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Inbreeding Depression in Scarlet Gilia: A Reply to Ouborg and Van Groenendael

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In a recent study we assessed the effects of variation in population size on fitness components in natural populations of scarlet gilia (*Ipomopsis aggregata*), in the San Francisco peaks region of northcentral Arizona (Heschel & Paige 1995). We showed that seed size and germination success were significantly reduced in small populations of scarlet gilia and that plants from small populations were more susceptible to environmental stress. We also provided experimental evidence that observed fitness reductions were due to genetic factors. We also addressed year-to-year variation in population size and its effects on plant fitness.

Ouborg and van Groenendael (1996) suggest that our paper is "laden with statistical and methodological problems." They raise five specific issues. First, as Ouborg and van Groenendael correctly point out, F values were incorrectly calculated in our nested analysis of variance: mean squares of one factor should have been tested against mean squares of the next, not the residual mean squares. But the highly nonsignificant F values estimated by Ouborg and van Groenendael are inconsistent with the trends shown in the data of our Figs. 1 and 2 (Heschel & Paige 1995). Here we present a corrected nested analysis table with the following alteration: population size ($\leq$100 versus $>$100) is used in an a priori planned comparison rather than as a nesting factor (Table 1). In retrospect, we realize that it is not statistically appropriate to test population size (small versus large) against population because population size is not a separate category in which populations are nested but represents by design a planned comparison (i.e., a contrast). As shown, the contrast supports our original contention that seed size is significantly reduced in small populations (those with $\leq$100 flowering plants) of scarlet gilia (Heschel & Paige 1995).

The second point made by Ouborg and van Groenendael is that data on seed size were analyzed by means of a t test following the nested analysis of variance (ANOVA) and that germination data were not tested with an ANOVA, only a t test. Contrary to their claims, seed-size data were not tested with a t test following the nested analysis of variance, and second germination data were tested with a one-way ANOVA (bottom of Fig. 2; Heschel & Paige 1995). More important, Ouborg and van Groenendael were concerned about germination data being pooled into small and large categories for comparison. To rectify this problem we reanalyzed our germination data using a contrast for population size instead of a t test; in other words, the comparison between small and large populations ($\leq$100 versus $>$100) was originally an a priori planned comparison. This comparison is legitimate, whether the population factor is significant or not. The results of our reanalysis using a contrast shows, as our original analysis did, significant differences in germination success between small and large populations in both 1991 and 1992 (Table 2).

The same issue is raised concerning our environmental stress experiment, in which data were pooled without prior testing for differences within groups. But there were no significant differences among small or among large populations (four small populations in plot 1 and plot 2, $\chi^2 = 2.67$, df = 3, $p > 0.45$ and $\chi^2 = 3.75$, df = 3, $p > 0.25$, respectively; four large populations in plot 1 and plot 2, $\chi^2 = 5.40$, df = 3, $p > 0.15$ and $\chi^2 = 0.758$, df = 3, $p > 0.75$, respectively). Therefore, the comparisons and the conclusions drawn in our original paper are correct.

The third issue raised deals with the limited number of populations (one large and two small) used in the pollen-transfer experiments, which measured two variables (seed mass and germination success), not one variable, as Ouborg and van Groenendael incorrectly assert. We agree that these data alone are not overwhelmingly convincing (nor were they presented as such, see page 131 of our discussion; Heschel & Paige [1995]). But these data, in combination with the common garden stress experiment, 2 years of population data on seed size and germination success, and data on population size variation and

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Table 1. Nested analysis of variance for population and maternal family effects on seed mass for 1991 and 1992, followed by a comparison of small and large papulations (≤ 100 versus > 100).

Source of variation	*Sum of square*	df	*Mean square*	f	p
1991					
Population	42.55	9	4.727	4.88	0.000
Seed family (within population)	93.06	96	0.969	5.19	0.000
Residual	175.54	940	0.187		
Comparison					
Small versus large (≤100 versus >100)	7.91	1	7.91	42.36	0.000
Residual	175.54	940	0.187		
1992					
Population	97.99	9	10.89	7.71	0.000
Seed family (within population)	111.59	79	1.41	8.13	0.000
Residual	133.58	769	0.174		
Comparison					
Small versus large (≤100 versus >100)	21.75	1	21.75	125.2	0.000
Residual	133.58	769	0.174		

fitness, are consistent with a genetic explanation for observed fitness reductions (Heschel & Paige 1995). In addition, we now have molecular data from four populations (two small and two large) that are also consistent with a genetic explanation for observed fitness reductions. The RAPD markers demonstrate a significantly higher percentage of band sharing within two of the small populations, 151/180 (62.3 ± 1.23%) and Gasline (66.3 ± 1.65%) than within two of the large populations, Northland (53.6 ± 1.76%) and Fern Mountain (49.1 ± 3.54%) (ANOVA F = 15.14, df = 3,159, p = 0.0000).

The fourth issue raised deals with seed size and germination success. Ouborg and van Groenendael argue that seed size needs to be factored out in an analysis of the effect of pollen source on germination because larger seeds have a higher germination success. We do not agree with this overly simplified statement. Results from our paper (Heschel & Paige 1995) provide evidence that seed size and germination success are not always concordant: large seed size does not always equate with higher germination success, and vice versa. For example, germination success in population 151-1Mi (n = 137) in 1992 was comparable to that of a small population (24.22 ± 5.64%; Fig. 2 in Heschel & Paige [1995]), even though this population produced the largest seeds documented (2.11 ± 0.25 mg; Fig. 1 in Heschel & Paige [1995]) among populations over the 2-year period of this study. Conversely, germination success in the Forest

Table 2. Analysis of variance for population effects on germination success for 1991 and 1992, followed by a comparison of large and small populations (≤ 100 versus > 100).

Source of variation	*Sum of square*	df	*Mean square*	f	p
1991					
Population	0.583	9	0.065	1.476	0.167
Residual	4.213	96	0.044		
Comparison					
Small versus large (≤100 versus >100)	0.305	1	0.305	6.944	0.01
Residual	4.213	96	0.044		
1992					
Population	1.104	8	0.138	3.56	0.002
Residual	2.674	69	0.039		
Comparison					
Small versus large (≤100 versus >100)	0.562	1	0.562	14.49	0.000
Residual	2.674	69	0.039		

Hills population ($n = 714$) in 1992 was comparable to that of a large population (40.60 ± 5.18%; Fig. 2 in Heschel & Paige [1995]), even though this population produced exceptionally small seeds, within the range of those of a small population (0.95 ± 0.05 mg; Fig. 1 in Heschel & Paige [1995]). Given these results, an assessment of germination success is appropriate without accounting for seed size in the analysis (Fig. 4 in Heschel & Paige [1995]). Nonetheless, we agree that it would have been interesting and informative to hold seed size constant and to assess germination success independent of seed size.

In their final point, Ouborg and van Groenendael argue that transfer of distant pollen, which bolsters seed size, may lead to untimely germination of seeds hastening a population decline, whereas a (larger?) proportion of the smaller seeds produced within the population will remain dormant, allowing the species to await better times and buffering the population against decline. This argument is contingent upon there being differences in dormancy between small and large seeds and/or small and large populations—that dormancy is inherently plastic in *I. aggregata*. Although we cannot address this possibility directly (and for that matter no one to our knowledge has the data to address this issue in this or any other system), if it were true, it is more likely that large seeds would still have a fitness advantage given that conditions are typically favorable (i.e., in the majority of years) for seed germination and subsequent seedling survival in the San Francisco Peaks region of north central Arizona (Paige, personal observation). The populations near Flagstaff, Arizona, are in neither highly stressful nor heterogeneous environments. Thus, delayed germination would, in the majority of years, result in a population decline. Also, among-species comparisons of temperate plant communities have demonstrated that perennial herbaceous plants do not exhibit dormancy to the degree that annual plants do (Rees 1993). Thus, given the monocarpic perennial habit of *I. aggregata* (i.e., having long-lived rosettes), dormancy may be moot to the discussion at hand.

In summary, we make the following points. First, due to a statistical error in our analysis and improper nesting of small versus large populations, we present a corrected nested analysis table using population size (≤ 100 versus > 100) in a planned comparison rather than as a nesting factor. Using population size as a nesting factor, in retrospect, was not appropriate because it is not a separate categorization factor, but instead represents an a priori planned comparison (i.e., a contrast). Our reanalyses support our original contention that there are significant differences in seed size between large and small populations. Second, Ouborg and van Groenendael were concerned about the germination data and the data from the environmental stress experiment being pooled into small and large categories for comparison without a priori testing for among-population differences. To rectify this problem, we reanalyzed germination data using a contrast instead of a t test: the comparison between large and small populations (≤ 100 versus > 100) was originally an a priori planned comparison. This comparison is legitimate, whether the population factor is significant or not. The results show, as our original analysis did, significant differences in germination success between small and large populations. In terms of the environmental stress experiment, there were no significant differences among small or large populations. Thus, the comparison and conclusions drawn in the original paper are correct. Third, in terms of the pollen-transfer experiments, even though only a limited number of populations were used, these data, in combination with data from the common garden stress experiment, two years of population data on seed size and germination success, data on population size variation and fitness, and recently incorporated molecular genetic data are consistent with a genetic explanation for observed fitness reductions. Fourth, although Ouborg and van Groenendael argue that seed size needs to be factored out in an analysis of the effect of pollen source on germination because larger seeds have a higher germination success, our study provides evidence that seed size and germination success are not always concordant. Thus, an assessment of germination success independent of seed size is appropriate and important. Fifth, the possibility exists that the transfer of distant pollen, which bolsters seed size, may lead to untimely germination of seeds in poor years hastening a population decline, whereas smaller seeds produced within the population remain dormant while awaiting better times. Even if this is true, however, it is more likely that large seeds would still enjoy a fitness advantage given that conditions are typically favorable for seed germination and subsequent seedling survival in the majority of years.

We believe that the results of our studies contribute to a much-needed empirical database on natural populations of restricted size and the effects of year-to-year variation in size. 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. Although we admit that we made a few minor errors in our initial presentation, we hope we have cleared up any misgivings on the part of our critics.

Literature Cited

Heschel, M. S., and K. N. Paige. 1995. Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). Conservation Biology **9**:126–133.

Ouborg, N. J., and J. M. van Groenendael. 1996. Demography, Genetics, or statistics: Comments on a paper by Heschel and Paige. Conservation Biology, this issue.

Rees, M. 1993. Trade-offs among dispersal strategies in British plants. Nature **366**:150–152.