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ORIGINAL RESEARCH

Surviving strategies in the Sahara: Understanding diel activity patterns of ungulates in hyper-arid regions

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activity pattern plasticity; anti-predator behaviour; camera trap methodology; *Canis lupaster*; desert ungulates; *Gazella cuvieri*; human-wildlife interactions; temporal niche partitioning.

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Abstract

Diel activity patterns provide insight into how animals adapt to environmental constraints, human disturbance, and community context. However, empirical information on diel activity of large, free-ranging ungulates in hyper-arid systems is limited, and much of the existing evidence comes from fenced enclosures or managed reserves. To investigate these mechanisms, we used Cuvier's gazelle *Gazella cuvieri*) as a model species to examine seasonal and ecological drivers of activity in a hyper-arid Saharan landscape. A total camera trap effort of 11 333 trap days was accumulated across four sites. We studied both abiotic (seasons, moon phase, and rainfall) and biotic factors (activity of the African golden wolf, Barbary sheep, and livestock). The influence of each factor was assessed using the activity overlap coefficient (Δ) and the non-parametric circular Mardia–Watson–Wheeler test. Period selection within the diel cycle was analysed using chi-square contingency tables and the 'Wi' parameter of the resource selection coefficients. Cuvier's gazelle exhibited predominantly diurnal activity with bimodal crepuscular peaks at dawn and dusk and reduced activity at midday. The main drivers were wet/dry periods and moon phase. In contrast, intra-guild factors did not produce significant effects, although temporal asynchrony with wolves and slight behavioural shifts in the presence of livestock were observed. Overall, gazelles avoided nocturnal hours and selected crepuscular periods. These findings strengthen our understanding of behavioural adaptations of an endangered species in hyper-arid environments and contribute to broader knowledge of ungulate activity patterns under extreme ecological constraints.

Introduction

Diel activity is a central axis of the temporal niche, describing how animals allocate time to balance access to resources and mating opportunities against costs, such as thermal stress, predation risk, and human disturbance. Because activity schedules are plastic, species can shift from diurnal to crepuscular or nocturnal, or become more flexible (cathemeral), in response to environmental constraints and biotic interactions (Gaynor et al., 2018; Hut et al., 2012).

Hyper-arid deserts provide a stringent test for activity theory, as extreme heat, chronic water limitation, and highly pulsed productivity can strongly constrain when animals can forage and move. Under such stressful conditions, intraspecific relationships may become more complex (Hart & Marshall, 2013) and competitive interactions gradually shape community structure, potentially leading to local extinctions of phylogenetically related species (Hardin, 1960; Schoener, 1974; Violle et al., 2011; Webb et al., 2002). Furthermore, disruptions in predator–prey dynamics caused by the extirpation of apex predators and increased human-ungulate interactions are clearly impacting communities and reshaping ecosystem structures (Estes et al., 2011; Pascual-Rico et al., 2021). Yet, empirical evidence for large mammals, particularly ungulates, in hyper-arid systems remains limited and is often derived from studies conducted in fenced enclosures or managed reserves, where movements, space use and exposure to predators and human activities may differ from fully free-ranging conditions (Hetem et al., 2012a, 2012b; Meliane et al., 2023; Ostrowski & Williams, 2006; Seri et al., 2018). As a result, field-based tests in open hyper-arid landscapes that jointly quantify abiotic forcing (e.g. rainfall pulses, seasonality and moonlight) and biotic context (e.g. predators, sympatric ungulates and livestock) remain scarce.

Among desert ecoregions, the Sahara Desert holds the greatest diversity of antelope species, although large-mammal populations have experienced a dramatic collapse during the past century, primarily due to overhunting and habitat loss (Durant et al., 2014; Newby et al., 2016). In this context of global change, advancing our knowledge of the ecological responses of Saharan ungulates is a pressing need for effective conservation planning (Cooke et al., 2016; Durant et al., 2014).

Understanding how desert ungulates adjust their activity under extreme environmental constraints and human-associated pressures can therefore inform both conservation and broader theory on temporal niche dynamics across ecosystems. Here, we focus on Cuvier's gazelle (*Gazella cuvieri*) as a model species to evaluate these mechanisms in an open Saharan landscape. Cuvier's gazelle is a medium-sized antelope endemic to northwest Africa. Its main range lies in the Atlas Mountains of Morocco, Algeria and Tunisia, but it also occurs in the Atlantic Sahara, where it harbours a key population of demographic and genetic significance (Gil-Sánchez et al., 2017; Silva et al., 2015, 2017). Classified as Vulnerable by the IUCN Red List due to its small population size and persistent threats (IUCN, 2018), the species belongs to the Sahelo-Saharan antelope group and is well adapted to hyper-arid conditions (Beudels-Jamar et al., 2006; Durant et al., 2014). In this region, Cuvier's gazelles persist under strong resource limitation and increasing overlap with livestock, while co-occurring with other ungulates and carnivores such as the African golden wolf (*Canis lupaster*) (Gil-Sánchez et al., 2017; Herrera-Sánchez et al., 2020, 2023), making this system well suited to evaluate drivers of temporal niche organization in a hyper-arid landscape.

In this study, we used motion-detecting digital cameras to investigate the factors influencing diel activity patterns of Cuvier's gazelle in the Sahara Desert, a non-invasive approach widely applied to scarce and endangered taxa (Frey et al., 2017; Gil-Sánchez et al., 2023; O'Connell et al., 2011; Ridout & Linkie, 2009). Specifically, we examined the effects of key abiotic and biotic factors, including daylight, moonlight, seasonality, apparent intra-guild competition, predator avoidance, and human disturbance, to test seven hypotheses summarized in Table 1.

Materials and methods

Study area

The study was conducted in the extreme north-western part of the Sahara Desert, between 28°20′ and 27°35′ N and 11°15′ – 9°50′ W (Fig. 1), within the Atlantic Sahara of Morocco. The area is characterized by prolonged droughts and erratic rainfall, and is considered part of the North Saharan Xeric Steppe and Woodland ecoregion of the northern Sahara (Dinerstein et al., 2017). The mean, minimum, and maximum temperatures are 22.7, 8.0, and 39.0°C in the western zones (closer to the Atlantic Ocean), 23.2, 0.0, and 43.0°C in the eastern zones, and 19.1, 10.7, and 29.0°C in the northern zone. Total annual precipitation is 138, 59, and 190 mm, respectively (recorded at climate stations at Smara, 26°46′ N, 11°31′ W; Tindouf, 27°40′ N, 8°07′ W; and Tan Tan, 28°26′ N, 11°06′ W), with high interannual variability. This variability includes prolonged droughts lasting several consecutive years with no recorded rainfall.

Information obtained from previous surveys on the target species (see Gil-Sánchez et al., 2017; Herrera-Sánchez et al., 2020) guided the selection of the sampling sites, following a stratified sampling strategy to encompass the full habitat variability of the study area. Accordingly, four sites were selected: Djebel Ouarkziz, Aydar Mounts, and the M'sied area, which are mountainous and hilly with numerous oueds (dry riverbeds) and, in the case of M'sied, include some scattered dune systems; and Oued Taclet, which lies along the stepped margin of the hamada (stony desert plateau), characterized by steep ravines and low hills. The dominant tree vegetation consists mainly of acacias (*Vachellia tortilis* subsp. *raddiana* and *V. flava*), along with some scattered individuals of *Balanites aegyptiaca*, *Maerua crassifolia*, the argan tree (*Argania spinosa*), and *Calotropis procera* (further details in Gil-Sánchez et al., 2017; Herrera-Sánchez et al., 2020).

Cuvier's gazelle shares this region with Barbary sheep (*Ammotragus lervia*) and dorcas gazelle (*Gazella dorcas*). The area also once supported the last wild population of the Mhorr gazelle (*Nanger dama mhorr*), which disappeared in 1968 (Cano, 1991). Although large predators have been lost, most notably the Saharan cheetah (*Acinonyx jubatus hecki*) last recorded in the 1990s, the carnivore community remains diverse, comprising 10 species from five families; however, the African golden wolf is the only predator consistently recorded in the study area and the only one showing evidence of regular presence and relative abundance (Aulagnier et al., 2017; Gil-Sánchez et al., 2025).

Camera trap survey

We deployed a total of 40 camera traps, arranged as four sampling blocks of 10 stations each, across the four survey sites between January to April 2017 and from September 2017 to September 2018 (Fig. 1; Table 2). Digital red-glow infrared cameras (Busnell, Moultrie, Covert, and Scoutguard brands), triggered remotely by infrared sensors, were deployed following a predesigned 1 × 1 km regular grid using ArcGIS 10.4. Grid points for the camera trap design were defined a priori and independently of human accessibility. In line with the stratified approach, mountainous/hilly habitats, oueds, and scattered dune systems present in M'sied were sampled. At Oued Taclet, although the site lies along the hamada margin, extensive flat plains were not sampled due to the low occurrence of

Table 1 Summary of predictions from seven hypotheses proposed to explain variation in the diel activity pattern of Cuvier's gazelle in the Atlantic Sahara

Hypotheses	Key predictions/rationale	References	Prediction support
H1-Crepuscular patterns of diel activity in arid environments	Cuvier's gazelles will adopt a bimodal pattern, avoiding midday and adjusting between nocturnal and diurnal behaviour depending on environmental conditions	Hetem et al. (2012a), Davimes et al. (2016, 2017)	Yes
H2-Intra-guild competition affects diel activity patterns	Intra-guild competition will drive temporal niche partitioning to reduce exploitative competition	Rivero et al. (2005), Ferreguetti et al. (2015), Frey et al. (2017)	no
H3-Extand predators do not affect diel activity patterns	Predator avoidance will have a limited impact on diel activity patterns, as current carnivores do not prey on gazelles	Stephens and Krebs (1986) Sarabia-Domínguez (2021)	Yes
H4-Seasons variation affects diel activity patterns	Seasonal factors will impact diel activity by reducing daytime activity to avoid excessive heat during the hottest months	Davimes et al. (2017), Abáigar et al. (2018), Seri et al. (2018)	No
H5-Drough periods affect diel activity patterns	The reduction in food availability during droughts will force an increasing in both daytime and nocturnal activity due to extended foraging time	Davimes et al. (2016), Meliane et al. (2023)	Yes
H6-Humans affect diel activity patterns	The presence of livestock will affect diel activity though human avoidance behaviour	Manor & Saltz, 2003, Groves et al. (2011)	Yes
H7-Moon phase affects diel activity patterns	Lunar phases are expected to influence the activity pattern through their effects predation risk and human avoidance	Kramer and Birney (2001), Groves et al. (2011), Pratas-Santiago et al. (2017)	Yes

Cuvier's gazelle (Gil-Sánchez et al., 2017; Herrera-Sánchez et al., 2020). Once each grid point was located in the field, cameras were installed at optimal locations along game trails and ravines, always facing north. Camera traps were mounted on large stones, acacia logs, or wooden stakes at a height of 25–30 cm above the ground. Devices were programmed to capture 1–3 pictures per detection event, with PIR (Passive Infrared) interval of 0–5 s. During a preliminary camera trap trial in the area, Iberian lynx (*Lynx pardinus*) urine proved to be an effective olfactory attractant for medium to large-sized mammals, including gazelles: individuals commonly paused to sniff upon arrival, and no overt fear or flight responses were observed. For African golden wolves (the only carnivore species included in this study), Iberian lynx urine also proved an effective olfactory attractant for surveying this species (Figures S1 and S2; see Gil-Sánchez et al., 2021, 2025). Accordingly, each station was baited with Iberian lynx urine applied to a menstrual tampon at the time of deployment and during each camera check to enhance detection rates (Gil-Sánchez et al., 2023). All cameras were checked every 4–5 months to replace batteries and memory cards. Despite the high number of thefts (23 cameras were stolen during the study), replacements were installed at the same or nearest feasible grid points during each visit, ensuring consistent spatial coverage. M'sied was the only site where camera-trapping continued uninterrupted for 9 months (January 2018–September 2018), as it was initially deployed in another area deemed unsafe for the integrity of the cameras. As a result, between 30 and 35 active camera traps remained active at any given time throughout the survey (mean distance between cameras: 919 metres ±70.80 SE). In addition, we assessed whether camera losses and subsequent rotations biased detection using rarefaction curves; the curves plateaued with no evidence of step changes, indicating that the remaining effort was sufficient and detection rates were stable (Figure S3).

Data processing

The data extracted from the memory cards were processed using the ZSL Camera Trap software (Amin et al., 2016). Prior to this, metadata (file name and timestamp) from the original ".jpg" files were automatically extracted using PIE software (version 7.00.1). Consecutive images of the same species and group of individuals taken within a 30-min interval were considered a single detection event to ensure event independence and reduce pseudoreplication (Brook et al., 2012; Monterroso et al., 2013; O'Connell et al., 2011; Wang et al., 2015). For livestock (sheep and goats), we applied a 1-h interval, as these species tend to move slowly and rarely remain stationary due to low food availability in front of the cameras and would otherwise generate multiple non-independent records; independence was verified by confirming that the flock did not reappear after this threshold. The relative abundance index (RAI) was calculated as the number of independent captures per 100 camera trap days (O'Connell et al., 2011).

Interannual rainfall in the study area is highly irregular (Gil-Sánchez et al., 2023), but two distinct periods were identified: a '*wet* period' following the autumn rains of 2016, and a '*dry* period' during the subsequent year, when virtually no rainfall was recorded until the end of the survey (Figure S4). The months of January to March 2017 were defined as the '*wet* period' and were compared with the same months in 2018, considered as a dry event and hereafter referred to as the '*dry* period' for analytical purposes. The driest and hottest

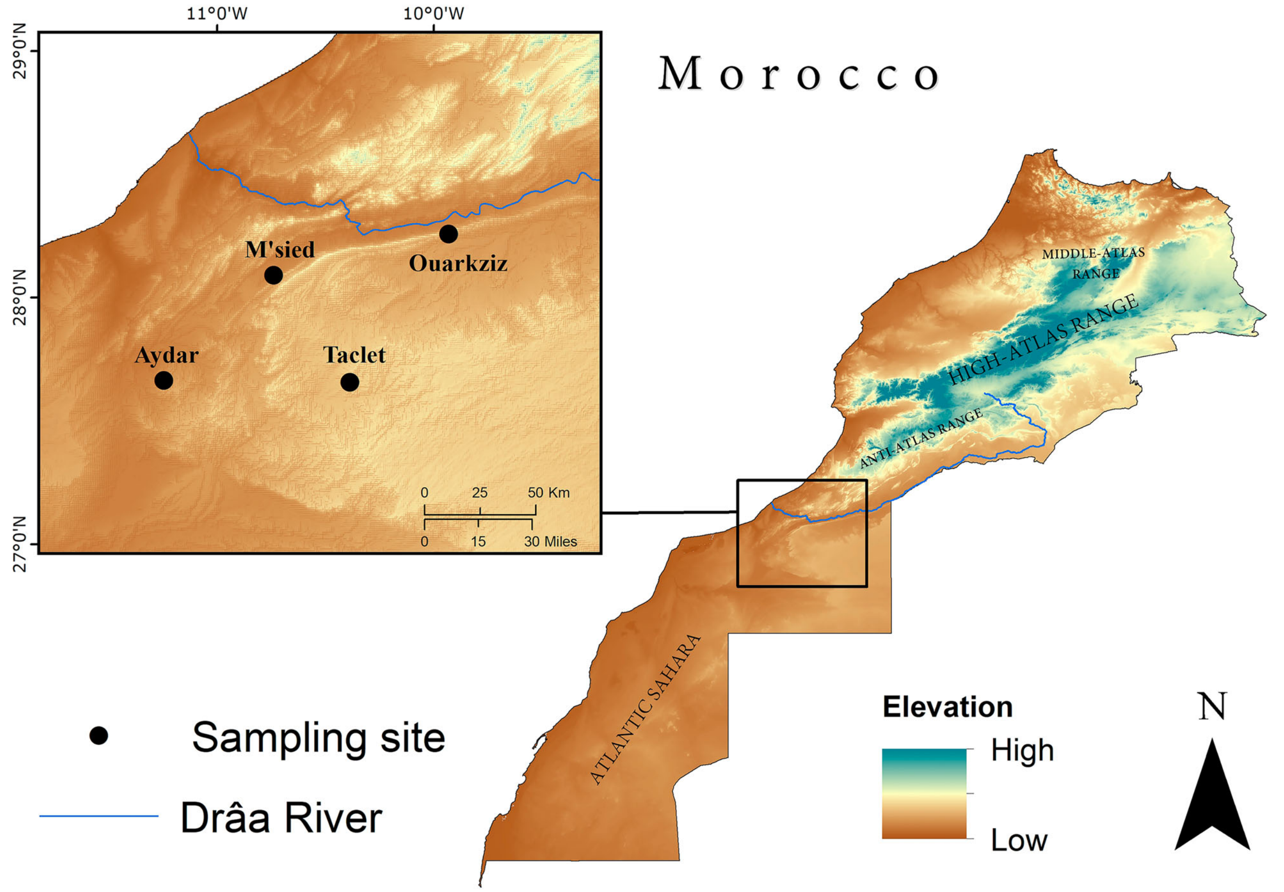


Figure 1 Location of the study area and sampling sites for the camera traps. The map also shows the topography using a digital elevation model (DEM).

Table 2 Sampling effort and number of events recorded at each site in the study area for both target species and livestock

				Events (*RAI*)			
Site	No of stations	Date of full survey	Full survey effort (trap days)	Cuvier's gazelle	Barbary sheep	African golden wolf	Livestock
Aydar	10	January 2017–April 2017 September 2017–September 2018	3620	71 (***1.96***)	0	69 (***1.91***)	22 (***0.61***)
Ouarkziz	10	January 2017–April 2017 September 2017–September 2018	4283	40 (***0.93***)	42 (***0.98***)	144 (***3.36***)	21 (***0.49***)
Taclet	10	January 2017–April 2017 September 2017–September 2018	1971	41 (***2.09***)	0	27 (***1.38***)	21 (***1.07***)
M'sied	10	January 2018–September 2018	1459	41 (***2.81***)	0	19 (***1.3***)	8 (***0.55***)
Total	*40*		*11 333*	*193*	*42*	*259*	*72*

The relative abundance index (RAI) per 100 camera traps day is shown in bold italics.

seasons in the region correspond to spring and summer, beginning in April, when average monthly precipitation drops to nearly zero. Conversely, the wet season, characterized by milder and lower night-time temperatures, corresponds to autumn and winter (Bergier et al., 2017). Based on this seasonal framework, we grouped detections into two climatic seasons: '*hot-dry*' (spring–summer) and '*mild-wet*' (autumn–winter), thereby reducing bias from small sample size (Lashley et al., 2018). To ensure the absence of livestock at each study site, only the corresponding months with no recorded events were considered. In contrast, the presence of livestock was included only for months with confirmed photo captures.

Statistical analysis

Based on the camera detections, we considered each event as a random sample derived from a continuous temporal distribution. Therefore, diel activity patterns were estimated using kernel density estimates (Ridout & Linkie, 2009) with the R package *overlap* (Meredith & Ridout, 2021). Pairwise comparisons between the targeted species (Cuvier's gazelle, Barbary sheep, African golden wolf, and sheep and goat herds) and environmental factors (mild-wet/hot-dry seasons, wet/dry periods, and moon phase) were conducted by estimating the overlap coefficient Δ_1 when the number of events was <50 detections, or Δ_4 when ≥50 detections. This coefficient was determined from a bootstrap estimation of 10 000 samples (Centore et al., 2018; Meredith & Ridout, 2021). The Δ coefficients range from 0 (no overlap) to 1 (complete overlap).

Diel activity records represent a 24-h circular distribution; thus, pairwise comparisons were analysed using circular statistics with the R package *circular* (Lund et al., 2022). For this purpose, the non-parametric Mardia–Watson–Wheeler test (MWW) was applied to detect differences between samples (Batschelet, 1981; Frey et al., 2017). An alpha level of 0.05 was used to determine statistical significance (Lund et al., 2022). Frequency Chi-square contingency tables were used to classify temporal activity into three diel categories: 'day', 'crepuscular', and 'night' (Bu et al., 2016; de Satgé et al., 2017). To support and confirm the Chi-squared tests, we calculated the '*Wi*' parameter of resource selection ratios (Manly et al., 2003) using Wide I. The Manly selectivity index (*Wi*: selection ratio = used/available) tests preference/avoidance for each period and was adjusted using the Bonferroni correction with a significance level of 0.016. Values above 1 indicate preference, whereas values below 1 indicate avoidance. This analysis was conducted using the R package *adehabitatHS* (Calenge, 2017). Sunrise and sunset times for each capture were calculated using the latitude and longitude of the corresponding sample site with the R package *suncalc* (Thieurmel & Elmarhraoui, 2022). Specifically, 'crepuscular' periods were defined as the 1-h interval before and after both sunrise and sunset. Seasons and moon phases were associated with each event using the R package *lunar* (Lazaridis, 2022). All statistical analyses were performed with R-software version 4.5.0 (R Core Team, 2022).

Results

A total of 11 333 trap-day (24-h periods) and 494 independent detections of the three target species were recorded across the four survey sites (Table 2). Cuvier's gazelle, African golden wolf, and livestock were detected at all sites, whereas Barbary sheep were only recorded at Ouarkziz.

Cuvier's gazelles exhibited a predominantly diurnal activity with bimodal crepuscular peaks, especially at dawn, while avoiding night activity and reducing activity at midday (Fig. 2Ia; *Wi*: crepuscular = 1.865, night = 0.46; see Table S2 for all Wi values and significance tests). No significant differences were found among sites (Table S1). Barbary sheep showed a similar bimodal crepuscular pattern, but with earlier afternoon activity and a sharper morning decline than gazelles (Fig. 2Ib,IIa). Although significant differences among diel categories were found for this species, no clear preference was identified after Bonferroni correction. The African golden wolf showed a significant preference for crepuscular hours and was otherwise predominantly nocturnal, with low activity during the middle of the day (Fig. 2Ic). Its evening peak was delayed compared with both ungulates (Fig. 2IIb, IIc) and its activity pattern differed significantly from that of Cuvier's gazelle (Fig. 2IIb; Table 3).

Across seasons and periods, Cuvier's gazelles concentrated more activity around midday and reduced nocturnal activity during the *hot-dry* season and *dry* period compared with the *mild-wet* season and *wet* period (Fig. 2IIIa,IVa). Although gazelles were generally crepuscular, diurnal activity increased during the *hot-dry* season (Table S2). Seasonal pairwise comparisons showed significant differences between Cuvier's gazelle and the African golden wolf for both the *hot-dry*/*mild-wet* seasons and the *dry* period (Fig. 2IIIc,d,IVd; Table 2). The African golden wolf avoided daylight in both seasons and during the *dry* period, whereas in the *wet* period it showed a cathemeral pattern with no diel category preferences (Fig. 2IIIb,IVb; Table S2). Twilight activity increased during the *hot-dry* season and the *dry* period, with nocturnal activity in the dry period concentrated in the early night. Consequently, significant differences were found between *wet* and *dry* periods (Fig. 2IVb; Table 3).

Livestock concentrated activity during the central hours of the day (Fig. 2Id), resulting in the lowest overlap coefficient with Cuvier's gazelle in the analyses (Fig. 2IId). Livestock were rarely detected in the hottest and driest months. No significant differences in gazelle activity patterns were observed between the presence and absence of livestock (Table 3). However, when livestock were absent, gazelles extended diurnal activity towards midday and exhibited a stronger second peak at dusk. In contrast, when livestock were present, gazelle activity was more concentrated at dawn, increased at midday, and declined towards dusk (Fig. 3Ia).

Moon phase strongly influenced gazelles: during the new moon they were more diurnal, strongly crepuscular at dusk, and avoided night activity, whereas during the full moon night avoidance was less pronounced (Fig. 3IIa). As a result, gazelle activity differed significantly between moon phases, whereas no such difference was found for wolves (Fig. 3IIb). Accordingly, significant differences in temporal overlap were observed between gazelles and wolves during the new moon, but not during the full moon (Fig. 3IIc,d; Table 2).

Discussion

This study explored, for the first time, the activity pattern of Cuvier's gazelle in the wild. Conducting long-term research on rare and elusive species such as Cuvier's gazelle in the Atlantic Sahara is particularly challenging due to the remoteness of the terrain and the extreme temperatures reached during the summer season. Despite a high number of stolen cameras, camera-trapping effort exceeded 1400 trap days across the four surveyed sites, surpassing the threshold estimated to minimize detection bias related to camera placement (Cusack et al., 2015). The camera-trapping design was successful in detecting both Cuvier's gazelle and the African golden wolf at all four surveyed sites. Barbary sheep were only detected at the Ouarkziz site, with a low number of records. However, this study provides the first data on diel activity of Barbary sheep in the wild, offering an important baseline for future research.

General activity patterns of Cuvier's gazelle

Our result demonstrate that Cuvier's gazelles are primarily diurnal with strong crepuscular peaks. This supports H1 and is analogous to patterns reported for desert-dwelling species, such as dorcas gazelle (Abáigar et al., 2018), addax, *Addax nasomaculatus* (Seri et al., 2018), and Arabian oryx, *Oryx leucory* (Davimes et al., 2016). The dawn peak was extended into the early morning hours before declining towards midday, which suggests that access to dew and reduced heat stress may be important drivers. This mechanism has also been proposed for other gazelles in arid environments (e.g., goitred gazelles, *Gazella subgutturosa*, Blank, 2023; addax antelopes, Seri et al., 2018). These results highlight the adaptive significance of temporal plasticity in desert ungulates.

Interspecific comparisons with barbary sheep

Although sample size was limited, Barbary sheep displayed partially overlapping but asynchronous activity with Cuvier's gazelles, a pattern that could be consistent with H2. Niche partitioning may be facilitated by distinct diel activity patterns, as well as by differences in habitat uses and dietary preferences (Abrams, 1983). Both species largely overlapped in the Djebel Ouarkziz; however, steeper terrain not represented in our sites would likely be more favourable to Barbary sheep, suggesting potential spatial segregation that remains to be explored. On the other hand, the diet of the Cuvier's gazelle is relatively well documented in the study area (Herrera-Sánchez et al., 2023), but no information is currently available on the feeding ecology of Barbary sheep in Saharan environments. Given the extremely low food availability in the region, some degree of interspecific overlap is likely. Thus, the observed temporal asynchrony could serve as a mechanism to reduce interspecific competition (Brannan et al., 1985; Gayot et al., 2004; Rivero et al., 2005), but further research is needed to confirm this hypothesis.

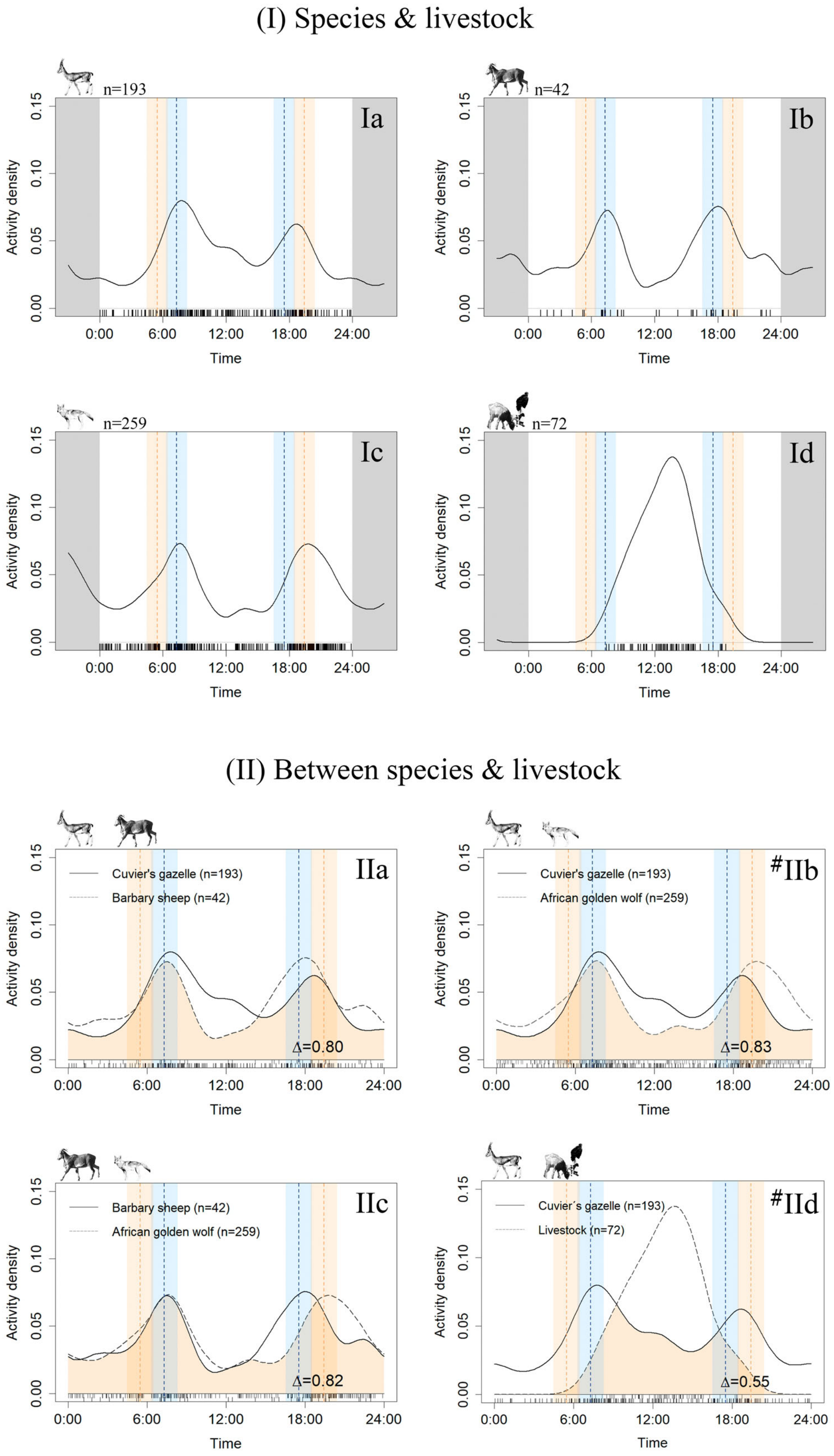
Relationship with African golden wolf

The clear asynchrony between gazelles and wolves suggests either active avoidance by gazelles or limited predation pressure by wolves (H3). Unfortunately, information on this predator–prey system is scarce. Shalmon et al. (2020) reported predation of fawns of dorcas gazelle and Arabian gazelle (*G. arabica*) by wolves (*C. lupus*), and Abáigar et al. (2016) suggested predation of dorcas gazelles by African golden wolves; however, both cases occurred in fenced reserves. In our study area, gazelles were not detected as a component of the wolves' diet (Sarabia-Domínguez, 2021), which supports the optimal foraging theory, suggesting that gazelles are not optimal prey due to unfavourable cost–benefit ratios and trade-offs (Schoener, 1971; Stephens & Krebs, 1986). Therefore, the observed diel activity patterns between both species may not reflect a direct predator–prey dynamic, as hypothesised in H5, but rather shared responses to abiotic factors and the nocturnal availability of alternative prey, such as lagomorphs, small mammals, and reptiles.

Seasonal and climatic drivers

Contrary to expectations (H4), gazelles increased their daylight activity during hot-dry conditions. This pattern resembled that of the dry period detected in our study (January–March 2017), a shorter period with lower temperatures than the hot-dry season (April–September). This behaviour may reflect the need to increase foraging effort (see rationale for H5 in Table 1), when gazelles are forced to exploit a wider range of plant species, which are scarcer and lower in nutritional quality (Herrera-Sánchez et al., 2023; Xia et al., 2011). Moreover, the body size of Cuvier's gazelle (mean adult male: 32.5 kg; female: 26.43 kg; Moreno & Espeso, 2008) may provide thermal inertia, in contrast to the small-sized antelopes that are more sensitive to high temperatures (du Toit & Yetman, 2005). Notably, Cuvier's gazelle is nearly twice the size of the Arabian sand gazelle (*G. marica*), a species capable of heterothermy (Hetem et al., 2012a; Ostrowski & Williams, 2006). Other gazelles, such as slender-horned gazelles (*G. leptoceros*), considered an ecotype of Cuvier's gazelle (Silva et al., 2017), have evolved a lighter coat coloration, enabling them to better reflect solar radiation. These behavioural and physiological traits may reflect an enhanced tolerance to high ambient temperatures in Cuvier's gazelle, allowing it to remain active under conditions that constrain less adapted ungulates.

Figure 2 Diel activity patterns of the three target species and livestock in the Atlantic Sahara. The y-axis shows kernel density estimates: (I, II) individual species/livestock activity, (III) by mild-wet and hot-dry seasons, and (IV) by wet/dry periods. The coloured shaded area represents the overlap, measured by the mean overlap coefficient Δ (95% CI). The "#" symbol indicates activity patterns that were significantly different according to the Mardia–Watson–Wheeler test ($P < 0.05$). Sunrise and sunset times are shown as vertical dashed lines for equinoxes and solstices: autumn (brown), winter (blue), spring (green), and summer (orange). Narrow shaded bands flanking sunrise and sunset (−1 to +1 h) indicate the crepuscular windows. Sample sizes (*n*, independent detections) are shown in each panel.


(I) Species & livestock
n=193
Ia
n=42
Ib
n=259
Ic
n=72
Id
Activity density
0.00
0.05
0.10
0.15
0:00
6:00
12:00
18:00
24:00
Time
(II) Between species & livestock
IIa
Cuvier's gazelle (n=193)
Barbary sheep (n=42)
Δ=0.80
#IIb
Cuvier's gazelle (n=193)
African golden wolf (n=259)
Δ=0.83
IIc
Barbary sheep (n=42)
African golden wolf (n=259)
Δ=0.82
#IId
Cuvier´s gazelle (n=193)
Livestock (n=72)
Δ=0.55

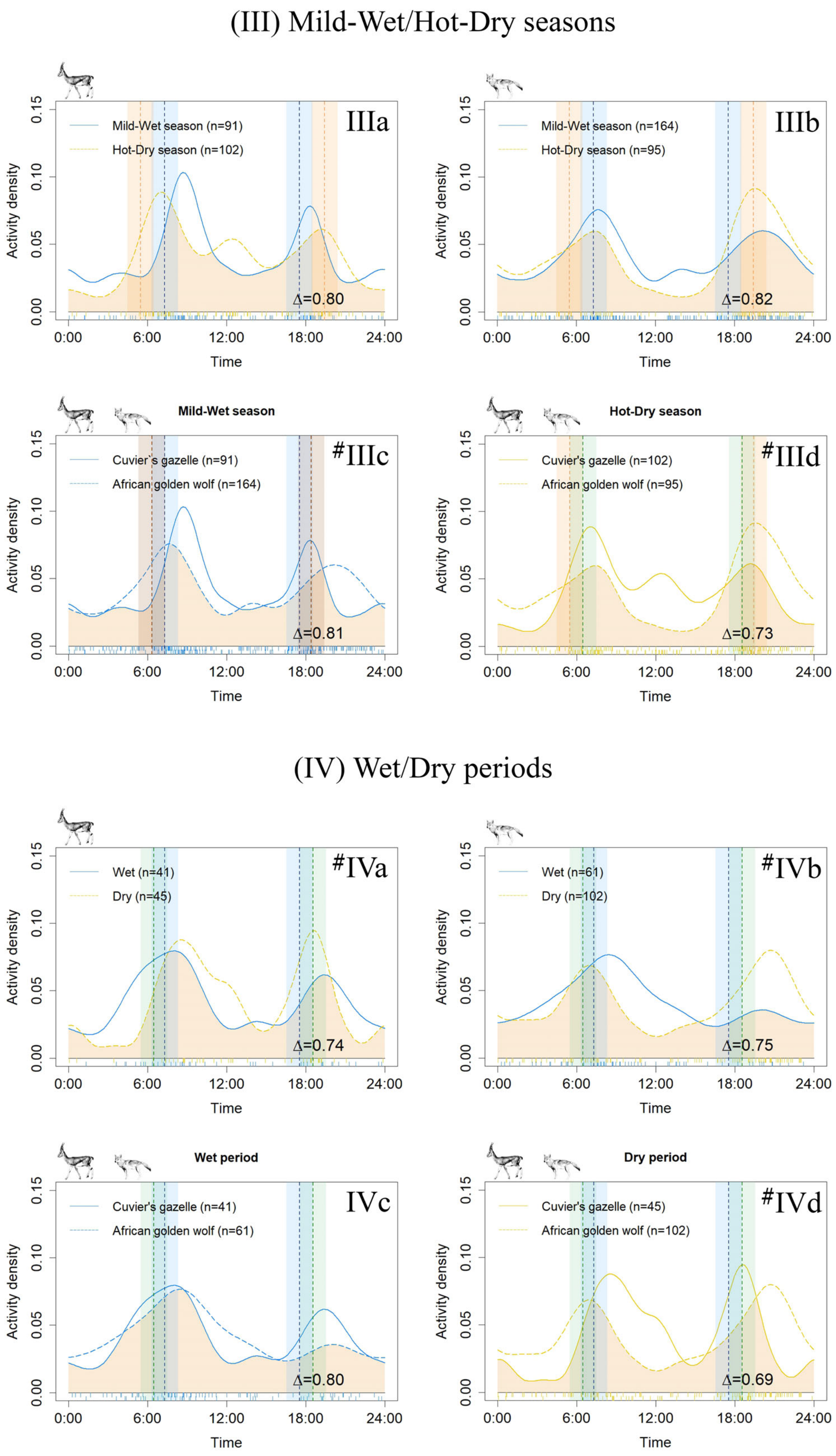


Figure 2 Continued

Table 3 Coefficient of overlap (Δ1 and Δ4) and mean Δ based on 10 000 bootstrap samples

Factor pairing	Δ	Bootstrap Δ (mean)	Δ 95% CI	Method	No of events (*n*|*n*)		Mardia–Watson–Wheeler test (W)	
Species								
GC/BS	0.84	0.80	0.74–0.95	Δ1	193	42	$P = 0.2245$	W = 2.9882, d.f. = 2
GC/AW	**0.84**	**0.83**	**0.77–0.91**	**Δ4**	**193**	**259**	$\mathbf{P < 0.001}$	**W = 18.246, d.f. = 2**
AW/BS	0.88	0.82	0.78–0.98	Δ1	259	42	$P = 0.6061$	W = 1.0016, d.f. = 2
Mild-wet/hot-dry seasons								
GC (mild-wet/hot-dry)	0.77	0.80	0.68–0.87	Δ4	91	102	$P = 0.7233$	W = 0.64799, d.f. = 2
AW (mild-wet/hot-dry)	0.84	0.82	0.75–0.93	Δ4	164	95	$P = 0.05549$	W = 5.7829, d.f. = 2
GC/AW (mild-wet)	**0.81**	**0.81**	**0.72–0.90**	**Δ4**	**91**	**164**	$\mathbf{P < 0.05}$	**W = 6.5225, d.f. = 2**
GC/AW (hot-dry)	**0.72**	**0.73**	**0.60–0.83**	**Δ4**	**102**	**95**	$\mathbf{P < 0.001}$	**W = 16.539, d.f. = 2**
Wet/dry periods								
GC wet/dry	**0.77**	**0.74**	**0.64–0.90**	**Δ1**	**41**	**45**	$\mathbf{P < 0.05}$	**W = 6.1961, d.f. = 2**
AW wet/dry	**0.78**	**0.75**	**0.66–0.89**	**Δ4**	**61**	**102**	$\mathbf{P < 0.05}$	**W = 7.8513, d.f. = 2**
GCwet/AWwet	0.87	0.80	0.75–0.99	Δ1	41	61	$P = 0.8432$	W = 0.34103, d.f. = 2
GCdry/AWdry	**0.68**	**0.69**	**0.55–0.80**	**Δ1**	**45**	**102**	$\mathbf{P < 0.001}$	**W = 15.629, d.f. = 2**
Livestock								
Presence/Absence	0.81	0.79	0.69–0.93	Δ4	71	54	$P = 0.7686$	W = 0.52647, d.f. = 2
GC/livestock	**0.51**	**0.55**	**0.41–0.61**	**Δ4**	**193**	**72**	$\mathbf{P < 0.001}$	**W = 65.98, d.f. = 2**
Moon								
GC full/new	**0.73**	**0.72**	**0.59–0.88**	**Δ1**	**51**	**38**	$\mathbf{P < 0.05}$	**W = 8.6312, d.f. = 2**
AW full/AW new	0.84	0.79	0.73–0.95	Δ4	60	60	$P = 0.5442$	W = 1.2168, d.f. = 2
GC full/AW full	0.86	0.80	0.75–0.98	Δ4	51	60	$P = 0.255$	W = 2.7331, d.f. = 2
GC new/AW new	**0.72**	**0.72**	**0.58–0.86**	**Δ1**	**38**	**60**	$\mathbf{P < 0.05}$	**W = 7.6344, d.f. = 2**

Mardia–Watson–Wheeler test (MWW) used to compare diel activity patterns under different factors. Bold rows indicate statistically significant differences.

AW, African golden wolf; BS, Barbary sheep; GC, Cuvier's gazelle.

Influence of humans and livestock

The concentration of livestock activity at midday may reflect their daily grazing routine, whereby herds leave the camps in the morning and return only in the evening, thus inverting the hours of daylight for grazing. Although not statistically significant, the presence of livestock appeared to shift gazelle activity towards earlier hours, suggesting behavioural avoidance (H6). Chammem et al. (2008) found no significant association between sheep and goat abundance, and dorcas gazelle occurrence. However, while their study focused on species occurrence, our approach assessed effects on diel activity patterns, providing complementary evidence of a potential behavioural response to human and livestock presence. In addition, illegal hunting events, although scarce due to current protection measures, were confirmed during the study period and may contribute to this avoidance behaviour, reinforcing the perceived risk associated with human presence.

Effects of moon phase

Moonlight strongly influenced gazelle diel activity, supporting H7. The reduced nocturnal activity during new moon phases may represent an ancestral anti-predator strategy, since moonlight may enhance the hunting efficiency of carnivores, thereby increasing predation risk (Pratas-Santiago et al., 2017). Alternatively, in the absence of predators, prey species may extend their activity into illuminated periods (Michalski & Norris, 2011; Pratas-Santiago et al., 2017). However, moonlight has been associated with the nocturnal activity of the mountain gazelle (*G. gazella*), probably due to the intensive pressure from human activity (Groves et al., 2011). In our context of low predator pressure and limited human activity, the effect of moon phase on Cuvier's gazelle activity may be more related to phylogenetic imprinting within the ungulate guild and their visual acuity (Prugh & Golden, 2014; Roll et al., 2006). It is worth noting that Cuvier's gazelles coexisted with cheetahs in the study area until very recently (Aulagnier et al., 2017). This felid is particularly specialized in hunting gazelles and the Saharan cheetah is more nocturnal than other subspecies (Belbachir et al., 2015; Sunquist & Sunquist, 2009). Consequently, the observed moon-related behaviour in Cuvier's gazelles could represent an atavistic response.

Limitations of our study

We acknowledge several potential limitations: (i) the use of Iberian lynx urine as a scent lure, while effective and with no overt fear or flight responses in our footage, may exert minor species-specific behavioural effects and limits replicability elsewhere due to procurement constraints; as mitigation, more cryptic camera deployments to reduce theft (e.g., camouflaged housings, lockboxes and cable locks, or concealed placements) could be considered; (ii) the theft and rotation of 23 camera traps could have affected detection probabilities across space and time, although rarefaction analyses indicated negligible

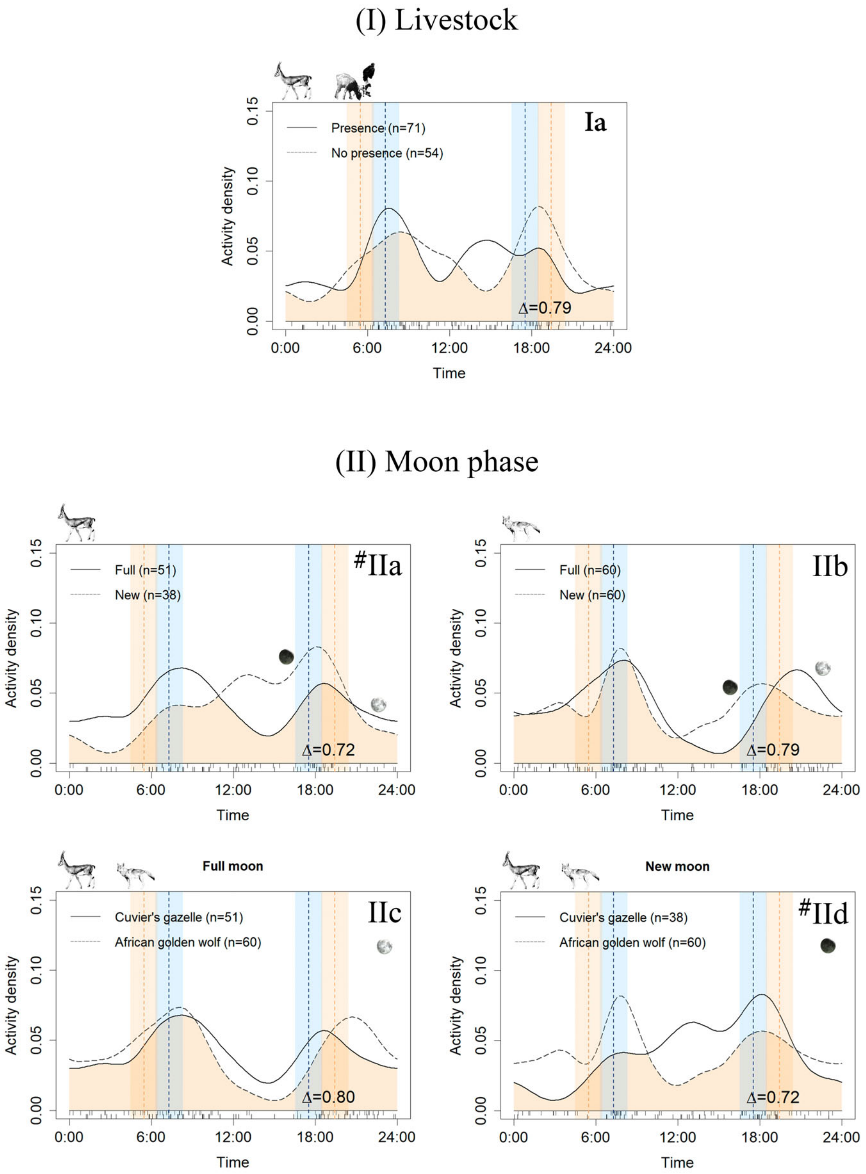


Figure 3 Diel activity patterns of Cuvier's gazelle, livestock, and African golden wolf in the Atlantic Sahara. The y-axis shows the kernel density estimates across two factors: presence of livestock (I) and moon phases (II). The coloured shaded area represents overlap, measured by the mean overlap coefficient Δ (95% CI). The "#" symbol indicates activity patterns that differ significantly according to the Mardia–Watson–Wheeler test. Sunrise and sunset times are shown as vertical dashed lines for the winter (blue) and summer (orange) solstices. Narrow shaded bands flanking sunrise and sunset (−1 to +1 h) indicate the crepuscular windows. Sample sizes (*n*, independent detections) are shown in each panel.

effects; (iii) unequal sampling effort across sites and seasons may have obscured local behaviours; and (iv) potential misclassification of diel activity linked to group-living dynamics, lure-related shifts, or short detection windows, which represents an inherent constraint of camera trap studies.

Conservation implications

By revealing strong temporal plasticity, our study underscores the adaptability of Cuvier's gazelle to hyper-arid conditions. This resilience, combined with its keystone role in Saharan ecosystems, suggests that the species could serve as a focal target for conservation actions in the face of climate change. Current diel patterns suggest slight temporal asynchrony between Cuvier's gazelle and livestock, pointing to incipient behavioural avoidance. While no drastic shifts were detected, increased grazing pressure could intensify not only trophic competition for key resources (Herrera-Sánchez et al., 2023) but also behavioural displacement. Monitoring and regulating livestock activity is therefore essential to prevent such cascading effects in hyper-arid ecosystems.

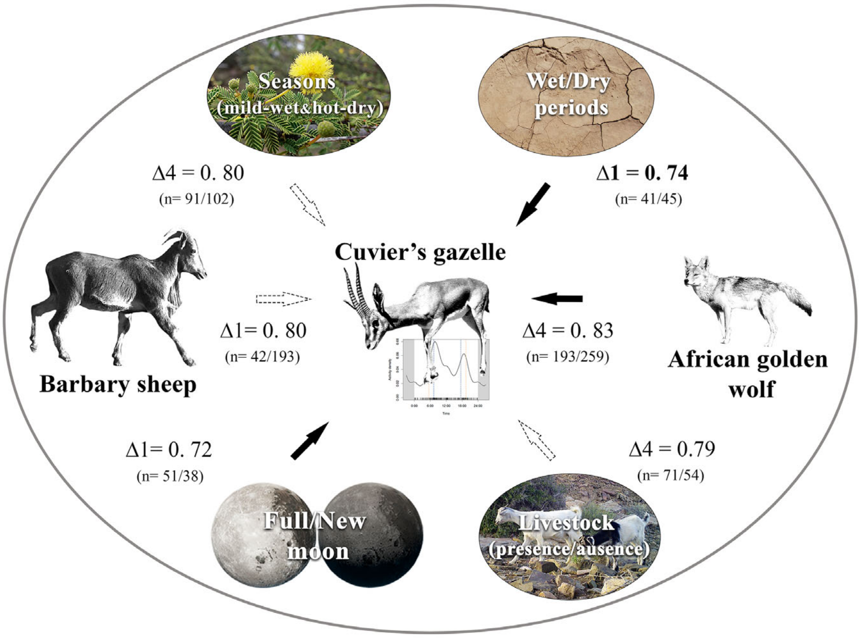


Figure 4 Conceptual diagram showing the effects of the analysed factors on the diel activity pattern of Cuvier's gazelle. Solid black arrows indicate factors for which differences in activity patterns were statistically significant based on Mardia–Watson–Wheeler test, while dashed arrows indicate non-significant differences. Diel activity pairwise comparisons include: mild-wet vs. dry-hot seasons, wet vs. dry periods, Cuvier's gazelle vs. African golden wolf, presence vs. absence of livestock, full vs. new moon, and Cuvier's gazelle vs. Barbary sheep. The mean overlap coefficient is represented by Δ1 and Δ4. Each comparison shows "*n*" (independent detections) used for activity/overlap estimates.

Conclusions

Despite limitations associated with sample size in some pairwise comparisons (Peral et al., 2022), our study adds to the scarce empirical evidence on diel activity of large ungulates in hyper-arid systems by providing a field-based assessment of temporal niche structure under extreme environmental constraints. We examined the temporal niche of an endangered, low-density species, integrating responses to co-occurring taxa, human activity, and environmental variability (Fig. 4). Cuvier's gazelle exhibited marked temporal plasticity, with activity patterns driven primarily by abiotic conditions and only limited modulation by biotic interactions. Taken together, these results indicate that environmental constraints dominate temporal niche structuring in hyper-arid ungulates, and that behavioural flexibility may underpin resilience in highly variable and stressful conditions. Finally, our findings provide a quantitative baseline to track future shifts in temporal niche structure as climate change, predator recovery, and land use intensify across Saharan landscapes.

Author contributions

FJH-S, TA, JMG-S, conceived the ideas and designed methodology; all authors participated in field work; FJH-S, TA, JMG-S analysed the data; FJH-S, TA, JMG-S, EV led the writing of the manuscript; all authors participated in funding. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Target species captured by camera traps: (a) adult and juvenile female of Cuvier's gazelle (*Gazelle cuvieri*), (b) solitary adult male of Cuvier's gazelle, (c) male Barbary sheep (*Ammotragus lervia*), and (d) a pair of African golden wolves (*Canis lupaster*).

Figure S2. Cuvier's gazelles sniffing Iberian lynx urine used as a scent lure: (A) Selected frames from a single photo sequence showing two individuals at the same camera station; (B) Different gazelle individuals recorded across four camera stations; the bottom row shows an African golden wolf and a male Barbary sheep sniffing Iberian lynx urine.

Figure S3. Rarefaction curve for the relative abundance index (RAI = independent captures/100 camera-days; total effort = 11 333 trap days) of Cuvier's gazelles, Barbary sheep, and African golden wolf. Points are monthly estimates coloured by sampling period (January–April 2017; September–December 2017; January–May 2018; June–September 2018); the solid line is the logarithmic fit.

Figure S4. Rainfall recorded in the study area from 2016 until 2018. The two camera trap survey periods are showed ('A' & 'B'), along with the drought event (gold line). Data source: Ventusky web – Wind, rain and temperature maps (https://www.ventusky.com).

Table S1. Mardia–Watson–Wheeler test (MWW) comparing surveyed site areas, presence/absence of Barbary sheep, pooled data across the four seasons (autumn, winter, spring and summer), and the tree focal species. Bolded rows indicate statistically significant differences. AW, African golden wolf; BS, Barbary sheep; GC, Cuvier's gazelle.

Table S2. Chi-square analysis and resource selection ratios outputs for diel categories (day, crepuscular, night), factors, and surveyed target species. AW, African golden wolf; BS, Barbary sheep; GC, Cuvier's gazelle.