Western North American Naturalist 64(4), © 2004, pp 482–491

DYNAMICS OF A DWARF BEAR-POPPY (*ARCTOMECON HUMILIS*) POPULATION OVER A SIXTEEN-YEAR PERIOD

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ABSTRACT.—A population of the dwarf bear-poppy (*Arctomecon humilis* Coville, Papaveraceae) at Red Bluff, Washington County, Utah, was monitored twice annually between 1987 and 2002. This is a narrowly endemic, gypsophilous species that has been formally listed as endangered since 1979. During the 16 years of observation, density of this species has fluctuated between 3 and 1336 individuals on the 0.07-ha monitoring plot. Moderate to large recruitments of seedlings occurred in 1992, 1995, and 2001. Seedling recruitments from a large, long-lived seed bank are triggered by abundant precipitation during the February–April period. At least 5.0 cm of rainfall is required during that interval to produce any seedlings. Seedlings experienced considerable mortality in the 1st few months of life in all observed cases. The average seedling initiated in the very large recruitment event of 1992 survived for only 2.6 years. Seedlings in that cohort that were alive 1 year after germination had an average longevity of 4.6 years. None of the seedlings that emerged in 1992 were still alive in October 2002. Mortality in this species was poorly correlated with fluctuations in precipitation or temperature. No epidemics of parasites or herbivores were observed. Mortality in the species appears to be caused by a variety of factors acting over a cohort's lifetime.

Key words: Arctomecon humilis, *demography, longevity, germination, seed bank.*

Arctomecon humilis Coville is a moderately short-lived perennial herb endemic to gypsiferous soils. It occurs only on soils derived from the Moenkopi Formation, a deep-water marine deposit of lower Triassic age. The formation is widely exposed in Washington County, extreme southwestern Utah. The species is a low-growing, evergreen plant that exists as light green rosettes during the nonflowering season. The plants form low (<5 cm high) mounds consisting of dead, persistent leaves and 1 to many short, leafy stem-tips arising from a branched caudex. Caudexes top an unbranched, deep (8–15 dm) taproot. Leaves bear a sparse to moderately dense vesture of hirtellous to long (<5 mm), pilose hairs. Leaves are cuneate to obovate and tipped by 3 or 4 triangular teeth. Each tooth is terminated by an acerose hair. The fancied similarity of such leaves to the foot of a bear is the source for the common name (bearclaw-poppy) for this species.

At flowering, few-flowered (1–5 flowers) inflorescences rise to the height of 1.5–2.5 dm and produce white-petaled flowers that may be up to 5.0 cm in diameter. Numerous bright yellow stamens surround the pistil during the 1st few hours after anthesis. The abundant pollen is quickly shed or collected by foraging bees, but stigmas may remain receptive to pollen for another 48 hours. Petals begin to wither within 72 hours but remain attached at the base of developing fruits and assist in seed dispersal. Individual plants may produce as many as 400 flowers in a single season (Nelson 1989, Nelson and Welsh 1993), but the average plant produces only a few dozen flowers.

Dwarf bear-poppy are restricted to habitats that are relatively barren of other herbaceous plants. The substrate weathers to form gently rolling mounds that are smooth, rock-free, and only sparsely covered by shrubs that might interfere with vehicular traffic. The few shrubs that do occur belong primarily to the species *Lepidium fremontii* (Fremont's pepperplant), *Atriplex confertifolia* (shadscale), *Ephedra torreyana* (Torrey's ephedra), *Hymenoclea salsola* (burrowbrush), and *Lycium andersonii* (Anderson's lycium). Herbs are uncommon on this parent material, but lichens, mosses, and cyanobacteria do form heavy covers (25%–100%) on sites where the poppy grows. This nonvascular plant cover probably contributes significantly

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to both erosion control and the availability of biologically usable nitrogen (Nelson and Harper 1991, Evans and Lange 2001).

Arctomecon humilis, like its congener, *A. californica,* exhibits large year-to-year fluctuations in population density (Nelson and Welsh 1993). A large and persistent soil seed bank of long-lived seeds is maintained by both species (Meyer 1987, Nelson 1989). Since climatic conditions conducive to germination of the seeds of these species often occur at intervals longer than longevity of most individuals in their populations, dramatic cycles in abundance are common (Nelson and Welsh 1993).

Arctomecon humilis was formally listed as endangered in 1979 under provisions of the Endangered Species Act of 1973. Among the reasons cited for listing the species were (1) its restriction to a single geological formation, (2) the threats to the species' habitat from rapid urbanization, and (3) the uncontrolled use of the habitat by off-road vehicles (U.S. Fish and Wildlife Service 1979).

The recovery plan for this species recommended that demographic studies be initiated to help managers separate changes in population density due to variations in climate from declines caused by human activities (Anderson and England 1985). This paper presents the results of monitoring the density of the species between 1987 and 2002 at the Red Bluff site near Bloomington, Utah.

STUDY SITE AND METHODS

Population dynamics of the dwarf bear-poppy are based on long-term observations of a population at a site northwest of Bloomington, Washington County, Utah. The study plot is in the northwestern quarter of section 9, Township 43 South, Range 16 West. Elevation at the site varies from about 845 m to 855 m above sea level (~2770–2805 feet). Geologic parent material at the site is the Shinabkaib Member of the Moenkopi Formation, a fine-textured, sedimentary deposit (Cook 1960). Soils at the study site have a pH of 7.2–7.5 and an average gypsum content of 39.3% by weight (Nelson and Harper 1991). Average precipitation is reported as 207 mm (8.16 inches) per year at the St. George weather station, which is located approximately 5.0 km (3.0 miles) from the study site. Annual mean monthly temperature is reported as 16.8°C (62.3°F) for that station (National Oceanographic and Atmospheric Administration 2000). The monitoring site occurs on land managed by the Bureau of Land Management (BLM), U.S. Department of the Interior.

The site was closed to motorized off-road vehicles in 1988, but access to the site by nonmotorized vehicles has continued to be legal to the present time. Bike trails are marked and managers have attempted to confine traffic to marked trails. That effort has been largely successful.

The site was partially fenced in the mid-1980s in a joint action by BLM and the Nature Conservancy. The BLM completed a fence around the entire Red Bluff population in 2002.

An initial monitoring site was established in 1987 by Nelson (1989). She placed a permanent grid over an area of 2.1 ha. At that time the area supported only 400 living plants of the dwarf bear-claw poppy. The grid consisted of 100-m^2 units (0.01 ha, each 10 m × 10 m). The grid units were marked at their corners by steel bars (4.5 dm long and 0.95 cm in diameter). Individual plants were marked at their base by a 2.5-cm-diameter aluminum disk, each uniquely numbered. Each disk was tied to a zinc-coated nail, 8 cm in length, with aluminum wire. To minimize vandalism on markers, when numbers were not being read, we folded the tags parallel to the anchoring nail and pushed both out of sight into the soil. Metal detectors were used to relocate marker tags.

The monitoring site was visited in May and late September or early October each year. At each visit we recorded rosette diameter of each plant as well as general health of the plant and any evidence of recent dieback in the rosette. When the visit was late enough in May, the number of flowers initiated and whether pollination had resulted in formation of a capsule were noted. When the spring visit was too early to provide a realistic estimate of total flowers produced by plants that year, we nevertheless noted whether a plant would flower that year as indicated by the presence of buds.

Unusually favorable conditions for germination of seedlings occurred in late winter and early spring of 1992. Such a large crop of seedlings had emerged by early May 1992 that we found it impossible to monitor all seedlings on Nelson's original grid network. Since we felt it expedient that a sizable cohort of seedlings be tracked from emergence to death, we limited

TABLE 1. Population dynamics of the dwarf bearclaw-poppy on a 0.07-ha monitoring plot near Bloomington, Washington County, UT. Number of living plants was determined in May and late September or early October of the year of concern. Mortality is based on deaths among established plants and seedlings discovered on the plot during the 12-month period preceding the mid-October date of the year of concern. The number of recruits still living when plants were permanently tagged in 1992 is noted in parentheses.

Year	Living plants in mid-October	Recruits during year	% mortality during year
1987	13	0	
1988	9	4	47
1989	7	1	30
1990	4	0	43
1991	3	1	40
1992	400	1333 (398)	70
1993	195	36	55
1994	159	1	19
1995	175	132	40
1996	122	0	30
1997	97	0	20
1998	86	20	27
1999	81	7	13
2000	61	0	25
2001	17	107	87
2002	5	0	71

our observation to 0.07 ha (7 units of 0.01 ha area each). In May 1992 we marked 1333 seedlings on that area with wooden toothpicks. By late September 1992 only 398 individuals survived on the 0.07-ha site. Those seedlings were permanently marked as well as all new seedlings that subsequently emerged on the plot over the period 1992–2002. The report that follows is based primarily upon the seedling cohort marked in September 1992.

RESULTS

Plant Density

Since the size of the monitoring plot was changed in 1992 to deal with the large number of seedlings that emerged in that year, we have gone back to raw field data to determine the number of established plants and recruits that occurred on that smaller monitoring plot in years prior to 1992. Data in Table 1 extend back to the initiation of the monitoring plot in 1987. Results show that this population has experienced only a single large recruitment event (1992) during the 16 years of observation. In 4 other years, at least 1 seedling per 100-m^2 grid unit survived long enough to be tagged during our October inventory (1993, 1995, 1998, and 2001). Nevertheless, the population has shown but a single "hump" in established plant density during the 16-year period. Numbers were very low from 1988 through early 1992. The recruitment pulse of 1992 declined steadily from that date to late 2000. Severe drought in that and subsequent years (2001 and 2002) precipitously reduced the population to very low numbers again.

Climatic Conditions

Precipitation and temperature at the St. George weather station are reported in Table 2. Water-year (1 Oct.–30 Sept.) precipitation varied widely over the 16 years of record, ranging from a high of 331 mm per year in 1995 to a low of 53 mm in water-year 2002. Late winter–early spring (Feb.–April) precipitation is well correlated [$r = + 0.685$, $P = 0.0034$; $Y = -72.6 + 16.5 X$, where Y represents number of new seedlings surviving to October and X represents precipitation (reported in tenths of cm) falling at St. George during the period 1 Feb.–30 Apr. of the year of concern] with seedling recruits that survived the growing season. This seasonal rainfall is also highly variable among years, ranging from 5 m to 155 mm. Neither autumn (1 Oct.–31 Dec.) or total water-year precipitation nor mean monthly temperature is significantly correlated with seedling recruitment in the dwarf bearclaw-poppy.

TABLE 2. Climatic conditions recorded at the St. George weather station for each year of concern for this study. Annual precipitation is reported for the "water-year" (October 1 of previous year through September 30 of year of concern), since that period seems more likely to influence plant performance than calendar-year precipitation and temperature. All data are from the National Climatic Data Center, Asheville, NC.

Year	Water-year precipitation (mm)	Feb.–April precipitation (mm)	Mean monthly temperature (°C) (water-year)
1987	189	54	17.3
1988	290	87	17.0
1989	153	31	17.6
1990	121	52	17.6
1991	116	55	16.3
1992	225	155	16.4
1993	319	92	17.2
1994	197	94	18.6
1995	331	131	17.8
1996	114	34	19.3
1997	327	25	18.1
1998	311	131	17.2
1999	214	37	17.7
2000	130	64	19.4
2001	191	88	18.3
2002	53	5	16.5

Percent mortality in this population is not significantly correlated with any environmental variable considered (Tables 1, 2). Mortality in this species varies greatly from year to year (13%–87% of plants alive at the end of the preceding growing season), but it appears to be dependent on a variety of factors rather than 1 or 2 triggering conditions. We observed no evidence of epidemic outbreaks of either insect or microbial pathogens or herbivores of any type during the course of study. However, larvae of an unknown butterfly species did destroy many flower buds during spring 1990.

Growth Rates

Growth of the individual plants in the 1992 cohort is reported in Figure 1. Interestingly, average plant size for this cohort reached a maximum value at the end of the 7th growing season and declined thereafter. Plant diameter averaged about 22 cm at the end of the 7th growing season. The few plants remaining alive (4) at the end of their 10th growing season had an average diameter of slightly less than 12 cm (Fig. 1), but variation in size among surviving plants was great. No members of the 1992 cohort were alive at the end of the 2002 growing season. The decline in average diameter of plants during the last 3 years of life is attributable to progressive death of the several stem tips produced by healthy plants.

Reproductive Events

Flowering in this cohort began during the 2nd growing season of life, when 23.5% of the individuals produced at least 1 flower. Plants that did flower produced, on average, slightly less that 4 flowers per individual (Fig. 2). During the 3rd growing season, about 62% of the living members of the 1992 cohort flowered, producing slightly more than 23 flowers per plant. In the next growing season, almost all members of the cohort flowered. The average plant produced slightly over 34 flowers during this 4th growing season.

The monitoring population was not always in full flower at the time of the spring inventory; thus, the number of flowers per individual was not determined in some years. The number of flowers per plant was not determined for survivors of the 1992 cohort in 1996, 1997, 1999, and 2000. The 1998 season was cool, and the average number of flowers per individual reported in Figure 2 (about 19) is an underestimate of the total flowers produced per plant, since we sampled well before the plants reached full flower. The number of flowers per individual reported for 2001 is probably a good estimate. Older plants vary greatly in size and vigor, and both of those variables markedly impact flower production.

Pollination success (fruit set) was carefully evaluated for the monitored population in the

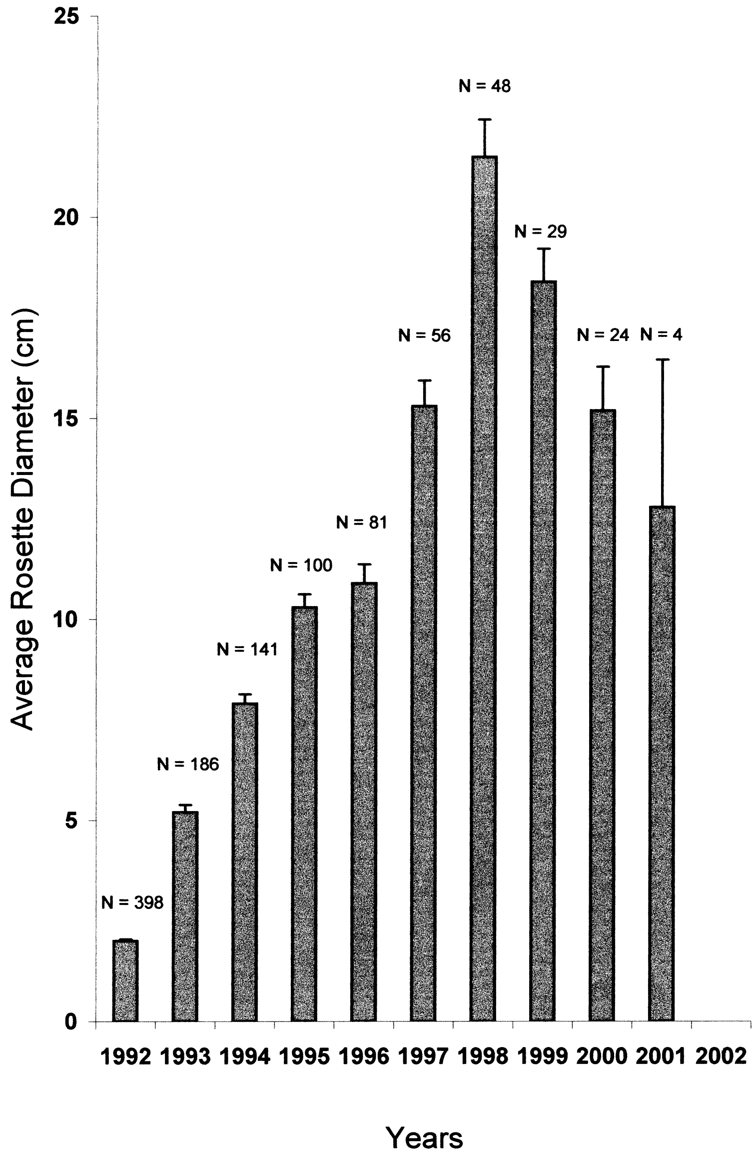

Fig. 1. Rosette diameter averages for all living members of the 1992 seedling cohort of *A. humilis.* Diameter values were taken annually in late September or early October. Bars represent average diameter of surviving members of the 1992 cohort in each year. The error bar atop each average diameter bar represents the standard error for that mean. The number of individual survivors represented in each annual mean is shown above the diameter bar.

years 1997 and 2000 (Table 3). Since precipitation in those years varied widely above (in 1997) and below (in 2000) the long-term average for the site, observed results probably bracket the long-term pollination and seedset success for this population. Our results published elsewhere (Harper et al. 2000) suggest that the high pollination success reported in Table 3 (~94%–82%) is typical of results obtained for 2 other populations of this species growing elsewhere in Washington County in year 2000. Seedfill results (84.5%–52.8%) also are similar to those obtained for the other 2 populations in 2000. We observed an average of 34 ovules per ovary in the 3 populations considered by Harper et al. (2000). If one assumes a worst case scenario

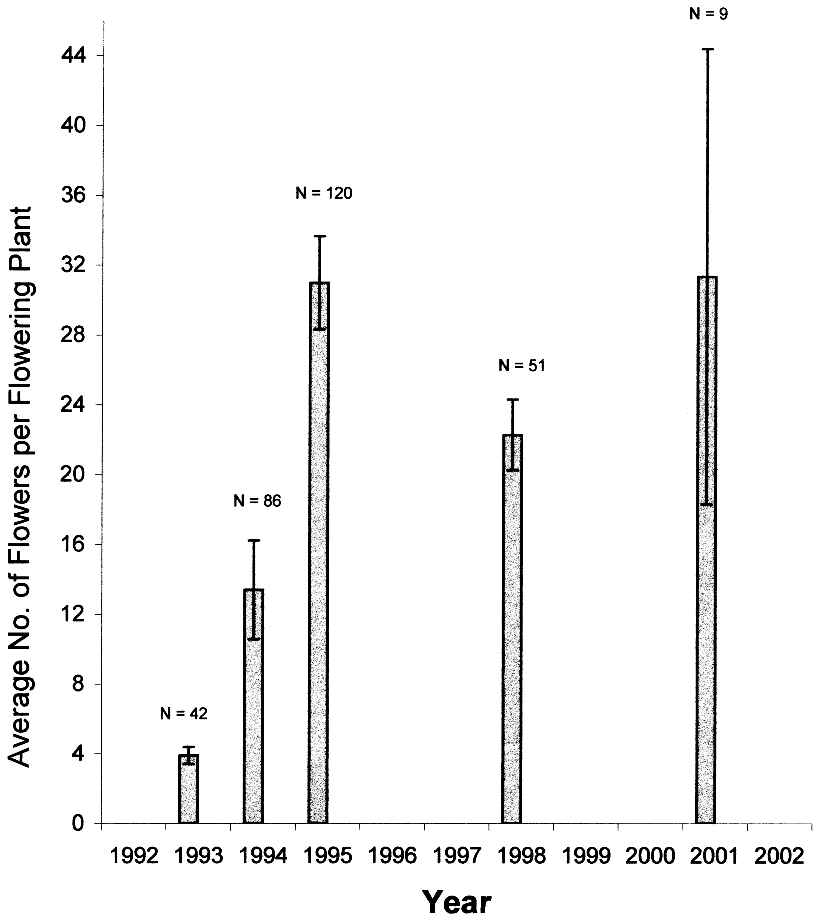

Fig. 2. Average number of flowers produced per flowering individual of the 1992 seedling cohort of *A. humilis* in a given year. The spring sample was sometimes too early to provide an acceptable estimate of the number of flowers produced per plant.

for percentage pollination and seedfill (i.e., 82% pollination and 52.8% of the ovules becoming filled seeds per fruit) and the flowering percentage and average number of flowers per age class reported above (Fig. 2 and text relative thereto) for the 1992 cohort and their progeny, one would predict that just slightly over 250,000 filled seeds would be produced over the 10-year period spanning the lifetime of any individual belonging to the 1992 cohort.

Although one must assume that some seed predation would occur in any population and some seeds would be expected to lose viability while in the seed bank, such losses are apparently not large. Nelson and Harper (1987) presented seeds of this species in a manner that made them readily available to rodent and bird granivores. Only 6.6% of the seeds presented could not be accounted for at the conclusion of the 2-week presentation period, which coincided with natural seed dispersal in the Red Bluff population. Since the seeds were displayed in glass saucers, some of the lost seeds could simply have been blown from the dishes by recurrent winds that swept the site during the study period.

Ants appear to be the principal dispersal agent. Seeds of this species showed an average weight of 2.0 mg based upon results from 7 lots of 50 seeds. Each seed has a narrow, elongate aril of white tissue running along the hilum edge of the seed. Seeds are jet black and the seed coat is hard. Ants are attracted to the arils and nibble at them, but seeds are

TABLE 3. Pollination and seedfill results for the Red Bluff monitoring population of *Arctomecon humilis* in 1997 and 2000.

	Year	
	1997	2000
Percentage of average water-year precipitation	159.4	63.4
Pollination (%)	93.9	82.0
Seedfill (%)	84.5	52.8

eventually abandoned between the point of discovery and the nest site. Thus, ants appear not to damage the viability of seeds and often deposit them below the soil surface and in places that are probably rarely discovered by larger seed predators.

Since 303 seedlings of the dwarf bearclaw-poppy emerged during the period 1998–2001 and survived long enough to be located and tagged on 1 of the 2 annual inventory visits each year, we know that the accumulating seed bank was depleted of some seeds by natural germination events. Such depletion was almost certainly small, however. Assuming only 1% survival of new seedlings, only approximately 30,000 seeds would have been lost to germination.

Nelson and Harper (1987) used the tetrazolium test to evaluate viability of seeds from herbarium specimens and seeds extracted from the soil seed bank. They found that most filled seeds taken from a 10-year-old herbarium specimen were still viable. They observed a 64% viability of seeds from the seed banks at the monitoring site. Assuming 250,000 seeds to have been produced by plants of the 1992 cohort and their progeny over the 10-year period of life of any member of that cohort, one would predict a possible loss of 19,800 seeds to predators, 30,000 to germination, and 36% of the remaining seeds may have become nonviable while in the seed bank. Nevertheless, that would still leave slightly over 160,000 viable seeds in the seed bank. Since those seeds would be spread over 0.07 ha, there may have been as many as 286 viable seeds per m^2 in the soil of the monitoring site at the end of the 2002 growing season.

Plant Longevity

Survivorship for the 1992 cohort is shown in Figure 3. Most mortality among that cohort occurred in the 1st growing season. Losses were also steeper during the 2nd year of life than during subsequent years. From 1993 to 2002, when the last members of the 1992 seedling cohort died, mortality progressed slowly and at a rather steady rate (Fig. 3).

The average seedlings of the initial 1992 cohort had a longevity of only 2.6 years. Seedlings of that cohort that were still alive 1 year after germination had an average longevity of 4.6 years.

DISCUSSION

Our study demonstrates the crucial role of the seed bank in persistence of bearclaw-poppy populations. Without a reserve of long-lived seeds, the species would probably disappear because of the long periods between climatic events that are capable of triggering significant recruitment. Data in Table 1 show that sizable recruitment events occurred in 1995 and 2001, but that those seedlings were almost completely lost during their 1st year of life. Survival of the species thus requires that many seeds remain dormant in the seed bank even when conditions are suitable for germination. Fortunately, bearclaw-poppy seeds are dormant at and, for an unknown duration (but probably more than 1 year), after dispersal, because of immature embryos (personal communication, Nancy Vivrette, Ranson Seed Laboratory, Santa Barbara, CA). Nelson and Harper (1987) observed that bearclaw-poppy seeds from the seed bank showed great variation in embryo size: some were fully mature, while most ranged in size from that observable in seeds ready for dispersal through all gradations to mature size. Accordingly, it seems likely that some seeds are dormant at the time of any germination event.

Our data suggest that the 1992 cohort had rebuilt a large seed bank during its lifetime. Even if it is assumed that the previous seed bank was totally depleted in the large germination event of 1992, by 2002 when the last member of that cohort died, the seed bank should have been large even when conservative estimating criteria are used.

Nelson (1989) estimated over 800 seeds per 1.0 m^2 in the seed bank extracted from 0.6-m-radius circular plots centered on large, dead poppy plants. Our estimate of 286 seeds per 1.0 m^2 at the Red Bluff monitoring site thus

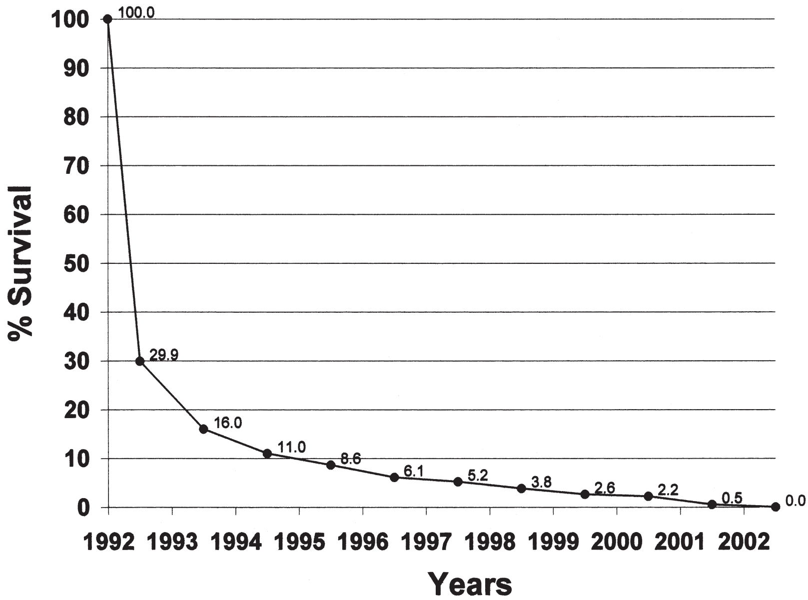

Fig. 3. Survivorship curve for 1333 individual seedlings of *A. humilis* that appeared in early May 1992. Percentage survival values are based on individuals of the cohort that were alive in late September or early October of each year, except for the 100% value, which is based on individuals observed in early May 1992. No member of the cohort survived to October 2002.

seems reasonable, especially since it is based on total plot area, not just the area around mature plants. In 2000 we (Harper et al. 2000) estimated that the average distance between bearclaw-poppy plants at the Red Bluff site was 1.66 m.

The recovery plan for this species (Anderson and England 1985) makes no recommendations concerning density of the plant on sites where it occurs. Although there seems little that managers could do to increase population density beyond that observed naturally after a major recruitment event, various kinds of human-caused disturbance can reduce density of bearclaw-poppy populations far below the number of plants successfully recruited. Therefore, following any large, episodic reproductive event, managers must ask the question, How many plants per unit area are desirable?

Harper et al. (2000) demonstrated that interplant distance has a significant effect on pollination success and, especially, on the percentage of ovules that become filled seeds. Their data showed that when interplant distances average 1.5 m (about 568 plants per acre), percentage flower pollination averaged slightly over 92% and seedfill averaged about 67%. When interplant distances average 3.5 m and 12.0 m (only about 119 and 10 plants per acre), flower pollination could be expected to decline to about 90% and 64% and seedfill would probably drop to about 50% and 35%, respectively.

In light of such an interplay between population density and seed production, human disturbances that severely reduce poppy populations below the naturally high densities that exist for a few years after a major recruitment event are likely to drastically reduce seed production. Obviously, low population density markedly reduces effectiveness of the insect pollinators that service bearclaw-poppy. It seems likely that human disturbances that create dust could cause fouling of stigmatic surfaces and reduce seed set, but studies of such relationships have not been done.

Large variations in density of the bearclaw-poppy through time observed at our monitoring site are apparently common for this species as well as for the California bear-poppy (Meyer 1987, Nelson and Welsh 1993). A sizable literature suggests that such large differences in population density that recur through time have a strong influence on genetic characteristics of a species (Ellstrand et al. 1978, Thomson

1981, Handel 1983, Schmitt 1983, Kunin 1997, Harper et al. 2000). These and other references suggest that dense populations attract numerous pollinators and receive such efficient pollinator services that fruit and seed set are greatly enhanced. Species that produce seeds that are long-lived in the soil (as the *Arctomecon* species do) may thus build up large seed banks when their populations are dense. Ellstrand et al. (1978) suggest that seed banks produced by such local, dense populations are likely to be deficient in heterozygotes. However, when populations are sparse, wide outcrosses can be expected (Ellstrand et al. 1978, Handel 1983). Seeds entering the seed bank at such times should be more genetically diverse at any given location. Species such as *Arctomecon humilis,* which experience large variations in population density and produce large, long-lived seed banks, should thus retain considerable genetic diversity even though average population size may not be large.

Our results (Harper et al. 2000) for *Arctomecon humilis* reproductive success at local density values, which varied from high to very sparse, support Kunin's (1997) conclusion that population density (number of individuals per unit area) is a more important variable than population size per se in plant conservation biology. Population size (number of individuals in a population) is a prominent variable in all considerations of rare species management and probability of local extinction (Ricklefs 1997), while population density is rarely mentioned. Kunin's (1997) results and those of Harper et al. (2000) demonstrate that population density deserves more attention.

Finally, we call attention to the large size difference observed among seedlings of the 1992 cohort. We have elsewhere documented (Harper and Van Buren 1996) that size differences persisted for at least 4 years and had large impacts on mortality rates (i.e., greater mortality among the smaller seedlings) among the several dozen seedlings initially assigned to each of the 2 categories in October 1992. Also, fewer small seedlings flowered each year during the first 4 years of life, and the smaller plants consistently produced fewer flowers than larger members of their cohort. Meyer (1987) observed similar persistent differences in size of seedlings of *A. californica*. Allphin et al. (1998) reported progressively more heterozygotes in samples of plants of the dwarf bearclaw-poppy that ranged from small- to large-flowering individuals. It is not clear from their data whether the size differences reflected age or growth rate differences, but it is possible that observed size differences among a single seedling cohort are related to genetic differences.

ACKNOWLEDGMENTS

We are indebted to Deanna R. Nelson for original design of the monitoring program and for much of our knowledge about bearclaw-poppy and its seed bank. Janet Cooper, Zachary Aanderud, Diane Carter, and Donna Barnes have provided assistance with collection of field monitoring data. Zachary Aanderud gave invaluable help in laboratory processing of seedfill data in both 1997 and 2000. We are grateful to those people for competent assistance. This work has been financed by the BLM primarily, with consistent contributions in space and supplies from both BYU and UVSC.

LITERATURE CITED

ALLPHIN, L., M.D. WINDHAM, AND K.T. HARPER. 1998. Genetic diversity and gene flow in the endangered dwarf bear-poppy, *Arctomecon humilis* (Papaveraceae). American Journal of Botany 85:1251–1261.

ANDERSON, J., AND J.L. ENGLAND. 1985. Dwarf bear-claw poppy, *Arctomecon humilis* Coville: recovery plan. Prepared by U.S. Fish and Wildlife Service, Region 6, Denver, CO. 26 pp.

COOK, E.F. 1960. Geologic atlas of Utah: Washington County. Utah Geological and Mineral Survey Bulletin 70. 119 pp.

ELLSTRAND, N.C., A.M. TORRES, AND D.A. LEVIN. 1978. Density and the rate of apparent outcrossing in *Helianthus annuus* (Asteraceae). Systemic Botany 3:403–407.

EVANS, R.D., AND O.L. LANGE. 2001. Biological soil crusts and ecosystem nitrogen and carbon dynamics. Pages 263–279 *in* J. Belnap and O.L. Lange, editors, Biological soil crusts: structure, function, and management. Ecological Studies Series 150. Springer-Verlag, Berlin.

HANDEL, S.N. 1983. Pollination ecology, plant population structure and gene flow. Pages 163–211 *in* L. Real, editor, Pollination biology. Academic Press, Inc., London.

HARPER, K.T., AND R. VAN BUREN. 1996. *Arctomecon humilis* Coville. Monitoring report for 1996. Report to Endangered Plant Specialist, Bureau of Land Management, U.S. Department of the Interior, Richfield, UT. 11 pp.

HARPER, K.T., R. VAN BUREN, AND Z.T. AANDERUD. 2000. The influence of interplant distance and the number of flowers on seed set in dwarf bear-poppy (*Arctomecon humilis*). Pages 105–109 *in* J. Maschinski and L. Holter, editors, Southwestern rare and endangered plants: proceedings of the third conference. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Proceedings RMRS-P-23.

KUNIN, W.E. 1997. Population size and density effect in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. Journal of Ecology 85:225–234.

MEYER, S.E. 1987. Life history of *Arctomecon californica*, a Mohave Desert endemic perennial herb. Unpublished manuscript, available from author, Shrub Sciences Laboratory, U.S. Forest Service, Provo, UT.

NATIONAL OCEANOGRAPHIC AND ATMOSPHERIC ADMINISTRATION. 2000. Utah climatological annual summaries 1961–1990. NOAA—Climatic Summaries, NCDD. Asheville, NC.

NELSON, D.R. 1989. Site characteristics and habitat requirements of the endangered dwarf bear-claw poppy (*Arctomecon humilis* Coville, Papaveraceae) and demographic and seed bank biology of *Arctomecon humilis* (Papaveraceae), a short-lived perennial. Master's thesis, Brigham Young University, Provo, UT. 53 pp.

NELSON, D.R., AND K.T. HARPER. 1987. Project summary: ecological study of the endangered dwarf bearclaw-poppy. Report to the Utah Native Plant Society. 134 pp.

______. 1991. Site characteristics and habitat requirements of the endangered dwarf bear-claw poppy (*Arctomecon humilis* Coville, Papaveraceae). Great Basin Naturalist 51:167–175.

NELSON, D.R., AND S.L. WELSH. 1993. Taxonomic revision of *Arctomecon* Torr. and Frem. Rhodora 95:197–213.

RICKLEFS, R.E. 1997. The economy of nature. 4th edition. W.H. Freeman and Co., New York.

SCHMITT, J. 1983. Density-dependent pollinator foraging, flowering phenology, and temporal pollen dispersal patterns in *Linanthus bicolor*. Evolution 37:1247–1257.

THOMSON, J.D. 1981. Spatial and temporal components of resource assessment by flower-feeding insects. Journal of Animal Ecology 50:49–59.

U.S. FISH AND WILDLIFE SERVICE. 1979. Determination that *Arctomecon humilis* is an endangered species. Federal Register 44(216):64250–64252.

Received 3 October 2003
Accepted 12 February 2004