



Dry conditions and predation risk shape the spatial ecology of introduced aoudad

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Abstract

Introduced non-native ungulates can alter ecosystem processes and generate management conflicts. Thus, understanding spatial behavior and habitat use in invaded landscapes is highly relevant. We investigated seasonal home range and habitat selection of the natively African mountain species aoudad *Ammotragus lervia*, introduced in the Southern Dinaric Alps, Croatia, using GPS telemetry data. We used Kernel Density Estimates to estimate seasonal home range size and assessed habitat selection in several temporal scales through integrated Step Selection Analysis. Aoudad exhibited marked seasonal variation in home range size, with more restricted space use during the warm period, potentially suggesting aggregation in more favorable microhabitats under drier conditions. Habitat selection revealed consistent preference for high elevations and steep slopes, while the species avoided north facing and east facing aspects and areas with high tree cover density in both warm and cold seasons. During the night, avoidance of tree covered areas intensified and selection shifted towards steeper terrain, consistent with patterns expected under increased perceived predation risk. Weather conditions further modulated habitat selection, with temperature and wind influencing selection of slope and elevation, respectively. Overall, our findings support the capacity of the African aoudad to persist under Mediterranean mountain conditions.

Keywords *Ammotragus lervia* · Barbary sheep · GPS telemetry · Habitat selection · Home range · Ungulates

Introduction

Understanding the behavior of introduced wild ungulate species is fundamental for predicting their ecological impacts, and guiding management strategies. Studies based on the behavioral ecology of the species can provide valuable insights about how introduced animal species interact with their novel environments, shaping environmental dynamics of flora and fauna, and altering ecosystem processes (Banks and Dickman 2007; Merkle et al. 2015; Richardson et al. 2000). Behavioral adaptability is required for invasion success, enabling species to exploit unfamiliar resources and evade local predators (Chapple et al. 2012; Holway and Suarez 1999). Because introduced species pose a threat to ecosystem functions through competition for resources, habitat modification, and pathogen spread (Simberloff et al. 2013), a detailed understanding of their behavioral and spatial ecology can help to mitigate their impact.

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Relevant advances in animal tracking technology during the last two decades have revolutionized the field of spatial ecology and the study of animal movement and habitat use (Cagnacci et al. 2010). These capabilities benefit research on movement and space use of wildlife species, including introduced animals (Recio et al. 2010, 2014; Recio and Seddon 2013), that are already or can potentially become invasive species. Data obtained through GPS tracking and accelerometers allow improved analyses of home range dynamics, habitat selection, and behavioral responses to environmental variability (Hebblewhite and Haydon 2010; Kays et al. 2015; Seigle-Ferrand et al. 2021). Such valuable data also support models of potential range expansion, habitat suitability assessments, and assist the design of management interventions able of minimizing the ecological footprint of introduced animal populations.

The aoudad or Barbary sheep *Ammotragus lervia* is a wild caprine native to the arid mountains of North Africa, initially imported to European zoos in the 19th century (Cassinello 1998) and later introduced across the continent for game/trophy hunting (Šprem et al. 2022). Non-native species are commonly introduced into new habitats to create or improve hunting opportunities, especially when native game species have become scarce. Today, free-ranging European populations of the aoudad are established in Croatia, France, Italy, and Spain (Leoncini et al. 2023; Stipoljev et al. 2021; Šprem et al. 2022), with an estimated total number of at least 3,500 mature individuals (Cassinello et al. 2025). Self-sustaining populations also occur in the United States and Mexico (Wright et al. 2024). The ecological flexibility of the aoudad, combined with behavioral traits such as social preferences, utilization of available food resources, and a high anti-predator vigilance, have facilitated its persistence across a wide range of environments (Šprem et al. 2022). To date, the aoudad's deleterious ecological impacts have been documented exclusively on La Palma (Canary Islands, Spain), where the endemic Macaronesian flora lacks evolutionary adaptations to large herbivores (Cassinello 2015). Nevertheless, increasing aoudad population densities in Spain have sparked human-wildlife conflicts, manifested primarily through crop damage and resource competition with livestock (Cassinello 2000).

Several studies have characterized the spatial ecology and behavior of the aoudad, focusing on distribution patterns, habitat selection, activity patterns, and home range requirements (Anadón et al. 2018; Cassinello 1998; Leoncini et al. 2023; Pascual-Rico et al. 2020; Prpić et al. 2020). However, studies utilizing GPS tracking in this species remain scarce, with current research

only available in Spain, where Pascual-Rico et al. (2018) provide results on home ranges and the use of feeding stations.

Furthermore, most of the aforementioned studies have been conducted on aoudad populations in the absence of large predators. However, it is well established that the presence of large predators can induce shifts in ungulate behavioral niches via antipredator strategies aimed at reducing predation risk. These shifts are typically reflected in altered habitat use (e.g., increased selection for rugged terrain; (Jones et al. 2022; Villepique et al. 2015), increased dispersal (e.g., relocation to safer areas; (Thaker et al. 2011), and changes in activity patterns, particularly a pronounced shift toward nocturnality and temporal avoidance of periods of heightened predator activity (Šprem et al. 2015).

Understanding the movement dynamics of introduced aoudad populations is essential for evaluating how this species uses novel Mediterranean environments, and for potential interactions with sympatric native ungulates, ultimately advancing evidence-based conservation and management. This research aims to provide pioneer insights into the spatial ecology of the aoudad within a European Mediterranean context outside of Spain by leveraging GPS tracking data. Given that aoudad is native to arid and mountainous regions of North Africa, where resources are often scarce (Cassinello et al. 2025), we expected that Mediterranean mountain conditions in coastal Croatia would be broadly compatible with the species' habitat requirements. We further hypothesized that wolf predation risk would shape habitat selection, driving aoudad towards safer habitats, particularly steeper terrain, and away from forest cover during the night, when predation risk is expected to be higher. In this vein, we specifically estimated seasonal habitat selection while accounting for seasonal space use and temporal variation in movement. In doing so, we seek to offer critical evidence on how introduced ungulates utilize space when colonizing novel environments.

Materials and methods

Study area

The study was conducted in the southern Dinaric Alps, on Mt. Mosor (43°31'54" N, 16°38'29" E), Croatia, with its highest point at Veliki Kabal (1,339 m a.s.l.), and a mean elevation of 591 (SD: ± 236) m (Fig. 1). The mountain is predominantly composed of Mesozoic limestone

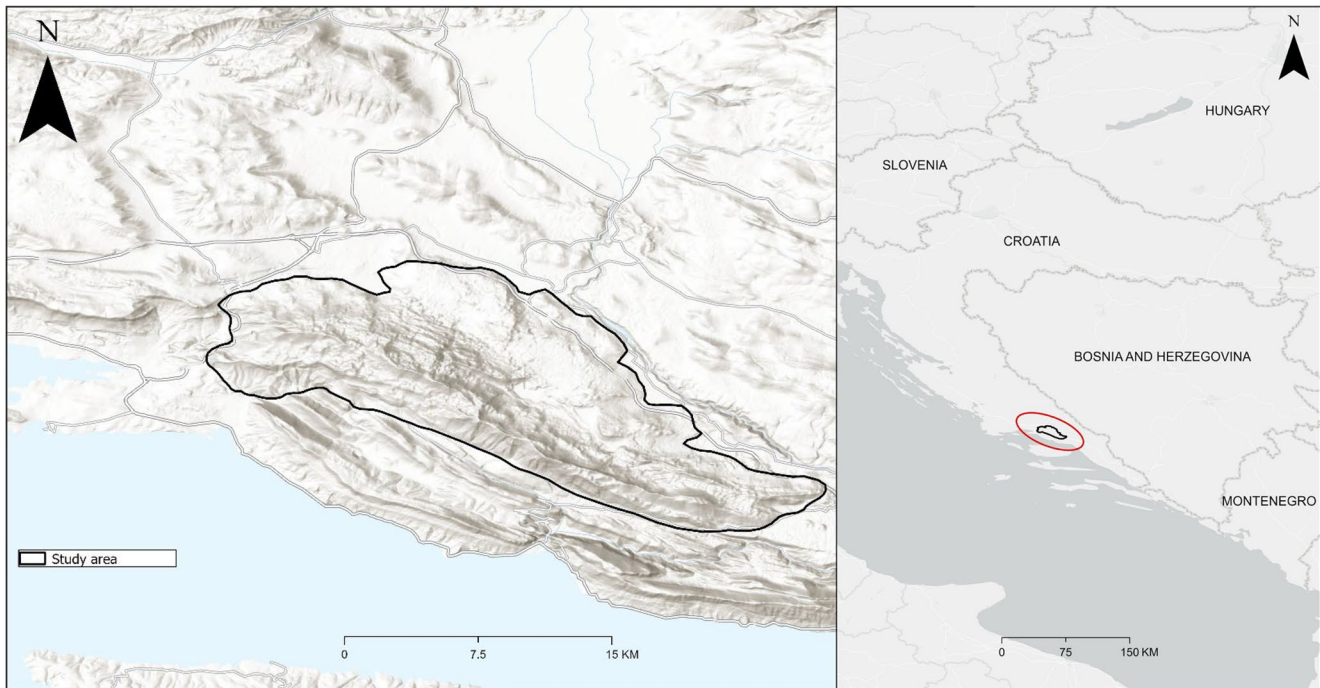


Fig. 1 Mt. Mosor study area in the southern Dinaric Alps, Croatia (173.1 km²)

sediments. Climatically, the Mediterranean zone dominates with a mean annual temperature of 10.8 °C and a mean annual precipitation of 1,665 mm. Beyond the 1,200 m mark, the climate shifts towards a montane climate. The topography is highly heterogeneous, characterized by gullies, depression, and prominent rocky outcrops. Vegetation primarily consists of sub-Mediterranean and Euro-Mediterranean scrubland and woodland communities (Prpić et al. 2020).

Study population

In 2002, three females and two males from the Czech Republic, Germany, and Slovakia, were illegally released in the Mosor Mountains of Croatia (Šprem et al. 2022; Stipoljev et al. 2021). The resulting established population has adapted well to the new environment and the Mediterranean climate. The current estimated population size is about 200 individuals (Lazarus et al. 2019), with approximately 25 individuals harvested annually. Besides aoudad, other ungulates occur in the study area, including the wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, European mouflon *Ovis aries musimon*, and Balkan chamois *Rupicapra rupicapra balcanica*. The study area is also home to two large carnivores, the brown bear *Ursus arctos* and the grey wolf *Canis lupus*.

Aoudad capture and telemetry data

Aoudad were captured between 2015 and 2019 using net enclosures. Individuals were lured with corn to a pre-established capture site, which was subsequently enclosed. After an acclimation period, captures were conducted by teams of 6–8 personnel. Sampling aimed to include individuals from different groups. No anaesthesia was used during handling; individuals were released immediately at the capture site following collar deployment. Animals were fitted with Lotek Wireless GPS 4000 telemetry collars programmed to record locations at two-hour intervals. A total of 11 animals (comprising seven females and four males, representing roughly 5% of the total population) were tracked for an average of 225 days per animal (range: 13–435). We used for our analyses a total of 30,355 GPS fixes collected on Mt. Mosor. The collars achieved a high GPS acquisition success (98.9% of scheduled fixes). Nevertheless, occasional missed fixes created irregular gaps between consecutive recorded locations, and 7.3% of all intervals between successive fixes exceeded the nominal 2-h schedule (range among individuals: 4.4 to 8.7%). Because we did not use anesthesia during capture and field observations indicated that animals resumed normal behavior immediately after release, we retained the full post-capture dataset for the analyses.

Environmental variables

We selected ten environmental variables related to topography, human disturbance, land cover, and climate to model habitat selection by the aoudad. We included topographic variables, as mountain ungulates are associated with high elevations and steep/rugged terrain. Elevation was obtained from a Digital Elevation Model (DEM) (Copernicus Data Space Ecosystem 2025). We derived slope and Terrain Ruggedness Index (TRI), respectively, from the DEM using the “terrain” function in the “terra” package (Hijmans et al. 2022) in R (version 4.3.3) (R Core Team, 2025). TRI measures terrain heterogeneity by calculating the sum change in elevation between a grid cell and its eight neighboring grid cells (Riley et al. 1999). We calculated northness and eastness as the cosine and sine of aspect, both ranging between -1 (full south or west in each case) to $+1$ (full north or east) (Hirzel et al. 2002; Wilson et al. 2007). We included distance to the nearest road as an index of potential human disturbance. We derived this variable from Open Street Map data (OSM 2025) and calculated using the “Distance Accumulation” tool in ArcGIS Pro (version 3.2.2). To reflect the diminishing influence of roads with increasing distance, we applied an exponential decay transformation of the form $e^{-\alpha d}$ where d was the distance in meters to a landscape feature, and α set at 0.002 (Nielsen et al. 2009). This approach ensures that areas in close proximity to roads are treated as strongly influenced, whereas the perceived impact decays with distance, reaching a point of negligible or zero influence in remote locations. To represent vegetation cover, which may influence both forage accessibility and shelter conditions, we used the Copernicus Tree Cover Density database (Copernicus Land Monitoring Service 2024) of 10 m resolution. Finally, we included three climatic variables that can influence thermoregulation and movement, namely hourly temperature ($^{\circ}\text{C}$), precipitation (mm), and wind speed (m/s), obtained from the nearest weather station (Split-Marjan). We standardized all environmental layers to the same spatial extent (study area) and resolution (30×30 m).

Home range

To identify differences in space use between seasons, we delineated annual and seasonal home ranges for both sexes using 95% Kernel Density Estimates (KDEs), which implies a probability of species occurrence in its range greater than 95% (Worton 1989), using the “adehabitatHR” package (Calenge 2006). We defined the warm

season as 1 April to 15 November and the cold season as 16 November to 31 March. We included in the analysis only individuals with at least 250 GPS fixes per season. We used this threshold as a pragmatic criterion to exclude very short monitoring periods and to retain only seasonal datasets with sufficient within-season coverage for robust home range estimation.

Habitat selection

We investigated seasonal habitat selection of the aoudad, accounting for day-night variation, applying an integrated Step Selection Analysis (iSSA) using integrated Step Selection Functions (iSSF) (Avgar et al. 2016). Integrated step selection analyses unify movement and habitat selection analyses (Signer et al. 2024). In contrast to Step Selection Functions (SSF), which assume that an animal selects habitat given its current movement state, integrated Step Selection Functions (iSSF) acknowledge that observed movement patterns arise from the interaction between the animal’s intrinsic movement capacity and habitat selection (Avgar et al. 2016). Attending to an iSSF framework, for each observed step, we generated ten random steps drawn from empirical movement distributions, fitting a gamma distribution for step lengths and a von Mises distribution for turning angles, implemented with the “amt” R package (Signer et al. 2019). We assigned each step to day or night periods using local sunrise and sunset times calculated with the “suncalc” package (Thieurmél et al. 2019). To account for missing or irregular fixes, we applied a dataset forgiveness of two, allowing inclusion of steps up to twice the regular sampling interval (4 h) (Hofmann et al. 2024). We treated intervals longer than 4 h as breaks in track continuity and split trajectories into separate movement bursts; we then generated used and available steps within bursts only, excluding steps that would span gaps > 4 h.

To improve comparability and interpretation of the modelling results, we log-transformed and normalized continuous variables to have a zero mean and unit standard deviation (Guidobaldi Stenbacka et al. 2025). Before model fitting, we assessed correlation among predictors using Spearman’s rank correlation (> 0.5). As a result, we excluded TRI, which was highly correlated with slope, and distance to road, which was highly correlated with elevation (Table S1).

For each season, we built separate generalized linear mixed models (GLMMs) with Poisson family and stratum-specific fixed intercepts, where each stratum corresponded to a single observed step and its associated set

of random alternative steps (Muff et al. 2020), using the R package “glmmTMB” (Brooks et al. 2017). In every model we included two random effects: one for each stratum ($1 | \text{step_id}$) and one for individual identity ($1 | \text{animal_id}$) (Guidobaldi Stenbacka et al. 2025). We did not model sex specific effects because of the limited number of males in the dataset ($n=2$). We modelled weather variables only as interaction terms because they were constant within each step specific choice set and therefore could not act as direct selection covariates. Instead, we used them to test whether short term weather conditions modified selection for landscape features. Specifically, we assessed interactions between temperature, precipitation, wind speed and topographic or cover variables, as we expected weather to modify thermoregulation, exposure, or movement decisions under changing weather conditions. Following Fieberg et al. (2021), we also visualized the distributions of the main environmental covariates for used and available steps, separately for the warm and cold seasons.

Results

Home range

Of the 11 collared aoudads, three individuals were predated by wolves (two females, one male), whereas the remaining eight (six females, two males) persisted throughout the study period and met our criteria (>250 GPS fixes). Eight aoudad were used in the analyses for the warm season and seven (five females, two males) for the cold season. Female aoudads exhibited considerable differences in home range size between the warm (mean = 9.8 ± 8.6 km²) and the cold season (mean = 25.5 ± 13.6 km²). Males had larger home ranges in both seasons, but this result is based on data from only two individuals (Table S2).

Habitat selection

During the warm season, aoudad avoided for east-facing (Estimate = -0.06 ; CI = $-0.08 - -0.04$) and north-facing (Estimate = -0.03 ; CI = $-0.06 - -0.01$) aspects and for areas with higher tree cover density (Estimate = -0.07 ; CI = $-0.09 - -0.05$), while selecting higher elevations (Estimate = 0.05 ; CI = $0.02-0.08$) (Fig. 2a, b, c, d) (Table S3). During the night, aoudad showed stronger avoidance of east-facing aspects (Estimate = -0.04 ; CI = $-0.07 - -0.01$) and tree cover (Estimate = -0.195 ; CI = $-0.2 - -0.15$) (Fig. 2a, c), but increased selection of

steeper slopes (Estimate = 0.1 ; CI = $0.06-0.12$) (Table S3). With increasing temperature, the avoidance of east-facing aspects (Estimate = 0.03 ; CI = $0.01-0.04$) and tree cover (Estimate = 0.03 ; CI = $0.008-0.05$) weakened, while the selection for steeper slopes increased (Estimate = 0.05 ; CI = $0.03-0.07$) (Fig. 2e, f, g). Aoudad also selected higher elevations under higher wind speeds (Estimate = 0.02 ; CI = $0.0007-0.04$) (Fig. 2h).

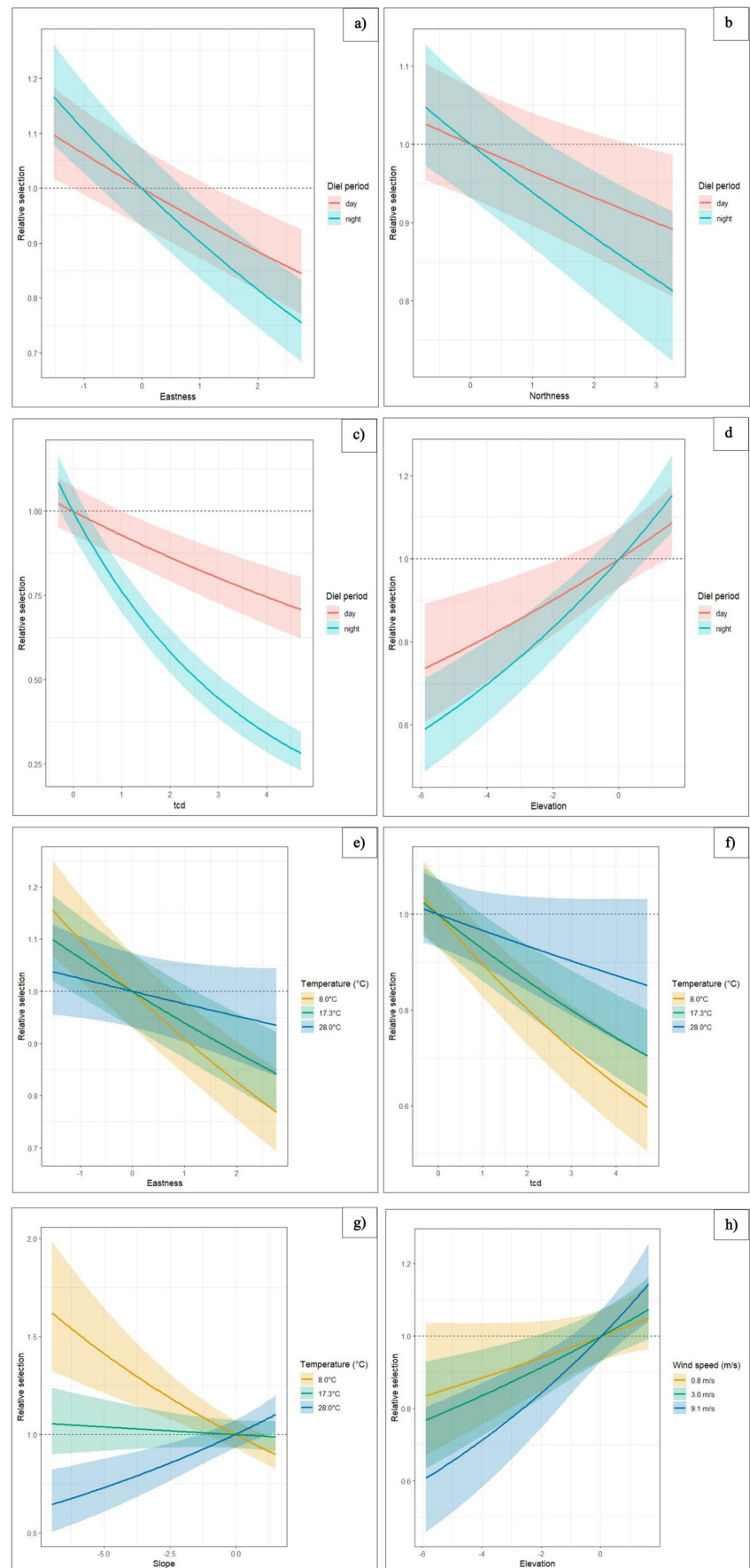
During the cold season, aoudad avoided east-facing (Estimate = -0.07 ; CI = $-0.1 - -0.03$) and north-facing (Estimate = -0.1 ; CI = $-0.1 - -0.04$) aspects, as well as areas with higher tree cover density (Estimate = -0.16 ; CI = $-0.2 - -0.1$), while continuing to select higher elevations (Estimate = 0.05 ; CI = $0.01-0.08$) (Fig. 3a, b, c, d) (Table S3). At night, avoidance of tree cover intensified (Estimate = -0.1 ; CI = $-0.2 - -0.08$) and selection shifted towards steeper slopes (Estimate = 0.3 ; CI = $0.26-0.4$) (Fig. 3c) (Table S3). With increasing temperature (Estimate = -0.04 ; CI = $-0.07 - -0.006$) and precipitation (Estimate = -0.06 ; CI = $-0.1 - -0.003$), selection for steep slopes decreased (Fig. 3e, f). The distributions of the main environmental covariates for used and available steps in each season are shown in Fig. S1.

Discussion

This study assessed the seasonal home range and habitat selection of the introduced aoudad in the southern Dinaric Alps, Mt. Mosor. The results indicate that Mediterranean mountain conditions in the study area are compatible with the species' ecological requirements, suggesting that this mountain ungulate can successfully persist under Mediterranean environmental conditions. These findings align with the documented capacity of the species to establish and expand following introduction (Cassinello 1998). We have also confirmed our main hypothesis, that predation risk can drive the aoudad habitat selection towards safer habitat during the night, when the risk is higher. However, this study was based on a relatively small number of tracked individuals, and the results should therefore be interpreted cautiously. In addition, the limited sample size did not support robust sex-specific comparisons of space use or habitat selection.

Based on results from female individuals, we found that aoudad showed extended variation in home range size between the warm and cold seasons. Seasonal differences in home range size of mountain ungulates often arise during the cold period because of environmental constraints, such as harsh winter conditions and limited food availability that

Fig. 2 Habitat selection of aoudad (*Ammotragus lervia*) during the warm season (1 April–15 November) in the southern Dinaric Alps, Mt. Mosor, Croatia, with respect to (a) eastness, (b) northness, (c) tree cover density (tcd), and (d) elevation, as well as interactions between (e) eastness-temperature ($^{\circ}\text{C}$), (f) tree cover density-temperature, (g) slope-temperature, and (h) elevation-wind speed (m/s). Relative selection strength represents the frequency ratio between realized and random steps, with values < 1 indicating lower relative selection strength, and values > 1 indicating higher relative selection strength. Each interaction is shown in a separate panel; predictions were generated for the focal interaction while holding all remaining covariates constant at their mean standardized value. For weather interactions, lines represent the 10th, 50th, and 90th percentiles of the observed seasonal distribution of the corresponding weather variable



restrict movements (Grignolio et al. 2007; Papakostas et al. 2026; Shakeri et al. 2021), or dry conditions and resource aggregation restricting space use during the warm period (Papakostas et al. 2025a). The seasonal range pattern might also remain stable under favorable environmental conditions (Papakostas et al. 2025b). In our study, female aoudad showed greater dispersal during the cold period, which likely suggests that environmental constraints limit space use during the warm period. We propose that, during the warm season, aoudad may aggregate in microhabitats with better water and forage availability as conditions become drier on Mt Mosor. Indeed, dry conditions and scarce water can restrict space use during the warm period, forcing ungulates to concentrate in microhabitats with higher resource availability (Papakostas et al. 2025a), or near artificial water troughs (Eliades et al. 2022; Ndachena et al. 2025). Previous research from Spain, also based on a limited sample size, reported smaller core home ranges of $1.65 \pm 0.67 \text{ km}^2$ (Pascual-Rico et al. 2018). This difference may partly reflect methodological differences between estimates of home range size and core area size but may also relate to differences in habitat quality or the absence of predation risk in the Spanish population, as predation pressure can influence the spatial use of ungulates (Tizzani et al. 2022). In contrast, aoudad populations in North America exhibit considerable variation in home range size, ranging from 2.6 to 33.6 km^2 (Šprem et al. 2022). This variability supports the hypothesis that large carnivores influence spatial behavior, given that the mountain lion *Puma concolor* represents the primary predator in these populations (Veals Dutt et al. 2023).

We found that aoudad avoided east facing and north facing aspects in both seasons (Fig. 2a, b) (Fig. 3a, b). During the warm season, avoidance of east facing slopes increased at night but weakened with increasing temperature. These patterns likely reflect a thermoregulatory response, as in our study area these aspects provide colder and windier conditions. The reduced avoidance at higher temperatures potentially appears because environmental conditions become milder during the warm season. Similar behavior has been reported for another introduced population in Italy, where aoudad selected southern and warmer aspects of the landscape (Leoncini et al. 2023), as well as for native European mountain ungulates such as chamois, which preferentially use aspects that allow better thermoregulation (Anderwald et al. 2024).

Aoudad preferred higher elevations in both seasons (Fig. 2d) (Fig. 3d), a pattern consistent with the native range in Northern Africa, where the species occurs at altitudes up to 2,000 m (Šprem et al. 2022). With higher wind speeds the selection for higher elevations increased in the warm season (Fig. 2h). This pattern may reflect differential wind exposure along the elevational gradient on Mt.

Mosor, with individuals shifting towards higher elevations (steeper slopes protected against wind) when wind conditions intensify.

We also found that aoudad avoided areas with tree cover in both seasons, with stronger avoidance during the night (Fig. 2c) (Fig. 3c), when individuals also selected steeper slopes (Table S3). This pattern likely reflects increased predation risk from wolves during nocturnal hours, as open areas combined with steep terrain enhance early detection of predators and provide escape terrain with improved visibility. Although aoudad generally also uses forested habitats in other introduced and native populations (Leoncini et al. 2023; Šprem et al. 2022), this pattern did not hold on to Mt. Mosor. Instead, avoidance of tree covered areas may result from the elevated predation risk in forested habitats, generating a landscape of fear shaped by wolf presence (Gaynor et al. 2019; Tizzani et al. 2022). Avoiding tree cover areas is a logical anti-predator behavior of aoudad on Mt. Mosor, as three individuals (two females and one male) were preyed upon by wolves in forested habitat type at night during this study. This response may also be influenced by sex specific behavior, as most GPS locations originated from female individuals, which often exhibit stronger antipredator strategies, particularly in the presence of offspring (Grignolio et al. 2007; Ruckstuhl and Neuhaus 2002). It is also noteworthy that forested vegetation occurs on less extreme terrain. Consequently, the avoidance of forests implicitly reflects a preference for the most rugged terrain, which offers aoudad protection from predators.

Higher temperatures during the warm season increased selection for steeper slopes (Fig. 2g). Aoudad typically occupies steep terrain in both their native and introduced ranges (Šprem et al. 2022), as well as in other regions where aoudad has been introduced (Acevedo et al. 2007; Cassinello 2000; Cassinello et al. 2006). In addition, during the calving season, females may shift towards steeper and more inaccessible areas at higher elevations, which can provide increased protection for offspring (Šprem et al. 2022), a pattern also reported in other mountain ungulates (Aycrigg et al. 2021; Blum et al. 2023; Hamel and Côté 2007).

Conclusions

This research provides essential baseline information for understanding the spatial behavior of *A. lervia* in non-native Mediterranean habitats. The species showed more restricted space use during the warm period, which may reflect aggregation in more favorable microhabitats. Consistent with its native range, aoudad also selected high

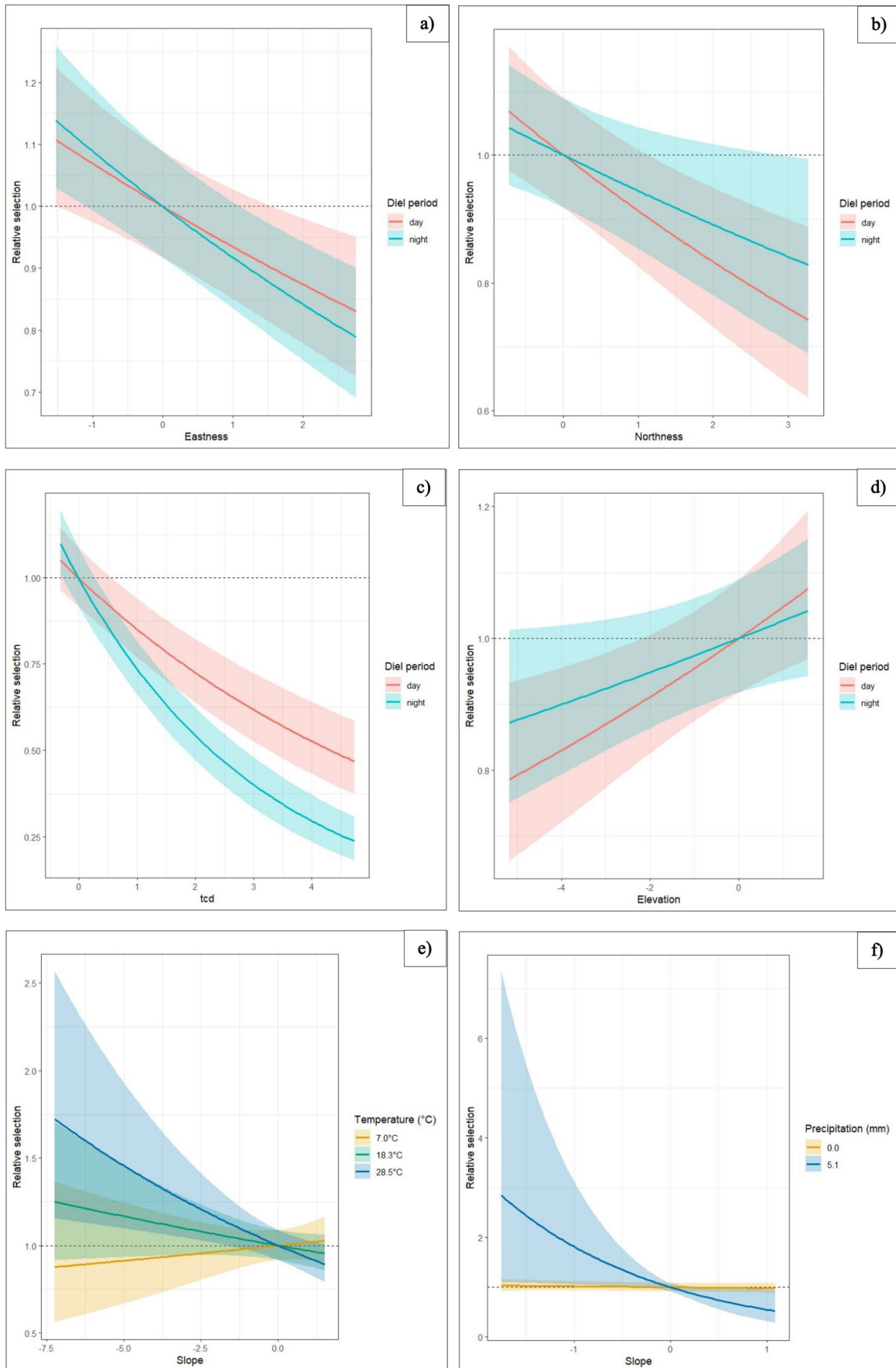


Fig. 3 Habitat selection of aoudad (*Ammotragus lervia*) during the cold season (16 November–31 March) in the southern Dinaric Alps, Mt. Mosor, Croatia, with respect to (a) eastness, (b) northness, (c) tree cover density (tcd), and (d) elevation, as well as interactions between (e) slope-temperature (°C), and (f) slope-precipitation (mm). Precipitation values were highly right skewed; therefore, predicted effects are shown for two representative conditions: 0 mm (no precipitation) and 5.1 mm (upper observed precipitation value). Relative selection strength represents the frequency ratio between realized and random steps, with values < 1 indicating lower relative selection strength, and values > 1 indicating higher relative selection strength. Each interaction is shown in a separate panel; predictions were generated for the focal interaction while holding all remaining covariates constant at their mean standardized value. For weather interactions, lines represent the 10th, 50th, and 90th percentiles of the observed seasonal distribution of the corresponding weather variable

elevation and steep terrain, while also exhibiting context dependent adaptations to the climatic and topographic characteristics of the study area. In addition, predation risk appeared to influence habitat selection, as reflected by avoidance of tree covered areas and increased use of open and steep terrain, particularly during the night. The influence of wolf predation is thought to be the main reason for the aoudad not spreading throughout the Dinarides, as Leoncini et al. (2023) previously concluded for the Italian population. Overall, our findings suggest that aoudad can successfully persist in Mediterranean mountain regions as previously concluded by Kavčić et al. (2020) based on life-history traits. These findings can also inform management strategies for the introduced aoudad in the region and support conservation planning for native mountain ungulates, particularly in view of the species' potential expansion towards nearby Balkan chamois habitat (Mt. Biokovo) and possible antagonistic interactions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10344-026-02106-7>.

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Author contributions NŠ and KP wrote first draft of the manuscript. KP, MRR analyzed the data. NŠ, KJ conceptualized the framework and supervised all stages of this work. NŠ, PG and KJ obtained and arranged raw data. All authors read and approved the final manuscript.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval The capture of animals was conducted using drop nets, according to the ethical and welfare standards presented in the Official Gazette of the Republic of Croatia (OG 102/2017, Animal Protection Act) and Regulation on the Protection of Animals Used for Scientific Purposes (OG 55/13), with the approval of the Bioethical Committee for the Protection and Welfare of Animals of the University of Zagreb Faculty of Agriculture (UR.BR. 251-71-29-02/11-19-2).

Competing interests The authors declare no competing interests.

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