Among people of all cultures there is an inherent appreciation of things that are rare and unique, whether a precious gemstone or green flash on the horizon at sunset. To the conservation scientist, rare organisms are of particular interest because they are genetically distinct aspects of living diversity that may be at risk of extinction, or may signify an impaired ecosystem. As stewards of the planet, most of us believe that we have an ethical obligation to preserve biodiversity and the ecological processes that sustain natural systems. This goal is especially challenging, given that our understanding of how healthy ecosystems function and the role that each life form plays is incomplete. The unique and diverse array of rare plants in the California deserts presents such a conservation challenge because the distributions and basic life histories of most species remain poorly documented.

While endangered mammals and birds often command more public attention, plants form the basis of all terrestrial life by providing energy, materials, and habitat structure. Globally, 25–40% of native vascular plant taxa (henceforth termed “species” in this article) are at risk (Pitman 2002). Within North America, numbers of imperiled plants may be most underestimated in our deserts because they have systematically received far less attention from botanists than other bioregions. In the California deserts, native plants are being added to the flora faster than any other region of the state. For more on this exceptional floristic frontier, see the other article by James M. André on page 3 of this issue.

The California Native Plant Society’s (CNPS) Inventory of Rare and Endangered Plants ranks 33% of California’s native vascular flora as being of conservation concern, but only 20% of the California desert flora is similarly ranked. There are at least three reasons for this lower percentage. First, endemism (where...
a species is only found in a restricted habitat or location) is lower in the California deserts than in the rest of California. Yet even though the California deserts represent only a fraction of the Great Basin, Mojave, and Sonoran Deserts, a striking 25% of the rare species in the California deserts are endemic to the state, highlighting the uniqueness of the California desert flora within the North American deserts. Second, because the deserts are, at present, relatively pristine compared to much of California, most rare desert plants are inherently rare, with only a handful driven to rarity by human activities. Third, we have underestimated the actual number of rare plant species in the California deserts—particularly given that the region is a hotbed for new species discovery—so most new additions to the flora will be rare.

The California deserts are undergoing rapid change as a result of increasing use by humans, especially on federal public lands targeted for widespread solar and wind energy development. Planning measures for rare plant protection will be based upon limited existing knowledge of the desert flora, and thus lack the necessary level of detail. Even after we document the distributions of rare plants, we are challenged to understand their unique biology.

In this article we focus on key factors that influence rarity in the California desert flora and provide a basis for establishing strategies for conservation. Our goal is to bring attention to the diversity of rare desert plants and to provide insight on their ecology that will be useful to those planning for their protection. We use case studies to illustrate some of the unique facets of rare desert plants that influence their management, highlighting additional research needs and priorities.

OPPORTUNISTS BY NECESSITY

Desert plants must be adapted to a harsh and variable climate to persist. These adaptations include the climatic responsiveness of an-
nuals, the seasonality of herbaceous and woody perennials, and the enduring architecture of many succulents and shrubs. Desert annuals arise from a long-lived dormant seed bank only when triggered by the right combination of temperature and moisture. Seed dormancy buffers annual populations from climatic fluctuations by permitting emergence only when conditions are likely to lead to high survival (Clauss and Venable 2000). Many desert annuals have a very limited period during which germination and emergence can occur, and it is highly dependent upon precipitation. In some cases, especially in the summer, this window may be only a few weeks. The absence of aboveground plants over multiple years can create the false impression that plant populations are no longer present, although they are merely lying in wait as viable seed in the soil for favorable germination conditions. One plant that demonstrates this dramatic year-to-year variation is the miniscule Barstow woolly sunflower (Eriophyllum mohavense), a rare winter annual found only near Kramer Junction and Edwards Air Force Base (photo on page 10).

The long dormancy periods of rare herbaceous desert perennials must be considered in the assessment of population densities and in developing long-term monitoring programs. The flowering phenology of some herbaceous perennials can be highly complex. For example, scarlet four o’clock (Mirabilis coccinea) typically flowers in response to localized summer precipitation, but may also respond to late winter rains and then flower in early summer. Some deciduous shrubs such as vera dulce (Aloysia wrightii) and desert milkwort (Polygala acaintholada) remain leafless until they receive sufficient precipitation. Many monsoon-responsive summer- and fall-flowering desert species such as desert purslane (Portulaca halimoides) apply a different photosynthetic pathway (C4) than the majority of plant species (C3), which allows them to more efficiently grow and reproduce in this warm climate with sparse and/or unpredictable rainfall.

The challenge of limited field documentation and periodic emergence is exemplified by Mojave milkweed (Asclepias nectaraginifolia), a tuber-forming perennial limited to the eastern Mojave. Prior to surveys for the construction of the Ivanpah Solar Electric Generating System (ISEGS)—a massive project that has been built on approximately 3,740 acres of federal public land—the milkweed was known in California from only four occurrences, all above 3,000 feet in elevation, and all at some distance from the project site. Mojave milkweed was thus assumed to have low potential to occur in Ivanpah Valley and was overlooked during initial project surveys, which were conducted during fairly dry years. Follow-up surveys in subsequent years of increased rainfall revealed numerous populations in the ISEGS footprint. These plants had been dormant and unaccounted for during the preliminary environmental review process.

RARE PLANT HABITATS

The causes of rarity in the desert are nearly as diverse as the rare flora itself (e.g. Rabinowitz 1981; Fielder 1986, 2001). Many rare desert species are narrow endemics that occur in a single restricted geographic area, and/or may be confined to a unique habitat to which they have adapted. They may have either recently evolved in place (neoendemics), or be ancient species (paleoendemics) that have become restricted and now persist in an isolated location such as a mountaintop. Unique desert habitats rich in endemic rare species include characteristic uplands...
such as sand dunes, gypsum clay deposits, and limestone substrates. Deserts also include localized wetland ecosystems that are home to many rare plants, including alkali meadows, non-alkali wetlands, freshwater springs, riparian systems, and infrequently inundated landscape features such as playas and washes (Favlik 2008).

Another challenge for rare habitat specialists is the limited extent, fragmentation, and disjunction of many of their specialized habitats. For example, species specialized on gypsum clay (gypsophiles) and limestone substrates such as California bearpoppy (Arctomecon merriamii) have populations scattered throughout suitable habitat patches that can be separated by many miles. Limestone ranges that extend into California from Nevada, such as Clark Mountain and the Nopah Range, house a suite of limestone specialists that are rare in California, but fairly common in Nevada where limestone substrates are abundant.

Rare species may also be distributed across a range of ubiquitous habitats, their distribution and rarity being driven by other factors. These include a long list of taxa such as Oroopia Mountains spurge (Euphorbia jaegeri), Mojave monkeyflower (Mimulus mojavensis), and the crucifixion thorn (Castela emoryi). These are fragmented or disjunct populations that are difficult to explain ecologically. Causes of rarity for such species might include geographic isolation due to long-term climate change, altered pollinator guilds, restricted gene flow, or other factors. Additional research is often required to discern whether such widely scattered populations are genetically isolated across the range of the species' distribution.

INFLUENCES OF REPRODUCTIVE BIOLOGY

In developing conservation strategies for rare desert plants it is of critical importance to first understand their diverse reproductive systems. Of the many factors that can influence rarity, the production and fates of seeds are often the most critical and least understood, and the complex interaction of flowers and fruits with animals warrants extensive research. Some rare species employ self-incompatibility, meaning that individuals need pollen from another individual to produce viable seed. These species, such as Little San Bernardino Mountains linanthus (Linanthus maculatus), need larger population sizes to persist than species that readily self-pollinate.

Idiosyncrasies of rare plants include atypical chromosome numbers, low genetic diversity, and relationships with specialist pollinators or dispersers. And these factors commonly compound to influence rare species. For example, Peirson's milkvetch (Astragalus magdalenae var. peirsonii) is restricted to the sands of the Algodones Dunes, is self-incompatible, and requires pollination by a single native bee species (Groom et al. 2007). In addition, its habitat has been severely degraded by off-road-vehicle use. Even when seeds are produced, their ability to survive, disperse, and persist in the seed bank is not assured. Rare plants at Ash Meadows and Piskah Crater can lose up to 90% of their total seed production due to herbivory by jackrabbits, sometimes for several consecutive years (Pavlik et al. 2009). Rapid construction of large-scale energy projects in the California desert could exacerbate seed losses due to local distortion of food webs.

NEEDS AND PRIORITIES

We must put our feet to the earth. There is an ongoing need for inventory and mapping of known rare plant species in the California deserts to better inform regional conservation and management. The majority of rare plant records occur within a mile of major roads, in historically popular botanical areas (e.g., New York Mountains, Mecca Hills), or

A PROFILE OF CALIFORNIA’S RARE DESERT FLORA

The 491 listed rare California desert species are an exceptionally diverse group with representatives in 70 vascular plant families. Nearly a quarter of these species (132) are either endemic to the California deserts or rare both here and elsewhere, placing them in the highest rarity class, California Rare Plant Rank (CRPR) 1B. A large proportion (209 species, 43%) are CRPR 2B, meaning they are rare in California but more common in other states. This is a relatively high percentage of 2B species in comparison to the rest of California. Another 118 plants are listed as CRPR 4, a watch list of species with limited distributions.

Of the CNPS-listed desert species, only 13 have federal listing status (are protected) under the Endangered Species Act, with 8 receiving protection as “Endangered” and the other 5 listed as “Threatened.” Federal listing of desert plants is often sidelined by other critical research needs or because officials may assume that rare species occurring on federal lands are sufficiently protected. Yet we have identified an additional 20–30 desert species that potentially meet criteria for federal listing status, and listing would greatly improve their prospects for research funding and protection.
White-margined beardtongue (*Penstemon albomarginatus*) in bloom near the Sleeping Beauty Mountains, Central Mojave Desert, California. Despite the numerous flowers in 2011, extremely few fruits and seeds were successfully produced because of strong herbivory and other unknown limits on fruit development. Photograph by Kara Moore.

...in areas surveyed prior to development. Geographic models can be used in some cases to estimate species ranges, but have important limitations when applied to rare and under-surveyed species (see article by Patrick McIntyre on page 15). Given that the California deserts remain a floristic frontier (we have added 183 species in the past two decades alone), extensive inventory is still needed to catalog additions to the native flora. Many undiscovered species will also be rare, and not afforded the necessary protections until their taxonomy is confirmed and their distributions mapped. A comprehensive desert-wide inventory will take institutional will, much expertise, and many decades to complete.

In addition, research on the ecology of California’s rare desert species is vital for stewarding populations amid rapidly increasing threats, such as from urbanization, utility-scale energy, mining, recreational activities, invasive species, and climate change. At present, status reports that document basic biology and perceived threats are available only for about a quarter of the 491 known rare desert plants, and fewer than 5% have accompanying conservation management plans. Of equal concern is the fact that established long-term monitoring or research programs exist for less than 1% of all rare plants in the California desert. We need to increase and extend species-specific research to provide a baseline understanding of a representative set of rare desert species.

Basic population studies that follow the fates of individual plants and their progeny are especially needed to make predictions about the effects of landscape fragmentation, population reduction, and climate change on the long-term persistence of species. A comprehensive life history approach that includes monitoring of all life stages, including seed banks, is necessary in order to make realistic predictions on population viability. Each stage of growth and reproduction can be greatly affected by other species in the community, some negatively (competition and herbivory) and some positively (pollination, seed dispersal). Therefore it is necessary to implement research that includes interacting species and is conducted over several decades. Such a time frame can better capture population responses to fluctuations in climate and variations in species interactions. Unfortunately, such long-term studies are extremely rare.

Currently, we are assembling 13 years of field data and observations on white-margined beardtongue (*Penstemon albomarginatus*), an herbaceous perennial known in Cali-
froma single population near Pisgah Crater. We are assessing how different life stages, precipitation, and species interactions affect its ability to persist. We found that caging plants from black-tailed jackrabbit herbivory increases survival and seed production, but perhaps not enough to protect the species from other factors that threaten local extinction. Increased drought frequency, as predicted by global climate change models, radically increases the probability of extinction. Additional demographic monitoring is needed to determine if this population will rebound or rapidly advance to California Rare Plant Rank 1A status (plants presumed extinct in the state).

For many desert rare plants, including the white-margined beard-tongue, perhaps the most curious and important life stage is the most challenging to study: the soil seed bank. Unknown factors include the longevity of seeds under field conditions, mechanisms and rates of dispersal, local density, and conditions that trigger germination. Seedling emergence, determined by environmental factors controlling germination and mortality in the soil, is often the most critical driver of population growth. When mathematical models are used to simulate populations of white-margined beard-tongue, small variations in the measured rates of seedling emergence can result in very different probabilities of population growth and persistence.

We also must improve our understanding of rare species’ interactions with other plants, pollinators, mutualists, and herbivores. Many plants endure strong herbivory, at least periodically, when populations of insects, jackrabbits, pocket gophers, wood rats, or other species reach high densities (often cyclic or due to a lack of predators), or during drought when food resources are limited. For example, in some years, alkali mariposa lily (Calochortus striatus) and crowned muilla (Muilla coronata) can be nearly impossible to observe before herbivores consume aboveground leaves and stems. However, for the majority of rare species, by far the most critical interactions are those they have directly and indirectly with humans.

A CALL FOR RESEARCH

Ongoing research is needed to determine the diversity, abundance, and distributions of rare desert plants and to understand the fundamentals of their ecology. We emphasize that the most critical facet of inventory and mapping for rare species is to remember that absence cannot be assumed from a single survey (or even a few) for species that have a dormant life phase. And with rapid and extensive changes in arid land use, we need to advance taxonomic research on both known species and those that are not yet described in order to forward their protection.

There is a pressing need for population biology research on rare plant species. Focal points must include research on the detection and function of dormant life stages and the positive and negative effects of species interactions. We must deepen our understanding of how both dormant life stages and interactions with other species vary with fluctuations in climate that are characteristic of these ecosystems. Furthermore, research to explore the effects of proximity to development, landscape fragmentation, soil erosion, altered hydrology, and other anthropogenic disturbances on rare plants is critical to their persistence.

Regional and global processes such as atmospheric nitrogen deposition and global climate change have far-reaching effects on local populations and must be included in the scope of studies. Although species-specific management is required by the biological uniqueness of rare species, clearly all forms of life are best served by protecting functioning ecosystem and landscape units. Preservation of large contiguous and diverse wildlands throughout the California deserts is the only way to ensure protection of its many rare species.

REFERENCES


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