Growth and Mortality in the Endangered Nichol's Turk's Head Cactus *Echinocactus horizonthalonius* Var. *nicholii* (Cactaceae) in Southeastern Arizona, 1995–2008

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GROWTH AND MORTALITY IN THE ENDANGERED NICHOL'S TURK'S HEAD CACTUS *ECHINOCACTUS HORIZONTHALONIUS* VAR. *NICHOLII* (CACTACEAE) IN SOUTHEASTERN ARIZONA, 1995–2008

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Abstract—Nichol's turk's head cactus *Echinocactus horizonthalonius* var. *nicholii* (Cactaceae) occurs in a few isolated populations in the Sonoran Desert of south-central Arizona (Pima and Pinal counties) and in one isolated population in Mexico. Populations of this variety are disjunct from the more widespread typical variety (*E. h.* var. *horizonthalonius*) that occurs in the Chihuahuan Desert of New Mexico, Texas, and Mexico. Variety *nicholii* occurs almost exclusively on Horquilla limestone substrate, and was federally listed as endangered in 1979. Since 1995, we have monitored study plots of this cactus in the Waterman Mountains, Pima County, Arizona, 32°20′N, 111°28′W, elevation 975 m, measuring size of plants, condition, and presence-absence of reproduction in ca. 200 individuals. Here we report data for 1995–2008. Rates of growth were slow, averaging 0.35 cm (*SD* ± 0.53) in height and 0.26 cm (*SD* ± 0.28) in diameter/year. Plants usually began flowering when they reached about 4 cm in height and 8 cm in diameter. Of 109 deaths recorded since 1995, 47% followed a visible decline in condition; the remainder of deaths were unanticipated. The study population declined from 129 individuals in 1995 to 89 in 2008.

Resumen—El cactus biznaga meloncillo *Echinocactus horizonthalonius* var. *nicholii* (Cactaceae) occurre en unas poblaciones aisladas en el desierto de Sonora en la zona sur y central de Arizona (condados de Pima y Pinal) y en una población aislada de México. Las poblaciones de esta variedad se encuentran geográficamente aparte de la variedad típica (*E. h.* var. *horizonthalonius*) que ocurre en el desierto de Chihuahua de Nuevo México, Texas, y México. La variedad *nicholii* ocurre casi exclusivamente en sustratos de caliza de Horquilla, y fue enlistada federalmente como una especie en peligro de extinción en 1979. Desde 1995, hemos monitoreado sitios de estudio con este cactus en las Montañas Waterman localizadas en el condado de Pima, Arizona, 32°20′N, 111°28′W, con una elevación de 975 m, midiendo el tamaño de la planta, su condición y presencia o ausencia de reproducción en aproximadamente 200 individuos. Reportamos datos de 1995 hasta 2008. Las tasas de crecimiento fueron lentas, con un promedio de 0.35 cm (±0.53 *DE*) de altura y 0.26 cm (±0.28 *DE*) de diámetro/año. La floración regularmente ocurrió cuando las plantas alcanzaron una altura de 4 cm y 8 cm de diámetro. De las 109 plantas muertas reportadas desde 1995, 47% habían mostrado una decaída aparente en cuanto a la condición; el resto de las muertes fueron inesperadas. La población estudiada declinó de 129 individuos en 1995 a 89 en 2008.

Six described species of *Echinocactus* grow in southwestern USA and Mexico. Of the two varieties of *Echinocactus horizonthalonius* described by Benson (1969), *E. horizonthalonius* var. *horizonthalonius* is widely distributed on limestone and calcareous soils at elevations of 900–1,650 m in the Chihuahuan Desert of southern New Mexico, western Texas, and northern Mexico (Benson, 1982; Turner et al., 1995). Plants treated as *E. horizonthalonius* var. *nicholii* occur only in a few locations in southeastern Arizona and in one mountain range in northern Mexico. This variety occurs almost exclusively on Horquilla limestone substrate in the Upland Division of Sonoran Desert Scrub at elevations of 600–1,100 m (Turner et al., 1995). These populations are markedly disjunct, by ca. 400 km, from the closest known occurrences of the typical variety.

Chamberland (1995) believed that the two varieties might not be as distinct in morphology as once believed, but preliminary results from a morphological analysis by M. Baker (in litt.) suggested that *E. h.* var. *nicholii* is sufficiently different to support variety status. There is no genetic study of either variety.

The three populations in Arizona are on or near the Vekol Mountains in the Tohono O'odham Nation, Pinal County, on Koht Kohl Hill (also in the Tohono O'odham Nation), Pima County, and on and around the Waterman Mountains, Pima County. Land comprising the Waterman Mountains includes parcels belonging to or administered by the Tohono O'odham Nation, Arizona State Trust, Bureau of Land Management, and private landowners (including active mines). In 1988, the Bureau of Land Management created the Waterman Mountains Area of Critical Environmental Concern in part to protect the cactus, and in 2000, the Ironwood Forest National Monument (administered by the Bureau of Land Management) was created. This includes the entire Waterman Mountains Area of Critical Environmental Concern and additional federal, state trust, and private lands outside of the Tohono O'odham Nation in Pima and Pinal counties.

In 1979, *E. h.* var. *nicholii* was listed as endangered due to its limited range and known threats to its existence (United States Fish and Wildlife Service, 1979). The perceived threats at the time of listing were mining of limestone deposits, off-road vehicles, and collection of plants. The most recent review of status recommends that this plant should remain classified as endangered (United States Fish and Wildlife Service, 2009).

Threats more recently identified include immigrant activity, drug smuggling, and associated law-enforcement activities (these have a considerable impact because the Waterman Mountains encompass important smuggling routes). In recent years, the invasive plants *Pennisetum ciliare* (buffelgrass) and *Brassica tournefortii* (Sahara mustard) have begun to colonize the Waterman Mountains, creating a new threat to survival of this population of cacti, fire (Thornton, 2007). The invasive species also can outcompete native vegetation. Off-road vehicles are another threat that we have seen on site. Riding off-road vehicles off the roads of the Monument is prohibited, but such prohibitions are not always obeyed. Finally, there is the threat of prolonged drought enhanced by climatic change (Intergovernmental Panel on Climate Change, 2007; Seager et al., 2007).

Data on populations of this endangered plant are of interest to land managers and conservationists. Demographic studies of other cacti have shown that the transition that makes the greatest contribution to lambda, the asymptotic rate of population increase, is survival of mature adults (Godínez-Álvarez et al., 2003). In this, cacti are no different from other long-lived, iteroparous, perennial plants.

Since 1995, we have monitored ca. 200 individuals on four study plots in the Waterman Mountains of southeastern Arizona. Size of the population has been estimated at ca. 2,000 (United States Fish and Wildlife Service, 2009) to 10,000 plants (May et al., 1986). Here we present data on size, growth, reproduction, recruitment, and mortality during 1995–2008.

Materials and Methods—Our study site is in the Waterman Mountains, ca. 40 km WNW Tucson, 32°20′N, 111°28′W, elevation 975 m, Pima County, Arizona. Four study plots were created on either side of a dirt track along a distance of ca. 0.5 km. At this location, the track runs along a ridge ca. 215 m above the valley floor. For three of four study plots, we selected locations with different orientations. Plots also differed in degree of slope. In three plots, we determined borders and size using a random-number generator to avoid favoring plots with an unusually high density of plants. One plot (B), 176 m^2, is nearly level; N plot, 275 m^2, slopes steeply to the north; S plot, 92 m^2, slopes gently to the south. The fourth plot, SW, 555 m^2, sloping to the southwest, was selected for convenience along both sides of a section of trail. Total area under study was 1,120 m^2.

During the initial survey in autumn 1995, we marked plants using numbered aluminum tags threaded on nails forced into the ground. At each subsequent census (usually in January–March), if we found new plants, we tagged them and added them to the survey. We tagged 129 plants in the initial survey, and found 75 new plants over the course of the study. During each census, we recorded height and diameter of each plant to the nearest 0.5 cm, noted presence-absence of fruits, and noted condition of each plant. If fruits were present at the apex of a plant, we assumed that the plant flowered the previous summer. Because of logistical problems, we were unable to survey in 2002–2003 and 2007–2008. In 2004–2005, to save time, we measured a subset of plants in our plots. We believed that rates of growth of juveniles were of the greatest interest, and we measured plants that in the previous year (2003–2004) had heights $\leq$3 cm and diameters $\leq$7 cm.

During our surveys, we noted condition of each plant. In some instances, plants sustained obvious trauma, such as being chewed, losing whole ribs or sections, or being uprooted. Other conditions included discoloration of surface, evidence of desiccation, such as puckering or wrinkling, irregularities of surface, such as blistering or flaking, and patches of dead or necrotic tissue. In 2006, we began to photograph each plant during each survey, including newly dead plants. Of the 109 plants that died over the course of the study, no trace was found of 14. We made notes on condition and appearance of 68 of the remaining plants. In 27 instances, we neglected to describe remains other than to note that the plant was dead.

To calculate rates of growth, we first averaged growth per year for each individual. We then took an average across plants. Because we did not measure every plant every year, some measurements of growth span 2 years instead of 1 year. In these instances, we halved the amount of growth, and this was counted as one data point. We removed the following outlier measurements: shrinkage in height ≥5 cm (six measurements removed), growth in height ≥6 cm (five measurements removed), and shrinkage in diameter ≥3.5 cm (three measurements removed). Outliers in height were likely errors in measurement because of plants that were leaning, on a steep slope, or had erosion or buildup of soil at the base of plants. Measurements of diameter that were removed were likely observer error. In all, 14 of 2,236 measurements of growth were removed (0.6%).

Results—In 1995, 129 plants were tagged during the first survey. Six were not found after initial measurements; descriptions of their localities were not detailed enough to allow us to determine their fate, and their tags also were not found. Over the course of the study, 75 new plants were found and added to the study for a total of 204 plants. During the study, 109 plants died, including 77 (60%) of the original 129. The overall population declined from 129 in 1995 to 89 in 2008 (129 + 75 new − 6 missing − 109 deaths = 89). Of the 75 new plants found, 37 (44%) were small juveniles, diameter ≤3.5 cm, and these may be considered new recruits to the population.

Rates of mortality among different size classes did not differ significantly, suggesting that there was no size class that was particularly vulnerable. However, we probably did not find many of the smallest seedlings and, thus, we do not have good data on mortality of plants <1 cm in diameter.

During the study, we added 75 plants to the survey on discovery in our study plots. Of these, 10 were adults of reproductive size (diameter >7.5 cm) and 28 were juveniles (diameter 4–7.5 cm). Plants in both groups likely were overlooked in previous surveys. There were 37 new recruits to the population (diameter <4 cm). Of the new recruits, 23 (62%) were at the base of larger plants; the rest were in isolated situations. Range of densities of plants across plots and years was 0.03–0.29 plants/m^2.

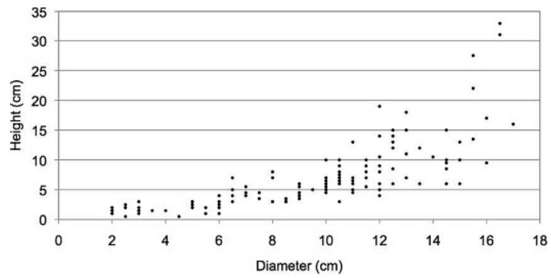

Fig. 1—Height and diameter of 129 Nichol's turk's head cacti *Echinocactus horizonthalonius* var. *nicholii* measured in the Waterman Mountains, Pima County, Arizona, 1996.

Plants were spherical when tiny (height and diameter <1 cm), later becoming flattened disks, and finally cylindrical to pyramidal as they matured. Diameter increased rapidly at first (until ca. 15 cm in diameter) then growth in diameter slowed (Fig. 1). Height continued to increase throughout life of the plant. Usually, height was greater than diameter in only the largest plants (Fig. 1). Height was greater than diameter in 15 (12%) of the 129 plants in Fig. 1.

Because growth in height continues indefinitely, whereas growth in diameter levels off, size classes based on height might be more useful than those based on diameter. However, it is easier to measure diameter more accurately than height. Measuring height was a painful challenge: plants had a dense crown of spines extending beyond the apex of the plant. Surface of the ground around plants was uneven and changed among years due to erosion, and plants often leaned significantly or grew between closely appressed and uneven rocks.

We depicted both size classes (height and diameter) to compare our data to those of Reid et al. (1983; Figs. 2a and 2b). Distribution of individuals among size classes based on height is similar for 1995 and 2008, although plants were more evenly distributed among size classes in 2008 than in 1995 (Fig. 2b).

Size at first reproduction is usually ca. 8 cm in diameter and 4 cm in height, although a few individuals as small as 6 cm diameter and 2 cm height had flowered (as determined by presence of a fruit or fruits at the apex). Therefore,

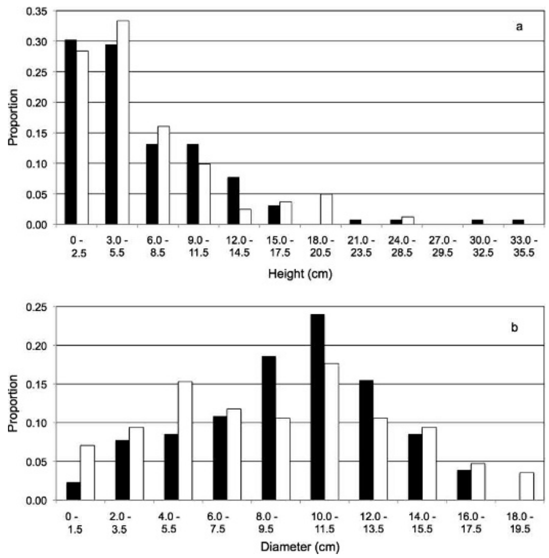

FIG. 2—Proportion of individual Nichol's turk's head cacti *Echinocactus horizonthalonius* var. *nicholii* studied in the Waterman Mountains, Pima County, Arizona, in size classes based on: a) height using intervals of 3 cm; b) diameter using intervals of 2 cm (1995, black bars, n = 129; 2008, white bars, n = 85).

individuals in height size class ≥2 and diameter size class ≥5 might be considered adults (Fig. 2). In any year, 50–88% of plants of reproductive size actually flowered (Table 1).

In total, we recorded 2,236 measurements of growth for 180 plants. Average number of years of measurements per plant was 6.2. Average growth in height was 0.35 cm/year (*SD* = 0.53, range = −2.5–3.0). Average growth in diameter was 0.26 cm/year (*SD* = 0.28, range = −0.5–2.0). Growth was highly variable from year to year, and in some years average growth per plant was negative (plants shrank in height, diameter, or both; Table 1). Rates of growth were not closely related to initial size (Figs. 2a and 2b), although growth in both height and diameter seemed to slow somewhat with increasing size.

During our surveys, we noted condition of each plant. Photographs illustrating these conditions are available on our website (http://indigo.cals.arizona.edu/turksheads/index.php). Commonly noted problems were signs of desiccation (shriveling, puckering), damage such as gouges or chewing, cuticle discoloration, necrotic flesh, and damaged or destroyed apex.

Over the 13 years of the study, 50 (47%) of the 109 deaths recorded were preceded by some problem in condition. In 10% of deaths, we found no remains, and in 25% of deaths, remains were more or less intact. In other deaths, remains were hollowed, torn apart, or only fragments or clusters of spines. Other circumstances associated with death included uprooted (four plants), eaten by rodents (three), and buried by rodent burrow or debris flow (two).

DISCUSSION—Reid et al. (1983) measured 174 individuals of *E. horizonthalonius* near El Paso, Texas, and created size classes based on 2-cm intervals of diameter (as we did). Distribution of individuals among size classes in their study was more irregular than on our plots, but in both studies, the proportion of individuals peaked in the size class of 10–12 cm diameter (Fig. 2b).

Previous studies have suggested that these plants require 10–32 years to reach a height of 5 cm (Arizona Game and Fish Department, in litt.). Extrapolating from our data for growth would give an age of 17 years for a plant 5 cm tall. These extrapolations are probably of limited value. For example, we noted that size at first reproduction is about 8 cm diameter and 4 cm height. Extrapolating from our rates of growth would give a cactus of this size an age of 14 years (based on height) to 44 years (based on diameter). May et al. (1986) suggested that plants of the same height and diameter might be different ages, and the high variance in rates of growth among individual plants that we observed is consistent with that suggestion. From our results, we can conclude that these plants grow slowly and take >10 years to reach reproductive size.

Because we only examined plants once a year in winter (≥6 months after flowering and fruiting), it seems likely that many fruits produced the previous summer had dispersed. Consequently, our data probably underestimated frequency of flowering. Our reported size at first flowering (8 cm diameter and 4 cm height) is larger (8 cm diameter and 2 cm height) than reported by the United States Fish and Wildlife Service (2009). It is reasonable to suppose that plants smaller than those we observed still bearing fruit in the winter have flowered and, thus, we might have overestimated size at first flowering.

Changes in height and diameter can be caused by changes in water status of the plant, but new areoles represent new tissue generated at the

Table 1—Annual precipitation (calendar year), growth, mortality, flowering, and size of samples of Nichol's turk's head cacti *Echinocactus horizonthalonius* var. *nicholii* in the Waterman Mountains, Pima County, Arizona.

Years[a]	Annual precipitation (cm)[b]	Mean growth in height (cm)	Mean growth in diameter (cm)	*n*	Number of deaths	Percent flowering
1995–1996	—	1.29	0.40	121	2	—
1996–1997	—	0.47	0.28	123	7	—
1997–1998	—	−1.36	−0.32	122	3	—
1998–1999	19.9 (1999)	0.39	0.47	118	7	—
1999–2000	35.0 (2000)	0.88	0.37	117	7	50
2000–2001	30.8 (2001)	0.67	0.29	116	2	70
2001–2003 (2 years)	11.1 (2002) 29.8 (2003)	−0.04	0.05	100	23	83
2003–2004 (only small plants were measured)	24.4 (2004)	0.51	0.61	40	14	65
2003–2005 (2 years, only large plants were measured)	—	−1.22	0.34	47	—	—
2004–2005 (only small plants were measured)	32.9 (2005)	−1.01	−0.22	43	5	88
2005–2006	27.1 (2006)	0.72	0.59	90	7	64
2006–2008 (2 years)	31.3 (2007) 31.5 (2008)	1.50	0.73	68	31	58

[a] Period between measurements at the end of the first year and the end of the second year.
[b] Measured at Silver Bell Mine, ca. 5 km NW of study plots, Pima County.

apical meristem. May et al. (1986) suggested that *E. h.* var. *nicholii* generates one new areole per rib per year. An alternate method for measuring growth would be to count number of new areoles that appear in a time period; perhaps, by marking the central spine of each cluster of spines (May et al., 1986). Our experience, however, suggests that this method is not practical. In any but the smallest of plants, the spines are too dense and interwoven to make it possible to find the central spine of each areole. Our study suggests that many new recruits to the population are seedlings that germinate at the base of the parent plant.

Our study was inspired in part by a monumental study of *Sclerocactus polyancistrus* following 350 individual plants over 15 years at six study sites (May, 1994). Of particular interest was the detailed analysis of causes of mortality. Careful observation and dissection of carcasses enabled the author to develop a unique system of classification of carcasses. Predation by small mammals resulted in open carcasses, in which the flesh of the plant was chewed, torn apart, or completely consumed, with mammal feces nearby. Closed carcasses could be attributed to infestation by insects, indicated by bore-holes, exit holes, and remains of pupal cells in the soil directly below the plant. Predation by mammals was more common than infestation by insects.

In our study, of the 68 plants whose appearance after death was noted, ca. 38% were more or less intact. In these instances, the plant was upright, in place, and apparently undisturbed and unharmed. These might be victims of infestation by insects. Dissection of living and dead plants would be needed to confirm possible presence of burrowing insects such as the cactus beetle (*Moneilema*, Cerambycidae). Although *Moneilema* has not been recorded on *Echinocactus*, it has been recorded as feeding on *Sclerocactus* (Kass, 2001) and *Ferocactus* (Clark et al., 2007).

During one year, our survey coincided with predation on two plants by small mammals. All that remained was the outer surface of the ribs with the clusters of spines attached, still in the shape of a living plant. The remaining flesh was green indicating that the herbivory was recent. We also documented nibbling of living plants, including size of teeth marks (small rodent).

One type of damage that we cannot explain is destruction of the apical meristem. We observed this type of damage on 21 plants (ca. 10% of the 204 plants). Plants can continue to live for years following this type of damage, but they cannot flower. Some carcasses were of standing intact plants that were hollow in the middle; perhaps, associated with this type of damage. We also observed plants with some spines chewed off, but we do not know if this is related to damage to the apical meristem.

Without further study, our notes on condition cannot accurately inform us about causes of death of plants in our study. For example, we classified wrinkling and puckering as signs of desiccation, but other signs such as discoloration of surface might also be due to desiccation. May (1994) reported that discoloration of stem was associated with infestation by insects. A distinction might also be made between proximate and ultimate causes of mortality; e.g., a plant weakened by drought might be more susceptible to infestation by insects. Finally, about one-half of plants that died during our study showed no evidence of distress during the previous year. This could suggest that predation caused the mortality, rather than environmental factors. However, environmental stressors could lead rapidly to necrosis and death. The fact that we observed plants only once a year, sometimes only once every 2 years, also makes it difficult to make conclusions about causes of mortality.

Short-term climatic stressors are a possible source of mortality in this plant. However, it is unlikely that extreme temperatures (not linked to drought) are a primary cause. Plants of *E. h.* var. *horizonthalonius* thrive near Rio Grande Village (elevation 564 m) in Big Bend National Park, Brewster County, Texas, where temperatures in May and June are higher than those in Tucson (National Park Service, http://www.nps.gov/bibe/planyourvisit/faq-4.htm). In addition, *E. h.* var. *horizonthalonius* also thrive in Las Cruces, Doña Ana County, New Mexico (elevation 1,219 m), where overnight low temperatures are on average below freezing for 3 months of the year (much colder than Tucson; Western Regional Climate Center, http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?nmstat). However, we do not know whether temperature constraints of *E. h.* var. *nicholii* are the same as those of *E. h.* var. *horizonthalonius*.

Rainfall might be more likely to be linked to growth and mortality. However, 2007 and 2008 both had high rainfall, but 2008 had a high number of deaths, even if divided by two to average over the 2 years (Table 1); 2005 had high rainfall and negative rates of growth. One possible correlation is the low rainfall of 2002 that was followed both by high deaths and low rates of growth. More years of data, plus the use of measures more meaningful than annual rainfall, such as the Palmer Drought Index (Pierson and Turner, 1998), would be needed to determine if climatic variables can be correlated with recruitment, growth, and mortality. Deaths were not correlated with rates of growth: 1998 had only three deaths, but negative rates of growth; 2004 had 14 deaths but one of the highest rates of growth in diameter; and 2008 had a high number of deaths, but good growth (Table 1).

To extend our knowledge of the demographics of this plant, the next step would be to collect data on reproductive output, seed bank (if any), rates of germination, and establishment of seedlings. This would enable us to use integrated projection models to predict rates of growth of populations and to determine sensitivities and elasticities of lambda to changes in demographic rates (Ellner and Rees, 2005; Miller et al., 2009). Traditional models of populations derived from matrices are not appropriate for long-lived, iteroparous, perennial plants, as they require using continuously varying traits, such as size or age, to classify individuals into arbitrary size or stage classes, which in turn creates potential artifacts that can influence output of models (Ellner and Rees, 2005). Methods using integrated projection models also can be extended to include factors related to dormant and active life stages, such as seed banks (Ellner and Rees 2005).

Even with 13 years of data, we still do not know much about regeneration cycles of this plant. For the saguaro cactus (*Carnegiea gigantea*), a plant that has an average lifespan of 125–175 years, 85 years of data were needed to detect the low-frequency (multiple-decade), high-amplitude peaks and troughs of regeneration (Pierson and Turner, 1998). For *E. h.* var. *nicholii*, which might have a lifespan of 35–95 years (United States Fish and Wildlife Service, 2009), we might need ≥30 years of data to get a good idea of patterns of regeneration. We do not know if regeneration occurs in distinct pulses, as it does for the saguaro cactus. Without such information, we cannot determine if the current steep decline in numbers we have observed is an irreversible trend. More importantly, we would need to collect data from other areas in the Waterman Mountains. In some areas, these plants appear to have lower mortality than those on our plots.

The number of plants in our study plots was declining. They grew slowly and they took >10 years to reach reproductive size. However, our study was limited to a few small patches of cacti, all in the same general area covering ca. 0.11 ha. Yet, the population in the Waterman Mountains is scattered across ca. 1,416 ha (United States Fish and Wildlife Service, 2009). Sources cited by the United States Fish and Wildlife Service (2009) suggest that our study area is one of the highest-density populations. To determine whether the entire population is declining would require systematic sampling across the population using standardized protocols. Comprehensive surveys have been attempted several times with limited success (United States Fish and Wildlife Service, 2009). Such a survey would be difficult to conduct. The terrain is rugged, access is limited and hazardous, and the plants are cryptic and unevenly distributed. In absence of systematic surveys that would sample the broader population, we cannot generalize from our plots to the entire population. However, our results indicate that current protected status is warranted and that these plants should continue to be monitored.

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