

# Bush encroachment influences nocturnal rodent community and behaviour in a semi-arid grassland in Gujarat, India

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## ABSTRACT

Bush encroachment is one of the major threats to grasslands globally. The increased cover due to bush encroachment can strongly influence the behaviour of animals adapted to a more open habitat. In this study, we explored the effects of bush encroachment on the foraging behaviour of nocturnal rodents the semi-arid Banni grasslands of western India, once one of India's largest tropical grassland habitats. We quantified foraging behaviour using the giving-up density (GUD) framework, across two sites that differed in the extent of bush encroachment. Rodents in the site with high bush encroachment (the dense site) exhibited higher foraging costs (higher GUD) in early summer compared to the site with low bush encroachment (the sparse site). Rodents in the dense site also had lower activity. The dense site supported higher richness and relative abundance of generalist rodents than the sparse site. Our results suggest that bush encroachment may be associated with higher foraging costs for nocturnal rodents and result in a change in species composition of rodents. Given the ecosystem engineering services performed by native grassland species, these results can have negative implications for grassland restoration.

## 1. Introduction

Savannas and grasslands account for a fifth of the global land surface (White et al., 2000). They are important in both agronomic and ecological contexts. However, grasslands are one of the most threatened ecosystems in the world, facing intense anthropogenic pressures due to agriculture and other land-use changes (Briggs et al., 2005). One of the major threats to grasslands is the natural or artificial increase in woody vegetation, a phenomenon termed shrub or bush encroachment (Archer, 1995). This can be due to changes in grazing practices (e.g. heavy grazing by domestic livestock (Archer, 1994)); fire suppression (Briggs et al., 2002) or due to the introduction of invasive species (Briggs et al., 2007). Bush encroachment in arid and semi-arid systems can alter biogeochemical processes, reduce plant species richness and result in ecosystem degradation (Briggs et al., 2005; Eldridge et al., 2011).

In India, semi-arid savannas account for ~13% of the landscape (Vanak et al., 2015). Although a neglected ecosystem, it supports a sizeable population of pastoralists and ~500 million livestock (Singh

et al., 2006). Bush encroachment due to afforestation and invasive species has converted many of India's grasslands into woodlands. For example, in the Banni grasslands of Gujarat, the alien invasive *Prosopis juliflora* which was systematically introduced in the 1960's, was found to occupy 50% of the total area in 2011 (Vaibhav et al., 2012).

Bush encroachment not only results in a physical reduction of grassland areas, but also a concomitant decline in associated obligate grassland species due to a change in habitat structure (Horncastle et al., 2005; Matlack et al., 2008; Sirami et al., 2009). What is relatively less known is the effect of bush encroachment on the behaviour of organisms that are adapted to relatively simpler, more open habitats. For instance, many open habitat species associate cover with predation risk due to the obstruction of sightlines (Iribarren and Kotler, 2012). In semi-arid grassland systems, bush encroachment can lower visibility (sightlines) and thus increase predation risk of foragers (Embar et al., 2011). Thus, it is necessary to study the foraging behaviour of consumers in response to increasing cover, allowing us to estimate foraging costs and hence fitness (Kotler and Brown, 1988).

In semi-arid grasslands, rodents are considered keystone species,

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due to their trophic effects (as herbivores and prey), and ecosystem engineering (Davidson et al., 2012). Their burrowing and grazing activities help to maintain the open habitat of grasslands and create important habitats for other species, thus increasing the overall habitat heterogeneity and biodiversity across the landscape (Davidson et al., 2012).

Rodent foraging behaviour is influenced by structural changes in vegetation. For example, high invasive shrub cover caused forest rodents adapted to low visibility, to exhibit increased foraging activity as these habitats served as a refuge (Dutra et al., 2011; Mattos and Orrock, 2010). Conversely, in shrub-dominated areas with reduced visibility, rodents adapted to high visibility habitats have high foraging costs (Wheeler and Hik, 2014). High foraging costs due to perceived predation risk can lead to individuals trading off feeding for safety, which can lead to a reduction in fecundity, and eventually, survival (Lima, 1998). If expressed at the population level, this can negatively affect the distribution and population abundance of rodents (Brown et al., 1999).

Given the importance of rodents in semi-arid grasslands, and the influence of cover on their foraging behaviour, rodents make a good model species to study the effect of bush encroachment on the behaviour of animals. Despite this, to the best of our knowledge, no studies have examined the effect of bush encroachment in semi-arid grasslands on rodent behavioural ecology. In this study, we examined how changes in habitat structure due to bush encroachment, affects the foraging behaviour of nocturnal rodents in the Banni grasslands of Gujarat, India. Banni, once among India's largest semi-arid grasslands, has experienced rapid invasion by *Prosopis juliflora*.

We tested how differences in bush encroachment mediated by abiotic factors such as moonlight, season and microhabitat influenced nocturnal rodent foraging behaviour and community composition. We expected that illumination due to moonlight, seasonal and microhabitat effects will interact with cover to influence foraging (see (Kotler et al., 2004)). In particular, we expected foraging costs to be higher in sites with dense cover compared to those with sparse cover, and during nights with high moonlight which are generally perceived as having the highest predation risk (Kotler et al., 2010, 1991). Season is likely to influence the effect of cover on foraging costs due to its effect on food availability and temperature. For example, desert gerbils foraged less from assay food patches in winter compared to summer, likely due to high thermoregulatory costs, the presence of alternative food sources in winter or lower population densities (Brown et al., 1994; mean population densities ranged from 1.5 and 6.8 individuals per hectare in winter and 3 and 10.7 individuals per hectare in summer for two of the most abundant species in the study, *Gerbillus pyramidium* and *Gerbillus allenbyi* respectively). Finally, differences in foraging costs between microhabitats is likely to be in contrast to the response of rodents to cover at the habitat scale, with rodents largely associating bushy microhabitats with safety and perceiving higher foraging costs in open microhabitats (Kotler et al., 1991). We expected that these foraging costs between microhabitats are likely to be exhibited only in the site with sparse cover due to a higher contrast between open and covered microhabitats.

## 2. Methods

### 2.1. Study area

This study was conducted between December 2015–March 2016 in the Banni Grasslands in the Kachchh district of Gujarat, India (23°19'N to 23°52'N and 68°56'E to 70°32'E; F). This semi-arid halophyte-dominated grassland covers an area of 2617 km<sup>2</sup>.

*P. juliflora* was introduced to Gujarat in the 1890s to check desertification (Tiawari, 1999). It was systematically introduced to the Banni Grasslands in the 1960s. Its rate of spread in Banni between 1980 and 1992 was estimated to be 25.5 km<sup>2</sup> per year (Jadhav et al., 1993). Currently, 50% of Banni is under *Prosopis* cover (Vaibhav et al., 2012).

The other vegetation types in Banni comprise *Suaeda* scrub, woody plants and grasses. Woody plants in the study area include *Acacia nilotica*, *Salvadora persica*, *S. oleoides*, *Pulicarya crispa*, and *Solanum* sp. Other vegetation includes grasses such as *Cenchrus ciliaris*, *Eleusine compressa*, *Cyperus rotundus*, *Aeluropus lagopoidis* and *Cressa cretica*. Livestock rearing is one of the main occupations of the people of Banni and overgrazing by livestock is perceived to be a cause of degradation of the grasslands (Joshi et al., 2009).

The nocturnal rodent species found in this area include *Millardia meltada*, *Tatera indica*, *Mus booduga*, *Millardia gleadowi* and *Gerbillus nanus*. The latter was rare during our study. *G. nanus* and *M. gleadowi* are the only desert-adapted fauna: *G. nanus* is found in sandy habitats and stabilised sand dunes (Idris, 2009) while *Millardia gleadowi* is found in thorny scrub habitats in arid and semi-arid regions of western India (Prakash et al., 2015). *M. meltada* is associated with both grasslands and irrigated croplands and agricultural fields (Idris, 2009). *T. indica* and *M. booduga* are largely associated with ruderal areas (Idris, 2009).

Potential predators of rodents in the study area include snakes, raptors such as the barn owl (*Tyto alba*) and spotted owl (*Athene brama*), jungle cat (*Felis chaus*), Indian fox (*Vulpes bengalensis*), desert fox (*V. vulpes pusilla*) and golden jackal (*Canis aureus*).

### 2.2. Study design

#### 2.2.1. Quantifying rodent foraging behaviour

Foraging costs were quantified using the giving-up density framework that provides an index of the costs of foraging at a patch (Brown, 1988). The giving-up density theory, which stems from an extension of the marginal value theorem, suggests that in a patch with diminishing returns, a forager should quit feeding from a patch when the returns from the patch becomes less than, or equal to, the costs of foraging from it (Brown, 1992, 1988). The amount of food left behind in the patch (i.e. when the forager 'gives-up') is referred to as the giving-up density (GUD). The GUD represents the costs of feeding at the patch which include the metabolic cost, predation cost and the costs of missed opportunity (e.g., of feeding elsewhere, or taking shelter; Brown, 1988) experienced by the forager. Thus higher the GUD, higher the foraging cost.

#### 2.2.2. Influence of bush encroachment on rodent foraging behaviour

Two adjacent sites that differed in woody vegetation cover were chosen for this study (see Appendix for representative pictures and how cover in the two sites was quantified). The two sites henceforth referred to as the 'dense' cover and 'sparse' cover sites were separated by a distance of 1000 m. Within each site (i.e. dense and sparse), two 5 × 6 trapping grids (20 m between stations, each covering an area of 8000 m<sup>2</sup> and separated by a distance of 150 m) were established.

Assay foraging patches were used to measure the foraging costs of rodents, a technique which has been used in several studies around the world (Johnson and De Leon, 2015; Kotler and Brown, 1988; Wheeler and Hik, 2014). Within each experimental grid there were four pairs of food patches (i.e. four stations). These were arranged as a square, separated by a distance of 40 m. This distance is greater than the radius of the average home range of the largest rodent, *Tatera indica* found in these habitats (Prakash and Rana, 1970). To test for microhabitat differences in foraging, one food patch was placed at each station under a *Prosopis* tree (the bush patch) and one placed 3.5 m away from the tree (the open patch).

Each assay foraging patch (henceforth, foraging patch) was a rectangular pit (38 × 27 × 7 cm) in the sand. The pit was first covered with newspaper and filled with 3 L of sifted sand, mixed with 3 g of pearl millet (*Pennisetum glaucum*) seeds. Each foraging patch had a 3 m track plot around it. Daily, in the evening (17:00–19:00), the track plots were smoothened after seeds were added to the foraging patch. The left over seeds (i.e. GUD) were collected in the morning. This was repeated for 4 consecutive nights, centered on four moon phases (full, waning,

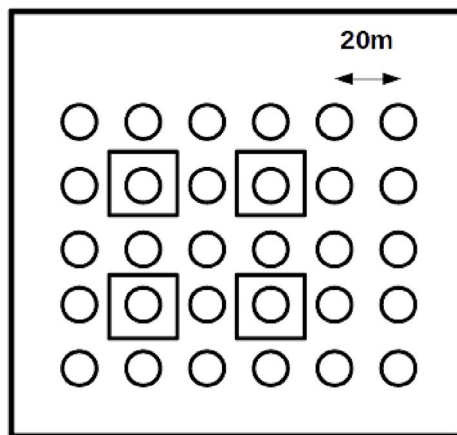


Fig. 1. Schematic of the experimental grid. Circles represent traps; squares represent feeding patches.

waxing and new moon).

We collected data from all four grids within 1 h, 30 min. Data collection began on the second day as the first day served as an acclimation period. We collected data on seeds remaining in each foraging patch (the GUD) and the number of footprints that entered a track plot (a measure of rodent activity). Any ants or bird tracks in and around the foraging patch were also recorded. If both gerbils and birds visited the feeding stations, the corresponding GUD data were discarded at the analysis stage. The seeds remaining in the foraging patch were sifted through a sieve, processed (debris removed) and weighed. We carried out this process over two months – winter (mid December 2015–January 2016) and early summer (late January–early March 2016), so that there were two replicates for each moon phase except the full moon phase, for which we could not collect data during early summer.

Rodent abundance and species composition was determined in the two sites (four grids) using live trapping. Sherman traps were arranged in a 5 × 6 grid (i.e., 30 traps) with a spacing of 20 m between each trap. The grids containing foraging patches were within this larger grid containing traps (Fig. 1). Trapping was carried out in the beginning, middle and end of the foraging study (from 19<sup>th</sup>–21<sup>st</sup> December 2015, 7<sup>th</sup>–10<sup>th</sup> January 2016, and 8<sup>th</sup>–14<sup>th</sup> March 2016). On trapping nights, the feeding experiment was not conducted. Thirty traps were placed in one of the two grids of both sites and baited with peanut butter mixed with wheat. The traps were baited in the evening and checked in the morning. If a rodent was captured, it was identified up to the species level, marked with non-toxic Sharpies, and released. Both the experiments and rodent trapping conform to the ARRIVE guidelines and are in accordance with the UK Animals (Scientific Procedures) Act 1986.

### 3. Analysis

We averaged rodent activity and GUD for each foraging patch across the three nights, for each moon phase (new, waxing and waning phase). Data for the full moon period were dropped, as we did not have data for early summer. We examined how rodent activity and GUD was explained by site (dense and sparse), moon phase (wane, new, wax), microhabitat (open and bush) and season (winter and early summer), using a linear mixed effects model (Bates et al., 2015). We started with the most complex model containing three-way interactions (site × moon phase × microhabitat, site × moon phase × season and site × season × microhabitat), two-way interactions (site × moon phase, site × microhabitat, site × season, moon phase × microhabitat, moon phase × season and season × microhabitat) and main effects. Three-way terms were removed from the model if they did not significantly explain variation in the response variable.

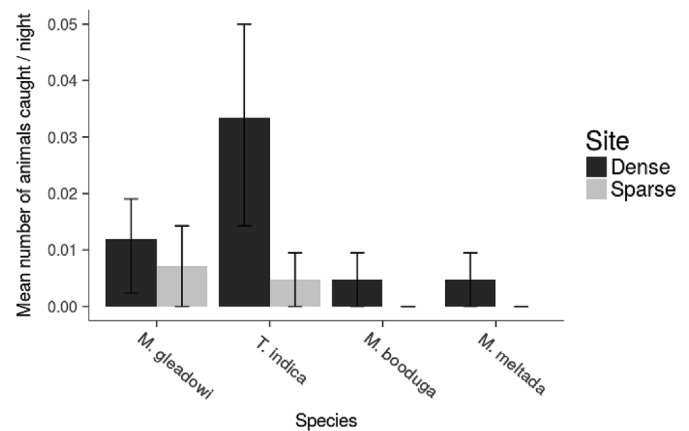


Fig. 2. Rodent species composition in the sparse and dense site, across 420 trap nights/site. Values are mean ± 95% CI.

Feeding station was treated as a random effect to account for repeated measures over multiple nights and seasons. Likelihood ratio tests were used to examine the significance of fixed effects. Tukey test (lsmeans package, Lenth (2016)) was used for post-hoc analysis of significant effects. Means of GUD data were squared to correct for heteroscedasticity.

Comparisons between rodent species composition and abundance in the two sites were made from 95% bootstrapped confidence intervals. All analyses were carried out using the R programming language, version 3.3.0 (R Core Team, 2013).

## 4. Results

### 4.1. Rodent species composition

Twenty-eight individuals belonging to four species of rodents were caught in the two sites, across 420 trap nights per site (Fig. 2). The species caught in the dense site were the Indian gerbil (*Tatera indica*; 14 individuals), sandy-coloured metad (*Millardia gleadowi*; n = 5), the common Indian field mouse (*Mus booduga*; n = 2) and the soft-furred rat (*Millardia meltada*; n = 2). In the sparse site, the species caught were the Indian gerbil (2 individuals) and sandy-coloured metad (n = 3). Overall, the dense site had a higher number of species, and a higher relative abundance of the Indian gerbil, compared to the sparse site.

### 4.2. Influence of bush encroachment on rodent activity

Rodent activity was affected by site, being significantly higher in the bush microhabitat (Tukey post-hoc  $p < .001$ ) compared to the open microhabitat in the sparse site (site × microhabitat × linear mixed effects model,  $p = .04$ ; Table 1; Fig. 3b), with higher overall activity in the sparse site (Fig. 3b). Activity also differed significantly between moon phases in the early summer season (moon phase × season × linear mixed effects model,  $p < .001$ ; Table 1, Fig. 3a), with significantly higher activity in the waning phase compared to the new (Tukey post-hoc  $p < .001$ ) and waxing moon phase (Tukey post-hoc  $p < .001$ ), in both sites. Activity was similar in both sites across the two seasons (site × season × linear mixed effects model,  $p = .47$ ; Table 1; see Table 2 for parameter estimates).

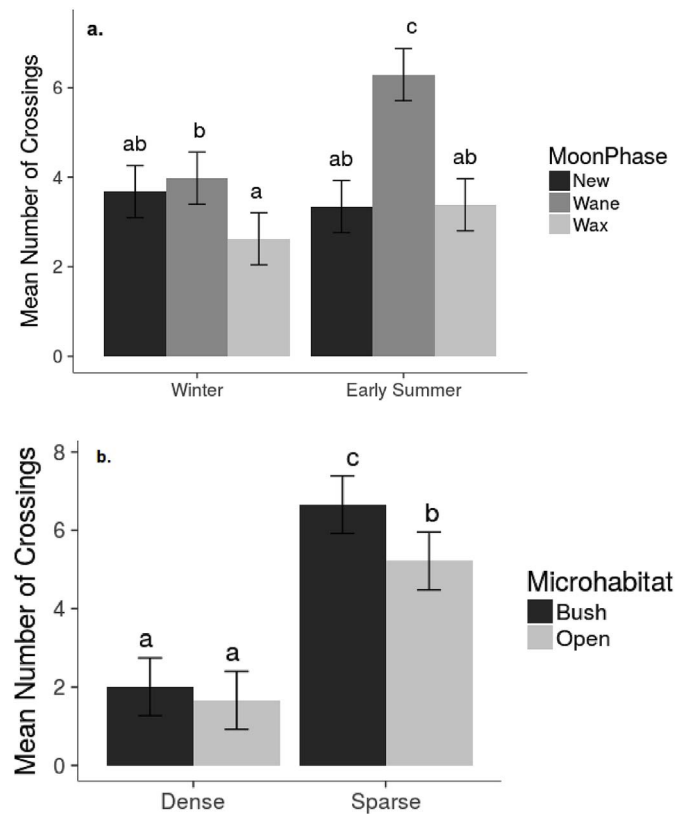
### 4.3. Influence of bush encroachment on rodent feeding behaviour

Rodent GUD was significantly affected by site and season (site × season × linear mixed effects model,  $p = .02$ ; Table 3, Fig. 4). During winter GUD between the two sites was similar, however during early summer, GUD was significantly lower in the sparse site compared to the dense site (Tukey post-hoc;  $p = .02$ ). Further, within the sparse site,

**Table 1**

Results of likelihood ratio test for mean rodent activity around foraging patches in Experiment 1,  $n = 192$  observations.

Effect	$\chi^2$	DF	Pr(> Chisq)
Moon phase	37.61	2	< 0.001
Site	11.39	1	< 0.001
Microhabitat	10.28	1	0.001
Season	10.25	1	0.001
Moon phase x Site	3.41	2	0.182
Moon phase x Season	16.22	2	< 0.001
Moon phase x Microhabitat	3.49	2	0.175
Microhabitat x Season	6.88	1	0.008
Site x Microhabitat	4.23	1	0.039
Site x Season	0.53	1	0.468
Moon phase x Site x Microhabitat	0.01	2	0.995
Moon phase x Site x Season	0.74	2	0.692
Site x Season x Microhabitat	3.11	1	0.070



**Fig. 3.** Variation in activity across (a) seasons, for different moon phases and (b) microhabitat in the two sites. Mean activity for the full moon phase during winter =  $1.12 \pm 0.25$  (values are mean  $\pm$  SE). Letters above the bars denote similar (same letter) or contrasting (different letters) values in post-hoc contrasts between (a) moon phase and (b) microhabitat.

GUD was lower in early summer compared to winter (Tukey post-hoc;  $p < .001$ ). GUD was similar in both sites, in the two microhabitats and across the three moon phases (Table 3; see Table 4 for parameter estimates).

## 5. Discussion

In a bush encroached grassland such as Banni, our results suggest that high woody cover affects both species composition and behaviour of nocturnal rodents. The dense site had higher relative abundance and species richness of rodents compared to the sparse site. However, as expected, rodents in the dense site had higher GUD in early summer and lower activity across both seasons, compared to the sparse site.

**Table 2**

Model estimates for the effects of site, moon phase, microhabitat and season on rodent activity.

Effect: level	Estimate	SE
Intercept	0.847	0.901
Moon phase: Wane <sup>a</sup>	3.198	0.781
Moon phase: Wax <sup>a</sup>	0.677	0.781
Site: Sparse <sup>b</sup>	4.17	1.273
Microhabitat: Bush <sup>c</sup>	0.764	0.737
Season: Winter <sup>d</sup>	0.556	0.737
Moon phase: Wane x Site: Sparse	0.708	1.105
Moon phase: Wax x Site: Sparse	-0.594	1.105
Moon phase: Wane x Season: Winter	-2.896	0.902
Moon phase: Wax x Season: Winter	-1.646	0.902
Moon phase: Wane x Microhabitat: Bush	-1.270	0.902
Moon phase: Wax x Microhabitat: Bush	-0.688	0.902
Site: Sparse x Microhabitat: Bush	0.118	1.104
Site: Sparse x Season: Winter	-1.84	1.104
Microhabitat: Bush x Season: Winter	0.472	0.736
Moon phase: Wane x Site: Sparse x Microhabitat: Bush	0.125	1.276
Moon phase: Wax x Site: Sparse x Microhabitat: Bush	0.021	1.276
Moon phase: Wane x Site: Sparse x Season: Winter	0.500	1.276
Moon phase: Wax x Site: Sparse x Season: Winter	1.104	1.276
Site: Sparse x Microhabitat: Bush x Season: Winter	1.847	1.041

<sup>a</sup> Moon phase reference level is 'New'.

<sup>b</sup> Site reference level is 'Dense'.

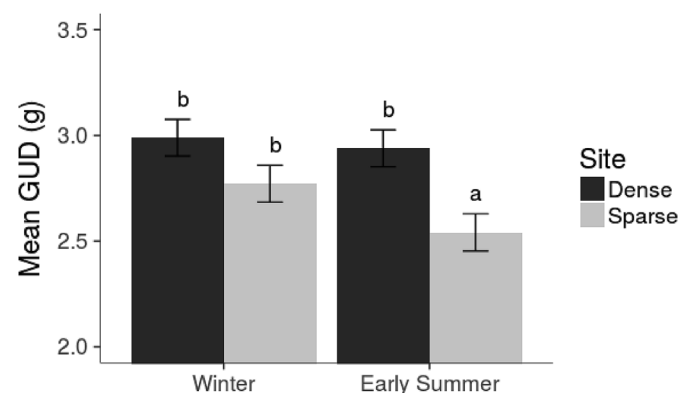
<sup>c</sup> Microhabitat reference level is 'Open'.

<sup>d</sup> Season reference level is 'Early Summer'.

**Table 3**

Results of likelihood ratio test for mean giving-up density around foraging patches in Experiment 1,  $n = 181$  observations.

Effect	$\chi^2$	DF	Pr(> Chisq)
Moon phase	2.510	2	0.285
Site	5.620	1	0.017
Microhabitat	0.337	1	0.561
Season	11.25	1	< 0.001
Moon phase x Site	1.343	2	0.511
Moon phase x Season	0.238	2	0.887
Moon phase x Microhabitat	0.139	2	0.932
Microhabitat x Season	3.039	1	0.081
Site x Microhabitat	0.149	1	0.698
Site x Season	5.220	1	0.022
Moon phase x Site x Microhabitat	0.943	2	0.624
Moon phase x Site x Season	1.260	2	0.532
Site x Season x Microhabitat	3.05	1	0.080



**Fig. 4.** Variation in mean GUD across seasons in the two sites. (values are mean  $\pm$  SE). Letters above the bars denote similar (same letter) and contrasting (different letters) values in post-hoc contrasts between the two sites.

The species diversity of rodents is known to be related to diversity in vegetation height and biomass (Kotler et al., 1988) where higher structural complexity of the habitat provides more niche space for



**Table 4**

Model estimates for the effects of site, moon phase, microhabitat and season on mean GUD.

Effect: level	Estimate	SE
Intercept	2.974	0.113
Moon phase: Wane <sup>a</sup>	−0.136	0.119
Moon phase: Wax <sup>a</sup>	0.005	0.111
Site: Sparse <sup>b</sup>	−0.320	0.161
Microhabitat: Bush <sup>c</sup>	−0.055	0.105
Season: Winter <sup>d</sup>	0.048	0.105
Moon phase: Wane x Site: Sparse	0.036	0.169
Moon phase: Wax x Site: Sparse	−0.084	0.157
Moon phase: Wane x Season: Winter	0.079	0.134
Moon phase: Wax x Season: Winter	−0.067	0.123
Moon phase: Wane x Microhabitat: Bush	0.118	0.132
Moon phase: Wax x Microhabitat: Bush	0.074	0.127
Site: Sparse x Microhabitat: Bush	−0.003	0.149
Site: Sparse x Season: Winter	0.019	0.149
	0.003	0.106
Moon phase: Wane x Site: Sparse x Microhabitat: Bush	−0.176	0.189
Moon phase: Wax x Site: Sparse x Microhabitat: Bush	−0.153	0.181
Moon phase: Wane x Site: Sparse x Season: Winter	−0.073	0.192
Moon phase: Wax x Site: Sparse x Season: Winter	0.135	0.181
Site: Sparse x Microhabitat: Bush x Season: Winter	0.268	0.153

<sup>a</sup> Moon phase reference level is 'New'.

<sup>b</sup> Site reference level is 'Dense'.

<sup>c</sup> Microhabitat reference level is 'Open'.

<sup>d</sup> Season reference level is 'Early Summer'.

species (MacArthur and MacArthur, 1961). The higher diversity in plant species and range in vegetation height in the dense site (refer Appendix) likely explains the higher number of rodent species (Fig. 2). Most of the species in the dense site are those generally associated with ruderal and agricultural habitats (*Mus booduga*, *Millardia meltada* and *Tatera indica* Idris (2009)), with the first two species absent in the sparse site (Fig. 2). This is likely due to the higher number of weedy species in more bush encroached habitats (Kumar and Mathur, 2014). Other studies have found an increase in woodland-associated species in areas with woody encroachment (Horncastle et al., 2005; Matlack et al., 2008). However, this was also associated with a decrease in fauna associated with open habitats and grasslands, which was attributed to high cover and a decrease in forage vegetation (Alford et al., 2012; Wheeler and Hik, 2014).

Bush encroachment may affect rodent foraging behaviour due to changes in food availability, costs of foraging (e.g. predation cost, missed opportunity cost; Brown, 1988), or both. Rodent GUD was higher in the dense site compared to the sparse site in early summer (Fig. 4) and rodent activity was lower in the dense site compared to the sparse site (Fig. 3b). This is in line with our expectations and suggests that rodents may perceive high predation risk in the dense site, likely due to high cover. However seasonal effects on temperature food availability may also explain GUD and rodent activity. Similar and high GUD between both sites in winter could be due to higher thermoregulatory costs (Kotler et al., 2004). Furthermore, winter in the Banni is also the post-monsoon season, when food resources such as seeds and vegetation are likely at their peak levels. As the dry season progresses towards summer, food resources are likely to dwindle, more so in the sparse site compared to the dense sites. This may explain why rodents forage more in the sparse site (i.e., lower GUD) in the summer.

Consistently high GUD across both seasons in the dense site may be due to other reasons. The diet of the rodents found in both sites is not primarily granivorous and consists of seeds, plant matter (stem, rhizomes etc.) and invertebrates (Prakash et al., 2015). Thus high GUD in the dense site may be explained by the higher relative abundance of more omnivorous species (*T. indica*, *M. booduga*, *M. meltada*) and the presence of alternate food sources. Similarly, low GUD in the sparse site may be due to lower forage availability (e.g. as a result of overgrazing, A. Jayadevan, pers. obs.), which may also explain the reduced number

of rodents in this site; more effective vigilance due to more open sightlines (Brown, 1999) and/or harvesting strategies such as grab-and-go foraging which reduces exposure to predators (Juliana et al., 2017).

Microhabitat differences in rodent activity suggest a strong effect of vegetative cover. In the sparse site, significantly higher activity in bush microhabitat compared to open (Fig. 3b) is in accordance with previous studies that have found that at the patch level, rodents associate bush microhabitats with safety (Kotler et al., 1993, 1991). The lack of microhabitat differences in activity in the dense site is likely due to low contrast between open and bush microhabitats, as a consequence of high shrub cover in this site. Unexpectedly, differences in activity between microhabitats in the sparse site, was not reflected in the GUD. This indicates that the rodents may be using other strategies (e.g. time allocation, apprehension (Kotler et al., 2004, 2002) to manage risk).

Moon phase affected rodent activity only during summer. In particular, highest activity was seen in the waning moon phase (Fig. 3a). This is likely due to rodents being at a lower energetic state following the full moon phase, a period where there is very low foraging due to high perceived risk of predation (Kotler et al., 2010). Seasonal effects on food availability and high thermoregulatory costs of foraging also likely explains why rodent activity was similar across the three moon phases in winter.

In order to robustly establish and generalize the association between high cover and perceived predation risk across broader spatial scales, we would require more replicates of sites and greater sample sizes. Further, to address the confounding factors of differences in rodent communities and forage availability in the two sites this study, future work should take into account the species identity of rodents at foraging patches and vegetation types in different sites, or compare foraging before and after bush removal within replicated habitats. As our study indicates that woody encroachment affects rodent communities, it would be instructive to examine changes in rodent communities and abundance following bush removal. Other studies that have examined the effect of bush removal on grassland flora and fauna have found rapid increases in abundance and a shift towards grassland-adapted rodents post bush removal (Alford et al., 2012). Further research is also needed to understand the role that different rodent communities play in either assisting or inhibiting bush encroachment.

The impact of bush encroachment on faunal assemblages is well documented. Studies have found decreased species richness and diversity of birds (Sirami et al., 2009), invertebrates (Steenkamp and Chown, 1996) and rodents (Matlack et al., 2008) associated with grasslands. This study suggests that bush encroachment is also associated with a higher number of generalist species. Given that rodents are considered keystone species in grasslands, our results may have negative implications for grassland restoration if, over time, the generalist species displace native grassland species which perform ecosystem engineering services.

Most studies that have explored the impact of bush encroachment on small mammals have not examined how the mammals' behaviour will be affected, which is often the first indication of population decline. Our results offer some evidence that bush encroachment may be associated with high foraging costs likely due to reduced visibility and higher food availability.

Bush encroachment is likely to increase in the grasslands of India due to afforestation (Vanak et al., 2015). In Banni, 95% of *Prosopis* encroachment has occurred in grasslands compared to other land cover types (Pasha et al., 2014). Globally, the trend of widespread increases in woody cover has been reported in many grassland ecosystems (Wigley and Hoffman, 2010). Our results indicate that bush encroachment may have important effects on the community and foraging behaviour of native prey species which, if expressed at the population level, can have a negative effect on their population dynamics (Preisser et al., 2005). Such changes in community composition and abundance of keystone species may result in a cascading effect on grassland plant species, with possible implications on habitat restoration.

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## Appendix. Vegetation characterization

Tree and bush density were not normally distributed, so a non-parametric Kruskal-Wallis test was used to examine differences in cover between the sparse and dense site.

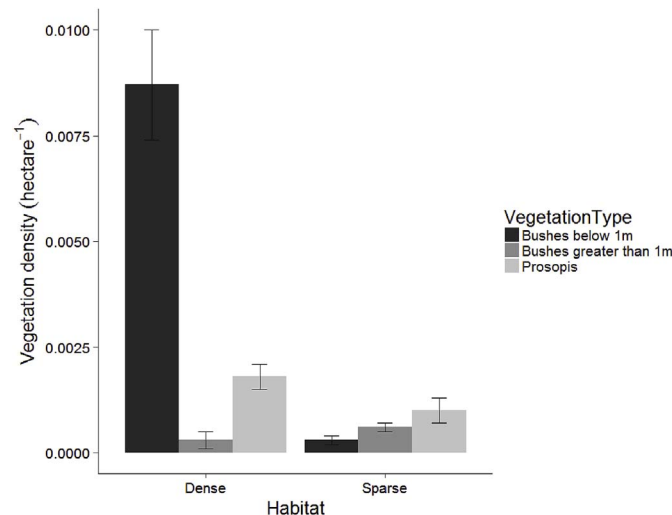


Fig. 5. Density of different classes of vegetation in the sparse and dense site (values are mean  $\pm$  SE).

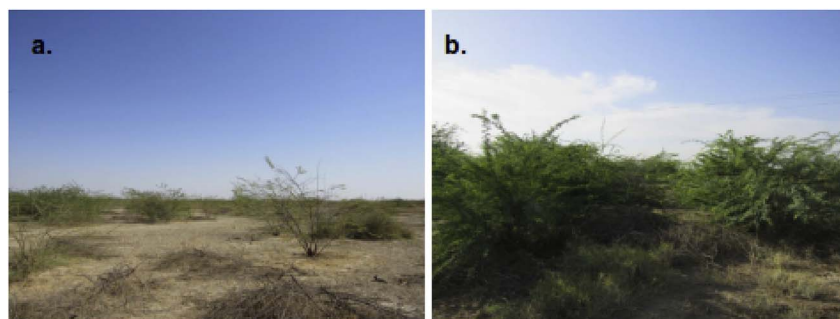


Fig. 6. Sites with low (a) and high (b) bush encroachment.

As expected total vegetation density is higher in the dense site (vegetation density<sub>dense site</sub> = 0.0035  $\pm$  0.0006 SE per hectare; vegetation density<sub>sparse site</sub> = 0.0006  $\pm$  0.0001 SE per hectare, Fig. 1) compared to the sparse site ( $\chi^2$  = 15.8,  $p$  < .001). Difference in vegetation density was mostly attributed to bushes less than 1 m in height (dense = 0.008  $\pm$  0.001 SE bushes per hectare; sparse = 0.0003  $\pm$  0.0001 SE per hectare,  $\chi^2$  = 30.77,  $p$  < .001).

## References

- Alford, A.L., Hellgren, E.C., Limb, R., Engle, D.M., 2012. Experimental tree removal in tallgrass prairie: variable responses of flora and fauna along a woody cover gradient. *Ecol. Appl.* 22, 947–958. <http://dx.doi.org/10.1890/10-1288.1>.
- Archer, S., 1995. Harry stobbs memorial lecture, 1993 herbivore mediation of grass-woody plant interactions. *Trop. Grasslands* 29, 218–235.
- Archer, S., 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns and proximate causes. *Ecol. Implic. Livest. Herbiv. West* 13–68.
- Bates, D.M., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Software* 67, 1–48. <http://dx.doi.org/10.1177/009286150103500418>.
- Briggs, J.M., Hoch, G.A., Johnson, L.C., 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5, 578–586. <http://dx.doi.org/10.1007/s10021-002-0187-4>.
- Briggs, J.M., Knapp, A.K., Blair, J.M., Heisler, J.L., Hoch, G.A., Lett, M.S., McCarron, J.K., 2005. An ecosystem in transition: cause and consequences of the conversion of mesic grassland to shrubland. *Bioscience* 55, 243–254. [http://dx.doi.org/10.1641/0006-3568\(2005\)055](http://dx.doi.org/10.1641/0006-3568(2005)055).
- Briggs, J.M., Schaafsma, H., Trenkov, D., 2007. Woody vegetation expansion in a desert grassland: prehistoric human impact? *J. Arid Environ.* 69, 458–472. <http://dx.doi.org/10.1016/j.jaridenv.2006.10.012>.
- Brown, J.S., 1999. Vigilance, Patch Use and Habitat Selection: Foraging under Predation Risk. pp. 49–71.
- Brown, J.S., 1992. Patch use under predation risk: I. Models and predictions. In: *Ann. Zool. Fenn. Finnish Zool. Publ. Board, Form. by Finnish Acad. Sci. Soc. Biol. Fenn. Vanamo, Soc. pro Fauna Flora Fenn. Soc. Sci. Fenn.*
- Brown, J.S., 1988. Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22, 37–47.
- Brown, J.S., Kotler, B.P., Mitchell, W.A., 1994. Foraging theory, patch use and the structure of a negev desert Granivore community. *Ecology* 75, 2286–2300.
- Brown, J.S., Laundre, J.W., Gurung, M., 1999. The ecology of Fear: optimal foraging, game theory, and trophic interactions. *J. Mammal.* 80, 385–399.
- Davidson, A.D., Detling, J.K., Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* 10, 477–486. <http://dx.doi.org/10.1890/110054>.
- Dutra, H.P., Barnett, K., Reinhardt, J.R., Marquis, R.J., Orrock, J.L., 2011. Invasive plant species alters consumer behavior by providing refuge from predation. *Oecologia* 166, 649–657. <http://dx.doi.org/10.1007/s00442-010-1895-7>.

- Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* 14, 709–722. <http://dx.doi.org/10.1111/j.1461-0248.2011.01630.x>.
- Embar, K., Kotler, B.P., Mukherjee, S., 2011. Risk management in optimal foragers: the effect of sightlines and predator type on patch use, time allocation, and vigilance in gerbils. *Oikos* 120, 1657–1666. <http://dx.doi.org/10.1111/j.1600-0706.2011.19278.x>.
- Horncastle, V.J., Hellgren, E.C., Mayer, P.M., Ganguli, A.C., Engle, D.M., Leslie, D.M., 2005. Implications of invasion by *Juniperus virginiana* on small mammals in the southern great plains. *J. Mammal.* 86, 1144–1155. <http://dx.doi.org/10.1644/05-MAMM-A-015R1.1>.
- Idris, M., 2009. Eco-biodiversity of rodent fauna of the thar desert. In: *Faunal Ecology and Conservation of the Great Indian Desert*, pp. 157–175.
- Iribarren, C., Kotler, B.P., 2012. Patch use and vigilance behaviour by Nubian ibex: the role of the effectiveness of vigilance. *Evol. Ecol. Res.* 14, 223–234.
- Jadhav, R.N., Kimothi, M.M., Kandiya, A.K., 1993. Grassland mapping/monitoring of Banni, Kachchh (Gujarat) using remotely-sensed data. *Int. J. Rem. Sens.* 14, 3093–3103. <http://dx.doi.org/10.1080/01431169308904422>.
- Johnson, M.D., De Leon, Y.L., 2015. Effect of an invasive plant and moonlight on rodent foraging behavior in a coastal dune ecosystem. *PLoS One* 10. <http://dx.doi.org/10.1371/journal.pone.0117903>.
- Joshi, P.N., Kumar, V., Koladiya, M., Patel, Y.S., Karthik, T., 2009. Local perceptions of grassland change and priorities for conservation of natural resources of Banni, Gujarat, India. *Front. Biol. China* 4, 549–556.
- Juliana, J.R.St, Kotler, B.P., Wielebnowski, N., Cox, J.G., 2017. Stress as an adaptation I: stress hormones are correlated with optimal foraging behaviour of gerbils under the risk of predation. *Evol. Ecol. Res.* 18, 571–585.
- Kotler, B.P., Brown, J., Mukherjee, S., Berger-Tal, O., Bouskila, A., 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. *Proc. R. Soc. B Biol. Sci.* 277, 1469–1474. <http://dx.doi.org/10.1098/rspb.2009.2036>.
- Kotler, B.P., Brown, J.S., 1988. Environmental heterogeneity and coexistence of desert rodents. *Annu. Rev. Ecol. Systemat.* 19, 281–307. <http://dx.doi.org/10.1146/annurev.es.19.110188.001433>.
- Kotler, B.P., Brown, J.S., Bouskila, A., Mukherjee, S., Goldberg, T., 2004. Foraging games between gerbils and their Predators: seasonal changes in schedules of activity and apprehension. *Isr. J. Zool.* 50, 256–271.
- Kotler, B.P., Brown, J.S., Dall, S.R.X., Gresser, S., Ganey, D., Bouskila, A., 2002. Foraging games between gerbils and their predators: temporal dynamics of resource depletion and apprehension in gerbils. *Evol. Ecol. Res.* 4, 495–518.
- Kotler, B.P., Brown, J.S., Hasson, O., 1991. Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology* 72, 2249–2260.
- Kotler, B.P., Brown, J.S., Mitchell, W.A., 1993. Environmental factors affecting patch use in two species of gerbilline rodents. *J. Mammal.* 74, 614–620. <http://dx.doi.org/10.2307/1382281>.
- Kotler, B.P., Gaines, M.S., Danielson, B.J., 1988. The effects of vegetative cover on the community structure of prairie rodents. *Acta Theriol. (Warsz)* 33, 379–391.
- Kumar, S., Mathur, M., 2014. Impact of invasion by *Prosopis juliflora* on plant communities in arid grazing lands. *Trop. Ecol.* 55, 33–46.
- Lenth, R.V., 2016. Least-squares means: the R package lsmeans. *J. Stat. Software* 69, 1–33. <http://dx.doi.org/10.18637/jss.v069.i01>.
- Lima, S.L., 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48, 25–34. <http://dx.doi.org/10.2307/1313225>.
- MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598. <http://dx.doi.org/10.2307/1932254>.
- Matlack, R.S., Kaufman, D.W., Kaufman, G.A., 2008. Influence of woody vegetation on small mammals in tallgrass prairie. *Am. Midl. Nat.* 160, 7–19. [http://dx.doi.org/10.1674/0003-0031\(2008\)160\[7:JOWVOS\]2.0.CO;2](http://dx.doi.org/10.1674/0003-0031(2008)160[7:JOWVOS]2.0.CO;2).
- Mattos, K.J., Orrock, J.L., 2010. Behavioral consequences of plant invasion: an invasive plant alters rodent antipredator behavior. *Behav. Ecol.* 21, 556–561. <http://dx.doi.org/10.1093/beheco/arq020>.
- Pasha, S., Satish, K.V., Sudhakar Reddy, C., Prasada Rao, P., Jha, C.S., 2014. Satellite image based quantification of invasion and patch dynamics of mesquite (*Prosopis juliflora*) in Great Rann of Kachchh, Kachchh Biosphere Reserve, Gujarat, India. *J. Earth Syst. Sci.* 123, 1481–1490. <http://dx.doi.org/10.1007/s12040-014-0486-0>.
- Prakash, I., Rana, B.D., 1970. A study of field population of rodents in the Indian desert. *Z. Angew. Zool.* 57, 129–136.
- Prakash, I., Singh, P., Nameer, P.O., Ramesh, D., 2015. South asian muroids. In: *Mammals of South Asia*, vol. 2. pp. 574–642.
- Preisser, E.L., Bolnick, D.I., Benard, M.F., 2005. Scared to death? The effects of intimidation and consumption in predator-prey interactions. *Ecology* 86, 501–509. <http://dx.doi.org/10.1890/04-0719>.
- R Core Team, 2013. R Core Team. R a Lang. Environ. Stat. Comput. R Found. Stat. Comput. Vienna, Austria.
- Singh, P., Rahmani, A.R., Wangchuk, S., Mishra, C., Singh, K.D., Narain, P., Singh, K. a., Kumar, S., Rawat, G.S., Chundawat, R.S., 2006. Report of the Task Force on Grasslands and Deserts.
- Sirami, C., Seymour, C., Midgley, G., Barnard, P., 2009. The impact of shrub encroachment on savanna bird diversity from local to regional scale. *Divers. Distrib.* 15, 948–957. <http://dx.doi.org/10.1111/j.1472-4642.2009.00612.x>.
- Steenkamp, H.E., Chown, S.L., 1996. Influence of dense stands of an exotic tree, *Prosopis glandulosa* Benson, on a savanna dung beetle (Coleoptera: scarabaeinae) assemblage in southern Africa. *Biol. Conserv.* 78, 305–311. [http://dx.doi.org/10.1016/S0006-3207\(96\)00047-X](http://dx.doi.org/10.1016/S0006-3207(96)00047-X).
- Tiwari, J.W., 1999. Exotic weed *Prosopis juliflora* in Gujarat and Rajasthan, India - boon or bane? *Tigerpaper* 26, 21–25.
- Vaibhav, V., Imamdar, A.B., Bajaj, D.N., 2012. Above ground biomass and carbon stock estimation from *Prosopis juliflora* in Banni Grassland using satellite and ancillary data. In: *The 33rd Asian Conference on Remote Sensing, Thailand*, pp. 26.
- Vanak, A.T., Kulkarni, A., Gode, A., Krishnaswamy, J., 2015. Extent and status of semiarid savanna grasslands in peninsular India. In: Rawat, G.S., Adhikari, B.S. (Eds.), *Ecology and Management of Grassland Habitats in India*, pp. 192–201.
- Wheeler, H.C., Hik, D.S., 2014. Giving-up densities and foraging behaviour indicate possible effects of shrub encroachment on arctic ground squirrels. *Anim. Behav.* 95, 1–8. <http://dx.doi.org/10.1016/j.anbehav.2014.06.005>.
- White, R., Murray, S., Rohweder, M., 2000. Grassland Ecosystems. Pilot Analysis of Global ecosystems., World Resources Institute. World Resources Insititute <http://dx.doi.org/10.1021/es0032881>.
- Wigley, B.J., Hoffman, M.T., 2010. Thicket expansion in a South African savanna under divergent land use: local vs. global drivers? *Global Change Biol.* 3, 964–976. <http://dx.doi.org/10.1111/j.1365-2486.2009.02030.x>.