

## MULTILEVEL SELECTION IN NATURAL POPULATIONS OF *IMPATIENS CAPENSIS*

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**Abstract.**—This study partitions selection in natural populations of jewelweed, *Impatiens capensis*, into group- and individual-level components. Group selection has been a subject of controversy for decades, yet this is the first study to partition phenotypic selection in a natural population. Using contextual analysis combined with path analysis, we measured the correlation between fitness components (survival rate to first reproduction, chasmogamous [open-pollinated] seed production, and cleistogamous [selfed] seed production) and several group- and individual-level traits. Survival rate was studied for 2 yr, and the reproductive traits were studied for 1 yr. For survival rate and cleistogamous seed production, both group and individual selection occurred, and the two types of selection were in opposition. For chasmogamous seed production, only individual selection was detected. Group selection may be responsible for the constant yield law in plants. It may be more common than previously believed because it may be mistaken for frequency-dependent selection. Evolutionary theory suggests different components of genetic variation are available to different levels of selection. Thus, the demonstration of group-level selection in nature challenges evolutionary biologists to consider new components of variation as raw material for selection. The results are discussed with respect to the evolution of altruism and the use of multiple regression versus path analysis in studies of selection.

Since Williams's (1966) book *Adaptation and Natural Selection*, group selection has been discounted by many evolutionary biologists. Williams suggested that it is more parsimonious to invoke individual selection than group selection to explain evolutionary adaptations. Although this argument may be useful for explaining existing patterns, only empirical studies can determine whether the process of selection occurs at multiple levels of population structure. Here we define *group selection* as variation in the fitness of an individual due to properties of the group or groups of which it is a member (Goodnight et al. 1992). *Multilevel selection* is defined as variation in the fitness of individuals due to both properties of the individual and properties of the group or groups of which they are members (Heisler and Damuth 1987; see Wilson 1983 and Sober 1984 for other definitions). Our group selection definition includes models of group selection that consider differential extinction of entire groups (Levins 1970; Wade 1978; Craig 1982;

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Goodnight 1985) as well as models that do not, such as Wright's definition of interdemic selection (1921; Wright 1977, p. 455; Crow et al. 1990; Wade and Goodnight 1991; Barton 1992; Kondrashov 1992) and the trait group models of D. S. Wilson (1975, 1980). Under our definition many forms of frequency-dependent selection have a component of group selection (Goodnight et al. 1992).

Although the evolutionary importance of group selection has been argued for almost 30 yr, this discussion has been largely a conceptual debate. The scant empirical work on group selection consists mainly of laboratory studies. Although the laboratory work demonstrates that group selection is an effective evolutionary force, it has done little to increase its acceptance among evolutionary biologists. Two studies demonstrate group selection of natural populations. Both examine larval survival in chrysomelid beetles (Breden and Wade 1989; McCauley 1994). In addition, a number of studies imply group selection (see, e.g., Gilpin 1975; Levin and Pimentel 1981; Wilson and Colwell 1981; but see Nunney 1985), and there is an extensive literature on interactions among kin, kin recognition, and kin selection, although actual documentation of kin selection occurring is rare (see Krebs and Davies 1991). A problem with field studies of group selection is correctly identifying the level of selection (Goodnight et al. 1992). Both individual (Williams 1966, 1992; Sober 1984; Heisler and Damuth 1987) and group (Wilson and Sober 1989) selection can be misinterpreted as selection at another level.

Recently, "contextual analysis" was proposed to extend the multiple-regression method of measuring selection (Christiansen and Frydenberg 1973; Arnold and Wade 1984a) to hierarchically structured populations (Heisler and Damuth 1987; Goodnight et al. 1992). Contextual analysis extends the traditional approach by including "contextual traits"—group traits (e.g., density, average size) that may influence fitness. Fitness, or more correctly an estimate of fitness, is measured only at the individual level. A significant regression of relative fitness on a contextual trait is evidence of group selection.

An alternative method for studying group selection is the Price covariance approach (Price 1970, 1972), in which the total variance in relative fitness is divided into within- and among-group components. The covariance approach can incorrectly identify indirect effects of individual selection as group selection, whereas contextual analysis correctly identifies the level of selection for models of pure group selection, as well as hard and soft selection (Goodnight et al. 1992).

We partitioned selection in a natural population of jewelweed, *Impatiens capensis*, into group- and individual-level components using contextual analysis. Jewelweed has been used in several studies of population ecology and evolution (see, e.g., Schemske 1978; Marden 1984; Schmitt et al. 1985; Mitchell-Olds 1986). There is density dependence in this species in the form of self-thinning (Schmitt et al. 1987a, 1987b). Self-thinning is particularly interesting because it is similar to soft selection (Wallace 1968, 1975) and includes a component of group selection (Goodnight et al. 1992). Selection can be separated into parts corresponding to segments of the life cycle (referred to as episodes of selection), and the direction and/or magnitude of selection on traits may vary from one life cycle segment to the next (Fisher 1930; Christiansen and Frydenberg 1973; Arnold and Wade 1984a, 1984b). One can draw conclusions about selection over any period of the

life cycle, even if no data are available before or after that period. We analyzed the following episodes of selection: survival rate from first census to first reproduction (1990 and 1991), cleistogamous (CL, self-pollinated) reproduction (1990), and chasmogamous (CH, open-pollinated) reproduction (1990).

We measured phenotypic selection at multiple levels. Evolution by natural selection can be viewed as phenotypic selection,  $S$ , and the genetic response to selection,  $R$ :

$$R = h^2 \cdot S,$$

where  $h^2$  is the heritability (see, e.g., Falconer 1989; but see Endler 1986). Selection causes within-generation changes in phenotypic distributions and can be described in purely phenotypic terms without considering inheritance. The evolutionary response to selection depends on both available genetic variation and inheritance. This view has been widely accepted for individual selection (see, e.g., Kalisz 1986; Mitchell-Olds and Bergelson 1990) and is equally appropriate for multilevel selection. Just as the variation in individual traits is due to genetic and environmental factors, the variation in contextual traits also results from both genes and the environment.

#### METHODS

Jewelweed is a hermaphroditic diploid ( $2N = 20$ ) herbaceous annual growing in moist woods, along streams and lakes in eastern North America. It has no seed bank (Leck 1979), and total fitness can be assessed at the season's end by counting seed production. It germinates in early spring and often grows in dense, almost monospecific stands. Both CL and CH flowers are produced and are easily distinguished by their positions on the plant and pedicel structure (Schemske 1978). We studied a contiguous population in a wooded area of the Kellogg Bird Sanctuary, a part of the Kellogg Biological Station, Kalamazoo County, Michigan. The plants are very delicate, so a portable scaffolding system was used to census the study plots. During the first censuses individuals were marked with numbered tags. The study plots consisted of 0.5-m diameter circles. There were six plots in 1990 and 10 in 1991.

To determine the appropriate plot size, in 1990 plants were measured in increasing concentric circles (0.5-, 1-, and 2-m diameter) around 0.25-m core plots. All of the plants in the core plots were measured, and 12 individuals in each of the outer circles were measured. Analyses of these data indicated that including plants up to 0.5 m in area increased the variance explained by the regression model. Beyond 0.5 m there was no increase in the variance explained, and the regression slopes became unstable. The regression analysis indicates that plants found within 0.5-m diameters appear to share a common selective environment, and we concluded that plots of 0.5 m were appropriate for this study.

In 1990, the individual traits measured were (table 1) number of fully expanded leaves on each plant at the first, second, and third censuses (number of leaves-1, -2, and -3); the average height at the first and second censuses (height-1, -2); the distance between the first and second internodes at the first census (internode-1);

TABLE 1  
LOADING OF EACH TRAIT FOR THE ROTATED INDIVIDUAL FACTORS IN 1990

TRAIT FACTOR	SURVIVAL RATE TO FIRST REPRODUCTION			REPRODUCTION	
	Large Size (RF1)	Low Herbivory (RF2)	Many Yellow Leaves (RF3)	Large Size (RF1)	CL Buds: Censuses 5, 6 (RF2)
Number of leaves-1	.74	-.20	.30	.83	.01
Number of leaves-2	.84	-.05	.20	.80	-.25
Number of leaves-3	.68	.06	.48	.86	.00
Height-1-2	.93	-.11	.02	.87	-.31
Internode-1	.86	-.13	-.04	.72	-.45
Stem diameter-2	.84	.05	.08	.83	-.11
Leaf length-3	.88	.11	.22	.91	-.14
Yellow leaves-3	.10	-.02	.95	.48	.40
Number of leaves eaten-3	.06	-.98	.01	.05	-.06
CH/CL buds-4				-.13	.33
CH buds-5				-.50	.53
CL buds-5				.07	.93
CH buds-6				-.59	.22
CL buds-6				.07	.93
CH buds-7				-.15	.25

NOTE.—CH, Chasmogamous (open-pollinated reproduction); CL, cleistogamous (self-pollinated reproduction); RF, rotated factors.

the diameter of the stem at the scar left by the cotyledons (stem diameter-2); the average length of the four longest leaves at the third census (leaf length-3); the number of yellow leaves at the third census (yellow leaves-3); the number of leaves damaged by herbivores at the third census (number of leaves eaten-3); the presence of CH or CL flower buds at the fourth census (CH/CL buds-4); the presence of CH flower buds at the fifth, sixth, and seventh census (CH buds-5, -6, and -7); and the presence of CL flower buds at the fifth and sixth census (CL buds-5 and -6; all plants had CL buds at the seventh census). One group trait was measured, density at the second census (density-2). The censuses dates were one on 5/22–29, two on 6/4–5, three on 6/11–13, four on 7/2–3, five on 7/9, six on 7/16–17, seven on 7/23, and eight on 8/13.

Chasmogamous and CL reproduction were estimated by counting the number of CH and CL petioles, respectively, at the final census. Chasmogamous pods produced an average of 1.46 seeds (SE = 0.08), and CL pods produced an average of 1.02 seeds (SE = 0.01); thus the number of each type of petiole was used to estimate of that type of seed production.

In 1991 traits were measured on all the individuals within each 0.5-m study plot and fewer traits were measured. We measured (table 2) number of fully expanded leaves at the first census (number of leaves-1), the height at the first censuses (height-1), the length of the longest leaf at the second census (leaf length-2), and density at the first census (density-1). Fitness was measured as survival rate until the first census at which flowers appeared, census 3. There

TABLE 2  
LOADING OF EACH TRAIT FOR THE ROTATED  
FACTORS IN 1991

TRAIT FACTOR	SURVIVAL RATE TO REPRODUCTION	
	Large Size (RF1)	Many Leaves (RF2)
Number of leaves-1	.35	.94
Height-1	.91	.28
Longest leaf-2	.83	.42

NOTE.—RF, Rotated factor.

was a different pattern of mortality in 1991, probably resulting from differences in the pattern of rainfall between the 2 yr. As a result, many of the plants died between first flowering and the final census, and we were unable to assess selection on CL and CH reproduction. Therefore, we restrict our discussion of selection to the first three censuses. Census 1 occurred on 5/15–18, 2 on 5/29, and 3 on 7/3.

Contextual analysis is a multilevel generalization of methods for estimating selection on correlated characters. We combined contextual analysis with path analysis (Wright 1921) as advocated by Crespi and Bookstein (1989). Path analysis is a system of portraying and analyzing systems of linear causation in which the system of linear causation is explicit (Li 1975). Multiple regression, factor analysis, and other systems of linear relationships can be expressed as a path analysis.

The relative merits of multiple regression versus path analysis are currently debated (Mitchell-Olds and Shaw 1987; Crespi and Bookstein 1989; Wade and Kalisz 1990). Multiple regression identifies the apparent selection on measured traits and can be used to predict a response to selection. However, it may be that the measured traits are merely correlated with unmeasured traits actually under selection (Crespi and Bookstein 1989). For example, multiple regression hypothesizes that selection is acting on "length of longest leaf on July 15," whereas path analysis hypothesizes that selection is acting on overall size, which is correlated with the measured trait. Our path analysis posits selection acts on unmeasurable traits such as "size" or "shape." A statistical advantage of path analysis is that increasing the number of correlated traits (colinearity) increases the ability to describe the underlying traits. As a consequence, it is relatively insensitive to the addition or deletion of traits.

The combination of path analysis and contextual analysis is new to evolutionary biology. Our path analysis couples a factor analysis with multiple regression. Individual traits and fitness components were measured on individuals ( $I_1$ – $I_k$ ; fig. 1), and the contextual trait (density) was measured for each group ( $C_D$ ; fig. 1). Principal components analysis was used to identify major factors (unmeasured traits). Those factors that explained more than 10% of the variance were retained. To maximize the variance explained (Anderson 1984), the factors were rotated

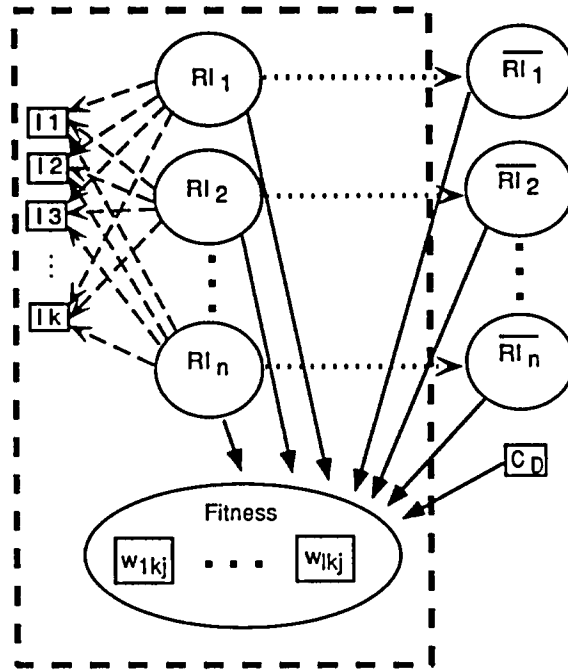


FIG. 1.—The path diagram used for partitioning selection in natural populations.  $C_D$ , Contextual trait (density);  $I_1$ – $I_k$ , individual traits. Factors enclosed in circles are unmeasured (and unmeasurable) underlying factors; factors enclosed in boxes are measured traits. Uncorrelated error 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.

using the Varimax method (SAS Institute 1989). The rotated factors (RF), the within-group mean of each RF ( $\overline{RF}$ ), and density ( $D$ ) were used in a multiple regression on each fitness component. Logistic regression and reduced models were used to determine exact  $\chi^2$  values for the discrete variables (survival rate), and standard regression analysis was used for the analyses of continuous variables (reproduction).

The regression model was

$$\begin{aligned}
 W_{kj} - W_{..} = & b_{RF1}(z_{1kj} - z_{1..}) + b_{RF2}(z_{2kj} - z_{2..}) \\
 & + \cdots + b_{RFn}(z_{nkj} - z_{n..}) + b_{\overline{RF1}}(z_{1..j} - z_{1..}) + b_{\overline{RF2}}(z_{2..j} - z_{2..}) \\
 & + \cdots + b_{\overline{RFn}}(z_{n..j} - z_{n..}) + b_D(y_j - y_{..}) + e_{kj},
 \end{aligned}$$

where  $W_{kj}$  is the fitness of the  $k$ th member of group  $j$ ,  $W_{..}$  is the population mean fitness,  $z_{ikj}$  is the value for the  $i$ th rotated factor measured on the  $k$ th member of group  $j$ ,  $z_{i..}$  is the mean value for the  $i$ th rotated factor measured in group  $j$ ;  $y_j$  is

the density of group  $j$ , and  $e_{kj}$  is the random error term for the  $k$ th member of group  $j$ . The individual-level coefficients,  $b_{RF1}, \dots, b_{RFn}$ , are the partial regression coefficients of fitness on each RF, controlling for both group- and other individual-level factors. Expressions  $b_{\overline{RF1}}, \dots, b_{\overline{RFn}}$  and  $b_D$  are the equivalents for group factors and density, respectively. The vector of partial regression coefficients is a composite gradient measuring the effects of directional selection on both the individual and group factors. Since it is a selection gradient vector, it is unaffected by changes due to selection on correlated factors: a significant partial regression of fitness on the group mean of a factor ( $b_{\overline{RF}}$ ) or on density ( $b_D$ ) demonstrates group selection.

## RESULTS

### *Survival Rate to First Reproduction—1990*

For survival rate to first reproduction in 1990, three factors each account for more than 10% of the variance in the observed independent variables (table 1): "large size" (RF1 has large loadings for number of leaves, height, internode, stem diameter, and leaf length), "low herbivory" (RF2 has a large negative loading for number of leaves eaten), and "many yellow leaves" (RF3 has a large loading for yellow leaves). Rotated factor 1 is normally distributed, and the remaining factors are approximately normally distributed.

Large size (RF1) and survival rate are significantly correlated at both the group and individual level ( $b_{RF1} = 1.74, \chi^2 = 32.02, P < .001$ ;  $b_{\overline{RF1}} = -3.03, \chi^2 = 10.93, P < .001$ ; fig. 2). Notice the slopes of the regressions of relative fitness on the individual- and group-level factors are opposite in sign, which indicates that group selection and individual selection for size are in opposition (fig. 1). Small size is selected for at the group level (negative slope), whereas large size is favored at the individual level (positive slope). These are the conditions that favor the evolution of altruism (Hamilton 1964a, 1964b; Goodnight et al. 1992). Low herbivory (RF2) is significantly correlated with survival rate only at the individual level ( $b_{RF2} = 0.87, \chi^2 = 8.48, P < .05$ ;  $b_{\overline{RF2}} = -2.57, \chi^2 = 3.51, P > .05$ ), and having many yellow leaves shows significant correlation only at the group level ( $b_{RF3} = 0.44, \chi^2 = 1.01, P > .05$ ;  $b_{\overline{RF2}} = 2.07, \chi^2 = 3.97, P < .05$ ). As plants grow and put out new leaves at the top, lower leaves often yellow and abscise. Groups with more yellow leaves show higher survival rate. The correlation between density and survival rate was nonsignificant ( $b_D = -0.05, \chi^2 = 1.36, P > .05$ ).

### *Reproduction—1990*

There were two factors included in the analyses of selection on reproduction (table 1). Rotated factor 1, a measure of size, is normally distributed, and RF2, presence of CL buds at the fifth and sixth censuses, is normally distributed after log transformation.

Both individual and group size have a significant correlation with CL reproduction ( $b_{RF1} = 0.51, F = 26.13, P < .001$ ;  $b_{\overline{RF1}} = -0.52, F = 5.46, P < .05$ ). As

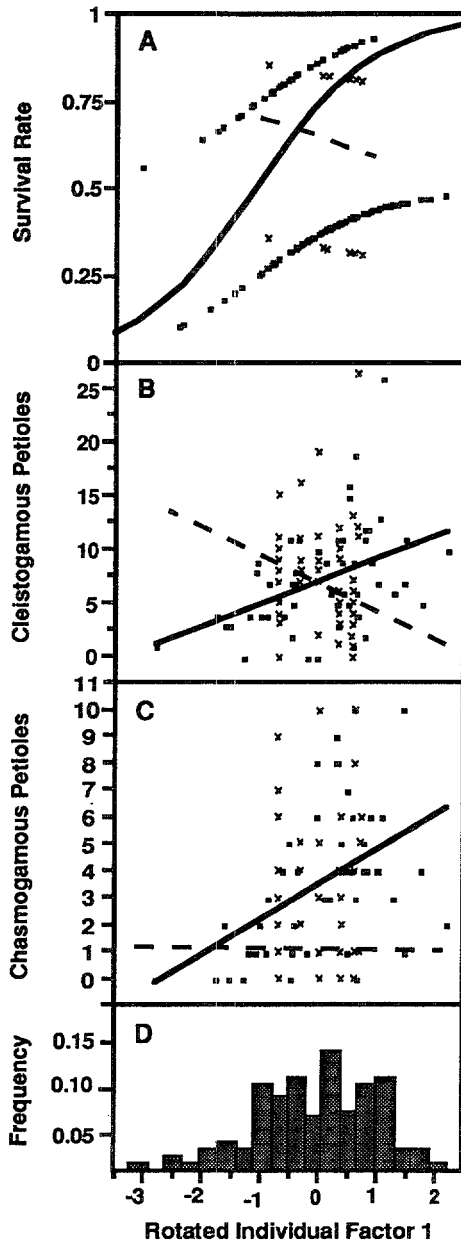


FIG. 2.—The correlation of size ( $RF1$ ,  $\overline{RF1}$ ) with (A) probability of survival rate to first reproduction, (B) number of cleistogamous petioles, and (C) number of chasmogamous petioles in 1990. The solid line is the log-linear regression of the individual trait ( $RF1$ ). The dashed line is the regression of the fitness component on the group trait ( $\overline{RF1}$ ). Solid squares are individual values, and x's are group values. D, The frequency distribution of the  $RF1$  for all individuals in the study. A significant regression indicates selection is acting; thus, individual selection favors large values of  $RF1$  (large size; see text) for all three traits, and group selection favors small values of for both survival rate and cleistogamous petioles.

with survival rate, selection at the two levels is in opposition: group selection favors small plant size, and individual selection favors large plant size. Also note that the slopes of the regressions at the group and individual level are equal and opposite in sign, which is expected if soft selection is acting (Goodnight et al. 1992). The regression between the presence of CL buds and CL reproduction is not significant at either the group or the individual level ( $b_{RF2} = -0.10$ ,  $F = 0.58$ ,  $P > .05$ ;  $b_{\overline{RF2}} = 0.51$ ,  $F = 0.81$ ,  $P > .05$ ). The correlation between density and CL reproduction is nonsignificant ( $b_D = 0.02$ ,  $F = 1.12$ ,  $P > .05$ ).

Selection on CH reproduction occurs only at the individual level. Individual size and the presence of CL buds at the fifth and sixth censuses both show significant correlations with CH reproduction ( $b_{RF1} = 0.54$ ,  $F = 13.66$ ,  $P < .001$ ;  $b_{RF2} = -0.34$ ,  $F = 4.61$ ,  $P < .05$ ). Neither of these traits is significant at the group level ( $b_{\overline{RF1}} = -0.10$ ,  $F = 0.15$ ,  $P > .05$ ;  $b_{\overline{RF2}} = 0.40$ ,  $F = 0.39$ ,  $P > .05$ ). The correlation between density and CH reproduction was nonsignificant ( $b_D = 0.02$ ,  $F = 0.97$ ,  $P > .05$ ).

#### *Survival Rate to First Reproduction—1991*

The factors included in the 1991 survival rate analysis are size (height and length of longest leaf; table 2) and number of leaves. Both are normally distributed. As with the 1990 data, survival rate has a positive regression with measures of individual size ( $b_{RF1} = 1.14$ ,  $\chi^2 = 69.26$ ,  $P < .001$ ;  $b_{RF2} = 0.55$ ,  $\chi^2 = 21.38$ ,  $P < .001$ ). There is significant group-level selection for size ( $b_{\overline{RF1}} = -2.41$ ,  $\chi^2 = 49.79$ ,  $P < .001$ ). Again, group and individual selection are in opposition. The regression for group selection on number of leaves is nonsignificant ( $b_{\overline{RF2}} = -0.18$ ,  $\chi^2 = 0.22$ ,  $P > .05$ ). The regression of survival rate on density was nonsignificant ( $b_D = -0.01$ ,  $\chi^2 = 1.49$ ,  $P > .05$ ).

#### DISCUSSION

We detect opposing individual and group selection in natural populations of *Impatiens capensis* and demonstrate the constant yield may result from the interaction of individual and group selection. Contextual analysis detected significant group selection for small size with respect to survival rate to first reproduction in 1990 and 1991 and for CL seed production in 1990. In these three cases group and individual selection were in opposition. There was also significant group selection for yellow leaves in 1990, although there was no individual selection for this trait.

Contextual analysis indicates that group and individual selection are acting in opposition, but it cannot reveal which of many possible ecological processes causes the selection. For example, there may be intraspecific competition for space and light. Nearly all plants surviving to the fifth census produced CL seeds, whereas only the largest plants produced CH seeds. Intraspecific competition could result in a significant survival and CL reproductive advantage for the largest individuals (individual selection), but the greatest overall survival rate and CL flower production may be in groups with large numbers of small individuals (group

selection). Selection for CH reproduction favoring large individuals may result because only the largest individuals produce CH flowers. There would be no analogous group selection for small size with respect to CH reproduction. There are other possible processes that could result in the same effects (competition for a fixed amount of a limiting nutrient, selective herbivory, etc.). Clearly, additional studies would be needed to determine the actual causal mechanism.

Altruism can evolve when group and individual selection are in opposition. An altruistic trait increases the fitness of other individuals in a group at the expense of the altruistic individual; consequently altruism is opposed by individual selection and favored by group selection (Hamilton 1964*a*, 1964*b*; Goodnight et al. 1992). We found individual selection favors large size, whereas group selection favors small size. The altruistic plant may forgo the individual advantage of large size "for the sake of" the increased survival rate and reproduction of the group.

The evolution of altruism depends on the cost to the altruist, the benefit to the group, and their relatedness (Hamilton 1964*a*, 1964*b*). In addition, the population genetic structure can affect the spread of an altruistic allele (Wilson et al. 1992). In *Impatiens*, relatedness within demes is likely to be high. All CL seeds are self-pollinated, and in some populations about 50% of the CH seeds are self-pollinated (Waller and Knight 1989). The seeds are ballistically dispersed, and primary dispersal is probably less than 1 m for more than 90% of seeds (Schmitt et al. 1985). The combination of high selfing and low seed dispersal may result in a local population genetic structure favoring a high heritability of contextual traits. However, this "population viscosity" may prevent the spread of group-advantageous traits. On the other hand, outcrossing from pollen dispersal favors the evolution of altruism (Wilson 1987). The consequences of these interacting factors for evolution demand further study (Queller 1992).

We found individual selection favors large size and presumably competitively superior individuals (e.g., individuals that successfully sequester resources and diminish the growth of nearby individuals). At the group level, individuals in groups of smaller average plant size perform better, perhaps because the resources are shared. Individual selection may be viewed as selecting for interference and group selection for cooperation (Griffing 1967). Theoretical and empirical studies conclude that group selection is the most efficient method of increasing yield when there is intraspecific competition (Griffing 1977; Goodnight 1985; Wright 1986). The population structure of *Impatiens* suggests individuals are likely to be competing with close relatives and enhances the potential importance of group selection in this species.

Our findings corroborate other studies using *Impatiens*. For example, Schmitt et al. (1987*a*, 1987*b*) observed size-based frequency-dependent selection and self-thinning. Our constant seed yield per plot, regardless of initial plant densities, is consistent with their results. Using contextual analysis, we conclude that the constant yield law may result from the interaction between group and individual selection. Yield has been observed to be independent of initial density in many plants (see Harper 1977, chap. 6, for a review). Our interpretation implies group selection via self-thinning may be common.

The constant yield regardless of initial density is a form of soft selection. In

soft selection the regression of relative fitness on the group mean of the selected trait will be equal and opposite in sign to the regression of relative fitness on the individual value of the trait (Goodnight et al. 1992). In our study, the partial regressions of CL flower production on plant size at the group and individual level are equal and opposite in sign. This result suggests the constant yield of CL seeds is due to soft selection on plant size. When soft selection acts on a heritable trait, group selection slows the response to individual selection.

Contextual analysis suggests frequency-dependent selection at the individual level may be an interaction of selection at multiple levels (Goodnight et al. 1992). Because group selection may be identified incorrectly as frequency-dependent selection (Uyenoyama and Feldman 1980, 1981; Damuth and Heisler 1988), it may be much more common in nature than previously considered.

Group selection does not have to be in opposition to individual selection; however, it is likely to go undetected when group and individual selection act in concert. Contextual analysis can detect group selection and individual selection in concert and in opposition. We feel the detection of the process of group selection can expand our understanding of evolution in both cases. When the two traits are in opposition, group selection adds a unique outcome: altruism can evolve. However, when both levels of selection are in concert, the detection of multilevel selection is important because higher levels of selection can act on nonadditive genetic variance that cannot contribute to a response to selection at a lower level. Thus, the detection of group selection challenges us to incorporate components of variance not previously considered important in evolution.

Contextual analysis, like commonly used models of individual selection (*dashed box*, fig. 1) (Kalisz 1986; Stewart and Schoen 1987), is a phenotypic selection model. It measures within-generation changes in mean phenotype, which includes both genetic (heritable) and environmental (nonheritable) components. What we detect as group-level selection is complex interactions between the traits of individuals, their fitness, and the microhabitat (defined as both abiotic factors and intraspecific interactions) in which they are found. These local environmental differences are the group-level equivalent of environmental variation at the individual level. In other words, the relative magnitude of these genetic and environmental factors determine the heritability of the contextual traits. Whether group selection will lead to a response to group selection depends on the relative magnitude of the genetic versus nongenetic components. Further study is needed to determine the genetic potential of populations to respond to multilevel selection. An important caveat when using contextual analysis, or any parametric regression approach, is that the data must conform to the statistical assumptions of regression (Mitchell-Olds and Shaw 1987). With contextual analysis, deviations from this assumption may result in apparent group selection when none is occurring. For example, if a data set is lognormally distributed and the data are not transformed, then group selection may be detected, even if it is not occurring.

We feel studies of selection using contextual analysis extend our understanding of evolution for three reasons. First, traditional analyses of selection (*dashed box*, fig. 1) neglect ecologically important effects of population structure (e.g., competition) on fitness. Second, contextual analysis provides a means of quanti-

fyng such interactions and their relative importance. Finally, these interactions can be governed by nonadditive gene effects that can contribute to a response to selection at the group level. Documentation of group selection in nature expands our potential to understand both selection and the potential genetic responses to selection.

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