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DEVELOPMENTAL FAILURE AND LOSS OF REPRODUCTIVE CAPACITY AS A FACTOR IN EXTINCTION: A NINE-YEAR STUDY OF *DEDECKERA EUREKENSIS* (POLYGONACEAE)

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ABSTRACT

Many long-lived perennial species exhibit lowered reproductive capacity. Early studies of reproductive success in *Dedeckera eurekaensis* (Polygonaceae) demonstrated that the species exhibited extremely low reproductive success, low seed/ovule (S/O) ratios (i.e., the percentage of ovules that produce filled seeds; 2.5%), low germinability of filled seeds (3.5%), low seedling survivorship (11.1%), and lack of recruitment in natural populations. These results were attributed to genetic load, but this elicited controversy, prompting long-term studies of the relationship between the S/O ratio and environment. After nine years of monitoring, however, the S/O ratio had not changed significantly (2.7%), and there was no significant correlation between precipitation and the S/O ratio. Controlled field experiments demonstrated that neither resource availability nor other ecological factors significantly influenced embryo abortion rates. Controlled self-pollinations ($N = 115$) matured only one questionably filled seed, whereas intrapopulation cross-pollinations ($N = 192$) produced significantly more seed (S/O = 12.0 %). Previous pollination studies demonstrated that the species has no primary pollinators and is only rarely visited by a few generalist insects. However, the flowers typically self-pollinate in 2–3 days following anthesis. Strong inference suggests that the loss of reproductive capacity in *D. eurekaensis* may be the result of inbreeding depression due to the superimposition of self-pollination on a normally outcrossed species carrying a high genetic/segregational load.

Key words: *Dedeckera*, fecundity, genetic load, reproductive capacity, seed/ovule ratio.

INTRODUCTION

According to Harper (1977), variation in reproductive capacity is a question at the heart of any science of population and evolutionary biology. A number of rare, long-lived, outcrossing plant species exhibit low reproductive success due to high levels of embryo abortion (Wiens 1984; Wiens et al. 1987, 1989a, b; Allphin and Harper 1997). Because reproductive capacity is essential for evolutionary fitness and long-term species survival, it is critical that biologists understand the factors contributing to low reproductive success in rare species and the implications of low fecundity on population dynamics and persistence.

Previously, Wiens et al. (1989a) documented excep-

tionally low levels of fecundity in *Dedeckera eurekaensis* Rev. & J. Howell (Polygonaceae), a monotypic genus and evolutionarily relict shrub endemic in the Mojave desert, California. Outcrossing perennials typically exhibit seed/ovule ratios (S/O, i.e., the percentage of ovules developing into filled seeds) averaging about 50% (Wiens 1984; Wiens et al. 1987). Annuals and short-lived perennials (generally self-pollinating) have S/O ratios approaching 90% (Wiens 1984; Wiens et al. 1987). By contrast, *Dedeckera* had a S/O ratio of only 2.5%. Germinability of filled seeds was only 3.5%, seedling survivorship was only 11.1% under glasshouse conditions, and recruitment was nonexistent in most populations (Wiens et al. 1989a).

Wiens et al. (1989a) attributed these results to genetic load, i.e., lowering of the mean fitness of a population compared with the fitness of the best genotypes. This explanation, however, elicited controversy (Bawa et al. 1989; Charlesworth 1989a, b, c; Wiens et

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al. 1989b). Most of the criticism centered around alternative explanations for the remarkably high rate of embryo abortion in *Dedeckera*, primarily resource limitation, resource allocation, and maternal effects by selective abortion.

Dedeckera is a longevous genus without vegetative reproduction. Previous studies of six populations in the White and Last Chance Mountains also showed that *Dedeckera* exhibited high levels of embryological abnormalities (Wiens et al. 1989a) and genetic variability (mean heterozygosity, $H_o = 0.269$; Nickrent and Wiens 1989). The numerous, small (2–3 mm) flowers are single-ovuled and adapted for outcrossing (protandry), but typically self-pollinate when the flowers close spontaneously 2–3 days following anthesis, or following intraplant insect pollination. The few single-seeded, indehiscent fruits (achenes) that mature occur randomly on expansive cymose inflorescences. Thus, position effects and genetically programmed phenomena influencing ovule survivorship in multiple-ovulate ovaries cannot explain the high embryo abortion rates in *Dedeckera* (Bawa et al. 1989; Wiens et al. 1989b).

Many authors suggest that embryo abortions in plant species are due to limitations in available resources for developing seeds (Bradbury 1929; Stephenson 1981; Nakamura 1986; Stanton 1987; Zimmerman and Pyke 1988; Charlesworth 1989a; Ehrlen 1992). Others have suggested that the maternal plant selectively aborts offspring of poorer quality, or offspring that may not be supportable under conditions of limited resources (Janzen 1977; Charnov 1979; Lloyd 1980; Willson and Burley 1983; Casper 1984; Stephenson and Winsor 1986; Stanton 1987; Marshall and Ellstrand 1988). However, in the previous studies of *Dedeckera*, these resource effects on S/O ratios were not explicitly considered.

Therefore, this study presents data from nine years of long-term monitoring and reproductive experiments in *Dedeckera* populations. The research, presented in this manuscript, considers the effects of environmental fluctuation over this nine-year period on S/O ratios in *Dedeckera* and the historical stability of these ratios. We also examine resource limitation and resource allocation effects on S/O ratios. Moreover, we compare S/O ratios in *Dedeckera* with those from co-occurring long-lived species at the Coldwater population. We also perform cross-pollinations to examine the differences in S/O ratios among self vs. outcrossed progeny.

MATERIALS AND METHODS

Seed/ovule ratios were monitored over a nine-year period for six natural populations of *Dedeckera*. Three of the monitored study populations occur in the White Mountains (Bishop, Coldwater Canyon (Fig. 1), and Gunter Canyon) and three populations occur in the

Last Chance Mountains (Lower *Dedeckera* Canyon, Upper *Dedeckera* Canyon, and Last Chance) of California, U.S.A. Generally, 100 ovules were sampled annually (when seeds were mature) from each of 10 randomly selected plants in each of the study populations. Seed/ovule ratios, or the proportion of ovules producing filled seed, were determined from these harvested ovules for each population and year. Significant differences were assessed among populations and years using Mann-Whitney *U*-tests and $P < 0.05$.

Precipitation data were obtained for the study area (from the weather station near Bishop, CA) over the nine-year time interval. The three populations in the White Mountains are approximately 7–13 km from Bishop and the three populations from Last Chance Mountains are approximately 80 km from Bishop and are both hotter and drier than Bishop. Pooled, mean S/O ratios, by year, for all six study populations of *Dedeckera* were compared with the nine years annual precipitation data (mm) using simple correlation (Pearson's correlation coefficient; Snedecor and Cochran 1980).

Seed/ovule ratios were determined from all ovules found in duff accumulation, or incompletely decomposed organic litter accumulation (ca. 10 cm deep), under four different plants (Coldwater Canyon), likely over 100 years old (Wiens et al. 1989a) to determine long-term (historical) stability of S/O ratios. Seed/ovule ratios represented the proportion of filled seeds over all of the ovules found in the duff accumulation. These were compared with the S/O ratios obtained from seed of plants from the current year to assess if *Dedeckera* exhibited long-term stability of low S/O ratios using a Mann-Whitney *U*-test and $P < 0.05$.

Seed/ovule ratios from duff accumulations were also obtained from two ecologically disparate sites in Coldwater Canyon (White Mountains) to determine if long-term stability of seed/ovule ratios occurs over varying environmental conditions. These disparate sites for *Dedeckera* at Coldwater Canyon vary with respect to elevation (2275 m and 1575 m) and dominant vegetation. The dominant vegetation at the upper site was juniper/pinyon and at the lower site salt bush/sagebrush (*Atriplex/Artemisia*). Ovules were collected from duff accumulations under four very old individuals (likely > 100 years old) at the upper elevation site and nine very old individuals at the lower elevation site. Significant differences were assessed between S/O ratios from the two ecologically distinct sites using a Mann Whitney *U*-test and $P < 0.05$.

Controlled field experiments were performed to assess the effects of resource limitation and resource allocation on seed/ovule ratios. Field resource treatments included: a) hand removal of 80% of the flowers on a plant just prior to anthesis, and b) removal of all but one flowering shoot from a plant rootstock just prior

to anthesis. Each of the experimental treatments were randomly assigned to at least three different individuals (a total of ten individuals received one experimental manipulation) in the Coldwater Canyon population and these were compared with ten adjacent but nonmanipulated plants (controls). At least 100 mature ovules were harvested from each of the control and treatment plants and S/O ratios were determined. Significant deviations of S/O ratios across the treatments from control plants were determined using a Mann-Whitney *U*-tests and a $P < 0.05$.

To determine the effects of local environmental variability on S/O ratios, we compared S/O ratios from a subpopulation of *Dedeckera* occurring on a perpetually moist seep to those S/O ratios obtained from plants on adjacent dry sites. Significant differences between seep and non-seep S/O ratios were determined utilizing the Mann-Whitney *U*-test. Significance was recorded at $P < 0.05$.

Finally, at the Coldwater Canyon site, the S/O ratios of five perennial species co-occurring with *Dedeckera* (1–10 m) and presumably having access to similar resources with *Dedeckera* were determined and compared with S/O ratios observed in *Dedeckera*. These co-occurring species (*Pericome caudata* A. Gray, *Stephanomeria paniculata* Nutt., *Chrysothamnus nauseosus* (Pallas) Britton, *Stanleya pinnata* (Pursh) Britton, *Eriogonum heermannii* Dur. & Hilg.) were located within 1–10 m of *Dedeckera* and, thus, likely had access to similar resources. Significant differences between *Dedeckera* and co-occurring species were determined utilizing the Mann-Whitney *U*-tests and significance was recorded at $P < 0.05$.

Earlier pollination experiments (Wiens et al. 1989a) resulted in no significant differences between S/O ratios of self- and intraplant-pollination crosses. However, these experiments were flawed by premature termination (15–21 days post-pollination, versus 33–42 days). Therefore, we performed additional controlled self-pollinations in this study to examine the effects of selfing versus outcrossing on S/O ratios in *Dedeckera*. Differential success of pollen tubes among treatments can not explain the differences in S/O ratios because over 90% of all flowers initiated ovary expansion in both of the treatments.

All pollination experiments were performed during the month of July in the natural populations. All open or fruiting flowers were removed from experimental inflorescences, after which they were enclosed with removable fine-mesh nylon covers mounted over a wire frame to prevent contact of the nylon with the flowers. Flowers were emasculated daily before anthesis. Stigmas were pollinated by contacting their sticky surfaces with a dehiscing anther after the styles had diverged and the stigmas became receptive. Due to the small size of *Dedeckera* flowers, all floral manipula-

tions were effected under a dissecting microscope mounted on a camera tripod.

For this study, we also made further attempts at germinating seed and growing seedlings of *Dedeckera*. Seed germination attempts were performed at room temperature in the greenhouse under mist bench conditions with complete water saturation of soils. Seeds were sown in a standard greenhouse potting medium. We removed the ovary wall on some of the seeds, but left the seed coat intact. On other seeds, we left the ovary wall intact. In addition, we made further attempts at growing seedlings in a standard greenhouse potting mix under typical glasshouse conditions.

RESULTS AND DISCUSSION

Seed/ovule ratios did not significantly differ among population or years over the nine-year study interval (Table 1). The pooled S/O ratio for the three White Mountain populations (Bishop, Gunter, Coldwater Canyon) over nine years averaged 2.8% (272 plants; 51,160 ovules). The populations from the Last Chance Mountains (lower *Dedeckera* Canyon, upper *Dedeckera* Canyon, Last Chance) averaged a S/O ratio of 2.5% (231 plants; 34,787 ovules; Table 1). The Bishop population had the lowest S/O ratio in 1997 (0.6%) and the Coldwater Canyon population had the highest S/O ratio in 1988 (4.7%). Interplant S/O ratios varied from 0 to 12% (Table 1).

The S/O ratios determined from duff accumulation (ca. 10 cm deep) under plants, likely over 100 years old, indicate long-term stability of low S/O ratios. There was no significant difference for S/O ratios obtained from the current year's seed crop ($N = 10$, 1128 ovules, S/O = 4.3%) and seed in duff layers under old living plants ($N = 4$, 428 ovules, S/O = 4.6%, $P = 0.09$). This is further evidenced by the constancy of S/O ratios over the nine years of monitoring (Table 1). These results are consistent with other reports, worldwide, indicating that S/O ratios remain constant over years and varying environmental conditions (Wiens 1984; Harper and Wallace 1987; Wiens et al. 1987; Lalonde and Roitberg 1989, 1994; Wiens et al. 1989a; Allphin and Harper 1997; Allphin et al. 2002).

Seed/ovule ratios from duff accumulations in two environmentally distinct populations in Coldwater Canyon (White Mountains) at elevations of 2275 m ($N = 4$, 428 ovules, S/O = 4.6%) and 1575 m ($N = 9$, 988 ovules, S/O = 3.0%) were likewise statistically similar ($P = 0.68$). However, the dominant vegetation at the upper site was juniper/pinyon and at the lower site salt bush/sagebrush (*Atriplex/Artemisia*). These ecosystems are characterized by pronounced differences in both mean precipitation and temperatures. Likewise the populations in the Last Chance Mountains occur in creosote bush, *Larrea tridentata* (DC) Cov.,

Table 1. Seed/ovule (S/O) ratios in six natural populations of *Dedeckera eurekensis* over nine years of monitoring. Mean S/O ratios for each population do not vary significantly ($P < 0.05$) across the nine years of study, as determined from Mann-Whitney U -tests. Yearly means of all populations also do not vary significantly at $P < 0.05$.

Population	1987			1988			1989			1990		
	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)
Bishop	0.6	1046	10	1.6	1624	10	2.7	26	10	4.4	1413	10
Gunter	2.1	1238	10	0.8	1482	10	2.4	1248	10	1.6	1153	10
Coldwater	4.2	1112	10	4.7	2875	10	4.3	1128	10	2.9	1171	10
Upper Dedeckera Cyn.	1.7	1230	10	4	1682	10	3.2	1121	10	2.1	997	9
Lower Dedeckera Cyn.	2.9	1265	11	4.3	1464	10	4.2	1203	10	1.8	1156	10
Last Chance	1.9	1184	10	—	—	—	—	—	—	—	—	—
Mean or Total	2.3	7075	61	3.3	9127	50	3.4	5657	50	2.6	5890	49
Standard Error	0.50			0.79			0.39			0.51		
Population	1991			1992			1993			1994		
	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)	S/O	N (ovules)	N (plants)
Bishop	1.9	1356	10	2.3	1128	10	3.1	1283	10	4.1	1225	10
Gunter	3.6	973	10	2.9	11,256	10	4.2	1590	10	1.8	1145	10
Coldwater	2.7	1208	10	2.1	7056	11	2.8	1688	10	2.9	1352	11
Upper Dedeckera Cyn.	1.5	1097	10	2.5	1217	10	2.7	1359	10	2.6	1423	10
Lower Dedeckera Cyn.	1.9	1186	10	2.4	1098	10	2.7	1342	10	1.7	1283	10
Last Chance	—	—	—	2.1	7257	11	3.1	1354	10	3.2	1178	10
Mean or Totals	2.3	5820	50	2.4	29,012	62	3.1	8616	60	2.7	7606	61
Standard Error	0.38			0.12			0.23			0.37		
Population	1995			Totals			SE					
	S/O	N (ovules)	N (plants)	Mean S/O	N (ovules)	N (plants)						
Bishop	2	1095	9	2.6	11,127	89	0.40					
Gunter	3.2	1207	10	2.7	21,292	90	0.36					
Coldwater	3.2	1160	11	3	18,750	93	0.29					
Upper Dedeckera Cyn.	1.8	1249	10	2.5	11,375	89	0.27					
Lower Dedeckera Cyn.	2.7	1199	10	2.8	11,196	91	0.32					
Last Chance	1	1243	10	2.2	12,216	51	0.33					
Mean or Totals	2.3	7153	60	2.7	85,956	503						
Standard Error	0.36											

desert communities, which are both hotter and drier than the other sites in the White Mountains.

Limited resources are widely believed to cause embryo abortion in plants (Charlesworth 1989c). Water is limiting in desert ecosystems and is also the resource to which plants are most sensitive (Kramer and Boyer 1995). However, in *Dedeckera* there is no correlation between precipitation and ovule survivorship even though rainfall varied widely ($r = 0.085$; Fig. 2). Annual precipitation, however, is directly proportional to plant growth during years of high precipitation (400% of normal, Fig. 2). *Dedeckera* in these years produces massive flower crops, but the S/O ratios remain constant (Table 1). Ambient environment may cause ovule death in some crop plants, e.g., high temperature in maize (Hanft et al. 1990), but we are unaware of such examples among noncultivated plants. Numerous studies demonstrate that resource availability can be correlated with greater flower and seed production and increased seed weight, but little evidence exists to suggest that resource availability is correlated with embryo abortion (Maun and Cavers 1971; Stephenson

1984; Harper and Wallace 1987; Lalonde and Roitberg 1989, 1994; Herrera 1991; Allphin and Harper 1997).

Various field manipulations and survivorship observations suggest that resource limitations are not likely a significant factor controlling the S/O ratio in *Dedeckera* (Tables 2, 3). Subpopulations of *Dedeckera* occurring on a perpetually moist seep and on an adjacent dry site exhibited statistically similar S/O ratios (Table 3). In addition, the S/O ratios of closely adjacent *Dedeckera* plants (1–2 m) may vary from 0 to 12%, yet presumably exploit similar resources (Table 1).

Many authors suggest that low S/O ratios are due to maternal selective abortion of offspring or differential allocation of resources to developing young under resource limiting situations (Janzen 1977; Charnov 1979; Lloyd 1980; Willson and Burley 1983; Casper 1984; Stephenson and Winsor 1986; Stanton 1987; Marshall and Ellstrand 1988). Under this hypothesis, one should expect to find lower S/O ratios, or an inability to fill all resource 'sinks' for individuals with larger numbers of inflorescences, when resources are



Fig. 1.—*Dedeckera eurekensis* growing at Coldwater Canyon, Inyo Mountains, California. Photo by W. H. Busby.

limiting. For *Dedeckera* the removal of 80% of the flowers on inflorescences and the removal of all but one flowering shoot from a rootstock did not significantly increase *S/O* ratios in *Dedeckera* (Table 2). Similar experiments, under greenhouse conditions, on *Cirsium* Mill. and *Erigeron* L. (Asteraceae) also produced no differences in *S/O* ratios between control and experimental plants with varying levels of inflorescence removal (Lalonde and Roitberg 1994; Allphin et al. 2002).

Finally, at Coldwater Canyon, five perennial species (listed in Materials and Methods section) co-occurring with *Dedeckera* (1–10 m) exhibited widely divergent

S/O ratios (17.1–64.7%; Table 4). These co-occurring species likely had access to similar resources and resource conditions. This result suggests that resources do not appear to be limiting in the area or that all species in this community are responding individually to current environmental conditions.

Histological analysis of 27 post-fertilization ovules in *Dedeckera* (Wiens et al. 1989a) showed a pattern of embryo abortion similar to that reported in *Epilobium* (Onagraceae) (Wiens et al. 1987; Seavey and Carter 1996). Aborted embryos clustered around the early stages of embryogenesis when the major tissue systems are initiated (Wiens et al. 1989a). This is appar-

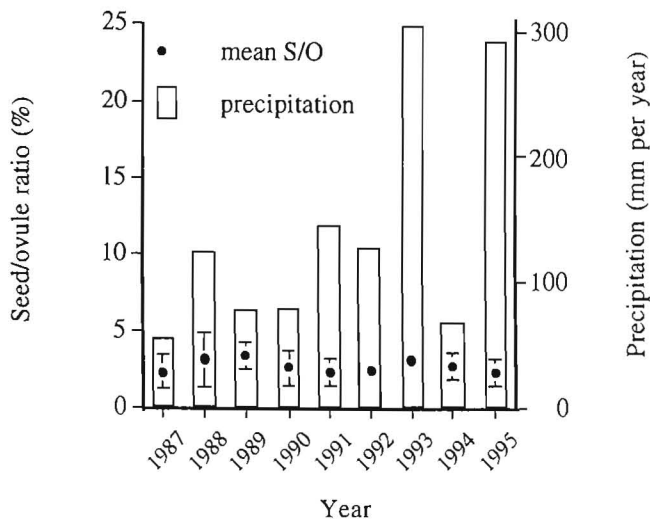


Fig. 2.—Pooled, mean seed/ovule (S/O) ratios, by year, for all six populations of *Dedeckera eurekaensis* over nine years, 2.7% (503 plants; 85,956 ovules), and precipitation at Bishop, California with 1-sigma error bars. Correlation coefficient between S/O and precipitation (r) = 0.085.

ently when the zygotic genome is first activated and lethal alleles associated with the developmental process are first exposed to selection. Of the 27 ovules examined, only one was normally developed. Clustering of abortions due to expression of lethal alleles at major differentiation events in development as the zygote genome is activated has been well demonstrated in *Drosophila* (Hadorn 1961). If limiting resources cause embryo abortions, clustering at these critical stages of development should not be expected because severe environmental perturbations serious enough to cause abortion would be random events. Interestingly, in spite of relatively early embryo abortion, approximately 50% of all initiated fruits continue development to full size achenes although they are empty at maturity (Wiens et al. 1989a).

Such a pattern of continued fruit development in ovules with aborted embryos is characteristic of various families, e.g., Pinaceae, Cycadaceae, Asteraceae, Polygonaceae, and various genera, e.g., *Adenostoma* (Rosaceae), *Galium* L. (Rubiaceae), *Mortonia* Gray (Celastraceae) (D. Wiens, unpublished data). Such development may be due to the continued production of hormones from endosperm or maternal tissue, but

Table 2. Experimental field manipulations performed at the Coldwater Canyon population of *Dedeckera eurekaensis*.

Experimental treatment	<i>N</i> Plants ^b	<i>N</i> Ovules	S/O (%)	<i>P</i> -value ^c
80% of flowers removed ^c	3	362	3.6	0.67
Single shoot retained ^d	4	167	3.6	0.74
Control	10	1112	4.2	

^a Probabilities based on Mann-Whitney *U*-test comparisons from S/O percentages in comparison with control.

^b Sample sizes were limited because of the small size of the existing population.

^c Removal of flowers and inflorescences occurred prior to anthesis.

^d Single shoot retained with all flowers intact just prior to anthesis, adjacent shoots within 20–30 cm removed.

should not be expected if limited resources (water and photosynthate) are the cause of embryo abortion.

Because resource limitations do not appear to affect S/O ratios in *Dedeckera* and neither occasional herbivory (beetles) nor pathogenic activity influences seed set (D. Wiens and L. Allphin, personal observation) alternative hypotheses for low fecundity in this species must be explored. Wiens et al. (1989a) originally ascribed the low S/O ratios in *Dedeckera* to balanced or segregational genetic load (Wiens et al. 1989a; heterozygote superiority) in response to increasing aridity in the Great Basin following uplift of the Sierra Nevada. However, mutational load is an alternative hypothesis (Klekowski 1984; Charlesworth 1989a).

All six study populations of *Dedeckera* are highly variable genetically with polymorphic loci averaging 56.8%, mean observed heterozygosity 26.9%, and mean expected heterozygosity 34.8% (Nickrent and Wiens 1989). Hypotheses for this high level of genetic diversity in *Dedeckera* and its evolutionary and reproductive implications are discussed in great detail in Nickrent and Wiens (1989). All of the study populations of *Dedeckera* are relatively large ($N > 167$), thus low seed set is not attributable to genetic homozygosity associated with small population size. Furthermore, three small satellite populations of the Gunter population ($N = 52$, $N = 26$, $N = 12$) averaged S/O ratios of 2.0% (Table 1), consistent with the large populations.

Prezygotic genetic self-incompatibility or pollen limitations cannot explain low fecundity in *Dedeckera*

Table 3. Seed/ovule ratios taken from seep and non-seep individuals at the Coldwater Canyon population over three years of monitoring (1987–1989).

Sampling year	Seep			Adjacent non-seep			<i>P</i> -value
	<i>N</i> (plants)	<i>N</i> (ovules)	S/O (%)	<i>N</i> (plants)	<i>N</i> (ovules)	S/O (%)	
1987	4	475	2.9	10	1112	4.2	0.40
1988	10	1463	4.0	10	2875	4.7	0.32
1989	9	979	3.6	10	1128	4.3	0.49

Table 4. Seed/ovule ratios of species co-occurring in natural populations with *Dedeckera eurekaensis* at Coldwater Canyon.

Species	N (plants)	N (ovules)	S/O (%)
<i>Dedeckera eurekaensis</i>	10	1128	4.3
<i>Pericome caudata</i>	7	1273	36.8
<i>Stephanomeria pauciflora</i>	8	858	33.8
<i>Chrysothamnus nauseosus</i>	4	178	47.8
<i>Stanleya pinnata</i>	10	225	64.7
<i>Eriogonum heermannii</i>	4	178	17.1

because approximately 90% of all flowers initiate ovary expansion (Wiens et al. 1989a). Hybrid dysgenesis commonly causes low fertility, but *Dedeckera* has no close relatives, meiosis is regular ($N = 20$ bivalents), and pollen is fully developed and stains normally with cotton blue and lactophenol.

Earlier pollination experiments (Wiens et al. 1989a) resulted in no significant differences between S/O ratios of self- and intraplant-pollination crosses (Table 5). These experiments were flawed by premature termination (15–21 days post-pollination, versus 33–42 days). Additional controlled self-pollinations performed in this study ($N = 115$) produced one filled seed (S/O = 0.9%). The S/O ratios of additional intrapopulation crosses ($N = 192$), however, remained similar (12.0%) to the previous result (11.4%; Wiens et al. 1989a; Table 5).

Further attempts to germinate intact, filled seeds ($N = 112$) under a mist bench were unsuccessful after four weeks. Previous tests of germination were also low (3.5%, $N = 360$) and 60 days of stratification likewise had no effect (Wiens et al. 1989a). However, when the ovary wall was removed, but the seed coat left intact, germination averaged 42% ($N = 672$) with little evidence of fungal infection. Ultimate seedling survivorship under glasshouse conditions, on the other hand, remained low (13.5%) after 74 days, as was seen in Wiens et al. (1989a; 11.1%). The seedlings were generally delicate and weak, particularly at the transition between epicotyl and hypocotyl. Seedlings frequently failed to develop normal root systems or apical meristems, and often died prior to cotyledon expansion.

Previous pollinator surveys in *Dedeckera* were un-

able to document any primary pollinators for the species (Wiens et al. 1986). Although the species appears to have lost its primary pollinators, its small flowers (2–3 mm) are most likely adapted for pollination by small, short-tongued Hymenoptera or Diptera. Intraplant cross-pollination by various generalist insects was found to be extremely rare (Wiens et al. 1986). The pollen of *Dedeckera* is also “sticky” and not readily wind dispersed (Wiens et al. 1988). Most pollinations are probably due to selfing, and we suspect that the few filled seeds are likely the product of rare recombinant gametes. The S/O ratios of a single, isolated plant (ca. 3–4 km) in lower Coldwater Wash had a mean S/O ratio of 0.8% over the years of monitoring ($N = 1462$ ovules), presumably the result of self-pollination. The filled seeds of this plant had similar germination and seedling survivorship values of other large study populations previously mentioned. Therefore, consistent selfing is the best explanation for the remarkable consistency of the S/O ratios for all six populations, and the approximately 90% of ovaries that initiate ovary expansion in the field.

Dedeckera can reproduce only by seed. Growth ring analysis indicates that older plants are approximately 150 years old (Wiens et al. 1989). The populations exhibit relatively similar age structures and consist of old plants (Wiens et al. 1989a). If the age data are correct (die-back and repeated sprouting from rootstocks could result in much older plants), the present populations were established sometime between 100–150 years before present at the close of the Little Ice Age (Graumlich 1993).

Concomitantly, we suggest that *Dedeckera* must have lost its effective cross-pollinating insects and by reverting to self-pollination lost its reproductive capacity due to its high genetic load. No seedlings of *Dedeckera* have been reported since its discovery in 1976 (Reveal and Howell 1976), despite continuing searches and favorable years for their occurrence (Fig. 1). Over nine years of monitoring, only three young plants have been observed in Coldwater Canyon at favorable sites, i.e., sparsely vegetated seeps. However, given seedling survivorship rates of 10^{-4} to 10^{-5} in some desert perennials (Turner et al. 1969), the long-

Table 5. Results of controlled pollination treatments in *Dedeckera eurekaensis*. Data are reported as mean percentage of ovules that produced filled seeds (S/O). Means followed by the same letter do not vary significantly at $P < 0.05$, based on Mann-Whitney U -tests.

Pollination treatment	N (plants)	N (ovules)	S/O (%)
Intrapopulation crosses	13	192	12.0 a
Self-pollinations (geitonogamous)	8	115	0.9 b
Interpopulation crosses (\times Gunter Cyn.) ^a	2	62	12.9 a
Spontaneous seed set in parental plants ^a	10	2875	4.7 c
Flowers isolated in nylon enclosures ^a	3	281	3.9 bc

^a Data summarized from Wiens et al. 1989a.

term evolutionary prospects for *Dedeckera* are not promising.

Extinction is often attributed directly to environmental causes, but in *Dedeckera* the immediate loss of reproductive capacity appears to be linked to genetic phenomena involving extensive self-pollination in plants with high genetic loads. Decreased reproductive success due to inbreeding in normally out-crossed species has been documented in other plant species, butterflies and birds (Keller and Waller 2002). However, populations with S/O ratios of $\leq 5\%$ may enter an extinction "red zone" where fitness is also affected by both low seed set and seedling survivorship (hard selection; Wallace 1968). Such genetically mediated loss of reproductive capacity is rare, but is now known in populations of other long-lived species in the northern Mojave Desert: *Eriogonum heermannii* Dur. & Hilg. (Polygonaceae), *Galium stellatum* Kellogg (Rubiaceae), *Mortonia utahensis* Nelson (Celastraceae), and *Scopulophila rixfordii* (Brandege) Munz & I.M. Johnston (Caryophyllaceae) (D. Wiens, unpubl. data). Other examples occur in the Chihuahuan Desert (*Mortonia sempervirens* Gray, Celastraceae), and California chaparral (*Adenostoma sparsifolium* Torrey, Rosaceae) (D. Wiens unpubl. data), and are reported from South Africa (Wiens et al. 1988) and Australia (Meney et al. 1997).

Reversion to self-pollination in plants with high genetic loads, as described for *Dedeckera*, however, cannot explain the low seed sets in some of the other species listed above, such as *Galium* and *Scopulophila*, because these two species are both obligate outcrossers (dioecious), yet most ovaries nonetheless initiate development and mostly mature full-sized fruits even though the developing seeds have aborted, as previously described. In *Adenostoma* high mutational genetic load related to great longevity is the most likely cause of lost reproductive capacity (D. Wiens and S. Davis, unpubl. data). Other examples may fit criteria of Haldane's (1957) argument that cost of selection may lead to extinction.

Conservation biologists, in particular, should be aware that populations of long-lived perennials comprising largely old individuals are likely characterized by low reproductive capacity. Such populations are often relictual elements of clades in evolutionary decline, usually as the result of environmental shifts. Short-lived species, on the other hand, are commonly edaphically restricted neoendemics with relatively high S/O ratios (20–70%; Wiens 1984). Because phylogenetically rare species (paleoendemics) possess more distinctive germplasm than neoendemics with close extant relatives, they should be given the highest priority in rare species conservation. Long-lived species with low reproductive capacities are not generally in immediate danger of spontaneous extinction, but are

probably highly susceptible to extinction via human environmental perturbations. Therefore, management strategies and conservation programs for such species should minimize any human disturbances in remaining populations.

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