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# The Influence of Neighbor Relatedness on Multilevel Selection in the Great Lakes Sea Rocket

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**ABSTRACT:** Natural selection can operate at the individual and group level in natural populations. This study investigates the ecological factors that determine the relative importance of individual versus group selection. In particular, it determines how the relatedness of interacting neighbors influences multilevel natural selection in a population of the Great Lakes sea rocket. Focal plants were grown in groups of siblings, groups of plants that were themselves siblings but unrelated to the focal plants, and groups of plants with mixed genotypes. Significant group selection on plant size was observed only when the neighbors were siblings but not when they were unrelated. In sibling groups, individuals with heavier stems had higher fitness, and individuals growing with heavier but shorter neighbors also had higher fitness. Thus, individual and group selection on stem weight operated in the same direction. The detection of group selection in sibling groups can be attributed in part to an increased opportunity for group selection in these groups since sibling groups differed more from one another than the other group types. In addition, the quality of the selective environment in sibling groups may have differed from that for the other group types. Group selection was therefore more prevalent in the most genetically structured sample, in which responses to group selection are also most likely to occur.

*Keywords:* competition, dispersal, genetic relatedness, group selection, levels of selection, natural selection.

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Natural selection can operate at more than one level simultaneously (Wade 1977, 1978, 1982*a*; Tuomi and Vuorisalo 1989; Goodnight et al. 1992; Pedersen and Tuomi 1995; Tanaka 1996). Fitness can be determined both by the phenotype of an individual itself and by the phenotypes of group members with whom an individual associates. The evolution of phenotypes therefore depends on the

fitness consequences of both individual and group traits, and in such cases, natural selection is said to be operating at both the individual and group levels (Wade 1982*a*; Goodnight et al. 1992; Queller 1992*a*, 1992*b*; Taylor and Frank 1996). Group traits can be either emergent properties of groups or simply the mean phenotype held by group members. When group members are related, group-level selection is often referred to as kin selection, although it is now widely recognized that kin selection (which employs the concept of inclusive fitness) and group selection (which focuses on among-group variation in phenotype and fitness) are mathematically equivalent (Queller 1992*b*, 1992*c*).

Empirical studies of natural selection have tended to focus on selection operating only at the level of individuals, although a small number have estimated the strength of selection at multiple levels (Breden and Wade 1989; Stevens et al. 1995; Tsuji 1995; Banschbach and Herbers 1996; Kelly 1996). Group selection can oppose individual selection or augment it, and populations can evolve in response to natural selection at both levels simultaneously (Wade 1977, 1982*a*; Goodnight and Stevens 1997). Despite the abundant theoretical support for the potential of group selection to contribute to evolutionary processes (e.g., Uyenoyama and Feldman 1980; Wade 1982*a*; Cheverud 1985; Queller 1992*b*), only empirical studies can determine whether group selection actually occurs. Group selection has, in fact, been detected in natural populations in the few studies that have estimated it, yet the ecological factors that mediate the relative strength of different levels of selection remain virtually unknown empirically (Goodnight and Stevens 1997).

Several ecological processes can influence the relative contribution of group selection to evolutionary dynamics. One of the most important is dispersal (Wright 1931; Wade 1982*b*; Wade and McCauley 1984; Wilson 1987; Moore and Tonsor 1994; Wade and Griesemer 1998). Dispersal can influence multilevel natural selection through two mechanisms. First, dispersal alters population structure, and population substructuring influences the opportunity for multilevel natural selection. In structured populations,

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groups can differ phenotypically. Phenotypic variation among groups creates the opportunity for among-group selection. Groups can also differ genetically, thereby enabling a response to group selection if it should occur. Response to group selection occurs most easily when genetic variation within groups is small and variation among groups is large (Cheverud 1985). Dispersal among groups can reduce both phenotypic and genetic differences among groups and thereby reduce the likelihood of evolution by natural selection at levels other than that of the individual.

Second, dispersal alters group composition and thereby can alter the quality of natural selection within the group when group members impose selection on one another (Griffing 1981*a*, 1981*b*, 1981*c*, 1981*d*, 1989; Goodnight and Stevens 1997; Wolf et al. 1998). For example, dispersal can alter the phenotypic similarity among interacting organisms, the density or the intensity of interactions, or the probability of interacting with individuals of particular phenotypes. Thus, it can influence the particular character of natural selection on group members and the relative importance of group versus individual traits in determining fitness.

This article focuses on variation in the genetic and phenotypic similarity among interacting individuals that results from different degrees of dispersal. Another study (Donohue, in press) addresses how dispersal influences multilevel selection by altering the intensity of competitive interactions among group members through changes in sibling density.

The role of dispersal in multilevel selection has recently been debated, particularly with respect to its ability to facilitate the evolution of altruism. Dispersal simultaneously alters population structure (or the distribution of variation among groups) and competitive interactions within groups. Population viscosity, or highly localized dispersal, increases the probability that positive interactions among group members will benefit relatives as opposed to unrelated individuals and thereby promote the evolution of altruistic behavior (Hamilton 1964; Wilson 1987). However, Taylor (1992) showed theoretically that, in viscous populations, competition can exactly counteract the advantage of being in a group with altruistic relatives such that limited dispersal ultimately does not influence the probability of the evolution of altruism (Queller 1992*a*, 1994; Taylor 1992; Wilson et al. 1992). The nature of competition in these models was highly generalized, however, depending solely on the number of individuals in the group regardless of their genetic composition, spacing, or any other variable. In essence, severe local density-dependent regulation and strict soft selection were assumed. Such conditions may not occur in many natural ecological contexts. If, for example, competition for resources depends on the genotypes of competitors, then the

two factors, altruism and competition, may not exactly balance. Therefore, specific information on the nature of competition within groups (Cheplick 1992) is necessary to understand the dynamics of multilevel selection and the influence of dispersal on it.

Much literature has proposed that density-dependent processes will be influenced by the genetic composition of group members in addition to the number of competitors. In particular, genetic and phenotypic similarity among competitors is hypothesized to influence competitive dynamics. Genotypic differences among competitors are thought to result in differences in resource use, and such resource partitioning is hypothesized to weaken competitive interactions (Maynard Smith 1976; Young 1981; Bell 1985; Schmitt and Ehrhardt 1987; Argyres and Schmitt 1992; Cheplick 1992). Minority genotypes in mixed stands may also have an advantage if pathogens or herbivores specialize on particular genotypes (Levin 1975; Jaenike 1978; Price and Wasser 1982), and there is some empirical support for a rare-genotype advantage in the presence of herbivores (Schmitt and Antonovics 1986). In addition, with variation among competitors, size or dominance hierarchies can result, with some individuals being larger than and possibly suppressing others within the group (Weiner and Solbrig 1984; Weiner 1985, 1990; Schmitt et al. 1986, 1987; Thomas and Bazzaz 1993). In such systems, performance of some genotypes may be greatly depressed while that of others is enhanced. Such variation in size among group members can potentially influence group and individual performance (Weiner 1985; Griffing 1989 and references therein; Tonsor 1989). In a few cases, it has been shown that individuals growing with genetically or phenotypically similar plants actually performed better than those growing with unrelated individuals (Willson et al. 1987; Tonsor 1989). Thus, increased neighbor relatedness has been shown to have either a positive (Willson et al. 1987; Tonsor 1989) or a negative effect (Antonovics and Ellstrand 1984; Schmitt and Antonovics 1986) on plant performance. Which physiological, morphological, or life-history characters are most favorable may also depend on the relatedness of neighbors, since neighbor relatedness can determine the intensity of competition for resources, susceptibility to herbivory, and asymmetry of interactions. Thus, multilevel natural selection on these characters is predicted to vary with the degree of neighbor relatedness.

The experiment presented here was a manipulation of group composition in order to simulate variation resulting from low, intermediate, and high frequencies of dispersal in a population. Specifically, the genetic relatedness among group members was manipulated in order to determine its effect on multilevel selection on size characters in the annual beach plant, *Cakile edentula* var. *lacustris*, or the

Great Lakes sea rocket. Size is a fundamental life-history character of great demographic importance that has been shown to be under multilevel natural selection in other plant systems (Goodnight 1985; Stevens et al. 1995; Kelly 1996). Size and height mediate competitive interactions in many plant systems, and variation in size has been shown to influence individual- and stand-level productivity (Griffing 1989 and references therein). Determining the relative importance of individual and group size characteristics to reproductive success can provide relevant information about mechanisms that create variation in stand or population productivity and mechanisms that cause differential contributions of genotypes to future generations.

By varying the relatedness among group members, the manipulation employed in this study simultaneously altered the genetic structure of the experimental populations and the quality of the competitive neighborhood experienced by group members. The manipulations were performed in the field in a naturally heterogeneous environment in order to characterize multilevel natural selection under ecologically realistic conditions. Through these manipulations, I addressed the following questions: How does the relatedness of group members influence size and fitness? Does the strength or direction of individual and group selection depend on group composition? Does group composition alter the opportunity and/or the quality of multilevel natural selection?

### Methods

*Cakile edentula* var. *lacustris* is an annual mustard (Brassicaceae) that grows on the shores of the Great Lakes of North America. It typically grows on the open beach or up on primary dunes. It has heteromorphic fruit segments that are usually single seeded (Rodman 1974). The proximal segments often remain attached to the dead maternal plant through germination. The distal segments frequently detach from the proximal segment and are dispersed independently by wind and water. Distal segments also become trapped within the branches of the maternal plant and germinate in its immediate vicinity (Donohue 1998). As a consequence, *C. edentula* often occurs in extremely high-density clumps, with hundreds of individuals within a 100-cm<sup>2</sup> area, and these clumps are usually composed of full or half siblings.

The experiment was conducted in the Indiana Dunes National Lakeshore near Michigan City, Indiana. Ripe fruit segments were collected from 14 maternal plants during the natural dispersal season in late summer, and the exact location of the maternal plant site was marked with a wooden dowel. Maternal plants were located by walking along the beach, beyond the range of typical beach traffic, and sampling plants arbitrarily at approximately 25-m in-

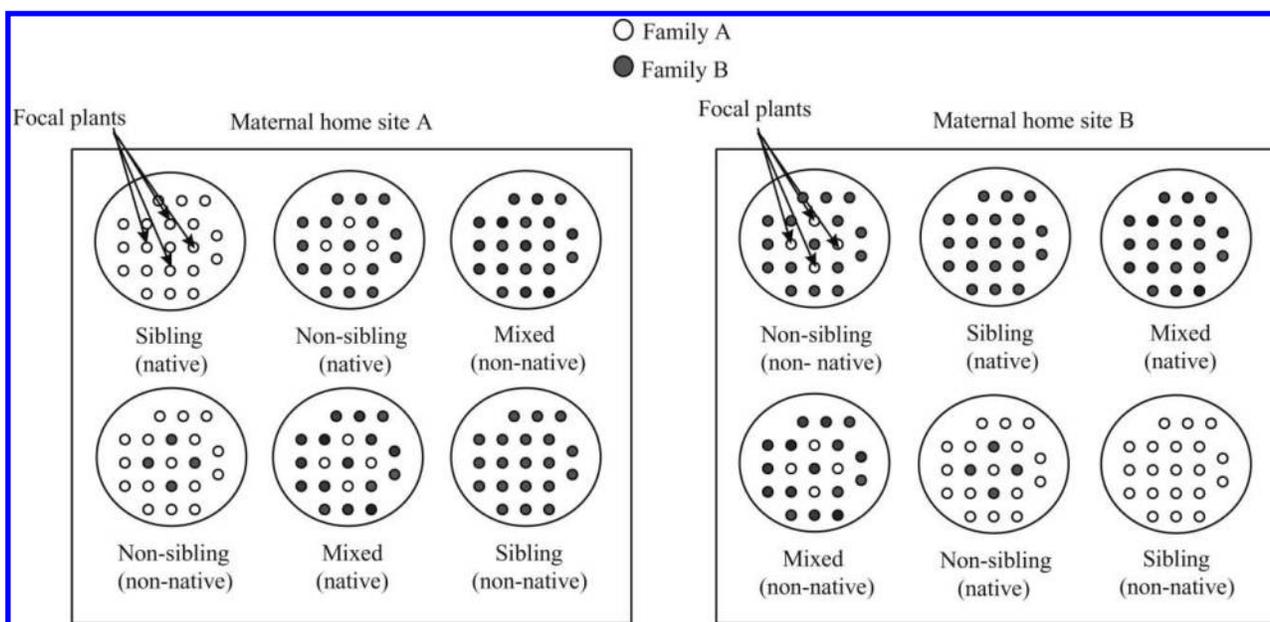
tervals. Seeds from these plants were full- to half-sibling groups ("families" hereafter) and were kept dry at room temperature until the following spring.

During March, seeds were weighed and then forced to germinate by imbibing the seeds and removing the seed coats. Seeds were planted into 3/4-inch plug trays in a 1 : 1 mixture of Pro-Mix artificial soil (Premier Brand) and Terragreen (baked clay) and maintained in the greenhouses of the University of Chicago. After the first true leaves appeared, seedlings were transplanted into the field.

Three competitor treatments (sibling, nonsibling, and mixed) and two location treatments (native and nonnative) were imposed in a factorial manner. In all treatments, four focal individuals were grown in competition with 16 nonfocal individuals to create clumps of 20 seedlings within approximately a 5-cm diameter area (fig. 1). At each maternal plant site, six such clumps were planted, with 20 cm between clumps. In three of the clumps, the focal individuals were offspring of the maternal plant that grew at that site, and in the other three clumps, the focal individuals were from one randomly chosen family. Members of the two paired families were reciprocally planted into the others' maternal site so each family had replicates at its native site and at a nonnative site. I refer to this manipulation of the site of planting as the "native" treatment hereafter.

At each site, three competitor treatments were imposed. In the first treatment, "sibling," focal individuals competed only with siblings (group members were all supplied by the same maternal plant). In the second treatment, "nonsibling," the focal individuals competed with individuals of the randomly chosen family with which it was paired. In the third treatment, "mixed," the focal individuals competed with a mixture of genotypes. All families contributed to the pool of seeds used for the mixed treatment, and 16 random individuals were selected from this pool of seeds for each mixed clump. At each maternal plant site, each treatment was planted for both the native and nonnative focal genotype.

These three competitor treatments represent three possible competitive environments likely to be experienced by *C. edentula* seeds depending on the frequency of dispersal in the population. The sibling competitive environment would occur when seeds are not efficiently dispersed, as happens frequently in this system when seedlings germinate from seeds that are still attached to the dead maternal plant. The nonsibling competitive environment could result when individually dispersing seeds are dispersed into an unrelated high-density clump. The mixed competitive environment occurs when dispersed seeds of many different genotypes are washed up together or accumulate in the same microsite. The sibling competitive environment would be common when dispersal is rare,



**Figure 1:** Experimental design. Each group (*large circles*) contained 20 plants (*small circles*), four of which were focal individuals. Six groups were planted at each maternal site (*boxes*), and two maternal sites are shown. Maternal home site A is the native site of family A and the nonnative site of family B. Maternal home site B is the native site of family B and the nonnative site of family A. Light and dark circles represent different families. Three competitor treatments (*sibling*, *nonsibling*, and *mixed* genotype) are shown for native and nonnative genotypes at each maternal site.

the nonsibling competitive environment would occur at an intermediate frequency of dispersal (since some seeds are dispersed while others are not), and the mixed competitive environment would occur most often when the frequency of dispersal in the population is high.

All focal seedlings were monitored throughout their life, and censuses were conducted every two weeks. During censuses, the number of flowers and fruits was recorded, and the date of death was recorded. At the time of death, a final fruit count was conducted, and the plant was collected. Nonfocal plants were also collected at the time of death. Height and stem weight of dead plants were determined. Fitness was estimated as the total number of fruit segments. Because fruit segments are usually single seeded, this is an accurate estimate of total lifetime seed production. The number of fruit segments was usually estimated as the total number of fruits and pedicles present at the time of collection times two (because there are two fruit segments in each fruit) and minus the number of abortions. Some plants blew away before collection, resulting in missing values for some focal and nonfocal plants.

The SAS Institute statistical package (1990) was used for all analyses. Data were natural log transformed to improve normality. To test for the effect of competitor treatment and the effect of growing at the native versus nonnative site, a mixed-model ANOVA was performed.

Competitor treatment and native treatment were crossed fixed factors, family was a random factor, and seed mass was a continuous covariate. Main effects of competitor and native treatments were tested over their interactions with family treatment. An alternative analysis substituted the maternal site for the native site in order to interpret the initial results. The maternal site was a random factor in that analysis. A MANOVA tested for significant main effects and interactions on plant height, stem mass, and number of fruit segments combined, while individual ANOVAs subsequently tested for significant effects on each trait separately. Many plants did not reproduce at all, so segment number data were nonnormal. The residuals of the analysis of segment number were leptokurtic, so probabilities are only approximate. For this reason, reproductive success, scored as whether or not plants reproduced, was analyzed with logistic regression (Proc Catmod; SAS Institute 1990) to test for main effects and interactions between competitor and native treatments. Other interactions could not be included in the model because of empty cells. Seed mass was used as a continuous covariate.

A nested analysis of variance was conducted to estimate the percentage of variation in traits expressed within versus between groups for each competitor treatment. In one analysis, only the focal individuals were used. In an additional analysis, focal and nonfocal individuals were used. The first analysis, using only focal plants, more precisely

assesses the effects of neighbor relatedness on the distribution of variance while controlling for family. The second analysis determines the distribution of phenotypic variance of all group members; it is therefore the more ecologically realistic representation of the consequences of neighbor relatedness for multilevel selection, since all group members are under selection. One-way ANOVAs using Proc GLM (SAS Institute 1990) were performed to test for significant among-group variation since sample sizes were somewhat unbalanced.

To determine the strength of multilevel natural selection on the size characters of height and stem mass, a contextual analysis (Heisler and Damuth 1987; Goodnight et al. 1992) was performed. This analysis uses multiple regression to estimate the effect of an individual's phenotype on that individual's fitness as well as the effect of the group mean phenotype on individual fitness. The selection coefficient for individual phenotypes can be interpreted as an estimate of the strength of individual-level selection, and the selection coefficient for the group mean phenotypes can be interpreted as an estimate of the strength of group-level selection (Goodnight et al. 1992; Stevens et al. 1995). Such a multiple regression approach is standard in many theoretical models of multilevel selection (e.g., Cheverud 1984; Queller 1992c; Wolf et al. 1999) and has the advantage of being able to employ thoroughly familiar methodology that has been developed to measure the strength of selection on correlated characters (Lande and Arnold 1983). In this analysis, all focal and nonfocal plants were used so that all group members could be included. The mean height and stem mass were calculated for each group, and these mean phenotypes were included in the regression analysis with the individual phenotypes for each member of the group. In this manner, the influence of the group mean phenotype can be estimated independently of the influence of the individual phenotype. In all analyses, family was initially used as an additional factor. However, results did not differ when family was excluded, so only results without family are presented here.

Three different methods of standardization were used. In the first method, which is the most common in the literature, traits were standardized within each competitor treatment to have a mean of 0 and SD of 1. Relative fitness was calculated as the fitness of each individual divided by the mean fitness of all individuals within each competitor treatment. In the second method of standardization, phenotypes were standardized within treatments, as before, but fitness was also standardized within treatment to have a mean of 0 and an SD of 1. This method constrains all treatments to have the same total variance in phenotypes and fitness. However, results of this second method of standardization did not differ much from the previous method, so these results are not presented here. In the last

method of standardization, traits were standardized across all treatments to have a mean of 0 and an SD of 1. Relative fitness was calculated as the fitness of each individual divided by the mean fitness of all individuals in all competitor treatments. This method of standardization differs from the others in that it permits the variance among groups to differ across treatments. Therefore, if competitor treatment influences the degree of variance among groups and consequently the opportunity for between-group selection, then such differences will be manifest using this last method of standardization but not the other methods, in which the variance is constrained to be 1 in all treatments.

Directional selection gradients were measured using multiple regression (Lande and Arnold 1983). Selection gradients are estimates of the strength of direct selection on characters while controlling for indirect selection acting through correlated characters. The strength of selection was compared across treatments using ANCOVA with relative fitness as the dependent variable; a significant interaction between the trait and the competitor treatment indicates that selection on that trait differed across treatments. Because the residuals of the selection analyses were not always normally distributed and sometimes were slightly leptokurtic, jackknife resampling was performed to estimate SEs of the selection gradients using the program *Freestat* (Mitchell-Olds 1989).

Nonlinear and correlational selection gradients were estimated by including the squared terms and cross products in a multiple regression. As before, jackknife SEs of the estimates were obtained using *Freestat* (Mitchell-Olds 1989). The coefficients for the squared terms provide estimates of stabilizing (if negative) or disruptive (if positive) selection. The coefficients of the cross products provide estimates of correlational selection, or how selection on one character depends on a second character. In contextual analysis, correlational selection coefficients can also provide information on how levels of selection interact; for example, the analysis can indicate whether the nature of individual selection depends on the group phenotype (Agrawal et al. 2001). Results of nonlinear selection are presented only from the last method of standardization since these results were similar to all methods of standardization.

In a heterogeneous environment, environmentally induced correlations between phenotypes and fitness can occur, and these environmental correlations alter estimates of natural selection (Mitchell-Olds and Shaw 1987; Rausher 1992). In order to control for environmentally induced correlations, separate selection analyses were conducted using the residuals of an ANOVA of variance that included the maternal site as the independent factor and fitness (number of fruit segments) as the dependent var-

**Table 1:** Results of ANOVA to test for treatment effects on plant characters and fitness

Source	ndf	ddf	<i>F</i> (Height)	ddf	<i>F</i> (Stem mass)	ddf	<i>F</i> (Fitness)
Seed mass	1	187	25.83***	188	29.69***	189	2.45
Treatment	2	29	2.76 <sup>+</sup>	29	1.23	27	4.63*
Native	1	14	.54	14	.06	14	.17
Family	13	15	.74	16	.61	25	1.15
Treatment × native	2	27	1.99	27	2.10	27	.47
Treatment × family	26	26	1.53	26	1.68 <sup>+</sup>	26	5.10***
Native × family	13	26	4.99***	26	4.06**	26	1.35
Treatment × native × family	25	187	1.26	188	1.31	189	1.19
<i>N</i>			271		272		273

Note: *F* ratios are given for each trait by column; results are based on type III sums of squares. ndf = numerator degrees of freedom; ddf = denominator degrees of freedom. One extreme outlier was excluded from the analysis of stem weight, but this exclusion did not change the results qualitatively.

<sup>+</sup>  $P < .1$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

table. In this manner, variation in fitness that was due to environmental variation in the landscape was factored out, and the residuals of fitness were analyzed. Therefore, these analyses test whether any observed association between phenotype and fitness was due solely to environmentally induced correlations. These analyses were conducted on traits that were standardized both within and across treatments, as described above. Fitness was not relativized by dividing individual fitness by the mean fitness because the mean value of residuals is 0. Results from the analyses of the residuals were similar to results based on relative fitness itself, so these results are not presented in the tables. Any differences between the results of residuals are indicated in the text. The similarity in results using these two methods indicates that the estimates of selection presented in the tables are not biased by environmental correlations at the scale of among-site environmental variation.

To further interpret the results from the contextual analysis, a path analysis (Kelly 1996) was also conducted. With path analysis, causal pathways known a priori can be included in the analysis of selection. In the case of multilevel selection, the influence of group phenotypes on individual phenotypes can be included as separate paths (Kelly 1996). Kelly argued that path analysis can reveal indirect effects of neighbor phenotypes on individual fitness—or indirect paths of group selection—that contextual analysis does not detect. That is, plastic responses of individual phenotypes to neighbor phenotypes reflect an additional contribution of group selection, since individual phenotypes and hence the opportunity for individual selection are actually in part due to characteristics of neighbors in addition to the genetic composition of the individual. Path coefficients were estimated on standardized traits and fitness using Proc Corr and Proc Reg (SAS Institute 1990). In contrast to

the contextual analysis, group mean traits were calculated only from nonfocal individuals so that the phenotype of focal individuals would not cause a spurious correlation with group mean phenotype. The effect of neighbor traits on the phenotype and fitness of focal individuals was estimated.

## Results

MANOVA detected significant effects of seed mass ( $F = 10.17$ ,  $P < .001$ ), competitor treatment ( $F = 2.40$ ,  $P < .05$ ), family ( $F = 1.81$ ,  $P < .05$ ), and significant effects of interactions between competitor treatment and family ( $F = 2.54$ ,  $P < .001$ ) and native site and family ( $F = 2.39$ ,  $P < .001$ ) on plant characters. Based on individual ANOVAs, plant height and stem mass were not influenced by competitor treatment or by whether the plant was growing in its native site (table 1; fig. 2). Plants did not necessarily grow larger when grown at their home site. Rather, the effect of growing in the native site depended on the family. Some families were taller and larger in their native site, and others were taller and larger in a nonnative site. When the maternal site was included as a random factor instead of the native treatment, no significant interactions were detected between family and site (site × family:  $F[\text{height}] = 1.79$ ,  $P > .05$ ;  $F[\text{stem mass}] = 1.48$ ,  $P > 0.05$ ; ndf = 6, ddf = 11 for both). These results indicate that differences in site quality influence fitness strongly; if both families within the pair were larger at the same site, then a site × native interaction would result without a site × family interaction, as was observed here. The lack of a significant main effect of site overall ( $F[\text{height}] = 3.15$ , ndf = 8, ddf = 2,  $P > .05$ ;  $F[\text{stem weight}] = 3.42$ , ndf = 8, ddf = 3,  $P > .05$ ) is likely to be due to the sig-

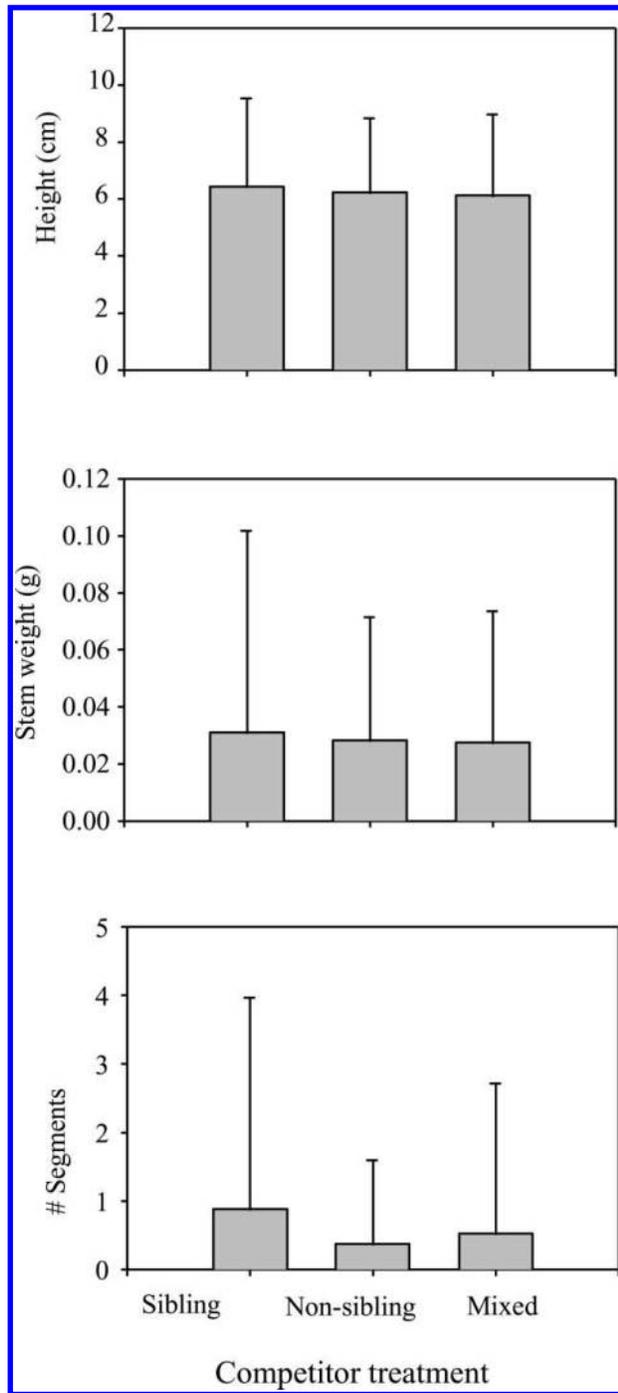


Figure 2: Means and SDs of untransformed plant traits for each of the three competitor treatments.

nificant or nearly significant three-way interactions such that the effect of site depended on the particular combination of family and competitor treatment (treatment  $\times$  site  $\times$  family:  $F$ [height] = 2.13,  $P$  = .02,

$ndf$  = 11,  $ddf$  = 87;  $F$ [stem weight] = 1.69,  $P$  = .08,  $ndf$  = 11,  $ddf$  = 188). This beach environment therefore is heterogeneous in site attributes that influence size, but these site attributes alone do not determine plant size.

Competitor treatment did influence fitness (table 1; fig. 2). Plants growing with siblings had more fruit segments, and plants growing with another family had the least number of fruit segments. Residuals of this analysis were leptokurtic, so statistical probabilities presented in table 1 are only approximate. In a logistic regression, neither native ( $\chi^2$  = .34,  $df$  = 1,  $P$  > .05) nor competitor treatment ( $\chi^2$  = 2.20,  $df$  = 2,  $P$  > .05) nor their interaction ( $\chi^2$  = 2.29,  $df$  = 2,  $P$  > .05) influenced whether plants reproduced. This result suggests that any effect of competitor treatment on fitness is more through the amount of reproduction rather than through survival to reproduce.

Family interacted with competitor treatment to influence fitness (table 1). Some families had highest fitness when competing with siblings whereas other families had higher fitness when competing with unrelated families or with mixed genotypes (fig. 3). Families that had high fitness in sibling groups also tended to have high fitness in nonsibling groups ( $r$  = .61,  $P$  < .05,  $N$  = 14; based on mean family fitness), but fitness in mixed groups was not correlated with fitness in sibling groups ( $r$  = .14,  $P$  > .05,  $N$  = 14) or nonsibling groups ( $r$  = -.05,  $P$  > .05,  $N$  = 14). Therefore, there is no evidence of trade-offs in performance across the different competitor treatments; families do not specialize to perform well in one competitive environment at the cost of performing poorly in a different competitive environment.

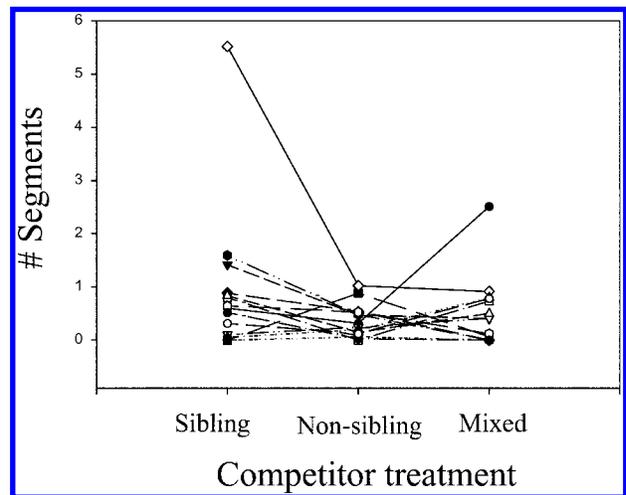


Figure 3: Mean number of fruit segments for each family in each of three competitor treatments. Omission of the extreme genotype with high segment production did not alter the significance of the family by treatment interaction ( $F$  = 7.66,  $P$  < .001 when that family was omitted).

Variance in height and stem mass of focal plants was distributed fairly evenly within and among groups when plants were grown with siblings (table 2, "Focal plants only"). Variance in height was also distributed evenly within and among groups for focal plants grown with nonsiblings, but more variation in stem mass was contained within groups than among groups in that treatment. When plants were grown with a mixture of genotypes, more variation was contained within groups than among groups for both height and stem mass. Thus, competitors of mixed genotypes appear to create microenvironmental variation within groups, which in turn causes greater variability among focal individuals derived from a single genotype. Likewise, genetically homogeneous competitors may create a less heterogeneous microenvironment, which leads to less variation in the focal individuals.

All or nearly all of the variance in the number of fruit segments was contained within groups when plants were not growing with siblings, indicating that the fitness of focal plants did not differ among groups in these treatments. When plants were growing with siblings, however, the variance in fitness among groups was similar to the variance in fitness among individuals within groups. Thus groups differ most in fitness when the groups are composed of siblings. The same pattern was observed when nonfocal individuals were included, but the differences among the competitor treatments were less pronounced (table 2, "All plants within groups"). This effect was caused in part by greater differentiation among groups in the mixed competitor treatment when considering nonfocal plants (12% variation among groups) than when considering just focal plants (which did not differ at all among groups in this treatment). Variations within sibling groups also increased when nonfocal siblings were included. These

differences in the distribution of phenotypic variation within and among groups when considering nonfocal individuals was unexpected, but random variation in the environment of peripherally located individuals (i.e., nonfocal plants) may have contributed to variation within groups of siblings. Likewise, spatial variation experienced by nonfocal peripheral plants and the stochastic sampling of mixed competitors could have contributed to variation in fitness among mixed-genotype groups. Therefore, in a naturally heterogeneous field environment, the influence of population structure on the distribution of phenotypic variation among individuals and groups appears to be less pronounced than would be expected under a uniform environment.

Variation in fitness among groups was observed in this study, with some groups contributing >100 times the number of seeds to the propagule pool than others (sibling groups: range = 0–151, SD = 30; nonsibling groups: range = 0–31, SD = 9; mixed groups: range = 0–75, SD = 16), leading to spatial variation in stand reproduction. In addition, fruit production by groups was significantly correlated to the mean size of individuals in the groups, indicating that soft selection was not observed in this experiment (sibling groups:  $r[\text{height}] = .84$ ,  $P < .001$ ,  $r[\text{stem mass}] = .95$ ,  $P < .001$ ; nonsibling groups:  $r[\text{height}] = .60$ ,  $P < .001$ ,  $r[\text{stem mass}] = .53$ ,  $P < .01$ ; mixed groups:  $r[\text{height}] = .63$ ,  $P < .001$ ,  $r[\text{stem mass}] = .59$ ,  $P < .001$ ).

Competitor treatment influenced patterns of multilevel selection. When values were standardized within each competitor treatment (table 3), higher fitness was significantly associated with larger stems (nearly significant in nonsibling groups). Taller plants had higher fitness when they competed in nonsibling groups (nearly significant

**Table 2:** Percentage variance explained within and among groups for the three competitor treatments

	Sibling		Nonsibling		Mixed	
	Among	Within	Among	Within	Among	Within
Focal plants only:						
Height	45***	55	43***	57	24*	76
Stem mass	42***	58	31**	69	29**	71
Segments	54***	46	2	98	0	100
df	26	63	26	59	27	63
All plants within groups:						
Height	37***	63	27***	73	35***	65
Stem mass	36***	64	27***	73	33***	67
Segments	26***	74	10***	90	12***	88
df	27	450	27	452	27	470

Note: Asterisks indicate the significance of among-group differences based on one-way ANOVA.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

**Table 3:** Multilevel selection gradients for each of three competitor treatments when standardized within each treatment

Character	Sibling $\beta$	Nonsibling $\beta$	Mixed $\beta$	$F$ interaction
Height	.42 (.33)	.77* (.31) <sup>b</sup>	.60 (.40)	.25
Stem mass	1.43*** (.36)	.61 <sup>+</sup> (.35) <sup>a</sup>	1.33* (.53)	1.67
Mean height	-.90* (.43)	-.34 <sup>+</sup> (.29) <sup>a</sup>	-.83 (.65)	.71
Mean stem mass	1.36** (.46)	.42 (.30)	.84 (.65)	1.81
$N$	478	480	498	1,456

Note: Jackknife SEs are shown in parentheses. Significant differences from 0 are indicated and are based on jackknife SEs. Mixed  $F$  interaction refers to the  $F$  ratio for the interaction between the trait and competitor treatment, and it tests whether the selection gradients differ significantly among the competitor treatments.

<sup>a</sup> Significant when based on residuals of fitness.

<sup>b</sup> Not significant when based on residuals of fitness.

<sup>+</sup>  $P < .1$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

when the analysis was done on residuals of site variation), but plant height was not significantly associated with fitness in the other treatments. Group-level selection was detected only in groups composed of siblings, although a similar trend for group selection on height was found in the nonsibling treatment. In sibling groups, plants had higher fitness when other members of the group were shorter and had larger stems. Thus individual-level and group-level selection on stem size operated in the same direction in these groups.

When residuals of fitness were analyzed after factoring out variation due to site, two trends in nonsibling groups became significant. The trend for heavier individuals to have higher fitness and the trend for plants growing with shorter neighbors to have higher fitness both became significant.

When values were standardized across all treatments,

the same patterns were observed as when values were standardized within each treatment (table 4). However, both individual and group-level selection on stem mass differed significantly across competitor treatments; both were strongest in sibling groups.

Disruptive selection was detected in sibling groups for group mean height and group mean stem weight such that plants had the lowest fitness when they grew within groups of intermediate-sized plants (table 5). Taller individuals had higher fitness if they also had larger stems, as indicated by the positive correlational selection coefficient between individual height and individual stem mass. Shorter neighbors were associated with higher fitness when those neighbors also had heavy stems (negative correlational selection for mean height  $\times$  mean stem mass). In nonsibling groups, no stabilizing or disruptive selection was detected, but significant correlational selection between individual

**Table 4:** Multilevel selection gradients for each of three competitor treatments when standardized across treatments

Character	Sibling $\beta$	Nonsibling $\beta$	Mixed $\beta$	$F$ interaction
Height	.62 (.48)	.49* (.20) <sup>b</sup>	.54 (.36)	.04
Stem mass	2.14*** (.54)	.38 <sup>+</sup> (.21) <sup>a</sup>	1.19* (.47)	6.65**
Mean height	-1.29* (.61)	-.24 <sup>+</sup> (.21) <sup>a</sup>	-.69 (.54)	1.95
Mean stem mass	2.15** (.73)	.30 (.21)	.64 (.50)	6.80**
$N$	478	480	498	1,456

Note: Jackknife SEs are shown in parentheses. Significant differences from 0 are indicated and are based on jackknife SEs. Mixed  $F$  interaction refers to the  $F$  ratio for the interaction between the trait and competitor treatment, and it tests whether the selection gradients differ significantly among the competitor treatments.

<sup>a</sup> Significant when based on residuals of fitness.

<sup>b</sup> Not significant when based on residuals of fitness.

<sup>+</sup>  $P < .1$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

**Table 5:** Nonlinear and correlational selection coefficients ( $\gamma$ ) for the three competitor treatments

Character	$\gamma$ -Sibling	$\gamma$ -Nonsibling	$\gamma$ -Mixed
(Height) <sup>2</sup>	-.65 (.42)	-.09 (.28)	.28 (.90)
(Stem mass) <sup>2</sup>	-.48 (.42)	-.35 (.29)	-.40 (.98)
(Mean height) <sup>2</sup>	1.30* (.51) <sup>b</sup>	.33 (.38)	.79 (.85)
(Mean stem mass) <sup>2</sup>	2.24*** (.60) <sup>b</sup>	.21 (.42)	.47 (.50)
Height $\times$ stem mass	2.59** (.88)	.91 (.58)	1.48 (1.95)
Mean height $\times$ mean stem mass	-3.39** (1.04)	-.60 (.70)	-1.19 (1.16)
Height $\times$ mean height	-.97 (.62)	1.07* (.51)	.16 (1.08)
Stem mass $\times$ mean stem mass	.29 (1.04)	1.50** (.55)	2.33 (1.35) <sup>a</sup>
Height $\times$ mean stem mass	1.82 <sup>+</sup> (.97)	-.80 (.54)	-.36 (.89)
Stem mass $\times$ mean height	-.61 (.95)	-1.80*** (.54)	-2.82 (1.80) <sup>a</sup>
<i>N</i>	478	480	498

Note: Values were standardized across all treatments. Jackknife SEs are shown in parentheses. Significant differences from 0 are indicated and are based on jackknife SEs.

<sup>a</sup> Significant when based on residuals of fitness.

<sup>b</sup> The minimum of the function was within the range of variation in the data set, indicating that intermediate phenotypes were associated with the lowest fitness.

<sup>+</sup>  $P < .1$ .

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

and group traits was found. Positive correlational selection was observed, such that tall individuals growing with tall neighbors and heavy individuals growing with heavy neighbors had higher fitness than individuals that differed from their neighbors in size. Negative correlational selection was detected such that heavy individuals had higher fitness if their neighbors were shorter. When residuals were analyzed, groups of mixed genotypes displayed positive correlational selection between individual and group stem mass and negative correlational selection between individual stem mass and group height, as was seen in the nonsibling groups.

Path analysis revealed positive relationships among most traits of neighbors and focal individuals (fig. 4). The mean stem mass of neighbors influenced the size of focal individuals most strongly in sibling groups. The effects of neighbor and individual traits on individual fitness were very similar to those obtained from the contextual analysis. However, in contrast to results from the contextual analysis, group selection on height in sibling groups was not

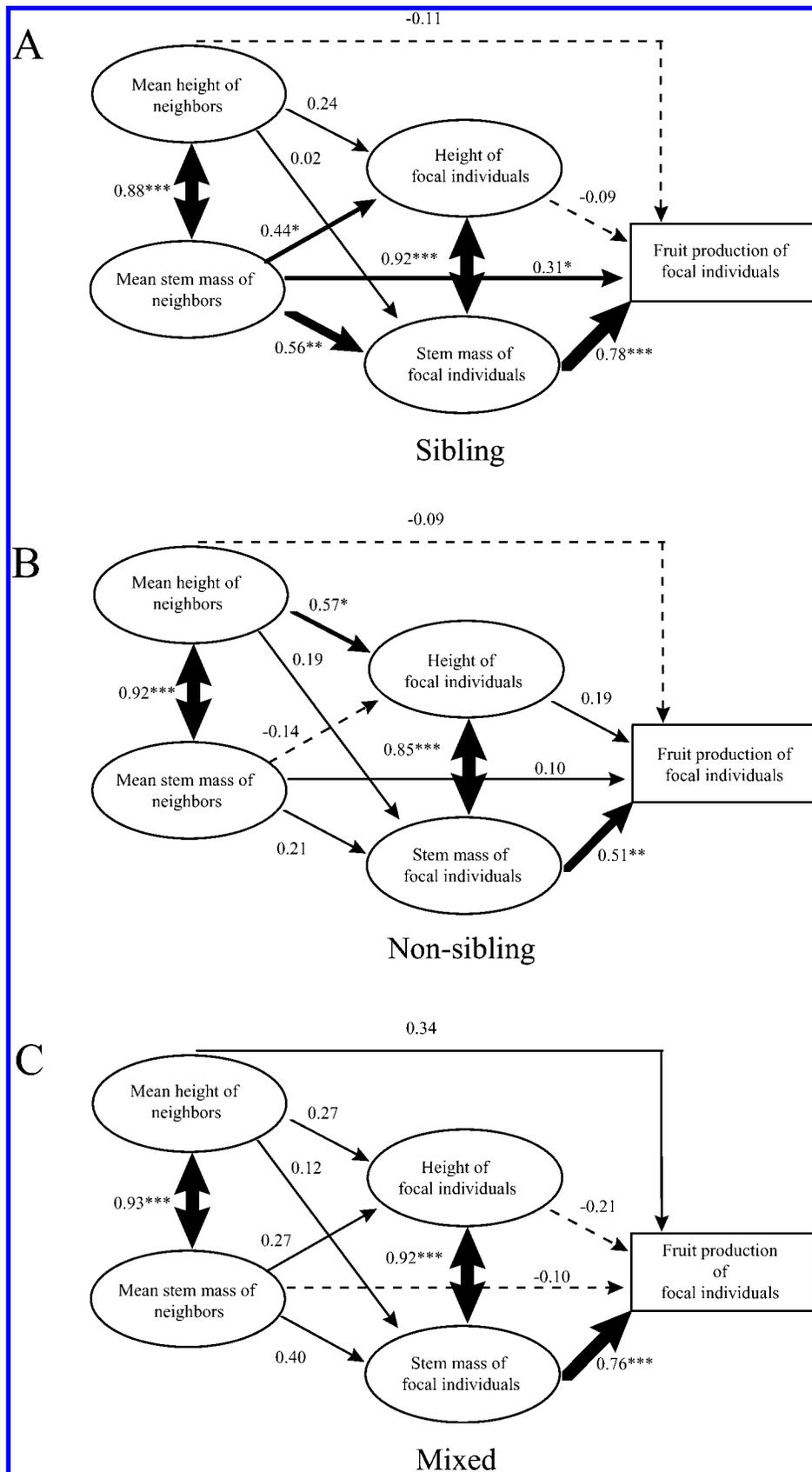
significant in the path analysis, nor was individual selection on height in nonsibling groups.

## Discussion

Neighbor relatedness significantly altered patterns of multilevel selection in a heterogeneous natural landscape. First, neighbor relatedness influenced reproductive success itself such that higher reproductive success was achieved when plants were growing with siblings than when growing with nonsiblings or with mixed genotypes. In addition, neighbor relatedness influenced multilevel selection on size. Individual selection on plant size was detected in all treatments, but group selection was detected in only sibling groups. In sibling groups, heavier plants growing with shorter and heavier neighbors had the highest fitness.

Neighbor relatedness influenced fitness overall, with the highest average fitness being obtained within sibling groups. In this population, high-density clumps of closely related seedlings are quite common, and intense compe-

**Figure 4:** Path diagram of the relationships between group traits, individual traits, and individual fitness for groups grown with siblings (A), nonsiblings (B), and mixed genotypes (C). Single-headed arrows indicate an a priori causal relationship, and double-headed arrows indicate correlation. The thickness of arrows is proportional to the significance of the path coefficient. Solid lines indicate positive path coefficients, and dashed lines indicate negative path coefficients. \* =  $P < .05$ ; \*\* =  $P < .01$ ; \*\*\* =  $P < .001$ .



tion with unrelated plants is less common. Thus, this population may have acquired adaptations that improve performance when plants compete with siblings but not when they compete with nonsiblings. Although a few previous studies have documented that plants perform better when they grow in competition with unrelated genotypes (e.g., Schmitt and Antonovics 1986), a small number of studies have demonstrated results similar to those in this article, namely, that plants perform better when grown with siblings (Willson et al. 1987; Tonsor 1989). Such an effect is rather unusual, as most studies that are designed to detect effects of neighbor relatedness on fitness did not detect any at all (e.g., Schmitt and Ehrhardt 1987; McCall et al. 1989; Argyres and Schmitt 1992; Burt and Bell 1992; Cheplick 1992). This study provides evidence against the "elbow room" hypothesis (Young 1981), which states that competitive interactions are less intense when competing genotypes differ. It also does not support the hypothesis of a rare-genotype advantage mediated by herbivore specialization (Levin 1975; Jaenike 1978).

Similar to the results of this experiment, Tonsor (1989) found that *Plantago lanceolata* had higher seed yield when grown with siblings than when grown with nonsiblings under suboptimal greenhouse conditions. He hypothesized that this advantage was caused by the more even size distribution of individuals within sibling groups than in groups of mixed genotypes. He argued that siblings did not suppress each other to the point of preventing reproduction. In mixed groups, however, larger plants suppressed smaller plants, causing a lack of reproduction in several group members and consequently lower mean reproduction under the conditions of the experiment (see also Weiner and Solbrig 1984; Weiner 1985, 1990). That is, only the largest genotypes were more suppressed in sibling groups than in the mixed groups such that, averaged over all groups, sibling groups had higher fitness. In *Cakile edentula*, plants within sibling groups were also less variable than those in mixed groups, suggesting that Tonsor's hypothesized mechanism may be operating in this system as well. The result that individuals in mixed groups perform better when they resemble their neighbors (table 5) also supports this interpretation.

In this experiment, the effect of neighbor relatedness on fitness depended on the family. Some families had higher fitness when competing with siblings, whereas others had higher fitness when competing with unrelated genotypes. The differences among families can be attributable both to genetic differences and to maternal effects, since the seeds used were collected from the field. This result suggests that dispersal influences the fitness of families differently; dispersal would be more advantageous for families that compete poorly with siblings. One therefore might predict associations between dispersal and perfor-

mance in sibling and nonsibling groups; families that perform well in sibling groups may have less dispersal than families that perform poorly. Many other factors such as density (Donohue 1998) and environmental heterogeneity also influence the adaptive value of dispersal, however, so neighbor relatedness is not likely to control such dynamics very strongly in this system.

The observation that competitive outcomes depend on the genetic composition of interacting group members emphasizes the need to investigate the ecological context of competition in plant populations (Cheplick 1992). Theoretical models that define competitive intensity to be solely a function of the number of individuals in a group have concluded that limited dispersal is unlikely to influence kin selection because the advantage of being in an altruistic group is exactly counterbalanced by increased competition (reviewed by Queller 1992a). Such precise balances need to be questioned in light of ecological factors that influence the intensity of competition among group members, such as neighbor relatedness and postdispersal density. The lack of soft selection in this system also argues against such strict balances. This study not only found evidence for group selection but also found an effect of a dispersal-dependent factor on the strength of group selection.

Group composition altered fitness itself, but it also influenced the strength with which other group attributes influenced fitness. The mean size of competitors significantly influenced fitness only in sibling groups. Plants had higher fitness if their sibling neighbors were heavier and shorter. Such neighbors could conceivably shade the soil and prevent evaporation without shading the individual. Phenotypic manipulations, such as those performed by Kelly (1996), would be necessary to test the functional predictions suggested by these results. Kelly found that plants growing in groups of more highly branched individuals had higher fitness, although Stevens et al. (1995) found that plants growing in groups of smaller individuals had higher fitness. Thus, multilevel selection on plant size may not always have a consistent pattern, even within a system, although the measurements of "bushiness" (Kelly 1996) and "size" (Stevens et al. 1995) were not directly comparable. In a separate experiment in the same natural population as was used in this study and in which sibling groups were grown at high density, heavier neighbors were also associated with higher fitness of focal individuals, although no group selection was detected when all members of the groups were analyzed in a contextual analysis (Donohue, in press).

Path analysis revealed an indirect pathway whereby neighbor size can influence individual fitness. Positive associations were observed between the size of neighbors and of focal individuals, particularly in sibling groups.

These positive associations are likely to be due in part to positive genetic and environmental associations between focal plants and neighbors, since the neighbors were siblings growing in the same location as the focal plants. Plasticity of focal individuals in response to neighbor size could also have contributed to the positive correlations. Such plasticity could contribute to group selection on size, since by altering individual size, neighbor size can thereby alter the opportunity for individual selection (Kelly 1996).

Unlike Stevens et al. (1995), who documented that group selection on size operated in the opposite direction of individual selection, these results show group and individual selection on stem mass operating in the same direction. Stevens et al. argue that the antagonism between group and individual selection that they observed may account for soft selection in their system, with each group contributing equal numbers of seeds to the progeny pool regardless of the mean size of individuals in the group. In contrast, the results of this experiment indicate that groups are likely to contribute differentially to the next generation. Variation in fitness among groups was, in fact, observed in this study, and fruit production by groups was significantly correlated to the mean size of individuals in the groups. Therefore, soft selection is not present in this sample. Fitness variation among groups, moreover, was more pronounced when groups were composed of siblings (table 2), and unrelated genotypes did not influence an individual's fitness as strongly as related genotypes. These results indicate that the differential contribution of genotypes to future generations occurs not only because of variation in fitness among genetically diverse individuals competing within groups but also because of variation in group performance among groups that differ genetically (i.e., groups of siblings). Therefore, the combined effects of individual and group selection can influence both the rate at which a given genotype can dominate a population and the rate of loss of genetic variation within the population.

This study demonstrated that group selection on size need not oppose individual selection, in contrast to other studies in plants (Goodnight 1985; Griffing 1989 and references therein; Stevens et al. 1995). This concurrence of individual and group selection may reflect an evolutionary history in which sibling competition was the predominant selective environment such that adaptations that increase both individual and group fitness were able to evolve, but this interpretation is completely speculative at this time. Allard and Adams (1969) found evidence in barley and wheat for adaptation to genotype-dependent competitive environments, suggesting that such evolutionary responses are possible, however.

This study also demonstrated that group and individual selection can interact to determine fitness. Selection on individual height and stem mass depended on how large

neighbors were in some treatments. The importance of interactions between levels of selection, or between individual and group traits, has recently been emphasized by Agrawal et al. (2001). They stressed the possibility that interactions may interfere with selection at both levels, causing anomalous responses to multilevel selection. In this study, however, most of the interactions were in the form of positive correlational selection, which would not interfere with, but rather complement, the direction of multilevel selection on size.

Group selection was strongest in the situation in which a response to group selection would be most likely, that is, when groups members are closely related to one another and members of different groups are unrelated (Wright 1951; Wade 1978, 1982*b*; Cheverud 1985). The result that selection differed significantly among competitor treatments most when values were standardized across all treatments indicates that neighbor relatedness influenced patterns of multilevel selection in part by determining the opportunity for between-group selection. Group selection was strongest in the treatment in which the groups differed most in fitness and phenotypes, namely the sibling competitor treatment. The same patterns of selection were present, however, when the variance was constrained to be the same in all treatments, suggesting that neighbor relatedness may influence the quality of natural selection in these different types of groups as well.

This experiment demonstrated that neighbor relatedness can influence patterns of multilevel selection under natural and heterogeneous ecological conditions. It did so by altering the opportunity for group selection and possibly also by altering the quality of the selective environment within groups. Individual selection on size was detected in all competitor treatments, but significant group selection was detected only in groups of siblings. Thus group selection was strongest in the most phenotypically and genetically structured sample—the sample in which a response to group selection would also be most likely. Therefore, dispersal, which determines group composition, can significantly alter patterns of multilevel selection in natural populations.

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