Population and behavioural responses of rodents and reptiles to woody encroachment in the Thar desert

by

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Under the supervision of

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AcSIR

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DECLARATION

I hereby declare that the work conducted under the thesis entitled **"Population and behavioural responses of rodents and reptiles to woody encroachment in the Thar desert",** is a record of original and independent research work done by me and subsequently submitted for the award of the degree of **Master's in Wildlife Science** at the **Academy of Scientific and Innovative Research**. This research work has been carried out under the guidance and supervision of **Dr. Sutirtha Dutta**, **Scientist- E**, and co-supervision of **Mr. Varun Kher, Scientist-C** of Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma, or any other qualification. I also declare that the thesis embodies my own work, analysis, observation, understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by **Himani Pawar** entitled **"Population and behavioural responses of rodents and reptiles to woody encroachment in the Thar desert"** is an original and independent research work submitted to the **Academy of Scientific and Innovative Research**, for the award of the degree of **Master's in Wildlife Science**.

Himani Pawar has put one semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other University or Institute for the award of any degree, diploma or distinction.

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Himani Pawar

July, 2026

EXECUTIVE SUMMARY

Woody encroachment is increasingly modifying open ecosystems worldwide, often altering trophic-level interactions and species composition. In the Indian Thar Desert, *Calotropis procera* is rapidly expanding across grassland and scrubland habitats, but its ecological consequences for desert fauna remain poorly understood. This study assessed the effects of varying levels of *Calotropis procera* encroachment on habitat structure, predation pressure, and behaviour and abundance of nocturnal rodents and two diurnal lizard species in and around Desert National Park, Jaisalmer.

Field surveys were conducted across no, moderate, and high encroachment levels of *C. procera* during 2025–2026. Responses of nocturnal rodent community were assessed through burrow counts and giving-up density (GUD) experiment. Reptile responses were assessed through abundance surveys and flight-initiation distance (FID) experiment, and clay model experiment was designed to quantify predation pressure.

Rodent abundance, measured through active burrow counts, declined from no encroachment plots to moderate and high encroachment levels. Conversely, giving-up density at artificial food patches was greater in no encroached plots - indicative of greater predation risk perception - compared to moderately and highly encroached habitats. Lunar illumination interacted with encroachment level to influence rodent foraging decisions, indicating the role of habitat structure and environmental conditions in shaping behavioural responses to predation risk.

Reptile species exhibited contrasting responses to woody encroachment. *Acanthodactylus cantoris* showed declines in abundance with increasing encroachment. Behavioural response mirrored this pattern. Flight-initiation distance of *Acanthodactylus cantoris* decreased

substantially with increasing encroachment. In contrast, *Trapelus agilis* occurred at higher densities in highly encroached areas than non-encroached areas and its FID was primarily influenced by refuge availability and starting distance rather than encroachment level.

Predation-risk experiment revealed context-dependent effects of encroachment. In scrubland habitat, predation was faster in moderate and high encroachment plots than in no encroachment. Habitat influenced predation pressure too, as clay models faced higher predation rate in grassland than scrubland.

This study demonstrates that woody encroachment produces species-specific ecological consequences, and continued expansion of *Calotropis procera* has the potential to reshape community composition through behavioural responses and trophic interactions, in the Thar Desert. Management interventions aimed at maintaining and preserving open habitats may therefore be important for conserving faunal diversity in this important conservation ecosystem.

1. INTRODUCTION

Woody plant encroachment is a global phenomenon observed across savannas, grasslands, and arid regions, driven by a combination of climate, and land-use related factors. Increases in atmospheric CO_2, shifts in rainfall regimes, and changes in grazing pressure have been shown to favour woody growth over herbaceous vegetation, gradually transforming open systems into shrub- or tree- dominated landscapes (Belay et al., 2013; Archer et al., 2017; Ding & Eldridge, 2024).

Such structural transformation has far-reaching ecological implications, influencing both bottom-up and top-down processes. At the bottom-up level, increased woody cover alters the quantity and quality of native vegetation, affecting food availability for small vertebrates (Smit & Prins, 2015). At the top-down level, encroachment modifies predator-prey interactions by changing visibility and refuge structure, thereby affecting perceived predation risk and behavioural responses (Loggins et al., 2019). These interacting effects influence individual fitness, local population abundance, and can shift species composition, and trophic relationships within ecosystems, including changes in predation success of aerial and terrestrial predators (Atkinson et al., 2022).

The Thar Desert harbours one of India's largest Open Natural Ecosystems (ONEs), but in recent decades, it has been facing multiple threats, including a rapid increase in woody cover, especially from *Calotropis procera*. The process of woody encroachment has been studied, though only sparsely, in semi-arid grasslands and savanna ecosystems. There remains a significant gap in understanding its effects in arid regions, particularly on sand dunes / plains. Previous studies have reported contrasting results, suggesting that different ecosystems respond

differently to woody encroachment (Stanton et al., 2018). Largely underexplored and often overlooked, this ongoing process highlights an urgent need to investigate its impacts on arid-zone fauna.

Calotropis procera is a woody shrub, native of Israel and is widely distributed in disturbed habitats in India (Saxena and Singh, 1976). It has proliferated naturally, spreading rapidly along such habitats due to its drought tolerance and efficient seed dispersal (Singh et al., 2020). Assessing its impacts on fauna is essential, as changes in vegetation structure can directly alter resource availability, shelter, and perceived predation risk for small vertebrates. Rodents and reptiles, which occupy key trophic positions as prey for numerous aerial and terrestrial predators and exhibit strong habitat associations, serve as suitable bioindicators for detecting such responses. The focal rodent species, *Gerbillus gleadowi, Gerbillus nanus and Tatera indica* form a widespread nocturnal rodent community adapted to sandy substrates, making them ideal for assessing population and behavioural variation across encroachment gradients. The selected reptile species, *Trapelus agilis* and *Acanthodactylus cantoris*, represent different microhabitat preferences, offering a comparative framework to study behavioural and abundance responses to changing habitat structures. Together, these focal taxa and questions align with the broader aim of quantifying faunal responses to ongoing vegetation transformation within one of India's largest, fragile arid ecosystems that is also an important ecological and conservation region of India, supporting the last viable population of the Critically Endangered Great Indian Bustard and habitats for many resident and migratory raptors.

1.1 Literature Review

1.1.1 International status

Many open ecosystems of the world have ancient origins and are typically maintained by disturbance regimes such as fire and grazing. These open formations include some of the planet's most biodiverse regions, and under appropriate disturbance regimes such as fire and regulated grazing, represent stable alternatives to closed-canopy forests (Bond, 2021). They now face multiple threats, including agricultural expansion, renewable energy development, afforestation for carbon sequestration projects, and widespread woody plant encroachment driven by altered rainfall patterns, rising atmospheric CO_2 concentrations, and land-use changes such as grazing intensification. Long-term trends towards greening of formerly open areas have been documented globally (Van Auken, 2009; Archer et al., 2017; Stevens et al., 2017). Early descriptive reports of woody expansion date back to the early twentieth century (e.g., Cook, 1908; Gleason, 1913), and by the mid-twentieth century researchers had already identified interacting drivers such as altered grazing regimes, fire suppression, and climate change (Brown, 1950; Humphrey, 1958). Since the 1990s, the field has increasingly focused on global syntheses and quantitative analyses that explicitly link woody encroachment to ecosystem processes and biodiversity change.

The effects of woody encroachment on animal communities are now among the fastest-growing areas of ecological research, and several consistent patterns have emerged despite important knowledge gaps. Experimental removal and before-after-control-impact (BACI) studies demonstrate that small mammal assemblages can respond rapidly to tree removal. Diversity, evenness, and community composition often shift towards grassland-associated assemblages within one to two years, although the extent of recovery depends on pre-treatment

woody cover and weather conditions (Alford et al., 2012). Gradient and space-for-time studies show that increases in woody cover are commonly accompanied by substantial declines in grass biomass and complete reorganization of herbivore communities, with meso-grazers tending to decline while browsers increase. Total herbivore biomass may nevertheless remain relatively stable through functional compensation (Smit & Prins, 2015).

Meta-analyses and global reviews indicate that vertebrate responses are highly taxon- and context-dependent. Mammals and herpetofauna are often most vulnerable in low-productivity systems, whereas birds show mixed responses, with many shrub-associated species expanding locally even as grassland specialists decline regionally (Stanton et al., 2018; Eldridge et al., 2011; Furtado et al., 2021). Several studies have explicitly quantified resource availability, including herbaceous biomass, Enhanced Vegetation Index (EVI), and ground cover, and linked these measures to faunal responses (Smit & Prins, 2015; Alford et al., 2012; Sepp et al., 2021).

Comparatively, reptiles and other ectotherms have received substantially less attention. The available literature suggests species-specific responses, with many open-habitat lizard species declining as shrub cover increases, while some shade-tolerant taxa become more abundant, indicating community reassembly rather than uniform declines (Meik et al., 2002; Eldridge et al., 2011). Shrub hummocks and woody patches frequently function as resource islands and centres of activity for soil-modifying fauna such as ants, scorpions, burrowing reptiles, and small mammals. Consequently, shrub removal can immediately reduce habitat availability for these taxa (Daryanto & Eldridge, 2012). Studies quantifying visual obstruction using methods such as Robel poles, Nudds boards, and Visual Obstruction Readings are common in avian ecology and nest-predation research and have been used to identify thresholds of woody cover beyond which grassland specialist distributions contract (Andersen & Steidl, 2019).

Fewer mammal studies have combined structural habitat metrics with behavioural indicators of predation risk, such as giving-up densities (GUDs) and activity measures. Existing evidence suggests that shrub cover often reduces perceived predation risk and alters rodent activity and foraging behaviour (Loggins et al., 2019; Wheeler et al., 2014). At the level of large predators, a small but growing body of literature demonstrates species-specific hunting outcomes across woody-cover gradients. Cursorial predators such as cheetahs may be disadvantaged by increasing woody cover, whereas ambush predators such as leopards and snakes may benefit from intermediate levels of vegetation cover (Atkinson et al., 2022). Overall, while many studies have quantified resource availability and structural habitat change, and a growing number have incorporated behavioural proxies of predation, few integrated multi-trophic investigations simultaneously measure visual obstruction, resource availability, and direct predation rates. This gap is particularly pronounced for reptiles.

1.1.2 National Status

Woody encroachment is increasingly recognised as a major threat to India's open natural ecosystems, including the semi-arid grasslands of Gujarat, the Thar Desert, and other open habitats. Much of this encroachment is driven by invasive woody species such as *Prosopis juliflora*. Studies in the Banni grasslands of Gujarat have shown that *Prosopis* invasion alters nocturnal rodent community composition and foraging behaviour, with shrub-adapted and generalist species increasing in abundance while open-habitat specialists decline (Jayadevan, Mukherjee & Vanak, 2018; Misher et al., 2022). *Prosopis* invasion also affects habitat use by the Indian desert fox (*Vulpes vulpes pusilla*), which has been found to prefer more open *Suaeda*-dominated saline habitats over dense *Prosopis juliflora* stands.

Classic ecological studies from the Thar Desert on species such as *Meriones hurrianae* and *Tatera indica* highlight the strong affinity of historically dominant rodent species for open habitats (Prakash, 1975). However, there is a lack of recent long-term monitoring to evaluate how ongoing woody encroachment is reshaping these communities. Reptiles remain particularly understudied in this context within India. The Thar Desert, one of the largest remaining contiguous open natural ecosystems in the country, has received limited attention with respect to the ecological consequences of woody encroachment. Addressing these knowledge gaps is increasingly important given the rapid land-cover changes occurring across the landscape in recent decades.

1.2 Fear ecology of small prey

Prey-predator interactions are one of the most widely studied topics in ecology. While predator-prey interactions were traditionally viewed through the lens of direct consumptive effects, predators also exert important non-consumptive effects by changing prey behaviour and decision-making. Prey species frequently modify vigilance, activity, movement, and foraging behaviour in response to perceived predation risk. These behavioural responses can influence energy acquisition, reproduction, and habitat selection, forming the basis of the "ecology of fear" hypothesis (Brown et al., 1999; Clinchy et al., 2013).

The ecology of fear framework emerged from behavioural ecology and Optimal Foraging Theory (OFT), which proposes that animals maximize energetic gain while minimizing costs associated with obtaining food, including exposure to predators (Pyke et al., 1977; Stephens & Krebs, 1986). Predation risk therefore acts as an important ecological cost influencing patch-use decisions. Prey may avoid profitable food patches if they are associated with elevated danger.

The integration of predation risk into foraging theory was further strengthened through the Marginal Value Theorem, which predicts that a forager should leave a patch when energetic gain declines below the environmental average. However, prey often abandon food patches earlier than predicted because continued foraging increases exposure to predators. Brown (1988, 1999) argued that patch departure decisions reflect energetic costs, missed opportunity costs, and predation risk, making patch use an indirect measure of perceived danger. These ideas contributed to the development of the "landscape of fear" concept, which describes how prey perceive spatial variation in predation risk across heterogeneous habitats (Laundré et al., 2001). Prey species modify movement, refuge use, and foraging activity according to perceived risk gradients rather than predator presence alone (Gaynor et al., 2019).

Habitat structure strongly influences risk perception by altering visibility, refuge availability, and predator detection. Open habitats may increase exposure to predators, whereas dense vegetation may provide concealment while simultaneously limiting visibility. Consequently, prey responses to habitat structure are often context dependent and nonlinear. Studies have shown that prey frequently concentrate activity near cover and reduce foraging in exposed habitats, highlighting the importance of structural complexity in shaping antipredator behaviour (Chalfoun & Martin, 2009).

These trade-offs are particularly relevant in ecosystems undergoing woody encroachment. Increasing shrub cover alters vegetation structure, movement pathways, visibility, and refuge availability, potentially modifying predator-prey interactions. Moderate encroachment may reduce perceived risk by increasing concealment opportunities, whereas excessive encroachment may restrict movement or reduce visibility. Structural variation may therefore influence prey behaviour through both resource distribution and altered perception of danger.

Temporal variation in predation risk may further shape behavioural responses. Optimal Risk Allocation Theory proposes that prey allocate antipredator behaviour according to both the intensity and duration of risk exposure (Lima & Bednekoff, 1999). When predation risk fluctuates, prey is expected to reduce foraging during risky periods while allocating safer periods toward feeding. In contrast, under chronically elevated risk, prey may continue to forage despite danger because prolonged avoidance imposes energetic costs and increases starvation risk. The interaction between foraging decisions and predation risk has frequently been quantified using Giving-Up Density (GUD) experiments. GUD refers to the amount of food remaining in an artificial food patch after a forager stops feeding. According to Brown's patch-use framework, prey abandon patches when the benefits of continued foraging no longer outweigh cumulative costs associated with metabolism, missed opportunities, and predation risk. Higher GUD values are therefore interpreted as indicators of increased perceived danger or reduced patch profitability (Brown, 1988; Bedoya-Pérez et al., 2013).

Together, these frameworks suggest that prey behaviour is shaped by interactions between energetic requirements, habitat structure, refuge availability, and perceived predation risk. Structural variation associated with woody encroachment may therefore influence prey activity, refuge use, and patch exploitation through fear-mediated behavioural mechanisms.

1.3 Importance of the Project in the Context of Current Status

Rodents and reptiles are key components of the trophic communities of open ecosystems and can serve as effective bioindicators of habitat change (Shacham et al., 2023). Their sensitivity to alterations in vegetation structure, including increasing shrub density, declining grass cover, and reduced visual openness, makes them particularly suitable for detecting ecological impacts

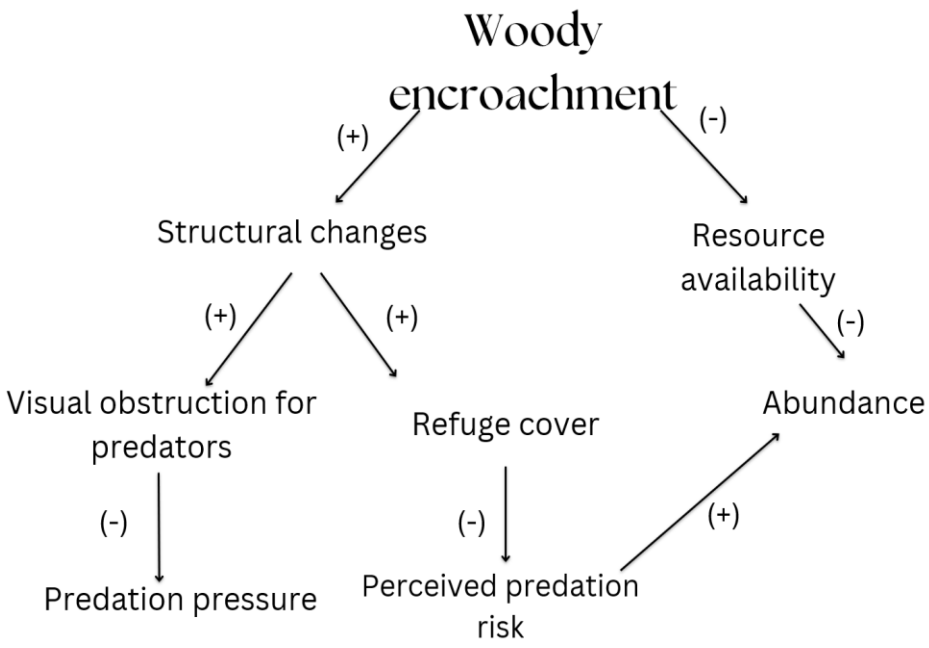
of woody encroachment before such effects become evident in larger vertebrates. Open landscapes in India, particularly the Banni grasslands of Gujarat and the Thar Desert of Rajasthan, are experiencing rapid expansion of shrubs such as *Prosopis juliflora* and *Calotropis procera*, potentially driven by changing precipitation regimes and livestock grazing. Singh et al. (2013) reported a progressive shift through personal observation in mammalian community composition following canal irrigation, with desert-adapted taxa such as *Gerbillus* becoming less prominent and mesic taxa such as *Bandicota* and *Mus* appearing several decades after irrigation. While rodent responses to shrub encroachment in Banni have been documented, revealing shifts in community composition and behaviour under increasing woody cover (Jayadevan et al., 2018), comparable studies on reptiles remain extremely limited. This highlights the need for empirical investigations examining the effects of encroachment on reptile communities in Indian open ecosystems.

Studies from Africa, Australia, and the Americas have demonstrated that shrub encroachment can alter predator-prey interactions, modify activity patterns, and reduce populations of open-habitat specialists (Meik et al., 2002; Eldridge et al., 2011; White et al., 2024). However, no study in India has explicitly quantified structural habitat variables such as visual obstruction and shrub architecture in relation to reptile and rodent responses. By measuring these attributes alongside faunal abundance and behavioural indicators, the present study will provide the first integrated assessment of how woody encroachment changes refuge conditions and perceived predation risk for small vertebrates in Indian sandy habitats. Given that open natural ecosystems are among the most threatened and least studied biomes in the country, the findings are expected to provide an important scientific basis for habitat management, invasive shrub control, and ecological restoration planning.

1.4 Study objectives

1.4.1 Aim

The overarching aim of this study was to examine the ecological consequences of woody encroachment in the Thar Desert. Specifically, the study investigated how increased visual obstruction associated with woody vegetation alters predation pressure by influencing predator detection and prey vigilance. It further assessed how the combined effects of visual obstruction and refuge cover shape perceived predation risk and influence the abundance of two key prey groups, rodents and reptiles. Below is the hypothesised mechanism of how woody encroachment can influence prey species:



1.4.2 Objectives and Research questions

1. **To compare visual obstruction and predation pressure across different levels of woody encroachment**
    a. How does visual obstruction vary across different levels of *Calotropis procera* encroachment?
    b. How does predation pressure differ across woody encroachment levels and habitats (grassland vs scrubland)?
2. **To assess the numerical responses of rodent and reptile to woody encroachment**
    a. How does number of rodent burrows change with woody encroachment?
    b. How does abundance of *Trapelus agilis* and *Acanthodactylus cantoris* change with woody encroachment?
3. **To assess the behavioural responses of rodents and reptiles to woody encroachment**
    a. How does Giving-up density of nocturnal rodents change with woody encroachment and other environmental variables?
    b. How does flight-initiation distance and escape tactics of *Trapelus agilis* and *Acanthodactylus cantoris* change with increasing woody encroachment and other environmental variables?

1.4.3 Hypothesis and predictions

Table 1: Hypothesis and predictions of the study in Thar desert (2025-2026)

S. No.	Hypothesis	Prediction
1.	Woody encroachment will negatively influence the visual coverage of predators, thus reducing detectability of prey species by predators.	Robel pole reading, proxy of horizontal visual obstruction (quantified by proportion of no. of bands covered by vegetation / no. of total bands) will increase with increase in encroachment levels. Percentage shrub cover will follow the same trend. Predation on the clay models (quantified by proportion of clay models with predation marks / removed) will reduce with increase in woody encroachment.
2.	Woody encroachment will affect the abundance of rodents and reptiles by two contrasting mechanisms, i.e., an increase in refuge cover and a decrease in resource availability.	Rodent and reptile abundance will reduce from non-encroached to encroached plots.
3.	Woody encroachment will negatively influence the perceived predation risk of rodents and reptiles due to increased refuge cover (Microhabitat selection hypothesis).	Giving-up density for rodents will decrease with increase in woody encroachment (Loggins et al., 2019). The flight-initiation distance will also decrease with increase in woody encroachment. This will signify

		lower perceived predation risk in high levels of encroachment.

2. METHODOLOGY

2.1 Study area

The study was conducted in the Thar landscape, specifically in and around Desert National Park (DNP) - actually a Wildlife Sanctuary, Rajasthan during December 2025 to May 2026.

The area falls in the Desert Biogeographic Zone, characterised by low erratic rainfall (100-450 mm annually with frequent droughts) and extreme temperatures with large diurnal ranges (Rao et al. 2012). The DNP is 3162 sq.km in area with 88 settlements. Lands are either agricultural, used for rainfed farming of (mostly) Guar (*Cyamopsis tetragonoloba*) in good rainfall years and left fallow to regenerate during dry months, or pastoral, used for free-range livestock grazing by goats, sheep, cows and camels, and often excessively grazed.

This landscape encompasses a mosaic of habitat types ranging from open grasslands to semi-stabilized and active sand dunes. The region has high vertebrate biodiversity, comprising 21 mammals such as the Chinkara (*Gazella bennetti*), Desert Cat (*Felis sylvestris*) and Desert Fox (*Vulpes vulpes pusilla*), 51 reptile species, and around 329 bird species, including many migrants of the Central Asian Flyway and threatened raptors. The diversity of small mammals and reptiles in this arid ecosystem is high. About 18 lizard species (Gaur, Kumar, & Rathore, 2013), along with approximately 18 rodent species (Idris, 2008*)* have been recorded in the Thar landscape. Both reptiles and rodents inhabiting this landscape are highly specialized, exhibiting unique adaptations to extreme arid conditions.

However, DNP and the surrounding Thar landscape face multiple, interacting threats that make it essential to study the impacts of woody encroachment. The construction of the Indira Gandhi Nahar/Canal (IGNP) has dramatically altered the hydrology of the region, "greening" parts of the desert, allowing mesic species to establish, and subtly shifting grazing regimes, all of which encourage shrubs and trees to invade formerly open dune and grassland habitats. Moreover, intensive and often unmanaged livestock grazing across large areas reduces herbaceous cover and promotes soil erosion, creating ideal conditions for woody invaders such as *Prosopis juliflora* and *C. procera.* Compounding these ecological drivers are anthropogenic pressures such as road and pipeline infrastructure, fencing, power lines (which pose mortality risks), free-ranging dogs and pigs, mining, and expanding human settlements, all of which fragment habitat and exacerbate the ecological impacts of encroachment.

As one of India's last relatively intact arid open ecosystems, this region naturally encompasses a gradient of woody cover, from completely open sandy areas to nearly treeless grass-shrub mosaics and even dense *Calotropis* thickets on sandy plains, providing a suitable gradient for detecting faunal responses. Parts of western Thar desert in Jaisalmer district have experienced rapid woody encroachment over the last decade. Subtle shifts in shrub density here can have outsized effects on microhabitats, thermoregulatory space, visibility, and resource distribution. Many open-habitat species, including *Saara hardwickii*, gerbils, and desert carnivores, are dependent on the park's sandy substrate, open foraging grounds, and unobstructed views.

Study species

The nocturnal rodent community of the Thar Desert is dominated primarily by gerbils belonging to the family Muridae. Common species reported from the region include the Indian

desert gerbil (*Meriones hurrianae*), Indian gerbil (*Tatera indica*), hairy-footed gerbil (*Gerbillus gleadowi*), soft-furred field rat (*Millardia meltada*), and lesser bandicoot rat (*Bandicota bengalensis*) (Prakash, 1996; Idris, 2008). These rodents exhibit several adaptations to arid environments, including nocturnal activity, extensive burrow systems, efficient water conservation, and granivorous or omnivorous feeding habits. Species such as *Gerbillus gleadowi* and *Gerbillus nanus* are strongly associated with sandy habitats and sparse vegetation, where they play important ecological roles in seed dispersal, soil turnover, and nutrient cycling. The Indian desert gerbil commonly constructs multi-entrance burrows beneath shrubs and feeds on seeds, roots, grasses, and insects, while *Gerbillus gleadowi*, *Gerbillus nanus* and *Tatera indica* are more solitary and construct simpler burrows (2-4 entrances) (Prakash, 1996).

Vegetation structure is considered an important determinant of habitat use among both nocturnal rodents and reptiles in the Thar Desert. Burrows are frequently constructed beneath shrubs such as *Capparis decidua*, *Ziziphus nummularia*, *Leptadenia pyrotechnica*, and *Calligonum polygonoides*, where vegetation cover may provide shade, reduced thermal stress, and protection from predators.

Reptilian species of the Thar Desert similarly exhibit clear associations with particular vegetation types and substrate conditions. *Acanthodactylus cantoris* is typically associated with open sandy habitats, interdunal plains, and sparsely vegetated dunes where loose substrate facilitates rapid locomotion and active foraging behaviour. The species is commonly observed in areas with scattered grasses and low scrub vegetation that support high arthropod abundance. *Trapelus agilis* occurs in sandy and rocky habitats with xerophytic shrub cover and preferentially use vegetation such as *Capparis decidua* and *Salvadora oleoides* as refuge sites,

particularly for burrow construction and shelter (Bhatnagar et al., 2012). Such vegetation may provide thermal buffering, concealment from predators, and structurally suitable microhabitats. Overall, the distribution and activity of desert reptiles appear closely linked to vegetation openness, shrub architecture, and substrate heterogeneity within the Thar landscape.

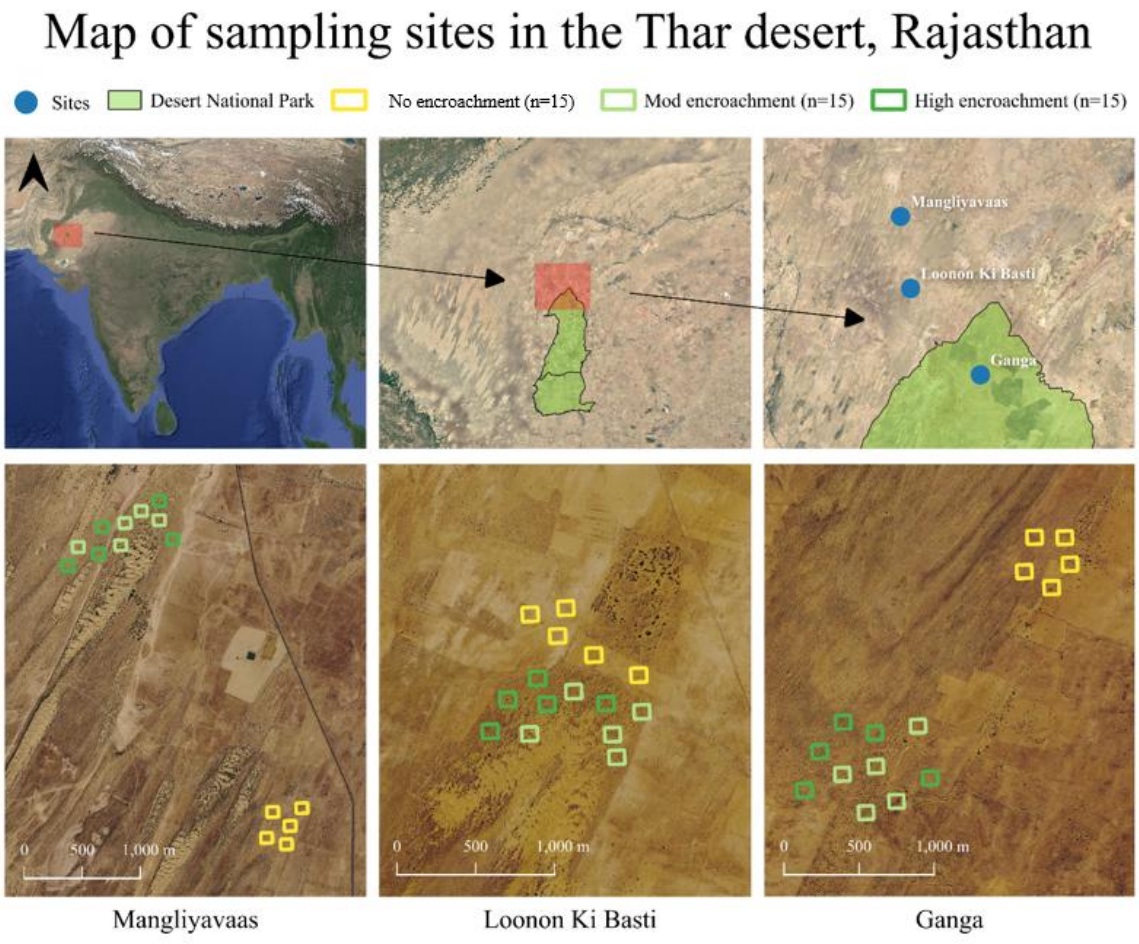


Figure 1: Location and distribution of sampling sites across the Thar Desert, Rajasthan, India, showing no, moderate, and high woody encroachment plots across the three study: Mangliyavaas, Loonon Ki Basti, and Ganga during 2025-2026

2.2 Site selection

Reconnaissance surveys were conducted during the initial one and a half months of the study period, from early December to mid-January, for site selection. Preliminary sites were identified beyond a minimum distance of 200 m from roads and 500 m villages to remove anthropogenic effects on distribution and behaviour of the study taxa. For paired treatment plots, at least a few hectares of coverage of varying levels of encroachment were identified. Calotropis encroachment was categorised ocularly during reconnaissance into no, moderate and high levels. Presence-absence of nocturnal rodents was assessed through preliminary installation of GUD trays and camera traps positioned at each tray.

Based on the reconnaissance, three sites were selected – all in sandy plains – but along a reasonably large linear stretch of ~19 km to ensure larger representativeness. Each site had varying levels of woody encroachment within a radius of 3 km from its center, such that predator density, anthropogenic disturbances and other ecological factors were similar among encroachment levels within a site but can be different between sites. Five plots were sampled per encroachment level that were either spatially aggregated or dispersed depending on habitat availability. Distance from roads was maintained at a minimum of 200 m, while distance from villages was maintained at a minimum of 500 m. Distance between plots ranged from 100 to 3000 m, while distance between sites ranged from 6.1 to 18.8 km.

For giving-up density (GUD) experimentation, one plot was selected per encroachment level at each site (n = 9). Each selected plot contained four identified active burrows of nocturnal rodents determined based on signs on baited peanut trays, deployed from late evening to early morning.

For nocturnal rodent burrow counts, three plots per encroachment level within each site were sampled (n = 27). Of these, two plots were selected randomly prior to obtaining information on rodent activity through preliminary camera trapping, while the third plot corresponded to the plot selected for GUD experimentation.

For reptile count and flight-initiation distance (FID) sampling, the three plots selected for burrow counts within each encroachment level were retained along with two additional plots, resulting in a total of 45 plots, for adequate samples, as reptile activity was relatively less compared to rodents.

Clay model experimentation for quantification of predation pressure was conducted across four sites. Two sites from the primary sampling sites - Ganga and Loonon ki Basti - were selected in scrubland habitat, while two additional sites, Ibrahim Ki Talai and Sudasari EF, were selected in grassland habitat. Within each site, three encroachment levels were identified with distances ranging from 150 to 1500 m apart. In each encroachment level, two transects were laid out approximately 50 m apart.

2.3 Field methods

1. Obstruction

To validate if sampling plots across different encroachment levels varied in terms of obstruction experienced by predators, visibility obstruction due to vegetation obscurement was quantified along vertical and horizontal fields. Horizontal obstruction was measured using Robel pole technique as the proportion of ten 10 cm bands on a 1m pole that was not visible from a distance of 10 m at the eye level of the observer at 1.7 m height (Robel et al., 1970; Frost & Powell, 2011). Whilst, vertical obstruction was characterized in terms of percentages

of shrub cover, *Calotropis* cover, grass cover, litter cover and bare ground cover in a 10 m radius circular plot that would cumulatively affect visibility of an aerial predator (Tempel & Tietje, 2006). These measurements were recorded at five plots per encroachment level at each site. At each plot, five readings were taken - at all corners and the centre of the plot, always from the north to the observer.

2. Clay model experiment

To understand how predation pressure on lizards varies with woody encroachment, clay models of *Trapelus agilis* were developed and deployed at four sites (Bateman, Fleming, & Wolfe, 2017). Two of the four sites were grasslands and the other two were scrubland sandy plains. To construct clay models, a mould was constructed out of silicon in the shape of *Trapelus agilis*. The body measurement was obtained from literature (Snout-to-vent length ~79cm, Tail length ~ 125 cm) (Shahamat et al., 2019) and the species' images were referred to for its body shape. The same mould was used to make 204 plasticine clay models (JOVI plastilina clay) to prevent variation in body shape and size (Yeager, Wooten, & Summers, 2011). Each clay model was painted with a base sandy-colour, and patterns of longitudinal and latitudinal streaks on the body using brown paint. The shade and type of colours were estimated ocularly from pictures of the species and copied in the absence of a spectrometer (Husak et al., 2006). Few test runs were done from January to February to understand if predators were detecting clay models. During these test runs, plastic lizards were placed in front of areas frequently visited by short-toed snake eagles, falcons or tawny eagles. Cameras were placed at each clay model. However, the plastic lizards were only visited by Desert fox and Bengal fox. The clay model study was conducted from the first week of March to the end of April. At each site, clay models were placed along two transects per encroachment level that 50 m away from each other, resulting

in 17 clay models per encroachment level and 51 clay models per site. Each clay model was placed at a distance of 20 m away from each other. They were placed in open ground or various types of refuges, approximately proportional to how they were detected during VES, within 1m width of the transect. A camera trap was placed at every 4th clay model, that is on 1st, 5th, 9th and 13th to identify the species that visited the clay models, and to quantify the time to predation at each model (Perry, 2018). The clay models were placed at 5:00 pm and the experiment was stopped after 72 hrs. Clay models were visited in grassland sites at 48 hrs and 72 hrs and in scrubland sites at 13 hrs, 24 hrs, 37 hrs, 48 hrs, 61 hrs and 72 hrs. Time to predation was obtained at fine scale using camera traps for grassland sites and at both fine using camera traps and coarse scale through visitations in mornings and evenings for scrubland sites.

Figure 2: Trapelus agilis in the wild (left) and clay model (right)

3. Numerical responses of rodents and reptiles

3.1 Numerical response of rodents

To understand if woody encroachment influences rodent numbers, burrow count was conducted in three plots per encroachment level per site, for 25 days in February 2026 (Cavia,

Cueto, & Suárez, 2012). Sampling was done using time-constrained space-constrained burrow search. The observer would walk a parallel belt transect of 100m length and 2m width, then take a perpendicular turn of 20 m, after which another transect was traversed, in a zig-zag fashion. Burrow counts were done from 9:30 to 11:30 am, after GUD experimentation, to ensure maximum retention of footprints of nocturnal rodents before the wind action obscured these signs through the day. Sampling was not done on very windy days. Every plot was sampled only once, and sampling was interspersed across encroachment levels and sites, such that every day a different encroachment level and site was selected randomly (without replacement), for sampling.

Identification of burrows:

Four species were targeted for burrow identification, as these are the most abundant rodent species found in sandy plains of Thar - *Gerbillus gleadowi, Gerbillus nanus, Tatera indica and Merroines hurrianae*. Of these, the latter (Indian Desert Jird or IDJ) is a diurnal rodent, which is not a focal species of this study, and lives in extensive multiple entrance burrow systems, ranging from 4-30 opening (Goyal & Ghosh, 1993). Hence, a radius of 5 m was taken from the centrality of the burrow system and no burrow entrance within this buffer around IDJ colonies was considered. Remaining rodent burrows were classified as putative nocturnal rodent burrows when fresh nocturnal rodent tracks were present and burrow architecture was consistent with solitary gerbil (*Gerbillus sp.)* or Indian gerbil (*Tatera indica*) burrows. Burrow classification was based on a combination of entrance diameter, number and clustering of openings, associated tracks, and evidence of recent activity. Species-level assignment was not attempted due to overlap in external burrow characteristics. Since plots were sandy plains, sand was used as a natural medium to detect tracks and counts of active vs inactive burrows were

recorded for each plot. The high wind speed in the study area ensured that inactive burrows with old footprints were not misidentified as active burrows.

Table 2: Burrow characteristics used for identification of nocturnal vs diurnal rodents in Thar during 2025 (Prakash I., 1981; Goyal & Ghosh, 1993) (ref Appendix 10 &11)

Species	**No. of entrances**	**Excavation marks**	**Size of burrow opening**
Indian Desert Jird (*Meriones hurrianae*)	Usually, 3-10 or more interconnected entrances	Prominent fresh soil mounds around active entrances	Large (5-8 cm diameter)
Indian Gerbil (*Tatera indica*)	Usually, 1-3 Y shaped entrances	Distinct fan-shaped soil heap near entrance	Medium to large (4-7 cm diameter)
Gerbillus spp. (*Gerbillus gleadowi* and *Gerbillus nanus*)	Usually, 1-2 entrances	Little or no conspicuous soil accumulation	Small (2-4 cm diameter)

3.2 Numerical response of reptiles

Two species of diurnal reptiles, native to Thar, were used as focal species of this study- Indian fringe-fingered lizard (*Acanthodactylus cantoris*) and brilliant ground agama (*Trapelus agilis*).

Five plots were sampled per encroachment level per site (n = 45 plots). In each plot, five belt transects of 100 m length and 2m width on either side of the observer, were laid 20 m from the next transect - to minimise double counting. Space and time constrained single-observer visual encounter surveys (VES) were used to count reptiles (Crump & Scott, 1994; Campbell & Christman, 1982). The transects were traversed in the same fashion as the burrow count transects. Whenever any lizard was encountered, the species identity would be recorded, where from the species' counts in the plot were computed.

3.3 Detection probability of reptiles in three levels of encroachment

Detectability of reptiles during VES can be biased by perception and availability biases. To correct for perception bias in count data caused by encroachment-induced visibility obstruction, detection probability was estimated for each encroachment level using the double observer method (Nichols et al., 2000) in a subset of the plots used for the count study. Two out of five plots per encroachment level were sampled using dependent double observer space and time- constrained VES. Two observers walked along the same transect paths from earlier study, 2 m away from each other, in a single file. The primary observer would inform the secondary observer of all detections by pointing out the location of the individual. The secondary observer would additionally record detections/ individuals missed by the primary observer.

4. Behavioural responses of rodents and reptiles

4.1 Camera trapping artificial resourced patches for nocturnal rodents

Forty artificial resource patches - in the form of GUD trays - were installed across the month of December, placed randomly in various plots, irrespective of burrow entrances, to determine

activity patterns of nocturnal rodents and understand their interaction with these resource patches (Loggins et al., 2019). GUD trays contained crushed peanut seeds and sand as substrate and were camera trapped. The trays were placed at an angle such that the interior was visible in camera view-frame. Ten spatially independent trays at various locations were visited by nocturnal rodents. Camera traps were set at a time lapse of one minute with five motion triggered captures. The artificial patches were installed at 4:00 pm and removed at 8:00 am next day, to understand the time activity of nocturnal rodents for GUD determining the duration of GUD experiments.

4.2 Giving-up density for rodents

To understand how predator risk perception varies with woody encroachment for nocturnal rodents, Giving-up Density experiments were conducted in winter - from mid-January to the first week of March (Brown et al., 1988). At each encroachment level, a plot of 1 hectare area was sampled using four trays, placed at 30-40 m distance from each other, to reduce spatial dependence (Prakash and Rana, 1970). Each tray was placed 2m from and facing an identified active rodent burrow, along runways (identified from repeated monitoring of footprints from the burrows). After the first day, the trays were shifted 1 m away radially, keeping the burrow as a central point such that the distance from it is always 2 m. This was done to minimise the familiarity of resource patch, which might reduce the overall cost of foraging. Each plastic tray was 400 (length) x 300 (width) x 100 mm (depth) in dimensions and was filled with 3 liter of sand and 4g of peanut seeds. Each peanut seed was broken by hand meticulously to 1/4th of size, so that they were almost of the same size, to minimise variation in handling time across trials. GUD trials were conducted simultaneously at 12 trays covering three plots and three encroachment levels at each site. At each site, data was not collected for the initial two days -

to minimise novelty of trays for nocturnal rodents - and was collected for the next five days (Bedoya-Perez et al., 2013). Further, GUD trials were repeated in two sessions, under low (<50%) and high (≥50 %) lunar illumination. Standard effort of 10 days was deployed at all sites, except for one site, where consistent thievery of GUD trays during high illumination forced the sampling to be curtailed after 7 days. During reconnaissance and test runs, it was found that rodent activity was restricted between 7:20 pm and 5:54 am (n=10). Hence, trays were activated between 5:30 - 6:30 am and removed early next morning between 6:30-7:45 am.

Confirmation that the animal visiting the GUD tray was a nocturnal rodent, was done by flattening the sand tracks around the GUD trays. Moreover, the visited trays showed distinct signs of disturbance like tail marks and footprints on the sand. To attract rodent visitation, a sliver of bait of peanut butter was added on the side of GUD trays.

4.3 Flight-initiation distance for reptiles

Simultaneously with reptile count, to understand the responses of lizards to an approaching predator, various behavioural metrics were recorded. The observer on detecting an individual would move sideways to an area front-facing the reptile. The starting distance (SD) before the predator simulation would be recorded. Flight initiation distance (FID) was taken as the distance between the observer and the lizard before it decided to flee and was used as a metric of the species' predation risk perception (McGowan et al., 2014). Starting distance was measured to examine if the FEAR (Flush early and avoid the rush) hypothesis in the optimal risk theory holds true for the two species. FEAR hypothesis states that a reptile that detects the presence of the predator early, might also flee early as continued monitoring of that predator

incurs costs (attention, lost foraging opportunities, etc) (Blumstein, 2010). The problem arises when different treatments might have different starting distances and thus, the difference in flight distance might be an artifact of starting distance rather than the property of treatment that is under investigation.

In the context of this study, higher levels of encroachment might naturally have lower starting distance because of high structural complexity leading to lower visibility or detection rates of the individuals until they are at an extremely short distance in comparison to longer distance detections in no encroachment plots. The best way to deal with such a problem is to standardise the starting distance across different conditions. However, in this study, the individuals are difficult to detect at larger distances, especially in *Calotropis* encroached areas. Thus, SD was included as a covariate in subsequent analyses to account for variation in approach conditions among observations. Other metrics like escape tactic, distance to the nearest refuge, type of the nearest refuge- categorised burrow, *Calotropis* or scrubs, distance to the refuge taken, and type of the refuge taken were recorded to explore escape strategies and decisions taken by different reptile species and different age class across encroachment levels. Distances till 5 m were measured using a tape and distances beyond 5 m were measured by range finder.

VES was done from 8:00 am-11:00 am. Data was not collected during cloudy or rainy days, as well as on the following day after the rain since substrate type (wet or dry sand) can change the readings of flight initiation distance and escape strategies. Surveys for this component were undertaken from mid-March to the end of April. Although livestock presence can impact the FID of reptiles, field observations indicated that all three encroachment levels experienced almost equal livestock presence. Whenever VES in a plot was underway and a livestock herd would approach or enter the plot, the survey was discontinued and a new plot would be visited.

The plot left would be revisited after a few days to reduce the impact of the halfway-done survey on FID of the reptiles.

2.4 Analytical methods

All statistical analysis and data visualisations were done in R version 4.5.

1. Habitat characteristics - Obstruction

Descriptive statistics and boxplots were used to quantify and visualise how Robel pole readings, % scrub cover, % *Calotropis procera* cover, % bare ground, % grass cover, % litter cover differed across *Calotropis* encroachment levels - no, moderate and high encroachment.

2. Clay model experiment

a) Predation rate of clay models

To examine if clay model predation varied with woody encroachment and land types, additive and interactive generalised linear mixed models were used, with clay model predation occurrence as binomial response, encroachment level and habitat as fixed effects, and site as random intercept. Candidate models were compared using an information-theoretic approach. Visualisation of the predicted values from the best model was done using the *ggpredict* function in *ggeffects* package.

b) Time to predation

To understand how time to predation differs across the three encroachment levels in sandy scrubland sites, each clay model was given a unique identification code and monitored repeatedly across survey intervals to determine the timing of predation events. The dataset was

structured in a start and stop interval format, where each row represented an observation interval for an individual clay model. The variables included study site, encroachment category, clay model identity, start hour, end hour, exposure duration, and predation fate (0 = survived, 1 = predated). Exposure duration represented the number of hours for which a model remained active during each interval.

To examine temporal variation in predation risk, survival analyses was done using Cox proportional hazards models (Function: *Coxph*) implemented in the *survival* and *survminer* package. The Cox model is a time-to-event model that assesses the instantaneous rate of an event which in this study is predation (Cox 1972; Rotella et al., 2004). For survival analyses, repeated monitoring records for each clay model were condensed into a single observation containing the final monitoring time till predation occurred and predation outcome. Clay models that were missing during the experiment were treated as predation events (Castilla et al., 1999). Clay models with predation marks from Rodentia were treated as opportunistic or novelty item predation and were not considered as predated in the analyses. Encroachment level was included as a fixed effect, and site-level variation was incorporated using a frailty term. Competing models with and without encroachment were compared using an information-theoretic framework.

The proportional hazards assumption was evaluated using Schoenfeld residual tests (function: *cox.zph*). Kaplan-Meier survival curves using *ggsurvplot* and *survfit* functions were made to visualise survival probability across encroachment categories over exposure time till predation event.

For all above analysis, candidate models were compared in an Information Theoretic framework (Burnham and Anderson 2002), and inferences on effects (direction and magnitude) were drawn from the least AICc model.

3. Numerical responses of rodents and reptiles

3.1 Active burrow count of nocturnal rodents

Count of active burrows per plot (response variable) across three encroachment levels (no, moderate, and high as fixed effect) were analysed using generalized linear mixed models (GLMMs), with site identity as a random effect. Initial analyses were conducted using a Poisson GLMM, however, model diagnostics displayed overdispersion in the residuals. Subsequently, negative binomial family (nbinom2) in *glmmTMB* package was used. Model containing encroachment levels as fixed effect was compared against the null model using an Information theoretic approach.

Mean and SE counts of active burrows were derived for each encroachment category and site that were visualized using the *ggplot2* package.

3.2 Lizard count

Detection probabilities for lizard counts were estimated using dependent double-observer sampling conducted on a dataset with subsampled number of plots (2 plots × 3 encroachment levels × 3 sites = 18 plots). Detection probability (p = Counts by Observer 1 / Total counts) was calculated separately for each species and encroachment category and was used to correct observed counts in the main dataset with n = 45 plots. Descriptive statistics of nondetection-adjusted counts was estimated separately for each species across encroachment categories.

The effect of *Calotropis* encroachment (predictor) on non-detection adjusted lizard counts (Poisson distributed response) was analysed independently for each species using generalized linear mixed models (GLMMs) implemented in *glmmTMB* package, with site identity as a random intercept. Model containing encroachment categories as fixed effect was compared against the null model using an information-theoretic framework. Mean and SE counts of each species and associated standard deviations were calculated for each encroachment category within each study site, and were visualized using the *ggplot2* package.

To evaluate difference in age/size composition across encroachment levels, proportions of juvenile and adult individuals were computed for each category and were visualised using stacked bar plots, separately for each species.

4. Behavioural responses of rodents and reptiles

4.1 Visitation patterns of nocturnal rodents to artificial food patches

Passive motion triggered camera trap photo captures were manually annotated to characterise the use of GUD trays by nocturnal rodents. For each visitation event, the time of entry into and exit from the tray was recorded, and the duration of the visit was calculated as the time between these two events. Cumulative time spent in each tray was obtained by summing the durations of all visitation events recorded for that tray during a sampling night. Some entry and exit events occurred within the same minute. To account for these short-duration visits, events in which the rodent remained inside the tray for at least two images within a five-image sequences were assigned a duration of 0.5 minutes. The time of the first and last detection was recorded, and temporal activity span for each tray was calculated as the time between these observations.

For each tray, additional metrics including the number of entry events, the number of ground detections without tray entry, latency to first entry defined as time between first ground capture and tray entry event, and mean residence time per visit (= Total time spent in a tray / No. of entry events) were calculated from the camera trap records. To quantify temporal patterns of tray use, the total number of tray entry events and the total time spent inside trays were summed across all trays for each hourly interval throughout the sampling period. Pearson's correlation analysis was done to assess the relationship between mean residence time and total number of entry events, and between total time spent in a tray and total number of entry events. Descriptive statistics along with visualisation using package *ggplot2* was done for all variables.

4.2 Giving-up density for rodents

The weight of peanuts remaining, out of the 4-gm offering, in each tray after the foraging period (giving-up density, GUD in grams) was used as the response variable. GUD values outside the range of 0.05-3.95 g were excluded from analyses, following standard practice. Two analytical approaches were used to examine the effect of woody encroachment on GUD. In the first approach, GUD values were averaged across trays in a plot to estimate mean GUD for each encroachment level (n = 3 plots) within a site on a sampling day (to account for daily variations), after which GUD differences for moderate and high encroachment levels from no encroachment were calculated, which was the reference category. The difference in GUD from no encroachment was modelled on linear mixed model with encroachment level and lunar illumination as predictors using linear model. In the second method, log transformed GUD (Gaussian distributed variable) value of each tray per plot was treated as an independent observation, with site, calendar date nested within the site and plot identity (representing the burrow / microsite where tray was placed) as random effects to account for repeated sampling

of the same plots across multiple days and moonlight sessions. Both approaches generated similar inference, but residual diagnostics of the first approach indicated violation of normality and homoscedasticity. Hence, the second approach with better residual diagnostics was used for inference. Additive, interactive, univariate, and null models were made to assess the effects of moonlight and encroachment on GUD values and were compared using an information-theoretic framework.

Mean and SE GUD were derived for each encroachment level and lunar condition for study sites that were visualized using the *ggplot2* package.

4.3 Flight-initiation distance of reptiles

The distance between the observer and the reptile individual before it flees - Flight Initiation Distance (hereafter, FID) - was analysed as the gaussian distributed response variable. FID and starting distance (SD) were log-transformed to reduce heteroscedasticity (Samia and Blumstein, 2015). The effect of *Calotropis* encroachment (predictor) on log-transformed FID was analysed independently for each species using generalized linear mixed models (GLMMs) implemented in *glmmTMB* package, with site identity as a random intercept. Candidate models included starting distance, distance to the nearest refuge, age class, and encroachment level were considered as explanatory variables. Candidate models with additive effects of these variables and null model were compared using an information-theoretic framework. Mean and SE FID of each species were derived for each encroachment level and site, and were visualized using the *ggplot2* package.

Escape tactics:

Descriptive statistics and visualizations using *ggplot2* were used to examine variation in distance to the nearest refuge across age classes and encroachment levels. Descriptive statistics were also used to assess the proportion of lizards using the nearest refuge and its variation across encroachment levels. Stacked bar plots were constructed to assess patterns in refuge type use. To evaluate whether the relationship between log-transformed flight-initiation distance (FID) and distance to the nearest refuge varied with encroachment or age class, additive and interactive models were compared using an information-theoretic approach. Predicted values from the best model were visualized using the *ggpredict* function in the *ggeffects* package.

3. RESULTS

3.1 Visibility obstruction due to woody encroachment

The Robel pole technique showed two-fold greater visibility obstruction in high encroachment plots (Mean 0.68 ± SE 0.02 proportion of bands that were not visible to the observer, n = 15 plots) compared to moderate (0.30 ± 0.02, n = 15 plots) and no (0.31 ± 0.03, n = 15 plots) encroachment plots. Percentage *C. procera* cover was 0 in no encroachment by design and increased from moderate (22.27 ± 1.62 %, n = 15 plots) to high (54.80 ± 1.45, n = 15 plots) encroachment plots. However, percent scrub cover (species other than *C. procera*) was greater in no encroachment (48.80±2.53 %, n = 15 plots) > moderate encroachment (12.40±2.03%, n = 15 plots) > high encroachment (26.67±1.31 %, n = 15 plots). Percent bare ground cover was similar in no encroachment (44.53 ± 2.63 %, n = 15 plots) and moderate encroachment (48.80±1.99 %, n = 15 plots) but considerably lower in high encroachment (26.67±1.31 %, n = 15 plots). Plots had very little litter and grass cover (Fig 3).

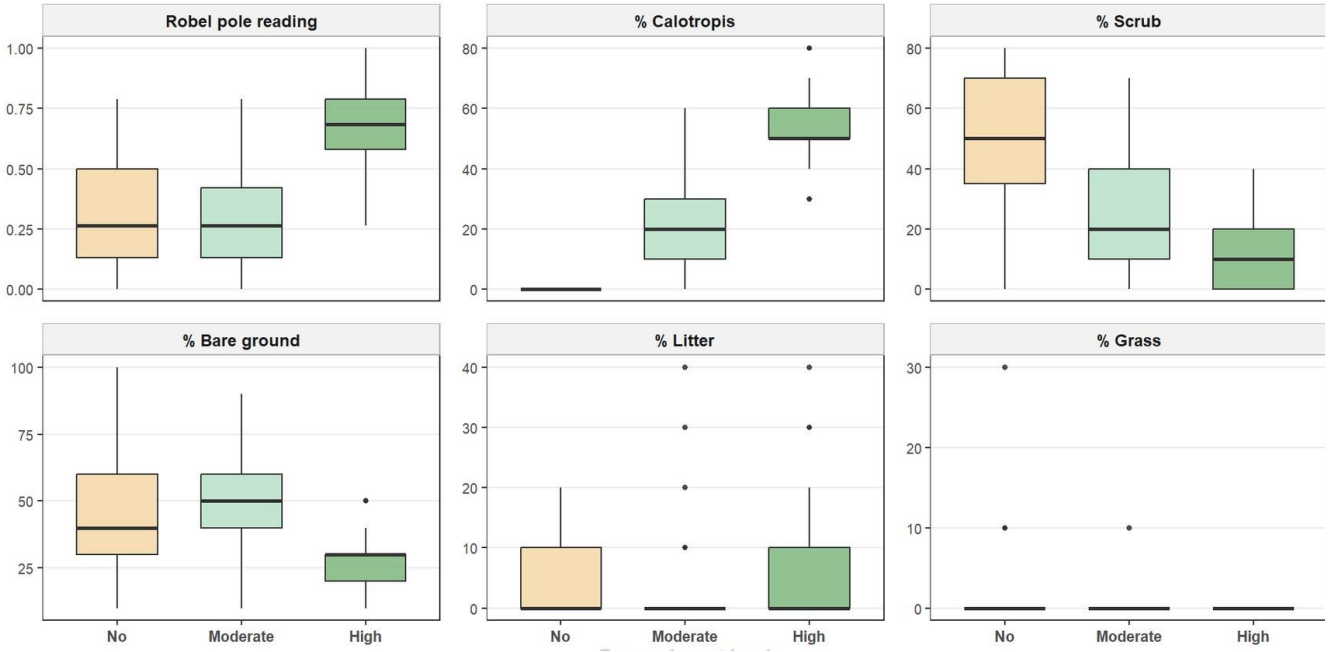


Figure 3:Boxplots depicting how habitat variables differ across different levels of C. procera encroachment in the study area in the Thar desert during 2025-2026

3.2 Predation pressure quantification across varying encroachment levels

a) No. of clay models predated against different habitat types and encroachment levels

Table 3: Summary and outcome of the clay model experiment to examine predation risk differences across encroachment levels in Thar desert (2026)

Sites	Encroachment	Total no. of models	No. of predated models	Land type

Sudasari EF	No	17	16	Grassland
Sudasari EF	Mod	17	8	Grassland
Sudasari EF	High	17	16	Grassland
Ibrahim ki talai	No	17	17	Grassland
Ibrahim ki talai	Mod	17	17	Grassland
Ibrahim ki talai	High	17	16	Grassland
Loonon	No	17	3	Scrubland
Loonon	Mod	17	6	Scrubland
Loonon	High	17	6	Scrubland
Ganga	No	17	6	Scrubland
Ganga	Mod	17	17	Scrubland
Ganga	High	17	12	Scrubland

Comparison of candidate models explaining count of predated clay models showed strongest support for the interactive model containing habitat and encroachment levels (Akaike weight =0.999, R2=0.271, Table 4).

Table 4: Summary statistics comparing models (hypothesis) explaining the variation in clay model predation occurence in Thar desert (2026)

Fixed effect	K	-2logL	AICc	Delta AICc	Akaike weight
Encroachment × Land type	6	192.66	205.1	0.00	0.999
Land	2	215.25	219.3	14.23	0.001
Encroachment + Land type	4	212.38	220.6	15.50	0.000
Null	1	253.80	255.8	50.73	0.000
Encroachment	3	251.45	257.6	52.49	0.000

In scrubland habitats, predation occurrence for clay models increased with encroachment level, as can be seen in Table 5. Moderate encroachment sites exhibited a higher number of predated

clay models (n = 23) relative to no encroachment scrublands (n = 9). Similarly, high encroachment scrubland showed higher predation occurrence (n = 18) compared to no encroachment scrubland. Under no encroachment conditions, grassland habitats showed substantially higher predation occurrence (n = 33) relative to scrublands (n = 9) (Fig 4).

Table 5: Parameter estimates of model relating clay model predation occurrence with land type and encroachment levels in Thar during 2026

Predictors	*Estimate*	*Std. Error*	*Z value*
(Intercept)	-1.02	0.39	-2.63
Encr [Mod]	1.76	0.53	3.29
Encr [High]	1.14	0.52	2.20
Land [Grass]	4.52	1.09	4.16
Encr [Mod] × Land [Grass]	-4.23	1.21	-3.50
Encr [High] × Land [Grass]	-1.86	1.35	-1.38
Observations	204		
R^2 Tjur	0.27		

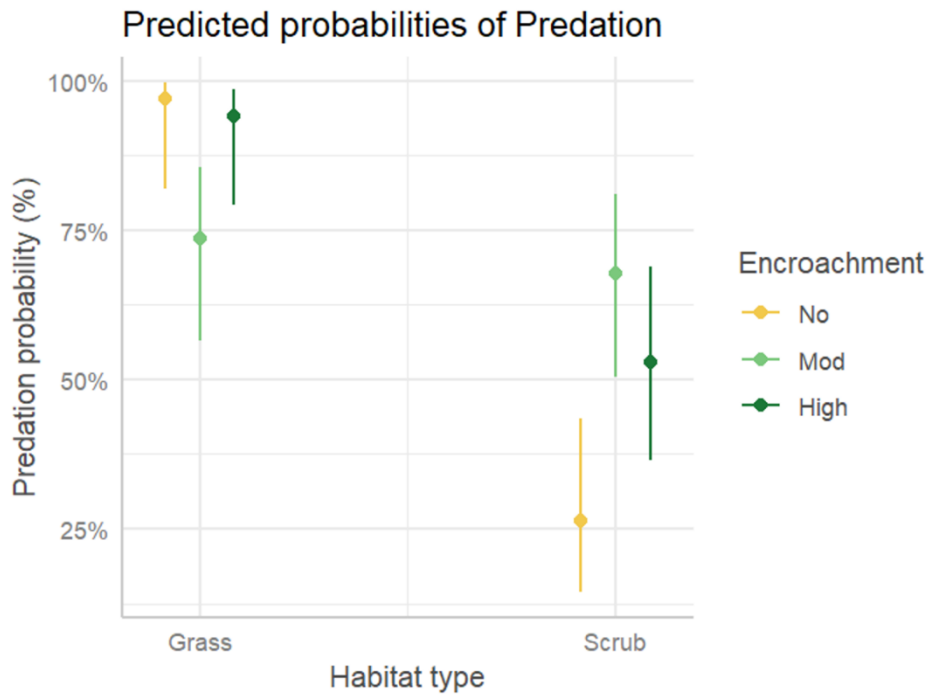


Figure 4: Graph depicting predicted predation probability under two land types (Grassland and Scrubland) across woody encroachment levels in Thar desert (2026)

b) Cox model and survivorship curve

Comparison of candidate models explaining predation risk through time showed strongest support for encroachment levels (Akaike weight =0.999, R2=0.33, Table 6).

Table 6: Summary statistics comparing models (hypothesis) explaining the variation in predation risk through time in Thar desert (2026)

	Fixed effects	K	-2logL	AICc	Delta AICc	Akaike weight

Coxmodel1	Encroachment	2	469.50	475.8	0.0	0.99
Null model	1	0	487.29	489.2	13.4	0.01

Results of survival analysis showed that clay model predation occurred substantially faster under moderate and high encroachment conditions compared to no encroachment habitats (Table 7 and Fig 5).

Table 7: Parameter estimates of model relating predation risk through time with encroachment levels in Thar during 2026

Predictors	*coef*	*Se (coef)*	*Chi.sq.*
encroachment [Mod]	1.30	0.3716	12.38
encroachment [High]	1.24	0.3676	11.36
frailty (Site)	23.71		
Observations	102		
R^2 Nagelkerke	0.33		

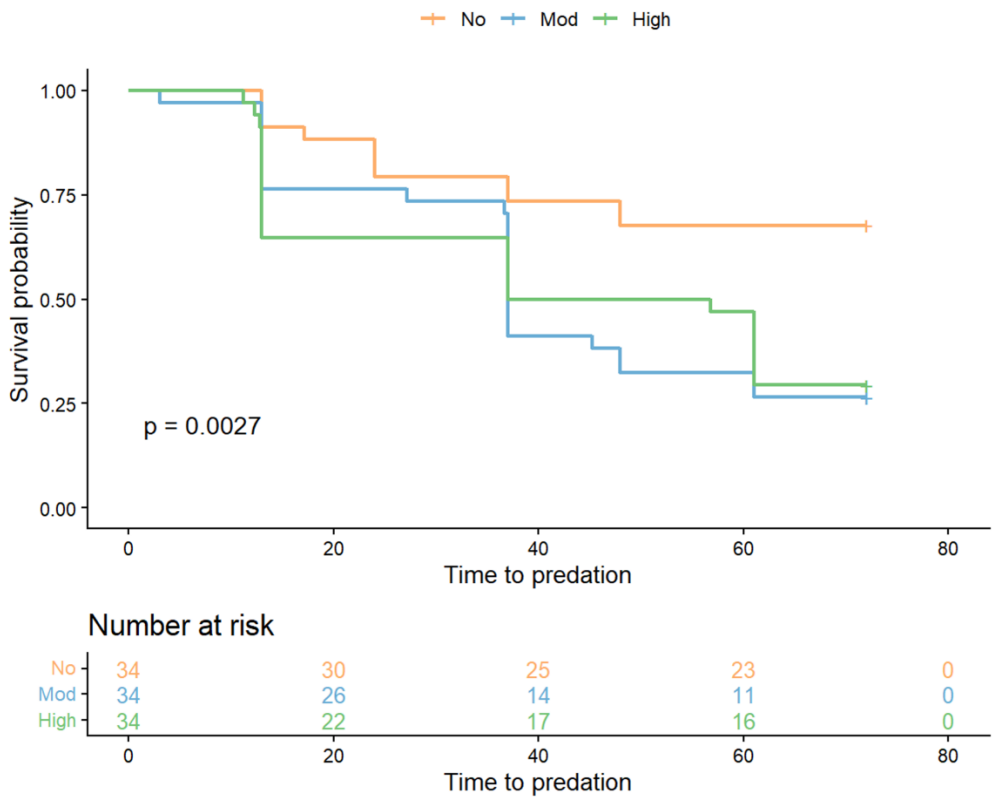


Figure 5: Kaplan-Meier survival curves showing time to predation of clay models across different encroachment levels with site (n=2) as a frailty term

3.3 Effect of *Calotropis procera* encroachment on numerical responses of rodents and reptiles

3.3.1 Burrow count of nocturnal rodents

The model explaining active burrow count as a function of encroachment level found stronger support from data than the null model (Ak wt. = 0.95, R2= 0.45, Table 8), showing an effect of encroachment level on rodent abundance (Table 8). Count of active rodent burrows per 1-ha plot was higher in no-encroachment sites (Mean = 30.67, SD = 6.89, n = 9 plots) than moderate

(Mean=16, SD= 8.67, n= 9 plots) and high (Mean=16, SD=10.16, n=9 plots) encroachment levels (Table 9 and Fig 6)

Table 8: Summary statistics comparing models (hypothesis) explaining the variation in number of active burrows count in 1-ha plots, in Thar desert (2026)

Model	K	-2logL	AICc	Delta AICc	Akaike weight
Encroachment	5	192.46	205.3	0	0.95
Null	3	204.16	211.2	5.89	0.05

Table 9: Parameter estimates of model relating active burrow counts of nocturnal rodents in 1-ha plots with woody encroachment levels in Thar desert (2026)

Predictors	*Estimate*	*Std. Error*	*z value*
(Intercept)	3.43	0.17	20.66
Encroachment [Mod]	-0.68	0.20	-3.39
Encroachment [High]	-0.67	0.20	-3.37
Random effects			

N_{Site}	3
Observations	27
Marginal R^2 / Conditional R^2	0.36 / 0.45

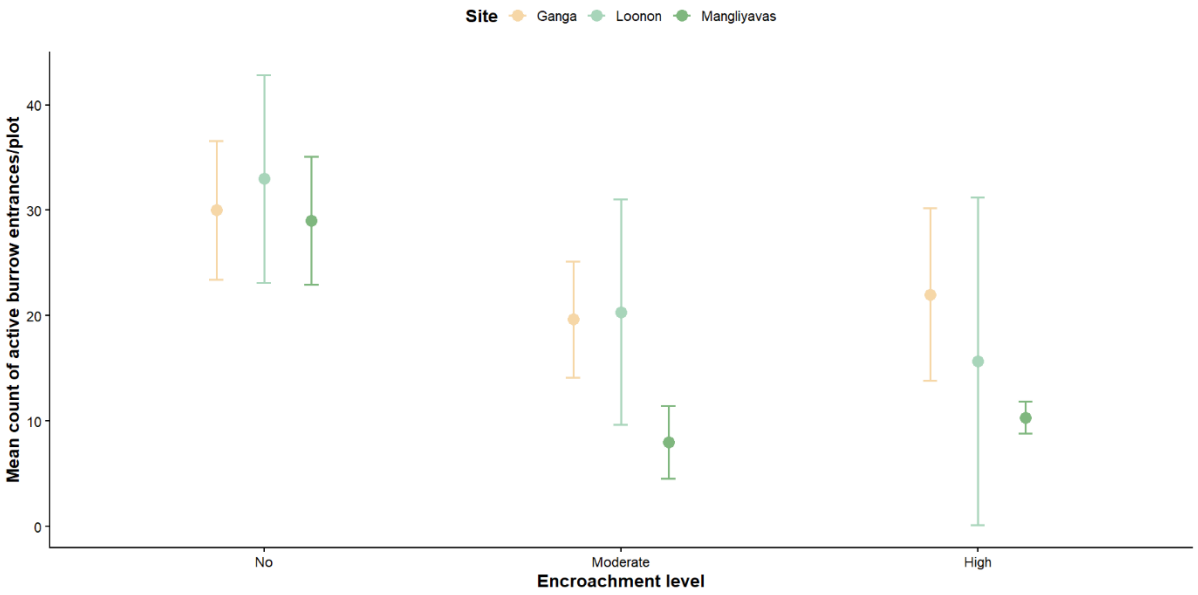


Figure 6: Mean count and SE (error bars) of active burrow entrances per plot across the three levels of encroachment (n=27 plots) in Thar desert (2026)

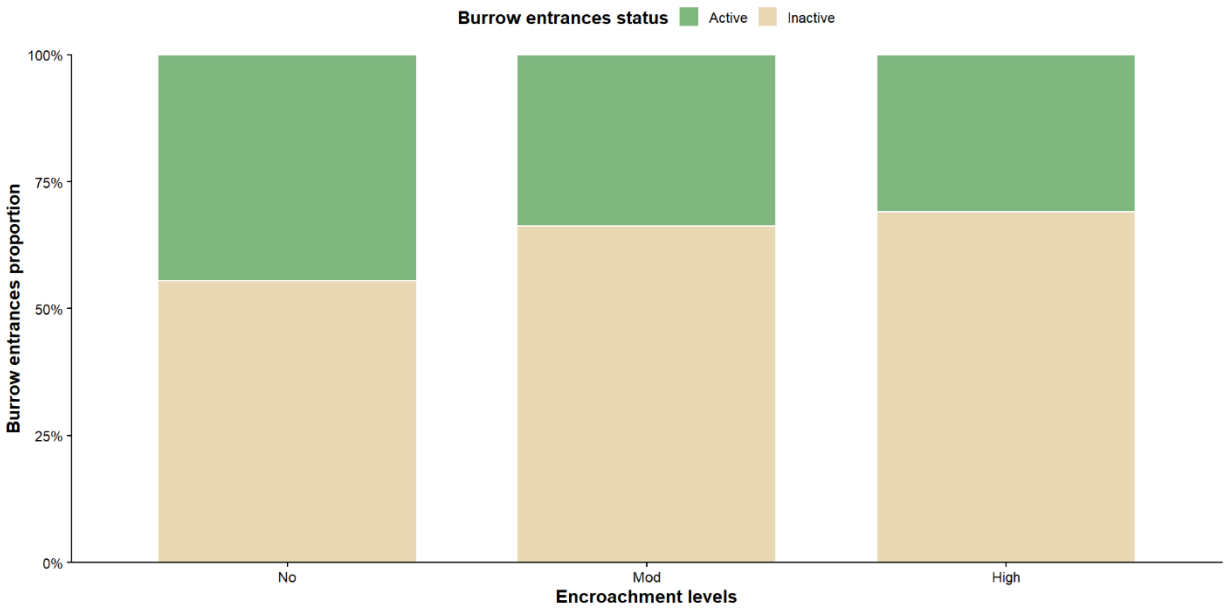


Figure 7: Stacked bar plot comparing frequency of active and inactive burrows across levels of Calotropis encroachment (n=27 plots) in Thar desert (2026)

3.3.2 Abundance of reptiles

a. Detection probability of reptiles in the three levels of encroachment

To correct for detection probability of lizards in a single observer framework (n = 45 plots), a subset of plots (n = 18 plots) was revisited with dependent double observer and detection probability of the main observer was calculated as shown in Table 10.

Table 10: Number of sightings of the two lizard species pooled across plots for the first observer and both observers and used to estimate detection probability using the dependent double-observer method across different encroachment levels in Thar desert (2026)

Species	Plots	Encroachment	Obs1	Total	Detection probability (p)
Brilliant	6	High	2	3	0.67
Brilliant	6	No	4	5	0.8
Brilliant	6	Mod	3	5	0.6
Fringe	6	High	4	5	0.8
Fringe	6	No	24	31	0.77
Fringe	6	Mod	10	14	0.71

b. Corrected counts of the two lizard species across three levels of encroachment

i. Acanthodactylus cantoris

Table 11: Summary statistics comparing models (hypothesis) explaining Acanthodactylus cantoris counts in 1-ha plots, in Thar desert (2026)

Model	K	-2logL	AICc	Delta AICc	Akaike weight
Encroachment	4	190.71	199.7	0.00	1
Null	2	240.05	244.3	44.62	0

The model explaining *Acanthodactylus cantoris* count as a function of encroachment level found stronger support from data than the null model (Akaike weight = 1, R2= 0.58, Table 11), showing an effect of encroachment level on *Acanthodactylus cantoris* abundance. Density (number / ha) of this species was greater in no-encroachment sites (Mean=6.54, SD=3.64, n=15 plots) than moderate (Mean=2.61, SD=1.74, n=15 plots) and high (Mean=1.83, SD=1.32, n=15 plots) encroachment levels (Table 12 and Fig 8).

Table 12: Parameter estimates of model relating counts of Acanthodactylus cantoris in 1-ha plots with woody encroachment levels in Thar during 2026

Predictors	*Effect size*	*Std. error*	*z value*
(Intercept)	1.86	0.15	12.56
Encroachment [mod]	-0.92	0.19	-4.86

Encroachment [high]	-1.27	0.22	-5.90
Random effects			
σ^2	0.24		
N_{Area}	3		
Observations	45		
Marginal R^2 / Conditional R^2	0.52 / 0.58		

ii. Trapelus agilis

The model explaining *Trapelus agilis* count as a function of encroachment level found stronger support from data than the null model (Akaike weight = 0.88, R2= 0.60, Table 13), showing an effect of encroachment level on *Trapelus agilis* abundance. Density (number / ha) of this species was greater in high-encroachment sites (Mean=1.7, SD=1.37, n=15 plots) than no (Mean=0.67, SD=1.14, n=15 plots) and moderate (Mean=0.78, SD=1.07, n=15 plots) encroachment levels (Given in Table 14 and Fig 8).

Table 13: Summary statistics comparing models (hypothesis) explaining the Trapelus agilis counts in 1-ha plots, in Thar desert (2026)

Model	K	-2logL	AICc	Delta AICc	Akaike weight

Encroachment	4	104.75	113.8	0.00	0.88
Null	2	113.40	117.7	3.94	0.12

Table 14: Parameter estimates of model relating counts of Trapelus agilis in 1-ha plots with woody encroachment levels in Thar during 2026

Predictors	*Effect size*	*Std. Error*	*Z value*
(Intercept)	-0.75	0.62	-1.21
Encroachment [mod]	0.15	0.43	0.36
Encroachment [high]	0.94	0.37	2.51
Random Effects			
σ^2	0.65		
N_{Area}	3		
Observations	45		
Marginal R^2 / Conditional R^2	0.11 / 0.60		

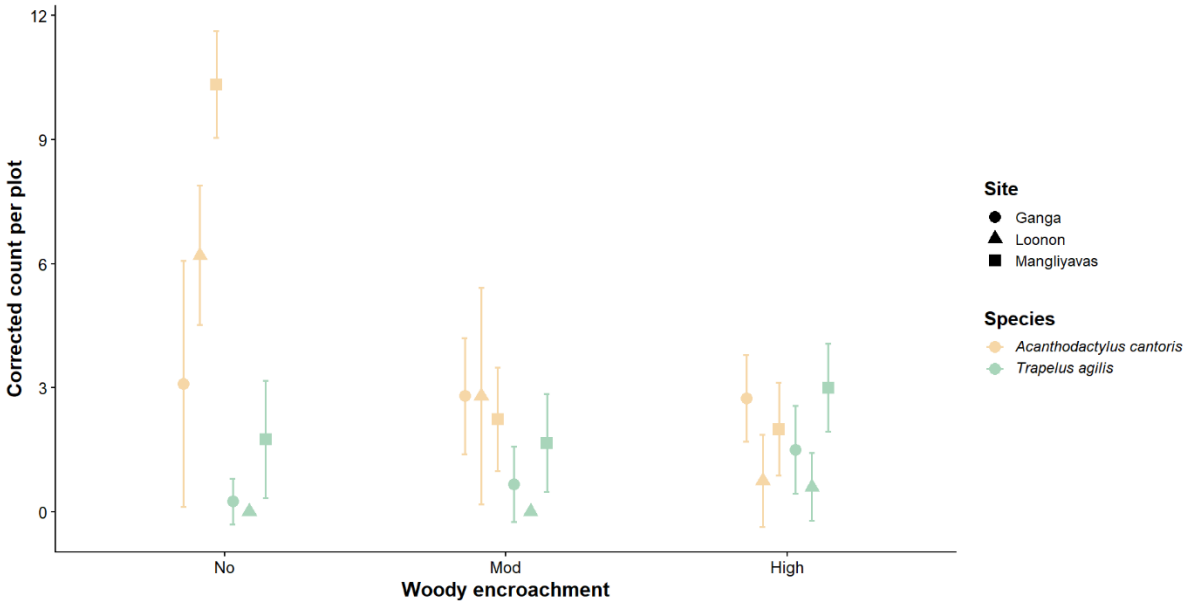


Figure 8: Mean count and SE (error bars) of Indian fringe-fingered lizard and Brilliant Ground Agama per plot across the three levels of encroachment (n=45 plots) in Thar desert (2026)

Adult-biased age structures were observed in both species, with adult: juvenile ratios of 15:1 in *Trapelus agilis* and 3.2:1 in *Acanthodactylus cantoris*. Age-class distribution did not vary substantially across encroachment levels (Fig 11).

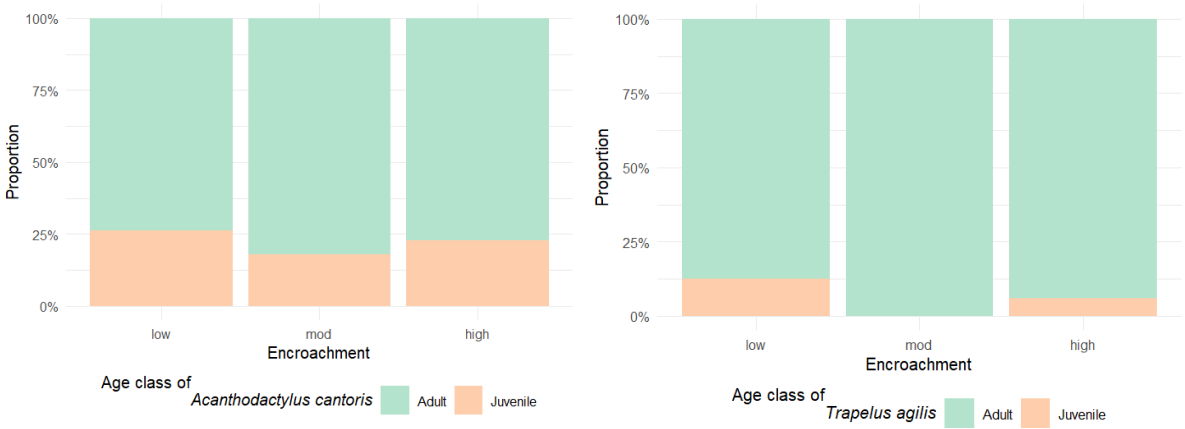


Figure 9: Stacked bar plot comparing frequency of adults and juveniles of Acanthodactylus cantoris (left) and Trapelus agilis (right) across the three levels of Calotropis encroachment in Thar desert (2026)

3.4 Effect of *Calotropis procera* encroachment on behavioural responses of rodents and reptiles

3.4.1 Description of nocturnal rodent activity and foraging patterns in artificial foraging patches

Table 15: Mean, standard deviation (SD), median, minimum and maximum values of rodent activity metrices in GUD trays (n = 10) in areas without Calotropis procera encroachment

Variable	Mean	SD	Median	Min	Max
Duration between first and last rodent visit (hours)	3.63	3.99	1.99	0.02	10
Total time spent in a tray	6.4	9.32	1.25	0	28
Total no. of entry events	5.6	7.66	1.5	0	23
No. of ground detections	2.1	3.57	1	0	12
Latency time (minutes)	10.65	14.83	0.5	0	37
Mean residence time (minutes)	1.03	0.37	1	0.5	1.5

Rodent activity varied through the night, with cumulative entry events and feeding duration peaking at 23:00 h, and indicative of cyclic bouts of activity rather than a fixed temporal pattern. Minimal activity was observed at 22:00 h and 2:00 h, and activity ceased between 6:00 and 18:00 h (Figure 10).

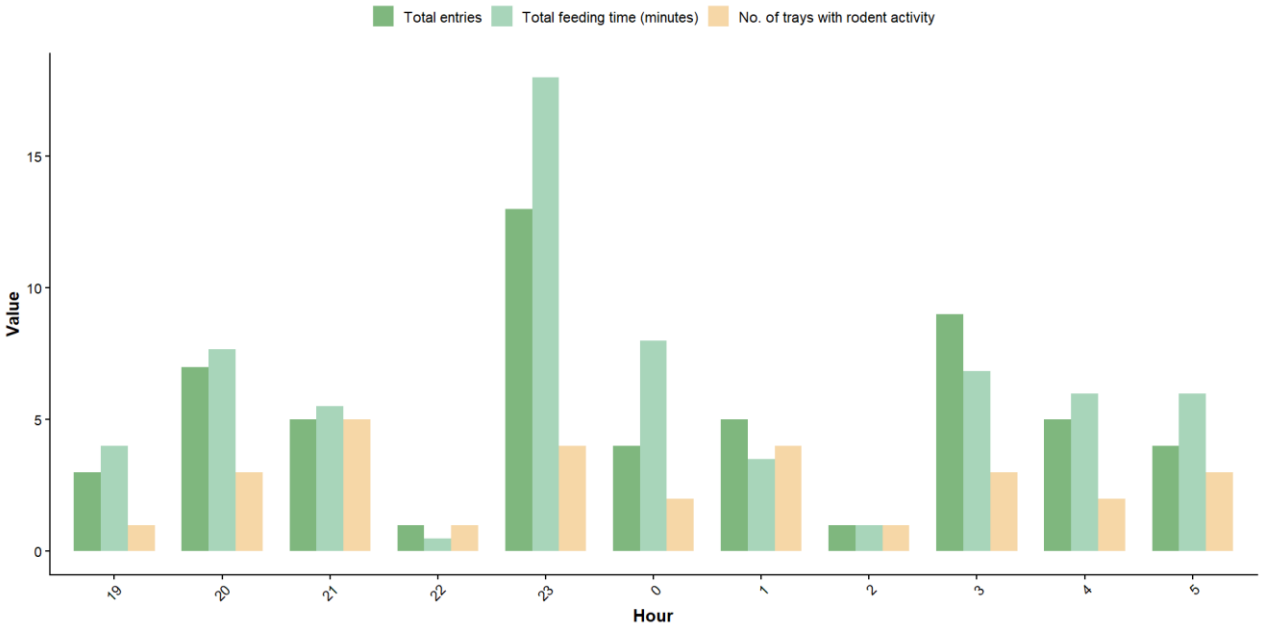


Figure 10: Hourly distribution of total entries, total feeding time and no. of trays displaying rodent activity across multiple GUD trays (n=10) in scrubland areas without Calotropis procera encroachment

Pearson correlation analysis showed weak positive association between mean residence time and number of entry events (r = 0.45) and a strong association between cumulative time spent in a tray and entry frequency (r = 0.99) (Figure 11).

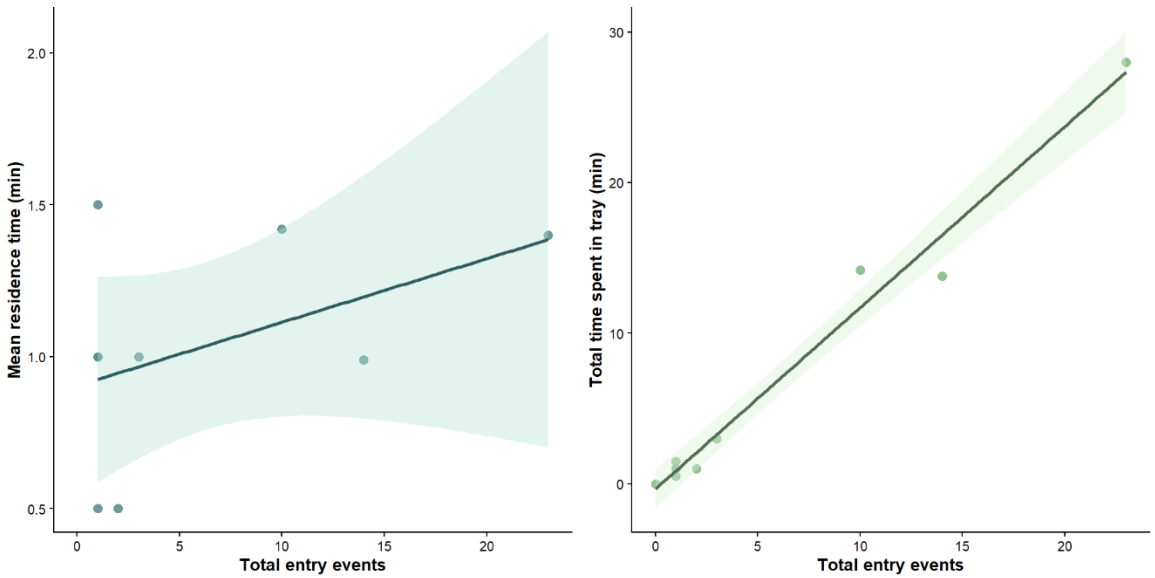


Figure 11: Graph depicting mean residence time in minutes (Left) and Total time spent in a tray in minutes (Right) against total entry events per tray in n = 10 trays

3.4.2 Giving-up density for rodents

Giving-up density (GUD) of nocturnal rodents was higher under no woody encroachment (Mean =2.05, SD=1.80, n= 3 plots) compared to moderate (Mean=0.50, SD=0.67, n= 3 plots) and high (Mean=0.54, SD=0.88, n=3 plots) levels of Calotropis encroachment (Fig 12).

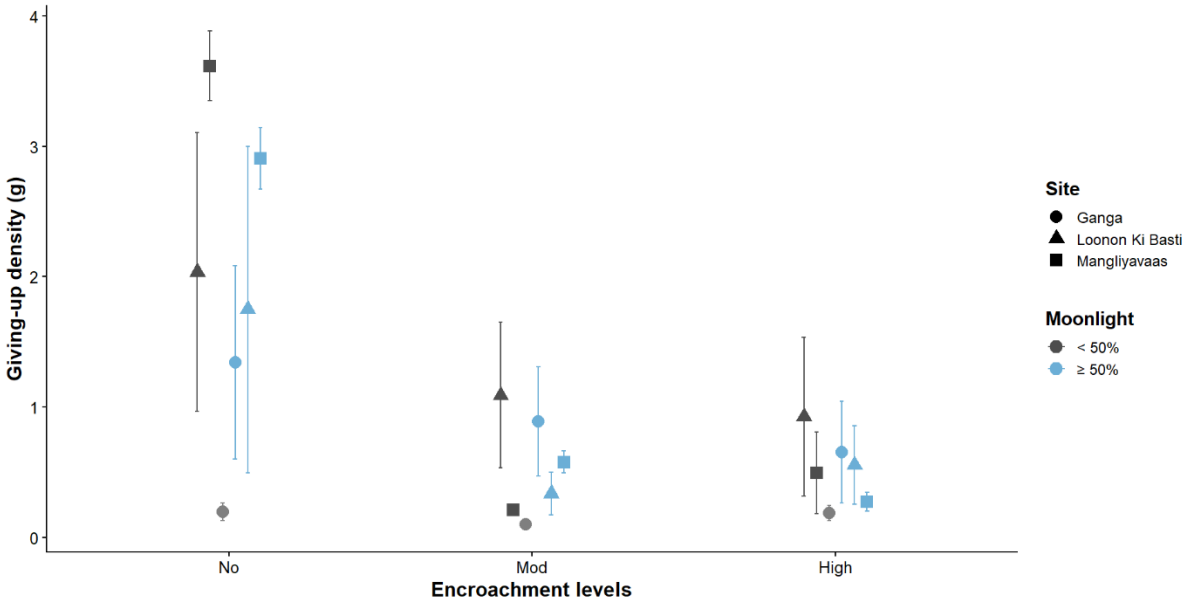


Figure 12: Mean and SE (error bars) of Giving-up density against levels of Calotropis encroachment across three sites and varying lunar illumination in Thar desert (2026)

Three models had ΔAIC < 1. Comparison of candidate models explaining GUD showed similar support for interactive and additive effects of woody encroachment and lunar illumination (Table 6). Interactive model was selected from them on the basis of best biological interpretation (Table 16). The least AICc model showed that woody encroachment reduced GUD and lunar illumination increased GUD under moderate levels of woody encroachment but not in no encroached and highly encroached plots (Table 17, Figure 13).

Table 16: Summary statistics comparing models (hypothesis) explaining the variation in Giving-up density in Thar desert (2026)

Model	K	-2logL	Delta AICc	Akaike weight

Encroachment × Moonlight	10	571.03	0.00	0.40
Encroachment + Moonlight	8	575.98	0.54	0.31
Encroachment	7	578.22	0.61	0.30
Moonlight	6	596.05	16.30	0.00
1	5	598.47	16.59	0.00

Table 17: Parameter estimates of model relating log-transformed Giving-up density of nocturnal rodents with woody encroachment levels and lunar phase in Thar during 2026

Predictors	*Estimates*	*Std. Error*	*z value*
(Intercept)	-0.09	0.38	-0.25
Encr [Mod]	-1.48	0.30	-4.92
Encr [High]	-1.50	0.31	-4.83
Lunar phase	0.07	0.32	0.22
Encr [Mod] × lunar	0.67	0.32	2.06
Encr [High] × lunar	0.34	0.32	1.04

Random effects	
σ^2	0.69
N_{Date}	23
N_{Site}	3
N_{Points_id}	35
Observations	200
Marginal R^2 / Conditional R^2	0.21/0.62

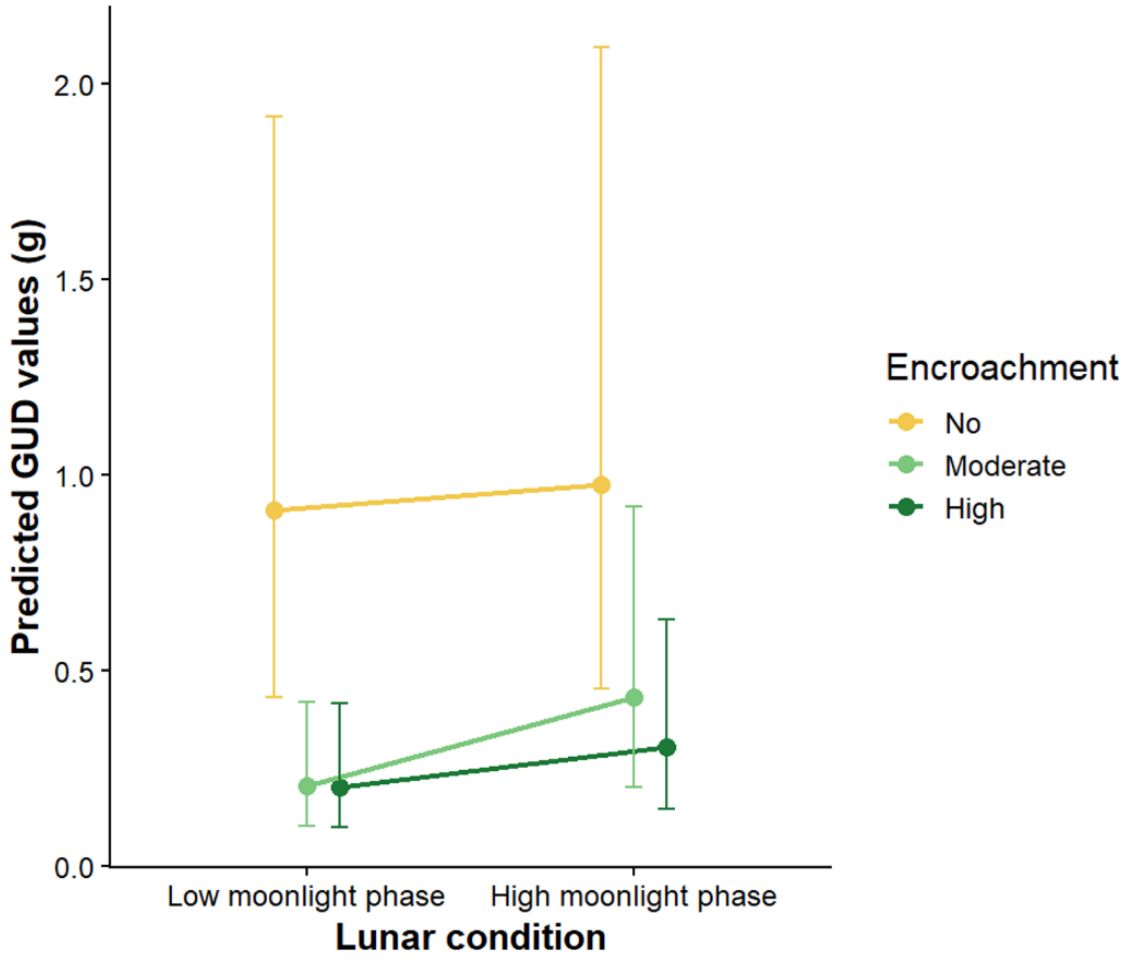


Figure 13: Graph depicting predicted GUD under binary lunar conditions (<50% illumination= low, =>50% illumination= high) across encroachment levels from a GLMM with interaction of Lunar condition and encroachment

3.4.3 Behavioural responses of lizards in three levels of encroachment

a. Flight-initiation distance

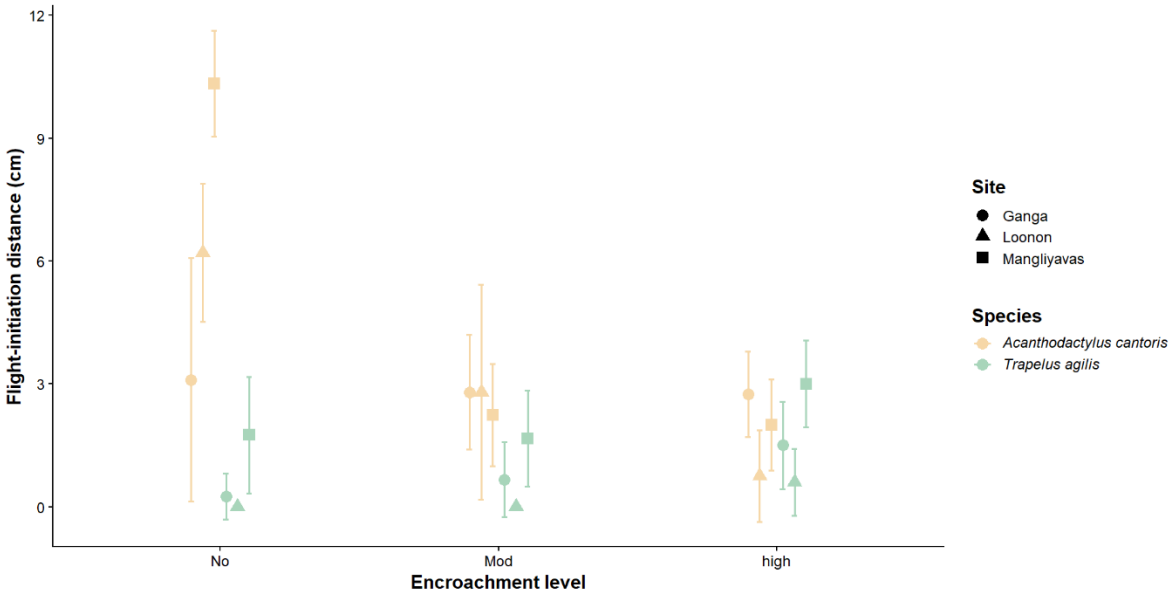


Figure 14: Mean and SE (error bars) flight-initiation distance against levels of Calotropis encroachment in two reptile species across three sites in Thar desert (2026)

i. Acanthodactylus cantoris

Comparison of candidate models explaining flight-initiation distance (FID) in *Acanthodactylus cantoris* showed strongest support for the model containing log-transformed starting distance and woody encroachment (Akaike weight = 0.67, R2 = 0.634, Table 18).

Table 18: Summary statistics comparing models (hypothesis) explaining the variation in Flight-initiation distance of Acanthodactylus cantoris in Thar desert (2026)

Model	K	-2logL	AICc	Delta AICc	Akaike weight

Log (starting distance) + encroachment	6	122.89	135.5	0.00	0.67
Log (starting distance) + encroachment + Distance to nearest shrub	7	122.87	137.7	2.20	0.22
Log (starting distance) + encroachment + Distance to nearest shrub+ Age class	8	122.07	139.2	3.67	0.11
Log (starting distance)	4	146.53	154.8	19.29	0.000
Null	3	259.60	265.8	130.25	0.000

Flight-initiation distance (FID) of *Acanthodactylus cantoris* was higher under no woody encroachment (Mean= 353 cm, SD=93 cm, n= 15 plots) compared to moderate (Mean=191 cm, SD= 93 cm, n= 15 plots) and high (Mean= 158 cm, SD= 54 cm, n= 15 plots) levels of Calotropis encroachment (Table 19 and Fig 14). Starting distance had a strong and precise effect on FID.

Table 19: Parameter estimates of model relating Flight-initiation distance of Acanthodactylus cantoris with woody encroachment levels and starting distance in Thar during 2026

Predictors	*Estimates*	*Std. Error*	*z value*
(Intercept)	0.64	0.42	1.54
starting distance [log]	0.83	0.07	12.15
encroachment [mod]	-0.23	0.08	-2.70
encroachment [High]	-0.45	0.09	-4.91
Random effects			
σ^2	0.14		
$\tau_{00\ site}$	0.00		
$N_{\ site}$	3		
Observations	137		
Marginal R^2	0.634		

ii. Trapelus agilis

Comparison of candidate models explaining flight-initiation distance (FID) in *Trapelus agilis* showed strongest support for the model containing log-transformed starting distance and age class (Akaike weight = 0.56, R2= 0.58, Table 20).

Table 20: Summary statistics comparing models (hypothesis) explaining the variation in Flight-initiation distance of Trapelus agilis in Thar desert (2026)

Model	K	-2logL	AICc	Delta AICc	Akaike weight
Log (Starting distance) + Age class+ Distance to nearest refuge	6	58.66	73.8	0.00	0.56
Log (Starting distance)	4	67.40	76.3	2.58	0.16
Log (Starting distance) + Encroachment+ age class + Distance to the nearest refuge	8	56.9	76.7	2.93	0.13
Log (Starting distance) + Encroachment+ Distance to the nearest refuge	7	60.44	77.3	3.54	0.10

Log (Starting distance) + Encroachment+ Age class	7	60.38	79.3	5.49	0.04
Log (Starting distance) + Encroachment	6	66.34	80.4	6.67	0.02
Null	3	99.94	106.5	32.74	0.00

Distance to the nearest refuge and starting distance had a strong and precise positive effect on FID of *Trapelus agilis* (Fig 15). Age class showed a weak and imprecise effect on flight-initiation distance, with juveniles exhibiting lower values relative to adults (Table 21). Woody encroachment did not have an effect on flight initiation distance of this species.

Table 21: Parameter estimates of model relating flight-initiation distance with starting distance, age class and distance to nearest refuge in Thar during 2026

Predictors	*Estimates*	*Std. Error*	*Z value*
(Intercept)	0.65	0.76	0.86
starting distance [log]	0.80	0.13	6.29
age class [juvenile]	-0.43	0.24	-1.79
Distance to nearest refuge	0.00	0.00	2.10

Random Effects	
σ^2	0.21
N_{site}	3
Observations	47
Marginal R^2	0.58

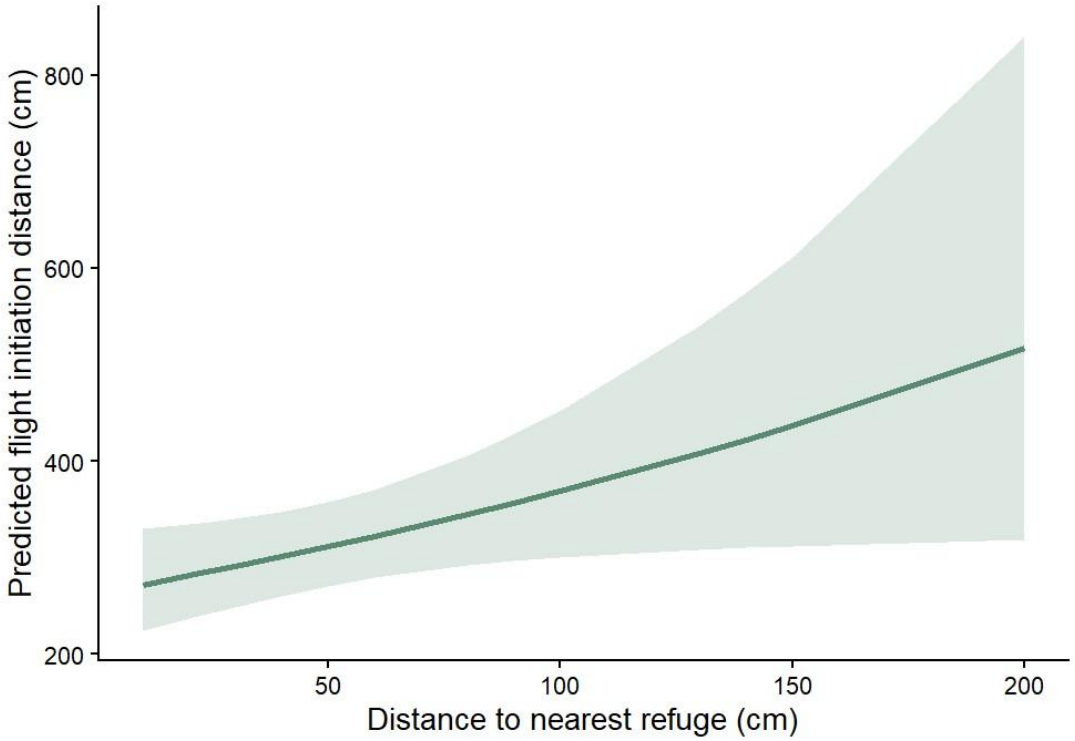


Figure 15: Predicted flight-initiation distance of Trapelus agilis across increasing distance to nearest refuge, derived from a GLMM with additive effects of age class and distance to nearest refuge.

b. Escape tactics

1) Does distance to nearest refuge differ across encroachment and age class

The distance to nearest refuge in *Acanthodactylus cantoris* was higher overall in adults (Mean=52.6 cm ± SE=3.93 cm) than in juveniles (36.0 cm ± 6.49 cm). In *Trapelus agilis*, similar but inconsistent pattern was seen, i.e., adult individuals' distance to nearest refuge (50.6 cm±6.84 cm) was greater than that of juvenile individuals (30 cm ± 10 cm) (Fig 16)

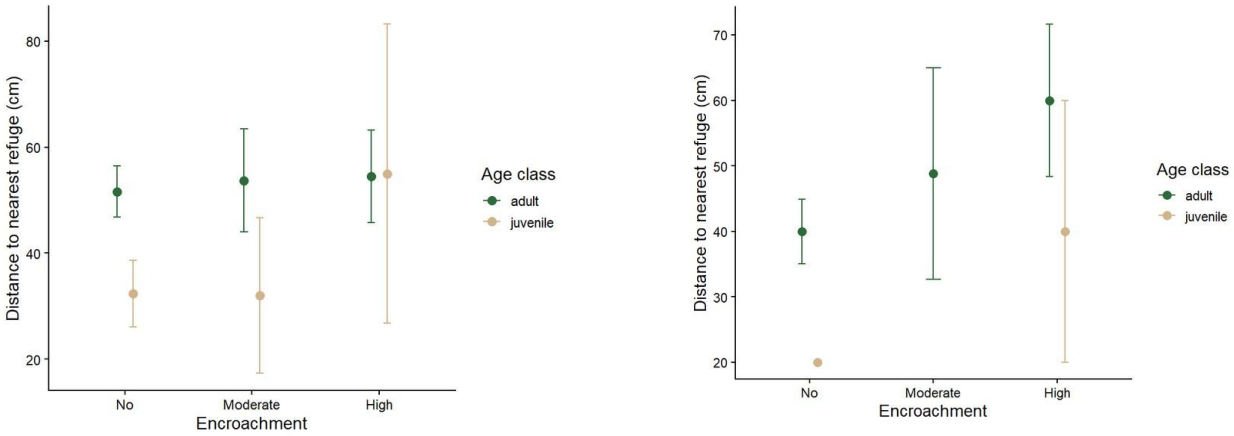


Figure 16: Mean and SE (error bars) distance of nearest refuge of adults and juveniles of Acanthodactylus cantoris (left) and Trapelus agilis (right) against levels of Calotropis encroachment across three sites in Thar desert (2026)

2) What is the proportion of lizards choosing the nearest shrub and is the preference changing with encroachment?

40 % of *Acanthodactylus cantoris* and 55 % of *Trapelus agilis* took the refuge closest to them. The proportion of individuals using nearest refuge was higher in high encroachment (Mean=0.85 ± SE=0.1) than in no encroachment (0.52 ± 0.07) for *Acanthodactylus cantoris.*

For *Trapelus agilis*, the proportion of individuals using nearest refuge was higher in moderate encroachment (0.69 ± 0.13) than in no encroachment (0.27 ± 0.11) (Fig 17).

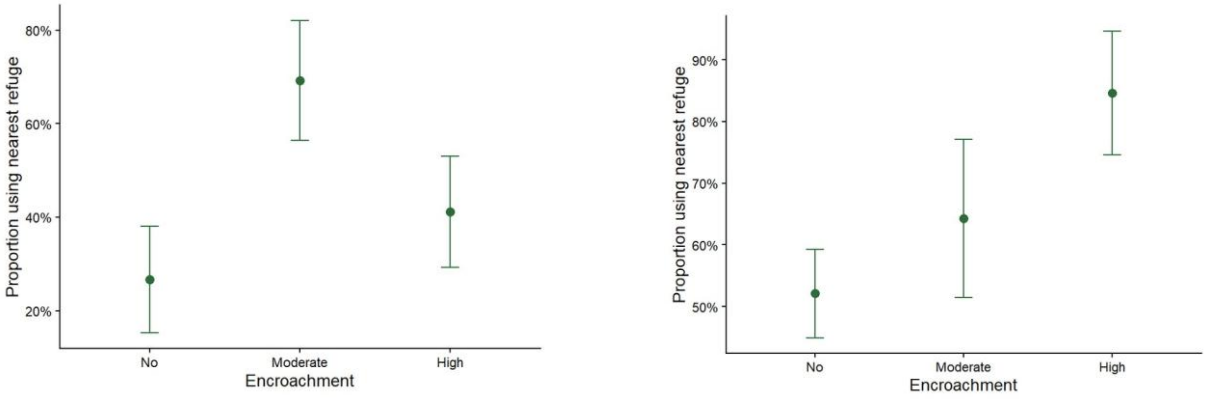


Figure 17: Mean and SE (error bars) proportion of individuals using nearest refuge against levels of Calotropis encroachment in Acanthodactylus cantoris (left) and Trapelus agilis (right) across three sites in Thar desert (2026)

3) How does the relationship between flight-initiation distance and distance to nearest refuge change with encroachment levels and age class of *Acanthodactylus cantoris*?

Comparison of candidate models explaining FID showed more support for interactive than additive effects of woody encroachment and distance to nearest shrub (Appendix 1, Akaike weight=1). The least AICc model showed that starting distance increases FID and increase in distance to nearest refuge decreased FID under moderate levels of woody encroachment but not in no encroached and highly encroached plots (Appendix 2) (Fig 18).

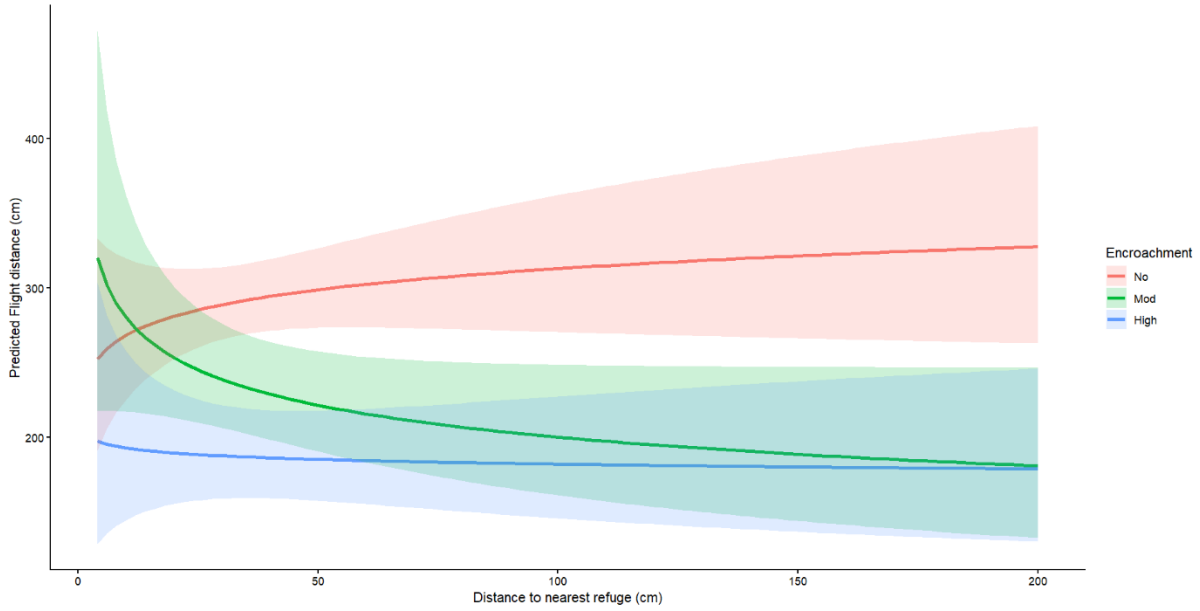


Figure 18: Graph depicting predicted flight-initiation distance with CI (error bars) as a function of distance to nearest refuge across levels of encroachment with site as a random effect in Thar desert (2026)

Comparison of candidate models explaining FID showed more support for interactive than additive effects of age class and distance to nearest shrub (Appendix 3, Akaike weight=0.93). The least AICc model showed that starting distance increases FID and increase in distance to nearest refuge decreased FID in juveniles but not in adults (Appendix 4) (Fig 19).

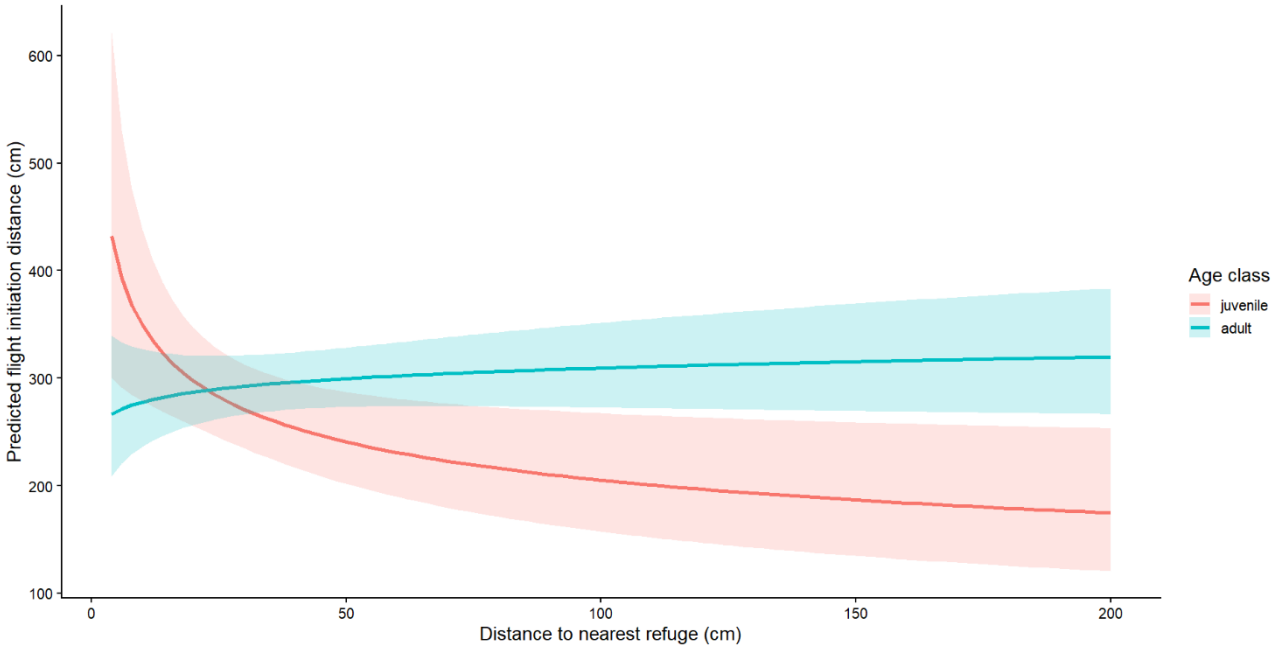


Figure 19: Graph depicting predicted flight-initiation distance with CI (error bars) as a function of distance to nearest refuge and age class with site as a random effect in Thar desert (2026)

4) What is the proportion of different refuge type use in different encroachment level?

Acanthodactylus cantoris predominantly uses shrubs while *T. agilis* uses both shrubs and burrows. Both species only sparsely use *C. procera* for refuge cover as can be seen in Figure 20.

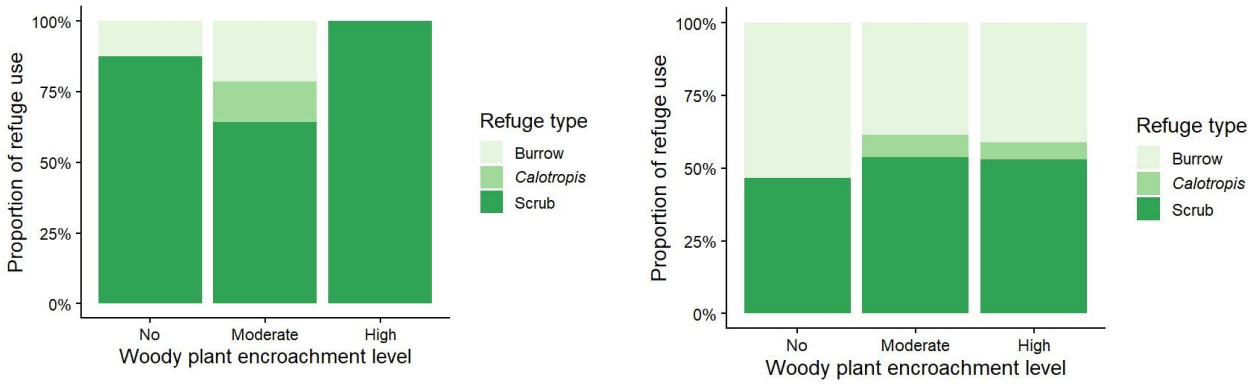


Figure 20: Proportion of use of different types of refuge across encroachment levels in Acanthodactylus cantoris (Left) and Trapelus agilis (Right) in Thar desert (2026)

4. DISCUSSION

This study expands upon our existing knowledge about the cascading effects of woody encroachment on behaviour, abundance and trophic relations of small vertebrates in Open Natural Ecosystem, with the recent expansion of *Calotropis procera* in the western Thar desert, as a case. Findings from field-based surveys and experimentation indicated that while active burrow count of nocturnal rodents declined with woody encroachment, their perceived risk perception was greater in non-encroached areas. Lizard species differed in their responses, with contrasting responses of abundance and predator risk perception to *Calotropis* encroachment between the two study species. Further, predation pressure differed between structurally different habitats – and woody encroachment thereof. These findings imply that the effect of woody encroachment is not straightforward but highly nuanced and can differ between species, thereby holding potential to reshape ecological communities and trophic interactions in Open Natural Ecosystems. These findings are discussed in detail below.

1) Quantifying predation pressure through clay models

The outcome of clay model experiment showed that grassland habitats faced more predation pressure than scrublands. Predation was mostly by Desert fox, Desert cat and Bengal fox, with only one documented predation by a bird (identified through claw marks left at the location of the clay model). A few of the predation events occurred immediately after the deployment of clay models (Time to predation ~ 0.5 hours as seen in camera traps). This difference in predation pressure across habitat types might be attributable to higher predator usage in grasslands than scrublands, perhaps because of the following reasons: a) predators may experience lower benefit to cost ratio in scrublands (compared to grasslands, wherein increased visual obstruction can reduce search efficiency and consequently reduce exploitation of food

patches, fitting in the framework of optimal foraging theory; or b) natural food resources might be more abundant in grasslands. Indeed, various group-living prey species (IDJ and Spiny-tailed lizard) exist in higher numbers in grasslands than in scrublands which might lead to higher search effort of predators in grasslands as prey capture rate might be higher there. Spiny-tailed lizards preferentially use compact grasslands (Dutta and Jhala 2007) and personal observations indicate greater number of IDJ in grasslands. Regardless of the possible explanations, the relationship between habitat structure, prey and predator species is deeply interlinked and is difficult to tease apart.

While predation pressure differences between grassland and scrubland could be attributed to structural variations, the predation pattern across encroachment levels within scrubland is difficult to explain through the lens of structural differences. Braun et al. (2024) used plasticine lizard models in a semi-arid Australian landscape and found that predation risk from red foxes was substantially lower in vegetated microhabitats, with 3.58 times lower predation than in bare ground. This is contradictory to results of the study undertaken in Thar, though can be explained by the selection of a spiky shrub by Braun et al. (2024) thus making it hard to distinguish between effects of protection against spikes and reduced visibility owing to the low predation attempts. Schooley et al. (2018) found that kit foxes were more abundant in landscapes with lower shrub cover. Within the Thar landscape, Misher and Vanak (2021) documented landscape-scale avoidance of dense *Prosopis juliflora* stands by the Indian desert fox in preference of Sueda-dominated habitats, though the habitat structures formed by Prosopis and Calotropis are structurally quite different. White et al. (2006) reported the avoidance of less complex habitats by *Vulpes vulpes* in an Australian riparian habitat during the day possibly for shelter during inactivity. Shepard (2007) through clay model experiment

found that habitat structure was the primary determinant of predator attack frequency on lizard models in the Brazilian Cerrado, with structurally complex habitats having higher frequency of predation. These findings hint at context-dependent changes in predator activities. Thus, the findings of this study, relating to increased predation in encroached habitats, cannot be explained currently.

Few methodological caveats in the study included colouring of clay models by ocular estimation of *Trapelus agilis* colour instead of replicating the spectrometric values and non-involvement of movement in clay models. These two shortcomings might explain the non-visitation of aerial predators on clay models, that have been found to depend on both movement (Shifferman and Eilam, 2004) and spectrometric colours of prey species (Lind et al. 2013). Furthermore, sample size (n = 2 sites) for each habitat type was too small to make generalisable inferences about predation patterns for the Thar landscape from the results.

2) Population and behavioural response of rodents to woody encroachment

a) Population response

Count of active burrow entrances was comparatively greater in no encroachment, suggesting that nocturnal rodent numbers decline with increasing woody encroachment in sandy scrublands. Active burrow counts did not differ between moderate and high encroachment plots. This pattern is consistent with a threshold response (non-linear), where rodents avoid using plots beyond a level of woody encroachment (Kluever et al., 2019; Misher et al., 2022; Smith et al., 2018).

Two opposing ecological mechanisms were expected to influence rodent abundance with increasing encroachment. Woody encroachment may negatively affect rodents through reduction in resource availability (Resource availability hypothesis), particularly vegetation and associated insect communities, but can simultaneously exert a positive effect through increased refuge availability and reduced perceived predation risk (Microhabitat selection hypothesis) (Lloyd & Vetter, 2019; Tait & Hovel, 2012). In the present study, shrub cover (other than *Calotropis*) decreased considerably from no to high encroachment. This potentially indicates a reduction in food availability for dominant nocturnal rodents such as *Gerbillus* spp. and *Tatera indica*, both of which are known to consume vegetative parts of shrubs and scrub vegetation especially during the winter season during which this study was conducted (Idris, 2008; Singla et al., 2017). Although insect abundance could not be quantified due to time constraints, studies from open ecosystems undergoing woody encroachment have reported declines in insect abundance and diversity due to habitat homogenisation and reduction in native vegetation heterogeneity (Anthelme et al., 2001; Ubach et al., 2020) Such changes could further reduce food availability for nocturnal rodents that opportunistically consume insects such as ants, beetles, and grasshoppers.

Even though GUD experiment suggested comparatively lower perceived predation risk in encroached habitats, rodent abundance still declined in encroached areas. This may indicate that resource limitation – which is often seen in homogenised woody habitat - has a stronger influence on the numerical response of nocturnal rodents than refuge-facilitated reduction in perceived predation risk.

If both increased refuge availability and reduced resource availability exerted comparable effects on rodent populations, a hump-shaped relationship between abundance and

encroachment might have been expected (Blaum et al., 2007), where moderate encroachment would have had the highest rodent abundance due to a balance between protective cover and decreased resource availability. Such a pattern was not observed in this case. Instead, the decline in active burrows from no to moderate encroachment suggest that the negative effects associated with resource reduction may outweigh the potential refuge benefits provided by encroachment.

Another possible explanation may relate to burrow-site selection and substrate characteristics. Rodents in the Thar Desert often prefer to construct burrows under vegetation cover in loose sandy substrates. Although *C. procera* may provide structural cover above ground, its growth pattern frequently results in mound formation and localised sand aggregation around the root system, potentially altering the suitability of the substrate for burrow construction. This interpretation remains speculative and falls outside the direct scope of the present study, particularly because burrow counts represented the entire nocturnal rodent community rather than species-specific responses. Moreover, not all species considered in this study possess the same substrate preferences. While *Gerbillus nanus* is known to preferentially burrow in sandy soils, species such as *Tatera indica* and *Gerbillus gleadowi* are also capable of occupying comparatively compacted or hardened substrates, including agricultural fallows (Prakash, 1997).

b) Behaviour of nocturnal rodents

Camera trap observations from artificial foraging patches in no encroachment scrublands indicated that nocturnal rodent activity fluctuated across the night rather than occurring continuously. Activity showed an oscillatory pattern (Mohr et al., 2003) with intermittent peaks

and declines, with the highest cumulative entry events and feeding duration observed around 23:00 h, suggesting more intensive foraging during this period.

The strong positive relationship between total entry events and cumulative feeding duration indicates that increased activity at trays was primarily driven by repeated visitation and prolonged exploitation of profitable food patches. In contrast, mean residence time showed only a weak relationship with entry frequency, suggesting that rodents frequently revisited trays without substantially increasing the duration of individual feeding bouts. Such short and repeated short-duration foraging bouts (mean~1 min) may point towards a strategy to balance energy requirements with predator avoidance.

Behavioural responses to woody encroachment:

A similar trend was also detected in the behavioural response of nocturnal rodent community, examined using giving-up density (GUD) as a proxy for perceived predation risk within the framework of optimal foraging theory. Encroached habitats showed comparatively lower GUD values, suggesting reduced perceived predation risk and increased willingness of rodents to forage within these habitats. This pattern is likely associated with microhabitat selection hypothesis where structural complexity of vegetation resulting from woody encroachment provides greater refuge availability (Blaum et al., 2007; Blaum et al., 2009; Scholes & Archer, 1997; Riginos, 2015; Smit et al., 2019).

To examine whether encroached habitats indeed differed structurally, two measures of habitat obstruction were quantified. Horizontal obstruction was measured using the Robel pole method. Horizontal obstruction in no and moderate encroachment did not differ substantially, while high encroachment exhibited relatively greater obstruction. Percent bare ground,

interpretated as an inverse proxy for vertical obstruction, showed similar values for no and moderate encroachment and was much lower in high encroachment. This suggests that visual obstruction was much higher in high encroachment than no and moderate encroachment.

Based on these structural patterns, it would be expected that perceived predation risk, represented by GUD values, would be relatively similar between no and moderate encroachment and lower within highly encroached habitats. However, the behavioural response did not completely follow this expectation. One possible explanation is that the structural measures used in the present study may not fully capture the aspects of vegetation complexity that are most relevant to nocturnal rodents and their predators. Although the Robel pole method is widely used to quantify vegetation obstruction (David et al., 2008; Lehman et al., 2017), several studies have noted limitations in its ability to capture fine-scale structural heterogeneity relevant to small mammals. Alternative approaches such as digital photography or cover-board methods may provide more precise estimates of concealment and visibility near the ground layer (Limb et al., 2007).

Another possible explanation is that GUD values in encroached habitats may reflect not only perceived predation risk, but also altered foraging decisions driven by resource limitation. Encroached habitats potentially contained lower natural food availability, while GUD trays provided a consistent and energetically rich food source in the form of fat-enriched peanut seeds. Under such conditions, rodents inhabiting resource-poor areas may adopt higher risk-taking strategies and forage for longer durations despite predation risk, resulting in lower GUD values. Consequently, the lower GUD observed in encroached habitats may represent the combined effects of refuge availability and increased energetic motivation to exploit

concentrated food resources (Brown, 1988; Kotler et al., 1993; Brown et al., 1994; Morris, 1997; Kotler et al., 2004; Prugh et al., 2008).

Drawing from the clay model experiment, nocturnal predation on clay models was lower in no encroachment compared to moderate and high encroachment areas. If predation pressure alone was determining perceived predation risk, lower predation within no encroachment would be expected to correspond with lower GUD values in these habitats. Such a pattern was not detected. Instead, the behavioural response observed through GUD experiments appeared to be only partially aligned with the predation patterns detected using clay models.

This pattern may also be explained by Optimal Risk Allocation Theory, which proposes that prey responses to predation risk depend not only on the intensity of risk but also on its temporal predictability and persistence (Lima & Bednekoff, 1999). When predation pressure fluctuates across time, prey is expected to reduce foraging activity during high-risk periods while allocating safer periods toward foraging. Under chronically elevated predation pressure, continuously maintaining strong antipredator responses may become energetically non-viable. As a result, prey may continue to forage despite elevated danger. The lower GUD and continued patch exploitation observed within moderate and highly encroached habitats, despite higher predation pressure, as indicated by clay model predation, may therefore reflect behavioural alterations under persistent risk conditions rather than reduced perception of danger.

This implies that GUD values are influenced not only by realised predation pressure, but also by multiple interacting ecological factors including refuge availability, food limitation, and behavioural trade-offs associated with foraging decisions. Rodents may perceive structurally complex habitats as relatively safer despite the presence of predators, particularly if vegetation

cover reduces immediate exposure during foraging activity. Whereas, reduced natural food availability in encroached habitats may reinforce the willingness of nocturnal rodents to forage from experimentally provisioned food trays. The compounded effects of these mechanisms likely explain the higher patch utilization under woody encroachment.

Moonlight illumination did not show a strong overall effect on giving-up density across encroachment levels. Increased moonlight illumination is generally expected to increase visibility for predators and therefore elevate perceived predation risk for nocturnal rodents (Prugh & Golden, 2013). However, the response detected in the present study varied across encroachment categories. Within no encroachment, moonlight did not influence GUD values. In moderate encroachment, high moonlight illumination resulted in notably higher GUD values, indicating that rodents gave up foraging earlier during brighter nights. High encroachment showed a similar directional trend, although the effect was weak and imprecise possibly due to limited sample size.

A contrasting pattern is expected based on habitat-mediated suppression of moonlight effect (Prugh & Golden, 2013). Greater vegetation cover within encroached habitats would likely reduce the amount of moonlight reaching the ground and provide increased concealment during foraging. Consequently, the behavioural effect of moonlight is expected to be stronger within open habitats characterised by no encroachment. Furthermore, if no encroachment represented habitats with higher perceived predation risk, increased illumination could potentially magnify this risk perception and result in earlier abandonment of food trays. Such a pattern was not observed.

A possible explanation is that since predation pressure (on clay models) was greater in moderate and high encroachment areas, perhaps due to greater predator activity, increased illumination may further enhance predator detection efficiency and therefore strengthen risk perception during foraging. The behavioural response to moonlight may therefore depend not only on habitat openness, but also on the underlying predation context associated with each habitat type (Prugh & Golden, 2013; predator-mediated lunar effects).

Another possible explanation relates to behavioural variability within no encroachment habitats. Considerable variation was observed in GUD values across sites and sampling nights, along with differences in foraging behaviour recorded through camera traps. Open habitats may permit greater flexibility in movement, vigilance behaviour, and patch use by nocturnal rodents, resulting in highly variable foraging responses that are difficult to detect statistically with limited sample size. Consequently, the absence of a clear moonlight effect within no encroachment may partly reflect high behavioural heterogeneity and insufficient sampling intensity rather than the absence of an ecological effect. Further sampling across seasons and lunar phases would be required to better understand how moonlight interacts with habitat structure and predation risk to influence nocturnal foraging behaviour in the Thar Desert.

Taken together, these results indicate that woody encroachment influences both the numerical and behavioural responses of nocturnal rodents within the sandy scrublands of the Thar Desert, although the mechanisms underlying these responses appear complex.

Rodent abundance, represented through active burrow entrances, declined consistently with increasing encroachment, suggesting that the negative effects associated with altered habitat composition and reduced resource availability may outweigh the refuge benefits provided by

increased vegetation structure. In contrast, behavioural responses measured using GUD suggested comparatively lower perceived predation risk within encroached habitats, highlighting that habitat structure may simultaneously provide concealment during foraging despite broader reductions in habitat suitability.

Several methodological limitations should also be considered while interpreting the findings. Active burrows represent an indirect estimate of rodent abundance of the whole nocturnal rodent community (due to inability to identify species-specific burrows based on signs) and may not fully capture species-specific occupancy or detectability differences across habitats. Similarly, GUD experiments integrate multiple behavioural processes beyond predation risk alone, including energetic state and foraging motivation. The clay model experiment was limited by low replication and inability to simulate natural prey cues such as scent, particularly for nocturnal predators relying heavily on olfactory cues. Consequently, the present study should be interpreted as an exploratory assessment of the ecological consequences of woody encroachment rather than a definitive mechanistic evaluation. Moreover, resource quantification which would have provided a better perspective of resource availability for the nocturnal rodents couldn't be quantified due to logistical constraints.

Despite these limitations, the study provides preliminary evidence that woody encroachment may alter ecological interactions within arid scrubland systems through simultaneous effects on habitat structure, resource availability, and behavioural decision-making of small mammals. Reduction in nocturnal rodent abundance may have broader ecological implications for the sandy scrublands of the Thar Desert. Rodents constitute an important prey base for several meso-carnivores within the landscape and therefore changes in rodent abundance could potentially influence predator activity, space use, and trophic interactions across the ecosystem.

Similar declines in small mammal abundance associated with woody encroachment have been linked to trophic restructuring and altered predator-prey dynamics in arid ecosystems elsewhere.

In addition to their role as prey, nocturnal rodents also influence vegetation dynamics through seed predation, caching, and seed dispersal. Consequently, the relationship between vegetation structure and rodent abundance is likely bidirectional. Although these broader ecosystem-level consequences were not directly examined in the present study, the observed decline in active burrow entrances with increasing encroachment suggests the possibility of wider functional changes occurring across trophic levels in the Thar landscape. Further studies integrating direct estimates of resource availability, rodent abundance, predator surveys, vegetation productivity, and seasonal resource dynamics would be necessary to better understand the long-term ecological consequences of woody encroachment in desert ecosystems

2) Abundance and flight-initiation distance of reptiles

a) Differences of escape tactics of the two lizards

The population and behavioural responses of two lizard species, i.e., *Acanthodactylus cantoris* (AC) and *Trapelus agilis* (TA) to woody encroachment were assessed. Both species showed contrasting responses to woody encroachment. The AC density reduced from no to moderate and high encroachment. This pattern could potentially be explained by reduction in resource availability with increase in encroachment. Percent native shrub cover decreased with increasing woody encroachment and since AC predominantly used native shrubs as refuge while fleeing from predators, reduction in shrub cover may reduce availability of refuge resources for the species.

On the contrary, TA used both shrubs and burrows as refuge. It was observed that individuals utilised both active and inactive rodent burrows. This behavioural flexibility may reduce the effect of woody encroachment on TA abundance by allowing utilisation of multiple refuge types despite changes in vegetation structure. This pattern raises the possibility that TA may have a competitive advantage under woody encroachment, reflected in higher abundance, due to greater behavioural flexibility in habitat use and resource acquisition.

Behaviourally, flight-initiation distance (FID), used as a proxy for perceived predation risk, was significantly higher for AC in no encroachment compared to moderate and high encroachment. Moderate and high encroachment did not differ much in FID, reinforcing the threshold-like response also observed in abundance of nocturnal rodent burrow, GUD and abundance of AC. TA, however, did not show any difference in FID across encroachment categories.

Field observations suggested substantial differences in escape behaviour between the two species. AC individuals were frequently observed actively foraging in open sandy areas. In no encroachment, even indirect predator approaches simulated from the side or behind frequently resulted in early fleeing responses. TA individuals, in contrast, were commonly observed basking near refuges, under shrubs, or partially inside burrows. TA individuals often did not flee during indirect approaches until the observer was extremely close. This may indicate differing antipredator strategies between the species. TA may rely more strongly on crypsis and camouflage, whereas AC may depend more on rapid escape towards refuge. Consequently, increase in woody encroachment may influence the escape behaviour of AC more strongly than TA.

The probability of selecting the nearest refuge for TA was lower in no encroachment than moderate encroachment, while a similar pattern was observed for AC between no and high encroachment. This could potentially indicate that no encroachment habitats provide greater refuge visibility and availability, allowing individuals to choose refuges based on quality rather than proximity alone. Earlier predator detection in open habitats may also provide greater decision-making time, enabling individuals to select refuges perceived as safer instead of simply escaping to the nearest available refuge (Cooper et al. 2009). These results suggest that TA might not be completely unaffected by woody encroachment but rather alter specific escape tactics in response to changing habitat structure.

The selective modification of antipredator tactics with encroachment is further supported by the refuge-use habits. For both species, the probability of taking refuge itself remained unchanged across encroachment levels, suggesting that refuge use remains a consistent component of escape behaviour irrespective of habitat structure. This suggests that although immediate refuge accessibility influences the timing of escape in TA (FID increased with distance to nearest refuge), it does not alter the overall tendency to use refuge following predator approach. Refuge use therefore appears to be a stable component of the antipredator behaviour of TA, while behavioural adjustments occur primarily through modification of escape timing and refuge selection.

FID for AC changed significantly with distance to nearest refuge only within moderate encroachment, where FID decreased with increasing distance to nearest shrub. This may indicate that individuals within moderate encroachment tolerate closer predator approach even when located farther from refuge. In contrast, within no encroachment, FID remained

consistently high irrespective of refuge distance, suggesting generally higher perceived predation risk within open habitats (Cooper & Whiting 2007; McElroy & McBrayer 2021).

b) Age- dependent escape tactics

AC showed different escape tactics depending on ontogeny of the individuals. The distance to nearest shrub was lower in juveniles as compared to adults. This aligns well with literatures showing juveniles have lower sprint speed, lower learned experience, high intrinsic mortality rate in comparison to adults, resulting in facilitation of more risk-aversive strategy so they can sprint to safety quickly by offsetting the distance to nearest refuge (Husak, 2006).

In AC, the flight-initiation distance of juveniles decreased with increasing distance to the nearest refuge while flight-initiation distance of adults remains mostly unchanged with distance to the nearest refuge. This difference might align with the theory that fleeing for smaller-bodied animals incur more cost and given their possibly reduced sprint speed, the chances of being intercepted mid-sprint increases for juveniles (Husak, 2006). Moreover, due to less learned experience, the latency to act might be greater. A combination of these reasons could possibly be delaying their response with increase in distance to nearest refuge.

Results from the clay model experiment could not be directly used to interpret behavioural responses of the reptile species since most predation events on clay models occurred nocturnally and were primarily attributed to Desert Foxes, Bengal Foxes, and Desert Cats. Both focal reptile species selected for the present study, *Acanthodactylus cantoris* and *Trapelus agilis*, are diurnal, and therefore are unlikely to experience similar predator assemblages or temporal predation pressures. Consequently, the clay model experiment may be more relevant in understanding predation dynamics associated with nocturnal fauna, particularly nocturnal

rodents. Further studies focusing on nocturnal reptiles may help clarify relationships between nocturnal predator activity detected through clay model experiments and behavioural measures of perceived predation risk in nocturnal desert species.

5. CONCLUSION

The overarching aim of this study was to understand the ecological consequences of woody encroachment in open ecosystems. The results indicate that woody encroachment does not lead to uniform shifts in trophic interactions. For both rodents and reptiles, measures of perceived predation risk showed strong dependence on microhabitat availability suggesting that structural changes introduce an altered distribution of risk and resources. The combined evidence from GUD, FID, and clay model experiments further indicates that the non-consumptive effects of predation are facilitated by interactions among visibility, refuge availability, and predator detection efficiency, which vary across encroachment levels and habitat types. Furthermore, abundance patterns in both taxa may be shaped by both behavioural adjustments and resource availability, producing context-dependent outcomes. These findings suggest that woody encroachment may shift prey-predator interactions and community dynamics, although the extent of generality remains uncertain without large-scale future studies. From a management perspective, these results highlight the importance of considering trophic-level responses while designing woody plant management programmes. In systems invaded by *Calotropis procera,* management interventions should account not only for changes in vegetation structure but also for their potential consequences for predator-prey interactions, habitat use, and the persistence of fauna associated with open habitats.

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7. APPENDIX

Appendix 1: Summary statistics comparing additive and interactive models (hypothesis) explaining the variation in Flight-initiation distance of Acanthodactylus cantoris in Thar desert (2026)

Fixed effect	K	-2logL	AICc	Delta AICc	Akaike weight
Encroachment × Log (Distance to the nearest refuge) + log (starting distance)	8	119.46	79.5	0	1

Encroachment +log (starting distance) + Log (Distance to nearest refuge)	6	122.81	135.5	5.94	0

Appendix 2: Parameter estimates of interactive model relating predictors encroachment level and distance to nearest refuge with the log-transformed FID of Acanthodactylus cantoris in Thar during 2026

	log(flight)		
Predictors	*Estimates*	*Std. Error*	*Z value*
(Intercept)	0.40	0.43	0.93
DNS [log]	0.06	0.06	1.09
encroachment [mod]	0.53	0.37	1.43
encroachment [High]	-0.12	0.39	-0.30
starting distance [log]	0.83	0.07	11.67
DNS [log] × encroachment [mod]	-0.21	0.10	-2.09
DNS [log] × encroachment [High]	-0.09	0.104	-0.875
Observations	47		

R^2 / R^2 adjusted 0.575 / 0.499

Appendix 3: Summary statistics comparing additive and interactive models (hypothesis) explaining the variation in Flight-initiation distance of Acanthodactylus cantoris in Thar desert (2026)

	Fixed effects	K	-2logL	AICc	Delta AICc	Akaike weight
Model 1	Log (Distance to nearest refuge) × Age class + log (starting distance)	8	144.42	131.5	0	0.934
Model 2	Log (Distance to nearest refuge) +Age class + log (starting distance)	7	121.96	136.8	5.28	0.066

Appendix 4: Parameter estimates of interactive model relating predictors age class and distance to nearest refuge with the log-transformed FID of Acanthodactylus cantoris in Thar during 2026

log(flight)			
Predictors	*Estimates*	*Std. Error*	*Z value*
(Intercept)	0.36	0.48	0.75
DNS [log]	0.05	0.05	0.94
age class [juvenile]	0.87	0.35	2.48
starting distance [log]	0.85	0.07	11.33
encroachment [mod]	-0.23	0.08	-2.68
encroachment [High]	-0.45	0.08	-4.96
DNS [log] × age class [juvenile]	-0.28	0.09	-2.78
Observations	137		
R^2 / R^2 adjusted	0.65 / 0.64		

Appendix 5: Visitation of Gerbillus sp. in GUD trays

Appendix 6: Trapelus agilis under Calotropis procera

Appendix 7: Acanthodactylus cantoris in high encroachment

Appendix 8: Clay model predation by Bengal fox

Appendix 9: Clay model predation by Desert fox

Appendix 10: Solitary burrow entrance of a nocturnal rodent

Appendix 11: Aggregated burrow entrances of a diurnal rodent (Meriones hurrianae)