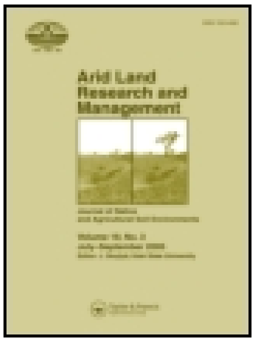

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Hyper-arid tall shrub species have differing long-term responses to browsing management

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ABSTRACT
Hyper-arid rangeland vegetation is typically dominated by large woody species which are often overlooked in herbivory studies. Long-term responses of tall shrub populations to herbivory change are poorly understood in the Arabian Peninsula. Population and size of 1559 individuals from four shrub species were assessed over an 11-year period under two herbivory regimes, one in which domestic livestock (camels) were replaced by semi-wild ungulates (Oryx and gazelles) before, and the other during, the study period. Each shrub species exhibited a different response to the change in herbivory. Populations of *Calotropis procera* decreased dramatically. Populations of both *Calligonum polygonoides* and *Lycium shawii* increased through sexual reproduction, but the spatial distribution of recruits indicated different modes of seed dispersal. Average lifespans were estimated at 22 and 20 years respectively. The persistence strategy of *Leptadenia pyrotechnica* was similar to tree species of this habitat in that vegetative regrowth was prioritized over recruitment, and average lifespan was estimated at 95 years. Shrub responses to changes in ungulate management are therefore species-specific. The response of individual plant size was faster than the response of population size, which was limited by slow sexual recruitment (*L. pyrotechnica*) or localized seed dispersal (*C. polygonoides*).

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Arid rangeland; gazelle; grazing impact; grazing recovery; *Oryx leucoryx*

Introduction

Hyper-arid rangeland vegetation is dominated by woody perennial species (Holechek, Pieper, and Herbel 2010). Large woody species form microhabitats that may benefit associated flora and fauna, and typically provide a richer diet for herbivores during dry periods when the nutritive value of non-woody plants is low (Ahamefule et al. 2006). Herbivory studies often omit woody perennial species due to the difficulty in obtaining reliable marginal biomass estimates (Louhaichi et al. 2017) or focus on the smaller perennial species only (e.g. Katz et al. 2016). Additionally, larger perennial species exist at a broader spatiotemporal scale than species with shorter lifespans. This necessitates the use of larger sample areas and longer time periods to study, the result of which is that fewer studies are

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completed. Population change for tree species has been assessed from satellite imagery (Andersen and Krzywinski 2007; Gomaa and Picó 2011) but not for shrubs. For the Arabian Peninsula, long-term tall shrub population responses to change in herbivory system has not been studied.

Camel (*Camelus dromedarius* Linnaeus, 1758) herbivory is frequently cited as the main cause of rangeland decline on the Arabian Peninsula (Batanouny 1990; Assaeed 1997; Ferguson, McCann, and Manners 1998; Abed and Hellyer 2001). Several fenceline studies comparing camel presence to absence have demonstrated increased plant biomass and biodiversity on the excluded side, particularly for herbaceous and smaller woody shrubs (Shaltout, El-Halawany, and El-Kady 1996; Gallacher and Hill 2006a, 2006b; Ouled Belgacem, Tarhouni, and Louhaichi 2013; Al-Rowaily et al. 2015), but complete exclusion from herbivory is a socio-politically unsustainable management option for most rangelands. A dramatic increase of domesticated camel populations over the last few decades has displaced smaller wild ungulates in Dubai (Gallacher and Hill 2006b), and although the establishment of the Al Marmoum conservation reserve (Khafaga, Simkins, and Gallacher 2018) has reversed this trend, camels still far exceed sustainable levels across the Arabian Peninsula. An increase in livestock numbers has devastated *Vachellia origena* (Hunde) Kyal. and Boatwr (syn. *Acacia origena*) woodlands of Yemen, *Juniperus procera* Hochst. ex Endl. forests of Saudi Arabia, and Acacia forests throughout the Arabian Peninsula (Chaudhary and Le Houérou 2006), but the impact of excess herbivory on plant communities is usually reversible (Dean and Macdonald 1994). Assessing persistent change in plant community structure requires a change in management that has persisted for at least 10 years (Ghazanfar and Osborne 2010), preferably much longer. To our knowledge, this is the first long-term study of the effect of herbivory on tall shrub communities in Arabia.

Native Oryx and gazelle species have, by contrast, little remaining impact on open-access Arabian rangelands due to diminished wild populations. All species are currently listed as ‘vulnerable’ by the IUCN. In 2011 *Oryx leucoryx* (Pallas, 1777) was the first species to have its ‘endangered’ status revert to ‘vulnerable’, due to increasing captive populations and some success with reintroductions to the wild (Hayward *et al.* 2015). The impact of these smaller ungulates on Arabian plant community structure has received scant attention from either herbivory or a seed dispersal viewpoint but is becoming increasingly significant for protected areas and private lands with expanding collections.

The present study investigates the long-term response to two herbivory regimes of four shrub species; *Leptadenia pyrotechnica* (Forssk.) Decne, *Lycium shawii* Roem. and Schult, *Calligonum polygonoides* subsp. *comosum* (L’Hér.) Soskov and *Calotropis procera* (Aiton) W. T. Aiton. It was believed that camel browsing suppresses all species studied except *C. procera* which then benefits from the reduced competition (Gallacher and Hill 2006b). However, population densities of all four species are lower in the Dubai emirate when access for the public, including camel herders, is permitted (Khafaga, Simkins, and Gallacher 2018). Camels can be selective; in a moister desert they avoided the low-height shrub *Artemisia monosperma* Del. even when palatable herbs and grasses became rare (Katz *et al.* 2016). Persistence of tree species in this environment is more dependent on vegetative resprouting than sexual recruitment due to the difficulty of seedling establishment (Andersen and Krzywinski 2007), but the persistence strategies of tall shrubs are unknown. The distribution of population recovery is reliant on seed dispersal, which is primarily affected by dispersal syndrome, growth form, and terminal velocity (Tamme et al. 2014), the latter of which has not been evaluated for these species. Seed morphology indicates that the dispersal syndrome of *L. shawii* is endozoochorous, while the other species are anemochorous (Table 1). Epizoochory might also occur for a tiny but significant fraction of seeds despite the lack of morphological adaption, as has been suggested for desert annual species (Venable et al. 2008). The influence of herbivory on functional traits of these species has also not been investigated.

The aim of the present study is to assess how population and plant size of these four species respond to a reduction in ungulate herbivory. We hypothesized that herbivory intensity would correlate positively with a number of *C. procera* individuals, negatively with the size of *C. polygonoides* and both size and number of *L. pyrotechnica* and *L. shawii* (Table 1). We further hypothesized that population recovery would be slower than plant size recovery since it is limited by low rates of seedling survival. However, prior to the study, we had no data on the typical lifespan or rate of recruitment of the species in this or any habitat and thus no baseline with which to predict if natural recovery would require a decade, a century, or longer. This study will thus enable better predictions of how arid shrublands might respond to changed land management, and the timescale required to realize these changes.

Materials and methods

Study site

This study was conducted at the Dubai Desert Conservation Reserve (DDCR) where two large areas with different herbivory regimes had been established. True replication across locations was unfeasible due to the requirement for a large spatiotemporal scale under stable long-term management. Instead, the study was conducted in a 300-m wide band either side of a fence that separated an internal enclosure of 27 km^2 (Al Maha) from the rest of the 225 km^2 DDCR. The 2.16 km^2 area sampled from Al Maha is referred to as WILD/wild and the 2.32 km^2 area sampled from the DDCR as DOM/wild (Figure 1), with capital letters signifying greater herbivory pressure during initial sampling, and 'DOM' signifying domesticated rather than semi-wild ungulates. This section of the fence was chosen because it was less affected by other anthropogenic factors (i.e. external DDCR fence, buildings, and human activities) and contained a mix of habitats with high- and low-density shrub populations. Soil types of the DDCR are predominantly typic torripsamments (sand dunes) with intermittently exposed typic torriorthents (gravel plains; Shahid et al. 2014). Study site elevation ranged from 203 to 250 m above sea level with substrates of stable dunes interspersed by shifting dunes and sandy plains (typic torriorthents covered thinly with sand). Rainfall is unpredictable, averaging 93.8 mm annually, mostly in winter and early spring (Gallacher and Hill 2006a). Rainfall prior to the 2017 survey had been above average and annual/biennial plants were abundant during the survey period. Vegetation of the study site is characteristic of the soil type in the emirate, in which the dominant species are *L. pyrotechnica*, *Haloxylon salicornicum* (Moq.) Bunge ex Boiss., *Cyperus conglomeratus* Rottb., and *Heliotropium ramosissimum* (Lehm.) Sieb. ex DC.

Table 1. General attributes of shrub species studied and hypothesized response to herbivory intensity.

	Calligonum polygonoides	*Calotropis procera*	*Leptadenia pyrotechnica*	*Lycium shawii*
Density at study site (plants km^{-2}, 2006)	6.3	6.3	255.1	14.7
Height at study site average/maximum (m)[a]	2.5/5.5	3.1/4.6	3.5/6.2	1.4/3.7
Canopy area at study site average/maximum (m)[b]	6.9/52.5	14.1/27.9	19.1/120.7	2.1/20.4
Assumed ungulate herbivory[b]	Leaves highly palatable, and a preferred species of camels	Leaves consumed by gazelles but not by camels (Gallacher and Hill 2006b)	Fruit and flowers palatable. Ungulates graze stems lightly	Leaves and fruits palatable. Roots might be palatable[c]
Herbivory defense mechanism	Temporal (deciduous)	Chemical (latex)	Stems: chemical (latex). Leaves absent or abscise early	Physical (thorns)
Plant response to repeated herbivory	Plant remains leafless until suitable growing conditions reoccur.	Lower branches disappear such that the plant becomes single-stemmed. Chemical response not researched	Chemical response not researched. Physical damage to plant structure is apparent in locations with high camel densities	Produces a hedged structure, where leaves are protected under a thorny, woody frame
Reproductive method	Sexual	Sexual	Sexual and possibly asexual[d]	Sexual
Diaspore unit[e]	Fruit	Seed	Seed	Fruit
Seeds per fruit[e]	1	300	50	1
Main diaspore dispersal time[e]	Rainy	Dry	Dry	Rainy
Diaspore dispersal structure[e]	Wings	Pappus	Pappus	Nutrients
Presumed dispersal mechanism[e]	Anemochory	Anemochory	Anemochory	Endozoochory
Hypothesized response to reduced camel herbivory	Increased population size. No change in plant size	Decreased population size due to increased competition for resources. No change in plant size	Increased population and plant size	Increased population and plant size
Hypothesized rate of population change	Slow, reliant on seedling success	Slow, reliant on natural mortality	Slow, reliant on seedling success	Slow, reliant on seedling success

[a]Vegetation above 3.1 m is not directly accessible to camels.
[b]Palatability studies have not been conducted for these species, to the authors' knowledge.
[c]Consumption of roots by *Oryx leucoryx* has been reported in Saudi Arabia (Asmodé 1990), but not observed in the Dubai Desert Conservation Reserve.
[d]Frequency of either reproduction method has not been studied in this species, to the authors' knowledge. [e]Diaspore information was obtained from Shabana (2019), and used to identify the presumed dispersal mechanism.

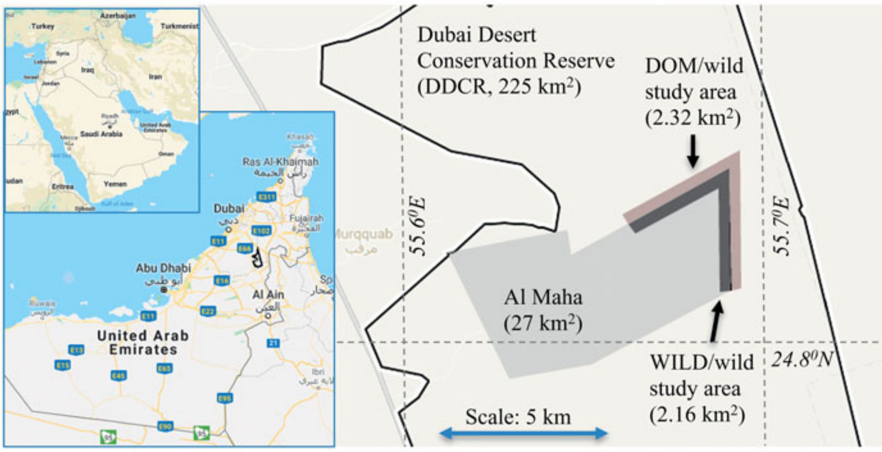

Figure 1. Map of the study site within Arabia (upper left), the United Arab Emirates (lower left) and with the Al Maha fence line (right; Map data ©2019 Google).

Due to the lack of true replication, a comparison of enclosures is justified only if a vegetation gradient across the fence line is shown to not exist. We tested for a gradient by separating 2006 data into six replicates according to the distance from the fence (100 m intervals) and analyzing using ANOVA with Tukey's comparison of means among distance categories as a fixed factor. Differences among intervals were attributable only to the fence line (Table 2), hence differences between WILD/wild and DOM/wild data could be attributed to herbivory management and not to a possible vegetation gradient.

All statistical tests were conducted using IBM SPSS v23 (IBM, Armonk, New York, USA).

Shrub species

Four large-shrub species occur in the study area (Table 1). All are common in the Northern Emirates of the United Arab Emirates (Jongbloed et al. 2003) and similar habitats of the Middle East and North Africa region, though community structure varies. In the United Arab Emirates, *C. polygonoides* subsp. *comosum* is widespread on sandy plains and low dunes. *L. pyrotechnica* and *C. procera* are also frequent in this habitat but are more tolerant of gravel substrates. *L. shawii* is commonly found on gravel substrate and low dunes

L. pyrotechnica is the dominant species in the study area and provides microhabitats in the form of large phytogenic mounds, a dense biomass of living and dead branches, and shelter from sun and wind. A size change of *L. pyrotechnica* will have the greatest impact on carbon sequestration (Singh et al. 2012) and may affect microhabitat availability for other species. *L. pyrotechnica* is widely distributed through the sandy deserts of Pakistan (Ullah et al. 2015) in Egyptian Eastern desert valleys (Migahid, Abdel Wahab, and Batanouny 1972), and is also found in India, Iran, Arabia, Sudan, Somalia, Chad, Libya and Algeria (Ali 2002; Boulos 2009).

Table 2. Effect of the distance from the fence that separated Al Maha and Dubai Desert Conservation Reserve (DDCR) regimes, on plant number, height and canopy size among four shrub species in 2006.

			Calligonum polygonoides subsp. *comosum*			*Calotropis procera*			*Leptadenia pyrotechnica*			*Lycium shawii*		
Regime	Distance from fence (m)	Area (ha)	*N*	Height (m) Mean (*SD*)	Equivalent diameter (m) Mean (*SD*)	*N*	Height (m) Mean (*SD*)	Equivalent diameter (m) Mean (*SD*)	*N*	Height (m) Mean (*SD*)	Equivalent diameter (m) Mean (*SD*)	*N*	Height (m) Mean (*SD*)	Equivalent diameter (m) Mean (*SD*)
WILD/wild (Al Maha)	0–100	73.8	10	2.53 (1.44)^{a}	1.57 (1.05)^{a}	0			205	3.49 (1.02)^{a}	4.02 (1.84)^{a}	15	1.84 (0.78)^{a}	1.82 (0.59)^{a}
	100–200	72	11	2.89 (0.76)^{a}	2.24 (1.20)^{a}	7	3.11 (0.51)^{a}	2.23 (0.90)^{a}	221	3.36 (0.98)^{a}	3.89 (1.80)^{a}	8	1.77 (0.19)^{ab}	1.61 (0.33)^{ab}
	200–300	70.2	7	2.90 (1.04)^{a}	2.21 (1.43)^{a}	2	3.19 (0.07)^{a}	2.74 (0.45)^{a}	271	3.25 (0.92)^{a}	3.77 (1.69)^{a}	9	1.93 (0.41)^{a}	1.77 (0.57)^{a}
DOM/wild (DDCR)	0–100	75.6	0			10	1.91 (0.86)^{a}	3.26 (1.09)^{a}	81	2.77 (0.87)^{b}	3.23 (1.31)^{b}	9	1.03 (0.33)^{c}	1.22 (0.50)^{abc}
	100–200	77.3	0			3	2.57 (0.75)^{a}	1.83 (1.33)^{a}	142	2.72 (0.88)^{b}	3.15 (1.31)^{b}	13	0.80 (0.34)^{c}	0.91 (0.48)^{c}
	200–300	79.1	0			6	3.26 (0.34)^{a}	3.79 (0.94)^{a}	130	2.81 (0.88)^{b}	3.17 (1.18)^{b}	11	1.08 (0.36)^{bc}	0.97 (0.25)^{bc}
df				2	2		4	4		5	5		5	5
F				0.219	0.953		5.667	3.109		21.15	10.746		10.208	7.394
P				0.805	0.399		0.003	0.035		2.87×10^{-20}	4.12×10^{-10}		7.48×10^{-7}	2.67×10^{-5}

Superscripts show Tukey's comparison of means among height and canopy means for each species, with distance category as a fixed factor.

L. shawii is broadly distributed through North Africa, Arabia and South Asia (Ali 2002; Boulos 2009), preferring gravel plains, hillsides, wadis and plantations.

C. polygonoides subsp *comosum* is highly palatable (Heneidy 1996) and common in active sand dunes where it plays a role in dune stabilization (Al-Farraj 1989). It is distributed from Northeast Africa, Egypt, Sinai, Palestine, Arabia to Pakistan (Ali 2002). Species of the genus are poorly discriminated by standard terrestrial plant barcoding primers, indicating that divergence is relatively recent (Li et al. 2014). The taxon *comosum* is used as a subspecies by some authors but as a separate species by others (*C. comosum*). *C. polygonoides* subsp *comosum* exhibits a considerable phenotypic variation (Taia and El-Etaby 2006; Taia and Moussa 2011) and its macromorphological structure varies from shrub to small tree (Western 1989; Karim and Fawzi 2007). The genus can withstand severe water stress (Mao and Pan 1986; Zhang 1992). Drought and summer adaptation includes the loss of leaves and branches (Dhief et al. 2009), and continued water stress results in a modified wood morphology (Al-Khalifah et al. 2006). It is a preferred food for camels, having a high level of crude protein, potassium, and calcium (Munton 1988) and is an indicator of non-saline groundwater (Western 1989). Seeds are anemochoric and exhibit dimorphism in color and germination attributes (Bhatt et al. 2019).

C. procera is broadly distributed through North Africa, Arabia, and South Asia (Ali 2002), preferring sandy desert plains, low dunes and gravel plains close to a disturbance source. It is a successful invasive species in Australia (Barreto, Evans, and Pomella 1999) and Brazil, invading scrublands, savanna, roadsides and pastures (Kissmann and Groth 1991). Camels do not eat it, even when it is the only species remaining (Western 1989).

Ungulate browsing

This study compares two areas with lesser (WILD/wild; Al Maha) and greater (DOM/wild; DDCR) exposure to ungulate herbivory. Timings of ungulate species' presence in each area are provided (Table 3). Domesticated camels were replaced by semi-wild Oryx and gazelles in both areas, but replacement occurred 10 years earlier in the WILD/wild sample. Ungulate species density in each enclosure is known but is not a direct indication of rangeland phytomass consumption for two reasons. Firstly, ungulates are provided externally sourced feed and water. This is the primary reason that Oryx and gazelles are classified as semi-wild. Secondly, ungulate spatial distribution within each enclosure is not uniform, being affected by anthropogenic disturbance and access routes. It is believed but not quantified that camel density was significantly higher in the DOM/wild sample area between 1999 and 2009 due to the influence of the fence corner on camel movement.

Shrub size and population change

All individuals of the four species within the study area were assessed between Oct 2005 and Feb 2006, and Feb-Mar 2017. GPS location of all shrubs was recorded to 5 and 1 m accuracy in 2006 and 2017 respectively. Height and two diameters were measured by

Table 3. Timeline of livestock access and data collection within the DOM/wild (Dubai Desert Conservation Reserve; DDCR) and the WILD/wild (Al Maha) herbivory regimes.

Time period	Event
Before 1999	The area contained 14 active 'farms', previously described (Gallacher 2010), with a combined camel herd of approximately 960 (4.3 camels km^{-2}). However the area was unfenced and camels entered on a day-basis.
Mid 1999	The 27 km^2 Al Maha boundary was fenced, and camel herders were prohibited entry. Three ungulate species were introduced; *Oryx leucoryx* (Pallas, 1777), *Gazella gazella cora* (Smith, 1827) and *G. subgutturosa marica* Thomas, 1897. Other livestock were present in limited numbers, including camels and horses for tourism associated with the Al Maha Desert Resort, and several other non-native ungulate species that were later removed (Gallacher and Hill 2006a).
Mid 2003	The 225 km^2 DDCR boundary was fenced. Entry for external camel herders was highly restricted but herders located within the DDCR were permitted to stay. Observations by the DDCR botanist indicated that the northern DDCR was being grazed particularly heavily at this time.
Oct 2005–Feb 2006	2006 survey of the present study was completed. Livestock at the time included:
WILD/wild (Al Maha):	9.2 Oryx and 7.5 gazelles km^{-2}. Oryx and gazelles present for 6.5 years Camels absent for 6.5 years
DOM/wild (DDCR):	4.3 camels km^{-2}.
Mid 2009	Camel herders were relocated to outside the DDCR, and access for all external camel herders ceased. Oryx and gazelle movement became unrestricted within the DDCR.
Mid 2011	Al Maha fence was removed
Feb–Mar 2017	2017 survey of the present study was completed. At this time, Al Maha and the DDCR were the same enclosure, with 2.0 Oryx and 2.1 gazelles km^{-2}. Camels had been excluded for 17.5 and 8 years respectively.

In general, herbivory intensity was greater in the first survey (represented by upper case letters) and in the DDCR, domesticated camels (represented by 'DOM') were replaced with semi-wild species (wild).

tape on all shrubs in 2006 and all *C. procera* and *L. shawii* shrubs in 2017, but on a representative sample of 242 *L. pyrotechnica* and 54 *C. polygonoides* shrubs in 2017. A paired *t*-test was used to assess differences among height and equivalent diameter, where equivalent diameter was calculated as the square root of the ellipse formed by the widest diameter and its perpendicular diameter.

Shrubs in 2017 were marked as survived, dead or missing since the 2006 survey, or as successful (alive) or unsuccessful (dead) recruits. A lack of above-ground green phytomass of tall shrubs was considered an indicator of mortality, but it is possible that some classified as dead will regenerate. *L. pyrotechnica* is capable of regrowth from roots. Shrubs were marked dead if they contained sufficient structure to identify the species but lacked green tissue, and missing if the 2006 location contained no plant recognizable as the species. Chi-square was used to test population changes among years and regimes.

Lifespan estimation

Lifespans were estimated by extrapolating mortality and recruitment rates between observed counts in 2006 and 2017 according to the formulae:

$$Lifespan\ (mortality) = \frac{T \times A}{M},\ Lifespan\ (recruitment) = \frac{T \times A}{R}$$

where T = time between observations (11 years), A = number of living plants at first observation (2006), M = number of plants that were dead or missing at the second observation (2017), and R = number of successful and unsuccessful new recruits at the

Table 4. Estimate of shrub species' average lifespans in each enclosure, by extrapolating mortality and recruitment data between population counts made in 2006 and 2017.

				Average lifespan estimate (years)		
	2006 population count	Survival (%)	Recruitment (%)	Survival	Recruitment	Average
Calligonum polygonoides subsp. *comosum*						
WILD/wild	28	50	489	22	n/a	22
DOM/wild	0					
Calotropis procera						
WILD/wild	9	0	0	n/a	n/a	
DOM/wild	19	11	0	n/a	n/a	n/a
Leptadenia pyrotechnica						
WILD/wild	697	89	16	102	68	
DOM/wild	353	90	12	114	95	95
Lycium shawii						
WILD/wild	32	63	75	29	15	
DOM/wild	33	18	45	13	24	20

n/a indicates insufficient data for estimation.

second observation (2017). More accurate age estimation of woody shrubs requires growth ring analysis, radiocarbon dating, or molecular markers of ramets (de Witte and Stocklin 2010), but each of these methods has limitations for desert species with highly varied growth rates and the ability to regenerate from the rootstock. Extrapolation of mortality data to estimate lifespan has been used previously to estimate species' lifespans in the Grand Canyon from tourist photos (Bowers, Webb, and Rondeau 1995).

Results

In 2006, *L. pyrotechnica* density in WILD/wild was double that of DOM/wild (697 vs 353 shrubs, Table 4) and shrubs were larger in both average height and equivalent diameter ($P < 0.0001$, Figure 2). WILD/wild contained the 20 largest canopies and the six tallest shrubs (Figure 3). By 2017 the size differences among surviving shrubs of each regime had disappeared, though new recruits in DOM/wild were larger than in WILD/wild in both height ($P = 0.0011$) and equivalent diameter ($P = 0.0015$). One patch of increased recruitment appeared in WILD/wild and one of mortality in DOM/wild. Survival and mortality data indicated an average lifespan of 95 years (Table 4). The relationship between shrub size in 2006 and change in size to 2017 was consistent between the regimes (Figure 4), indicating that the long-term equilibrium occurs at an average height of 4.3 m and median canopy area of 27.5 m^2. This canopy area has been reached in WILD/wild but not in DOM/wild.

In 2006 there were 65 individuals of *L. shawii* distributed throughout WILD/wild and DOM/wild. Recruitment was similar in each enclosure, but mortality was greater in DOM/wild ($P = 0.0003$). Surviving individuals exhibited no change in height over the 11-year period (Table 5), but their average canopy across the study area decreased from 3.8 to 2.0 m^2 ($P = 0.0038$). Survival and mortality data indicated an average lifespan of 20 years (Table 4).

The proportion of *L. shawii* plants growing within a *L. pyrotechnica* shrub canopy increased from 2006 to 2017 (28 to 53%, $P = 0.0047$), such that they were found under 3.4% of WILD/wild and 1.7% of DDCR *L. pyrotechnica* canopies. Recruitment was

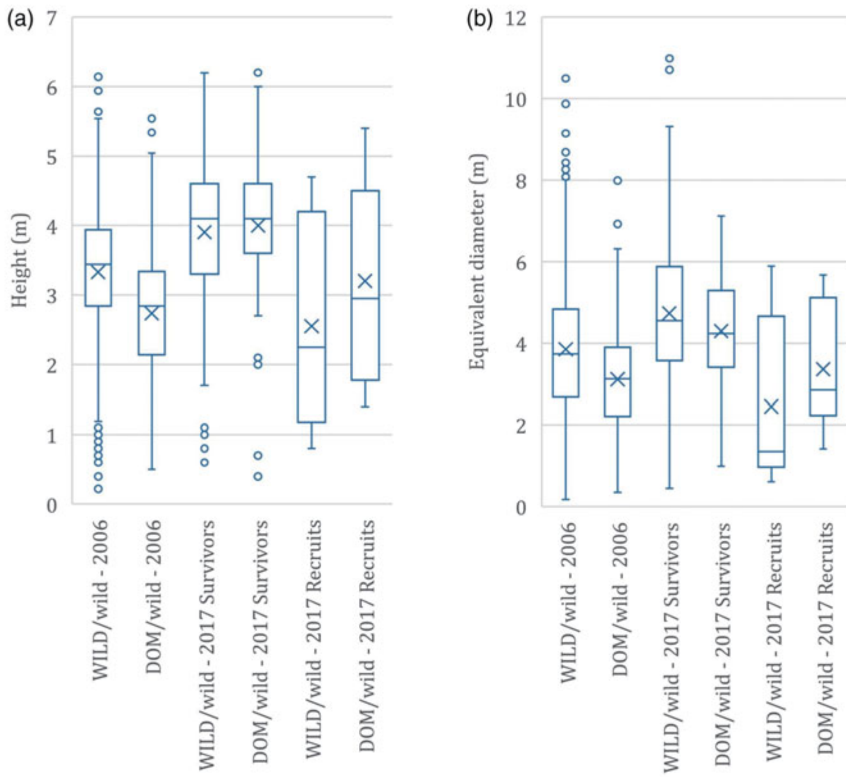

Figure 2. Height (a) and canopy size (b) changes in *Leptadenia pyrotechnica* among two regimes (DOM/wild and WILD/wild) from 2006 to 2017. 'Survivors' and 'recruits' indicates shrubs established before and after 2006.

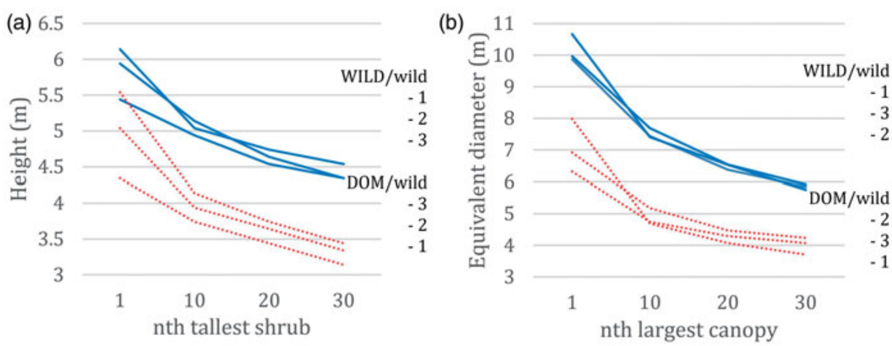

Figure 3. Height (a) and canopy size (b) of the 1st, 10th, 20th and 30th largest *Leptadenia pyrotechnica* shrubs in 2006 under two herbivory regimes. Each regime was separated into three 100 m wide replicates, with 1 indicating closest to, and 3 furthest from the fence.

more common within *L. pyrotechnica* canopies (59% of recruits) and recruits appeared more likely to remain alive, though data was insufficient for statistical verification. Shelter under *L. pyrotechnica* canopies had no effect on survival or on equivalent diameter (Figure 5), and the effect on height was marginal ($P = 0.0274$). The average

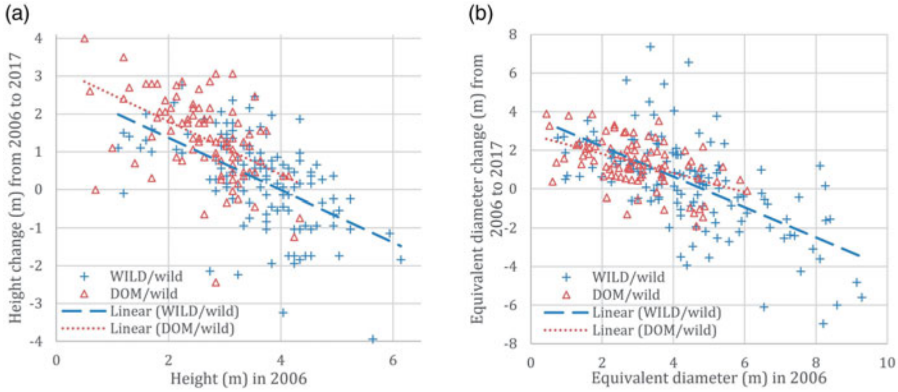

Figure 4. Relationship between *Leptadenia pyrotechnica* height (a) and the canopy size (b) in 2006, and change to 2017 under two herbivory regimes. All linear regression lines were significant ($P < 0.001$).

Table 5. Size change of shrubs that were alive in both 2006 and 2017, assessed using a paired *t*-test.

		Canopy area (m^2)			Height (m)		
	N	2006 Mean (*SD*)	2017 Mean (*SD*)	*P*	2006 Mean (*SD*)	2017 Mean (*SD*)	*P*
Calligonum polygonoides subsp. *comosum*							
WILD/wild	14	7.8 (6.11)	20.1 (13.44)	0.0006	3.26 (0.949)	3.17 (0.868)	n.s.
Calotropis procera							
DOM/wild	2	9.0 (0.33)	18.4 (10.66)	n.s.	2.89 (0.636)	3.45 (1.626)	n.s.
Leptadenia pyrotechnica							
WILD/wild	130	23.3 (18.98)	26.1 (21.2)	n.s.	3.59 (0.959)	3.90 (1.039)	0.0044
DOM/wild	88	10.2 (7.86)	20.0 (11.0)	<0.0001	2.63 (0.803)	4.00 (0.987)	<0.0001
Lycium shawii							
WILD/wild	17	4.1 (2.04)	3.4 (4.67)	n.s.	1.96 (0.584)	1.61 (0.767)	n.s.
DOM/wild	5	1.2 (0.69)	1.0 (1.09)	n.s.	1.32 (0.278)	1.38 (0.716)	n.s.
Sheltered	5	2.2 (0.60)	5.9 (8.39)	n.s.	1.72 (0.272)	1.92 (1.268)	n.s.
Unsheltered	17	3.8 (2.37)	2.0 (1.51)	0.0014	1.85 (0.662)	1.45 (0.522)	n.s.

n.s: non significant *P* value.

L. pyrotechnica shrub harboring *L. shawii* was 90 cm taller and twice the canopy area of the species average. Thus most (81% in 2017) of the incidences of *L. shawii* appearing under *L. pyrotechnica* appeared in WILD/wild, where the larger *L. pyrotechnica* shrubs were located.

In 2006 *C. polygonoides* was distributed throughout WILD/wild but absent in DOM/wild. By 2017 the population had increased fivefold, distribution had become clustered, and the canopy area of surviving shrubs had increased 158% while height remained the same (Table 5, Figure 6). Two clusters contained almost all the successful (130 of 131) and unsuccessful (6 of 6) recruits, seven of which appeared in DOM/wild. Survival of individuals from 2006 was higher within clusters, though this was not statistically significant (8 of 10 survived within, 5 of 16 outside clusters, 1 of 2 ambiguous). Survival data indicated an average lifespan of 22 years (Table 4), but data for estimating average lifespan of this species was insufficient for an accurate result.

In 2006 there were 28 individuals of *C. procera* throughout the study area, with most (19) located in DOM/wild. By 2017 only two survived, both in DOM/wild, and most of

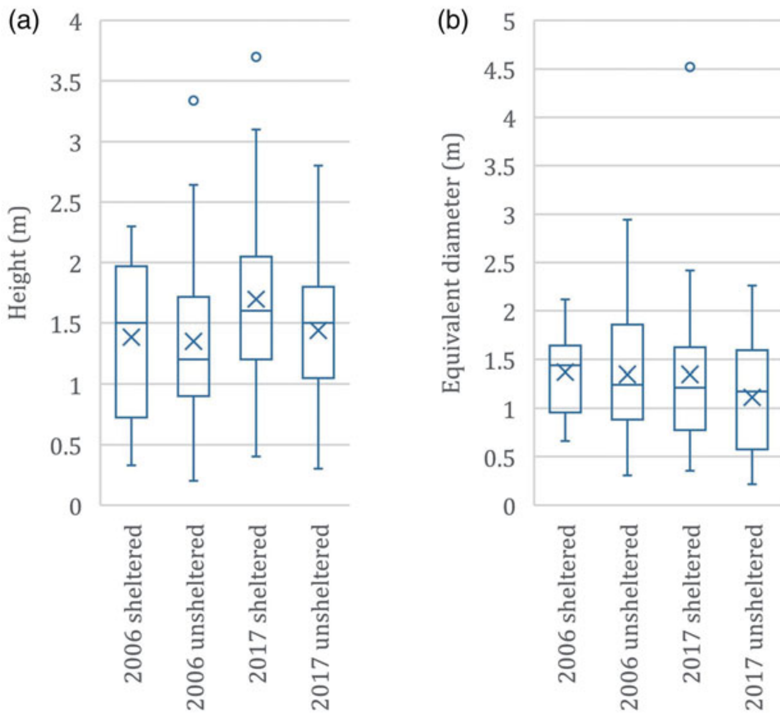

Figure 5. Height (a) and canopy size (b) of *Lycium shawii* growing independently (unsheltered) and within the canopy of a *Leptadenia pyrotechnica* (sheltered), including data from both herbivory regimes.

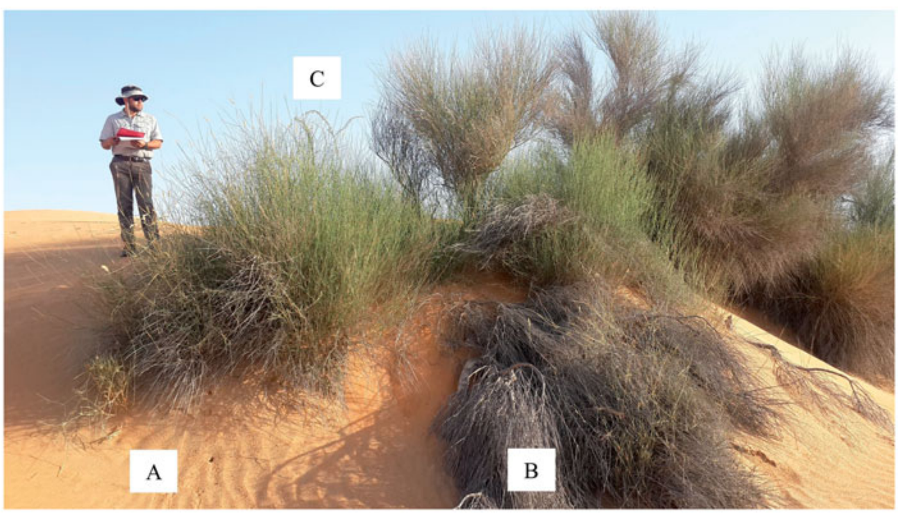

Figure 6. *Leptadenia pyrotechnica* shrub with three species growing within its canopy; *Cenchrus divisus* (A), *Panicum turgidum* (B), and *Lycium shawii* (C).

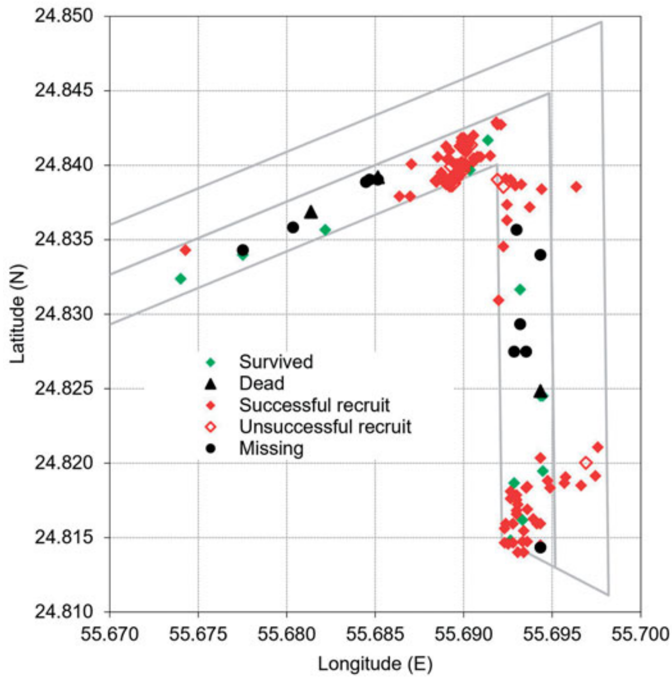

Figure 7. Distribution of *Calligonum polygonoides* across the study area in 2017. Plants observed in 2006 were classified in 2017 as survived, dead or missing, and new recruits were classified as successful (alive) or unsuccessful (dead).

the remaining plants had disappeared completely. Of the two surviving, one had grown substantially but the other remained at approximately the same size. Data were insufficient to estimate average lifespan.

Discussion

Each shrub species exhibited a different response to the change in herbivory from livestock to semi-wild ungulates. Population changes were as hypothesized (Table 1) but plant size changes differed from our expectations. Populations of *C. procera* decreased dramatically. Populations of both *C. polygonoides* and *L. shawii* increased through sexual reproduction, but the spatial distribution of recruits supported the different presumed modes of seed dispersal; recruitment of *C. polygonoides* was very high but localized around maternal plants (Figure 7), while recruitment of *L. shawii* was slower and partially associated with the canopies of *L. pyrotechnica*. The strategy of *L. pyrotechnica* was most similar to that previously reported for tree species in this habitat, in which vegetative reproduction is more frequent than sexual (Andersen and Krzywinski 2007). Individuals of *L. pyrotechnica* had a high survival rate despite sometimes large reductions in plant size, resulting in a relatively long estimated life span. For *L. pyrotechnica*, the response of average plant size to changed herbivory occurred within the 11 years, but the response of population density was still in the early stages.

Substantial differences in the tall shrub populations were observed in 2006, when camels were present in DOM/wild and had been absent in WILD/wild for 6.5 years. *C. polygonoides* was absent from DOM/wild, *L. shawii* shrubs were smaller, and *L. pyrotechnica* shrubs were smaller and less densely distributed. Some of these differences were visibly clear; six of eight farm owners who were interviewed in a 2005 ethnobotanical study (Gallacher 2010) reported an increase in *C. procera* populations over the previous decade, and three reported a decline in *C. polygonoides*, but they did not mention changes in the density or structure of *L. pyrotechnica*. Density of this species is spatially heterogeneous, making it difficult for ground observers to detect even the large differences measured here. Size of *L. pyrotechnica* was also affected, as was hypothesized, resulting in a much greater frequency in WILD/wild of the microhabitats that are produced by the largest shrubs in this habitat. Larger shrubs were significantly associated with under canopy *L. shawii. L. pyrotechnica* was observed to shelter perennial grasses *Cenchrus divisus* (J.F.Gmel.) Verloove, Govaerts and Buttler and *Panicum turgidum* Forssk. (Figure 6), and the bulk of seed production of these species within this habitat appeared to occur within the shelter of *L. pyrotechnica* canopies. Camels appear to cause greater mechanical damage to *L. pyrotechnica* than do Oryx or gazelles when they forage through the shrubs for these more palatable associated species.

By 2017 the size differences of *L. pyrotechnica* among enclosures had largely disappeared but density differences remained. The number of new recruits was similar among enclosures, though they had grown larger in DOM/wild. Therefore, this species recovers from heavy camel browsing by increasing both size and density, but the former is much faster than the latter, as hypothesized. Successful recruitment is normally very rare in perennial shrubs of arid ecosystems (Ackerman 1979). Average lifespan was estimated at 95 years, differing markedly from the 15–20 years average lifespan reported previously (Gondaliya and Rajput 2017). These observations also indicate that the 2006 population difference among enclosures was caused by a decline of population in DOM/wild, rather than a recovery of population from prior over-browsing in WILD/wild.

Recruitment of *L. shawii* showed a loose proximal association with potential maternal plants, but it is unclear from this study whether this is attributable to seed dispersal mechanism or suitability of microhabitat (dune stability). Recruitment was more common under the shelter of *L. pyrotechnica* canopies. Two possible explanations for this are that faunal dispersers of *L. shawii* seeds also frequent *L. pyrotechnica* canopies, or that seedlings are more protected from herbivory in this microhabitat. Survival of established *L. shawii* plants was unaffected by *L. pyrotechnica* protection. Reproductive success of *L. shawii* may have been affected by the grazing regime. Plant size is often a better indicator of fecundity and survival than age, and may, therefore, be a preferable measure of life history (Harper 1977; Shaltout, Sheded, and Salem 2009). It is not known why a higher mortality of *L. shawii* was observed in DOM/wild during the study. It is possible that they are preferentially browsed by *Oryx* more than camels. Domesticated Oryx in Taif, Saudi Arabia, were observed to eat both leaves and roots of *L. shawii*, the latter by digging around the base of the plant with their front hooves (Asmodé 1990), but this behavior has not been observed in the DDCR.

Distribution of *C. polygonoides* recruitment was tightly clustered into two groups, indicating that seeds had dispersed into DOM/wild from two surviving maternal individuals located in WILD/wild. This clustering pattern has been observed elsewhere throughout WILD/wild, and is consistent with seeds being anemochoric. The habitat is similar to dune deserts in Oman that have been classified as a Prosopis-Calligonum vegetation type (Ghazanfar 2004), indicating that a much larger density of *C. polygonoides* may have occurred previously. Recovery from camel over-browsing is relatively slow since destruction was more complete, and most recruitment occurs within a few hundred meters of a surviving plant.

Camels avoid *C. procera* but eat most other plants, thus the species thrives in areas of dense camel populations. The almost complete decline of the species in 2017 is likely due to gazelle herbivory. Lower leaves on the two surviving plants, and others throughout DOM/wild, have been removed and plant structure modified from multiple to a single stem. It is likely that this species was historically uncommon in this habitat, and its demise represents a return toward a former ecological balance.

Two plant size observations were contrary to our hypotheses. *L. shawii* plants did not increase in size with reduced herbivory, indicating that the heavier grazing pressure of the 2006 DDCR regime did not substantially modify plant structure. *C. polygonoides* plants did not increase in height, as predicted, but their canopies increased substantially. Camel herbivory thus appears to affect woody stems in addition to the palatable leaves of this species. This might be through direct mechanical damage, or through the plant abandoning branches that lack photosynthetic tissue.

Conclusion

The change in herbivory from camels to Oryx and gazelles resulted in a decline of *C. procera* and an increase in the other three species as was hypothesized, but the response differed markedly among species. Existing *L. pyrotechnica* shrubs responded rapidly in size but recruitment was slow, with the species exhibiting a long lifespan and relying more on recovery and/or recruitment from rootstock than sexual reproduction. In contrast, *C. polygonoides* and *L. shawii* exhibited a short lifespan and showed no evidence of asexual reproduction. *C. polygonoides* relies on rapid growth and sexual recruitment, and the population can recover quickly around the maternal plant. However, heavy camel browsing can destroy established plants and the soil seed bank, resulting in local extinctions. *L. shawii* population recovery is slower but more dispersed. The species benefits from but is not reliant on its association with large *L. pyrotechnica* shrubs, which appear in the absence of heavy camel browsing.

A healthy tall shrub community in this habitat can be recognized by an abundance of *C. polygonoides*, infrequent occurrences of *C. procera*, and large *L. pyrotechnica* shrubs that show little sign of mechanical damage from camels. Recovery from heavy camel herbivory would be hastened by (1) artificially distributing seeds of *C. polygonoides* and (2) promoting the presence of large unbrowsed *L. pyrotechnica* shrubs. A ten-year timeframe is sufficient to see only the early stages of plant community recovery.

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