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Cattle trampling increases dormant season mortality of a globally endangered desert milkvetch

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ABSTRACT

Conflicting priorities for livestock grazing management in the context of rare plant conservation are common worldwide, especially in semiarid and arid ecosystems, where open-range livestock grazing is a primary land use. Detailed information on the interaction between livestock impacts and rare plant demography would facilitate improved management, yet this information is most often not available. In this study we examined the direct impacts of cattle trampling on dormant season survival of *Astragalus holmgreniorum* (Fabaceae), a globally endangered perennial spring ephemeral of the northeastern Mojave Desert, USA. Current management restricts livestock access to the dormant season, when plants are not active above-ground, but monitoring indicates possible population decline under this regime. We tagged > 2100 *A. holmgreniorum* plants to document dormant season survival and quantified cattle trampling and other disturbance impacts in small plots at six sites with contrasting disturbance regimes. We documented disturbance impacts on survival at the site, plot, and individual plant level across two dormant season iterations. We consistently found significant negative relationships between plant dormant season survival and cattle impacts. Plants at sites with heavy cattle trampling were up to five times more likely to experience mortality than those at sites with low cattle impact. Other surface disturbances (rodent activity, human impacts, water erosion) were also quantified but contributed substantially to reduced survival in only one case of water erosion disturbance. We conclude that grazing management in *A. holmgreniorum* critical habitat on federal land may require modification to reduce extinction risk for this federally listed endangered species.

1. Introduction

The interface between biodiversity conservation and livestock grazing has been the topic of considerable study and controversy (Jensen, 2001). Most studies on grazing impacts have been carried out at the landscape or community scale and have focused on species richness. The interaction between grazing and species richness is dependent on a complex set of factors that include climate, vegetation type, and both long-term and short-term grazing history and management. In mesic grassland ecosystems that supported herding wild ungulates in the past, the relationship for plants is often positive, for example, in semi-natural grasslands across northern Europe, where livestock can act as keystone species that maintain increased species diversity (Dolek & Geyer, 2002; Luoto, Pykälä, & Kuussaari, 2003; Pykälä, 2003). These studies showed that grazing decreases competition from the dominant grasses and trampling creates openings for seedling recruitment, resulting in increased abundance of rare species and increased species richness. Studies from tall grass prairie (Polley, Derner, & Wilsey, 2005) and from semiarid grasslands and Mediterranean ecosystems have also demonstrated increased species richness with grazing (Marty, 2005; Minckley, 2013; Verdú, Crespo, & Galante, 2000). Grazing impacts on native species in semiarid ecosystems can also be negative, however (Kimball & Schiffman, 2003; Valone & Sauter, 2005).

In more arid environments, grazing effects on vegetation and soils most often tend to be negative (Jones, 2000). Studies examining cattle grazing impacts on species richness in deserts have frequently shown decreased native species richness in more heavily grazed areas (e.g., Brooks, Matchett, & Berry, 2006 in the Mojave Desert, Waser & Price, 1981 in the Sonoran Desert). Other studies have shown no effect of grazing on species richness (Fensham, Fairfax, & Dwyer, 2010 in the Simpson Desert of central Australia). This may reflect the much shorter history of cattle grazing (20 years) in the latter study.

Studies of possible positive effects of livestock grazing in semiarid

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and arid systems have focused on trampling, both as a mechanism for seed burial (Winkel, Roundy, & Blough, 1991) and for improvement of the seed bed microenvironment prior to revegetation seeding, presumably through local redistribution of water (Winkel & Roundy, 1991). Others have argued that trampling creates a microenvironment that is deleterious to seedling establishment and may be one reason why recovery of native grasses following cessation of abusive grazing is often so slow (Valone & Sauter, 2005).

There are apparently few scientific studies that directly address livestock impacts on plant species of conservation concern. In a demographic study of the rare perennial *Gentiana pneumonanthe* in hay meadows and heathland in the Netherlands, Oostermeijer, Van't Veer, and Den Nijs (1994)) showed that population structure improved with grazing (i.e., grazing increased recruitment), both through the reduction in grass competition and the creation of safe sites for establishment. *Ranunculus aestivalis*, a critically endangered buttercup of lowland wet meadows in Utah, USA, also benefitted from cattle grazing, primarily because reduction in grass cover decreased vole herbivory (Skopec et al., 2018). In contrast, small globular desert cacti experience high risk of damage or death from livestock trampling, and the risk of trampling is directly related to stocking rate (Guthery & Bingham, 1996). For example, *Pediocactus winkleri*, a threatened species of semiarid habitats in central Utah, USA, was shown to be vulnerable to cattle trampling (Clark, Clark, Duniway, & Flagg, 2015).

In this study, we directly address the impact of cattle trampling on a federally listed endangered species of the northeastern Mojave Desert, *Astragalus holmgreniorum* Barneby (Fabaceae). All known populations of this species occur within 15 km of a rapidly expanding urban area (St. George, Utah, USA), and the only extensive population that is protected on federal land is located within the State Line pasture of the US Department of the Interior, Bureau of Land Management, Curly Hollow Wash cattle grazing allotment. Monitoring trend studies indicate possible long-term decline of this population (Meyer, 2018, based on studies by R. Van Buren and A. Searle; report on file at the Bureau of Land Management, St. George Field Office, St. George, Utah USA).

Astragalus holmgreniorum is a spring ephemeral perennial species (Rominger, Meyer, Van Buren, & Searle, 2019). Seedlings emerge in early spring, establish as recruits during the spring growing season, then enter dormancy at the onset of hot summer weather. They remain dormant through the summer, fall and winter. In early spring of the year following the recruitment year, surviving plants re-emerge as returning adults that can flower and produce seeds. The species is a hemicryptophyte, i.e., its dormant meristems are located at or very near the soil surface, where they are likely to be highly vulnerable to trampling. In this study, we asked whether surface disturbance and specifically cattle trampling could impact dormant season survival both of newly recruited juvenile *A.holmgreniorum* plants and of adult plants that have already survived at least one dormant season. We measured survival of tagged plants over the dormant season in small plots at an array of sites with different degrees of cattle disturbance and quantified disturbance at the plot level at these sites. We then statistically examined the relationship between cattle disturbance and dormant season survival.

Our study was designed to address the following hypotheses: 1) Dormant season survival of *A. holmgreniorum* plants will be negatively correlated with the level of cattle trampling disturbance at the site, plot, and individual plant level, 2) Cattle trampling will be shown to be the principal source of surface disturbance in critical habitat for this species within the State Line pasture of the Curly Hollow Wash grazing allotment, 3) Negative cattle trampling impacts incurred during the current dormant season as measured at the time of evaluation will be greater than long-term impacts as measured at the time of tagging. 4) Adult plants will have higher survival probabilities than recruited juveniles, and this difference will be more pronounced at sites with more cattle trampling impact, and 5) Survival probability for recruited juveniles will be positively correlated with their size at tagging.

2. Material and methods

2.1. Study site selection

The field experiment was carried out in two iterations, 2016 − 2017 and 2017 − 2018. Five study sites were established for the first iteration in late spring 2016. Four sites were selected from within critical habitat (see US Fish & Wildlife Service, 2006, for location information) in the State Line population, on federal land managed by the Bureau of Land Management (BLM). These sites are located within a pasture that is designated for fall-winter seasonal cattle grazing, i.e., grazing only when *A. holmgreniorum* plants are dormant. The cattle range freely over ca. 20 square km within this pasture and their impacts are consequently unevenly distributed, with some areas much more heavily impacted than others. Based on observed levels of cattle trampling in *A. holmgreniorum*-occupied areas, the Demo and Salt Lick sites were selected as highly disturbed sites, while the Overlook and Wash sites were selected as moderately disturbed sites. The fifth site, located within the Central Valley population on school trust land managed by the State of Utah and not grazed by livestock, was selected as a low-disturbance site.

For the second experimental iteration in spring 2017, the same five study sites were included, and an additional moderately disturbed site at Atkinville, also located within the State Line population, was included. Atkinville was the site of the long-term demography study reported in Van Buren, Searle, Rominger, and Meyer (in press), so that its current status was of specific interest. At Central Valley, the study was moved to a different site just north of the first-year site. The new site was chosen because it better matched the habitat at the State Line sites. The original Central Valley site was in a sloping overland flow area with heavy biological soil crust dissected by numerous small washes with evidence of serious soil erosion in spring 2017. This could have compromised the results there and made them less comparable with results from the State Line sites. Data from Central Valley for both iterations are included in the formal analysis.

2.2. Experimental design

At each site for each iteration, twenty 2m × 2m (4 m^2) plots were selected (16 plots at Atkinville). Plots were placed without regard to disturbance within each site, but with the restriction that each plot include living *A. holmgreniorum* plants within its boundaries. There was no formal randomization procedure. For each iteration, a different set of plots was selected at each site, i.e., there was no resampling of plots across iterations.

2.3. Survival data collection

Within each plot the first spring of each iteration, each *A. holmgreniorum* plant was marked with a numbered aluminum tag nailed into the ground. Plant diameter and age class (juvenile or adult) were recorded for each tagged plant. A minimum of 100 plants was tagged at each study site for each iteration (range 125–210 per site for the first iteration, 172–283 per site for the second iteration). On the second spring visit at each site, all sample plots were relocated and tagged individuals were recorded as dead (did not re-emerge) or alive (re-emerged successfully). For tags that could not be relocated, plants were removed from the data set. For the first iteration, plants were tagged between March 31 and April 9, 2016 and plots were revisited between April 28 and May 6, 2017. For the second iteration, tagging took place between April 28 and May 6, 2017 and plots were revisited between April 21 and April 28, 2018.

2.4. Disturbance data collection

Disturbance data were collected using a modification of the nested frequency method of Smith and Bunting (1986). This method utilizes a series of nested quadrats and was originally designed to optimize quadrat size for simultaneously measuring frequencies of multiple species that vary in abundance. In the modification of the nested frequency method used here, the minimum size of the quadrat needed to detect the presence of disturbance was used as an index of disturbance extent (Van Buren & Harper, 2003). The logic was that more extensive disturbances within each plot were more likely to be encountered in smaller subplots than less extensive disturbances. Each 4 m^2 plot was sectioned into four nested quadrats of decreasing size (4, 2, 1 and 0.25 m^2) and the quadrats were assigned disturbance index values of 1, 2, 3 and 4, respectively.

Disturbance in each plot was evaluated by type at the time of tagging and at the time of evaluation a year later, and reported as 0 (no disturbance), 1 (disturbance present only in the 4 m^2 quadrat, not evident in smaller nested quadrats), 2 (disturbance present in the 2 m^2 nested quadrat), 3 (disturbance present in the 1 m^2 nested quadrat, or 4 (disturbance present in the 0.25-m^2 nested quadrat). Each plot was examined for cattle, rodent, human (foot, bicycle, or motorized vehicle), and water erosion disturbance types. For each type of disturbance, a value was recorded depending upon the size of the smallest subplot within which the disturbance was found. Plots with no disturbance received a value of 0 for all disturbance types. It was theoretically possible to detect disturbance of multiple types within a single plot, as disturbance types were scored independently. However, it was rare to encounter two types of disturbance in a single plot, especially in cattle-disturbed plots, which tended to be heavily trampled throughout, obliterating any sign of other disturbance.

2.5. Statistical analysis

We used several different approaches to test our hypothesis that survival would be negatively correlated with cattle disturbance at the site, plot and individual plant levels. First, we used analysis of variance (ANOVA) for a binomial response variable (plants surviving/plants tagged) to examine survival proportion as a function of study site for each iteration (SAS Proc Glimmix), with survival proportions for plots within a site as replicates. Iterations were kept separate for analysis because of the unbalanced design (different numbers of sites) and the change in Central Valley site location. Least squares means separations from the analysis were used to detect significant differences in survival among sites for each iteration. We did not formally test the hypothesis that cattle trampling was the principal source of disturbance at sites within the State Line pasture because this result was obvious by inspection of the data (Fig. 1).

We used correlation analysis (SAS Proc Corr) to look for a relationship between mean survival proportion and mean disturbance score at the site level. Overall disturbance score (sum of all disturbance scores for each plot, including cattle disturbance) and cattle-only disturbance score were used in this analysis. These tests had limited power because of small sample size, i.e., a small number of sites. For this reason, we also performed analyses examining the correlation between survival and both overall disturbance and cattle disturbance at the plot level, using scores for individual plots pooled across sites for each iteration. To test the hypothesis that current dormant season disturbance would have a stronger negative effect than long-term disturbance measured at tagging, we performed separate analyses for disturbance scores at installation (pre-dormant season) and at evaluation (post-dormant season) for the 2017 − 2018 iteration. Excessive missing data precluded the use of installation disturbance data for the 2016 − 2017 iteration; consequently only disturbance at evaluation could be included in the analysis.

To test the hypothesis of negative cattle trampling impacts on survival at the individual plant level, plants were classified according to survival (surviving or dead), and plot disturbance scores associated with each tagged plant were treated as the dependent variable. These data were subjected to ANOVA (SAS Proc GLM) to determine whether surviving plants had significantly lower disturbance scores than plants that suffered mortality. A significant decrease in disturbance scores for surviving vs. dead individuals was interpreted as evidence that reduced survival was associated with higher levels of disturbance. We performed this analysis for both overall disturbance and cattle disturbance and for both pre-dormant season and post-dormant season scores. As P values tended to be uniformly very low in these analyses (i.e., very large effect of disturbance on survival), we used the relative magnitude of F-ratios as a guide in interpreting treatment effects.

We tested the hypothesis that adults and juveniles would have different survival probabilities as a function of site, and by proxy cattle trampling disturbance, in an ANOVA (SAS Proc GLM) with age class and site as independent variables and survival as the dependent variable. Each plant was assigned a value of 1 or 0 depending on whether it was surviving or dead, and these values were averaged to calculate survival probability for each age class by site combination.

Individual plant-level ANOVA (SAS Proc GLM) was also used to test the hypothesis that plant size (rosette diameter) at tagging would affect patterns of dormant season survival overall. We asked whether plant size affected survival differentially for adult versus juvenile plants by treating age class and survival class as independent variables and plant size at tagging as the dependent variable.

3. Results

3.1. Site level analysis

Dormant season survival of *A. holmgreniorum* plants varied significantly among sites in both the 2016 − 2017 iteration (d. f. = 4, 95, F = 25.57, $P < 0.0001$; range 12–69 % survival) and the 2017 − 2018 iteration (d. f. = 5, 110, F = 40.99, $P < 0.0001$; range 11–54 % survival; Fig. 1A, B). Mean scores for overall disturbance and cattle trampling disturbance also varied widely among sites (Fig. 1C, D). Most of the disturbance was from cattle trampling, especially at the three sites most heavily impacted by cattle. Dormant season survival was significantly negatively correlated with overall disturbance at the site level for both iterations (Table 1). It was significantly negatively correlated with cattle disturbance at the site level in the 2017 − 2018 iteration, but not in the 2016 − 2017 iteration. This was due to results at the ungrazed Central Valley site in 2016 − 2017, where relatively low survival was due to natural disturbance from water erosion in the wet spring of 2017. The most cattle-trampled sites had significantly lower dormant season survival than sites with less cattle disturbance in the State Line population in both study iterations (Fig. 1). These results show that surface disturbance had a major negative impact on dormant season survival of *A. holmgreniorum* at the site level, and that the principal source of surface disturbance within the State Line critical habitat was cattle trampling.

3.2. Plot-level analysis

All correlation coefficients in the plot-level correlation analysis for the relationship between disturbance and survival were negative and highly significant, confirming results at the site level (Table 1). In the 2016 − 2017 iteration, the negative correlation coefficients for the relationship of survival to overall disturbance and to cattle disturbance were similar, likely because of low survival in some plots at Central Valley not related to cattle trampling. However, the relationship with cattle disturbance remained highly significant in this plot-level analysis. In the 2017 − 2018 iteration, negative correlation coefficients for the relationship between survival and cattle disturbance were substantially higher than those for the relationship to overall disturbance. The highest correlation coefficient was for cattle trampling measured after the dormant season, supporting the hypothesis that direct impacts of current-year trampling would be more important than cumulative effects of cattle disturbance over time.

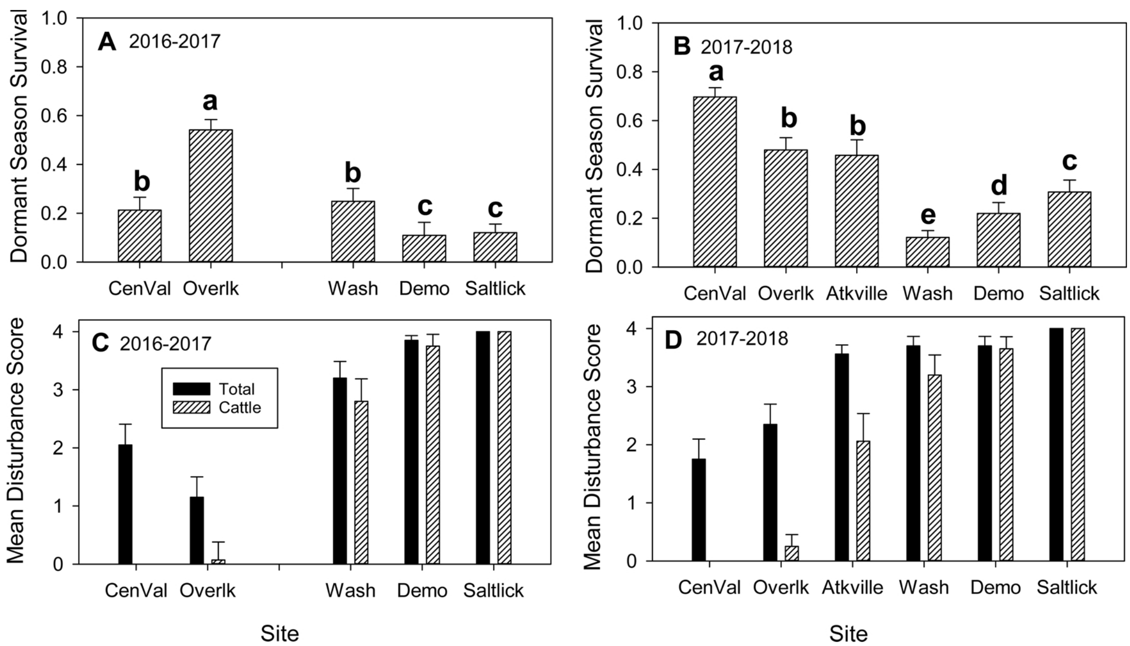

Fig. 1. Mean over-dormant season survival of *Astragalus holmgreniorum* plants (A, B) and mean total and cattle disturbance scores (C, D) at 5 sites in 2016-2017 (A, C, first iteration) and 6 sites in 2017-2018 (B, D, second iteration). Sample size = 20 plots at each site for each iteration (except Atkinville, which included only 16 plots and was included only in the second iteration). Error bars represent standard error of the mean. For dormant season survival in each iteration, bars headed by the same letter are not significantly different at P < 0.05 based on analysis of variance for the binomial response variable surviving plants/tagged plants (SAS Proc Glimmix).

3.3. Individual plant-level analysis

Individual plant-level analysis for tagged plants pooled across sites using the plot disturbance score associated with each tagged plant also confirmed the hypothesis of a negative relationship between disturbance and specifically cattle disturbance and plant survival (Table 2, Fig. 2). Disturbance scores for plants that survived were significantly lower than scores for plants that suffered mortality in both iterations and at both evaluation times in the 2017 − 2018 iteration. Differences in disturbance scores for surviving versus dead plants were especially strong for cattle disturbance, with substantially lower cattle disturbance scores for surviving plants. This effect was also evident in the magnitude of the F-ratios from ANOVA for the 2017 − 2018 iteration, which were much larger for cattle disturbance than for overall disturbance (Table 2). F-ratios were also larger at evaluation than at installation, reflecting the greater difference between disturbance scores for surviving and dead plants when measured after current-year disturbance. We also used plant-level analysis to test whether patterns of survival were different for adult versus juvenile plants. There were far more juvenile plants (current-year recruits) than adult plants (survivors of at least one prior dormant season) present on the plots at tagging (2016: 171 adults, 605 juveniles; 2017: 50 adults, 1361 juveniles). Dormant-season survival was significantly higher for adults than for juveniles in both iterations (2016 − 2017: d.f. = 1, 775, F = 7.278,

Table 1
Correlations at the site and plot levels between *Astragalus holmgreniorum* dormant season survival and disturbance score for overall (total) disturbance and cattle trampling disturbance.

Disturbance Factor	Sample Number	Correlation Coefficient	Significance Level
Site Level Correlations			
2016 − 2017			
Total Disturbance at Evaluation	5	−0.882	0.048
Cattle Disturbance at Evaluation	5	−0.772	0.126
2017 − 2018			
Total Disturbance at Installation	6	−0.559	0.249
Total Disturbance at Evaluation	6	−0.837	0.038
Cattle Disturbance at Installation	6	−0.845	0.034
Cattle Disturbance at Evaluation	6	−0.850	0.032
Plot Level Correlations			
2016 − 2017			
Total Disturbance at Evaluation	100	−0.378	< 0.0001
Cattle Disturbance at Evaluation	100	−0.354	0.0003
2017 − 2018			
Total Disturbance at Installation	116	−0.274	0.0029
Total Disturbance at Evaluation	116	−0.475	< 0.0001
Cattle Disturbance at Installation	116	−0.455	< 0.0001
Cattle Disturbance at Evaluation	116	−0.573	< 0.0001

Table 2
Analysis of variance (SAS Proc GLM) for the response variables total and cattle disturbance score with survival class (surviving vs. dead *Astragalus holmgreniorum* plants) as the independent variable and with data pooled across sites for each iteration. Analyses were performed for disturbance score at evaluation for the 2016-2017 iteration, and for disturbance score at installation and at evaluation for the 2017-2018 iteration. Each individual tagged plant was considered a replicate in either the surviving or dead survival class.

Iteration and Disturbance Source	Degrees of freedom	F-ratio	P-value
2016 – 2017 Iteration			
Total Disturbance at Evaluation	1, 775	51.70	$P < 0.0001$
Cattle Disturbance at Evaluation	1, 775	59.49	$P < 0.0001$
2017 – 2018 Iteration			
Total Disturbance at Installation	1, 1409	55.99	$P < 0.0001$
Cattle Disturbance at Installation	1, 1409	170.48	$P < 0.0001$
Total Disturbance at Evaluation	1, 1409	130.61	$P < 0.0001$
Cattle Disturbance at Evaluation	1, 1409	212.85	$P < 0.0001$

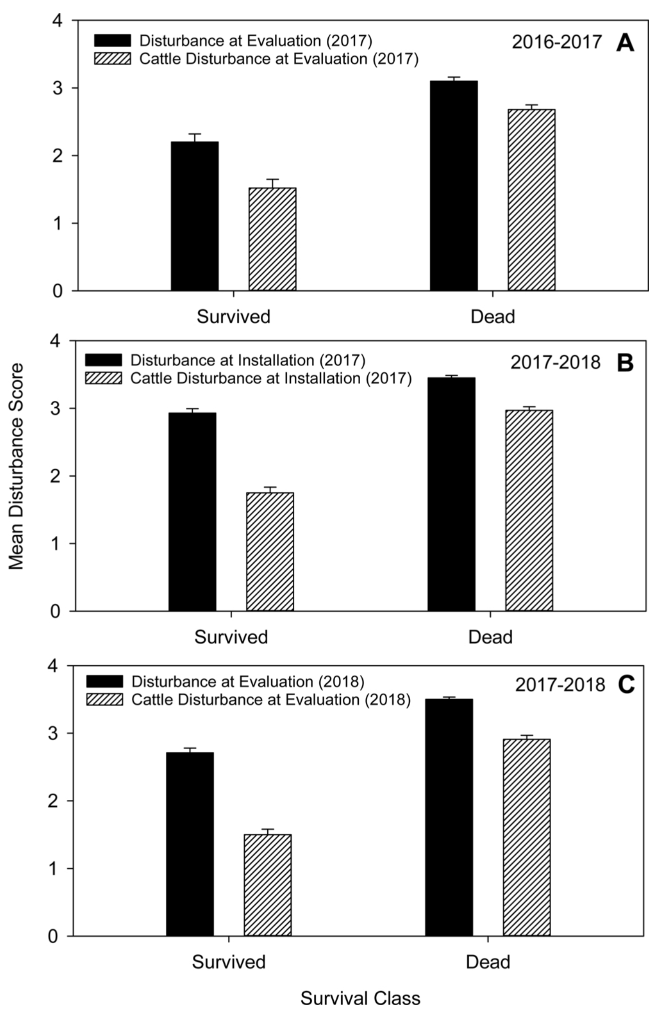

Fig. 2. Mean plot disturbance scores (total disturbance and cattle disturbance) for surviving and dead plants for: A) disturbance at evaluation for the first iteration, B) Disturbance at installation for the second iteration (2017-2018) and C) Disturbance at evaluation for the second iteration (2017-2018). Error bars represent standard errors of the mean. See Table 2 for statistical analysis.

$P < 0.0001$, adult survival 40.9 %, juvenile survival 17.5 %; 2017 – 2018: d.f. = 1, 1409, F = 3.96, P = 0.0467, adult survival 51.5 %, juvenile survival 38.1 %).

In ANOVA using individual plant-level data to compare adult versus juvenile survival as a function of site (and by proxy, of cattle disturbance), the age by site interaction was marginally significant for the first iteration (d.f. = 4, 767, F = 2.22, P = 0.0652). Adult probability of survival (47.4 %) was > 26 times higher than juvenile survival probability (1.8 %) at the most heavily cattle-disturbed Salt Lick site ($P < 0.0001$), and it was 4 times higher than juvenile survival probability (25 % vs. 6%, P = 0.0602) at Demo, which also had heavy cattle disturbance (Fig. 1C). At the least cattle-disturbed sites (Overlook and Central Valley), adult survival probability was < 2 times higher than juvenile survival. These results provide some support for the idea that juvenile plants are more likely to be killed by heavy trampling disturbance than adult plants. Results for the second iteration showed no pattern of adult versus juvenile survival by site disturbance level, likely because of low sample size for adults (mean < 9 adults per site).

Finally, we tested the hypothesis that size prior to the initiation of the dormant period would affect the probability of survival differentially for juveniles versus adults in a two-way ANOVA for each iteration with age class and survival class (alive or dead) as the independent variables and rosette diameter as the response variable. Not surprisingly, age class was highly significant in both analyses, as adult plants were much larger on average than juvenile plants (Fig. 3, Table 3). Size did not affect survival overall in either iteration, but there was a highly significant interaction between age and survival class in both cases. This was because size had no effect on survival probability for adult plants (no significant effect of survival class on size in either iteration), whereas for juvenile plants, smaller individuals were much less likely to survive (2016 – 2017: d.f. = 1,605, F = 46.31, $P < 0.0001$; 2017 – 2018: d.f. = 1,1361, F = 42.10, $P < 0.0001$). Juvenile plants that died in the 2016 – 2017 iteration averaged 3.7 cm at tagging whereas those that survived averaged 4.4 cm (Fig. 3). The difference was even greater in 2017 – 2018, 2.71 cm vs. 4.53 cm. These results suggest that the higher survival of adults in heavily trampled areas could be a function of size, with larger plants less likely to suffer trampling-caused mortality.

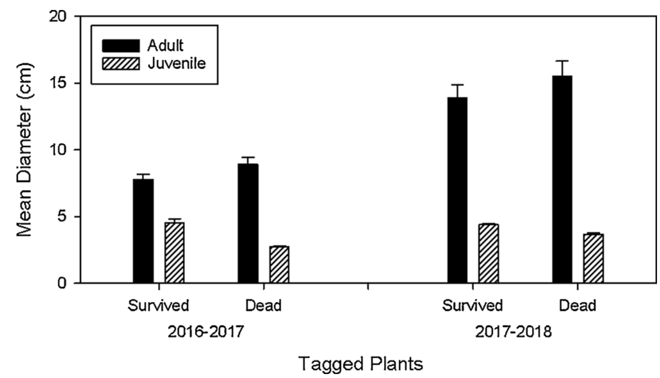

Fig. 3. Mean plant diameter at tagging for surviving versus dead plants of the adult and juvenile age classes in the 2016-2017 and the 2017-2018 iteration. Error bars represent standard errors of the mean. See Table 3 for statistical analysis.

Table 3
Analysis of variance (SAS Proc GLM) by iteration (2016-2017 and 2017-2018) for the response variable diameter at tagging, with age class (adult vs. juvenile) and survival class (surviving vs. dead) as the independent variables.

	Degrees of Freedom	F-ratio	P-value
2016 – 2017 Iteration			
Age Class	1, 773	283.7	< 0.0001
Survival Class	1, 773	1.29	0.2562
Age x Survival	1, 773	28.38	< 0.0001
2017 – 2018 Iteration			
Age Class	1, 1407	1209.9	< 0.0001
Survival Class	1, 1407	2.44	0.1187
Age x Survival	1, 1407	14.67	< 0.0001

4. Discussion

We have shown in previous studies that survival through the dormant season is a weak link in the life history strategy of *A. holmgreniorum* (Van Buren et al., in press). Because dormant meristems are so close to the surface, the plants can suffer both from the extreme heat of the soil surface in summer and from periods of drought at any period during the dormant season. In the 22-year demographic study cited above, two exceptionally dry years (2002 and 2007) resulted in complete failure to survive dormancy, so that no adult plants were present. The species is able to recover from these extreme events through episodic high seed production in favorable years and the ability to form a persistent seed bank that permits the population to reestablish in a subsequent favorable year. These life history traits, along with the ability to recruit new seedlings in most years, provide a buffer that may also compensate to some degree for trampling-caused dormant season mortality. This could explain how the species has managed to coexist with some level of cattle grazing in this desert shrubland community during the 170 years since settlement.

Juvenile dormant-season survival probability had a strong impact on likelihood of extinction in population viability analysis for this species (Van Buren et al., in press). Any factor that substantially increases juvenile dormant season mortality risk and that can be mitigated through improved management needs to be addressed. The study we report here has shown that cattle trampling substantially increases dormant season mortality risk, particularly for juvenile plants. Heavily trampled sites in the State Line population had dormant season mortality up to five times higher than sites with minimal trampling disturbance.

Our study is observational rather than manipulative, but it has produced statistically robust evidence that cattle trampling can substantially reduce dormant season survival in *A. holmgreniorum*. One advantage of our observational study is that the levels of trampling are undeniably realistic, and the reduction in survival is directly linked to trampling disturbance that has actually occurred. This provides a strong case not only that cattle trampling can kill *A. holmgreniorum* plants, but that this trampling impact is currently occurring on the ground in established critical habitat for the species.

One difference between weather-caused dormant season mortality and the effects of cattle trampling is that negative weather impacts are episodic, permitting periods of recovery, whereas cattle grazing is most often a chronic disturbance that occurs seasonally every year. On the other hand, weather-caused dormant season mortality is relatively uniform across the entire range of the species, whereas cattle disturbance shows an uneven pattern across the landscape, with some areas much more impacted than others in any given year. The positioning of water tanks can have a major effect on cattle distribution on desert ranges, (Brooks et al., 2006). In the State Line pasture the cattle have access to river water, apparently obviating the need for water tanks that would concentrate their impact. However, salt licks can have a similar concentrating effect. In our study the area around a salt lick was chosen as the most cattle-disturbed site. Placing salt licks far from areas with high concentrations of *A. holmgreniorum* plants would be one simple management change that could potentially reduce recruit mortality substantially.

Cattle could potentially have many other effects on *A. holmgreniorum*, both positive and negative, in addition to their negative effect on dormant-season survival. Potential positive effects alluded to earlier are the planting of seeds and the creation of water-collection microsites that might be more favorable for seedling establishment, but there are no quantitative data to address these potential effects. We have data to show that seeds of this species must be buried in order for seedlings to establish successfully in the field and that seedlings can emerge in greenhouse soil from 3-centimeter depth (K. Rominger, Utah Valley University, unpublished data). However, we also have field data showing that most seeds are likely buried in mud soon after dispersal from their pods by water action, obviating the need for another burial agent (Houghton, Stevens, & Meyer, in press). Also, burial too deep for emergence is a potential negative effect of cattle hoof action. When the soil is wet, hoof prints can penetrate to much greater depths than would permit seedling emergence, and these hoof prints are then silted in over relatively short time periods. It is likely that the fine, silty soils of the Virgin Limestone member of the Moenkopi Formation where this species is found are especially susceptible to cattle disturbance impacts.

Other possible negative effects of grazing and trampling include destruction of nests of the ground-nesting native bees that this species relies upon for pollination, and decrease in alternative nectar and pollen sources for these bees (Barlow & Pavlik, 2017; Tepedino, 2005). A more indirect cause of harm that can only putatively be assigned to cattle grazing is the documented increase in the cover of exotic annual bromes that potentially compete both directly with *A. holmgreniorum* plants and also with other native plant species that provide resources for pollinators (Meyer 2018, report on file at the Bureau of Land Management St. George Field Office). Annual brome proliferation also greatly increases the risk of wildfire (Brooks et al., 2004), a factor with unknown impacts on *A. holmgreniorum*, which typically occupies plant communities with very low cover and consequently low fuel loads.

5. Conclusions

This study of the effects of cattle trampling on demography of a globally endangered plant provided quantitative evidence that: (1) dormant season mortality in this species is strongly correlated with levels of cattle disturbance, (2) smaller, juvenile plants are more susceptible to this threat, and (3) the mortality is apparently caused directly by trampling that occurs during the current dormant season and not by chronic habitat degradation. Our study also demonstrates the utility of a small-plot approach to quantification of cattle trampling and its impacts on plant survival. This methodology is best applied in desert systems with low plant cover and with species that occur at relatively low density, making it possible to track the fate of individual plants through time. The method permitted the tracking of many hundreds of plants and the quantification of disturbance on over two hundred plots, providing large sample sizes for statistical analysis. It has provided a clear demonstration that cattle trampling can be directly damaging to an endangered plant species within its critical habitat, and also provides a framework for consideration of management actions that could potentially mitigate this damage. These options range from simple resource manipulations (e.g., changing salt lick placement) that shift patterns of cattle use away from sensitive areas to the removal of all cattle grazing from the pasture.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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