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Arctomecon humilis (Papaveraceae) across a quarter century:
unraveling of a pollination web?

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REPRODUCTION AND POLLINATION OF THE ENDANGERED DWARF BEAR-POPPY *ARCTOMECON HUMILIS* (PAPAVERACEAE) ACROSS A QUARTER CENTURY: UNRAVELING OF A POLLINATION WEB?

Vincent J. Tepedino¹, John Mull², Terry L. Griswold³, and Gerald Bryant⁴

ABSTRACT.—*Arctomecon humilis*, a rare gypsophile of the extreme northeastern Mojave Desert, is restricted to a few isolated populations in Washington County, Utah, USA. At several times in the past quarter century, we have studied the breeding system and reproductive success of this endangered species, recorded its pollinators, and tested the feasibility of human-assisted gene flow by performing reciprocal crosses between 2 isolated “populations” approximately 4 km apart. *Arctomecon humilis* possessed a mixed breeding system in the population studied (Beehive Dome in 1988); some plants exhibited self-compatibility but produced significantly fewer fruit/flowers and seeds/fruit for geitonogamous self-pollinations than for cross-pollinations. Few fruits and seeds were produced in the absence of pollinators. The results of cross-pollination treatments did not differ from unassisted open-pollinations (controls), suggesting that pollinators were not limiting reproductive success. Our more recent results (2012) suggest that some populations may be more at risk than others. Although all 7 populations surveyed produced $\geq 70\%$ fruits/flower, they differed significantly in fruit set and in average seed number/fruit and seed weight. Possible reasons for these differences (i.e., inbreeding, genetic load, insufficient mating types, pollinator scarcity, etc.), are all potentially important for conservation management and should be investigated. Over the past 2 decades, the pollinator community appears to have changed dramatically from one composed of specialist and generalist bees to one where pollination is presently being accomplished by generalist foragers alone. The health of one of these generalists, the honey bee *Apis mellifera*, is a current global concern, and its future presence as a pollinator of *A. humilis* is unclear. Our reciprocal crosses between the White Dome and Webb Hill populations provide support for our proposal that human-mediated gene flow through interpopulation cross-pollinations be undertaken every 5 years to increase the genetic variability of populations. We make several other recommendations for research that would improve the ability of land managers to conserve this species.

RESUMEN.—*Arctomecon humilis*, una rara gipsófila del extremo noreste del Desierto de Mojave, está restringida a unas cuantas poblaciones aisladas en el condado de Washington, Utah (EE.UU.). En varias ocasiones en el último cuarto de siglo, hemos estudiado el sistema de cultivo y el éxito reproductivo de esta especie en peligro de extinción, registramos sus polinizadores y comprobamos la viabilidad de una corriente de genes asistidos, por humanos, al realizar cruces recíprocos entre dos “poblaciones” aisladas aproximadamente a 4 km de distancia entre una y la otra. Descubrimos que el *A. humilis* posee un sistema de reproducción mixto en la población estudiada (Cúpula de Colmena en 1988); algunas plantas exhibían auto-compatibilidad, pero producían significativamente menos frutos/flores y semillas/frutos en las autopolinizaciones geitonógamas que en las polinizaciones cruzadas. Se produjeron pocos frutos y semillas en ausencia de polinizadores. Los resultados de los tratamientos de polinización cruzada no difirieron de las polinizaciones abiertas no asistidas (controles), sugiriendo que los polinizadores no limitaban el éxito reproductivo. Nuestros resultados más recientes (2012) sugieren que algunas poblaciones pueden estar en más riesgo que otras. Aunque las siete poblaciones analizadas produjeron $\geq 70\%$ frutos/flores, difirieron significativamente entre el tipo de fruto, entre el número promedio de semillas/frutos y entre el tamaño de las semillas. Las posibles razones de estas diferencias (i.e., endogamia, carga genética, tipos de cruce insuficientes, escasez de polinizadores, etc.) todos potencialmente importantes para los tratamientos de conservación, deberían ser investigadas. La comunidad polinizadora parece haber cambiado dramáticamente durante las últimas dos décadas, de abejas especialistas y generalistas a una donde la polinización se lleva a cabo actualmente sólo por abejas generalistas. La salud de una de estas generalistas, *Apis mellifera*, la abeja de la miel, es de interés mundial y su futura presencia como polinizadora de *A. humilis* no es clara. Nuestros cruces recíprocos entre las poblaciones de Cúpula Blanca y Webb Hill proporcionan apoyo a nuestra propuesta de que la corriente de genes asistidos a través de polinizaciones cruzadas entre poblaciones se realice cada cinco años para aumentar la variabilidad genética de las poblaciones. Concluimos haciendo varias otras recomendaciones para la investigación que podrían mejorar la capacidad de los responsables de estas tierras de conservar esta especie.

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A critical question confronting plant conservationists is how to facilitate reproduction by their rare wards. After all, the maintenance or resurgence of rare plant populations and the acquisition of propagules to restore former populations and initiate new ones are ultimately contingent on seed production, especially in plants that do not reproduce vegetatively. Seed production, in turn, is usually dependent on healthy populations of pollinators: a recent study estimates that about 80% of temperate-zone angiosperms depend on animals, usually insects, to deposit viable pollen on receptive stigmas (Ollerton et al. 2011). Most rare plants in the western USA fit this finding (Tepedino 2000).

Managing for reproductive success of many rare plant species is difficult because so little is known of their reproductive biologies. Dwarf bear-poppy, *Arctomecon humilis* (Papaveraceae), is an example, though it is relatively well-studied for a rare plant. Demographic studies show it to be a short-lived perennial (with about a 5-year lifespan) that begins to flower in the second year; seedlings rarely survive and population numbers fluctuate widely (Harper and Van Buren 2004; unpublished information from several BLM monitoring sites, R. Douglas, personal communication). Seed production may be related to plant size and density (Harper et al. 2000). Aside from a few estimates of fruit production (Harper et al. 2000, Harper and Van Buren 2004) and an undocumented assertion that *A. humilis* has a self-incompatible breeding system (Harper et al. 2000), little else is known of its reproduction, and nothing is known of its pollination or pollinators.

Arctomecon humilis is one of a trio of closely related species confined to the hot desert regions of Arizona, California, Nevada, and Utah in the southwestern USA (Nelson and Welsh 1993). The plants are particularly striking when in bloom and have many large, open, white, fragrant 4-merous flowers subtending numerous bright yellow-orange anthers. *Arctomecon humilis* is recognized as one of the rarest plant species in the USA with endangered status under the Endangered Species Act (USFWS 1979). The species is gravely imperiled by several criteria: (1) it is a gypsophile of the extreme northeastern Mojave Desert, limited in global extent to 13–16 km² of the Shinob Kibe member of the Moenkopi geological formation in Washington County, Utah (Nelson and Harper

1991); (2) there are about 7 small, somewhat isolated populations (we use population to refer to continuous groups of plants that are at least 3 km from the nearest population without any implication of genetic isolation); (3) none of these populations are large, but several are very small and all are fragmented (i.e., surrounded by unfriendly habitat due to rapidly expanding human activity); (4) as a taxon with only 2 congeners, one of which (*A. californica*) is also imperiled, *A. humilis* is also a phylogenetic rarity (Nelson and Welsh 1993); and (5) there is evidence that some populations are isolated, genetically impoverished, and in danger of extinction (Simpson 2012).

Our specific objectives were to (1) describe the plant's breeding system, specifically addressing whether pollinators are needed to effect sexual reproduction and whether plants are self-compatible (this is especially relevant because sexual reproduction is negatively affected by habitat fragmentation, and self-incompatible species are at heightened risk; Aguilar et al. 2006); (2) compare reproductive success in 1988 with that of 2012; (3) examine the feasibility of performing reciprocal intersite crosses; (4) identify pollinators at 3 times in the past 25 years and describe how they may have changed; (5) discuss what such changes may mean for the continued *in situ* existence of *A. humilis*; and (6) suggest research that would provide needed tools for conservation managers.

METHODS

Study Sites

Plant reproduction was studied experimentally in 1988/1989 at the Beehive Dome site, the most southeastern known population of *A. humilis* (Fig. 1). This site was chosen because of its relatively large and healthy population, and because it was somewhat removed from human activity. In 2012, plants at 7 sites were selected for studies of reproductive success (Fig. 1). Part of Shinob Kibe (SK) and White Dome (WD) are owned and managed by The Nature Conservancy, and Atkinville (AT) is located on SITLA (School and Institutional Trusts Lands Administration) lands administered by the state of Utah. All other sites are located on Bureau of Land Management (BLM) land administered by the U.S. Department of the Interior. General soil and habitat characteristics of the sites are described by Nelson

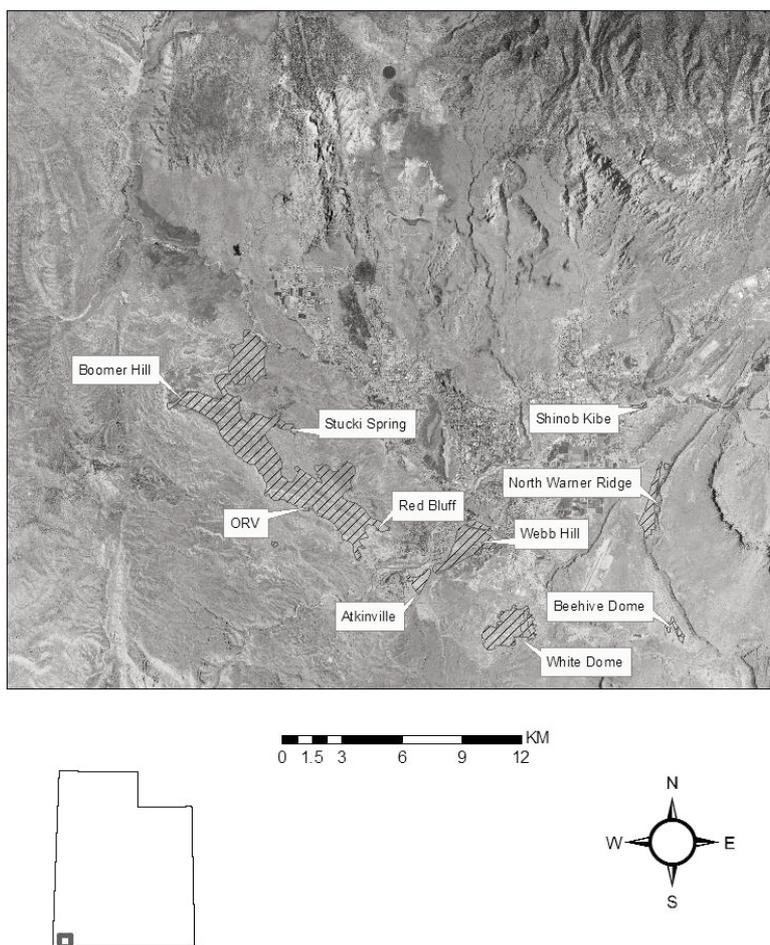


Fig. 1. Location of the 10 sites used in this study. Hatched areas indicate the distribution of *Arctomecon humilis* in Washington County, Utah. Five of the sites—Shinob Kibe, North Warner Ridge, Webb Hill, Beehive Dome, and White Dome—are recognized names of dwarf bear-poppy populations; some regard Atkinville and Webb Hill, separated in 1974 by a busy interstate highway, as a single population, though we have treated them as separate. The other 4 sites—Red Bluff, ORV, Boomer Hill, and Stucki Spring—are individual sampling sites within the large, sinuous Red Bluff population.

and Harper (1991), and the distances between some are approximated in Allphin et al. (1998).

Experimental Pollinations

To describe flower maturation, we closely followed several flowers, each on a separate plant, over several days, paying special attention to movements and color changes of reproductive parts.

Breeding system experiments were conducted on flowers in bagged inflorescences on large plants that had the many inflorescences needed for multiple experimental flowers. Large plants were also advantageous for their

vigor and their distribution throughout the population. Prior to the opening of any flowers, we bagged inflorescences using bags fashioned from pale-colored Saran Cloth[®] (mesh size 121/cm²); bags were equipped with a drawstring to facilitate a snug, gentle fit about the base of the stem.

Each breeding system treatment was delivered to a different flower on each inflorescence: (1) agamospermy—flower emasculated in the bud before anther dehiscence but otherwise unmanipulated; (2) autogamy—flower untreated; (3) geitonogamy—flower pollinated on the first day of anthesis with fresh donor

pollen from another bagged flower in the same inflorescence (in the few cases when a fresh pollen donor was unavailable, we used pollen from another inflorescence on the same plant); and (4) xenogamy—flower pollinated on the first day of anthesis with fresh donor pollen from a flower on another plant >4 m distant. On a separate bagged inflorescence on the same plant, we conducted experiments on stigma receptivity using flowers in the following stages: Bloom Day 2 AM and Bloom Day 3 AM. These were crossed with fresh outcross pollen from a plant >4 m distant. For all treatments, pollen was transferred from donor to recipient using a supply of small paintbrushes cleaned between pollinations by dipping in alcohol, wiping, and drying. Treatments on each plant were randomly delivered to remove any effect of position in the inflorescence (Lee 1988). An unbagged, open-pollinated flower was marked on another inflorescence of the treatment plant as a control in 1988, but not in 1989. Treated flowers were marked by loosely tying color-coded threads about their base. All plants did not always receive all treatments. Flowers (except controls) were bagged at all times except when experimental pollen transfers were made. When strong winds blew bags off inflorescences, all data were discarded and another inflorescence was used. We repeated the geitonogamy and xenogamy treatments in 1989 and also compared 2 stigma receptivity treatments: Day 1 PM, and Day 2 AM. We also tested pollen viability of second-day flowers when delivered to a bagged first-day stigma on a different plant. Finally, in 1989 at 8:30 on a warm morning (to ensure pollinator activity), we bagged first-day flowers so that we could measure fruit production.

The fruits of all experimental flowers from 1988 and 1989 were collected at maturation and examined later in the lab to record the percentage of fruit set and number of seeds/fruit. Only filled seeds were counted.

Reproductive Success

In 2012, we compared fruit and seed production on 20 open-pollinated plants at each of 7 sites: Webb Hill (WH), White Dome (WD), Red Bluff (RB), Beehive Dome (BD), North Warner Ridge (NWR), Atkinville (AT), and ORV, which is part of the larger RB population (Fig. 1). We marked 2 flowers on each plant with embroidery floss tied lightly to the base of the

pedicel on the day before opening, when mature buds had a distinctive, swollen appearance that distinguished them from more immature buds. When possible, large plants bearing multiple flowers were chosen. The number of available plants was limited at AT, and plants were widely dispersed at NWR. In these populations, some small plants were used.

The fruits of all marked flowers from 2012 were treated as described above, except that seeds from each fruit were dried and weighed *en masse* on an electronic balance and then counted. Average seed weight was obtained by dividing seed mass by seed number.

Reciprocal Crosses

Reciprocal crosses used 35 plants at each of the WD and WH sites, 3.5–4.0 km apart (Fig. 1). To facilitate the efficient collection and transfer of pollen, the largest available plants were selected from the densest sections of these populations. On the day before opening, one flower on each plant was bagged with nylon bridal veil fabric (98 squares/cm²) and secured to the flower pedicel with a twist tie. On the morning of anthesis, a fresh stamen was clipped from each bagged flower, placed individually in a small plastic bag, and transported in a cooler to the recipient site, where the donor anther was gently and repeatedly rubbed over the stigmatic surface of the marked recipient flower. Each recipient flower also served as a pollen donor for its partner in the other population. Crosses were accomplished over the course of 2 days (20 on day 1, 15 on day 2). On each day, all crosses were completed before noon. Bags remained on flowers until fruit maturation began. The bags were then removed, and each experimental flower was marked with a piece of embroidery floss tied on the pedicel. Fruits were collected at maturation and subsequently treated as described in the open-pollinated fruit survey.

Statistical Analysis

We used parametric statistics (*t* tests, one-way ANOVA) when possible and nonparametric tests (Mann–Whitney *U* tests, Kruskal–Wallis test) when variances exceeded acceptable limits ($P < 0.05$), determined using Bartlett's test for homogeneity of variance (Snedecor and Cochran 1967). Fruit set comparisons were made using contingency tables and their partitions (Maxwell 1961). For 2012, at each fruiting

survey site, we initially compared seed number using only those plants that produced fruits from both flowers (paired *t* test). As none of these comparisons approached significance (all $P \geq 0.10$), we compared the combined data set to seeds/fruit for plants that produced only one fruit of the 2 treated flowers. Again, there was no significant difference for any site (all $P > 0.05$). These results enabled us to combine all data for each site for intersite comparisons. Seed weight data were treated identically and yielded similar results.

Insect Collections and Observations

Insect collections and observations were made opportunistically, during other activities, in 1988 (and a few in 1989) at BD and at the large and sinuous RB population (sometimes previously termed Bloomington Hills, South Bloomington, West Bloomington, or Bloomington Dump), which included Boomer Hill (BO) and Stucki Spring (SS) (Fig. 1). Collections were not equally distributed over sites; BD, for example, was visited most frequently, and RB next most frequently. Other sites were visited as time allowed. Voucher specimens reside in the USDA-ARS Pollinating Insects Research Unit at Utah State University, part of the U.S. National Pollinating Insects Collection.

In 1993, we observed the rare poppy oligocele, *Perdita meconis*, to determine its role as a pollinator of *A. humilis* and attempted to circumscribe its distribution in southern Utah. Bees were observed and collected at the flowers of 7 dwarf bear-claw poppy populations: AT, BD, BO, NWR, RB, WD, and WH (Fig. 1). In addition, blooming individuals of *Argemone* (Papaveraceae), the sister group of *Arctomecon* (Schwarzbach and Kaderet 1999) and the only other taxon that *P. meconis* is known to collect pollen from (Griswold et al. 2006), were visited throughout Washington County, Utah, USA, and surrounding areas. Our frequent forays (16 May–12 June) took us from Kanab, Kane County, Utah, in the east, to the Lincoln County, Nevada, border in the west, and from Milford, Iron County, Utah, in the north, to Mt. Trumbull in the Arizona Strip (that part of Mojave County, Arizona, above the Colorado River) in the south.

In 2012, we collected bees visiting *A. humilis* flowers at 6 sites (BD, NWR, RB, SK, WD, and WH; Fig. 1) on 12 days between 18 April and 14 May. Total collecting time was

estimated at 30 hours, most of which was done before 10:00.

Bee specimens collected in 2012 were examined under a dissecting microscope for the presence of *A. humilis* pollen, following methods similar to those outlined by Motten (1986). Forceps were used to gently remove pollen from the scopae when possible. Pollen was placed on a slide with a drop of alcohol. Once the alcohol had evaporated, a drop of cotton blue stain and a coverslip were applied to the preparation. A small piece of agar was dabbed on other parts of the body where pollen was concentrated, and embedded grains were removed and transferred to a slide. The agar was then slowly melted, and the stain and coverslip were applied to the slide. Pollen grains were compared to similarly prepared *A. humilis* pollen taken directly from flowers.

RESULTS

Flower Development

In both 1988 and 1993, dwarf bear-poppy began blooming in early April. Flowers are fragrant and typically last 2 days; unpollinated flowers may be viable for a third day. Expanding flower buds generally split and dislodged their caduceus sepal cap in the early morning (sometimes before sunup) as the temperature rose. The petals opened rapidly and reflexed until they touched the stem, revealing stamens closely attending the pistil and its sessile stigma. Pollen shedding appeared to be temperature dependent and usually began while the anthers were near to the stigma; stamens continued to shed as they gradually bent away from the stigma. By mid-to-late afternoon of the first day, stamens were usually brown, shriveled, and spent; they typically abscised completely during the second day.

Stigma Receptivity

In 1988 we compared receptivity of bagged flowers on the second and third mornings of anthesis (Table 1). We found that Day 2 flowers set fruit significantly more often than did Day 3 flowers ($\chi^2 = 6.5$, $df = 1$, $P < 0.02$). There was no difference between treatments in seeds/fruit for flowers that set fruits (Mann-Whitney *U* test: $P > 0.05$), but both produced significantly fewer seeds/fruit than did controls (Mann-Whitney *U* test: $P < 0.001$).

TABLE 1. Fruit set (%F) and mean seeds/fruit (SF with standard deviation in parentheses) for several experimental breeding system and reproductive treatments at Beehive Dome in 1988 and 1989. Treatment abbreviations: AG = agamospermy, AU = autogamy, G = geitonogamy, X = xenogamy, C = control. All treatments beginning with "D" are stigma receptivity treatments: D1P = Day 1 PM; D2A = Day 2 AM; D3A = Day 3 AM; PD2 = Day 2, pollen; B830 = bagged at 08:30. *N* = sample size.

	Treatment	<i>N</i>	%F	SF (SD)
Breeding system				
1988	AG	14	2.4	—
	AU	24	8.3	25.0 (0.0)
	G	21	42.9	7.7 (8.8)
	X	21	100.0	23.1 (8.8)
	C	19	100.0	25.9 (4.1)
1989	X	36	97.2	23.3 (9.2)
	G	34	73.5	15.1 (10.1)
Other treatments				
1988	D2A	13	92.3	13.6 (8.4)
	D3A	13	46.2	13.2 (10.2)
1989	D2A	21	100.0	22.6 (8.9)
	D1P	23	87.0	19.2 (9.0)
	PD2	14	92.9	18.2 (8.5)
	B830	6	83.3	20.8 (10.7)

In 1989, to refine our comparisons further, we compared the results of treating flowers pollinated on Day 1 PM with flowers pollinated on Day 2 AM (Table 1). There was no difference between treatments in percent fruit set ($\chi^2 = 2.9$, *df* = 1, $P > 0.05$) or in number of seeds/fruit ($t_{39} = 1.23$, $P > 0.20$).

Anther Age

In 1989, after watching anthers mostly shed their pollen and wither in the late afternoon of the opening day of bloom in 1988, we examined the virility of second-day pollen when applied to bagged first-day flowers. We found that viable pollen remained in second-day anthers: 13 of 14 treated flowers produced fruits and the number of seeds/fruit was indistinguishable from Day 2 stigmas pollinated in the morning with Day 1 pollen ($\chi^2 = 1.5$, *df* = 1, $P > 0.10$; Table 1).

Breeding System

There was a significant difference in the percentage of fruit set among the 4 breeding system treatments in 1988 ($\chi^2 = 46.0$, *df* = 3, $P < 0.001$; Table 1). In the first contingency table partition, there was a highly significant difference ($\chi^2 = 32.3$, *df* = 1, $P < 0.001$) between treatments not requiring a pollinator (agamospermy, autogamy) and treatments requiring a pollinator (geitonogamy, xenogamy). Treatments requiring a pollen vector produced many more fruits. A second partition found no significant difference between treatments not

requiring a pollinator (agamospermy, autogamy; $\chi^2 = 0.005$, *df* = 1, $P > 0.9$). Conversely, the final partition found that the outcrossing treatment (xenogamy) produced significantly more fruits than did the pollinator-assisted selfing treatment (geitonogamy; $\chi^2 = 13.8$, *df* = 1, $P < 0.001$). Among those treatments producing sufficient fruits for analysis, the comparison was significant; the geitonogamy treatment produced significantly fewer seeds/fruit than the xenogamy or control treatments, which did not differ from each other (Kruskal–Wallis statistic = 14.0, $P < 0.001$).

To be confident of our results, we repeated the geitonogamy and xenogamy treatments in 1989. We again found that the xenogamy treatment produced a significantly greater percentage of fruits ($\chi^2 = 8.0$, *df* = 1, $P < 0.01$; Table 1) and a significantly greater number of seeds/fruit than did the geitonogamy treatment ($t_{58} = 3.3$, $P < 0.002$).

Reproductive Success

In 1988, all open-pollinated control flowers at BD produced fruits (Table 1). In 2012, fruit set at the 7 surveyed sites ranged from 70% to 100% (Table 2). There were significant differences among sites ($\chi^2 = 16.4$, *df* = 6, $P < 0.02$), with fruit set varying from 100% at BD to a low of 70% at AT. At 5 sites, fruit set was lower than 80%. We also found significant differences in seeds/fruit among sites (Kruskal–Wallis test: $P < 0.0001$). Three groups were demarcated ($P = 0.05$); 2 sites

TABLE 2. Survey results from 2012 of fruit set (% fruits/flower, FS), seeds/fruit (SF with standard deviation in parentheses), and average seed weight (SW with standard deviation in parentheses) at 7 sites in Washington County, Utah. Sample size is 40 for all FS samples; N_s = sample size for seeds/fruit and seed weight. Values within the columns SF and SW with the same superscript letter are not significantly different.

Site	FS	SF (SD)	N_s	SW (SD)
Atkinville (AT)	70	15.3 (6.6) ^{b,c}	28	1.89 (0.31) ^a
Beehive Dome (BD)	100	24.2 (11.3) ^a	40	1.84 (0.23) ^a
North Warner Ridge (NWR)	72.5	10.6 (6.4) ^c	29	1.45 (0.36) ^b
ORV	75	20.5 (9.8) ^{a,b}	30	2.13 (0.42) ^a
Red Bluff (RB)	77.5	25.6 (11.1) ^a	31	1.44 (0.22) ^b
White Dome (WD)	77.5	28.0 (8.6) ^a	31	1.55 (0.28) ^b
Webb Hill (WH)	87.5	20.9 (9.9) ^{a,b}	35	1.47 (0.32) ^b

TABLE 3. Fruit set (% fruits/flower, FS), mean seeds/fruit (SF with standard deviation in parentheses), and average seed weight (SW_p with standard deviation in parentheses) for crosses between plants at Webb Hill (WHX) and White Dome (WDX) and their respective controls (WHN, WDN; SW_t with standard deviation in parentheses). Webb Hill crosses have WH pollen recipients and WD pollen donors; White Dome pollen recipients have WH pollen donors. N_f = sample size for fruit set; N_s = sample size for seeds/fruit and seed weight for all fruits for each treatment; N_{sp} = sample size for paired seed weight comparisons between WD and WH.

	N_f	FS	SF (SD)	N_s	SW_t (SD)	N_{sp}	SW_p (SD)
WDX	35	80.0	22.3 (7.5)	28	1.31 (0.19)	16	1.32 (0.15)
WHX	35	62.9	20.3 (8.3)	22	1.27 (0.28)	16	1.24 (0.32)
WDN	40	77.5	27.7 (8.4)	31	1.55 (0.28)	—	—
WHN	40	87.5	20.9 (9.9)	35	1.47 (0.32)	—	—

(AT, NWR) produced the fewest fruits/flower and seeds/fruit. There was also a significant difference among sites in seed weight (Kruskal–Wallis test: $P < 0.0001$) with 2 distinct groups of sites ($P = 0.05$; Table 2).

Reciprocal Crosses

Fruit set for the reciprocal crosses between plants in the WH and WD populations were compared with each other and with their respective controls (Table 3); there was no significant difference among the 4 treatments ($\chi^2 = 6.7$, $df = 3$, $P > 0.05$). We then compared seeds/fruit between the paired reciprocal treatments using only pairs where both plants had produced fruit ($N = 16$); again, we found no significant difference ($t_{15} = 0.67$, $P > 0.50$). Seeds/fruit and seed weight were also compared between each cross and its control by using the full complement of crossed plants that produced fruits (Table 3). We found no difference in seed number for the WD comparison ($t_{57} = 1.51$, $P > 0.10$); seed weight of controls, however, was significantly greater than the crosses (Kruskal–Wallis test: $P = 0.005$). Results at WH were similar: there was no difference in seed number ($t_{55} = 0.23$, $P > 0.80$), but seeds from the control were significantly heavier than seeds from the crosses ($t_{55} = 2.44$, $P < 0.02$).

Insect Collections and Observations

Like its sister species *A. californica* (Hickerson 1998, Simpson 2012) and members of its sister genus *Argemone* (Schneider and Nichols 1984, Schneider et al. 1987, Schwarzbach and Kaderet 1999), the flowers of *A. humilis* produce copious pollen but no nectar, and are visited by a moderate number and variety of pollen-collecting bees. From 1988 to 1989 and in 1993, we collected 18 species of bees visiting *A. humilis* flowers at 6 sites (Table 4). The “parasitic” bee, *Stelis anthocopae*, can be eliminated as a reliable visitor as it does not collect pollen. Other uncommon species are also unlikely to play an important role in pollination.

Four bee taxa were prominent pollinators: 2 species of *Perdita*, *Eucera quadricincta*, several species of *Lasioglossum*, and the introduced honey bee *Apis mellifera*. Many more individuals of *P. meconis*, *E. quadricincta*, and *A. mellifera* were observed on the flowers than were collected, especially in 1993, when our objectives were to document pollinator presence and describe pollinator behavior. Of these most abundant visitors, the honey bee *A. mellifera* is an extreme generalist whose hive members visit many species of flowers for pollen; members of most species of the genus *Lasioglossum* also visit the flowers of many taxa (Hurd 1979) and

TABLE 4. Bee species collected while individuals foraged on the flowers of *Arctomecon humilis* in 1988 or 1993. *N* = number captured; date indicates range of capture. Site abbreviations: AT (Atkinville), BD (Beehive Dome), RB (Red Bluff), BO (Boomer Hill), SS (Stucki Spring), WD (White Dome), NWR (North Warner Ridge). An asterisk (*) indicates species with many more sighted, but uncollected individuals.

Family/species	<i>N</i>	Years	Dates	Sites
Andrenidae				
<i>Perdita meconis</i> **	36	1988, 1993	18 Apr–20 May	BD
<i>Perdita mohavensis</i>	19	1993	29 Apr–6 May	RB
<i>Perdita</i> sp.	1	1993	30 Apr	NWR
<i>Perdita turgiceps</i>	1	1988	24 Apr	BD
Apidae				
<i>Anthophora lesquerellae</i>	2	1993	22 Apr–6 May	BD
<i>Apis mellifera</i> **	9	1988, 1993	12 Apr–22 May	AT, BD, BO, RB
<i>Eucera quadricincta</i>	25	1988, 1993	12 Apr–22 May	BD, BO, RB, SS
Halictidae				
<i>Lasioglossum alium</i>	18	1988	13 Apr–5 May	BD, WD
<i>Lasioglossum hyalinum</i>	1	1988	11 May	BD
<i>Lasioglossum perparvum</i>	1	1988	9 May	RB
<i>Lasioglossum semicaeruleum</i>	1	1988	13 May	BD
<i>Lasioglossum sisymbrii</i>	20	1988, 1993	14 Apr–22 May	BD, BO, RB, SS
<i>Lasioglossum</i> sp.	14	1988, 1993	12 Apr–10 May	BD, RB
Megachilidae				
<i>Megachile</i> aff. <i>furcata</i>	1	1988	18 May	BD
<i>Megachile fucata</i>	1	1988	12 May	BD
<i>Megachile</i> sp.	1	1988	12 May	BD
<i>Megachile subanograe</i>	1	1993	23 Apr	WD
<i>Stelis anthocopae</i>	1	1993	30 Apr	NWR

are regarded as generalized foragers (Linsley 1958). *Perdita meconis*, a rare oligolege, collects pollen only from species in 2 poppy genera (*Arctomecon* and *Argemone*), whereas *E. quadricincta* females appear to be opportunistic pollen-collectors that are constant to *A. humilis* only when its flowers are abundant. In 1993, the first bees, honey bees, were not seen until 11 April, 8 days after first bloom; the first *P. meconis* was not seen until 19 April, over 2 weeks into the blooming season. The first *Lasioglossum* was seen on 12 April.

Members of the abundant taxa of bees varied in their foraging behavior. *Eucera quadricincta* females tended to forage rapidly and earlier in the day, and they visited relatively few flowers per plant before moving to other plants. *Apis mellifera* workers tended to appear on the flowers later and worked more deliberately, slowly collecting pollen and visiting many flowers on a plant before moving on. They greatly preferred polleniferous first-day flowers.

Both females and males of *P. meconis* were common on *A. humilis* flowers at BD in 1988 and 1993 (hundreds of sightings were made in 1993). They were active mostly between 09:00 and 12:00, depending on ambient temperature, and rarely were they seen after noon.

As the season progressed and early mornings became warmer, bees flew earlier. Sunlit plants were visited far more often than were shaded plants, especially earlier in the day. Females foraged similarly to those described visiting *A. californica* in Nevada (Hickerson 1998). Females stripped the pollen from the anthers with mandibles and forelegs as they pulled the stamens towards them with their midlegs. Pollen was then passed to the hindlegs for packing into the scopa, where it was tamped down and smoothed by midlegs and abdominal movements. Females commonly contacted the stigma when landing or departing from flowers, or when scrabbling around collecting pollen. Some females visited more than one plant on a foraging bout. The frequency of such activity was impossible to determine; their small size made following individuals extremely difficult in the sometimes breezy conditions.

The primary objective of males appeared to be the location of females. Males landed frequently on the abaxial side of the petals and crawled into the flowers where they lurked beneath overhanging stamens and prepared to pounce on foraging females. But they also displayed restiveness; they scrabbled about the flowers or took flight after a few minutes

TABLE 5. Bee species collected while individuals foraged on the flowers of *Arctomecon humilis* in 2012. *N* = number captured, *PS* = number collecting pollen, *PB* = number with pollen on body other than scopa; date indicates range of capture. Site abbreviations with number of collecting episodes: BD (Beehive Dome, 6), NWR (North Warner Ridge, 3), RB (Red Bluff, 1), SK (Shinob Kibe, 1), WH (Webb Hill, 4), and WD (White Dome, 1). Species collected in previous years are marked with an asterisk (*).

Family/species	<i>N</i>	<i>PS</i>	<i>PB</i>	Date	Sites
Andrenidae					
<i>Perdita albonotata</i>	1	1	1	9 May	NWR
Apidae					
<i>Apis mellifera</i> *	11	7	6	18 Apr–9 May	BD, NWR, RB, WH
<i>Centris cockerelli</i>	1	1	1	9 May	BD
Colletidae					
<i>Colletes covilleae</i>	1	1	1	9 May	BD
<i>Colletes salicicola</i>	1	1	1	9 May	NWR
Halictidae					
<i>Lasioglossum ?alium</i> *	4	0	0	2–10 May	BD, SK, WH
<i>Lasioglossum hudsoniellum</i>	2	2	1	14 May	WH
<i>Lasioglossum hyalinum</i> *	2	1	1	30 Apr–9 May	BD, RB
<i>Lasioglossum pimpavidum</i>	1	0	0	18 Apr	WH
<i>Lasioglossum perparvum</i> *	2	0	0	14 May	WH
<i>Lasioglossum</i> sp.	1	0	0	29 Apr	BD
<i>Lasioglossum</i> sp. 1	1	0	0	9 May	BD
<i>Lasioglossum</i> sp. 5	15	5	3	23 Apr–10 May	BD, NWR, RB, SK, WH, WD
Mellittidae					
<i>Hesperapis</i> sp.	1	1	0	9 May	BD

residence. It was not uncommon to find more than one male in a flower.

Mating in the flowers is common for *Perdita* species (e.g., Danforth 1991, Neff and Danforth 1991) and *P. meconis* males enjoyed a fair amount of success in encountering females. Females may be forced to acquiesce to male advances to gain access to pollen. Numerous mating pairs of *P. meconis* were found in the flowers or sometimes beneath them on the ground (they sometimes tumbled out while in copulo). Mating by females was frequently bracketed by pollen collecting; as soon as copulation ended, females returned to foraging.

The behavior of male and female *P. meconis* rendered them vulnerable to predation by crab spiders (Thomisidae), which were common flower residents. In 1993, crab spiders were present with the first bloom, 2 weeks before the first *P. meconis* was seen. Numerous dead *P. meconis* individuals of both sexes were seen in the possession of thomisids.

In 2012, collections were made with varying intensity at 6 sites from 18 April to 14 May (Table 5). Three sites could only be visited once and yielded few bees. In total, 44 specimens were collected in 12 species. Roughly one-third of all individuals belonged to *Lasioglossum* sp. 5, the only species recorded at all 6 sites. The second most abundant species was the honey

bee, recorded at 4 sites. Most species were recorded at BD, the site we collected at most intensively because of our interest in confirming the continued presence of *P. meconis*. Although we visited BD 6 times between 18 April and 9 May, we did not find either *P. meconis* or *E. quadricincta*, another important native bee pollinator of *A. humilis*.

Individuals of several taxa were either collecting *A. humilis* pollen in their scopae or were carrying poppy pollen on their bodies (Table 5). Seven of 11 *Apis* workers were collecting pollen and of the 7 collectors, 6 also had poppy pollen on their bodies. Five of 15 *Lasioglossum* sp. 5 were collecting pollen, and 3 of the 5 carried poppy pollen elsewhere on their bodies. In total, 45% of individuals captured were collecting pollen, and 75% of pollen collectors carried pollen on their bodies.

DISCUSSION

We began by noting the several criteria by which *A. humilis* meets the definition of a gravely imperiled plant species: (1) extremely limited distribution, (2) few populations, (3) small size of most populations, (4) genetic impoverishment of some populations, (5) isolation of most populations due to habitat loss, and (6) few congeners. Our present findings suggest that there are several additional reasons to be

concerned for the welfare of *A. humilis*: (1) a reproductive system that depends on pollinating bees; (2) a pollinator community in which native bee species, particularly specialists, are now absent from some sites or exist at very low numbers; and (3) a current dependency on generalist pollinators, especially the alien honey bee, which has health problems of its own (Aizen and Harder 2009, Potts et al. 2010). We address these in turn.

The breeding system of *A. humilis* is mixed, at least at the BD population (Table 1), where it was composed of self-compatible plants (approximately 60%) and self-incompatible plants (approximately 40%). Fruits from xenogamy treatments contained significantly more seeds than did fruits from geitonogamy treatments. However, it is not uncommon for species to vary in compatibility among populations (e.g., Busch 2005); thus, our results may not be indicative of the breeding system at all populations. The report of Harper and Van Buren (2004) that plants at RB (Van Buren personal communication) were “highly self-incompatible” should be confirmed and extended, because self-incompatible populations of rare plants, particularly small ones, are at greater risk of local extinction than are those that are self-compatible (Aguilar et al. 2006, Busch and Schoen 2008). A prime reason for this is genetic: genetic diversity of populations of self-incompatible species is significantly lower after fragmentation than is that of self-compatible species (Aguilar et al. 2008). For example, the number of S-alleles declines markedly in small populations, reducing the likelihood of successful pollinations in self-incompatible populations (Aguilar et al. 2008, Busch and Schoen 2008). In addition, pollen and nectar resources tend to accumulate in flowers where pollinators are scarce, necessitating fewer between-plant flower visits by pollinators to collect a complete pollen and/or nectar load than if pollinators were more abundant. Fewer between-plant visits in a self-incompatible species mean fewer effective pollinations.

The breeding system of *A. humilis* requires that conservation managers protect pollinators as well as plants (Kearns et al. 1998, Aguilar et al. 2006). Our results from 2012 suggest that pollinators of *A. humilis* have not only become scarce over the last 2 decades, but also that the composition of the pollinator community has been simplified in worrisome ways.

Such simplification is characterized by the decrease or disappearance of specialized pollinators and the ascendance of generalists (Tepedino 1979; see also Ashworth et al. 2004). To illustrate, an important pollinator at BD, *P. meconis*, is a specialist that collects pollen only from poppies in the genera *Arctomecon* and *Argemone* and is itself a rare species (Griswold 1993, Griswold et al. 2006). *Perdita meconis* is now either extinct in Utah or present at disquietingly low numbers. Another native, *E. quadricincta*, a facultative specialist, was also absent from the flowers of *A. humilis* in 2012, either because it was foraging on more rewarding flowers of other species or because its numbers have also dwindled at poppy sites in southern Utah. (Both species were also absent from collections made in 2014; O'Brien and Tepedino unpublished data). The absence of *E. quadricincta* is less troubling because it is a large, fairly common species in southern Utah, so it is likely to recolonize sites where it was not recorded in 2012, given adequate floral resources and nesting habitat. This is hardly the case for *P. meconis*, a diminutive bee whose nearest known population is approximately 100 km to the southwest in the Lake Mead National Recreation Area in Nevada, in association with sister species *A. californica* (Hickerson 1998, Griswold et al. 2006). Its recolonization of Utah sites from Nevada seems improbable.

Presently, *A. humilis* appears to rely for pollination on individuals of 2 generalist flower-visiting taxa. One of these, the beleaguered honey bee *A. mellifera*, has seen its feral populations plummet in the northern hemisphere in recent years (Potts et al. 2010, Jaffe et al. 2010), and its managed populations come under great pressure due to growing demand for crop pollination (Aizen and Harder 2009). (An exception appears to be urban areas of the Sonoran Desert, where feral Africanized honeybees are increasing; S. Thoenes personal communication). Pollinator partnerships between alien and native species sometimes succeed, at least temporarily (Dick 2001, Aguilar et al. 2006), and the honeybee has been visiting poppy flowers in Washington County for at least 25 years (Harper et al. 2000 also found it to be a common poppy-flower visitor); however, the prognosis for the continued presence of *A. mellifera* as a pollinator of *A. humilis* is unclear. It is more likely that the primary

pollinators of the future will be a suite of species in the genus *Lasioglossum* (Table 4, 5). Though ubiquitous, *Lasioglossum* species are notoriously inconstant in their foraging habits; many students of bees and pollination regard them as little more than unreliable opportunists (e.g., Linsley 1958). Certainly a poppy population dependent for pollination on individuals of *Lasioglossum* will experience fewer conspecific interplant flower visits than one serviced by *P. meconis*, because visits by the latter are always intraspecific visits, whereas those of *Lasioglossum* are far less so. Self-incompatible populations, if such exist, would especially be at risk.

At $\geq 70\%$, fruit set was high for all populations examined (Table 2; Harper et al. [2000] reported lower fruit set, but only for small and/or isolated plants). Nevertheless, plants at the AT and NWR sites produced significantly fewer fruits/flower and seeds/fruit than did plants in other populations, and this finding suggests that they may be at greater risk of decline. Possible reasons for lower fruit and seed production are many (inbreeding, genetic load, mate limitation, pollinator scarcity, etc.) and should be investigated. What is unexpected about these low fruit set and seed production results is that one of the sites (AT) is a purported member of a central site cluster of several populations, which seems to serve as a partial conduit for gene flow between more eastern and western populations (Simpson 2012). Perhaps AT, a population with relatively few plants (R. Douglas personal communication), is effectively isolated from eastern populations (by heavy traffic on the interstate highway that forms its eastern boundary) and from western populations (by housing and business developments). The other site (NWR) clusters with the SK population (Simpson 2012), which is the smallest, most isolated, and most threatened population of *A. humilis*; thus, it is not surprising to find the NWR population with low fruit set. The low seed weight at NWR only adds to concern for this site. Another population of potential concern is BD, which, despite its high fruit set, seed production, and seed weight, is relatively isolated and appears to have lost important pollinators. All of these populations should be carefully monitored. Other smaller populations, such as those at BO and SS, are actually contiguous with the large BR

population with which they almost certainly trade genes (Simpson 2012).

Despite the positive prognosis offered by some researchers (e.g., Simpson 2012), the plight of *A. humilis* seems to have worsened over the past 2 decades, even though most populations have been protected by reserves and fruit set continues to be high. Population declines in some fragments may not yet be manifest. Genetic erosion increases with time from initial impacts on rare populations (Aguilar et al. 2008), and there is reason to believe that the habitat loss and fragmentation experienced by *A. humilis* is quite recent and may not yet be fully evident. Prioritizing the risk of the various populations would be aided by filling information gaps in several areas, which would expand the options available to conservation managers. First, fairly frequent surveys of all populations would yield better estimates of numbers of ramets and refine estimates of distances among populations. Surveys should include the periodic estimation of reproductive success of ramets (i.e., fruit set and seeds/fruit), because declining reproduction can be a warning sign of inbreeding, genetic load, pollinator scarcity, and so forth, and can presage a subsequent decline in seedling and adult population numbers.

Second, as discussed above, the claim that some sites other than Beehive Dome are self-incompatible (Harper and Van Buren 2004) should be investigated, and data on fruit set and seed production should be compared with sites where self-compatibility occurs. Self-incompatible sites are at greater risk for reproductive failure (Aguilar et al. 2006) and genetic impoverishment (Aguilar et al. 2008), and thus should be unmasked.

Third, for several reasons, methods need to be developed to germinate seeds, grow seedlings, and transplant young individuals (older plants have proved impossible to successfully extricate because of their long taproots). Reared transplants could be used to augment present populations and to initiate new ones; the Purgatory Flat area mentioned by Nelson and Harper (1991) is a possible target as are other more promising areas delimited by M.A. Bowker (D. Roth and T. Arundel personal communication). By expanding the periphery of known populations, transplants might be used to reduce the distance between adjacent populations, thereby increasing the

likelihood of natural gene flow (Aguilar et al. 2008). Because *A. humilis* is a horticulturally desirable species, transplants could be made available to interested amateurs for planting in local backyard and community gardens as part of a community-wide conservation effort (Rudd et al. 2002, Goddard et al. 2009). Such plantings might serve as stepping-stones (Menz et al. 2010) to encourage gene flow and support populations of native bees. Natural colonization of extant populations by pollinators would also be more likely, especially for diminutive species like *P. meconis*.

Fourth, human-assisted gene flow between populations should be explored. All populations might benefit from an infusion of genes from other populations, as has been the case for some other species (Richards 2000, Willi et al. 2007, Lopez et al. 2009, Bermingham and Brody 2011). With the rapid development of Washington County as a retirement mecca, we cannot assume continued presence of healthy pollinator populations to effect gene flow. As we have seen, 2 important native bee species are already at low numbers, and the numbers of one alien generalist, the honey bee, are under pressure for several reasons. It may be time to begin an assisted breeding program in which interpopulation pollinations are performed manually every 5 or so years (the average life span of ramets). The successful hybrid experiments reported here testify to the feasibility of this management tool, although the finding that seed weights of controls significantly exceeded those of hybrids for both sites is concerning due to the size-fitness relationship for seeds (Westoby et al. 1992). Learning how to germinate seeds and grow seedlings would enable us to test the viability of hybrid seeds under controlled conditions.

Fifth, an effort should be made to locate and describe nesting sites of important native pollinators so that the location and substrate for such sites can be identified and protected. It is even possible to transplant overwintering bees of some ground-nesting species into appropriate habitat (Cane 1997), and such a management tool might be employed if pollinator populations continue to decline.

The growth projections for Washington County for the next several decades are a cause for concern for the continued existence of dwarf bear-poppy; we must employ every

weapon in our arsenal to assure that it remains a part of the southwestern Utah landscape.

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