INVESTIGACIÓN DE FAUNA AMENAZADA EN MEDIOS REMOTOS: EL CASO DE LA GACELA DE CUVIER (*Gazella cuvieri* Ogilby, 1841) EN EL DESIERTO DEL SAHARA

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Programa de Doctorado en Biología Fundamental y de Sistemas

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TESIS DOCTORAL

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Mira siempre lo humano como efímero, de poca monta: ayer mocos mañana embalsamiento y ceniza, de modo que pasa este breve tiempo de acuerdo con la naturaleza, termina alegre, como una aceituna madura que cayera a tierra bendiciendo a quien la produjo y agradecida al árbol que la crio

Marco Aurelio. Meditaciones, Libro IV, 48

Índice

Resumen

En las últimas décadas, los estudios empíricos sobre fauna y flora que implican trabajos sobre el terreno han disminuido, a pesar de que falta información básica sobre aspectos clave de la biología y ecología de numerosas especies. Esta escasez de conocimiento ha afectado negativamente a las decisiones tomadas por los gobiernos en relación con los planes de conservación de la biodiversidad. La necesidad de aumentar nuestro conocimiento básico sobre la situación y ecología de las especies es más urgente que nunca, particularmente en zonas remotas del planeta, donde la ausencia de información es muy notable. El desierto del Sahara es una de esas zonas remotas en la que faltan datos básicos para desarrollar acciones de conservación bien diseñadas. Allí, la caza excesiva y la destrucción de hábitats tienen un impacto nefasto sobre el ecosistema, que como consecuencia ha pedido gran parte de su integridad y funcionalidad. La gacela de Cuvier (*Gazella cuvieri* Ogilby, 1841) es un ungulado de tamaño medio endémico del norte de África que se encuentra precisamente amenazado por esas presiones antrópicas. A pesar de estar catalogada como "Vulnerable" por la Unión Internacional de Conservación de la Naturaleza (IUCN), el escaso conocimiento sobre su biología y el estado real de conservación puede estar conduciendo a una falta de protección e incluso a extinciones locales.

La gacela de Cuvier forma parte del grupo de antílopes Sahelo-Saharianos, gremio que ha desarrollado estrategias fisiológicas y de comportamiento para sobrevivir en condiciones extremas. La población más meridional de la gacela de Cuvier se localiza en el cuadrante atlántico del desierto del Sahara, en una región de clima hiperárido dentro de la ecorregión de la Estepa Xerófila y Bosques del Norte del Sahara. A pesar de las condiciones límites en las que habita esta población, esta especie sobrevive allí debido a su gran resiliencia y adaptación a las condiciones extremas del ambiente.

Esta tesis se llevó a cabo en un área aproximada de 20.000 km^2 de dicha región del desierto del Sahara, más concretamente en el sector noroccidental del Sahara Atlántico. El objetivo general consistió en evaluar el estado de conservación regional de la especie y ampliar el conocimiento de su biología, rasgos ecológicos y adaptaciones en el límite suroccidental de su distribución. Los objetivos específicos incluyeron la evaluación de su distribución y tamaño poblacional, la identificación de los factores que determinan su presencia con la generación de modelos predictivos de distribución, y el análisis de su dieta, ritmo de actividad y relaciones con los predadores y el hombre. Cabe destacar el carácter pionero del presente trabajo, no solo por su magnitud (tanto espacial como temporal) y por los aspectos cubiertos, sino también por haber tenido como objeto de estudio a una población totalmente silvestre de un ungulado

norteafricano. Sorprendentemente, se trata de un enfoque excepcional en el contexto reciente de la investigación de los ungulados saharianos, en el que son norma los estudios realizados en poblaciones reintroducidas en régimen de semilibertad (dentro de áreas cercadas).

En el **Capítulo 1** se evaluó la eficacia y eficiencia de dos métodos de campo ampliamente utilizados en el estudio de ungulados: el análisis de datos indirectos como huellas y excrementos (depósitos de heces y letrinas), y la observación directa de ejemplares. A través de 10 expediciones desarrolladas entre 2011 y 2014, se muestrearon 67 zonas en la que se llevaron a cabo 194 transectos a pie con un total de 2.169 km recorridos. Se detectó la presencia de la especie en el 74.62% (50/67) de los puntos muestreados y se avistaron gacelas en 21 sitios (61 individuos), lo que permitió calcular una densidad mediante estimas de distancias de 0.08 ± 0.02 individuos/km^2. La identificación de excrementos a través de análisis genéticos tuvo una tasa de acierto del 95.12%. Se encontró que los recorridos a pie superiores a 2.15 km y el aumento de las repeticiones (2-3 réplicas) redujeron significativamente el efecto de la detección imperfecta (falsos negativos). Por otro lado, hubo una relación positiva entre los avistamientos de la gacela de Cuvier y los índices indirectos de abundancia, lo que sugiere que estos métodos son eficaces para su uso en el seguimiento a largo plazo de la población en medios desérticos.

Los resultados de presencia/ausencias en los muestreos llevados a cabo en el **Capítulo 1** fueron utilizados en el **Capítulo 2** para el desarrollo de modelos predictivos de distribución a gran escala, lo que permitió identificar las áreas más favorables para su supervivencia y protección. La distribución proyectada para la presencia de la gacela de Cuvier estuvo fuertemente relacionada con zonas montañosas de terreno heterogéneo y alejadas de grandes asentamientos humanos, por encima de otros factores ecológicos que tuvieron un menor impacto en la presencia y distribución de la especie. También se realizó una estimación cuantitativa del área de distribución potencial de la gacela de Cuvier en el sur de Marruecos, identificando dos zonas clave bien delimitadas. Estas dos zonas contienen actualmente suficiente terreno favorable y de carácter remoto como para sustentar a esta especie en este duro entorno desértico. Además, se ha puesto en relieve la necesidad de la aplicación de planes de conservación para la gacela de Cuvier como "especie paraguas", lo que conferiría una protección eficaz a las zonas de hábitat de mayor calidad y a las especies cohabitantes, dando lugar a un desarrollo sostenible y ecológicamente responsable en la región.

Para evaluar la ecología alimentaria de la gacela de Cuvier en el desierto del Sahara, utilizamos un enfoque múltiple que combinó muestras fecales, observaciones directas y el análisis de signos indirectos de alimentación (**Capítulo 3**). Nuestra hipótesis pronosticó que el ramoneo sería la mejor estrategia de alimentación para la especie en entornos hiperáridos, principalmente debido a los largos periodos sin oportunidades de forrajeo. De forma complementaria, exploramos los efectos de varios descriptores ambientales (precipitaciones, temperatura, altitud y el índice de Vegetación de Diferencia Normalizada -*NDVI*-) sobre los patrones de alimentación y la calidad de la dieta. Observamos que la dieta de Cuvier se basó principalmente en acacias (*Vachellia tortilis* y *V. flava*) y ocasionalmente en la rosa de Jericó *Anastatica hierochuntica*. En conjunto, se registraron dieciocho especies (cinco árboles, nueve arbustos, tres herbáceas y una gramínea) pertenecientes a quince familias. Nuestros resultados confirmaron la característica ramoneadora y oportunista de esta especie, que aumentó la diversidad de la dieta en condiciones desfavorables. Las acacias destacaron como especies claves consumidas en el límite más meridional de su área de distribución. Los futuros planes y estrategias de conservación que se diseñen habrán de tener en cuenta el estado de conservación y extensión de estos árboles saharianos como factor determinante de la supervivencia de la gacela de Cuvier en ambientes desérticos.

En el **Capítulo 4**, se estudiaron los patrones de actividad diarios de la especie, puesto que pueden proporcionar información valiosa tanto sobre su adaptación al hábitat desde un punto de vista ecológico, como sobre los cambios inducidos por el hombre y la estructura de la comunidad. Para investigar los factores que influyeron en los patrones de actividad de la gacela de Cuvier, se utilizaron cámaras trampa instaladas en el área durante un año y cinco meses, muestreándose todas las épocas del año. Como factores abióticos se exploró el efecto de las estaciones del año, las fases lunares y las precipitaciones, y en cuanto a factores bióticos se testó el efecto de la actividad del lobo dorado africano (*Canis anthus*) como depredador potencial, las relaciones intragremiales en las áreas de coincidencia de la gacela y el arruí sahariano (*Ammotragus lervia*), la presencia de los pastores nómadas, y las posibles diferencias entre machos y hembras en sus patrones de actividad. Para evaluar la influencia de cada factor, utilizamos el coeficiente de solapamiento de actividad (Δ) y la prueba circular no paramétrica de Mardia-Watson-Wheeler. También analizamos la selección de un período específico del ciclo diario mediante tablas de contingencia chi-cuadrado y el parámetro "Wi" del coeficiente de selección de recursos. Observamos que la gacela de Cuvier mostró un patrón diurno bimodal con picos de actividad al amanecer y al atardecer, siendo este carácter crepuscular más claramente definido en las hembras que en los machos. Los efectos más significativos fueron provocados por la estacionalidad (estaciones y periodos húmedos/secos) y la fase lunar, mientras que los factores antropogénicos o intragremiales no ofrecieron resultados significativos. Tanto la gacela de Cuvier como el lobo dorado africano y el arruí mostraron un patrón bimodal y crepuscular compartido. Sin embargo, se observaron discrepancias significativas en la selección de periodos entre la gacela de Cuvier, que evitaron claramente las horas nocturnas, y los lobos dorados africanos, que evitaron las horas diurnas.

Como resumen final podemos afirmar que la presencia de gacela de Cuvier en su área de distribución más meridional se relaciona estrechamente con las características locales de un hábitat remoto, en el que se dificulta el acceso por pistas y carreteras a los seres humanos; ello gracias a una compleja red de barrancos y colinas; lo que, además, proporciona refugio vital ante las inclemencias del ambiente desértico y una adecuada disponibilidad de alimento, con un papel fundamental de las especies saharianas de acacias. Por otro lado, las gacelas de Cuvier son capaces de adaptar sus patrones de actividad diaria para optimizar su relación con las duras condiciones ambientales del desierto, circunstancia probablemente relacionada con capacidades fisiológicas propias de su herencia filogenética. A nivel metodológico, en zonas de baja densidad de la especie son de gran utilidad los datos procedentes de muestreos indirectos de presencia, a fin de estimar su distribución y abundancia. Además, las estimaciones de densidad basadas en el muestreo de distancias si bien requieren de un esfuerzo considerable, pueden ser efectivas para obtener datos sobre la dinámica poblacional. Finalmente, los modelos de distribución identificaron las áreas favorables para su protección, así como para otras especies amenazadas. En un contexto de cambio climático, taxones como la gacela de Cuvier podrán ser claves para el mantenimiento de los procesos ecológicos en ambientes áridos, por lo que es urgente la aplicación de políticas de conservación orientadas tanto a su protección directa como a la del ecosistema desértico en su conjunto.

Research on threatened fauna in remote environments: the case of the Cuvier's gazelle (*Gazella cuvieri* Ogilby, 1841) in the Sahara Desert.

Summary

In recent decades, empirical studies on fauna and flora involving fieldwork have declined, although basic information on key aspects of the biology and ecology of many species is lacking. This lack of knowledge has negatively affected decisions made by governments regarding biodiversity conservation plans. The need to increase our basic knowledge of the status and ecology of species is more urgent than ever, particularly in remote areas of the planet, where the absence of information is very noticeable. The Sahara Desert is one such remote area where basic data are lacking to develop well-designed conservation actions. There, overhunting and habitat destruction have a disastrous impact on the ecosystem, which has consequently lost much of its integrity and functionality. Cuvier's gazelle (*Gazella cuvieri* Ogilby, 1841) is a medium-sized ungulate endemic to North Africa that is threatened by precisely these anthropogenic pressures. Despite being listed as "Vulnerable" by the International Union for Conservation of Nature (IUCN), the lack of knowledge about its biology and actual conservation status may be leading to a lack of protection and even local extinctions.

Cuvier's gazelle is part of the Sahelo-Saharan antelope group, a guild that has developed physiological and behavioural strategies to survive in extreme conditions. The southernmost population of Cuvier's gazelle is located in the Atlantic quadrant of the Sahara Desert, in a region of hyper-arid climate within the ecoregion of the Xerophytic Steppe and Forests of the Northern Sahara. Despite the limiting conditions in which this population inhabits, this species survives there due to its great resilience and adaptation to the extreme conditions of the environment.

This thesis was carried out in an area of approximately 20,000 km^2 in this region of the Sahara Desert, more specifically in the north-western sector of the Atlantic Sahara. The general objective was to assess the regional conservation status of the species and to increase knowledge of its biology, ecological traits and adaptations at the southwestern limit of its distribution. The specific objectives included the evaluation of its distribution and population size, the identification of the factors that determine its presence with the generation of predictive distribution models, and the analysis of its diet, activity rhythm and relationships with predators

and humans. The pioneering nature of this work should be highlighted, not only because of its magnitude (both spatial and temporal) and the aspects covered, but also because it has focused on a totally wild population of a North African ungulate as the object of study. Surprisingly, this is an exceptional approach in the recent context of research on Saharan ungulates, where studies on reintroduced populations in semi-freedom (within fenced areas) are the norm.

Chapter 1 evaluated the effectiveness and efficiency of two field methods widely used in the study of ungulates: the analysis of indirect data such as tracks and scat (faecal deposits and latrines), and the direct observation of individuals. Through 10 expeditions developed between 2011 and 2014, 67 areas were sampled in which 194 foot transects were carried out with a total of 2,169 km covered. The presence of the species was detected in 74.62% (50/67) of the points sampled and gazelles were sighted in 21 sites (61 individuals), which allowed us to calculate a density using distance sampling of 0.08 ± 0.02 individuals/km^2. Identification of scat through genetic analysis had a 95.12% success rate. We found that walking distances greater than 2.15 km and increased repetitions (2-3 replicates) significantly reduced the effect of imperfect detection (false negatives). On the other hand, there was a positive relationship between Cuvier's gazelle sightings and indirect indices of abundance, suggesting that these methods are effective for use in long-term population monitoring in desert environments.

The presence/absence results of the surveys conducted in **Chapter 1** were used in **Chapter 2** for the development of large-scale predictive distribution models, allowing identification of the most favourable areas for survival and protection. The projected distribution of Cuvier's gazelle was strongly related to mountainous areas of heterogeneous terrain and away from large human settlements, over and above other ecological factors that had less impact on the species' occurrence and distribution. A quantitative estimation of the potential range of Cuvier's gazelle in southern Morocco was also carried out, identifying two well-defined key areas. These two areas currently contain sufficient remote and favourable terrain to support this species in this harsh desert environment. In addition, the need for the implementation of conservation plans for Cuvier's gazelle as an "umbrella species" has been highlighted, which would confer effective protection to areas of higher quality habitat and cohabitant species, leading to sustainable and ecologically responsible development in the region.

To assess the feeding ecology of Cuvier's gazelle in the Sahara Desert, we used a multiple approach combining faecal samples, direct observations and analysis of indirect signs of feeding (**Chapter 3**). Our hypothesis predicted that browsing would be the best foraging strategy for the species in hyper-arid environments, mainly due to long periods without foraging opportunities. Complementarily, we explored the effects of several environmental descriptors (precipitation, temperature, altitude and the Normalised Difference Vegetation Index -*NDVI*-) on feeding patterns and diet quality. We observed that Cuvier's diet was mainly based on acacias (*Vachellia* *tortilis* and *V. flava*) and occasionally on rose of Jericho *Anastatica hierochuntica*. Altogether, eighteen species (five trees, nine shrubs, three forbs and one grass) belonging to fifteen families were recorded. Our results confirmed the browsing and opportunistic characteristic of this species, which increased dietary diversity under unfavourable conditions. Acacias stood out as key species consumed at the southernmost limit of their range. Future conservation plans and strategies will have to take into account the conservation status and extent of these Saharan trees as a determining factor for the survival of Cuvier's gazelle in desert environments.

In **Chapter 4**, diel activity patterns of the species were studied, as they can provide valuable information both on its adaptation to the habitat from an ecological point of view, as well as on human-induced changes and community structure. To investigate the factors influencing the activity patterns of Cuvier's gazelle, camera traps were used in the area for one year and five months, sampling all seasons of the year. As abiotic factors we explored the effect of seasons, lunar phases and rainfall, and as biotic factors we explored the effect of the activity of African golden wolf (*Canis anthus*) as a potential predator, the intra-guild relationships in the areas of coincidence of the gazelle and Saharan Barbary sheep (*Ammotragus lervia*), the presence of nomadic herders, and the possible differences between males and females in their activity patterns. To assess the influence of each factor, we used the activity overlap coefficient (Δ) and the non-parametric Mardia-Watson-Wheeler circular test. We also analyse the selection of a specific period of the diel cycle using chi-square contingency tables and the "Wi" parameter of the resource selection coefficient. We observed that Cuvier's gazelle showed a bimodal diurnal pattern with peaks of activity at dawn and dusk, this crepuscular character being more clearly defined in females than in males. The most significant effects were caused by seasonality (seasons and wet/dry periods) and lunar phase, while anthropogenic or intra-gremial factors did not provide significant results. Cuvier's gazelle, African golden wolf and Saharan Barbary sheep all showed a shared bimodal and crepuscular pattern. However, significant discrepancies in period selection were observed between Cuvier's gazelle, which clearly avoided nocturnal hours, and African golden wolves, which avoided diurnal hours.

As a final conclusion, we can state that the presence of Cuvier's gazelle in its southernmost range is closely related to the local characteristics of a remote habitat, where access by tracks and roads is difficult for humans, thanks to a complex network of ravines and hills, which also provides vital shelter from the harshness of the desert environment and adequate food availability, with a fundamental role of Saharan acacia species. On the other hand, Cuvier's gazelles are able to adapt their diel activity patterns to optimise their relationship with the harsh environmental conditions of the desert, a circumstance probably related to physiological capacities inherited from their phylogenetic heritage. At a methodological level, in areas of low density of the species, data from indirect presence sampling are very useful to estimate its distribution and abundance. In addition, density estimates based on distance sampling, although requiring considerable effort, can be effective in obtaining data on population dynamics. Finally, distribution models identified favourable areas for their protection, as well as for other threatened species. In a context of climate change, taxa such as Cuvier's gazelle may be key to the maintenance of ecological processes in arid environments, so it is urgent to implement conservation policies aimed at both their direct protection and that of the desert ecosystem as a whole.

SECCIÓN I. INTRODUCCIÓN Y OBJETIVOS

1. INTRODUCCIÓN Y OBJETIVOS

Los estudios empíricos sobre fauna y flora que implican trabajos de campo han disminuido sensiblemente en las últimas décadas (Ríos-Saldaña, 2018). Y ello a pesar de que falta información básica sobre aspectos clave de la biología y la ecología de numerosas especies (Noss, 1996; Tewksbury *et al.*, 2014; IUCN, 2023). Como consecuencia, se suceden efectos negativos en las decisiones que toman los gobiernos y que influyen en las tan necesarias medidas de conservación de la biodiversidad (Margules & Pressey, 2000). Además, la puesta en marcha de políticas medioambientales es cada vez más urgente ante la evidente pérdida de hábitats y biodiversidad a consecuencia del cambio climático (Pimm, 2008; Cardinale *et al.*, 2012). Ante este crítico escenario ahora, más que nunca, es necesario aumentar nuestro conocimiento básico sobre la situación y ecología de las especies, particularmente en zonas remotas del planeta, donde la ausencia de información es muy notable (Brito *et al.*, 2009, 2016; Brugière & Scholte, 2013).

El desierto del Sahara posee esa temible etiqueta de remoto. Allí, cualquier estudio sobre el terreno implica serios desafíos, tanto logísticos como derivados de la propia seguridad de los investigadores, lo que ha motivado que el conocimiento ecológico sobre esta región sea muy escaso (Durant *et al.*, 2014; Brito *et al.*, 2018). El estado de conservación y distribución de la fauna del Sáhara es un caso paradigmático que ilustra esta falta de datos básicos para desarrollar acciones de conservación bien diseñadas. En ese escenario, la caza excesiva y la destrucción de los hábitats son las principales amenazas, habiendo causado ya varias extinciones locales (globales en el caso del órix de cuernos de cimitarra, *Oryx dammah*) y una situación crítica de conservación de todo el conjunto de ungulados y grandes carnívoros (Duran *et al.*, 2014; Brito *et al.*, 2016). En consecuencia, los ecosistemas saharianos han perdido por completo su integridad ecológica, tras la desaparición de grupos funcionales clave (Gil-Sánchez & Sánchez-Cerdá, 2023).

El desierto del Sahara contiene en su sector atlántico una región de enorme interés conocida como Sahara Atlántico. La biodiversidad que alberga es alta, con una notable cantidad de endemismos y taxones relictos, lo que conforma un área clave que actuaría como refugio de fauna y corredor faunístico entre ecorregiones (Brito *et al.*, 2014). La dificultad de acceso y la dureza del terreno, así como la inseguridad de la zona como consecuencia de varios conflictos sociales aún sin resolver, han hecho que sean muy escasos los estudios de campo sobre el estado actual de conservación de su fauna amenazada, o sobre el funcionamiento ecológico del conjunto del ecosistema. El último de estos conflictos mantiene esta región contaminada de minas terrestres y restos de explosivos como consecuencia de un continuado conflicto armado (MINURSO, 2023).

Habitando el Sahara Atlántico se encuentra la amenazada gacela de Cuvier (*Gazella cuvieri* Ogilby, 1840), un ungulado de tamaño medio endémico del norte de África. La existencia de una población situada al noroeste del Sahara no se descubrió hasta mediados del siglo XX (Valverde, 1957). Esta gacela ha sufrido en el último siglo una importante fragmentación de sus poblaciones y su número ha disminuido drásticamente hasta los 2.360-4.560 individuos, debido principalmente a la caza excesiva y a la pérdida de hábitat (Beudels-Jamar *et al.*, 2006; Cuzin, 2008; Bounaceur *et al.*, 2016; IUCN, 2018). Este hecho hace que la gacela de Cuvier esté catalogada como "En peligro" en Marruecos, Argelia y Túnez (Beudels-Jamar *et al.*, 2006), y globalmente como "Vulnerable" por la Unión Internacional de Conservación de la Naturaleza (UICN). El escaso conocimiento sobre su biología y estado real de conservación puede estar conduciendo a una falta de protección e incluso a extinciones locales, como ha ocurrido con otros taxones (p.ej. es bien conocido el caso del lince ibérico, *Lynx pardinus*, Guzmán *et al.*, 2004). De hecho, tres especies de antílopes han sido ya erradicadas de la región en el pasado siglo: la gacela dama mohor (*Nanger dama mhorr*), el órix de cuernos cimitarra y el adax (*Addax nasomaculatus*) (Valverde, 1957, Beudels-Jamar, 2006). La puesta en marcha de estudios de campo encaminados a entender aspectos básicos de la gacela de Cuvier como son: su distribución y abundancia actual, biología y adaptaciones a ambientes desérticos, y estado de conservación, podrán proporcionar el conocimiento necesario con los que diseñar medidas de conservación a largo plazo en esta región de importancia crucial para las especies desérticas.

1.1 La gacela de Cuvier

Esta especie es un artiodáctilo de porte mediano que pertenece a la familia Bovidae, subfamilia Antilopinae, tribu Antilopini y una de las veinte especies que conforman el género *Gazella* (Wilson & Mittermeier, 2011). La gacela de Cuvier es la mayor de tres especies de este género que conviven actualmente en el norte de África, las otras dos son: la gacela dorcas (*G. dorcas*) y la gacela de Loder (*G. leptoceros*). Localmente se la conoce por varios nombres vernáculos como son: *damah* (bereber, este de Marruecos), *harmush* (hassania, sur-oeste de Marruecos), *Ledm*, *Edem* o *Edmi* (árabe, Argelia y Túnez) (Beudels-Jamar *et al.*, 2006). Posee un cuerpo robusto y desarrolla un cierto dimorfismo sexual (pesos medios: 26.43 kg ♀ & 32.5 kg ♂, Moreno & Espeso, 2008). De pelaje marrón oscuro y franja lateral negra, mantienen un vistoso contraste con los blancos del vientre y el escudo anal. Además, posee el rayado típico en la cara propio de género de las gacelas (Fig. 1).

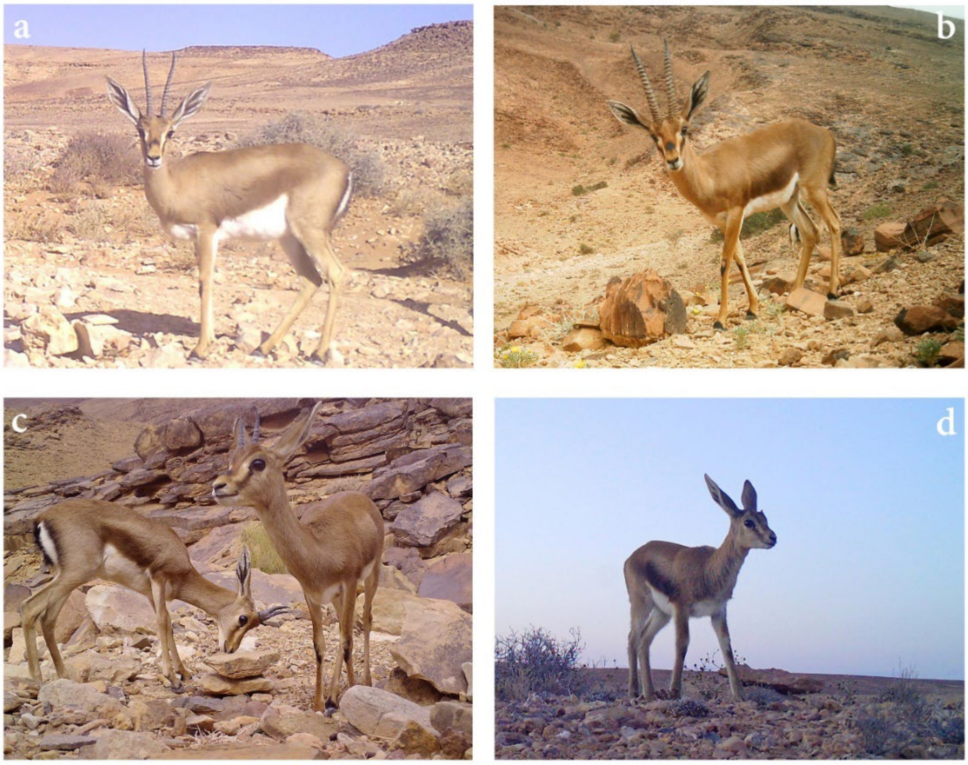

Figura 1. Fotografías de gacelas de Cuvier obtenidas mediante cámara trampa durante el trabajo de campo en el Sahara Atlántico: a) hembra adulta, b) macho adulto, c) macho y hembra juveniles procedentes de un parto gemelar, d) cría.

El tiempo de gestación para la especie suele estar entre 161-165 días (Cano, 1991; Escós, 1992) y pueden tener dos nacimientos al año (primavera/otoño). Además, los partos gemelares son comunes, al igual que sucede con la gacela persa (*G. subguturosa*) y la gacela Loder (Abáigar & Cano, 2005).

Con una distribución histórica más amplia, actualmente la gacela de Cuvier se encuentra restringida a pequeños parches aislados del Atlas y estribaciones montañosas de Marruecos, Argelia y Túnez, además de en estepas mediterráneas áridas (IUCN, 2018). La aparente plasticidad de la especie, le permite sobrevivir en una amplia gama de hábitats. La podemos encontrar habitando desde monte espeso de tuya mediterránea (*Tetraclinis articulata*) o escasamente abierto de *Rosmarinus officinalis, Phillyrea angustifolia, Pistacia lentiscus* y *Globularia alypum,* a estepas mediterráneas de *Stipa tenacissima* y *Artemisia herba-alba* e incluso en zonas de cultivo de cereal cuando la presión cinegética desaparece (Cuzin, 2003; Beudels-Jamal *et al.*, 2006; Bounaceur *et al.*, 2016; Boualem, 2017; El Alami, 2018).

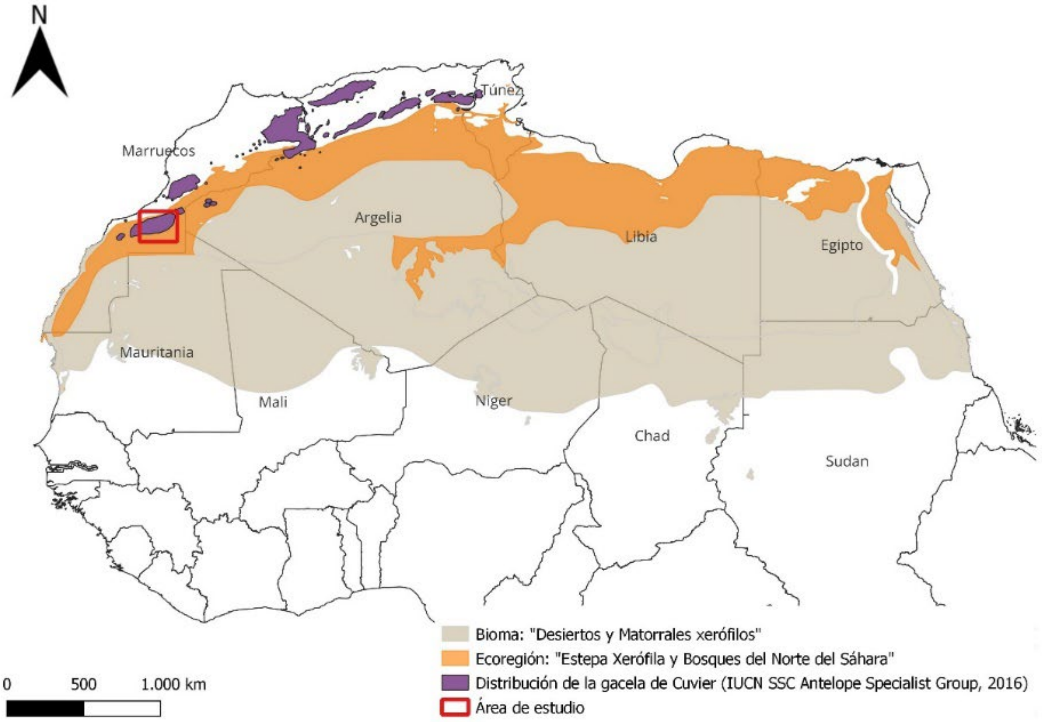

Figura 2. Localización del área de estudio y distribución de la gacela de Cuvier según la IUCN (IUCN SSC Antelope Specialist Group 2016). El mapa también muestra la ecorregión “Estepa Xerófila y Bosques del Norte del Sahara” y el bioma “Desierto y Matorrales Xerófilos” (Dinerstein *et al.*, 2017).

En el cuadrante atlántico del desierto del Sahara, la gacela de Cuvier alcanza su distribución más meridional, habitando biotopos muy diferentes de los paisajes típicos que ocupa en las montañas del Atlas y estepas áridas, donde las condiciones climáticas dan lugar a entornos más productivos que en el Sáhara (IUCN, 2018; Fig. 2). Esta región posee un clima hiperárido (Trabucco & Zomer, 2009), y se sitúa en el sector occidental de la ecorregión de la “*Estepa Xerófila y Bosques del Norte del Sáhara*” contenida en el bioma “*Desierto y Matorrales Xerófilos*” (Dinerstein et al., 2017). Dicha ecorregión delimita la extensión septentrional del Gran Desierto del Sáhara, con precipitaciones irregulares durante el frío invierno, seguidas de un verano caluroso, seco y largo (Naia & Brito, 2021). El hecho de que esta especie sobreviva en este ambiente hiperárido demuestra una gran resiliencia a las condiciones extremas. Es por ello que se la incluye en el grupo de antílopes Sahelo-Saharianos junto con la gacela dama, la gacela dorcas, la gacela de Loder, el órix de cuernos de cimitarra y el adax. Estos ungulados han desarrollado diferentes estrategias fisiológicas y de comportamiento ante la escasa disponibilidad de agua y la exposición extrema a la radiación solar, por lo que están bien adaptadas a la vida en las condiciones extremas de esta región (Beudels-Jamar *et al.*, 2006; Durant *et al.*, 2014).

1.2 Objetivos

En el área de estudio de este trabajo, la gacela de Cuvier debe haber desarrollado diferentes estrategias de supervivencia como respuesta a los factores limitantes que encuentra en ambientes desérticos, tal como debe suceder en la región del noroeste del desierto del Sahara, límite sur de su distribución. Los objetivos generales de este estudio son: 1) evaluar el estado de conservación de la gacela de Cuvier en el Sahara Atlántico, y 2) ampliar el conocimiento de su biología, rasgos ecológicos y adaptaciones de esta especie, que le permiten sobrevivir en el límite suroccidental de su área de distribución. Los objetivos específicos son:

i) Determinar su estatus en términos de distribución y número, realizando una evaluación previa de las metodologías disponibles. **Capítulo 1.**

ii) Determinar cuáles son los factores abióticos y bióticos que determinan la presencia de la especie y generar modelos predictivos de distribución, a gran escala, para ser utilizados en el diseño de áreas protegidas. **Capítulo 2.**

iii) Determinar los rasgos adaptativos en términos biológicos y ecológicos; particularmente: su dieta, ritmo de actividad y relaciones con los predadores y el hombre. **Capítulos 3 y 4.**

1.3 Hipótesis genéricas

H1.- Debido a: 1) la presumible baja detectabilidad de individuos, a consecuencia del desarrollo de un comportamiento de evitación y huida frente al hombre, 2) su previsible baja densidad en un ambiente *a priori* subóptimo, y 3) limitaciones logísticas relacionadas con las condiciones de trabajo (en un escenario remoto e incluso peligroso), los métodos de estudio más eficaces serán técnicas indirectas y no invasivas (detección de heces y huellas, fototrampeo, etc.), los cuales también suponen un menor esfuerzo.

H2.- En un contexto geográfico, el Sahara, donde la extinción de su gran fauna especialmente por persecución directa ha sido la norma a lo largo del siglo XX, la presencia de esa población marginal de gacela de Cuvier estará relacionada con factores locales asociados tanto a la estructura del hábitat como a los usos del terreno por parte del hombre.

H3.- "A priori", la población objeto de estudio se sitúa en el límite del óptimo ecológico de la especie, habitando un medio de condiciones ambientales extremas. La gacela de Cuvier en regiones saharianas deberá presentar una serie de adaptaciones particulares en sus rasgos biológicos y ecológicos, particularmente los que se refieren a: i) su alimentación, en relación a la predictibilidad y abundancia del alimento, ii) sus ritmos de actividad circadiana (por ejemplo, para evitar las temperaturas extremas), iii) su relación con los depredadores.

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SECCIÓN II.
METODOLOGÍA

2. METODOLOGÍA

La región estudiada se localiza en el sector norte del Sahara Atlántico y cubre una superficie aproximada de unos 20.000 km^2 (Fig. 1). Esta enorme extensión planteó problemas logísticos (principalmente de abastecimiento agua y gasoil), y por ello se diseñó un estudio sistemático a gran escala teniendo en cuenta las limitaciones temporales y económicas. Se llevaron a cabo 17 campañas de muestreo que comenzaron en el 2011 y tuvieron fin en el 2018. La duración de cada una de las campañas fue de 10-15 días, y se recorrieron entre 2.500-3000 km en vehículos 4x4 por expedición. En cada **Capítulo (1-4)** se detalla en profundidad la metodología empleada. Para los siguientes apartados se describe la metodología de manera sintética y general.

2.1 Área de estudio

El área de estudio se sitúa en el extremo noroccidental del desierto del Sahara (28°30′N-26°50′N y 11°40′-9°25′W) dentro de la región de Guelmim-Es Smara de Marruecos. Delimitando el área hay dos importantes accidentes geográficos: el cauce bajo del río Drâa al norte y la cuenca alta del Sequiat Al Hamra al sur (Fig. 1). Esta vasta región posee un paisaje típicamente sahariano con temperaturas medias que oscilan entre 22.7 °C en las zonas occidentales (más próximas al océano Atlántico) y los 23.2 °C en el área más oriental. Las precipitaciones anuales totales (con gran variabilidad interanual) registradas en las estaciones climáticas de Tan Tan (28°26′N, 11° 06′W), Es-Smara (26°45′N, 11°39′W) y Tinduf (27°40′N, 8°8′W) varían entre 190, 138, 59mm respectivamente. La zona presenta un relieve diverso (Fig. 2) con zonas accidentadas montañosas (*djebels*), depresiones salinas (*sebjas*), mesetas (*hammadas*), llanuras arcillosas (*dayas*) y pedregosas (*regs*), y algunas pequeñas agrupaciones de dunas (*ergs*). Los grandes relieves montañosos los conforman los montes Aydar (zona occidental), tres djebeles principales: Zini, Rich y Ouarkziz, este último con una longitud total aproximada de 400 km (250 km en Marruecos), y la hammada de Tindouf extremo oriental.

El área de estudio es un punto de contacto de diferentes tipos de vegetación típicos de las regiones sahelo-árabe, mediterránea y macaronésica (Le Houérou 1986,1987; Casañas, 1999). La vegetación leñosa es escasa y se localiza principalmente en barrancos y *oueds* (efímeros ríos de cuencas arenosas), con bosques abiertos tipo sabana principalmente formados por acacias (*Vachellia tortilis* subsp. *raddiana* y *V. flava*), que a veces son acompañados por datileras del desierto (*Balanites aegyptiaca*) y por el manzano de Sodoma (*Calotropis procera*). Otras especies que destacan son el argán (*Argania spinosa*), árbol endémico de Marruecos que alcanza aquí su límite más meridional, el tamarisco africano (*Tamarix africana*), abundante en *gueltas* (charcas permanentes de agua) y el cardón *Euphorbia officinarum*, este último especie clave de la región macaronésica continental. También destacan los arbustos de *Periploca laevigata*, *Launaea* *arborescens*, *Searsia tripartita*, *Nitraria retusa*, *Saharanthus ifniensis*, *Salsola tetragona y Lycium shawii*, y entre las gramíneas *Panicum turgidum*, *Andropogon laniger*, *Stipagrostis pungens* y *Cymbopogon schoenanthus*. Como ejemplo de vegetación extremófila que sobrevive en las hammadas, regs y ergs, aparecen dispersas la rosa de Jericó (*Anastatica hierochuntica*) y la tuera (*Citrullus colocynthis*).

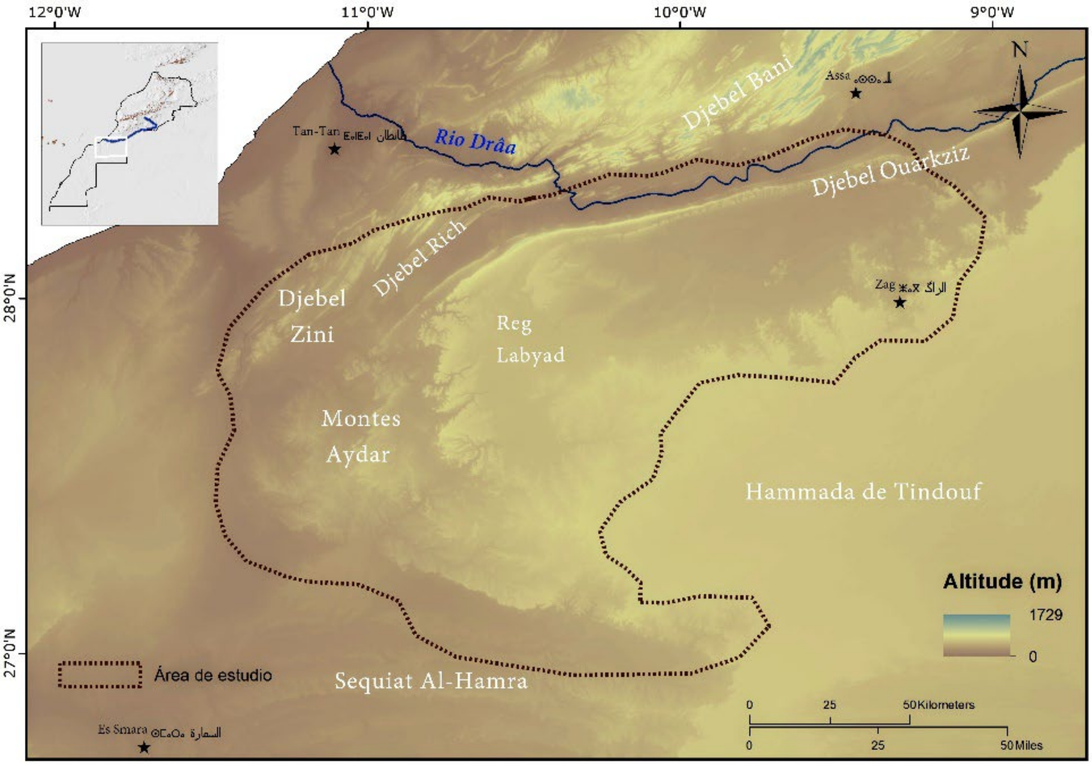

Figura 1. Localización del área de estudio. En el mapa están indicados los nombres de los accidentes geográficos y ciudades más importantes.

Respecto a los grandes vertebrados, estos han sufrido una enorme regresión debido principalmente a la caza ilegal, acompañado por un declive general en toda el área sahelo-sahariana (Durant *et al.*, 2014). El guepardo sahariano (*Acinonyx jubatus hecki*) probablemente se extinguió a finales del siglo XX y los últimos avistamientos de la gacela dama mohor (*Nanger dama mhorr*) se produjeron a mediados del mismo siglo (Cano, 1991; Aulagnier *et al.*, 2017). Actualmente podemos encontrar conviviendo con la gacela de Cuvier (*Gazella cuvieri*) dos ungulados en el área de estudio: la gacela dorcas (*G. dorcas*) y el arruí sahariano atlántico (*Ammotragus lervia atlantica*), recientemente identificado como subespecie gracias a los muestreos desarrollados para esta tesis (Pizzigalli, 2023).

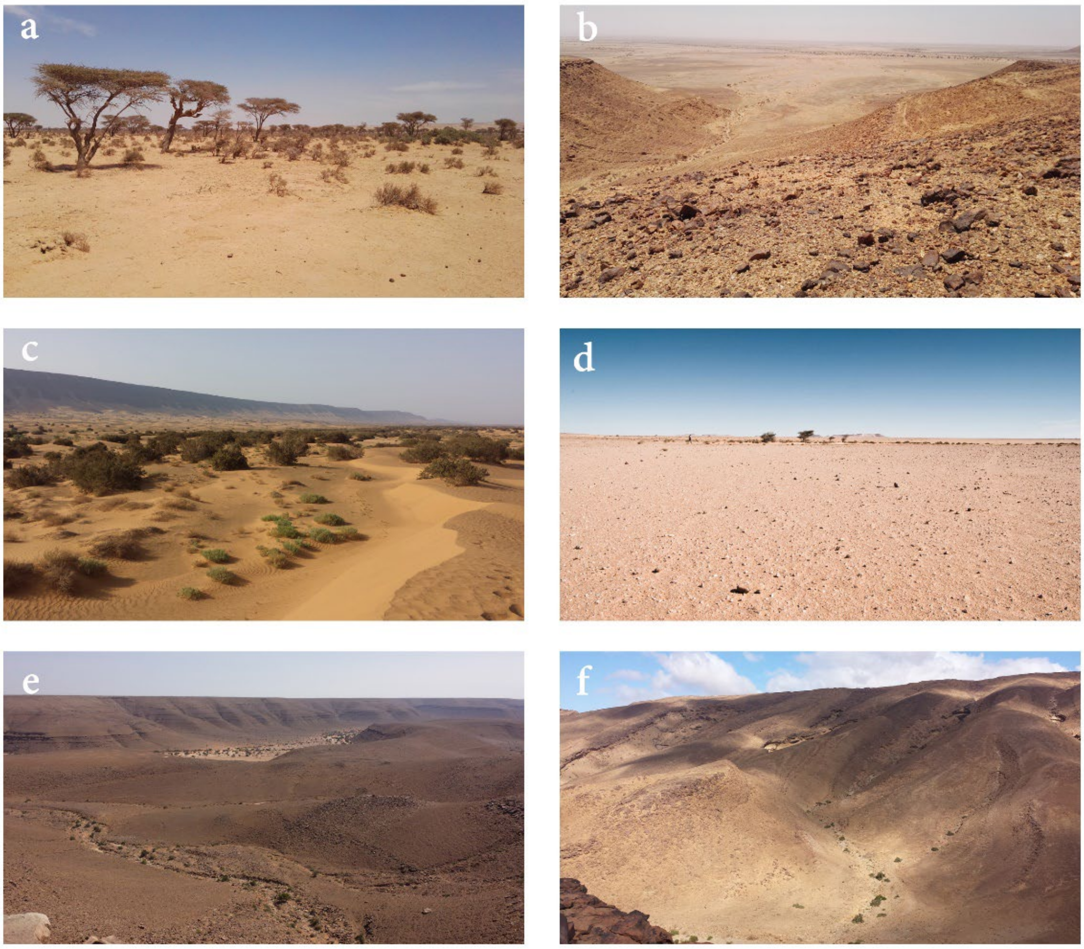

Figura 2. Ejemplos de la diversidad paisajística del área de estudio: a) lecho y márgenes de un *oued*, b) escalón de la hamada de Tindouf, c) ergs de M'sied, d) reg Labyad, e) montes Aydar y f) djebel Ouarkziz.

La comunidad de mamíferos carnívoros la conforman 12 especies pertenecientes a 6 familias (Aulagnier *et al.*, 2017): cuatro cánidos (el lobo dorado africano *Canis anthus*, el zorro rojo *Vulpes vulpes*, el zorro de Ruppell *V. rueppellii* y el fenec *V. zerda*), tres félidos (el caracal *Caracal caracal*, el gato montés africano *Felis lybica* y el gato de las arenas *F. margarita*), dos mustélidos (el ratel *Mellivora capensis* y la zorrilla líbica *Ictonyx libycus*), un vivérrido (la gineta común *Genetta genetta*), un herpéstido (el meloncillo *Herpestes ichneumon*) y un hiénido (la hiena rayada *Hyanea hyanea*).

2.2 Muestreos: recorridos a pie

En expediciones de 7 a 15 días de duración, se llevaron a cabo recorridos a pie, en los cuales se usaron dos métodos comúnmente aceptados y utilizados en estudios de mamíferos silvestres: (i) observaciones directas (Lawes & Nanni, 1993; Dunham, 1997; Abáigar *et al.*, 2005a; Chammem *et al.*, 2008; Cunningham & Wronski, 2011; Attum & Mahmoud, 2012), (ii) búsquedas de indicios/rastros de presencia (huellas, pilas de excrementos aisladas y letrinas) (Abáigar *et al.*, 2005b; Chammem *et al.*, 2008; Wronski & Plath, 2010; Attum *et al.*, 2014).

La selección de los recorridos/transectos a pie fue establecida previamente a través de imagen satelital con el *Google Earth*, lo que aseguró un muestreo estratificado que cubrió todas las formaciones paisajísticas y biotopos (ramblas, roquedos, agrupaciones de acacias, llanuras pedregosas o *regs*, etc.). Los recorridos a pie durante los meses de verano fueron evitados debido a las extremas temperaturas y a la escasa disponibilidad de agua en el área de estudio; el agua debe de ser trasportada y almacenada para su uso y consumo lo que conllevó, por tanto, un serio factor limitante. Los datos obtenidos en cada transecto fueron georreferenciados con GPS. Se llevaron a cabo dos tipos de muestreos:

a) *Transectos para la observación directa y detección de rastros de presencia*. Los recorridos se realizaban antes del amanecer por equipos de 2-3 personas; uno con la función de guía adelantado (100 m), buscando contacto visual con binoculares, mientras el resto del equipo tomaba datos de la presencia de huellas y recogía excrementos que se almacenaron en sobres de papel. La función del guía avanzando fue la de detectar gacelas en un paisaje abierto con gran visibilidad donde su distancia de huida es alta. Los avistamientos recopilados por el guía se trataron como un muestreo de distancias. Usando ArcGIS e imagen satelital (ESRI, i-cubed, GeoEye) se calculó la distancia perpendicular por el método de biangulación (Millspaugh & Marzluff, 2001), y por GPS en caso de avistamientos cercanos; además, se identificó la clase de edad y el sexo de cada gacela en base a su tamaño corporal, y forma y longitud de la cornamenta en los casos que fueron posible (**Capítulos 1, 2**; Fig. 3).

b) *Transectos exclusivos de indicios indirectos*. Recorridos llevados a cabo a cualquier hora del día por una o dos personas y cuyo objetivo fue la búsqueda de huellas y excrementos de gacelas (**Capítulos 1, 2**). Al mismo tiempo, cuando se detectaron rastros de gacelas en sustratos arenosos, se anotaron las especies vegetales disponibles a lo largo de cada rastro y cuáles fueron consumidas (Schulz *et al.*, 2013; Wronski *et al.*, 2015). Estos datos se completaron con observaciones directas de gacelas alimentándose, lo que suministró información para el estudio de la ecología trófica (**Capítulo 3**).

2.3 Identificación de indicios/rastros: excrementos y huellas

Los excrementos de gacelas Cuvier se diferencian claramente de los de cabra u ovejas domésticas debido a su morfología, aunque pueden ser confundidos con los de gacela dorcas, presente en el área de estudio. Ambas gacelas normalmente defecan creando pilas aisladas y letrinas de excrementos. Se realizaron análisis genéticos de los excrementos en los laboratorios del Instituto Universitario de Investigación en Biodiversidad (CIBIO) de la Universidad de Oporto y se calculó la tasa de acierto en la identificación de *visu* de los indicios de la especie diana (**Capítulo**

1). Cabe desatacar que estas muestras formaron parte de dos publicaciones científicas, donde pueden consultarse los detalles metodológicos del análisis molecular (Silva *et al.*, 2015, 2017).

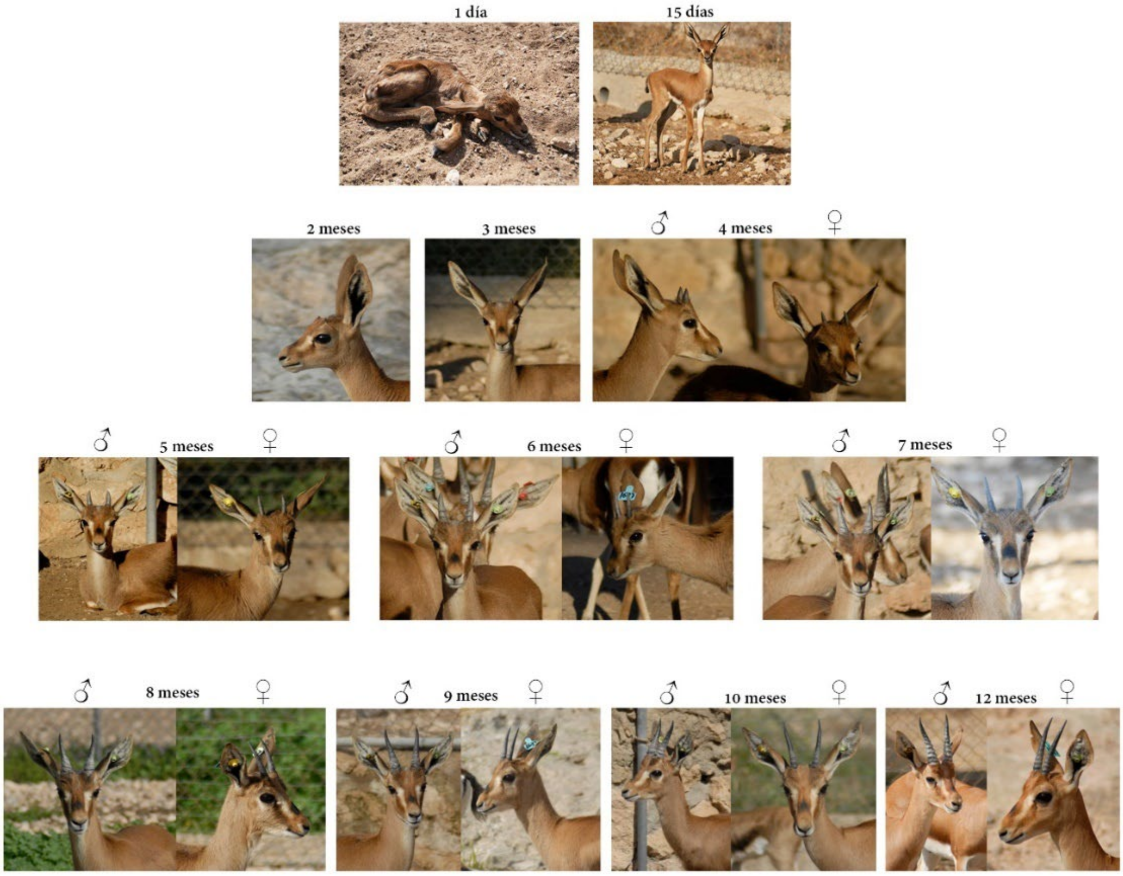

Figura 3. Desarrollo de los cuernos respecto a cada mes de crecimiento de una pareja de hermanos de gacela de Cuvier, nacidos de un parto gemelar en la Finca Experimental La Hoya (EEZA- CSIC, Almería, España). Imágenes obtenidas en el transcurso de esta tesis.

Las huellas de gacelas tienen una forma particular de corazón invertido que las distinguen del resto de ungulados de la zona de estudio (Fig. 4). Solo se tuvieron en cuenta rastros recientes y muy claros. Además, las huellas de juveniles de gacelas de Cuvier pueden ser confundidas con los de gacelas dorcas (<4.5 cm; Wacher *et al.*, 2011), por tanto, fueron consideradas solo cuando estuvieron asociadas con adultos.

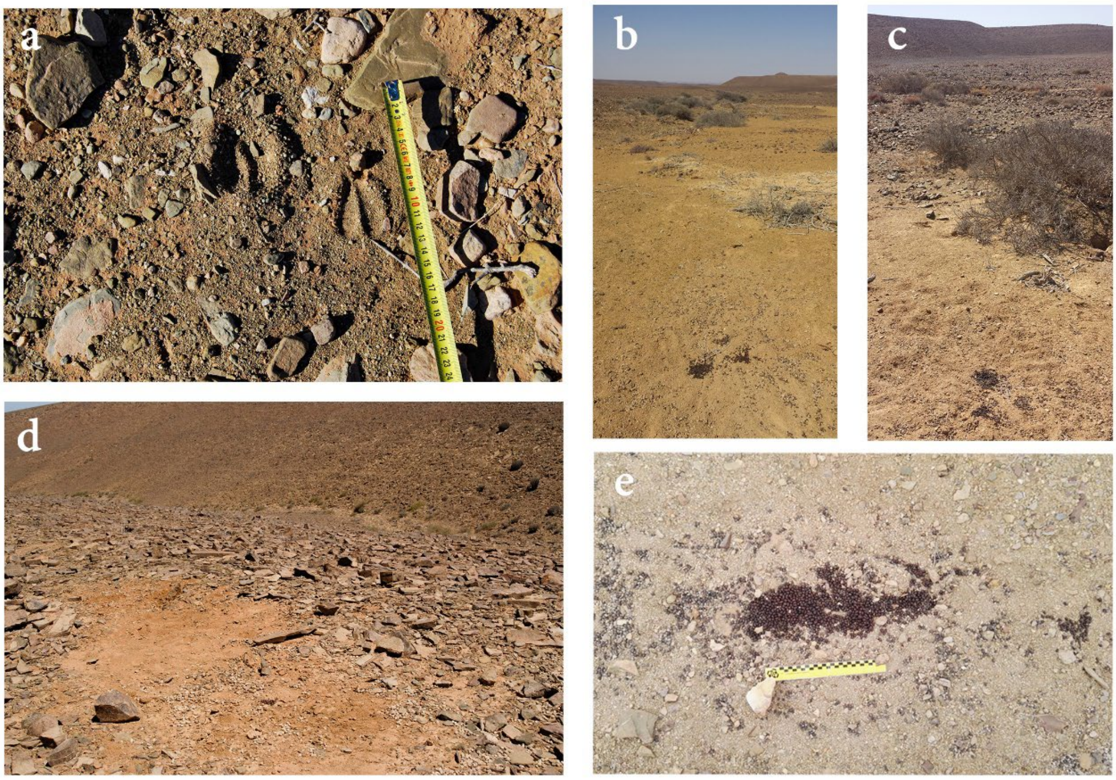

Figura 4. Indicios indirectos de gacela de Cuvier detectados durante el trabajo de campo: a) huellas, b) y c) punto de marcaje con pilas de excrementos recientes, d) encame junto a una letrina, e) detalle de una deposición reciente sobre una letrina.

2.4 Fototrampeo

El fototrampeo es un método no intrusivo basado en el registro fotográfico mediante cámaras-trampa. Esta herramienta es ampliamente usada para el seguimiento de fauna debido a su objetividad, facilidad de uso y capacidad para generar información sobre un amplio espectro de especies (O'Connell *et al.*, 2011). En el área de estudio se usaron cámaras digitales con sensor de infrarrojo pasivo colocadas en sendas, barrancos y pasos de animales, separadas 1-2 km entre sí formando una malla de muestreo. Los sitios de muestreo fueron elegidos donde expediciones previas confirmaron la presencia de la gacela de Cuvier. Esto permitió obtener información para el diseño de un estudio de larga duración que consistió en cuatro áreas de fototrampeo, dispuestas de manera estratificada cubriendo todas las estaciones del año (**Capítulo 4**). En total, se utilizaron simultáneamente 10 cámaras por área de fototrampeo. El objetivo fue obtener datos sobre: 1) el ritmo de actividad diaria, y 2) las relaciones interespecíficas (intragremiales y con los depredadores potenciales) y con la actividad humana (pastoreo y caza furtiva).

2.5 Manejo de datos y análisis estadísticos

a) *Evaluación de métodos y estima poblacional* (**Capítulo 1**). Para analizar la viabilidad, en términos de esfuerzo necesario y precisión de los resultados obtenidos mediante las observaciones directas y muestreos de indicios indirectos, se llevaron a cabo análisis de ocupación mediante el programa PRESENCE (Mackenzie *et al.*, 2006). Esto permitió estimar la probabilidad de detección en los muestreos a pie, y calcular la probabilidad de ocupación. Además, se hicieron cálculos de detección imperfecta en áreas de presencia conocida, que ofrecieron una valoración cuantitativa complementaria de la eficacia de los muestreos. Por otro lado, se llevaron a cabo estimas de densidad mediante el software DISTANCE aplicado a los muestreos de distancias a partir de las observaciones directas (Buckland *et al.*, 2004; Thomas *et al.*, 2010).

b) *Modelización de la distribución y selección de hábitat* (**Capítulo 2**). Se usaron dos softwares ampliamente utilizados para el modelado de hábitat: (1) MAXENT, en el que emplea un algoritmo basado en la máxima entropía y (2) modelos lineales generalizados (GLM); ambos mediante el software R (R Core Team, 2020), en el que se empleó una aproximación logística contrastando presencias *vs* ausencias. Se evaluaron variables descriptoras del relieve (pendiente, irregularidad topográfica, altitud e índices de cálculo de régimen de temperatura-humedad de suelo), gradientes geográficos (distancia a la costa) y climáticos (temperatura media anual y precipitaciones), lejanía a poblaciones humana y vegetación. Mediante el paquete '*biomod2*' de R (Thuiller *et al.*, 2009), se analizaron tres enfoques del modelo de forma conjunta (GLM, MAXENT y el modelo de consenso entre ambos) para evaluar la contribución y la respuesta de las variables a los factores de predicción. Creamos un mapa de promedios utilizando el modelo del conjunto de todos los algoritmos para predecir la posible presencia espacial en el área de distribución; con ello se evitó el sesgo de selección de un único modelo (Araújo *et al.*, 2007; Marmion *et al.*, 2009).

c) *Alimentación* (**Capítulo 3**). Para determinar la selección de alimento por la gacela de Cuvier se compararon las frecuencias de las especies consumidas con las frecuencias de las especies disponibles, mediante una aproximación clásica de selección de recursos. Para ello se calculó el índice de selección de Ivlev´s (Ivlev, 1961), aplicado a los datos obtenidos del seguimiento de rastros de alimentación. La información sobre el espectro alimenticio se completó mediante el análisis de excrementos, aplicándose técnicas microhistológicas basadas en el análisis de las cutículas vegetales (Bartolomé *et al.*, 1998). Además, se emplearon la espectrofotometría de infrarrojo cercano (NIRS) para estimar el contenido fecal de nitrógeno y fibra (Villamuelas *et al.*, 2017). Finalmente, a través de análisis de correlación de Pearson y un análisis de Componentes Principales (PCA), se exploraron las relaciones existentes entre las variables ambientales (altitud, temperatura media anual, precipitación media anual y productividad primaria medida mediate el índice de vegetación de diferencia normalizada "NDVI"), la calidad de la dieta (nitrógeno y fibra), especies consumidas y diversidad trófica a través del índice de diversidad de Shannon.

d) *Ritmos de actividad* (**Capítulo 4**). A partir de las capturas fotográficas obtenidas mediante las cámaras trampa se calculó el índice de abundancia relativa (RAI, acrónimo en inglés), definido como el número de capturas independientes por cada 100 trampas día. En base a la esperable correlación positiva entre la abundancia y la probabilidad de detección, este índice permite realizar comparaciones temporales y espaciales si los muestreos están suficientemente estandarizados (Tanwar *et al.*, 2021). El patrón diario de actividad y los factores que pueden influir en el mismo (estaciones, fase lunar, competencia interespecífica, sexo, depredadores potenciales y presencias de pastores nómadas) se analizaron mediante el coeficiente de solapamiento de actividad (Δ), a través de estimas no paramétricas con el método Kernel (Ridout & Linkie, 2009). Mediante la prueba circular no paramétrica de Mardia-Watson-Wheeler se buscaron diferencias entre estos factores (Batschelet, 1981; Frey *et al.*, 2017). Por último, se analizaron los periodos diarios seleccionados a través de test de chi-cuadrado y el parámetro "Wi" de selección de recursos (Manly *et al.*, 2002) mediante las funciones Wide I, y Wide II en el caso del sexo (hembras y machos). Para estos análisis se emplearon 3 paquetes estadísticos en R: '*overlap*' (Meredith & Ridout, 2021), '*circular*' (Lund *et al.*, 2022) y '*adehabitatHS*' (Calenge, 2017).

Por último, aunque no fue objetivo de esta tesis, se obtuvo información sobre la estructura poblacional, el tamaño y la composición de grupos, la fenología de la reproducción y el comportamiento. Se adquirieron así datos inéditos para la especie, de gran utilidad para futuros estudios.

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SECCIÓN III.
RESULTADOS

CAPÍTULO 1.

Evaluating methods for surveying the Endangered Cuvier's gazelle *Gazella cuvieri* in arid landscapes

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Evaluating methods for surveying the Endangered Cuvier's gazelle *Gazella cuvieri* in arid landscapes

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Abstract

The Endangered Cuvier's gazelle *Gazella cuvieri* is an endemic ungulate of north-western Africa. Information on the species has been based primarily on non-systematic surveys, and the corresponding status estimates are of unknown quality. We evaluate the effectiveness and efficiency of two field methods for systematic surveys of populations of Cuvier's gazelle in arid environments: distance sampling (based on sightings) and sampling indirect sign (tracks and scats). The work was carried out in the north-western Sahara Desert, in Morocco, where what is possibly the largest population of Cuvier´s gazelle persists. A logistically viable survey was conducted over a total area of c. 20.000 km^2 in 10 expeditions during 2011–2014. A total of 67 sites were surveyed, with 194 walking surveys (2,169 km in total). Gazelle signs were detected at 50 sites, and gazelles were sighted at 21 sites (61 individuals). We found a relationship between sightings and abundance indices based on indirect sign, which could be useful for population monitoring or ecological studies. Additionally, the data could be used in occupancy modelling. Density estimates based on distance sampling required considerable effort; however, it is possible to survey large areas during relatively short campaigns, and this proved to be the most useful approach to obtain data on the demographic structure of the population.

Keywords. Distance sampling, endemic species, *Gazella cuvieri*, Morocco, occupancy, Sahara Desert, ungulate.

1. INTRODUCTION

Cuvier's gazelle *Gazella cuvieri* is categorized as Endangered on the IUCN Red List (Mallon & Cuzin, 2008), with a distributional range restricted to portions of three countries of north-west Africa: Morocco, Algeria and Tunisia (Huffman, 2011; Beudels et al., 2013). The most recent population estimate for the species is 1,750– 2,950 individuals (Beudels-Jamar et al., 2006), in a few scattered and largely fragmented populations, with the majority in Morocco (900–2,000 individuals). However, these estimates should be viewed with caution, as no description is provided of how data were collected in most areas (but see Abáigar et al., 2005b). Most information on the distribution and status of Cuvier's gazelle has been based on opportunistic records and/or nonsystematic surveys (Sellami et al., 1990; de Smet, 1991; Loggers et al., 1992; Cuzin, 1996, 2003; Cuzin et al., 2008).

Cuvier's gazelle was previously known to inhabit both open areas and Mediterranean forests of the Atlas Mountains, from sea level to 2,600 m (Beudels et al., 2013). However, in the mid-20th century a population was discovered inhabiting a true desert environment in the extreme north-western Sahara Desert (Morales Agacino, 1950). This was described as being the largest population of the species (Beudels-Jamar et al., 2006), with subjective estimates of 200–500 individuals based on anecdotes and non-systematic surveys (Cuzin, 2003). However, more recent information suggested the species had declined (Cuzin et al., 2008) and could soon, if not already, be extirpated from the region (Huffman, 2011).

Implementation of appropriate conservation strategies for Cuvier's gazelle is essential and urgent action may be needed to secure a viable future for the species. The first step is to obtain current, scientifically robust information on its distribution and abundance. Thus, we present standardized surveys of the north-western Sahara, using systematic sampling methods. We report on the viability, in terms of effort required and accuracy of results, of distance sampling and indirect sign sampling techniques. These findings provide the first analytical data on the species, and a foundation for further studies on the distribution, abundance and demographics of this Endangered gazelle in a harsh desert environment.

2. METHODS

2.1 Study area

The study area comprised the region between the lower Draa River and the upper basin of the Sequiat Al Hamra, Morocco (c. 20,000 km^2; Fig. 1). It is a typical Saharan landscape, with a subtropical desert and low-latitude hot, arid climate (Köppen–Geiger classification, Kottek et al., 2006). 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 at the northern limit. Total annual precipitation (with large annual variability) is 138, 59 and 190 mm, respectively (recorded at climate stations at Smara, 26°46′N, 11°31′W; Tindouf, 27°40′N, 8°7′W; and Tan Tan, 28°26′N, 11°06′W). The terrain is a mix of rough and hilly areas (*yebels*), flat areas with saline depressions (*sebjas*), plateaux (*hammadas*), clay plains (*dayas*), stony plains (*regs*) and some small dune areas (*ergs*). The altitude is 290–770 m. Ancient rivers spread throughout the region in a complex network, some collecting seasonal waters. The main rivers, the Draa and the Chebeika, hold permanent waters called gueltas. Vegetation is scarce except in the dry river basins, where important open savannah-like forests of thorn trees *Acacia raddiana* still survive, sometimes together with *Acacia ehrenbergiana*, *Balanites aegyptiaca*, *Calotropis procera* and *Panicum turgidum*, and along the gueltas, where there are abundant *Tamarix africana* bushes. The argan tree *Argania spinosa*, endemic to Morocco, reaches its southern most limit here, with scattered individuals sheltered in the valleys of the yebels.

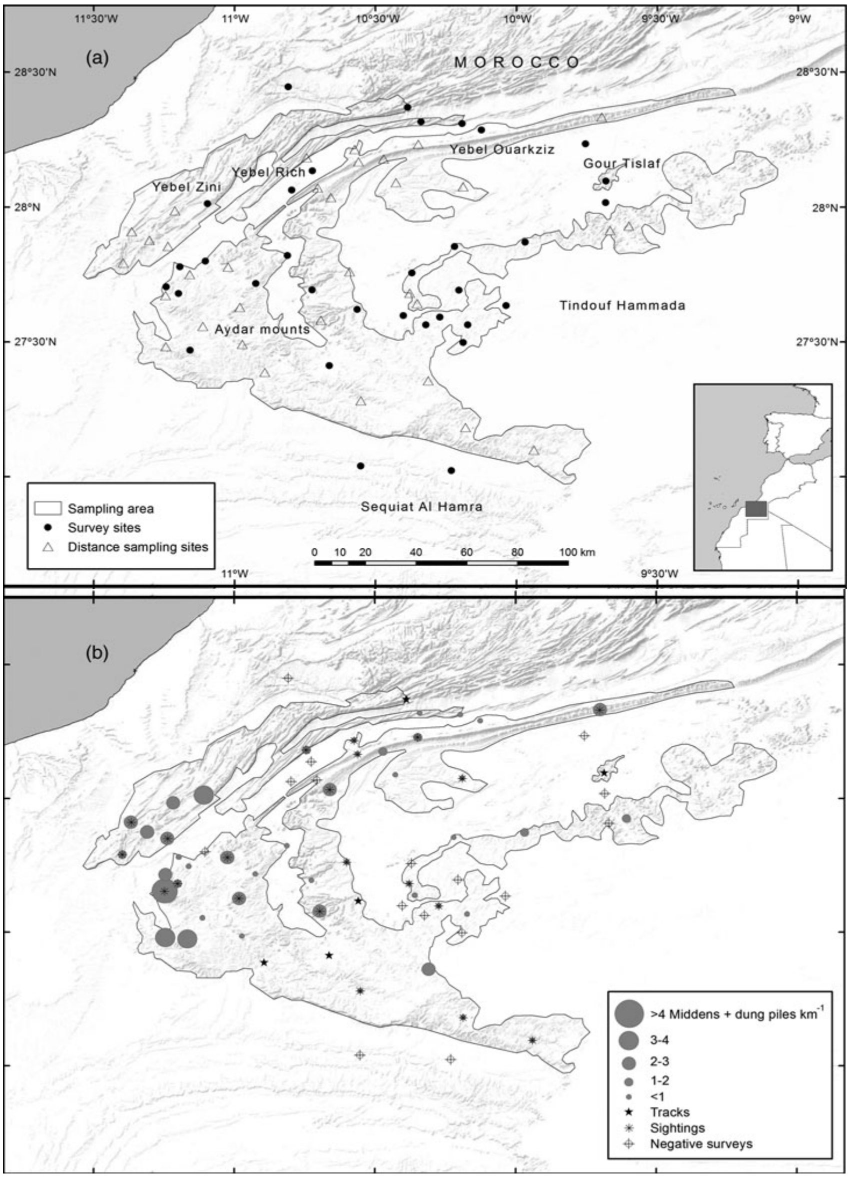

Figure. 1 (a) The study area in the north-western Sahara Desert, Morocco. (b) The distribution of Cuvier's gazelle *Gazella cuvieri* inthe study area.

The region is home to key threatened ungulates of north-west Africa, such as Cuvier's gazelle, the western dorcas gazelle *Gazella dorcas neglecta* and the Saharan Barbary sheep *Ammotragus lervia sahariensis* (Cuzin, 1996). There are six human settlements in the region, each with fewer than 100 inhabitants. The region is also used by traditional nomads, who move their temporary camps and herds of goats, sheep and dromedaries across the desert landscape in search of seasonally available forage. There is an extensive network of 4 × 4 vehicle trails and unpaved roads across the region, facilitating easy access for wildlife poachers, usually coming from the nearby cities of Tan Tan and Guelmin.

2.2 Overall survey design

Ten expeditions of 7–10 days each were conducted by 2–11 persons in 1–3 4 × 4 vehicles. Five expeditions were carried out in spring (March, April and May), three in winter (December and January) and two in autumn (October). We avoided conducting field work during summer months because of the extreme weather conditions in the area at this time. We logged a total of 50 effective survey days (5 days per expedition over 10 expeditions), with a mean of seven persons per expedition, amounting to 350 person-days of effort in the field.

Our sampling unit was the survey site, defined as an area where a set of walking surveys was carried out. The number and distribution of survey sites were influenced by logistics and accessibility; however, we attempted to achieve a large sample size of spatially independent surveys and regular distribution of sampling effort across the various habitats within the study area. During the two first expeditions we observed that gazelles were absent from flat areas (*sebjas*, *hammadas*, *dayas*, *regs* and *ergs*), and therefore we concentrated subsequent efforts within rugged hilly terrain (*yebels*; Fig. 1). We surveyed 67 study sites during April 2011–April 2014 (Fig. 1). Within each study site 1–4 walking surveys were carried out simultaneously by teams of 2–4 observers. We conducted a total of 194 walking surveys, each with a specific route designed according to local terrain conditions. The mean distance covered in a walking survey was 12.08 ± SE 0.72 km (range 3.8–22.5 km; accumulated distance 2,169 km); survey length varied according to time and logistical limitations. We did not use vehicle surveys to detect gazelles (Attum et al., 2014) because of the rugged terrain and poor preliminary results (only six gazelles were sighted from a vehicle during the entire study).

Cuvier's gazelles were detected exclusively within or close to rugged areas (< 1,000 m), and therefore we excluded flat areas (< 5% slope) from our estimated sampling area by deleting these areas from our relief shape file of the terrain (ASTER GDEM v. 2, NASA, Washington, DC, USA, & METI, Tokyo, Japan) in *ArcGIS v. 9.7* (ESRI, Redlands, USA). The estimated sampling area was 12,176.8 km^2, in four patches: Yebel Zini–Yebel Rich: 2,153.1 km^2; Gour Tislaf: 46.5 km^2; Yebel Ouarkziz–Aydar Mountains–Upper Sequiat Al Hamra: 8,323.4 km^2; northern slope of the Tindouf Hamada: 1,653.6 km^2 (Fig. 1).

2.3 Field data collection techniques

We selected two methods of field data collection commonly used for gazelle surveys in arid and semiarid environments: (1) direct observations or sightings (Lawes & Nanni, 1993; Dunham, 1997; Abáigar et al., 2005b; Chammem et al., 2008; Cunningham & Wronski, 2011; Attum &

Mahmoud, 2012), and (2) indirect signs, such as tracks, isolated dung piles and latrines or middens (Abáigar et al., 2005a; Chammem et al., 2008; Wronski & Plath, 2010; Attum et al., 2014). We developed two kinds of walking surveys to sample direct sightings and indirect sign (Fig. 1). The first type was a sighting survey, where 2–3 persons walked the same route, beginning just before sunrise; one person (the guide) walked c. 100 m ahead, scanning the open landscape (with the naked eye and using binoculars) for gazelles (direct sightings), and the other(s) followed, looking for tracks and pellets. Indirect sign surveys were similar to sighting surveys but were conducted at any time of the day, with observers looking only for indirect signs. Indirect sign was sampled at all 67 survey sites, whereas active searches for direct sightings were carried out at only 33 sites. Survey routes were initially determined using *Google Earth* (Google Inc., Mountain View, USA). Subsequently, exact routes were recorded in the field using global positioning systems (GPS). Surveys were stratified in an effort to proportionally cover most of the microhabitats of each survey site. Therefore, upon arrival at each site the routes were amended to include and properly represent valley bottoms and mid-slope and hill-top sections of rugged terrain. At most sites 2–3 surveys were carried out simultaneously, in different cardinal directions to avoid overlap or interference with gazelle sightings. The sighting surveys were designed as distance sampling surveys (Buckland et al., 2004; Abáigar et al., 2005b), in which the location of gazelles observed far from the survey transect was estimated using the biangulation method (Millspaugh & Marzluff, 2001). For gazelles sighted closer to the transect, their exact GPS location was recorded. Using *ArcGIS*, we calculated the perpendicular distances of sightings from the transect. When possible, age and sex of gazelles were recorded, based on body size and shape, and size of horns. Some individuals observed in the distance or moving quickly away from the observers could not be categorized accurately. Age categories were defined as follows: calves (6 months old), subadults (7–18 months) and adults (18 months) (T. Abáigar, Parque de Rescate de la Fauna Sahariana de la Estación Experimental de Zonas Áridas, Almería, Spain, pers. comm.).

To ensure correct identification of indirect sign we sent 73 faecal samples visually identified as belonging to Cuvier's gazelle to the Research Centre in Biodiversity and Genetic Resources at Porto University, Portugal, for genetic identification following methods described in Silva et al. (2015). Of the 73 samples, 41 were identified to species through genetic analysis (39 to Cuvier's gazelle, one to dorcas gazelle and one to domestic goat). Thus, field identification of dung samples was correct in 95.12% of cases tested. Only fresh and clear tracks were included in the data (Plate 1), specifically to avoid confusion with domestic ungulates (mainly goats) and Barbary sheep. There was a risk of misidentifying the tracks of dorcas gazelles as those of Cuvier´s gazelles, and therefore we only included tracks identified *in situ* by our team using reference data from Wacher *et al.* (2011), and rejected tracks < 5 cm long of isolated individuals.

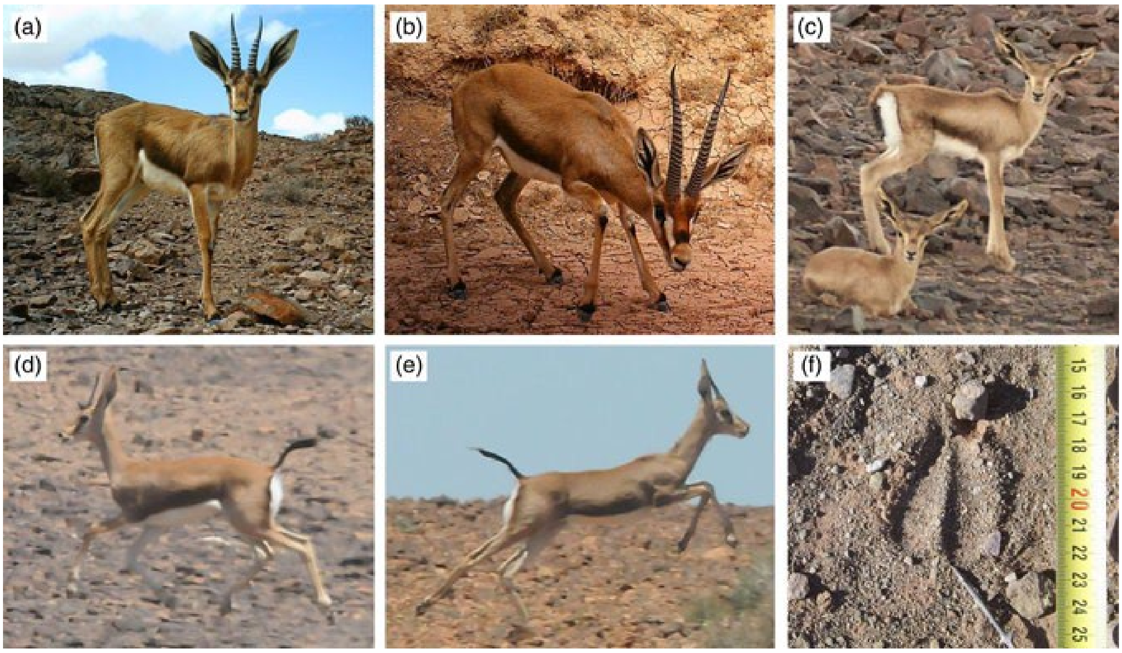

Plate 1. Photographs of Cuvier's gazelles of various age categories and sex taken during surveys in the study area: (a) subadult male; (b) adult male; (c) calves; (d) subadult female; (e) adult female; and (f) a typical track left by a Cuvier's gazelle (the heart shape distinguishes Cuvier´s gazelle tracks from those of goats, sheep and Barbary sheep). (a) and (b) were taken by camera traps.

2.4 Data analysis and evaluation of methods

We analysed the effect of season on gazelle detections. We divided data into two periods: spring (March–May, 40 study sites) and autumn/winter (October–January, 27 study sites). We compared the effect of season on the percentage of study sites with confirmed gazelle presence, and on the abundance of indirect signs and of gazelles sighted, both standardized as kilometric abundance index (sighted gazelles per km; signs per km), using U-Mann Whitney tests. We calculated the effort required (km walked) to detect gazelles, and identified the type of data that first confirmed gazelle presence at each site (pellets, tracks or direct sightings).

An imperfect detection analysis (MacKenzie et al., 2006) was carried out to determine whether the number of surveys per site had any influence on the effectiveness of detection of indirect signs (measured as detection rates, see below). We selected those sites where gazelles were sighted (hereafter, real positive sites) that had three simultaneous surveys of > 5 km each (16 sites and 48 (16 × 3) surveys in total). We used a cut-off of 5 km because our data showed that if no sign was found within 5 km, increasing the search effort did not increase the likelihood of detecting sign. The detection rates (positive surveys/total surveys) and the percentage of false absences ((1 – detection rate) × 100) were calculated simulating one survey per site (48 chances), two surveys per site (48 chances) and three surveys per site (16 chances).

The relationship between the relative abundance (kilometric abundance index) of isolated dung piles and middens (subsequently pooled together) and the abundance of sightings (gazelles per km) was analysed using the Pearson correlation. We excluded tracks from this analysis because the ability to detect tracks depended largely upon substrate type, which varied. Only sites with gazelle presence were considered in this analysis and, to avoid redundancy, the various replicates of each site were pooled together (29 sites).

We tested the utility of the pooled data for occupancy and density approaches. Firstly, we used *PRESENCE v. 6.2* (MacKenzie et al., 2006) to calculate occupancy probability (Ψ) using presence/absence site occupancy data analysis, with single-season survey-specific p analysis, applied to the 28 sites containing three replicates (surveys) each. A detection history of 28 rows (number and order of sites) and three columns (number and order of surveys per site) of zeros (0, gazelles not detected) and ones (1, gazelles detected) was built for the occupancy analysis (note that indirect sign was detected for all instances of 1). Secondly, we used *DISTANCE v. 6.0* (Thomas et al., 2010) to calculate the density from the distance sampling surveys (Buckland et al., 2004). The detection function was half-normal, as (1) the data set did not facilitate either uniform or hazard-rate functions, and (2) the half-normal function yielded more conservative results than the negative exponential function. The estimated population size (N) was then calculated using the equation $N = \mathrm{A} \times D$, where A is the estimated sampling area and D is the density.

3. RESULTS

Gazelles were detected at 50 of the 67 study sites (74.63%), and 61 individuals in 28 groups were sighted at 21 locations (Fig. 2). We recorded 48 sightings with sufficient accuracy to determine sex, age class and group size (mean = 2.17 individuals per group) for describing population structure (Fig. 3). Isolated dung piles were the most frequently collected type of data, and sightings were the rarest (Table 1). Middens were always associated with more abundant isolated dung piles nearby. Of the 50 positive sites 10% (n = 5) had gazelle presence confirmed by tracks alone. Twelve of 17 negative surveys (70.59%) were in flat areas.

Seasonal effects on surveys. No seasonal variation was found for the three variables tested: percentage of sites with gazelles detected (spring 77.5%, autumn/winter 70.3%; $U = 501.0$, $Z = -0.65$, $P = 0.51$), kilometric abundance index of indirect signs (spring 0.64, autumn/winter 0.49; $U = 490.0$, $Z = -0.49$, $P = 0.62$), and kilometric abundance index of gazelles sighted (spring 0.028, autumn/winter 0.05; $U = 465.0$, $Z = -1.02$, $P = 0.30$).

Effort required to detect Cuvier's gazelles. A mean survey distance of 2.15 ± SD 1.74 km (range 0.02–5.69) was required to detect any sign of gazelle presence. The first sign detected was tracks at 66.66% of sites, dung piles at 30.76% and middens at 2.56%. No gazelles were sighted prior to detection of indirect sign.

Imperfect detection analysis. The imperfect detection analysis yielded the following estimations of detection rates and false absences within real positive study sites: (1) detection rate = 40/48 = 0.83 and 17% false absences for one survey per site; (2) detection rate = 45/48 = 0.94 and 7% false absences for two surveys per site; and (3) detection rate = 16/16 = 1 for three surveys per site and 0% false absences. At two of the five sites with no detected gazelle presence (Yebel Zini and Yebel Rich, Fig. 1) the survey effort was sufficient (3 transects > 5 km each) to have detected gazelles had they been present, and therefore real absences can be assumed. Surveys at the other three sites were < 5 km, and thus the results could be false negatives.

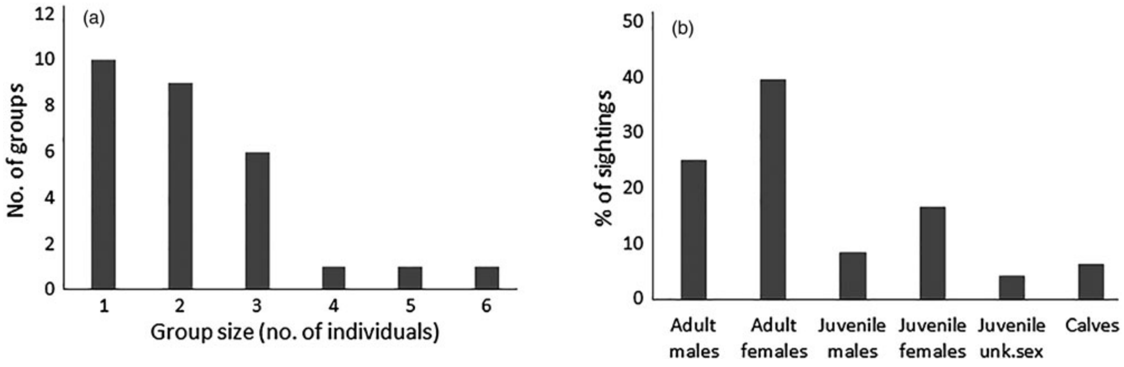

Figure 2. (a) Sex and age composition of Cuvier's gazelles, from 48 discernible observations (of a total of 61 sightings) and (b) numbers of groups of various sizes observed in the study area (Fig. 1).

Relationships between indices of abundance. We calculated a mean kilometric abundance index of 0.29 ± SE 0.085 km^{-1} and 0.22 ± SE 0.059 km^{-1} for isolated dung piles and middens, respectively. The abundances of isolated dung piles and middens were positively correlated ($Rs = 0.82$, $P < 0.0001$; Fig. 4), and therefore they were pooled together (mean kilometric abundance index = 0.52 ± SE 0.13; Kolmogorov–Smirnov (K–S) test for normality: $Z = 1.05$, $P = 0.22$). We found a positive relationship ($Rp = 0.69$, $P = 0.026$; Fig. 4) between indirect signs (as dependent variable) and the abundance of sightings (mean kilometric abundance index or encounter rate from distance sampling = 0.081 ± SE 0.019 gazelles km^{-1}; K–S test: $Z = 1.10$, $P = 0.17$).

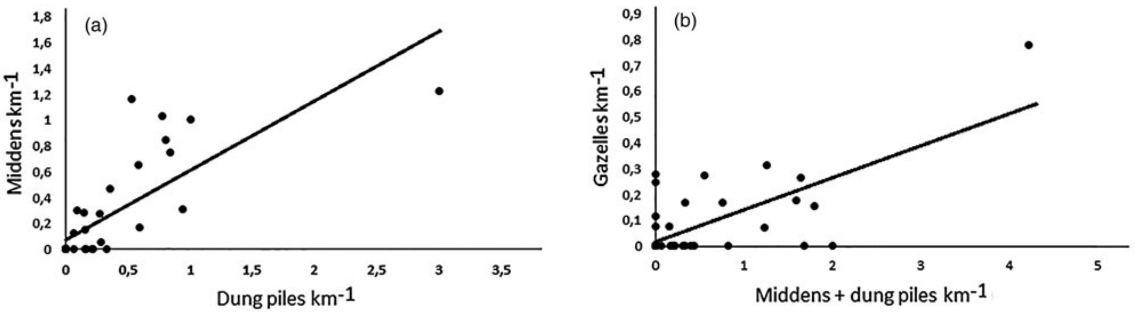

Figure 3. Relationships between (a) two types of indirect signs (middens and dung piles), and (b) indirect signs and direct sightings of Cuvier´s gazelles in the study area (Fig. 1).

Occupancy and density estimates. The estimated value of Ψ was 0.85 ± SE 0.061 (95% CI 0.68–0.94). The effort for the distance calculations was 707.1 km over 64 surveys, resulting in 26 clustered observations (57 gazelles) and a maximum detection width of 1.08 km. The half-normal function without any adjustment term (corrected Akaike's information criterion, AICc = 346.33) was selected over the half-normal function with cosine adjustments of order two (AICc = 348.54) and over the half-normal function with simple polynomial adjustments (AICc = 347.16), offering a good value of adjustment to the observed distribution of sightings (K–S test: Z = 0.23, P = 0.12; Fig. 4); the half-normal function with hermite polynomial adjustments was not possible with the data set. The resulting population estimate for Cuvier's gazelle in the study area is 935 individuals (95% CI 597-1607).

Table 1. The number and percentage of sites at which various types of data on Cuvier´s gazelle *Gazella cuvieri* were recorded in the arid landscapes of the north-western Sahara Desert, Morocco (Fig. 1).

Type of data	No. of sites	% sampled sites	% positive sampled sites
Sightings	20	29.85	41.66
Isolated dung piles	38	56.71	75.00
Middens	28	41.79	56.25
Tracks	30	44.77	60.41

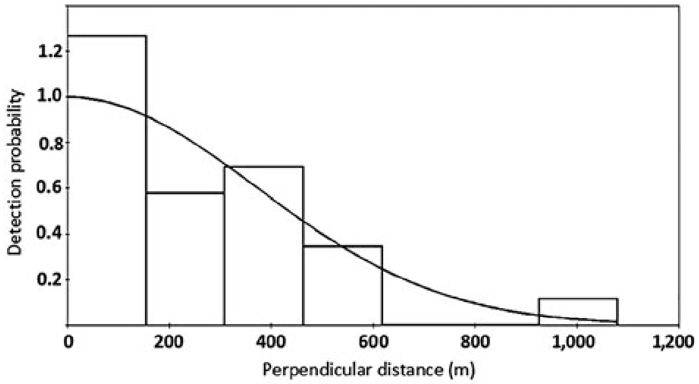

Figure 4. Detectability function and distance distribution of observed Cuvier´s gazelles in the study area (Fig. 1).

4. DISCUSSION

We found that sampling indirect sign can yield optimal results for Cuvier's gazelle, even in situations of low or very low density. Moreover, the species' sign is usually easy to recognize, especially the middens, which are not likely to be confused with those of other species. Similar findings have been reported for the mountain gazelle *Gazella gazelle* (Attum et al., 2006; Wronski & Plath, 2010). Our results suggest that it is feasible to obtain sufficient sample sizes for occupancy models or ecological studies (Abáigar et al., 2005a; Attum et al., 2006; Wronski & Plath, 2010) with relatively low effort. In < 2 effective sampling months of combined effort we detected gazelles in 74.62% of all surveys and determined that a survey distance of 2.15 km is sufficient to detect gazelles if present. Moreover, imperfect detection (the biases produced by false negative surveys; MacKenzie et al., 2006) was observed in few samplings, and could be avoided by increasing the effort at some sites. Only track surveys produced a low rate of positive detection. This is not surprising, as detecting this type of indirect sign depends not only on effort but also, more importantly, on substrate. The difficulty of detecting tracks in rocky areas, as well as environmental circumstances (e.g., rain, wind) that can quickly destroy this type of sign, could lead to false negative surveys. However, the rate of negative points within the area of Yebel Zini and Yebel Rich (Fig. 1) was low (2 of 52 survey sites), and therefore the effects of this limitation (which could result in underestimation of the population) were negligible. As we found a significant positive relationship between sightings of gazelles and indirect indices of abundance, the latter could also be used for population monitoring, both at spatial and temporal scales.

The distance surveys did not provide additional information or improve upon the results from the indirect surveys in terms of distribution data and relative abundance. Moreover, distance surveys increased the effort required, as it was necessary to walk longer distances to see gazelles than to find indirect sign. It seems that the distance results were affected not only by the low density of gazelles but also by their shy and vigilant behavior (authors, pers. obs.; Manor &

Saltz, 2003). Although distance sampling (with wide confidence intervals) was the only way to estimate gazelle density, our density estimate must be viewed with caution, as it was based on data from surveys that spanned a long sampling period (2011–2014), during different seasons, and with low sample sizes (see criticisms in Buckland et al., 2004). We have, however, demonstrated that with sufficient effort it is possible to gather enough field data for distance analysis. Furthermore, the distance survey was useful in gathering data on the demographic structure of the population.

Table 2. Results of the distance analysis of data on Cuvier's gazelle in the study area (Fig. 1).

Parameter (unit)	Estimate ± SE	%CV	95% CI
Detection probability	0.42 ± 0.065	11.41	0.33–0.54
Effective strip width (m)	461.76 ± 52.69	11.41	365.32–583.66
Density of groups (groups km^{-2})	0.039 ± 0.008	22.34	0.025–0.061
Expected group size (no. of individuals)	2.03 ± 0.24	12.17	1.58–2.60
Density of individuals (individuals km^{-2})	0.08 ± 0.02	25.44	0.049–0.132

Even considering the limitations of our density estimation it is clear that the species is scarce within the study area. Reference densities for comparison are not available; however, the mountain gazelle has been found at densities of 0.64–15.0 individual's km^{-2} in arid but well-protected areas (Dunham, 1997; Cunningham & Wronski, 2011). We assume that the observed abundance of Cuvier's gazelle is not strongly limited by natural factors, as this population lives under optimal conditions for the species in an arid habitat (Cuzin, 2003). Rather, poaching may have a significant impact on population dynamics. Poaching has traditionally been a major factor in the decline and extinction of ungulate species throughout the Sahara Desert (Beudels-Jamar et al., 2006), including in Morocco (Morales Agacino, 1950; Valverde, 1957; Loggers et al., 1992; Cuzin et al., 2008). During our field work we observed three poaching parties, and two more poachers were photographed by a hidden camera trap. Although more information is needed, we fear that poaching may be a significant threat to this population, and further protection may be necessary to secure a viable future for the species.

Our study highlights some limitations of previous estimates of the local populations of Cuvier's gazelle, which were based on subjective estimates. Cuzin et al. (2008) estimated that the studied population comprised only 100–300 individuals, and regarded it as a secondary and less important focus for Morocco´s Wild Ungulates Action Plan. However, our results suggest that this population requires increased attention from managers, as it is the only extant population with an effective population size close and is therefore the most genetically viable in the long term (Frankham et al., 2014). Considering a recent prediction that 'Cuvier's to gazelle might be soon extirpated from the Western Sahara, if not already' (Huffman, 2011), our population estimate of 600–1,600 individuals is a cause for optimism. Nonetheless, given the potential impact of poaching on the population, there is an urgent need for regular monitoring and conservation action.

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CAPÌTULO 2.

Identifying priority conservation areas in a Saharan environment by highlighting the endangered Cuvier's Gazelle as a flagship species.

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Identifying priority conservationareas in a Saharan environment by highlighting the endangered Cuvier's gazelle as a flagship species

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Abstract

Monitoring populations and designing effective conservation actions for endangered species present significant challenges. An accurate understanding of current distribution, ecological traits and habitat requirements is imperative in formulating conservation strategies. Recent surveys on the southernmost Cuvier's gazelle (*Gazella cuvieri*) population, an ungulate endemic to North Africa, showcase its importance in terms of numbers and genetic diversity. This population inhabits a remote region in the extreme north-western portion of the Sahara Desert and has not been well studied. Here, we examine the potential distribution of Cuvier's gazelle and the environmental factors limiting the species in a Saharan environment, by combining broad-scale field survey data and species distribution models. Our objective was to identify high priority conservation areas in the southernmost known portion of the species' distribution by modelling habitat selection at the landscape scale using a predictive distributionmap. Our results show that the distribution of Cuvier's gazelle is strongly related to mountainous areas with heterogeneous terrain and remoteness from large human settlements over other ecological factorsthat had less impact on the species' presence and distribution. We also provide a quantitative estimate of the potential distribution range of Cuvier's gazelle in southern Morocco, identifying two well- demarcated key areas. The two core areas currently contain enough rugged terrain isolated from humanencroachment to support the endangered species in this harsh desert environment. We encourage the implementation of conservation planning for Cuvier's gazelle as an "*umbrella species*", which will confer effective protection to higher-quality habitat zones and co-occurring species, leading to sustainable and ecologically responsible development in the region.

1. INTRODUCTION

Knowledge of the population distribution and dynamics of threatened species in the wild is key to effective conservation actions[1,2]. While this may seem obvious, at present, there are many examples of endangered wildlife for which their current situation is unknown, especially in remote areas of the world and in less developed[3]. Field research through large-scale surveys plays a key role in obtaining quality data on species status; however, unfortunately, empirical field studies have decreased appreciably in the past several decades[4,5]. A recent study has shown that the proportion of fieldwork-based investigations in the conservation literature has dropped significantly from the 1980s until today: fieldwork-based publications decreased by 20% in comparison to a 600% and 800% increase in synthetic modelling and data analysis studies, respectively[6]. As a direct result, key decisions establishing national and global priorities in biodiversity conservation are lacking observational data. Researchers, funders and journals have been urged to conduct, fund and disseminate relevant field research[6].

The conservation status and distribution of the Sahara's megafauna is a paradigmatic case to illustrate this lack of fundamental and key data for well-designed conservation actions in remote areas. Field studies are becoming increasingly necessary because of the collapse in Saharan wild ungulate and mammalian carnivore populations over the last century[7]. In this remote region of northern Africa, any field work faces great logistical and safety challenges, due to remoteness, lack of infrastructure, extreme environmental conditions and, in many cases, ongoing armed conflicts[8]. One of the species that inhabits this desert is the endangered Cuvier's gazelle (*Gazella cuvieri* Ogilby, 1840), a medium-sized ungulate endemic to North Africa. Over the last century, the Cuvier's gazelle population has undergone major fragmentation and its numbers have declined dramatically to 2,360–4,560 individuals due to overhunting and habitat loss[9–13]. Currently, the distribution of Cuvier's gazelle is limited to the Atlas Mountains and the neighbouring mountain ranges in Morocco, Algeria and Tunisia[11,13–15]. It is included within the subset of Sahelo-Saharan antelopes along with dama gazelle (*Nanger dama*), dorcas gazelle (*Gazella dorcas*), slender horned gazelle (*G. leptoceros*), scimitar-horned oryx (*Oryx dammah*) and addax (*Addax nasomaculatus*). These species are well-adapted to life in the extreme conditions of this region, such as high temperatures, drought and a seasonal lack of food[7,10]. Like other Sahelo-Saharan antelopes, Cuvier's gazelle is poorly studied due mainly to its elusiveness and remote habitats[7,16]. Therefore, the limited knowledge about its biology and actual conservation status may lead to a lack of protection and even local extinctions. Cuvier's gazelle is defined as "Endangered" in Morocco, Algeria and Tunisia[10] but globally classified as "Vulnerable" to extinction[3]. Given its importance in North Africa, the IUCN has elaborated an international strategy that includes several actions focused on protection from illegal hunting, management of habitat, monitoring and environmental sensibility to achieve better preservation and recovery of populations[13]. Only through increasing knowledge regarding its natural history and habitat requirements will it become possible to identify the areas that need protection for more effective conservation of the species.

Changes are currently being proposed that would reclassify Cuvier's gazelle as a mountain ecotype of slender-horned gazelle[17], a species strictly associated with the great sand desert and ergs of the Sahara[18]. Covering a wide variety of habitats from sea level to 2600 metres, Cuvier's gazelle mainly lives in mountain ranges and associated plateaus, such as semiarid open Mediterranean forests of cork oak (*Quercus suber*), holm oak (*Quercus ilex*), *Pinus* spp., sandarac (*Tetraclinis articulata*), Atlas cedar (*Cedrus atlantica*), argan (*Argania spinosa*) and Phoenicean juniper (*Juniperus phoenicea*), but also in steppes, maquis or scrubland areas, and even in cereal fields in Algeria and Morocco[9,11,14,15,19]. In contrast, Cuvier's gazelle appears to avoid areas covered in heavy snow at high altitudes in winter and ranges to the Sahara Desert on rocky mountains and desert plateaux, limited to areas with argan and thorn trees *Acacia* spp. forests[9]. In this environment, recent surveys in the Bas Drâa-Aydar region (Morocco) show promising distribution and numbers of Cuvier's gazelle[20], since this population has been described as one of the largest populations of the species, with 935 individuals (95% CI 597–1607)[20]. This population of Cuvier's gazelle inhabits the extreme north-western portion of the Sahara Desert and is probably the most important in terms of numbers and genetic diversity, making it essential to the species' longevity and conservation[20]. In this region, with apparently suboptimal conditions, the topography, food availability and extreme climatic conditions may be crucial factors determining the species' presence, but human settlements may also play a role and may restrict Cuvier's gazelle presence and usable habitat[9].

In this study, we applied species distribution models, also known as habitat suitability models, a technique that combines information on species occurrence or abundance with environmental estimates and/or spatial characteristics[21–23]. Species distribution models are mainly used to address the potential effects of climate change on species distribution[24–26] but are also used to improve the understanding of ecological factors for conservation planning and to detect unknown potential distribution areas for rare species[27–29]. Our goal is to identify the main ecological features of the southernmost subset of the Cuvier's gazelle population in the Sahara; for this purpose, we integrated data from a broad-scale field survey carried out from 2011 to 2014 and species distribution models to model habitat selection at the landscape scale, using a predictive distribution map. The final purpose of this study is to contribute to the biological conservation management of Cuvier's gazelle by identifying the extent of its potential habitat and high priority areas to ensure the species' survival in the southernmost area of its distribution.

2. MATERIAL AND METHODS

2.1 Study area

The survey was conducted in the extreme north-western part of the Sahara Desert between 28°30′–26°50′N and 11°40′–9°25′W in the Guelmim-Es Semara region (Fig. 1). The area is delimitated by two important geographical features: the lower Drâa River to the north and the upper basin of the Sequiat Al Hamra to the south. It is a typical Saharan landscape with a subtropical desert and a low-latitude hot, arid climate (Köppen-Geiger classification[30]). 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 (with large interannual variability) is 138, 59 and 190 mm, respectively (recorded at climate stations at Smara, 26°46′N, 11°31′W; Tindouf, 27°40′N, 8°7′W; and Tan Tan, 28°26′N, 11° 06′W).

The area contains diverse terrain with rough and hilly areas (*jbels*), flat areas with saline depressions (*sebjas*), plateaux (*hammadas*), clay plains (*dayas*), stony plains (*regs*) and some small dune areas (*ergs*). There are large mountainous reliefs: Aydar Mountain (western zone); three main *jbels*: Zini, Rich and Ouarkziz, the last with an approximate total length of 400 km (250 km in Morocco), and at the eastern edge, the Hammada of Tindouf. The whole region is a contact point between two ecoregions: The Sahelo-Arabian and the Macaronesian regions. Thus, is it possible to find features typical of Mediterranean, tropical vegetation and Macaronesia[31–33]. Woody vegetation is scarce and is mainly located in ravines and *oueds* (ephemeral sandy rivers) with open savannah-like forests of horn trees such as acacia (*Acacia raddiana*), sometimes along with balanites (*Balanites aegyptiaca*) and calotrope or sodom apple (*Calotropis procera*), and abundant African tamarisk (*Tamarix africana)* bushes along the gueltas. Other typical species are argan (an endemic tree of Morocco that reaches its southernmost limit here), *Periploca laevigata*, *Launaea arborescens*, sumac (*Rhus tripartitum*), *Maerua crassifolia* and *Euphorbia officinarum*, this latter being a key species from a more continental Macaronesian region. There is also important extremophilic vegetation that survives in the *hammadas*, *regs* and *ergs*, such as rose of Jerico (*Anastatica hierochuntic*), *Panicum turgidum*, *Nucularia perrinii*, colocynth (*Citrullus colocynthis*) and *Mesembryanthemum cryptanthum*.

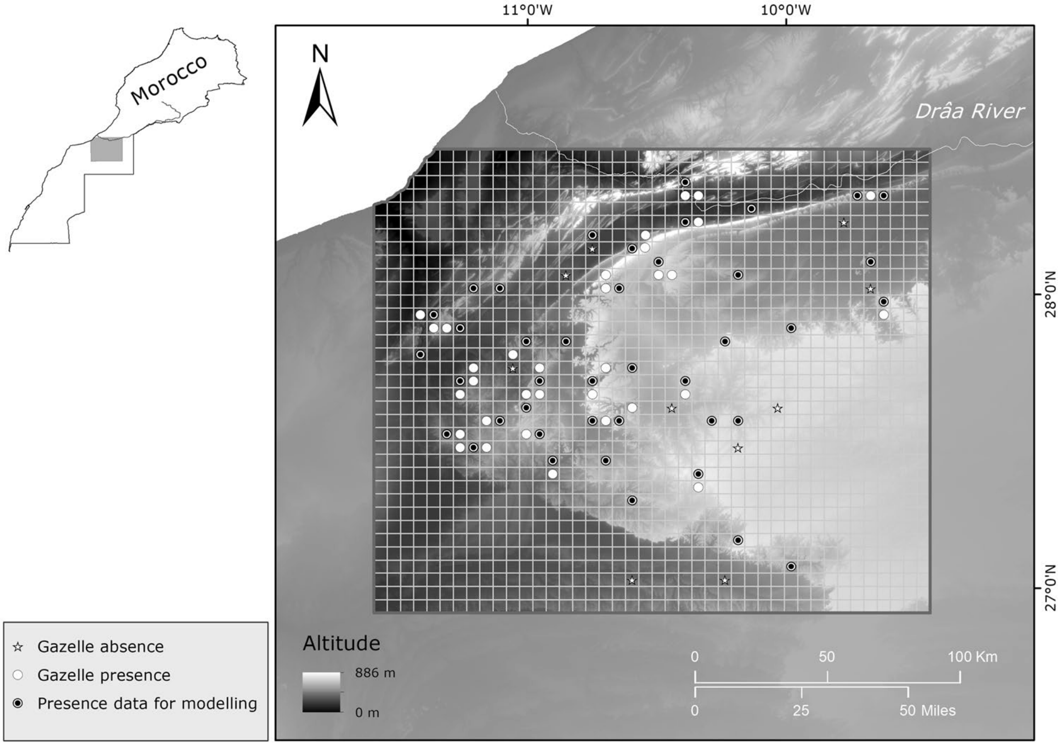

Figure 1. Location and topography of the study area in the north-western Sahara Desert, Morocco. Presence-absence data collected are shown in plots of 5 × 5 surveyed grids by *white dots* and *white stars*, respectively. *Black dots* show final presence data for building the species distribution model. Base map image by Shuttle Radar Topography Mission (SRTM)[38].

2.2 Field surveys and environmental predictor variables

Presence-absence data were collected from April 2011-April 2014 by completing walking surveys and sampling direct sightings and indirect signs, such as tracks, isolated dung piles and dung middens (accumulations of dung piles in latrines)[34–37]. After 194 transects on foot counting a total of 2169 km, 615 dung points were georeferenced and 61 gazelles sighted at 21 different sites. The mean distance covered by walking surveys was 12.08 ± SE 0.72 km (range 3.8–22.5 km). The correct identification of indirect signs was tested by genetic analyses at the Research Centre for Biodiversity and Genetic Resources at Porto University, Portugal, using methods described in Silva *et al.*[17]. For more detailed descriptions on the field data, see Gil-Sánchez *et al.*[20].

To develop models that predict habitat suitability and determine the influence of variables on Cuvier's gazelle presence, we selected a set of previously published metric variables ranked in five categories (Table 1).

Table 1. Description of the environmental predictor variables used to fit the species distribution models for Cuvier's gazelle.

Variables	Selected for modelling	Units	Source	Description	Calculation
Topographic morphology					
Altitude (ALT)	yes	meters	Elevation above sea level from SRTM (Shuttle Radar Topography Mission). 1 arc-second (~30 m^2)	Elevation above sea level	
Slope (SLOPE)	no	degree		Terrain slope	Slope function. Toolbox. ArcGIS 10.4
Topographic Ruggedness Index (TRI)	yes	meters		[65]Topographic roughness. Calculated as the difference between the value of a cell and the mean of an 8-cell neighbourhood of surrounding cells	[66]Geomorphometric and Gradient Metrics Toolbox. ArcGIS 10.4
Temperature-moisture regime					
Heat Load Index (HLI)	no		Elevation above sea level from Shuttle Radar Topography Mission (SRTM). 1 arc-second (~30 m^2)	[67]Potential direct incident radiation in relation with slope and aspect transformation	Geomorphometric and Gradient Metrics Toolbox. ArcGIS 10.4
Compound Topographic Index (CTI)	yes			[68,69]Flow accumulation by catchment size (wetness index) described as a function of both the slope and the upstream contributing area per unit width orthogonal to the flow direction and a quantification of catenary topographic convergence.	
Topographic distance and human factor					
Distance to Coast (DISTCOAST)	no	meters	ArcGIS server	Terrain border	Euclidean distance. ArcGIS 10.4
Distance to Cities and Urban Villages (DISTSETT1)	yes		OpenStreetMap project and Haut Commissariat au Plan, Royaume du Maroc	Distance to the nearest human settlement with more than 1500 inhabitants	
Distance to Rural Villages (DISTSETT2)	yes			Distance to the nearest human settlement with less than 1500 inhabitants	
Vegetation					
Annual of Maximum Green Vegetation Fraction (AMGVF)	yes		USGS Land Cover Institute (LCI). 30 arc-seconds (~1km^2)	Green vegetation fraction estimated from Normalized Difference Vegetation Index (NDVI)	Values calculated on 12 years (2001-2012) of Collection 5 MOD13A2 normalized difference vegetation index (NDVI)
Climatic variation					
Annual Mean Temperature (BIO1)	yes	degrees Celsius	WorldClim database 2.0, 30 arc seconds (~1km^2).	Annual Mean Temperature	
Annual Precipitation (BIO2)	yes	millimetres		Annual Precipitation	

Mean values for topographic morphology metrics (altitude, slope and topographic ruggedness index) and two temperature-moisture metrics (heat load index and compound topographic index) were obtained from Shuttle Radar Topography Mission (SRTM) with 1 arc-second (~30 m2) spatial resolution[38]. For topographic distance and human factor metrics, we used the Euclidean distance computed in ArcGIS 10.4[39], measuring the distance to the coast and a two-tiered settlement size classification (DISTSETT1 and DISTSETT2). To describe vegetation, we used a primary productivity parameter: the average annual maximum green vegetation fraction or AMGVF[40]. AMGVF data are based on 12 years (2001–2012) of Collection 5 MOD13A standardised difference vegetation index (NDVI) data, with a spatial resolution of 30 arc-seconds (~1 km^2). Finally, from 19 climate variables in the WorldClim database[41], we selected variables that captured the main environmental gradients in the study area: mean annual temperature (BIO1) and annual precipitation (BIO12). WorldClim data were downloaded at a spatial resolution of 30 arc-seconds (~1 km^2). The original spatial resolution of predictor variables was maintained to calculate the average of pixel values in each grid-cell by focal analysis. We then resampled the pixel size to 1 × 1 km to equal data scale for data processing. All spatial analysis were conducted using ArcGIS 10.4[42,43].

We analysed the pairwise correlation between explanatory variables: first removing those strongly correlated with coefficients of correlation above 0.80[44] and then testing for multicollinearity in the data with the Variance Inflation Factor (VIF), by using stepwise elimination of highly inflating variables with a threshold of 10[23]. After these analyses, we removed slope, heat load index and distance to coast (Supporting Information, Appendix S1), resulting in eight variables selected for modelling: topographic ruggedness index, altitude, compound topographic index, annual maximum green vegetation fraction, annual mean temperature, annual precipitation, distance to cities and urban villages, and distance to rural villages.

2.3 Species modelling strategy

The study area was enclosed in a 29 UTM (Universal Transverse Mercator) grid-cell measuring 5 × 5 km (Fig. 1). Due to the high mobility of gazelles, all records were gathered in each 5 × 5 km plot[45] with a measure of occurrence (presence/absence). Presence was determined by dung middens and direct observations. To avoid imperfect detection in the absence of data (i.e., false negative surveys), we only included grids with transects of more than 5 km repeated at least twice[20]. Of the 84 surveyed grids, we removed those sites within a radius of 5 km to avoid spatial correlation, thus obtaining 51 grid-cells in all (41 positive cells and 10 negative cells). We then computed the nearest neighboring index in ArcGIS 10.4 to prevent using clustered data[42] (Supporting Information, Appendix S2).

To build a species distribution model, we used the R package ‘biomod2’[46] for R 3.6.2[47]. We used two algorithms common in distribution modelling: (1) Generalised Linear Model[48] (GLM) and (2) Maximum entropy modelling of species distributions implemented in MAXENT 3.0.4 beta software[49], to ultimately obtain an assembled model based on the variables we had selected. The use of an ensemble model or consensus algorithms in species distribution model is a powerful tool that prevents the selection of one single best model and thus eliminates or limits model selection bias while improving predictions of the current range of a species[23,50,51]. GLM is a flexible method and an extension of the linear regression models, which allows the response variable to follow a non-linear distribution and non-constant variance function. We fit GLMs for binary responses (the presence-absence data) using a logic link function, quadratic terms for each predictor and an automatic stepwise procedure with AIC. MAXENT is a reliable, effective technique based on a machine learning algorithm known as maximum entropy, which can use only presence, but also performs well when compared with presence-absence procedures that utilise both real and pseudo-absence data[52]. MAXENT was set up with 200 maximum iterations, with linear, quadratic, product, threshold and hinge features. We ran 10 sets of pseudo-absences (PA) and equaled the number of pseudo-absences as available presences to prevent a sampling bias[53]. To build a consensus ensemble forecasting model, we chose a mix of both algorithms that had shown good performance and therefore used them to project the potential spatial distribution in the region (Fig. 2).

2.4 Model evaluation and spatial forecasting

The predictive power of occurrence in the models was tested using a split-sample cross-validation approach. To do this, the dataset was randomly split into two subsets: 75% for training data and 25% for testing data. This process was repeated 20 times for each model (× 10 pseudo-absence samplings × 2 algorithms). Therefore, 400 models were built in total. Models obtained through cross-validation were compared using a predictive accuracy metric: the area under the receiver operating characteristic curve (AUC). Only predictive models with a value of over 0.8 AUC were selected to create a final ensemble model. Differences in the predictive accuracies of different algorithms were tested using a Wilcoxon signed rank test. The models with a threshold that optimises AUC (above 0.8) were transformed into one single model by binary transformation, using the committee average approach in the training area[23,51,54]. In this process, the selected models are given equal probability levels by averaging the results of binary transformation and allowing direct comparisons across models[46,50]. To determine which environmental variables were most important, we selected 10 permutations to estimate variable importance in two ensemble methods: using algorithms and with all models. Then, the three ensemble model approaches (GLM, MAXENT and the consensus model) were analysed to assess the contribution and variable response of the predictive factors. To integrate results of different methods and avoid model selection bias[50,51], we created a committed averaging map using the ensemble model of all algorithms to forecast the potential spatial occurrence in the southernmost known distribution area of Cuvier's gazelle. The threshold value below which the species was considered absent was <0.5[55] with a range for probability of occurrence: low (0.5) to high (1). Then, the potentially suitable area was calculated by adding together all of the 5 × 5 km presence grid-cells, considering the species' geographic Atlantic Saharan population border to be the Drâa River.

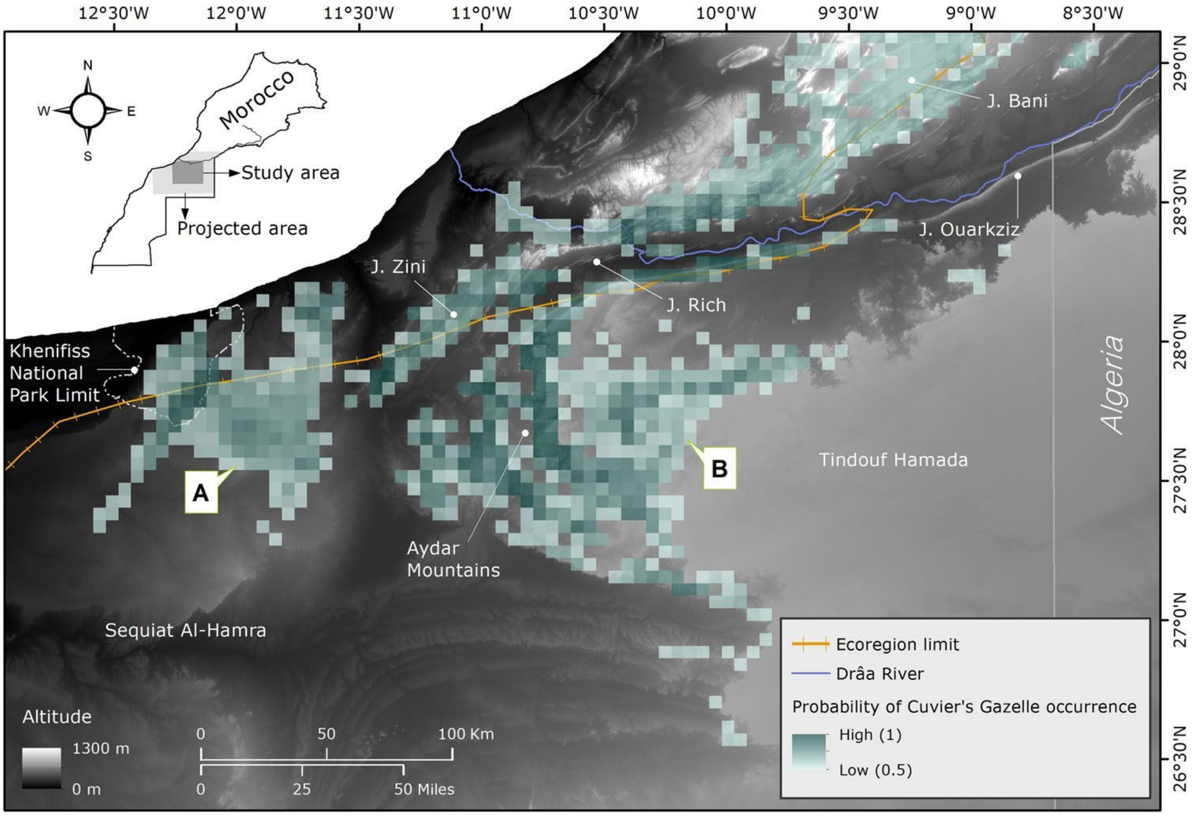

Figure 2. Spatial projection of the ensemble forecasting model to identify occurrence and suitable habitat of Cuvier's gazelle in the study area and surroundings. The probability of occurrence is ranked from low (0.5) to high (1) and shows two key areas "A" and "B" to consider in Cuvier´s Gazelle conservation plans. In dark orange the boundaries between ecoregions[70] and in dark blue the Drâa River, considered as the northern limit of the Saharan population of the species. The forecast map also provides the main mountainous reliefs (Aydar Mountains, Jbel Zini, Jbel Rich, Jbel Ouarkziz and Jbel Bani). Basemap image by Shuttle Radar Topography Mission (SRTM)[38]. Software used: ArcGIS 10.4 (http://www.esri.com/)[39] and R 3.6.2 (http://www.R-project.org/)[47].

3. RESULTS

3.1 Evaluation of models and habitat inferences

Only 97 GLM and 43 MAXENT models with good accuracy (above 0.8 AUC) were selected to build three ensemble models. Significant differences were found between the two algorithms (W = 2682, p-value = 0.006), though GLM models performed better (AUC mean value: GLM, AUC = 0.86 SD = 0.048 and MAXENT, AUC = 0.83 SD = 0.039). However, the committee averaging ensemble model for MAXENT had the highest AUC value (Table 2). The eight variables selected for modelling showed different response curves, but the shape was similar for each variable in all ensemble models, except for distance to rural villages in MAXENT (Fig. 3a). The topographic ruggedness index and distance to cities and urban villages were key variables determining gazelle presence for the three ensemble models, though its respective contribution showed some differences were key variables determining gazelle presence for the three ensemble models, though its respective contribution showed some differences (Fig. 3b): topographic ruggedness index was the most important variable for the consensus model and MAXENT, whereas distance to cities and urban villages was most important in GLM.

Table 2. Predictive accuracy of ensemble models by binary transformation using the committee average approach in the training area for: a) GLM (EMbyGLM), b) MAXENT (EMbyMAXENT) and c) both algorithms(EMbyAll).

Type of ensemble model	AUC	Sensitivity	Specificity
a) EMbyGLM	0.86	92.68	69.28
b) EMbyMAXENT	0.90	87.81	77.74
c) EMbyAll	0.88	95.12	67.40

In both cases, the probability of the Cuvier's gazelle occurrence increased with higher rugged terrain index and longer distances to cities and urban villages. Variables such as annual mean temperature in GLM and in the combined model, and distance to rural villages in MAXENT played a secondary role. In this instance, higher temperatures and a decrease in distance to rural villages affected negatively to gazelle presence. The rest of the variables in the different approaches showed low contribution determining gazelle presence (Fig. 3b).

3.2 Predicted distribution range and priority conservation areas

Considering the northern limit of our study area to be the Drâa River, the predicted suitable Cuvier's gazelle habitat resulting from the consensus ensemble forecasting model yielded an area of 15820 km^2 (Fig. 2). The forecasted potential spatial occurrence at its southernmost limit of distribution revealed two well-demarcated areas: "A" and "B," with estimated areas of 4385 km^2 and 11315 km^2, respectively (Fig. 2). These areas are regions lacking formal protection, with only a relatively low percentage (5%) included in Khenifiss National Park. Presence of Cuvier's gazelles was higher in the eastern area of Khenifiss National Park, on the steep slopes of the Hammada of Tindouf, in the mountainous terrain of Aydar and across the large reliefs in the area (Jbels Zini, Rich and Ouarkziz). The consensus ensemble forecasting model showed a continuous suitable habitat strip to the north of the Drâa River, in the Jbel Bani and beyond the limits of the ecoregion.

4. DISCUSSION

Our study illustrates an example of how to successfully deal with a lack of key data in developing well-designed wildlife conservation actions in remote areas, such as the hard environment of the Sahara Desert, through combining large scale field surveys and distribution modelling. This approach has clear applications for any type of study on the population distribution and dynamics of threatened species that live in these types of regions, not only wild ungulates but also carnivores or other mammals of medium to large size. The present study provides robust ensemble models that achieved a good estimate of the importance of the variables and their response curves[23,46,56]. Our analyses confirm that the species presence and distribution of Cuvier's gazelle in the study area are primarily influenced by the variability or complexity of the terrain and the increasing distance to large human settlements. As a result, we found a higher projected probability of Cuvier's gazelle presence in zones with a complex network of hills and ravines and in remote areas with a low human population density and less accessibility (e.g., paved roads). These results are consistent since Cuvier's gazelle is well-adapted to rugged mountain areas[57], where they can find shelter from predation and poaching, but also where environment conditions are more favorable against the extreme Saharan climate. In such areas, Cuvier's gazelle can feed in ravines and dry river basins, where vegetation remains productive throughout the year. However, we were able to confirm that they avoid the more productive *oueds*, which are located in flat areas, probably because of greater pressure from livestock and human presence, factors that may hold great importance in habitat selection in the area[20]. This is consistent with the annual maximum green vegetation fraction and the compound topographic response curves, both positively correlated to the size of river basins, and therefore more productive *oueds*. The human factor represented by the distance to the nearest large human settlement is one of the many factors constraining the potential distribution of the species. A similar phenomenon was described in Chammem *et al.*[35], in which the species presence and distribution for dorcas gazelle in Tunisia seemed to be affected negatively by human presence and land use, rather than habitat characteristics. The projected species distribution model area probably reflects a shelter range that allows survival in apparently suboptimal conditions, due to both poaching and the extreme Saharan environment, where the species reaches the southernmost limit of its range. The impact of illegal wildlife hunting is one of the causes or the main cause of decline and extinction of ungulate species throughout the Sahara Desert[7,8,10,16,58], as it is in Morocco[59,60]. Therefore, the better-preserved Cuvier's gazelle populations in Morocco may currently be related to remote territories that have a low human population density. Furthermore, the species shows high environmental heterogeneity throughout its range in North Africa[18]. Cuvier's gazelle and slender-horned gazelle were suggested to inhabit two different ecotypes of mountain and low- land sand dunes, respectively, with a parapatric population structure[17], which may explain the ecological flexibility of Cuvier's gazelle and thus its survival under extreme environmental conditions. In the study area, other threats such as overgrazing and habitat loss must be studied, but at least do not seem to have had major effects thus far, in principle. Nevertheless, this situation appears to be changing. Recently, we noticed an increase in the number of domestic grazers and local pastoralists. This appears to be related to the opening of new roadways (some paved) and the use of large flexible plastics for water storage, allowing for more stable livestock exploitation in areas far from water sources.

4.1 Implications for conservation policies

At present in Morocco, two main populations of Cuvier's gazelle have been identified: the Bas Drâa-Aydar region (our study area) and the western Anti-Atlas[57]. Moreover, small populations are located in the Western High Atlas (north of Agadir) and on the south side of the central High Atlas and East Atlas[60]. We extended the species distribution model forecast area to the south of its known distribution area, identifying two well-delimited key areas for Cuvier's gazelle (A-B; Fig. 2), a result consistent with the previous scattered and opportunistic records inside and outside of the study area, which resemble our species distribution model[9,57,60].

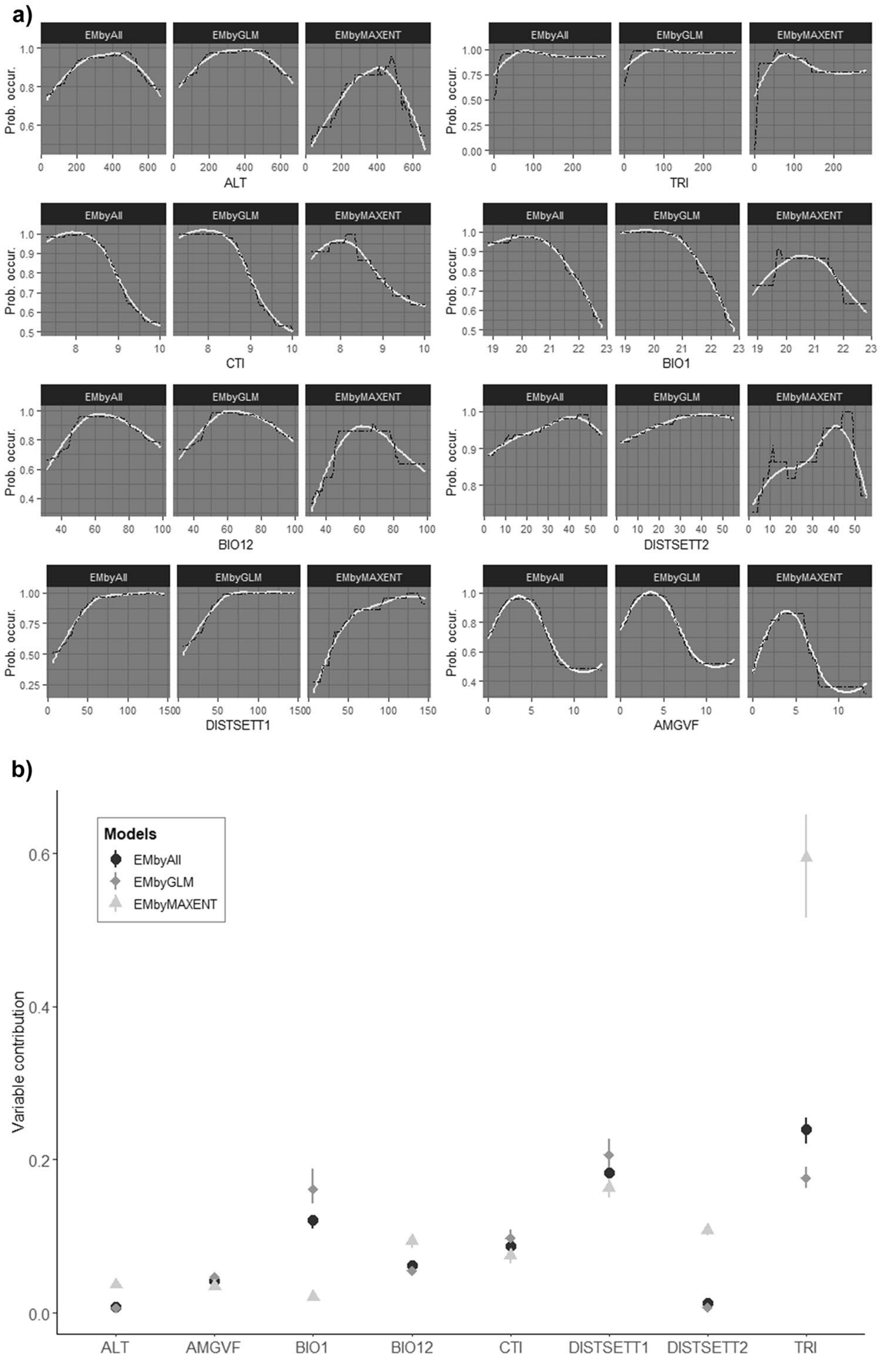

Figure 3. (**a**) Response curve and (**b**) variable contributions of the predictor variable selected for the different statistical approaches to model distribution of Cuvier´s Gazelle. Black curves in (**a**) are from original outputdata and grey curves by smooth processing. Models: ensemble model by GLM (EMbyGLM), ensemble model by MAXENT (EMbyMAXENT) and ensemble model by both algorithm (EMbyAll). Variables: altitude (ALT), annual of maximum green vegetation fraction (AMGVF), annual mean temperature (BIO1), annual precipitation (BIO12), compound topographic index (CTI), distance to cities and urban villages with >1500inhabitants (DISTSETT1), distance to rural villages with <1500 inhabitants (DISTSETT2) and topographic ruggedness index (TRI).

Within both areas, our species distribution model identified sectors with high Cuvier's gazelle probability of presence (close to 1). These locations hold a suitable habitat where action aimed at conservation is urgent. The whole region is considered public land under the Moroccan government's management, with nomads moving about in temporary camps with herds of goats, sheep and dromedaries. During the field surveys, we observed that these people opportunistically try to hunt gazelles, whereas groups of poachers coming from the nearest large cities operate at will. Moroccan authorities planned to declare one national park (Bas Drâa NP), one Biological and Ecological Interest Site (Oued Tirhzer) as well as two hunting reserves (Messeied-Abeteih and Oued Chbeyka)[61,62]. However, the surface area covered by these planned protected areas is insufficient to protect a key space for Cuvier's gazelle (i.e. a viable population), since it would cover just 25% of the range we have estimated and, moreover, these projects have been stalled for more than two decades. Moreover, local Cuvier's gazelle densities are quite low (0.08 individuals/km^2) and the total population has been estimated at 935 (95% CI 597–1607) individuals[20]. Our results show the need to extend the protected areas designed in the Moroccan strategy for the preservation of endangered species[60], as well as the urgency in the implementation of this national strategy to protect the current natural populations of Cuvier's gazelle. New protection areas forming a backbone for the region's sustainable development with proper protection (in terms of poaching) and a low human impact will be crucial to preserving the species. The Cuvier's gazelle population inhabiting this region will have a better chance against any harsh conditions (water shortages and extremely high temperatures) in a changing climate scenario[7]. Furthermore, the region has been proposed as a dispersal corridor and fauna shelter for the Sahara-Sahel region[16]. These features make this part of Morocco a crucial area not only for the Cuvier's gazelle preservation, but also for other endangered ungulate species still present in the region such as dorcas gazelle and Saharan barbary sheep (*Ammotragus lervia sahariensis*), and carnivores such as striped hyaena (*Hyaena hyaena*), sand cat (*Felis margarita*), caracal (*Caracal caracal*) and, in all likelihood, the critically endangered Saharan cheetah (*Acinonyx jubatus hecky*). The latter could find a strategic area for recovery here, the area could also aid in the recovery of other extinct ungulate species like mhorr dama gazelle (*Nanger dama mhorr*), scimitar-horned oryx and addax, through reintroduction projects. Some of these species have begun to be reintroduced in the Souss-Massa region[63,64]. The current work can provide a basis for the definitive design of protected areas and reintroduction projects.

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SUPPLEMENTARY INFORMATION

Appendix S1. Matrix of correlation coefficients and Variance Inflation Factor (VIF) analysis[1]. Pre-selection of variable by removing environment metrics highly correlated and with multicollinearity problems. Variables removed in "red".

- Matrix correlation table

	Alt	*Slope*	*Tri*	*Hli*	*Cti*	*Amgvf*	*BIO1*	*BIO12*	*Distcoast*	*Distcities*	*Distvillages*
Alt	1.00										
Slope	0.04	1.00									
Tri	0.06	0.96	1.00								
Hli	0.03	0.89	0.86	1.00							
Cti	0.10	-0.85	0.73	0.73	1.00						
Amgvf	0.42	0.19	0.19	0.14	0.22	1.00					
BIO1	0.17	-0.37	0.35	0.32	0.30	-0.39	1.00				
BIO12	0.03	0.50	0.49	0.44	0.38	0.33	-0.80	1.00			
Distcoast	0.63	-0.35	0.31	0.31	0.23	0.03	0.62	-0.69	1.00		
Distcities	0.40	-0.28	0.31	0.24	0.15	0.04	0.45	-0.70	0.63	1.00	
Distvillages	0.26	-0.24	0.24	0.24	0.19	0.00	0.01	-0.28	0.27	0.21	1.00

- Variance Inflation Analysis.

a) 1 variables (Distcoast) from the 9 input variables had collinearity problem.

b) After excluding the collinear variables, the linear correlation coefficients ranges between:

min correlation (distvillages ~ amgvf): 0.0029392

max correlation (BIO12 ~ BIO11): -0.7952318

-------- VIFs of the remained variables --------

	VARIABLES	VIF
1	Alt	1.685919
2	Tri	2.494449
3	Cti	2.268704
4	Amgvf	1.478186
5	BIO1	3.483616
6	BIO12	6.110327
7	Distcities	2.91219
8	Distvillages	1.349295

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CAPÍTULO 3.

Feeding Ecology of the Cuvier's Gazelle (Gazella cuvieri Ogilby, 1841) in the Sahara Desert

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Feeding Ecology of the Cuvier's Gazelle (*Gazella cuvieri* Ogilby, 1841) in the Sahara Desert

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Simple summary

The Sahara desert is home to the greatest diversity of ungulates of all deserts. In this harsh environment, the endangered Cuvier's gazelle finds at the southernmost limit of its distribution a key population for its survival. A better understanding of the feeding ecology of the species may improve our understanding of the biological requirements for implementing conservation measures. In this study, we analysed the diet and feeding strategy of a desert population by combining different approaches such as faecal sampling, recording indirect signs of feeding, and direct observations of individuals. Our results revealed that Cuvier's gazelles displayed a feeding behaviour similar to that of browsing ruminants, with acacias as key species for the survival of the species in the harsh environment of the Sahara. Consequently, the current increasing grazing pressure in remote areas and on acacias calls for measures to mitigate this emerging and possibly worsening impact due to imminent climate change.

Abstract

Knowledge of the feeding ecology of ungulates in arid biomes offers an interesting model for understanding the drought resistance of large desert-adapted herbivores, a crucial issue in the face of increasing desertification due to climate change. To assess the feeding ecology of the endangered Cuvier's gazelle (*Gazella cuvieri*) in the Sahara desert, we used a multi-method approach combining faecal samples, direct observations, and the recording of indirect signs of feeding. We hypothesised that browser behaviour is the best foraging strategy for species living in hyper-arid environments, mainly due to long periods without grazing opportunities. Complementarily, we explored the effects of the main environmental descriptors (rainfalls and NDVI) on feeding patterns and diet quality. We found that Cuvier’s diets are based mainly on acacias (*Vachellia tortilis*, *V. flava*) and occasionally on the annual forb *Anastatica hierochuntica*. In total, eighteen species (five trees, nine shrubs, three herbs, and one grass) belonging to fifteen families were recorded. Our result confirmed the browsers’ characteristic of this species, reaffirming its ability to settle in a hostile environment. Acacias stand out as key species consumed at the southernmost limit of their range; hence, future conservation plans and strategies should take this into account for the survival of Cuvier’s gazelle in desert environments.

Keywords: *Gazella cuvieri*; climatic change; diet; deserts ecology; Sahara; wild ungulates; wildlife conservation; acacia.

1. INTRODUCTION

Deserts comprise the hyper arid regions (aridity index, AI < 0.05) of the Earth and the surrounding arid zones (AI < 0.2), occupying almost a quarter of the Earth’s surface, some 33.7 million square kilometres [1]. The scanty annual rainfall, with less of 250 mm as a rule but even complete absence in some years [2], imposes extreme conditions for the survival of any form of life. Desert-dwelling species have evolved different physiological and behavioural strategies in the face of scarce water availability and extreme exposure to solar radiation. These strategies may even differ according to the size of the animal, as in the case of burrowing desert rodents or the heterothermy of arid-adapted ungulates, which allows them to survive in harsh desert environments. In this context, adaptations in terms of food quality and active foraging in relation to their trophic ecology may further condition the type of survival strategies in deserts, including for obtaining water under extreme conditions [3]. Unfortunately, large desert mammals not only have to cope with the harsh desert conditions, but they are also mostly endangered in the Sahara with extreme cases such as the critically endangered addax (*Addax nasomaculatus* [4]) or the critically endangered Saharan cheetah (*Acinonyx jubatus hecki* [5]). The Sahara desert is home to the highest diversity of antelope species of any desert ecoregions in the world, namely the scimitar-horned oryx (*Oryx dammah*), addax, dama gazelles (*Nanger dama*), slender-horned gazelles (*Gazella leptoceros*), Cuvier’s gazelles (*G. cuvieri*), and Dorcas gazelles (*G. dorcas*) [6,7]. The recent decline in these populations has been due to overhunting, and habitat destruction [6] has not been followed by an increase in the research efforts on existing populations to develop conservation plans [8–10], most likely due to the hostile conditions of their habitats and the political instability that makes conditions unsafe for researchers [11]. However, knowledge of the ecology of wild ungulates in arid environments is a hot topic in the current climatic change scenario [12]. In this sense, understanding the feeding strategies of large mammals in desert biomes becomes a key goal.

Desert environments are characterised by low and variable rainfall (both spatially and temporally), resulting in minimal and unpredictable pulses of primary production lasting for a few weeks [3,13]. In this environment, herbivores must adapt their foraging strategy to the high uncertainty of food availability and its quality. The quality provided by the plants is deduced from the concentration of nitrogen and fibre which are measured by different methods. Two common procedures are direct observation of consumption in certain plants for which the chemical composition is known and detailed analysis of faecal composition. Both tend to show that woody plants are a poorer-quality source compared to fresh herbaceous taxa [3,13,14]. Similarly, the quality of the diet can be largely determined by the environmental conditions that, in arid and desert environments, greatly limit the abundance of vegetation and productivity [3,13]. In fact, deserts usually host scattered sclerophyllous or deciduous woody plants, often spiny or/and with tiny leaves, low palatable perennial graminoids, and annual plants with a phenology dependent on erratic rainfall [3,13].

In relation to the preference for feeding on herbaceous plants or the ability to consume woody plants, ruminants are conventionally classified as "grazers" with a mainly bulk/grass diet, "browsers" with a concentrated diet of browsers or herbs, and "intermediate" for opportunists and mixed feeders [15,16]. In addition, some physiological adaptations make ungulates more energetically efficient at grazing or browsing [14]. In semi-arid and desert environments, browsing species become an important component of the diet during hot and dry summers, as a rapid decline appears in quality and herbaceous availability [2]. The alternation between grazing and browsing is well known and depends on the frequency and intensity of rainfall as well as the extent of grazing for many species (e.g., Eland (*Taurotragus oryx*) [17], Dorcas gazelle [18], Dama gazelle (*Nanger dama*) [8], and Mountain gazelle (*Gazella gazella*) [19]). Hence, to survive in deserts, ruminants could alternate between the following feeding behaviours: (1) grazing opportunistically to take advantage of eventual pulses of ephemeral grasses and forbs that grow after occasional rainfalls, possibly in conjunction with nomadic movements (e.g., the case of addax [20]); or (2) browsing on more stable resources such as perennial shrubs and trees growing in desert massifs. This second strategy could be the selected one for long-term survival in the case of sedentary species that have to endure long periods of drought that preclude grazing. This scenario might be the case of the Cuvier's gazelle, as its Saharan population is strictly restricted to the main massifs [10,21] with no opportunities for long migrations.

Cuvier's gazelle is an ideal model for studying the survival strategies of ruminants in deserts. This medium-sized ungulate is endemic to north-western Africa [22]. However, over the last century, long-term overhunting and recent habitat loss have drastically reduced its population sizes and subsequent assessments of extinction risk as a vulnerable species [23]. The species occupies a wide range of habitats from Mediterranean scrubland and open Aleppo pines (*Pinus halepensis*), arar tree (*Tetraclinis articulata*), oaks (*Quercus* spp.) and junipers (*Juniperus* spp.) to the Sahara desert [22,24]. However, the extant populations are now restricted to small and isolated patches in mountainous terrain in the Maghreb highlands of Morocco, Algeria, and Tunisia, and also in arid Mediterranean steppes and the Atlantic Sahara desert [22,25]. The Atlantic Sahara desert is one of the last strongholds of the endangered Cuvier's gazelle [10,21]. Here, it reaches its southernmost distribution, inhabiting biotopes very different from the typical landscapes it occupies in the Atlas Mountains, where the climatic conditions give rise to more productive environments than in the Sahara [22]. Therefore, a better understanding of the adaptive traits that enable the survival of this species in this hyper-arid environment is crucial to implement effective conservation measures [10,25,26]. However, the current scientific knowledge on the diet of Cuvier's gazelle is very scarce. Only two studies on free-ranging gazelles have been published but restricted to the Mediterranean population of Djebel Messaâd Forest, Algeria [27,28], and another one has focused on a reintroduced group in a small fenced area in Tergou reserve, Morocco [29].

In this study, we analyse the feeding strategy of Cuvier's gazelle in the Sahara. In particular, we examine the diet of Cuvier's gazelle and its components that could play a key role in their survival and, thus, their ability to be sedentary in a Saharan environment. We hypothesise that the foraging strategy of Cuvier's gazelle in this environment is mainly based on browsing, due to both the long periods without rain and its proximity to mountains where trees and bushes are common [10]. To achieve our objective, we use a multi-method approach combining faecal-based analysis, direct observations of foraging behaviour, and recording indirect signs of feeding. Secondly, we explore the relationships between key environmental descriptors (precipitation, primary production assessed through the NDVI, altitude, and temperature), the observed consumption patterns, and diet quality. Finally, beyond improving the knowledge of our targeted species, we provide baselines that could be useful for studying the feeding ecology of other wild ungulates in remote and harsh deserts environments.

2. MATERIALS AND METHODS

2.1 Study Area

We studied the diet of Cuvier's gazelles in a vast region between the lower Draa River and the upper basin of the Sequiat Al Hamra, within the Atlantic Sahara of Morocco (Figure 1). The study area extends over 20,000 km^2 and is a typical Saharan landscape, with a subtropical desert at low-latitude (Köppen–Geiger classification [30]) and hyper-arid climate [1]. The area falls inside the North Saharan Xeric steppe and woodland ecoregion with prolonged droughts and irregular rainfalls [31]. 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; 19.1, 10.7, and 29.0 °C at the northern limit, respectively. Total annual precipitation (with large annual variability) is 138, 59, and 190 mm, respectively (recorded at climate stations at Smara, 26°46′N, 11°31′W; Tindouf, 27°40′N, 8°7′W; Tan Tan, 28°26′ N, 11° 06′W).

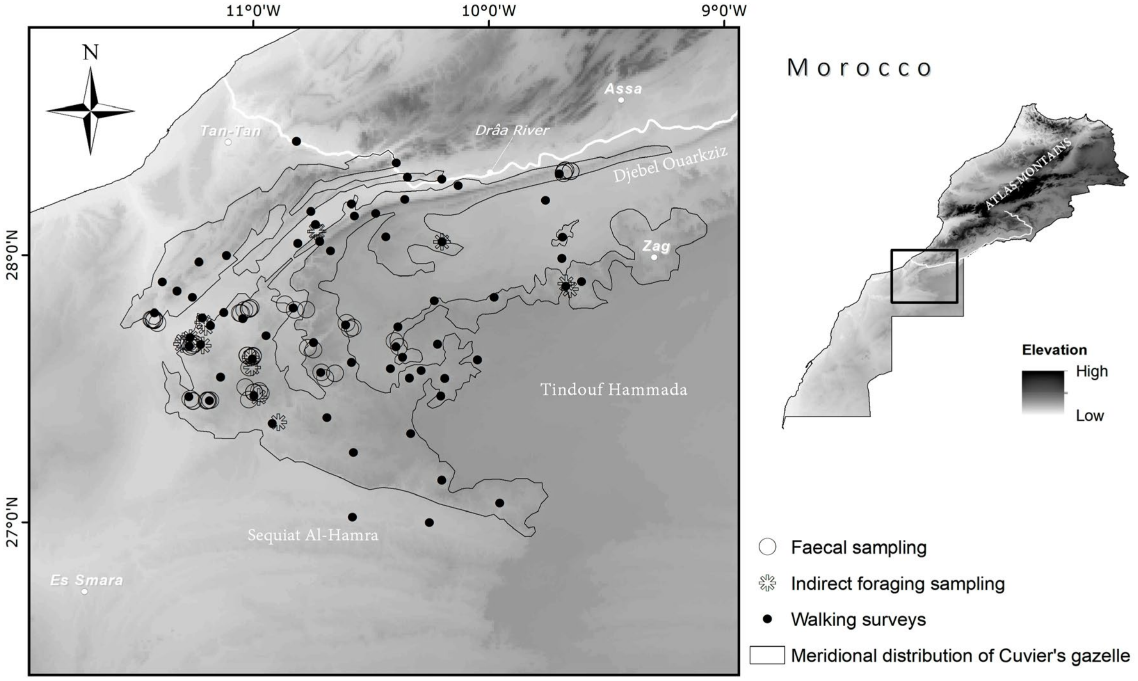

Figure 1. Study area with sampling sites. Relief is represented by a raster digital elevation model (DEM) and is expressed by a colour gradient from darker (higher altitude) to lighter (lower altitude). The map also shows the main towns and distribution of Cuvier's gazelle south of the Drâa River, considered its southernmost range [10,21].

The study area is typically mountainous with rocky plateaus and a complex network dry rivers of which only the Draa and Chebeiqa rivers can maintain permanents pools of water. The whole region is a transition point between the Saharan and Macaronesian ecoregions [2,32,33]. In this context, the presence of plant species such as the argan tree (*Argania spinosa*), a Moroccan endemism, and the presence of Macaronesian elements such as *Euphorbia officinarum* are noteworthy but very limited to some mountain refuges. Vegetation is very sparse and is mainly associated with mountainous areas and ravines that favour higher soil humidity. Acacias (*Vachellia tortilis* subsp. *raddiana* and *V. flava*) along with some scattered specimens of *Balanites* *aegyptiaca*, *Maerua crassifolia*, and *Calotropis procera* form the dominant tree vegetation. *Periploca laevigata*, *Launaea arborescens*, *Searsia tripartita*, *Nitraria retusa*, *Saharanthus ifniensis*, *Salsola tetragona,* and *Lycium shawii* stand out as shrub vegetation, and *Cymbopogon schoenanthus* as grass. Other species that thrive mainly on hammadas (*plateaux*), regs (*stony plains*), and ergs (*dune areas*) are *Anabasis articulata*, *Hammada scoparia*, *Helianthemum lippii*, and *Nucularia perrinii* among perennial shrubs, and *Anastatica hierochuntica*, *Citrullus colocynthis*, *Mesembryanthemum cryptanthum*, *Cullen plicatum*, *Panicum turgidum*, *Stipagrostis plumosa*, and *Pennisetum divisum* among ephemeral forbs and perennial grasses that experience short-term pulses, lasting for a few months (or weeks) only during the years with enough rainfall [34].

As a result of a massive general decline in the region's large vertebrate fauna [6] and following the last sightings of the Dama gazelle after the mid-20th century, there are currently three ungulates remaining in the study area: Dorcas gazelle, Barbary sheep (*Ammotragus lervia*), and Cuvier's gazelle [35]. Here, Cuvier's gazelle population is one of the most important, if not the most, of its global range, with an estimated 1000 individuals distributed over 12,000 km^2, resulting in a very low density of 0.08 ± 0.02 individuals per square kilometre [21]. This population is severely affected by poaching and habitat destruction related to overgrazing by goat and sheep, habitat fragmentation due to roads and water cisterns construction, and timber harvesting [36].

2.2 Data Collection

First, it is important to take into account two main limitations of our survey in the study area: (1) the remoteness, which includes high limitations for displacements due to the scarcity of roads, mostly represented by unpaved roads only accessible by 4WD vehicles; (2) the very low density of Cuvier's gazelle. To overcome both challenges, we accomplished walking surveys to collect samples for three types of data: faecal samples, direct observations, and indirect records. Fieldwork was carried out during 18 expeditions with a maximum of 15 persons per expedition, conducting 67 sampling points every March–April and December–January annually from 2012 to 2019, to avoid the harsh conditions during the rest of the year (temperatures > 45 ◦C); the other four expeditions were during May (2), September (1), and October (1). Each study site was located in the different habitats of the study area to make a spatially independent distribution covering the entire area of interest. In a typical walking survey (12.08 ± 0.72 km by 2–3 persons), we looked for sightings of individuals and indirect signs such as footprints, scats, and signs of grazing/browsing activity (see further details in [21]). The long sampling period allowed us to capture the typical rainfall variability of the study area.

Faecal samples (FSs) provide a good approximation of the diet of ungulates [37], including desert gazelles [27,38]. The collected FSs were confirmed as belonging to Cuvier's gazelle by genetic analysis (see details in [39]). During field surveys, foraging behaviour was recorded by direct observation (DO) of individuals using binoculars or spotting scopes of high-magnification. Plants that were eaten and those that were visited but not consumed were counted (see [40,41] for another desert gazelle species). Indirect signs of feeding (IF) were recorded from the detected fresh tracks of Cuvier's gazelle using footprints in sandy terrain, which were followed for as long as possible. Plants with associated tracks (see examples in Figure 2A,B) were examined in situ for fresh bites on leaves and branches recording the species consumed (Figure 2) (see [42] for IF applied on Addax or [43,44] on moose (*Alces alces*) by tracking in the snow). Plants < 2 m from the track were considered ignored and, therefore, not consumed. The tracks of the smaller Dorcas gazelle may be confused with those of our target species, but this gazelle is almost absent in our study area in areas inhabited by Cuvier's gazelle (data from our surveys); in any case, tracks < 5 cm in length of isolated individuals were rejected [45]. As for domestic ungulates, both the number of tracks left and the clear morphological differences of the footprints (as for Barbary sheep) were easily identified and discarded.

2.3 Faecal Cuticle Microhistological Analysis of FSs

For the analysis of FSs, we used microhistological techniques based on the analysis of the plant cuticles, following [46]. This technique is widely used to determine the diet of herbivorous mammals, e.g., [46–48], including our target species [27,28]. We added 1 g of faecal samples in 5 mL of HNO_3, concentrated in test tubes, and this preparation was introduced in a hot water bath (80 °C) for 1 min. After this time, the content of these tubes was poured into 200 mL of distilled water. This solution was passed through a 0.125 mm filter to separate the liquid from the solid sample. To prepare the slides, we added 3 drops of 50% aqueous glycerine solution; then, we took the solid that had remained on the filter and added it to the slide, distributing everything homogeneously. When everything was homogenised, we mounted the coverslip with DPX microhistological varnish. All these samples were prepared in duplicate. We let the samples dry for one or two days and then performed the analysis with a microscope. The samples were examined under 10–40 magnification. One hundred plant fragments were counted per slide and identified to species level on the basis of epidermis and trichomes morphology [49].

Figure 2. Examples of Cuvier's gazelle indirect feeding (IF) data obtained in the study area duringthe surveys: (**A**) Footprints recorded while one group was feeding on *Vachellia tortilis*. (**B**) Damage in *Lavandula coronopifolia* by browsing. (**C**) *Calotropis procera* consumed by a Cuvier's gazelle. (**D**) Leaf of *C. procera* partially consumed by Cuvier's gazelle.

2.4 Diet Quality

Diet quality was assessed through faecal nitrogen (FN), which is widely used in diet quality assessment [14,50,51]. In addition, the use of neutral detergent fibre (NDF = Cellulose + Hemicellulose + Lignin), acid detergent fibre (ADF = Cellulose + Lignin), and acid detergent lignin (ADL = lignin) is useful to complement the information given by FN as both follow opposite patterns [52,53]. As FN is the combination of metabolic and food residue nitrogen excreted in faeces, FN/NDF, hereafter called FNc, was calculated as a proxy for the protein contents of diets [52]. Near-Infrared Spectrophotometry (NIRS) was used to predict faecal nitrogen and fibre contents [51]. Briefly, the samples were placed in 35 mm diameter quartz beakers and analysed in a NIRSystem 5000 spectrometer (FOSS, Hillerød, Denmark) using wavelengths from 1100 to 2500 nm. Data were obtained at 2 nm intervals as log 1/R, where R is the reflectance. Each sample was scanned in duplicate by making a 180° turn of the glass. If the amount of sample was too small, the base of the glass was not completely covered, but a beaker was added to reduce the surface by half so that two readings could be taken, each with its duplicate. Faecal nitrogen data were obtained using the multispecies equation [51].

Subsequently, faecal nitrogen was corrected with neutral detergent fibre [52]. For fibre content, 10 samples were analysed in the laboratory following the Van Soest method [54] using the Ankom 200 Fiber Analyzer (ANKOM Technology, Macedon, NY, USA). Afterwards, the values obtained from the 10 samples were used to readjust the NIRS equation and to obtain more accurate data due to the correction provided by this method.

2.5 Environmental Descriptors

We selected six environmental descriptors that could affect the foraging behaviour of Cuvier's gazelles: normalised difference vegetation index NDVI (per year, seasonal, and weekly scales), annual precipitation, annual temperature, and altitude. The values of the NDVI index were extracted from the map of the USGS Land Cover Institute (LCI) website (available at https://earthexplorer.usgs.gov/; accessed on 15 September 2022). Climatic variables and elevation data were taken from the WorldClim–Global Climate Data (available at http://worldclim.com/version2; accessed on 14 June 2022) and the DIVA-GIS websites (available at https://www.diva-gis.org; accessed on 3 May 2022), respectively.

2.6 Data Analyses

As we were only able to observe very few individuals feeding, this type of data was not used for statistical analysis. For the other two approaches, we first compared the information obtained by FSs and IF through (1) the taxonomic richness (number of consumed species) and (2) the contribution (% of occurrence) of each consumed plant, using Chi^2 tests on 2 2 contingency tables with Bonferroni's correction to detect significant differences. Each consumed species was classified as woody species (trees and shrubs), forbs, or grasses (Table 1), to define the feeding strategy resulting from each methodological approach (i.e., browser, grasser, or intermediate).

Second, plant species selection was examined using the IF data set; for this, we compared the contribution of consumed species with the contribution of non-consumed species detected for each monitored trackway. We pooled all data on a single sample and calculated the Ivlev's selectivity index [55], also tested by Chi^2 tests on 2 2 tables with Bonferroni's correction.

Third, we used the FS data to explore the multiple relationships between diet composition (proportion of consumed plants), diet quality (FNc, NDF, ADF, and ADL), and environmental descriptors (rainfalls and NDVI).

Table 1. Species consumed by Cuvier's gazelles, category and detection method.

Species	Family	Category	Method [1]
Vachellia flava	Leguminosae	Tree	DO, IF, FS
V. tortilis subsp. *raddiana*	Leguminosae	Tree	IF, FS
Anastatica hierochuntica	Brassicaceae	Forbs	FS
Argania spinosa	Sapotaceae	Tree	IF
Asparagus altissimus	Asparagaceae	Shrub	DO, IF
Asteraceae (sp. unidentified)	Asteraceae	Forbs	IF
Calotropis procera	Apocynaceae	Tree	IF
Citrullus colocynthis	Cucurbitaceae	Forbs	IF
Convolvulus trabutianus	Convolvulaceae	Shrub	IF
Cullen plicatum	Leguminosae	Shrub	IF
Helianthemum lippii	Cistaceae	Shrub	FS
Lavandula coronopifolia	Lamiaceae	Shrub	IF
Lycium shawii	Solanaceae	Shrub	DO
Maerua crassifolia	Capparaceae	Tree	IF
Nitraria retusa	Nitrariaceae	Shrub	IF, FS
Pennisetum divisum	Poaceae	Grass	FS
Periploca laevigata	Apocynaceae	Shrub	DO, IF
Searsia tripartita	Anacardiaceae	Shrub	IF

[1] Direct observations (DOs), indirect data of feeding recorded from fresh tracks (IF), and faecal samples of Cuvier'sgazelles (FSs).

We began by exploring the relationships between diet quality descriptors, the occurrence of consumed species, and some environmental variables through Pearson's correlations. Then, we carried out a Principal Component Analysis (PCA) [56]. In our PCA modelling, the dietary components of gazelles (plants and the faecal indicators of diet quality) were used to build the PCA dimensions (active variables), whereas the descriptors for the environmental variation were considered as supplementary quantitative variables. The Shannon's diversity index was also included in the set of active variables. PCA was performed in the FactoMineR 1.63 version [57] package of the statistical software R 4.2.1 version (R Core Team 2022).

3. RESULTS

3.1 Diet Composition and Feeding Behaviour

The IF after 15 tracks (mean length 624 m, range 300–1600 m) provided information on at least 27 gazelle individuals (11 tracks during April, and 1 track during December, January, March, and September). These IF records were made on 144 individual plant species and 14 species of trees and shrubs (Table 1, Figures 1 and 3). On four independent occasions, seven gazelles were directly observed feeding on *P. laevigata* (1), *L. shawii* (1), *Asparagus altissimus* (8), *V. flava* (6), and other unidentified species (twelve times, probably small forbs), amounting to at least 4 species and 28 individuals. We obtained 57 samples (independent groups of pellets) for FS analysis (Figure 1), 21 collected during December– January and 36 during March–April. The FS analysis provided 5766 cell fragments with acacias being the best represented with a total of 2337 fragments (40.54%), followed by unidentified plant taxa with 1808 fragments (31.37%), *A. hierochuntica* with 1298 fragments (22.51%), *H. lippii* with 206 fragments (3.57%), *N. retusa* with of 93 fragments (1.61%), and *P. divisum* with 23 fragments (0.40%).

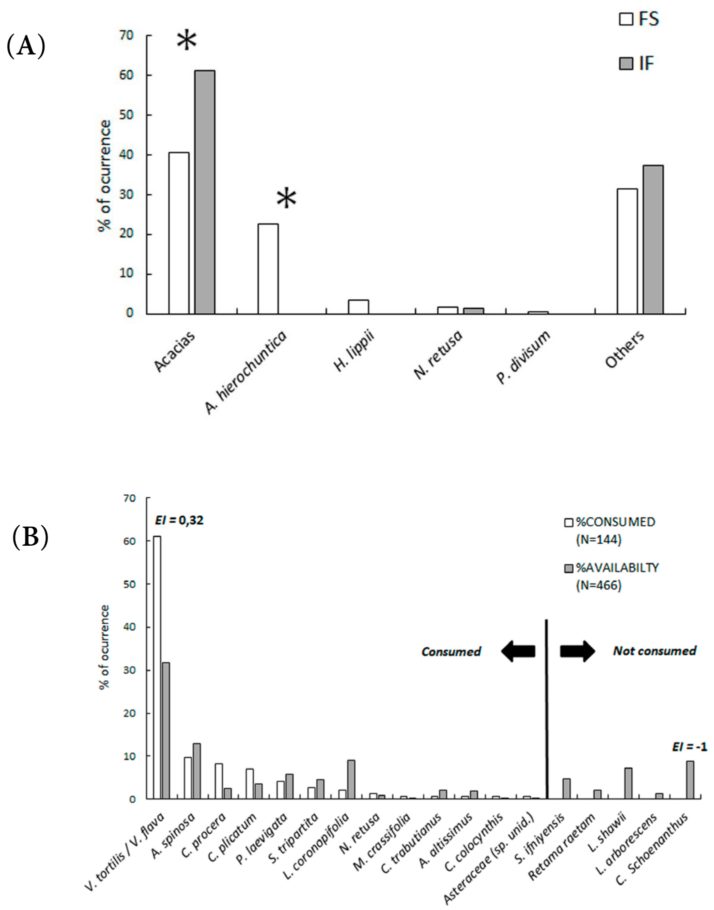

Figure 3. (**A**) Contribution of plant species to the diet of Cuvier's gazelles in the Sahara desert: from faecal samples (FSs) and indirect feeding (IF) data; * $p < 0.001$ of Chi^2 tests with Bonferroni's correction. (**B**) Diet selection from IF; Ivlev's electivity index (*EI*) is shown only for species with $p < 0.0027$ of Chi^2 tests with Bonferroni's correction for acacias (*Vachellia tortilis* and *V. flava*) and *Cymbopogon schoenanthus*.

Therefore, only five or six species were identified from the faecal samples (the two acacia species could not be differentiated). It is remarkable that *A. hierochuntica* was not detected by tracking despite its contribution to the diet (Figure 3). In our study area, Cuvier's gazelles feed on eighteen species (five trees, nine shrubs, three forbs, and one grass), belonging to fifteen families (Table 1, Figure 3). The percentage of trees and shrubs depends on the method of analysis used and varies between 45.72% for FS, 57.1% for DO, and 98.6% for IF (Figure 3).

There were important differences in diet composition between the FS and the IF data sets. The IF offered a higher contribution of trees, a null contribution of *A. hierochuntica*, and a lower contribution of the other species (Figure 3A). In terms of taxonomic selection, the tracked Cuvier's gazelles showed a preference for acacias while they tended to consume all other species according to their availability, except for the grass *Cymbopogon schoenanthus*, which was neglected by the monitored gazelles (Figure 3B). A group of three gazelles tracked over 1.6 km did not consume ripe argan fruits in fifteen available trees.

3.2 Effects of Environmental Factors

A summary of diet composition and diet quality from FSs is shown in Table 2. Eleven PCA components were obtained, but the first two explained more than half (54.43%) of the variability observed in the dietary elements (Figure 4C). In the first PCA component (which retains 32.5% of the observed variability), the variables with the highest contribution were ADF and NDF fibre, followed by the proportion of unidentified plants and ADL fibre. In contrast, the lowest contribution was for the proportions of *P. divisum* and *N. retusa*. The second component accounted for 21.9% of the observed variability in our set of diet variables and was mainly represented by the proportion of acacias, the diet quality, and the Shannon index.

Table 2. Mean ± SD, minimum, and maximum concentrations (%) of the assessed items in 57 faecal samples from Cuvier's gazelles collected in December, January, March, and April from 2012 to 2019in the Sahara desert, Morocco.

	Feacal items[1]	**Mean ± SD**	**Range**
Diet composition	*Anastatica hierochuntica*	22.77 ± 23.80	0 – 80.00
	Acacias	41.01 ± 16.42	9.00 – 82.00
	Others	31.73 ± 13.9	6.00 – 71.00
	Helianthemum lippii	3.61 ± 8.18	0 – 40.00
	Nitraria retusa	1.63 ± 4.72	0 – 33.00
	Pennisetum divisum	0.04 ± 2.91	0 –22.00
Diet quality	FNc	0.18 ± 0.06	0.0.79 –0.034
	NDF	37.71 ± 4.63	27.80 –50.70
	ADF	26.30 ± 3.02	19.8 – 34.3
	ADL	11.72 ± 2.20	7.8 – 16.30

[1] Faecal nitrogen (FNc), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL). "Other" refers to plant species not identified in the microhistological analysis of the faecal cuticle and "Acacias"includes *Vachellia tortilis* and *V. flava*.

The proportion of *A. hierochuntica* and NDF and ADF fibres were also important for the second PCA component. The PCA correlation circle (Figure 4D, see data in Supplementary Material Table S1) reflects a relatively complex net of relationships with the following remarkable results: (1) for diet quality descriptors, fibres showed a negative relationship with FNc (as expected), acacias consumption was weakly associated with FNc, and fibres were associated with the "Others" category and negatively associated with *A. hierochuntica*. (2) As for environmental descriptors, primary production at different time intervals (annual, seasonal, and weekly), annual precipitation, annual temperature, and altitude had very little relationship with plant consumption or with faecal indicators of diet quality. (3) In terms of relationships between the consumed species, *A. hierochuntica* was negatively correlated with acacias and with the "Others" category, and trophic diversity was negatively related to acacias.

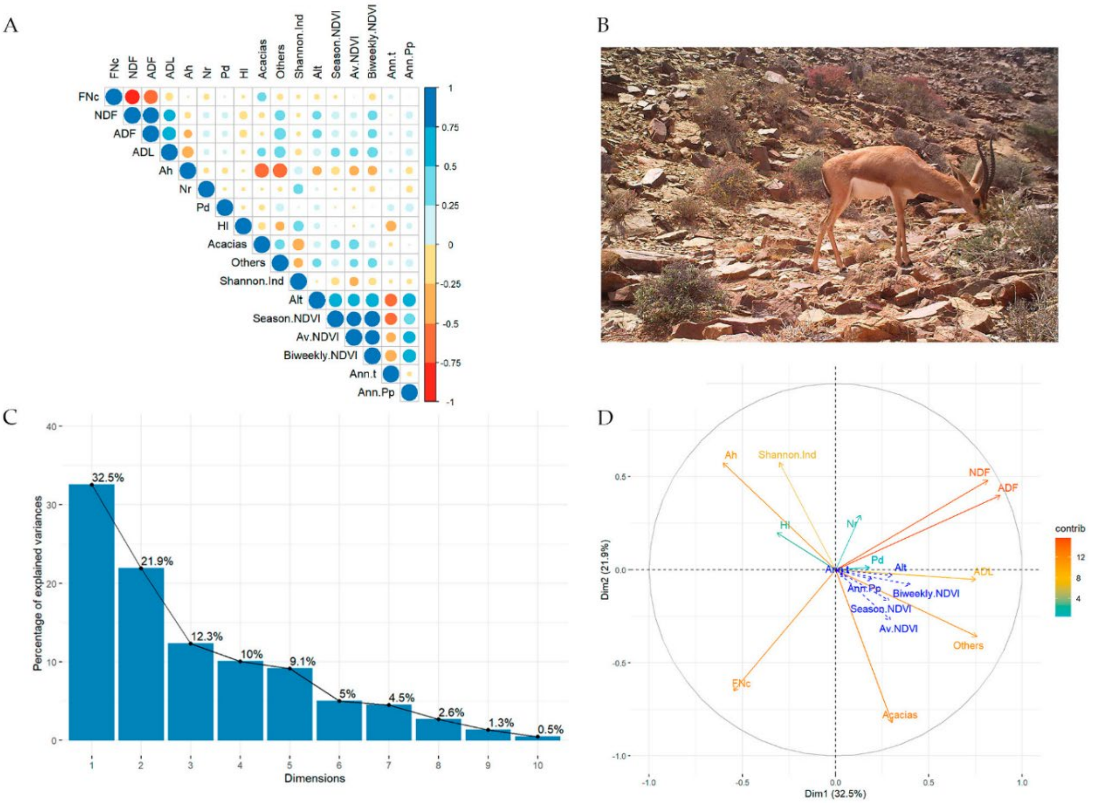

Figure 4. (**A**) Correlation panel showing Pearson's coefficients between pairs of variables; positive relationships are represented in blue, negative ones in red. (**B**) Photo capture by camera-trapping of a male Cuvier's gazelle feeding on *Asparagus altissimus* in the study area. (**C**) Bar plot representing the proportion of variance explained by the dimensions extracted from the PCA. (**D**) PCA results for relationships between the species consumed, Shannon's index, diet quality, and selected environmental factors. Abbreviations: plants consumed: Ah (*Anastatica hierochuntica*), Nr (*Nitraria retusa*), Pd (*Pennisetum divisum*), Hl (*Helianthemum lippii*); Alt (Altitude), Annual temperature (Ann.t), Annual precipitation (Ann.Pp); NDVI: per year (Av.NDVI), weekly scales (Biweekly.NDVI), and seasonal (Season.NDVI); Shannon's diversity index (Sannon.Ind). For all other abbreviations, see text.

4. DISCUSSION

4.1 Limitations of the Study

Our results highlight the great difficulties of wildlife research in the Sahara. First, we obtained a relatively low sample size for IF and DO after a great effort surely due to the very low density of Cuvier's gazelles [21], their shy behaviour resulting from constant poaching (confirmed during field surveys), and the limitations for fieldwork in such a rocky terrain. The latter circumstance determined the non-detection by IF of important species for the feeding ecology in the Sahara, as was the case of *A. hierochuntica*, a widespread annual forb in the study area. However, IF resulted in a significantly higher number of identified consumed plants and, in addition, this method allowed the only approach to food selection in a free-ranging population of Cuvier's gazelles of which we are aware, confirming a strong preference for acacia species as a key result.

In contrast to DO and FI, FSs were relatively easy to find [21], but we obtained a very low identification success of species consumed, which was a handicap for the description of the foraging behaviour (i.e., for testing our hypothesis). This result contrasts with the FS analyses by Benamor et al. [27,28], who obtained a higher identification success in FSs of Cuvier's gazelles in a Mediterranean population. The discrepancy may be partly explained by: (1) the large differences detected in the taxonomic composition of the diet between the Saharan and the Mediterranean studies [27], and/or (2) differences in the degree of field preservation of collected pellets. Although this problem may be solved through DNA identification of the plants consumed (see, e.g., the case of Dorcas gazelle [38]), another limitation was the expensive costs of genetic analyses; in fact, we obtained many more samples (see [21]) that could not be used, due to lack of budget for laboratory work.

Poor success in identifying the species consumed by FSs limited the correct classification of the foraging strategy, and DOs were inconclusive due to the low sample size. The IF method was much more capable of classifying the foraging behaviour of Cuvier's gazelle as a browser than of revealing its diet composition.

Finally, our samples were biased to December–January and March–April, particularly due to the limitations of surveying the rest of the year in such a hostile environment. In any case, this circumstance did not affect the prediction for our main hypothesis (that is, Cuvier's gazelles are browsers in the Sahara) as we sampled during the seasons of maximum rainfall and, thus, during the maximum availability of herbs and grasses. However, this seasonal sampling bias could affect the relationships between diet and environment descriptors, so these results should be assumed to be representative of winter and spring only.

4.2 Feeding Strategy

Following our hypothesis, the results suggest that Cuvier‘s gazelles are mainly browsers in the

Sahara desert, showing a strong preference for trees, as can be deduced from (1) the resource selection patterns observed in the analysis of IF data, and (2) the negative relationship between this plant category and diet diversity in the analysis of FS data, as predicted by the optimal foraging theory [58–61]. Moreover, the tracked gazelles avoided some available grass species, even when these plants were growing after rainfall (the case of *C. schoenanthus*). Cuvier‘s gazelles had previously been considered as an intermediate feeder (i.e., browser-grazer) based on a study carried out in their Mediterranean range, where the diet is totally different from that of the Sahara, with *Stipa tenacissima* grass and the *Artemisia herba-alba* shrub as the predominant food items among the 29 species of consumed plants [27,28]. Therefore, this ungulate is an adaptable ruminant that switches its foraging behaviour according to plant availability, following a typical opportunistic feeding strategy [60,61]. In the Atlantic Sahara, the other *Gazella* pecies present is the smaller Dorcas gazelle, which seems to be a browser-grazer intermediate in this region, basing its diet on acacias and the succulent species *N. perrinii* and *M. cryptanthum* [62]. This strategy is probably favoured by nomadic movements following rain pulses [63], allowing Dorcas gazelles to have a much wider distribution than Cuvier’s gazelles in the Atlantic Sahara, as they also inhabited the vast flat regions south of the study area, where our targeted species is absent [35].

The presence of trees such as acacias and argan trees plays a key role in the survival of Cuvier‘s gazelles in the case of the Sahara desert and, in particular, acacias as the most consumed and selected tree species. In fact, this genus also fulfils an essential role in the diets of Sahelo-Saharan antelopes [20] and other desert gazelles such as Acacia gazelle (*G. acaciae*) and Arabian Desert gazelle (*G. cora*), especially *V. tortilis* [64,65]. Acacias belong to the family Leguminosae, a group with a high nitrogen content and, therefore, probably with higher nutritional quality than other Saharan species. IF showed that acacias were more selected compared to argan, although the latter tree species also plays an important role in the local feeding ecology of Cuvier’s gazelles. However, our IF data were inconclusive due to the small sample size, and did not confirm the consumption of the fruit of this tree by Cuvier‘s gazelles, as has been previously mentioned [35].

A. hierochuntica was the most important alternative species after trees, supporting the opportunistic condition of Cuvier‘s gazelles. The contribution of this annual forb to the diet suggests a key role during drought periods, an aspect discussed below. The consumption of *C. procera*, previously cited for Arabian Desert gazelles [65], is an interesting result as this tree is a highly toxic species, particularly its latex [66]. Gazelles only fed on one or two leaves per visited tree, taking only a few pieces of each leaf (see Figure 2). This behaviour may allow the avoidance of latex secreted by the plant in response to browsing bites. In this respect, there is some risk to the gazelles, but it is probably worth the reward, as *C. procera* has one of the broadest leaves of all Saharan plant species, rich in water content.

We found only weak effects of primary production on observed foraging patterns and diet quality during winter and spring. The rugged habitat of the study area provides sheltering conditions for trees and shrubs at the micro-habitat level by maintaining humidity in ravines and canyons, and reducing evapotranspiration due to the shade provided by the relief, thus helping to mitigate periods of drought [3,67]. This scenario favours the resilience of Cuvier´s gazelles to Saharan conditions, thanks to a relatively constant food supply, which would partly explain the habitat selection patterns observed in this region [10]. The results only allow us to hypothesise that gazelles would probably increase forbs consumption during periods of drought (lower NDVI), as an adaptive response to low food availability. During periods of drought, Saharan woody species adopt a deciduous strategy by removing most, if not all, leaves in extreme situations [68]. This scenario probably forces gazelles to increase their foraging effort, consuming species that should be avoided when primary production is higher, such as *A. hierochuntica* and the toxic *C. procera*.

5. CONCLUSIONS

There are important limitations to the correct description of the Cuvier's gazelle diet in desert environments if only FS approaches are used. Therefore, further research is needed to determine the reasons for this low success of plant tissues identification. In the meantime, in the absence of optimal resources to carry out genetic approaches, we recommend combining all available non-invasive techniques to maximise the dataset in the study of remote areas, especially considering the logistical constrains that make it challenging to study wild ungulates in such regions.

Moreover, we detected strong evidence of foraging strategies that allow Cuvier's gazelles to live at the edge of their optimal habitat conditions. Through our combined approaches, we confirmed the marked plasticity of this species, which adapted to browser behaviour in the stressful conditions of the Sahara desert. In this sense, the presence of acacias probably represents the last resort for its survival there, being a key result for the design of correct conservation strategies for this threatened ungulate. An immediate recommendation applied to the conservation of this key population is to urgently study the impact on the trees of the large number of herds of goat and sheep that invade this region during the rainy season. This emergent problem is related to the improvement of trucks transport thanks to new roads and the construction of a considerable network of water cisterns, resulting in intensive land use that is very different from the traditional nomadic pastoralism of the Atlantic Sahara. Lastly, the observed patterns of feeding ecology of Cuvier's gazelles in desert conditions provide an interesting model for understanding the drought resistance of desert-adapted large herbivore species, an issue that will be crucial in the face of increasing desertification due to climate change.

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SUPPLEMENTARY MATERIAL

Table 1. Link of variables with the first two dimensions of the PCA. For variables descriptions and variables, see text.

	DIMENSION 1		DIMENSION 2	
VARIABLES	correlation	p-value	correlation	p-value
ACACIAS	0,30	2,24E+04	-0,82	5,40E-09
ADF	0,88	8,96E-14	0,40	2,12E+03
ADL	0,75	1,69E-05	-0,05	7,01E+05
ANASTATICA HIEROCHUNTICA	-0,60	6,56E-01	0,57	2,95E+00
ALTITUD	0,31	2,09E+04	-0,03	8,27E+05
ANNUAL PRECIPITATION	0,20	1,42E+05	-0,05	6,95E+05
ANNUAL TEMPERATURE	0,05	6,99E+05	-0,04	7,75E+05
AV.NDVI (PER YEAR)	0,29	2,66E+04	-0,27	4,27E+04
BIWEEKLY.NDVI	0,40	2,06E+03	-0,08	5,55E+05
FNC	-0,55	1,06E+01	-0,65	4,09E-02
HELIANTHEMUM LIPPII	-0,31	1,76E+04	0,20	1,40E+05
NDF	0,82	1,03E-08	0,48	1,55E+02
NITRARIA RETUSA	0,13	3,25E+05	0,29	2,66E+04
OTHERS	0,76	9,29E-06	-0,36	6,05E+03
PENNISETUM DIVISUM	0,18	1,75E+05		
SEASON.NDVI	0,29	3,14E+04	-0,16	2,22E+05
SHANNON.IND	-0,30	2,24E+04	0,58	2,77E+00

CAPÍTULO 4.

Diel activity of Cuvier's gazelle (*Gazella cuvieri*) in the desert: living side by side with African golden wolf (*Canis anthus*), Barbary sheep (*Ammotragus lervia*) and nomadic herders

Herrera-Sánchez, F. J., Abáigar, T., Rodríguez-Siles, J., Sáez, J. M., Lahlafi, T., Arredondo, A., Valenzuela, G., Cancio, I., Pérez, J., Sánchez-Cerdá, M., Martín-Sánchez, J.M., Díaz-Portero, M.A., Castillo, S., Qninba, A., Virgós, E. & Gil-Sánchez J. M. (2023). Diel activity of Cuvier's gazelle (*Gazella cuvieri*) in the desert: living side by side with African golden wolf (*Canis anthus*), Barbary sheep (*Ammotragus lervia*) and nomadic herders. En preparation / *In process*

Diel activity of Cuvier's gazelle (*Gazella cuvieri*) in the desert: living side by side with African golden wolf (*Canis anthus*), Barbary sheep (*Ammotragus lervia*) and nomadic herders

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Abstract

Under stressful environmental conditions, activity patterns can provide valuable information on species adaptation to the habitat from an ecological point of view, but also on human-induced changes and community structure. We deployed a camera trap survey in a remote region of the Sahara Desert to investigate the factors that determine the activity patterns of Cuvier's gazelle. Abiotic (seasons, moon phase and rainfall) and biotic factors (activity of the African golden wolf, Barbary sheep, nomadic herders and sex) were studied. The influence of each factor was assessed using the activity overlap coefficient (Δ) and by the non-parametric circular Mardia-Watson-Wheeler test. The selection of a period in a diel cycle was analysed using chi-square contingency tables and the "Wi" parameter of the resource selection coefficients. Cuvier's gazelle showed a bimodal diurnal pattern with peaks of activity at twilight (better delimited in females) and predominant activity in the early hours of the day and at dusk. The most significant effects were induced by seasonality (seasons and wet/dry periods), and the phase of the moon. In contrast, anthropogenic or intra-gremial factors did not produce significant differences, suggesting no clear temporal niche differentiation for both species. In addition, there was synchrony between the three species studied with a shared bimodal and crepuscular pattern. However, significant discrepancies in period selections were observed between Cuvier's gazelles, which clearly avoided nocturnal hours, and African golden wolves, which avoided diurnal hours. Our results contribute to understanding the adaptations of this endangered gazelle to a hyper-arid environment and its relationships with keystone species and humans.

Keywords. *Gazella cuvieri*, *Canis anthus*, *Ammotragus lervia*, human activity, diel activity pattern, Morocco, Sahara Desert, temporal niche.

1. INTRODUCTION

Deserts are resource-poor environments where there are huge variations in environmental quality over space and time (Ward, 2008). Consequently, desert-dwelling species have developed adaptations to the harsh conditions of the environment where competition can be extremely important to face of scarce water and resources availability (Whitford & Duval, 2019). Under these stressful conditions, intraspecific relationships become more complex (Hart & Marshall, 2013) and competitive interactions gradually shape community structure, even leading to local extinctions in phylogenetically related species (Hardin, 1960; Schoener, 1974; Webb *et al.*, 2002; Violle *et al.*, 2011). Furthermore, alterations in the dynamics of predator-prey through the extirpation of apex predators and human-ungulate interactions are creating a clear impact on communities and reshaping the ecosystem structures (Estes *et al.*, 2011; Pascual-Rico *et al.*, 2021; Gil-Sánchez & Sánchez-Cerdá, 2023).

Of all desert's ecoregions, the Sahara Desert is home to the greatest diversity of antelope species, however, the large mammals have suffered a massive collapse in the last century (Durant *et al.*, 2014; Newby *et al.*, 2016). It is more than necessary today, given the evident loss of habitats and climate change, to conduct studies on the conservation status of the Saharan megafauna and to increase knowledge of their ecological relationships (Durant *et al.*, 2014; Cooke *et al.*, 2016). Recently, Cuvier's gazelle (*Gazella cuvieri*) has been presented as a paradigm for the study of desert ecosystems, alternatively, it could represent an umbrella species that can help to implement conservation measures and to understand the interspecific relationships in these ecosystems (Gil-Sánchez *et al.*, 2017; Herrera-Sánchez *et al.*, 2020, 2023).

Cuvier's gazelle is a medium-size ungulate endemic to northwest Africa, listed as Vulnerable in the IUCN's Red List of Threatened Species, principally due to its small population (IUCN, 2018). This ungulate belongs to the group of Sahelo-Saharan antelopes, which are well adapted to life in extreme conditions (Beudels-Jamar *et al.*, 2006; Duran *et al.*, 2014). Cuvier's gazelle inhabits a region in the north-western edge of the Sahara Desert, called the Atlantic Sahara, where a key population remains in terms of numbers and genetic diversity (Gil-Sánchez *et al.*, 2017; Silva *et al.*, 2015, 2017). This region is also the distribution area of the Barbary sheep (*Ammotragus lervia*) and the Dorcas gazelle (*Gazelle dorcas*), and hosted the last population of Mhorr gazelle (*Nanger dama mhorr*) disappeared in 1968 (Cano, 1991). In addition, there is still an important carnivore community including African golden wolf (*Canis anthus*), despite the eradication of the large apex predators such as Saharan cheetahs (*Acinonyx jubatus hecki*), with the last sightings of in the 1990s (Aulagnier *et al.*, 2017). In this context, it has been observed that Cuvier's gazelles are able to adapt to hostile environments where food resources are limited in quantity and quality, while competing with nomadic herders for this resource (Gil-Sánchez *et al.*, 2017; Herrera-Sánchez *et al.*, 2020, 2023).

How Cuvier's gazelles coexist with sympatric species and the impact of human activities on them could be reflected in the variation of activity patterns and their partitioning along the time axis of their niche, an essential dimension of animal behaviour (Schoener *et al.,* 1974; Frey *et al.,* 2017). The niche concept introduced by Hutchinson (1957) defines it as a multidimensional space delineated by the range of resources in which a species survives and reproduces. Niche differentiation occurs along different dimensions, one of them -with a crucial importance- is time (Kronfeld-Schor & Daya, 2003; Dunbar *et al.,* 2009). The study of the temporal niche has attracted attention in a multitude of research and is a highlighted topic (e.g. Delibes & Beltran, 1985; du Toit *et al.,* 2005; Roll *et al.,* 2006; Gerber *et al.,* 2012; Wang *et al.,* 2015; Karssene *et al.,* 2019). The diel temporal niche of a species, usually defined as the time of day when its individuals show locomotor activity, can, in turn, be defined as nocturnal, diurnal, crepuscular or cathemeral species (Hut *et al.,* 2012). In this regard, the species-specific activity pattern is ultimately the result of intra- and interspecies interactions, evolutionary physiological adaptations, accessibility to resources and predation, but also environmental conditions (Monterroso *et al.,* 2013; Roll *et al.,* 2006; Abáigar *et al.,* 2018; Seri *et al.,* 2018). Among the most common abiotic and biotic factors that may influence activity patterns in ungulates are the following: temperature (Davimes *et al.,* 2017; Abáigar *et al.,* 2018; Blank, 2023), seasonal changes/availability of resources (Moncorps *et al.,* 1997; Seri *et al.,* 2018), photoperiod (Davimes *et al.,* 2017), moon phase (Pratas-Santiago *et al.,* 2017), livestock movements/human activity (Schaller, 1998; Xia *et al.,* 2011; Wang *et al.,* 2015), sex (Ruckstuhl & Neuhaus, 2002; Xia *et al.,* 2011) and prey avoidance (Brown *et al.,* 1999; Kotler *et al.,* 2002) .

Under the optimal foraging theory, survival and reproduction are ultimately about coping with the problem of how to obtain energy and use time (Bunnell & Harestad, 1986). Hence, animals must balance feeding advantages, predation risks and thermal constraints (Owen-Smith & Goodall, 2014). A key adaptation of arid-adapted ungulates is the heterothermy that it is associated with desert dwelling ungulates as Arabian oryx (*Oryx leucoryx*) and Arabian sand gazelles (*Gazella marica*) (Ostrowski & Williams, 2006; Hetem *et al.*, 2012a). Commonly these species develop a bimodal or crepuscular pattern (Blank, 2023; Seri *et al.,* 2018), that can change to a more nocturnal rhythm during the hot dry season (Hetem *et al.,* 2012a; Davimes *et al.,* 2017; Meliane *et al.,* 2022; Abáigar *et al.,* 2018). Accordingly, daytime inactivity and avoidance of excess heat during the hottest months were also related to the selection of a cooler microclimate in the form of shade-seeking (Hetem *et al.,* 2012b). Furthermore, bimodal activity peak has been linked to predator avoidance but also to response to daytime heat load and solar radiation avoidance in Arabian oryx (Davimes *et al.,* 2017).

In this study, we use motion detecting digital cameras to study the factors that determine the diel activity patterns of Cuvier's gazelle in a hyper-arid environment (Frey *et al.,* 2017; Gil-Sánchez *et al.,* 2023; O'Connell *et al.,* 2011; Ridout & Linkie, 2009). As biotic factors, we tested the effect of the sex, the presence of Barbary sheep as a potential intraguild competitor, the expected predatory effect of the African golden wolf and the presence of nomadic herders. Moon phases, seasons and wet/dry periods were studied as abiotic factors.

Due to the stress-full abiotic conditions of hyper-arid environments, the niche time activity could be affected by both biotic and abiotic factors. Therefore, based on previous studies, we formulated the following six hypotheses (H). H1) Among difference strategies (diurnal, crepuscular, nocturnal and cathemeral behaviours), Cuvier's gazelle will choose a crepuscular bimodal pattern, avoiding the middle of the day, as mechanism of adaptation to arid environments switching between nocturnal and/or more diurnal patterns depending on environmental conditions (Hetem *et al.,* 2012b; Davimes *et al.,* 2016, 2017). H2) Similar to other ungulates that inhabit deserts, seasonal factors will impact on diel activity patterns. During the hottest month, we expect a decrease of daytime activity and the avoidance of excess heat, which is related with the selection of a cooler microclimate in the form of shade-seeking behaviour (Davimes *et al.,* 2017; Abáigar *et al.,* 2018, Seri *et al.,* 2018). H3) The presence of nomadic herders will determine the diel activity of the target species, resulting in avoidance behaviour caused by human presence and/or to prevent the risk of poaching (Manor & Saltz, 2003). H4) Predator avoidance will have limited impact on diel activity in the study area since the top predator resulted after the extinction of cheetah -African golden wolf- is not adapted to chase fast-moving ungulates as gazelles, which requires higher energy expenditure according to optimal foraging theory (Stephens & Krebs, 1986). H5) Moonlight will drive the patterns, with the nocturnal activity being weaker at new moon in order to reduce predation risk, as innate behaviour resulted of the former co-existence with cheetahs (Kramer & Birney, 2001; Pratas-Santiago *et al.,* 2017). Finally, H6) due to the body dimorphism of the species, females may be less efficient than males at digesting forage, resulting in longer foraging times for females compared to males (activity budget hypothesis: Main *et al.,* 1996; Ruckstuhl *et al.,* 2002). Consequently, males would have longer periods of inactivity than females (Ruckstuhl, 1998). Furthermore, as females are more vulnerable to predation due to the need to protect their offspring and/or their smaller size than males, so they would be less nocturnal and/or diurnal than males (predation risk hypothesis: Jakimchuk *et al.,* 1987; Ruckstuhl *et al.,* 2002).

2. MATERIAL AND METHODS

2.1. Study area

The survey was conducted in the extreme north-western part of the Sahara Desert between 28°20′ – 27°35′ N and 11°15′ – 9°50′ W (Fig. 1). Here, we find a vast region between the lower Draa River and the upper basin of the Sequiat Al Hamra, within the Atlantic Sahara of Morocco. The area is characterised by prolonged drought and erratic rainfall, and is considered part of the

North Saharan Xeric steppe and woodland ecoregion of the northern Sahara (Dinerstein *et al.*, 2017). Four survey sites (Aydar Mountains, djebel Ouarkziz, oued Taclet, and M´sied area) were selected due to the previously confimed presence of Cuvier's gazelle (Gil-Sánchez *et al.*, 2017). All sites contain a typical Saharan landscape with a subtropical desert at low-latitude (Köppen–Geiger classification, Kottek *et al.*, 2006) and hyper-arid climate (Trabucco & Zomer, 2009). The altitude range varies from the highest point in djebel Ouarkziz to the lowest point in the lower Draa River (743-125 m a.s.l, respectively). The "Ouarkziz", "Aydar" and "M'sied" sampling sites are mainly mountainous areas with numerous wadis or oueds and some scattered dune areas in the case of M'sied. The "Taclet" sampling site is part of a hamada step, with steep ravines, hills, and oueds. The whole area is a transition point between the Saharan and Macaronesian ecoregions (Le Houérou, 1997; Casañas, 1999). The dominat tree vegetation is conformed by acacias (*Vachellia tortilis* subsp. *raddiana* and *V. flava*) along with some scattered specimens of *Balanites aegyptiaca*, *Maerua crassifolia*, the argan tree (*Argania spinosa*) and *Calotropis procera*. In the area, *Periploca laevigata*, *Launaea arborescens*, *Searsia tripartita*, *Nitraria retusa*, *Saharanthus ifniensis*, *Salsola tetragona* and *Lycium shawii* stand out as shrub vegetation, and *Panicum turgidum, Andropogon laniger, Stipagrostis pungens*, and *Cymbopogon schoenanthus* as the main grasses.

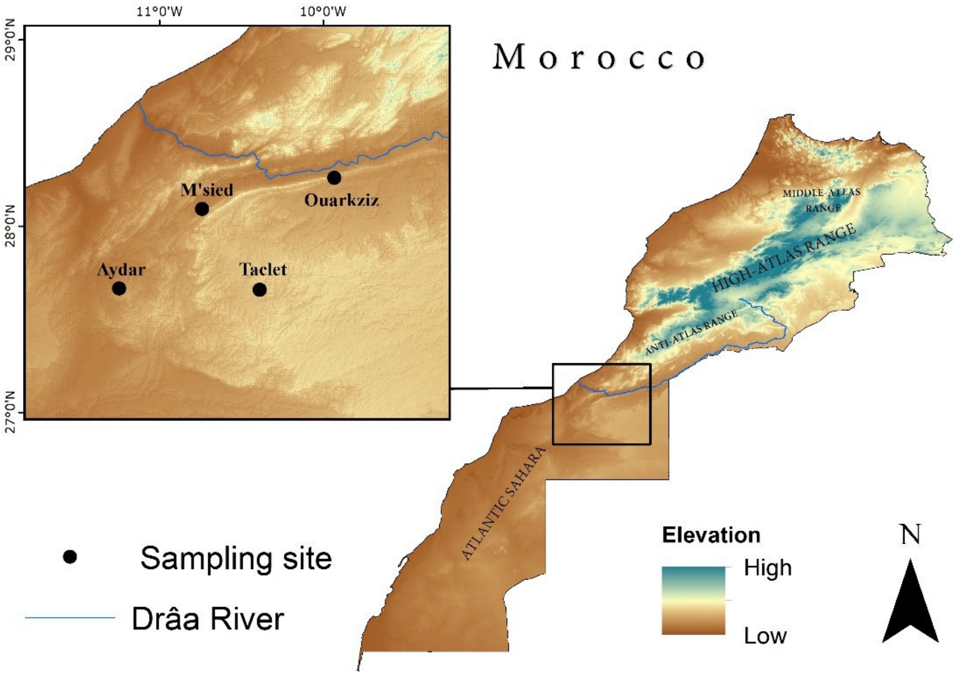


Figure 1. Location of the study area and sampling sites for the camera traps. The map also shows the relief using a raster digital elevation model (DEM).

The information obtained in previous surveys on the target species (see Gil-Sánchez *et al.*, 2017; Herrera-Sánchez *et al.*, 2020) allowed the selection of the sampling sites, following a stratified sampling strategy to cover all the habitat variability that defines the study area. Due to the remoteness and difficulty of the terrain, and in order to achieve the objectives, expeditions of 1 to 2 weeks were planned using 4 × 4 vehicles for setting up photo-trapping stations and checking of camera traps.

2.2. Camera trap survey

We placed 10 sampling stations of one camera trap in four survey sites between January to April 2017 and September 2017 to September 2018 (Fig. 1 and Table 1). Digital red glow infrared cameras (Busnell, Moultrie, Covert and Scoutguard brands), remotely triggered by an infrared sensor, were placed on a regular grid of 1x1 km previously designed in ArcGIS 10.4. Once the camera point was located, the best sites were sought on game trails and ravines to place the north-facing cameras. Camera traps were installed on large stones, acacia logs or wooden stakes at a height of 25-30 cm above the ground. Cameras were programmed to take 1–3 pictures per event, with 0–5 s of PIR interval. In a preliminary camera trap training in the area, we positively tested Iberian lynx urine as an optimal attractant for medium to large mammals. Therefore, each station was baited with Iberian lynx urine on a menstrual tampon at the start and at each camera check to improve capture rates (see Gil-Sánchez *et al.*, 2023). Every 4 months we visited all cameras to verify the condition of the batteries and replace the memory cards. Despite the high number of stolen cameras (23 cameras during the entire study), they were replaced at each control, so that in total 35-30 camera traps were simultaneously active during the study (mean distance: 919 metres ± 70.80 SE). M'sied was the only site where camera-trapping took place for nine months (from January 2018 to September 2018), as it was initially deployed in another location that proved to be unsafe for the integrity of the cameras.

2.3. Data processing

The data extracted from the memory cards was initially processed with the ZSL Camara Trap software (Amin *et al.*, 2016). Previously, the metadata (file name and date) of the images were automatically extracted from the original "jpg" file using PIE software version 7.00.1. Consecutive images of the same species within 30 min. interval were considered as the same event to ensure that events were independent and to reduce pseudoreplications (O'Connell *et al.*, 2011; Brook *et al.*, 2012; Monterroso *et al.*, 2013; Wang *et al.*, 2015). Only events produced by domestic livestock (sheep and goats) and shepherds, call *nomadic herder factor*, within a period of 1 hour were taken into account, once it was verified that the captures were not repeated and after this interval and could be considered as independent events. The relative abundance index (RAI) was estimated as the number of independent captures by the camera traps per 1000 camera days of effort (O'Connell *et al.*, 2011).

Cuvier's gazelles were assigned to 3 age classes (calf < 6 months, juvenile 6-12 months, adult > 12 months) based on morphological characteristics and horn size. To distinguish age and sex classes, the photo captures of the specie were compared with a reference catalogue obtained from specimens of known age at the Experimental Field Station "La Hoya" (EEZA-CSIC, Almería, Spain), where captive breeding programmes are carried out.

Inter-annual rainfall is very irregular in the study area (Bergier *et al.*, 2017; Naia & Brito, 2021) but two periods could be distinguished, a "*wet* period" after the autumn rains in 2016 and a "*dry* period" that occurred during the consecutive year, in which hardly any rainfall was recorded until the end of the survey (SD Fig. 1). The months of January to March 2017 were determined as the "*wet* period" and were compared to the same months of 2018 considered as a dry event, and called "*dry* period", for the analysis. On the other hand, the driest and hottest seasons are spring and summer, starting with April, when the average accumulation of precipitations per month is even close to zero; and the wet season, with milder and night-time lows temperatures, corresponds to autumn and winter seasons (Bergier *et al.*, 2017). Under this approach, we have grouped the detections into two seasons, "*hot-dry*" (spring-summer) and "*mild-wet* " (autumn-winter) seasons, and thus reduced the bias of low size effects (Lashley *et al.*, 2018). Finally, to determine and ensure the absence of nomadic herders at each study site, only the correlative months in which no events occurred were taken into account. Instead, the presence of domestic livestock was only counted in the months in which photo-captures were recorded. Seasonality and moon phase analyses have not been carried out for Barbary sheep due to the low number of detections (<25).

2.4. Statistical analysis

Based on the camera detection, we considered each event as a random sampled derived from a continuous temporal distribution. Therefore, the diel activity patterns were estimated from kernel density estimates (Ridout & Linkie, 2009) with the R package *overlap* (Meredith & Ridout, 2021). Pairwise comparisons between factors and species were conducted by estimating the overlap coefficient Δ_1 in case of the number of events was <50 detections or Δ_4 with ≥50 detections. This coefficient was determined from bootstrap estimation of 10.000 samples (Centore *et al.*, 2018; Meredith & Ridout, 2021). The coefficients Δ can vary from 0 when there is no overlap to 1 when the overlap is considered to be total.

The records for diel activity represent a 24-hour circular distribution, thus data according to groups (location, season, pool species) and pairs (sex, season, species, presence-absence of Barbary sheep and nomadic herders and moon phase) were compared by circular analysis through the R package *circular* (Lund *et al.*, 2022). For this purpose, the non-parametric Mardia-Watson-Wheeler test (MWW) was used to detect differences between samples in mean or variance (Batschelet, 1981; Frey *et al.*, 2017). We used an alpha level of 0.05 to determine statistical significance (Lund *et al.*, 2022). Frequency chi-square contingency tables were used to determine temporal groups for three diel categories: "day", "crepuscular" and "night" (Bu *et al.*, 2016; de Satgé *et al.*, 2017). To support and confirm chi-squared tests we calculate "*Wi*" parameter of resource selection ratios (Manly *et al.*, 2003) through Wide I, and Wide II functions in the case of sex (SM *vs* SF). The Manly selectivity measure (*Wi*: selection ratio = used/available) test the preference / avoidance for each period, and it was adjusted using the Bonferroni correction with a significance level of 0.016. Values above 1 indicate preference and values below 1 indicate avoidance. This analysis was carried out using the R package *adehabitatHS* (Calenge, 2017). The latitude and longitude corresponding to each survey site was calculated by the R package *suncalc* (Thieurmel & Elmarhraoui, 2022). To associate the season and the moon phase to each event, we use the R package *lunar* (Lazaridis, 2022). All statistical analyses were performed with R-software version 4.2.2 (R Core Team, 2022).

3. RESULTS

3.1 Camera-trapping

A total of 11333 trap day (24 h periods) and 494 independent detections of the three target species were recorded at the four survey sites (Table 1). Cuvier's gazelle, African golden wolf, and nomadic herders were present at all sites surveyed. In contrast, only in Ouarkziz was detected the presence of Barbary sheep.

Table 1. Effort and events recorded at each site surveyed in the study area for species and nomadic herders. The relative abundance index (RAI) estimated for 1000 camera traps day is shown in bold italics.

				Events (*RAI*)			
Site	Nº of Stations	Date of full survey	Full survey effort (trap days)	Cuvier´s gazelle	Barbary sheep	African golden wolf	Nomadic herders
Aydar	10	Jan. 2017 - April 2017 Sept. 2017 - Sept. 2018	3620	71 ***(19.6)***	0	69 ***(19.1)***	22 ***(6.1)***
Ouarkziz	10	Jan. 2017 - April 2017 Sept. 2017 - Sept. 2018	4283	40 ***(9.3)***	42 ***(9.81)***	144 ***(33.6)***	22 ***(5.1)***
Taclet	10	Jan. 2017 - April 2017 Sept. 2017 - Sept. 2018	1971	41 ***(20.8)***	0	27 ***(13.7)***	21 ***(10.7)***
M'sied	10	Jan 2018 - Sept. 2018	1459	41 ***(28.1)***	0	19 ***(13)***	8 ***(5.5)***

Significant differences in RAI (Table 1) were found between surveyed sites for Cuvier´s gazelle ($\chi^2 = 9.19$, $df = 3$, $P < 0.05$) and African golden wolf ($\chi^2 = 13.83$, $df = 3$, $P < 0.01$) but not in nomadic herders ($\chi^2 = 2.9$, $df = 3$, $P = 0.407$).

3. 2 Diel Activity Patterns

The three focal species displayed a bimodal crepuscular pattern with mean coefficients of overlap above 0.80 (Fig. 2, I & II, Table 2). Cuvier's gazelle showed a diurnal activity with a bimodal pattern in the twilight hours (mainly at dusk) and more activity in the early hours of the day (Fig. 2, IIa), while avoiding the night hours and decreasing its activity in the central hours of the day (*Wi*: crepuscular = 1.865, night= 0.46, $P < 0.001$). A similar crepuscular bimodal pattern but with weaker activity in central hours was observed in Barbary sheep (Fig. 2, IIc). Instead, African golden wolf exhibited nocturnal activity with a marked crepuscular pattern, where peaks were observed both at dawn and dusk, and low activity during the central hours of the day (Fig. 2, IIb). Significance differences in the use of temporal category of periods were found for Barbary sheep ($P < 0.05$), but no clear preference could be determined by applying the Bonferroni correction (supp. data Table 2). As well, similarities were found in African golden wolf (Fig. 2, IIb) with a predominance of activity at twilight, but in contrast to both ungulates, it trended to avoid daylight hours (*Wi*: crepuscular = 1.714, day = 0.743, $P < 0.01$). The diel cycle was statistically different between African golden wolf and Cuvier's gazelle but not for the rest of paring species (Table 2).

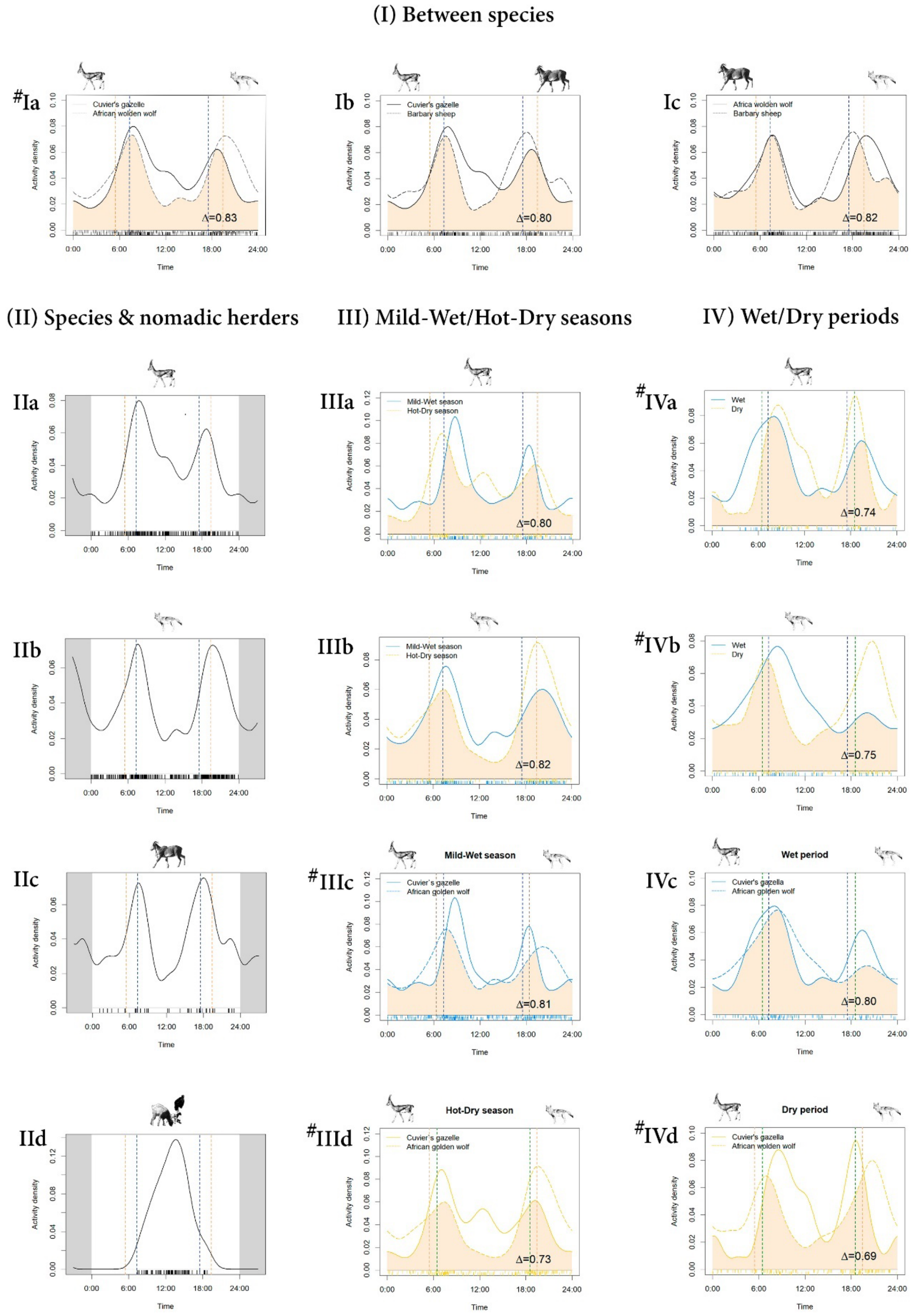


Figure 2. Activity patterns of the three target species and nomadic herders in the Atlantic Sahara. The y-axis shows the kernel density estimates between species, mild-wet & hot-dry seasons, and wet/dry periods. The coloured shaded area shows the overlap measured by the mean overlap coefficient Δ (95% IC), The "#" symbol shows those activity patterns that were significantly different in the Mardia-Watson-Wheeler test (95%). Sunrise and sunset times are displayed in vertical dashed colour for equinoxes and solstices: autumn (brown), winter (blue), spring (green), and summer (orange).

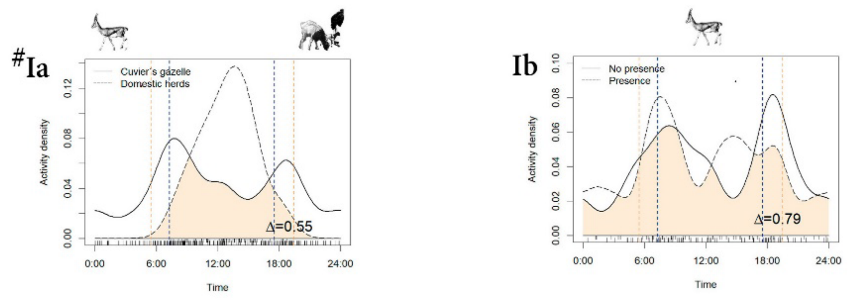
3.3 Seasonal and wet/dry period effect

Cuvier's gazelle displayed a higher concentration of activity towards midday and lower nocturnal activity in both the *hot-dry* season and *dry* period, compared to the *mild-wet* season and *wet* period (Fig. 2, IIIa & IVa). Furthermore, the activity preference in all seasons and periods was markedly crepuscular (supp. data Table 2), but additionally diurnal in the *hot-dry* season (*Wi*: day = 1.294, crepuscular = 2, night = 0.306, $P< 0.001$). During the *dry* period, the activity pattern was concentrated in the early hours of the day and markedly twilight at dusk (Fig. 2, IVa). In contrast, both the *mild-wet* season and *wet* period showed less activity in the middle part of the day. Significant differences were found in the pairwise analysis between Cuvier's gazelle and African golden wolf in the *hot-dry*/*mild-wet* seasons, and *dry* period (Fig. 1 IIIc-d, IVd; Table 2). African golden wolf tended to avoid daylight hours in both seasons and in the *dry* period (Fig. 1 IIIb & IVb), but in *wet* period the species exhibited a cathemeral pattern and no significant differences were found between temporary categories. Additionally, African golden wolf was more active during twilight in both the *hot-dry* season and *dry* period (*hot-dry* season *Wi*: day =0.707, crepuscular=1.895. $P < 0.05$; *dry* period *Wi:* day =0.565, crepuscular=1.706, $P < 0.001$), and during the *dry* period its main nocturnal activity occurred in the early evening hours (Fig. 2 IVb). Consequently, significant differences were found between the two periods for African golden wolf (Table 2).

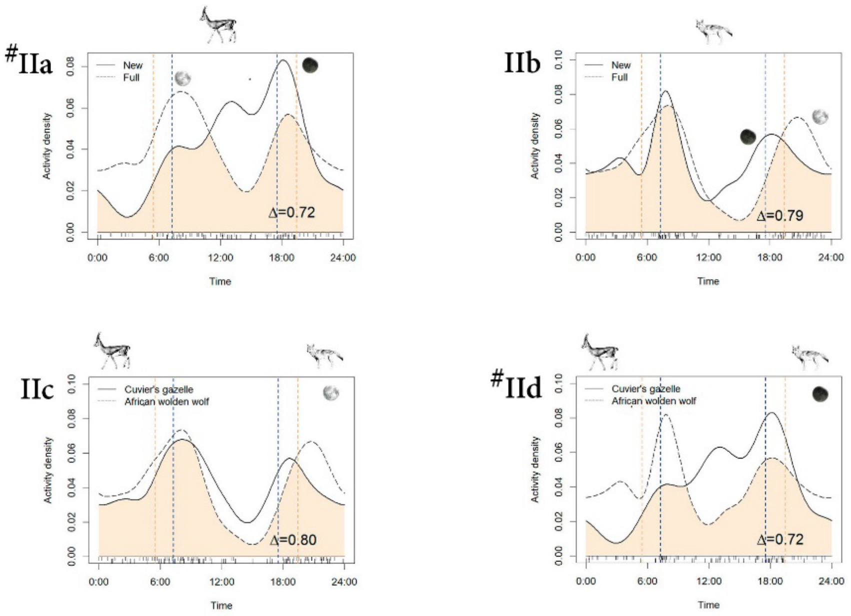
3.4 Human factor

The activity pattern of nomadic herders was concentrated in the central hours of the day (Fig. 2, IId). The mean overlap coefficient with Cuvier's gazelle was the lowest recorded in the analyses (Δ=0.55, Fig. 3, Ia). No significant differences in activity patterns of the gazelles were observed between the presence and absence of nomadic herders, but Cuvier's gazelle, apparently, showed a shift in both peaks of activity. When nomadic herders were not present, diurnal activity was prolonged during the first hours of the day and the second peak of activity was more concentrated at dusk, whereas when nomadic herders were present, activity was concentrated and short during the first hours of dawn, rising again in the middle hours of the day until falling off at dusk (Fig. 3, Ib).

(I) Nomadic herders



(II) Moon phase



(III) Sex

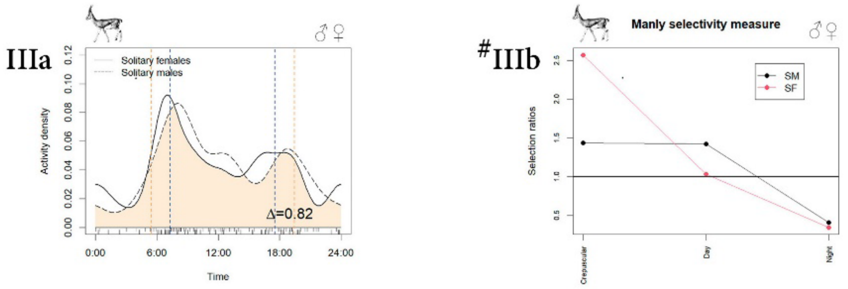


Figure 3. Diel activity patterns of Cuvier's gazelle, nomadic herders, and African golden wolf in the Atlantic Sahara. The y-axis shows the kernel density estimates between three factors: presence of nomadic herders, moon phases, and sex. The coloured shaded area shows the overlap, measured by the mean overlap coefficient Δ (95% IC). The "#" symbol shows those activity patterns that are significantly different in the Mardia-Watson-Wheeler test. Sunrise and sunset times are displayed in vertical dashed colour for the winter (blue) and summer (orange) solstices. SM: Solitary females & SM: Solitary males of Cuvier's gazelle.

Table 2. Coefficient of overlap (Δ1 and Δ4) and mean Δ from 10000 bootstrap samples. Mardia–Watson–Wheeler test (MWW) between the activity patterns of factors pairing species. Bolded rows indicate statistically significant differences. GC: Cuvier's gazelle, BS: Barbary sheep, AW: African golden wolf, GC (sf): solitary females, GC (sm): solitary males. Significant results are shown in bold type.

Factor pairing	Δ	Bootstrap Δ (mean)	Δ 95 % ci	Method	Nº 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, df = 2
GC/AW	**0.84**	**0.83**	**0.77 - 0.91**	**Δ4**	**193**	**259**	**P < 0.001**	**W = 18.246, df = 2**
AW/BS	0.88	0.82	0.78 - 0.98	Δ1	259	42	P = 0.6061	W = 1.0016, df = 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, df = 2
AW (mild-wet/hot-dry)	0.84	0.82	0.75-0,93	Δ4	164	95	P = 0.05549	W = 5.7829, df = 2
GC /AW (mild-wet)	**0.81**	**0.81**	**0.72-0.90**	**Δ4**	**91**	**170**	**P < 0.05**	**W = 6.5225, df = 2**
GC/AW (hot-dry)	**0.72**	**0.73**	**0.60-0.83**	**Δ4**	**102**	**96**	**P < 0.001**	**W = 16.539, df = 2**
Wet/Dry periods								
GC wet/dry	**0.77**	**0.74**	**0.64-0.90**	**Δ1**	**41**	**45**	**P < 0.05**	**W = 6.1961, df = 2**
AW wet/dry	**0.78**	**0.75**	**0.66-0.89**	**Δ4**	**61**	**102**	**P < 0.05**	**W = 7.8513, df = 2**
GCwet/AWwet	0.87	0.80	0.75-0.99	Δ1	41	61	P = 0.8432	W = 0.34103, df = 2
GCdry/AWdry	**0.68**	**0.69**	**0.55-0.80**	**Δ1**	**45**	**105**	**P < 0.001**	**W = 15.629, df = 2**
Nomadic herders								
Presence/Absence	0.81	0.79	0.69-0.93	Δ4	71	54	P = 0.7686	W = 0.52647, df = 2
GC/nomadic herders	**0.51**	**0.55**	**0.41-0.61**	**Δ4**	**193**	**72**	**P < 0.001**	**W = 65.98, df = 2**
Moon								
GC new/full	**0.73**	**0.72**	**0.59 - 0.88**	**Δ1**	**38**	**51**	**P < 0.05**	**W = 8.6312, df = 2**
AW new/AW full	0.84	0.79	0.73 - 0.95	Δ4	60	60	P = 0.5442	W = 1.2168, df = 2
GC new/AW new	**0.72**	**0.72**	**0.58 - 0.86**	**Δ1**	**38**	**60**	**P < 0.05**	**W = 7.6344, df = 2**
GC full/AW full	0.86	0.80	0.75 - 0.98	Δ4	51	60	P = 0.255	W = 2.7331, df = 2
Sex								
GC (sf)/GC (sm)	0.87	0.82	0.76-0.97	Δ1	49	71	P= 0.7139	W = 0.67403, df = 2

3.5 Moon phases

The moon phase had a powerful effect on Cuvier's gazelle by modifying its diel activity pattern in the new moon, with an increase in diurnal activity, a greater preference for twilight hours at dusk, and an increasing aversion to night hours (Fig. 3, IIa; *Wi*: crepuscular = 2.526, night = 0.253, $P < 0.001$). On the other hand, there were slight differences between diel periods during the full moon, with less night-time avoidance (*Wi:* night = 0.706, $P < 0.05$). The diel activity of Cuvier´s gazelle was significantly different between full and new phases, but not for African golden wolf (Fig. 3, IIb). Consequently, there were significant differences in pairing patterns with new moon between Cuvier's gazelle and African golden wolf, but not at full moon (Fig. 3. IIc-d, Table 2).

3.6 Sex factor

In terms of sex differences, no significant differences were found in activity patterns between solitary males and solitary females, but females showed a stronger preference for twilight hours, and males were more diurnal (Fig. 3, Vb; *Wides II*: $P > 0.05$).

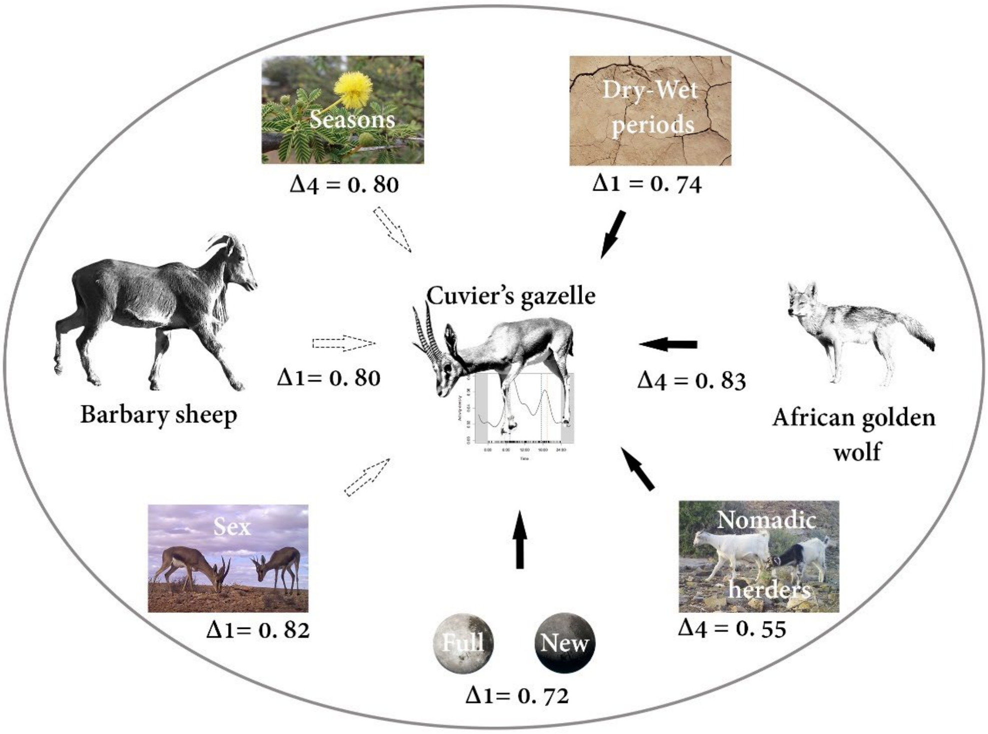


Figure 4. Conceptual diagram showing the analysed factors on the diel activity pattern of Cuvier's gazelle. The black arrows represent the factors for which asynchrony in activity patterns was found to be significant through the Mardia-Watson-Wheeler test, and the dashed arrows represent non-significant differences. The mean coefficient of overlap of Δ1 and Δ4 for the paired factors is shown. Diel activity pairing factors: mild-wet *vs* dry-hot seasons, wet *vs* dry periods, Cuvier's gazelle *vs* African golden wolf, presence *vs* absence of nomadic herders, full *vs* new moon, solitary female's *vs* solitary males, Cuvier's gazelle *vs* Barbary sheep.

4. DISCUSSION

In this work, for the first time, the activity pattern of Cuvier's gazelle was explored. Long-term studies of rare and elusive species such as Cuvier's gazelle in the Atlantic Sahara was challenging due to the remoteness of the terrain and the high temperatures that can be reached in the summer season. Despite the high number of stolen cameras, camera-trapping effort exceeded 1400 trap day in the four sites surveyed, a threshold estimated to rule out bias in the detection of target species due to the placement of camera stations (Cusack *et al.*, 2015). The camera-trapping design was successful for Cuvier's gazelle and African golden wolf at all four sites surveyed. On the other hand, Barbary sheep was only detected at Ouarkziz site. The small number of detections of this species prevented the study of the effect of the different factors on its activity pattern. However, we provide for the first-time data on diel activity of Barbary sheep in the wild and an interesting line of research for future studies.

Table 3. Summary of predictions from the six hypotheses that could modulate the diel activity pattern of Cuvier's gazelle in the Atlantic Sahara.

Hypothesis	Key predictions	References	Prediction support
H1	Cuvier's gazelle will choose a bimodal pattern, avoiding midday, and switching between nocturnal and/or more diurnal patterns depending on environmental condition	Hetem *et al.* (2012b); Davimes *et al.* (2016, 2017)	yes
H2	Seasonal factors will impact diel activity reducing daytime activity and avoidance of excess heat during the hottest months	Davimes *et al.*, (2017); Abaigar *et al.* (2018), Seri *et al.* (2018)	no
H3	The presence of nomadic herders will affect diel activity	Manor & Saltz, 2003	no
H4	Predator avoidance will have limited impact on diel activity	Stephens & Krebs (1986)	yes
H5	Nocturnal activity will be weaker at new moon	Kramer & Birney (2001); Pratas-Santiago *et al.* (2017)	yes
H6	Females and males will develop a different activity pattern	Jakimchuk *et al.* (1987); Main *et al.* (1996); Ruckstuhl (1998); Ruckstuhl *et al.* (2002)	yes

4.1 Diel activity patterns

We found high values of overlap coefficient and similarities in activity patterns, but significant differences were observed between the three species. These differences lay mainly in the use of diel periods. Cuvier's gazelle showed diurnal behaviour with peaks of activity in the twilight hours (more pronounced in females) especially at dusk and in the morning. This supports our "hypothesis 1" of a bimodal activity pattern in this environment, and shares parallels with the cases reported of desert-welling species, for examples: Dorcas gazelle (Abáigar *et al.,* 2018), addax (Seri *et al.,* 2018), and Arabian oryx (Davimes *et al.,* 2016). Furthermore, Cuvier's gazelles were more active in the morning than in the afternoon, similar to what was observed in goitered gazelles in arid environment (Blank, 2023) and addax antelope (Seri *et al.,* 2018). Barbary sheep also showed a crepuscular bimodal pattern but both peaks of activity were symmetrical with increased activity delayed to the afternoon. Compared to the Cuvier´s gazelle, Barbary sheep were somewhat more nocturnal, and showed a more pronounced diurnal central period in which they appear to rest.

This bimodal activity pattern may have two advantages: 1) to take advantage of the morning dew (Whitford *et al.,* 2019; Gutterman, 2002) and 2) to take advantage of the cooler period of the day in the early morning hours, and the favourable period of temperature with less insolation in the afternoon, when the highest temperatures drop significantly before dusk (Blank, 2023). African golden wolf showed nocturnal activity but with a markedly crepuscular pattern in which peaks were observed at both dawn and dusk. A similar pattern was obtained in arid environment by Meliane *et al.,* 2022, but some differences were found by Gil-Sánchez *et al.* (2021) in southern Middle Atlas of Morocco, where African golden wolf' main activity was in the early morning hours, and by Karssene *et al.* (2019) in southern of Tunisia, who observed a continuous activity throughout the day in all seasons. These differences are probably due to the opportunistic behavior of the species, and in consequence, due to differences in environmental conditions and availability of resources between areas.

4.2 Seasonality

Contrary to what we expected in hypothesis 2 of a clear daytime inactivity and avoidance of excess heat during the hottest months, the *hot-dry* seasons resulted in more activity in the morning and during daylight hours than in the *mild-wet* season. Although, in general, a decrease in activity towards the central hours of the day was evident, it was surprisingly delayed and maintained until the afternoon in the hot-dry season. The fact that this pattern of activity was similar to the *dry* period detected in our study (January to March 2017), a shorter period and without temperatures as high as in the hot-dry season (April-September), suggests that it was probably due to the need to increase their foraging effort, when they are forced to consume a greater variety of plant species, more scarce and of low quality, and, therefore, to spend more time foraging (Xia *et al.,* 2011; Herrera-Sánchez *et al.,* 2023). On the other hand, Cuvier's gazelles were more active in the mornings than in the afternoons, especially in the hottest season (*hot-dry* season). This may be related to the diurnal fluctuations in temperatures, when the coolest period of the day is during the morning hours, and the evenings have shorter periods when the highest temperatures drop significantly, with two hours before dusk (Blank, 2023). Furthermore, Cuvier's gazelles increased their diurnal activity in the *hot-dry* season. This could be due to the average size of Cuvier's gazelle (32.5 kg average weight of adult male / 26.43 kg average weight of adult female, Moreno & Espeso, 2008), which could provide thermal inertia, contrary to the lower thermal inertia of other small-sized antelopes that are less tolerant to high temperatures (Du Toit & Yetman, 2005). It is remarkable that the size of this gazelle is twice that of the Arabian sand gazelle (*Gazella marica*), which according to Hetem *et al.* (2012a) attributed to it the adaptive capacity of heterothermy. We haven't considered body temperature, which has been found to influence the activity patterns of some desert-welling species that avoid the hottest parts of the day once they reach a certain body temperature threshold (Hetem *et al.*, 2012b). In contrast, other gazelles, such as slender-horned gazelles (*G. leptoceros*), have developed a lighter coloration that enables them to reflect excess heat, a species which is considered to be an ecotype of Cuvier's gazelle (Silva *et al.*, 2017). In the case of African golden wolf, it maintained a bimodal and crepuscular pattern in all seasons except the *wet* period, when they shifted to a cathemeral pattern, probably due to the availability of food and softer temperatures. The effect of temperature probably modulates more strongly the activity pattern of African golden wolves, a species probably less adapted to the harsh desert conditions than Cuvier's gazelle (Meliane *et al.*, 2022).

4.3 Human factor

Although nomadic herders were present at all four study sites and remained for long periods of time (several months), as we expected in hypothesis 3, they did not clearly influence the activity patterns of Cuvier's gazelle, probably because these nomads generally consisted of a small nomadic family covering a large area; despite this, there seems to be a shift in the use of daylight y hours when nomadic herders are present. Without the presence of nomadic herders, diurnal activity of Cuvier's gazelle was prolonged in the first hours of the day and whereas with nomadic herders, activity was brief during the first hours of dawn, increasing again in the middle hours of the day before decreasing at dusk. The months in which no domestic herds were detected were July and August, thus the apparent differences observed may be due to the effect of seasonality.

Overgrazing may ultimately cause a greater need for foraging, with similar effects to those caused by the *dry-hot* season or *dry* period. Furthermore, feeding conditions could become particularly difficult for Cuvier's gazelle when livestock arrived after the rains and occupied the most suitable habitat (Xia *et al.*, 2011). In this respect, Benamor *et al.* (2021) found a moderate degree of overlap between the diet of domestic sheep/goats and Cuvier's gazelle in semi-arid Mediterranean areas. In our study area acacias play a crucial role for the Cuvier´s gazelle (Herrera-Sánchez *et al.*, 2022). This dependence on a resource that is also exploited by domestic livestock (goats) in an unproductive environment could result in the effect of nomadic herders having a strong impact on Cuvier's gazelle. The improvement of truck transport due to the construction of newer roads and the installation of a considerable network of water cisterns are leading to an intensive land use in the area that is very different from the traditional nomadic pastoralism of the Atlantic Sahara (Herrera-Sánchez *et al.*, 2022). It is most likely that we are in the early stages of an emerging problem for the species in this region.

4.4 Predation effect

Significant differences in activity patterns for the pairwise comparison of Cuvier's gazelle and African golden wolf were observed in the *mild-wet/hot-dry* seasons, the *dry* periods and with all pool data. The main differences between the two were the wolf's more nocturnal behaviour, and differences in the wolf's use of daylight hours. In most cases, noticeable discrepancies can be noted at some point during the 24-hour cycle. These subtle differences can have significant consequences in terms of adaptation, especially when no distinction is made between different types of activities (resting, feeding, moving, etc.). Our result could suggest that Cuvier's gazelle may be avoiding the wolf or that wolves does not actively seek out gazelle as a potential prey item. This latter fact is consistent with the results on the diet of African golden wolf obtained by Karssene *et al.* (2019), who describes it as an opportunistic diet based on small mammals, fruits, livestock, and invertebrates, and by Sarabia *et al.* (2023) with similar results in our study area. On the other hand, Shalmon *et al.* (2020) suggested that predation by wolves (*Canis lupus*) affected the population size of Dorcas gazelle and Arabian gazelle (*Gazella arabica*), through predation on fawns. Similarly, Abáigar *et al.* (2016) was able to associate most of the Dorcas gazelle carcasses with African golden wolves, although it could not be determined whether this was due to scavenging or predation. In both cases the study took place in a fenced nature reserve, which probably favoured wolf encounters with prey.

The game theory model proposes that the predator's activity should match the pattern of its prey and the prey will drive the temporal dynamics of the game, in other words, when the prey is more active, the predator should also be more active (Brown *et al.*, 1999; Kotler *et al.*, 2002), although, in a scenario where prey is abundant, the predator does not need to express this complete synchrony in seeking prey (Martín-Díaz *et al.*, 2018; Monterroso *et al.*, 2013). After the disappearance of large predators, there may be an increase in opportunistic mesopredators (Brook *et al.*, 2012), however, in a stressful environment such as deserts, resources are reduced and become a limiting factor. In our study area, according to the theory of optimal foraging, gazelles are probably not optimal prey due to the cost–benefit ratio and trade-offs. The seasonality effect of the observed gazelle patterns, their asynchrony with African golden wolf, and the apparent limited contribution in the wolf's diet confirms our fourth hypothesis based on a low impact of predator avoidance on the activity pattern of Cuvier's gazelle.

4.5 Moonlight effect

As expected in the fifth hypothesis, in which lunar phases will shape the pattern of activity of Cuvier's gazelle, during the new moon phase Cuvier's gazelle avoided the night even more intensely, and increased its diurnal activity. Moonlight can be considered an increased predation risk, a period when predator may be more efficient hunters, and consequently prey can allocate their activity to the darkest hours of the day (Pratas-Santiago *et al.*, 2017). This fact could explain the increased nocturnal activity of African golden wolf in the full moon. On the other hand, without predation pressure prey can extend their activity to lighted periods (Michalski & Norris, 2011; Pratas-Santiago *et al.*, 2017), which would respond to the effect observed in the gazelle, and consequently the greater overlap with wolves during the full moon. Additionally, full moon nights may be used for animals to avoid exposure to high temperature (Wacher, 2006; Seri *et al.*, 2018). Furthermore, moonlight was associated with the nocturnal activity of the mountain gazelle (*Gazella gazella*), probably due to the alteration of natural conditions by intensive pressure from human activity (Huffman, 2011). In any case, in the context of low predator pressure and low human activity (although probably not in the case of illegal hunting), the effect of moon phase on Cuvier's gazelle activity could be more related to a phylogenetic imprinting within the ungulate guild and their visual acuity (Roll *et al.*, 2006; Prugh & Golden, 2014). It's important to note that Cuvier's gazelles coexisted with cheetahs (*Acynonyx jubatus*) in the study area until very recent times (Alagnier *et al.*, 2017), being this a felid particularly specialized in predation on gazelles. Therefore, the observed nocturnal activity could be indeed argued as an atavistic behaviour.

4.6 Sex factor

No significant differences were found between the activity patterns of the two sex categories studied (solitary females and males), so no asynchrony in activity patterns was observed that would confirm our sixth hypothesis. However, it should be noted that solitary males were less crepuscular and more diurnal than solitary females. These differences could be explained in the context of the predation risk hypothesis, where females would be less exposed to daylight, rather than in the context of the activity budget hypothesis, where females would need to spend more time feeding than males because of energy requirements due to smaller size than males (Ruckstuhl *et al.*, 2002).

5. CONCLUSIONS

There is an increasing need for research to address the difficulties in remote desert areas due to the collapse of the Saharan populations of wild ungulates and carnivorous mammals over the last century (Durant *et al.*, 2014). The non-invasive methods of camera-trap is a methodology that can address these issues and minimise cost (Rowcliffe *et al.*, 2014), and has proven as a very useful tool for study rare and elusive Saharan mammals (Gil-Sánchez *et al.*, 2023; the present study). While our results should be taken with caution due to the low sample size in some analysis for pairwise comparisons (Peral *et al.*, 2022), with a sufficient number of spatially distributed cameras trap (>30-35 camera-trap), we have achieved to study, for the first time, the temporal ecology niche of a rare and scare species, and its relationships with other sympatric keystone taxa and humans. Cuvier's gazelle showed great adaptability to desert environments, where seasonality modulated diel activity. Furthermore, due to its resilience to harsh conditions, Cuvier's gazelle could be a keystone species in the face of climate change in arid ecosystems. On the other hand, further work remains open to deepen the spatio-temporal relationship in Saharan environments with the Barbary sheep, dorcas gazella, and even apex depredators, in those places where they coexist.

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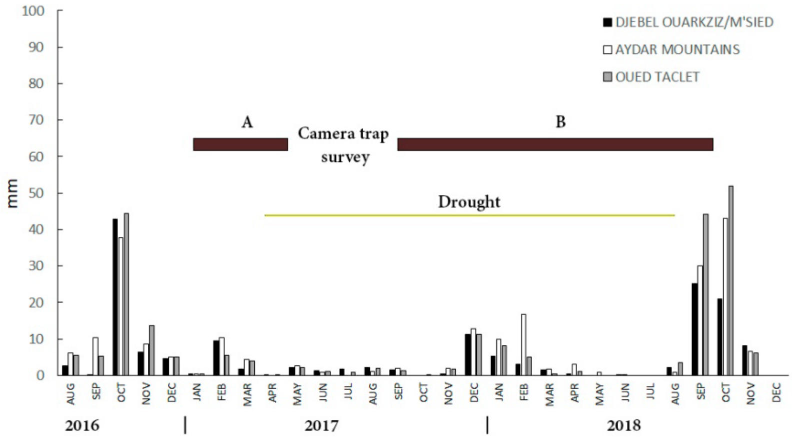
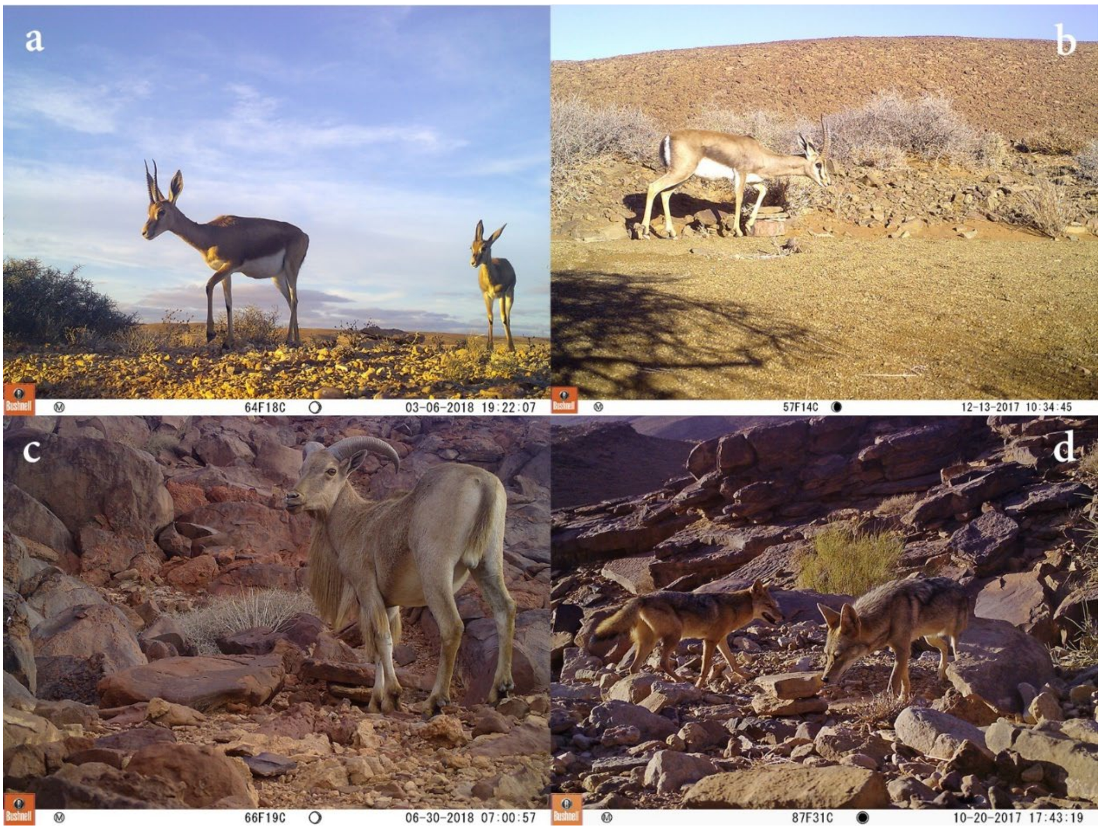
SUPPLEMENTARY DATA



Supplementary data Figure 1. Rainfall recorded in the study area since 2016 until 2018. The two camera trap survey periods are showed ("A & "B") and the drought event (gold line). Ventusky web source - Wind, rain and temperature maps https://www.ventusky.com



Supplementary data Figure 2. Target species captured by camera traps: a) adult and juvenile females of Cuvier's gazelle (*Gazelle cuvieri*), b) solitary adult male of Cuvier's gazelle, c) male of Barbary sheep (*Ammotragus lervia*) and d) couple of African golden wolves (*Canis anthus*).

Supplementary data Table 1. Mardia–Watson–Wheeler test (MWW) for pairing surveyed site area, presence/absence of Barbary sheep, pool of all data for the 4 season (autumn, winter, spring and summer) and the 3 focal species. Bolded rows indicate statistically significant differences. GC: Cuvier's gazelle, BS: Barbary sheep, AW: African golden wolf.

FACTOR	**Nº of events**		**MWW (W)**	
GC AREA	Aydar (71); M'sied (41); Ouarkziz (40); Taclet (41)		P= 0.1517	W = 9.411, df = 6
GC presence and absence of BS	33*	160	P= 0.09192	W = 4.7736, df = 2
GC Seasons	193		P= 0.2417	W = 2.8404, df = 2
SPs (all)	**GC (193); AW (259); AR (42)**		**P < 0.001**	**W = 18.701, df = 4**

*Only in camera-trapping stations where both species were present.

Supplementary data Table 2. Chi-square analysis and resource selection ratios output for the diel categories (day, crepuscular, night), factors, and target species surveyed. GC: Cuvier's gazelle, BS: Barbary sheep, AW: African golden wolf, SF: solitary females, SM: solitary males.

Species/Factors	Chi-squared tests (diel temporal category)		Post hoc analysis*			Resource selection ratios (*Wi*)**			
			day	crepuscular	night	wides I & II	day	crepuscular	night
SPECIES									
GC	**P < 0.001**	$X^2 = 50.544$, df = 2	"*"	"****"	"****"	**P < 0.001**	-	**1.865**	**0.460**
AW	**P < 0.001**	$X^2 = 30.325$, df = 2	"***"	"****"	"n.s."	**P < 0.01**	**0.723**	**1.714**	-
BS	P = 0.1775	$X^2 = 3.4571$, df = 2	-			**P < 0.05**	-	-	-
CUVIER`S GAZELLE									
SEASON									
Mild-Wet Season	**P < 0.01**	$X^2 = 13.097$, df = 2	"n.s."	"**"	"**"	**P < 0.001**	-	**1.714**	**0.633**
Hot-Dry Season	**P < 0.001**	$X^2 = 41.153$, df = 2	"*"	"****"	"****"	**P < 0.001**	**1.294**	**2**	**0.306**
Wet period	**P < 0.01**	$X^2 = 11.712$, df = 2	"n.s."	"***"	"n.s."	**P < 0.001**	-	**2.195**	-
Dry period	**P < 0.001**	$X^2 = 17.5$, df = 2	"n.s."	"**"	"***"	**P < 0.001**	-	**2.045**	**0.327**
NOMADIC HERDERS									
Presence	**P < 0.01**	$X^2 = 12.222$, df = 2	"n.s."	"*"	"**"	**P < 0.001**	-	**1.778**	0.41
Absence	**P < 0.001**	$X^2 = 23.208$, df = 2	"n.s."	"****"	"**"	**P < 0.001**	-	**2.195**	0.540
MOON									
Full	P = 0.11	$X^2 = 12.222$, df = 2	-			**P < 0.05**	-	-	**0.706**
New	**P < 0.001**	$X^2 = 23.895$, df = 2	"n.s."	"****"	"***"	**P < 0.001**	-	**2.526**	**0.253**
SEX									
SM	**P < 0.001**	$X^2 = 17.918$, df = 2	"**"	"n.s."	"****"	**P < 0.05** (wides II)	**1.224**	**2.003**	0.37
SF	**P < 0.001**	$X^2 = 29$, df = 2	"n.s."	"****"	"***"				
AFRICAN GOLDEN WOLF									
SEASON									
Mild-Wet Season	**P < 0.001**	$X^2 = 15.122$, df = 2	"**"	"***"	"n.s."	**P <0.05**	**0.732**	-	-
Hot-Dry Season	**P < 0.001**	$X^2 = 16.234$, df = 2	"*"	"****"	"n.s."	**P < 0.001**	**0.707**	**1.895**	-
Wet period	P = 0.9228	$X^2 = 0.1607$, df = 2				P = 0.877	-	-	-
Dry period	**P < 0.001**	$X^2 = 17.518$, df = 2	"***"	"**"	"n.s."	**P < 0.001**	**0.565**	**1.706**	
MOON									
Full	P =0.289	$X^2 = 2.48$, df = 2	-			P = 0.119	-	-	-
New	P = 0.221	$X^2 = 3.02$, df = 2	-			P = 0.105	-	-	-
BARBARY SHEEP									
Mild-Wet Season	P = 0.792	Fisher's Exact Test	-			P = 0.099	-	-	-
Hot-Dry Season (nº events <20)	-	-	-			-	-	-	-

*Assignment of significance levels to different categories, based on the results of the residuals test; "n.s" not significant; single asterisk is used to indicate a p-value < 0.05; double asterisk is used to indicate p-value < 0.01; and so on.

**Resource selection ratios (*Wi*) and Bonferroni test level (only significant ones are shown; values greater than 1 indicate positive selection and values less than 1 (red) indicate negative selection. Test wide I except for Sex (wide II)

SECCIÓN IV.
DISCUSIÓN GENERAL Y CONCLUSIONES

4. DISCUSIÓN GENERAL Y CONCLUSIONES

4.1 Hipótesis genéricas

Las tres hipótesis genéricas con las que partió el presente estudio de la gacela de Cuvier en el Sáhara Atlántico se han podido evaluar adecuadamente, gracias a la realización de un ambicioso trabajo de campo, pionero en su contexto biogeográfico. La primera de ellas (**H1**) establecía que, debido a un conjunto de particularidades tanto propias de la especie como locales, los métodos de estudio más eficaces serían técnicas indirectas y no invasivas (las cuales también suponen un menor esfuerzo); y en efecto, con medios relativamente limitados se pudo llevar a cabo el sondeo poblacional más detallado y a mayor escala espacial que se ha desarrollado hasta la fecha en poblaciones (silvestres) de este ungulado. Sin embargo, cabe destacar que el conteo directo de individuos también ofreció resultados importantes, dando lugar a la única estima poblacional con base científica disponible hasta la fecha para esta amenazada especie. En segundo lugar, se estableció que la presencia de esa población marginal de gacela de Cuvier estaría relacionada con factores locales asociados tanto a la estructura del hábitat como a los usos del terreno por parte del hombre (**H2**); y de nuevo se cumplieron las predicciones asociadas a esta hipótesis, ya que la complejidad del relieve y la lejanía a los núcleos de población fueron factores clave que explicaron en gran medida los patrones de presencia observados en este ambiente desértico. Por último, se hipotetizó que la gacela de Cuvier debería presentar, en las condiciones hiperáridas de las regiones saharianas, una serie de adaptaciones particulares en sus rasgos biológicos y ecológicos (**H3**); esta hipótesis se pudo confirmar en el caso de su alimentación, en relación a la predictibilidad y abundancia del alimento (con las acacias saharianas como elemento clave), y en relación a sus ritmos de actividad circadiana, adaptados a las condiciones de aridez y temperaturas extremas.

4.2 Desafíos del estudio de campo

El área de estudio de esta tesis doctoral se situó en la frontera de un conflicto bélico que perdura desde 1973 (UN, Secretary-General, 2022). Además, la ausencia de agua, las altas temperaturas y la lejanía de los centros de población más cercanos condicionaron notablemente el diseño del muestreo, ya que supusieron grandes retos logísticos debido a la escasa o nula disponibilidad de recursos básicos, tales como el agua potable y el gasoil. Todas estas condiciones implicaron que el trabajo de campo se tuviera que llevar a cabo con grandes vehículos (todoterreno 4x4), y siempre disponiendo de los permisos gubernamentales pertinentes (condición crítica dado el delicado escenario político regional). A pesar de estas limitaciones, se pudo desarrollar satisfactoriamente uno de los pocos estudios de campo sobre una población totalmente silvestre y no reintroducida de un antilopino, llevados a cabo en el noroeste de África, en el que cabe destacar su magnitud a escalas espacial y temporal. Se trata de un enfoque marcadamente pionero en el contexto reciente de la investigación de los ungulados saharianos, en el que son norma los estudios realizados en poblaciones reintroducidas en régimen de semilibertad (dentro de áreas cercadas).

La escasez de la especie objeto de esta tesis, la gacela de Cuvier (*Gazella cuvieri*), junto a un deficiente conocimiento previo, han sido otros de los desafíos que ha enfrentado este trabajo. Así, las estimas previas de su población en el Sáhara Atlántico no superaban los 100-300 individuos (Cuzin, 2008). De hecho, se pronosticaba su desaparición a corto plazo o incluso se indicaba que ya se encontraba erradicada del área (Huffman, 2011a). Además, solo se habían llevado a cabo dos trabajos científicos de la especie dentro de un estudio general sobre la distribución de grandes mamíferos en Marruecos, realizados mediante información no sistemática y con frecuencia de segunda mano (Loggers, 1992; Cuzin, 2003). La mayor parte de las aportaciones científicas sobre la gacela de Cuvier procedían de Argelia, aunque casi siempre con datos muy vagos sobre su ecología (Sellami *et al.,* 1990; Sellami & Bouredjli, 1991; De Smet, 1991; Arbouche *et al.,* 2012). No fue hasta el 2016 cuando, a las contribuciones de esta tesis, se han unido nuevos trabajos sobre la gacela de Cuvier en otros países del norte de África (*Argelia*: Aouad *et al.*, 2016; Benamor *et al.*, 2019, 2021, *Marruecos*: El Alami *et al.*, 2018). Paralelamente se han ido desarrollando publicaciones científicas en condiciones de semilibertad (*Túnez*: Abáigar *et al.,* 2005; Moreno *et al.,* 2020, *Marruecos*: Hanane & Amhaouch 2021 a, b), a la par que para otras especies de antílopes sahelo-saharianos (p.ej. gacela dorcas *G. dorcas*, órice de cuernos de cimitarra *Oryx dammah,* gacela de Loder *G. leptoceros* y adax *Addax nasomaculatus*: Ait Baamrane *et al.,* 2012; Abáigar *et al.,* 2016: Cooke *et al.,* 2016; Meliane *et al.,* 2022; Melanie *et al.,* 2023: Seri *et al.,* 2018). Esta escasez de estudios no es sino un reflejo y consecuencia de las dificultades que conlleva cualquier trabajo con especies esquivas y escasas en medios remotos que, a su vez, en el contexto actual del Sahara, se ven agravadas por cuestiones geopolíticas y de seguridad (Brito *et al.,* 2018).

La disminución paulatina de estudios empíricos de campo (Ríos-Saldaña *et al.,* 2018) es acorde con el bajo número de publicaciones científicas que hay disponibles para la gacela de Cuvier. La principal aportación y valor de este trabajo es el de proveer conocimiento, hasta ahora inédito, sobre la biología y la ecología de la gacela de Cuvier en un ambiente desértico, además de remoto y hostil.

4.3 Cómo, cuántas y dónde

Teniendo en cuenta los retos que imponía el área de estudio, se planificaron expediciones *ad hoc* con los objetivos de: 1) evaluar en campo las limitaciones logísticas en cuanto al abastecimiento de recursos básicos (distancia a pueblos, gasolineras, estado de pistas, etc.) y 2) confirmar la presencia de la especie. Las campañas de muestreo se sustentaron particularmente (pero no exclusivamente) en el empleo de técnicas indirectas y no invasivas (Sutherland, 2006).

En el **Capítulo 1** se evaluó el uso combinado de datos indirectos como huellas y excrementos (pilas y letrinas), junto con la observación directa de ejemplares. Los resultados arrojaron un 74.62% (50/67) de los puntos muestreados con presencia para la especie y una densidad estimada de 0.08 ± 0.02 individuos/km^2. Esta baja densidad resultó ser incluso inferior a la obtenida por Strauss *et al.*, (2009) para la gacela arábiga en ambientes desérticos (0.2 individuos/ km^2). A pesar de ello, y debido a la enorme extensión del área prospectada, la población estimada fue de 935 individuos (IC 95%: 597-1607). Tomando los valores más pesimistas, la población resultante estaría cerca de los 500 individuos y, por tanto, sería de una importancia crucial para la especie (IUCN, 2018) tanto por su tamaño poblacional como por diversidad genética (Silva *et al.*, 2015, 2017). Hasta la fecha y en base a nuestro conocimiento, no hay ninguna otra publicación en la que la estima de la abundancia de la gacela de Cuvier esté basada en datos empíricos, dado que la mayor parte de los trabajos basaban la abundancia de la especie en encuestas y aproximaciones locales, siendo la mayoría de hace más de veinte años (IUCN SSC Antelope Specialist Group, 2016). Además, las estimas (no empíricas) subestimaron la importancia de la población del Sahara Atlántico, relegándola a un papel secundario dentro de los planes de acción para los ungulados silvestres de Marruecos (Cuzin *et al.*, 2008).

A nivel metodológico, los recorridos a pie de 2.15 km fueron suficientes para detectar la especie, en tanto que, para evitar falsos negativos, el aumento de réplicas (2-3) disminuyó significantemente el efecto de la detección imperfecta (MacKenzie *et al.*, 2006). La tasa de acierto en la identificación de excrementos, testada mediante análisis genético, fue del 95.12 % (**Capítulo 1**). Además, este trabajo ha formado parte de dos publicaciones científicas realizadas en base a la identificación genética a través de las heces (Silva *et al.*, 2015, 2017). Por otro lado, se encontró una relación positiva entre los avistamientos de las gacelas de Cuvier y los índices indirectos de abundancia (IKA; pilas + letrinas), lo que permitiría su uso en el seguimiento de la población a largo plazo en este tipo de medios. Los indicios indirectos dejados por la gacela de Cuvier son fácilmente identificables, especialmente las deposiciones y letrinas, las cuales no se confunden con otras especies en nuestra zona de estudio, debido a la práctica ausencia de gacelas dorcas dentro del área ocupada por la especie diana. Además, el muestreo de indicios indirectos puede producir resultados óptimos para la gacela de Cuvier en medios desérticos, incluso en situaciones de baja o muy baja densidad, lo que le convierte en una herramienta útil para el seguimiento a largo plazo tanto temporal como espacial.

Los modelos de distribución combinan información sobre la presencia o abundancia de especies con variables medioambientales y/o características espaciales (Guisan & Zimmerman, 2000; Elith & Leathwick, 2009; Guisan *et al.*, 2017). El **Capítulo 2** analiza los datos de presencia/ausencia del muestreo a gran escala obtenidos en el **Capítulo 1,** desarrollando modelos predictivos de distribución de especies. Para ello, se utilizó la información de presencia proporcionada por los avistamientos (61 gacelas en 21 puntos), la recogida de excrementos (615 pilas/letrinas en 2169 km recorridos) y los datos de ausencia, y se combinó con variables topográficas (altitud, pendiente, rugosidad del terreno), índices de temperatura y humedad del relieve, distancias de la costa y a poblaciones, e índices de vegetación y climáticos. Los resultados arrojaron una mayor probabilidad de presencia de gacela de Cuvier en zonas con una compleja red de colinas y barrancos, y en áreas remotas con una baja densidad de población humana y, *por ende*, con una menor accesibilidad (carreteras asfaltadas). Estos resultados fueron coherentes con los descritos previamente, ya que se considera a la gacela de Cuvier como un ungulado bien adaptado a zonas montañosas (Aulagnier *et al.*, 2017; Huffman, 2011a), donde puede hallar refugio para evitar tanto la depredación como la caza furtiva, y donde también encuentra condiciones ambientales más favorables frente al clima extremo sahariano (Batanouny, 2001). En Túnez se observaron efectos similares para las gacelas dorcas en cuanto a la presencia humana como factor limitante, que tuvo más peso que las características de hábitat (Chammem *et al.*, 2008).

Las gacelas se cazan por su carne, pero también por su piel, cuernos e incluso huesos, que se utilizan en algunas prácticas de terapias tradicionales y magia (El Alami, 2018). El impacto de la caza excesiva, impulsada por la aparición de los 4x4 y las armas de fuego durante el siglo XX, persiste a día de hoy, situando la caza ilegal como la principal causa del declive y extinción de los ungulados silvestres en todo el desierto del Sáhara, y por tanto de la región (Valverde, 1957; Logger *et al.*, 1992; Beudels-Jamar *et al.*, 2006; Cuzin *et al.*, 2008; Durant *et al.*, 2014; Brito *et al.*, 2014, 2018; Aouad *et al.*, 2016; Newby *et al.*, 2016). En este sentido, el área proyectada por el modelo de distribución para la gacela de Cuvier reflejaría una zona de refugio que permite la supervivencia en condiciones aparentemente extremas (ver **Capítulo 2**), donde la especie alcanza el límite más meridional de su área de distribución.

En Marruecos, se delimitan dos poblaciones que serían vitales para la especie en cuanto al número que las conforman: la población de la región del Bas Drâa-Aydar (la zona de estudio) y la población del Anti-Atlas occidental. El resto de su distribución estaría compuesta por pequeños núcleos poblacionales en el Alto Atlas occidental, y la vertiente sur del alto Atlas central y del Atlas oriental (Beudels-Jamar *et al.*, 2006; Aulagnier *et al.*, 2017). Estos datos junto, con la información generada por esta tesis, sugirieren que las poblaciones remanentes en Marruecos estarían limitadas a áreas remotas y con una baja densidad de población humana.

La proyección del modelo de distribución más allá del área de estudio, identificó dos áreas bien delimitadas que podrían ser claves para la supervivencia de la gacela de Cuvier en la región (**Capítulo 2**). Una englobaría el entorno próximo al área de estudio, y la segunda se situaría al oeste, junto a la costa Atlántica, zona que comprende una pequeña proporción del sector occidental del parque Nacional Khenifiss. El área de presencia estimada para la especie se asemeja a la descrita por Aulagnier *et al.* (2017), lo que podría corroborar el modelo de distribución proyectado. Tan solo un 5% del área de distribución de la gacela de Cuvier en nuestra área de estudio y en áreas adyacentes se encuentra bajo alguna categoría de protección (parque nacional Khenifiss, desde 2006); esta circunstancia puede suponer un riesgo para la futura supervivencia de la población, y sería recomendable ampliar las zonas protegidas hasta incluir la mayor parte posible de los sectores más importantes del área de distribución potencial de la especie.

Teniendo en cuenta el importante declive y fragmentación de las poblaciones que ha sufrido este ungulado durante el pasado siglo XX, las áreas identificadas podrían ser de una importancia crucial para asegurar su supervivencia en el área más meridional de su distribución. Estas áreas podrían garantizar condiciones adecuadas contra las duras condiciones del desierto, además de proporcionar refugio por ser áreas remotas con bajo impacto humano. La proyección de nuevas áreas protegidas en base a los resultados obtenidos en el **Capítulo 2** no solo favorecería a nuestra especie focal, sino que sería garante, por contener un hábitat adecuado, para la recuperación de otras especies de ungulados presentes (gacelas dorcas y arruí sahariano) o incluso para la reintroducción de aquellos extintos (la gacela dama mohor *Nanger dama*, órix cimitarra y adax). En definitiva, la protección de la gacela de Cuvier podría ejercer un efecto paraguas, que no solo favorecería a otro ungulados presentes, sino que además beneficiaría a otros taxones, como sería a la diversa comunidad de carnívoros presente en la región (según datos de nuestro estudio): p. ej. hiena rayada (*Hyaena hyaena*), gato de las arenas (*Felis margarita*), lobo dorado africano (*Canis anthus*), ratel (*Mellivora capensis*) y posiblemente caracal (*Caracal caracal*), entre otros, o incluso aportar escenarios adecuados para futuros proyectos de reintroducción del críticamente amenazado guepardo sahariano (*Acinonyx jubatus hecky*).

4.4 Adaptaciones al desierto

Los ungulados desérticos se enfrentan a factores que retan su capacidad de termorregulación y mantenimiento del equilibrio hídrico, debido a las altas temperaturas ambientales, a la elevada radiación solar, la falta de agua y cobertura, y a la presencia de recursos alimenticios impredecibles (Cain *et al.*, 2006). Este último factor está determinado por la escasez e irregularidad de precipitaciones, que dan lugar a pulsos imprevisibles de producción primaria (Reynolds *et al.*, 2004; Whitford & Duval, 2019), que condicionan a las especies a adaptar sus estrategias alimentarias a periodos de incertidumbre en cuanto a la disponibilidad y calidad de los alimentos.

En estudios previos sobre la alimentación realizados en su área mediterránea, se ha comprobado que la gacela de Cuvier se comporta como una especie ramoneadora y pastadora intermedia (Benamor *et al.*, 2019, 2021; Hanane & Amhaouch 2021b). Por el contrario, los resultados obtenidos en el **Capítulo 3** revelaron que la especie en el desierto del Sahara es principalmente ramoneadora, mostrando una fuerte preferencia por los árboles, y entre ellos las acacias (*Vachellia* sp.). Este género juega un papel relevante en la dieta de los antílopes Sahelo-Saharianos (Beudels *et al.*, 2006) y en concreto, *Vachellia tortilis*, que es una especie clave para especies como la gacela de las acacias (*G. acaciae*, Huffman *et al.*, 2011b), la gacela del desierto de Arabia (*G. cora*, Huffman *et al.*, 2011c) o la gacela dama (Valverde, 1957; Grettenberger & Newby, 1986). Las acacias pertenecen a la familia Leguminosae, un grupo con un alto contenido en nitrógeno y, probablemente, con una calidad nutricional superior a la de otras especies vegetales saharianas. Por otro lado, la rosa de Jericó (*Anastatica hierochuntica*) destacó en la dieta de la gacela de Cuvier como la especie consumida más importante después de los árboles. La contribución de esta especie en la dieta sugiere un papel clave, dependiente de los pulsos estacionales, y en el que en periodos de sequía se incrementa la diversidad de taxones en la dieta.

El carácter rugoso del medio proporciona a los árboles y arbustos condiciones de refugio a nivel de microhábitat, manteniendo la humedad en barrancos y cañones, y reduciendo la evapotranspiración debido a la sombra proporcionada por el relieve, contribuyendo así a mitigar los periodos de sequía (Batanouny, 2001; Whitfor & Duval, 2019). Los patrones de selección de hábitat observados en el **Capítulo 2** explicarían la resiliencia de las gacelas de Cuvier a las condiciones saharianas gracias a un suministro de alimento relativamente constante. Sin embargo, se pudo confirmar que evitan los *oueds* más productivos, situados en zonas llanas, probablemente debido a la mayor presión del ganado y a la presencia humana; estos dos factores son de gran importancia en la selección de hábitat, a todas las escalas, por parte de las gacelas. Asimismo, los resultados obtenidos en el **Capítulo 3** indican que la especie se adapta y cambia su comportamiento de alimentación en relación con la disponibilidad de plantas, siguiendo una estrategia típica de alimentación oportunista (Stephens & Krebs, 1986; Futuyma & Moreno, 1988).

La supervivencia y la reproducción consisten, en última instancia, en hacer frente al problema de cómo obtener energía y utilizar el tiempo (Bunnell & Harestad, 1986). En este sentido el **Capítulo 4** aborda esta cuestión. En áreas hiper-áridas y con temperaturas extremas durante los meses más calurosos, es previsible una inactividad diurna para evitar el exceso de calor durante las horas centrales, mientras que se selecciona un microclima más fresco en forma de búsqueda de sombra (Davimes *et al.*, 2016, 2017). Por lo general, en ungulados desérticos se produce un patrón de actividad bimodal o crepuscular (Davimes *et al.*, 2016; Seri *et al.*, 2018, Blank, 2023), que puede cambiar a un ritmo más nocturno durante la estación seca y cálida (Hetem *et al.*, 2012; Davimes *et al.*, 2016, 2017; Meliane *et al.*, 2022; Abáigar *et al.*, 2018). Mediante el foto-trampeo se determinó que la gacela de Cuvier muestra una actividad prácticamente diurna en la zona de estudio, con picos en el crepúsculo (mejor delimitado en las hembras) y un periodo central de actividad reducida. Las mañanas fueron importantes, con un pico de actividad al amanecer que decrece a lo largo de la mañana y que remonta al atardecer cerca del crepúsculo. Este patrón podría estar asociado a las variaciones de las temperaturas entre las primeras horas de la mañana y la tarde, siendo más frías las horas de la mañana que la de las tardes, estas últimas con periodos más cortos en donde la insolación y el descenso de las altas temperaturas es menos acusado (Blank, 2023). Por lo contrario, en los periodos secos y caluros, y en contra de lo que cabría esperar, aumentó la actividad diaria. La explicación más probable es que las gacelas se ven obligadas a invertir más tiempo en la búsqueda de alimento dado que, en este periodo, disminuye tanto en número de especies vegetales disponibles como su calidad alimentaria (Xia *et al.*, 2011; **Capítulo 3**).

Este patrón diurno en la época más calurosa, podría indicar gran capacidad de resiliencia a las altas temperaturas. Una adaptación clave asociadas a los ungulados adaptados a zonas desérticas es la heterotermia. Esta consiste en disminuir la pérdida de agua mediante el almacenamiento de calor corporal durante el día y su disipación durante la noche para reducir la evapotranspiración (Cain *et al.*, 2006). La capacidad de heterotermia se ha asociado al órix árabe (*Oryx leucoryx*) y a la gacela de arena de Arabia (*G. marica*) (Ostrowski & Williams, 2006; Hetem *et al.*, 2012). Por otro lado, Silva *et al.* (2017), proponen reclasificar la gacela de Cuvier como un ecotipo de montaña de la gacela de Loder (la gacela típica de los tórridos *ergs* saharianos), mientras que Hassanin *et al.* (2012) asignan como subespecies de la gacela de Cuvier a la gacela de Loder y a la gacela de arena de Arabia, ambas asociada a *regs* y *ergs* (Huffman, 2011 d,e). El grado de parentesco con estas especies, a través de la herencia filogenética, podría explicar la resiliencia de la gacela de Cuvier a las altas temperaturas, la falta de agua o incluso su capacidad potencial de heterotermia.

El **Capítulo 4** también analiza la relación de la gacela de Cuvier con el arruí sahariano, el hombre y el lobo norteafricano en cuanto a sus patrones de actividad. Por un lado, no se encontró una segregación temporal importante con el arruí presente en simpatría, aunque relegado a las zonas más abruptas del área de estudio. Por otro lado, el impacto por la presencia de pastores nómadas no fue significativo a pesar de permanecer durante largos periodos de tiempo (varios meses) en el área de estudio. En la región los pastores nómadas, generalmente, están formados por pequeños grupos familiares, que se desplazan siguiendo los pastos y dependen de disponibilidad de agua (pozos); un uso tradicional que puede cambiar radicalmente en la zona, tal como se comprobó durante el trabajo de campo.

En un ambiente con recursos limitados, especies claves como las acacias son también explotados tanto por el ganado doméstico como alimento, como por el hombre para hacer carbón; por tanto, el aumento de la presión ganadera en la zona puede provocar un fuerte impacto sobre los ungulados (Xia *et al.*, 2011). La mayor accesibilidad debido a la creciente construcción de nuevas carreteras asfaltadas, junto con la instalación de una red considerable de cisternas portátiles de agua, podrían potenciar un uso intensivo de la tierra, muy diferente del pastoreo nómada tradicional del Sáhara Atlántico. Por tanto, es muy probable que nos encontremos en las primeras fases de un problema emergente para la especie en esta región.

Respecto a la depredación potencial por el lobo norteafricano y su impacto en la actividad de la gacela de Cuvier, cabe mencionar que, en el contexto sahariano, las gacelas no son una presa óptima debido a la relación coste-beneficio según la teoría de la búsqueda óptima de alimento (Brown *et al.,* 1999). Si bien las asincronías detectadas en los patrones de actividad entre lobos y gacelas podrían ser interpretadas como un comportamiento de evitación por parte del herbívoro, sin embargo, un reciente trabajo que abarca a la ecología trófica del lobo dorado africano en el área de estudio, pone en evidencia que las gacelas no forman parte de su dieta (Sarabia *et al.*, 2023). En cualquier caso, el elevado solapamiento de la actividad observado entre lobos y gacelas (del 80% aproximadamente) probablemente se relacione con limitaciones fisiológicas compartidas, más que con un caso aparente de relación depredador-presa.

La fase lunar moduló significativamente la actividad de las gacelas, con una menor actividad nocturna con luna nueva (menor luminosidad) y un aumento de la actividad diurna. Mientras que durante la luna llena (mayor luminosidad) aumentó el grado de solapamiento y sincronía entre lobos y gacelas. Este aumento de la actividad nocturna durante las noches más luminosas en depredadores se ha asociado al hecho de que pueden ser cazadores más eficientes y, en consecuencia, las presas pueden asignar su actividad a las horas más oscuras del día (Pratas-Santiago *et al.*, 2017). Sin embargo, este no sería el caso de estudio, que ya ha sido discutido previamente. La actividad nocturna podría ser beneficiosa para evitar las altas temperaturas diurnas (Wacher 2006; Seri *et al.,* 2018), pero también sería esperable que las presas extiendan su actividad hacia la noche en un contexto de baja presión de predadores (Michalski & Norris, 2011; Pratas-Santiago *et al.,* 2017). Por otro lado, la actividad nocturna se puede relacionar con la alteración de las condiciones naturales en un escenario de intensiva presión humana (Huffman, 2011f). Con todo ello, en el contexto de una previsible baja presión por depredación y bajo impacto humano, el comportamiento observado por las fases lunares podría estar más relacionado con una impronta filogenética que asociaría las noches menos luminosas con un aumento del riesgo de depredación (Roll *et al.,* 2006). De hecho, la extinción del guepardo en la zona de estudio es relativamente reciente (años 90s del siglo XX; Aulagnier *et al.*, 2017), siendo un depredador precisamente especializado en gacelas.

En cuanto a la biología de reproducción, si bien no forma parte de los objetivos de la tesis, esta información es de gran interés para el adecuado conocimiento de la especie y sus adaptaciones a ambientes desérticos. En base a foto-trampeo de chotos (< 6 meses) y juveniles (<1 año), se han estimado dos épocas de nacimientos, una primaveral (marzo-mayo) y otra otoñal (septiembre y octubre). Datos similares fueron obtenidos en cautividad, con un pico en marzo y otro en noviembre ("bajo condiciones sin el control de reproducción"; Abáigar & Cano, 2005). También, Dunham (1997) encontró en la gacela de montaña (*G. gazella*) de la península arábica un pico de nacimiento a finales de invierno/primavera (febrero-marzo) y otro a finales de verano/principios de otoño (septiembre). Estos datos sobre reproducción son los primeros obtenidos en ambientes desérticos pata la gacela de Cuvier y podrían apoyar su alta adaptabilidad a estos medios.

4.5 Conclusiones

1. En áreas de baja densidad de gacelas de Cuvier y donde las condiciones de trabajo requieren logísticas especiales y adecuadas a zonas alejadas de núcleos de población, los datos indirectos de presencia son razonablemente adecuados para estimar tanto su distribución como abundancia relativa.

2. Las estimaciones de densidad basadas en el muestreo de distancias requieren un esfuerzo considerable; sin embargo, es posible prospectar grandes áreas durante campañas relativamente cortas para obtener datos adecuados sobre la estructura demográfica de la población.

3. El 74.62% (50/67) de los puntos muestreados fueron positivos para la presencia de la especie, con una densidad de 0.08 ± 0.02 individuos/km^2 lo que resulto en 935 individuos (IC 95%: 597-1607) en el área de estudio. Este resultado sugiere que se trata, con diferencia, de una de las poblaciones más importantes de la especie, con una relevancia clave a nivel global.

4. La distribución de la población más meridional de gacela de Cuvier está relacionada con la topografía, la distancia a las zonas habitadas (la presión humana) y probablemente la disponibilidad de alimento. La irregularidad del terreno actuaria a diferentes escalas favoreciendo la resiliencia de las especies vegetales óptimas y su disponibilidad, además de proporcionar refugio frente el clima extremo y la caza.

5. Los modelos de distribución de gacela de Cuvier han identificado áreas importantes, tanto para su protección como para otras especies saharianas amenazadas en el área de estudio, como por ejemplo el arruí sahariano o la gacela dorcas; e incluso para futuros proyectos de reintroducción de la extinta en libertad gacela dama mohor o del críticamente amenazado guepardo sahariano.

6. En la dieta de la gacela de Cuvier se identificaron dieciocho especies pertenecientes a quince familias, que indicaron una estrategia trófica marcadamente ramoneadora y parcialmente oportunista en ambientes semiáridos.

7. Las acacias (*Vachellia tortilis* y *V. flava*) destacaron como las especies más consumidas, desempeñando un papel clave en la ecología de la gacela de Cuvier en el Sáhara Atlántico. Este resultado debe ser tenido en cuenta en los futuros planes y estrategias de conservación.

8. La gacela de Cuvier exhibió una actividad diurna con picos al amanecer y al atardecer, aunque el patrón crepuscular fue más acusado en las hembras que en los machos. La estacionalidad, los periodos de humedad y sequía, y la fase lunar fueron los factores con efectos más significativos en los patrones de actividad.

9. Se observó una elevada sincronía en los patrones de actividad entre la gacela de Cuvier, el arruí sahariano y el lobo dorado africano, con un patrón bimodal y crepuscular compartido. Sin embargo, se observaron diferencias significativas en la selección de período entre las gacelas de Cuvier y los lobos dorados africanos, aunque, en cualquier caso, estos resultados no se relacionarían con un escenario de interacciones-depredador-presa. En contraste, no se encontraron diferencias significativas relacionadas con la competencia con el arruí sahariano.

10. El todavía limitado pastoreo tradicional nómada en la zona no afectó significativamente a los patrones de actividad de la gacela de Cuvier, probablemente en relación a la relativamente baja intensidad de esta actividad humana.

11. En un contexto de cambio climático, taxones como la gacela de Cuvier, con gran capacidad de resiliencia a las duras condiciones de escasez de agua y altas temperaturas, podrían llegar a ser claves para el mantenimiento de los procesos ecológicos en ambientes norteafricanos donde se van a incrementar las condiciones de aridez. Por tanto, es urgente la aplicación de políticas de conservación orientadas tanto a la protección directa de la especie, en particular reducir su caza ilegal, como dirigidas a evitar el sobrepastoreo emergente. Estas medidas supondrían la protección eficiente de un ecosistema de gran valor, donde habita su población más meridional junto con una, todavía, diversa comunidad faunística.

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