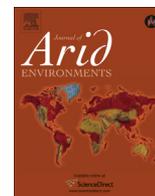


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Assessing regional differences in predation of endangered species: Implications from Texas populations of the endangered star cactus (*Astrophytum asterias*)



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ABSTRACT

Understanding threats to endangered species is one of the most critical components of implementing a successful recovery plan. For the endangered star cactus *Astrophytum asterias*, both mammalian and insect herbivory have been documented as a major threat to populations in Mexico. Herein, we focus on populations of *A. asterias* in Texas, examining how mortality threats differ from populations found in Mexico as well as among sites within Texas. Our study supports insect and mammalian herbivory as a major threat to *A. asterias* in Texas, with reductions in population sizes ranging between 16 and 54%. However, our study highlights that both regional and local differences can influence rates of mortality even in a range-restricted species such as *A. asterias* and highlights the need to assess threats at both of these levels for effective development and implementation of endangered species recovery plans.

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1. Introduction

The U.S. Endangered Species Act of 1973 (ESA; [United States Code, 1973](#)) requires that a recovery plan be developed for every species listed as threatened and endangered. The objective of these species specific plans is to assist in the recovery of listed species such that their populations become self-sustaining and no longer threatened with extinction ([Clark et al., 2002](#)). Despite this mandate, researchers and policy-makers alike have identified short-comings associated with these recovery plans ([Clark et al., 2002](#); [Foin et al., 1998](#); [National Research Council, 1995](#); [Schemske et al., 1994](#); [Tear et al., 1995](#)). [Clark et al. \(2002\)](#) identified

that threats to species had received insufficient attention in recovery plans and that those plans that linked recovery goals to species specific biological information were more likely to improve the species' status.

For endangered plants of arid systems, identifying which threat is most critical to long-term population persistence can be difficult ([Valverde et al., 2004](#)). Despite this difficulty, particular groups of plants tend to share suites of similar threats. For arid-land cacti, these threats often include over-collection for the horticultural trade ([McIntosh et al., 2011](#)), habitat disturbance ([Martorell and Peters, 2005](#)), and disease or predation ([Martínez-Ávalos et al., 2007](#)). Although documentation of individual threats at the species-specific level are available for several arid-land cacti ([Godínez-Álvarez et al., 2003](#) and references therein), very few species have been examined for regional and or local differences in relation to specific threats such as predation. Without a detailed understanding of how threats may differ among proximal or distant populations of arid-land, endangered plants, construction of effective recovery plans will remain a challenge.

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For the federally endangered star cactus (Cactaceae: *Astrophytum asterias*), the 2003 recovery plan identified the following threats: habitat destruction, over-collection by cactus enthusiasts, inadequate regulatory protection, reduction of genetic variability through diminution of population size, and disease or predation (USFWS, 2003). Martínez-Ávalos et al. (2007) reported that damages caused by the plant pathogen *Phytophthora infestans*, a cerambycid beetle, and the Mexican ground squirrel (*Spermophilus mexicanus*) led to a reduction in population size of more than 50% in *A. asterias* in Mexico. Of these threats, Martínez-Ávalos et al. (2007) identified herbivory from *S. mexicanus* as the most important cause of death.

Although Martínez-Ávalos et al. (2007) identified threats to populations of *A. asterias* in Mexico and documented impacts of these effects on different life stages, anecdotal data collected from sites in Texas (USFWS, 2003) indicated that the demographic impacts of herbivory as well as those species responsible for herbivory-induced deaths differed from those found in Mexico. This information meant that even for a geographically restricted species such as *A. asterias*, threats facing populations may differ enough to require regional contexts to be incorporated into recovery plans. To determine how regional differences in threats may impact the existing recovery plan of the endangered *A. asterias* we sought to 1) document the species of herbivores posing a threat to *A. asterias* in Texas, 2) examine rates of mortality among different sites of *A. asterias* in Texas, and 3) relate herbivore-induced mortality to environmental variables and life-stages of *A. asterias*. In addition, we sought to compare our results from sites of *A. asterias* in Texas to the results collected from Mexican populations by Martínez-Ávalos et al. (2007). Given our different methodological approaches, geographically distinct populations, and distinct habitat types, contrasting our results to those of Martínez-Ávalos et al. (2007) provides an excellent case study to explore how regional and or local differences in mortality might influence the effective recovery of endangered species. Our comparative approach synthesizes data on mortality in *A. asterias* while highlighting differences in herbivore-induced mortality among geographically disparate populations further supporting the hypothesis that recovery plans for endangered cacti (prone to mammalian or insect-induced mortality) need to consider population variability in mortality rates at both a local and regional scale. Taking such variation into account could ultimately lead to the development of more effective recovery plans for endangered arid-lands plants such as *A. asterias*.

2. Materials and methods

A. asterias is a small, globose cactus 0–3 cm tall and 2–15 cm in diameter with flat-ribbed stems divided by grooves into 8 ribs (Strong and Williamson, 2007). The plant is an obligate outcrosser whose hermaphroditic, yellowish-orange flowers can open to 15 cm in diameter (Strong and Williamson, 2007; USFWS 2003). The species is predominantly bee pollinated with *Diadasia rinconis* acting as the most important pollinator (Blair and Williamson, 2008). Oval to round fruits 1–2 cm in size contain glossy seeds with a flaring collar surrounding the hilum (Benson, 1982). Although little is known regarding seed dispersal, evidence gathered from pollen dispersal indicates that genetic neighborhoods are small enough to subdivide large patches of *A. asterias* (Blair and Williamson, 2010). The current distribution of *A. asterias* is restricted to 25 sites with one to 12 local clusters of cacti per site, covering a 145 km² area in south-central Starr County, Texas (Janssen et al., 2010) and 9 additional populations in Mexico, 2 in Nuevo León and 7 in Tamaulipas (Martínez-Ávalos et al., 2004). Despite its restricted distribution, *A. asterias* does not appear to have strict habitat requirements as it is found in both saline-sodic and non-saline soils, protected by nurse plants or fully exposed, and in areas either dominated by or completely devoid of *Varilla texana*. Habitats in Texas and Mexico from which *A. asterias* is known differ from one another in vegetation and soil characteristics (Birnbaum, 2009; Martínez-Ávalos et al., 2007).

In order to assess herbivore-induced mortality of *A. asterias* in Texas, we employed two methods: motion-sensor cameras and permanent plot surveys. All monitoring focused on five study sites in southern Starr County, Texas, USA (Sites 1–5, Table 1, Fig. 1). These sites were chosen based on accessibility as well as the presence of *A. asterias* (Janssen et al., 2010). Due to risks of illegal collecting activities, the exact coordinates for each of these sites have been withheld. However, a map depicting the locations of the study sites, in relation to the geographic distribution of *A. asterias*, has been included (Fig. 1).

Six vegetation transects, following a stratified random sampling design, were conducted among Sites 1, 2, 3, and 4. Each transect was 75 m (three 25-m transects) and were sampled using the line-intercept method to document the plant species within the *A. asterias* patches and determine percent dominance (cover) and percent relative dominance of these species (Birnbaum, 2009). An additional 9 patches of *A. asterias* were sampled using this method within our 75.6 km² study area. All vegetation surveys were

Table 1

Descriptions of five study sites used for monitoring herbivore-induced mortality of *Astrophytum asterias* in Starr County, Texas, March 2008–September 2009.

Site	Ownership	Property size	Recreational activities	Dominant vegetation (in order of dominance)	Description
1 ^a	The Nature Conservancy	415-ha	Prohibited (none)	<i>Varilla texana</i> <i>Acacia rigidula</i>	Multiple patches of <i>A. asterias</i> on property.
2 ^a	Private	32-ha	Cattle ranching, hunting	<i>Opuntia leptocaulis</i> <i>Varilla texana</i> <i>Prosopis glandulosa</i>	Two verified patches of <i>A. asterias</i> .
3 ^a	Private	4-ha	Goat/cattle ranching	<i>Opuntia leptocaulis</i> <i>Varilla texana</i> <i>Opuntia leptocaulis</i>	Single, isolated patch of <i>A. asterias</i> next to ranch house and livestock pens.
4 ^a	Private	161-ha	Hunting	<i>Prosopis glandulosa</i> <i>Varilla texana</i> <i>Prosopis glandulosa</i>	Two verified patches of <i>A. asterias</i> .
5 ^b	Private	168-ha	Hunting	<i>Opuntia leptocaulis</i> <i>Varilla texana</i> <i>Prosopis glandulosa</i> <i>Opuntia leptocaulis</i>	Multiple verified patches of <i>A. asterias</i> , relatively unmodified habitat.

^a Vegetation data from vegetation transects directly adjacent to or within study plot.

^b Vegetation data based upon visual assessments of the major plant species present in the plot.

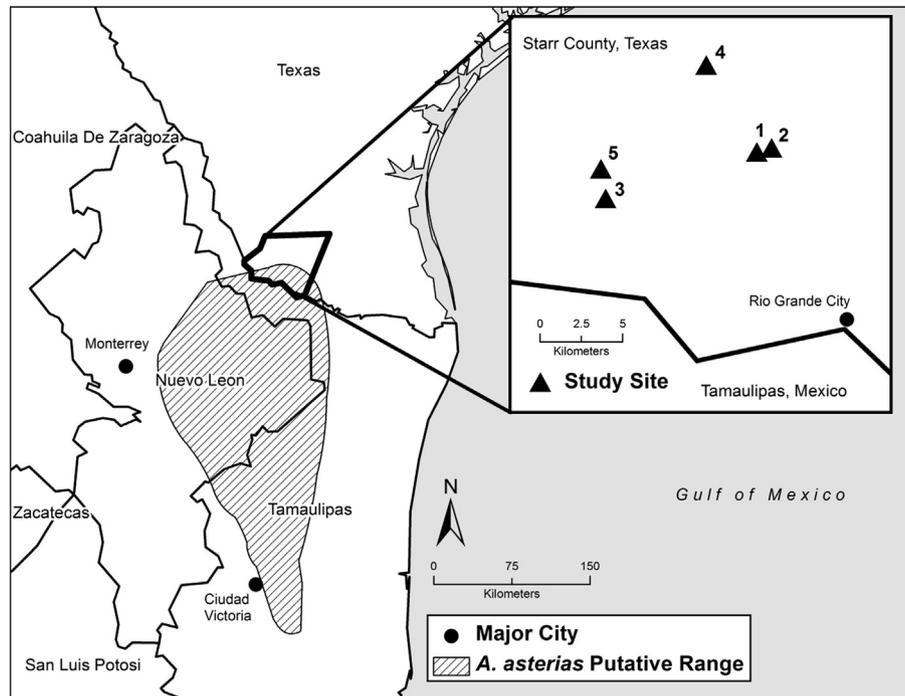


Fig. 1. Location of five study sites within Starr County, Texas (inset) in relation to the putative geographic distribution of *Astrophytum asterias* (adapted from www.cactusconservation.org, Martínez-Ávalos pers. com.).

conducted in March and May 2006. Site 5 was not sampled for vegetation as *A. asterias* was not discovered at that site until 2007. The species with greatest percent cover for our study sites (in order of dominance) were: *V. texana*, *Prosopis glandulosa*, *Opuntia leptocaulis*, *Acacia rigidula*, *Ziziphus obtusifolia* var. *obtusifolia*, *Castela erecta* subsp. *texana*, *Parkinsonia texana* var. *macra*, *Monanthochloe littoralis*, *Sporobolus airoides* subsp. *airoides*, and *Bouteloua trifida*. Dominant species recorded at our study sites differed slightly from those found among the populations studied in Mexico, which were dominated by *Karwinskia humboldtiana*, *P. texana*, *Schaefferia cuneifolia*, *P. glandulosa*, *Porlieria angustifolia*, *Z. obtusifolia* in the Tamaulipan thronscrub and *Acacia berlandieri*, *Acacia coulteri*, *A. rigidula*, *Acacia greggii*, *Astrocasia neurocarpa*, *Chloroleucon pallens*, *Chloroleucon frutescens*, *Cordia boissieri*, *Castela tortuosa*, *Forestiera angustifolia*, *Fraxinus greggii*, *Gochnathia hypoleuca*, *Helietta parvifolia*, *Lycium berlandieri*, *Mimosa leucaenoides*, *Rhus virens*, *Neopringlea integrifolia*, and *Yucca filifera* in the Piedmont thronscrub (Martínez-Ávalos et al., 2007). Most of the soils along the vegetation transects have a clay component and are classified as clay or clay loam with varying levels of salinity. Detailed information regarding soil analysis and composition as well as vegetation data can be found in Birnbaum (2009).

Trailmaster[®] motion sensor camera systems were used to document mammalian herbivores feeding upon *A. asterias*. Pilot camera surveys were conducted on Sites 1 and 2 in March 2006. After successful documentation of mammalian herbivory, an additional 8 cameras were added to the two sites for a total of 10 cameras, 5 cameras on Site 1 and 5 cameras on Site 2. Cameras required constant upkeep and maintenance, and were all permanently removed in July 2007 due to extensive damage to the units by rodents.

Beginning in February 2008, 10,000 m² permanent plots were established on each of the five study sites. Plots were systematically surveyed using a minimum of four people in a grid-like fashion, and all observed cacti were measured to the nearest 0.10 cm using rulers and drafting stencil circles and marked with fluorescent pin flags for

future monitoring. Equal efforts were made to search both densely vegetated portions of the plots as well as bare soil/exposed rocky cobblestone as *A. asterias* individuals were found both protected and unprotected by nursery plants among all sites. Individuals were grouped into ten 1 cm size classes based on these measurements. For example, size class one individuals were ≤ 1 cm in diameter and size class two individuals were > 1 cm to ≤ 2 cm in diameter. Beginning in March 2008, previously marked cacti within the monitoring plots were resurveyed for new evidence of herbivory or other causes of mortality every other month until September 2009. Although additional causes of mortality have been recorded in *A. asterias* (see Martínez-Ávalos et al., 2007), we found identification of exact causes of death to be quite difficult in the field. Thus, we focused our efforts exclusively on those factors which we believed could be unequivocally assigned as a cause of death: mammalian herbivory and insect herbivory attributable to *Moneilema armatum* (Coleoptera: Cerambycidae). Identification of mortality factors were similar to those used by Martínez-Ávalos et al. (2007), although mammalian herbivory was not identified to species based on incisor markings (see Results) and insect induced damage was attributed only to *M. armatum* when the larva or pupation chamber was discovered in the cactus. We found reliance on the characteristic bore hole (see Fig. 2B in Martínez-Ávalos et al., 2007) to be misleading at our study sites, as *M. armatum* were observed pupating in the lateral portions of the cacti (Ferguson and Williamson, 2009). In addition, the hollow root chamber that remained after the death of a cactus often resembled a bore hole even in the absence of any sign of *M. armatum* infestation. We did not find that all instances of herbivory lead to death of the plant involved; thus, we quantified the extent of damage on a percentage scale using the 8 ribs of the plant to assess percent damage attributable to the two causes of death (see Fig. 2A).

3. Statistical analysis

Percentage estimates of extent of damage were arc-sine square-root transformed for all analyses (Quinn and Keough, 2002). We



Fig. 2. (A) Partially consumed individual of *Astrophytum asterias* with 3 of 8 ribs consumed (37.5% damage, black arrow); (B) photo of a *Peromyscus* sp. next to a healthy *A. asterias*; (C) photo of *Sylvilagus audubonii* consuming *A. asterias*; (D) *Spermophilus mexicanus* investigating an *A. asterias*.

used two way contingency-table analyses and general linear models (ANOVA) to assess whether mortality differed among size classes and across study sites. Tukey's post-hoc HSD was used to identify pairs of means that differed significantly from one another, and resulting homogeneous subsets. Due to the low incidence of confirmed deaths induced by *M. armatum* we pooled both insect and mammalian herbivory into a single herbivory category partitioned among the 5 sites. We assumed that damage greater than or equal to 75% of the plants' ribs led to death of that individual. This assumption was supported by field observations which indicated that individuals with less than 75% of their flattened stem removed were able to survive whereas those with approximately 6 of their 8 ribs entirely destroyed succumbed to death more frequently. The response variable was treated as binary (0 = alive, 1 = dead) and represented the number of deaths for both categories of herbivory-caused mortality (mammalian and *M. armatum* induced). We used a general linear model (ANCOVA) to assess whether mortality differed among sites after accounting for size class, and Tukey's HSD to identify pairs of means that significantly differed from one another. Seasonal variation among mortality rates was visualized using a survivorship curve and tested for heterogeneous survivorship rates using a randomized ANOVA (Good, 2006; 5000 iterations) based on estimates of daily mortality rates due to the small number of sampling dates. Seasonal heterogeneity in mortality was assessed using all mortality combined among the five sites in contrast to all other analyses, which treated sites independently. Daily mortality rates were used only for seasonal analysis. Daily mortality rates were estimated in SAS using the following equation: $\text{dailyRate} = \text{deaths} / \text{living} / \text{dDays}$ where 'deaths' is defined as the total number of dead cacti per each sampling date (9 sampling dates in total) and 'living' defined as the total number of living plants for a particular sampling date minus the number of deaths at time t . 'dDays' is the number of Julian days between contiguous collection dates.

Environmental data were collected from a Hobo weather station (Pocasset, MA) at Site 1. Environmental variables included total monthly rainfall (mm), mean monthly air temperature ($^{\circ}\text{C}$), monthly maximum air temperature ($^{\circ}\text{C}$), and monthly minimum air temperature ($^{\circ}\text{C}$). These Site 1 data were temporally incomplete, and so were compared to environmental data collected from the National Climatic Data Center's annual climatological summary

from the Rio Grande City weather station (# 417622/99999) using Principal Component Analysis (PCA) to determine whether the data sets were sufficiently similar to permit Rio Grande City data to be used as a proxy for the Site 1 data. Environmental data were subsequently used in a Principal Component regression to examine potential patterns between mortality and environmental conditions.

4. Results

A total of 277 photographs were recorded between March 2006 and July 2007 (10 cameras operated for 17 months). Twenty-seven species of animals were recorded, including four potential mammalian herbivores: *Sylvilagus audubonii* (Audubon's cottontail), *S. mexicanus* (Mexican ground squirrel), *Neotoma micropus* (Southern Plains woodrat), and *Peromyscus* sp. (Deer mouse, Fig. 2B–D). Most photographs were of birds ($n = 119$ or 43.0%) followed by *S. audubonii* ($n = 74$, 26.7%) and *S. mexicanus* ($n = 39$, 14.1%). *N. micropus* and *Peromyscus* sp. accounted for 1.1% ($n = 3$) and 2.2% ($n = 6$) of all photographs, respectively. Each of these species is considered native to this region. Although cameras were only deployed at Sites 1 and 2, all potential herbivores photographed were recorded at each individual site either through direct observation, live trapping, or sign surveys (with the exception of Site 3 which lacked direct evidence for *N. micropus* in proximity to the isolated patch of *A. asterias*).

A total of 1606 *A. asterias* were marked and monitored across the five sites from 22 March 2008–6 September 2009. After ignoring plants that were unsuitable for inclusion in analyses (due to other causes of mortality, missing plants preventing classification of extent of damage, or removal of flags by livestock) a total of 1473 individual *A. asterias* were available for statistical analyses. A total of 367 individual deaths ($\geq 75\%$ extent damage) attributable to either mammalian ($n = 349$) or insect ($n = 18$) herbivores were recorded among all five sites. Other causes of mortality accounted for only 81 deaths during our study period, including 63 'unknown', 7 'desiccations', 7 'fungus/pathogen', 3 'rot', and 1 'anthropogenic' although these categorizations were considered dubious (see **Materials and Methods**). No herbivory was attributed to livestock. Population sizes varied among the sites (range = 128–444), as did the sizes of *A. asterias* found within those populations ($F = 40.8$, $df = [4, 1468]$, $p < 0.001$). Mortality significantly varied among the ten size categories ($\chi^2 = 41.3$, $df = 9$, $p < 0.001$; Fig. 3A), with higher mortality rates occurring among plants whose diameters ranged from 3 to 6 cm. Plants between 3 and 4 cm in diameter had the highest rate of mortality among all five sites. Mortality also varied among sites ($\chi^2 = 104.8$, $df = 4$, $p < 0.001$; Fig. 3B) with Sites 1 and 5 having the highest mortality rates (55.7% and 37.7%, respectively). Sites 2, 3, and 4 were not significantly different from one another according to the Tukey's HSD test, and all incurred similar levels of mortality (20.1%, 15.9%, and 22.2%, respectively). After accounting for variation in mean size class among the five sites, we still found significant differences in mortality among sites ($F = 24.1$, $df = [5, 1467]$, $p < 0.001$). The pattern among sites was the same as described in the absence of the factor of size class, with Sites 1 and 5 experiencing different rates of mortality in comparison to Sites 2, 3, and 4. The survivorship curve depicted a large decrease in survivorship between October and December 2008, with a steady decline in survivorship thereafter. The large decrease in survivorship between October and December 2008 (Fig. 3C) was reflective of a large increase in mortality documented at Site 3 during this time frame. Heterogeneity in estimated daily mortality rates among seasons was not significant due to low statistical power ($F = 4.73$, randomized, $p = 0.088$; Fig. 3D), but the highest daily mortality rates occurred in winter (Dec–Feb).

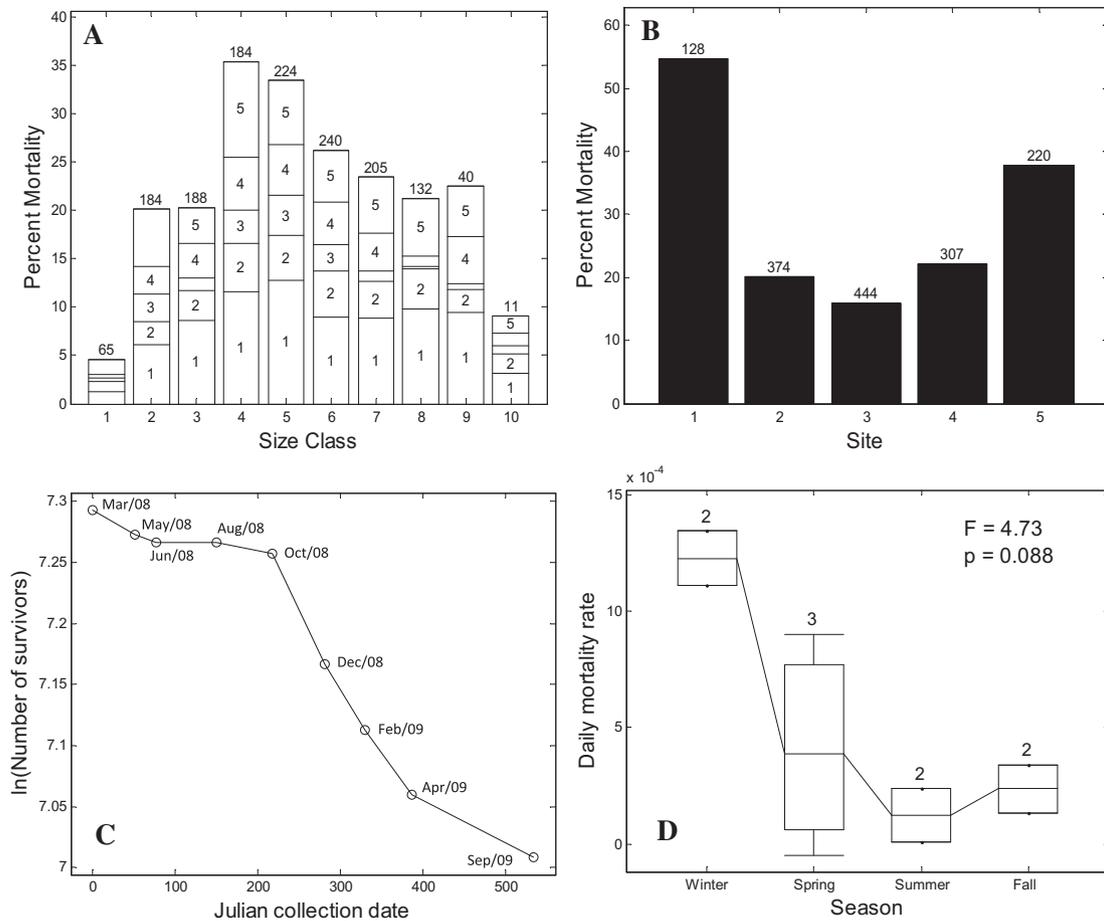


Fig. 3. Total percent mortality (extent damage to plant $\geq 75\%$) of *Astrophytum asterias* in relation to (A) 1 cm size class categories and (B) among the five different sites. Sample sizes are displayed on top of histogram bars. For 3A, bars are labeled with appropriate site identifiers, moving from Site 1 to Site 5 from bottom to top. (C) Survivorship curve for mortality among all five sites on a continuous Julian-date scale; circles indicate sampling dates. (D) Daily mortality rates depicted among four major seasons sampled-number above the plots indicate the number of sampling periods per season. Standard error bars for winter, summer, and fall were too small to print.

Principal Component Analysis revealed that weather data collected from the Hobo station at Site 1 were consistent with weather data collected from the Rio Grande City weather station (# 417622/999999) in their patterns of variation, based on eigenvector coefficients (Table 2). Thus, in the subsequent Principal Component regression of mortality (extent damage $\geq 75\%$) on PC scores, only weather data collected from the Rio Grande City weather station were used because the station had data available for the entire study period. Principal Component regression helps deal with effects of collinearity that stem from correlated predictor variables such as temperature and rainfall (Quinn and Keough, 2002). The

first two principal components accounted for 98.9% of the variance among the original variables, with Principal Component 1 (PC1) and Principal Component 2 (PC2) explaining 83.8% and 15.1% of the original variance respectively. PC1 was mainly correlated with temperature ($r = 0.54$) and rainfall ($r = 0.39$), whereas PC2 was positively correlated with rainfall ($r = 0.89$) and negatively correlated with maximum temperature ($r = -0.41$). Although statistically significant ($F = 6.21$, $df = [2, 440]$, $p = 0.002$), the regression failed to explain a reasonable proportion of the variance associated with mortality among the five sites ($r^2 = 0.03$) and neither temperature or rainfall patterns were related to either increases or decreases in mortality rates.

Table 2

Principal coordinate coefficients for first two principal components generated from PCA between environmental data gathered from Site 1 weather station and environmental data collected from the Rio Grande City NCDC Climate Station 417622/999999 (RGC). Together PC1 and PC2 explained 99% of the variation in the data.

Variable/site	PC1	PC2
Total monthly rainfall (mm)/Site 1	0.289	0.624
Total monthly rainfall (mm)/RGC	0.276	0.669
Mean monthly temperature (°C)/Site 1	0.375	-0.168
Mean monthly temperature (°C)/RGC	0.376	-0.159
Maximum monthly temperature (°C)/Site 1	0.371	-0.199
Maximum monthly temperature (°C)/RGC	0.372	-0.192
Minimum monthly temperature (°C)/Site 1	0.375	-0.130
Minimum monthly temperature (°C)/RGC	0.376	-0.129

5. Discussion

One major goal of research involving endangered species is to provide scientific data for improving conservation plans and management tactics in the field (Salafsky et al., 2002). The differences recorded between our study and that of Martínez-Ávalos et al. (2007) highlight the fact that managerial tactics may require regional adjustment to protect populations of *A. asterias*. Our camera data indicated that *S. audubonii* poses a serious threat to *A. asterias*. Serial photographs demonstrated that *S. audubonii* would consume an entire cactus plant in one feeding period. In contrast, photos rarely showed *S. mexicanus* inflicting serious damage to *A. asterias* individuals. Although few photos existed of

N. micropus and other non-sciurid rodent species, two intense periods of herbivory with associated sign (feces and observations) at different sites indicated that *N. micropus* and *Sigmodon hispidus* can inflict serious damage to *A. asterias* populations. Thus, our study found a greater diversity of mammalian herbivores (6 vs. 1) preying upon *A. asterias* than reported by Martínez-Ávalos et al. (2007). This community of herbivores poses a serious threat to the persistence of individuals, indicating that managing solely for *S. mexicanus* predation could grossly under-protect populations of *A. asterias* in Texas. Our study also differed from Martínez-Ávalos et al. (2007) with regard to impacts of insect herbivores. We found the beetle *M. armatum* to be the main insect herbivore impacting *A. asterias* (Ferguson and Williamson, 2009), but mortality due to this insect only accounted for 4.9% of total mortality in comparison to 19.9% reported for populations from Mexico (Martínez-Ávalos et al., 2007). However, these differences could be due to differences in methodologies used to assess damage attributable to cerambycid beetles and other herbivores (see Materials and Methods above and in Martínez-Ávalos et al., 2007).

Although we found differences between our study and the work conducted by Martínez-Ávalos et al. (2007), our results were similar in several regards. We found herbivory-induced mortality of *A. asterias* to comprise a serious threat to local populations (leading to reductions in individuals ranging from 16 to 54%). Our estimates of mortality are conservative as in that our assessment of mortality assignment was limited to plants with $\geq 75\%$ damage and several months of mortality data were excluded from the analyses due to methodological issues. For example, Site 1 had 8 plants displaying herbivory damage less than 75% and thus all were treated as alive for our analyses. However, assuming these 8 plants would not survive would increase the percent mortality estimate from 54.7% to 60.9%. Despite these conservative estimates, herbivore-induced mortality comprised the major cause of death among our 5 study sites. Our data also indicated that smaller individuals (ranging in size from 3 to 6 cm) were at greater risk to mortality induced by herbivores than larger individuals, as was the case in Mexican populations (Martínez-Ávalos et al., 2007).

Although we found no explanatory relationships between weather conditions and herbivore-induced mortality among our 5 study sites, understanding how local abiotic conditions influence herbivory rates could provide information useful for protecting local populations. Our lack of explanatory power could be confounded by behaviors of small mammals not accounted for by local weather patterns, or other factors besides rainfall or temperature that might explain differences in mortality rates among and within populations of *A. asterias*. Future research on *A. asterias* should focus on identifying factors influencing mortality rates, including the context of surrounding habitats and current land-use practices. In addition, research into the long-term impacts of predation on population dynamics and colonization patterns of areas once suitable but now devoid of *A. asterias* would be beneficial. Given the site-level variation we observed, our study also helps to lay the foundation for implementing manipulative experiments to test the effects of particular land-use practices/management strategies (e.g. exclusion of livestock, brush control, insect/lagomorph/rodent control) on predation rates.

Understanding regional differences in mortality risks and local forces that may be influencing demographics of endangered arid-land plants such as *A. asterias* is critical to conserving such species. Our research demonstrates that even in a range-restricted species, threats may differ among local sites, requiring local, adaptive management strategies to effectively conserve the species. The fact that predation rates and predators can differ among local sites of such a range-restricted cactus could have direct implications for conserving additional arid-land cacti, including many of

the endemic and or geographically rare cacti of Mexico (Hernández et al., 2010). Studies on Mexican species such as *Mammillaria magnimamma*, have demonstrated that local populations can experience differential growth rates (Valverde et al., 2004), which when combined with differential predation rates, as demonstrated in this study, could spell disaster for localized populations of endangered succulents. Our results also indicate that mortality differed among size classes, with higher mortality occurring among individuals ranging in size from 3 to 6 cm. Such information, in light of the fact that one of the greatest threats to populations of arid-land cacti is mortality of mature individuals (Godínez-Álvarez et al., 2003), clearly indicates that small mammal/insect herbivory should be taken into account when managing populations of endangered arid-land cacti. Our study demonstrates the need to better understand how spatial patterns of plant mortality in arid ecosystems differ at both the local and regional scale. Investigations of such patterns in other arid-land systems known to be impacted by herbivorous rodents (Bagchi et al., 2006; Borruel et al., 1998) could prove useful in understanding whether or not spatial variability in mortality is a conservation concern for other arid plants besides cacti. Future studies of such systems should explicitly take such local and or regional variation in mortality into account to provide effective recovery plans for endangered arid-land plants.

Disclosure statement

Adam W. Ferguson – was employed by Paula S. Williamson and Texas State University-San Marcos (the institution that administered the Texas Parks and Wildlife Department grant) during the field component of this study. He has no professional ties to Texas Parks and Wildlife Department or The Nature Conservancy which helped fund and give access to survey sites respectively. He designed, implemented, and led the study, collected data from the field, and composed the final manuscript.

Richard E. Strauss – has no conflicts of interests to declare. Rich contributed substantially to the statistical analyses and experimental design of the project helping run all the statistics. He also reviewed and edited the manuscript.

Anna W. Strong – was employed by Paula S. Williamson and Texas State University-San Marcos (the institution that administered the Texas Parks and Wildlife Department grant) during the field component of this study. She has no professional ties to Texas Parks and Wildlife Department or The Nature Conservancy which helped fund and give access to survey sites respectively. Anna assisted in choosing and setting up Trailmaster camera locations for the pilot and extended study to document herbivores. Anna also maintained cameras and reloaded and developed film through May 2007.

Sandra J. Birnbaum – is employed by Texas Parks & Wildlife Department, the state agency that awarded and administered the funding for the project. She also completed her Master of Science degree at Texas State University—San Marcos under Dr. Paula Williamson. Sandra conducted vegetation transects and soil analyses as part of her thesis research (Habitat characterization and pilot reintroduction of star cactus [*A. asterias*]). Some of this data is included in the manuscript. She also participated in discussions regarding methodology employed in this study and assisted with one of the first plot surveys. Sandra also reviewed drafts of the manuscript.

Jackie M. Poole – works for Texas Parks and Wildlife Department, the state agency that awarded and administered the funding for the project. However, because she was working on the project, she did not review it. As she was doing long-term demographic monitoring to determine population size class distribution within populations, growth rate, size relation to reproductive state, and

recruitment and mortality (including causes of mortality), she discussed plot design and effective and efficient ways to monitor the cacti within the plots. She helped the senior author set up and monitor the cacti within the first plot. She also helped monitor the cameras and reviewed the manuscript.

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Paula S. Williamson – has no conflicts of interests to declare. Paula contributed substantially to the conception of the research study. She reviewed the manuscript for intellectual content and edited the manuscript.

All authors have approved the final version of this article as submitted to the Journal of Arid Environments.

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