Title: A review of *Arctomecon californica* (Papaveraceae) with a focus on the species' potential for propagation and reintroduction and conservation needs

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Summary

Las Vegas bearpoppy (*Arctomecon californica*) populations have declined during the past twenty-five years, and habitat is threatened with continued development in the Las Vegas Valley. *A. californica* was petitioned for listing under the Endangered Species Act in 2019 and is under consideration to determine whether listing is warranted (Department of Interior, Fish and Wildlife Service 2020). This review updates species information for *A. californica* and includes recent insights into the species' seed ecology, habitat requirements and suitability models, propagation and reintroduction, and pollinator biology. We include information from the past twenty years in these areas that supplement conservation and restoration actions for the species. We also identify topics with scarce information available and highlight areas for future study including: preserving the genetic diversity through germplasm collections, identifying the mechanisms driving its soil endemism, understanding pollinator habitat to maintain *A. californica* – pollinator relationships, determining the viable seed fraction and its longevity in the soil seed reserves, and predicting population response to regional climate change based on demographic modeling.

Introduction

Arctomecon californica is a short-lived, herbaceous perennial in the Papaveraceae family and grows on unique substrates in the Mojave Desert of southeastern Nevada and northwestern Arizona (Thomson and Smith 1997). *A. californica* has been heavily studied when compared to other rare, endemic plants of the Mojave Desert; however, much species and habitat information is unknown or remains equivocal. *A. californica* is listed as critically endangered by the state of Nevada and is covered by Clark County's Multi-Species Habitat Conservation Plan, is listed as a special-status species in Arizona (WRA Environmental Consultants 2018), and a petition was submitted for federal listing under the Endangered Species Act in July 2019 (Cornelisse and Tyler 2019).

Arctomecon californica populations are highly variable over the species range due in part to the influence of timing and amount of precipitation on population structure and health and the fragmentation of habitats. Bureau of Land Management's comprehensive survey in 1993 estimated 830,000 plants on 39,500 acres across 99 populations (91 in Clark County, Nevada and 8 in Mohave County, Arizona), although these estimates may represent a peak in population cycles influenced by above-average rainfall for the region during 1992 – 1993 (Mistretta et al. 1996). *A. californica* populations have declined since 1996 (Cornelisse and Tyler 2019), and the species' range has been reduced by half since 1994 surveys, estimated at 20,000-24,000 acres in 2000 (The Nature Conservancy 2007, Nevada Natural Heritage Program 2017). Population declines are difficult to differentiate between disturbance effects on plant fitness or weather-driven fluctuations in recruitment and senescence. The abundance of plants is not the only variable informing population persistence because population reductions can result from senescing plants while seeds persist in the soil in a dormant state awaiting appropriate conditions to emerge (The Nature Conservancy 2007). For example, many fragmented populations in the Las Vegas Valley were declared extirpated during 1996 and 1998 surveys, yet field checks conducted following above-average 2004 – 2005 winter rainfall found plants at 5 of the 10 populations presumed extirpated in 1998 (The Nature Conservancy 2007). However, because *A. californica's* seed dispersal distance is several orders of magnitude less than the distance between suitable habitat patches, and pollinator limitations in the Las Vegas Valley may reduce gene flow between populations, it is possible that these western populations may be extirpated with further loss of habitat (The Nature Conservancy 2007, Meyer and Forbis 2006). The eastern populations on protected lands are considered stable when accounting for climate pulse (above-average precipitation) and inter-pulse (below-average precipitation and warm seasonal temperatures) periods that drive recruitment and senescence, respectively (The Nature Conservancy 2007).

Previous reviews of *A. californica* focused less attention on practices to augment populations or reintroduce plants into unoccupied habitats that appear suitable for sustaining populations. Mistretta et al. (1996) is a comprehensive review of *A. californica* and concludes that a seed storage program for conserving germplasm and investigating production of commercially available stock may alleviate collection pressure for landscape purposes. In their low elevation multi-species review, The Nature Conservancy (2007) recommended salvaging *A. californica* surface soils containing seeds and seedlings as mitigation, in the managed Nellis Dunes OHV Recreation Area in particular, where loss and damage of rare plant habitat would require exceptional means to reclaim and restore. We update these reviews and other *A. californica* information in our status of knowledge of the species and refer to earlier information on habitat description and life history strategy to provide context for conservation actions. We direct readers to earlier literature for the historic perspective and comprehensive treatment of *A. californica* taxonomy, species description, distribution, status and trends, surveys and population trends, and threats. Our review draws from published and unpublished literature and focuses on recent findings to evaluate conservation and restoration actions needed for long-term protection of *A. californica*. Specifically, we summarize information on habitat, seed ecology, and pollination biology and how this information relates to propagation, reintroduction, and habitat management.

Habitat

Vegetation and soil associations

Arctomecon californica inhabits sparsely vegetated areas within creosote bush (*Larrea tridentata*) and salt-bush (*Atriplex* spp.) dominated communities where physical crusts limit establishment of dominant vegetation (Megill et al. 2011, Meyer et al. 1992, Mistretta et al. 1996, Romão and Escudero 2005). *A. californica* is positively associated with shadscale (*Atriplex confertifolia*) and negatively correlated with white bursage (*Ambrosia dumosa*), desert trumpet (*Eriogonum inflatum*), broom snakeweed (*Gutierrezia sarothrae*), and Mojave woodyaster (*Xylorhiza tortifolia*; Megill et al. 2011). *A. californica* shares its distribution with silverleaf sunray (*Enceliopsis argophylla*), and the two species are commonly surveyed together in and around Lake Mead National Recreation Area (Bangle et al. 2010).

Invasive annual species that are problematic in upland desert shrublands are not as well documented for gypsic soils. Sahara mustard (*Brassica tournefortii*), African mustard (*Strigosella africana*), red brome (*Bromus madritensis* ssp. *rubens*) and Mediterranean grass (*Schismus barbatus*) have been noted in *A. californica* habitat, usually along disturbance trails (The Nature Conservancy 2007, Bangle et al. 2010), but the direct (competition) and indirect (wildfire fuels) impacts of these species on *A. californica* have not been quantified. Seed bank emergence trials have shown abundant seeds of invasive species in *A. californica* habitat, especially Mediterranean grass; although not represented in above-ground vegetation, disturbance events potentially allow these invasive plants to become established (Pereira 2019). African mustard was documented on gypsic soils at a greater frequency than on other soil types during five years of survey that fluctuated greatly in annual precipitation (Abella et al. 2009), and the potential threat of competition with *A. californica* placed invasive plants as a high priority among research and management needs (The Nature Conservancy 2007). Invasive species may not be a widespread threat to *A. californica* where vegetation is typically sparse but may encroach where soils in fragmented populations are disturbed; thus, quantifying presence/absence of invasive plants at a minimum during population surveys will help trigger early intervention for removal.

Fine scale soil mapping at the northern edge of Las Vegas Valley demonstrates *A. californica* occurring on map units typical of spring deposits and basin floor sediments that lack a thick surface veneer of extremely gravely alluvium, while map units with deep and gravely soils do not support *A. californica* (Boettinger et al. 2010). Surface soils and 3-dimensional soil profiles that were sampled and analyzed indicate that *A. californica* inhabits finely disseminated calcium carbonate soils with petrocalcic horizons (carbonate-cemented layers), many carbonate nodules, and small (5%) to trace (< 0.1%) amounts of gypsum (Boettinger et al. 2010). *A. californica* has a narrow distribution on the highly calcareous basin floor, as compared to the wider range of shrub vegetation on alluvial fans, the basin floor, and drainages (Boettinger et al. 2010). Geomorphic surface (e.g., spring deposit, basin floor) and fine scale soil map unit were proposed as better indicators of *A. californica* habitat than surface soil chemistry (Boettinger et al. 2010), and have been included in habitat suitability models (see "*Habitat suitability models*").

Gypsophile?

Early studies considered *A. californica* a gypsophile, a species restricted to soils with high gypsum content (36-69%; Meyer 1986, Sheldon 1994, Thompson and Smith 1997), or a gypsocline, a species primarily found on gypsum but also on other unusual or mixed soils, such as soils with high boron or lithium (Meyer 1986). Thompson and Smith (1997) described soils in *A. californica* habitat as whitish in color, fluffy in texture, spongy and mineral-rich, and forming raised crusts that are easily disturbed, with higher levels of sulfur, calcium, and soluble salts and lower phosphorus levels than adjacent soils. Despite the unique chemistry of gypsum soils, the effects of these elements are likely secondary to the physical structure and crust characteristics of the soil – such as biological crust cover, rock cover, and spongy texture with low bulk density –

that are associated with *A. californica* (Thompson and Smith 1997, Meyer 1986). Indeed, true gypsophiles occur on soils only when the gypsum content is high enough to change the physical properties of the soil, emphasizing the potential importance of physical factors rather than chemistry (Meyer 1986).

More recent research confirms that *A. californica* can occur on a wide range of soils and parent material and is not a gypsum-obligate (Saxena 2005, Childers 2004, Drohan and Merkler 2009, Boettinger et al. 2010). Gypsum soils are nutritionally impoverished due to the exchange of calcium and magnesium for other ions and are toxic to some plants because of high sulfate levels (Meyer et al. 1992, Palacio et al. 2007, Moore et al. 2014). Unlike specialist gypsophiles adapted to accumulate high foliar concentrations of sulfur, calcium, magnesium, nitrogen, phosphorus, and ash (Palacio et al. 2007, Parsons 1976), foliar analysis of *A. californica* (Drohan and Merkler 2009) compared with that of 69 species that grow on gypsum soils (Merlo et al. 2019) indicates *A. californica* maintains moderate levels of foliar calcium and sulfur and may avoid the accumulation of these elements through selective uptake (Moore et al. 2014, Duvigneaud and Denaeyer-de Smet 1968 cited in Moore et al. 2014). The calcium and sulfur levels in *A. californica* leaves suggest it is an "indicator species," or one without a specialized physiological mechanism for coping with high levels of these select elements (Merlo et al. 2019). Further study exploring the leaf chemical compositions of *A. californica* growing in gypsum and non-gypsum soils, or a comparison between *A. californica* and known gypsophiles in the Southwestern U.S. (e.g., *Acleisanthes lanceolata, Tiquilia hispidissima,* and *Nama cornosum*; Muller 2017, Moore et al. 2014) would be more definitive, especially as some sites where *A. californica* occurs have a minimal difference in soil chemistry between occupied and neighboring unoccupied areas (Meyer 1986). In fact, soil surveys reveal that some *A. californica* populations have small (5%) to trace (< 0.1%) amounts of gypsum in the subsoil and a total lack of gypsum in surface horizons (Boettinger et al. 2010). Furthermore, based on 2,575 *A. californica* observations, 65.4% occur on gypsic soils, while the remaining 34.5% occur on calcid soils originating from limestone parent material with shallow calcium carbonate layers and accumulated high levels of calcium carbonate (Childers 2004).

Collectively, recent studies recognize *A. californica* as a "gypsovag," a species that can occur on soils with or without gypsum (Drohan and Merkler 2009, Boettinger et al. 2010). Isolated populations of *A. californica* may represent ecotypes that tolerate different soil chemistries among other factors (Bangle et al. 2010). For example, four geographically isolated populations of *A. californica* in Grand Canyon exhibit unique morphology and genetics, potentially comprising an undescribed variant (Mistretta et al. 1996, Simpson 2014). Such soil chemistry-based differentiation has been found both for a widespread California arid land annual (*Lasthenia californica*) when growing on serpentine outcrops (Rajakaruna 1998) and an edaphic endemic perennial herb (*Lomatium cookii*) growing in two isolated wetlands with different soils (Silvernail 2008).

Habitat characteristics

Soils with low aggregate stability may be at risk for erosion and for surface crusting and sealing; exposed gypsum also creates hardened soil crusts when gypsum recrystallizes as water evaporates from the soil surface (Watson 1979). Communities of living organisms within the soil surface – known as cryptogamic, cryptobiotic, microbiotic or biotic crusts – occupy some *A. californica* population sites in addition to physical crusts; however, it is difficult to separate the relative effects of biotic and physical crusts on plant establishment in these environments (Moore et al. 2014). Dense gypsum horizons and the penetration resistance of gypsum soils can also limit root growth and lead to sparse plant cover (Gibbens and Lenz 2001). Regionally dominant shrubland species are typically excluded from gypsum soils when these soils are exposed on the surface but establish when a thin layer of alluvium covers the surface of the gypsum soils (Meyer 1986, Meyer et al. 1992). Thus, the physical nature of the surface crust of these soils limits shrub establishment and reduces plant density, leading to less resource competition for *A. californica* (Meyer 1986, Megill et al. 2011, Palacio et al. 2007).

Spring deposit material, petrocalcic horizons, and petrogypsic horizons are soil layers that can limit downward movement of water during the winter and spring and store moisture within the rooting zone of plants (Duniway et al. 2007). Petrocalcic horizons increase the near surface soil water holding capacity, augmenting available soil moisture during drier periods (Duniway et al. 2010, Buxbaum and Vanderbilt 2007, Herbel et al. 1972). Winter precipitation that is absorbed by these carbonate-cemented horizons is stored deep enough so that the subsoil moisture is not depleted by evaporation but shallow enough for roots of many aridland shrub and perennial forb species to access (typically less than 50 cm deep; Duniway et al. 2010). Petrocalcic horizons were noted at approximately 30 cm depth for one *A. californica* population, with roots embedded in the petrocalcic layer (Winkel 2004). Petrogypsic horizons, cemented gypsum-derived layers structurally similar to petrocalcic horizons, could increase water availability on gypsum-rich soils in the same way (Casby-Horton et al. 2014). Usually these hardened horizons are described as root-limiting layers, with root mats observed on the upper surface; however, petrogypsic horizons broken apart showed presence of interior roots (Casby-Horton et al. 2014). Plants growing in gypsum-rich soils may additionally benefit from physical properties that allow water to move readily through the soil column, such as low water-holding capacity coupled with high hydraulic conductivity (Meyer and Garcia-Moya 1989, Meyer et al. 1992, Reading et al. 2012), although this dynamic has not been directly measured in *A. californica* habitat (Drohan and Merkler 2009).

Diverse arbuscular mycorrhizal fungi communities are often associated with gypsum plant communities (Alguacil et al. 2009, Moore et al. 2014, Palacio et al. 2012), but species in Papaveraceae do not commonly form mycorrhizal associations, and their potential role for *A. californica* is unknown (Meikle et al. 2006). Arbuscular mycorrhizal fungi associations occur for both gypsophile and gypsovag species and promote tolerance of the nutrient and soil structure deficiencies of gypsum soils (Alguacil et al. 2009, Palacio et al. 2012) by increasing nutrient uptake, improving plant tolerance, and contributing to soil structure and quality (Wang 2017). The direct role that mycorrhizal colonization may play in supporting the persistence of gypsovags on gypsum soils is unclear because studies have analyzed colonization solely on gypsum soils without comparison to non-gypsum soils (Palacio et al. 2012). Mycorrhizal vesicles, arbuscules, and internal fungal hyphae were not detected in the roots of two *A. californica* plants examined for endomycorrhizal colonization (Meikle et al. 2006), but this sample size is too small to definitively confirm or refute arbuscular mycorrhizal fungi association for the species. Establishment of *A. californica* seedlings does seem to be enabled by the presence of cryptogamic crusts (Bailey 2019), although the mechanism is unclear in light of preliminary data showing more experimental units of dead crusts supporting seedlings than live crusts (6 on dead crusts vs. 1 on live crust, and 3 on no crust). Improved establishment may be largely a result of crust structure and nutrient inputs or moisture retention, but mycorrhizae can also be influenced by presence of cryptogamic crusts, and the relationship remains unclear (Harper and Pendleton 1993, Pendleton et al. 2003).

Habitat suitability models

Quantitative models of species distribution and associated habitat variables can expand searches for new populations and identify which habitats should be prioritized for protection and management actions including restoration and re-introduction. Modeling efforts for *A. californica* have been challenging due in part to the coarse resolution of available geologic maps. A model for *A. californica* for the Gold Butte region identified suitable habitat close to gypsiferous topsoil layer (66.6% variable contribution), low elevation (20.0%), with specific surficial geology (10.8%) and dominant bedrock material (2.6%). However, the authors note that this model potentially overpredicts suitable habitat because it did not account for habitat loss associated with human activities (Nussear et al. 2010). A model expanded to include Clark County was based on soil-based parameters (Natural Resources Conservation Service, Soil Survey Geographic Database data), an elevation constraint of 300-1120 m, and Advanced Spaceborne Thermal Emission and Reflection satellite imagery (Hamilton and Kokos 2011). Addition of climate variables (BioClim) to this county-wide model did not refine the soils-based model more than using elevation in the soil-based model, likely because climate is closely tied to elevation at a fine scale (Hamilton and Kokos 2011). The model with climate showed that *A. californica* populations tended towards warmer temperatures with a lower range of diurnal temperatures often associated with lower elevations and low isothermality, a measure of day-to-night temperature oscillations relative to annual oscillations (Southwest Ecology 2018, Hamilton and Kokos 2011). There are several additional issues that these recent models highlighted. For example, the presence of gypsum is largely based on the bedrock geology of an area, and surficial geology maps are not helpful in mapping gypsiferous regions. Using different geological maps can also make refining models difficult as geologic unit types might not be uniform or might be outdated, confusing bedrock lithology with soil type, geologic unit names, and/or landform type (Robins et al. 2014). *A. californica* can also occur in patches much smaller than the resolution of geologic units or not detectable by satellite imagery, or on map units that are not mapped as gypsiferous but contain gypsum due to erosion from neighboring units, further complicating modeling (Hamilton and Kokos 2011).

Seed and seedling ecology

Pollination and seed set

Arctomecon californica is largely self-incompatible, requiring pollen transfer between different individuals and not between flowers within an individual for fertilization (Sheldon 1994, Mistretta et al. 1996, Thompson and Smith 1997). However, self-compatibility can vary both within and between populations of a species (Faegri and van der Pijl 1979). For example, the closely-related *A. humilis* was previously asserted to be self-incompatible (Harper et al.

2001), but a subsequent study found that the breeding system was mixed for one population with 60% self-compatible and 40% self-incompatible plants, although this ratio of mixed self-compatibility may not hold for all *A. humilis* populations (Tepedino et al. 2014). Studies focusing on self-compatibility for different populations of *A. californica* will elucidate the importance of pollinators to species conservation and could reveal changes in *A. californica*'s breeding system, with possible shifts to self-compatibility in areas that are heavily fragmented or isolated. Modeling indicates the advantage of self-compatibility is greatest when site occupancy rates are low, such as along the margins of a species' range (Pannell and Barrett 1998). For one restricted annual herb (*Leavenworthia alabamica*), populations at the center of its range retain self-incompatibility, while peripheral, isolated populations display adaptations for self-fertilization, enabling reproduction despite pollinator limitations (Busch 2005).

Reproductive failure in *A. californica* is primarily the result of tissue abortion of buds and capsules rather than insect herbivory (Thompson and Smith 1997). High attrition may occur when buds develop late in the flowering season and abort at the onset of environmental stress during spring (Thompson and Smith 1997). However, *A. californica*'s reproductive attrition is low compared to other Mojave Desert perennials such as *Larrea tridentata* (Boyd and Brum 1983). Thus, low seed set may not play a primary role in the rare, restricted status of *A. californica* even though it may affect total fitness (Thompson and Smith 1997).

Seed dormancy

Upon ripening and prior to dispersal, seeds of species in the Papaveraceae family commonly display morphophysiological dormancy (Baskin and Baskin 2014), characterized by a rudimentary or linear embryo combined with physiological inhibiting mechanisms (Pereira et al. 2021). *A. californica* seeds fit this type of dormancy, with underdeveloped linear embryos and germination occurring only in response to specific incubation regimens (Meikle et al. 2006).

Seed dispersal

Arctomecon californica's seed dispersal is facilitated by more than one vector, a mode of dispersal known as diplochory. While a small proportion of seeds fall and are trapped within the basal rosette, wind disperses *A. californica* seeds from the capsules to the ground within 1 m of the parent during primary dispersal, and ants subsequently collect and disperse seeds across the landscape during secondary dispersal (Megill 2007). A small proportion of seeds disperse further from the parent plant, and seeds have been found up to 8 m away from the nearest adult plant (Megill 2007). Seed deposition in a northerly direction from the parent plant is in accordance with seasonal wind patterns after seed set (Megill 2007, Sheldon 1994).

Secondary dispersal of *A. californica* seeds by ants (known as myrmecochory) has been documented through seed dispersal trials and direct observations (Megill 2007). Over 99% of 23,253 intact *A. californica* seeds examined had elaiosomes, or white, fatty structures along the seed's hilum (attachment scar) that facilitate seed dispersal by ants (Fig. 1; Megill 2007). Ants transport seeds to their nests and feed the lipid-rich elaiosomes to their larvae, discarding the otherwise intact seeds on the soil surface. This dispersal of seeds away from the parent plant can help seedlings avoid direct competition with adults and deter seed predators foraging close to adult plants (Giladi 2006). Intact *A. californica* seeds discarded on the surface of nests without elaiosomes suggests that ants transport the seeds into their nests and discard intact seeds after elaiosomes are removed (Megill 2007). Heteromyid rodents, in contrast, generally prefer seeds larger than the average available in the soil (Price 1983, Brown et al. 1979), and the size of *A. californica* seeds (2 mm) may not be calorically rich enough to provide foraging reward (Reichman 1979). Alternately, the seeds' elaioisomes may act as a rodent repellent as in the case of *Corydalis aurea* (Hanzawa et al. 1985, Megill 2007), but additional studies are needed to confirm a potential role of rodent granivory or dispersal for *A. californica*. Seeds of the closely-related *A. humilis* also have elaiosomes and are removed by both ants and rodents, although it is not known how each impacts seed germination (Farrall and Mull 2010).

Figure 1: Position of elaiosome on hilum side of *A. californica* seed (left, drawing by A. Stosich); juvenile (pre-reproductive) *A. californica* with four rosettes (center, photo by L. DeFalco); adult *A. californica* in flower (right, photo by S. Sciulla).

Seed reserves

Several studies have shown that following dispersal, dormant seeds of *Arctomecon californica* accumulate over time in the soil seed reserves[1] awaiting conditions for germination. Far fewer *A. californica* seeds have been detected in studies that use emergence methods (i.e., surface soils collected from habitat are repeatedly watered in a greenhouse until germination ceases; Pereira 2019, Abella et al. 2013) compared with extraction methods (soils are sieved in a laboratory to separate seeds from soil; Sheldon 1994, Megill 2007, Megill et al. 2011, Pereira 2019). This difference occurs in part because emergence methods trigger germination of live seeds by simulating environmental cues – such as through repeated wetting and drying, or mechanical or chemical treatments – that shift seeds from a dormant to a germinable state (Baskin and Baskin 2014). Extraction methods determine total seeds, including those that may be nonviable (i.e., unfilled, decomposing or old seed). The viable fraction is sometimes assessed

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[1] The terms "seed reserves" and "seed banks" are both used in the literature to describe the natural accumulation and persistence of seeds in a dormant state within the topsoil awaiting favorable conditions for germination and seedling emergence. We use the former term in this context to avoid confusion with the latter, which is also used to reflect human-collected seeds maintained in a repository for future use in conservation or to safeguard declining populations against possible extinction (see *Further research for species conservation*).

after extraction through dissection of seeds and/or staining with tetrazolium dye, but determining viability this way is not definitive for small seeds such as those of *A. californica* (Pereira 2019). Early emergence studies for *A. californica* recorded minimal numbers in seed reserves (Pereira 2019, Abella et al. 2013), but a subsequent study confirmed that *A. californica* requires one or more seasons of chilling to stimulate germination (Pereira et al. 2021). Determining the viable seed reserves is important for understanding population viability and guiding potential seed reserve salvage or supplementation efforts. Thus, adding cold stratification to the emergence method may distinguish viable from nonviable seed fractions, but sorting the remaining soils using a combination of extraction and viability tests (e.g., poke test, dissection, or tetrazolium; Baskin and Baskin 2014) ensures that all viable seeds are accounted for.

Despite population-wide attrition of adult plants that occur during periods of drought (The Nature Conservancy 2007), *A. californica* relies on long-lived seed reserves for population persistence (Megill et al. 2011, Mistretta et al. 1996). In contrast to seed dispersal distances, distribution of seed reserves may be less clustered. In one study, total seeds extracted from soils did not decline in number out to 150 cm from adult plants (Winkel 2004), although nonviable seeds were not differentiated from viable seeds, which tend to be more clustered around adult plants (Megill et al. 2011). The combination of high output of seeds that can remain germinable for 19 years (Meyer, pers. comm., 2005 cited in The Nature Conservancy 2007) and persistence of viable seed in the soil (Megill 2007) allows *A. californica* to accumulate large seed reserves in the soil (Harper and Van Buren 2004). When plant populations are sparse, broad outcrossing due to greater pollinator foraging distances among plants is known to produce genetically diverse seed in other species, because distant plants are more likely to be unrelated (Ellstrand et al. 1978). In this way, *A. californica*, which has large interannual fluctuations in population densities, may potentially retain high genetic diversity in seed reserves despite small population sizes (Harper and Van Buren 2004). Population persistence depends on adequate seed production to replenish sizable seed reserves (Philips and Philips 1988 cited in The Nature Conservancy 2007). However, a population viability analysis of *A. californica* indicated that small, fragmented populations like those in Las Vegas Valley have low seed set due to pollinator limitations and may exist largely on their long-developed seed reserves (Meyer and Forbis 2006). These populations would become extirpated if their seed reserves become depleted without periodic inputs during years with successful seed set.

Arctomecon californica has been found at sites after 15 years of absence (Powell and Walker 1993 and Meyer 1996, both cited in Megill 2007), which may reflect dormant seeds awaiting favorable temperature and precipitation patterns that favor seedling emergence or seeds deep in the soil being brought to the surface through bioturbation to germinate (e.g., rodent digging, ant nest construction). Megill (2007) found *A. californica'*s seed reserves to be heterogeneously distributed, with a 34% of seed reserves at 0-2 cm, 22% at 2-4 cm, 18% at 4-6 cm, and 26% at 6-15 cm depth for 2,973 seeds recovered across five sites. Approximately 10.5% of the seeds recovered were determined to be viable in a tetrazolium stain test, with no significant difference between soil depths (Megill 2007). In addition to the presence of viable seeds in the soil profile, *A. californica* displays other characteristics indicating persistent seed reserves (Christoffoleti and Caetano 1998, Megill 2007) including long-lived seeds (Meyer, pers.

comm., 2005 cited in The Nature Conservancy 2007) and delayed germination of fresh seeds containing immature embryos. Seeds may travel deep into the soil profile due to their small size relative to the soil particle sizes at sites (Megill 2007), where seeds more than 7 cm below the surface are safe from most foraging granivores (Reichman 1979). Most seedlings of desert species cannot emerge from greater than 2 cm depth (Cabin and Marshall 2000, Bond et al. 1999), so these deeply buried seeds would produce seedlings only if bioturbation brought them nearer to the surface (Megill 2007).

Seedling recruitment

Emergence of *A. californica* seedlings has been noted during the winter or early spring months after unusually high winter precipitation (Meyer 1987 cited in Pereira 2019, Meyer and Forbis 2006). Based on these observations, Meyer (1987) surmised that winter rainfall sufficient for seedling establishment may occur as infrequently as once every nine years (Mistretta et al. 1996), while the exact temperatures, and amount and timing of favorable rainfall events remains unknown. Although untested, it has been suggested that rainfall events heavy enough to wash away or dilute sulfate mineralogy from surface soils are needed before germination can take place (Bangle et al. 2010). Seedlings tend to establish near adult plants at sites where *A. californica* is dense, a pattern that diminishes when disturbance limits adult plant abundance (Megill et al. 2011). High seedling mortality, typical of desert perennials, ranged between 60-87% for three sites around Lake Mead (Thompson and Smith 1997). Individual plants usually live 4-5 years and can have multiple flowering events over the plant's lifetime beginning in their second season (Thompson and Smith 1997). Individuals develop multiple rosettes as they grow older (Fig. 1), which can increase the plant's reproductive output (Thompson and Smith 1997, Meyer 1979 cited in Mistretta et al. 1996).

One recent study suggests that cryptogamic crusts may promote *A. californica* seedling establishment, although the mechanism and field dynamics of this relationship are only recently under investigation (Bailey 2019). *A. humilis*, a sister species with similar growth requirements, occurs on sites where biocrust cover contributes 84% or more of the total living cover, and seeds are captured within the cryptogamic crusts (Nelson and Harper 1991, Nelson and Welsh 1993). *A. californica* habitat has been described as having heavy cryptogamic cover as well (Mistretta et al. 1996, Thompson and Smith 1997, The Nature Conservancy 2007). However, some population sites support minimal biocrust cover (Megill et al. 2011), and studies have not found a direct relationship between cryptogamic cover and *A. californica* distribution (Bangle et al. 2010, Megill et al. 2011). *A. californica* plants have even been observed growing in disturbed spots (hoof prints) within heavily crusted areas (Bangle et al. 2010), on topsoil piles awaiting reclamation (Cayenne Engel, Nevada Division of Forestry; Lara Kobelt, BLM, Southern Nevada District Office, pers. comms.), and at sites previously inundated by Lake Mead (Engel et al. 2014). *A. californica* seedlings also established sporadically during 2003 – 2006 along an unimproved road at Lake Mead National Recreation Area along sections where deep soil compaction was alleviated with heavy machinery during late fall 2002 (U.S. Geological Survey, unpubl. data).

Weather influence

Careful *a priori* selection of weather variables for correlating important life stages (seedling, pre-reproductive juvenile, adult) and phenological stages (onset of flowering, fruit maturity, plant senescence) is essential for discriminating among the environmental triggers under our current climate and for forecasting future demographic and population trends. Seasonal temperatures and precipitation, variation in timing of precipitation, and combinations of current year and previous year temperature and precipitation patterns influence reproduction and fruit production, phenology, and complex relationships between plant species and their pollinators for other arid land species (Meyer and Pendleton 2015, St. Clair and Hoines 2018). Although preliminary, an analysis of *A. californica* numbers as influenced by site-specific weather variables revealed maximum humidity in May, minimum humidity in November, and high July rainfall were correlated with greater numbers of *A. californica* (Bangle et al. 2010), yet the ecological mechanism for humidity to promote recruitment or survival was unclear. Multiple stations that record daily maximum and minimum temperatures and daily rainfall across *A. californica* populations will discriminate between climate-driven limitations (e.g., low reproductive output, recruitment events, seedling and adult survival) and limitations driven by land use. Local long-term weather stations are also pivotal to validating the use of larger scale climate data such as Oregon State University's PRISM Climate Group, which can justify the extrapolation of spatial weather data across the species' range.

Propagation

Seed

Propagation from seed has held the most promise for developing nursery stock for habitat augmentation or reintroduction. *Arctomecon californica* seeds require an extended period of cold dry or cold wet conditions (known as stratification) to induce germination (Pereira et al. 2021, Pereira 2019, Meikle et al. 2006). This stratification requirement for *A. californica* germination resembles intermediate complex morphophysiological dormancy where the development of the embryo is not complete at the time seeds disperse, and embryo growth begins under cold stratification between 0-10 °C regardless of when the seeds mature in nature (Baskin and Baskin 2014). One recent germination trial with *A. californica* seeds encompassed cold-dry storage at 4 °C for 3.5 months, alternating moderate-wet incubation at 23°/13 °C and cold-wet stratification at 4 °C for 5.5 months, and a final cold-wet stratification for another 4 months, resulting in 4.9% germination over the first nine months and 18.7% germination during the final four months (Pereira et al. 2021). An unpublished report from Meyer (1996) used a similar protocol with comparable results (Pereira 2019). Increased germination during the final cold stratification indicates that one long or multiple short cold stratification events are needed to produce high germination rates, but the number and duration of these chilling events is unclear (Pereira et al. 2021). Field-stratified seeds of *A. californica* had much lower germination rates (0.4 ± 0.8%), demonstrating that year-to-year temperature variability across *A. californica* habitats may not always be cold enough or long enough, may not be frequent enough, or soil moisture may be inadequate for seeds to imbibe water during cold events during many years (Meyer 1987 cited in Mistretta et al. 1996, Pereira et al. 2021).

For species with intermediate complex morphophysiological dormancy, gibberellic acid is used to shorten the period of cold stratification (Baskin and Baskin 2014). *A. californica* seeds exposed to 100 ppm and 1000 ppm gibberellic acid produced radicles but no shoots, showing that some level of cold stratification remains necessary for embryo development (Meikle et al. 2006). One trial with gibberellic acid achieved 26% germination with cold-moist stratification at 2-4 °C for 40 days followed by treatment with 100 ppm gibberellic acid and incubation at 2-4 °C for 10 days and then at 8°/18 °C until germination occurred after about 10 days (Meikle et al. 2006). For some species with this seed dormancy type, dry storage or warm stratification prior to cold stratification can also shorten the period of cold stratification needed (Baskin and Baskin 2014), but this has not been tested for *A. californica*.

Arctomecon californica seeds are covered by a waxy cuticle that is water permeable and does not inhibit water imbibition, although it may delay embryo development and germination by reducing levels of gas and water exchange to some degree (Pereira 2021, Meikle et al. 2006). *A. californica* seeds treated with sulfuric acid (a seed pre-treatment to simulate gypsum releasing sulfate ions in solution) and subjected to cold treatment germinated more rapidly than seeds exposed to cold treatment alone (Pereira et al. 2021). *A. californica* seeds placed in an incubator for 10 minutes at 45 °C with subsequent scraping away of the waxy cuticle had significantly higher germination compared to intact seeds, with no effect on embryo growth (Meikle et al. 2006). Elevated germination of *A. californica* seeds exposed to acid or physical removal of the cuticle suggests that scarification – the mechanical or chemical weakening of the seed coat to promote the processes that lead to germination – could potentially improve seedling establishment in a restoration context.

Seed reserves

Raising plants germinated from the soil seed reserves is a potential strategy for propagating rare desert plants but has not been formally tested for *Arctomecon californica*. Although the emergence method is not suited for determining total numbers (viable + dead) of seeds in the seed reserves, this method has successfully identified the viable portion of seed reserves across a wide diversity of native and invasive plant taxa in desert shrublands (DeFalco et al. 2009, Scoles-Sciulla and DeFalco 2009, Esque et al. 2010, Jurand and Abella 2013). This method adapted to Mojave Desert shrublands promotes the germination of viable seeds from field-collected surface soils through repeated wetting and drying cycles in a greenhouse in combination with dormancy-breaking chemicals such as potassium nitrate and gibberellic acid (Esque 2004). By germinating seeds within the soils where *A. californica* grows, an emergence approach may improve seedling establishment over direct propagation from seed using nursery soil mixtures. An emergence method, including a cold stratification treatment, is currently being tested in this context for the rare Mojave Desert species *Penstemon albomarginata*, *Eriogonum viscidulum*, and *Astragalus geyeri* var. *triquetrus* (Clark County Desert Conservation Program project #2019-USGS-190A).

The cryptogamic crusts that are often found in *Arctomecon californica* habitat could play a role in seedling establishment (Bailey 2019), although the mechanism may be more complex than originally thought. In a growth chamber, seeds that germinated without biocrust did not develop into seedlings, while those that germinated with either live or dead biocrust reached seedling stage; the presence of live soil from the rhizosphere and the location of the seed above or below the crust did not influence initial germination (Bailey 2019). Subsequently, seeds in water permeable pouches were buried between soil and biocrust in the field in October and retrieved the following March, resulting in seedlings that developed true leaves (Lydia Bailey, pers. comm.). When these seedlings were moved from the growth chamber to the greenhouse, they died within five months, indicating that suitable greenhouse conditions have not yet been determined for *A. californica* seedlings (Lydia Bailey, pers. comm.).

Cuttings

Trials on stem or root cuttings for propagating *A. californica* plants are unknown. Whereas Mojave Desert perennials have been successfully propagated in a nursery setting using stem cuttings (Richardson et al. 1979, Everett et al. 1978), most species were woody shrubs. Unsurprisingly, propagation of herbaceous perennials is less common for desert species, particularly for herbs that lack organs from which they naturally reproduce asexually, such as rhizomes, stolons, or bulbils. Though challenging, vegetative propagation from cuttings of *A. californica* could be a useful tool in restoration because developing mature *A. californica* plants from seed is difficult (Lydia Bailey, pers. comm.). For the rare Rocky Mountain medicinal herb *Ligisticum porteri* (Apiaceae) that arises from a single taproot, crown cuttings collected during early spring were more successful than root cuttings and provided better plant development than did propagation from seed (Panter et al. 2004). *A. californica* emerges as a basal rosette of leaves from which a single inflorescence arises, although typically not during its first year (Fig. 1), and multiple rosettes accumulate as plants age (Sheldon 1994). Propagation of *A. californica* from an excised basal rosette, potentially using growth hormones that are known to establish roots in other herbaceous plants (Mladenović et al. 2016), shows some promise but has not been tried for *A. californica* to our knowledge. Rosette propagation, if successful, should limit injury and death of the donor plants, such as collecting rosettes after above-average winter precipitation or watering donor plants prior to collection to augment water status, and collecting in winter or early spring before belowground resources are mobilized for reproduction.

Micropropagation

Micropropagation techniques that use small parts of plant tissues grown on nutrient agar to produce new plants are becoming popular for mass production of plants that are difficult to grow using conventional horticultural methods. However, most micropropagation efforts seek to produce medicinal and ornamental plants, food for humans and livestock, and lumber (Kant et al. 2010, Chokheli et al. 2020). Little research has explored micropropagation for augmenting declining populations by reintroducing rare plants.

Reintroduction

Options for reintroducing *Arctomecon californica* plants into suitable habitat include outplanting nursery-raised seedling stock, salvaging seed reserves from topsoil, sowing or broadcasting seeds (pre-treated with cold stratification, scarification, or with no pre-treatment), or transplanting established plants within habitat (also known as plant salvage).

Outplant of nursery stock

Raising *Arctomecon californica* for outplanting is the most resource intensive approach to reintroduction due to pre-planting costs (labor and nursery costs for 6-mo to 1-yr commitment to grow robust seedlings) and post-planting effort (regular supplemental irrigation during establishment and herbivore protection, although leaf alkaloids in *Arctomecon* species are known to deter rodents and lagomorphs, Raynie et al. 1990, 1991). This approach is also the most challenging due to the difficulties of overcoming seed dormancy, reducing seedling mortality due to fungal infection (i.e., damping off), and promoting healthy growth and survival through to outplanting (Meikle et al. 2006). We were unable to find examples where outplanting has been attempted for *A. californica* specifically.

Soil salvage

Salvage of soil seed reserves by removing surface soils prior to disturbance is also resource intensive as it requires heavy machinery and space for storing topsoil piles, but it has been carried out as a mitigation measure for large-scale activities such as urban development and power pole placement. This mitigation method has not always been successful. At the Springs Preserve in Las Vegas, two of five known populations (each about 800 ft^2) had no living plants for over three years and were under the proposed footprint of major construction. In 2001, the top 2" of soil (with seed reserves) was set aside and 4" of the subsoil was salvaged and placed next to a third population. The topsoil was then spread on top of the subsoil. No *A. californica* plants were observed from the salvaged soil (Von Winkel, Southern Nevada Water Authority, pers. comm.). Additional soil salvage efforts also resulted in failed *A. californica* emergence: 40 cubic yards of gypsum soil obtained in 2005 from Nellis Air Force Base to enlarge a population at Springs Preserve, and a similar volume of soil obtained in 2006 from a stockpile at the Nevada Division of Forestry collected near Tule Springs (Von Winkel, pers. comm.). In contrast, during a recent salvage effort in *A. californica* habitat, topsoil was removed in December 2018 and replaced after completion of a transmission line in the Rainbow Gardens region near Pabco Mine. After late rains during winter 2019 – 2020, roughly 80 seedlings were found growing over approximately 150 linear feet of these topsoil piles, although the majority had died by late 2020 following below-average rainfall (Cayenne Engel, Nevada Division of Forestry, and Lara Kobelt, BLM, Southern Nevada District Office, pers comms.). Topsoil salvage using heavy machinery can significantly dilute Mojave Desert seed reserves when the surface soil layer is inadvertently mixed with deeper soil fractions lacking seed reserves (Scoles-Sciulla and DeFalco 2009), but when collected for nursery use, soils may also improve establishment of salvaged or greenhouse-grown plants. Alternately, surface soils collected near existing plants using shovels should capture the majority of seeds (Sheldon 1994), but this would be practical only on a small scale.

Direct seeding

Direct seeding is the least resource-intensive approach to reintroducing *Arctomecon californica*, but little research exists on this method. Anecdotally, *A. californica* was believed to be successfully introduced into an area in Utah after seeding by a local landowner (Mistretta et al. 1996). Most recently, *A. californica* plants successfully established at Rainbow Gardens and Gold Butte sites seeded in spring 2018 and 2019 as part of an ongoing restoration study (Lydia Bailey, pers. comm.). An additional seeding trial in combination with biocrust treatments was carried out at Rainbow Gardens in fall 2020, with results yet to be reported (Lydia Bailey, pers. comm.). Direct seeding trials that evaluate multiple treatments – including tests of seed pre-treatments, granivore protection, and supplemental irrigation – and revisited over multiple years to account for the influence of field conditions on germination and seedling establishment, will strengthen our understanding of this reintroduction strategy in comparison to others.

Plant salvage

The transplanting of salvaged *Arctomecon californica* plants is intermediate in resource intensity between outplanting and seeding and has received the most attention as a viable strategy. The largest challenge in transplanting *A. californica* is preserving the single fragile taproot that can reach the top of the petrocalcic layer with many growing into or through this layer (Winkel 2004). The greatest depth that taproots can grow into the petrocalcic layer is unknown, but penetration may be enabled by wet conditions (Winkel 2004, Casby-Horton et al. 2014). Because the taproot grows directly under the rosettes, excavating a column of soil that is slightly larger than the above-ground portion of the plant is sufficient for salvaging *A. californica*, but taproot depth cannot be predicted by above-ground plant size (Winkel 2004). For example, one plant with two rosettes had a taproot over 33 cm in length (the root went further but broke off at the petrocalcic layer), while another plant with 31 rosettes had a 26 cm taproot (Winkel 2004).

In the late 1990s and early 2000s, Las Vegas Valley Water District and Southern Nevada Water Authority made several attempts to salvage and transplant *Arctomecon californica* either directly into habitat or into pots using methods meant to avoid injuring the taproot (Winkel 2004). Shallow collection down to 30 cm depth was not successful for adult plants, while some adults collected with soil to 60 cm depth survived for almost two years in pots, and the majority of living plants also flowered and produced seeds in spring with hand pollination (Winkel 2004). The ability of *A. californica* to survive in pots for many months and produce seed is useful in cases when plants cannot be immediately transplanted (Winkel 2004) and could provide a means for seed increase. Two subsequent salvage trials of seedlings were conducted with 30 cm depth soil collection in December when the plants were dormant or in late March when plants were actively growing, transplanted into soil salvaged from the collection site and irrigated. Eighty percent of the December-collected seedlings survived for 19 months after transplanting and produced seed, while 73% of the plants salvaged in March died within 5 weeks of transplant (Winkel 2004). The late March collection occurred right before *A. californica* plants begin to produce new rosettes and flowers, and transplantation and irrigation may have negatively impacted the physiology of the plants (Winkel 2004). Seedlings with shallow taproots were easier to salvage than larger adult plants and have the potential of living longer after transplanting, suggesting that salvage efforts should focus primarily on seedlings (Winkel 2004). Most salvaged *A. californica* that reproduced died shortly after seed production in all trials, likely because they diverted a large amount of energy to reproduction (Winkel 2004).

In December 2019, sixteen *Arctomecon californica* seedlings were salvaged and relocated to the Lima gypsum mine reclamation area, using a stovepipe to collect a 30 cm deep column of soil around the taproot (Lydia Bailey, pers. comm.). Unlike previous salvage efforts, the plants were not watered after initial transplant, but eleven of the plants flowered and set seed in spring 2020, and seven remained alive after 10 months (Lydia Bailey, pers. comm.). Continued monitoring of current and future salvage attempts is needed, but the rapid die-off of plants during most past efforts suggests that there may be additional factors influencing survival that have not been addressed. For example, an understanding of *A. californica*'s mycorrhizal associations could inform potential research into mycorrhizal inoculation of disturbed or salvaged soil to help the plants weather transplant shock.

Pollinators

Pollinator diversity

Seed production ensures that populations of *A. californica* are resilient to environmental changes yet ultimately depends on healthy populations of pollinators. *A. californica* is most commonly pollinated by the rare Mojave poppy bee (*Perdita meconis*), Encelia megandrena (*Megandrena enceliae*), and European honey bee (*Apis mellifera*; Portman et al. 2018, Hickerson 1998 cited in Portman et al. 2018). During surveys in 2017, *A. mellifera* only visited *A. californica* flowers at sites with 45 or more plants in bloom and commonly visited alternate floral hosts, gathering pollen from just one or a few *A. californica* flowers per visit (Portman et al. 2018). However, the pollinator efficiency of *A. mellifera* increased when aggressive interactions with male *P. meconis* forced *A. mellifera* to visit multiple *A. californica* plants (Portman et al. 2018). The solitary *M. enceliae* was historically regarded as a specialist on the widespread creosote bush (*Larrea tridentata*), but surveys in 1995 and 2017 showed that this pollinator is an effective cross-pollinator for *A. californica* due to its large size and tendency to visit flowers on multiple plants during a single foraging trip (Hickerson 1998 cited in Portman et al. 2018, Portman et al. 2018). *Perdita meconis,* despite its small size, is also an effective pollinator of *A. californica* and was the dominant flower visitor at many recently surveyed sites (Portman et al. 2018). This species is a solitary ground-nesting bee, is a strict specialist on *Arctomecon* and *Argemone* species, and has recently been petitioned for listing under the Endangered Species Act (Cornelisse 2018).

Many desert bee species, especially foraging specialists, follow the same environmental cues as desert annual plants for emergence (Danforth 1999). The closely related *Macrotera portalis* (formerly *Perdita portalis)*, a specialist on plants in the genus *Sphaeralcea*, follows a bet-hedging emergence pattern where only a portion of the larvae pupate under optimal conditions and can remain in diapause for multiple years, emerging upon exposure to high humidity (rainfall), which helps synchronize bee emergence and host-plant germination (Danforth 1999). It is possible that this delayed emergence and induced emergence triggered by rainfall occurs in many species of specialist desert bees across a range of bee families (Danforth 1999).

Pollinator foraging in A. californica *habitat*

Plant population size and density both play a vital role in the reproductive health of *Arctomecon californica*. For *A. humilis*, greater distance between plants is correlated with lower pollination rates and seed fill, especially for plants with fewer than 10 flowers: less than 20% seed fill for plants ≥ 10 m apart compared with 51% seed fill for plants separated by 3 m or less (Harper et al. 2001). *A. californica* flowers produce more seed if they are available to pollinators for the full two days when stigmas are receptive (Tepedino and Hickerson 1996 cited in Bangle et al. 2010), suggesting that maximum fertilization may require multiple visits by pollinators, as is the case for *A. humilis* (Harper et al. 2001). Pollen deposited from multiple outcrosses raises competition in reproduction and can positively impact the vigor and genetics of the offspring (Bjorkman 1995, Mitchell 1997). *A. humilis* and *A. californica* are most efficiently pollinated by similar species of native solitary bees: declines in plant population density will have more impact on specialist pollinators that forage near their nest compared with those that are generalists and/or regularly travel great distances between nesting sites and plant populations (Harper et al. 2001). Whereas the foraging range of pollinators for *A. californica* is not directly known, the foraging distance of bee species is generally a function of body size, with smaller bees traveling disproportionately shorter distances than larger bees (Greenleaf et al. 2007). Most solitary bees require nest and host plant sites to overlap within 100 m of each other (Zurbuchen et al. 2010), but this distance may be an overestimate for *P. meconis*, with its small size and strict specialization (Cornelisse 2018). The female of a similar desert specialist, *P. coreopsidis*, forages less than 5 m from its nest (Danforth 1989).

Pollinator trends and habitat fragmentation

Arctomecon californica pollinator diversity and densities were relatively unchanged in 2017 compared with previous surveys conducted in 1995 on Lake Mead National Recreation Area and Bureau of Land Management lands (Hickerson 1998, Portman et al. 2018). Populations of *A. californica* in the western Las Vegas Valley, on the other hand, have suffered fragmentation and habitat loss, decreasing connectivity concurrent with reduced pollinator numbers and diversity (Hickerson and Wolf 1998, Mistretta et al. 1996). Fragmented *A. californica* populations in the Las Vegas Valley are becoming more isolated and differentiated from one another as insect pollination and corresponding levels of gene flow decline within and between populations (Hickerson and Wolf 1998). This shift reflects a decline in specialist pollinators and reliance on less effective generalist pollinators (Hickerson and Wolf 1998, Tepedino and Hickerson 1996 cited in The Nature Conservancy 2007). Therefore, plants at fragmented sites have two to three times lower seed set compared to plants in unfragmented habitat at Lake Mead National Recreation Area (Tepedino and Hickerson 1996 cited in The Nature Conservancy 2007). Follow-up pollinator surveys have not been conducted in these more fragmented Las Vegas Valley populations since 1995, yet the western portion of *A. californica* habitat may be comparable to *A. humilis* habitat in Utah around the St. George area where pollinator populations have significantly changed (Portman et al. 2018). *A. humilis* pollinators have become scarce, and diversity has declined over the last twenty years in southern Utah; specialized pollinators are declining in numbers and generalist pollinators are increasing (Tepedino et al. 2014). If trends continue, pollinator abundances in the region may increasingly represent the genus *Lasioglossum*, a prominent genus of bees that are infamously variable and unreliable in their pollinating habits (Tepedino et al. 2014).

In comparison to heavily developed land surrounding populations within the Las Vegas Valley, Lake Mead National Recreation Area and Bureau of Land Management lands surrounding the eastern portion of *A. californica* habitat promote pollinator habitat (Portman et al. 2018). *A. californica* does not produce nectar, so pollinators commonly visit other genera, including *Stanleya, Enceliopsis,* and *Larrea* (Griswold et al. 2006, Tepedino et al. 1997), making these plant associates important for pollinator persistence. *P. meconis* has been extirpated from southern Utah following Africanized honey bee invasion in 2000 (Tripodi et al. 2019), while Africanized honey bee invasion in 1998 had much less impact on populations of *Perdita* in southern Nevada. When Africanized honey bees arrived in Utah, alternative bee forage was low, driving Africanized honey bees to *A. humilis* flowers and driving away *P. meconis* (Portman et al. 2018). In contrast to *A. humilis* in Utah, *A. californica* sites have much higher floral diversity, partially due to Mojave desert tortoise (*Gopherus agassizii*) conservation efforts, which lead to retiring most grazing allotments on lands at Lake Mead National Recreation Area and Bureau of Land Management in Clark County (Portman et al. 2018). Portman et al. (2018) observed that many alternative flowering plants at *A. humilis* Utah sites (e.g., *Eriogonum* and *Sphaeralcea*) were heavily grazed, while other plants that are pollinator attractants in Nevada were reduced or entirely missing from Utah sites (e.g., *Phacelia* and *Psorothamnus*).

For management actions that target the reproductive health of *A. californica* populations, a better understanding of native pollinator nesting and foraging behavior is needed. Nests of solitary, ground-nesting bees are difficult to locate and site characteristics such as exposed bare ground, litter cover, soil compaction, sloping ground, and ground cavities are often used as a proxy (Sardiñas and Kremen 2014). *Perdita meconis* is known to nest in open patches of gypsum soil (Clark County Department of Comprehensive Planning 2000a cited in Cornelisse 2018), while even this basic description of nesting sites is not known for less-studied pollinators such as *M. enceliae*. Bee emergence traps can be used to directly associate ground nesting locations with on-site nesting resources (Sardiñas and Kremen 2014), and this information could be used to monitor and protect nesting sites, which are vulnerable to surface disturbance (Hickerson and Wolf 1998).

Further research for species conservation

We reviewed and presented here a body of information on *Arctomecon californica* that follows several notable reviews and contributions from more than a decade ago. We attempted to build on existing knowledge, with reference to relevant information previously reported that provided context to our current understanding of the species, especially with regard to its propagation potential, reintroduction into protected habitat, and its conservation as a rare perennial desert herb existing in heavily fragmented habitats throughout its range. Our understanding of *A. californica's* reproductive ecology and habitat needs has developed immensely since these earlier reviews, and we highlight topics where study is still needed.

Preserve germplasm for the future

A conservation strategy that preserves germplasm (seeds and other tissues for propagation) in the event of extirpation of populations enables plants to be introduced into new habitats designated for protection and for repatriating previously extirpated sites throughout *Arctomecon californica*'s range. Genetic diversity within current populations, while still high, is at risk of inbreeding depression and genetic drift due to habitat fragmentation (Hickerson and Wolf 1998). Rigorous guidelines for germplasm collection and conservation already exist for rare California species including collecting adequate numbers of seeds and matrilines (Wall 2009, Meyer et al. 2014) and can direct future management of *A. californica* with little impact to intact populations.

Understand edaphic endemism

Managing populations of *A. californica* depends in part on identifying whether this species requires the chemical or physical attributes characteristic of the substrate, or tolerates the often physiologically stressful conditions of these soil types when other vegetation competitively excludes it from less stressful habitats (Allphin and Harper 1994, Houle and Valéry 2003). Habitat suitability models can guide site selection for carefully planned mechanistic experiments that introduce *A. californica* plants (by direct seeding and protection from harvester ants, by planting nursery-raised seedlings, or both) into known habitats versus perceived less-suitable habitat. Furthermore, complementary greenhouse experiments can distinguish the roles of biocrusts, soil structure, chemistry, and soil moisture and temperature dynamics to provide a more complete picture of the habitat needs of this unique species. Cryptogamic crusts and potentially mycorrhizal inoculation could improve *A. californica* propagation and salvage efforts (Bailey 2019) but are largely untested; however, propagation and plant salvage experiments using cryptogamic crust are currently underway (Lydia Bailey, pers. comm.). Potential mycorrhizal associations with *A. californica* cannot yet be refuted with the limited information available warranting further study. Elucidating the relationship between germination/seedling success and cryptogamic crusts in intact and disturbed habitat is also desirable to optimize reintroduction efforts.

Promote A. californica *– pollinator relationships*

Protecting habitat for key pollinators is pivotal to *Arctomecon californica* population persistence by promoting gene flow between populations of *A. californica* and maintaining habitat patch connectivity. Fundamentally, studies are needed to understand the nesting requirements, the cues for bee emergence, and foraging limits for the primary pollinators of *A. californica.* When integrated with *A. californica* population monitoring, studies of flower and fruit production and seed fill will signal inbreeding depression, genetic load, and pollinator scarcity, which can in turn portend population decline (Tepedino et al. 2014). Periodic study of *A. californica*'s self-incompatibility across the range of its populations would track whether populations on the periphery of the species' range will develop self-compatibility and adaptations to self-fertilization over time (Busch 2005). For the most degraded habitats, reintroducing nectar plants that support *A. californica'*s pollinators (such as *Stanleya pinnata, Enceliopsis argophylla,* and *Larrea tridentata* produced from locally-sourced seeds) could serve as an effective ecosystem-based conservation approach (Tepedino et al. 1997) in combination with artificial pollination or active import of pollinators to restore gene flow and genetic variation for *A. californica* (Hickerson and Wolf 1998, Tepedino et al. 2014). Such an integrated conservation program requires rigorous implementation and monitoring to meet management goals including promoting the role of nectar plants (Does outplanting promote native bee visitation?), the role of pollinators (Does import of pollinators improve *A. californica* seed set), and the desired increased fitness for *A. californica* (Does enhanced seed bank support seedling recruitment?).

Protect soil seed reserves

Seed reserves and seed dispersal dynamics can be better elucidated with broadened sampling (different methods, multiple years, wider range of sites). Combining seed reserve extraction and emergence methods, and including new information about germination requirements in emergence methods, would describe the distribution of viable and nonviable seeds in the soil seed reserves, which would support soil salvaging efforts and update seed dispersal knowledge (Abella et al. 2013). Methods for tracking seeds in seed dispersal trials (for example, see Vander Wall et al. 2006) and characterizing abundance of seed predators in degraded and intact habitats could better elucidate primary (distance from parent plants) and secondary (ant versus rodent removal and movement) dispersal. In addition, the longevity of *A. californica* in the seed reserves is unknown, and seed burial trials would also inform population viability analyses needed for managing degraded and intact habitats (Baskin and Baskin 2014). *A. californica's* short-lived adults and persistent seed reserves highlights the need for continued, standardized surveys of existing, historic, and suitable habitat, especially in years following exceptional rainfall, in order to gain a more robust understanding of demography and population dynamics.

Predict responses to climate change and land use

The southwestern United States is a regional climate change hotspot with projections predicting increasingly variable precipitation and potentially a shift to more spring-dominant rainfall (Seager et al. 2007, Diffenbaugh et al. 2008). This climatic trend could significantly impact *A. californica*'s germination, which is currently believed to be dependent upon cold winter rains (Meyer 1987 cited in Mistretta et al. 1996). High reproductive attrition for *A. californica* at the bud and capsule stages may be linked to delayed development with onset of environmental stress in spring (Thompson and Smith 1997) or to asynchrony between flowering and abundance of pollinators, both of which can be exacerbated by changing temperatures. Better describing this reproductive attrition and knowing the temperature requirements for bud and capsule development would help assess the reproductive health of *A. californica* populations. Less well known is how changing temperature and rainfall cues will affect synchrony between pollinators and *A. californica* flowering, flower and fruit production, seed viability and dormancy, and whether potential increases in invasive species in disturbed habitats will suppress *A. californica* recruitment. Ongoing surveys that collect information on invasive species abundance (e.g., presence/absence, frequency of plots) and on *A. californica* life stages (e.g., seedling, pre-reproductive, reproductive adult) may require little additional effort, and combined with the emerging availability of spatial climatic information will reveal how seedling emergence cues and/or germination timing are changing through time and across habitats with varying levels of disturbance.

Acknowledgements

We are grateful for Stefanie Ferrazzano (Clark County Desert Conservation Program) and her support of our review of *Arctomecon californica*. We also thank Lydia Bailey (Northern Arizona University) for sharing her graduate research with us prior to publishing her results and Von Winkel (Southern Nevada Water Authority, Springs Preserve) for sharing reports and insights into propagation of desert plants. The *Arctomecon californica* community is a passionate one, and we are grateful for the provocative discussions during the July 2020 virtual meeting for the Rapid Species Status Assessment for Las Vegas Bear Poppy and follow-up communications with Cayenne Engel (Nevada Department of Forestry), Lara Kobelt (BLM, Southern Nevada District Office), Tiffany Pereira (Desert Research Institute), and Carrie Norman (NPS, Lake Mead National Recreation Area). We thank Tiffany Pereira and Von Winkel for reviewing this report and providing valuable feedback that improved an earlier draft. This work was supported by the Clark County Desert Conservation Program and funded by Section 10, as project #2019-USGS-1990A to further implement or develop the Clark County Multiple Species Habitat Conservation Plan. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

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