



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

Anisha Jayadevan^{a,b,*}, Shomen Mukherjee^{c,d}, Abi Tamim Vanak^{d,e,f}

^a Postgraduate Program in Wildlife Biology and Conservation, National Centre for Biological Sciences, Bengaluru 560065, India

^b Wildlife Conservation Society – India Program, Centre for Wildlife Studies, Bengaluru 560 070, India

^c Azim Premji University, Electronic City, Bengaluru 560100, India

^d Ashoka Trust for Research in Ecology, and the Environment, Bengaluru 560064, India

^e Wellcome Trust/DBT India Alliance Program, India

^f School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa

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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 1960s, 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,

* Corresponding author. Postgraduate Program in Wildlife Biology and Conservation, National Centre for Biological Sciences, Bengaluru 560065, India.
E-mail address: anishaj@ncbs.res.in (A. Jayadevan).

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 km².

P. juliflora was introduced to Gujarat in the 1890s to check desertification (Tiware, 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 km² 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 m² 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 smoothed 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,

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