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Mortality of Adult Joshua Trees (*Yucca brevifolia*) Due to Small Mammal Herbivory at Joshua Tree National Park, California

Prepared by

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Executive Summary

In October of 2001, National Park Service staff and visitors observed damage to the trunks of Joshua trees (*Yucca brevifolia*) in Joshua Tree National Park (JTNP). The bark-like tissue on the trunks of Joshua trees, known as the periderm, was removed by small mammals thus exposing large, light colored patches of underlying tissue. The U.S. Geological Survey initiated a study to determine the extent of the damage to Joshua tree populations and the consequences of damage to Joshua tree survivorship within the park.

During the 2002 hydrologic year (October 1, 2001 through September 30, 2002), JTNP received 20 mm of precipitation, well below the 54-year average of 103 mm. As a result, germination of annual plants failed in winter 2001/02 and very little new growth and flowering of perennial plants occurred. Coincident with low rainfall and plant productivity, small mammals, including antelope ground squirrels (*Ammospermophilus leucurus*), Botta's pocket gophers (*Thomomys bottae*) and black-tailed jackrabbits (*Lepus californicus*), which normally forage on seeds, fruits, shoots and roots of annual and perennial plants, removed the periderm from Joshua trees.

The survivorship of damaged trees was measured at three sites at JTNP during the summers of 2002 and 2003. During that time 95% of undamaged trees survived, but only 42% of trees with periderm damage survived. The survivorship of the damaged trees was associated with the percent of periderm removed by herbivores: 60% of trees with <5% periderm damage were alive in 2003, but none of the trees with >25% damage survived. On density plots established in the summer of 2003, 12% of the Joshua tree population had periderm damage, which is approximately 4.4 trees ha^{-1}. Although incidence of periderm damage was low during the summer of 2002, a subsequent roadside survey of Joshua tree stands demonstrated that by July 2003 there were no areas of the park free from periderm damage.

The widespread occurrence of Joshua tree damage, the low survivorship of damaged trees, and the recent drought within the park have contributed to the loss of potentially thousands of trees. Large-scale management action to suppress this natural occurrence would not be feasible. However, simple methods, such as wire screening to exclude small mammals, could be used to protect individual trees of particular cultural value, where such actions do not conflict with other management objectives.

While drought and herbivory on Joshua trees are not uncommon in the Mojave Desert, their combined effects over the past 2 years will likely impact the demography of the species at JTNP. While these events pose challenges to natural resource management, they also allow us to learn more about the life history of a long-lived plant species and effective management strategies necessary to preserve natural populations while presenting an excellent opportunity to educate the public about interactions between plants and animals.

Abstract

The widespread damage to adult Joshua trees (*Yucca brevifolia*) by small mammals in a year with below average precipitation and low plant productivity was studied at Joshua Tree National Park. Antelope ground squirrels (*Ammospermophilus leucurus*) were observed climbing the upper branches of Joshua trees and removing large continuous patches of the periderm (i.e, the outer bark-like plant tissue). Deep, wide tooth marks on periderm that was removed below a trunk height of 30 cm distinguished periderm damage by black-tailed jackrabbits (*Lepus californicus*) from that by other small mammals. In contrast, damage to interior vascular tissues was likely due to Botta's pocket gophers (*Thomomys bottae*), which weakened stem support and resulted in toppling of entire trees. More than half of the Joshua trees with periderm damage in summer 2002 died the following summer, which was dramatically greater than the mortality of trees due to drought in the same year. Whereas herbivore damage to Joshua trees by small mammals during most years is not novel, large losses of individual trees due to widespread herbivory during drought years could have severe consequences for plant demography of this long-lived plant species. Although large-scale management action to suppress this natural occurrence would not be feasible, simple solutions, such as wire screen, could be used to protect individual trees of particular cultural value, where such actions do not conflict with other management objectives.

Introduction

In October 2001, park staff at Joshua Tree National Park observed severe damage to the trunks and limbs of Joshua trees (*Yucca brevifolia*) growing between the Pinto/Wye junction on Park Route 12 and Queen Valley. The outer tissue that resembles tree bark, called the periderm (Simpson 1975), was removed from the entire trunk and along branches of trees extending as high as 4 m from the ground exposing large light-colored patches of vascular tissue. Tooth marks on periderm samples were initially presumed to be from small mammals, although the species of mammals responsible for the damage was unknown. The same damage to Joshua trees was observed in the Spring Mountains and the Mormon Mountains in Clark County, Nevada during fall 2001 (TCE, pers. obs.).

In response to the widespread occurrence of tree damage, we initiated a study to determine the extent of the damage to Joshua tree populations and the consequences of damage to Joshua tree survivorship within the park. We assumed this degree of periderm removal by rodents was a rare occurrence at Joshua Tree National Park because periderm damage (1) has never been documented by park personnel, (2) was observed on a small percentage of approximately 1000 widely dispersed Joshua trees studied during spring 2001-2003, and (3) is not documented in the literature as a major influence on plant survivorship. This study provides park personnel with information on (1) the animals that are responsible for the removal of periderm from Joshua trees, (2) the percentage of periderm removal that was required to kill a Joshua tree, and (3) the area of the park with Joshua trees damaged by periderm removal. This study complements other USGS studies at Joshua Tree National Park and the Nevada Test Site (southern Nevada), and contributes to our long-term understanding of demography and ecology of Joshua trees influenced by multiple disturbances (i.e., drought and wildfire).

Research objectives of this study include:

(1) Identify the herbivores removing the periderm from Joshua trees using direct observation and light-beam triggered cameras.

(2) Quantify the density of damaged trees through field surveys at three study areas, and extrapolate the distribution of damage within the park from road surveys.

(3) Compare the amount of precipitation from the time recent periderm damage occurred with the long-term average to understand the likely interval of such disturbances at Joshua Tree National Park and across the Mojave.

(4) Monitor long-term effects of periderm damage on Joshua tree survivorship by marking individual Joshua trees and following their survival over the course of years.

Study area

Three study areas with relatively heavy periderm damage were selected after a visual survey of the park on June 29, 2002. Lost Horse Valley site is located south of Hidden Valley Campground and north of Cap Rock on the east and west sides of Park Boulevard, but excludes trees in the area burned in 1999 on the west side of the road. Queen Valley site is north of Park Boulevard in Queen Valley. Jumbo Rocks site is northeast of Jumbo Rocks Campground, south of Park Boulevard, west of Pinto Basin Road, and northwest of Belle Campground. Both the Lost Horse Valley and Queen Valley sites occur on flat ground with little or no discernable slope. The

Jumbo Rocks site is located on a gentle slope (~3°) with a northeast aspect.

Methods

Precipitation. Precipitation data were acquired from the National Oceanic and Atmospheric Administration, and summarized by hydrologic year, which occurs between 1 October and 30 September.

Remote Cameras. On July 14-16, 2002, two damaged trees at the Queen Valley study area were equipped with 35 mm Canon cameras to capture diurnal and nocturnal rodent activity. Trees that appeared to have very recent damage, such as tooth marks and rodent fecal pellets on perches, were selected. Each camera was installed midday and remained in place for 48 h to capture movements on slide transparency film (200 ISO) triggered by an infrared motion sensor (Trailmaster 500, Goodson & Associates, Lenexa, Kansas, USA). Additionally, during the aboveground activity periods of diurnal rodents (e.g. *Ammospermophilus leucurus*) we posted an observer in the vicinity of the damage with telescope, binoculars and 35 mm camera to capture periderm removal on film.

Density of Damaged Joshua Trees. On July 22-24, 2003, permanent plots were established to quantify the density of Joshua trees damaged by small mammals. Three 100 m × 100 m plots were established within each study area (Lost Horse Valley, Queen Valley, and Jumbo Rocks). Plots were oriented so the perpendicular edges lined up with the north-south and the east-west azimuths. Plot corners were marked with 50 cm tall wooden stakes (2.5 cm × 5 cm), with 15 cm visible above ground after placement. All four stakes were tagged to indicate plot number and corner, and UTMs of each stake were recorded with a GPS unit.

Joshua trees were counted on each plot by two observers walking transects spaced 5 m apart through the entire plot. Particular attention was focused on shrubs and perennial grasses, which serve as nurse plants for Joshua tree seedlings (Brittingham and Walker 2000). Once a tree was located, GPS location and status (e.g., height, live vs. dead, percent periderm damage, presence/absence of sprouts, and nurse plant species) were recorded. Only trees that were alive or were estimated to have died within approximately one year (i.e., no signs of decay, leaf blades still tan or straw colored) were included in the survey in order to estimate the effects of herbivory and drought on the population.

Joshua Tree Survivorship. On June 29 and July 12-14, 2002 Joshua trees were selected within each study area to quantify declines in survivorship associated with periderm damage. Because damaged Joshua trees were distributed non-randomly, Joshua trees were selected based on a modified wandering quarter method (Catana 1963), where every other damaged tree and its second closest undamaged tree were selected along a wandering transect until a total of 50 damaged and 50 undamaged trees were selected (3 study areas × 2 treatments (damaged vs. undamaged) × 50 trees = 300 trees). GPS coordinates of each tree were recorded using North America Datum 1927. Plants were tagged and numbered with an aluminum tag near the base of the trunk on the south side or on a side out of the line of sight of hiking trails. Each tree was photographed at a distance of 10 m on the side where the tree was tagged, but if the tree was too small or too large for this distance to be practical, it was photographed from an appropriate distance to fill the frame. Damaged trees were photographed on the side that best displayed the periderm damage. A second photo was taken of damaged trees 180º from the position of the first photograph.

Tree dimensions and periderm damage were recorded for each tree in 2002 when they were first selected and again on May 17-18, 2003 to determine if damaged trees survived almost 1 yr later. An ocular estimate of old damage was estimated as the area of the trunk with underlying tissue weathered gray, which was usually < 5 ft^2 per tree. New damage (area of the trunk with periderm removed and underlying tissue tan in color) was estimated as a percentage of the whole tree. These estimates were based on an average of three or more observers' visual assessments after walking 360º around a tree. The height of each tree was measured from the ground to the top of live leaf blades using a fiberglass telescoping measuring rod (36'/11m 9 Section CMR Fiberglass Measuring Ruler Round Rod, Crain Enterprises, Mound City, Illinois, USA). The largest diameter of the main stem at 1 m height was measured using calipers (Haglöf Mantax aluminum 50 cm calipers, Haglöf Sweden AB, Långsele, Sweden). The number of live terminal buds and basal (< 10 cm) and stem sprouts (> 10 cm) were recorded, as well as the presence/absence of chewed sprouts and presence/absence of fallen limbs. We used a conservative definition of "live" as a tree with green, presumably photosynthetically active leaf material.

Six to ten damaged trees in each study area were monitored in greater detail. Additional measurements included close-up digital photographs of damaged trunks and notations on the presence or absence of carpenter bees, fungus, bird damage or other types of damage that might impact the survival of the trees. These trees will be revisited in subsequent years so that damage can be rephotographed and digitized over time and rates of change in damage can be analyzed. Matched photographs as well as observational data will serve both to document deterioration of the damaged trees and to identify possible causes.

Statistical Analyses. All analyses were conducted using SAS statistical software (version 8; Cary, NC, USA). Densities of Joshua trees damaged by herbivores were compared among sites in a single fixed factor ANOVA (N = 3 plots per site). The percent survivorship of damaged Joshua trees 1 yr after they were marked was arc-sin square root transformed to meet the assumption of equal variance and analyzed in a single factor, random complete block design with site as a random blocking factor (N=3 sites) and damage treatment (periderm removal vs. no periderm removal) as a fixed factor. The amount of periderm damage required to kill a Joshua tree was analyzed as the mean percent survivorship regressed across individual tree damage intervals (1-5%, 6-10%, 11-15%, etc.) in a simple linear regression.

Roadside Surveys. On July 24, 2003, road and field surveys were conducted through most areas of Joshua Tree National Park to determine the distribution, and estimate the severity of, periderm damage. The survey started at the south end of the gravel road in Upper Covington Flat, continued through Lower Covington Flat, and out of the Park on La Contenta Road. The survey continued by entering the park at the West Entrance and driving southeast on Park Boulevard. We took the turnoff for Barker Dam and proceeded east through Queen Valley on gravel roads, then headed south on the Geology Tour Road. We drove the one-way loop at the end of the Geology Tour Road, and headed back to Park Boulevard. From there we drove west along Park Boulevard, turned south at Cap Rock and drove to Keys View. We drove back up to Park Boulevard and drove north through Lost Horse Valley. We then drove east on Park Boulevard to the North Entrance.

We climbed boulder piles when they were available (alternatively the parked vehicle was used for a vantage point) to view large areas of the park, and binoculars were used to determine presence or absence of periderm damage, relative density of damaged trees, and the relative level of damage (i.e., amount of periderm removed from individual trees) up to about 1.5 km away. We did not survey large portions of some flats, valleys and slopes, and could not scan these areas with binoculars. These areas included: the region between Lost Horse Valley and Juniper Flats; the valley to the north of Smith Water Canyon; the northern parts of the valley traversed by the Boy Scout Trail; the western part of the valley to the east of Ryan and Lost Horse Mountains; most of the valley traversed by Berdoo Canyon Road (south of Pleasant Valley); and the area southeast of Jumbo Rocks, north of Hexie Mountains, and west of White Tank.

Areas burned by fire were not included in the damage survey (or in any other aspect of this study) because periderm exfoliation due to fire injury could confound estimates of damage due solely to herbivores. Closer examination of trees within the burned areas is necessary to determine relative numbers that are affected by rodents vs. fire.

Results

Precipitation. Joshua Tree National Park received 20 mm of precipitation during the 2002 hydrologic year (October 1, 2001 through September 30, 2002), well below the 54-year average of 103 mm (Fig. 1). Only 1956 (8 mm) and 1972 (5 mm) were drier than 2002 during the period of record. Total precipitation in these years did not exceed the 15-25 mm considered critical to trigger germination of annual plants and break dormancy in perennial plants in the Mojave Desert (Went 1948, Beatley 1974).

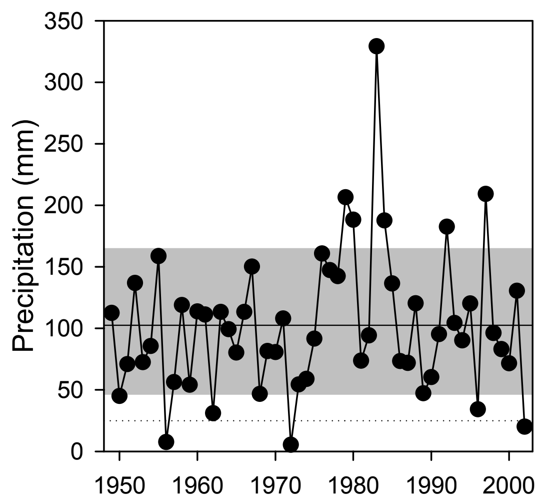

Figure 1. Mean precipitation (± 1 SD, shaded) for the hydrologic year (October 1 – September 30) at Twenty-nine Palms, CA, 1949-2002 (NOAA, 2003). The value of 25 mm precipitation, required for germination of annual species (Beatley 1974), is also shown (dotted line).

Photo Surveys and Observations. Damaged Joshua trees had the periderm removed from the entire trunk and along branches of trees extending as high as 4 m from the ground. The removal of this bark-like tissue resulted in large light-colored patches of exposed vascular tissues (Fig. 2a). Tooth marks on periderm samples were approximately 1-2 mm wide (Fig. 2b) and initially presumed to be from small mammals.

On June 29, 2002, we observed an antelope ground squirrel (*Ammospermophilus leucurus*) climb a large Joshua tree with previous damage and remove the periderm in pieces < 1 cm in diameter. Botta's pocket gophers (*Thomomys bottae*) and black-tailed jackrabbits (*Lepus californicus*) also contributed to injury of Joshua trees, yet both species compromised Joshua trees differently. Pocket gophers ate roots and hollowed out trunks from the inside, traveling up the interior of the trunk as they ate (Fig. 2c).

Occasionally a fallen tree broke at a point where a gopher hollowed the trunk to within 1 or 2 cm of the trunk surface, severely weakening the trunk at that point. Hollowing of Joshua tree trunks was observed up to 2 m above the ground surface. Jackrabbits, however, chewed trunk tissue from the outside at the base of the tree (Fig. 2d). This chewing was deeper than the damage left from periderm removal by *A. leucurus*: 1 to 3 cm deep but not higher than about 30 cm above ground. Furthermore the individual tooth marks were much wider (> 3 mm) than those of *A. leucurus*. Therefore, the extent and type of damage throughout the tree canopy indicates that periderm removal by *A. leucurus* was the most prevalent source of damage in this year.

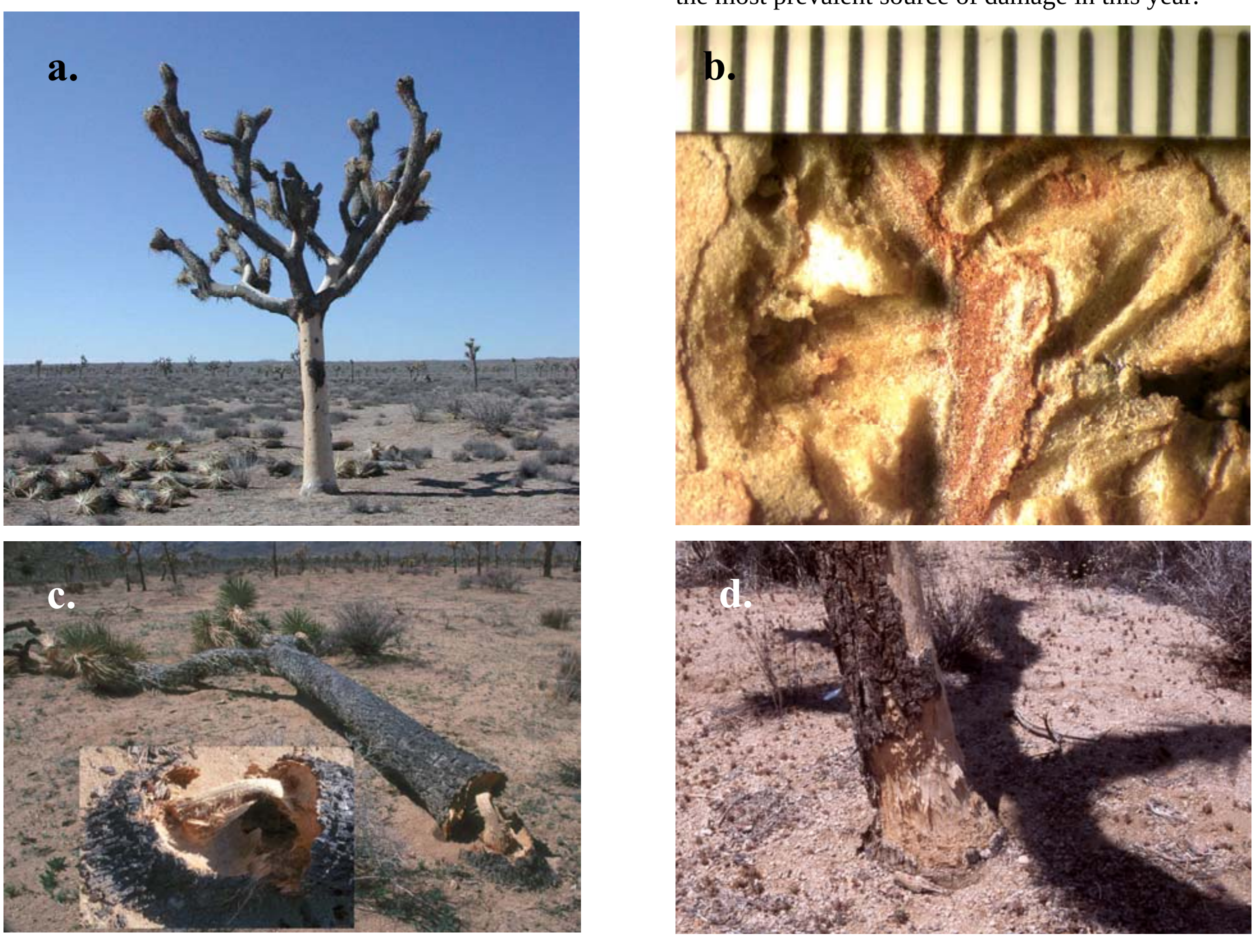

Figure 2. (a). A Joshua tree (*Yucca brevifolia*) with periderm removed from the base of the trunk to a height of several meters and among the many branches, (b) close-up of rodent tooth marks (likely antelope ground squirrel, *Ammospermophilus leucurus*) on periderm removed from adult Joshua tree (scale = 1 mm increments), (c) fallen adult Joshua tree (*Yucca brevifolia*) due to chewing of inner vascular tissues (inset), and (d) base of Joshua tree stem likely chewed by black-tailed jackrabbit (*Lepus californicus*).

Despite our efforts to photograph herbivory on Joshua tree periderm in action, none of the photographs triggered by remote cameras captured this activity. More than 600 photographs were triggered by the cameras, likely by movements in branches and debris blowing in the wind, but no photographs had signs of small mammals of any kind during the 48 hour period of recording.

Density of Damaged Joshua Trees. The three study areas were selected because of the noticeably high density of Joshua trees in these areas within the park that had periderm damage to the trunks. Mean densities (± SE) of Joshua trees (damaged + undamaged) were 35 ± 1 ha^{-1}, 37 ± 5 ha^{-1}, and 47 ± 14 ha^{-1} for Queen Valley, Jumbo Rocks and Lost Horse Valley sites, respectively, but were not statistically different ($F_{2,6}$ = 0.53, P = 0.61). In addition, the percent of trees that had periderm damage was not statistically different among sites (Fig. 3, $F_{2,6}$ = 0.81, P = 0.49). Thus, the average percent of the total number of trees with damage was 12 ± 2%. This percentage translates into an average of 4.4 trees ha^{-1} with periderm damage.

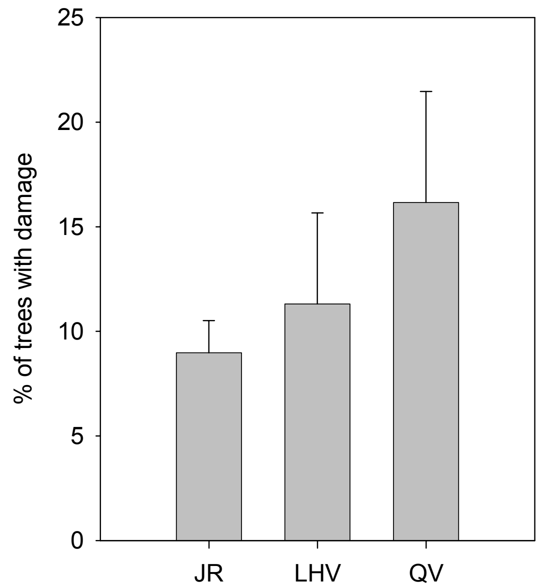

Figure 3. Extent of periderm damage at the Jumbo Rocks (JR), Lost Horse Valley (LHV) and Queen Valley (QV) sites at Joshua Tree National Park. Bars are means (± SE) for three plots per site.

Joshua Tree Survivorship. At the time Joshua trees were marked in summer 2002, none were considered dead because all the trees had green pigmentation in the leaf blades. Periderm damage significantly reduced the survival of Joshua trees ($F_{1,4}$ = 70.44, P < 0.01). Most of the undamaged trees alive in 2002 (as inferred from the presence of green leaves) were still alive in 2003, but more than half of the damaged trees that were alive in 2002 were dead in 2003 (Fig. 4). The survivorship of Joshua trees damaged by periderm removal was lowest in Queen Valley (22 %), followed by Jumbo Rocks (40 %) and Lost Horse Valley (64 %), whereas the survivorship of undamaged trees was relatively constant across sites (94, 94, and 96%, respectively).

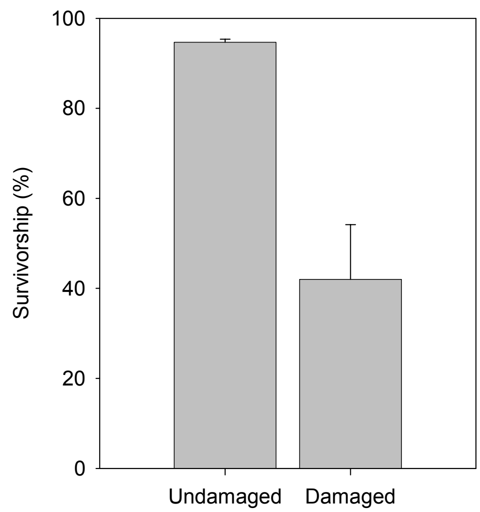

Figure 4. Survivorship of Joshua trees (*Yucca brevifolia*) 1 yr after trees were marked. Each bar represents the mean (± SE) for 3 sites where 50 damaged and 50 nearby undamaged trees (150 of each, total) were marked in 2002 and revisited in 2003.

Predicting Survivorship of Damaged Trees. Joshua trees with high periderm damage in 2002 had lower survivorship in 2003 (Fig. 5). Trees with 1-5 % of the periderm removed had a mean survivorship of 63%, but survivorship dropped to 0% for trees with 26-30% damage (r^2 = 0.94, $F_{1,4}$ = 64.45, P < 0.01). Trees with >30% damage were not included in this analysis due to extremely low sample size.

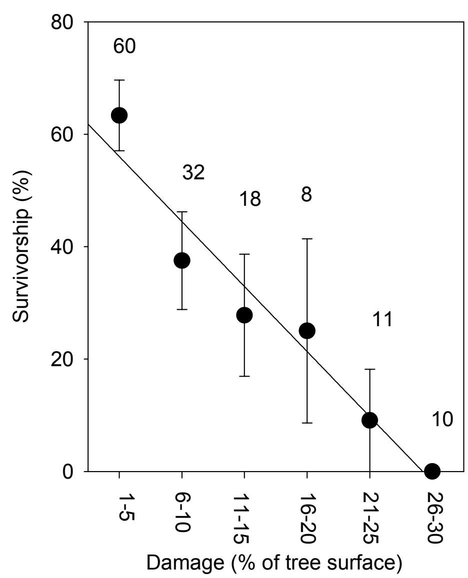

Figure 5. One-year survivorship of damaged Joshua trees (*Yucca brevifolia*) associated with an ocular estimate of the periderm damage. Each point represents the mean (± SE) for trees within each damage interval. Number of trees per damage interval is denoted above each mean.

Roadside Surveys. The extent of periderm damage in the park was limited in summer 2002, but by July 2003, no area of the park was free of damaged trees. In some areas, trees with periderm damage were clustered (i.e. where one tree had damage, the nearest trees were likely to have damage as well, DFH, pers. obs.).

A map was created to illustrate the extent of damaged trees observed in road surveys within the park (Fig. 6). Two subjective factors were combined to develop the relative levels of damage: density (the percentage of trees that show signs of damage), and damage (the percent of periderm removed from individual trees). Generally, areas with high densities of damage also had high percentages of damage on trees. Relative levels of damage ranged from very low, having very few trees with generally < 5% damage; low, with scattered density and a maximum of 15% damage; medium, regular occurrence of damage up to 30%; high, with dense damage up to 45%; and very high, with very dense damage across the landscape and up to 60% damage observed. Some subtleties of estimated damage are not represented on the map. For example, there was a gradient of damage in Queen Valley, with the highest damage observed in the western and central regions of the valley and a gradual decrease toward the east. Also, areas that appeared to have the most damage occurred immediately south of the North Entrance Station where Joshua trees first occur, and in the southern part of Pleasant Valley.

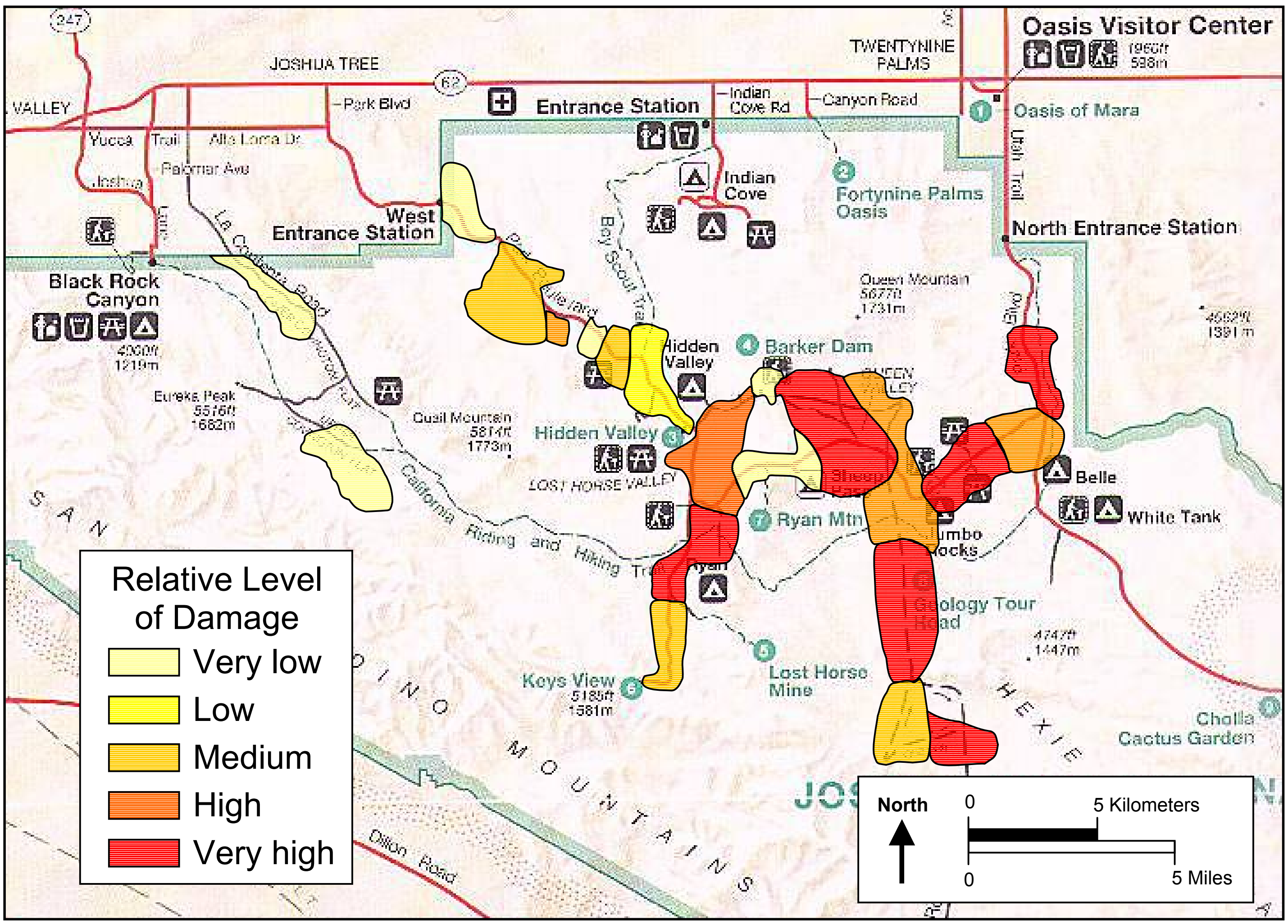

Figure 6. Survey of Joshua tree bark damage in Joshua Tree National Park, 24 July 2003. Only areas that could be accessed by vehicle (excluding burned areas) are represented.

Discussion

Between 2002 and 2003, the presence of periderm damage to Joshua trees in the park expanded from isolated areas (especially our study areas) to all areas of the park where Joshua trees occur. Generally, more trees in the eastern region of the park were impacted than the western areas, but there were no other notable patterns in the disturbance. Areas of very low damage sometimes occurred immediately adjacent to areas with a very high level of damage.

In our study areas, we registered an average of 4.4 trees ha^{-1} with signs of herbivory (estimated from density plots), and an average of 42% survivorship among those Joshua trees 1 yr after they were marked (estimated from marked trees on transects). Based on this estimate of survivorship for damaged trees in the study areas, combined with the presumed higher survivorship in adjacent areas with lower damage, we estimate that thousands of Joshua trees died in 2003. Comanor and Clark (2000) studied Joshua trees from 1975-1995, a relatively wet time period (Fig. 1) at 3 sites across the Mojave Desert. Estimates of survivorship based on their values indicate 100% (21 out of 21 trees), 95% (18 out of 21 trees), and 81% (25 out of 31 trees) over a 20-year period. It remains to be seen whether the 5% loss (95% survivorship) of undamaged trees in the one year of our study is comparable to Comanor and Clark (2000) or if this 5% loss reflects sensitivity to drought.

The pronounced decline in survivorship one year after periderm damage observed in the park (42%) is equivalent to survivorship of burned trees two years after the 1999 Juniper Fire at JTNP: 79% in 2000 (398 out of 503), and 42% in 2001 (209 out of 494) (Esque et al. unpublished data). In respect to survivorship, therefore, the immediate combined effects of periderm damage from rodents and drought have been more damaging than a moderate-intensity wildfire. We predict that survivorship will continue to decline for several years, as has been the case with burned Joshua trees (Esque et al. unpublished data).

The occurrence of herbivore damage appears to have been triggered by the lack of herbaceous plant production during a drought that affected the JTNP area and the warm deserts in general. Coincident with the below normal precipitation, annual plant growth in JTNP was much lower than normal in 2002 and 2003 (Matthew Brooks, USGS, pers. comm.). Similarly, few perennial plants had new growth or flowered in both years. Antelope ground squirrels rely heavily on seeds and green shoots for forage through most of the year (Bradley 1968), so without their typical diet squirrels probably resorted to removing periderm to get to the succulent tissues underneath. We believe this same lack of forage is the likely cause of the gopher and jackrabbit damage to Joshua trees.

Periderm damage by antelope ground squirrels was not confined to JTNP. During late fall 2001, fresh periderm damage was observed on Joshua trees in the north end of the Spring Mountains and the south end of the Mormon Mountains in Clark County, Nevada (TCE, pers. obs.). This damage was not as heavy or as widespread as that observed throughout JTNP, but has the potential to influence the population structure of Joshua trees in these areas.

Reduced Joshua tree survivorship due to the combined effects of drought and herbivory has changed the population structure of impacted Joshua tree stands by thinning out mature trees. The future of Joshua tree stands depends on whether or not additional severe and widespread disturbances occur in coming decades. Although thousands of Joshua trees are estimated to have died in the past two years, this dramatic phenomenon should serve as an opportunity to focus research and public education on interactions between plants and animals. Although herbivores and drought caused severe damage recently, there is growing evidence that the same small mammals play an irreplaceable role in placing seeds in appropriate microsites for germination and establishment in a renewal phase for our tree yuccas (VanderWall and Esque, unpublished data). We will continue to monitor effects of herbivores and drought on Joshua tree populations, which will improve our knowledge of life history and management strategies for the preservation of natural populations.

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