Reproductive Biology of *Larrea tridentata*: A Preliminary Comparison Between Core Shrubland and Isolated Grassland Plants at the Sevilleta National Wildlife Refuge, New Mexico

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Abstract—Expansion of diploid creosote shrubs (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville)) into grassland sites occurs exclusively through seed production. We compared the reproductive biology of *Larrea* shrubs located in a Chihuahuan desert shrubland with isolated shrubs well-dispersed into the semiarid grasslands at the Sevilleta National Wildlife Refuge. Specifically, we examined (1) reproductive success on open-pollinated branches, (2) the potential of individual shrubs to self-pollinate, and (3) bee pollinator guild composition at shrubland and grassland sites. Sampling of the bee guild suggests that there are adequate numbers of pollinators at both locations; however, the community composition differs between shrub and grassland sites. More *Larrea* specialist bee species were found at the shrubland site as compared with the isolated shrubs. Large numbers of generalist bees were found on isolated grassland bushes, but their efficiency in pollinating *Larrea* is currently unknown. Higher percent seed fill of unbagged, open-pollinated shrubs at the shrubland site, compared with isolated grassland shrubs (76 versus 57 percent) suggests that bee specialists may increase plant pollination success. Isolated grassland shrubs varied greatly in the number of seeds produced in pollinator-exclusion bags, whereas the number of self-pollinated seeds produced by shrubland plants was more uniform. Overall, the difference in seed produced by bagged and unbagged branches of isolated shrubs was much less than the difference produced by plants located at the shrubland site. These trends will be explored in greater detail in future years.

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Introduction

Chihuahuan Desert shrubland is expanding into semiarid grasslands of the Southwest. Creosote (*Larrea tridentata*) seedling establishment in grasslands is a key factor in this conversion. Diploid *Larrea* plants of the Chihuahuan Desert are not clonal as has been reported for some hexaploid Mojave populations (Vasek 1980). Consequently, *Larrea* establishment in semiarid grasslands of New Mexico must occur exclusively through seed. At McKenzie Flats in the Sevilleta National Wildlife Refuge, there exists a gradient in *Larrea* density stretching from dense *Larrea* shrubland (4,000 to 6,000 plants per hectare) to semiarid desert grassland with only a few scattered shrubs. This study investigated the effects of spatial isolation on *Larrea* pollination and seed production. We compared the reproductive biology of *Larrea* shrubs located in the *Larrea* shrubland community with isolated shrubs well dispersed into the grasslands of McKenzie Flats. Specifically, we compared (1) reproductive success on open-pollinated branches, (2) the potential of individual shrubs to self-pollinate, and (3) bee pollinator guilds at shrub and grassland sites.

Methods

Flower and seed production of *Larrea* shrubs occurs most reliably in spring, but can also occur in late summer or early fall depending on the timing and amount of monsoonal precipitation. This study took place in the spring of 2005. We used mesh bags to exclude pollinators from four branches per plant of six isolated and six shrubland *Larrea* plants. After flowering was complete, we bagged four additional branches per shrub with mesh bags to prevent insect damage and facilitate collection of all flowers and fruits. Flowers that did not develop fruit could still be counted because the bag mesh size was small enough to retain remnant gynoecia. Once the fruits had ripened on the branch, all bags were collected and returned to the lab for processing. For each sampled branch, we counted total numbers of flowers, developed fruits, and filled seeds to determine percent fruit set, percent seed fill, and return on investment calculated as the average number of filled seeds per flower (five possible). Seed fill was determined using a cut test.

Bee pollinator guilds at shrubland and grassland sites were sampled twice weekly from May 21 to June 17, once in the morning and once in the afternoon. Five shrubs at each site were sampled for 15 minutes per bush per visit. Bee collections were later pinned and provisionally identified to species using available literature. Determinations were later confirmed at the USDA-ARS Bee Biology and Systematics Laboratory in Logan, Utah. Classification as generalist or specialist pollinators followed Minckley and others (1999). Bee species not specifically identified in that paper as *Larrea* specialists were considered to be generalists. Identifications have so far been performed only for female specimens. We assume females comprise the primary pollinating agents, because they collect pollen with which to provision their nests (Simpson and others 1977). Males will be included in the analysis when identifications are completed.

Results and Discussion

Larrea Reproductive Biology

We were able to recover open-pollinated seed from only two of the six isolated shrubs. Because of unusually high numbers of grasshoppers present in the grassland in 2005, flowers not protected by pollinator-exclusion bags were subject to herbivory, the severity of which varied with shrub. Consequently, seed and fruit production numbers for open-pollinated branches of isolated shrubs are based on two shrubs, resulting in a high standard deviation.

Average fruit set (percentage of flowers developing fruit) for open-pollinated branches of shrub (91 percent) and grassland (93 percent) *Larrea* was nearly identical (fig. 1A). Average percent seed fill for shrubland plants was substantially higher than for isolated shrubs (76 compared to 57 percent), resulting in a higher number of filled seed produced per flower (fig. 1B, 1C). Although the difference in seed fill was not significant due to the low number of sampled shrubs (two isolated shrubs), it does suggest greater pollination success for shrubs located within the shrubland population.

Individual grassland shrubs varied greatly in the number of seeds produced in pollinator-exclusion bags, whereas the number produced by shrubland plants was more uniform (see error bars in fig. 1). Percentage fruit set of self-pollinated branches ranged from 15 to 83 percent for isolated shrubs, and from 26 to 51 percent for shrubland plants. Overall, however, isolated shrubs had higher fruit set and seed fill on self-pollinated branches than did shrubland plants. The reason for this difference is not clear, but may be due to a redistribution of resources within the shrub. Shrubland *Larrea* plants had greater seed fill for open-pollinated branches and may have directed resources to those branches and away from selfed branches (Knight and others 2006). Conversely, isolated shrubs that lost potential open-pollinated flowers to herbivory may have directed available resources into self-pollinated fruit production. Mixed pollination systems, in which plants produce seed through outcrossing or by selfing, constitute a bet-hedging strategy that allows for seed production in the absence of successful cross-pollination (Kalisz and others 1999).

Our results on seed production of self- and open-pollinated flowers are comparable to those reported previously.

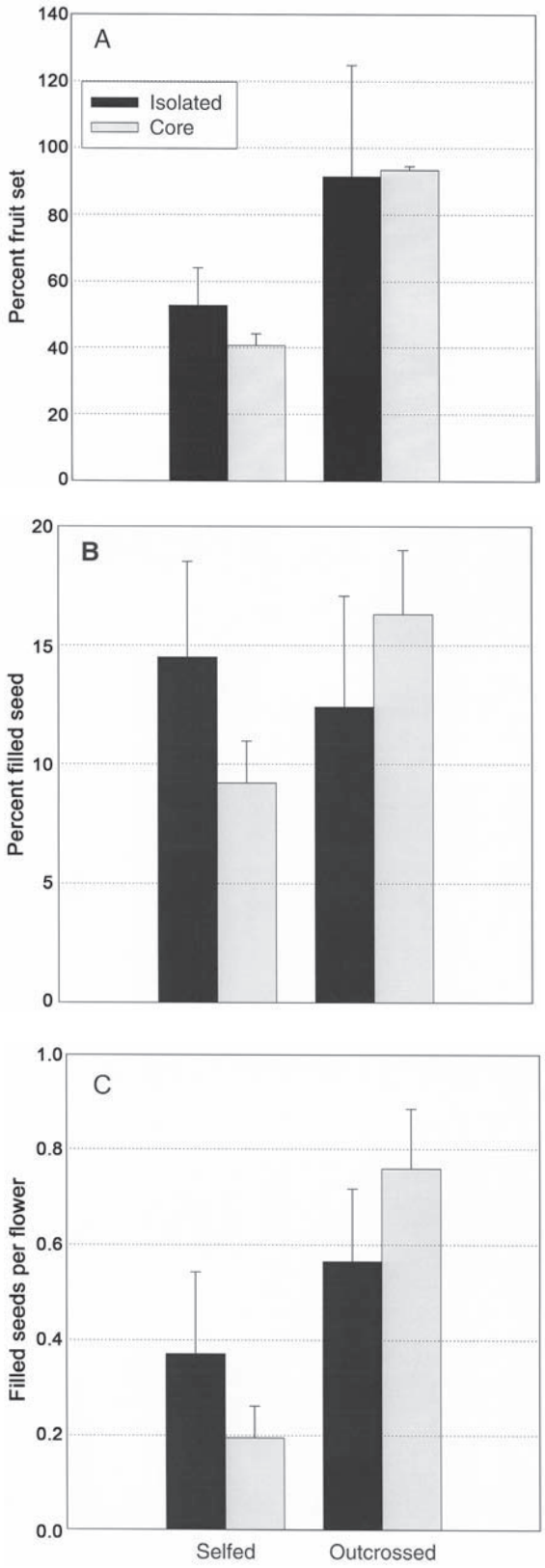

Figure 1—Means and standard errors for (A) percent fruit set, B) percent seed fill, and (C) number of seeds per flower of selfed and open-pollinated branches of isolated grassland and shrubland *Larrea*. For open-pollinated branches of isolated shrubs, n = 2. For all other groups, n = 6.

Tetraploid plants growing near Tucson, Arizona, produced an average of 0.41 filled seeds per flower for mesh-bagged branches (Simpson and others 1977). This is roughly equivalent to the average we found of 0.37 seeds per flower for isolated shrubs, but higher than the mean of 0.20 seeds per flower in the shrubland. Open-pollination of the Tucson shrubs resulted in 0.79 seeds per flower, compared to our 0.76 seeds per flower for shrubland plants. Again, the greater disparity in seed production of selfed and out-crossed branches in shrubland as opposed to isolated grassland shrubs may be due to differential resource allocation.

In creosote shrublands, *Larrea* is likely to be an over-abundant pollen source for visiting bees in years with prolific flowering, resulting in proportionately fewer successful cross-pollinations (Simpson and others 1977). The relatively low number of filled seeds per flower reported both here and by Simpson and others (1977) for open-pollinated shrubs occurred in years with abundant spring moisture. Higher seed fill is likely to occur in years of low flowering. High temporal variation in precipitation patterns associated with desert ecosystems may promote the retention of self-pollination as a back-up reproductive mechanism in *Larrea* (Simpson and others 1977).

Bee Pollination Guilds

Bees are by far the most important group of *Larrea* pollinators (Simpson and others 1977). Over 120 species of native bees visit *Larrea* flowers (Minckley and others 1999). Several species are oligolectic, collecting pollen exclusively from *Larrea* even in the presence of alternate potential pollen sources. Others are polylectic, collecting pollen from multiple sources. *Larrea* provides both pollen and nectar resources to visiting insects. Nectar feeders generally do not restrict their visitation to a particular plant species. Conversely, some pollen foragers specialize on productive, dependable hosts such as *Larrea* (Minckley and others 1999).

Results from our bee guild sampling suggest that there are adequate numbers of pollinators at both locations; however, the community composition differs between shrubland and grassland sites (table 1). More than three times as many bees were collected from isolated shrubs within the grassland. This may suggest resource limitation for generalist bees in the grassland. The large numbers collected from isolated bushes primarily reflect the abundance of three species of presumed generalists, *Colletes salicicola*, *Halictus tripartitus*, and *Lasioglossum pruinosiformis*. Simpson and others (1977) report that *C. salicicola*, while considered a generalist, appeared to prefer *Larrea* and *Prosopis* as pollen sources, which may explain the relatively high numbers also collected from plants in the shrubland. The relatively low numbers of bees collected from the shrubland site is not unusual. Simpson and others (1977) reported that pure stands of *Larrea* were consistently characterized by low pollinator densities. However, we found a notable difference in pollinator composition between sites. Five of the six *Larrea* specialist bee species were found at the shrubland site, whereas only three of the six were found on the isolated bushes. Also, the number of individuals of specialist species was more than five times the number on isolated bushes, even though the total number of bees collected from isolated bushes was much higher (table 1).

Recent research by Cane and others (2006) investigated the effects of fragmentation of *Larrea* populations on the bee pollination guild. They reported differences in bee functional guilds based on dietary breadth (generalist or specialist feeders) and nesting substrate. Population fragmentation had a negative effect on *Larrea* specialists and on ground-nesting bees. Our study investigated the extreme in fragmentation of a *Larrea* population, namely isolated shrubs within a semiarid grassland. We found a similar negative effect on *Larrea* specialists, but no effect on ground-nesting bees. Ground-nesting bees were found in abundance at both locations, whereas stem and cavity-nesting bees (four species) were found only in the shrubland site. The lack of stem and cavity-nesting bees in the grassland site reflects a lack of nesting substrate, a resource well-represented in the fragmented urban *Larrea* populations studied by Cane and coworkers (2006).

Bee numbers may be limited by appropriate nesting sites, as well as by the abundance of floral resources (Cane 2001). For ground nesting bees, suitable nest sites should be relatively constant between shrubland and grassland, and therefore, the spatial density of bees is likely to be constant between the two sites. The apparent higher abundance of bees that we report for grassland shrubs likely reflects attraction to an abundant concentrated food resource in what is otherwise a relatively homogeneous grass-dominated landscape. Conversely, the superabundant floral resources present in the shrubland would create an apparently lower density per bush because individuals would visit shrubs closest to their nest site.

The effects of fragmentation on *Larrea* reproduction have not previously been examined. While some studies report reduced pollination success with fragmentation, others argue that an abundance of floral generalists may contribute more to successful seed production than infrequent visits by specialists (Cane and others 2005; Minckley and Roulston 2006). In this study, large numbers of bees were collected from isolated shrubs, but their pollination efficiency is unknown. The higher seed fill of open-pollinated branches in the shrubland compared to isolated grassland shrubs suggests that bee specialists may indeed increase plant pollination success.

Our results are from one flowering season. The amount of floral resources provided by *Larrea* can vary greatly among years and between spring and fall growing seasons. The number of bee species collected in *Larrea* shrublands is also quite variable seasonally and annually (Cane and others 2005; Minckley and others 1999; Simpson and others 1977). The majority of bee individuals collected come from a few common species, with the remainder comprised of a small number of individuals from multiple species. A high degree of variation in bee abundance and composition has often been reported in other studies (Williams and others 2001). Additional research is now underway to determine if the results reported here are consistent among years.

Table 1—Numbers of female bees collected from isolated grassland and core shrubland *Larrea* plants. Bee species considered to be *Larrea* specialists are in bold.

Family	Scientific name	# Collected from isolated bushes	# Collected from core bushes
Andrenidae	*Andrena prunorum*	1	0
	Perdita semicaerula	1	28
Apidae	*Anthophora* sp. 1	1	0
	Apis mellifera	1	3
	Bombus morrisoni	2	0
	Centris caesalpiniae	4	4
	C. cockerelli	2	0
	C. ferrisi	0	1
	Diadasia rinconis	0	1
	Epeolus mesillae	0	2
	Melissodes sp. 1	10	2
	Triepeolus sp. 1	0	1
	Xylocopa californica	0	2
Colletidae	***Colletes clypeonitens***	6	0
	C. covillae	2	9
	C. hyalinus	4	0
	C. louisae	4	4
	C. salicicola	66	18
	C. sphaeralceae	1	1
	C. wootoni	3	0
Halictidae	*Agapostemon angelicus*	4	2
	Halictus ligatus	1	0
	H. tripartitus	248	6
	Lasioglossum sp. 3	8	2
	L. sp. 5	5	2
	L. morrilli	7	1
	L. pruinosiformis	72	46
	L. sisymbrii	2	3
	Nomia sp. 1	1	0
Megachilidae	*Anthidium cockerelli*	0	1
	Ashmeadiella bigeloveae	0	1
	A. meliloti	0	1
	Hoplitis biscutellae	0	2
	Megachile spinotulata	7	0
	M. sp. 1	7	0
	M. sp. 2	1	0
	Trachusa larreae	0	7
Mellitidae	***Hesperapis* sp. 1**	0	1
Total number of individuals		473	151
Total number of species		27	26
Total number of specialist species		3	5
Total number of specialist individuals		9	47
Number of site specific species		12	11

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References

Cane, J.H. 2001. Habitat fragmentation and native bees: a premature verdict? Conservation Ecology. 5(1): 3. [online] Available: http://www.consecol.org/vol5/iss1/art3 [11/20/06].

Cane, J.H.; Minckley, R.L.; Kervin, L.J.; Roulston, T.H. 2005. Temporally persistent patterns of incidence and abundance in a pollinator guild at annual and decadal scales: the bees of larrea tridentata. Biological Journal of the Linnean Society. 85: 319-329.

Cane, J.H.; Minckley, R.L.; Kervin, L. J.; Roulston, T.H.; Williams, N.M. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Applications. 16: 632-644.

Kalisz, S.; Vogler, D.; Fails, B.; Finer, M.; Shepard, E.; Herman, T.; Gonzales, R. 1999. The mechanism of delayed slefing in Collinsia verna (Scrophulariaceae). American Journal of Botany. 86: 1239-1247.

Knight, T.M.; Steets, J.A.; Ashman, T.-L. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. American Journal of Botany. 93: 271-277.

Minckley, R.L.; Cane, J.H.; Kervin, L.; Roulston, T.H. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. Biological Journal of the Linnean Society. 67: 119-147.

Minckley, R.L.; Roulston, T.H. 2006. Incidental mutualisms and pollen specialization among bees. In: Waser, N.M.; Ollerton, J., eds. Plant-pollinator interactions: from specialization to generalization. Chicago, IL: University of Chicago Press: 69-98.

Simpson, B.B.; Neff, J.L.; Moldenke, A.R. 1977. Reproductive systems of Larrea. In: Mabry, T.J.; Hunziker, J.H.; DiFeo, D.R., Jr., eds. Creosote bush: biology and chemistry of Larrea in New World deserts. US/IBP Synthesis Series 6. Stroudsburg, PA: Dowden, Hutchinson & Ross, Inc.: 92-114.

Vasek, F.C. 1980. Creosote bush: long-lived clones in the Mojave Desert. American Journal of Botany. 67: 246-255.

Williams, N.M.; Minckley, R.L.; Silveira, F.A. 2001. Variation in native bee faunas and its implications for detecting community changes. Conservation Ecology 5(1): 7. [online] Available: http://www.consecol.org/vol5/iss1/art7 [11/20/06].