

2021 Status Assessment of white-margined beardtongue
(*Penstemon albomarginatus*) using population viability
analysis

Final Report



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Abbreviations

ACEC	Area of Critical Environmental Concern
AGOL	ArcGIS Online
AIC	Akaike Information Criterion
BLM	Bureau of Land Management
CNDDB	California Natural Diversity Database
DRI	Desert Research Institute
GBIF	Global Biodiversity Initiative Forum
GIS	Geospatial Information System
GPS	Global Positioning System
NNHP	Nevada Natural Heritage Program
NTS	Nevada Test Site
PPT	Precipitation
PVA	Population Viability Analysis
USFWS	United States Fish and Wildlife Service

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I. Executive Summary

White-margined beardtongue (*Penstemon albomarginatus*) is a rare, psammophytic perennial forb endemic to the Mojave Desert. It occurs in 4 disjunct population centers: Pisgah Crater California, Dutch Flat Arizona, Clark County Nevada and Nye County Nevada. It is considered Endangered in California, Imperiled in Nevada, and Critically Imperiled in Arizona, but currently has no Federal listing status. In 2019, the Center for Biological Diversity informed the U.S. Fish and Wildlife Service (USFWS) of an intent to petition the species for federal listing based on threats of extensive habitat modification and development in the small range that the species occupies. Previous viability analysis of the Pisgah Crater population showed alarming declines in population abundance, and a high probability of quasi-extinction under current climate conditions that was made worse under increased drought scenarios. The Pisgah Crater population occurs at the driest and warmest extent of the species' range, and anecdotal observations indicate that individuals in the Pisgah population have shorter lifespans and are smaller and less robust than individuals in the Clark County and Dutch Flat populations; thus, trends and projections for the Pisgah Crater population may not apply to the population as a whole.

To inform a potential petition for Federal listing, a range wide status assessment of PENALB was conducted by documenting habitat conditions, threats, abundance and demographic attributes at 75% of known occurrence records of the species in each of its 4 population centers. Current habitat conditions and threats, abundance and population structure in each population center were compared to each other, and compared to historic data. Climate trends for each population center were compared to determine if climatic differences could explain differences in population attributes. Demographic population models, using 10 years (1996-2006) of demographic monitoring data collected on the Clark County population, were constructed to estimate transition rates, population growth rates, and extinction risks for this population. Two years (2013-2014) of monitoring data for the Pisgah Crater that had not been previously analyzed were added to PVA models for Pisgah Crater. We examined how increasing seed to seedling transition rates and different precipitation regimes affected population growth and persistence. Quasi-extinction probabilities within 50 years were estimated for each of the 4 population centers using population abundance and structure estimated in the 2021 field survey and transition matrices constructed for Clark County and Pisgah Crater.

2021 was among the driest and warmest on record for the Mojave Desert; consequently, emergent PENALB abundance in each population center was very low in 2021 relative to previous surveys. Apparently dormant plants were the dominant life stage observed at each population except for Dutch Flat. Flowering individuals were common at Dutch Flat, not observed at Clark or Nye County, and only 1 observed at Pisgah Crater; however, no successful reproduction was observed for the entire population as all plants were eaten or senesced by early June. Population viability analysis showed that like Pisgah Crater, the Clark County population is on a trajectory of decline, although the likelihood of extinction in this population is lower. Extinction risk increased with increased frequency of drought, and was lower with increased

reproductive success. Quasi-extinction probabilities within 50 years ranged from 50% at Nye County to 100% at Pisgah Crater, and increased with increasing aridity.

Chapter 1—Introduction

White-margined beardtongue (*Penstemon albomarginatus*; hereafter PENALB) is a rare perennial forb restricted to the Mojave Desert, where it occurs in 4 disjunct populations, occurring in California, Nevada and Arizona (figure 1). PENALB is a State of California Endangered (G2, S1) species. It is considered a Sensitive List (G2, S2) species by the Nevada Natural Heritage Program (NNHP 2021), and is listed as Imperiled in Nevada (NNHP 2001, NatureServe 2021). It is a State of Arizona Critically Imperiled (S1) species (NatureServe 2021). It is considered a BLM Sensitive Species (NNHP 2021). The species has no current Federal status, but the Center for Biological Diversity notified the state of Nevada that it will seek federal protection under the Endangered Species Act for PENALB in March 2019 (Center for Biological Diversity 2019).

Previous viability analysis of the Pisgah Crater population, based on 12 years (1994-2003 and 2011-2012) of demographic monitoring data, showed significant declines in population abundance, and a high probability of quasi-extinction under current climate conditions that was made worse under increased drought scenarios (Moore and Pavlik 2014). The Pisgah Crater population occurs at the driest and warmest extent of the species' range, and anecdotal observations indicate that individuals in the Pisgah population have shorter lifespans and are smaller and less robust than individuals in the Clark County and Dutch Flat populations; thus, trends and projections for the Pisgah Crater population may not apply to the population as a whole. Understanding how habitat condition, threats, and population dynamics may drive future population trends in each population center is essential for determining the overall status of PENALB, and for determining management needs.

To inform a potential petition for Federal listing status, and determine how each population functions in the overall health of the species, we conducted a range-wide status assessment of PENALB that included surveying habitat, health and demographic characteristics of 75% of known PENALB occurrences throughout its range, and by using 2 existing long term demographic monitoring datasets to build demographic population viability assessment (PVA) models from which factors contributing to population persistence could be examined and compared among the 4 populations.

This status assessment sought to answer the following questions:

1. What is the current population status and threats facing PENALB as a whole, and within each of its 4 population centers?
2. How do the 4 population centers differ in terms of population abundance, structure, likelihood of extinction and threats?
3. How do projected climate change impacts impact population persistence in each population center?

Our scope of work was as follows:

1. We assembled known occurrence records of PENALB and surveyed 75% of these records for habitat condition, demographic population attributes and threats in each population center.
2. Data collected in part 1 were used to compare habitat characteristics, abundance, and threats among the 4 populations. The role of climate in explaining population differences was examined by comparing precipitation and temperature patterns among the 4 population centers. Demographic population viability models were constructed for the Clark County Nevada population using 10 years of monitoring data, and models built for the Pisgah Crater population (Moore and Pavlik 2014) were expanded with 2 more years (2013-2014) of data that had not been previously analyzed. Population growth rates, transition rates, and extinction probabilities were compared between the 2 populations. Because lack of reproductive success in dry years was observed in the 2021 survey and in both historic demographic datasets that could potentially be improved with management (e.g., herbivore exclusion), we examined how increasing seed to seedling transition rates affected population growth rates.
3. Quasi-extinction probability was estimated from the above PVA models for Clark County using observed climate patterns, increased drought frequency and no drought. We estimated quasi-extinction probability based on initial population vectors for each of the 4 population centers measured in 2021 using Clark County matrices for Clark County, Nye County and Dutch Flat, and Pisgah Crater matrices for Pisgah Crater, and simulated effects of increased drought.

This project was initially intended to be 2-3 years in duration, allowing for population specific collection of plant traits and vital rates over multiple years, which are necessary to build accurate PVA models. However, due to contractual issues only 1 year of data collection was possible for all populations except for Pisgah Crater. Further, 2021 was exceptionally dry, and no seeds were produced throughout the range of PENALB, so per inflorescence and per plant fruit production is available only for Pisgah Crater. Therefore, we could not construct PVA models for Nye County and Dutch Flat.



Figure 1. Range wide distribution of PENALB.

Background

Species description

PENALB is a rare perennial psammophytic hemicryptophyte, typically 15 to 35 cm tall, with several to many stems arising from a buried root crown (figure 2). Stems emerge for the winter-spring growing season, flower March to May, fruit May to June, and die back in the heat of summer (Baldwin et al. 2012, Moore and Pavlik 2014). Sufficient monsoonal precipitation in summer may initiate re-emergence of stems, and insufficient winter-spring precipitation may inhibit or reduce emergence. Stems that emerge in response to summer precipitation have not been observed to successfully reproduce (Moore and Pavlik 2014, André pers. comm.). Plants have the ability remain dormant underground for several years, and to shift aboveground distribution (Nevada BLM unpublished data). Showy, pink to purple flowers are 13 to 17 mm and contain 50-52 ovules (Scogin 1989, Baldwin et al. 2012, Moore and Pavlik 2014). Seed set is low relative to the number of ovules, with seeds produced per fruit ranging from 2 to 35 (Scogin 1989, Baldwin et al. 2012, Moore and Pavlik 2014). Seed and fruit production is highly variable among plants and years (Moore and Pavlik 2014, Nevada BLM unpublished data). Seedling emergence is episodic with wet years, and is rarely observed during dry years (Scogin 1989, Etyemezian et al. 2010, Moore and Pavlik 2014).



Figure 2. A. Large *Penstemon albomarginatus* individual at Pisgah Crater, California. B. Close up of *Penstemon albomarginatus* flowers. PHOTOS: Wendy Boes, March 2020.

Habitat description

PENALB is typically restricted to deep stabilized or semi-stabilized deposits of windblown sand or sandy alluvium (Smith 2001, Etyemezian et al. 2010, Baldwin et al. 2012, Moore and Pavlik 2014). It often occurs in or near small dry drainages, and also occurs on valley floors, foot-slopes, or alluvial terraces (Smith 2001). It occurs on all aspects at elevations between 780 and

1090 meters (Smith 2001). Vegetation of preferred habitat is typically sparse, with less than 20 percent shrub cover (Etyemezian et al. 2010). Associated species include *Hilaria rigida*, *Abronia villosa*, *Tiquilia plicata*, *Larrea tridentata*, *Krameria erecta*, *Ambrosia dumosa*, *Achnatherum hymenoides*, *Krascheninnikovia lanata*, *Ephedra nevadensis*, *Menodora spinescens*, and *Yucca brevifolia*. Surrounding vegetation includes *Larrea tridentata* – *Ambrosia dumosa* shrublands in California and Nevada, and *Yucca brevifolia* – mixed shrubs in Arizona (Anderson 1999, Smith 2001, Etyemezian et al. 2010, Moore and Pavlik 2014).

Distribution

PENALB is known from 4 disjunct population centers: Pisgah Crater California, Clark County Nevada, Nye County Nevada, and Dutch Flat Arizona (figure 1). The California population is comprised of many small subpopulations (figure 3), that ranged in size from 2 to 29 individuals for the period 1994 to 2012 (Moore and Pavlik 2014). Population size may fluctuate dramatically with precipitation availability. The total Pisgah Crater population size was estimated to be greater than 450 individuals in 1989 (Scogin 1989), 4,420 in 1993 (Smith 2001), 2,200 adult individuals in 1997, and only 67 plants in 2012 (Moore and Pavlik 2014). Historical occurrences are reported near Ludlow, Cadiz Summit, and Bagdad Chase Mine, California, but a search for PENALB in California failed to locate any individuals farther than 15 miles from Pisgah Crater (Moore and McIntyre 2015).



Figure 3. Known Pisgah Crater California occurrences of PENALB.

The Clark County Nevada population consists of 9 subpopulations located in the Jean Lake area, south of Las Vegas (figure 4). Four of these subpopulations are very large, consisting of thousands of individuals occupying approximately 2 to 8 square miles (figure 4). Sheldon (1994) reported that 7 of the Clark County occurrences totaled approximately 8,775 plants covering 324 ha (Blomquist et al. 1995). Smith (2001) estimated that a total of 68,164 plants occurred in Nevada (Clark and Nye County). Etyemezian et al. (2010) quantified abundance in the Nevada populations using multiple transects to estimate density within large subpopulation boundaries. They estimated a total abundance of 125,825 plants in the Clark County population, 5 times larger than what had been estimated by Smith (2001). The authors think that rather than a true increase, more precise estimates of abundance explained this increase (Etyemezian et al. 2010). An isolated occurrence near Camp Patosi, Clark County Park was determined to be a misidentification (Smith 2001, Jim André pers. comm.).

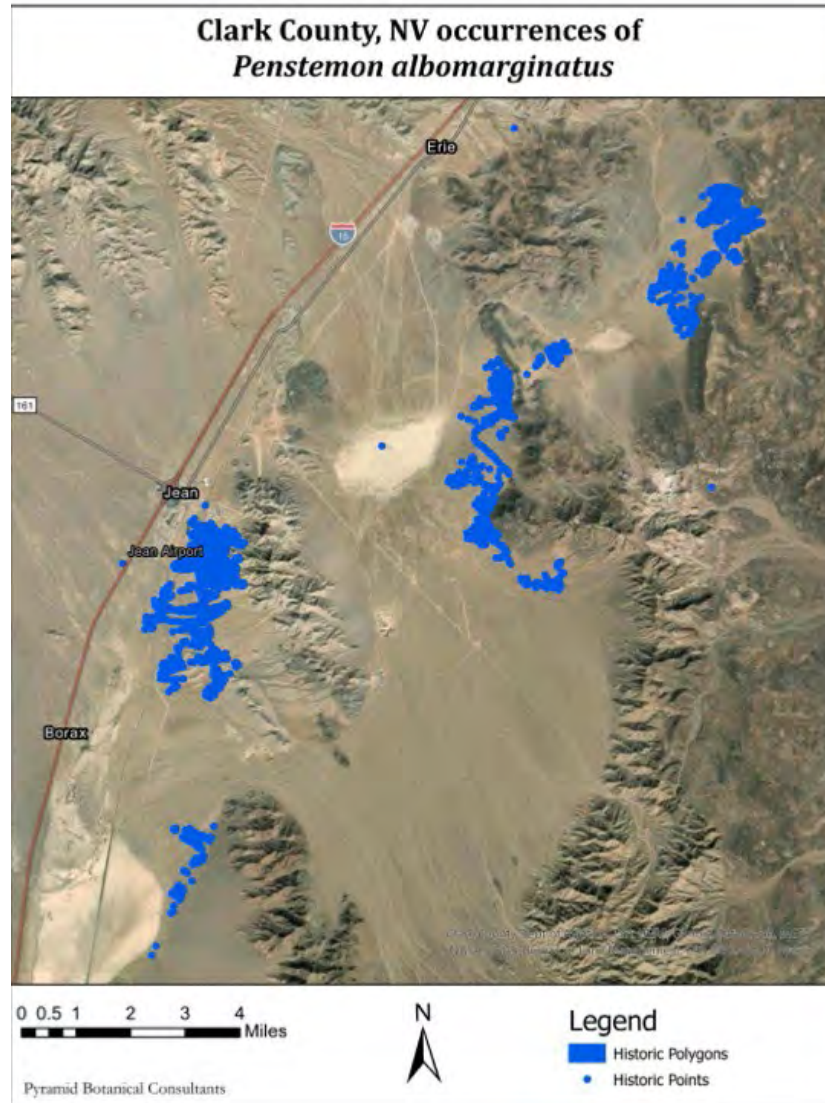


Figure 4. Known Clark County Nevada occurrences of PENALB.

The Nye County Nevada population consists of 9 subpopulations located northeast of Amargosa Valley and south of the Nevada Test Site (NTS), along Highway 95 (figure 5). Blomquist et al. (1995) surveyed 5 known occurrences located within 11 km from the NTS boundary in 1992 and 1994. Plant abundances ranged from 600 to 1,900 with the total number of plants approximately 6,200 and occupying an area of approximately 54 ha. Additional surveys around the southern border of the NTS site did not find any additional occurrences. Two herbarium locations along Highway 95 could not be found, and the authors speculate that they may have been extirpated by highway maintenance activities. Etyemezian et al. (2010) estimated 78,954 plants total for this population, approximately twice the abundance estimated by Smith (2001).

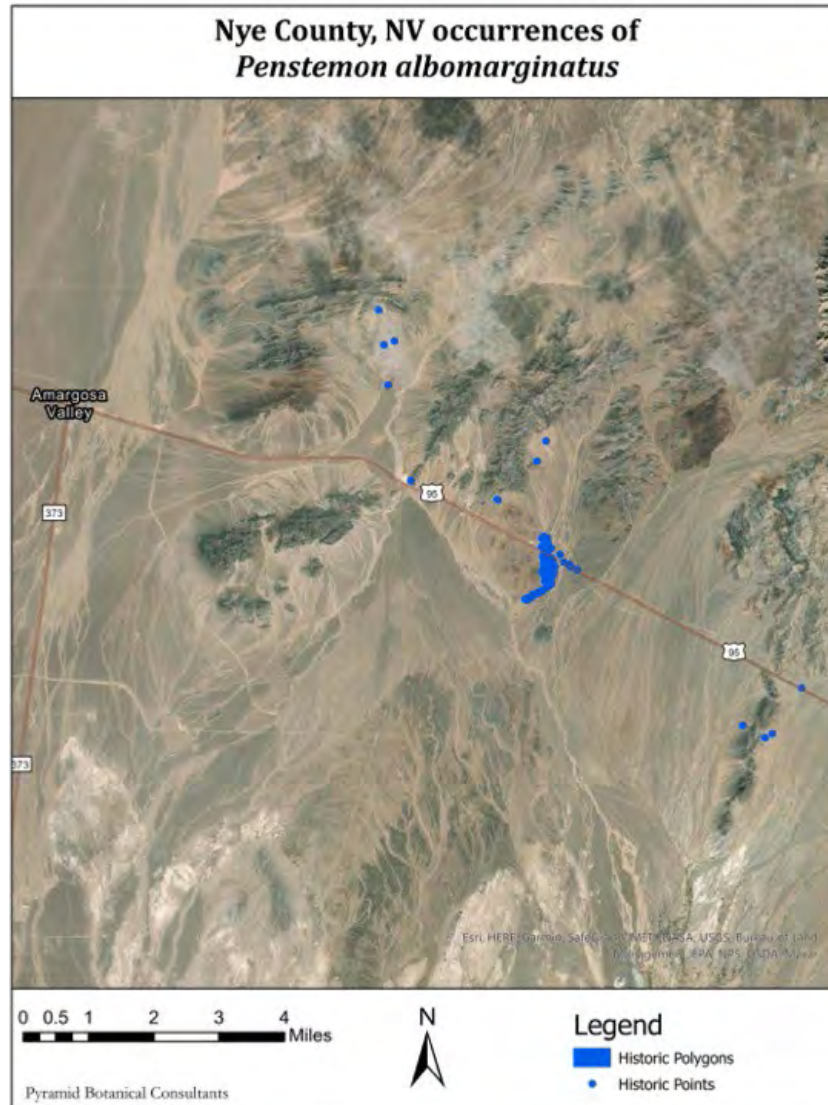


Figure 5. Known Nye County Nevada occurrences of PENALB.

The Dutch Flat Arizona population consists of 20 occurrences located primarily in the Dutch Flat area, east of Yucca Arizona (figure 6). One occurrence occurs near Kingman Arizona and 1 occurs north of Bill Williams National Wildlife Refuge (figure 6). The Dutch Flat population has been described as the largest single population, occupying a range of 15 miles by 5 miles (Anderson 1999). Sheldon (1994) described the Arizona population as in the thousands. Smith (2001) estimated approximately 100,000 plants occurred in this population. Part of this area was designated an Area of Critical Environmental Concern (ACEC) for PENALB in 1993, but the ACEC encompassed a checkerboard of BLM and private land (Anderson 1999). A land exchange between the BLM and the Santa Fe Railroad (Hualapai Mountains Land Exchange) resulted in 70,000 contiguous acres containing the highest quality and highest density PENALB habitat being transferred to the BLM (Anderson 1999). Half of the known Arizona EOs of PENALB occur on private land, and development of private land parcels significantly threatens this population (Anderson 1999, André pers. comm.).



Figure 6. Known Dutch Flat Arizona occurrences of PENALB.

The Pisgah Crater population occupies the warmest and driest conditions of the range of PENALB, and individuals in this population are thought to be smaller, have shorter lifespans, exhibit no to low rates of dormancy, and be at higher risk of extinction relative to the other populations due to more extreme aridity (Moore and Pavlik 2014, Jim André pers. comm.). Increased total precipitation and a greater proportion of summer precipitation in the Clark County and Dutch Flat populations may offer buffering to adverse climate trends (Moore and Pavlik 2014).

Threats

Land development projects in PENALB habitat is the greatest threat facing the large populations that occur in Clark County Nevada (Etyemezian et al. 2010, Center for Biological Diversity 2019, NatureServe 2021). Urban development is the dominant threat to the Dutch Flat Arizona

population (Anderson 1999, Smith 2001). Solar development may threaten the California population (NatureServe 2021). Off highway vehicle (OHV) use is a significant threat within the sandy habitats of this species throughout its range. Trash dumping, activities associated with transmission line and pipeline, highway construction and maintenance, cattle grazing, and military activities also threaten PENALB (Blomquist et al. 1995, André and Clark 2011, NatureServe 2021). In addition, invasive species such as Russian thistle (*Salsola* spp.), (Asian mustard) *Brassica tournefortii*, and Mediterranean grass (*Schismus* spp.), may modify habitat and/or directly compete for resources. Population viability analysis showed that the California population may be imminently threatened with quasi-extinction, with risk increasing with increasing drought frequency (Moore and Pavlik 2014). Herbivory by jackrabbits may also cause severe impacts to the California population (Moore and Pavlik 2014).

Previous research

Population genetics

Genetic differentiation and diversity were examined in each of the 4 population centers (Wolfe et al. 2016). PENALB populations were most genetically similar within their geographic regions, but were fairly similar overall, and generally did not show signs of inbreeding (Wolfe et al. 2016). Northern populations (Clark and Nye County Nevada) were more closely related, with genetic diversity greatest in southern populations, suggesting that PENALB spread from south to north post glaciation (Wolfe et al. 2016).

Demographic Monitoring and Population Viability Analysis

Pisgah Crater California

Demographic monitoring of the Pisgah Crater California population took place from 1994 to 2003 (Jim André, UC Granite Mountains Desert Research Center), and from 2011 to 2012 (Moore and Pavlik 2014). Moore and Pavlik (2014) attempted to relocate André's subpopulations, but in all but 2 cases locations had been extirpated due to unknown reasons. Subpopulations were fully enumerated, with all plants greater than 3 cm tagged and monitored. Maximum diameter, number of inflorescences, and fruit per inflorescence were measured. Seedlings smaller than 3 cm were censused during a subset of monitoring years. The population at Pisgah Crater fluctuated significantly both overall and within subpopulations over both time periods (Moore and Pavlik 2014).

Survival rates for 12 years of monitoring did not differ among subpopulations, and were driven by herbivory and climate patterns that impacted the population as a whole (Moore and Pavlik 2014). Individuals survived for a mean of 5.2 years during the sampling period, and the study documented only 2 individuals that lived longer than 10 years (Moore and Pavlik 2014). Larger plants had higher rates of survival, with juveniles more likely to die during drought episodes (Moore and Pavlik 2014). Seedling mortality rates were high, with only 16.2% of a cohort of seedlings that emerged in 2011 surviving to 2012 (Moore and Pavlik 2014).

Fruit and seed production may be limiting in this species, with fecundity negatively affected by severe herbivory, desiccation, and/or possibly lack of pollinators (Moore and Pavlik 2014). Plants that had flowered prolifically were observed with no fruit at all, or with low fruit output (mean of 1.8 fruits/inflorescence) despite the presence of 20-40 flowers. In 2012 only 4

individuals produced mature fruit. Aborted fruits and flowers are also prevalent in herbarium specimens (Moore and Pavlik 2014).

Moore and Pavlik (2014) used this dataset to build demographic population models (Caswell 2001, Morris and Doak 2003) to estimate population growth rates, and the sensitivity and elasticity of population growth to changes in fitness components, variations in climate, and impacts of herbivory. Estimates of the asymptotic population growth rate (λ) were derived using deterministic and stochastic methods. This analysis showed that the Pisgah population had been in decline over the period of study, with a trajectory towards possible extinction. Population growth rates were most sensitive to plant growth progression to larger stage classes, with survival, and seed to juvenile transition and seed production having much smaller effects. Population growth rates were positively affected by growing season precipitation. Juvenile survival was positively correlated to growing season precipitation, but there was no relationship between growing season precipitation and adult survival. Simulations showed that increased frequency of drought had a strong negative effect on population growth rate, and growth rates responded more strongly to increased drought frequency than a long-term reduction in growing season precipitation. Quasi-extinction (defined as population size at or below 10 individuals) was predicted as 80% probability within 27 years under current climate conditions. With higher frequency of drought, time to quasi-extinction was reduced to 19 years (Moore and Pavlik 2014).

Jean Lake Exclosure, Clark County, Nevada BLM

A subpopulation at Jean Lake, Clark County Nevada (Jean Lake Exclosure) was monitored between 1996 and 2006 by Gayle Marrs Smith with Nevada BLM. Plants were monitored on 8 60 meter by 5 meter transects, with individuals mapped with x and y coordinates along the transects. Canopy width and the number of shoots with flowers were recorded annually. Like the Pisgah Crater population, the monitored subpopulation at Jean Lake showed large fluctuations in abundance over the decade of monitoring. Plant survival were higher than in the Pisgah Crater population, with many plants surviving longer than 10 years (unpublished data, BLM). In contrast to the Pisgah Crater population, the BLM monitoring data show that plants are capable of long periods of dormancy, and adults may re-emerge after multiple years.

We used the Jean Lake dataset to build demographic matrix projection models, based on the above Pisgah Crater models, to estimate transition rates, population growth rates, and the sensitivity and elasticity of population growth to changes in fitness components, variations in climate, and impacts of herbivory for the Clark County Nevada population. These are described later in this report.

Clark and Nye Counties, Desert Research Institute

The Desert Research Institute (DRI) monitored 3 subpopulations of PENALB in the Clark County population (Hidden Valley, Jean Lake Exclosure and Roach Lake) and 1 subpopulation (2 transects) at the Nye County population from 2008 to 2009 (Etyemezian et al. 2010). Sixty plants in each location were tagged and monitored for 2 years. For each plant, the number of shoots, shoot height, canopy area, number of shoots with flowers, number of shoots with fruit, and number of shoots impacted by herbivory were recorded. Results showed a possible 1% mortality rate between the 2 sampling years, although the failure of a plant to appear could have been due to dormancy rather than mortality.

Chapter 2—Methods

Current Status, Abundance and Threats – 2021 Survey

Compile occurrence records

To determine the current known extent of PENALB, occurrence records were assembled from multiple sources, including the California Natural Diversity Database (CNDDDB), SEIN.net (<https://swbiodiversity.org/seinet/index.php>), GIS records from the Nevada BLM, and Nevada Natural Heritage Program, and the Global Biodiversity Initiative Forum (GBIF, <https://www.gbif.org/>). Occurrence records from these data sources were merged to create a single shapefile in ArcGIS Pro. Since many of these records represented a single occurrence (i.e., within 0.25 miles and not separated by a natural barrier) records had to be parsed to identify each unique occurrence. To accomplish this, a 0.25 mile buffer was created around each point, and the buffered points were merged into a polygon using the overlay option in ArcGIS Pro. When historic records that had been visited and determined to be extirpated, or an identification error (Smith 2001, Moore and McIntyre 2015), or that occurred on private lands and outside of the scope of the present work were removed, approximately 35 occurrences in California, 9 occurrences in Clark County Nevada, 9 occurrences in Nye County Nevada and 10 occurrences in Arizona remained. Ten of the total Arizona occurrences fell on private lands. Approximately 319 acres of the Clark County Roach Lake North subpopulation occurs on private land around the Jean airport (figure 4).

A map containing occurrence record; locations of all previous demographic and genetic monitoring; background imagery; data collection with mapping forms for occurrence surveys and demographic data was created in ArcGIS Pro and published to ArcGIS online (AGOL) for use as a Collector app to navigate to occurrences, collect data electronically, and serve as a geodatabase for PENALB survey data.

2021 Field Survey

Survey site selection

To meet the objectives of this contract, 75% of known occurrences were selected for survey (see Appendix A for maps with survey locations). For the first year of data collection (the original intent of the project was at least 2 years of data collection), survey sites were selected based on efficiency of visiting the maximum number of sites possible; therefore, sites within the core areas of each population center were selected for survey. In addition, sites that had a history of previous demographic (Moore and Pavlik 2014, Etyemezian et al. 2010) or genetic research (Wolfe et al. 2016) were prioritized for survey. Sampling locations in the large Clark County and Nye County subpopulations where spatial data were available were first selected at sites where previous monitoring had occurred. Additional locations for survey were selected within

subpopulation boundaries using a stratified approach where sample locations fell within both high and low density areas, and were spatially distributed throughout the subpopulation boundary. Areas around sampling locations were searched for PENALB, with plants mapped on discovery, and the search area mapped to calculate plant density.

For occurrences at Pisgah Crater and Dutch Flat, where subpopulations were under 100 individuals, demographic parameters were collected for each individual in each occurrence where PENALB was found. Clustered sampling (Elzinga et al. 1998) was used to sample the large occurrences at the Nye and Clark County populations. For a subset of locations where PENALB was found, demographic data were collected along variable length 10 meter wide transects, with the starting point and azimuth of the transect randomly chosen in the field.

Demographic monitoring

To maximize trend analysis, demographic data collection methods were based on those described in Moore and Pavlik (2014). Occurrences were initially surveyed April 10-17, 2021, to coincide with peak reproduction. Each emergent or dormant individual with identifiable aboveground material was tagged with a numbered metal tag. For each emergent plant the following data were collected: Canopy width (cm), measured as the largest diameter and its perpendicular; maximum height (cm); current phenology (dormant, vegetative, budding, flowering, fruiting); number of inflorescences; number of buds, flowers and fruits on 3 randomly chosen inflorescences; and percent of the plant impacted by herbivory (0%, 1-25%, 26-50%, 51-75%, 76-100%). Although it was not possible to tell whether an apparently dormant plant was alive or dead without excavation, apparently dormant plants were tagged, and phenology was recorded as dormant. Monitoring in subsequent years will determine whether these plants are alive. Monitoring sites were revisited June 1-6, 2021 to re-assess reproductive output, collect fruit and count seeds produced per fruit, but at this time plants were either gone, nearly completely browsed, senesced, or had minimal vegetative material remaining.

Habitat and threat data

At each surveyed occurrence, habitat characteristics including aspect, slope, soil surface texture, associated species, habitat description, and land use was collected, as well as whether PENALB was found, abundance, and phenology (percent vegetative, flowering, and fruiting), and threat information including visible disturbance and threats. To show where plants were found and where they were not, the surveyed area was mapped as a polygon whether plants were present or not. Entering survey data into the CNDDDB database was a requirement of this contract, so habitat, general population, and threat data were collected on a Collector form adapted from the CNDDDB field survey form (California Department of Fish and Wildlife 2021).

Analysis

Population abundance, stage class structure, habitat characteristics and threats were summarized for each of the 4 population centers. Plant size, reproductive status, and rates of herbivory were compared among the 4 population centers using linear mixed effects models with population as a fixed effect and occurrence as a random effect. Herbivory was transformed to the median of the severity class for analysis. Climate data, including total monthly precipitation, and mean, minimum and maximum monthly temperatures for the last 27 years (when PENALB was first monitored at Pisgah Crater) were downloaded from PRISM (PRISM Climate Group 2021) for each population center. Total annual precipitation, winter (October to April) and summer (May to September) precipitation, and mean, minimum and maximum temperatures were calculated

for each year. Differences in these climate variables among the 4 population centers were tested using Anova with Tukey's HSD tests.

Because different stage classes of PENALB are known to have different rates of survival and reproduction (Moore and Pavlik 2014), emergent plants observed in the 2021 dataset were assigned to the size classes used in the Pisgah Crater PVA, and differences in size class distribution among populations were compared using Fisher's exact test with simulation. Differences in plant size among populations were examined using mixed effect models with population as a fixed effect and site as a random effect. Since only Dutch Flat had reproductive plants in 2021, relationships between plant size and probability of reproducing, plant size and total reproductive output, and plant size and rate of herbivory were examined for this population using mixed effects models with site included as a random effect. Data manipulation and analysis were done using RStudio (RStudio 2021).

Population Viability Analysis

Demographic matrix projection models (Caswell 2001, Morris and Doak 2003) were constructed from the 1996-2006 Jean Lake Exclosure, Clark County demographic monitoring dataset and for the Pisgah Crater dataset to include 2013-2014 monitoring data that had not been included in the original analysis done by Moore and Pavlik (2014). Population growth rates, transition estimates and the importance of matrix elements and climate on population growth and quasi-extinction probability were calculated. Projection matrices were constructed for each pair of monitoring years, and deterministic and stochastic population growth rates were estimated from the complete dataset. Size class distributions, transition rates, growth estimates and extinction probabilities were compared between the Clark County and Pisgah Crater population. The set of demographic matrices for Clark County was used to estimate quasi-extinction probabilities based on 2021 estimates of abundance and size class distribution for Nye County, Clark County and Dutch Flat, while the set of matrices for Pisgah Crater was used to estimate quasi-extinction probabilities based on the 2021 Pisgah Crater population vector. Models were constructed using the popbio library in RStudio (Stubben and Milligan 2007).

Estimation of stage structure

To facilitate comparison between PVA for the Pisgah Crater and Clark County populations, projection matrices were constructed based on individual size classes used in the Pisgah Crater demography study (Moore and Pavlik 2014). For each year of the 1996-2006 dataset, plants were assigned to 1 of 5 size classes based on average diameter (mean of 2 maximum perpendicular diameters) recorded at peak flowering: J = 0-10cm, A1 = 11-20cm, A2 = 21-30cm, A3 = 31-40cm, A4 = 41+cm. A dormant class was added to each dataset since many plants reappeared after 1 or more years with no above ground growth in Clark County, and dormant plants were observed in the 2012-2014 monitoring dataset for Pisgah Crater, that had not been included in the earlier analysis. Plants in the J class at the Pisgah population included new recruits and small adults, and plants in this size class were not to be reproductive in the 1994-2011 monitoring set (Moore and Pavlik 2014), but plants as small as 5 cm were reproductive between 2012-2014 (unpublished data). In the Clark County study, the minimum size that plants were observed to be reproductive was 5 cm. New recruits in Clark County dataset were identified as plants that were smaller than 5 cm that were not associated with a previously mapped plant.

For any given pair of years, plants could remain the same size (stasis), grow to a larger size class, regress to smaller size classes, go dormant or die. We also built models separating seedlings from J class individuals for Clark County. These resulted in slightly higher population growth rates due to higher mortality rates in true seedlings versus J size class individuals, but differences were very small, and we present only the models using the Pisgah Crater size classes described above.

Relationships between plant size and survival, number of inflorescences, probability of reproducing, and probability of dormancy were examined using mixed effects models with plant size and year as fixed effects and transect included as a random effect. To examine relationships between dormancy and reproductive fitness, we tested whether plants were more likely to go dormant after being reproductive including reproductive status in year 1 as a fixed effect with fate in year 2 as the response. To examine whether dormancy impacted reproductive status, we included size class in year 1 as a fixed effect and reproductive status in year 2 as the response. Since rainfall is known to be a key factor influencing the emergence of PENALB, the effects of winter and summer precipitation, and the effects of mean, minimum and maximum annual temperatures on the above variables were tested by including them in the mixed effects models and evaluating models by comparing Akaike Information Criterion (AIC).

Fecundity estimates

Fecundity was estimated as the mean seed to seedling transition of total population seed output in year 1 to total seedlings observed in year 2 (Morris and Doak 2003). Since no estimates of seed production per fruit or per inflorescence were available for the Clark County population, mean seed production per inflorescence estimated from the Pisgah Crater population (Moore and Pavlik 2014) was used to estimate per plant seed production for the Clark County dataset, and for the updated Pisgah Crater analysis. Several monitoring years had no reproductive individuals, and 2 years had no seedlings, with the number of seedlings low in any given year. Since small seedlings could have been missed during monitoring, and no population specific seed outputs were available, we explored what the effects of increasing the seed to seedling transition rate were on population growth rate.

Chapter 3—Results

2021 Field Survey

Population abundance, structure and plant traits

Seventy-five percent of known occurrences on public lands throughout the range of PENALB were surveyed April 10-17, 2021. These included 26 occurrences at Pisgah Crater, 8 at Dutch Flat, 7 at Clark County and 8 at Nye County (table 1; Appendix A). For the large occurrences where sampling was necessary, we surveyed a total of 31 samples at Clark County and 13 samples at Nye County. Among all populations, emergent plants were observed at 44% of sites visited, with a total of approximately 1,553 emergent plants observed. Many apparently dormant plants that appeared to have reproduced in 2020 were observed at each population except Dutch Flat, where only emergent plants were observed (table 1).

Table 1. 2021 PENALB surveyed sites, with presence and abundance of emergent and apparently dormant plants in each population center. For large populations in Clark and Nye County, occurrences were sampled, and the number of samples is given in parentheses after the number of occurrences.

Population	# Occurrences surveyed (# subsamples within site)	Occurrences or samples with emergent plants	Occurrences or samples with emergent or dormant plants	# Emergent Plants	# Total plants	# Reproductive plants
Pisgah	26	10	11	14	35	1
Dutch Flat	8	6	6	189	189	56
Clark County	7 (33)	4	10	12	1,039	0
Nye County	8 (13)	12	12	1352	3861	0

All populations were dominated by apparently dormant individuals, except for Dutch Flat, where no dormant individuals were observed (figure 8). Among emergent plants, smaller size classes (J and A1) dominated in all populations, with few large individuals observed in 2021. Dutch Flat had more large individuals than Pisgah Crater or Nye County (figure 7, Fisher's exact test, $P < 0.0004998$).

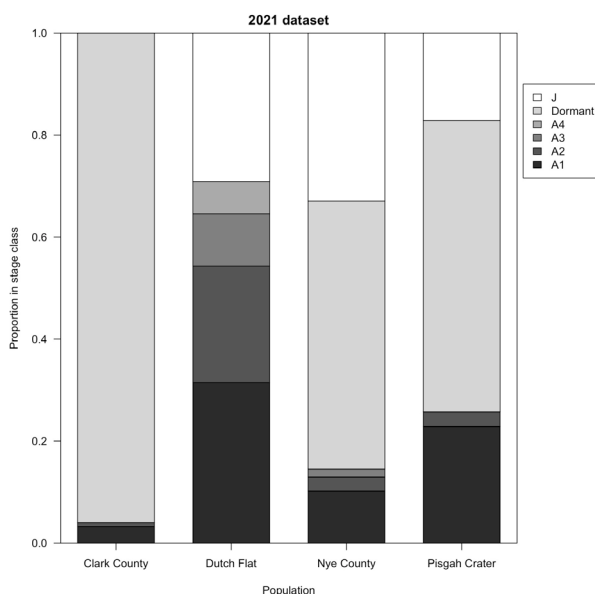


Figure 7. Size class distributions in 4 PENALB populations surveyed in 2021.

Large differences in abundance and phenology were observed among the 4 populations. Only emergent plants were observed at the Dutch Flat population with 32% of these reproductive. Fourteen emergent plants and 1 reproductive plant was observed at Pisgah Crater. The vast majority of plants at Clark County were apparently dormant, and no reproductive plants were observed. Nye County had the highest abundance, and on average 35% of plants were emergent and none were reproductive (table 2). While mean diameters in the Dutch Flat and Clark Count populations were higher than in Nye County and Pisgah Crater (table 2), the difference was significant only in Clark County (t-value 2.934, $p < 0.0036$). No seedlings were observed in any population in 2021. All observed plants at the Pisgah Crater and Dutch Flat populations were tagged for demographic monitoring, while a sample of observed plants at each of the remaining populations were tagged. Tagged plants were re-visited May 27-June 4 to remeasure reproductive output and estimate seed per fruit production. At this time, all plants had either senesced, been browsed to the ground (figure 8), or had minimal vegetative material and no successful reproduction appeared to have occurred.

Table 2. Summary of PENALB phenology and mean plant size measured in April 2021 in the 4 population centers.

Population	#Subpopulations	#Total plants	% Budding	% Dormant	% Flowering	% Vegetative	Diameter (cm)	
							Mean	SD
Pisgah	12	35	0	60	1	40	11.8	6.54
Dutch Flat	5	175	19	0	13	68	19.67	12.34
Clark County	8	124	0	98	0	2	15	4.87
Nye County	7	255	0	53	0	47	8.60	7.92



Figure 8. A browsed PENALB plant typical of the condition of plants observed on the June revisit (plant PENALB AZ8-19).

Habitat

All 4 populations occurred in a matrix of creosote bush (*Larrea tridentata*) – burrobush (*Ambrosia dumosa*) shrublands on sandy to sandy loam soils. Ephemeral washes through the habitat were frequent, with PENALB plants often more abundant within small rivulets. Vegetation and soils of the Dutch Flat population differed from the other 3 populations, with Joshua Tree (*Yucca brevifolia*), Saguaro (*Carnegiea gigantea*) and crucifixion thorn (*Castela emoryi*) frequent associates along with creosote bush and burrobush (figure 9a-b), and finer, more stable soils, often with a gravelly surface. Pisgah Crater subpopulations occurred at the lowest elevations on fine sandy soils, with less stable soils than the other 3 populations. Vegetation of Pisgah Crater subpopulations was characterized by large, widely spaced creosote bush with big galleta (*Hilaria rigida*) and burrobush. Most occurrences were found on stabilized soils (figure 9c), but several occurred on semi-stabilized sand sheets and sand ramps with little vegetation (figure 9d). Small washes through the habitat were frequent, and PENALB plants were often associated with washes or road banks. Clark County subpopulations were typically found on loamy sand to sandy loam soils (figure 9e), but dense subpopulations were also found on soils with a high gravel component. Nye County subpopulations occupied the highest elevations, soils frequently had a gravelly to cobbly surface (figure 9e), and most subpopulations were associated with outwash fans and rivulets.

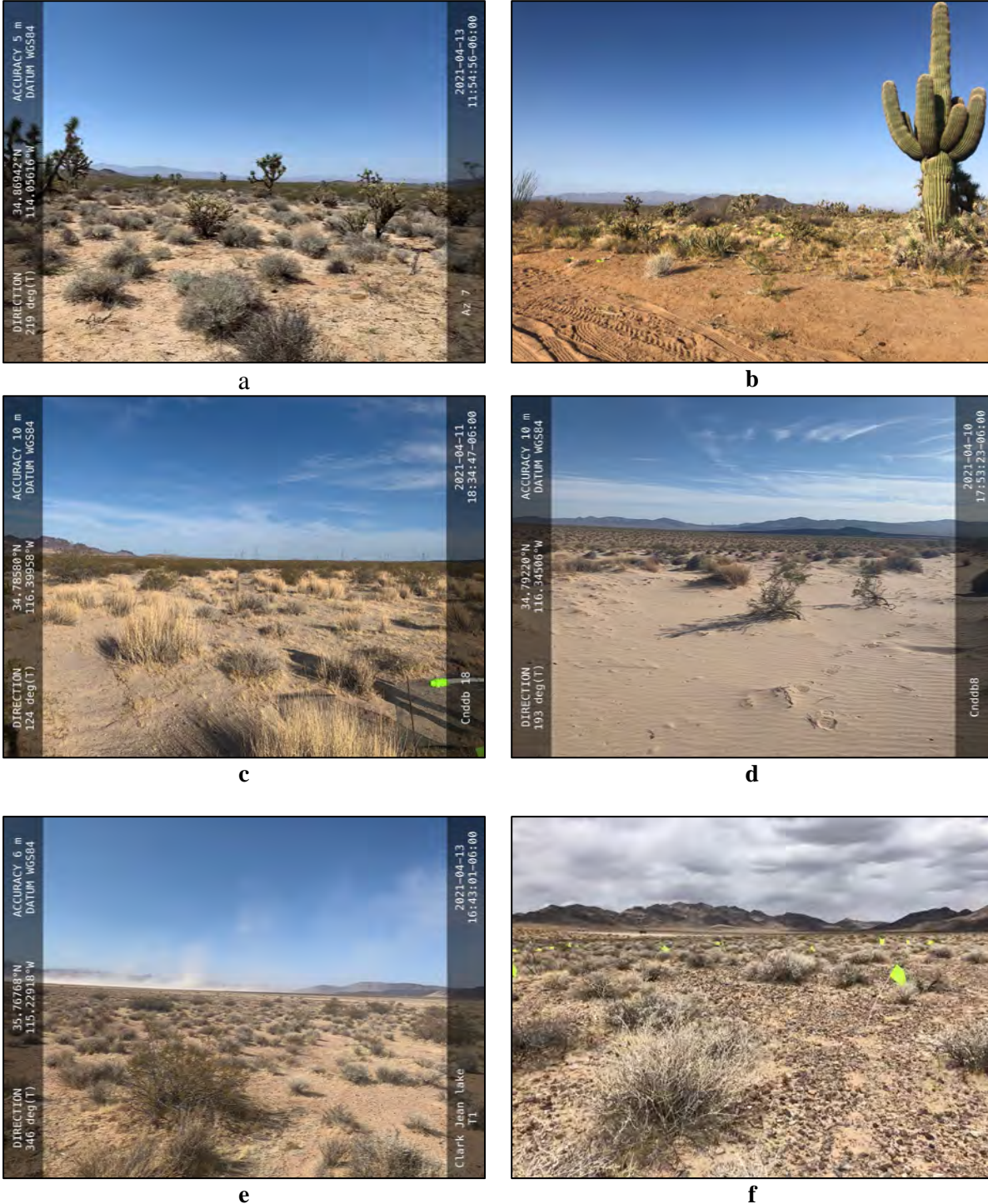


Figure 9. Habitats typical of the 4 PENALB population centers: a) Joshua tree – creosote bush shrublands, AZ7, Dutch Flat; b) Saguaro – Joshua Tree shrublands, AZ8, Dutch Flat; c) Stabilized fan apron with big galleta, creosote bush and burrobush, CNDDb18, Pissgah Crater, d) Sparsely vegetated sand sheet, CNDDb8, Pissgah Crater; e) Stabilized fan apron, Jean Lake Enclosure, Clark County; and f) Fan terrace with gravelly-cobbly surface, Nye T2, Nye County.

Threats

The severe drought of 2021, with very little winter precipitation throughout the range of PENALB, was the most prevalent threat impacting all populations of PENALB, with very low aboveground emergence, no seedling recruitment and no successful reproduction in 2021. Each population also faced multiple additional threats, with invasive species, OHV use, proximity to dirt roads and herbivory the most frequent (table 3). Nye County was the least disturbed of the 4 population centers. The frequency and severity of observed threats varied by population and survey site. Invasive plants were present at the majority of sites surveyed at Pisgah Crater, Clark County and Nye County, but were not observed at Dutch Flat (table 3). Mediterranean grass (*Schismus* spp.) was the most prevalent invasive plant present, observed at all Pisgah Crater sites and most Clark and Nye County sites. Asian mustard was locally abundant at Pisgah Crater and Nye County, and Russian thistle was infrequently observed at Clark and Nye County.

Off-highway vehicle use posed a significant threat at the majority of sites surveyed at Pisgah Crater and Clark County, with tracks observed within sites at numerous occurrences. Off-highway vehicle use was observed at only 2 occurrences in Nye County, and was not observed within subpopulations surveyed at Dutch Flat, though recreational OHV use was observed in the general area. All populations were threatened by proximity to roads and road maintenance activities (table 5). Pisgah Crater and Clark County sites occur in energy infrastructure corridors, and may be threatened by energy corridor maintenance and additional construction (table 3).

Herbivory was noted in all populations except for Clark County where nearly all plants were dormant in 2021. Herbivore impacts were generally mild in April (table 4). Populations did not significantly differ in severity of herbivory, but Pisgah Crater had a higher incidence of herbivory than Dutch Flat or Nye County (table 4). Herbivore impacts became severe in late spring, with all Dutch Flat and most Nye County plants decimated between April and June, and no successful reproduction observed.

The Dutch Flat population was most threatened by cattle grazing, which was observed in all subpopulations, and by urban development, with subpopulations occurring on or close to private property parcels, with roads and land development occurring throughout the area. Each population is discussed in more detail below.

Table 3. Frequency of threats documented at PENALB survey sites, 2021.

Population	Threat	Frequency observed
Pisgah Crater	Invasive plants (<i>Schismus</i> spp. <i>Brassica tournefortii</i>)	100%
	OHV	92%
	Proximity to road	46%
	Energy corridor, infrastructure	27%
	Railroad maintenance	31%
	Herbivory	38%
	Garbage dumping	7%
Dutch Flat	Cattle grazing	63%
	Proximity to roads	75%
	Urban development	75%
	Herbivory	100%

Population	Threat	Frequency observed
Clark County	OHV	67%
	Invasive species ((<i>Schismus</i> spp. <i>Salsola tragus</i>)	64%
	Proximity to roads, road migration	19%
	Cattle grazing	13%
	Energy corridor maintenance	13%
	Shooting range	3%
	Garbage dumping	3%
Nye County	Invasive plants (<i>Schismus</i> spp. <i>Brassica tournefortii</i> , <i>Salsola tragus</i>)	85%
	Herbivory	38%
	OHV	15%
	Road proximity, construction	15%
	Hydrological modification (berms, flooding)	23%
	Mining	8%

Table 4. Frequency and mean severity (percent of plant impacted) of herbivory observed in PENALB demography plots, 2021. Frequency of herbivory was significantly higher at Pisgah Crater, while remaining values were not significantly different among populations.

Population	Frequency of herbivory	Mean Severity
Pisgah Crater	0.80 ¹	3.73
Dutch Flat	0.35	1.25
Clark County	0	NA
Nye County	0.30	6.35

¹(t-value=2.706, p<0.017)

Population Center Descriptions

Pisgah Crater

A total of 35 PENALB individuals were observed at the Pisgah Crater population, occurring in 12 of the 26 PENALB sites surveyed (table 2, Appendix A). Of these 35 plants, only 14 had active growth (figure 10a) and only 1 was reproductive (figure 10b). Apparently dormant plants had been large and reproductive in 2020 (figure 10c). Eighteen of the observed individuals had tags that were part of the 2011-2012 demographic monitoring study (Moore and Pavlik 2014), with the majority of plants observed in 2021 either within or near herbivore exclusion cages (figure 10d), indicating that protection from herbivory has been a critical for long-term survival in this population. Our observations of emergent and apparently dormant tagged plants from 2011 also show that some PENALB individuals may survive for at least 10 years at the Pisgah population, and suggests that these plants are capable of dormancy. Mammalian herbivory was observed impacting on all but 2 of the emergent plants at Pisgah, but was typically minor, affecting less than 1% of the individual plant (figure 11d). Two plants had 1-25% herbivory.

The June revisit found 12 plants still in a vegetative state, with the remainder dormant. Herbivory incidence and severity had not increased from April observations.

Threats observed during the April survey included drought impacts, dirt roads in the vicinity of most occurrences, OHV use, invasive species, and energy construction. The extreme drought conditions of 2021 were the most pervasive threat impacting the Pisgah Crater population, with the lowest number of emergent plants observed to date in this population, and no successful reproduction. The invasive Mediterranean grass was present at most sites surveyed (figure 11a) and Asian mustard was abundant on sand ramps near occurrences in Giant Wash (figure 11b). Off-road vehicle tracks were observed within or adjacent to most occurrences at Pisgah Crater, and were especially abundant in the semi stable sand habitats adjacent to and northwest of Giant Wash (figure 11c). Off-road vehicle use threatens this population by direct impacts to plants and by destabilization of the sandy habitats that PENALB occurs in at Pisgah Crater. Giant Wash, which is the center of the PENALB population at Pisgah Crater, is a corridor for OHV users, and in addition to OHV tracks in this area, trash dumping, and a small recent fire were observed in the vicinity of historic PENALB occurrences at the north end of the wash.

Many of the Pisgah Crater occurrences are directly adjacent to a dirt road. This poses threats to population persistence through road maintenance and OHV use along dirt roads. Several Pisgah Crater occurrences occur under a major energy transmission corridor, and energy corridor maintenance activities, including road maintenance pose a significant threat to the Pisgah Crater population. An active energy construction project was occurring at the time of survey, with a large area of soil and vegetation disturbance south of CNDBB_011 (Appendix A).



a



b



c

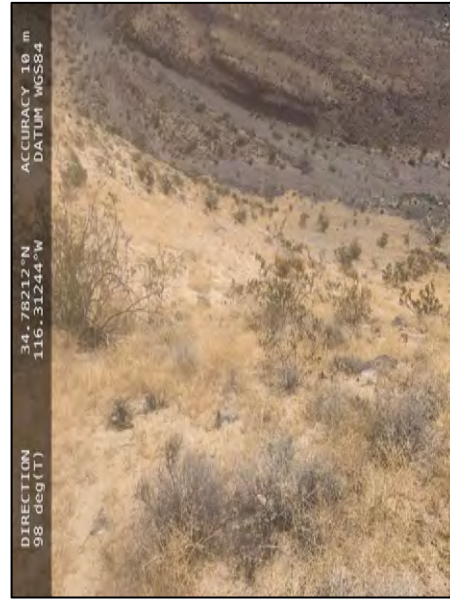


d

Figure 10. April 2021 Pisgah Crater PENALB, including a) Vegetative PENALB at CNDDB_09; b) Budding PENALB at CNDDB_19; c) Large dormant or dead PENALB at CNDDB_11; d) Cages with dormant and active PENALB at Main Drag 2.



a



b



c



d

Figure 11. Threats observed at the Pisgah Crater population, including a) Mediterranean grass (*Schismus* spp.) at CNDDDB_21; b) Dense Asian mustard (*Brassica tournefortii*) on sand ramp above PENALB occurrences in Giant Wash; c) OHV tracks within PENALB habitat in Giant Wash; d) Minor mammalian herbivory on PENALB leaves.

Dutch Flat

PENALB plants were observed at 6 of the 8 occurrences surveyed at Dutch Flat (table 2, Appendix A). The 2 occurrences where plants were not found were historic herbarium records from 1973 in Rocky Creek (Appendix A), and location accuracy for these records was poor. The entire area around these 2 sites was actively grazed at the time of survey. Habitat surrounding record 73-463 was higher elevation slopes with very rocky soils and vegetation dominated by

Utah juniper (*Juniper osteosperma*). Record 463 was within the Rocky Creek drainage channel. Searches of the channel and surrounding slopes did not find any sign of PENALB (Appendix A). The remaining occurrences were on northwest to west facing, gently sloping bajada with vegetation dominated by mixed Joshua tree – creosote bush shrublands at lower elevations (figure 12a) to Saguaro – Joshua tree-mixed shrublands at higher elevations (figure 12c).



Figure 12. PENALB habitat and plants observed at the Dutch Flat population, April 2021, including: a) Joshua tree – creosote – burrobush shrubland, AZ7; b) Large flowering PENALB at AZ7; c) Saguaro – Joshua tree shrubland with flagged PENALB, AZ8; d) Flowering PENALB, AZ8.

Approximately 189 PENALB individuals were observed among the 7 locations where plants were found at Dutch Flat, with subpopulation sizes ranging from 1 to 73 plants (table 1). Of these, all were emergent in 2021, with approximately 32% reproductive (table 1). No apparently dormant individuals were observed at Dutch Flat. Herbivory was observed impacting approximately 35% of individuals. Severity of herbivory was typically low, but severe herbivory

was observed (figure 13a). Herbivory included mammalian bites on leaves, and desert leafcutter ants (*Acromyrmex versicolor*) (figure 13b) were observed completely decimating 3 individuals in about 3 minutes.

The June revisit found plants either completely gone, browsed stems, or senesced, and no evidence of successful reproduction in any individuals.

Threats observed during the April survey included cattle grazing within all surveyed sites, dirt roads in the vicinity of all sites, herbivory, and urbanization and development with plants occurring on or adjacent to private land.

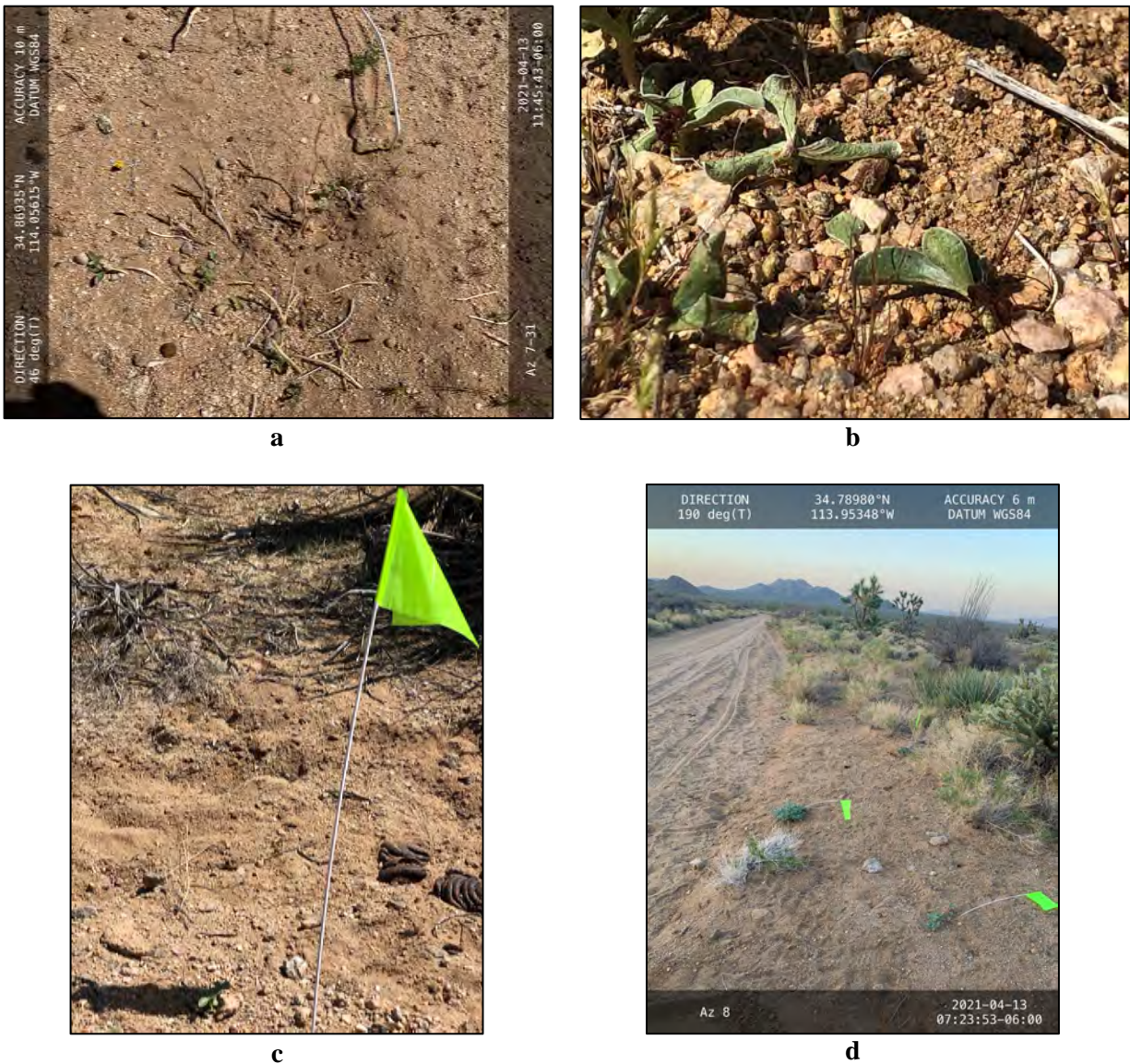


Figure 13. Threats to PENALB at the Dutch Flat population, including: a) Severely browsed PENALB; b) Desert leafcutter ants harvesting PENALB; c) Small PENALB plant near cowpie and cattle trail; d) PENALB plants growing beside road.

Clark County

Since the 4 main subpopulations of the Clark County population are very large, these occurrences were sampled by surveying previous demographic monitoring locations as well as randomly choosing survey locations within occurrence boundaries. This resulted in 31 survey locations within the Clark county population (Appendix A). Approximately 1,060 PENALB individuals were found among these survey sites, nearly all of which were apparently dormant (figure 14b). Only a handful of emergent individuals (figure 14b) were observed; these were found at the Jean Lake and Hidden Valley subpopulations. Habitat throughout the area was gently sloping creosote bush – burrobrush – big galleta shrublands with sandy soils. Density and abundance of PENALB was variable among survey sites, with none or few plants found in some areas, and hundreds of plants found in others (Appendix A). Dormant plants with pins from the 2008-2009 DRI study (Etyemezian et al. 2010) were found at all DRI demography sites, indicating that some of these plants have survived for 13 years. Herbivory was not observed in this population, but most plants did not have live growth.

The June revisit found only dormant individuals with no evidence of reproduction in 2021 in Clark County.



Figure 14. PENALB plants observed at the Clark County population, April 2021, including a) Dormant PENALB with pin flag from 2008, Roach Lake North; b) Emergent PENALB, Hidden Valley.

In addition to the pervasive effects of the 2021 drought, off-road vehicle use was the dominant threat facing the Clark County PENALB population. Motorcycle tracks through populations were observed in the Roach Lake North and South subpopulations (figure 15a), and heavy use was observed in many areas (figure 15c). Grazing impacts were observed in the Jean Lake area, with extensive areas of vegetation and soil loss and no PENALB observed. Invasive species including Mediterranean grass and Russian thistle posed a threat at many locations, but were most severe within areas of the Hidden Valley subpopulation (figure 15d). Trash dumping was observed in several locations. Roads and energy corridors pose a threat to this population, with dirt roads occurring in the vicinity of many sites, and a large energy corridor extending

through the Roach Lake South population. The two southernmost occurrence sites in the Roach Lake South population occurred beneath power pylons, and no plants were observed in this disturbed habitat.

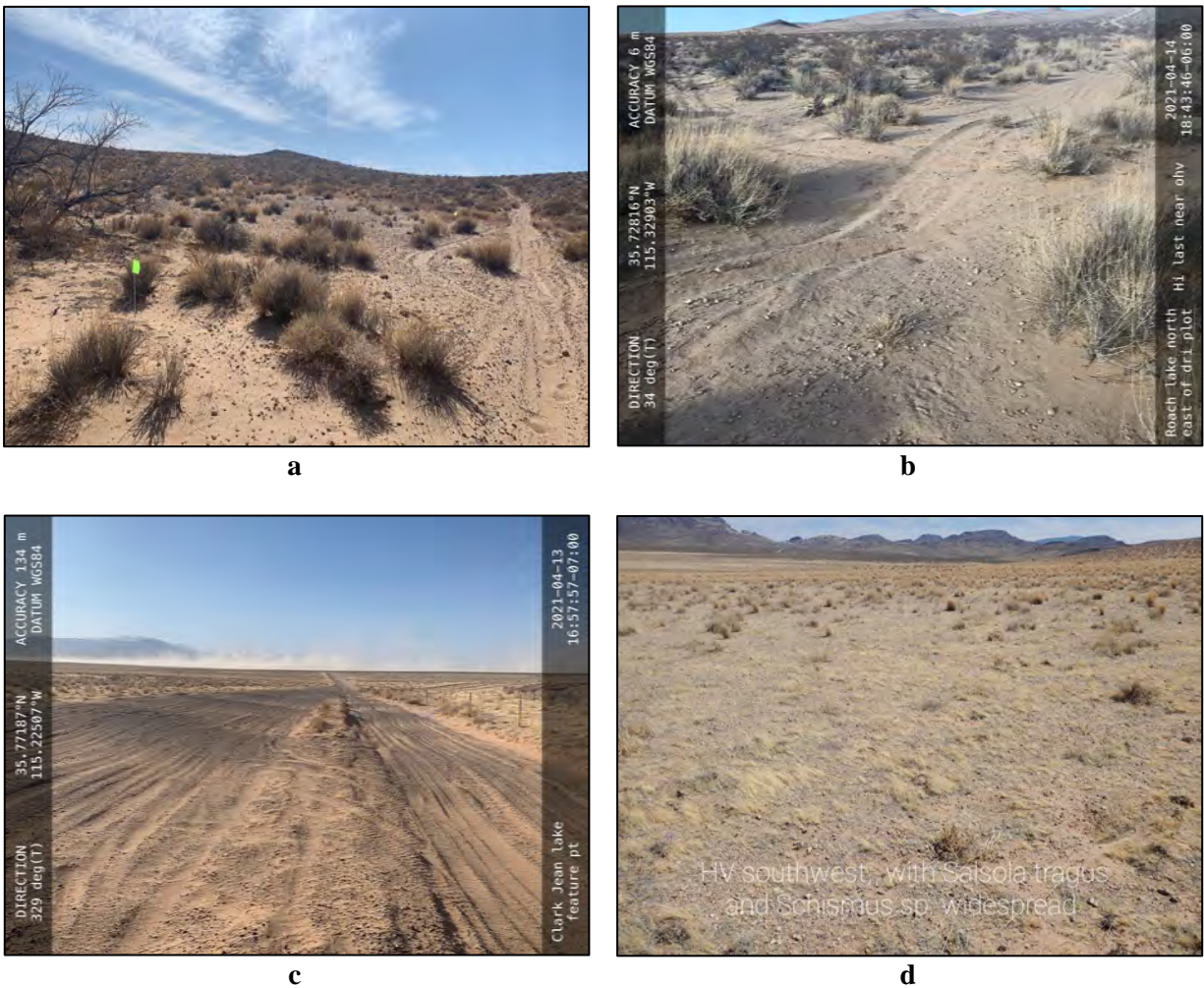


Figure 15. Threats to PENALB at the Clark County population, including: a) Motorcycle trail through PENALB site; Roach Lake North; b) OHV tracks through large population, Roach Lake North; c) Extensive road widening, Jean Lake; d) Abundant invasive plants, Hidden Valley.

Nye County

All but 1 of the 8 occurrences surveyed in the Nye County population had PENALB individuals, and abundance was highest in this population (table 2, Appendix A). The only occurrence without plants occurred in a heavily disturbed area immediately adjacent to Highway 95 (Appendix A). Habitat included ephemeral washes, terraces, outwash fans and sand ramps dominated by creosote bush – burrobrush shrublands (figure 16a-d). Soils were fine sands, often with a gravelly to cobbly surface layer (figure 16c-d). Approximately 3,361 individuals were observed across the remaining 7 sites. Approximately 38% of observed individuals were emergent at the time of survey, with the remainder apparently dormant, and 1 budding plant observed. Herbivory impacted approximately 32% of observed plants. As in the Clark County

population, pin flags associated with plants monitored in the 2008 DRI study were found at the Nye County population, indicating that some of these plants may survive for at least 13 years.

The June revisit found only 2 vegetative individuals on demography transects, with the remainder either dormant or senescent and no evidence of successful reproduction in 2021.



a



b



c



d

Figure 16. PENALB habitat and plants observed at the Nye County population, April 2021, including: a) Sandy soils in creosote bush – burrobush shrublands, Nye 5; b) Large PENALB in Nye_5; c) Cobbly soil surface, Nye T1; d) Flagged PENALB plants, Nye T2.

The Nye County population was the least disturbed of the 4 locations, and habitat conditions were generally considered good to excellent. However, invasive species including Mediterranean grass and Asian mustard were observed near several occurrences. Off-road vehicle tracks were observed within 2 occurrences. Berms near habitat that direct sediment flow towards subpopulations or prevent water from reaching subpopulations were observed in 2 occurrences.

Climate differences among population centers

Climate conditions in the 4 PENALB populations differed over the past 27 years in terms of amount of winter (October – April), summer (May – September) and total annual precipitation received, and in terms of mean, minimum and maximum annual temperatures (figure 17, table 5). Dutch Flat was the wettest population in terms of all precipitation components, followed by Clark County (figure 17, table 5). Nye County and Pisgah Crater were not significantly different in terms of winter or total precipitation, but Nye County typically received more summer precipitation than Pisgah Crater (figure 17, table 5). Pisgah Crater was the warmest of the 4 populations in terms of mean, minimum and maximum temperatures, followed by Dutch Flat (figure 17, table 5). Minimum temperatures at Nye County were significantly cooler than the other 3 population centers (figure 17, table 5). Maximum temperatures in Nye County and Clark County were not significantly different (figure 17, table 4).

While precipitation and temperature values were different among the population centers, annual patterns of drought and wet, and warming and cooling were similar across the region, with all populations typically experiencing drought and/or warming at the same time (figures 18-19).

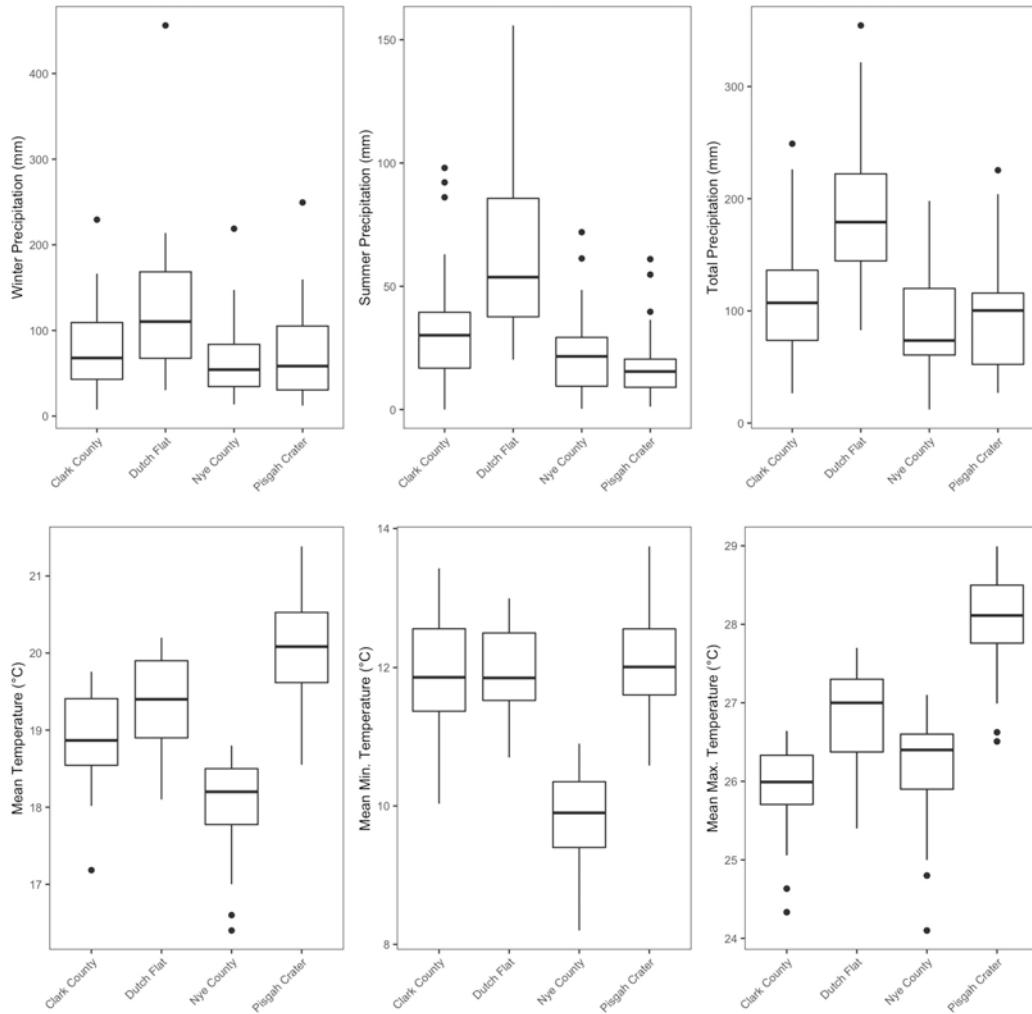


Figure 17. Boxplots of climate variables including mean winter (Oct-April), summer (May-Sept) and total precipitation, and mean, minimum and maximum annual temperatures for the 4 PENALB populations.

Table 5. Mean winter (Oct-April), summer (May-Sept) and total precipitation, and mean, minimum and maximum annual temperatures for the 4 PENALB populations. Values sharing the same letters are not statistically different.

Population	Mean winter ppt (mm) ¹	Mean total ppt (mm) ²	Mean summer ppt (mm) ³	Mean annual temp. (°C) ⁴	Mean min. temp. (°C) ⁵	Mean max. temp. (°C) ⁶
Clark County	78.30 ^a	114.75 ^a	33.92 ^a	18.81 ^a	11.91 ^a	25.87 ^{ac}
Dutch Flat	123.57 ^b	188.24 ^b	63.72 ^b	19.39 ^b	11.97 ^a	26.81 ^b
Nye County	66.85 ^c	90.55 ^c	22.37 ^c	18.01 ^c	9.85 ^b	26.18 ^c
Pisgah Crater	71.39 ^c	98.02 ^c	18.20 ^d	20.04 ^d	12.08 ^a	28.00 ^d

¹ F-value = 5.0512, P<0.00259, ² F-value= 17.146, P<0.0001, ³ F-value = 19.474, P<0.0001, ⁴ F-value = 43.963 P<0.0001,

⁵ F-value = 64.796, P<0.0001, ⁶ F-value=59.971, P<0.0001.

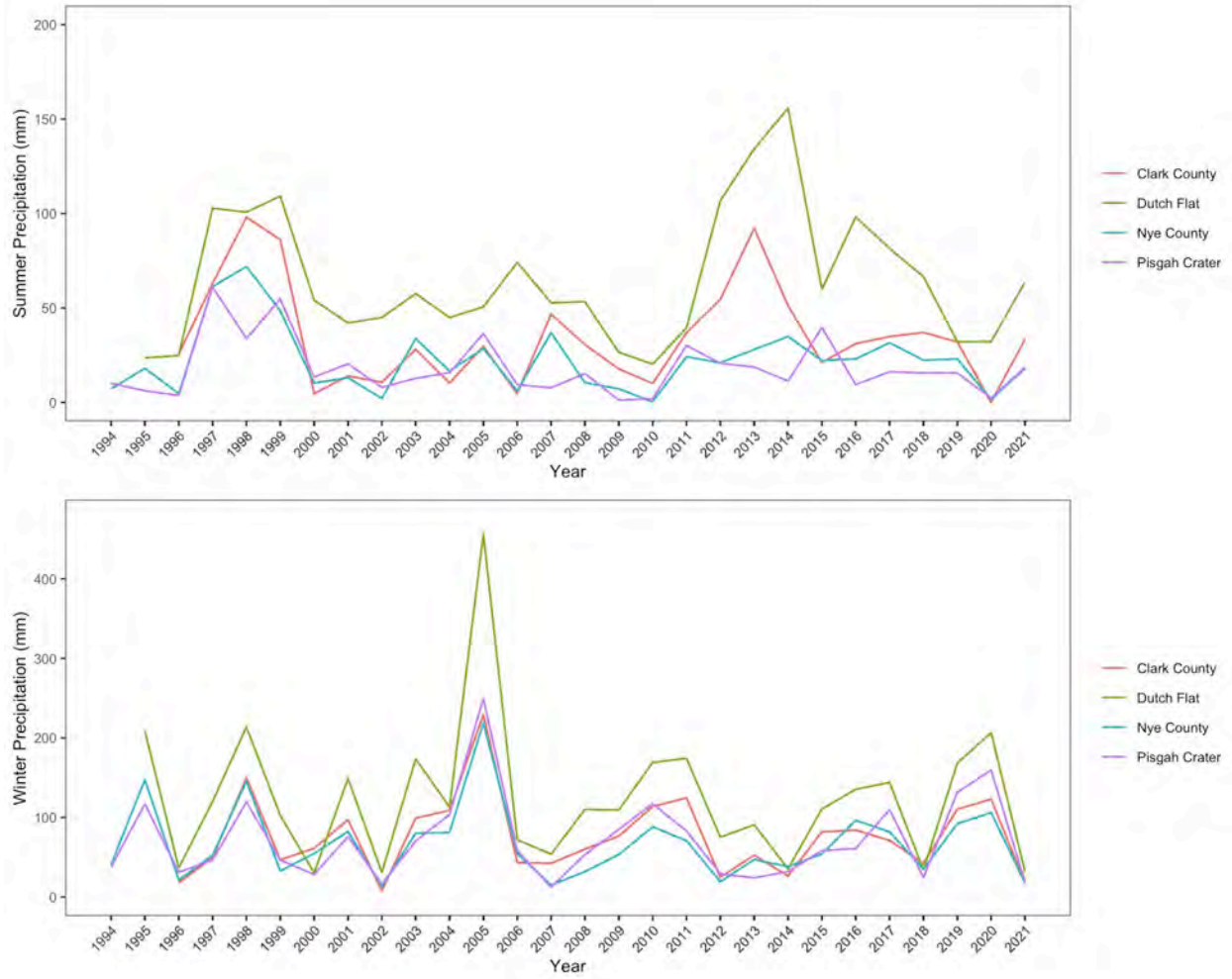


Figure 18. Winter (October – April) and summer (May – September) precipitation totals (mm) for 1994 – 2021 for the 4 PENALB population centers.

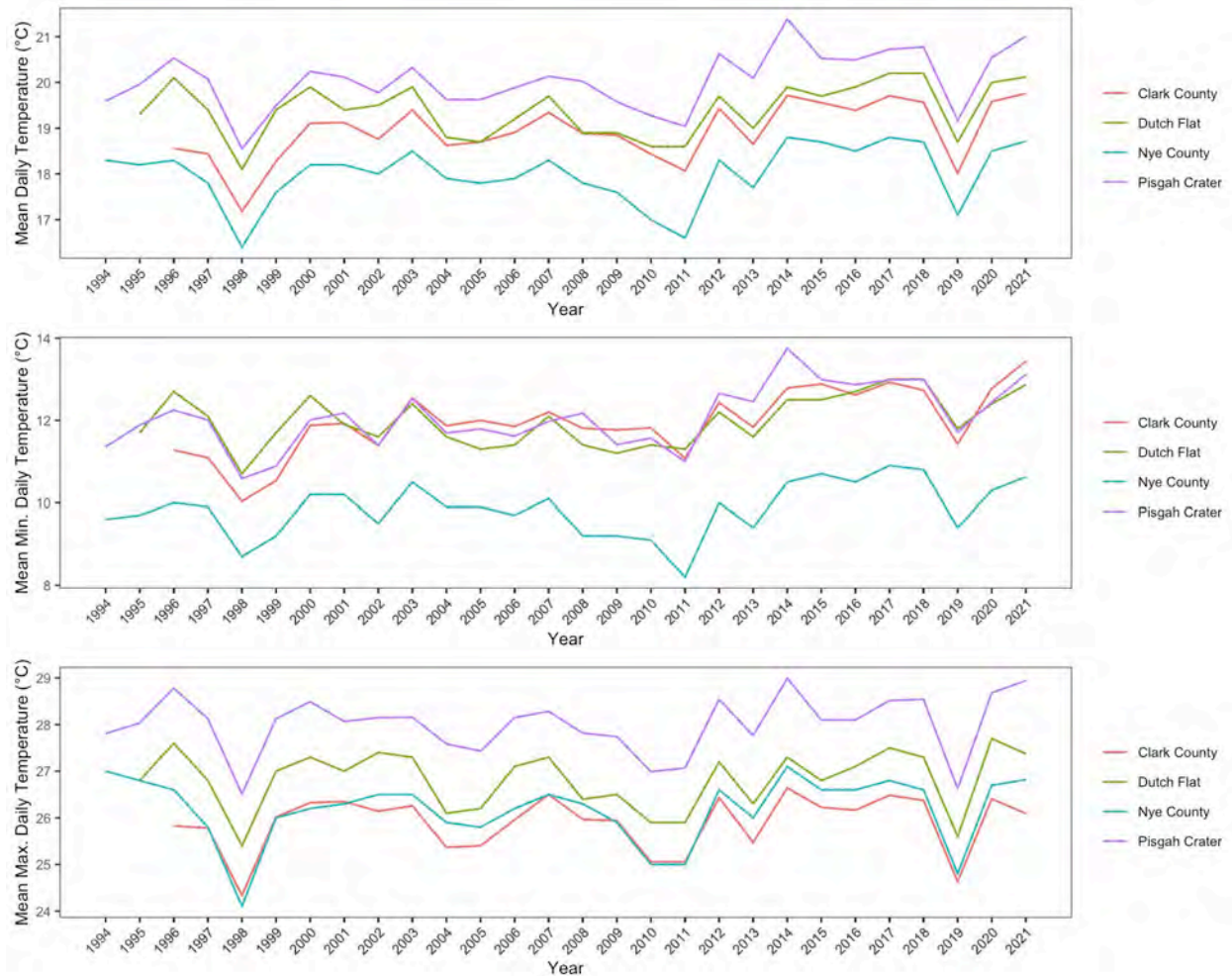


Figure 19. Mean, mean minimum and mean maximum annual temperatures for 1994 – 2021 for the 4 PENALB population centers.

Population viability analysis

Population size

In both the Pisgah Crater and Clark County long-term demographic monitoring studies, PENALB population size fluctuated significantly among years (figure 20, table 6). Fluctuations were more dramatic in the Pisgah Crater monitored population, with a low of 19 plants in 2004 to a high of 461 in 2011, while the largest difference at Clark County was a low of 169 plants in 2004 to a high of 400 plants in 1997 (table 6). Both populations showed a net decrease in abundance over their respective monitoring periods. The Pisgah Crater population showed a steady decline between 1995 and 2004, while the Clark County population had periods of both increases and decreases over this time period (figure 20, table 6). Plant size (mean diameter) also fluctuated among years, with plant size patterns more consistent between the 2 populations (figure 20, table 6).

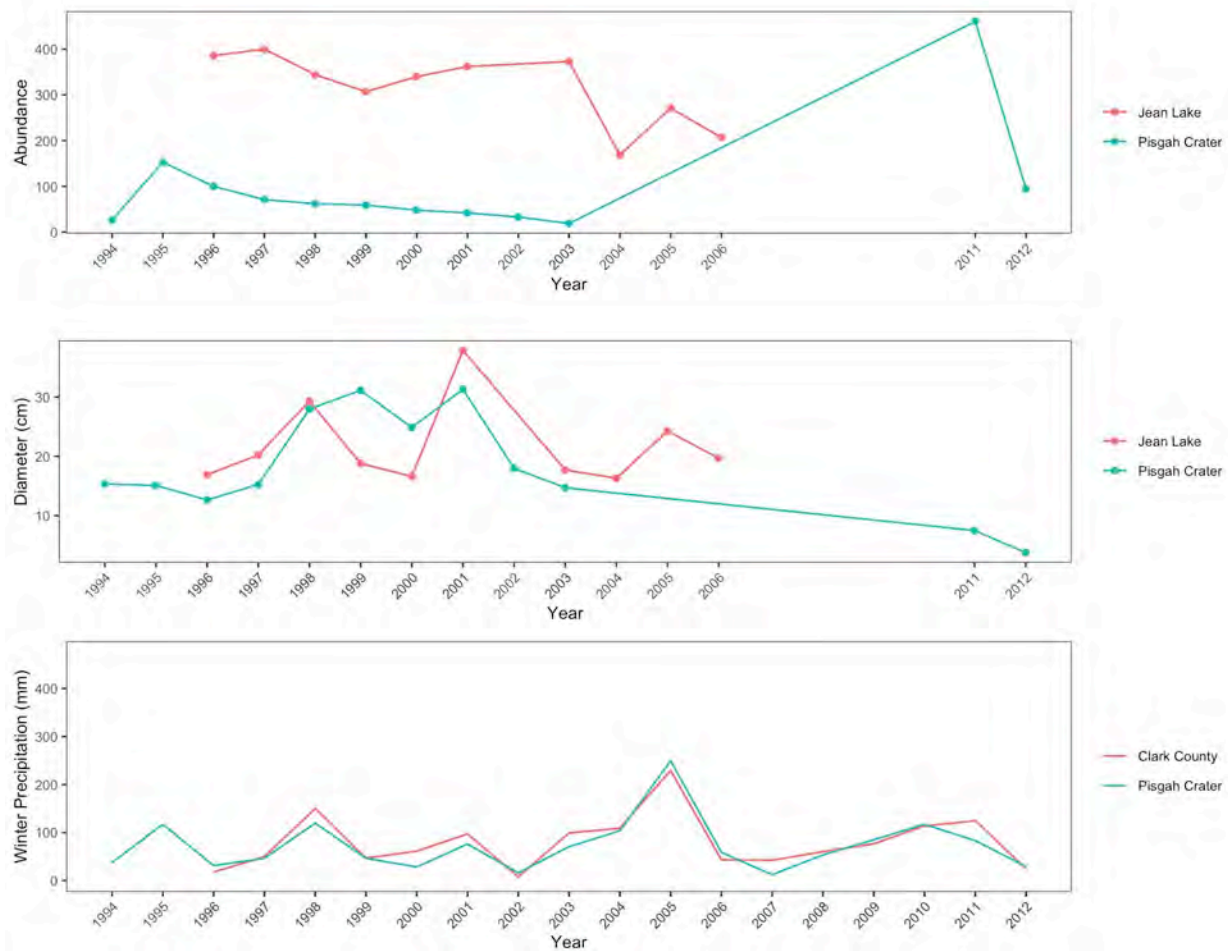


Figure 20. Population size and mean diameter (cm) for the 1994-2012 Pisgah Crater demographic monitoring and the 1996-2006 Clark County demographic monitoring, with total precipitation (mm) over the monitoring period.

Table 6. Population size with mean diameter (cm) for the 1994-2012 Pisgah Crater demographic monitoring and the 1996-2006 Clark County demographic monitoring.

Pisgah Crater 1994-2012 Demographic Monitoring			Diameter (cm)	
Year	#Subpopulations	#Plants	Mean	SD
1994	1	26	15.35	13.32
1995	9	158	15.09	13.28
1996	9	152	12.65	12.74
1997	9	101	15.25	12.99
1998	9	71	27.96	15.11
1999	9	62	31.11	12.41
2000	9	59	24.86	14.45
2001	9	48	31.29	15.15

Pisgah Crater 1994-2012 Demographic Monitoring			Diameter (cm)	
2002	9	42	17.98	11.42
2003	9	33	14.70	14.23
2004	9	19	NA	NA
2011	9	461	7.49	11.44
2012	9	269	3.77	6.76
2013	9	110	NA	NA
2014	9	86	25.1	12.0
Jean Lake Exclosure 1996-2006 Demographic Monitoring			Diameter (cm)	
Year	#Transects	#Plants	Mean	SD
1996	8	386	16.90	7.82
1997	8	400	20.22	7.46
1998	8	344	29.30	11.79
1999	8	307	18.79	8.07
2000	8	340	16.60	8.18
2001	8	362	37.84	15.95
2003	8	373	17.70	9.48
2004	8	169	16.30	6.92
2005	8	271	24.26	13.82
2006	8	207	19.67	11.24

Size class distribution and transitions

Size class distributions and transition rates differed among years within the Pisgah Crater and Clark County populations (figure 21, table 7). Differences and similarities in transition rates occurred between the Clark County and Pisgah Crater population, with the presence of a large proportion (13 to 77%) of individuals in a dormant stage in all monitoring years in Clark County the biggest difference (figure 21). Both monitored populations had years where no seedlings were observed. Clark County had 2 years (1999 and 2000) where no reproduction was recorded, and Pisgah Crater had 1 year where very low rates of successful reproduction occurred (Moore and Pavlik 2014). Both populations had years where no large size classes (>41 cm) were present (figure 21), and this occurred more frequently in the Pisgah Crater population.

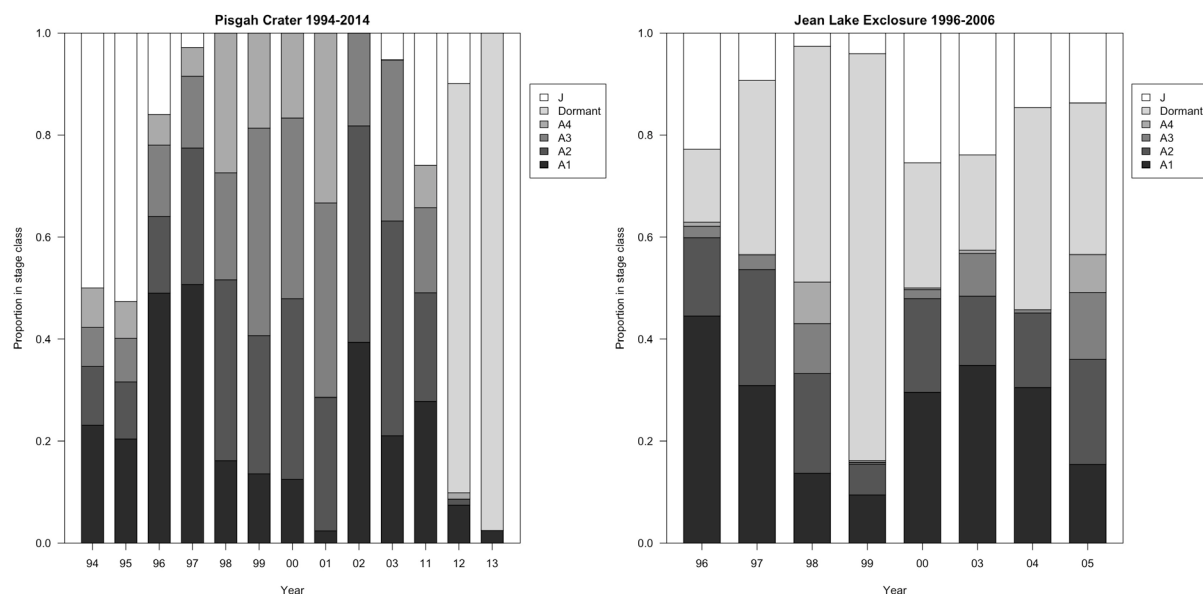


Figure 21. Size class distributions in the 1994-2012 Pisgah Crater dataset and 1996-2006 Clark County dataset.

Survival and dormancy

Dormancy buffered Clark County population abundance, with mortality rates ranging from less than 1% to 13% among monitoring years. Survival of Clark County individuals was best predicted by a model that included initial size class and winter precipitation in year 2, with significantly higher rates of mortality among juvenile, A1 and A2 size classes, and mortality rates declining with increasing plant size and lowest in dormant individuals (table B1).

Dormancy rates ranged from 14% to 77%, and was best predicted by a model that included size class and year, with smaller individuals and already dormant individuals most likely to be dormant in the following year (table B2). While a model with year instead of winter precipitation had a lower AIC, indicating that factors other than precipitation also explain dormancy, rates of dormancy were lower in years with higher winter precipitation (t-value -6.07, $p < 0.001$). There was no effect of previous year's reproductive status on probability of dormancy. All size classes were more likely to go dormant or regress in size during years of low winter precipitation, e.g., between 1998 and 1999 when winter precipitation was 35% of normal, the transition to dormancy was the dominant transition for all size classes (table 7). During good years, all size classes were more likely to rapidly grow e.g., between 2000 and 2001 the transition to the A4 size class was the dominant transition for all stages, except for juveniles where it was the only year that a juvenile to A4 transition was observed (table 7). Large individuals (A4) were more likely to exhibit stasis than other size classes (table 7).

Without the buffering capacity of dormancy during adverse conditions, Pisgah Crater mortality rates ranged from a low of 5% in 1998 to 100% in 2003. Like Clark County, smaller individuals were also more likely to die in the Pisgah Crater population, with mortality of new recruits especially high (Moore and Pavlik 2014). Dormancy was observed in the Pisgah Crater population from 2012-2014, with most of monitored plants dormant in 2012 and 2013 in this population (figure 21).

Fecundity

In the Clark County population, smaller plants were much less likely to be reproductive. Reproductive rates were highest in the A3 size class and declined in the A4 size class, and plants that had been dormant were least likely to reproduce in the following year (table B3). Smaller plants were also much less likely to be reproductive at the Pisgah Crater population, but in the Pisgah Crater population the probability of reproduction increased with size, with no peak in reproduction as observed in the Clark County population. The mean transition rate from seed to seedling was estimated to be lower in the Clark County population (0.000113 vs. 0.00305), with more years with no observed reproduction in this population, and a lower proportion of reproducing adults observed over the monitoring period. Since no data on per plant seed production was available for Clark County, and the intensity of seedling searches was unknown, this rate may be higher and should be refined with Clark County specific fecundity estimates.

The probability of reproducing was also lowest for juveniles in the Dutch Flat population in 2021 (the only population where reproduction trends could be examined in 2021). Plants in the A1 stage class were most likely to be reproductive, with no other significant differences in reproduction among plant size (table B4). Total reproductive output was lowest in the juvenile stage class then increased with plant size except for A3 size individuals; however, most of the differences among stages were not significant (table B5). Since 2021 represented exceptionally dry conditions, these relationships should be examined under wetter conditions.

Table 7. Annual variation in PENALB size class transition rates and number of plants in each stage class for each transition year for the 1996-2006 Clark County dataset. T is the transition rate between stage classes for each pair of transition years. N is the number of plants in the stage class.

Transition Years		1996-1997		1997-1998		1998-1999		1999-2000		2000-2001		2001-2003		2003-2004		2004-2005		2005-2006	
From	To	T	N	T	N	T	N	T	N	T	N	T	N	T	N	T	N	T	N
J	J	0.225	20	0.094	3	0	0	0.167	2	0.070	6	0.313	3	0.243	9	0.292	7	0.124	3
	A1	0.236	21	0.160	5	0	0	0.250	3	0.233	20	0.005	9	0.190	7	0.292	7	0.376	9
	A2	0.034	3	0.125	4	0	0	0.083	1	0.244	21	0	2	0	0	0.333	8	0.083	2
	A3	0	0	0.031	1	0	0	0.083	1	0.174	15	0	0	0	0	0	0	0	0
	A4	0	0	0	0	0	0	0	0	0.081	7	0	0	0	1	0	0	0	0
	Dormant	0.315	28	0.563	18	1.00	8	0.417	5	0.105	9	0.125	2	0.027	20	0.042	1	0.083	2
	Dead	0.191	17	0.031	1	0	0	0	0	0.093	8	0.563	8	0.541	2	0.042	1	0.333	8
A1	J	0.023	4	0.009	1	0.10	2	0.036	1	0.020	2	0.278	3	0.037	24	0.020	1	0.111	3
	A1	0.322	56	0.149	15	0.02	4	0.357	10	0.021	2	0.093	13	0.448	5	0.222	11	0.490	13
	A2	0.247	43	0.217	23	0	1	0.321	9	0.210	21	0	4	0.093	0	0.400	20	0.148	4
	A3	0.006	1	0.104	11	0	0	0	0	0.220	22	0	1	0	0	0.200	10	0.037	1
	A4	0	0	0.047	5	0	0	0	0	0.380	38	0	1	0	0	0.020	1	0.037	1
	Dormant	0.270	47	0.311	33	0.76	32	0.250	7	0.120	12	0.167	5	0.426	23	0.140	7	0.185	5
	Dead	0.132	23	0.170	18	0.07	3	0.036	1	0.030	3	0.472	0	0.000	0	0	0	0	0
A2	J	0.000	0	0.013	1	0.03	2	0.056	1	0	0	0.266	1	0.048	1	0	0	0.028	1
	A1	0.168	10	0.087	4	0.08	5	0.222	4	0.020	1	0.285	18	0.263	5	0.019	0	0.534	18
	A2	0.300	18	0.205	16	0	0	0.556	10	0.016	1	0.047	9	0.286	6	0.083	2	0.250	9
	A3	0.083	5	0.051	4	0	0	0	0	0.161	10	0.016	4	0	0	0.375	9	0.111	4
	A4	0	0	0.128	10	0	0	0	0	0.613	38	0	0	0	0	0.417	10	0	0
	Dormant	0.283	17	0.333	26	0.83	50	0.111	2	0.145	9	0.250	4	0.429	9	0.125	3	0.111	4
	Dead	0.167	10	0.218	17	0.05	3	0.056	1	0.048	3	0.172	0	0	0	0	0	0	0
A3	J	0	0	0	0	0.03	1	0	0	0	0	0.088	0	0.154	2	0	0	0	0
	A1	0	0	0.095	0	0.13	4	0	0	0	0	0.494	2	0.181	2	0	0	0.300	2
	A2	0.222	2	0.000	0	0.13	4	1.000	1	0	0	0.113	11	0.385	5	0	0	0.478	11
	A3	0.333	3	0.200	2	0	0	0	0	0.333	2	0.050	7	0	0	0	0	0.304	7
	A4	0	0	0.500	5	0	0	0	0	0.667	4	0.013	2	0	0	1.000	1	0.087	2
	Dormant	0.222	2	0.200	2	0.60	18	0	0	0	0	0.125	1	0.308	4	0	0	0.043	1
	Dead	0.222	2	0.100	1	0.10	3	0	0	0	0	0.225	0	0	0	0	0	0	0
A4	J	0	0	0	0	0	0	0	0	0	0	0.074	0	0	0	0	0	0	0
	A1	0	0	0	0	0.16	4	0	0	0	0	0.360	1	0.032	0	0	0	0.248	1
	A2	0	0	0	0	0.12	3	0	0	0	0	0.269	3	0	0	0	0	0.231	3
	A3	0	0	0	0	0.04	1	0	0	0	0	0.120	6	1.000	1	0	0	0.462	6
	A4	0	0	0	0	0.04	1	1.000	1	1.000	1	0.019	0	0	0	0	0	0	0
	Dormant	1.000	3	0	0	0.60	15	0	0	0	0	0.194	3	0	0	0	0	0.231	3
	Dead	0	0	0	0	0.04	1	0	0	0	0	0.065	0	0	0	0	0	0	0

Transition Years		1996-1997		1997-1998		1998-1999		1999-2000		2000-2001		2001-2003		2003-2004		2004-2005		2005-2006	
Dormant	J	0.054	3	0.026	3	0.05	7	0.262	62	0.048	4	0.091	2	0.241	7	0.062	4	0.038	2
	A1	0.339	19	0.145	17	0.08	11	0.283	67	0.120	10	0.159	3	0.207	7	0.138	9	0.058	3
	A2	0.214	12	0.137	16	0.07	10	0.143	34	0.205	17	0.159	0	0	6	0.092	6	0	0
	A3	0.018	1	0.103	12	0	0	0.021	5	0.253	21	0.045	1	0	0	0.062	4	0.019	1
	A4	0	0	0.051	6	0	0	0	0	0.205	17	0	0	0	0	0.015	1	0	0
	Dormant	0.375	21	0.538	63	0.80	114	0.291	69	0.169	14	0.545	46	0.310	9	0.631	41	0.885	46
	Dead	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA

Population growth

Deterministic population growth rates varied by observation year for both the Pisgah Crater and Clark County populations (table 8, Moore and Pavlik 2014), and mean deterministic and stochastic asymptotic population growth rate indicated a declining population for both (table 9, Moore and Pavlik 2014). Updating the Pisgah Crater PVA models with 3 years of monitoring data that included significant rates of dormancy increased population growth rates for this population (table 9).

Table 8. Deterministic population growth rate (λ_a), by observation year for Clark County, 1996-2006.

Year	λ_a
1996-1997	0.8973
1997-1998	0.8212
1998-1999	0.99156
1999-2000	1
2000-2001	1
2001-2003	0.759413
2003-2004	1.000869
2004-2005	0.74331
2005-2006	0.992474

Table 9. Mean deterministic (λ_a) and stochastic (λ_s) population growth rates estimated for the Clark County and Pisgah Crater (with and without dormancy) populations.

Population	λ_a	λ_s
Clark County	0.940	0.933
Pisgah Crater no dormancy	0.926	0.778
Pisgah Crater with dormancy	1.180	0.971

Sensitivity and elasticity

Growth and survival of dormant and A1 and A2 individuals had the biggest effects on population growth rate in the Clark County population (table 10). For the Pisgah Crater population growth and survival of larger size class individuals had the biggest effect on population growth rates (Moore and Pavlik 2014). Sensitivity and elasticity analysis are based on small changes in matrix elements (Morris and Doak 2003). Our fertility estimates for the Clark County population are uncertain (based on seeds per inflorescence estimates from Pisgah Crater). Further, increasing fecundity through management actions such as protection from herbivores is a realistic scenario. Therefore, we examined how increases in the seed to seedling transition rate impacted population growth rates in Clark County. Increasing the seed to seedling transition rate to that estimated for Pisgah Crater (from 0.000113 to 0.00305), increased the mean deterministic population growth rate from 0.940 to 1.149, and the stochastic population growth rate from 0.938 to 1.11. Further increases to the seed to seedling transition rate increased population growth rates (Table 11).

Table 10. Sensitivity and elasticity matrix for Clark County, 1996-2006.

Sensitives						
	J	A1	A2	A3	A4	Dormant
J	0.03433	0.271	0.2452	0.04895	0	0.3147
A1	0.03639	0.2874	0.2599	0.0519	0	0.3336
A2	0.03454	0.2727	0.2467	0.04926	0	0.3166
A3	0.0303	0.2393	0.2164	0.04321	0	0.2778
A4	0.04722	0.3728	0.3372	0.06733	0	0.4328
Dormant	0.04237	0.3345	0.3026	0.06042	0	0.3884
Elasticities						
	J	A1	A2	A3	A4	Dormant
J	0.008596	0.006944	0	0	0	0.018786
A1	0.009577	0.103069	0.04858	0	0	0.126142
A2	0.001298	0.075116	0.08248	0.0122	0	0.075616
A3	0	0.001533	0.0201	0.01605	0	0.005528
A4	0	0	0	0	0	0
Dormant	0.014855	0.100705	0.09555	0.01496	0	0.162309

Table 11. Deterministic population growth rate (λ_a), by observation year for Clark County, with effects of increasing the seed to seedling transition rate on λ_a . T Observed represents the mean transition rate observed over the 1996-2006 monitoring period. T=0.003 is the mean rate estimated in the Pisgah Crater monitoring period.

Year	λ_a T Observed	λ_a T=0.003	λ_a T=0.008	λ_a T=0.05
1996-1997	0.8973	0.904	0.916	1.006
1997-1998	0.8212	1.223	1.767	1.770
1998-1999	0.99156	0.992	0.992	0.992
1999-2000	1	1	1	1
2000-2001	1	1	1	1
2001-2003	0.759413	0.864	1.034	2.685
2003-2004	1.000869	1.123	1.307	2.626
2004-2005	0.74331	0.841	1.055	2.410
2005-2006	0.992	1.2482	1.534	2.798

Quasi-extinction probabilities

The monitored Clark County population had a 50% chance of quasi-extinction within 50 years under the climate conditions observed over the study period (figure 22). Doubling the frequency of drought increased this probability to over 80%, while eliminating drought reduced the chance

of extinction to almost zero (figure 22). Increasing the seed to seedling transition rate for Clark County to that estimated for Pisgah Crater reduced the likelihood of extinction for Clark County to zero, even under increased drought (results not shown). Quasi-extinction in the Pisgah Crater population was similarly projected as highly likely with an increase in drought frequency, and also likely under the observed climate conditions (Moore and Pavlik 2014).

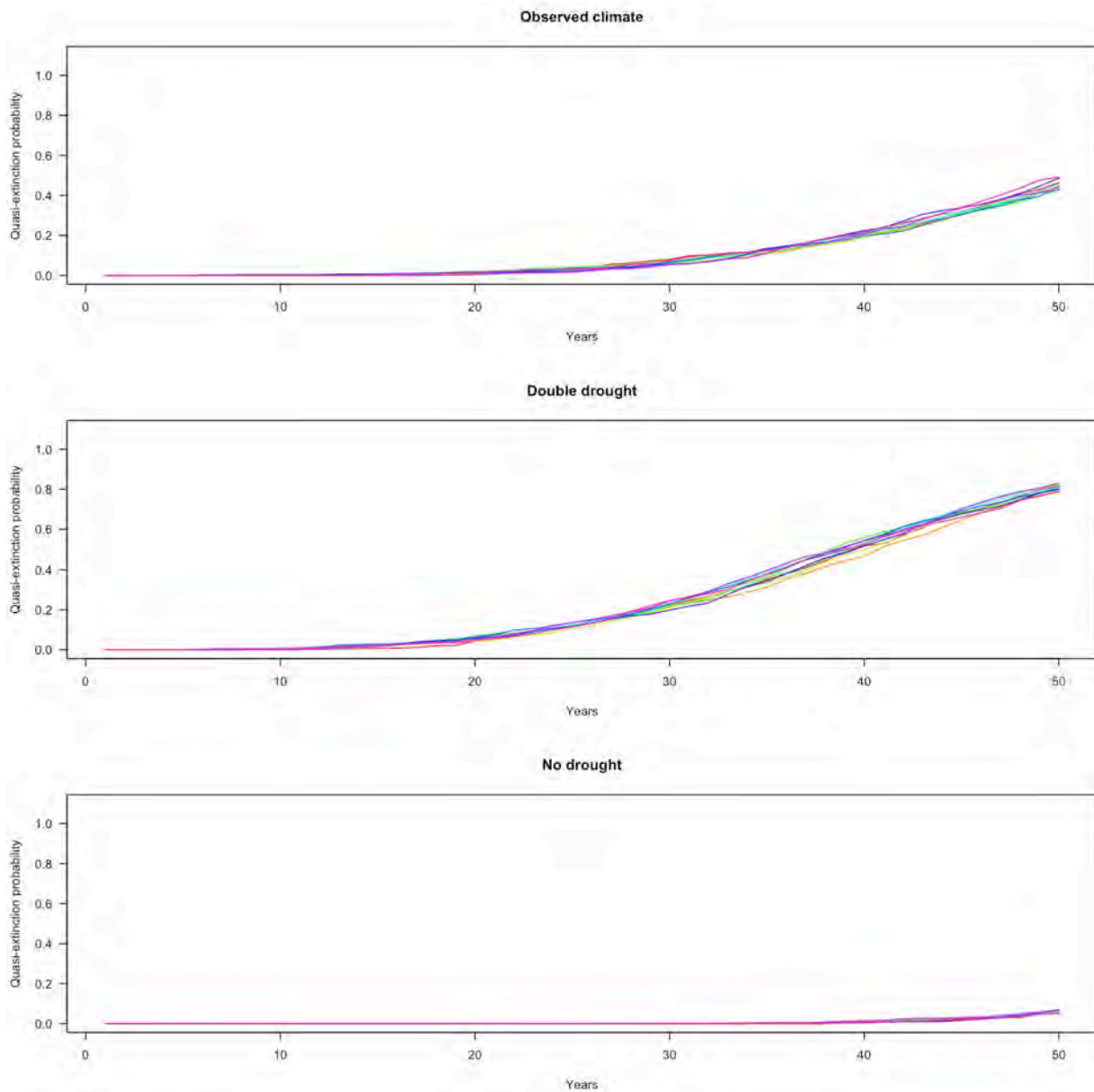


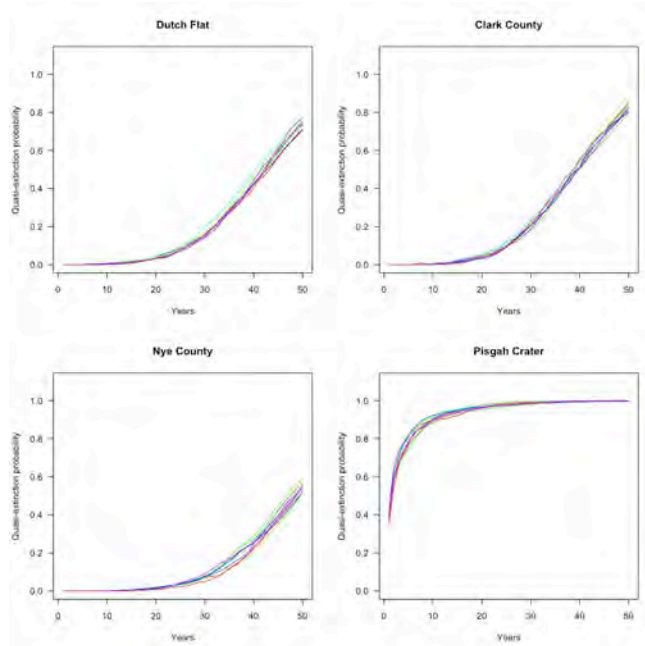
Figure 22. Quasi-extinction probabilities in 50 years for the Clark County 1996-2006 dataset with the monitoring period observed climate, double drought, and no drought. Quasi-extinction is defined as fewer than 10 individuals.

Quasi-extinction probabilities 2021 Dataset

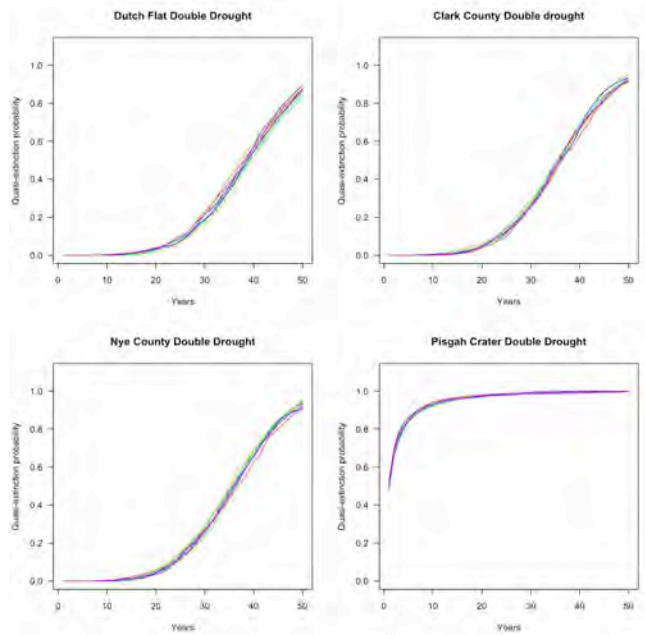
Quasi-extinction probabilities with the 2021 population starting vectors showed a significant likelihood of quasi-extinction for all populations within 50 years (figure 23). The Nye County population was lowest at 50%, while Pisgah Crater was highest at 100% (figure 23). Doubling

drought frequency increased the probability of extinction slightly for Dutch Flat and Clark County and substantially for Nye County, with the probability of extinction increasing from 50% to over 80% (figure 23B). These projections are based on the starting population size and size class distribution measured in 2021; thus, Pisgah Crater CA and Dutch Flat AZ represent all plants observed in the survey sites visited, while Clark County and Nye County are a sample of much larger populations.

These projections are based on transition rates estimated from roughly a decade ago, and seed production estimates are based on a small sample from Pisgah Crater. For Clark County and Nye County, the Clark County transition rates are likely a fair representation of the variability in transition rates, but cooler temperatures and lower disturbance rates in Nye County could result in higher rates of survival, or other differences in population vital rates. Likewise, greater winter and summer precipitation in the Dutch Flat population was shown to ameliorate drought effects in 2021, and certainly will result in differences in vital rates in this population.



A.



B.

Figure 23. Quasi-extinction probabilities in 50 years for 4 PENALB population centers with starting population vectors based on the 2021 dataset. A. Observed drought scenario, B. Double drought frequency scenario. Quasi-extinction is defined as fewer than 10 individuals. Probabilities for Dutch Flat AZ, Clark County NV, Nye County NV were drawn from the 1996-2006 Clark County dataset. Probabilities for Pisgah Crater CA were drawn matrices from the 1994-2014 Pisgah Crater dataset.

Chapter 4—Discussion and Recommendations

A survey of PENALB in 75% of its known occurrence sites throughout its range in 2021, coupled with population viability assessment using 9 to 12 years of demographic monitoring data in 2 of its 4 population centers, showed that the species is severely threatened by drought, catastrophic herbivory (the severity of which may be increased during drought), invasive species, and anthropogenic disturbances including OHV recreation, energy infrastructure and urban development. Population growth and persistence throughout the range of PENALB is limited by little to no reproduction during dry years due to a combination of few emergent plants, plants that emerge but do not flower or produce viable fruit, lack of seedling recruitment, and catastrophic herbivory of aboveground material. Population persistence in Clark and Nye County is buffered by the ability to avoid adverse climatic conditions by remaining in a dormant state for 1 to at least 5 years. Adults in the Clark County population may survive for 13 plus years, with many plants surviving at least 10 years. Individuals in the Pisgah population may live at least 9 years, but appear to be shorter lived with reduced rates of dormancy to buffer climatic adversity. Populations occurring in either wetter (Dutch Flat) or cooler (Nye County) conditions may be more resilient to climate impacts.

Current status of PENALB

The current status of PENALB, as informed by a 2021 range wide survey, is dire, with abundance in each population center much lower than observed in past assessments (Anderson 1998, Smith 2001, Etyemezian et al. 2010, Moore and Pavlik 2014, Moore and McIntyre 2015). Abundance in the Pisgah Cater population has declined dramatically since 1993, when the population was estimated to contain 4,420 individuals (Sheldon 1994). While abundance in this population has fluctuated since then with wet and dry years, abundance has been nowhere near even 1,000 individuals (Moore and Pavlik 2014), and the 14 plants observed in 2021 was the lowest abundance observed to date. Abundance in the Clark County population was estimated as 125,825 plants in 2009 (Etyemezian et al. 2010). Our rough estimate of abundance for Clark County in 2021 was 33,735 plants. Abundance in Nye County was estimated as 78,954 plants in 2009 (Etyemezian et al. 2010). Our rough estimate of abundance for Nye County in 2021 was 34,606 plants. Smith (2001) estimated 100,000 plants occurred over the Dutch Flat population; our survey only took place on public land, and did not cover 25% of occurrences, but we

observed only 189 PENALB plants in 2021, and these were found among a matrix of developed land parcels.

In addition to very low abundance in 2021 among all population centers, PENALB did not successfully reproduce across its entire range. Flowering was essentially absent in all populations except for Dutch Flat, and even at Dutch Flat, all plants were decimated by herbivory or had senesced before fruit production could occur.

The abundance and phenology data collected across the range of PENALB in 2021 are an important snapshot of PENALB responses to extreme drought conditions, and confirm that population responses to drought (low emergence rates, lack of reproduction and recruitment) observed in long-term demographic monitoring of Pisgah Crater and Clark County, apply to the population as a whole. However, while our results provide an important ‘worst case scenario’, given that much higher abundance is expected during years with more precipitation, they do not present a complete picture of the status of PENALB.

Differences among population centers

Current Status

The 4 population centers of PENALB differed in terms of abundance in 2021, life stage distribution and phenology, habitat, threats and climate. Data on reproduction were too sparse to accurately examine differences in reproductive attributes among populations. Plants were small in all populations in 2021, with most individuals smaller than 20 cm in diameter. While climate trends across the range of PENALB are similar, with all populations experiencing the effects of drought and warming in a given year, the magnitude of these trends is different among populations. Dutch Flat and Nye County, which are respectively the wettest and coolest population sites, had more emergent plants, and Dutch Flat was the only population with significant flowering observed in 2021.

Population Persistence

Long-term demographic monitoring

Population decline was also observed in long-term (10-12) years of monitoring of the Pisgah Crater and Clark County populations. Reflecting harsher climatic conditions, population growth rates at Pisgah Crater were lower than at Clark County; this, coupled with a much smaller population size, means this population is at the highest risk of quasi-extinction in the near future. High rates of dormancy during periods of climatic stress, with higher longevity of adults in the Clark County population, made population growth rates higher in Clark County relative to Pisgah Crater.

A lack of reproduction and low seedling recruitment in dry years is limiting population growth and persistence in both populations. No population specific per plant seed production data were available for the Clark County population, and seedling counts among the monitoring transects may have been underestimated. Experimentally increasing the seed to seedling transition rate in matrix projection models for the Clark County population to the rate estimated for Pisgah Crater resulted in a positive stochastic population growth rate for this population.

Accurate fecundity rates collected over multiple precipitation regimes in this population will allow for refinement of population viability models.

Quasi-extinction estimation in the 4 population centers, based on 2021 population vectors, and mean matrices from the Clark County and Pisgah Crater datasets, show all 4 monitored populations have a significant (50%-100%) probability of extinction within 50 years, with quasi-extinction likelihood higher with increased drought frequency.

Threats to persistence

Climate change

Global climate change is the most pervasive threat to the long-term persistence of PENALB, with impacts observed throughout the range of the species in 2021, and documented in 2 long-term demographic studies in 2 of its population centers. 2021 was 1 of the driest and warmest years on record for the Mojave Desert, with the entire range of PENALB in Extreme to Exceptional Drought status (Drought.gov 2021). Consequently, PENALB emergence was very low relative to historic records throughout its range. Dutch Flat AZ and Nye County NV are respectively wetter and cooler relative to the Pisgah Crater and Clark County populations, and the ameliorating effects of these conditions were seen in the 2021 survey, with over a thousand emergent plants observed in April at Nye County, and over 100 at Dutch Flat. However, by June all emergent plants had been decimated by herbivory or were senescent, and no successful reproduction was observed for the entire population in 2021. Very low emergence, failure to reproduce and/or no seedling recruitment was also documented in the Pisgah Crater population in 2002 and 2012, and in the Clark County population in 1996, 1998 and 1999.

Climate change, with increased heat and aridity, is already impacting Mojave Desert region ecosystems and species (e.g., Munsen et al. 2015, Wuebbles et al. 2017, Riddell et al. 2021, Wilkening et al. 2021). Climate change projections for the Mojave Desert region include increased heat, aridity, and increased frequency and intensity of extreme events including drought (Breshears et al. 2005, Archer and Predick 2008, McKechnie and Wolf 2009, Lenihen et al. 2003, Dominguez et al. 2010, Randall et al. 2010, Adlam et al. 2017).

Anecdotal observations saw widespread mortality of even common species in the Mojave Desert in 2021, and large-scale die off of common vegetation in response to drought has been observed over the last 3 decades (e.g., Mueller et al. 2005). Impacts on rare species, with small populations and/or limited range sizes already under pressure from anthropogenic threats, are likely to be critically threatened by climate change. Wilkening et al. (2021) found most federally listed plant species in the Mojave Desert are moderately to extremely vulnerable to climate change. Population viability analysis of the rare Sonoran Desert shrub *Purshia subintegra* showed slowing declining populations with higher risks of extinction with increased aridity (Maschinski et al. 2006). Demographic monitoring and PVA of the Endangered Sonoran Desert *Corypantha scheeri* var. *robustispina* found that the species is declining within its survey area, and projected to rapidly decline in coming years, likely due to climate change impacts (Molano-Flores et al. 2021).

The ability to maintain periods of dormancy for 1 to several years provides some buffering for PENALB populations to withstand unfavorable climatic conditions, as with many other species adapted to the inherent climatic variability of dryland ecosystems (e.g., Chesson et

al. 2004, McCluney et al. 2011). Dormancy is a relatively common feature of geophytes such as PENALB, and is often associated with drought or other environmental stress (e.g., Lesica and Steele 1994, Kery et al. 2005, Lesica and Crone 2007, Shefferson et al. 2017, Shefferson et al. 2018). Dormancy allows plants to avoid the costs of producing aboveground structures when resources are not available and when reproduction is unlikely to be successful, but it may come at a cost, such as reduced fecundity, regression in growth or reduced survival following dormancy (Lesica and Crone 2007, Shefferson et al. 2018). Dormant individuals in the Clark County population were more likely to re-emerge as small size class individuals, and had reduced rates of reproduction relative to plants that had not been dormant, but in favorable years could emerge as large size classes. Dormancy increased survival of Clark County individuals during periods of drought, with mortality in the Clark County population much lower than Pisgah Crater; survival and growth of dormant individuals had the biggest impact on population growth in this population. Many apparently dormant individuals were observed throughout the Clark and Nye County PENALB populations in 2021. No dormant individuals were observed at Dutch Flat, and how dormancy impacts population dynamics at Dutch Flat is unknown. Dormancy was not observed in the 1994-2004 monitoring at Pisgah Crater (Moore and Pavlik 2014), but did occur between 2011 and 2014 dormancy. Adding these years with dormancy increased the population growth rate for Pisgah Crater, and continued monitoring over the next 2 years may allow further quantification of dormancy rates for Pisgah Crater PVA models.

While dormancy has provided a buffer for PENALB to persist in the natural cycles of variation in moisture availability typical for the Mojave Desert, without recruitment population growth rates are ultimately on a declining trajectory, even with high rates of dormancy. Increases in the frequency and severity of drought may inhibit adequate population growth in response to larger precipitation events, and further reduce the ability of populations to grow and persist (Chesson et al. 2004, McCluney et al. 2011).

Herbivory

Extreme drought also appears to increase herbivore impacts on PENALB, with catastrophic herbivory observed on the 2 population centers with widespread emergent plants in 2021, and observed at the Pisgah Crater population during demographic monitoring. Protection from herbivores increased seedling survival and seed production in the Pisgah Crater population, even during a drought year, and increased projected population growth rates (Moore and Pavlik 2014). Mammalian herbivory was observed in 2021 at Pisgah Crater and Nye County, and active cattle grazing occurred throughout the Dutch Flat AZ population. Severe impacts from mammalian herbivory, particularly black-tailed jackrabbits (*Lepus californicus*) have been documented on a number of rare Mojave Desert plant species (e.g., Pavlik and Moore 2011).

In addition to mammalian herbivory, we observed complete decimation of PENALB plants in the Dutch Flat population by desert leafcutter ants. We did not observe ant activity at other population sites in 2021, and could not find references for ant foraging impacts on PENALB or other *Penstemon* species. It is unknown whether the behavior we observed was a chance event or a regular occurrence, or whether it impacts other PENALB sites. Desert leafcutter ants are more common in the Sonoran Desert, but do extend as far as Southern California. Leafcutting ants may be more abundant in areas with increased disturbance such as roadsides (Schowalter and Ring 2017).

Species interactions, including plant-herbivore interactions, are likely to change with the disturbances caused by global climate change (Tylianakis et al. 2008, Hamann et al. 2020), and

these changes may be accelerated in desert ecosystems where species are already on the edge of climate extremes (McCluney et al. 2011). Although the way interactions change may be highly variable, herbivory intensity frequently increases under drying and warming, switching from a neutral effect in periods of adequate moisture availability to a deleterious effect during periods of low moisture availability (Tylianakis et al. 2008, McCluney and Sabo 2009, McCluney et al. 2011). Generally, the effects of climate change have been shown to increase foliar herbivory in plant-insect interaction (Hamman et al. 2020). If drought occur after periods of good moisture availability, during which herbivore numbers may increase due to high availability of resources, the effects of herbivory may be particularly severe (McCluney et al. 2011); this pattern has been observed impacting multiple rare plant species at Ash Meadows National Wildlife Refuge (Miller 2020).

Invasive species

Invasive species were widespread in all populations except for Dutch Flat. Mediterranean grass was the most prevalent, present at nearly every site visited in the Pisgah Crater, Nye County and Clark County populations. Generally, cover of Mediterranean grass was low, but given the very dry conditions of 2021, is likely to be much higher in years with more precipitation. High cover of Mediterranean grass in wetter years could compete with PENALB seedling establishment. High cover of Mediterranean grass may also promote fire in creosote bush habitat; to our knowledge, fire has not been documented in PENALB habitat and the effects of fire on the species are unknown. Asian mustard skeletons were locally dominant in areas of Pisgah Crater, and in parts of the Hidden Valley subpopulation in Clark County. The density of Asian mustard observed has the potential to dominate resources and inhibit PENALB establishment and possibly reduce fitness. Russian thistle was present in Hidden Valley, though at low abundance in the dry conditions of 2021. This species has the potential to become dominant, especially in disturbed, sandy substrates that are typical of many PENALB locations.

Anthropogenic threats

Off-highway vehicle use was observed in most PENALB survey locations except for Dutch Flat, and was especially prevalent in Clark County and Pisgah Crater. Motorcycle trails directly through PENALB subpopulations were observed frequently in Clark County. The disturbance from OHV use has the potential to directly impact plants, as well as reduce habitat quality through loss of vegetation and soil stability. Cattle grazing was prevalent in the Dutch Flat population, with trailing and trampling impacts observed within surveyed sites. Cattle grazing of PENALB individuals did not appear to be widespread, but trampling could damage plants and compress soils, making them less suitable for new plant establishment. Urban development in the Dutch Flat population was significant, and increased roads, development, and overall use of the area is reducing the habitat available for PENALB, and reducing population abundance. Energy infrastructure occurs throughout the Pisgah Crater and Clark County populations; with energy corridors and maintenance roads running through these populations. Two historic locations of PENALB in the Roach Lake South area appear to have been extirpated due to pylon construction. Large solar field have been erected in areas surrounding the Clark County population, and are under consideration for Pisgah Crater.

Recommendations

Survey and demographic monitoring in average to high rainfall years

The current status of PENALB, as informed by our 2021 range wide survey, is dire, with abundance in each population center much lower than observed in past assessments (Anderson 1998, Smith 2001, Etyemezian et al. 2010, Moore and Pavlik 2014, Moore and McIntyre 2015). However, abundance is likely to be much higher in average and good years, and additional survey is required to capture these conditions. Population-specific vital rates for the Dutch Flat and Nye County populations are likely to be different in the more benign environmental conditions that these populations occur in, and are necessary to build accurate PVA models for these populations. Population viability assessment that incorporates the spatial variability among and within PENALB populations would provide a more accurate picture of the overall risk of extinction to PENALB. Fecundity estimates, including seeds per fruit and seeds per inflorescence are necessary for Nye County, Clark County and Dutch Flat, to build more accurate PVA models. Additional survey and demographic monitoring in years with a range of precipitation conditions, and especially during years with higher rainfall, is recommended to provide a complete understanding of the current status of PENALB.

Management

Population viability assessment provides an excellent experimental framework for evaluating management actions (Caswell 2001, Morris and Doak 2003, Knight 2012, Regan et al. 2016), as was demonstrated by herbivore caging experiments in the Pisgah Crater population (Moore and Pavlik 2014). Herbivore cages were shown to improve plant survival in the short term at Pisgah Crater (Moore and Pavlik 2014), and in the long-term, with most observed plants at Pisgah Crater in 2021 either within or near cages erected in 2011. Our LTRE showed that management that increases the seed to seedling transition rate will increase population growth rates. This, with the severe herbivory effects observed in 2021, indicate that caging should be trialed at the other 3 populations to determine how protection from herbivory may increase reproductive output and recruitment.

The Clark County population already has fencing that excludes OHV and grazing from some transect locations; population transition rates and growth could be compared in areas protected from OHV versus not (e.g., Maschinski et al. 2003), and OHV protection could be implemented at Pisgah Crater and Nye County. Similar experiments could be done with cattle grazing excluded from Dutch Flat monitoring sites.

Transition rates and population growth rates in occurrence sites with abundant invasive species infestations versus no or low levels could be compared.

Conclusion

PENALB is imminently threatened by climate change across its range, with additional anthropogenic stressors in each of its 4 population centers. Management that seeks to mitigate disturbances that can be controlled, such as OHV use, herbivory and cattle grazing, additional development in PENALB habitat, should be implemented, and evaluated with a PVA framework

that can use the monitoring sites established here and described in Moore and Pavlik (2014). Additional survey and monitoring in years with average and above average precipitation are necessary to comprehensively describe the current status of PENALB across its range.

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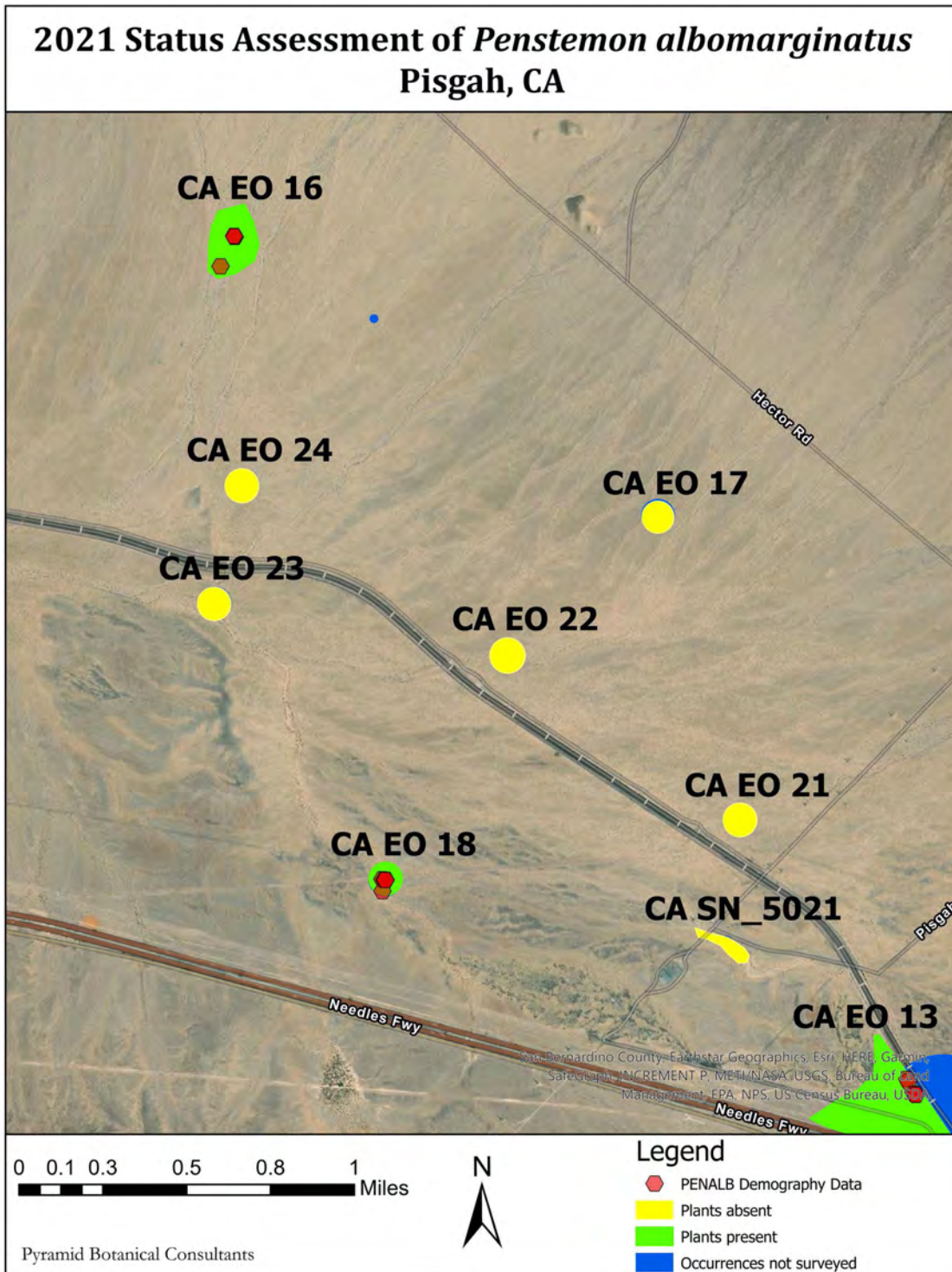
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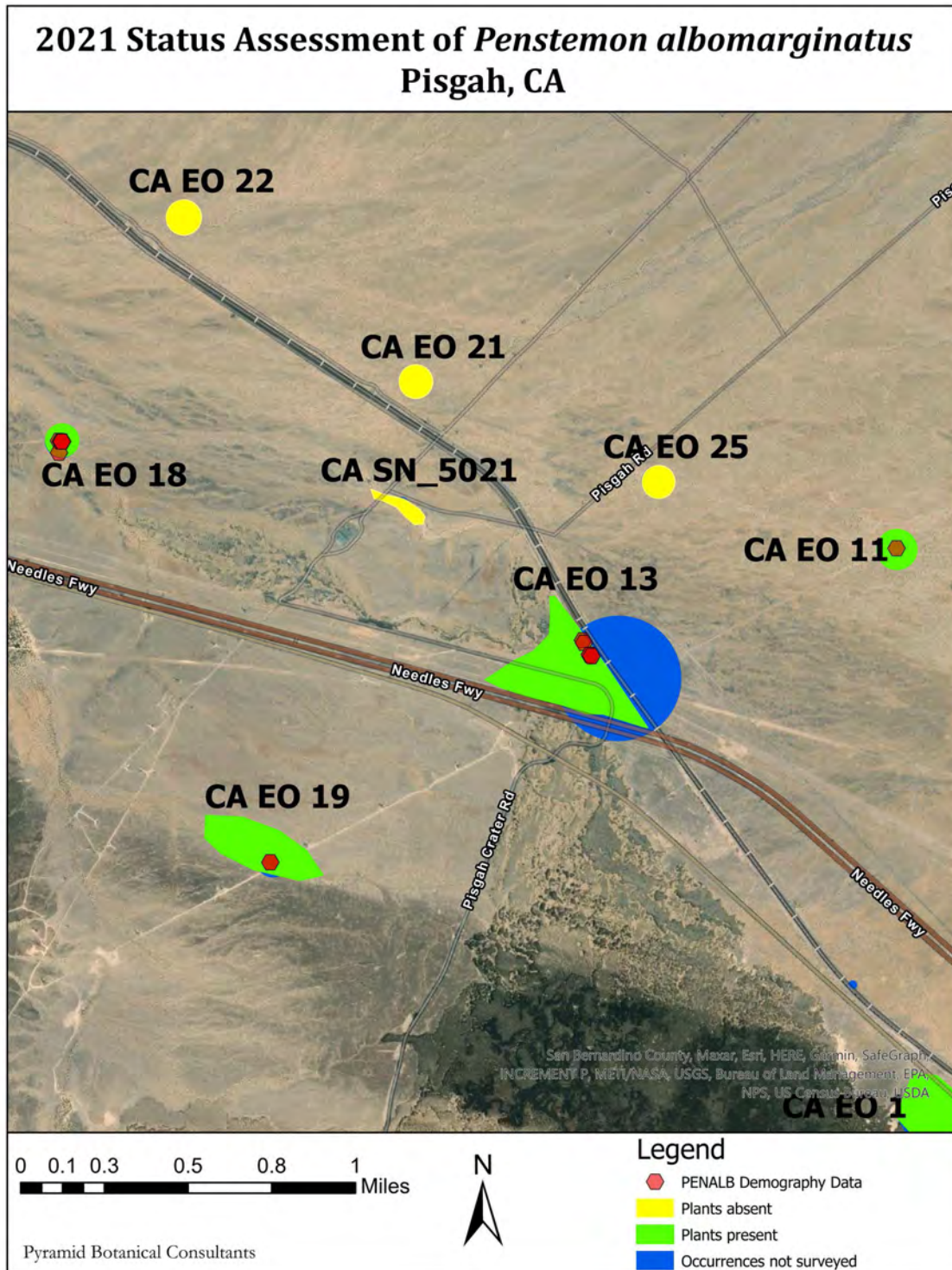
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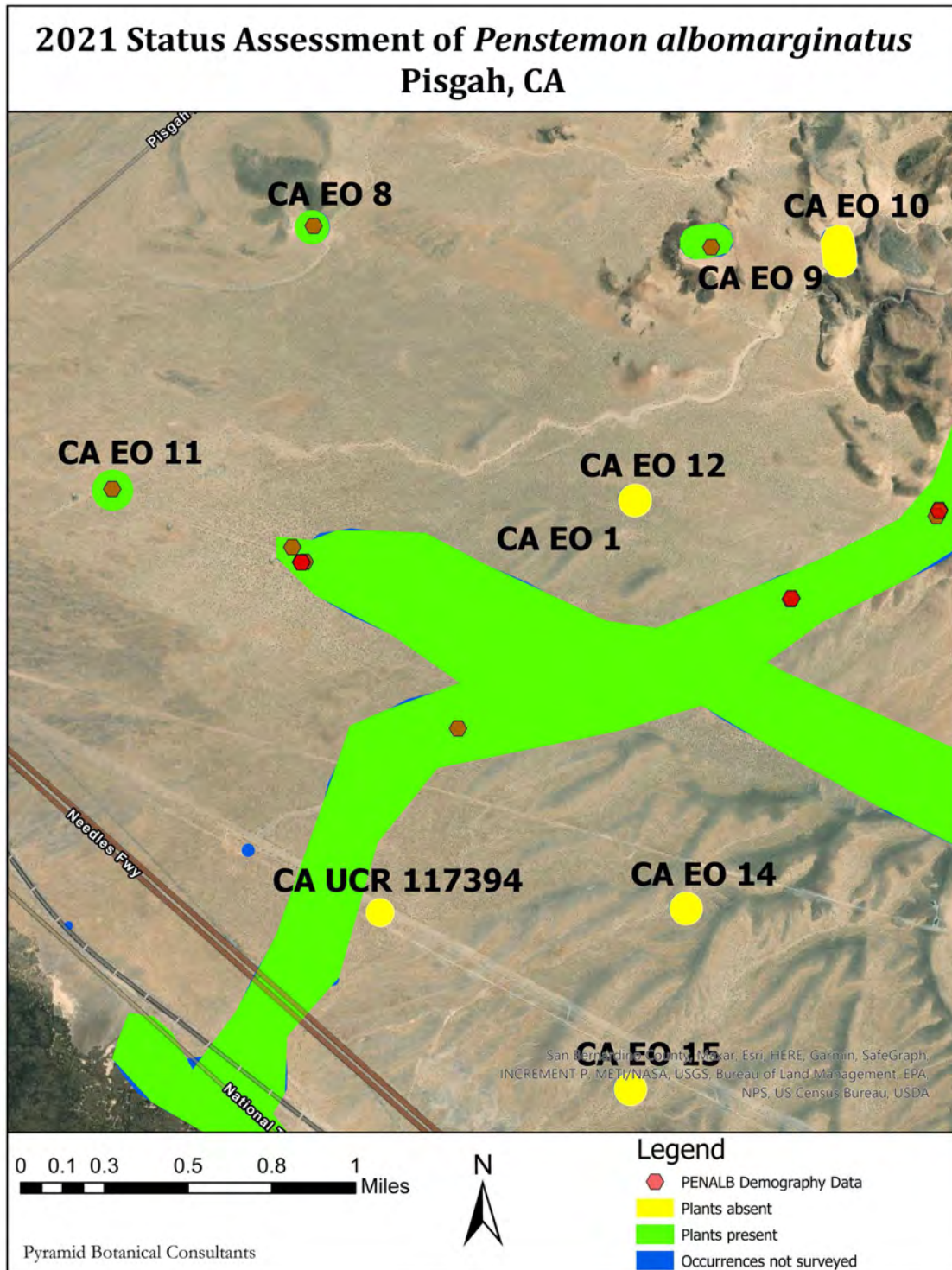


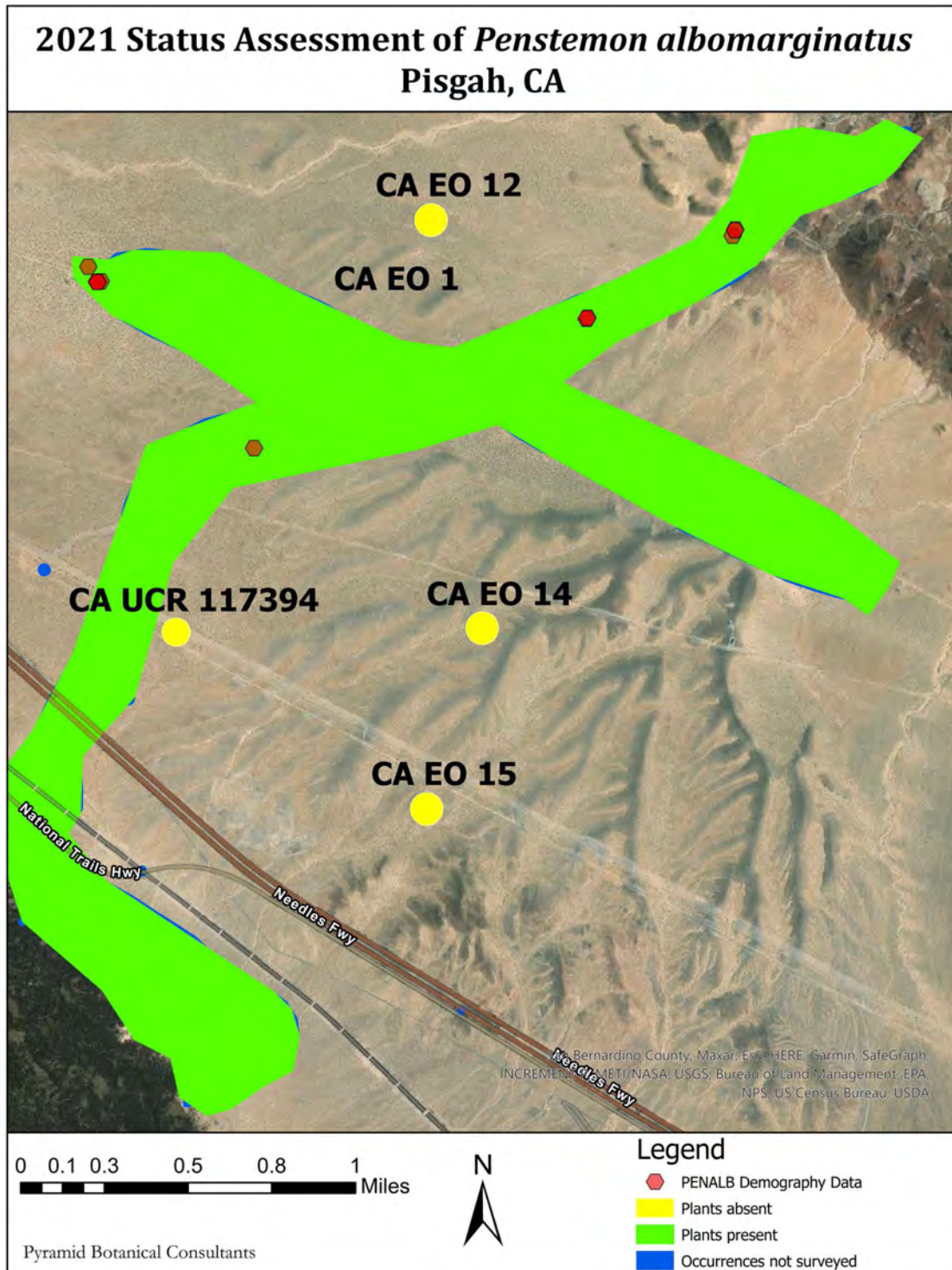
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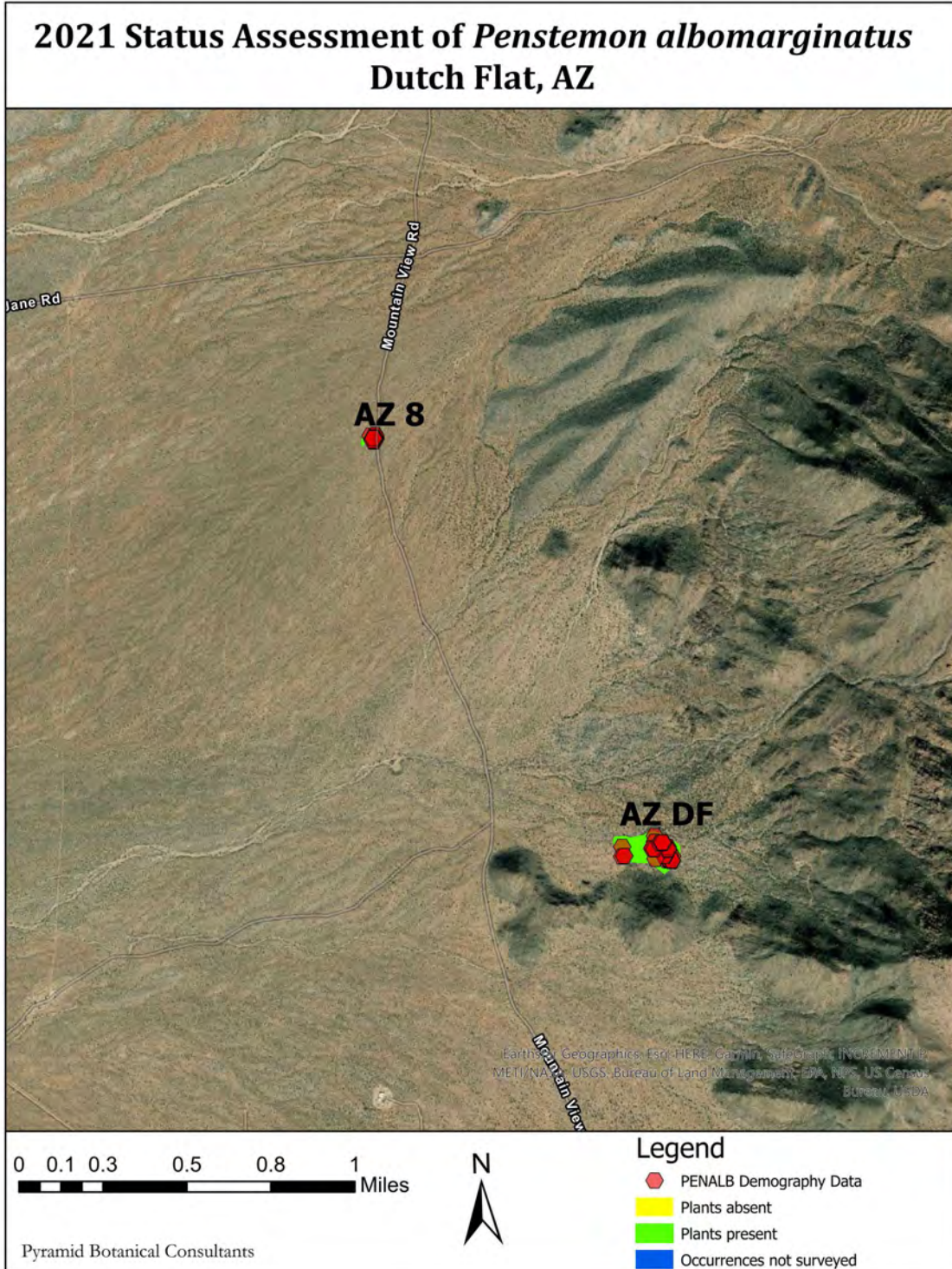
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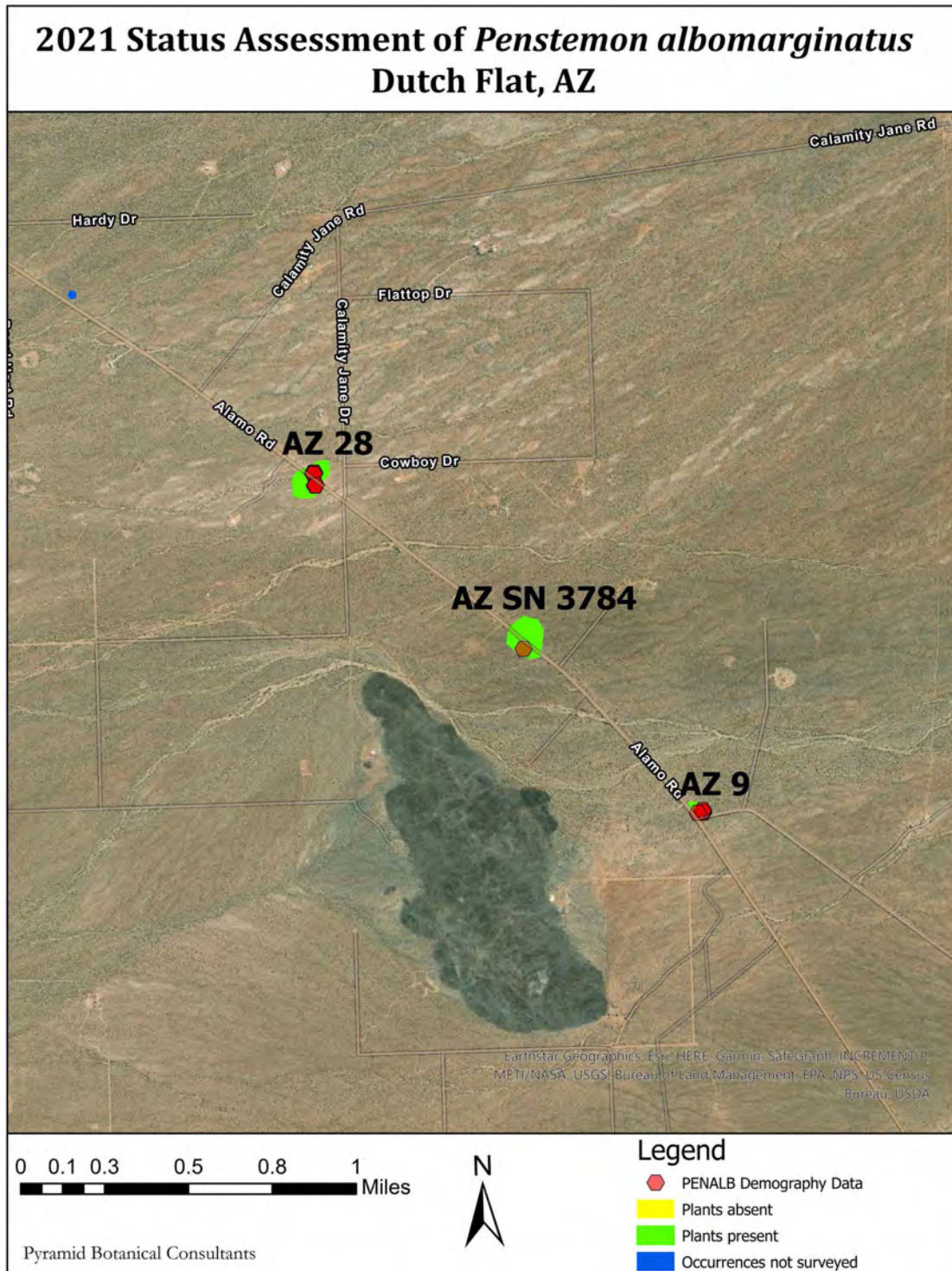




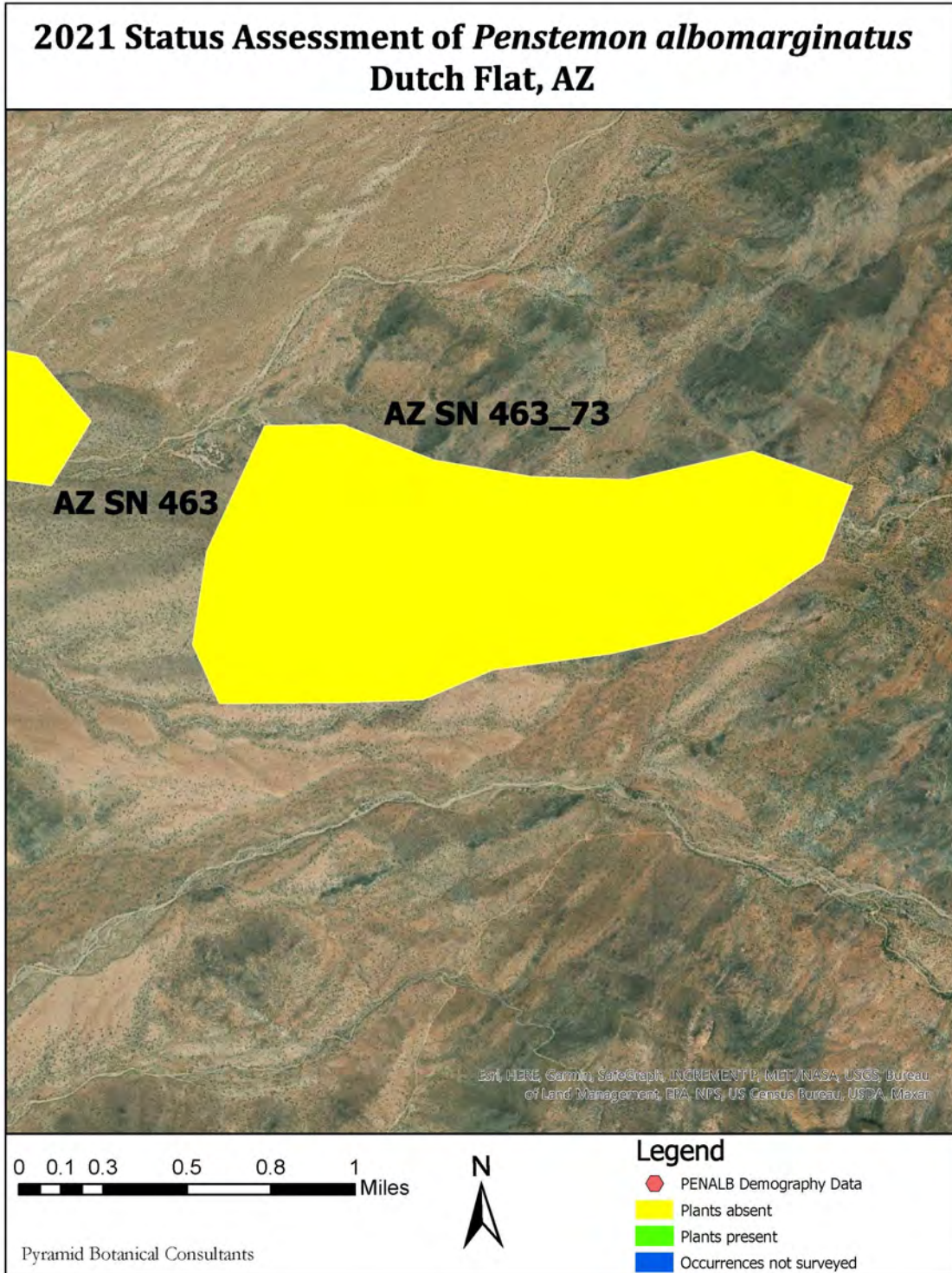


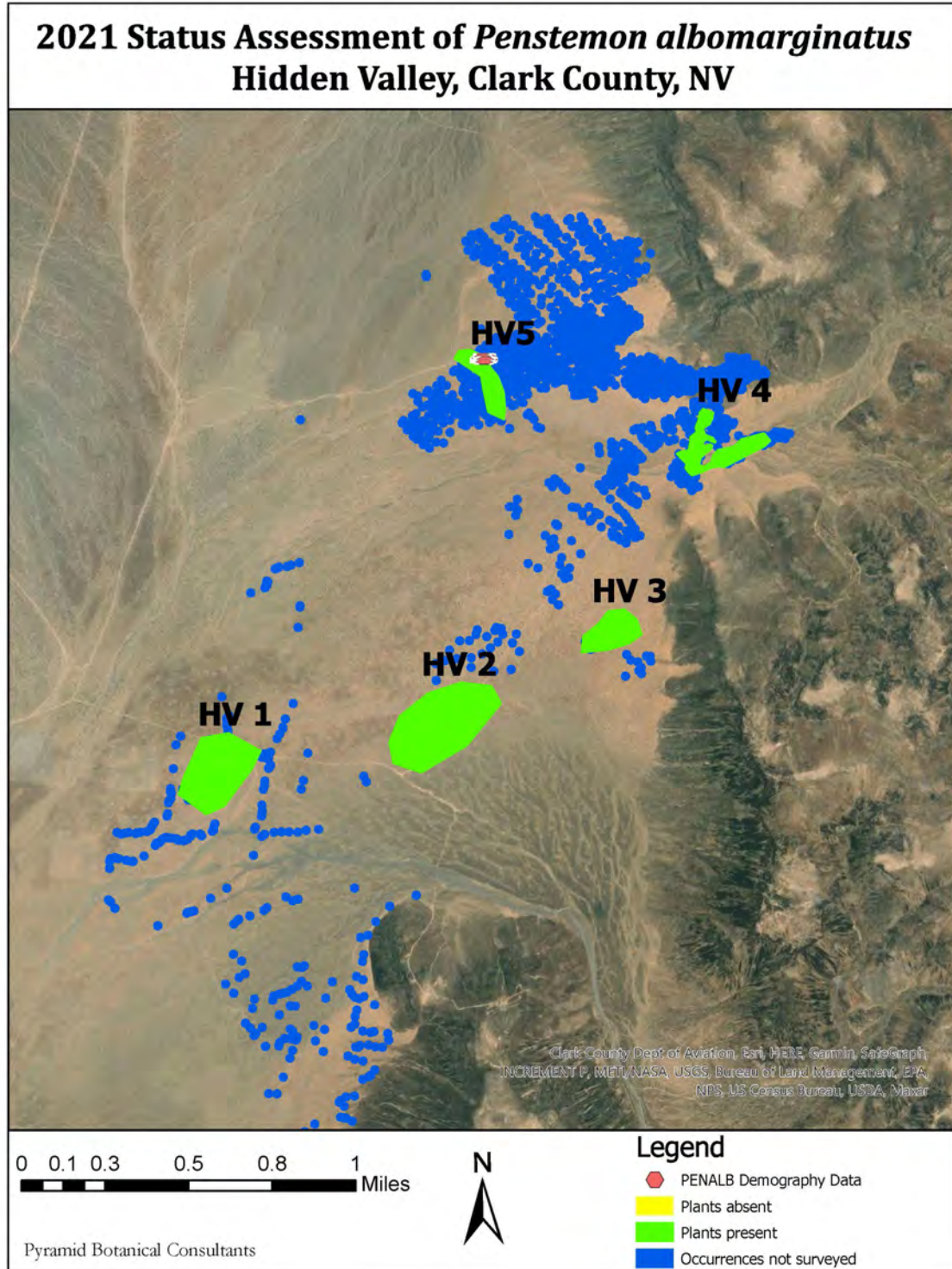




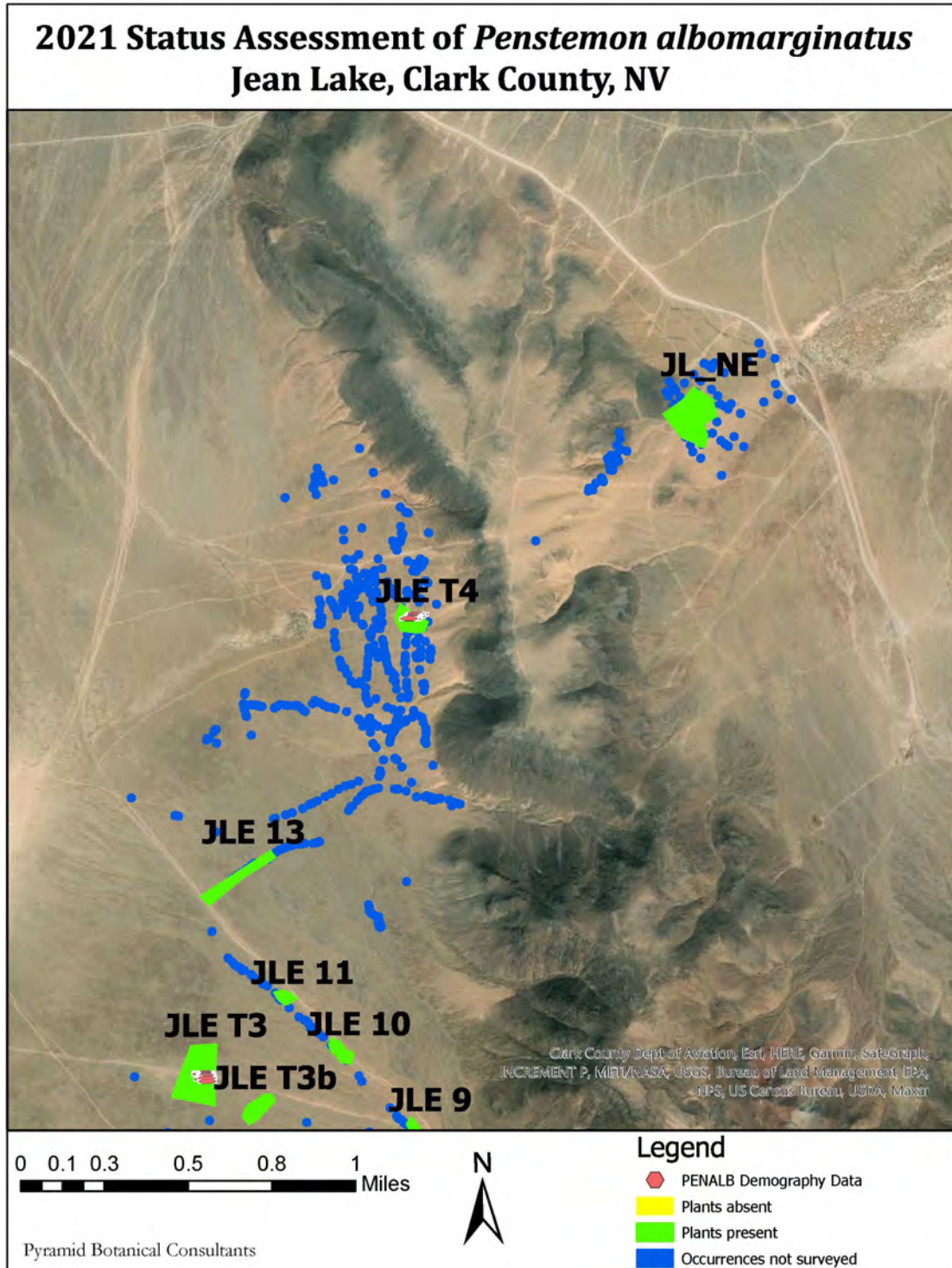


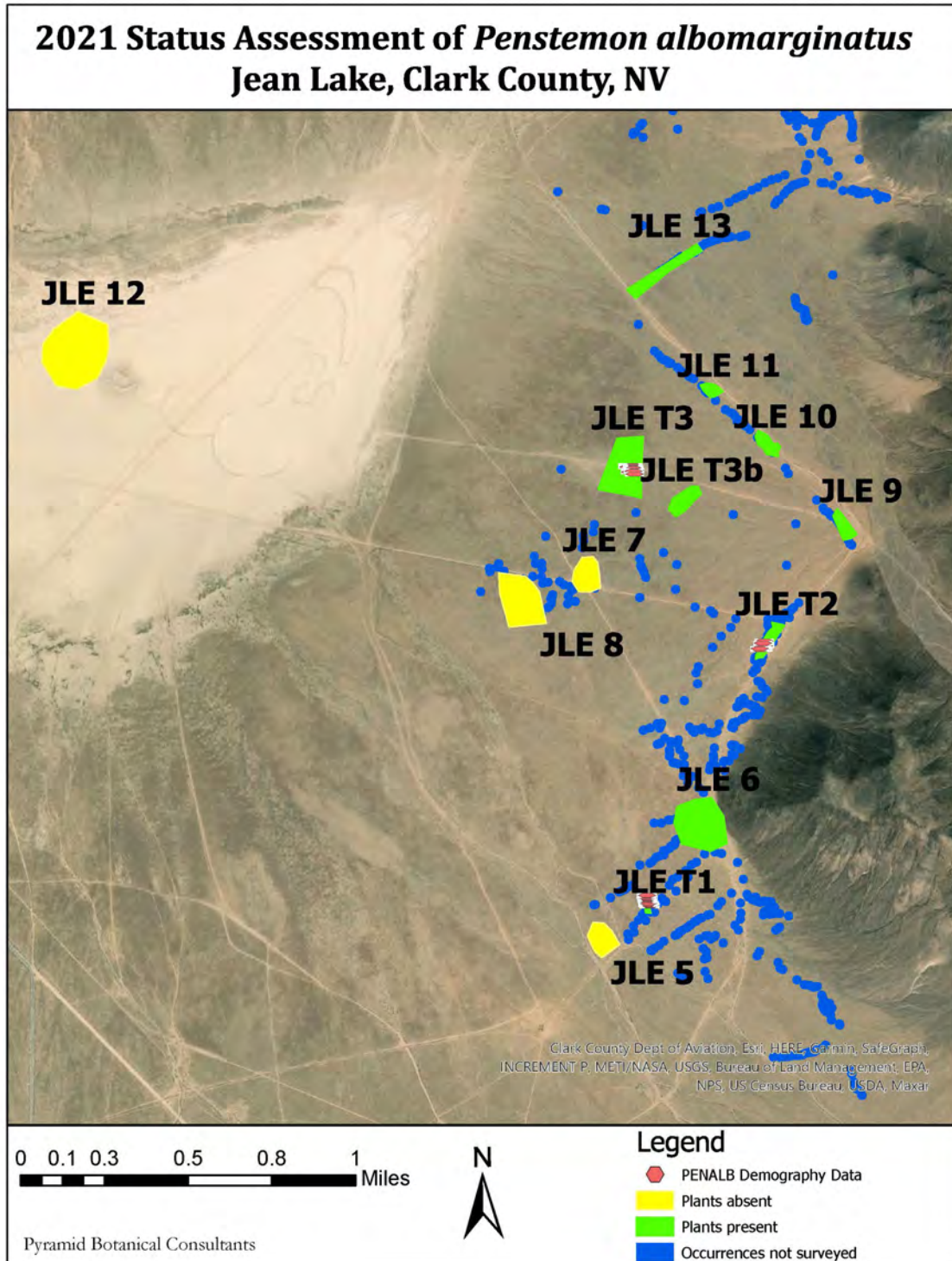


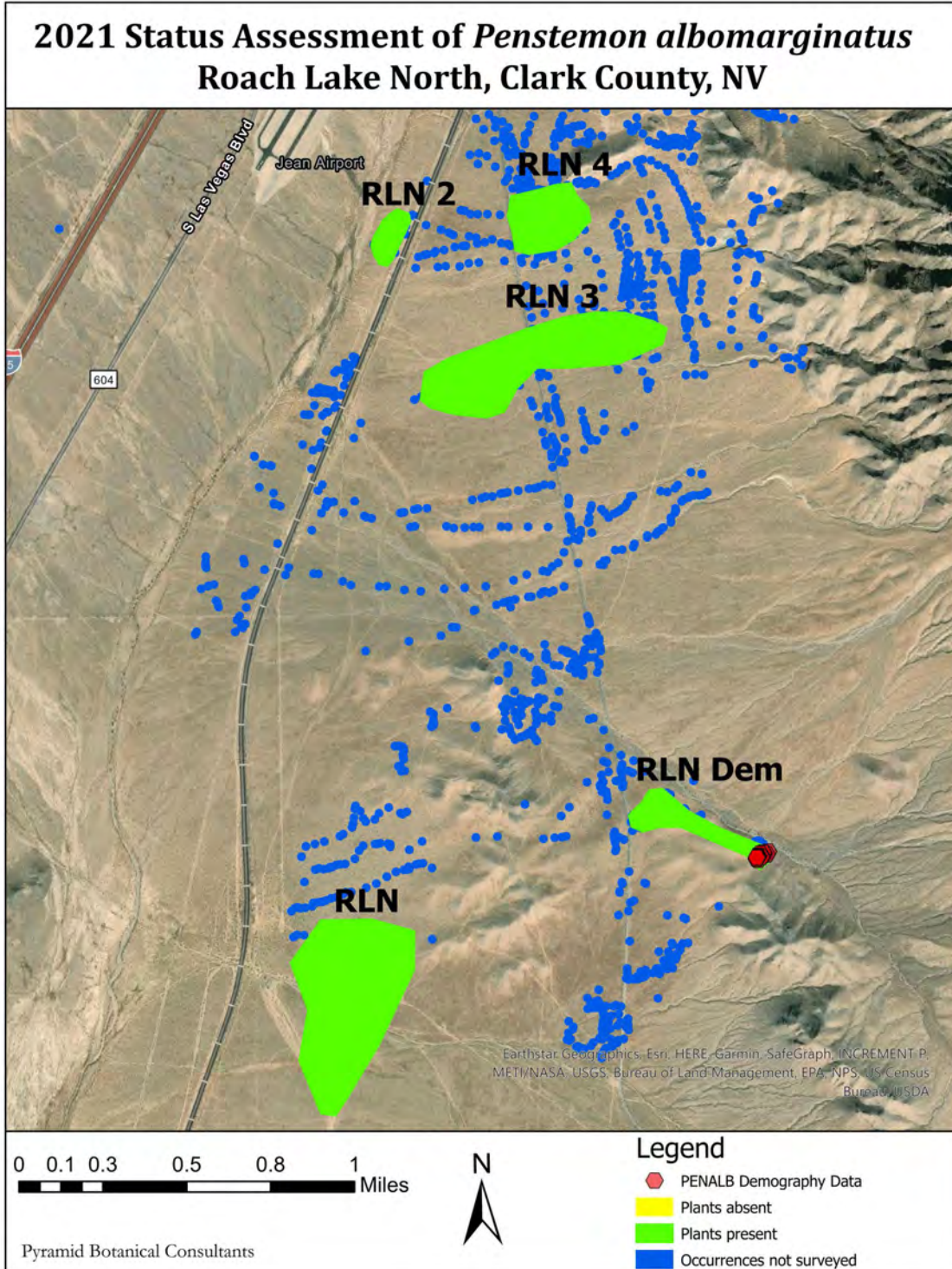


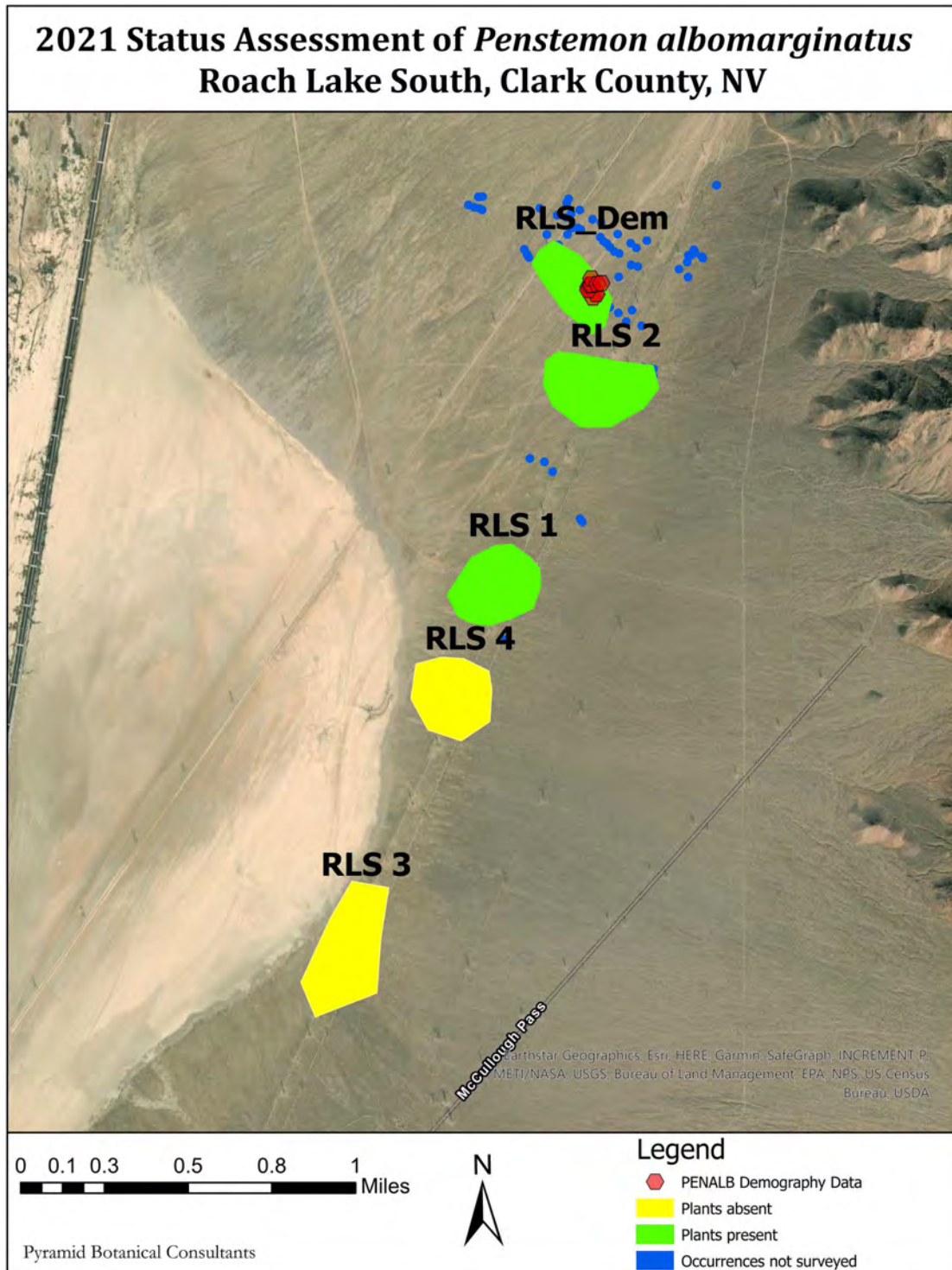


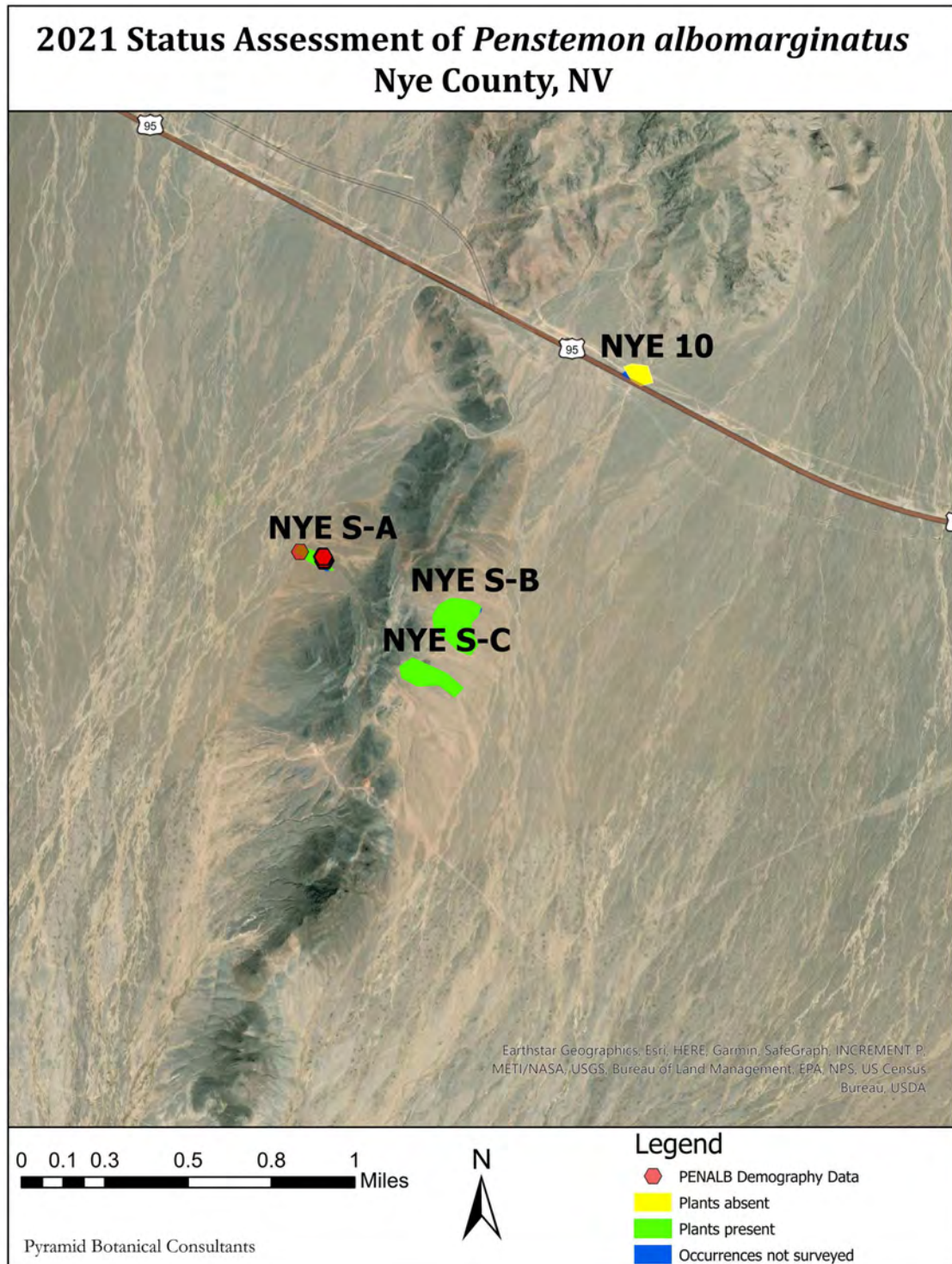


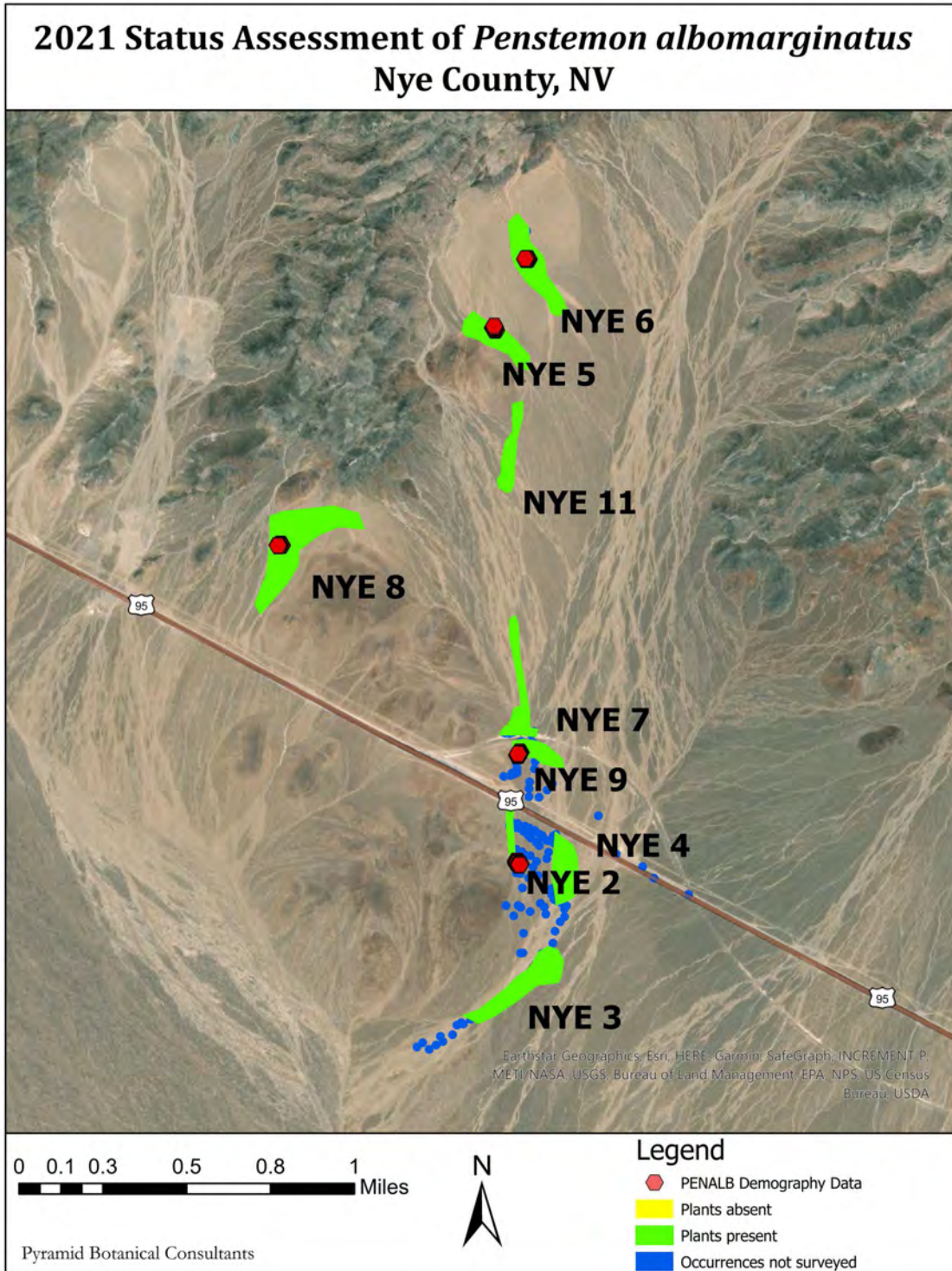














Appendix B

Supplemental Results

Table B1. Best-fit generalized linear mixed effects model of PENALB survival in the 1996-2006 Clark County demography dataset, with initial stage and winter precipitation as fixed effects and transect included as a random effect.

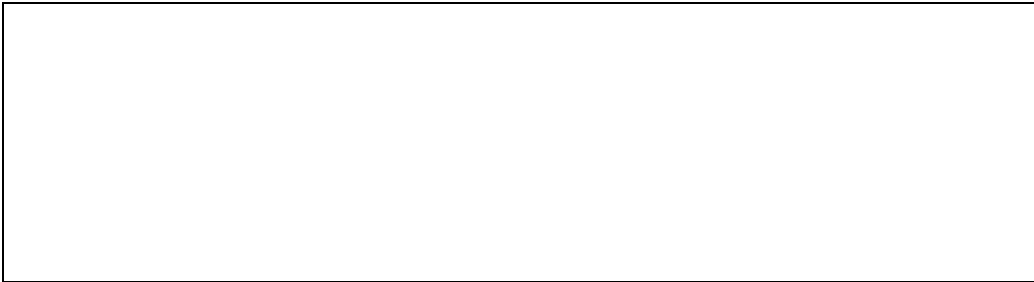


Table B2. Best-fit generalized linear mixed effects model of PENALB dormancy in the 1996-2006 Clark County demography dataset, with initial stage and year pairs as fixed effects and transect included as a random effect.

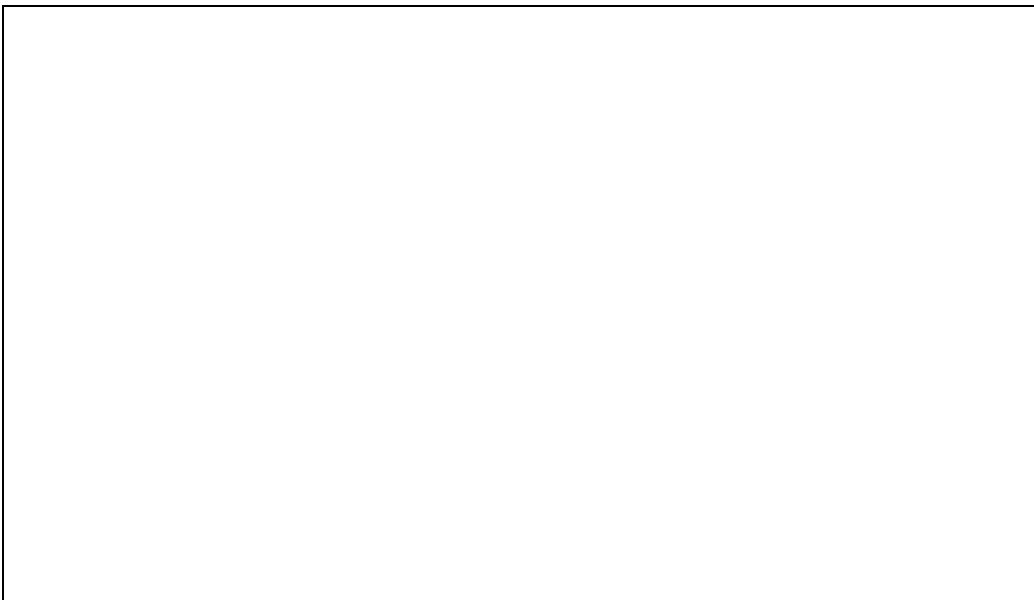


Table B3. Best-fit generalized linear mixed effects model of PENALB probability of reproduction in the 1996-2006 Clark County demography dataset, with initial stage and year pairs as fixed effects and transect included as a random effect.

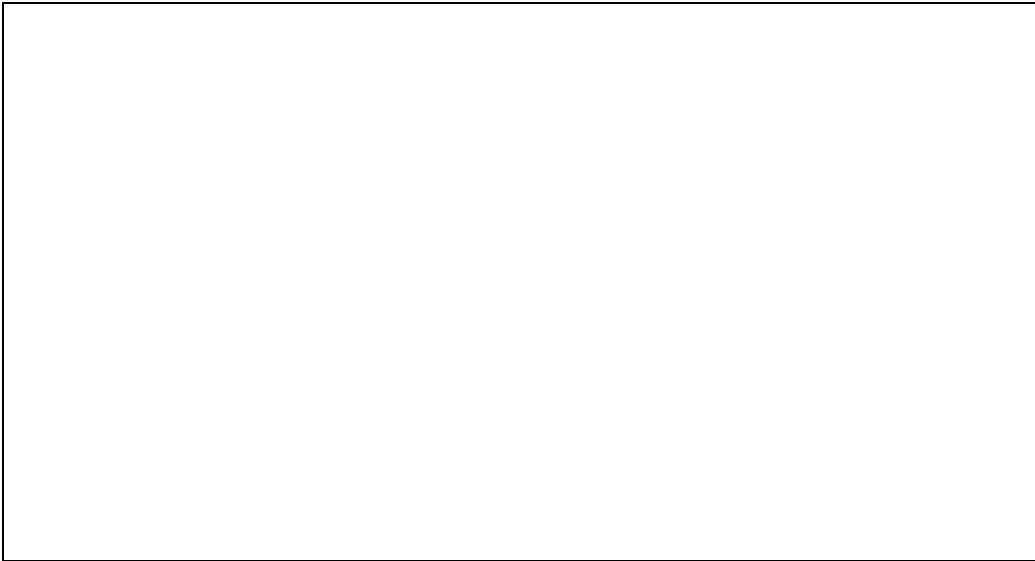


Table B4. Best-fit generalized linear mixed effects model of PENALB probability of reproduction in the 2021 Dutch Flat demography dataset, with stage as the fixed effect and survey site as the random effect.

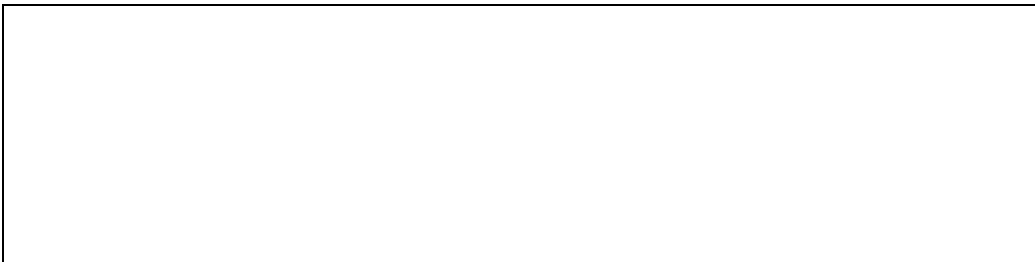


Table B5. Best-fit generalized linear mixed effects model of total reproductive output (sum of buds and flowers) observed in April in the 2021 Dutch Flat demography dataset, with stage as the fixed effect and survey site as the random effect.

