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Inbreeding Depression, Environmental Stress, and Population Size Variation in Scarlet Gilia (*Ipomopsis aggregata*)

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Abstract: *Despite a large body of theory, few studies have directly assessed the effects of variation in population size on fitness components in natural populations of plants. We conducted studies on 10 populations of scarlet gilia, Ipomopsis aggregata, to assess the effects of population size and year-to-year variation in size on the relative fitness of plants. We showed that seed size and germination success are significantly reduced in small populations (those ≤ 100 flowering plants) of scarlet gilia. Plants from small populations are also more susceptible to environmental stress. When plants from small and large populations were subjected to an imposed stress (combined effects of transplanting and experimental clipping, simulating ungulate herbivory) in a common garden experiment, plants from small populations suffered higher mortality and were ultimately of smaller size than plants from large populations. In addition, experimental evidence indicates that observed fitness reductions are genetic, due to the effects of genetic drift and/or inbreeding depression. When pollen was introduced from distant populations into two small populations, seed mass and percentage of germination were bolstered, while pollen transferred into a large population had no significant effect. Year-to-year variation in population size and its effects on plant fitness are also discussed. In one small population, for example, a substantial increase in size from within did not introduce sufficient new (archived) genetic material to fully overcome the effects of inbreeding depression.*

Depresión de endocria, stress ambiental y variación en el tamaño poblacional de *Ipomopsis aggregata*

Resumen: *A pesar de la existencia de una gran base teórica, son pocos los estudios que han evaluado directamente los efectos de los cambios en el tamaño poblacional sobre los componentes de la condición de poblaciones naturales de plantas. Conducimos estudios sobre diez poblaciones de Ipomopsis aggregata, con el fin de evaluar los efectos del tamaño poblacional y su variación interanual sobre la condición relativa de las plantas. Demostramos que el tamaño de las semillas y el éxito en la germinación son reducidos significativamente en poblaciones pequeñas (aquellas con menos de 100 plantas en floración) de I. aggregata. Las plantas de poblaciones pequeñas son también más susceptibles a stress ambiental. Cuando las plantas de poblaciones pequeñas y grandes fueron sujetas a tensión (el efecto combinado del transplante y la poda experimental para simular pastoreo por ungulados) en un experimento en vivero, las plantas de poblaciones pequeñas sufrieron una mayor mortalidad y fueron finalmente de menor tamaño que las plantas de poblaciones grandes. Además, la evidencia experimental indica que las reducciones en condición observadas son genéticas, debido al efecto de la deriva genética y/o la depresión de endocria. Cuando se introdujo polen de poblaciones distantes en dos poblaciones pequeñas, la masa de las semillas y la germinación porcentual fueron reforzadas, mientras que el polen introducido en poblaciones grandes no tuvo ningún efecto significativo. También se discute la fluctuación interanual en el tamaño poblacional y los efectos resultantes sobre la condición de las plantas. Por ejemplo, en una población pequeña, un incremento substancial en tamaño originado en forma interna (crecimiento), no introdujo suficiente material genético nuevo como para contrarrestar totalmente los efectos de la depresión de endocria.*

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Introduction

Small populations generally face appreciable risk from the effects of environmental variation, demographic stochasticity, and reduced genetic variation (Shaffer 1981; Menges 1991). Each process, or the interaction of all three, can reduce population viability and persistence time (Gilpin & Soulé 1986).

Genetic variation, in particular, is generally regarded as important in maintaining high levels of fitness and allowing populations to adapt to changing environmental conditions. As populations become smaller, however, they tend to lose genetic variability due to genetic drift (Wright 1931). Random sampling of successively smaller subsets from generation to generation can also mimic the effects of nonrandom mating by increasing the inbreeding coefficient (Hartl 1988). An increase in the inbreeding coefficient, or level of homozygosity, can manifest itself as a loss in individual fitness (Franklin 1980). Thus, a given population can suffer the consequences of inbreeding as a result of size reduction, even if mating within the population is random (Crow 1986).

To date, most studies have focused either on the effects of inbreeding on yield components in cultivated species or on mating system and inbreeding depression within natural populations of plants (for a review, see Barrett & Kohn 1991). Studies of variation in population size and measures of inbreeding depression are virtually undocumented for natural populations of plants (Menges 1991), despite a large theoretical base. Only two studies (Jennerstein 1988; Menges 1991) have attempted to look at the effects of population size and isolation on fitness components in plants. However, these studies did not ascertain whether observed fitness reductions were due to genetic factors.

Here we assess the effects of varying population size on relative fitness across 10 populations of scarlet gilia, *Ipomopsis aggregata*, ranging in size from 12 to 4500 flowering individuals. Specifically, we address the following questions: (1) What is the relationship between population size, seed mass, and percentage of germination success? (2) Are plants from small populations more susceptible to environmental stress than plants from large populations? (3) Are observed fitness reductions due to genetic or ecological factors? (4) Is there year-to-year variation in population size and, if so, what are the consequent fitness effects?

Methods and Materials

Organism and Study Sites

Scarlet gilia, *Ipomopsis aggregata* (Polemoniaceae), is a common, monocarpic, self-incompatible, biennial/perennial herb of western montane regions that flowers from early/mid-July through late September (Paige &

Whitham 1985, 1987; Paige 1992). Following seed germination, scarlet gilia develops into a leafy rosette and, after 1–8 years of vegetative growth, a single paniculate-racemose inflorescence is produced (Paige 1992). Following stem elongation, the plant flowers, reproduces, and then dies.

Field studies on scarlet gilia were conducted during the summers of 1991, 1992, and 1993 in 10 populations located along Highways 80 and 151 in the San Francisco Peaks region north of Flagstaff, Arizona. Most populations were separated by at least 2 km, with the exception of one population, which was located only 0.32 km from another. No individuals of scarlet gilia were found between populations (populations are discrete), and all populations occurred within the same habitat type: openings among ponderosa pine. Only flowering plants were incorporated into population counts. At the onset of the study, the 10 populations included 12, 31, 36, 61, 71, 72, 189, 280, 398, and approximately 4500 flowering individuals. Although the long-term histories of these populations are unknown—when and how they were established—most populations remained small (≤ 100) or large (> 100) in terms of the numbers of flowering individuals over the past 10 years.

Population Size and Fitness

To assess the effects of plant population size on fruit production, approximately 10 plants similar in size (as measured by stem diameter) were chosen within each of nine populations, and the total number of fruits per plant were counted. These data were collected at the end of the 1992 flowering season.

To assess the effects of population size on seed mass and germination success, in September 1991 approximately 10 ripened fruits were collected from each of 10 haphazardly chosen plants from each of 10 populations. Numbers of seeds per fruit were not assessed due to the fact that all dehiscing fruits per plant were pooled upon collection, ultimately mixing seeds. Fifty seeds were randomly chosen from each plant, and the first 10 selected were weighed to the nearest tenth of a milligram. All seeds (50/plant) were germinated under aphotic conditions at room temperature between two pieces of moistened Whatman #1 filter paper placed in petri dishes over a three-week period. All seeds were stored at 4°C prior to germination. These studies were replicated in 1992. Due to fungal attack, however, no assessment of germination success was made for the largest population (151) in 1992.

An experiment was also conducted to assess the differential effects of stress on plants from small and large populations. In mid-June of 1992, two (replicate) common garden plots were established on Fern Mountain (population size 602 in 1992). One hundred and sixty single-stemmed plants from eight populations (20

plants/population) were transplanted into one of two common garden plots (10 plants/population/plot, or 80 plants/plot) and clipped (2 cm from the base, removing approximately 95% of the above-ground biomass to simulate herbivory by mule deer and elk). Transplants were taken from four small populations (<100 individuals/population) and from four large populations (>200 individuals/population). All plants were similar in size and developmental stage. We assumed that the combined effects of both the transplant and clipping treatment imposed a significant physiological stress. At the end of the flowering season an assessment of survivorship was made. Ultimate plant height was also determined by measuring the distance from the base of the plant to the tip of the tallest regrowth stem. Stem diameter was used as a covariate to further adjust for the effects of plant size differences on regrowth rate. Stem diameter is a relatively accurate measure of plant size (positively correlated; for example, with plant height, $R^2 = 0.571$, $n = 60$, $p < 0.0001$; biomass, $R^2 = 0.535$, $n = 25$, $p < 0.0001$; and flower production, $R^2 = 0.655$, $n = 25$, $p < 0.0001$; Paige 1992).

To determine whether observed reductions in seed size and germination success were due to genetic factors, pollen transfer experiments were conducted in August 1992 and in July and August 1993. Experiments were conducted in 1992 in two small populations (Forest Hills and 151/80) and in 1993 in one large population (Museum of Northern Arizona, MNA). Ten plants were randomly chosen in each population and caged with nylon-tricot covered wire cages. Three treatments were performed on each plant: pollen was transferred by hand from a distant large population (approximately 2.0 km, 4.8 km, and 6.4 km away for MNA, Forest Hills, and 151/80, respectively), pollen was transferred by hand within the population (from approximately 10 meters away—the “optimal outcrossing” distance of scarlet gilia [Waser & Price 1989]), and pollen was transferred naturally by pollinators within the population. Because scarlet gilia is essentially self-incompatible (Hainsworth et al. 1985), a treatment assessing the effects of self-pollination was not incorporated. Two flowers per treatment, for a total of six flowers per plant in each population, were assigned to one of three positions

(top, middle, bottom) on the plant, marked with colored thread prior to opening, caged and—when receptive—pollinated. Hand-pollination treatments were completed first, and each pollinated flower was bagged with nylon mesh. Cages were then removed, and pollinators were allowed to complete the natural treatment. Upon dehiscence, in mid-September, seeds were collected, weighed, and germinated on petri plates as noted above. On average, plants produce 10.8 seeds per fruit (Paige 1992). The two small populations were pooled for analysis of germination success due to small sample sizes. No assessment of germination success was made for the large population, MNA.

Results

A nested analysis of variance showed there was significant seed size variation between plants within populations, between populations, and between small and large populations (those with ≤ 100 and > 100 flowering individuals, respectively; Table 1). Seed size reductions were not further compounded by reductions in fruit set, with no significant differences among populations ($F = 1.93$, $df = 1, 7$, $p = 0.21$).

Individual population data on seed mass and germination success are shown in Figures 1 and 2. On the average, in both 1991 and 1992, populations with 100 or less individual flowering plants produced significantly smaller seeds than larger populations (1.44 ± 0.05 [± 1 S.E.] versus 1.58 ± 0.05 mg, $p < 0.0000$, 1991; 1.21 ± 0.08 versus 1.50 ± 0.07 mg, $p < 0.0000$, 1992; Table 1). In addition, mean germination success was, on the average, significantly lower in populations with 100 or less flowering individuals (27.88 ± 2.79 versus $38.32 \pm 2.93\%$, $t = 2.58$, $df = 104$, $p = 0.011$, 1991; 22.68 ± 4.12 versus $38.57 \pm 2.87\%$, $t = 3.25$, $df = 76$, $p = 0.0017$, 1992). Mean germination success was also found to be positively correlated with mean seed size across populations over the two-year period of this study ($R^2 = 0.401$, $n = 19$, $p = 0.0036$).

In 7 of the 10 populations studied in 1991, seed sizes were not significantly different in 1992. In two of the populations (Hart/80, $n = 12$ in 1991 and $n = 20$ in

Table 1. Nested analysis of variance for population size, population, and maternal family effects on seed mass for 1991 and 1992.

Source of Variation	Sum of Squares		df		F		Significance	
	1991	1992	1991	1992	1991	1992	1991	1992
Seed Family								
(within population)	93.06	111.87	96	79	5.32	7.93	0.0001	0.0001
Population	42.11	87.20	9	9	25.70	54.13	0.0000	0.0000
Small vs. Large								
(≤ 100 vs. > 100)	4.60	7.61	1	1	25.27	42.51	0.0000	0.0000
Residual	170.94	137.35	939	768				

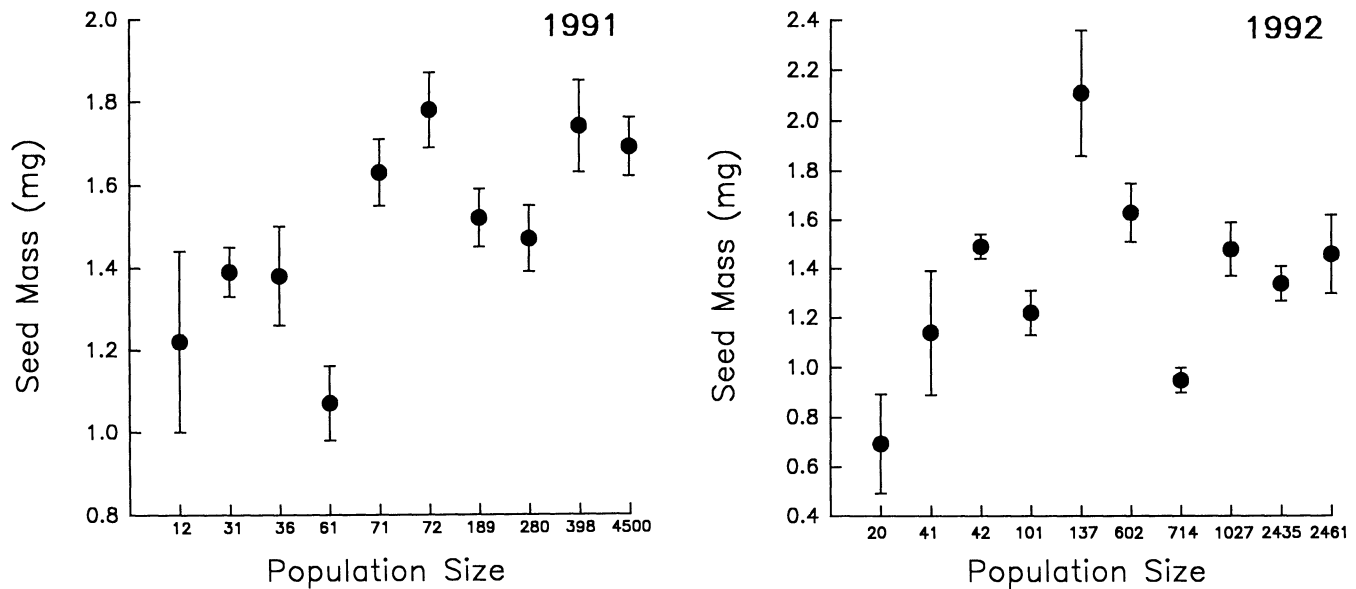


Figure 1. Individual population data on seed mass for 1991 and 1992. Means \pm 1 S.E. are shown.

1992; Gasline, $n = 72$ in 1991 and $n = 41$ in 1992, respectively). However, seed size was significantly reduced, and in one population (151-1Mi, $n = 71$ in 1991 and $n = 137$ in 1992) seed size was significantly larger in 1992 (Table 2). Only one of these populations, Gasline, showed a decrease in population size from a large population (with seed size and germination success equivalent to a large population in 1991) to that of

a small population (Table 2). The other two populations (Hart/80, 151-1Mi) remained either large or small (greater than or less than approximately 100 flowering individuals); seed size, likewise, showed a similar pattern. Furthermore, no significant differences in germination success were found (Table 2). One population, Forest Hills, increased dramatically in size (approximately 12-fold, from 61 to 714 flowering individuals)

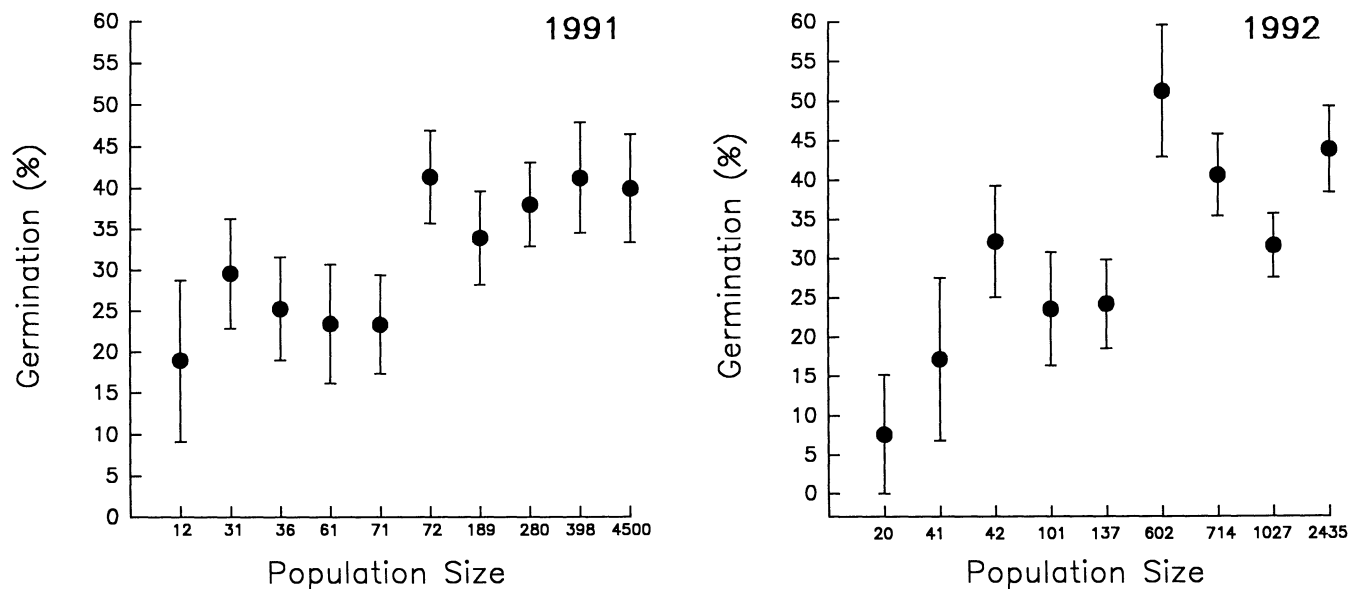


Figure 2. Individual population data on percentage of seed germination success for 1991 and 1992. Means \pm S.E. are shown ($F = 1.48$, $df = 9,96$, $p = 0.168$, 1991, although not statistically significant, the trend is in the same direction as seed size data; $F = 3.56$, $df = 8,69$, $p = 0.0016$, 1992).

Table 2. Variation in population size, seed mass, and percentage of germination from 1991 to 1992 for 10 populations of scarlet gilia.^a

Population	Year	N	Seed Mass (± 1 S.E.)	Germination (% ± 1 S.E.)
Hart/80	1991	12	1.22 \pm 0.22 ^b	18.97 \pm 9.81
	1992	20	0.69 \pm 0.20	7.60 \pm 7.60
Hilltop 80	1991	31	1.39 \pm 0.06	29.60 \pm 6.72
	1992	101	1.22 \pm 0.09	23.56 \pm 7.22
151/80	1991	36	1.38 \pm 0.12	25.28 \pm 6.31
	1992	42	1.49 \pm 0.05	32.18 \pm 7.10
Forest Hills	1991	61	1.07 \pm 0.09	23.42 \pm 7.28 ^b
	1992	714	0.95 \pm 0.05	40.60 \pm 5.18
151-1Mi	1991	71	1.63 \pm 0.08 ^b	23.34 \pm 6.03
	1992	137	2.11 \pm 0.25	24.22 \pm 5.64
Gasline	1991	72	1.78 \pm 0.09 ^b	41.32 \pm 5.60 ^b
	1992	41	1.14 \pm 0.25	17.20 \pm 10.3
MNA	1991	189	1.52 \pm 0.07	33.94 \pm 5.70
	1992	2435	1.34 \pm 0.07	43.80 \pm 5.44
Northland	1991	280	1.47 \pm 0.08	37.98 \pm 5.08
	1992	1027	1.48 \pm 0.11	31.60 \pm 4.07
Fern	1991	398	1.74 \pm 0.11	41.20 \pm 6.66
	1992	602	1.63 \pm 0.12	51.20 \pm 8.36
151	1991	4500	1.69 \pm 0.07	39.91 \pm 6.55
	1992	2461	1.46 \pm 0.16	—

^a Means ± 1 S.E. are shown.^b Significant differences at the 0.05 level (LSD multiple range test).

from 1991 to 1992. The significant increase in size came from the large number of nonflowering rosettes within this population. Although the large increase in population size did not alter seed size, germination success was significantly higher.

Experiments on the differential effects of stress on plants from large and small populations demonstrated that plants from small populations (<100) experienced significantly higher mortality than plants from large populations (>200; 28.8% versus 12.5%, $X^2 = 6.45$, $df = 1$, $p = 0.012$). Because there were no significant differences in response between plots for plants from small populations ($X^2 = 0.549$, $df = 1$, $p < 0.25$) or between plots for plants from large populations ($X^2 = 0.00$, $df = 1$, $p = 1.0$), plots were pooled for analysis. In addition, final plant heights were significantly lower for plants from small versus large populations by the end of the flowering season (23.6 ± 1.38 cm versus 27.4 ± 1.24 cm, $F = 4.23$, $df = 1, 124$, $p < 0.042$). As noted earlier, stem diameter was used as a covariate to adjust for the effects of plant size differences on regrowth rate. Because there were no significant differences in height between plots for plants from small populations ($t = 1.17$, $df = 56$, $p > 0.25$) or between plots for plants from large populations ($t = 1.17$, $df = 69$, $p > 0.25$), plots were pooled for analysis.

At the population level, seed size was significantly bolstered when pollen was transferred into each of the small populations over pollen transferred from within (Fig. 3). However, no significant differences in seed size were found among the three treatments within the large population (Fig. 3). Mean germination success was also

higher when pollen was transferred into each of the small populations (Fig. 4). No assessment of germination success was made for the large population.

Discussion

Fitness Reductions and Plant Population Size: Genetic Effects

Although there was significant seed size variation among plants within populations, much of the variation existed between small (<100 flowering individuals) and large (>100) populations (Table 1). Our studies also showed that seed germination was substantially reduced in small populations of scarlet gilia. These results are consistent with those of Menges (1991), who studied the effects of population size and isolation on seed germination in *Silene regia*. Menges showed that large populations (>150 plants) had higher percentages of seed germination than small populations (those <150). Although Menges (1991) proposed several possible mechanisms to explain the observed patterns, such as inbreeding depression, reduced pollinator activity, and changes in the source of pollen (from predominantly between-plant to within-plant crosses as a result of reduced population size), he did not attempt to assess the mechanisms involved.

Here, we provide experimental evidence that fitness

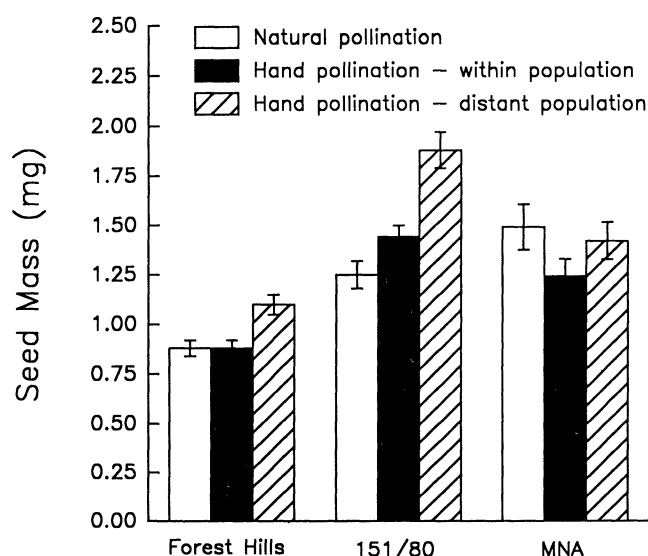


Figure 3. Mean seed mass as a result of three pollen transfer treatments in three populations (Forest Hills and 151/80, each with less than 100 flowering individuals, and MNA, with much more than 100 flowering individuals) of scarlet gilia. Means ± 1 S.E. are shown ($F = 8.55$, $df = 2, 208$, $p < 0.0003$ for Forest Hills; $F = 15.40$, $df = 2, 81$, $p < 0.0001$ for 151/80; $F = 1.55$, $df = 2, 52$, $p = 0.221$ for MNA).

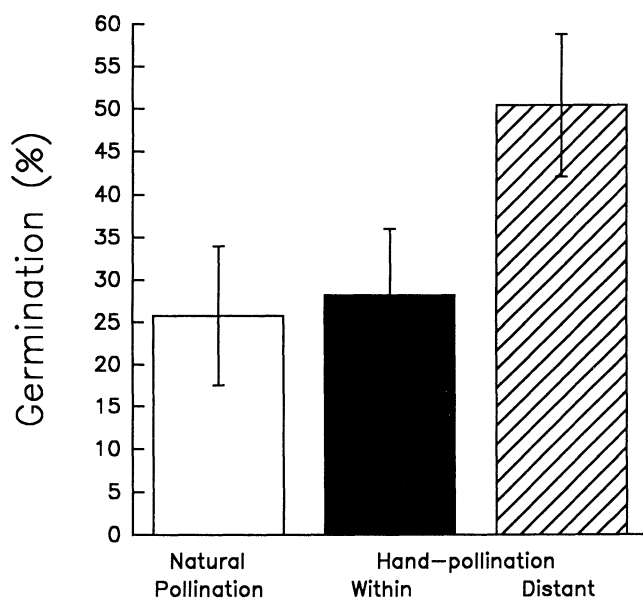


Figure 4. Mean germination as a result of three pollen transfer treatments in two small populations (Forest Hills and 151/80, each with less than 100 flowering individuals) of scarlet gilia. Means \pm 1 S.E. are shown ($F = 2.68$, $df = 2,46$, $p = 0.079$; although only marginally significant, the trend is in the predicted direction).

reductions observed in small populations of scarlet gilia are, at least in part, genetic. To our knowledge, these results represent the first empirical evidence of genetically-based fitness reductions as a result of restriction of population size within a species under natural conditions. When distant pollen was introduced into each of two small populations (Forest Hills and 151/80), seed size and germination success were substantially bolstered (Figs. 3 and 4), while pollen transferred into a large population (MNA) had no significant effect (Fig. 3). These comparisons, however, should be viewed with caution. Pollen transfers were conducted in different years in small and large populations, and the effects of yearly variation on the outcome of such experiments is at present unknown.

Significant differences in seed size between natural and within-hand-pollination treatments were also found within the 151/80 population (Fig. 3). Seeds produced from pollen transferred by hand within the population were significantly larger than seeds produced from pollen transferred naturally by pollinators. These results may be explained by considering pollinator behavior. Less than 1% of the pollen moved by hummingbirds is in excess of 5 meters (Campbell 1991). This distance is less than the optimal outcrossing distance of 10 meters (Waser & Price 1989) used in our within-hand-pollination treatment; thus, pollinators could act to increase the level of inbreeding. Of course this assumes

that the optimal outcrossing distance is similar to the distance reported in Waser and Price (1989), which may or may not be the case. The optimal outcrossing distance likely depends upon characteristics of the individual population, including its density, spatial distribution, genetic relatedness, and inbreeding history.

We can only surmise why only the 151/80 population showed these treatment differences while the Forest Hills population did not (Fig. 3). Perhaps it is a result of the difference in the configuration and spacing of plants, which could have altered pollinator behavior and levels of outcrossing. Plants at Forest Hills were in a more linear array and spread out, while plants at 151/80 were clumped and closely distributed.

Although pollinator activity was not directly assessed, mean fruit set was not significantly different among populations, suggesting that pollinator activity was not reduced in smaller populations (as shown for *Dianthus deltooides*, Jennerstein 1988). Numbers of seeds produced per fruit were not assessed, however, which would provide a more accurate measure of pollinator behavior and activity. Furthermore, an increase in the number of within-plant pollinations would not contribute directly to reductions in seed size or germination due to the fact that *I. aggregata* is self-incompatible.

Results from our common garden experiments also indicate that fitness reductions in small populations of scarlet gilia are due to genetic factors. When plants from small and large populations were subjected to an imposed stress (combined effects of transplanting and experimental clipping, simulating ungulate herbivory) in a common garden experiment, plants from small populations suffered higher mortality and were ultimately of smaller size than plants from large populations.

From a mechanistic perspective, fitness reductions are likely the result of inbreeding depression. As population size decreases, sampling accidents lead increasingly to random losses of genetic variation. Random sampling of successively smaller subsets from generation to generation can also lead to an increase in the inbreeding coefficient (Wright 1931). Thus, one possible effect of genetic drift is inbreeding depression due to loss of heterozygosity and expression of deleterious alleles, manifested as a loss in individual fitness (Franklin 1980).

Population differences in fitness can also result from the interactive effects of site and inbreeding depression (Schmucke 1983; Dudash 1990). Limited results suggest there may be significant environmental differences among sites affecting traits such as seed size. For example, seed sizes were significantly different between our experimental populations even after the introduction of pollen into the populations (Fig. 3). We are presently conducting fertilization and pollen transfer experiments in small and large populations in an effort to assess the

interactive effects of site and inbreeding depression on seed size and germination success in scarlet gilia.

Changes in Population Size and Fitness

During the two-year period of this study, two populations showed significant change in size and relative fitness. One population, Gasline, decreased from a relatively large population with large seed size and high germination success to a small population with significantly smaller seed size and lower germination success (Table 2). The decrease in population size was the result of human disturbance (road construction), constricting the population to a small patch of plants. Because the population was constricted to a small patch, the remaining plants were likely of higher genetic similarity. Spatially adjacent plants are closely related as a result of limited seed dispersal in *I. aggregata*. Thus, the observed reduction in offspring fitness is likely the result of matings between relatives. These results are consistent with the findings of Waser and Price (1989): when outcrossing of *I. aggregata* occurs over a relatively short distance (less than 10 m) fitness declines as a result of inbreeding depression.

The second population, Forrest Hills, represented a small population in 1991, producing seeds significantly smaller with lower germination success than populations larger in size. Pollen transfer experiments conducted within this population also demonstrated a genetic basis for observed reductions in relative fitness. Pollen brought in from a distant population bolstered seed size and germination success. In 1992, however, the number of flowering individuals increased dramatically in size (approximately 12-fold, from 61 to 714). The significant increase in size came from the large number of nonflowering rosettes within this population. Although the large increase in population size did not alter seed size, germination success was significantly higher in 1992.

The only plant study addressing the issue of whether populations can recover from the ill effects associated with restricted population size when population size is restored to adequate levels is one conducted by Polans and Allard (1989) on *Lolium multiflorum*, an outbreeding grass. In part, they showed that restrictions in size resulted in significant phenotypic effects. Smaller populations flowered more slowly and were shorter, with fewer tillers and seeds, than plants from larger populations. Furthermore, when sizes of experimental populations of *Lolium* were increased from within, some of the detrimental effects were still discernible. However, in composite populations formed by mixing genotypes from several small inbred populations, the expression of these traits recovered to levels similar to those in the original population after a single generation of random mating. These results are consistent with our findings.

Even though the Forest Hills population increased substantially in size, evidence of inbreeding depression was still discernible (plants were still producing small seed). But pollen transferred into the population from a distant population alleviated signs of inbreeding depression (seed size and germination success). In general, these results indicate that an increase in population size from within does not introduce sufficient new (archived) genetic material (or combinations) to fully overcome the effects of inbreeding depression. Of course this assumes that additional effects occur following germination because germination success was higher following the increase in population size. Eldridge and Griffin (1983) showed that inbreeding depression increased steadily with age in mountain ash (*Eucalyptus regnans*): by 12.5 years inbreds had 57% poorer survival and were smaller than plants that were outcrossed. Nonetheless, it will be necessary to follow plants beyond the germination stage to determine the ultimate outcome.

Evolutionary/Conservation Implications

Overall, the results of our studies contribute to a much-needed empirical data base on natural populations of restricted size and the effects of year-to-year variation in size. Considering the sessile habit of plants and the ease with which they can be counted, data on variation in plant population sizes are surprisingly sparse in the literature (Barrett & Kohn 1991). Size variation may be important to the long-term fate of a population. For example, populations that remain small for long periods are likely to be genetically less diverse than those that have only recently become small and have rapidly regained large size or those that have never experienced a substantial reduction in size (Wright 1931; Kimura & Crow 1964). In other words, it is perennial low numbers that erode genetic variation. Although the long-term histories of the populations studied here are unknown—when and how they were established or the long-term history of size variation—casual observation and observed fitness reductions suggest that most populations have remained perennially small (<100) or large (>100) for at least 10 generations (the time period for which studies have been conducted on scarlet gilia; Paige, personal observations). Genetic studies are presently being conducted to directly assess levels of genetic variation among these populations.

In addition to reducing fitness, such loss of variation is thought to reduce the ability of populations to adapt to changing environments as well as to increase their susceptibility to pests, pathogens, and other stresses of the environment. The results of our studies are consistent with the idea that plants from small populations are more susceptible to environmental stress. Plants from small populations suffered higher mortality and were ultimately of smaller size than plants from large popu-

lations when subjected to an imposed stress in a common garden setting. More recent results also indicate that plants from small populations are more susceptible to high levels of secondary herbivory (see Paige 1992; Paige 1994) by mule deer and elk than plants from large populations (Paige, unpublished data).

Overall, gene flow among populations of scarlet gilia is limited at best. As noted earlier, less than 1% of pollen moves in excess of 5 meters in *I. aggregata* populations (Campbell 1991). The likelihood of pollen transfer between populations is further reduced by interspecific pollen transfer by hawkmoths and hummingbirds, which visit a variety of plant species while foraging (Koptur 1984). Because alleviation of the detrimental effects associated with small population size seems unlikely in the absence of gene flow (which is limited), the long-term evolutionary consequence of size restriction in *I. aggregata* may ultimately be local extinction.

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