



Black-Tailed Prairie Dog (*Cynomys ludovicianus*) Reintroduction Can Limit Woody Plant Proliferation in Grasslands

Sarah L. Hale*, John L. Koprowski and Steven R. Archer

School of Natural Resources and the Environment, The University of Arizona, Tucson, AZ, United States

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*Correspondence:

Sarah L. Hale
shale16@gmail.com

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Tree and shrub proliferation has been widespread in grasslands worldwide, and has altered ecosystem function and wildlife habitat. Several causes have been proposed for the woody plant encroachment phenomenon. The widespread eradication of a native keystone herbivore in North American grasslands, the prairie dog (*Cynomys* spp.), is one potential contributing factor that has received relatively little attention. We hypothesized prairie dogs would have historically suppressed woody plants by creating “browse traps” through their systematic clipping of vegetation. We tested this hypothesis by conducting surveys and experimentally manipulating shrub accessibility via exclosures and artificial saplings on and around recently reestablished black-tailed prairie dog (*Cynomys ludovicianus*) colonies in southeastern Arizona, United States. Shrubs were common on the nascent colonies (mean \pm SE = 132 ± 32.7 plants ha⁻¹), but at substantially reduced densities compared to off colonies (305 ± 94.9 plants ha⁻¹). Among branches placed on colonies to simulate “saplings” 89% were damaged within 3 days of “planting,” whereas those placed off colonies were virtually untouched. This was true for both a deciduous, N₂-fixing shrub (velvet mesquite, *Prosopis velutina*) and an evergreen non-N₂-fixing shrub (creosote bush, *Larrea tridentata*). Prairie dogs on newly established colonies did not extirpate woody plants over the time-frame of our study, but reduced their abundance and suppressed their growth, which would ostensibly prevent them from achieving dominance. Implications for extending the longevity of widely practiced “brush management” grassland restoration treatments are discussed in the context of perceptions of prairie dogs as rangeland pests. Prairie dogs represent an enigma in keystone conservation. Whereas the reintroduction of large or charismatic keystone species [e.g., sea otters (*Enhydra lutris*)] are conducted to restore critical ecological function, reintroductions of other keystone species, such as gray wolves (*Canis lupus*) and in our case, prairie dogs, are highly controversial. Our findings suggest reintroductions of this negatively perceived small herbivore could function as a tool to locally suppress woody plant proliferation that is widely regarded as an impediment to livestock production. Accordingly, prairie dogs could promote restoration efforts to re-establish and maintain habitat for grassland endemics while promoting biological diversity and other ecosystem services.

Keywords: black-tailed prairie dog, browse trap, ecosystem engineer, exclosure, grassland, keystone species, reintroduction, woody plant encroachment

INTRODUCTION

Woody plant encroachment, the proliferation of trees and shrubs within grasslands and savannas, is a phenomenon occurring in arid and semiarid grasslands and savannas worldwide. This proliferation may involve increases in the density, stature and cover of native trees and shrubs within their historic ranges or the introduction of non-native woody plants (Archer et al., 2017). Shifts from grass to woody plant dominance affects a variety of ecological processes and the allocation of numerous ecosystem goods, and provisioning (e.g., forage production), supporting (e.g., primary production, biodiversity), and regulating (e.g., carbon sequestration) services (Eldridge et al., 2011; Archer and Predick, 2014). Increases in woody cover also substantially alters wildlife habitat, favoring some species and adversely affecting others (Fulbright et al., 2018). Increases in atmospheric CO₂ and changes in climate and fire regimes have been proposed as causal factors; however, the direct and indirect effects of intensification of livestock grazing over the past century appears to be a primary driver (Archer et al., 2017). Perspectives on shrubs in grasslands vary widely (Archer et al., 2017). Commercial ranching enterprises based on cattle have traditionally viewed shrub proliferation as an impediment to livestock production; pastoralists raising goats, camels or other domesticated browsers see shrubs as a potentially important forage resource and may look favorably on increases in their abundance; conservation biologists have biodiversity concerns that shrub proliferation will threaten grassland and savanna ecosystem types and the plants and animals endemic to them (Archer et al., 2017). These contrasting perspectives pose challenges for managing lands for multiple uses.

Coincident with the intensification of livestock grazing in North America was the widespread eradication of the prairie dog (*Cynomys* spp.), a rodent traditionally viewed as an impediment to livestock production (Vermeire et al., 2004; Derner et al., 2006; Detling, 2006). Although prairie dogs have been recognized as contributing to the maintenance of grassland ecosystems (Hoogland, 1995; Kotliar et al., 1999), the consequences of their removal have received relatively little attention in the context of regulating grass-woody plant interactions. In Africa, herbivores of varying sizes mediate woody plant abundance through browsing activities [e.g., elephants (*Loxodonta* spp.), dik-diks (*Madoqua* spp.), impala (*Aepyceros melampus*); Sankaran et al., 2013]. Systematic browsing maintains woody vegetation at a small stature, thereby creating a “browse trap” that also contributes to a “fire trap” (Bond and Keeley, 2005; Staver et al., 2009; Sankaran et al., 2013). For the purpose of this manuscript, “browse trap” and “fire trap” refer to the maintenance of woody vegetation at small stature by herbivores and frequent, low-intensity wildfires, respectively. Woody plants caught in a fire or browse trap are unable to achieve dominance until the suppressing pressure is removed. We suggest that prairie dogs in North America historically prevented woody plant recruitment or created and maintained browse traps that suppressed shrubs and trees. In the former case, prairie dog eradication would have opened the door for woody plant establishment. In the latter

case, prairie dog removal would have released established, but diminutive, woody plants from the browse trap. In both cases, removal of the suppressing pressure, i.e., prairie dogs, would have permitted woody plants to reach adult stature in grasslands throughout the prairie dog’s former range.

Prairie dogs, once widely distributed across the North American west (Proctor et al., 2006), were deemed a rangeland pest in competition with livestock, leading to widespread and highly successful eradication efforts beginning in the early 1900s (Andelt, 2006; Forrest and Luchsinger, 2006; Reeve and Vosburgh, 2006). Historic population sizes are hard to pin-point (Vermeire et al., 2004), but at the most conservative estimate, active eradication, habitat loss, and sylvatic plague (*Yersinia pestis*; Luce et al., 2006) appear to have reduced prairie dog populations to 2% of historic numbers (Whicker and Detling, 1988; Miller et al., 1994), and range occupancy to ≤1% (Luce et al., 2006). Prairie dogs are grazers, but systematically gnaw, clip, and girdle other vegetation to maintain plants on their colonies at small stature (<30 cm; King, 1955; Hoogland, 1995; Weltzin et al., 1997) and thereby maximize predator detection. Accordingly, their removal would have removed an impediment to woody plant establishment and growth.

Woody plant proliferation in grasslands has led to the implementation of “brush management” practices involving heavy equipment, herbicides, and/or prescribed fire to reduce the cover of trees and shrubs (Hamilton et al., 2004; Collins et al., 2015). Such techniques are typically expensive with short-lived effects, and hence are seldom cost-effective (Archer et al., 2011). We sought to investigate whether the black-tailed prairie dog (*Cynomys ludovicianus*; hereafter “prairie dog”) might constitute a natural, potentially long-term, sustainable “biocontrol” solution for deterring woody plant encroachment and proliferation in grasslands. We hypothesized that reintroduced prairie dogs would suppress woody plant growth on their colonies, and create a “browse trap” through their systematic felling of vegetation. If our hypothesis was supported, we predicted that woody plants on newly established prairie dog colonies would be less abundant than those off-colony, that shrubs occurring outside of exclosures on prairie dog colonies would have slower growth and higher mortality rates than protected shrubs, and that disturbance to introduced artificial “simulated saplings” would be greater on colonies than off colonies.

From a broader perspective, our study was also intended to determine whether the reintroduction of a keystone herbivore following a prolonged absence could restore the browse trap that historically excluded woody plants or prevented them from expressing dominance in grassland systems. Studies involving keystone species typically seek to assess ecosystem effects while the species of interest is present or absent from the landscape (e.g., Reisewitz et al., 2006); however, studies assessing the ecosystem-level effects of keystone species reintroductions are more rare (Hale and Koprowski, 2018). A study in northwestern Mexico investigated independent and interactive effects of existing prairie dogs and cattle on woody encroachment in an elegant field experiment (Ponce-Guevara et al., 2016), wherein plots received one of four treatments: prairie dogs only, cattle only, prairie dogs + cattle, and neither prairie dogs nor cattle.

Results indicated that prairie dogs played an important role in suppressing woody encroachment, and that their role was amplified in the presence of cattle. The study we report here similarly assesses the effects of black-tailed prairie dogs on shrubs in an arid grassland, but differs in that we had the unique opportunity to ascertain whether a *reintroduced* population of prairie dogs could influence shrub encroachment. Our study is among the first to investigate consequences of the reintroduction of a keystone species, and the extent to which that reintroduction might be justified as part of an integrated, comprehensive plan to more effectively address ecosystem management challenges in grasslands.

MATERIALS AND METHODS

Study Site

Las Cienegas National Conservation Area (hereafter Las Cienegas) is a 17,000 ha working cattle ranch managed by the Bureau of Land Management, and is located 72 km southeast of Tucson, AZ, United States in Santa Cruz County. The study area is a representative of the natural regional grasslands occurring across central and southern Arizona, southwestern New Mexico, and northern Mexico (Gori and Enquist, 2003; Gori and Schussman, 2005; Bodner and Simms, 2008). Mean annual precipitation is 405 mm, mostly falling during the summer monsoon months (July–September); mean annual temperature is 15.7°C (Bodner and Robles, 2017). During our study (2013–2015) annual precipitation and temperature (\pm SE) averaged 350 \pm 47 mm and 16.2 \pm 0.2°C (Empire Remote Area Weather Station; QEMA3)¹. Grasslands at Las Cienegas are located between 1300 and 1500 m in elevation, and soils are primarily gravely, sandy, and clay loam (Bodner and Robles, 2017).

Semi-desert grasslands in Arizona support a variety of herbivores, including peccaries (*Pecari tajacu*), mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), pronghorn (*Antilocapra americana*), and historically, supported black-tailed prairie dogs, which were extirpated by 1960 (Bock and Bock, 2000; Underwood and Van Pelt, 2000). The Arizona Game and Fish Department began reintroducing black-tailed prairie dogs at Las Cienegas in 2008 using animals obtained from populations in New Mexico, United States, and Sonora, Mexico. We conducted our experiments on four of these colonies.

Colonies were situated on sites with similar soils (fine, deep, well-drained), slopes (0–15%), and elevations (1367–1412 m). One colony was initiated per year starting in 2008 and ending in 2011. The Arizona Game and Fish Department prepared sites via mechanical removal of large (>~1 m height) shrubs, mowing, and installation of 25 artificial burrows within a 4 ha area (see Hale et al., 2013 for details). Managers re-mowed colonies in 2011 to facilitate prairie dog establishment.

Throughout our study, three of the four colonies remained occupied by prairie dogs; however, one colony (hereafter referred to as the “control site”) failed and was unoccupied during 2014

and 2015. The Arizona Game and Fish Department initially prepared this site in the same manner as the other colonies, but the colony lacked prairie dogs throughout the majority of our study period (<10 prairie dogs present in May 2013; the site was vacant by October 2013). We only used the control site for our simulated sapling experiment.

Woody Plant Surveys

We surveyed woody plants on each occupied colony in May of 2013 and 2014. We conducted eight belt (5 m width) transect surveys, wherein transects originated at the center of each colony and extended to and slightly beyond the colony boundary. We considered colony boundaries to be where the junction of short, prairie dog-defoliated grass and burrows met tall, unclipped grass and an absence of burrows. Off-colony transects extended up to 100 m beyond the colony perimeter for four transects at colonies A and B, and six transects at colony C. Some off-colony transects did not extend to the full 100 m due to logistical or topographic constraints (e.g., one transect was cut short by a deep, wide wash). We counted shrubs with stems originating within the transect belts, and noted the presence and degree of disturbance in the form of clipping, chewing, or girdling of their stems on a scale of 0–3 (0 = no disturbance, 1 = few stems disturbed, 2 = many stems disturbed, 3 = majority of stems disturbed). We considered colony to be the experimental unit ($n = 6$; two surveys at three colonies).

Exclosure Experiments

Among the woody plants encountered in our 2013 survey, we tagged plants of a random subset of the two most abundant species (velvet mesquite, *Prosopis velutina* and catclaw acacia, *Acacia greggii*; $n = 40$) for monitoring on each occupied colony (typically $n = 20$ on-colony and 20 off-colony). We installed exclosures around half of the plants at each on-off colony location ($n = 10$), with the other half remaining unprotected. We used garden fencing (mesh size 5.1 cm \times 7.6 cm) to exclude prairie dogs and larger mammals (e.g., lagomorphs) for half of the exclosures ($n = 5$), and hardware cloth (mesh size 0.6 cm \times 0.6 cm) for the remainder of the exclosures ($n = 5$) to exclude prairie dogs and smaller mammals [e.g., northern pygmy mice (*Baiomys taylori*), pocket mice (*Chaetodipus* spp., *Perognathus* spp.), kangaroo rats (*Dipodomys* spp.), woodrats (*Neotoma* spp.), grasshopper mice (*Onychomys* spp.), deer mice (*Peromyscus* spp.), harvest mice (*Reithrodontomys* spp.), and cotton rats (*Sigmodon* spp.)]. We left exclosures in place for ~3 months (mid-May through August) in 2013 and 2014 and for ~5 months (mid-May through late October) in 2015. We measured the canopy diameter of plants along their longest axis and perpendicular to their longest axis at the time of exclosure installation and again at the time of exclosure removal. We standardized change in shrub canopy area (CA), (m², computed as an ellipse) to a monthly basis (30 days). We followed the same plants each year; if a plant measured on the previous year had died, we made note of it and replaced it with the nearest live individual of the same species.

¹<http://mesowest.utah.edu>

Simulated Sapling Experiment

We removed foliated branches [average (\pm SE) length = 47 ± 0.6 cm; diameter = 1.1 ± 0.02 cm] from mature shrubs in nearby off-colony areas, and inserted them ~ 10 cm into the ground along four transects that originated at the center of each colony and extended 100 m beyond the colony boundary in randomized directions. We also installed transects of “simulated saplings” on the unoccupied control site that had been prepared in the same manner as the occupied colonies (see section “Study Site”).

We hypothesized that prairie dog responses to artificial “simulated saplings” would indicate how they would react to the appearance of new woody plants. We spaced saplings ($n = 10$) evenly along transect segments on the colonies (the spacing distance varied for each transect segment, depending on its absolute length), and at 10 m intervals along the off-colony transect segments ($n = 10$). We considered three simulated saplings on each transect to be “periphery” saplings: the sapling installed on the colony boundary, and the closest sapling inside and outside of the colony boundary (Supplementary Figure S1). We also sought to ascertain whether prairie dogs would respond to familiar vs. novel shrubs in the same manner, so we used two woody species: velvet mesquite (*P. velutina*; hereafter “mesquite”), a native shrub common on and around the prairie dog colonies, and creosote bush (*Larrea tridentata*), also a native shrub, but one that did not occur on or near the colonies on the Las Cienegas. Both species are abundant across the Sonoran Desert and on landscapes within the study area. Mesquite is a thorny, N_2 -fixing deciduous shrub (Fabaceae), whereas creosote bush is thorn-free, non- N_2 -fixing evergreen shrub (Zygophyllaceae) that dominates many landscapes in each of the three North American hot deserts.

We measured saplings for height (cm) and recorded the number of secondary stems arising from the primary stem (typically several for mesquite and none for creosote bush). After 3 days of exposure to prairie dogs, we re-measured saplings and recorded the extent of damage (i.e., chewing, clipping, or girdling). We quantified damage as the proportion of stems disturbed on mesquite saplings and the relative proportion of height change of creosote bush saplings (since there were rarely secondary stems present). We conducted the experiment with mesquite in May 2014, and repeated it in late July/early August 2014. We conducted the experiment with creosote bush saplings in early September 2015, and repeated it in late September 2015. We generated different sets of random transects for each trial, so considered temporal replicates independent of one another for statistical analysis. For our 2014 experiment, we used branches of various heights (11–156 cm) and basal diameters (2.2–24.5 mm) to ascertain if prairie dog treatment of small, less visible plants would differ from that of larger more prominent plants.

Data Analysis

We performed statistical analyses in JMP (1989–2007). We assessed shrub density on and off colonies using a Student’s *t*-test, with location (on-colony, off-colony) as the explanatory variable. We removed outliers (points $> \pm 2$ SD’s from the

mean; $n = 7$ of 320 shrub canopy area data points) from analysis based on examination of histograms and residual plots. We log transformed changes in shrub canopy area ($m^2/month$) in enclosure experiments to normalize the data and assessed relationships using a full factorial two-way ANOVA with enclosure mesh size (prairie dogs and larger mammals excluded, or all mammals excluded) and location (on-colony, off-colony) as main effects. Additionally, we assessed change in shrub canopy area using a four-way ANOVA with location (on-colony, off colony), enclosure presence (yes, no), colony (A, B, or C), and year (2013, 2014, 2015) as main effects.

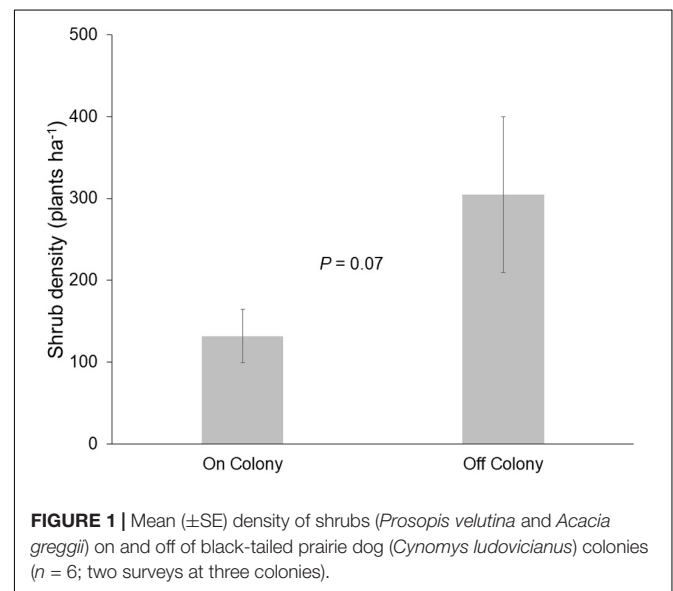
To assess the simulated sapling experiment, we performed a full factorial three-way ANOVA with trial number (first or second), species (mesquite or creosote bush), and location (on-colony, colony periphery, off-colony, on-control, control periphery, off-control) as independent variables, and proportion of total plants disturbed or degree of disturbance as the dependent variables. We considered colony to be the experimental unit ($n = 16$; four temporal replicates per colony).

When significant differences were indicated by ANOVA ($\alpha \leq 0.05$), we used Tukey’s honest significant difference (hsd) tests (where statistical significance was set at 0.05 divided by the total number of comparisons in each test) to evaluate differences among means. In cases where no interactions occurred between effects having only two levels, we performed Student’s *t*-tests on each effect with $\alpha \leq 0.05$.

RESULTS

Woody Plant Surveys

Mean (\pm SE) shrub density (plants ha^{-1}) was greater off of colonies (305 ± 94.9) than on colonies (132 ± 32.7 ; $P = 0.07$; Figure 1). The frequency of disturbance was greatest for shrubs on colonies [85% ($n = 329$ plants)] compared to only 9% ($n = 279$) in off-colony locations.



Exclosure Experiments

Shrub mortality during our study was low: only three of the 116 tagged mesquite plants died. Survival of mesquite was comparable on (95 ± 2.0%) and off of colonies (100 ± 2.0%; $P = 0.10$), and inside (95 ± 2.0%) and outside of exclosures (100 ± 2.0%; $P = 0.10$).

Changes in the canopy area of individual shrubs (m^2/month) were statistically comparable in exclosures of differing mesh size ($F_{1,159} = 0.01$, $P = 0.918$; **Table 1**) so we pooled these data for subsequent analysis. Additionally, changes in shrub canopy area were statistically comparable among colonies ($F = 0.412$, $P = 0.663$; **Table 1**), so we also pooled these data for subsequent analysis. We examined data to determine if there might be a size threshold above which shrubs might be more consistently damaged by prairie dogs, but we found no indication of such.

Change in canopy area was affected by location ($F_{2,297} = 20.06$, $P < 0.001$; **Table 1**), year ($F_{2,297} = 9.67$, $P < 0.001$; **Table 1**), exclosure presence ($F_{2,297} = 29.68$, $P < 0.001$; **Table 1**), and the interactive effects of location × year ($F_{2,297} = 10.48$, $P < 0.001$; **Table 1**) and exclosure presence × year ($F_{2,297} = 8.14$, $P < 0.001$; **Table 1**). On average, (i) canopies of shrubs protected by exclosures expanded more than those of unprotected shrubs ($P < 0.001$), (ii) levels of canopy expansion of shrubs on colonies ($0.14 \pm 0.03 \text{ m}^2/\text{month}$) was greater than that of shrubs off colonies ($0.00 \pm 0.02 \text{ m}^2/\text{month}$; $P < 0.001$), and (iii) canopies of shrubs expanded more in 2013 ($0.15 \pm 0.02 \text{ m}^2/\text{month}$) than in 2014 ($0.03 \pm 0.02 \text{ m}^2/\text{month}$; $P < 0.001$) or 2015 ($0.03 \pm 0.02 \text{ m}^2/\text{month}$; $P < 0.01$). Interaction effects were largely driven by year, with shrubs on colonies in 2013 expanding significantly more than all other groups (**Table 1**), and shrubs inside exclosures in 2013 expanding more than all other groups (**Table 1**).

Simulated Sapling Experiments

Size of simulated saplings did not affect whether or not they were disturbed [X^2 ($df = 3$, $n = 638$) = 1.309, $P = 0.73$], so we pooled size classes for subsequent analysis. Colony had no effect on the proportion of saplings disturbed or degree of disturbance, so we pooled these data across occupied colonies as well. Neither trial number (first or second; $F_{1,47} = 0.17$, $P = 0.688$) nor shrub species (creosote or mesquite; $F_{1,47} = 0.19$, $P = 0.671$) influenced the proportion of saplings disturbed, but location (on-colony, colony periphery, or off-colony, on-control, control periphery, off-control) did ($F_{1,47} = 61.63$, $P < 0.001$). The proportion of saplings disturbed was greatest on colonies ($89 \pm 4.0\%$; see **Figure 2** for illustration of disturbance), followed by colony peripheries ($39 \pm 4.0\%$; Tukey's hsd, $P < 0.001$); disturbances off-colony were essentially nil (0–2%; **Figure 3A**). Expressed as a spatial continuum, the proportion of saplings disturbed was consistently high (74–100%) among on-colony transect positions, decreasing sharply at the colony periphery locations, and was consistently low to nil for off-colony positions and the control site (**Figure 4**).

Similarly to the proportion of plants disturbed, neither trial number (first or second; $F_{1,47} = 1.43$, $P = 0.243$) nor shrub species (creosote or mesquite; $F_{1,47} = 2.27$, $P = 0.145$) influenced the

degree of sapling disturbance. Conversely, location (on-colony, colony periphery, or off-colony, on-control, control periphery, off-control) was significant ($F_{1,47} = 44.35$, $P < 0.001$). Degree of sapling disturbance was greatest on colonies (0.54 ± 0.03), intermediate on colony peripheries (0.22 ± 0.03), and least off of colonies (0.05 ± 0.03) and on control sites (on: 0.06 ± 0.05 , periphery: 0.05 ± 0.05 , off: 0.05 ± 0.05 ; **Figure 3B**).

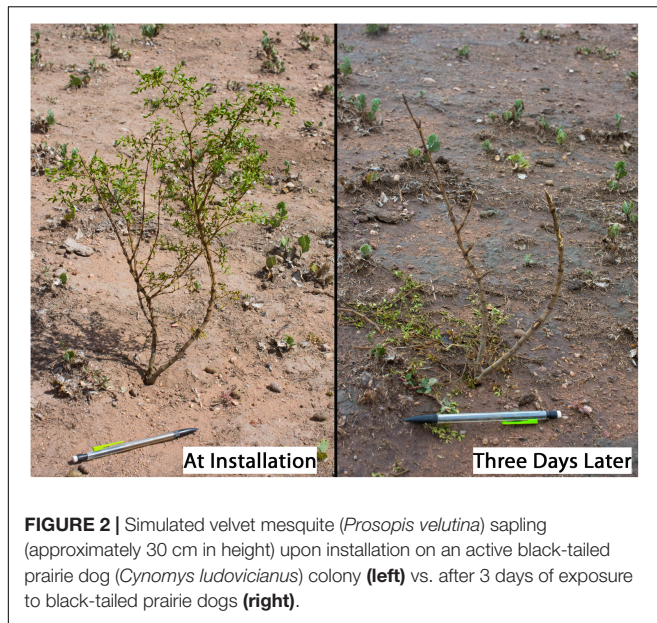
DISCUSSION

Woody plant encroachment is a threat to grasslands and their endemic plants and animals (Archer et al., 2017). Chemical, mechanical and pyric approaches to reducing woody plant abundance and restoring shrub-encroached grasslands have been widely practiced (collectively known as “brush management”), but are typically expensive and their effects are short-lived (Archer and Predick, 2014). Our results suggest that the reintroduction of prairie dogs subsequent to “brush management” could prolong the effectiveness of those treatments while concurrently resuscitating ecosystem processes that would sustain long-term success and promote biodiversity. In this respect, prairie dog re-introductions represent another example of how “rewilding” may revive ecosystem structure, function, and health in a cost-effective manner (e.g., Guyton et al., 2020).

Our exclosure experiments indicated that herbivory was reducing shrub growth both on and off the colony, but more so off-colony than on-colony. One hypothesis to account for this counter-intuitive result would be that above- vs. belowground allocation patterns differed for shrubs on- and off-colony, wherein on-colony shrubs were preferentially allocating more resources to aboveground growth. Another hypothesis would be that growth of protected on-colony shrubs was enhanced by reductions in competition resulting from the felling of surrounding plants by prairie dogs, while growth of protected off-colony shrubs was muted or suppressed owing to the relatively higher levels of competition from surrounding plants. In any case, our observations, surveys, and sapling experiments collectively suggest that benefits gained by potential release from competition or increased allocation to aboveground growth were more than offset by high levels of damage to on-colony shrubs. We directly observed prairie dogs gnawing and clipping shrubs (including those that escaped the broad-scale mechanical treatment and those that re-sprouted following mechanical treatment) and our simulated saplings, consistent with their well-documented habit of systematically felling plants to maintain vegetation in a short-statured state to aid in visual detection of predators (King, 1955; see Figure 5.18 in Hoogland, 1995). Small-statured shrubs that remained on colonies after the mechanical removal of adult shrubs were disturbed more frequently than those located on colony peripheries and off of colonies, as substantiated by observational results (surveys), and experienced the greatest degree of disturbance as indicated by our simulated sapling experiments. Prairie dogs were thus able to substantively mitigate shrub abundance and stature on these nascent colonies. The introduced prairie dogs did not eliminate the small shrubs remaining on their colonies over the time-frame of this study,

TABLE 1 | Summary of ANOVA outcomes for enclosure experiments and coefficients for main effects and significant interactions.

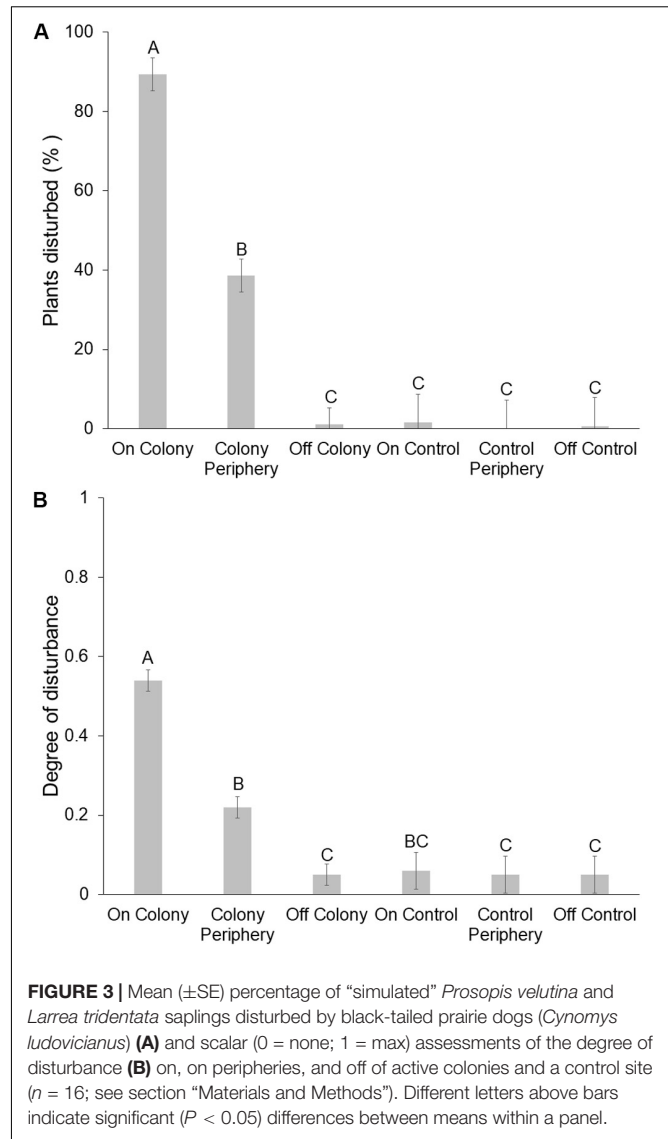
Main effects	F-value Coefficient	df	P	Interactions	F-value Coefficient	df	P
Exclosure mesh size two-way ANOVA							
Location (L)	14.18	1, 159	<0.001	L × ES	0.99	1, 159	0.321
On colony	0.22						
Off colony	0.07						
Exclosure mesh size (ES)	0.01	1, 159	0.918				
Small	0.15						
Large	0.14						
Four-way ANOVA							
Location (L)	20.06	1, 297	<0.001	L × E	1.10	1, 297	0.296
On colony	0.13			L × C	3.41	2, 297	0.035
Off colony	0.01			Off, A	0.03		
Exclosure (E)	29.68	1, 297	<0.001	Off, B	0.05		
Yes	0.14			Off, C	−0.05		
No	0.00			On, A	0.14		
Colony (C)	0.41	2, 297	0.663	On, B	0.08		
A	0.08			On, C	0.16		
B	0.06			L × Y	10.48	2, 297	<0.001
C	0.06			Off, 2013	0.01		
Year (Y)	9.67	2, 297	<0.001	Off, 2014	0.01		
2013	0.15			Off, 2015	0.01		
2014	0.03			On, 2013	0.30		
2015	0.03			On, 2014	0.04		
				On, 2015	0.04		
				E × C	1.00	2, 297	0.370
				E × Y	8.14	2, 297	<0.001
				Yes, 2013	0.30		
				Yes, 2014	0.07		
				Yes, 2015	0.05		
				No, 2013	0.01		
				No, 2014	−0.02		
				No, 2015	0.01		
				C × Y	0.18	4, 297	0.951
				L × E × Y	0.80	2, 297	0.452
				L × E × C	0.21	2, 297	0.812
				L × Y × C	3.10	4, 297	0.016
				Off, 2013, A	0.08		
				Off, 2013, B	0.10		
				Off, 2013, C	−0.16		
				Off, 2014, A	−0.01		
				Off, 2014, B	0.02		
				Off, 2014, C	0.02		
				Off, 2015, A	0.02		
				Off, 2015, B	0.02		
				Off, 2015, C	0.00		
				On, 2013, A	0.26		
				On, 2013, B	0.22		
				On, 2013, C	0.41		
				On, 2014, A	0.09		
				On, 2014, B	−0.02		
				On, 2014, C	0.04		
				On, 2015, A	0.05		
				On, 2015, B	0.05		
				On, 2015, C	0.03		
				E × Y × C	0.47	4, 297	0.760
				L × E × Y × C	0.25	4, 297	0.911



but the density of shrubs on colonies was 40% that of off-colony sites (Figure 1). This suggests that prairie dogs may reduce recruitment and, over longer time-scales, induce shrub mortality on their colonies.

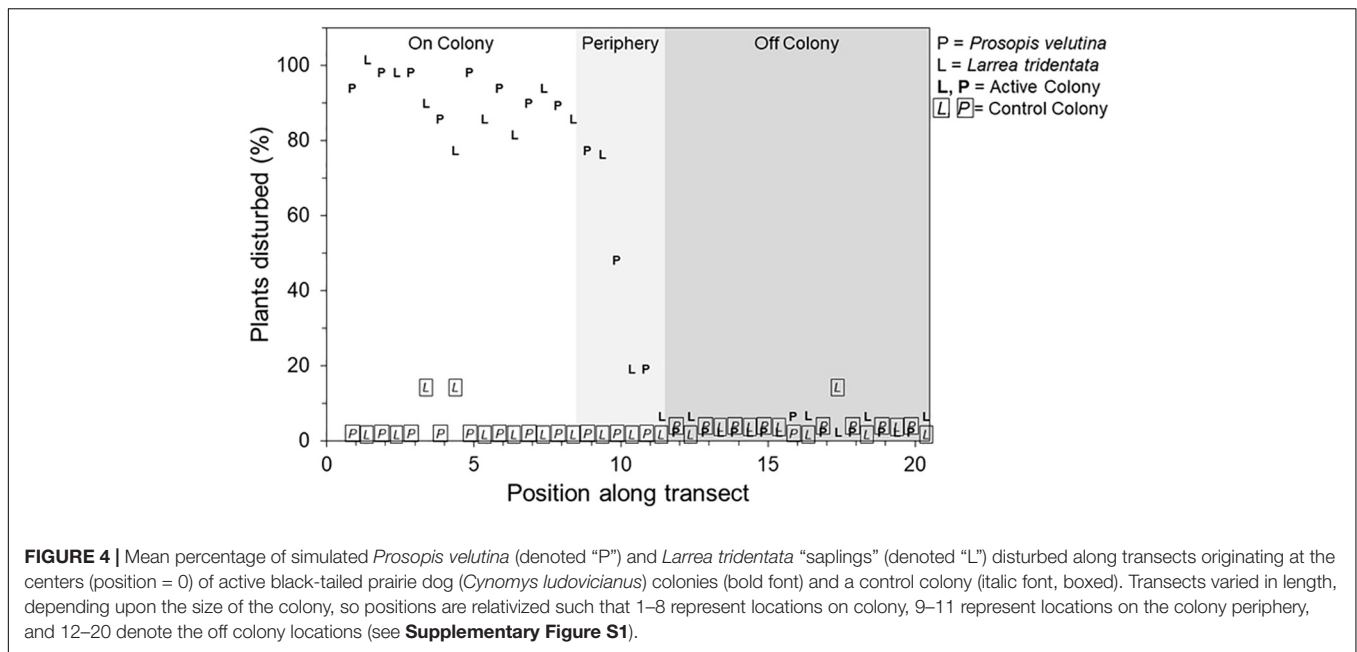
Prosopis velutina and *A. greggii*, the two main shrubs on our site, have the ability to vegetatively regenerate from basal meristems following removal of aboveground biomass (Glendening and Paulsen, 1955; Cross and Wiedemann, 1997). Accordingly, prairie dogs on these nascent colonies did not affect shrub survival, demonstrating that shrubs at this site are capable of persisting even under heavy levels of herbivory. This is reminiscent of the “browse trap” phenomenon. We would expect that the loss of prairie dogs from this site, which had been mechanically cleared of adult woody plants, would release small shrubs or those recruiting from the seed bank from the browse trap. These expectations are consistent with those from studies on well-established prairie dog colonies (Weltzin et al., 1997; Ceballos et al., 2010; Ponce-Guevara et al., 2016). Such a release would allow shrubs to re-gain dominance and thus neutralize the “brush management” effort to restore this former grassland. The fact that simulated saplings placed on a recently failed prairie dog colony received no damage (Figures 3, 4), despite their being highly conspicuous to lagomorphs and other rodents, suggests that prairie dogs, not other small mammals, were regulating shrubs within colonies. This interpretation is consistent with another study showing that small rodents on prairie dog colonies did not influence rates of shrub seed disappearance (Weltzin et al., 1997).

There was little evidence that large herbivores contributed to a browse trap for shrubs in this region. Native (e.g., American bison, *Bison bison*) and non-native ungulates, such as domestic cattle (*Bos taurus*) have diets that consist primarily of grasses and forbs (Meagher, 1986; Beck and Peek, 2005) so their preferential foraging on prairie dog colonies (e.g., Coppock et al., 1983)



would not be likely to constrain the development of communities dominated by woody plants prior or subsequent to prairie dog removal. This would be particularly so for highly unpalatable shrubs such as mesquite and creosote bush (Campbell and Taylor, 2006; Brock et al., 2014; Bovey, 2016). Pronghorn (*Antilocapra* spp.) are also known to preferentially forage on prairie dog colonies (King, 1955; Krueger, 1986; Hoogland, 1995), but given the abundance of shrubs in other portions of their range [e.g., sagebrush (*Artemisia* spp.) in the Intermountain West and northern Great Plains] it does not seem likely they exert sufficient browsing pressure to keep shrubs in check. The browse trap in this system thus appears to center around prairie dogs and their activities, which could, in turn, be enhanced by cattle grazing (Ponce-Guevara et al., 2016).

A coincidence between the elimination of small native grazers and woody encroachment is not restricted to North America. In Australia, native granivorous rodents may have historically limited shrub recruitment following fire events, but rodent



populations have declined due to pastoral activity, and their declines have coincided with shrub encroachment (Gordon and Letnic, 2019). Plains vizcacha (*Lagostomus maximus*) in Argentina and burrowing bettong (*Bettongia lesueur*) in Australia exhibit similarities to prairie dogs not only in their ecology and behavior, but also in their pest status, which has led to elimination from parts of their range (Jackson et al., 1996; Noble et al., 2007). Likewise, plateau pikas (*Ochotona curzoniae*) in China play a keystone role analogous to that of prairie dogs, but have also been subjected to eradication efforts (Smith and Foggin, 1999; Delibes-Mateos et al., 2011; Fahong et al., 2012). As with the elimination of prairie dogs in North America, elimination of these perceived small mammalian pests has had the unintended consequence of promoting woody plant proliferation (Brandt et al., 2013; González-Roglich et al., 2015). Such trade-offs should be considered in rangeland management and conservation plans where the maintenance of grasslands and the organisms endemic to them are a priority.

Woody plant proliferation in grasslands has prompted the implementation of “brush management” practices aimed at reducing shrub cover to enhance livestock production (Hamilton et al., 2004) and restore habitat for grassland wildlife (Fulbright et al., 2018). These practices often involve herbicides, heavy equipment (e.g., cutting, shredding, or chaining), and prescribed burning alone or in combination (Collins et al., 2015). Such endeavors are costly, short-lived, and require repeated application (Archer et al., 2011). Prairie dogs rely on short vegetation for visual detection of predators (Hoogland, 1995; King, 1955), so are unlikely to colonize areas with dense woody vegetation and would not be likely to persist if introduced into a landscape with well-developed woody cover (Milne-Laux and Sweitzer, 2006). However, our study suggests that reintroductions of prairie dogs following brush management can succeed and could extend the shrub treatment longevity and reduce or

perhaps eliminate the need for follow-up treatments, while simultaneously promoting the restoration of grassland habitats and the plants and animals endemic to them (Whicker and Detling, 1988; Kotliar et al., 1999, 2006; Ceballos et al., 2010).

Our sapling experiments suggest that prairie dogs are not limited by previous experience with woody species, as the Las Cienegas prairie dogs felled both a species they encountered regularly (*P. velutina*) as well as a species they had never encountered (*L. tridentata*). This suggests that (i) prairie dogs can restore the browse trap even when source and reintroduction sites differ in woody species composition, and (ii) prairie dog reintroduction within areas of their former range could simultaneously function as a natural, cost-effective, and sustainable option for limiting woody plant encroachment in present-day grasslands and for restoring grassland structure, function and biodiversity where shrub encroachment has occurred. These positive facets of prairie dogs may compensate for or more than off-set the traditional negative perspectives associated with prairie dog-livestock competition for forage and declines in forage and livestock production (O’Meilia et al., 1982; Derner et al., 2006). A comprehensive assessment of these complexities in livestock-prairie dog interactions and the various trade-offs that emerge would require a landscape-scale accounting of livestock grazing intensity, seasonality, and patterns and prairie dog colony locations, sizes and ages. When prairie dog re-introductions are contemplated, where best to locate them and how colonies might subsequently expand should be given careful consideration.

The conservation and reintroduction of large or charismatic keystone species [e.g., gray wolves (*Canis lupus*) and sea otters (*Enhydra lutris*)] can restore critical ecological function to ecosystems (Estes and Palmisano, 1974; Callan et al., 2013). However, similar to the historical perception of wolves, small keystone herbivores are often viewed as pests that are targeted

for eradication rather than conservation (Delibes-Mateos et al., 2011). Accordingly, the ecological implications of reintroducing small keystone herbivores has not been widely investigated. We add to this understanding, and highlight the ability of small keystone herbivores to address significant ecological issues, such as woody encroachment, immediately following their reintroduction and in conjunction with other land management practices. Our results indicate the important role(s) that small keystone herbivores can potentially play in maintaining diverse, healthy ecosystems, and the substantial ecological consequences that can result from their removal (Weltzin et al., 1997; Davidson et al., 1999, 2012, 2014; Miller et al., 2000; Kotliar et al., 2006; Brandt et al., 2013; González-Roglich et al., 2015). A better understanding of such species and their reintroduction after extirpation will be important for the restoration and conservation of grassland ecosystems throughout the world.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

The animal study was reviewed and approved by the University of Arizona Institutional Animal Care and Use Committee (protocol 11-251).

AUTHOR CONTRIBUTIONS

SH contributed to the research design, collected data in the field, performed the experiments, analyzed the data, and wrote

the manuscript. JK and SA contributed to the research design, data analysis, and provided valuable edits and revisions to the manuscript. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2020.00233/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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