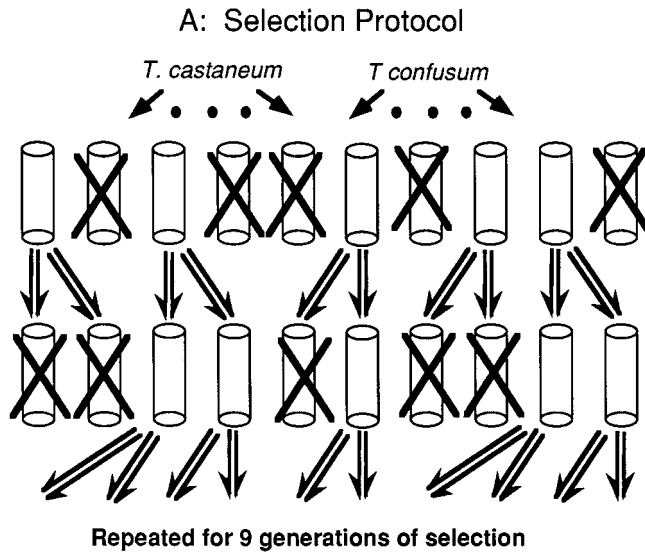
tions among hens (Craig and Muir 1996). Are the traits examined a special subset of fitness components? Probably many traits can be affected by interactions among individuals or nonadditive genetic effects. The traits described above include morphological, behavioral, and group-emergent traits.

Why was individual selection ineffective in some experiments (Craig 1982; Goodnight 1985), when it is generally appreciated that individual selection is always effective (e.g., Hartl and Clark 1989, p. 441)? Griffing's (1977, 1981a, 1981b, 1981c, 1981d, 1982a, 1982b, 1982c, 1982d, 1982e, 1982f) models provide an answer. Individual selection experiments often use methods minimizing interactions among individuals. For example, when selecting at the individual level for egg production, the hens are typically housed in individual cages (Muir 1996). Eliminating interactions among individuals prevents negative responses to individual selection because of aggressive interactions. In two of the experiments described earlier (Craig 1982; Goodnight 1985), the individual selection was performed in the intact populations. In accordance with Griffing's theory, selection increased the aggressive interactions resulting in no response (Craig 1982) or a negative response (Goodnight 1985).

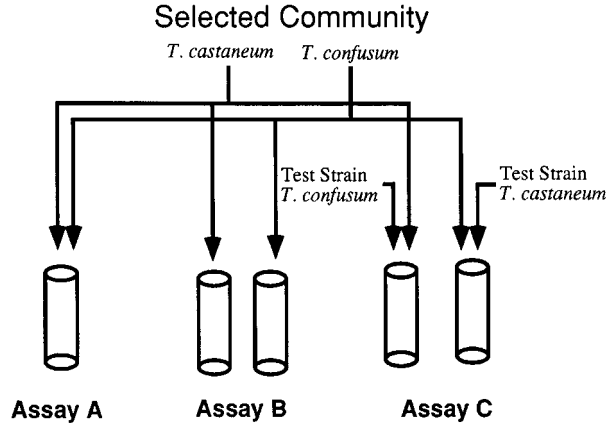
Genes in one individual, such as cannibalism or interspecific predation rate, can affect the fitness of other individuals of the same or different species. In previous studies (Goodnight 1990a, 1990b), the role of such ecological interactions was examined among individuals on the response to group selection. Selection was performed on two species communities of *Tribolium castaneum* and *Tribolium confusum* (fig. 3A). There were four pairs of community selection treatments (eight treatments total): selection for increased or decreased population size in *T. castaneum*, selection for increased or decreased population size in *T. confusum*, selection for increased or decreased emigration rate in *T. castaneum*, and selection for increased or decreased emigration rate in *T. confusum*. Because of Wade's earlier observation of the efficacy of the propagule pool model over migrant pool migration in promoting a response to group selection, these experiments selected at the community level by keeping the two species groups intact when founding each generation.

As with the previous group selection experiments, a rapid response occurred for all treatment pairs. Correlated responses to selection were measured by assaying all four traits in all treatments. Correlated responses occurred both within and between species. For example, selection for increased *T. castaneum* population size was correlated with a significant increase in the emigration rate of *T. confusum*. Interspecies correlated responses to selection must be mediated through ecological interactions among individuals. Thus, these interspecies correlated responses to selection are clear evidence that ecological interactions are contributing to the response to community selection (Goodnight 1990a).

To further analyze the role of interspecies interactions (Goodnight 1990b), following the final generation of selection, the selected populations were subjected to three treatments (fig. 3B). In assay A, the intact communities were raised in the standard manner. This treatment was identical to the conditions under which the communities were selected. In assay B, the two species were separated and raised as single-species populations. Both the ecological and genetic



B: Assays performed on each community



3.—A, The selection protocol used in a previous experiment (Goodnight 1990a). Each treatment consisted of 10 two-species communities. Each generation the communities were assayed for four traits (population size and emigration rate in both species), and selection was performed based on the value of the trait under selection. B, The assays performed following the final generation of the selection experiment (Goodnight 1990b): *assay A*, an analysis of the coevolved communities established in the same manner as the original communities used in the selection experiment; *assay B*, an analysis of single-species populations established from the species that made up the original coevolved communities; and *assay C*, an analysis of the reconstructed communities in which one of the species was drawn from the original coevolved community and the other species was drawn from a naive test strain.

effects of the presence of the second species were removed. In assay C, the two species were again separated, but a second "test strain" of the competing species was added to each population. Assay C was ecologically identical to the original conditions; however, only one of the species had been subjected to community selection, whereas the second species was a naive test strain.

In the intact communities, all communities showed the response to selection that had occurred in the selection experiment. In the single-species populations, there were no significant differences between any of the selection treatments (i.e., the significant responses exhibited in the communities were absent when the lines were raised as single species). In the reconstructed communities, two pairs of selection treatments, selection for high and low emigration rate in both species, showed a significant response to selection, and two pairs of selection treatments, selection for high and low population size in both species, showed no response to selection (fig. 4).

All of the community selection treatments resulted in a response to selection, but in all cases the response was only expressed in a community setting. Changing the ecological conditions by removing either of the coevolved constituents eliminated the response to selection. However, the ecological setting is not always sufficient to ensure that the response to selection is maintained. For two traits, population size in both species, the response to selection was expressed only in the intact communities, which indicates that the genetically based ecological interactions between the two strains is contributing to the response to selection. These among-species changes can only occur if there are genetically based ecological interactions among individuals. For example, population size in *T. castaneum* was in part due to genes in the particular coevolved strain of *T. confusum*.

The role of ecological interactions in the response to selection were the focus of subsequent experiments (Goodnight 1991). Ten two-species communities were allowed to differentiate for 16 generations. The communities were divided into single-species populations and factorially recombined into the 100 possible two-species communities. These reconstructed communities were measured for the four traits described earlier, emigration rate and population size in both species. The experiment documented significant genetic variation for all traits in both species. As an example, the genetic variance for *T. confusum* population size was greater in *T. castaneum* than in *T. confusum*. In addition, one of the traits, population size in *T. confusum*, showed a significant genetic variance because of the interaction between the two species.

Griffing (1989) performed an experiment using *Arabidopsis* designed to examine his models of the quantitative genetics of interactions among individuals. He examined the fresh weight of individuals in populations of two individuals of *Arabidopsis thaliana* growing in a sterile agar medium. He found that these two individual populations had significant genetically based associate effects, or interactions among individuals, for plant fresh weight. Furthermore, he found the predicted negative genetic correlations between direct effects (the effect of an individual on itself) and associate effects (the effect of an individual on its neighbors).

Nonadditive genetic variance can contribute to a response to group-level se-

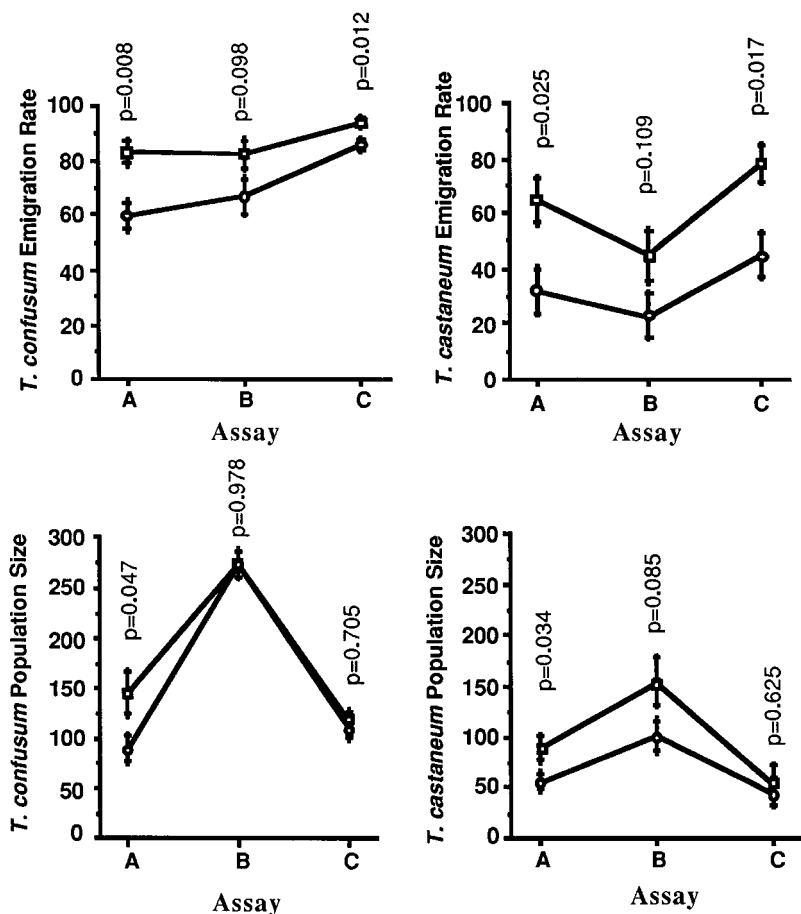


Fig. 4.—The means \pm 1 SD for each of the treatments in the three assays reported earlier (Goodnight 1990b). Means are only reported for communities in which the coevolved strain of the species expressing the selected trait is present. Squares indicate treatments with selection for increased value of the trait, and circles indicate treatments with selection for decreased value of the trait. Significance levels are listed above each assay.

lection. Experiments clearly demonstrate that genetically based interactions among individuals are contributing to group differences and to the response to group and community selection. Thus, group selection is far more effective than predicted because it can act on genetic interactions both within and among species. These genetic interactions among individuals—and, to a lesser extent, other forms of nonadditive genetic variance—are almost universally ignored in discussions about higher levels of selection.

how common is group selection in nature?

Laboratory experiments have established that group selection is very effective, that it can occur with weak selection differentials ($S \leq 0.05$), and that it

TABLE 2
Field Studies of Group Selection in Natural Populations

Study	Organism	Trait(s)	Special Features
Breden and Wade 1989	<i>Plagiodera versicolora</i>	Cannibalism	Demonstration of simultaneous group and individual selection
Stevens et al. 1995	<i>Impatiens capensis</i>	Survivorship, flower production	Use of contextual analysis and path analysis to examine multilevel selection
Tsuji 1995	<i>Pristomyrmex pungens</i>	Reproductive allocation	Within- and among-colony selection acting in opposition
Kelly 1996	<i>I. capensis</i>	Fruit production	Manipulative experiment examining kin selection
Banschbach and Herbers 1996	<i>Myrmica punctiventris</i>	Reproductive/worker allocation	Nest- vs. colony-level selection

Note. — All studies detected significant group selection.

occurs even with little genetic differentiation among populations (F_{st} , 0.10). Many organisms have population structures that are similar to those used in the empirical studies, which attests to their appropriateness as model systems for examining the efficacy of group selection. Although laboratory experiments demonstrate the plausibility of group selection, we can determine the importance of group selection in nature only by measuring selection in natural populations.

Published studies of group selection in natural populations are listed in table 2. Although all of these studies detected selection above the level of the individual, more studies are needed to establish the importance of group selection in nature. Within the adaptationist school, there are also a number of studies indicating that higher levels of selection are important in evolution (see Wilson 1983 for a review).

Some studies (Stevens et al. 1995; Tsuji 1995; Banschbach and Herbers 1996) use a statistical technique, contextual analysis, recently introduced into biology (Heisler and Damuth 1987; Goodnight et al. 1992). Contextual analysis was developed in the social sciences where it is used to predict an individual's opinion (e.g., political party preference) based on both individual (e.g., sex, age, education) and community (e.g., number of churches, mean annual income) characteristics (Boyd and Iversen 1979).

Contextual analysis is used to measure selection at multiple levels. As discussed earlier, equation (1) separates evolution by natural selection into two processes, selection and the response to selection. Contextual analysis is a means of detecting group and individual selection, but it cannot predict the response to group or individual selection. The studies of group selection are similar to studies of individual selection in that they document selection but do not demonstrate evolutionary change. The laboratory studies discussed here demonstrate that group selection can be a powerful evolutionary force.

Multilevel selection studies using contextual analysis are an extension of a standard selection analysis (Lande and Arnold 1982; Arnold and Wade 1984). A fitness component such as seed number or survival is the dependent variable in a regression analysis with any number of individual traits, such as leaf area, plant height, and photosynthetic rate, as independent variables. To detect group selection, contextual traits are also measured. Contextual traits are group-level phenotypes and include both the group means of the individual traits (e.g., mean leaf area, mean plant height, mean photosynthetic rate) and traits that are only expressed at the neighborhood or group level (e.g., population density, percentage ground cover). Multiple-regression analysis examines the relationship among individual relative fitness (the fitness of an individual divided by the metapopulation mean fitness) and the individual and contextual traits. Group (or neighborhood) selection is inferred from a statistically significant partial regression of relative fitness on a contextual trait. Multilevel selection in this context is broader than classic definitions of group selection (e.g., Maynard Smith 1976). Group selection occurs whenever a component of individual fitness can be attributed to its context. Theoretical analysis shows that contextual analysis successfully identifies classic group selection as well as the partitioning selection into group- and individual-level components when they are acting simultaneously (Goodnight et al. 1992). Classic results such as Hamilton's (1964, 1975) rule concerning the evolution of altruism can be expressed with contextual analysis in terms of conflicting group and individual selection (Goodnight et al. 1992). In addition, contextual analysis interprets many forms of frequency-dependent selection as multilevel selection.

Contextual analysis will be illustrated using a study of selection in *Impatiens capensis* (Stevens et al. 1995). The population of *Impatiens* used was a large, homogeneous stand in which neighbors within 10 cm interacted sufficiently to influence each other's fitness. Thus, contextual traits were measured in the 10-cm circle surrounding the focal individuals (fig. 5). Three measures of relative fitness were examined: the number of chasmogamous (open-pollinated) flowers, the number of cleistogamous (self-pollinated) flowers, and survival to first reproduction (fig. 6). The largest plants produced the most chasmogamous flowers and therefore had the highest fitness. The number of chasmogamous flowers was determined solely by individual characteristics (i.e., density did not affect chasmogamous flower production, nor did plants with tall neighbors produce more chasmogamous flowers than did plants with short neighbors). This result indicates only individual selection influences chasmogamous flower production. The largest individuals in the smallest neighborhoods had the highest survival and produced the most cleistogamous flowers. Because survival and number of cleistogamous flowers was determined both by characteristics of the individual (height, size) and characteristics of the neighborhood (height of neighbors), contextual analysis indicates that selection is acting at both the individual and group levels.

The interaction between individual selection for large size and neighborhood or group selection for small size results in a constant yield of seeds over a wide range of plant densities. Dense populations with many small plants produce approximately the same number of (cleistogamous) seeds as low-density popula-

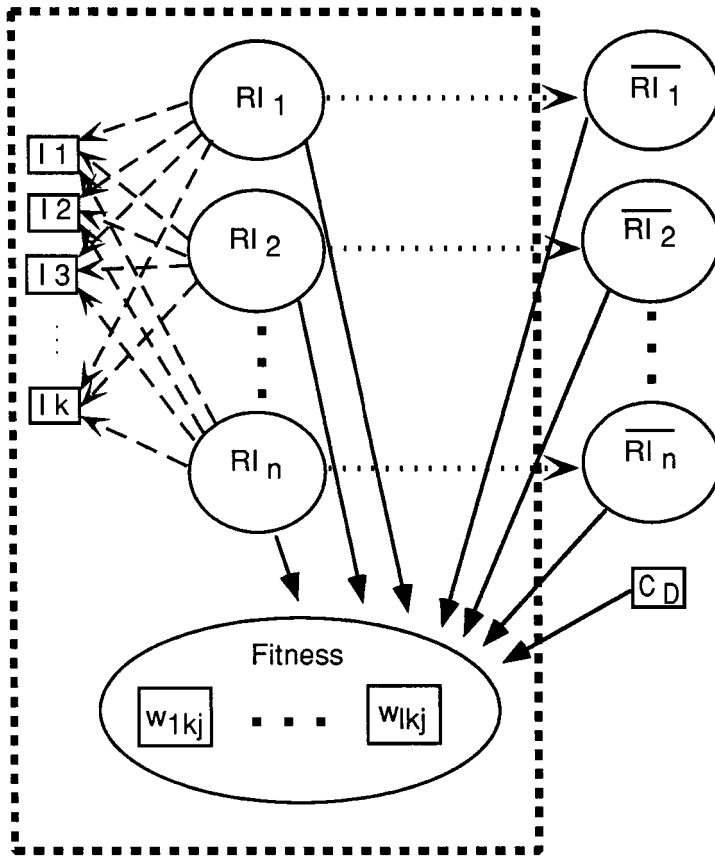
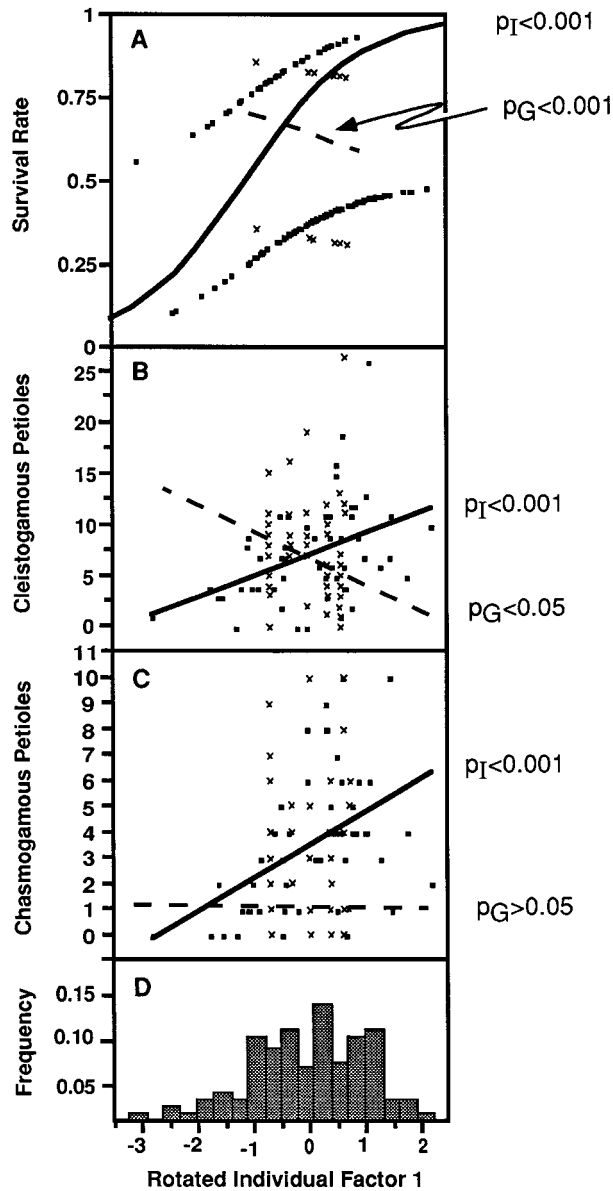


Fig. 5.—The path diagram used for partitioning selection in natural populations. Here C_D is contextual trait (density), and I_1 I_2 I_k are individual traits. Factors enclosed in circles are unmeasured (and unmeasurable) underlying factors; factors enclosed in boxes are measured traits. Uncorrelated 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. The box encloses traits measured on the individuals that would be used in a standard selection analysis. Factors that are unique to contextual analysis lie outside the box. (Redrawn from Stevens et al. 1995.)

tions with large plants. This constant-yield law has been observed in both other *Impatiens* studies (Schmitt et al. 1987) and other plants (Harper 1977, pp. 205–208). If the constant-yield law and the related self-thinning processes frequently found in plants have a component of neighborhood selection, this will suggest that multilevel selection may be common in plants.

An individual's relative fitness is frequently dependent on the biotic context in which it is found, which suggests that the results of the *Impatiens* study (Stevens et al. 1995) are not unusual—multilevel selection may be far more com-



6.—The correlation of the rotated first principal component (size; RI_1 in fig. 5) and the neighborhood mean of the first principal component RI_1 in fig. 5) with (A) probability of survival to first reproduction, (B) number of cleistogamous petioles, and (C) number of chasmogamous petioles in 1990. The solid line is the regression (log-linear regression in A) of the fitness component on the individual trait. The dashed line is the regression (log-linear regression in A) of the fitness component on the group trait. Solid squares are individual values, and x's are group values. D, The frequency distribution of the individual trait for all individuals in the study. Significance levels for partial regression on an individual trait (p_I) and the group trait (p_G) are shown to the right of each graph. A significant regression indicates that selection is acting. (Redrawn from Stevens et al. 1995.)

mon than previously suggested. It is likely that the reason it is not more frequently detected is that we have lacked statistical tools for detecting it. Contextual analysis provides such a tool.

conclusions

Careful reading of Williams's (1966, especially chap. 4) book reveals that he considered only additive genetic effects in his critique of the likelihood of group selection explaining adaptations. In genetic systems with only additive effects, group selection results in novel evolutionary outcomes only under very restrictive conditions. As the amount of nonadditive genetic effects increases, the restrictions are relaxed and higher-level selection becomes both more likely and more novel in its evolutionary contributions. Experimental studies confirm that gene interaction, and especially genetically based interactions among individuals, contribute to a response to group selection. Thus, models with only additive effects are inappropriate for predicting the effectiveness of group selection.

The five published studies using the genetic approach to study group selection in nature (table 2) are not enough to draw general conclusions; however, they do indicate that group selection may be more common than previously supposed. Theoretical analysis indicates that many commonly accepted processes, such as kin selection and many forms of frequency-dependent selection, are mathematically a combination of group and individual selection. Experimental analysis indicates that there is individual selection in *Impatiens* for large size and group selection for small size. These opposing forces of selection result in an ecological process frequently observed in plants: a constant seed yield regardless of planting density. If constant yield or self-thinning in plants typically includes a component of group selection, then multilevel selection may indeed be common.

Experimental studies of group selection are remarkable in that they highlight the inadequacy of theory based on additive gene effects and the dearth of data from natural populations. The challenge to theoretical biology is to incorporate nonadditive gene effects into models of multilevel selection. The challenge to empirical biology is to continue to document multilevel selection in natural populations, determine how frequently contextual traits influence fitness, and quantify the role of group selection in nature.

acknowledgments

We thank D. S. Wilson, N. Gotelli, M. Wade, and an anonymous reviewer for thoughtful comments on the manuscript. This work was supported by the Vermont Experimental Program to Stimulate Competitive Research (National Science Foundation EPSCoR).

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