The Influence of Interplant Distance and Number of Flowers on Seed Set in Dwarf Bear-Poppy (*Arctomecon humilis*)

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Abstract: Samples from three isolated populations of the dwarf bear-poppy (*Arctomecon humilis* Cov.) demonstrate that both flower pollination (fruit set) and seed set per fruit decline as interplant distances increase and the number of flowers per plant declines. Interplant distance and number of flowers per plant tend to interact with reproduction. Seed set per plant is most impaired on plants that produce few flowers and are far from other flowering, conspecific individuals. Such data warn that the number of surviving individuals alone is not a safe criterion for evaluating reproductive health of a plant population. Population density (number of individuals per unit area) strongly influences the reproductive success of this species. Other studies suggest that large reductions in the pollen deposited on stigmas may eliminate competition among pollen grains for access to ovules and adversely affect the vigor of the next sporophyte generation.

The dwarf bear-poppy is a local endemic confined to gypsiferous soils in Washington County, Utah and the adjacent edge of Mohave County, Arizona (McDougall 1973, Welsh et al. 1993). The species is formally listed as endangered by the U.S. Fish and Wildlife Service (1979).

It is a low-growing (rarely over 2 cm tall in flower), evergreen herb that usually survives for only 5 or 6 years. The dwarf bear-poppy flowers in April and early May and produces as many as 200 flowers per plant. Individual flowers are white and about 4 cm in diameter: Each flower displays a mass of numerous, bright yellow anthers at its center for a few hours after opening. Flowers remain attractive and reproductively receptive to pollen for 2 or 3 days (Nelson 1989). As many as 8 or 10 new flowers open each day and flowering individuals are rendered even more conspicuous by retention of petals indefinitely after anthesis. The shriveled, off-white petals enfold the developing fruit and are abscised with it at maturity.

The dwarf bear-poppy was pollinated in presettlement time by two native, solitary bees, species of *Perdita* and *Synhalonia* (Borror et al. 1976, Buchmann and Nabhan 1996). The domestic honeybee (*Apis mellifera*) has also become a regular pollinator of the species. In fact, our observations suggest that the honeybee is currently the most frequent visitor to dwarf bear-poppy flowers. Pollinator visits appear to be rewarded with pollen only: Nectar is apparently not produced by the flowers.

Our earlier work has shown that the dwarf bear-poppy is highly self-incompatible (Harper et al., unpub. data). Plants enclosed in mesh cages rarely produce fruits, whereas plants open to natural pollinators show high percentages of fruits set per flower (consistently over 90% in dense populations). More than 85 percent of the ovules in fruits produced in dense populations produced viable seeds in a sample taken at the Red Bluff (Washington County, Utah) monitoring site in 1997, a year of better than average precipitation.

The dwarf bear-poppy displays large variations in population size at all known sites of occurrence. The population at Red Bluff has been monitored annually since 1987. During that period the population varied from a high of 425 plants per 0.1 ha in April of 1993 to a low of 19 plants per 0.1 ha in October of 1987 (Harper et al. 2000).

In this study, we have attempted to determine the effect of variable interplant distances on seed set for *Arctomecon humilis*. Because interplant distances inescapably increase as population density declines, one might expect this insect-pollinated species to reproduce less effectively when pollinators are forced to commute greater distances between plants. However, little information exists concerning the effects of interplant distances on the behavior of common pollinators of the dwarf bear-poppy. Likewise, the influence of interplant distance on frequency of pollinator visits or the number of pollen grains that are deposited on individual stigmas after a single visit is not known for this bear-poppy. Other studies have demonstrated that many plant species rarely produce maximum seed set after a single visit from a pollinator (Primack and Silander 1975, Silander 1978, Rathcke 1983). Such studies have also shown that pollinators differ widely with respect to their ability to effect high seed set after a single visit to flowers of any specific species.

Methods

To obtain data that are broadly representative of the influence of interplant distance on seed production of the dwarf bear-poppy, we have drawn our sample from three separate populations of the species. Allphin et al. (1998) have shown that the three populations sampled show genetic differences from each other in respect to allele frequencies at selected loci.

The Red Bluff population that we sampled is near the community of Bloomington and north of the Virgin River. We have also sampled the White Dome and the Beehive Dome populations. The White Dome population is roughly 10 km south of St. George and almost on the Utah-Arizona border. Beehive Dome is approximately 15 km southeast of St. George, near the Arizona border, on Warner Ridge.

All of the sample sites occur on the Shinabkaib member of the Moenkopi Formation at about 875 m elevation. The Shinabkaib shales are strongly impregnated with gypsum, 25–50 percent by weight (Nelson and Harper 1991). Annual precipitation averages about 200 mm across the sample area. The mean annual temperature at St. George is 16.8° C (Nelson and Harper 1991).

The annual precipitation is both highly variable over these study areas and of critical importance for seed germination, seedling establishment, and seed production for the dwarf bear-poppy. The coefficient of variation for annual precipitation at St. George is almost 32 percent over the 100 years that the station has operated (National Oceanographic and Atmospheric Administration 2000). Perhaps more pertinent is the fact that annual precipitation has ranged from a low of 90.2 to a high to 425.5 mm during the period of record at that station. To more accurately document influential climatic variables for seed production by this bear-poppy, we have determined precipitation at the St. George station for the 7 months preceding sampling dates for seed production. That period includes the coolest months of the year at this location, so most of the precipitation falling during the period enters the soil and is available for flowering and fruiting of the dwarf bear-poppy, which occurs in April and early May.

Samples were collected from approximately 20-ha plots at each of the three sites. Ten sample points were taken within each study plot; they were positioned at the intersections of a grid across the surface of each study area. Grid lines were 50 m apart. At each intersection a peg was pushed into the ground and the area around that point was divided into four quadrants of equal size (90° angles). These points became centers for the quarter method, a distance method used to sample plant populations in which individuals are often far removed from each other.

The quarter method provided a crude estimate of poppy density at each site and quantified the degree to which plants were aggregated in space; it also provided an objective method for selecting plants to evaluate the effects of interplant distance on pollination and seed set (Cottam and Curtis 1956). Operationally, a point positioned at a grid intersection became the center for four quadrants erected around the point. The distance from the point to the nearest object of interest (in this case, the nearest bear-poppy) was recorded for each quadrant. In a population of randomly dispersed objects, the average point-to-object distance provides an accurate estimate of the square root of the mean area per individual in the population (when area and distance are recorded in the same basic units—e.g., in m^2 and m, respectively). We have used the ratio of average point-to-object distance and the variance of that value as an estimator of population aggregation, because statisticians have long known that the ratio approaches 1.0 for randomly dispersed objects (Steel and Torrie 1960).

The nearest poppy plant in quadrants 1–3 became the base plant for interplant distance analyses. In each quadrant, the closest plant was taken as the base plant if it was flowering. If the nearest plant was not flowering, the nearest flowering individual in the quadrant was located and the nearest flowering poppy to that plant was chosen for analysis. The distance between those two individuals was recorded and the nearest neighbor individual was studied for number of flowers produced and number of developing fruits. Finally, one of the larger fruits present on the nearest neighbor plants was harvested and placed in a 5 cm x 10 cm paper envelope, which was sealed. Plant number and collection site were recorded on the envelope. Thirty randomly chosen plants were thus inventoried at each of the three sites.

In the laboratory, fruits were opened and the number of well-filled, apparently viable seeds was recorded. The numbers of aborted seeds (shriveled) and unexpanded ovules in the fruit were also recorded. Ultimately, percent pollination (percent of flowers that produced expanded fruits) and percentage of seed set (the proportion of ovules in each fruit that produced filled seeds) was correlated with the interplant distance associated with individual inventory plants. Preliminary analyses suggested that the number of flowers produced by inventoried plants was interacting with interplant distance to determine percentage pollination and seeds set per fruit of individual plants. Accordingly, the joint effects of interplant distance and flower number on flower pollination and fruit set were evaluated using multiple regression (Steel and Torrie 1960).

Results

The spatial distribution of bear-poppy plants at the three study sites is considered in Table 1. The average point-to-plant distances obtained using the quarter method show that plants in all populations are widely spaced and highly aggregated. Small, disjunct subpopulations are widely separated from other subpopulations. Plants appear to prefer tops and southern exposures of ridges in the gently undulating terrains that develop on weathered exposures of Moenkopi shale. Because all populations show strong aggregation of individuals into small, variably spaced subpopulations, reliable estimates of plant density are not possible; such estimates are based on the assumption that all objects sampled are randomly dispersed in space. We do know the exact number of plants on a 0.07 ha monitoring site at Red Bluff—that area contained 74 plants (~106 plants per 0.1 ha) in October of 1999. Using the assumption that the average point-to-plant distance (2.78 m in Table 1) equals the square root of the mean area per plant for randomly dispersed objects (Cottam and Curtis 1956), one would estimate approximately 129 plants per 0.1 ha. Thus, even though the distances obtained with the quarter method are not randomly dispersed about their mean, they do permit an estimate of population density that is reasonably close to actual density values observed on a portion of the larger sample area. It should be noted, however, that poppy populations at Beehive Dome and White Dome are much more aggregated than at Red Bluff. Thus point-to-plant distances could be expected to yield less reliable estimates of true density.

Table 1. Population characteristics for dwarf bear poppies at three sample sites.

Site	Average point-to-plant distance (m)	Aggregation Index*
Red Bluff	2.78	9.9
Beehive Dome	9.54	50.0
White Dome	11.78	37.9

*The aggregation index is the ratio of each average point-to-plant distance divided into the variance for that average.

The extreme aggregation within the bear-poppy populations provides a wide variation in interplant distances. Both pollination and seed fill are strongly influenced by interplant distance and number of flowers per plant (Table 2). The data suggest that for the dwarf bear-poppy and the pollinators involved in our area, pollination is not adversely affected by interplant distance until it exceeds 10 m. The effect is slight for plants that produce more than 30 flowers, but becomes progressively more influential as flower number declines. The effects of flower number and interplant distances on seed fill were strong even when interplant distances were less than 3 m. When distances exceeded 10 m, plants with less than 10 flowers filled less than 20 percent of potential seed, on average.

Table 2. Percent pollination and seed fill for 90 randomly selected plants separated into classes based on flower number and distance to nearest flowering conspecific. Sample size (n) is given for each compartment. Data are based on a sample taken in year 2000.

Interplant distance classes (m)	Number of flowers per plant: 1–10	11–30	≥ 31
Percent Pollination			
≤ 3.0	96.4 ± 2.83 (12)	92.6 ± 3.72 (11)	95.9 ± 1.58 (13)
3.1–10.0	93.5 ± 4.37 (7)	92.6 ± 4.05 (6)	90.4 ± 3.25 (16)
≥ 10.1	56.9 ± 14.01 (6)	64.9 ± 13.79 (4)	89.6 ± 2.70 (15)
Percent Seed Fill			
≤ 3.0	51.3 ± 9.92 (12)	66.7 ± 7.53 (11)	72.5 ± 6.67 (13)
3.1–10.0	41.3 ± 13.48 (7)	49.8 ± 11.00 (6)	71.5 ± 5.73 (16)
≥ 10.1	19.4 ± 12.29 (6)	35.2 ± 20.36 (4)	67.1 ± 6.52 (15)

Pollination success and seed fill appear to be dependent on the conspicuousness of the floral flag. Increasing distance or fewer flowers per plant both appear to reduce the attractiveness of the floral signal for foraging pollinators, effectively reducing the number of pollinator visits. Pollination appears to be less sensitive to the number of pollinator visits than percentage seed fill. The results of multiple regression analyses (Table 3) demonstrate that interplant distance and number of flowers per plant both exert statistically significant effects on pollination and seed set. For pollination the interaction between distance and number of flowers per plant was significant.

Because we have preliminary interplant distance data, and we know its influence on pollination and seed fill from Red Bluff for reproductive year 1997, a year of far better moisture relations than 2000, we can make a rough evaluation of the relative impacts of abiotic resources (water availability) and interplant distances on pollination and seed fill. During the 7-month period (October 1996–April 1997) preceding flowering and fruiting of the dwarf bear-poppy in 1997, 196.3 mm of precipitation fell at the St. George, Utah weather station (137.8% of the long-term mean for that period). The pollination percentage was 93.9 at the Red Bluff site, and the seed set percentage averaged 84.5 in 1997. When results for 2000 are averaged across all interplant distance and flower number classes, pollination averaged 82.0 percent and seed fill was 52.8 percent. Precipitation for the preceding 7 months in 2000 was only 65.5 mm (46.0% of the long-term average).

These data demonstrate that resources do exert a strong impact on flower pollination and seed fill in developing fruits of the dwarf bear-poppy. Nevertheless, the year 2000 results demonstrate significant effects of interplant distance and flower number on pollination and seed fill independent of those of abiotic resources.

Discussion

Our results demonstrate that the number of surviving plants alone is not an adequate indicator of the reproductive health of rare plants. When interplant distances become too great, both percentage pollination and percentage seed fill can be expected to decline. That decline may be especially great for species that produce few or inconspicuous flowers. Results for interplant distance will undoubtedly vary with pollinators. Flowers ser-

Table 3. Multiple regression results of the combined (above) and independent (below) effects of number of flowers per plant and interplant distance on percentage fruit set (pollination) and percentage seed fill. The interaction of number of flowers per plant and distance between flowering plants on percentage of flowers setting fruit or filling seeds is also tested.

Source of variation	Degrees of freedom	Sum of squares	Mean sum of squares	Probability of F value	Larger F
Pollination combined effects					
Model	8	10,171.78	1,271.47	6.25	<0.0001
Error	81	16,490.85	203.59		
Corrected total	89	26,662.63			
Pollination independent effects					
Distance	2	7,861.35	3930.67	19.31	<0.0001
No. flowers per plant	2	1,815.46	970.73	4.46	0.0146
Distance-flower interaction	4	4,200.77	1050.19	5.16	0.0009
Seed fill combined effects					
Model	8	22,072.64	2,759.08	3.42	0.0019
Error	81	65,275.25	805.87		
Corrected total	89	87,347.90			
Seed fill independent effects					
Distance	2	6,577.33	3,288.67	4.08	0.0205
No. flowers per plant	2	17,705.08	8,852.54	10.99	<0.001
Distance-flower interaction	4	2,759.21	689.80	0.86	0.4941

viced by pollinators that habitually make long commutes between floral resources and nesting sites would probably be less handicapped by large reductions in density than plants serviced by pollinators less prone to search large areas.

Because seed production is the product of percentage pollination times percentage seed fill, reductions in these processes can have large effects on seed production per plant in any given year. For the bear-poppy considered here, small plants that were far removed from other flowering individuals experienced reductions in potential seed set of more than 75 percent.

Windsor et al. (2000) have demonstrated that maximum seed set in the desert vine, *Cucurbita foetidissima*, was never achieved after a single pollinator visit. Maximum fertilization was dependent upon multiple visitations. They further demonstrated that pollen competition occurred in the species when it received abundant pollen. Progeny tests demonstrated that seedlings emerging from seed produced by heavily pollinated fruits consistently showed greater vigor for several characteristics than seedlings from fruits that received insufficient pollen to experience pollen competition. Their results suggest that not only may seed set suffer when population density falls below a critical level among reproductively active plants, but vigor of individuals in the next generation may also be eroded. That hypothesis is supported by studies that show a significant correlation between vigor of gametophyte and sporophyte generations in several species. (See Mulcahy et al. 1983 and Willson 1979 for reviews of pollen tube competition and its potential effects on sporophyte genotype and vigor.)

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