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in a Winter Annual, *Collinsia verna***



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FITNESS CONSEQUENCES OF MATING SYSTEM, SEED WEIGHT, AND EMERGENCE DATE IN A WINTER ANNUAL, *COLLINSIA VERNA*

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Abstract.—Selfed and outcrossed progeny of 60 maternal parents were produced to investigate the joint and individual effects of mating system, seed weight, and emergence date on the expression of characters related to fitness and adult fecundity. A series of analyses of variance investigated these effects through time and indicated that 1) mating system explained 56% of the variance in seed weight, 2) seed weight explained 51% and mating system explained 38% of the variance in emergence date, and 3) mating system explained 71% and seed weight explained 15% of the variance in fecundity. Outcrossed-seed means differed significantly from selfed-seed means for all traits measured. On average, outcrossed seeds were larger, germinated earlier, had higher percentage emergence, and produced plants that were more fecund than selfed seeds. The coefficient of inbreeding depression increased through time in this study, from 0.05 for seed weight to 0.23 for fecundity. Seed weight and emergence date were positively correlated, both phenotypically and genetically, for both mating systems. Genetically, this indicates that genes that increase the value of seed weight also increase the value of emergence date and vice versa. Phenotypically, the positive correlation indicates that larger seeds germinate later. Outcrossed seeds were significantly larger but germinated earlier than selfed seeds, suggesting that mating system has an overriding effect in influencing fitness. In light of the selection on emergence date quantified in a previous study, seed weight, emergence date, and mating system may be functioning as a cluster of characters on which selection acts jointly in this species.

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Selection on characters that are expressed early in a species' life cycle has the potential to influence the evolution of life histories in two main ways: by affecting the amount of phenotypic variance available for natural selection at later stages in the life cycle and by causing indirect responses in genetically correlated characters. If selection acts early in the life cycle on a character that is phenotypically correlated with a trait expressed later in the life cycle, then selection on the early character will cause a change in the phenotypic variance available to selection in the character expressed later. If selection is stabilizing, the variance in such later characters will be decreased. Selection on early characters may thus constrain subsequent evolutionary change by limiting the amount of later phenotypic variance on which selection can act. An ecological correlate of this idea can be found in the "critical age classes" of demographic analyses referred to by Charlesworth (1980). Conversely, if selection acts disruptively on the early character, then phenotypic variance in the phenotypically correlated later character will increase, resulting in more phenotypic vari-

ance available to selection later in the life cycle. Second, if there are genetic correlations between characters expressed early and late in the life cycle (e.g., Roach, 1986), then genetic covariance between traits can tie the response to selection of one trait to that of another. If the traits are highly genetically correlated, the success or failure of whole suites of characters can occur if selection is acting early on one trait. The type of mating that produces a seed (i.e., selfed or outcrossed) and seed characters (such as weight and emergence date) are some of the earliest phenotypic traits of plants upon which selection can act. However, the influences of mating system (Charlesworth and Charlesworth, 1987) and seed characters (Roach and Wulff, 1987) on fitness and the evolution of plant life histories are poorly understood in natural plant populations.

The positive and negative genetic and ecological consequences of selfing in plant populations and the conditions under which selfing could evolve have been discussed extensively in the literature (e.g., Stebbins, 1957; Jain, 1976; Solbrig, 1976; Charlesworth and Charlesworth, 1978; Lloyd, 1979;

Schoen, 1983; Holsinger et al., 1984; Waller, 1984; Mitchell-Olds and Waller, 1985; Lande and Schemske, 1985; Schemske and Lande, 1985; Charlesworth and Charlesworth, 1987). Despite the wealth of theoretical treatments of these topics, fewer studies have investigated the fitness effects for progeny produced by selfing or outcrossing in the field or greenhouse (reviewed by Charlesworth and Charlesworth [1987]). The conclusion from these investigations is that mating system does significantly affect progeny fitness, with outcrossed progeny generally exhibiting higher fitness than progeny produced by selfing (henceforth, "selfed progeny"). While all of these studies addressed the percentage germination of seeds produced by the two mating systems, few addressed the relationship between mating systems and seed weight or emergence date in terms of influencing fitness at later stages (but see Waller [1985]).

Some of these studies were conducted with species having separate chasmogamous and cleistogamous flowers. This morphological distinction between "open-pollinated" and "self-pollinated" flowers provides a direct sample of seeds potentially produced by outcrossing and seeds definitely produced by selfing. In plants with a mixed mating system, the mating system that produced a particular seed is not readily apparent. However, "it remains possible that substantial inbreeding depression will exist even in partially selfing populations" (Charlesworth and Charlesworth, 1987 p. 252). For this reason, controlled-pollination studies that produce selfed and outcrossed progeny are necessary to provide initial information on the effects of mating system on fitness.

In addition to the fitness effects of mating system, seed weight and emergence date can have important effects on fitness components during various stages in the life cycle. Seed weight has been shown to influence the time of germination, early seedling establishment, competitive ability, survival, and fecundity in several species (e.g., Black, 1956, 1958; Stanton, 1984; Gross, 1984; Winn, 1985, 1988) and therefore, to contribute directly to fitness. Emergence date has been shown to influence the probability of establishment, survival, and adult plant performance as well (e.g., Marks and Prince,

1981; Howell, 1981; Kalisz, 1986; Miller, 1987).

In this paper, I examine the hierarchical fitness effects of mating system (selfing vs. outcrossing), seed weight, and emergence date in *Collinsia verna*. Emergence date in a field population has been shown to be under strong directional selection in this species (Kalisz, 1986). To quantify the effects of mating system and seed traits on components of fitness, selfed and outcrossed progeny were produced by hand-pollinations, and the progeny were germinated and grown to fruit maturation in the greenhouse. Although outcrossed progeny of a single parent are generally expected to exhibit greater variances in fitness than selfed progeny of that parent, selfed progeny may have greater variance due to decanalization of development, probably accompanied by lower mean fitness. Differences in variance among progeny could be attributable to heterosis in the outcrossed progeny, inbreeding depression in the selfed progeny, or a combination of these influences. The degree to which heterosis or inbreeding depression is expressed is a function of the mating history of the population. I investigated the extent to which the magnitude of the coefficient of inbreeding depression (Lande and Schemske, 1985) changed during the life cycle. The major goal of this study was to investigate the extent to which mating system, seed weight, and emergence date, through their phenotypic and genetic correlations with each other, have the potential to influence the opportunity for selection and evolution in this species.

Life History of Collinsia verna

Collinsia verna, a winter annual, is cued to germinate by diurnal temperature fluctuations that occur at the soil surface in the autumn (Baskin and Baskin, 1983; Kalisz, 1985). In the study population in the Raccoon Grove Forest Preserve, Will County, Illinois, USA, emergence date among plants was highly variable (ranging from early September through late November, a 60-day span; Kalisz, 1986). The date of emergence was found to be significantly negatively correlated with overall survivorship and with seed production in a two-year field study (Kalisz, 1986). Field-collected seed weights

are also highly variable among plants in this population ($\bar{x} \pm SD = 332 \pm 96 \mu\text{g}$), ranging from 50 μg to more than 600 μg . The extent of outcrossing in this population depends upon the frequency of visitation by insect vectors; flowers that are not visited by pollinators are automatically selfed. In the field, pollinators were extremely abundant during the spring of 1983 and relatively scarce in the spring of 1984 (approximately 10% of the number in the previous year (Kalisz, pers. observ.)). Therefore, it is likely that this population has a high variance among plants and among years in the percentage of outcrossed flowers, ranging from predominately selfing plants to predominately outcrossing plants. The extent to which the mating system fluctuates will be a function of the biotic and abiotic environmental factors that influence both pollinators and plants. The actual rates of selfing versus outcrossing within a generation and the long-term average selfing rate for this population are unknown. However, Greenlee and Rai (1986) estimated that the average per-locus heterozygosity of seven loci ranged from 0.31 to 0.46 for 12 populations of *Collinsia verna*, which had previously been considered a selfing species. These values were consistently higher than those for two congeners, *C. heterophylla* and *C. tinctoria* (0.24 and 0.13, respectively), which are considered to be outcrossing species. The results of Greenlee and Rai (1986) suggest that, in general, partial outcrossing is taking place, and populations of *C. verna* may have a mixed mating system.

MATERIALS AND METHODS

In late May 1982, one fruiting plant of *Collinsia verna* was collected every three meters along each of three 75-meter transects (3 transects \times 25 plants per transect = 75 plants) in the study population. All seeds from each plant were collected. Since these seeds were the result of natural pollinations, it was not known whether they were produced by selfing or outcrossing. The seeds ($N = 1,500$) were individually weighed and planted one seed per well (approximate volume = 4 cm^3) to a uniform depth in 16 96-well flats (52 \times 25 cm) filled with a soil-less potting mixture. The flats were placed

in the greenhouse and watered to maintain uniform moisture. The flats received ambient summer conditions in the greenhouse until mid-August. At that time the flats were moved to a cold frame, where they received ambient autumn temperature and light. Germination was censused weekly. At the end of November, the flats were moved into a growth chamber for vernalization (5°C, 12L:12D) for two months. In February, these plants were transplanted into four-inch pots and grown to flowering in the greenhouse. To produce the selfed and outcrossed progeny for this study, 120 plants were chosen at random from the 1,500 plants available. Sixty were used as seed parents, and 60 were used as pollen parents. Ten flowers on each seed parent were emasculated and pollinated: five with self pollen and another five with outcrossed pollen (following the methods of Garber [1975]). Anthers were removed from the pollen parents and used to transfer pollen directly to the receptive stigma of the emasculated flowers of the seed parent. Each seed parent was crossed to a single pollen parent.

From each of the 60 seed parents, six outcrossed seeds and six selfed seeds were collected, weighed, and planted as described for the field-collected seeds ($N = 720$ seeds). The seeds were kept under a 28°C-day : 20°C-night summer treatment in a growth chamber for three weeks. To simulate autumn daily temperature fluctuations in the field, a temperature regime of 15°C-day : 4°C-night was imposed, following the methods of Baskin and Baskin (1983). The flats were censused daily for newly emerged seedlings. These plants were grown to fruit maturation at 23°C under a 15L:9D photoperiod.

Seed weight was measured to the nearest μg on a Mettler balance. Emergence was defined as the protrusion of the epicotyl from the soil. The date of emergence was scored as the number of days after the first noted emergence in the experiment. Number of whorls was scored by counting all of the whorls on all stems. Regression of the number of whorls on the number of fruits produced in the natural population for two years was highly significant (1983: $R^2 = 0.88$, $P < 0.0001$; 1984: $R^2 = 0.80$, $P < 0.0001$). Therefore, the number of whorls was used as an estimator of fruit production and

overall plant fitness and will be referred to as fecundity.

Data Analysis

The relationships of interest in this study can be summarized as follows:

- 1) mating system may influence seed weight;
- 2) mating system and seed weight may influence emergence date;
- 3) mating system, seed weight, and emergence date may influence fecundity.

This sequence reflects the natural chronology of events in the life cycle. These effects were examined in three hierarchical mixed-model analyses of variance. Seed parent (PAR) and mating system (MATE) were main effects, and the two-way interactions were included in each model. In addition, seed weight (SW) was included as a covariate in the second and third models, and emergence date (ED) was included as a covariate in the third model. The three models used were:

- 1) $SW = MATE + PAR + (\text{two-way interaction}) + \text{error};$
- 2) $ED = SW + MATE + PAR + (\text{two-way interaction}) + \text{error};$
- 3) $\text{fecundity} = ED + SW + MATE + PAR + (\text{two-way interaction}) + \text{error}.$

In these models, mating system is a fixed effect, and seed parent and the interaction terms are random effects (Sokal and Rohlf, 1981 pp. 193–198). The assumption of parallel slopes necessary for including the covariates in the models was tested for the second and third models. The three-way interaction term $SW \times MATE \times PAR$ was included in the second model and found to be nonsignificant ($F_{[119,633]} = 0.76, P < 0.96$). The three-way interactions $SW \times MATE \times PAR$ and $ED \times MATE \times PAR$ were included in the third model and also found to be nonsignificant ($F_{[76,352]} = 1.29, P < 0.15$ and $F_{[70,352]} = 1.08, P < 0.38$, respectively). Accordingly, I tested parent and the interaction over the error mean squares and mating system over the interaction mean squares. Emergence date and fecundity were log-transformed to normalize their distributions, and the transformed values were

used in all analyses. The analyses were performed using PROC GLM in the SAS statistical package (SAS Institute, 1982). Type-IV sums of squares were used in all analyses.

The aim of these analyses was to determine the relative importance of early characters in influencing the expression of juvenile and adult fitness. Analyzing these effects in this series is analogous to the selection of a path diagram in path analysis (Wright, 1934; Li, 1975). This approach differs from formal path analysis on continuous variables in that both continuous variables (seed weight and emergence date) and discrete variables (parent and mating system) are included. Since mating system has only two states (selfed or outcrossed), the partial-regression and correlation analyses used in path analysis are not appropriate. Analyses of variance with covariates included in the model represent the best method for combining the class and continuous variables that are necessary for addressing the questions in this study.

To investigate sequentially the relative importance of mating system, seed weight, and emergence date to the dependent variables in the models (see above) and the change in importance through time, I calculated the variance components for the effects (based on the type-IV mean squares). Variance components were expressed as a percentage of the total variance explained.

To investigate overall fitness differences due to mating system, I compared selfed and outcrossed progeny for seed weight, emergence date, and fecundity, using Tukey's HSD method (Sokal and Rohlf, 1981 p. 245). I calculated the coefficient of inbreeding depression, δ , using the formula of Lande and Schemske (1985); if w_o is the mean estimator of fitness of the outcrossed progeny and w_s is the mean estimator of fitness of the selfed progeny, then

$$\delta = 1 - \frac{w_s}{w_o}.$$

I determined the value of δ for four characters that are directly related to fitness: seed weight, percentage emergence, seedling emergence date, and adult fecundity. To determine the phenotypic correlations among seed weight, emergence date, and fecundity,

TABLE 1. The results of three hierarchical ANOVAs testing the effects of parent, mating system, seed weight, and date of emergence on seed weight, emergence date, and fecundity. *F* values are reported for type-IV sums of squares.

Source	<i>F</i>		
	Seed weight	Emergence date	Fecundity
Emergence date	—	—	0.01
Seed weight	—	29.50***	3.49
Seed parent	4.66*	12.53***	12.32***
Mating system	4.38**	4.51***	1.78**
Seed-parent × mating-system	1.68**	43.71***	1.34
	$R^2 = 0.38$	$R^2 = 0.47$	$R^2 = 0.44$

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0001$.

I calculated Pearson product-moment correlations among these three variables for selfed progeny and for outcrossed progeny. Genetic correlations were calculated using Pearson product-moment correlations on family means (Via, 1984). Significant differences between paired selfed and outcrossed correlations were tested for differences using the test of homogeneity among correlation coefficients (Sokal and Rohlf, 1981 p. 588).

RESULTS

The roles of mating system, seed weight, and emergence date in influencing the expression of fitness changed in magnitude during the lifetime of the plants. The results of the hierarchical analyses of variance and the percentage of the total variance explained by each effect in the models are given in Tables 1 and 2, respectively. All three models tested explained similar amounts of the total variance in the dependent variables, approximately 38–47% (Table 1). Significant amounts of variance in seed weight were explained by each of the factors seed parent, mating system, and the interaction of parent and mating system (Table 1). Mating system accounted for the greatest percentage of the variance (56%), with seed parent accounting for nearly a third (32%; Table 2). However, the coefficient of inbreeding depression (δ) for seed weight was only 0.05 and that for percentage germination was also low (0.09; Table 3). Similarly, for emergence date, all effects in the model were significant. The covariate, seed weight, accounted for the greatest percentage of the variance (51%), mating system explained

38%, and seed parent and the interaction term (mating-system × seed-parent) each explained less than 9% (Table 2). The coefficient of inbreeding depression for emergence date was 0.11 (Table 3). For fecundity, seed parent and mating system had the only significant effects in the model. However, mating system explained 71% of the total variance, seed weight explained 15%, and seed parent only explained 8% (Table 2). The coefficient of inbreeding depression for fecundity was 0.23 (Table 3).

There were significant effects of mating system early and late in the life cycle. The mean weight of selfed seeds was significantly lower than that of outcrossed seeds, selfed seeds germinated later, and adults produced by selfing produced significantly fewer seeds than did outcrossed adults (Table 3). In addition, for seed weight and percentage emergence, selfed seeds had higher coefficients of variation than did outcrossed seeds (Table 3). Outcrossed progeny had higher coefficients of variation for emergence date and fecundity than did selfed progeny. Phenotypic and genetic correla-

TABLE 2. Percentage of the total variance explained by emergence date, seed weight, mating system, parent and parent × mating-system interaction for the three hierarchical models.

Source	Percentage variance explained		
	Seed weight	Emergence date	Fecundity
Emergence date	—	—	0
Seed weight	—	51	15
Seed parent	32	8	8
Mating system	56	38	71
Seed-parent × mating-system	12	3	6

TABLE 3. Table of means and standard deviations ($\bar{x} \pm SD$), coefficients of variation (CV) and coefficients of inbreeding depression (δ) of selfed and outcrossed progeny. *P* values are from Tukey's HSD test of the difference between selfed and outcrossed progeny.

Character	Selfed progeny			Outcrossed progeny			δ	<i>P</i>
	<i>N</i>	$\bar{x} \pm SD$	CV	<i>N</i>	$\bar{x} \pm SD$	CV		
Seed weight	360	324.3 \pm 97.9	30.2	360	340.1 \pm 94.2	27.7	0.05	<0.02
Percentage emergence	300	83.5 \pm 37.2	44.6	331	91.7 \pm 27.6	30.2	0.09	<0.05
Emergence date	300	11.1 \pm 7.2	64.9	331	10.0 \pm 8.1	81.0	0.11	<0.001
Fecundity	176	34.3 \pm 14.7	42.9	182	44.5 \pm 31.5	70.8	0.23	<0.0001

tions for selfed and outcrossed progeny are presented in Table 4. Over both mating types, there was a significant positive phenotypic correlation between seed weight and emergence date, indicating that larger seeds germinated later. The phenotypic and genetic correlations between seed weight and fecundity and between emergence date and fecundity were not statistically significant, either for selfed or outcrossed progeny (Table 4). Seed weight and emergence date were significantly genetically (and phenotypically) correlated in both mating systems, but the correlations for selfed and outcrossed progeny were not significantly different from each other.

DISCUSSION

Implications for Mating System

The consistently higher fitnesses of outcrossed progeny relative to selfed progeny, and the magnitudes of the coefficients of inbreeding depression suggest that this population has a mixed mating system. If inbreeding depression results from the expres-

sion of deleterious recessive alleles, then the negative effects of inbreeding and the degree of hybrid vigor in a population will be a function of the population's inbreeding history (Crow and Kimura, 1970 Ch. 3). Populations that are primarily outcrossing can carry deleterious recessive alleles in moderate frequencies and can display substantial inbreeding depression upon selfing. Schemske (1983) and Schoen (1983) have calculated coefficients of inbreeding depression exceeding 0.55 for highly outcrossing populations. This loss of vigor is generally ascribed to the expression of rare, recessive deleterious alleles in the homozygous condition with the remaining inbreeding depression due to genes of small effect on fitness (Wright, 1977 Ch. 2; Charlesworth and Charlesworth, 1987). If a population is primarily selfing, then repeated inbreeding over several generations is expected to cull recessive deleterious alleles from the population. Such populations are expected to have relatively high fitness values, lower frequencies of deleterious recessive alleles, and lower coefficients of inbreeding depression

TABLE 4. Phenotypic correlations (above diagonal) and genetic correlations (below diagonal) for selfed and outcrossed progeny of 60 female parents. *P* values (in parentheses) correspond to tests of the null hypothesis that the correlation is zero. Data for emergence date and fecundity were log-transformed prior to analysis.

Progeny type	Character	Seed weight	Emergence date	Fecundity
Selfed	seed weight	—	0.27 (0.0001)	-0.002 (0.98)
	emergence date	0.35 (0.005)	—	0.02 (0.84)
	fecundity	-0.12 (0.36)	0.09 (0.48)	—
Outcrossed	seed weight	—	0.26 (0.0001)	0.04 (0.60)
	emergence date	0.29 (0.02)	—	-0.03 (0.72)
	fecundity	-0.02 (0.88)	-0.14 (0.29)	—

relative to outcrossing populations experiencing a single generation of selfing (Wright, 1977 Ch. 2; Falconer, 1981 pp. 57–62). My lower estimates of the coefficient of inbreeding depression (0.05–0.23) suggest that the population studied here is likely to have a mixed mating system, with a substantial amount of selfing.

The negative effects of inbreeding were detected throughout the life cycle in this study. In addition, the negative effects of selfing, measured as the coefficient of inbreeding depression, increased through time (from 0.05 for seed weight to 0.23 for fecundity). However, the largest coefficient of inbreeding depression was generally lower than those estimated for highly outcrossing species (reviewed by Charlesworth and Charlesworth [1987]). This trend of increasing inbreeding depression through time is seen in 11 of 13 empirical studies with gymnosperms in which inbreeding depression was measured at more than one point in the life cycle (Charlesworth and Charlesworth [1987 table 2]). Fewer studies estimating inbreeding depression throughout the life cycle have been conducted with angiosperms, and no trend is apparent (Charlesworth and Charlesworth, 1987 table 3). If inbreeding results in the loss of developmental canalization, then an increase in the coefficient of inbreeding depression can be expected: the later in development one looks, the more off-course the phenotype will be. These differences in performance between selfed and outcrossed progeny may be increased under the natural, stressful and competitive conditions experienced by plants in the field (Allard, 1965; Antonovics, 1968; Levin, 1986). Schemske (1983) detected an increase in the level of inbreeding depression in three species of *Costus* when selfed and outcrossed progeny were grown in shady (stressful) versus sunny habitats. Similarly, Dudash (1987) found increasing inbreeding depression in *Sebatia angularis* in a series of environments ranging from a greenhouse common garden to the field. Greater fitness differences between selfed and outcrossed progeny in the field are expected for this population as well.

The relative numbers of seeds produced by each pollination type may also be an important source of inbreeding depression,

but this was not investigated in this study. It has been hypothesized that competition among seeds produced by selfing and outcrossing within the same fruit will result in differential survivorship of the embryos. Shields (1982) suggests that the greatest effect of inbreeding depression can be expected at the embryo stage, manifest in differential abortion of inbred seeds. In this view, the highest levels of inbreeding depression would be expected at early stages due to the expression of lethal recessive alleles, with little inbreeding depression expressed late in the life cycle. Outcrossed and selfed embryos were not competing within the same fruit in this study. Studies that have looked at differential embryo abortion in fruits from self pollinations versus fruits from outcrossing have yielded mixed results. Schoen (1983) and Karron (1989) found no difference in embryo abortion between selfed and outcrossed fruits, while Saki et al. (1989) found inbreeding depression in seed maturation. If differential abortion of inbred seeds occurred here, then the above results provide a conservative estimate of the effects of inbreeding. While seed-abortion rates were not measured in this study, it is still clear that the role of mating system in influencing fitness increased rather than decreased through time. A potential mechanism for this compounding effect may be the positive effects of outcrossing on other early characters, such as seed weight and emergence date. Small positive (or negative) increments in traits that influence fitness components and are expressed early may produce higher-order positive (or negative) effects on final plant fitness than increments expressed later in the life cycle. Both heterozygote advantage and mutational load (deleterious genes of small effect) may be contributing to the variance in fitness between selfed and outcrossed progeny in the population studied here.

Fitness Consequences of Early Characters

The fitness consequences of the characters investigated in this study were manifested both early and late in the life cycle of *Collinsia verna*. Seed weight, the earliest estimate of fitness in this study, was influenced by mating system. Outcrossed seeds were significantly heavier than seeds pro-

duced by selfing. In other species, heavier seeds have been shown to have higher probabilities of seedling establishment due to their larger starting capital (Black, 1956, 1958; Harper and Obeid, 1967). Since my experiment was designed to maximize the probability of establishment of the seeds that germinated, plants were grown singly, with no interspecific competition among individuals. However, fitness effects of seed size may be manifested only under competitive conditions in the field. For example, Waller (1984), Stanton (1984), and Wulff (1986) have shown that larger seeds and larger early seedlings are associated with increased fitness of adults under competitive conditions in three species. Seedlings of *Collinsia verna* often experience intense intraspecific competition in the field, with an average of 180 individuals in a 40-cm \times 40-cm area. Insofar as seed weight can be expected to influence seedling success, the variance in seed weight and the differential effects of mating system on seed weight could influence overall plant fitness. In natural populations, heavier seeds may confer a fitness advantage to both seedlings and adults.

Both seed weight and mating system affected the expression of emergence date. Early emergence confers higher fitness in *C. verna*. As discussed in Kalisz (1986), *C. verna* plants that emerged earliest in the field had a significantly greater probability of survival and significantly greater fecundity than plants that emerged later. Mating system and seed weight explained significant percentages of the variance in emergence date (seed weight: 51%; mating system: 38%; Tables 1, 2). In addition, the only significant phenotypic or genetic correlations in this study were between seed weight and emergence date: both the phenotypic and the genetic correlations were positive. This suggests that genes that increase the mass of a seed also cause seeds to germinate later. However, these phenotypic and genetic trade-offs are tempered by the degree of inbreeding. Generally, heavier seeds emerged later than lighter seeds, and outcrossed seeds were heavier than selfed seeds; however, outcrossed seeds emerged earlier than selfed seeds. Thus, there appears to be an overriding importance of mating system relative to seed weight in influencing emergence date.

Variation in the frequency of selfing and outcrossing in the field may therefore be generating some of the phenotypic variation in emergence date that was observed in the natural population (Kalisz, 1986). The extent to which mating system (relative to seed weight) can influence emergence date will depend on the frequency of selfing and outcrossing in the field.

In the analysis of the effects of mating system, seed weight, and emergence date on fecundity, only mating system had a significant effect (Table 1). While emergence date significantly influenced fecundity in the field study (Kalisz, 1986), the design of the present study (no competition and no seasonal decline in habitat quality) would minimize the positive effects of early emergence as compared to those measured in the field. Seventy-one percent of the variance explained in the model was due to mating system, and 15% was due to seed weight. In general, seed weight is expected to influence adult fecundity under field competitive conditions. Schaal (1984) described a greenhouse study in *Lupinus texensis* in which the effects of seed weight on plant performance were evident in the seedling and juvenile stages but showed no correlation with plant performance after six weeks or with the fecundity of adults. In contrast, Stanton (1984) found positive effects of seed weight on adult fecundity under competitive conditions in the field for *Raphanus sativus*. A competitive greenhouse study with *Impatiens capensis* (Waller, 1985) provided similar results to those of Stanton. Therefore, although the effect of seed weight on adult fecundity was not statistically significant in this study ($F_{[1, 301]} = 3.49, P < 0.06$), there may be an important effect in the dense populations of *C. verna* in the field. These results suggest that seed size and mating system may be important traits influencing the evolution of traits expressed later in the life cycle of *C. verna*, partially through their indirect effects on emergence date.

The results of this study suggest ways in which characters expressed early in the life cycle, such as mating system, seed size, and emergence date, have the potential to influence the evolution of correlated characters and fitness. If selection acts on the variation in single characters, then characters that are

genetically correlated with the character under selection will be dragged along, due to indirect selection acting through the genetic correlations. Adaptation in the life history of the organisms will then involve balancing the negative and positive effects of changes in each trait to maximize fitness. Conversely, if selection acts on the variation among clusters or suites of correlated characters, then selection may act on the covariances themselves, resulting in the production of different "suites" coexisting in the population. These data suggest that selection on emergence date measured in the field (Kalisz, 1986) may in fact have been attributable to selection on suites of characters that were phenotypically or genetically correlated.

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