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Animal Biodiversity and Conservation 49.1 (2026)
DOI: 10.32800/abc.2026.49.0011

Research paper

Habitat occupancy and microhabitat use of *Uromastyx acanthinura* in arid regions of Tunisia

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Handling Editor:
Gregorio Moreno-Rueda

Received: 23/12/2025
Cond. acceptance: 12/02/2026
Final acceptance: 07/05/2026
Published: 26/05/2026

Cite:
Kechnebbou M, Belliure J, Chammem M, 2026. Habitat occupancy and microhabitat use of *Uromastyx acanthinura* in arid regions of Tunisia. *Animal Biodiversity and Conservation* 49.1, e0011. DOI: https://doi.org/10.32800/abc.2026.49.0011

Abstract

Habitat occupancy and microhabitat use of Uromastyx acanthinura *in arid regions of tunisia.* Understanding species distributions and the factors shaping them is an important topic in ecology and conservation. This study explores the spatial distribution and habitat requirements of the desert lizard *Uromastyx acanthinura* in desert and arid areas of southern Tunisia. From February 2016 to November 2018, repeated field surveys were conducted across 50 sampling sites to locate individuals and active burrows of *U. acanthinura*. For each plot, microhabitat characteristics (altitude, burrow entrance direction, mountain slopes orientation, distance to nearest road, agricultural areas, and urban areas) were recorded. The abundance of predators such as diurnal carnivores (foxes and wolves) and prey (insects), as well as plant abundance, was also noted. Generalized linear mixed models were used to identify the main drivers of *U. acanthinura* occurrence in Tunisia. Our results indicate that lizard occurrence is positively associated with rocky habitats located near agricultural and urban areas, and with mountain slopes oriented between southwest and southeast exposures. In addition, food availability played a key role, as both plant and insect abundance were significantly higher in occupied plots and positively correlated, indicating that the species is more likely to occur in sites with higher resource availability. These findings further indicate that habitats located near agricultural and urban areas may provide enhanced foraging opportunities for the species.

Key words: Desert lizard, Habitat occupancy, Spatial distribution, Anthropic disturbance

Introduction

Understanding the habitat requirements of animal species is essential for developing effective conservation plans and guiding the management of threatened populations (Wone 1992, Díaz et al 2005, Souter 2006). For reptiles, especially lizards inhabiting arid and desert environments, habitat use is strongly constrained by environmental conditions, making the identification of key habitat features critical for understanding species distribution and persistence (Todd et al 2010, Elbahi et al 2023).

In these extreme environments, lizards exhibit a variety of habitat use strategies driven by thermoregulation, predator avoidance, and access to food resources (Martín and López 2002, Kearney and Porter 2009, Kechnebbou et al 2025). They often rely on specific structural elements such as rocks, vegetation, burrows, and crevices for thermal buffering and protection, and their habitat use may vary seasonally in response to changing environmental conditions (Ortega et al 2016, Kechnebbou et al 2021). In addition, resource availability, reflected by vegetation abundance, can indirectly influence trophic resources such as invertebrates, potentially shaping habitat suitability (Pianka 1986, Zeng et al 2014).

The North African spiny-tailed lizard *Uromastyx acanthinura* is a large, predominantly herbivorous agamid listed as Near Threatened by the IUCN (Wagner et al 2021). It is the only *Uromastyx* species known to occur in Tunisia (Wilms et al 2009a, Kechnebbou et al 2020), with a distribution spanning eastern Algeria, southern Tunisia, and northwestern Libya. In these regions, summer temperatures can exceed 50 °C, making thermal refuge critical for survival (Wilms et al 2009a, Tamar et al 2017).

Although the causes of the decline of this species have not been well identified, human-related habitat loss is thought to be a major threat (Kechnebbou et al 2021, Elbahi et al 2023). Habitat fragmentation, agricultural expansion, and the removal of rocks for construction have reduced the availability of suitable shelter sites (Wilms et al 2010, Kechnebbou et al 2019a). Additionally, *U. acanthinura* is subject to intense poaching for food, traditional medicine, and international pet trade. Road mortality and climate change further exacerbate these pressures (Kechnebbou et al 2019a, 2019b, 2021).

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ISSN: 1578-665 X eISSN: 2014-928 X

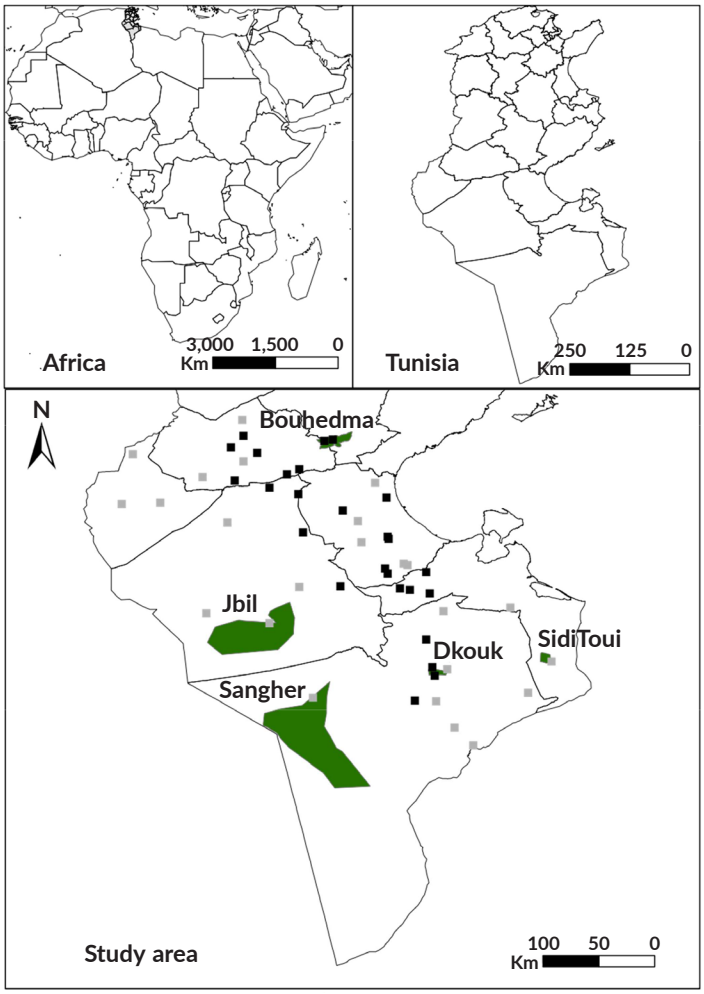

Fig. 1. Study area showing the presence (black symbols) and absence (grey symbols) of *Uromastyx acanthinura*, and the location of protected areas (green).

In Tunisia, the species is primarily associated with mountainous areas and rocky substrates. However, baseline ecological data remain limited, constraining both our understanding of its habitat requirements and the formulation of appropriate management strategies. Previous studies in the region have described aspects of the species' ecology and morphology, spatial distribution, and the relationship between physiological stress and human disturbance (Kechnebbou et al 2019a, 2019b), but have not quantitatively evaluated the relative importance of microhabitat characteristics or the combined effects of habitat structure, food availability, and human disturbance on species occurrence.

The objective of this study is to characterize habitat use of *U. acanthinura* in southern Tunisia and to identify the environmental factors influencing its occurrence, with the aim of informing future conservation and management actions. We evaluated key habitat components, including: (1) human disturbance (e.g., proximity to roads and urban areas), (2) refuge availability (e.g., presence of rocky burrows, slope orientation, and burrow entrance direction), (3) food resources (e.g., prey abundance and the presence of agricultural fields), and (4) predator abundance. These components were compared between sites where lizards were present and adjacent areas where they were absent.

Material and methods

Study area

This study was conducted in arid and desert regions of southern Tunisia, spanning from 31.08° to 34.70°N and 7.85° to 11.18°E. Five protected areas located within this region were included in this study (fig. 1). The study area covered approximately 85,000 km² and encompassed three bioclimatic zones: lower arid, lower Saharan, and upper Saharan stages (Nouira 1996). These zones span diverse topographies, including mountainous regions, steppe plains, and chott basins. The region experiences a highly variable thermal desert climate. Average minimum temperatures during the coldest month (January) range between 4 °C and 7 °C, while average maximum tempe-

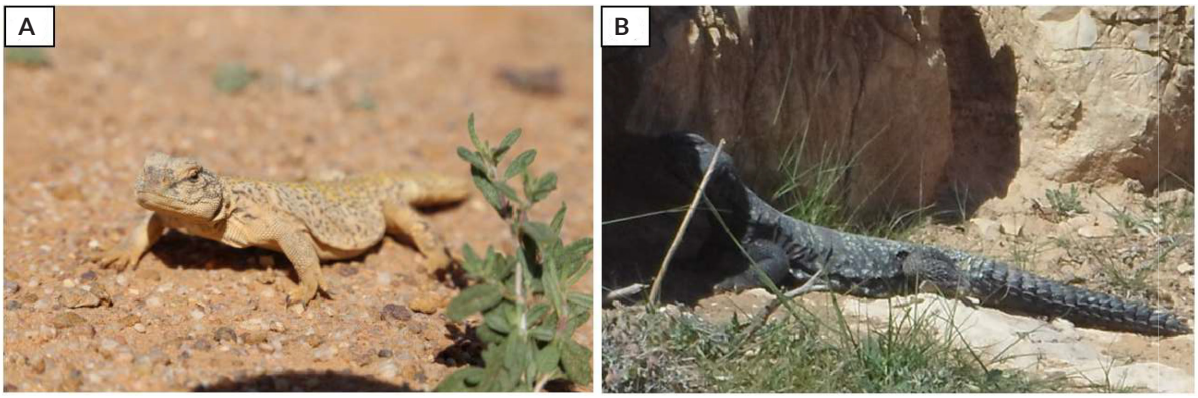

Fig. 2. Photographs of *Uromastyx acanthinura* in its natural habitat: A, adult female; B, adult male.

ratures in the hottest month (August) reach above 31 °C along the coast and up to 36 °C in the interior. Extreme temperatures can rise above 50 °C in the shade due to the influence of the sirocco (Chehili), a hot and dry wind originating from the south or southwest, which also contributes to relative humidity levels dropping below 10 %. Annual precipitation is scarce and irregular, ranging from 100 to 200 mm, with most rainfall concentrated in short episodes (Christidis et al 2023, Kechnebbou et al 2025).

Sampling method and habitat variables

Fieldwork was carried out during the active period of *U. acanthinura* (fig. 2), from February 2016 to November 2018, covering spring, summer, and autumn seasons. A total of 50 sampling sites, each measuring 4 km², were distributed across the study area using a Geographic Information System (GIS) to intensively search for individual U. acanthinura and their burrows. Site selection was guided by the known distribution of the species in the region. Within each site, three plots (500 × 500 m each), spaced approximately 2 km apart, were selected, resulting in a total of 150 plots. The distance between sampling sites ranged from 17 to 50 km (fig. 1).

Field surveys were conducted from 08:00 to 17:00h, under sunny weather conditions, 3-4 days per week. Each site was surveyed repeatedly (3-4 visits per site) to ensure reliable detection and to confirm species presence/absence. Three observers conducted visual surveys using binoculars (Leica Trinovid 10 × 50 BA), a telescope (Leica Televid 77, 20-60 BA), and spotlights to detect individuals and active burrows. A sampling plot was classified as occupied when at least one active burrow was identified. Burrows were considered active if an individual was directly observed or if signs of recent activity –such as tail-drag marks or fresh fecal matter– were present near the entrance. In contrast, unoccupied plots were defined as those where no burrows or signs of lizard activity were detected, despite repeated visits and confirmation from local residents.

For each sampling plot, several habitat variables were recorded to characterize local environmental conditions. Geographic coordinates and altitude (Alt) were recorded in the field using a GPS. Burrow entrance orientation (Asp_bur) was measured for occupied plots, and a single value corresponding to the first active burrow detected within each plot was used in the analysis. Mountain slope orientation (Asp_loc) was recorded for each plot. Distance to nearest agricultural area (Dist_agr), Distance to nearest urban area (Dist_urb), Distance to nearest regional road (Dist_road) were calculated using ArcView GIS 3.3 (Environmental Systems Research Institute, Redlands, CA, USA), based on the minimum distance from each sampling plot to the nearest corresponding landscape feature, following the approach described in Kechnebbou et al (2019b). Predator abundance (Abun_pred) was estimated as an index of relative abundance based on counts of carnivore tracks and fecal pellets (e.g., foxes and wolves) recorded along a 200 m transect randomly placed within each plot, following sign-based survey methods commonly used in wildlife ecology (Gompper et al 2006, Carreras-Duro et al 2016).

Plant abundance was estimated using the aligned point quadrat method (Levy and Madden 1933, Daget and Poissonet 1971). Vegetation sampling was conducted in 44 of the 50 sampling sites. At each of these sites, one plot was selected for vegetation assessment, within which a 1 m² quadrat was established. Vegetation was recorded at 10 cm intervals along linear transects within the quadrat (100 points per plot). At each point, the intercepted plant species was identified. Plant availability was expressed as the proportion of contacts per species relative to the total number of sampling points.

Insect abundance was estimated using pitfall traps (n = 50; 95 mm in diameter). Insect sampling was conducted in one plot per site, which was considered representative of local insect availability at the site scale. Traps were partially filled with 70 % ethanol, closed overnight, and operated for two consecutive days in each plot during the spring sampling period, corresponding to the main activity period of the species, over three consecutive years. Captured insects were identified to major taxonomic groups (Hymenoptera, Lepidoptera, Coleoptera). Although pitfall traps do not capture the entire insect

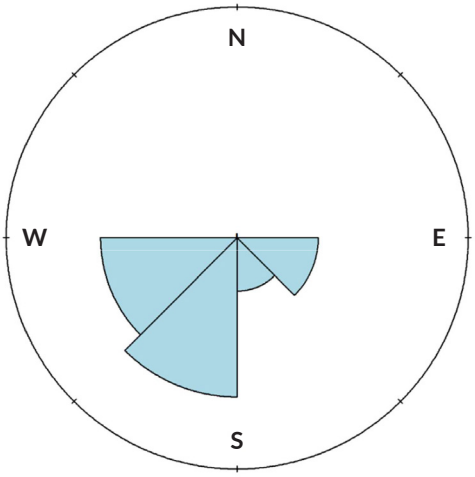

Fig. 3. Circular histogram showing the slope orientation of sampling plots where *Uromastyx acanthinura* burrows were recorded. The distribution indicates a predominance of burrows on slopes with western and south-western exposure.

community, they effectively sample ground-active insects, which are part of the diet of *U. acanthinura* (Bendami et al 2018, Kechnebbou et al 2019a). Insect relative abundance (Abun_insect) was quantified as the total number of individuals captured per trap (Pianka 1986, Bestelmeyer et al 2000).

Statistical analyses

Generalized Linear Mixed Model (GLMM) with a binomial error distribution and logit link function was used to assess the effects of environmental variables on the occurrence of *U. acanthinura*. Prior to model fitting, collinearity among explanatory variables was assessed using pairwise correlations, and no strong correlations were detected ($|r| < 0.3$). The initial set of explanatory variables included altitude (Alt), distance to roads (Dist_road), distance to urban areas (Dist_urb), distance to agricultural areas (Dist_agr), predator abundance (Abun_pred), slope orientation (expressed as sine and cosine components: sin_loc and cos_loc), and rock presence (Rock_pres). Sampling site was included as a random effect to account for the non-independence of plots within sites. Continuous variables were standardized (mean = 0, SD = 1) prior to analysis. Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc), and model averaging was applied to models with $\Delta AICc < 4$.

In addition, differences in plant abundance (Plant_abun) and insect abundance (Insect_abun) between occupied and unoccupied plots were assessed using non-parametric Wilcoxon rank-sum tests based on one representative plot per sampling site (44 plots in total). These variables were analyzed separately and were not included as explanatory variables in the GLMM. The relationship between plant and insect abundance was evaluated using Spearman's rank correlation.

The orientation of burrow entrances was analyzed using circular statistics. A circular histogram (rose diagram) was constructed to visualize the distribution of burrow entrance directions. All mean values are reported as mean ± standard error (SE), and all statistical analyses were performed using R software (version 4.5.2).

Results

Burrow distribution and orientation

Active burrows were detected in 26 of the 50 sampling sites. Out of the 150 sampling plots, *U. acanthinura* was recorded in 58 plots, while 92 plots were classified as unoccupied.

A total of 405 burrows were recorded across the study area, of which 176 (43.46 %) were classified as active. Active burrows showed a clustered distribution, with 1-8 clusters per site and 1-13 active burrows per cluster. Burrow density ranged from 1 to 18 burrows/km², with the highest number of active burrows recorded in Dkouk National Park (n = 44).

Distance between neighboring active burrows, obtained from a matrix of pairwise distances, ranged from 25.5 ± 7 m to 2550 ± 80 m. Sex was determined for 173 individuals (65 males, 108 females) based on external morphological characteristics. Mean inter-burrow distance was significantly greater for males (male-male distances: 623.90 ± 150.70 m) than for females (female-female distances: 158.80 ± 55.27 m; $F_{1,88} = 122.93$, $P < 0.0001$). Active burrows were predominantly located on sloped terrain with scattered rocks and sparse vegetation. The orientation of burrow entrances showed a non-random distribution, with a predominance of western and south-western exposures (fig. 3).

Habitat occupancy

Generalized Linear Mixed Model (GLMM) identified several environmental variables influencing the occurrence of *U. acanthinura* (table 1). The probability of species presence decreased significantly with increasing distance from urban areas ($\beta = -20.99$, $p < 0.001$) and agricultural areas ($\beta = -25.04$, $p = 0.024$), as well as with increasing predator abundance ($\beta = -28.19$, $p < 0.001$). In contrast, the presence of rocks strongly increased the probability of occurrence ($\beta = 68.99$, $p < 0.001$).

Slope orientation showed a significant effect, with the sine component (sin_loc) negatively associated with species occurrence ($\beta = -23.68$, $p = 0.044$), indicating a higher probability of presence on slopes oriented between southwest and southeast. Altitude, distance to roads, and the cosine component of slope orientation (cos_loc) did not have significant effects on species occurrence.

Food availability

Plant abundance and insect abundance were both significantly higher in plots where *U. acanthinura* was present compared to unoccupied plots (Wilcoxon tests, $p < 0.001$ in both cases). Mean plant abundance was substantially higher in occupied plots, and a similar pattern was observed for insect abundance. In addition, plant abundance was positively correlated with insect abundance (Spearman's $\rho = 0.54$, $p < 0.001$), indicating that plots with higher vegetation availability also supported higher insect abundance.

Table 1. Results of model averaged GLMM testing the effects of environmental variables on the presence/absence (P/A) of *U. acanthinura* lizards. Significant probabilities are marked in bold. Note: Estimates are model-averaged coefficients based on full averaging across candidate models from GLMM fitted with binomial error distribution and logit link, with site included as a random effect. Continuous variables were standardized.

Variable	Estimate	SE	z	p
Intercept	-78.69	13.65	5.77	**<0.001**
Dist_agr	-25.04	11.06	2.26	**0.024**
Dist_urb	-20.99	6.23	3.37	**<0.001**
Abun_pred	-28.19	7.96	3.54	**<0.001**
Rock_pres	69.00	14.39	4.79	**<0.001**
Sin(Asp_loc)	-23.68	11.78	2.01	**0.044**
Alt	-0.48	4.45	0.11	0.914
Dist_road	-0.62	1.52	0.41	0.681
Cos(Asp_loc)	0.47	1.16	0.41	0.683

Discussion

Habitat requirements

This study provides the first quantitative evidence of habitat occupancy of adult *U. acanthinura* in Tunisia and demonstrates that both anthropogenic and environmental factors shape its distribution. Species occurrence was strongly influenced by proximity to urban and agricultural areas, whereas distance to regional roads had no detectable effect. The higher occurrence observed near urban and agricultural areas may reflect indirect ecological effects rather than a direct positive influence of human activities. Agricultural areas may increase vegetation cover, trophic resources, and habitat heterogeneity, factors that can improve local habitat conditions in arid environments (Díaz et al 2005, Zeng et al 2014). This interpretation is supported by the positive relationship observed between plant and insect abundance, indicating that areas with higher primary productivity may offer greater foraging opportunities for the species. In addition, the positive association observed with urban areas may arise because both human activities and *U. acanthinura* are concentrated in sites with higher primary productivity. Under this scenario, the observed relationship would reflect shared habitat selection rather than facilitation. This spatial overlap may also indicate potential conservation conflict, as productive habitats are often exposed to increasing anthropogenic pressure (Balmford et al 2001). The absence of a significant effect of road proximity may reflect the relatively low traffic intensity in the study region, which may reduce the potential impacts of roads on habitat use and mortality.

U. acanthinura is primarily herbivorous (Wilms et al 2010, Bendami et al 2018, Kechnebbou et al 2019a), although the consumption of invertebrates has also been reported. In this study, insect abundance was significantly higher in occupied plots, suggesting that invertebrates may contribute to local resource availability. However, plant and insect abundance were positively correlated, indicating that higher insect abundance may reflect more productive environments with greater vegetation availability. Consequently, the relationship between insect abundance and species occurrence may be both direct (through prey consumption) and indirect (through its association with vegetation), highlighting the importance of resource availability in shaping habitat occupancy (Díaz and Carrascal 1991, Milne 1999, Nordberg et al 2017).

Predator abundance was negatively associated with species occurrence, indicating that predation pressure is an important factor shaping habitat occupancy. Similar patterns have been reported in other lizard species, where increased predator activity can reduce habitat use or alter spatial behavior to minimize risk (Díaz and Carrascal 1991, Martín and López 2002). In this context, the selection of habitats providing effective refuges is likely a key strategy to mitigate predation risk.

Our results further confirm a marked association with mountainous terrain characterized by scattered rocks and sparse vegetation, consistent with previous studies across the species' range (Wilms et al 2010, Kechnebbou et al 2019a). Substrate structure is a key determinant of desert lizard distributions, as it influences both thermal buffering and refuge availability, thereby reducing predation risk (Souter 2006, Wilms et al 2011).

Burrow characteristics emerged as a critical component of habitat suitability. Burrows provide protection from predators, mitigate thermal extremes, and contribute to water balance in arid environments (Souter 2006, Wilms et al 2010). The preference for sloped terrain and burrow entrances oriented between west and southwest likely reflects an adaptive strategy to maximize solar radiation during key activity periods while minimizing exposure to prevailing northeasterly winds. Similar orientation patterns have been reported in other populations of *U. acanthinura* and *U. a. microlepis* (Cunningham 2000, Wilms et al 2009b), although the absence of consistent trends in some regions suggests that burrow orientation may vary in response to local climatic conditions (Al-Ogily and Hussain 1983).

Implications for conservation management

Despite the presence of five protected areas within the distribution range of *U. acanthinura* in Tunisia, the species was detected in only a subset of these areas (Bouhedma National Park and the Dkouk Conservation Area). However, sampling within protected areas was limited and does not allow a robust assessment of habitat conditions where the species was not detected. The occurrence of the species in three protected areas nevertheless suggests that these areas can provide suitable conditions, although protection status alone may not be sufficient to ensure its persistence.

Our results highlight the importance of habitat structure and resource availability in shaping species occurrence. In particular, rocky substrates appear to be a key component of suitable habitat, providing essential refuges for thermoregulation and protection from predators. The conservation of these structural elements should therefore be a priority, especially in landscapes increasingly

affected by agricultural expansion and construction activities (Corbett 1989, Díaz et al 2005, Kechnebbou et al 2019a). In addition, the association of the species with areas closer to agricultural and urban environments suggests that certain human-modified landscapes may provide locally favorable conditions, likely through increased resource availability. This emphasizes the importance of maintaining habitat heterogeneity and limiting practices that reduce vegetation cover or remove natural refuges.

In areas where rocky substrates have been degraded or removed, habitat restoration actions such as the preservation or addition of stones and boulders may help improve local habitat suitability. Similar approaches have been shown to enhance refuge availability and occupancy in other reptile species (Hecnar and McCloskey 1998, Webb and Shine 2000, Mateo 2004, Souter 2006).

Given the species' cryptic behavior and the rugged environment it inhabits, future research would benefit from the use of radio-telemetry to better understand movement patterns, home-range size and fine-scale habitat use (Whitaker and Shine 2003, Salvador et al 2004). Such information would be valuable for refining habitat management and improving conservation planning.

Conclusion

This study provides new insights into the environmental factors associated with the occurrence of *U. acanthinura* in arid regions of Tunisia. Our results show that species occurrence is shaped by a combination of habitat structure, resource availability, and biotic interactions. In particular, rocky substrates and proximity to human-modified environments were positively associated with occurrence, while predator abundance had a negative effect. In addition, the positive relationship between plant and insect abundance highlights the role of resource availability in structuring suitable habitats. Together, these findings emphasize that both natural habitat features and landscape context are important in determining species distribution. Improving our understanding of these factors is essential for developing effective conservation strategies for this species in rapidly changing arid ecosystems.

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Acknowledgements
We thank Belgacem Khchira and Ali Zaidi for their assistance during fieldwork. We are also grateful to the Editor and the two anonymous reviewers for their constructive comments and suggestions, which helped improve the quality of the manuscript.

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M Kechnebbou: Conceptualization, methodology, fieldwork, data analysis, visualization, and writing of the original draft and revised manuscript; **J Belliure:** Methodology, supervision, and manuscript revision; **M Chammem:** Methodology, supervision, and fieldwork.

Conflicts of interest
The authors declare no conflicts of interest.

Funding
The authors received no financial support for this study. Fieldwork was supported by the Livestock and Wildlife Laboratory, Arid Lands Institute, Medenine, Tunisia.

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