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La portada

Couple of grey brocket deer in a pond in Calakmul Biosphere Reserve. Grey brocket deer (*Mazama pandora*) are common inhabitants of the Yucatán peninsula forest in Southern México and of the Northern forest of Guatemala and Belize. The species is a common prey for subsistence hunters of the area and prefer non-perturbed tropical forest of the area. The Grey brocket deer is a quasi-endemic species with a limited distribution range. Scientific attention and conservation actions are necessary actions to conserve this amazing species of brocket deer (Photo Rafael Reyna-Hurtado).

Nuestro logo "Ozomatli"

El nombre de "Ozomatli" proviene del náhuatl se refiere al símbolo astrológico del mono en el calendario azteca, así como al dios de la danza y del fuego. Se relaciona con la alegría, la danza, el canto, las habilidades. Al signo decimoprimero en la cosmogonía mexica. "Ozomatli" es una representación pictórica de los mono arañas (*Ateles geoffroyi*). La especie de primate de más amplia distribución en México. " Es habitante de los bosques, sobre todo de los que están por donde sale el sol en Anáhuac. Tiene el dorso pequeño, es barrigudo y su cola, que a veces se enrosca, es larga. Sus manos y sus pies parecen de hombre; también sus uñas. Los Ozomatin gritan y silban y hacen visajes a la gente. Arrojan piedras y palos. Su cara es casi como la de una persona, pero tienen mucho pelo."

Therya

Volumen 15, número 1 enero 2024

Contenido

EDITORIAL

ARTICLES

fascículo 43 http://www.revistas-conacyt.unam.mx/therya/index.php/THERYA/issue/view/43

DERECHOS DE AUTOR Y DERECHOS CONEXOS, año 15, No. 1, enero-abril del 2024, es una publicación cuatrimestral editada por la Asociación Mexicana de Mastozoología A. C. Hacienda Vista Hermosa 107, Colonia Villa Quietud, Coyoacan 04960. Distrito Federal, México. Telefono (612) 123-8486, www.mastozoologiamexicana.org, therya@cibnor.mx. Editor responsable: Dr. Sergio Ticul Álvarez Castañeda. Reservas de Derechos al Uso Exclusivo No. 04-2022-032919260800-102, ISSN: 2007-3364 ambos otorgados por el Instituto Nacional de Derechos de Autor. Responsable de la última actualización de este número, Unidad de informática de la Asociación Mexicana de Mastozoología A. C. Dr. Sergio Ticul Álvarez Castañeda. Instituto Politécnico Nacional 195. La Paz, Baja California Sur, C. P. 23096. Tel. (612) 123-8486, fecha de la última modificación 30 enero 2024.

Therya

El objetivo y la intención de *THERYA* es ser una revista científica para la publicación de artículos sobre los mamíferos. Estudios de investigación original, editoriales y artículos de revisión son bienvenidas.

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Editorial

Sonia Gallina influences on the study of other ungulates in México: honoring a professor and a dear friend

Sonia Gallina-Tessaro, a distinguished Mexican professor residing in Central México, has been a foundational pillar at the Instituto de Ecología, A. C. for over 47 years (Figure 1). A trailblazer in the study of deer not only in México but possibly across Latin America, Sonia's pioneering contributions have prompted many of us to continue doing research with deer and other ungulates. The following recompilation of contribution on ungulates is a small tribute to her work by presenting this special issue of THERYA, the scientific journal of the Mexican Society of Mammalogist (AMMAC by its Spanish initials), with a set of selected new articles about ungulates with special emphasis on deer.

Sonia is the clear example of enthusiasm and vitality that can be transmits to the students and to all of us who have ever crossed her path (Figure 2). Her long and illustrious carrier in the mammalogy have motivated many persons in the study of different aspect of the mammalogy, having the ability to reproduce that energy and spare among many of us. In opinion of many of the colleagues with whom we interact to carry out this issue, they mentioned that the most important aspect of Sonia is her cheerful personality and ability to tackle many challenges. Sonia has been described as a person with a deep passion to study and conserve mammals, but also a person able to transmit that passion to her students, a person that encourages young people to follow their academic dreams, a person that transmits trust. She uses her strong and powerful voice to convey clear and direct messages to her students and general persons, even in classrooms a floor away.

Figure 1. Dr. Sonia Gallina in Xalapa, Veracruz (2005; Photo Alberto González).

Figure 2. Dr. Gallina is pregnant of her second son Alejandro, almost due to give birth and still working in her office at the Instituto de Ecología, A. C. The institute was inside of the Museo de Historia Natural de la Ciudad de México, in section II of Chapultepec (1984; Photo Alberto González).

Sonia began its "passionate relationship" with deer since she was as student at the Universidad Nacional Autónoma de México when she began with her bachelor thesis in 1978 and continues to its PhD. Over the years, Sonia has mentored more than 65 students who conducted their research under her guidance in México. Many of these students have since become esteemed professors in various Mexican universities and institutes, specializing in deer studies across different regions of the country and in other countries as well.

With an impressive academic output that includes 10 books, 72 book chapters, over 90 papers, and 104 lectures, Sonia is also a member of the National System of Researchers of CONAHCYT (by its Spanish initials), holding the distinction of Level II. In the Asociación Mexicana de Mastozoología A. C. she is a very active member, the most outstanding contribution of her was to be president from 2008 to 2010 and her support to the creation of Therya, which now is a consolidated journal and is already a publishing house with three journals, including one of popular sciences. Sonia also organized the X Congreso Nacional Maztooología and the I Congreso Latinoamericano de Mastozoología (2010). In 2019 she was awarded the Ticul Álvarez Solórzano award in addition to U.S. Fish and Wildlife Service (Figure 3).

Ungulates are mammals with hooves and the group is composed by two orders of mammals, the Perissodactyla order containing rhinos, equine and tapirs, and Artiodactyla, an order that contains all bovids, ovid, deer, suids and peccaries of the world among others. Some ungulates are among the best studied mammals of the world (white-tailed deer, red deer, wild boar, etc.), but some have been neglected by science in several ways. For example, in a study about forest ungulates of Neotropical forest Taber *et al.* (2017) found that of 22 species of forest ungulates in Neotropical forest, 60 % of them were in some degree of risk of extinction in 2008, according to the red list of the IUCN (https://www.iucnredlist.org/), considerably larger than the 21 % of world mammals at risk of that time. In addition, there were 279 papers published about these 22 species from 2000 to 2009 with a rate of 1.3 papers per species per year (Taber *et al.* 2017), a contrasting figure with almost 20 papers per year about jaguar and pumas (charismatic carnivores of the Neotropical forests also). There were even 11 species of forest ungulates with no formal publication at all in all these years (Taber *et al.* 2017).

Figure 3. Receiving the Ticul Álvarez Solórzano award during the XV Congreso Nacional de mastozoología in Chihuahua City, October 19, 2022. In the photo from left to right Dr. Enrique Martínez Meyer president of the AMMAC, Dra. Cristina Mac Swiney González vicepresident of the AMMAC, Dr. Sonia Gallina awarded, and Dr. Gerardo Sánchez Rojas who presented her as the one recognized with the 2020 award (Photo Fernando González).

Ungulates are very important in the world because they are among the largest (and sometimes the numerous) species of the ecosystem, they are among the largest prey for native predators and for humans that still practice subsistence hunting, they remove large amount of plants, they disperse seeds, they remove soils and plan some seeds while destroy other seedlings, ungulates perform some of the largest and impressive migrations on the world (caribous in the Artic circle and Wildebeest and Zebras in Eastern Africa; Figure 4).

At the same time, ungulates are among the mammals that have suffered population reduction in large amounts. Ripple *et al.* (2015) in an influential paper, argues that 60 % of the world's largest herbivores (most of them ungulates) are at risk of extinction. The main reasons for the extinction of these groups of animals are the fact that are some of the largest preys for human hunters, and most of them (due to the large size) need large amount of habitat to maintain a viable population. Humans have hunted animals in all the natural ecosystems and forests are being fragmented and lost at alarming pace every day, the largest animals are the

Figure 4. Dr. Gallina on an island in Lake Victoria, Tanzania, Africa during a safari in July 2019 where she visited several sites in Tanzania and Kenya to witness the great migration of ungulates between the plains of the Masai Mara to the Serengeti National Park and Ngorongoro crater (Photo Fernando González).

one that are being impacted in a great way due to the ecological requirements.

In this context, Sonia Gallina's work on ungulates has been of extreme importance. Sonia began studying deer in the late 1970's and coauthored a book in early 1980's. Her primary focus species have been the white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), red brocket deer (*Mazama temama*) and bighorn sheep (*Ovis canadensis*), although her work is much more extensive and she has worked with many more species of mammals, either at the level of populations or communities, throughout all of México, in temperate forests, dry forest, jungles, and deserts.

Her work marks the beginning in México of the research on game wildlife and its management. Sonia began her research by studying the diet of deer in La Michilia, Durango. Later in her career, she expanded her expertise to the dry, arid regions of Sonora, Baja California, and Chihuahua. Her pioneering studies emerged during a time when wildlife in México was largely understudied. At that time, large mammals like the white-tailed deer were primarily assessed using indirect methods, such as feces or track counts. Direct counts were not yet common practice, and emerging technologies, such as telemetry radio-collars, were still in their early stages. She incorporated a long-awaited sustainability that we considered as a great tool to conserve biodiversity. For the data interpretation, Sonia and some of its colleagues developed some mathematical models for the estimation of density and relative size composition to its long-term studies that covered up to two decades of data.

Figure 5. After the 1970 women's world cup. In 1971 the biology students had a friendly game against the chemistry students, on the islands in Ciudad Universitaria, UNAM in Mexico City. The photo shows Sonia Gallina and Cecilia de la Torre (Photo unknown).

Sonia's research was groundbreaking, not only because it filled critical knowledge gaps but also because it signaled a significant milestone: a Mexican researcher was dedicating herself to understanding and conserving local wildlife populations. Many recognized and were inspired by the fact that Sonia, a Mexican scientist, was taking the lead in this important work. Moreover, Sonia exemplifies the resilience and determination of a female scientist. She navigated not only the scientific challenges of her field but also personal challenges. For instance, she continued her research while pregnant with her first child and even traveled to reserves in the then (now extinct), Soviet Union. She broke barriers in a male-dominated field, succeeding against the odds (Gallina 2012; Figure 5).

This special issue of Therya is a living tribute to a person who has dedicated her life to studying one of the largest mammals of México, a person that has dedicated uncountable hours of her life to form students, who has spent days, weeks, and month in the field enduring hard conditions to collect ecological information of a wildlife species, even up to today she teaches a fieldwork course of one month. She is passionate about it, but overall, she is a person who is a good friend and who can transmit trust and confidence to students that want to continue with research on ungulates. Sonia is a great friend, and we hope that she enjoys this issue and that continues working and inspiring many of us about studying the amazing group of ungulates, a group that she chose first! (Figure 6).

Figure 6. For Dr. Gallina, family has always been very important. In this photo taken in 1998, she appears with her two sons, Alberto Jr. on her right and Alejandro on her left. At the end her husband Dr. Alberto González (Photo Pia Gallina).

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Revisiting the conservation genetics of Pampas deer (*Ozotoceros bezoarticus*)

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The Pampas deer (*Ozotoceros bezoarticus*) is a unique species of neotropical cervid, that inhabits a wide range of open habitats including grasslands, pampas, savannas, and cerrado (Brazil) from -5° to -41° S. The reduction of the area encompassed by these habitats has been dramatically reduced to less than 2 % by human activities such as agriculture, urbanization, and poaching. Three decades ago, we initiated a molecular genetic study of the Pampas deer based on representative samples from throughout their geographic range. Our aim is to reevaluate the effect that habitat fragmentation has had on gene flow among eight wildlife Pampas deer populations and one from the captive breeding centre *Estación de Cría de Fauna Autóctona* (ECFA). We examined DNA sequences from three mitochondrial markers: the control region (*D-loop*), Cytochrome b (*Cytb*), and Cytochrome Oxidase I (*COI*). Furthermore, we compared the resolution of the different mitochondrial markers to elucidate the phylogenetic and phylogeographic patterns of the species to define Evolutionary Significant Units (ESU`s). The amount of gene flow was correlated with geographic distance among groups and populations and was consistent with limited dispersal being the primary determinant of genetic differentiation between populations. Our results showed that the *D-loop* was the most appropriate marker for defining Evolutionary Significant Units. We found that the critically endangered Paraná population showed significant genetic distance from the others and revealed unique haplotypes with all the mitochondrial markers. The molecular genetic results provide a mandate for habitat restoration and design a management plan to conserve these relictual populations.

El venado de las pampas (*Ozotoceros bezoarticus*) es la única especie de cérvido neotropical, que habita en una amplia gama de hábitats abiertos que incluyen pastizales, pampas, sabanas y cerrado (Brasil) desde -5° a -41° S. Se ha reducido drásticamente su hábitat a menos del 2 % por las actividades humanas como la agricultura, la urbanización y la caza furtiva. Comenzamos hace tres décadas un estudio de genética molecular del venado de las pampas basado en muestras representativas de todo su rango geográfico. Nuestro objetivo es el de reevaluar el efecto de la fragmentación del hábitat sobre el flujo de genes entre ocho poblaciones de ciervos de las pampas silvestres y una del centro de cría en cautiverio Estación de Cría de Fauna Autóctona (ECFA). Examinamos las secuencias de ADN con tres marcadores mitocondriales: la región de control (*D-loop*), el citocromo b (*Cytb)* y el citocromo oxidasa I (*COI*). Además, comparamos la resolución de los diferentes marcadores mitocondriales para dilucidar los patrones filogenéticos y filogeográficos de las especies que definen las Unidades Evolutivas Significativas (ESU`s). El grado de flujo génico se correlacionó con la distancia geográfica entre grupos y poblaciones siendo consistente con la dispersión, la principal limitante y determinante de la diferenciación genética entre poblaciones. Nuestros resultados mostraron que *D-loop* es el marcador adecuado para definir Unidades Evolutivas Significativas. La población de Paraná se encuentra en peligro crítico de extinción al tener una distancia genética significativa de las demás y haplotipos únicos con los marcadores mitocondriales. Los resultados de la genética molecular proporcionan un mandato para la restauración del hábitat y el diseño de un plan de gestión para conservar estas poblaciones relictuales.

Keywords: Cervidae; *COI*; *Cyt b*; *D-loop*; genetic management units.

Introduction

The Pampas deer (*Ozotoceros bezoarticus*) was once a widespread and abundant species occupying a wide range of open habitats, including grasslands, pampas in Argentina and the Brazilian savanna known as the Cerrado (Cabrera 1943; Jackson 1987; Merino *et al.* 1997; González *et al.* 2002; Weber and González 2003; González *et al.* 2010). Historical records showed that this species had a wide range distribution in southeastern South America (from -5° to -41° S), reported by several naturalists mentioned in their records as Charles Darwin (Darwin 1860). The area encompassed by these habitats has been dramatically reduced to less than 2 % by human activities such as agriculture, urbanization and poaching of that present in 1900 (González *et al.* 2023). Currently, Pampas deer populations are generally small and isolated (Jackson and Langguth 1987; Pinder 1994; González *et al.* 2010, Figure 1).

Mitochondrial DNA has been the most widely used tool for reconstructing population and species histories, presumably because it is relatively easy to amplify, typically non-recombining, supposedly nearly neutral, and highly variable between and within species (Taberlet 1996; Avise 1998). Furthermore, this molecular marker of maternal inheritance is useful for the genetic analysis of populations in fragmented habitats, such as those of the Neotropical deer (Avise 1992, 1995). Most deer species usually have: 1) asymmetric genetic flow and dispersal rate, females frequently being phylopatric. 2) Females and fawns are spatial associated. 3) A strong maternal lineages structuration resulting in demographic autonomy among populations in an ecological scale (González *et al.* 1998; Márquez *et al.* 2006; González *et al.* 2010). Historical population sizes based on mtDNA control region sequences were estimated to be several magnitudes larger than present day estimates. Gene flow patterns also showed high levels of genetic differentiation among isolated populations using representative samples of Pampas deer from throughout its geographic range. In that study, González *et al.* (1998) identified five conservation genetic units for the six localities surveyed: two in Brazil (Emas National Park and Pantanal da Nhecolandia), two in Uruguay (Salto and Rocha), and one in Argentina (composed of two populations: Samborombón Bay and San Luis).

The comparative craniometric analysis of the different Pampas deer populations revealed that differentiation was concordant with the levels of genetic differentiation found with mitochondrial markers. Furthermore, two new subspecies were recognized in the Uruguayan northwestern (*O. b. arerunguaensis*, Salto Department) and eastern (*O. b. uruguayensis*, Rocha Department) grasslands (González *et al.* 2002).

This species is currently considered Near Threatened (NT) in the global IUCN Red List (González *et al.* 2016). In their southern range of South America, the most threatened populations occur in Argentina, Bolivia, Paraguay, and Uruguay with fewer than 2,500 mature individuals. This is reflected by the Red List categories of the subspecies: *O. b. celer*, -Argentina-: Endangered [EN B1ab(iii)]; *O. b. arerunguaensis* -Uruguay- [CR B1ab(iii); O. *b. uruguayensis* -Uruguay- [CR B1ab(iii)]; *O. b. bezoarticus* -Brazil- (DD); *O. b. leucogaster* - Argentina, Bolivia, Brazil; Paraguay- Near Threatened (NT) (González *et al.* 2016). The species is also included in CITES Appendix I (Giménez-Dixon 1987).

Three decades ago, we conducted the first molecular genetic study of the Pampas deer based on representative samples from throughout their geographic range (González *et al.* 1998). We aimed to deduce genetic units for conservation (Moritz 199514) and to better understand the effect of habitat fragmentation on gene flow and genetic variation. In this study, we evaluated the effects of habitat fragmentation on gene flow among eight wild Pampas deer populations and one from the captive breeding centre Estación de Cria de Fauna Autóctona (ECFA) in Uruguay. We examined DNA sequences from three mitochondrial markers: the control region (*D-loop*), Cytochrome b (*Cytb*), and Cytochrome Oxidase I (*COI*) to determine levels of genetic differentiation among isolated populations. Additionally, we compared the resolution of the different mitochondrial markers to elucidate the phylogenetic and phylogeographic patterns of the species and to define Evolutionary Significant Units (ESU`s).

Almost thirty years later, we increased the sample size from the previous locations and incorporated new sites from its wide geographic range to revisit the genetic characterization of Pampas deer by implementing additional mitochondrial markers. Our results will be providing a comprehensive approach for understanding the current genetic status and the future viability of the species.

Materials and methods

Sample collection. We analyzed 164 Pampas deer samples from eight geographic localities across the species range from Argentina, Bolivia, Brazil, and Uruguay and one captive population in Uruguay, ECFA (Figure 1; Supplementary Material Table 1). This captive stock was founded in 1980 with 10 individuals from the wild population from Salto.

DNA extraction and PCR amplification. Genomic DNA was extracted from tissue samples (50 mg, see details on Supplementary material) following González *et al.* (1998) protocol. DNA from fresh feces that were stored in ethanol and refrigerated was extracted using the commercial QIAamp® Fast DNA Stool Mini Kit (QIAGEN, Hilden, Germany) following manufacturer's instructions. All PCRs reactions were carried out in an automatic TC 9639 Thermal Cycler (Benchmark Scientific) in a mixture of final volume of 15 uL containing 3 ng/ul of sample genomic DNA, 7.5 µL of Immomix™ mastermix (Bioline), 0.5 µL of each primer (10 µM, Table 1) and ultra-pure water.

The profile consisted of an initial denaturation at 95°C for 10 min, followed by 35 cycles of denaturation at 95°C for 1 min, an annealing step for 2 min (Table 1), an extension at 72°C for 1.5 min, and a final extension at 72°C for 7 min. Positive and negative controls were included in every PCR to check for contamination in different experiments.

PCR products were purified with DNA Clean and Concentrator™ (Zymo Research™) kit and diluted to an equal final concentration using a Nanodrop 1000™ Spectrophotometer (Thermo Fisher Scientific). The amplicons were sequenced by the Sanger method on an automatic sequencer ABI 3130 (Applied Biosystems) at the Pasteur Institute (Montevideo, Uruguay) and on an automated ABI 3730xl System Sequencer (MACROGEN Inc., Korea).

Bioinformatic Analysis. Sequences were aligned and edited in MEGA11 (Molecular Evolutionary Genetics Analysis software version 11,Tamura *et al.* 2021) and compared with the nucleotide database available in the National Center for Biotechnology Information (https://www.ncbi.nlm.nih.gov/) using BLAST (Basic Local Alignment Search Tool) utility. We calculated the number of paired differences for each mitochondrial marker. Diversity indexes as haplotype, nucleotide diversities and the number of polymorphic sites were calculated using DnaSP v. 6.12.3 (Rozas *et al.* 201714). The evolutionary genetic distances among haplotypes were determined by the Kimura 2-Parameter distance (Kimura 1980). Nucleotide sequence data were analyzed using maximum parsimony (MP) and neighbor joining (NJ) in the software MEGA11 (Tamura *et al.* 2021), as well the cluster support trees were evaluated with 1000 bootstrap pseudo-replicates.

Haplotype networks. To evaluate the evolutionary relationships among haplotypes and their geographic distribution, we constructed two haplotype networks (from *Cyt*b and *D-loop* sequences) using the median-joining network approach (Bandelt *et al.* 1999) implemented on PopART 1.7 (Leigh and Bryant 2015).

Patterns of geographic subdivision and gene flow. We used AMOVA (Analysis of Molecular Variance) to deduce the significance of geographic divisions among local and regional population groupings (Excoffier *et al.* 1992; Schneider *et al.* 2000). We calculated the fixation index within populations (ΦST) and among populations (ΦSC), as well as within groups and between groups (ΦCT). We also estimated the average number of migrants per generation (using ΦST estimates between populations) to measure the degree of isolation of populations or the degree of subdivision among populations. The significance of F-statistic analogues was evaluated by 1,000 random permutations of sequences among populations. We experimented with various grouping of populations as suggested by the analysis of DNA sequences and population trees. The groupings which maximized values of ΦCT and were significantly different from random distributions of individuals were assumed to be the most probable geographical subdivisions (Excoffier *et al.* 1992; Schneider *et al.* 2000).

Gene flow within and among regions was approximated as Nm, the number of female migrants occurring between populations units per generation and was estimated using the expression Fst = 1/ (1+2Nm) where N is the female effective population size and m is the female migration rate (Slatkin 1987; 1993; Baker *et al.* 1994). We used pairwise estimates of ΦST as surrogates for FST among regional groupings of populations (*e. g.* Stanly *et al.* 1996).

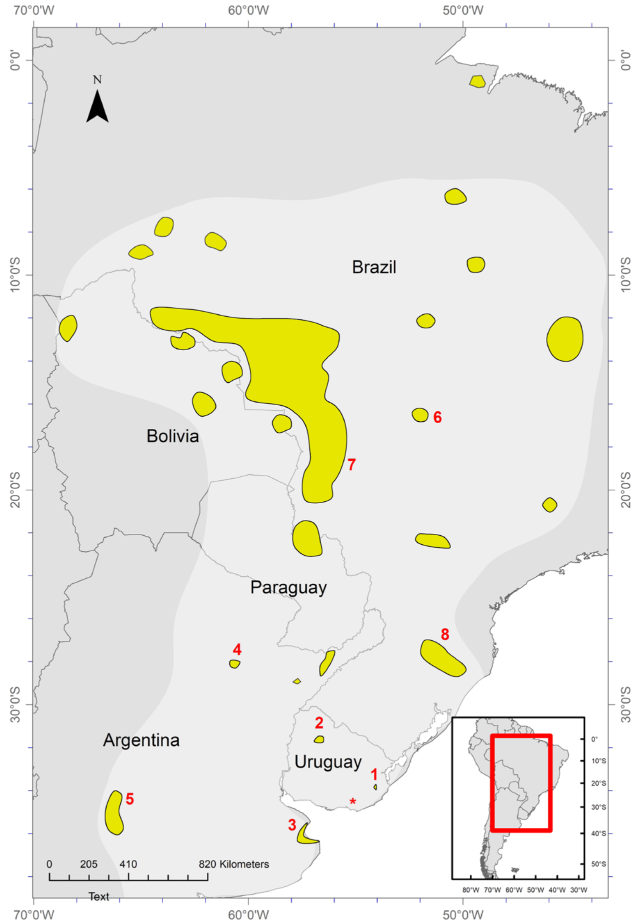

Figure 1. Distribution map of Pampas deer populations. Grey shadow indicated the presumed past distribution of the species. Yellow shaded areas represent the current distribution. Numbers indicated the 8 localities sampled: 1. Rocha; 2. Salto; 3. Samborombón Bay; 4. Santa Fé; 5. San Luis; 6. Emas National Park; 7. Pantanal da Nhecolandia; and 8. Paraná. Asterisk (*) shows ECFA (Estación de Cría y Fauna Autóctona) locales in Maldonado, Uruguay.

Phylogenetics and evolutionary rate estimation of three mtDNA regions. The phylogenetic relationships and evolutionary rates based on three markers (*D-loop*, *Cytb* and *COI*) were estimated using the Neighbour Joining algorithm. Trees were drawn to scale with the length of the branches in the same units as the evolutionary distance used to infer the phylogenetic tree. The genetic distances were calculated using the Kimura 2-Parameters algorithm and the units are the number of base substitutions per site.

We used the divergence time between the Pampas deer *O. bezoarticus* and the grey brocket deer *Subulo gouazoubira* based on Duarte *et al.* (2008), to estimate the evolutionary rate of the three mitochondrial markers *Cytb*, *COI*, and *D-loop*.

Table 1. Primers sequences annealing temperature and amplicon length.

Mitochondrial region	Primer sequence	Annealing temperature (°C)	Amplicon length (bp)	Reference
COI	LCO1490 5' -GGTCAACAAATCATAAAGATATTGG-3´ HC02198 5' - TAAACTTCAGGGTGACCAAAAAATCA-3´	55	710	Folmer *et al.* 1994
Cytb	H15149 5'-GCCCCTCAGAATGATATTTGTCCTCA-3' L14724 5'- CGAAGCTTGATATGAAAAACCATCGTTG- 3'	57	480	Maldonado *et al.* 1995
D-loop	Thr-L 15926 5' -CAATTCCCCGGTCTTGTGAACC -3' DL-H 16340 5' -CCTGAAGTAGGAACCAGATG -3'	50	603	Kocher *et al.* 1989

The evolutionary rate of *Cytb* was estimated using sequences deposited in GenBank by Duarte *et al.* (2008; accession numbers: DQ789173-DQ789231) together with additional sequences retrieved from GenBank and employed by the authors in the phylogenetic analysis. To calculate the evolutionary rate of the *D-loop* mitochondrial region, we used Pampas deer sequences and grey brocket deer available in GenBank (Accession numbers: AF012556-AFO12602).

Results

We sequenced 138 individuals of the mitochondrial control region (an amplicon of 603 bp). We analyzed a 423 bp fragment and found 87 different haplotypes in the eight localities defined by base-pair substitutions (Table 2). As was reported previously, this species has a polymorphic dinucleotide TA repeat sequence within this amplicon that had four to eight tandem repeats beginning at nucleotide position 186, with position 1 as the first nucleotide of our control region sequence (González *et al.* 1998). Because the same allele sizes were found in divergent sequences from geographically distant populations (*e. g.* Emas and Rocha) this region has a high degree of homoplasy and we excluded the tandem repeat region from the analysis, leaving 423 base pairs of DNA sequence to be analyzed.

Patterns of geographical subdivision and gene flow revealed by D-loop region. We analyzed samples from nine geographic locations that showed high levels of polymorphism (Table 3). The highest value obtained for the average number of pairwise differences within population (PiX) was in the Paraná samples and the lowest in Samborombón Bay.

Geographic distribution of control region sequences. The control region haplotypes were perfectly segregated as no locality shared haplotypes except for the Salto population that shared haplotypes with the individuals from the Breeding center ECFA. Sequences from the same locality tend to be clustered together in minimum spanning networks (Figure 2). The nine groups according to the haplotype's geographic distribution and the taxonomic criteria were arrange in six populations (Groups: 1 Salto and EFCA, 2 Rocha, 3: Paraná. 4: Emas, 5: Pantanal da Nhecolandia and North Argentina, and 6: Samborombón Bay and San Luis (Table 4). This is because the haplotype diversity present in each population, where most of the haplotypes found for each, are unique and not shared with other populations.

The AMOVA results showed high levels of differentiation among populations within groups (ΦST = 0.439), among groups (ΦSC = 0.240), and as well as within populations (ΦCT = 0.262; Table 5). The Argentinean populations (Samborombón Bay and San Luis) clearly are more closely related to each other than are those from Brazil or Uruguay.

Genetic differences among and within populations. The mtDNA control region showed a rapidly evolving pattern compared with more conserved genes such as the *COI* and *Cytb*. The *COI* gene showed phylogenetic relationships among Pampas deer populations in the recent past, where many migrants per generation were exchanged between populations, and population genetic structure

Table 2. Pampas deer individuals from locations analyzed *Dloop* haplotype, repetitions subspecies and Accession Numbers.

Location	Haplotype	Sequences	Repeated	Subspecies	Acc. number
Rocha- Uruguay	SGO2		1	*O. b. uruguayensis*	AF012589.1
33°45'S; 54°02'W	SGO7	SG13	2	*O. b. uruguayensis*	AF012591.1
	SG19	SG15	2	*O. b. uruguayensis*	AF012590.1
	SG34		1	*O. b. uruguayensis*	AF012588.1
	SG91		1	*O. b. uruguayensis*	OR805768
	SG109		1	*O. b. uruguayensis*	OR528919
	SG118		1	*O. b. uruguayensis*	OR528922
	SG126		1	*O. b. uruguayensis*	OR528923
	SG134	SG117, SG123, SG124, SG125, SG127, SG128, SG129, SG130, SG131, SG132, SG133	12	*O. b. uruguayensis*	OR805767
	SG1738		1	*O. b. uruguayensis*	AF012597.1
	SG245		1	*O. b. uruguayensis*	OR528924
	SG329		1	*O. b. uruguayensis*	OR528927
EL TAPADO- Uruguay	SG01		1	*O. b. arerunguaensis*	AF012601.1
31°65'S; 56°43'W	SG04	SG60, SG110, SG111, SG251, SG259, SG274, SG289ECFA, SG319, SG320, SG370, SG371, SG372, SG375, SG382, SG383, SG384	17	*O. b. arerunguaensis*	AF012583.1
	SG09		1	*O. b. arerunguaensis*	AF012598.1
	SG10		1	*O. b. arerunguaensis*	AF012586.1
	SG11		1	*O. b. arerunguaensis*	AF012587.1
	SG16		1	*O. b. arerunguaensis*	AF012585.1
	SG17		1	*O. b. arerunguaensis*	AF012602.1
	SG20		1	*O. b. arerunguaensis*	AF012600.1
	SG49		1	*O. b. arerunguaensis*	AF012596.1
	SG76	SG328, SG330, SG331, SG377, SG380	6	*O. b. arerunguaensis*	OR528934
	SG95		1	*O. b. arerunguaensis*	OR528938
	SG112		1	*O. b. arerunguaensis*	OR528920
	SG113		1	*O. b. arerunguaensis*	OR528921
	SG378	SG381	2	*O. b. arerunguaensis*	OR528929
	SG379		1	*O. b. arerunguaensis*	OR528930

Table 2. Continuation...

Location	Haplotype	Sequences	Repeated	Subspecies	Acc. number
	SG1623		1	*O. b. arerunguaensis*	AF012584.1
ECFA -Uruguay	SG252		1	*O. b. arerunguaensis*	OR528925
34°48'S; 55°14'W	SG281		1	*O. b. arerunguaensis*	OR528926
	SG369		1	*O. b. arerunguaensis*	OR528928
	SG385		1	*O. b. arerunguaensis*	OR528931
Paraguay Unknown location	SG94		1	*O. b. leucogaster*	OR528937
PARANA- Brasil	FB39	FB40, FB42, FB49, FB52	5	*O. b. sp.*	OR528912
24°11'S; 49°46'W	FB38	FB41	2	*O. b. sp.*	OR528911
	FB46	FB47, FB48	3	*O. b. sp.*	OR528913
	FB51		1	*O. b. sp.*	OR528914
EMAS- Brasil	SP13	SP12	2	*O. b. bezoarticus*	AF012558.1
18°15'S; 52°53'W	SP14	SP18	2	*O. b. bezoarticus*	AF012559.1
	SP15		1	*O. b. bezoarticus*	AF012560.1
	SP17	SP20	2	*O. b. bezoarticus*	AF012561.1
	SP19		1	*O. b. bezoarticus*	AF012599.1
	SP51		1	*O. b. bezoarticus*	AF012592.1
	SP52		1	*O. b. bezoarticus*	AF012562.1
	SP53		1	*O. b. bezoarticus*	AF012593.1
	SP54		1	*O. b. bezoarticus*	AF012563.1
	SP55		1	*O. b. bezoarticus*	AF012564.1
	SP56		1	*O. b. bezoarticus*	AF012565.1
PANTANAL- Brasil	SP36		1	*O. b. leucogaster*	AF012566.1
18°15'S; 52°53'W	SP38		1	*O. b. leucogaster*	AF012567.1
	SP41		1	*O. b. leucogaster*	AF012568.1
	SP42		1	*O. b. leucogaster*	AF012569.1
	SP43		1	*O. b. leucogaster*	AF012571.1
	SP44		1	*O. b. leucogaster*	AF012570.1
	SP40	SP45, SP47, SP48, SP49	5	*O. b. leucogaster*	AF012572.1
	SP46		1	*O. b. leucogaster*	AF012573.1
	SP50		1	*O. b. leucogaster*	AF012574.1
SAMBOROMBON- Argentina	SG24		1	*O. b. celer*	AF012581.1
35°30'S; 56°45'W	SG39		1	*O. b. celer*	AF012594.1
	SG40		1	*O. b. celer*	AF012578.1
	SG42		1	*O. b. celer*	AF012579.1
	SG43		1	*O. b. celer*	AF012580.1
	SG52		1	*O. b. celer*	AF012582.1
	SG72		1	*O. b. celer*	OR528933
SAN LUIS- Argentina	SG18	SG84, SG105	3	*O. b. celer*	AF012576.1
34°22'S; 65°44'W	SG66	SG85, SG88	3	*O. b. celer*	AF012575.1
	SG67		1	*O. b. celer*	AF012595.1
	SG68		1	*O. b. celer*	AF012577.1
	SG83		1	*O. b. celer*	OR528935
	SG86		1	*O. b. celer*	OR528936
	SG104		1	*O. b. celer*	OR805766
	VEN006		1	*O. b. celer*	OR528939
	VEN012		1	*O. b. celer*	OR528940
	VEN013		1	*O. b. celer*	OR528941
	VEN015		1	*O. b. celer*	OR528942
	VEN035		1	*O. b. celer*	OR528943
	VEN040		1	*O. b. celer*	OR528944
	VEN049		1	*O. b. celer*	OR528945
	VEN057		1	*O. b. celer*	OR528946
	VEN061		1	*O. b. celer*	OR528947
	VEN067		1	*O. b. celer*	OR528948
	VEN070		1	*O. b. celer*	OR528949
SANTA FE- Argentina	PV2		1	*O. b. leucogaster*	OR528916
31°38'S; 60°41'W	PV3		1	*O. b. leucogaster*	OR528917
	PV7		1	*O. b. leucogaster*	OR528918
CORRIENTES- Argentina	PV11		1	*O. b. leucogaster*	OR528915

Table 3. Above diagonal: Average number of pairwise differences between populations (PiXY). Diagonal elements: Average number of pairwise differences within population (PiX). Below diagonal: Corrected average pairwise difference (PiXY-(PiX + PiY)/2).

	1	2	3	4	5	6	7	8	9
1	**6.009**	6.872	10.710	8.014	13.920	10.893	8.975	11.619	15.208
2	2.261	**3.213**	10.824	7.445	12.923	11.303	9.234	8.312	11.598
3	5.666	7.178	**4.079**	9.093	14.633	11.552	10.923	14.953	18.434
4	3.792	4.620	5.836	**2.435**	10.627	9.139	9.159	11.706	15.481
5	5.489	5.889	7.167	3.982	**10.853**	14.031	12.354	16.087	20.244
6	3.778	5.586	5.402	3.810	4.493	**8.222**	11.593	15.540	18.929
7	1.593	3.250	4.506	3.563	2.549	3.104	**8.756**	12.437	15.844
8	4.816	2.907	9.116	6.691	6.863	7.631	4.261	**7.596**	12.433
9	5.299	3.087	9.489	7.359	7.913	7.913	4.561	1.730	**13.810**

1. Rocha; 2. Salto; 3. ECFA; 4. Samborombóm Bay; 5. North Argentina (Santa Fe); 6. San Luis; 7. Emas National Park; 8. Pantanal da Nhecolandia; and 9. Paraná.

was almost non-existent. On the other hand, the characteristic *D-loop* hypervariable region reflects the phylogenetic relationships among contemporary populations of Pampas deer, where populations are genetically isolated without gene flow.

The results of the different mitochondrial markers showed that the *D-loop* has unique haplotypes within populations. The haplotype diversity value for *COI* gene was 0.35, the average nucleotide diversity by site was $\pi = 0.00391$ (s. d. = 0.0000003). The populations that exhibited the highest values were Paraná, Rocha, San Luis, and Salto.

We found 18 haplotypes of 63 samples in the *Cytb* gene sequence fragment of 417 bp in Pampas deer populations, and a diversity index of 0.28 (Table 6). These three mitochondrial markers provide resolution at different scales and allow us to elucidate different scenarios and the spatial connections of haplotypes to make inferences about demographic and evolutionary processes of this species (Figure 2, Table 7).

On the other hand, we found lower evolutionary rates for the *COI* gene than *Cytb*. From the nucleotide differences matrix between pairs of *COI* sequences we determined 18 haplotypes. The minimum spanning network constructed has the H1 and H5 haplotypes with an ancestral position and has a wide distribution (Figure 2). This is consistent in terms of geographic location of the different populations. The number of migrants per generation that is exchanged between these populations is less than one migrant per generation, in the case of Paraná and Santa Fe was the lowest value of migrants, Nm = 0.286.

The AMOVA results for the *CO*I region analysis showed a lack of structure amongst populations. To explain this, we put forward the hypothesis that this lack of structure detected among populations is that millions of years ago these populations were connected. The mitochondrial control region (*D-loop*) analysis shows a later stage to this connection between haplotypes of the populations occurring after isolation by habitat fragmentation. The existence of high genetic variation featuring Pampas deer today indicates that the decrease in population size was recent.

Table 4. Migrants estimations (M = Nm for haploid data) in bold above diagonal. The average number of pairwise differences within population (PiX) is shown on the diagonal numbers in italic. Below diagonal, Slatkin (1995) linearized FSTs as t/M=FST/(1-FST).

	1	2	3	4	5	6
1	*6.14159*	**0.48088**	**0.76385**	**0.66852**	**1.41493**	**0.96551**
2	1.03976	*4.07854*	**0.31033**	**0.44385**	**0.70567**	**0.46762**
3	0.65458	1.61120	*2.43542*	**0.92304**	**1.18.19**	**0.74569**
4	0.74792	1.12650	0.54169	*10.85335*	**1.54293**	**0.83842**
5	0.35337	0.70854	0.42116	0.32406	*9.68892*	**0.98286**
6	0.51786	106.924	0.67052	0.59636	0.50872	*12.79634*

References: Groups 1. El Tapado and EFCA, 2. Los Ajos, 3. Paraná, 4. Emas, 5. Pantanal and North Argentina, and 6. Buenos Aires and San Luis Provinces.

Discussion

Past Genetic Variation. The direct ancestor of the Pampas deer first appeared in the Pampean Formation during the Pleistocene and may be associated with a glacial event approximately 2.5 million years ago at the boundary between the Gauss and Matuyama chrons (Bonadonna and Alberdi 1987; Marshall *et al.* 1983). For analyzing the past genetic variation, we used two mitochondrial markers the *Cytb* and *COI* genes.

The divergence time estimated between the two species, Pampas deer and gray brocket deer (*Subulo gouazoubira*) was approximately 4.77 million years. The evolutionary rate found for the *Cytb* gene is 1.07 x10^{-8} than it found

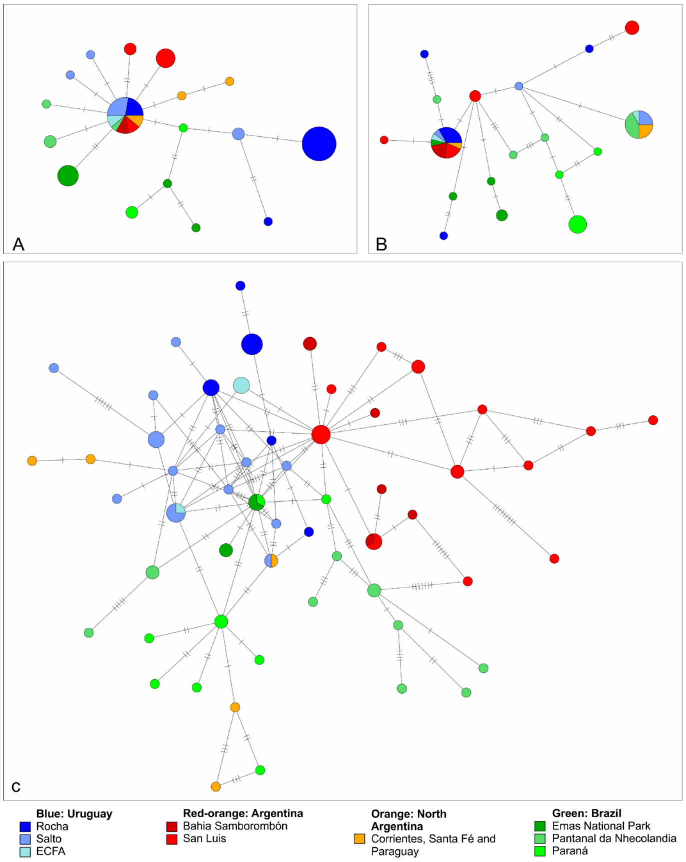

Figure 2. Minimum Spanning haplotype networks of mitochondrial regions showing the genetic relationships between Pampas deer individuals: A) Cytb b) COI and C) D loop. Mutational steps between haplotypes are shown as marks across connection lines. Circle sizes are proportional to haplotype frequencies and colours represent the respective sample localities.

Table 5. Summary of Analysis of Molecular Variance (AMOVA) results for *D-loop* region analysis in different groupings of the populations. Fixation indexes: between groups (ΦSC), among populations within groups (ΦST), within populations (ΦCT).

Source of Fixation	**D.f.**	**Sum of squares**	**Variance components**	**Percentage of variation**	**Fixation indexes**
Among groups	5	301.377	1.69008 Va	26.25	ΦSC : 0.240022 *p-value* = 0.00000
Among populations within groups	3	38.823	1.14089 Vb	17.72	ΦST : 0.43964 *p-value* = 0.00000
Within populations	126	454.658	3.60840 Vc	56.04	ΦCT: 0.2624 *p-value* = 0.00000
Total	134	794.858	6.43937		

Note: Distance method: Kimura 2P. $p < 0.000001$, after 1023 permutations.

for the *COI* gen 9.6 x10 $^{-9}$ nucleotide substitution events per site per year would be happening (See Figure 2). The sequences for the *D loop* regions analyzed with 423 base pairs fragments showed an evolutionary rate of 1.4 x10 $^{-8}$. The obtained divergence values for Pampas deer using the two mitochondrial markers, show that, as expected, the *D-loop* evolves faster than the *COI* gene.

The inference through the calculated evolutionary rate is that the *COI* gene could reflect another stage of the Pampas deer population history being more appropriate to analyze phylogenetics relationships. *Cytb* and *COI* genes are not able to resolve recent demographic events linked to habitat fragmentation (Tobe *et al.* 2010). Estimation of migrants per generation showed a high gene flow among the populations studied, and because of this, we found less genetic population structure according to the *COI* gene.

On the other hand, nucleotide diversity per site for Pampas deer through the *COI* gene is 0.391 %. The Paraná population had the highest nucleotide diversity value (0.87 %) while the lowest one was evidenced in the Emas population (0.16 %). The nucleotide diversity among populations of Pampas deer, through analysis of the control region obtained by González *et al.* (1998), ranged between 1.1 % to 2.5 %, and Argentina's population had the lowest value. Their slower evolutionary rate than *D-loop* showed that existing populations in the past maintained a closer relationship, showing that the structure is a recent phenomenon and could be a consequence of genetic populations' isolation. A similar finding was observed in another endangered species like the Asian elephant (*Elephas maximus*), whose populations are rapidly declining and *D-loop* marker was suitable for analyzing genetic variation and to infer other processes such as introgression/hybridization (Srikulnath *et al.* 2023).

Our results confirm the previous findings by González *et al.* (1998) that the control region of the Pampas deer is one the most polymorphic of any mammal. The large number of haplotypes and high level of nucleotide diversity in the Pampas deer suggest that this species was more abundant and widespread in the recent past. Since variability was lost rapidly from these populations, sizes have remained small

Table 6. Pampas deer haplotypes of partial *COI* gen.

Haplotype	**Individuals**	**Repetitions**	**Subspecies**	**Accession Number**
H1	SG38, SG52, SG56, SG89, SG95, SG100, SG105, SG123, SG144, SG147, SG150, SG207, SG217, PV11, FB03	15	*O. b. arerunguaensis* *O. b. bezoarticus* *O. b. celer,* *O. b. leucogaster* *O. b. uruguayensis* *O. b. sp.*	OR659038
H2	SG85, SG103	2	*O. b. celer*	OR659039
H3	SG83, SG99, SG102	3	*O. b. celer*	OR659040
H4	SG104	1	*O. b. celer*	OR659041
H5	PV2, PV3, PV7 SP13, SP15, SP31, SP32, SP56, SG227, SG48, SG49, SG1623	12	*O. b. arerunguaensis* *O. b. bezoarticus* *O. b. leucogaster* *O. b. uruguayensis*	OR659042
H6	SP35, SP36, SP37, SP46, SP50	5	*O. b. leucogaster*	OR659043
H7	SP48	1	*O. b. leucogaster*	OR659044
H8	SP40	1	*O. b. leucogaster*	OR659045
H9	FB52	1	*O. b. sp.*	OR659046
H10	FB47, FB49	2	*O. b. sp.*	OR659047
H11	FB51	1	*O. b. sp.*	OR659048
H12	SG143	1	*O. b. uruguayensis*	OR659049 OR659050
H13	SG13	1	*O. b. uruguayensis*	OR659051
H14	SG109	1	*O. b. uruguayensis*	OR659052
H15	SG10	1	*O. b. arerunguaensis*	OR659053
H16	SP27	1	*O. b. bezoarticus*	
H17	SP14	1	*O. b. bezoarticus*	OR659054 OR659055
H18	SP25	1	*O. b. bezoarticus*	
TOTAL		**51**		

References: Haplotype (H) identification, individuals ID, subspecies and the GenBank accession numbers.

Table 7. Pampas deer haplotypes of partial *Cyt b* gen.

Haplotype	Sequences	Repetitions	Subspecies	Acc. number
I	SG02, SG04, SG07, SG13, SG18, SG40, SG43, SG60, SG105, SG111, SG112, SG113, SG126, SG1623, SG320, SP19, P15, PV3, PV6	19	*O. b. arerunguaensis* *O. b. bezoarticus* *O. b. celer* *O. b. leucogaster* *O. b. uruguayensis*	MH593537.1
II	SG09	1	*O. b. arerunguaensis*	OR546559
III	SG19, SG34, SG91, SG117, SG123, SG124, SG125, SG127, SG128, SG129, SG130, SG131, SG132, SG133, SG134, SG1738	16	*O. b. uruguayensis*	OR546557
IV	SG44	1	*O. b. arerunguaensis*	OR546556
V	SG94	1	*O. b. leucogaster*	OR546555
VI	SG95, SG378	2	*O. b. arerunguaensis*	OR546554
VII	SG109	1	*O. b. uruguayensis*	OR546558
VIII	SP22, SP53	2	*O. b. bezoarticus*	OR546553
IX	SP36, SP42	2	*O. b. leucogaster*	OR546552
X	SP38	1	*O. b. leucogaster*	OR546551
XI	SP55	1	*O. b. bezoarticus*	OR546550
XII	FB21, FB38, FB41, FB48, FB49, FB52	6	*O. b.sp*	OR546563
XIII	FB39	1	*O. b. sp*	OR546562
XIV	FB51	1	*O. b. sp*	OR546561
XV	PV2	1	*O. b. leucogaster*	OR546560
XVI	VEN035	1	*O. b. celer*	OR546549
XVII	VEN012	1	*O. b. celer*	DQ789191.2
XVIII	VEN057VEN013, VEN015, VEN049, VEN040	5	*O. b. celer*	OR546548
Total		63		

References: Left column number of haplotype identification, the repetitions, subspecies and the GenBank accession numbers. Total number of *Cyt b* sequences obtained.

for long periods of time (Ballou 1994). However, currently Pampas deer are endangered in Argentina, south of Brazil and Uruguay, with fewer than 2,500 mature individuals. The levels of genetic diversity in populations from these locations suggest that historic population sizes were several orders of magnitude larger, and that recently populations have decreased dramatically, thus providing a strong mandate for restoration and augmentation. This population decline was due to habitat loss and unregulated hunting beginning in the last century and, most recently, to control efforts by ranchers who believe that deer compete with livestock. Pampas deer numbers might increase if protected from poaching in areas where natural habitats remain and if some grazing land, as a buffer, could be designated for dual use by deer and livestock (Castro *et al.* 2021).

González *et al* (1998) had estimated the historic population size based on the relation $\boldsymbol{\Theta} = 2N\mu$ where N is the effective number of females and µ is the mutation rate per site. Using coalescent likelihood methods incorporated in the COALESCE program by Kuhner *et al.* (1995), the parameter $\boldsymbol{\Theta}$ can be calculated from a population sample of DNA sequences. Our estimate of 2Nµ is 0.173 and assuming a mutation rate of 2.5×10^{-8} per nucleotide site per year for the control region (based on sequence divergence between the Pampas and brocket deer, as above), the effective number of breeding females would be approximately 3,460,000. The total census size of females is likely to be at least double this value (*e. g.* Nunney and Elam 1994). Therefore, both comparative and theoretical estimates indicate a substantial reduction in population size has occurred since the total present-day number of deer is between 64,000 and 80,000 individuals (González *et al.* 2010).

Conservation Implications. Genetic units for conservation have been based on criteria such as reciprocal monophyly (evolutionary significant units) or differences in genotype frequency (management units; Moritz 1995). The numerous reticulations in the minimum spanning network (Figure 2) show that none of the neighboring Pampas deer populations are reciprocally monophyletic and indicate the occurrence of past episodes of migration.

The highest level of genetic differentiation was observed in Uruguayan populations, especially the Rocha population. This differentiation is explained, with the UPGMA algorithm, establishing a divergence time of 2 million years and considering mean genetic distance and *D-loop* mutation rate (Figure 3). Probably this separation is linked to events occurring during the Pleistocene.

However, except for the Argentinean populations from Samborombón Bay and San Luis, belonging to *O. b. celer*, and North Argentinean and Pantanal belonging to *O. b. leucogaster*, all the other populations are significantly or marginally differentiated, thus they might be classified as management units experiencing low to modest rates of gene flow. A pronounced sequence divergence exists between Brazilian populations from Emas National Park and Pantanal da Nhecolandia and North Argentinian populations (Figure. 3), corresponding to the different subspecific designation recognized by Cabrera (1943). These populations may have been historically isolated in different habitats. In fact, the population in Emas National Park is located in the

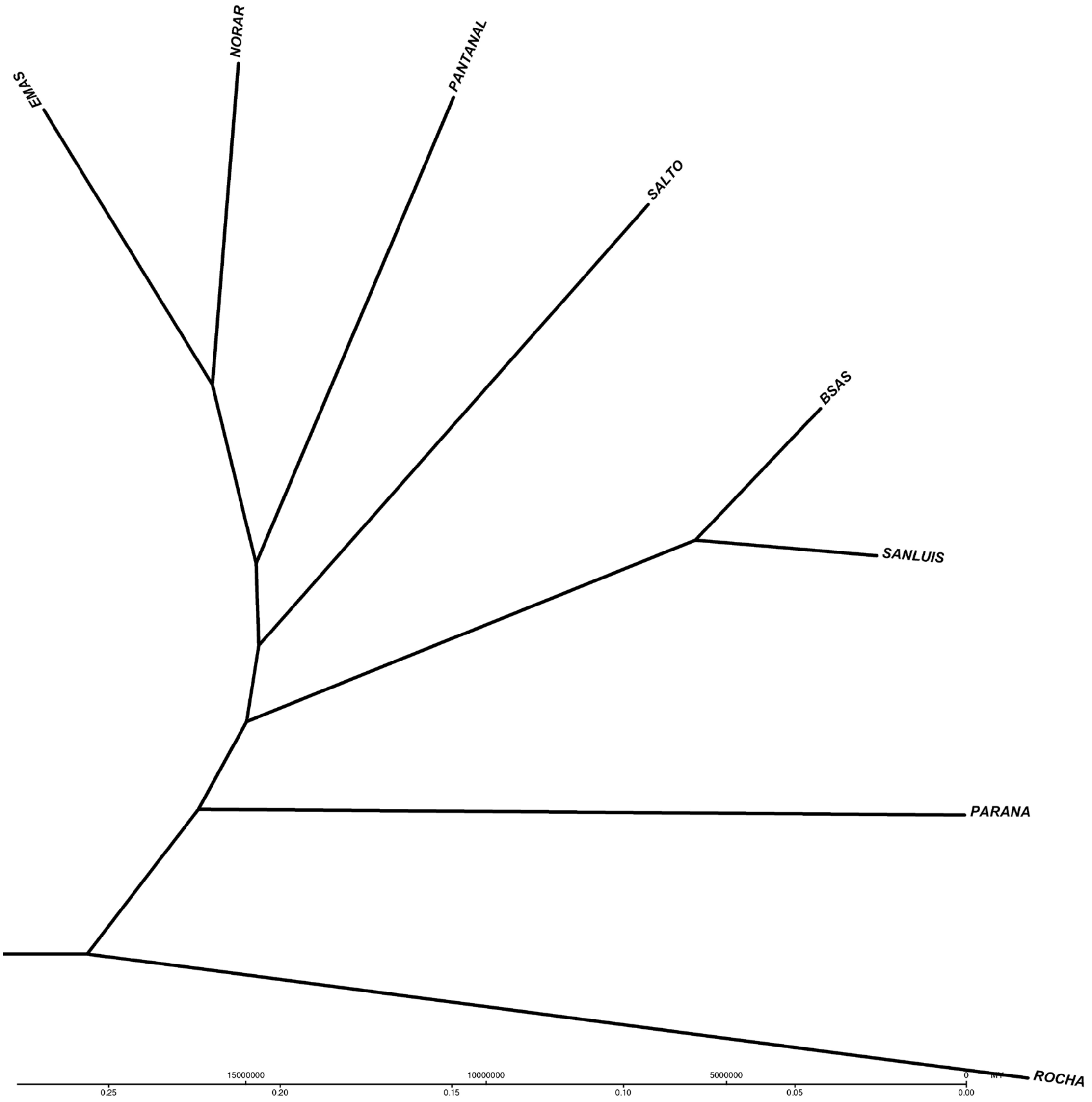

Figure 3. Evolutionary relationships of populations. The optimal tree with the sum of branch length = 1.43701786 is shown. The tree is drawn to scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree. The evolutionary distances were estimated with Kimura 2 parameter and the analyses were conducted in MEGA11.

cerrado of central Brazil, 650 to 1,000 m elevation, which has a distinct dry season, whereas the population in El Pantanal is found in wetlands below 100 m. Although based on limited evidence, these physiological differences may indicate differences in the timing of the reproductive cycle and hence, if of genetic origin, may be an important reason why the populations should not be interbred or used as a source for cross-translocation. Supporting differentiation between these populations are discrepancies in their physiology. In the Emas National Park population, antlers are shed in April, whereas in the Pantanal this occurs in June and July (González *et al.* 2010). The individuals belonging to Paraná showed differentiated genetic distance and low number of migrants less than 1. This population is critically endangered, making it urgent to reduce activities such as poaching that may be severely affecting its conservation, and to promote conservation management actions and design mitigation measures to assure long-term survival.

Our results suggest that Pampas deer have the potential to exist over a much greater area and historical data demonstrate a much wider distribution for the species. Therefore, if the goal of conservation is to maintain long term population stability and preserve genetic variation, conservation efforts should focus on the restoration of deer habitats over a wide geographic area. Finally, we conclude that the genetic dynamic shown by Pampas deer allows us to identify the *D-loop* as the marker of choice for defining management units for conservation of this species.

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Following the trail of the grey brocket deer (*Mazama gouazoubira*) in Argentina: new locality records, activity patterns and habitat use

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The brown brocket deer (*Mazama gouazoubira*) is a species of neotropical ungulate that inhabits several countries in South America. In Argentina, it is distributed in the northern portion of the country, while historical records do not mention it in the province of Mendoza. However, in the Categorization of Mammals of Argentina (2019), the NE of Mendoza is proposed as a potential distribution area of the species. In this work we confirm the presence of the brown brocket deer in the province of Mendoza (locality of Desaguadero - RAMSAR Site), and we also evaluate its activity patterns and habitat preferences. We established 1 km^2 grids in three environments: salt flats, shrublands, and forests. A camera trap ($n = 38$) was placed in each grid, active for 55 days between October 2022 and April 2023 for fauna survey. In addition, NDVI values (Normalized Difference Vegetation Index) were calculated from LANDSAT-8 images as an estimator of vegetation cover for each grid. We obtained 25 independent records of 11 individuals (5 males and 6 females) from a sampling effort of 51,072 hours of camera operation (2,090 night/trap = 55 night * 38 camera). The males were individually identified based on the presence of antlers, their size, dimension and texture, while the females by their body size and gestation condition. In terms of activity patterns, we observed that these animals are most active in the afternoon (16 to 19 hs) and morning (8 to 9 hs), avoiding the moments of greatest solar radiation (Rayleigh-test $r = 0.99$, $p < 0.001$). NDVI was significantly different among the three environments ($Chisq = 32.98$; $p < 0.001$), with the forest having the highest vegetation cover. Finally, generalized linear models with binomial distribution were used to evaluate the effect of vegetation on the presence of brown brocket deer. We found that the higher the NDVI value, the higher the probability of presence of the deer ($z = 2.27$; $p < 0.05$). These results expand the distribution of the species and increase the diversity of mammals for Mendoza province, which generates added value to the planning of the proposed protected area for Desaguadero in the RAMSAR site Lagunas de Guanacache, Desaguadero y del Bebedero.

La corzuela parda (*Mazama gouazoubira*) es una especie de ungulado neotropical que habita varios países de Sudamérica. En Argentina se distribuye en la porción norte del país, mientras que los registros históricos no la mencionan en la provincia de Mendoza. Sin embargo, en la Categorización de Mamíferos de Argentina (2019) se propone el NE de Mendoza como un área de distribución potencial de la especie. En este trabajo confirmamos la presencia de la corzuela parda en la provincia de Mendoza (localidad de Desaguadero - Sitio RAMSAR), y evaluamos también sus patrones de actividad y las preferencias de hábitat en dicha provincia. Para los relevamientos de fauna se establecieron cuadrículas de 1 km^2 en 3 ambientes: salares, arbustales y bosques. En cada cuadrícula se colocó una cámara trampa ($n = 38$) activa durante 55 días entre octubre 2022 y abril 2023. Además, para cada una de las cuadrículas se calcularon valores de NDVI (Normalized Difference Vegetation Index) a partir de imágenes LANDSAT-8 como un estimador de la cobertura vegetal. De un esfuerzo de muestreo de 51,072 horas de operación de cámara (2,090 noches/trampa = 55 noches * 38 cámaras), obtuvimos 25 registros independientes de 11 individuos (5 machos y 6 hembras). Los machos fueron identificados a nivel individual a partir de la presencia de astas, tamaño, dimensión y textura de las mismas, mientras que las hembras por su contextura, tamaño corporal y condición gestacional. En cuanto a los patrones de actividad, observamos que estos animales presentan mayor actividad durante la tarde (16 a 19 hs) y la mañana (8 a 9 hs), evitando los momentos de mayor radiación solar (Rayleigh-test $r = 0.99$, $p < 0.001$). En los tres ambientes estudiados, el NDVI fue significativamente diferente ($Chisq = 32.98$; $p < 0.001$), siendo el bosque el de mayor cobertura vegetal. Finalmente, se utilizaron modelos lineales generalizados con distribución binomial para evaluar el efecto de la vegetación en la presencia de corzuela parda. Encontramos que cuanto mayor fue el valor de NDVI, mayor fue la probabilidad de presencia de la corzuela ($z = 2.27$; $p < 0.05$). Estos resultados amplían la distribución de la especie e incrementan la diversidad de mamíferos para la provincia de Mendoza, lo cual genera valor agregado a la planificación del área protegida propuesta para Desaguadero en el sitio RAMSAR Lagunas de Guanacache, Desaguadero y del Bebedero.

Keywords: Activity patterns; brown brocket deer; forest; habitat use; Mendoza.

Introduction

The brown brocket deer (*Mazama gouazoubira*), also known as the "corzuela parda", is a neotropical ungulate species that inhabits various countries of South America, such as Brazil, Bolivia, Paraguay, Uruguay, and Argentina (Silva-Caballero and Ortega 2022; Figure 1). This species occupies a great variety of habitats and ecoregions, such as the Chaco, Pantanal, Cerrado, Espinal, Bosque Atlántico, Pampas, and Caatinga (Silva-Caballero and Ortega 2022; and references in there). Due to its wide distribution and ecological importance, the "corzuela parda" has attracted considerable attention from researchers aiming to understand its biology, behavior, and conservation status. In recent years, the "corzuela parda" had been categorized as Least Concern, both internationally (IUCN; Black-Décima and Vogliotti 2016), and locally in Argentina (CMA; Juliá *et al.* 2019), Brazil (Duarte *et al.* 2012), Paraguay (Asociación Paraguaya de Mastozoología y Secretaría del Ambiente 2017), and Bolivia (Aguirre *et al.* 2009).

The "corzuela parda" is one of the largest herbivores in native forests of South America; it feeds on a wide variety of species, being mostly a browser but with several pulses of frugivory (Serbent *et al.* 2011; Silva-Caballero and Ortega 2022), thus becoming an important seed disperser agent. It exhibits a predominantly solitary behavior although some authors suggest the presence of complex social interactions, including territoriality and mating systems (Juliá 2002; Black-Décima *et al.* 2010). Its lifestyle is mainly crepuscular, with individuals primarily active during dawn and dusk (Leeuwenberg *et al.* 1999; Rivero *et al.* 2005). The species' adaptability to different environments has allowed it to thrive across a diverse range of ecosystems, including forested habitats, tropical and subtropical forests, as well as grasslands and savannas. This species tends to occupy areas in good conservation status (Periago *et al.* 2015), or areas providing some cover, such as riverine forests (Silva-Caballero and Ortega 2022) becoming an important indicator species for assessing ecosystem health. However, "corzuela parda" also uses modified habitats like agricultural patches-lots or fragmented forests (Juliá *et al.* 2019; Silva-Caballero and Ortega 2022). Despite its ecological significance, the brown brocket deer has faced numerous challenges, including habitat loss, fragmentation, and hunting pressure, which have led to population declines in certain regions (Juliá 2002; Juliá *et al.* 2019).

In Argentina, the "corzuela parda" had been recorded in five biogeographic regions: Chaqueña, Espinal, Paranaense, Monte, and Yungas (Chebez and Johnson 1985; Romero and Chatellenaz 2013; Cirignolli *et al.* 2011), but most research on life history had been done in the Yungas (Tucumán province; Black-Décima 2000; Juliá 2002; Black-Décima *et al.* 2010) and the Chaco regions (Códoba province; Periago and Lyenaud 2009a,b; Serbent *et al.* 2011; Periago *et al.* 2012; 2015). Barquez et al (1991) mentioned its presence in Mendoza province, but there were not accurate records that prove its presence further west of the Desaguadero River (Juliá *et al.* 2019). According to Roig (1988; 1989) the "corzuela parda" does not appear in historical records of naturalists who visited Mendoza, nor in regional archaeological records from the specialized literature. Recent studies conducted in the Central-Eastern part of the province have not yielded any records of this species, even using camera traps or in interviews with forest inhabitants (Moreno 2023). Recently, Juliá *et al.* (2019) published a distribution map of the "corzuela parda" for Argentina, including a little portion of the east limit of Mendoza province, which neighbors with San Luis province. Nevertheless, in their description they mentioned as doubtful the presence in Mendoza because of the previous data.

In this paper, we confirm the presence of a new population of the brown brocket deer in the Eastern portion of Mendoza province (Desaguadero locality), thereby increasing the number of native species for the province and adding a new taxonomic group to its previous biodiversity records. We also provide information about the population inhabiting this new locality, their activity patterns and habitat preferences. With this information we aim to underscore the importance of evaluating effective conservation actions and management strategies to ensure the long-term survival and sustainable coexistence of the "corzuela parda" with its changing environment in Argentina.

Materials and methods

Study site. This research is part of the project "Aportes científico – técnicos al proceso de creación y gestión de la Reserva Natural Municipal Lagunas del Desaguadero, La Paz, Mendoza – ImpaCT.Ar Desafío N° 40" granted by Ministerio de Ciencia, Tecnología e Innovación of Argentina. The project focuses on the creation of a protected area around the Desaguadero River, through scientific-technical research which links natural and socio-cultural assets of the area.

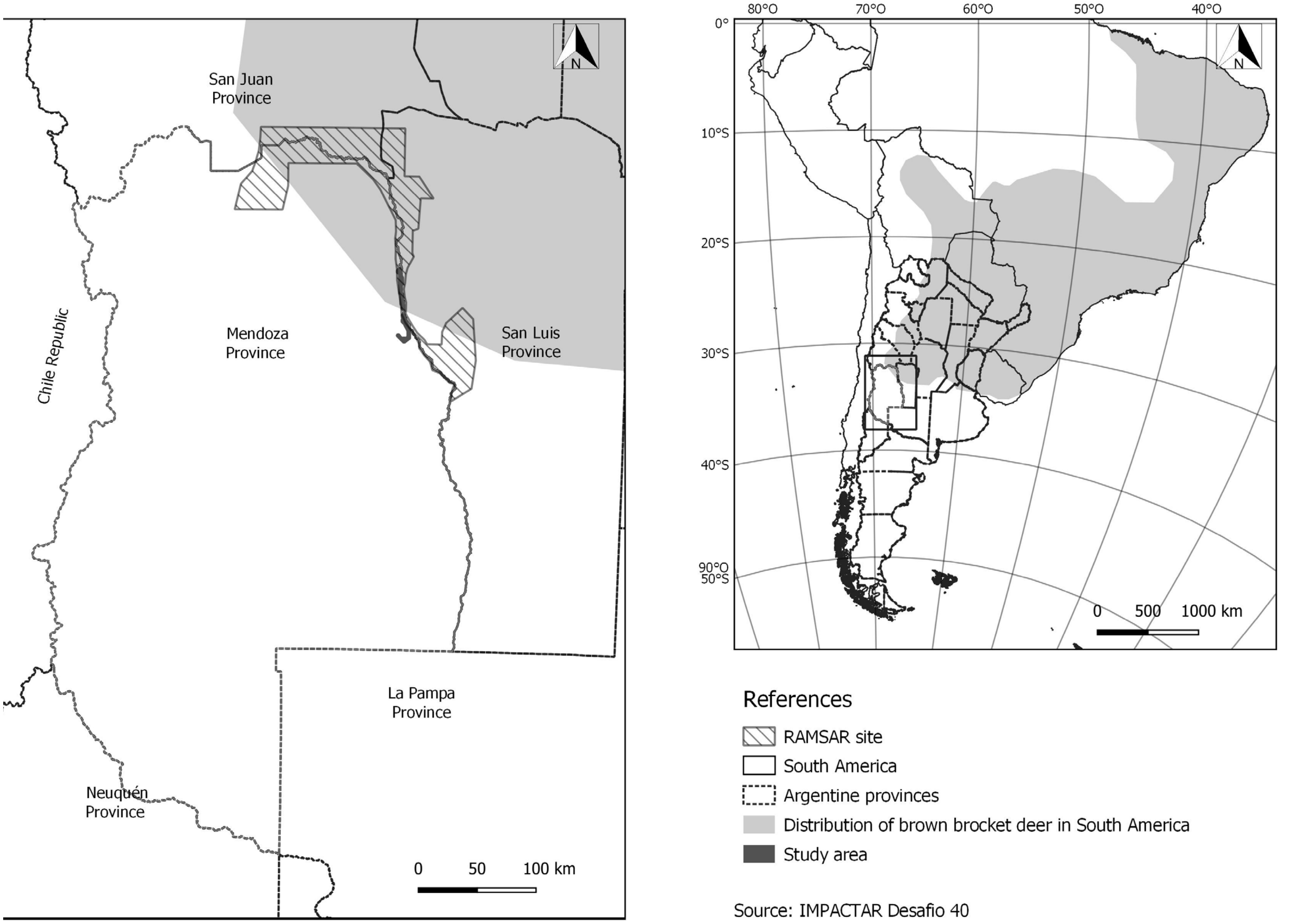
The study site is located in the Monte biogeographic region, specifically in the Central-East of Mendoza province, Argentina (Figure 1). The climate in this area is semi-arid to arid, characterized by pronounced seasonality and a wide daily temperature range. The average annual temperature is approximately 17 °C. Precipitation is concentrated in the summer and decreases from East to West. The mean annual rainfall is around 300 mm (Labraga and Villalba 2009). Within this region, there are multiple streams of the Tunuyán River that flow from West to East, forming an alluvial fan. The runoff is collected by the Desaguadero River (Figure 1). The study area includes 2 dams or "azudes" constructed in 2014 on the Desaguadero River to temporarily retain water.

A closed gallery forest, conformed mainly by *Neltuma flexuosa* (Hughes *et al.* 2022; "algarrobo dulce", ex *Prosopis*) trees, occupied the banks of the streams. The floodplain is covered by different plant communities, such as open *Neltuma* forests of lower density and coverage, as well as shrublands, and salt flats (Suplementary material 1). Typical species of Monte region, such as *Larrea* spp., *Condalia* *microphylla, Licium* spp., among others, are present in the area (Villagra *et al.* 2010; Del Olmo 2012). The study site is adjacent to the Chaco Seco ecoregion, separated by the Desaguadero river, and as a result, some species of plants form the Chaco, such as *Celtis tala* (tala), *Aspidosperma quebracho-blanco* (quebracho blanco) and *Acacia caven* (espinillo), can also be found in the study site (Villagra *et al.* 2010).

Sampling design. Grids of 1 km^2 were established to survey mammal assemblage in 3 main plant communities, classified a priori according to their physiognomy as: salt flats, shrublands and forests. Salt flats are open areas with low cover of halophyte shrubs, such as *Allenrolfea vaginata* or *Suaeda divaricata*. Shrubland community has a patchy cover of shrubs, mainly composed by *Larrea* spp., *Condalia microphylla and Lycium* spp. Forest includes open forest and gallery forest where *N. flexuosa* is the main species, accompanied by *Neltuma nigra*, *Geoffroea decorticans*, *Capparis atamisquea* and *Larrea* spp., among others. In the gallery forest, species incoming from the Chaco ecoregion are also present, such as *Celtis tala*, *Schinus fasciculatus,* and the exotic *Tamarix* spp.

Camera traps stations were placed in each grid according to logistic possibilities: 11 in shrublands, 15 in Salt flats and 12 in forests (*n* = 38 stations) (Figure 2). Each station contains 1 camera trap. Camera traps sampling was conducted in the period of highest population abundance of the animal species, coincident with the wet season: ends of spring 2022 and early summer 2023. Cameras were active during a total of 55 consecutive days on each station, over a 24 hs, period (2,090 night/trap = 55 night * 38 camera). Camera traps (Browning Patriot) were mounted on a 0.50 m high backing and vegetation surrounding the detection zone was cleaned to allow animal identification. The cameras took 3 consecutive pictures whenever animal movement was detected, with a 1 second delay between shoots. Individuals were identified from photos based on presence of antlers (size and texture), fur color, tail and body length and other species specific physical traits (Silva-Caballero and Ortega 2022).

Data Analysis. To shape the new distributional southern limit of the species within Mendoza province, we used not only records of camera trap but also opportunistic records by colleagues of brown brocket deer next to the main road



Source: IMPACTAR Desafio 40

Figure 1. "Corzuela parda" distribution in South America by Silva-Caballero and Ortega 2022. The square indicates the south-west actual distributional limit and the rectangle indicates the study site in Mendoza Province were new records of "corzuela parda" are located.

and i-Naturalist records published online. To evaluate daily activity patterns, we defined independent events (or activity records) as camera trap photographs in which the delay between two consecutive images of an individual exceeded 2 hours. With this information, circular statistic was used to unveil the daily activity patterns of the "corzuela parda". The analyses were performed using R v.3.2.5 environment and language (R Core Team 2023). The daily wind rose diagram, which convert data into a circular object, was performed with the "circular" package (Lund *et al.* 2022). To test for significant differences in the circular distribution among hours, we used the Rayleigh test (Zar 2010). Here, the null hypothesis assumes a uniform circular distribution across 24 hours, indicating the absence of preferred activity hours for the "corzuela parda". We used the "CirStats" package (Agostinelli and Agostinelli 2018) to perform the Rayleigh test.

To evaluate habitat use, NDVI index (Normalized Difference Vegetation Index) was estimated for each of the 38 cells of the grid. This index identifies the presence of green vegetation on the surface and characterizes its spatial distribution. NDVI values were obtained from a LANDSAT-8 image, OLI Sensor, from December 2022 with a pixel size of 30 m by 30 m. Because each index is estimated over a surface of $10 m^2$, an average of all the cells included in the grid was estimated as the NDVI of each sampling site. Differences in the NDVI between plant communities were assessed using the Kruskal-Wallis test. When significant differences were observed, *post-hoc* comparisons were conducted using a Dunn test (Zar 2010). Subsequently, generalized linear models with a binomial distribution were used to evaluate the effect of vegetation (as measured by NDVI) on the presence of "corzuela parda". All records, including those obtained from this study and external sources, were used in the model. R^2 coefficient was calculated to assess the goodness of fit. Graphic methods were used to test assumptions of normality and homogeneity of residuals. All analyses were performed using R v.3.2.5 environment and language (R Core Team 2023). Kruskal-Wallis test was performed with "agricolae" package (Mendiburu 2020). GLM was fitted with "stats" (R Core Team 2023), "DHARMa" (Hartig 2020) and "visreg" (Breheny and Burchett 2017) packages.

Results

New records. In this paper, we report 4 new site records from camera traps, 1 new record from personal observation of a CONICET colleague and include 3 iNaturalist reports added last spring (Table 1). These new records, located on the Central-East part of La Paz department, not only confirm the presence of the species on Mendoza province as previously mentioned by naturalists, but also rearrange the map proposed by Juliá *et al.* 2019 (Figure 2).

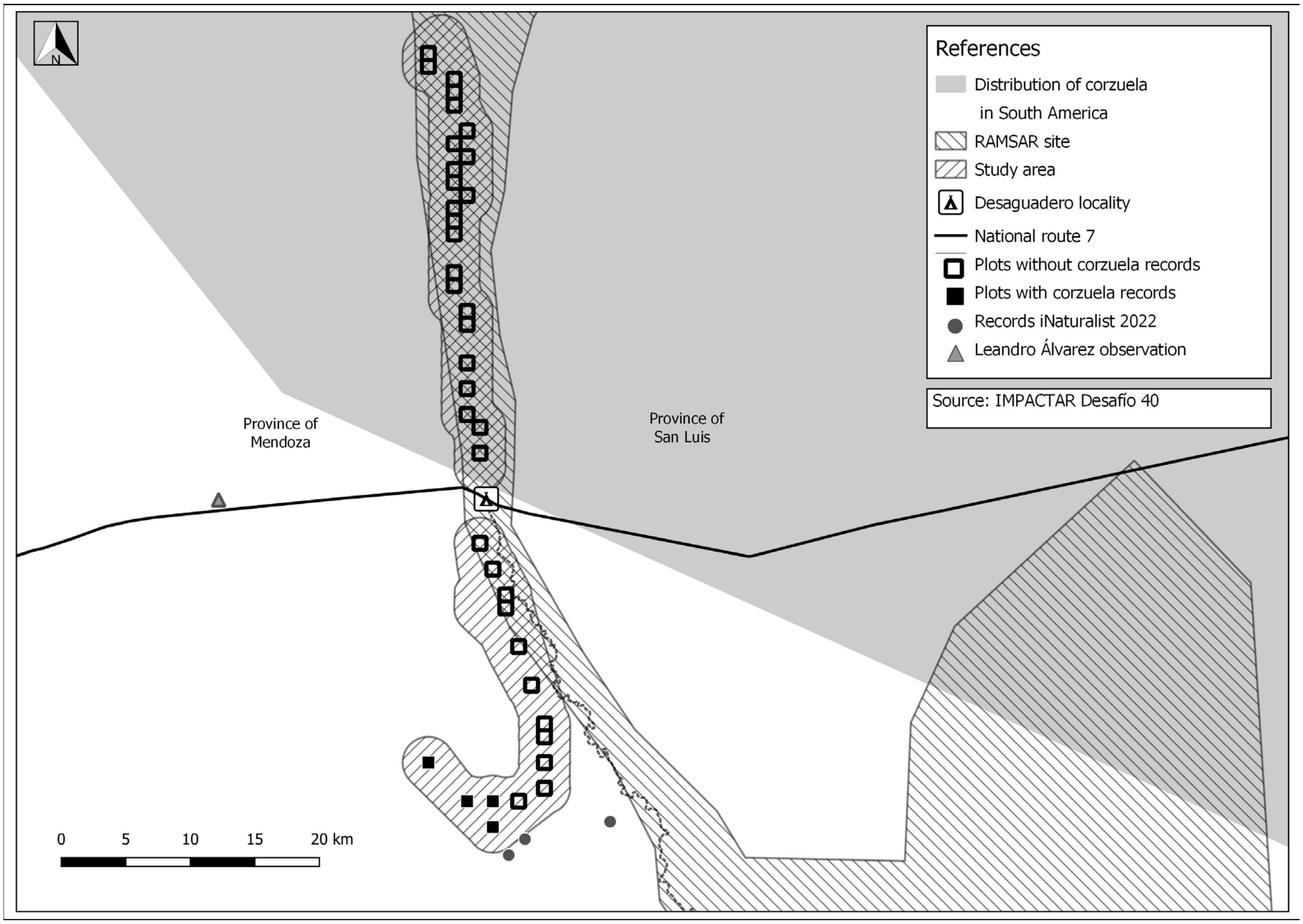


Figure 2. Location of camera traps stations in the study site.

Table 1. List of records of *Mazama gouazoubira* in Mendoza Province.

Latitude	Longitude	Source	Date
33° 37′ 58″ S	67° 8′ 57″ W	This study-B05	Summer 2023
33° 36′ 55″ S	67° 8′ 54″ W	This study-B03	Summer 2023
33° 35′ 26″ S	67° 12′ 1″ W	This study-B01	Summer 2023
33° 37′ 4″ S	67° 10′ 4″ W	This study-B02	Summer 2023
33° 24′ 38″ S	67° 22′ 39″ W	Leandro Alvarez observation	Autumn 2023
33° 38′ 24 “ S	67° 7′ 4″ W	iNaturalist-Quentin Vandem	Spring 2022
33° 37′ 36 “ S	67° 2′ 48″ W	iNaturalist-Damian Gamine	Spring 2022
33° 39′ 4″ S	67° 7′ 51″ W	iNaturalist-Damian Gamine	Spring 2022

Population. From a total sampling effort of 50,160 hours operation camera, we obtained 25 independent records of *M. gouazoubira*: three records in B01, two in B02, 11 in B03, and nine in B05. Eleven individuals of *M. gouazoubira* were identified, with five of them being adult males and six adult females. The males were primarily distinguished from the females by the presence of antlers, and among themselves, by their size, dimension and texture (Figure 3b, c). One male stood out for having a cut on the left ear and was photographed in the company of a female (Figure 3c, e). For the distinction among the females, their body size was taken into account (Figure 3a, d), with one female being identified as highly probably pregnant (Figure 3a). One individual from camera B01 could not be identified as it was camouflaged among the bushes. All individuals recorded in the camera trap photos exhibited a good overall physical condition.

Figure 3. Photos of "corzuela parda" in Mendoza province, Argentina, captured by the camera trap during the sampling period: a- Pregnant female, b-Adult male, c-Adult male with a cut on the left ear, d-Adult female, e-Male with a cut ear with an adult female.

Activity patterns. The 25 independent camera trap events are represented on a wind rose based on their time record. The brocket deer has higher activity between 8 and 9 am in the morning and then between 16 and 19 pm hours (Figure 4), avoiding the peak radiation hours (12 to 16 hours) during the summer season of 2023. Rayleigh test confirmed that these time preferences were statistically significant ($r = 0.99$, $p = 3.6062^{e-10}$).

Habitat use. The plant communities exhibited significantly different NDVI values among them, being the NDVI of the forest twice as high as that of the salt flat (*Chisq* = 32.98; $p < 0.00001$) (Figure 5). The higher the NDVI of the vegetation, the higher the probability of presence of the "corzuela parda" ($z = 2.27$; $p < 0.05$) (Figure 6). The NDVI explained about 36 % of the variance in the probability of presence.

Discussion

In this paper we report a new locality of "corzuela parda" in Argentina, particularly in Mendoza province, extending the distribution of the species to the South-West of its previous range. We also report the habitat use and activity patterns of "corzuela parda" in the new locality, suggesting a preference for habitats with higher complexity and NDVI, and being mostly active during the dawn and dusk time. Our results not only support the previous hypothesis of Juliá *et al.* (2019), who suggests the possible presence of "corzuela parda" in Mendoza, but also confirm that there is a stable and reproductive population in this new province.

By revising the distribution maps of the "corzuela parda", we found three different distributions according to different authors (Black-Décima 2010; Juliá *et al.* 2019; Silva-Caballero and Ortega 2022). However, none of them include our study site as part of the species' distribution

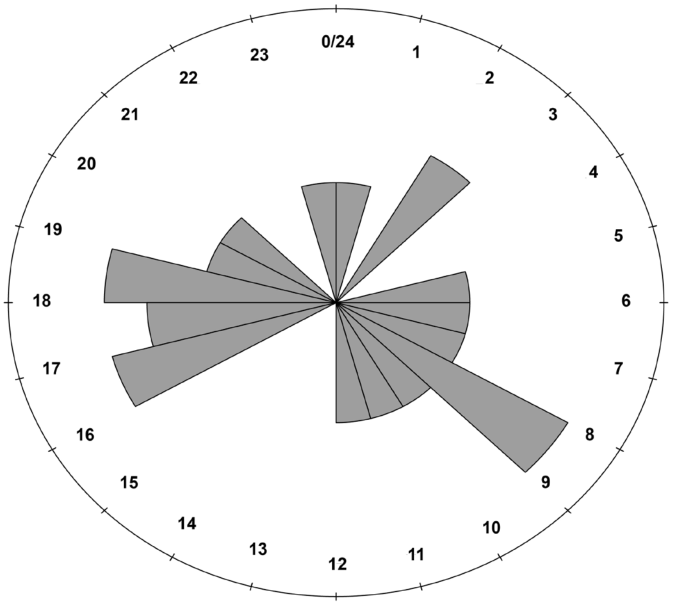


Figure 4. Wind rose recording daily activity pattern of the "corzuela parda" in Mendoza Province, Argentina. Numbers indicate daily hours. Longer arms indicate a higher number of independent records of corzuela captured on camera traps.

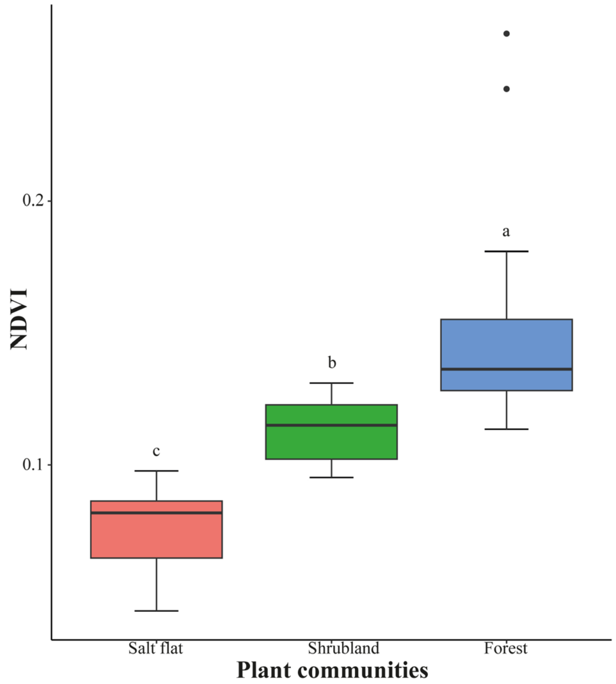


Figure 5. Box-plot of NDVI for different plant communities: salt flat, shrubland and forest. Different letters indicate significant differences among plant communities.

area. Considering the one proposed by Silva-Caballero and Ortega (2022), our records increase the South-West limit of "corzuela parda" of about 25 km, and confirm its presence in the province. While this work was being writing, the Mendoza government reported a new record of "corzuela parda" in the Central-West portion of Mendoza province (https://www.mendoza.gov.ar/prensa/fue-registrada-una-nueva-especie-de-la-fauna-silvestre-protegida-en-la-provincia/). Particularly, the sighting was at the Southern limit of the Ñacuñan protected area, about 90 km apart from our study site in the South-West direction. The precise record had not been provided in newspaper notices, so we could not include it here. Also, it is important to mention that recent studies carried out in the area, that included sampling with camera traps and surveys of residents, did not find records of this cervid (Moreno 2023). Future research that focuses on this species in Mendoza province will allow us to confirm or deny new records of populations presence, and probably the distribution area will change within a short time.

According to the ecology of the species, previous studies report that adult males mostly do not overlap their home range (Silva-Caballero and Ortega 2022). Nevertheless, some pairs of animals had been reported, mother and fawn or male and female or adult male and young male (Black-Décima 2000; Chebez and Johnson 1984; Juliá 2002). In our study, we found not only solitary individuals in all camera sites but also the presence of three different males (male #1,# 2 and #3) and two females (female #1 and #2) in a single sampling site (W03). Although there are no records of two or three males sharing the habitat at the same time, we found that presence records have a range of five and 17 days between different males. Moreover, the record of the three males and the two females was sequential, which means that during the first 20 days, only male #1 and female #1 used the area. After that period, and during the next month, male #2 and female #2 were recorded sharing the site. Finally, male #3 was recorded at the end of the sampling period only once. Therefore, this population could share its home range in space, but not in time. This pattern had not been previously reported in literature and became a new behavior for this species.

Records of activity patterns were consistent with literature, which mentions changes in the feeding behaviour of "corzuela parda" according to seasonality. During the spring and summer seasons, the "corzuela parda" is mainly found during the twilight periods, with individuals primarily active during dawn and dusk (Leeuwenberg *et al.* 1999; Rivero *et al.* 2005; Pautasso *et al.* 2008; Barrientos and Maffei 2000; Noss *et al.* 2003; Ferreguetti *et al.* 2015; Oliveira *et al.* 2016; Grotta-Neto *et al.* 2019). Although particular hours vary according to the biogeographic region of the sampling sites and seasonality (Bolivia, Brazil, Argentina), all studies reported two main activity peaks, one in the early hours of the morning, and the other in the latest hours of the day. This behavior avoids the exposition to the highest temperatures during the snap time, which can reach up to 45 °C in the summer time in our study site (Morello *et al.* 2018). During autumn and winter, "corzuela parda" would use all daily hours for foraging, besides dawn and dusk, something reported previously in other small ruminants (Putman 1988). This behavioral strategy, which prioritizes quality over quantity, would be responsible for the rhythm of activity previously described, in which "corzuela parda" invests a lot of time in food selection (Richard and Juliá 2004).

Habitat use of "corzuela parda" is one of the best known characteristics of this species across their entire range of

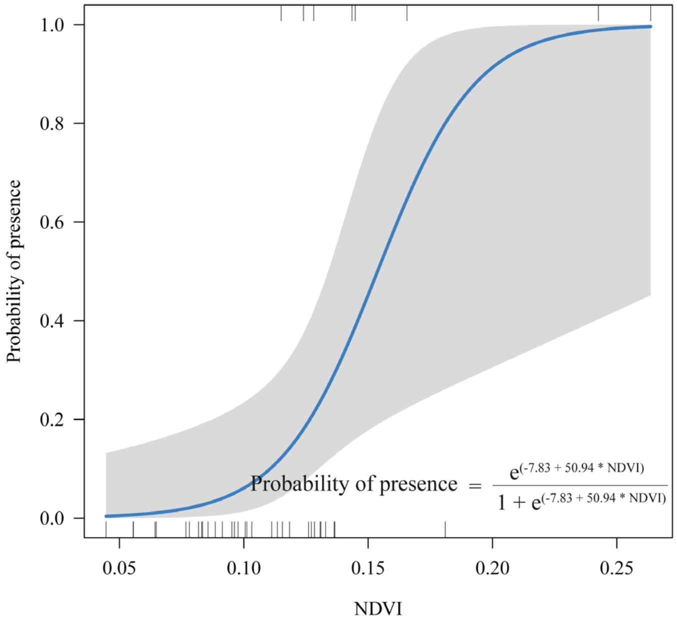


Figure 6. Probability of presence of "corzuela parda" in relation to the NDVI in Mendoza Province, Argentina. The solid blue line indicates the estimated parameter and the gray area represents the confidence intervals.

distribution. Non-anthropic terrestrial environments are optimal for the species, such as jungles, forests, shrublands, and grasslands, while anthropic environments such as agricultural crops, forest plantations, and cattle pastures are considered suboptimal (Juliá *et al.* 2019). In humid habitats, like the Brazilian savannah (Cerrado ecoregion), the "corzuela parda" mostly used forest habitats or bushy grasslands (Leeuwenberg *et al.* 1999; Grotta-Neto *et al.* 2019) and disturbed or agricultural habitats like Eucalyptus plantations (Rodrigues *et al.* 2014, 2017). In Argentina, the secondary forests of Parque Nacional El Rey are more frequently used than the mature forests of tropical forest habitat (Yungas), the difference being greater in the dry season compared to the wet season (Lepera *et al.* 2005). In North-East portion of Argentina, (Santa Fe and Misiones provinces), "corzuela parda" was recorded on gallery and Espinal forests, savannah and shrublands (Pautasso *et al.* 2008; Cirignoli *et al.* 2011). In Misiones jungle, a population growth was observed, favored by the fragmentation of the landscape and the increase in pine plantations (Juliá *et al.* 2019). In more arid habitats, such as the Chaco ecoregion in Argentina, "corzuela parda" is mostly present in habitats with a greater tree and bare soil cover and a less shrub cover (Periago *et al.* 2012). Our results show a higher presence probability on higher NDVI areas, supporting the hypothesis of the need of arboreal cover as a main habitat requirement of this species (Caraballo 2009; Desbiez *et al.* 2009). Because of our study site is next to the Chaco Seco ecorregion, the intrusion of elements of the Chaco into our study area could creates a propitious environment for the presence of the "corzuela parda". Particularly, riparian forests like the one present in our study site, could act as a corridor not only for "corzuela parda" individuals, but also their associated vegetation.

Finally, it is important to highlight that this portion of Mendoza Province has an ecological condition that allows the development of a *M. gouazoubira* population. Moreover, the political limit between Mendoza and San Luis provinces is also a biogeographic limit between Monte and Chaco Seco, so the Desaguadero river, and particularly the intersection between it and the Tunuyan River, could be acting as a biological corridor for the expansion of this species. The creation of the new protected area around Desaguadero and Tunuyan rivers, joint with the new record of "corzuela parda" in the nearby of Ñacuñan protected area, emphasize not only the importance of keep protecting these protected areas, but also the protection of surrounding habitats which was the potential of being used by "corzuela parda" to travel between patches.

Acknowledgments

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Appendix 1

Main plant communities in the study site: a) Salt flat, b) Shrubland, and c) Forest.

Supplementary material

Residuals of the Presence probability model

https://www.revistas-conacyt.unam.mx/therya/index.php/THERYA/article/view/5158/5158_Supplementary%20material

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Baird's Tapir social interactions, activity patterns, and site fidelity at ponds of the Maya Forest

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The Baird's tapir is an endangered species of the Neotropical Forest. The Maya Forest of southern México hold one of the most important populations of the species. Tapir are solitary, shy, and nocturnal animals of which behavioral observations are very limited. Using camera traps, we revised the social behavior of tapirs that are visiting ponds in the Calakmul Biosphere Reserve along 10 years. In these sites, locally named "aguadas", and that are sites where social interaction may take place, we have found that tapirs are solitary animals, but dedicated some percentage of their time to socialize with other individuals and these associations can last for months, maybe years. We reported on individuals that have visited some specific sites for periods of 4 and 10 years. There is a male biased sex ratio among the individuals we could identified sexually, and tapirs are nocturnal most of the time, but preferences for early hours of the night was recorded. This is a unique study because it is the first time that social behavior, site fidelity, and sex ratio are presented for the species for several sites, and along 10 years. We hope to advance in the knowledge of the social and ranging behavior of this endangered species of the Neotropical forests.

El tapir de Baird es una especie en peligro de extinción de los bosques Neotropicales. La Selva Maya del sureste de México mantiene la población más grande de la especie en toda su área de distribución. El tapir de Baird es un animal solitario, nocturno y del cual las observaciones sobre su comportamiento son muy limitadas. Usando cámaras trampa revisamos el comportamiento social de los tapires que visitaron algunos cuerpos de agua en la Reserva de la Biosfera de Calakmul por 10 años. Estudiando estos cuerpos de agua, llamados localmente "aguadas" como posibles sitios de encuentro de individuos, encontramos que los tapires son solitarios la mayor parte del tiempo, pero dedican un porcentaje de su tiempo a interactuar con otros individuos y que estas interacciones pueden durar algunos meses. Reportamos algunos individuos que han visitado ciertos cuerpos de agua por grandes periodos de tiempo, desde meses hasta 10 años. Existe un sesgo hacia los machos en el número de individuos registrados por las cámaras en los cuerpos de agua. Los tapires son nocturnos, pero más activos en las primeras horas de la noche. Es la primera vez que se reporta el comportamiento social, fidelidad de sitio y radio sexual de la especie en diversos cuerpos de agua a lo largo de 10 años. Esperamos que podamos comprender más sobre el comportamiento de esta especie difícil de observar y que está en grave peligro de extinción.

Keywords: Activity patterns; aguadas; Calakmul Biosphere Reserve; social behavior; *Tapirus bairdii*.

Introduction

In the last 40 years several mammalian species across the globe have suffered a decline in their populations due to human activities such as hunting, deforestation, habitat fragmentation and introduction of exotic species in the native habitats of the world. Tropical and large species of ungulates are the ones that have suffered the greatest reductions in their populations (Ripple *et al.* 2015). The Baird's tapir (*Tapirus bairdii;* although *Tapirella* is also used for this species; Álvarez-Castañeda *et al.* 2017) is a species that belongs to Tapiridae family and the order Perissodactyla, that lives in the Neotropical forests, and it is distributed from México to Colombia, but its distribution range has been highly reduced in the last 40 years due to habitat encroachment and hunting (Naranjo 2018). Tapirs have been described as one of the last megafauna of the Neotropics and also a unique species (from the evolutionary perspective) that is on the risk of extinction (Issac *et al.* 2007; Ripple *et al.* 2015).

Tapirs have been described as solitary, nocturnal animals, that visit frequently water bodies to reduce their corporal temperature and to escape from danger due to predators (Meyer *et al.* 2022; Calme *et al.* 2022; Reyna-Hurtado *et al.* in press). They disperse seeds of some trees and also defecate in water bodies filling an important ecological role as material and seed transporters and dispersers (O'Farrill *et al.* 2014). Tapirs are associated to some pieces of the landscape visiting frequently ponds and other water bodies (Reyna-Hurtado *et al.* 2016). Although there have been some documented attempts of predation of tapirs by jaguars (Pérez-Flores *et al.* 2020), it is not clear yet if adult tapirs can be preyed by jaguars due to the massive size and hard skin of tapirs.

The Maya Forest, a forest composed by protected areas in México, Guatemala, and Belize, is one of the last remaining pieces of Neotropical forests in good stage of conservation in Mesoamerica and the largest in the region. In México, in the Maya Forest, the Calakmul Biosphere Reserve (CBR) is the core area along with several other reserves in México, in Guatemala and in Belize that hold probably, the largest population of Baird's tapir in Mesoamerica (Schank *et al.* 2020). The CBR is the largest protected tropical forest of México and despite an increase of infrastructure around the reserve like highways and railways, the CBR is still the most important protected area for species like tapirs that need large areas to sustain a viable population (Reyna-Hurtado *et al.* 2019).

In the CBR there are not major rivers and most of the water that fell by precipitation goes underground due to the Karstic soil materials, and just in few sites of the ground surface the water remains (Reyna-Hurtado *et al.* 2010). These sites are locally called "*aguadas*" (ponds hereafter) and play an important role as source of water for wildlife during the critical dry season and even for human communities that live on the periphery of the CBR (Reyna-Hurtado *et al.* 2010, 2012, 2019).

In the last years, biologists trying to investigate wildlife habits, behavior, and population parameters in dense environments such as tropical forest, have relied on camera traps (Nichols *et al.* 2011). Camera traps are an essential technique because they function remotely every time an object that has a higher temperature than the environment is moving in front of the detection field of the camera, allowing researchers to capture species that live in dense, remote habitats that are shy or nocturnal, or that live in low densities. The technique has been refined in the last years and nowadays camera traps are cheaper, more sensible, durable and lighter. In terms of ecological analyses, camera trap data are useful to estimate several parameters of the population of species, of the behavior of individuals, of the associations of species, of habitat use and preferences, and even of the poaching or human perturbation levels (O'Connell *et al.* 2011).

Since 2008, camera traps have been deployed in ponds of CBR with the goal of estimate population parameters of endangered wildlife species, especially endangered ungulates (Reyna-Hurtado *et al.* 2010, 2016, 2019). The number of cameras varied from 3 to 17 but since 2014 at least 10 cameras have been working permanently in the same number of ponds. This camera trap monitoring research have been combined with radiotelemetry research on two species of ungulates, the Baird's tapir and the white-lipped peccary (*Tayassu pecari*) in the CBR. This combination of research technique has allowed us to combine data in terms of movement ecology (radiotelemetry) and population dynamics (camera traps).

For forest dwelling species such as Baird tapir (Reyna-Hurtado *et al.* 2016), Malaysian tapir (*Tapirus indicus*; Tawa *et al.* 2021), Bongo antelope (*Tragelaphus eurycerus*; Klaus-Hügi *et al.* 2000), Forest buffalos (*Syncerus caffer nanus*; Melletti *et al.* 2007), and Forest elephants (*Loxodonta cyclotis*; Turkalo and Fay 1995; Reyna-Hurtado *et al.* 2023) among others, the use of salt licks, or water sources such as ponds, can be important for resources acquisition (water, minerals), but also as "social arenas", sites where animals frequently visit to interact with other conspecifics, to search for mates, to strengthen social networks, or sites where young can learn to socialize, or probably sites where conspecifics exchange social information (Turkalo and Fay 1995).

In this study we used data from a long-term study to investigate to what extent Baird's tapir are solitary, or if they have social interactions while visiting ponds (a key piece of the landscape), we also described the sex ratio of the adult population and when individuals could be recognized, we described site fidelity. Finally, we described the tapir's daily activity patterns. These characteristics of the Baird's tapir population rarely have been described elsewhere and never in the long term and for several sites and with the sample size of this research. We expect to advance into the knowledge of the social behavior and natural history of this endangered species of the Maya Forest.

Material and methods

Study site description. The Calakmul Biosphere Reserve (CBR) with 7,289 km^2 is the largest protected tropical forest in México and is located at the core of the Maya Forest in Southern Mexico at 18° 07'21" N and longitude of -89° 48' 56" W (Figure 1). The area is a semi-perennial tropical forest where trees height reaches up to 25 meters in most of the landscape. CBR is a flat area with some rolling hills of karstic origin, the Calakmul climate is warm and sub-humid (Aw), with a mean annual temperature of 24.6 °C. There is seasonal rainfall, mainly in summer and early fall, with an annual average of 1,076 mm. Of the different forest associations (Pennington and Sarukhan 1998), four are widely distributed: Medium Sub-Perennial Forest (Medium), the more humid of the region, where trees are between 15 to 25 m high; Low-Flooded Forest (Flooded) that gets seasonally inundated after 2 to 3 months of heavy rains, and where trees are between 5 to 15 m high; and the Medium and Low Semi-Deciduous Forests, which both can be classified as dry forest (Dry) where trees range from 8 to 25 m high, but species composition differs from that of the Medium Semi-Perennial Forest. These four types of forest are highly intermingled within the area, although the humidity from northwest (driest) to southeast (wettest) has an impact on the forest types too. The water in the area is obtained through precipitation since there is no permanent river system. Most of the rainfall percolates through the limestone, but some drains superficially and stores in ponds ("*aguadas*"). These ponds constitute the only source of water for wildlife through the dry season (Reyna-Hurtado *et al.* 2010).

Study Design. As part of an ongoing research on ungulates of the Maya Forest some camera traps were deployed in as many ponds as possible since 2008. The number of ponds monitored range from 3 to 17, but since 2014 the number of ponds monitored ranged from 10 to 17. The ponds were selected so as to occur at least 1.5 km from each other. All these ponds are in the southern area of the CBR, an area that is isolated from any human community by two checkpoints of the CBR authorities, and have one single road that leads to an archeological site but with very few cars every day (less than 10 on average). These ponds were monitored by setting up a single camera trap (Reconyx PC800 Hyperfire professional Reconyx, Inc., Cuddeback Inc

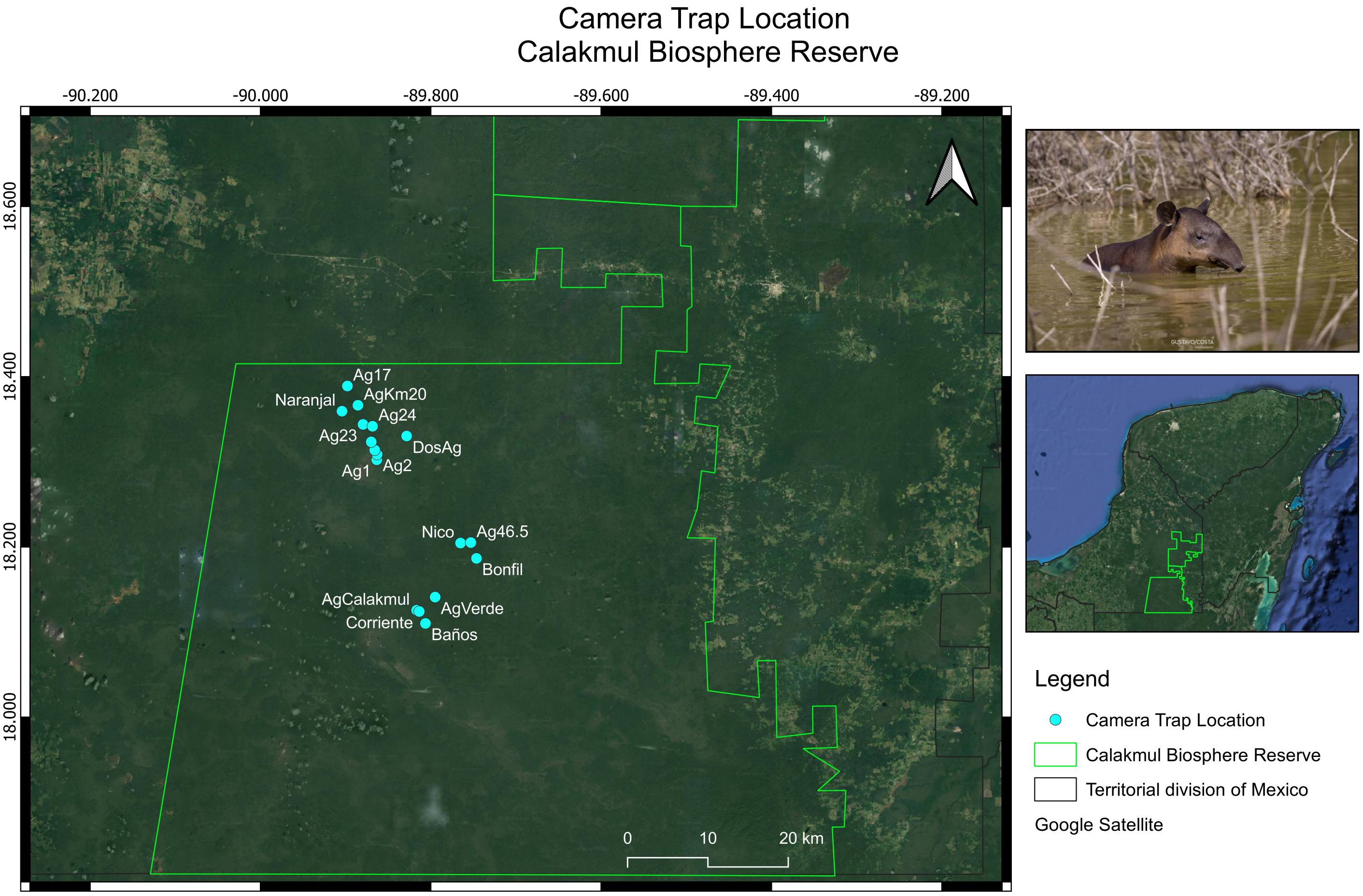

Figure 1. Map of the ponds (“*aguadas*”) where camera traps were deployed on this study and the Calakmul Biosphere Reserve, Campeche, México.

and Browning Strike force Co.) at 50 cm high in some ponds from February 2014 to August 2023. The cameras were programmed to take five consecutive photos (one photo per second) each time the sensor detected movement and were checked every two months in average in the period 2014 to 2023 to change batteries and memory cards.

The photos obtained were sorted by species and here, we analyzed all the photos obtained of Baird’s tapirs (13,068) from February 2014 to mid 2023. Then, we examined these records and counted the number of independent events (separated by 60 minutes) where tapirs were solitary, or when they had some social interactions. For social interactions we described any associations between two individuals, either female with newborn or juvenile, or male and female, or male and male, or female and female, or male and female with a juvenile, or more than two tapirs, etc. In addition, we counted the number of females and males when it was possible to identified sexually the individuals. The photos were also examined to visually identify as many as possible different individuals in each pond. We looked for scars in the face, for cuts in the ears, or scars in the back of the individuals, also other characteristics such as unique color marks, or leg problems (individuals limping). With these marks we tried to recognize individuals in the same pond but different years or in different ponds. Finally, we used a couple of tapirs (“Emiliano” and “Eli”) that were radio-collared with purposes of studying their movement patterns (Reyna-Hurtado *et al.* 2016). At the time these tapirs were collared, there were no other tapir with collar in the whole Maya Forest, so these individuals could be identified without doubt.

Analyses and software used. Once we selected a record every 60 minutes, it turned out to be 834 independent records. These records were analyzed with the statistical software R, using RStudio 2023.09.0 version (R Core Team 2023). Using the package “*CamptrapR*”, and “*Activity*” and an R-Code developed by Andrade *et al.* (2022), we analyzed the time that Baird’s tapirs were active in these years and in these sites and we constructed a graphic that shows the time preference along 24 hours for Baird’s tapirs in the CBR.

Results

Tapir social behavior and sex ratio. The independent records of tapirs visiting ponds collected over 10 years in 17 different ponds of the Maya Forest confirmed that tapirs are predominantly solitary animals but have a number of social interactions of some way in a percentage of their life. Here, 87 % of their records were recorded as solitary animals, but 13 % of the records showed more than one tapir interacting in some way with another individual.

Of the social interactions recorded in the 17 sites and over 10 years the more common one was an association between male and female (59 % of which we recorded one that lasted for more than three months), followed by an association between female and juvenile (28 %) and the rest (13 %) were rare associations between two males (fighting) and a male following a female and a juvenile (Figure 2). Of the adult tapirs that visited the ponds that could be identified in term of sex, we recorded a male biased sex ratio of 67 % males *versus* 33 % females.

Tapir site fidelity. This long-term study showed that tapirs show fidelity at some sites and for times up to 10 years or more. We have information on at least three tapirs that presented distinguished characteristics such as marks in the ear, or that we radio-collared, that we could distinguish over several years and allowed us to describe how many years they were present in some sites. Table 1 shows the long-term persistence of three tapirs: "Oreja mocha", "Emiliano" and "Eli". "Oreja mocha" has been sighted by 10 years at least, and we followed "Emiliano" for four years, and "Eli" only for nine months, however in an intensive way due to the radio-collar we deployed on it. These three tapirs showed fidelity to some sites always coming back to some specific sites. "Oreja mocha" was highly attached to "Bonfil" and we saw it for first time in May 2011 (with a short camera monitoring program that was not included in this study), then in 2014, 2015, 2020 and 2021 in the same pond (Figure 3); while Emiliano was a frequent visitor of "Aguada Verde", "Baños", "Calakmul", and "Corriente" ponds visiting them frequently during the four years we followed it (Figure 4). "Eli" was followed intensively due to the radio-collar that was recording geographic positions every two hours, we recorded "Eli" in five sites several times during the nine months with "Aguada Km 17" being the most visited pond (Figure 5).

Tapir activity patterns. The 834 independent records of visits to ponds determined that tapirs are nocturnal and that the peak of activity occurs between 19:00 to 22:00

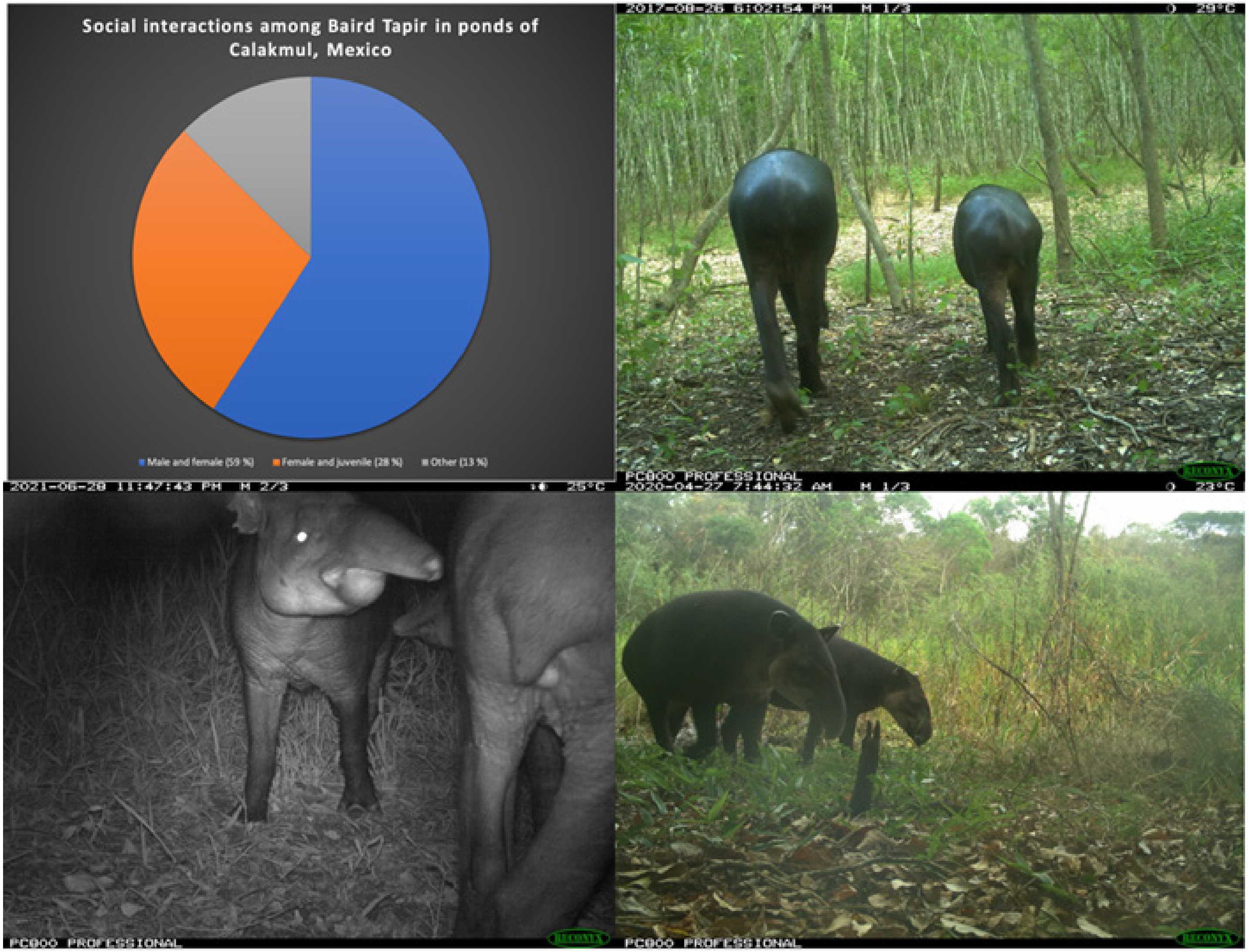

Figure 2. Percentage and photos of different social associations of *Tapirus bairdii* visiting ponds of the Calakmul Biosphere Reserve, México. Top left: Percentage of social interactions found in Baird's tapir from 2014 to 2023. Top right: a mother and a calf. Bottom left: a male ("Oreja mocha") and a female. Bottom right: another male and female.

Table 1. Individuals of *Tapirus bairdii* that were recognized over several periods of time in ponds of Calakmul Biosphere Reserve, México.

Tapir name	Description	First time sighted	Last time sighted	Site (ponds)
"Oreja mocha"	Male with right ear severed cut	May 2011	June 2021	"Bonfil"
"Emiliano"	Radio-collared male	May 2011	Jul 2015	"Verde", "Baños", "Calakmul", "Corriente"
"Eli"	Radio-collared male	Apr 2022	Jan 2023	"Naranjal", "Km 15", "Km 17", "Km 23", "Km 24"

hours (Figure 6). These data were collected across several sites, seasons, years and with an estimation of at least 30 (but could be more than 45) different individuals making it one of the most solid estimations of activity patterns of the species in the Maya Forest and in the whole distribution range of the species.

Discussion

Tapir social behavior. Here we demonstrated that despite Baird's tapir has been described as solitary species, it associates to some degree of their lives in rich social interactions with other individuals, while showing site fidelity that can last for several years. We confirmed that is a nocturnal species but preferences for being active early in the night was found.

It has been described that Baird's tapir is a solitary species where individuals travel and live most of their lives alone but that occasionally partner with other individuals for some part of their lives (Calme *et al.* 2022; Meyer *et al.* 2022). Our study, which confirm the previous sentences, was done across several years, sites, and individuals, so the finding of a small percentage of their live as social individuals is important because reflects the real degree of social relationships that tapir performs in the Maya Forest across seasons and years in different conditions.

Despite the percentage of social relationships was small (13 %), some of these associations lasted for several

Figure 3. "Oreja mocha" photos from 2015 to 2021 in Bonfil pond of Calakmul Biosphere Reserve, México.

Figure 4. "Emiliano" photos from 2011 to 2015 in several pond of Calakmul Biosphere Reserve, México.

months (male and female) and probably for years (female and juvenile pairs were seeing repeatedly in same sites in consecutive years). Here, we documented some associations between male and female that lasted at least four months and we found associations between female and juvenile in same site, but several years, that probably are the same individuals, however there were no definitive marks that allowed us to recognized them with certainty. It has been found that juveniles spent some time with their mother after being born. This time varies from one year (Naranjo 2014) to more than a year (Calme *et al.* 2022; Garcia 2016). The possibility of, larger than one-year associations, between female and newborn is evident here due to the photos of similar pairs (female and newborn) being showing consistently in the same sites but different years. That is a topic for future research using camera traps or genetic techniques to identify individuals with certainty. Castellanos *et al.* (2021) found similar results for the mountain tapir (*Tapirus pinchaque*), where they found associations among recognized tapirs that lasted more than two years (mother and calf), and they also found mountain tapirs to aggregate in temporal groups from three to nine (Castellanos *et al.* 2021).

We found a male biased sex ratio of the fraction of the population we could identify. There is not sex ratio reported previously in this species so we have no means to compare our results. This is contrasting with a population of the Amazonian tapir (*Tapirus terrestris*) where a female biased population was found in the adult section, and a male biased among the juvenile population that visited a salt lick place in the Colombian Amazon forest (Montenegro 1998). In that case, the researcher argue that female adults and male juveniles may have a higher minerals requirement (Montenegro 1998). In our case, our results could mean that the

Figure 5. "Eli" photos from 2022 to 2023 in several pond of Calakmul Biosphere Reserve, México. Top right photo credit: Daniel Nuñez.

population is truly male biased, or that males travel more and are visiting the ponds with higher frequency. However, the male sex ratio has been described previously in camera traps for jaguars and has been attributable to differences in behavior and ranging patterns, rather than population differences, with females being a lot less captured by camera traps than males, and probably avoiding camera traps deliberately (Srbek-Araujo *et al.* 2018). There is no information on the behavior of the female tapir, neither on the differences in the ranging behavior. In this study we got information from two males that were captured and attached with radiotelemetry collars but we have not followed any female yet. The fact that we found a great male-biased sex ratio raises a couple of interesting question, these are: Do females' tapirs move less and have smaller ranges than males' tapirs? and, do females' tapirs avoid camera traps, or ponds, deliberately?

There are very few studies of Baird's tapir movement patterns. In Nicaragua, Jordan *et al.* (2019) followed actively only two males as the female they captured dropped the collar short after they radio-collared her. In Belize, Martinez *et al.* (in press) followed a female that ranged similar distances than two males they followed for several months with radiotelemetry collars.

There is the need of more studies to confirm if the male sex ratio we found is due to population parameters, or due to behavior differences between the sex. We hope that in the near future the ranging behavior of females can be described in greater detail.

Tapir site fidelity. We found Baird's tapirs to show high fidelity so some sites and that that fidelity can last for years. The fact that one individual was sighted after 10 years in the same site was an interesting one that demonstrated that tapirs could associate themselves to some sites and remain, or visit, these sites for long periods of time. In 2011, when we sighted for first time "Oreja Mocha" he was already a full-grown adult tapir that showed several scars at that time already. This individual showed itself several times along 10 years in the same site and in 2021 he was there associated with a female and in apparently good health status. Two more tapirs that we followed by radiotelemetry also showed close associations to some sites for some periods of time, "Emiliano" who is probably using spatial memory to find and reach some ponds as was reported in Reyna-Hurtado *et al.* (2016) and "Eli" who was sighted several times returning to specific ponds (R. Reyna-Hurtado unpublished).

Tapirs ranging behavior can be complex and interesting. Probably, they are using the spatial memory to reach small ponds that are located in a flat, uniform, and extensive environment such as the CBR and that are found in low densities (Reyna-Hurtado *et al.* 2012; 2016). The knowledge of the location of these ponds can be a very valuable skill to survive in dense tropical forest and here we demonstrated that tapirs returned repeatedly and for several years to some specific sites located in dense environments of the CBR. More studies on this topic following individuals through radiotelemetry techniques can be very interesting to confirm it and elucidate the ways they associate with ponds and other features of the landscape.

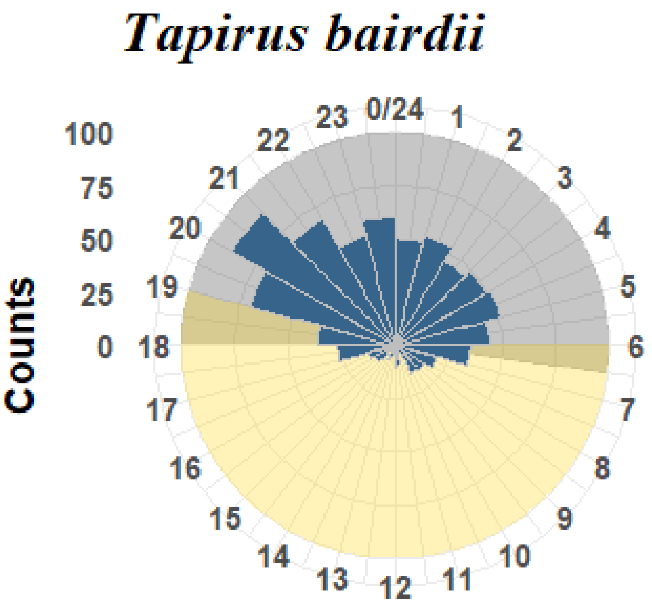

Figure 6. Activity patterns of *Tapirus bairdii* from 2014 to 2023 in several pond of Calakmul Biosphere Reserve, México.

Tapir activity patterns. Previously we have found that tapirs are more active at night and that they were affected by moon light in some way (Sanchez-Pinzon *et al.* 2019). Here we confirmed these patterns and also found that there is a preference for early hours of the night to be active. The 834 independent records showed that tapirs are more active at night but especially between 19:00 to 24:00 with a peak between 19:00 to 22:00 hours. These nocturnal patterns were consistent among several years, sites and seasons showing that tapirs are well adapted to the environment by moving at night and visiting repeatedly some specific sites. Probably, these behavioral patterns were adaptations to the hot environment of tropical forest such as CBR. It was evident that in the instances when tapirs were photo-captured during the day, they were visiting the ponds to cool down in the water in very hot days. Similar results were found for several Amazonian tapirs in Colombian forest that were visiting salt lick sites in a behavior markedly nocturnal with a peak between 18:00 to 04:00 (Montenegro 1998).

Tapirs are shy, elusive, nocturnal species that live in low density populations across a Neotropical forests range that is being decreasing every year. Information on the social behavior, sexual ratio, movement patterns and the site fidelity like the ones presented in this study may help to elaborate informed conservation actions. Research like this, also pointed out in the direction of more needed research to advance in the ecological knowledge of this enigmatic species, that has been described as a conservation priority (Isaac *et al.* 2007) and the tenth rarest species of the Neotropics mammals (Dobson and Yu 1993). Here, we presented information about social behavior, sex ratio, activity patterns and site fidelity of a long-term study across several sites, years, and individuals. We also showed that ponds can be places where different social interaction are occurring. In the future, we need to test these sites to find if they are been used as "social arenas" for tapirs. We hope that in a near future, studies about ranging patterns, genetic composition, and population dynamics can be conducted and we learn more about this endangered species of a Neotropical ungulate.

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Occupancy, relative abundance and activity patterns of three sympatric deer associated to ponds

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Calakmul Biosphere Reserve is one of the largest tropical forests in the Americas, home to three species of deer, the white-tailed deer, *Odocoileus virginianus*, the Yucatán brown brocket deer, *Odocoileus pandora*, and the Central American Red brocket deer, *Mazama temama*. Important ecological aspects on the conservation of these species have been poorly studied. The aim of this study was to determine the occupancy, relative abundance and activity patterns of these species through nine years of camera-trapping in ponds of a Neotropical Forest in southern México, contributing to the understanding of the ecological patterns and conservation of Neotropical deer. To determine abundance, occupancy and activity patterns, we monitored 17 ponds from 2014 to 2022. To calculate abundance, we used the general relative abundance index and the temporal kernel density to evaluate the overlap in daily activity of the species. To obtain the occupancy, local colonization, local extinction and detection probabilities we utilize the dynamic occupancy model, while to assess the interaction of water and species we utilize the species co-occurrence occupancy models. White-tailed deer were the most abundant during the nine years of the study, with low pond occupancy, but with a high probability of colonization. The Brown brocket deer was the one with the highest probability of occupancy, showing a low abundance, followed by the red brocket deer, with a very low occupancy and abundance. Interaction with water was positive in two of the three analyzed species and activity was diurnal for *Odocoileus* species and cathemeral for *Mazama*. The use of ponds by deer varied in quantity and activity, but they are important places for their survival. The protection of the ponds should be fundamental for the conservation of the species in the area, these are water sources and places of food and shelter for wildlife.

La Reserva de la Biosfera de Calakmul es uno de los bosques tropicales más grandes de América, hogar de tres especies de venados, el venado de cola blanca, *Odocoileus virgininaus*, el temazate pardo de Yucatán, *Odocoileus pandora*, y el temazate rojo centroamericano, *Mazama temama*. Los aspectos ecológicos importantes para la conservación de estas especies han sido poco estudiados. El objetivo de este estudio fue determinar la ocupación, abundancia relativa y patrones de actividad de estas especies a través de nueve años de fototrampeo en aguadas de un bosque Neotropical en el sureste de México, contribuyendo a la comprensión de los patrones ecológicos y la conservación de los venados neotropicales. Para determinar la abundancia, ocupación y patrones de actividad, se monitorearon 17 aguadas entre 2014 y 2022. Se utilizó el índice de abundancia relativa general para calcular la abundancia y la densidad temporal de Kernel para evaluar la superposición en la actividad diaria de las especies. El modelo de ocupación dinámica se utilizó para obtener la probabilidad de ocupación, colonización, extinción y detección, mientras que los modelos de ocupación de coocurrencia de especies se utilizaron para determinar la interacción del agua y las especies. El venado cola blanca fue la especie más abundantes durante los nueve años de estudio, con baja ocupación en las aguadas, pero con alta probabilidad de colonización. El temazate pardo presentó la mayor probabilidad de ocupación, mostrando una baja abundancia, seguida del temazate rojo, con una ocupación y abundancia muy baja. La interacción con el agua fue positiva en dos de las tres especies analizadas y la actividad fue diurna para las especies del género *Odocoileus* y catemeral para *Mazama*. El uso de las aguadas por parte de los venados es variado en cantidad y actividad, pero son lugares importantes para su sobrevivencia. La protección de las aguadas debe ser fundamental para la conservación de las especies de venados dentro de la reserva, ya que son una de las pocas fuentes de agua semiperennes y también lugares de alimento y refugio para la vida silvestre.

Keywords: Abundance; colonization; detection; extinction; *Mazama temama*; *Odocoileus pandora; Odocoileus virginianus*; ponds.

Introduction

Calakmul Biosphere Reserve is one of the largest natural protected areas in México with 7,231 km^2 (Comisión Nacional de Áreas Naturales Protegidas 2023). It belongs to the Mayan rainforest, the biggest extension of tropical forest of North and Central America, and the second in America, just below the Amazon basin (Secretaria de Medio Ambiente y Recursos Naturales 2018; Reyna-Hurtado and Sanchez-Pinzón 2019). Emblematic large mammals such as the jaguar (*Panthera onca*), the white lipped peccary (*Tayassu pecari*), and the Central American tapir (*Tapirus bairdii*) still inhabit this forest (Carabias-Lillo *et al.* 1999; Reyna-Hurtado and Sanchez-Pinzón 2019), as well as species of high cultural and alimentary importance for local communities, such as the white-tailed deer (*Odocoileus virginianus*) and two species of brocket deer (*Odocoileus pandora* and *Mazama temama*; Weber 2000, 2005; Reyna-Hurtado and Tanner 2005). However, this protected area is subjected to water extraction, logging, road construction, agriculture and extensive livestock farming (Weber 2008). In addition, in recent years, land clearing has increased due the construction of the "Tren Maya" megaproject and the touristic-urban complex "Hotel Maya" within the reserve, and these projects are expected to generate barrier effects (blocking of movement and trampling) and edge effects (due to noise; Alayón-Gamboa *et al.* 2019; Benítez *et al.* 2021).

The white-tailed deer (Figure 1c) is the most widely distributed deer in the Americas, historically ranging from southern Canada (60° North Latitude), to southern Peru (15° South Latitude), and has been introduced to New Zealand, Czechoslovakia and Finland (Ceballos 2014; Gallina *et al.* 2014; Gallina and López-Arévalo 2016). Its wide distribution is due to its high adaptability, evident in its high morphological, physiological, biochemical and behavioral variation (Weber 2014; Gallina *et al.* 2014; Gallina and López-Arévalo 2016). The tropical subspecies have a dark coat color in humid rainforest, being reddish in subtropical environments (Weber 2014; Gallina and López-Arévalo 2016). They are usually medium to small sized, with males weighting less than 60 kg and females less than 35 kg (Gallina *et al.* 2010; Weber 2014). In the greater Calakmul Region, in areas with little hunting it has been described as an "opportunistic", using habitat by its availability, showing preference for secondary vegetation and agricultural areas (Weber 2005; Reyna-Hurtado and Tanner 2005; Weber 2008; González-Marín *et al.* 2008), preferring the low-flooded forest in areas with high hunting pressure (Reyna-Hurtado and Tanner 2005; Briceño-Méndez and Contreras-Moreno 2020).

Yucatán brown brocket deer (Figure 1b), recently classified within the genus *Odocoileus* (Gutiérrez *et al.* 2017), is a medium-sized cervid. In the Great Calakmul Region the average weight of 13 captured male brocket deer was 20.5 kg, and that of eight adult females was 17.3 kg (Weber and Medellín 2010; Weber 2014). The dorsal coat is uniform brown to brown grayish, becoming paler in the ventral area. It has a tuft of bristle-like stiff hair between the eyes and in the forehead. The antlers have massive pedicels and are large, divergent, often curving so the tips are convergent, but with a wide space between them (Weber 2014). The brown brocket deer is distributed in the Yucatán Peninsula, in the states of Yucatán, Campeche, and Quintana Roo, México and in northern Guatemala and northern Belize (Weber and Medellín 2010; Weber 2014; Weber *et al.* 2016). It has been described as a generalist species, using habitat due to its availability, showing no preference for a vegetation type (Weber 2005; Weber 2014).

Central American red brocket deer (Figure 1a) is the smallest of the three deer species we discuss (Weber 2014) weighting 12 to 32 kg; in the Greater Calakmul Region the average weight of five adult males was 16.3 kg and that of four adult females was 13.2 kg (Bello-Gutiérrez *et al.* 2010). Its dorsal coat its deeply red, with darker tones on neck and head, and whitish ventral parts of the body and tail. Antlers are simple, lacking ramifications, growing no more than two inches (Bello-Gutiérrez *et al.* 2010; Weber 2014). The limits of its distribution are unclear, having records in México, in the states of Tamaulipas, San Luis Potosí, Veracruz, Puebla, Oaxaca, Chiapas, Tabasco, Campeche, and Quintana Roo, northern and central Belize, Guatemala, El Salvador, Costa Rica, Nicaragua, Honduras, Panama, and western Colombia (Bello-Gutiérrez *et al.* 2010; Bello *et al.* 2016; Moreira-Ramírez *et al.* 2019). It is a habitat specialist, occupying well-preserved humid forest (Medellín and Equihua 1998; Weber 2005; Tejeda-Cruz *et al.* 2009; García-Marmolejo *et al.* 2013; García-Marmolejo *et al.* 2015), occasionally using secondary vegetation, as long as there are well-preserved surrounding forest or vegetation that constitutes a high percentage of its diet, like the palm *Sabal mexicana* (Tejeda-Cruz *et al.* 2009; García-Marmolejo *et al.* 2015), in areas with high hunting pressure, it uses low-flooded forest (Reyna-Hurtado and Tanner 2005).

Camera-trapping has been an important tool for the study of these and other medium-sized and large mammals, covering aspects ranging from species richness, abundance indices, density, occupancy, activity patterns, and even more complex aspects such as intraspecific, interspecific and environmental interactions (Mandujano 2019). In recent years, occupancy models are being used more frequently to evaluate the presence or absence of cryptic species and the relationship of the species with several variables of the landscape (MacKenzie *et al.* 2011). The advantage of occupancy models is that they incorporate the probability of detection, a parameter that can vary when species are cryptic, shy, exist in low densities, or when the environment changes make it difficult to sample the presence of a specific species (MacKenzie *et al.* 2011).

Through occupancy models and several others ecological estimators of wildlife populations parameters, knowledge about fauna has expanded, allowing for more structured conservation strategies (Bruner *et al.* 2001). Food, water sources, type and vegetation cover, distance from roads and human presence are factors that limits the presence, movement and size of populations of ungulates. The effects of those vary among species and from regions (Lira-Torres and Naranjo Piñera 2003; Weber 2008; Pérez-Cortez *et al.* 2012; García-Marmolejo *et al.* 2013). However, basic ecological aspects as activity patterns, occupancy and the factors involved in these, have been poorly studied for these deer species (Ramírez 2016; Moreira-Ramírez *et al.* 2019). The aim of this study was to evaluate the probabilities of occupation, local colonization, local extinction, detection, activity patterns, activity overlap and relative abundance of the three species of deer in the ponds of Calakmul Biosphere Reserve, through nine years of photo-trapping, contributing to the understanding of the ecological patterns and conservation of Neotropical deer that live in sympatry.

Materials and methods

Study area. Calakmul Biosphere Reserve (CBR) is a protected area decreed in 1989, with an extension of 7,231 km^2, located in the municipality of Calakmul, southeast Campeche, 19° 15′ 17″ N, -90° 10′ 89″ W (Carabias-Lillo *et al.* 1999). The reserve

Figure 1. a) Central American red brocket deer (Mazama temama). b) Yucatan brown brocket deer (Odocoileus pandora). c) White tailed-deer (O. virginianus).

presents a tropical sub-humid climate, with a rainy season in summer (Jun to November), having an annual mean temperature of 24.6 °C, and an annual mean precipitation of 1,076 mm (Martínez and Galindo-Leal 2002). The reserve's hydrography is determined by the amount of rainfall, which is capable of flooding lowlands and forming temporary and permanent ponds and surface stream beds Carabias-Lillo *et al.* 1999). The ponds are vital components of the landscape for wildlife, being one of the few water sources of the region in the dry season (Reyna-Hurtado *et al.* 2010; Pérez-Cortez *et al.* 2012). The main vegetation types in Calakmul are high evergreen forest, medium sub evergreen forest, low evergreen and deciduous forest, savanna and hydrophytes (Pennington and Sarhukan 1998; Carabias-Lillo *et al.* 1999; Martínez and Galindo-Leal 2002).

Camera trapping. As part of a long-term study focused on wildlife uses of ponds in CBR conducted by R. Reyna-Hurtado and collaborators, camera trapping survey was conducted from February 1st 2014 to December 31st 2022 in as many as 17 ponds (Figure 2). A single camera trap was installed in each of a set of 10 to 17 ponds that were monitored along these years (Reconyx PC800 Hyperfire professional Reconyx, Inc., Cuddeback Inc and Browning Strike Force Co.). Cameras were positioned 50 cm above the ground, and programmed to take five pictures every time the sensor detected movement. The cameras were checked every two months on average to change batteries and memory cards.

Relative abundance. To ensure the independence of the records, photographs obtained of the same species where individuals could not be recognized were selected in a 60-minute period, considering them as a single event (Tobler *et al.* 2008). To estimate the relative abundance index, we took the number of independent records of a selected species divided by the number of camera-nights, multiplied by 100 (O'Brien 2011; Mandujano 2019).

Occupancy. Following the methodology used by Louvrier *et al.* (2017) to calculate the probability of occupancy, local colonization, local extinction, and detection in the ponds over the nine years of camera-trapping, we used the dynamic model of occupancy designed by MacKenzie *et al.* (2003). The sampling units were the years from 2014 to 2022 and the secondary occasions were defined according to the months of the year (1 to 12). We created a detection history per species, where we pooled the records of detection (1) and non-detection (0) per periods. Assuming that occupancy (Ψ) is the probability that a site is occupied by the target species, p_{tj} is the probability of detecting the target specie, given presence, in survey j within primary period t (MacKenzie *et al.* 2003). Local colonization (γ) is the probability that an unoccupied site in a primary sampling period (t) is occupied in $t + 1$, and local extinction (ϵ) is the probability that an occupied site in a primary sampling period (t) is unoccupied in $t + 1$ (MacKenzie *et al.* 2003). For model selection we used the Akaike's information criterion (AIC; Burnham and Anderson 2002), models were performed using the *Unmarked* package in R (Kellner *et al.* 2023).

To limit the number of models we followed a hierarchical approach (Olson *et al*. 2005; Betts *et al.* 2008), and to evaluate the goodness of fit and the dispersion parameter (c-hat) of the best single species model we followed the procedure used by Andrade-Ponce *et al* (2022). First, we created a model for each of the covariates to see their effects on the detection of the species, applying the Akaike's selection criterion to select the best one, similarly we performed these steps for occupation, local colonization and local extinction. The resulting models were contrasted with Akaike's selection criterion to choose the best model(s).

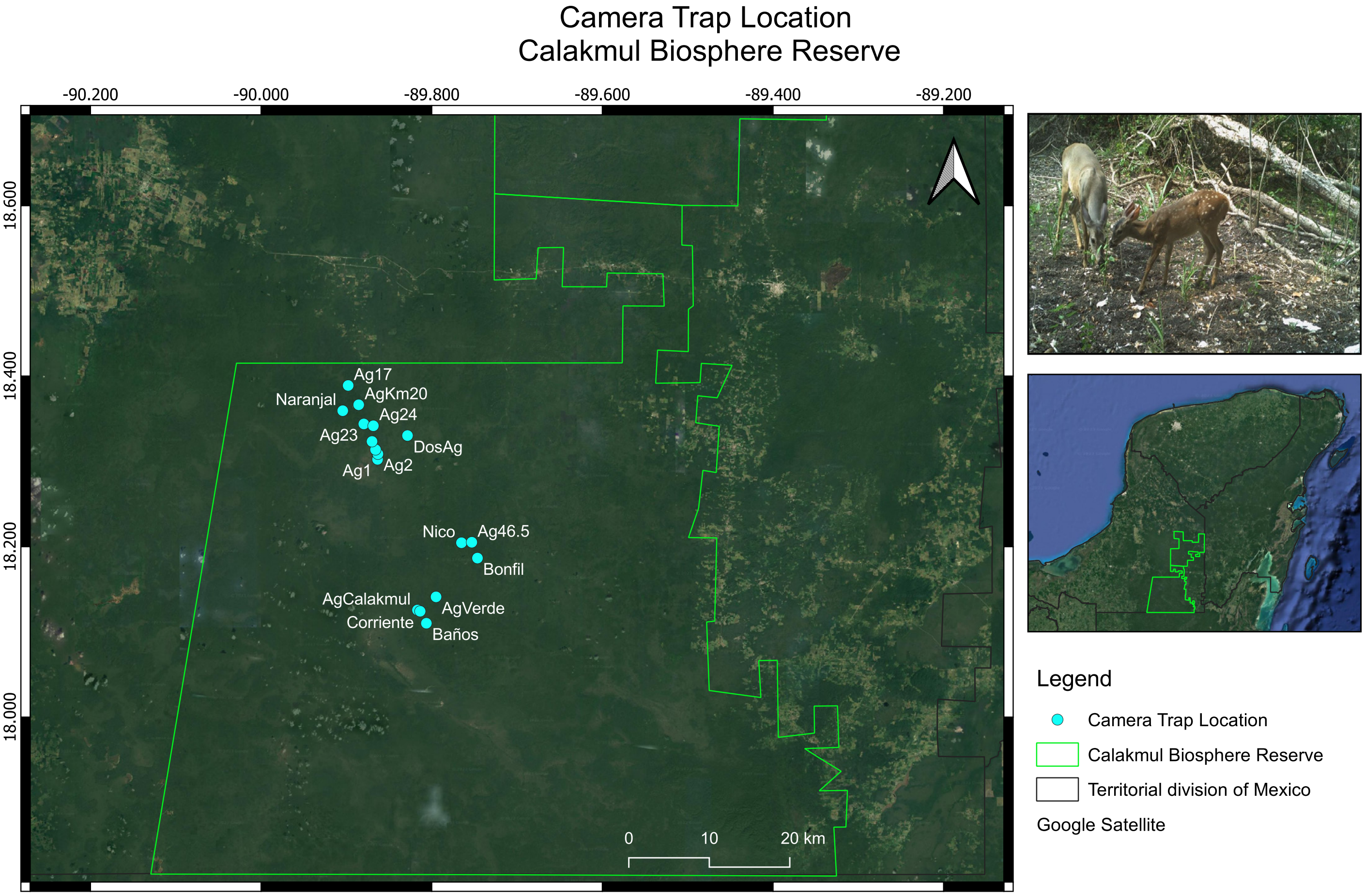

Figure 2. Geographic location of Calakmul Biosphere Reserve and sampled ponds.

The covariates used in this study were selected according to the possibility of their importance for the species at the time of visiting the ponds. a) The distance from the ponds to the road. b) The type of vegetation that predominates around the ponds following the classification of Pennington and Sarhukan (1998). c) Disturbance, measured as the influx of people to the ponds, being a "medium" level, when they are visited by this or another research group and/or having a medium level of tourism and being a "low" level, when they are only visited by our research group. d) The presence or absence of water. e) The year as a linear effect.

To determine a possible relationship between deer species occupancy and the presence of water, we used a multispecies model, since single-season or multi-season occupancy models consider that the variables affecting occupancy do not change during the entire study period (MacKenzie *et al.* 2003), while the presence or absence of water in the ponds varies over months and years. Therefore, to see its possible effect, water presence was analyzed as another species, solely for analysis purposes in the unmarked program (Kellner *et al.* 2023). The multispecies model allows estimating the probability of two or more species occurring simultaneously, as a function of covariates, using a multivariate Bernoulli distribution (Rota *et al.* 2016). For the analysis, a detection history was created for the presence of water and a null occupancy model was performed, to visualize if there was any type of interaction, and if it was significant. Finally, the species interaction factor (*SIF*) was estimated to corroborate the type of interaction between deer and water, where values equal to one suggest independence, values less than one indicate an inversely proportional relationship and values greater than one indicate a positive relationship (Richmond 2010). The analysis was performed through the *Unmarked* package in R (Kellner *et al.* 2023).

Activity patterns. Following the methodology used by Andrade-Ponce *et al.* (2022) we used the Kernel density estimation method, with the Von Mises distribution for circular data to estimate the overlap activity patterns (Ridout and Linkie 2009). To compare the overlap of daily activities of a pair of species we use the overlap coefficient (*Δ*), where values close to one reflect a similar activity pattern and values close to cero mark different activity patterns. In addition, we calculated the 95 % CI of each overlap coefficient with 10,000 bootstrap tests (Ridout and Linkie 2009). To assess whether the overlap coefficient was statistically significant, a randomized test was performed. If the resulting *P*-value is less than 0.05 it can be inferred that the Kernel circular probability distributions differ and therefore the resulting overlap is the result of chance. The packages *Activity* and *Overlap* were used to perform the tests in R version 2023.09.1+494 (Ridout and Linkie 2009; Rowcliffe 2023; R Core Team 2023).

Results

Relative Abundance. During the nine years of camera-trapping, with an effort of 31,217 camera-nights, 225 independent records were obtained for Yucatan brown brocket deer, only 16 for Central American red brocket deer and 2,026 for white-tailed deer, the last species having the highest relative abundance (*RAI.* = 6.49; Table 1), followed by the Yucatan brown brocket deer (*RAI.* = 0.72; Table 1), and Central American red brocket deer having the lowest value (*RAI.* = 0.05; Table 1).

Of the nine study years, the one with the highest relative abundance for *Odocoileus virginianus* was 2022 (*RAI.* = 13.29; Table 1) and the lowest was 2014 (*RAI.* = 3.47; Table 1). For *Odocoileus pandora* the highest year was 2019 (*RAI.* = 1.51; Table 1) and the lowest was 2020 (*RAI.* = 0.21; Table 1). *Mazama temama* was not recorded in six of the nine camera-trapping years, the one with the highest relative abundance was 2021 (*RAI.* = 0.81; Table 1) and the lowest 2022 (*RAI.* = 0.03; Table 1).

Occupancy. Odocoileus pandora. The probability of occupancy ($\Psi = 0.98$), colonization ($\gamma = 0.0001$), and extinction ($\epsilon = 0.05$) of *O. pandora* was not related to any of the variables under analysis, however, the probability of detection was negatively influenced by low to medium disturbance of the ponds respectively, with values ranging from $p = 0.500$ ($\beta = 0.002$, *P-value* = 0.99) to $p = 0.077$ ($\beta = -2.47$, *P-value* = 0.001; Table 2; Figure 4a). The more human visitation the water pond received, the lower the detection of the species by the cameras. It presented a slightly positive interaction with respect to the presence of water in the ponds (*SIF.* = 1.01, *P-value* = 2.85E-43; Figure 4c).

Odocoileus virginianus. Similar to *Odocoileus pandora*, the probability of occupancy ($\Psi = 0.36$), colonization ($\gamma = 0.86$), and extinction ($\epsilon = 0.06$) were not affected by any of the covariates analyzed for *O. virginianus*. Detection probability was affected by the type of vegetation surrounding the ponds, with values ranging from $p = 0.50$ ($\beta = 0.18$, *P-value* = 0.82) in lowland dry forest, $p = 0.41$ ($\beta = -0.28$, *P-value* = 0.71) in the mid-humid forest and flooded lowland ecotone, $p = 0.23$ ($\beta = -1.16$, *P-value* = 0.08) in mid-humid forest, and $p = 0.19$ ($\beta = -1.73$, *P-value* = 0.01) in mid-dry forest (Table 2; Figure 4b). While interaction with water was also slightly positive (*SIF.* = 1.03 *P-value* = 7.24E-08; Figure 4e).

Table 1. Relative abundance index in each of the nine years of photo-trapping.

Species	2014	2015	2016	2017	2018	2019	2020	2021	2022	9 years
Odocoileus pandora	0.48	1.17	0.88	0.96	0.96	1.51	0.21	0.41	0.89	0.72
Mazama temama	0.00	0.00	0.00	0.078	0.00	0.00	0.00	0.81	0.039	0.05
Odocoileus virginianus	3.47	10.63	3.97	7.53	7.29	4.96	3.64	5.50	13.29	6.49

Mazama temama. Probably due to the few independent records obtained for the Central American red brocket deer, none of the variables under analysis had any effect on the probability of occupancy ($\Psi = 0.001$), colonization ($\gamma = 0.99$), extinction ($\epsilon = 0.65$), and detection ($p = 0.01$; Table 2). Being the interaction with water slightly negative (*SIF.* = 0.93, *P-value* = 1.84e-01; Figure 4d).

Activity patterns. We detected a predominant diurnal activity in two of the three deer species, white-tailed deer showed two peaks of activity (7:00 to 10:00 and 13:00 to 16:00; Figure 3d), and the Yucatan brown brocket deer showed a relatively constant activity during the day with a large peak from 11:00 to 13:00 (Figure 3a), while the Central American red brocket deer showed a cathemeral activity, having several activity peaks during the whole day (7:00 to 8:00, 10:00 to 11:00, 14:00 to 13:00, 17:00 to 18:00 and 23:00 to 24:00; Figure 3b). We found a high overlap in the daily activities of the three species ($\Delta > 0.7$), the pair of species with the highest overlap coefficient were white-tailed deer and Yucatan brown brocket deer ($\Delta = 0.86$, P-value = 0.63; Figure 3d), followed by white-tailed deer and Central American red brocket deer ($\Delta = 0.78$, P-value = 0.7; Figure 3f), and finally Yucatan brown brocket deer and Central American red brocket deer ($\Delta = 0.73$, P-value = 0.6; Figure 3e).

Discussion

The type of human disturbance, behavior, habitat and parameters of the deer biology can explain the results obtained for the relative abundance and occupancy of the ponds. The White-tailed deer, despite not occupying a large number of ponds, presented greater abundance, probably due to the ponds being open environments, with a large amount of food in their surroundings. On the other hand, both Gray and Red brocket deer showed a low abundance throughout the nine years, which may be due to their elusive behavior and their more frugivorous diet (Weber 2005), and especially for *M. temama*, due to their preference for closed environments with dense humid vegetation (Bello-Gutiérrez *et al.* 2010). This differs from studies conducted in the same area with transects and track counts, in which a greater abundance of Brocket deer is reported relative to White-tailed deer, but because they are different methods, the results often differ from each other (Weber 2005; Reyna-Hurtado and Tanner 2007).

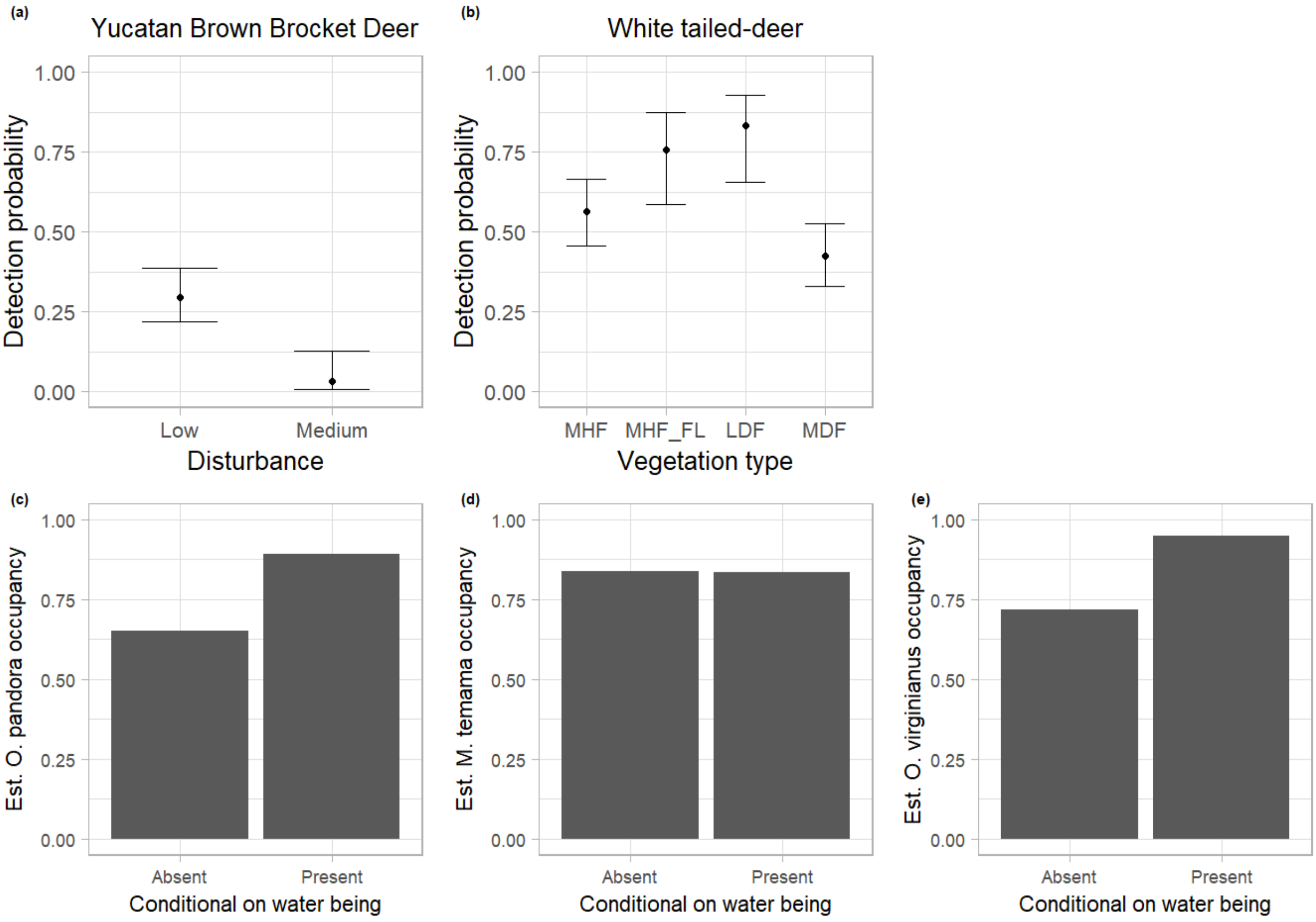

Figure 4. a) Relation between O. pandora Detection and level of disturbance. b) Relation between O. virginianus detection and vegetation type. c-e) Interaction between the presence or absence of water and the occupancy of the three deer species, in ponds of Calakmul Biosphere Reserve, México. MHF = Mid Humid Forest, MHF_FL = Mid Humid Forest and Flooded Lowland, LDF = Low Dry Forest, MDF = Mid Dry Forest.

Table 2. Dynamic occupancy models for the three deer species in Calakmul Biosphere Reserve from 2014 to 2022. Covariates: Disturbance (Pert); Year; Distance to road (Dist_road); Presence of water (Water); Vegetation type (Veg). Ψ = Occupancy, γ = Colonization, ϵ = Extinction, p = Detection, K = Number of parameters, AICc = Akaike Information Criterion, ΔAICc = Delta Akaike, AICcw = Akaike weight.

Model	K	AICc	ΔAICc	AICc$_w$
Odocoileus pandora				
Ψ(1);γ(1);ϵ(1);p(Pert)	6	309.54	0	0.95
Ψ(1);γ(1);ϵ(Pert);p(1)	6	316.99	7.45	0.02
Ψ(1);γ(1);ϵ(1);p(1)	4	318.38	8.84	0.01
Ψ(1);γ(Year);ϵ(1);p(1)	5	318.38	9.26	0.01
Ψ(Pert);γ(1);ϵ(1);p(1)	6	321.27	11.73	0.00
Ψ(1);γ(1 + Year);ϵ(1 + Pert);p(Pert)	9	334.46	24.92	0.00
Mazama temama				
Ψ(1);γ(1);ϵ(1);p(1)	4	34.77	0	0.40
Ψ(1);γ(Year);ϵ(1);p(1)	5	37.20	2.43	0.12
Ψ(1);γ(Dist_road);ϵ(1);p(1)	5	37.20	2.43	0.12
Ψ(1);γ(1);ϵ(1);p(Year)	5	37.85	3.09	0.08
Ψ(1);γ(1);ϵ(1);p(Water)	5	37.85	3.09	0.08
Ψ(1);γ(1);ϵ(1);p(Pert)	6	37.85	3.09	0.08
Ψ(1);γ(1);ϵ(1);p(Dist_road)	5	37.85	3.09	0.08
Ψ(1);γ(Pert);ϵ(1);p(1)	6	40.59	5.83	0.02
Ψ(1);γ(1);ϵ(Pert);p(1)	6	40.62	5.86	0.02
Ψ(1);γ(1 + Year + Dist_road + Pert);ϵ(1 + Pert);p(1 + Year + Water + Pert + Dist_road)	15	288.96	254.19	0
Odocoileus virginianus				
Ψ(1);γ(1);ϵ(1);p(Veg)	8	418.35	0	0.93
Ψ(1);γ(1);ϵ(1);p(1)	4	424.24	5.89	0.05
Ψ(1);γ(1);ϵ(Year);p(1)	5	426.80	8.44	0.01
Ψ(1);γ(1);ϵ(Pert);p(1)	6	430.44	12.08	0.00
Ψ(1);γ(1);ϵ(1 + Year + Pert);p(Veg)	11	449.66	31.31	0.00

Similarly, other studies throughout México report abundances of *M. temama*, being the highest in the El Triunfo Biosphere Reserve in Chiapas (Lira-Torres and Naranjo-Piñera 2003) and in the ejido of Nuevo Becal, Campeche (Ramírez 2016), with the species been more abundant in humid well-conserved areas. In the case of *O. virginianus*, its abundance is very fluctuating, due to its ability to adapt to disturbed areas, for example in San Luis Potosí, it presented an abundance of 5.6 in ecosystems of early successional stages and an abundance of 2.8 in those of medium successional stages. The abundance of *O. pandora* has been poorly studied outside of Campeche, and most studies lump the two brocket deer species into a single group (Weber 2005; Reyna-Hurtado and Tanner 2007), making it difficult to compare the abundance of these species. However, the results obtained in this study should be taken with caution, as they may be biased, because the positioning of the cameras was not random, but were placed specifically in ponds (Reyna-Hurtado *et al.* 2019).

The Yucatan brown brocket deer had the highest probability of occupancy in the ponds out of the three deer species throughout the nine years (despite not being very abundant), and therefore presented very low probabilities of colonization and extinction; however, none of the variables analyzed had an effect on these. This could be due to the fact that this species has been defined as a generalist species (Weber 2005), adapting well to the diverse types of environments that the CBR has (Reyna-Hurtado and Tanner 2005), and to the different degrees of disturbance, either by human presence and/or distance to the roads. Previous studies have shown the adaptability of *O. pandora* to these environments, presenting high abundances for the species (Weber 2005; Reyna-Hurtado and Tanner 2007; Ramírez 2016), however, it has also been reported that this species is susceptible to hunting and that the presence of this activity has a negative effect on occupancy (Urquiza-Haas *et al.* 2009). The probability of detection was affected by the disturbance at the watering holes, decreasing with increased human presence, probably due to the species solitary and nervous nature, leading them to a selective use of watering holes with little human influx (Weber 2014).

White-tailed deer showed a low occupancy of the ponds, but with a high probability of colonization, and a low probability of extinction, this can be explained by the high amount of food found in these forest clearings, where herbaceous plants are abundant and are important resources for this species (García-Marmolejo *et al.* 2015; Ramírez 2016), although none of the variables had an effect on these, as in studies conducted in Nicaragua (Zeller *et al.* 2011). On the other hand, detection probability was influenced by the type of vegetation, varying among the four types of vegetation analyzed. Although this species is clas-

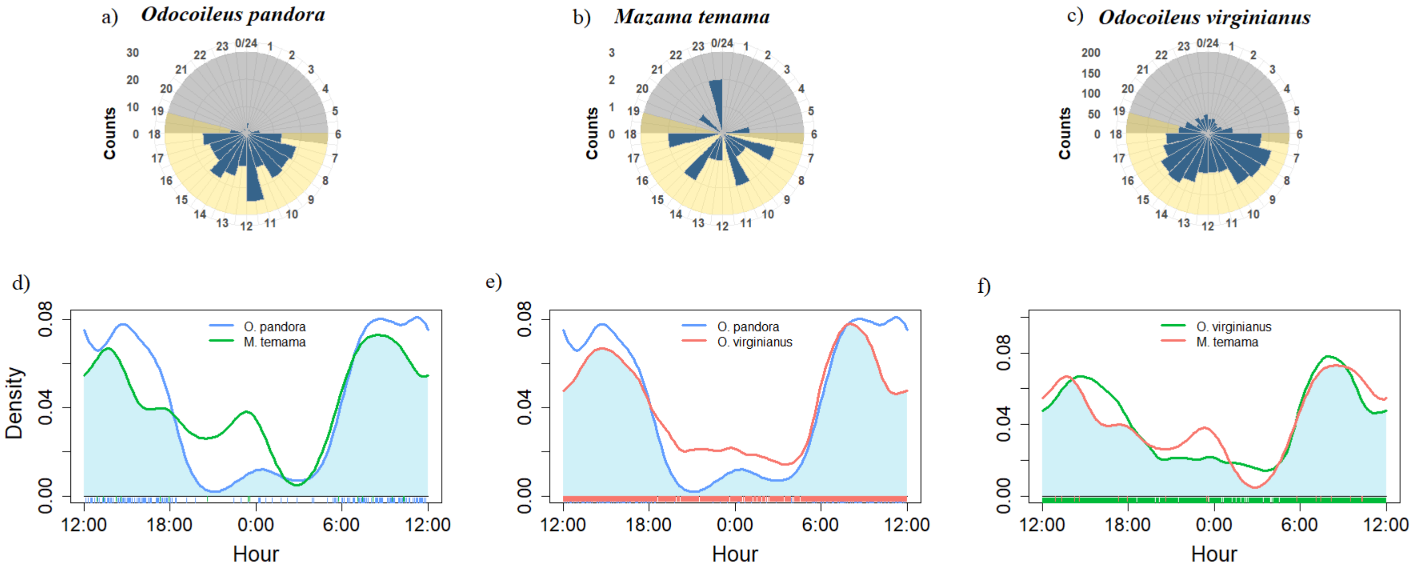

Figure 3. a-c) Number of records per hour for Odocoileus pandora, Mazama temama and O. virginianus. d-f) Kernel activity overlaps between each pair of species in Calakmul Biosphere Reserve, México.

sified as a generalist (Weber 2005) and has great plasticity, allowing it to inhabit a wide variety of ecosystems (Weber 2014; Gallina *et al.* 2014; Gallina and López-Arévalo 2016), it has shown a preference for dry and flooded lowland in the CBR. These habitats presented the highest probability of detection, followed by medium-humid and dry forests, which the species uses in proportion to their availability (Reyna-Hurtado and Tanner 2005).

In the case of Central American red brocket deer, both the probability of occupancy and detection were very low and the probability of colonization and extinction were high, probably due to the low abundance of this species in the reserve in this and other studies (Weber 2005; Ramírez 2016), as well as to the prevalence of non-optimal environments for this species, which prefers tropical forests with high humidity and high and dense vegetation cover, as a means of protection against predators (Bello-Gutierrez *et al.* 2010; Ramírez 2016). In studies conducted in a nearby community forest (Ejido Nuevo Becal) the presence of this species was higher (Ramírez 2016) and there is even a sport hunting company focusing entirely on legally harvesting this species (Reyna-Hurtado pers. Obs.). Studies conducted in Los Chimalapas, Oaxaca, showed that the distance to the villages had a positive effect on the occupancy of *M. temama* and that the probability of detection is low, due to its cryptic behavior (Pérez-Irineo and Santos-Moreno 2016). Similarly, it has been detected that the presence of hunting has a negative effect on the occupancy of this species (Urquiza-Haas *et al.* 2009). On the other hand, in Costa Rica, it was determined that the colonization by *M. temama* was favored in areas with ecologically similar species as the temperature increased. Conversely, in areas with ecologically dissimilar species, colonization was favored as the temperature decreased (Beaudrot *et al.* 2019).

The presence of water in the ponds was an environmental variable of special interest in this work, because it has been demonstrated that it is a vital resource for other ungulate species in the reserve (Reyna-Hurtado and Tanner 2005; Reyna-Hurtado *et al.* 2012; Pérez-Cortez *et al.* 2012; Sandoval-Seres *et al.* 2016; Sánchez-Pinzón *et al.* 2020). White-tailed deer as well as Yucatan brown brocket deer showed a slight positive interaction with the presence of water, allowing us to infer that the presence of the resource may be a factor that influences the visit to the ponds, however it is uncertain if it is for consumption or for some other reason, such as a greater amount of some herbaceous species. In other regions, water has been found to be a determining factor in the activities of white-tailed deer, altering their behavior (Gallina *et al.* 1998) or extending their home range when the resource is scarce (Kroll 1992; Contreras-Moreno *et al.* 2021). The importance of water availability in the behavior and survival of this species (and probably of other cervids) is clear (Bello *et al.* 2001). The interaction of the Central American brocket deer with water was slightly negative. This finding is inconsistent with other studies in the tropics, which report the importance of water for the brocket deer species (Zeller *et al.* 2011). The CBR represents the driest portion of the area and *M. temama* prefers humid areas, such as the adjacent community areas to the CBR, where the species seems to be more abundant (Ramírez 2016; Reyna-Hurtado unpublished data). This discordance also may be due to the low number of records we obtained for this species.

Two of the three deer species studied, the white-tailed and the Yucatan brown brocket deer showed daily diurnal activity; the white-tailed deer had activity peaks during most of the day, but avoiding the hottest hours (11:00 to 13:00), agreeing with other studies for this species in the east and center of Mexico (Hernández-SaintMartín *et al.* 2013;

Soria-Díaz and Monroy-Vilchis 2015; Ramírez 2016; Soria-Díaz *et al.* 2016; Moreira-Ramírez *et al.* 2019) and Costa Rica (Botts *et al.* 2020), although contrasting with studies done in arid environments and in Sierra Madre Occidental (Beier and McCullough 1990; Gallina *et al.* 2005), where activity peaks were reported at dawn and dusk. Likewise, the Yucatan brown brocket deer was active during the day, presenting a large peak between 11:00 and 12:00, agreeing with previous works in Campeche and Guatemala (Ramírez 2016; Moreira-Ramírez *et al.* 2019). In contrast, the Central American red brocket deer showed cathemeral activity, which is consistent with most studies for this species, both in México (Pérez-Irineo and Santos-Moreno 2016; Moreira-Ramírez *et al.* 2019; Pérez-Irineo *et al.* 2021; González *et al.* 2021; Salazar-Ortiz *et al.* 2022) and Central America (Arroyo-Arce *et al.* 2016; Arroyo-Arce *et al.* 2017; Moreira-Ramírez *et al.* 2019; Botts *et al.* 2020), varying at diurnal or nocturnal times in few cases (Ramírez 2016; Pérez-Irineo *et al.* 2021; Moreno *et al.* 2023).

Activity overlap was high among the three deer species ($\Delta > 0.7$), which lead us to hypothesize that they are able to coexist in the same environment due to the clear separation in behavior and diet specialization. The white-tailed deer being a habitat generalist browser with high consumption of leaves and stems throughout the year and a few fruits during the wet season; the Yucatan brown brocket deer is also a habitat generalist but is mainly frugivorous during the dry season and a browser in the wet season; and the Central American red brocket deer is a specialist frugivorous of well-conserved and dense habitats (Weber 2005).

In this study it was shown that among the variables analyzed there is not one that influences deer occupancy in the ponds, so it is likely that this is due to a combination of multiple factors and interactions among these species, however, it was seen that these species, like other ungulates, have a positive interaction with the presence of water. Ponds are vital resources in the Calakmul Biosphere Reserve, being one of the few semi-perennial water sources for wildlife during the dry season. Increasing temperatures, desiccation, changing rainfall patterns and human disturbance in the ponds threaten these unique microenvironments, endangering the natural habitats of the species and the biotic community in general, making them priority areas for biodiversity conservation. The CBR is a unique place that hold population of three sympatric species of deer. We hope that this research helps to understand the ecological requirements of these interesting species and how they have coexisted in this tropical, semidry environment.

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Applicability of DNA barcoding-based analyses on the diet of the Gray brocket deer (*Subulo gouazoubira*) in xeric hillside forests

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In this study, we explore the applicability of DNA barcoding, specifically targeting the chloroplast DNA (cpDNA) sequences, particularly the *trn*L (UAA) intron region, to analyze the diet of gray brocket deer. This approach offers improved taxonomic resolution and the ability to identify species with greater precision compared to traditional methods. The study was conducted in the "Reserva Natural Salus" in Uruguay, covering a range of vegetation types, where gray brocket deer coexist with other exotic ungulates. A local reference database of *trn*L (UAA) sequences was established, incorporating both GenBank data and sequences obtained from native species in the study area. Fecal samples were collected in summer and winter, and DNA was extracted and amplified for metabarcoding analysis in pooled samples for each season. For each sample 28,229 and 33,588 reads were obtained respectively, which together corresponded to 25 Operational Taxonomic Units (OTUs). The species *Rubus ulmifolius* and *Schinus engleri* were the most represented in the diet with 69.6 % of the summer reads, whereas in winter, 68.7 % of the reads corresponded only to *Schinus engleri*. These findings indicate that gray brocket deer consume species that have higher nutritional value, which may be linked to their capacity to thrive in young and productive ecosystems. This study demonstrates the feasibility of DNA barcoding for dietary analysis in gray brocket deer and provides valuable insights into their food habits in the "Reserva Natural Salus". Further improvements to increase the reference databases of native species and the exploration of additional genetic markers are recommended for enhanced species-level discrimination in dietary analysis studies. This methodology is promising for future research as diet studies have an impact on species management, habitat conservation and biodiversity conservation efforts.

En este estudio, exploramos la aplicabilidad de los códigos de barras de ADN, utilizando la región de intrón del cloroplasto *trn*L (UAA), para analizar la dieta del guazubirá. Este enfoque ofrece una buena resolución taxonómica y la capacidad de identificar especies con mayor precisión que con los métodos tradicionales basados en análisis microhistológicos de fragmentos vegetales. El estudio se realizó en la "Reserva Natural Salus" de Uruguay, que presenta distintos tipos de vegetación, incluyendo bosques nativos, plantaciones de pinos y eucaliptos, y afloramientos rocosos, donde el guazubirá convive con otros ungulados exóticos. Para el estudio se estableció una base de referencia local de secuencias *trn*L (UAA), incorporando registros de GenBank y secuencias obtenidas de especies nativas en el área de estudio. Se recolectaron muestras fecales en verano e invierno, se extrajo y amplificó el ADN para análisis de metabarcoding, agrupando las muestras colectadas en cada estación. Para cada uno de los muestreos se obtuvieron 28,229 y 33,588 lecturas respectivamente, que en conjunto representaron 25 Unidades Taxonómicas Operativas (UTOs). Sin embargo, las especies *Rubus ulmifolius* y *Schinus engleri* fueron las más representadas con el 69.6 % de las lecturas de verano, para invierno el 68.7 % de las lecturas fueron para *Schinus engleri*. Estos hallazgos indican que el guazubirá consume especies que tienen alto valor nutricional, lo cual podría relacionarse con la habilidad de esta especie a adaptarse a ecosistemas jóvenes y altamente productivos. Este estudio demuestra la viabilidad de estudios de dieta basados en códigos de barras de ADN para ciervos neotropicales y proporciona información valiosa sobre los hábitos alimentarios del guazubirá en la "Reserva Natural Salus". Se recomienda ampliar las bases de secuencias de referencia de especies nativas y explorar otros marcadores genéticos adicionales para mejorar el poder de discriminación a nivel de especie en los estudios de metabarcoding de especies vegetales. Esta metodología es prometedora para futuras investigaciones, ya que los estudios de dieta tienen un impacto en el manejo de especies, la conservación del hábitat y los esfuerzos de conservación de la biodiversidad.

Keywords: DNA metabarcoding; food habits; mammal; neotropical cervids; noninvasive; species identification; *trn*L (UAA).

Introduction

Subulo gouazoubira (Bernegossi *et al.* 2022) is the only native deer that inhabits Uruguayan wooden environments (Black-Décima *et al.* 2010). Like other deer, it plays a relevant role in forest species composition, stand and canopy structures, and complexity (Vavra *et al.* 2007; Reed *et al.* 2022). The diet of gray brocket deer mainly involves fruits, leaves, fibers, and flowers (Prado 2013), and shows significant changes in composition associated with different ecosystems (Gayot *et al.* 2004; Kufner *et al.* 2008, Serbent *et al.* 2011).

Different complementary techniques have been used to evaluate the diet composition for large herbivores (Rayé *et al.* 2010; Nakahara *et al.* 2015). Diet studies of Neotropical cervids have been conducted mainly by microhistological analysis of plant fragment recovery from feces and stomach contents (Bodmer 1991; Pinder 1997; Gayot *et al.* 2004; Kufner *et al.* 2008; Cosse *et al.* 2009; Serbent *et al.* 2011). Although this is a non-invasive method that provide information in terms of species composition, the microhistological analysis is complex and often leads to the ambiguous identification of species in many plant groups (Garnick *et al.* 2018). The use of molecular techniques for species identification (DNA metabarcoding) reduces taxonomic identification errors (Taberlet *et al.* 1999; Miller and Waits 2003; Waits and Paetkau 2005; Deagle *et al.* 2013; Alberdi *et al.* 2019; Deagle *et al.* 2019), allowing for a more precise taxonomic resolution than with classic microscopic analysis. For example, the DNA contained in the feces can be amplified by PCR, allowing the fast production of large amounts of genetic information and, by contrasting with DNA barcodes in reference databases, the species present in the samples can be correctly identified (Davison *et al.* 2002). The power of the technique is based on the chosen genetic marker, which must have sufficient sequence-level differences between the species to be identified (barcode gap), and the level of completeness of the reference database. A marker widely used in DNA metabarcoding of plants is the chloroplast *trn*L (UAA) intron (Taberlet *et al.* 2007), a small DNA fragment, variable at sequence level in different species and amplified with universal primers.

Our aim was to evaluate the applicability of DNA barcoding for gray brocket deer dietary analysis related to: i) the resolution level at which the DNA-based method can describe the diet, using a global database enriched with a local acquired database, and ii) the diet composition focusing on native and alien species. To achieve these goals, we conducted next-generation sequencing of the chloroplast *trn*L (UAA) region from fecal samples obtained by non-invasive sampling to assess the diet of gray brocket deer in a patch of xeric, hillside forest of Uruguay.

Materials and methods

Study site. The study was carried out in the "Reserva Natural Salus (RNS)" in Lavalleja Department, Uruguay (34° 23′ 36.79″ S; -55° 18′ 58.54″ W) covering 1,500 ha. The altitudes vary around 497 masl, with the dominant vegetation types being grasslands, hillside shrublands, and native forests limited in extension to hillsides (see Bonifacino and Rossado 2016) for a more detailed description of the study area). In addition, eucalyptus and pine plantations also occur. Gray brocket deer (*Subulo gouazoubira*) coexist in the area with two exotic ungulates: wild boar (*Sus scrofa*) and axis deer (*Axis axis*).

Completion of the local reference database of the trnL (UAA) intron sequences. A local species list was created based on the technical report "Reserva Natural Salus Flora" (Bonifacino and Rossado 2016) and records of observations made by local park rangers (*pers. comm.* 2022) of highly palatable shrubby species cultivated in residential gardens in the vicinity of the study area and accessed by deer. A local database of *trnL* (UAA) intron reference sequences for chloroplast DNA (Taberlet *et al.* 2007) was retrieved from GenBank (Benson *et al.* 2013) based on matching records with the local species list. Also, *trnL* (UAA) sequences were generated to cover some missing taxa and local variants of the native species. Native plant species were gathered from various locations, including the botanical garden "Museo y Jardín Botánico de Montevideo", the gardens of the "Facultad de Agronomía-Udelar" the greenhouse of the "Instituto Nacional de Semillas" and the IIBCE Mimosoideae collection at the "Instituto de Investigaciones Biológicas Clemente Estable". Plant vouchers were herborized following standard protocols (Bridson and Forman 1992) and deposited at MVFA herbarium at Facultad de Agronomía-Udelar (see supplementary data). Plant tissue samples were preserved in silica gel until they were dried.

DNA extraction from reference plant specimens was conducted using dried young leaves following Fazekas *et al.* (2012). FastPrep®- 24 (MP Biomedicals) and lysing matrix beads were used for tissue homogenization and cell disruption. DNA extracts were amplified with the universal c–d primer pair (Taberlet *et al.* 2007), amplifying the entire *trn*L (UAA) intron (c: 5′-CGAAATCG GTAGACGCTACG-3′; d: 5′-GGGGATAGAGGGACTTGAAC-3′). Each PCR reaction contained 1X Buffer (Invitrogen), 1.5 mM MgCl (Invitrogen), 0.04 U Taq polymerase (Invitrogen), 0.05 mM each dNTP, 0.2 mg/mL BSA and 0.5 µM forward and reverse primers in a final volume of 20µl. The thermal profile consisted of an initial denaturation step at 94 °C for 3 min, followed by 35 cycles at 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 1 min, and a final extension step at 72 °C for 15 min. Amplification success was confirmed by 1.5 % agarose electrophoresis using GoodViewTM nucleic acid stain (SBS Genetech Co., Ltd., Beijing). PCR products were purified using an enzymatic method with 0.8 U/µl of Exonuclease I and 0.2 U/µl of Thermosensitive Alkaline Phosphatase (FastAP; Thermo Fisher Scientific), following the manufacturer's instructions. Forward and reverse sequencing was conducted using the Macrogen Korea sequencing server. For each reference plant, a consensus sequence was obtained and used to build a local reference database of *trnL* (UAA) intron sequences.

Feces sampling. Samples were collected in two seasons: summer and winter. We performed six 100-meter transects across three different environments: native forests, pine and eucalyptus plantations, and grassland to reach 600 meters (Figure 1). Each transect was visited only one time per sample season to reduce the probability of resampling the same individual. Fecal sampling was performed opportunistically on a visual basis along the transects. We collected fecal pellets randomly chosen from each fresh fecal pile and preserved them in 70 % alcohol. Each sample was treated independently.

DNA extraction and PCR of the feces samples. DNA extraction was performed using the Stool Kit QIAGEN®. Sterile materials were used, and extraction was performed in an isolated room. Each sample was confirmed for species assignment (Aristimuño 2013) using a 159 pb fragment of the mitochondrial DNA D-loop region.

We performed PCR experiments to amplify a fragment of approximately 141 bp corresponding to a region of the intron of the gene *trn*L (UAA) of the chloroplast using the primers c (5′-CGAAATCGGTAGACGCTACG-3′) and h (5′-CCATTGAGTCTCTGCACCTATC-3′), as described by Taberlet *et al.* (2007). These primers had non-barcode and barcode adapter sequences for Ion Torrent-PGM® (Life Technologies). We used two barcode adapters (BC54 and BC57) on forward primers to distinguish two pooled samples based on the season sampling time. The PCR was done in a final volume of 10 µl, containing 1x buffer Invitrogen, 1.5 mM MgCl2, 0.2 of BSA, 0.05 mM of each dNTP, 0.5 pM of each primer, 0.25 U of DNA Taq Polymerase (Invitrogen), and 1 µl of DNA (Taberlet *et al.* 2007). The thermocycling conditions consisted of an initial denaturation at 94 °C for 3 min; 35 cycles of initial denaturation at 94 °C for 45 s, followed by 54.5 °C for 30 s and 72 °C for 60 s; and a final extension at 72 °C for 20 min.

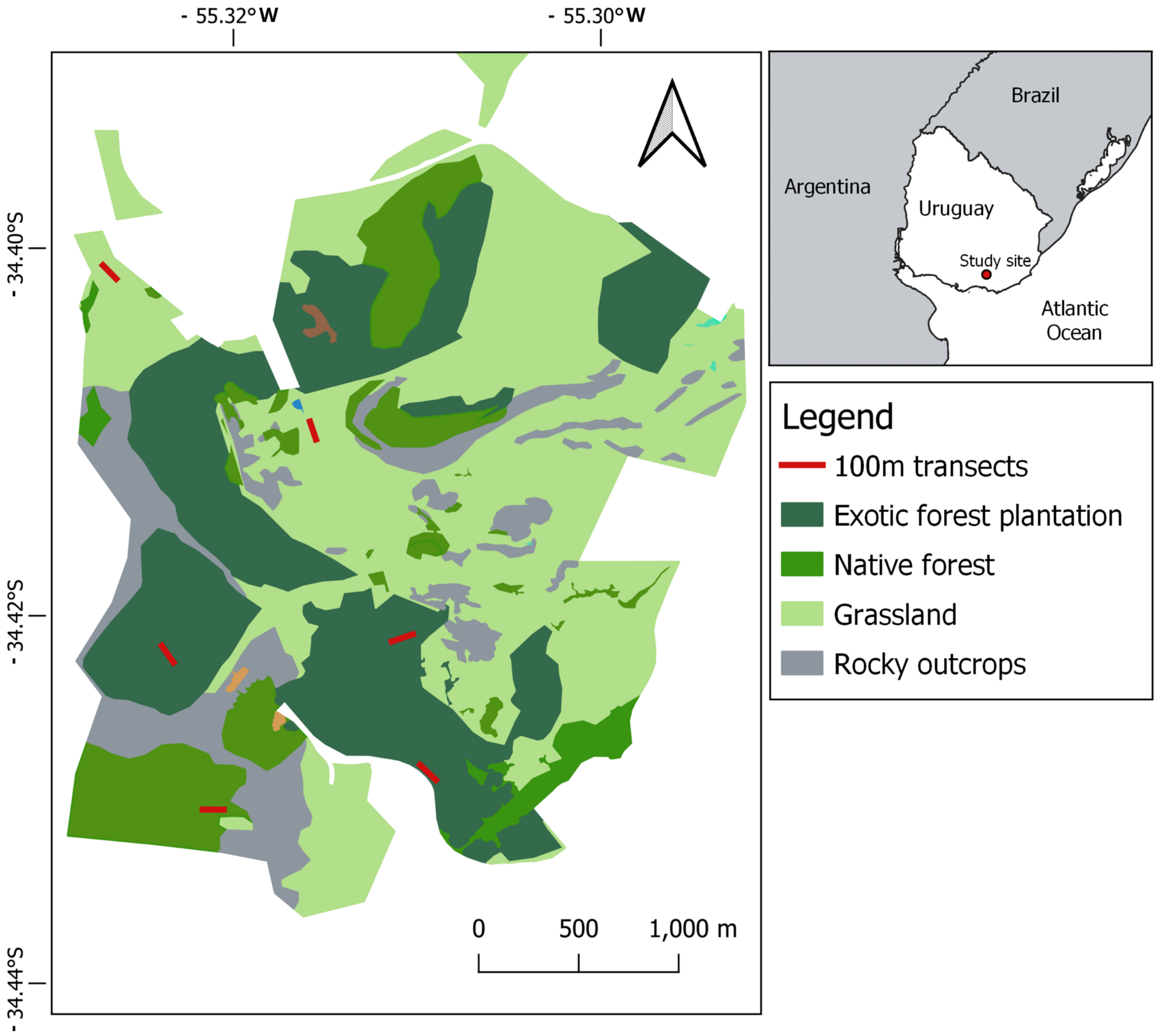

Figure 1. Habitat mosaics inside the 'Reserva Natural Salus' (RNS)'s. Red lines represent the location of each survey transect where gray brocket deer samples were collected. Right: Location of the RNS (red point) in Uruguay.

PCR products were purified using the same protocol as the reference sequences and pooled for each season according to the protocols for NGS by Moreno *et al.* (2016). The mixture was quantified using a QubitR 2.0 Fluorometer (Life Technologies, USA) and diluted to obtain almost the same number of molecules per pooled PCR product. The run was performed using the Ion Torrent-PGM® (Life Technologies) platform from IIBCE facilities with a 316 chip. A 5000x coverage was achieved. The metadata are available in the NCBI BioSample database (http://www.ncbi.nlm.nih.gov/biosample/) under accession number: SAMN39224164 and SAMN39224165.

Bioinformatic Analyses. The software SEED2 (Větrovský *et al.* 2018) was used for amplicon high-throughput sequencing data analysis from FastQ files. The pipeline excluded short sequences (< 50 bp), low-quality sequences (mean quality value < 27), and chimeras. In addition, we performed clustering of similar sequences (97 %) into molecular taxa or Operational Taxonomic Units (OTUs) using the algorithm implemented in Vsearch (Rognes *et al.* 2016). We then used the G-Ins algorithm from SEED2 (Větrovský *et al.* 2018) to align sequences representing each cluster. The aligned sequences were cut to 148 bp, including gaps. Taxonomic assignment of the OTUs was carried out using the BLAST alignment software (Altschul *et al.* 1997). Clusters with fewer than 10 reads were not included in the analyses to prevent misidentification of plants owing to sequencing errors and to increase the reliability of species composition (Nikodemova *et al.* 2023). BLAST in SEED2 was executed twice, using: i) the local reference database constructed with *trnL* (UAA) intron sequences from the local species list, and ii) the global reference database from GenBank (Benson *et al.* 2013). Species assignment was based on the "Parque Salus" species list (Bonifacino and Rossado 2016) and records of local park rangers (*pers. comm.* 2022) and the best score on similarity and cover for both references used (local or global GenBank). Once the clusters were taxonomically assigned, the relative abundance was calculated by dividing reads for each taxon count by the total number of reads classified as species, genus, or family (frequency of each OTU). The importance of each item was evaluated by calculating the relative read abundance (RRA) of the items identified through DNA metabarcoding (Deagle *et al.* 2019; Tosa *et al.* 2023).

Results

Local reference database of trnL (UAA) intron sequences. The list of flora species from the "Reserva Natural Salus" (Bonifacino and Rossado 2016) included 488 species, 268 genera, and 80 families. In the global base of sequences GenBank (Benson *et al.* 2013), *trnL* (UAA) intron sequences were found for 226 (51.6 %) of the species listed for the Reserve. In addition, 211 (48.2 %) representative species of the same genera were retrieved from this reference base. The local reference database generated includes the recovered sequences from GenBank (Benson *et al.* 2013) and 138 sequences of native species or local varieties of exotic species, comprising 71 genera and 32 families obtained in this study and from the "CENUR-Rivera, Udelar" *trnL* (UAA) sequence collection. In total, 496 species from 302 genera and 85 families were included. The local base of reference was created with 1,050 sequences that represented all genera in the area and more than one specimen for some species.

Diet Analyses. Forty-eight feces were collected in summer and 51 in winter, however more than half did not provided good enough DNA quality required for PCR. From the DNA extraction of these samples, it was possible to confirm the identity of the deer species in nine and five samples collected in summer and winter respectively. For the summer sampling, three PCR products of the TrnL (UAA) region were obtained and pooled, generating 43,906 reads. After filtering for quality and size, 28,229 reads were assigned to 21 OTUs. For winter sampling (June), three samples were pooled, which generated 52,136 reads, reducing to 33,588 after filtering to obtain 16 OTUs. With the two pooled samples, we obtained a total of 25 OTUs belonging to 17 families. At the family level, five families were represented in one of the two samples by more than 3 % of the reads. The dominant families were Anacardiaceae and Rosaceae, representing 77 % of the reads obtained in each sampling season (Figure 2).

We found that the amplified *trnL (UAA)* region does not exhibit sequence differences within certain species from the Anacardiaceae, Myrtaceae, Leguminosae, and Vitaceae families. Consequently, in these cases, taxonomic assignment was only possible at the genus or family level. To address this limitation, we conducted a broad comparison of all potential species assignable to an OTU with the list of flora species documented in the 'Reserva Natural Salus'. In certain instances, the flora of Parque Salus featured only a single species within a specific genus, allowing for the precise determination of the consumed species (*e. g.*, *Schinus engleri*, Anacardiaceae). However, in other cases, particularly within the Myrtaceae and Leguminosae families, the study area harbored several species, preventing us from assigning OTUs to a particular genus or species within these families.

Taxonomic assignment showed two species as the more frequent items in the deer diet. For summer samples, *Rubus ulmifolius* (Rosaceae) represented 42.4 % of reads, followed by *Schinus engleri*, with 27.2 % of reads. In addition, *Schinus engleri* was the most abundant in winter, representing more than 68.7 % of the reads obtained. Other species present in the diet had a minor representation of less than 8 % in both samples (Table 1).

Discussion

Several studies have been conducted on the trophic aspects of *Subulo gouazoubira*, which vary in their methods and scope. They also focused on different aspects of feeding behavior, such as food selection, preferences, and dietary seasonality, among others. Most studies have focused on

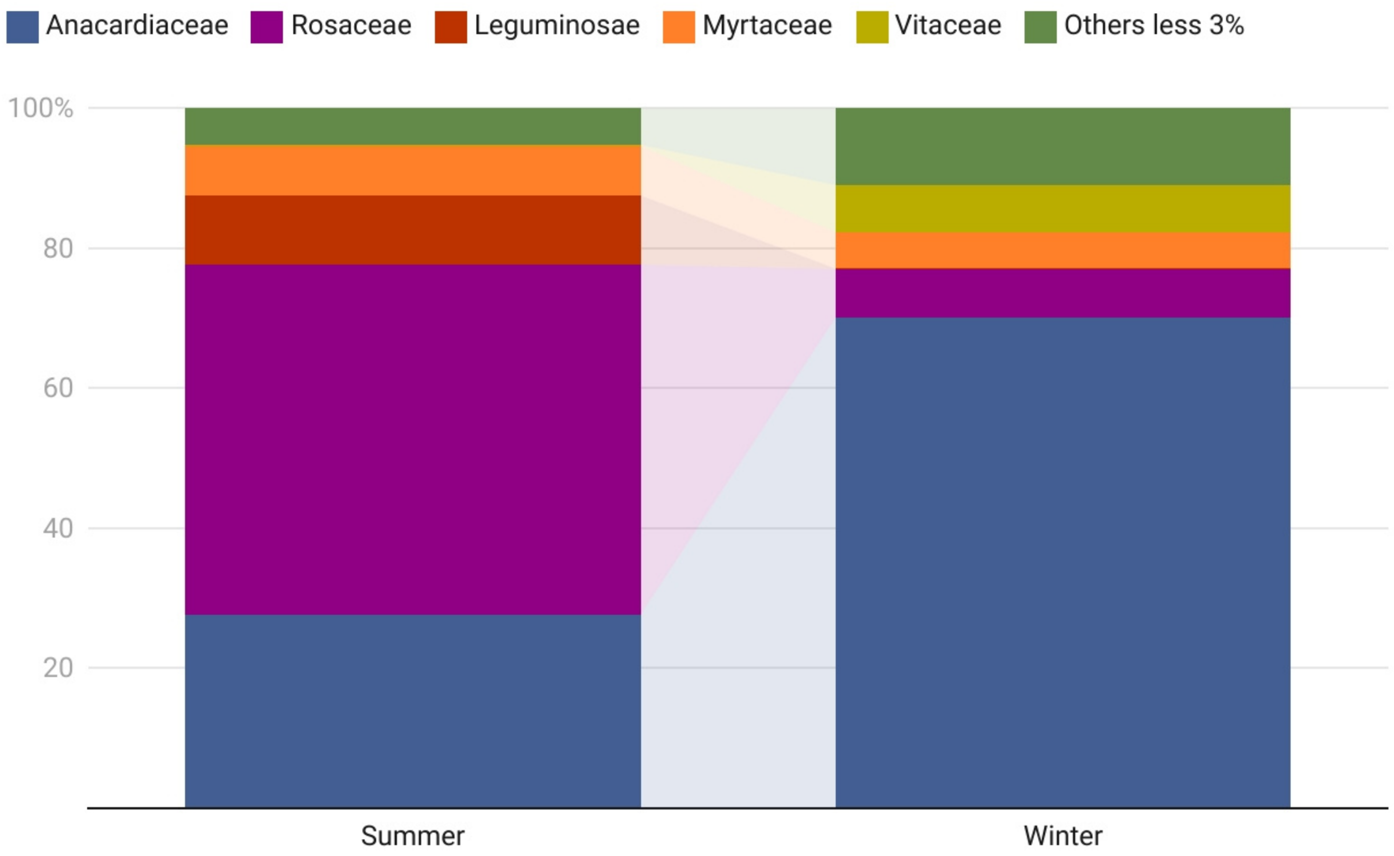

Figure 2. Frequency of reads for the most abundant families in feaces on summer and winter sampling dates.

determining whether a species is frugivorous or consumes a higher proportion of leaves and grass (browsers). In Argentina, Paraguay, and the Bolivian Chaco, it has been observed that this species of deer feed on a wide variety of species, ranging between 25 and 100 species present in their diet, primarily consisting of leaves and fruits (Richard *et al.* 1995; Juliá and Richard 2001; Kufner *et al.* 2008, Serbent *et al.* 2011). The incidence of fruits and seeds varies in these regions, ranging from 11 % to 40 % of their diet; however, occasional consumption of specific fungi (Richard *et al.* 1995) and cacti, which can account for up to 30 % of their consumption, has also been observed (Cartes 1998; Caballero 2001). In Paraguay, the type of fruit (hard and dry or soft and fresh) depends on the season, which can be dry or wet (Stallings 1984). In contrast, in the Brazilian Pantanal, Pinder (1997) found a low incidence of fruits in the diet (with a peak of 19.2 % and annual average of 4.3 %). In the Peruvian Amazon rainforest, fruits constitute 80 % of the diet of the gray brocket deer (Bodmer 1989).

This study presents the first characterization of the diet of gray brocket deer through DNA barcoding, focusing on the *trn*L (UAA) intron region. This technique provides an approach to understanding the diversity of consumed species but does not provide information about the consumed structures (fruit or leaves). In turn, small sample sizes and pooled samples were employed. For a more accurate characterization of the gray brocket deer's diet, it is desirable to increase the sample size, use of replicates and analyze individual samples independently. This approach allows better estimations of taxonomic richness, to ensure that rare taxa are not overlooked (Alberdi *et al.* 2019) and an evaluation of individual variability, whereas, in our analysis sample discrimination is limited to season-based distinctions. The sequences obtained from the two samples included 25 species belonging to 17 families. Most of these species represented less than 10 % of the total reads obtained. Estimating abundance from sequence counts involves addressing biases caused by factors such as DNA copy number, sample DNA degradation, and variations in PCR extraction and amplification efficiency (Pompanon *et al.* 2012). Therefore, while some studies suggest a positive correlation between RRA and the percentage of plant mass consumed (Willerslev *et al.* 2014), it is essential to recognize that RRA serves as a semi-quantitative indicator of dietary composition (Deagle *et al.* 2019). However, considering the existence of different biases, the gray brocket deer's diet in the "Reserva Natural Salus (RNS)" was dominated by two species (*Rubus ulmifolius* and *Schinus engleri*). These results are consistent with those observed by Serbent *et al.* (2011), who identified 20 species in the gray brocket deer diet but only five represented 60 % of the diet. These authors found that deer consume a few preferred species, making a strong selection for those that contain higher-quality nutrients. This is supported by our results on the high consumption

Table 1. List of species present on *Subulus gouazoubira* diet for summer and winter samples from "Reserva Natural Salus (RNS)." The genera with asterisks refer to the species not mentioned on the list but observed in home gardens from the area. Number of reads (N), relative percentage of reads (%).

			Summer		Winter	
Order	**Family**	**Gender**	**N**	**%**	**N**	**%**
Sapindales	Anacardiaceae	*Schinus engleri*	7,677	27.20	23,073	68.69
Rosales	Rosaceae	*Rubus ulmifolius*	11,964	42.38	2,259	6.73
Rosales	Rosaceae	*Pyracantha coccinea*	2,159	7.65	83	0.25
Myrtales	Myrtaceae	*Psidium sp./Myrcianthes sp./Eugenia sp.**	1,914	6.78	1,706	5.08
Vitales	Vitaceae	*Cissus striata*	38	0.13	2,179	6.49
Fabales	Leguminosae	Leguminosae Genera	1,619	5.74	0.00	0.00
		Species representing 1 - 3%	1,867	6.60	1,973	5.90
		Species representing less than 0.99%	991	3.50	2,315	6.90
Total			28,229	100	33,588	100

of blackberry (*Rubus ulmifolius*) in the summer when a large number of fruits are produced by this species. Studies of the cafeteria in this species under semi-captive conditions have evaluated their preferences among *Morus nigra*, *Psychotria carthagenensis*, and *Rubus boliviensis* (Richard and Fonturbel-Rada 2006). The authors found a clear preference for *M. nigra* and a rejection of *R. boliviensis*. These species differ in their nutritional characteristics, *M. nigra* has lower fiber content and higher crude protein content than *R. boliviensis*. In our study, the most represented species in summer, *Rubus ulmifolius*, has fiber values of 1.66 ± 0.06, even lower than *M. nigra*, and a higher carbohydrate content (Ahmad *et al.* 2015), which makes *Rubus ulmifolius* a high nutritional content food.

Small deer, less than 20 kg, such as the gray brocket deer, are generally classified as concentrated selectors or browsers (Hofmann and Stewart 1972; Hofmann 1989). Bodmer (1990) suggested the existence of a continuum between browsers and frugivores in which species can adjust their eating behavior in response to environmental changes. Our results agree with those of Richard and Fontúrbel-Rada (2006) and Serbent *et al.* (2011), which indicated that *S. gouazobira* is a selective and opportunistic species (Putman 1988), preferring a few species with high nutritional content. The dietary variations observed in the different habitats occupied by this species could be linked to the need to consume components with high energy content, as well as their plasticity to take advantage of young and highly productive ecosystems (Geist 1998; Serbent *et al.* 2011). This flexibility in their diet contributes to their success in different habitats and wide geographical distribution (Pinder 1997; Cartes 1998; Caballero 2001; Serbent *et al.* 2011).

It would be interesting to understand how the gray deer plays a role in the regeneration of native forests, as it is the only native deer species with a wide distribution in Uruguay. Understanding their role as dispersers or predators of invasive and native species seeds is crucial to accomplish this. This role is partly due to the size of the seeds; medium or large seeds appear to be destroyed during rumination (Bodmer 1989), whereas smaller seeds may remain intact when passed through the digestive tract (Gayot *et al.* 2004). In turn, the rumen bacterial communities (Bodmer 1989) of deer can digest different components of the seeds, softening the cuticles of the palms, but cannot degrade lignified covering present in the seeds of other species. It is necessary to carry out experiments on seed banks from the feces of *S. goauzaoubira* to determine the effect they can have on the germination rate of the different seeds they consume.

This is the first approximation of a diet determination technique in *Subulo gouazoubira* by metabarcoding. Our study focuses on evaluating the applicability of DNA barcode-based diet analysis of native herbivores with national capabilities. Although the number of samples was limited and the samples collected during the same sampling season (summer and winter) were processed together, relevant results could be obtained concerning the diet of this species in the "Reserva Natural Salus (RNS)" and the dominance of blackberries reads in the diet during the fruiting period of this species. Regarding the completeness of the reference base for barcode sequences of native species, it is necessary to advance into the generation of sequences of local populations and identify other markers, such as *matK, trnH-psbA, rbcL,* and *ITS2* (Fazekas *et al.* 2012), which have better species-level discriminatory power for some families, such as Anacardiaceae, Myrtaceae, and Leguminosae. It is important to highlight that progress in this methodology is relevant, as the results of these types of studies are of great importance for species management plans, land management, and diversity conservation.

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Spatial variation of population density and age structure of White-tailed deer (*Odocoileus virginianus*) in a Colombian moor

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Wildlife population density is affected by resource availability, predators and competitors, and anthropogenic stressors. Its analysis and the factors affecting it are important for conservation, use, or population control. Based on estimates of density and population parameters, together with niche modeling, previous studies considered that the white-tailed deer population at the Chingaza National Natural Park (NNP) is undergoing exponential growth due to the marginal influence of factors regulating its abundance, such as predators. The aim of this study was to evaluate the population density and age structure of the white-tailed deer in the Chingaza NNP, Colombia. To evaluate the population density and age structure of white-tailed deer in the Monterredondo and La Paila sectors of the Chingaza NNP, 10 transects were installed with circular plots in each. These were visited twice; in each visit, we collected all deer pellet groups, measuring each pellet to estimate its volume. Population density was calculated using the Eberhardt and Van Etten method and the semi-automated PELLET procedure using FSC and FAR techniques; the age structure was estimated by k-means and fuzzy clustering analyses. With the FAR technique, the estimated deer density was 2.09 ind/km2 in Monterredondo and 0.94 ind/km^2 in La Paila. With PELLET, these values were 0.37 ± 0.4 ind/km^2 for Monterredondo and 0.16 ± 0.2 ind/km^2 for La Paila. The proportion of age classes (adult, juvenile, and fawn) was 1:0.29:0 for Monterredondo and 1:0.57:0.04 for La Paila. The population density of white-tailed deer in two sectors of the Chingaza NNP is not homogeneous, but shows temporal and spatial variations. Population density has decreased versus reports from previous studies in this same area, with the highest deer abundance recorded in 2004, mostly in the Monterredondo sector. The proportion of age classes suggests that the population is stable, as the largest proportion of individuals corresponds to the adult stage.

La densidad poblacional se ve afectada por la disponibilidad y oferta de recursos, la presencia de predadores y competidores, y la influencia antrópica. Su análisis y el de los factores que la afectan son importantes en la conservación, aprovechamiento o control de poblaciones. A partir de estimaciones de densidad y parámetros poblacionales junto con modelamientos de nicho, se considera que la población del venado cola blanca en el Parque Nacional Natural (PNN) Chingaza está creciendo exponencialmente por la baja influencia de factores que regulan su abundancia, como los depredadores. El objetivo de este estudio fue evaluar la densidad poblacional y estructura de edades del venado cola blanca en el PNN Chingaza. Para evaluar la densidad poblacional y estructura de edades del venado cola blanca en los sectores de Monterredondo y La Paila del PNN Chingaza, Colombia, se instalaron 10 transectos con parcelas circulares en cada sector y se revisaron en dos ocasiones de muestreo, en las que se recogió la totalidad de los grupos fecales de venado y se midió cada pellet para estimar su volumen. La densidad poblacional se calculó utilizando el método de Eberhardt y Van Etten utilizando las técnicas FSC y FAR y el procedimiento semiautomatizado PELLET, y la estructura de edades se estimó por medio del agrupamiento con k-medias y con k-medias difuso. Con la técnica FAR la densidad de Monterredondo fue de 2.09 ind/km^2 y en La Paila fue de 0.94 ind/km^2. Con PELLET estos valores para Monterredondo fueron de 0.37 ind/km^2 ± 0.4 y 0.16 ind/km^2 ± 0.2 para La Paila. La proporción en las clases de edad (adulto, juvenil y cervatillo) para el sector Monterredondo fue 1:0.29:0 y para La Paila fue de 1:0.57:0.04. La densidad poblacional de venado cola blanca estudiada en dos sectores del PNN Chingaza, no es homogénea, presenta variaciones que son tanto temporales como espaciales así, la densidad poblacional ha disminuido en comparación con lo reportado por estudios anteriores en esta misma área, donde se estima que la mayor abundancia de venados se registró en 2004 y espacialmente las mayores abundancias se han registrado en su mayoría hacia el sector Monterredondo. La proporción de individuos por edades sugiere que la población se encuentra estable ya que en la clase de adultos se encuentra la mayor proporción de individuos y hay presencia de juveniles y algunos cervatillos.

Keywords: Age classes; pellet-group counting; pellet groups; moor; population estimates.

Introduction

Estimating the population density of a species allows carrying out comparisons over time and identifying trends in wild populations (Gallina 1994). According to Brown (1984) and Naoki *et al.* (2006), the factors affecting the distribution and abundance of individuals in a population are the availability and supply of resources in the habitat of each species. In mammals, population density is related to aspects such as habitat size and the supply of food, shelters, and water. In this way, the highest densities are associated with habitats that provide the appropriate resources for each species in quantity and quality (Pettorelli *et al.* 2001; Marsden and Whiffin 2003).

The white-tailed deer is a mammal species belonging to the family Cervidae that is widely distributed in America from southern Canada to the northern Amazon, ranging from 0 m to 4,000 m above sea level. Its ecological plasticity allows it to settle in tropical rainforests, scrublands, marshlands, and Andean moors, but the savannah is usually the most favorable biome (López-Arévalo *et al.* 2020). The white-tailed deer has been one of the most studied species throughout its range. Most studies have been carried out in the United States and Canada. In Latin America, the country with the largest number of studies on this species is Mexico (Mandujano 2014); in Colombia, these studies are still very scarce (Mateus-Gutiérrez *et al.* 2020).

The population density of white-tailed deer throughout its range varies according to the availability of food, water, and shelters, local weather conditions, the presence of predators and competitors, and habitat alterations. The largest abundances have been associated with habitat complexity and vegetation types such as scrub (Gallina 1994; Gallina *et al.* 1998; Villarreal 1999; Delfín-Alfonso and Gallina 2007; Gallina *et al.* 2010; Stewart *et al.* 2011). The anthropic influence related to hunting and proximity to human communities also affects the population dynamics, reflected in a lower deer density in areas closer to human settlements (Flores-Armillas *et al.* 2011; Ramos-Robles *et al.* 2013).

On the other hand, the analysis of the age distribution of a population, *i. e.*, the proportion of individuals belonging to a given age class, is a central component of population dynamics, since it provides information about the past and current status of a population, in addition to suggesting future trends (Ojasti 2000). Estimating and analyzing these parameters and the environmental factors that influence them represent baseline information to preserve, use, or monitor wildlife populations (Mandujano 2011). It is believed that a high proportion of juveniles indicates an expanding population, whereas the predominance of adults is characteristic of a stationary or declining population (Ojasti 2000).

In Colombia, the white-tailed deer are distributed throughout most of the territory. However, there are few studies on its population density, and it is considered that the largest populations thrive in La Orinoquia and the Andean region in the Chingaza National Natural Park (NNP; Rojas-Pardo 2010; Mateus-Gutiérrez 2014; Gómez-Castellanos 2017). In the first, population densities between 13 individuals/km^2 and 43 ind/km^2 have been estimated in two localities of the department of Casanare by direct count along transects (Pérez-Moreno *et al.* 2020). For the Chingaza NNP, Mateus-Gutiérrez (2014) estimated between 17.8 ind/km^2 (Monterredondo) and 23.2 ind/km^2 (La Mina) based on counts of fecal groups. For Monterredondo, Gómez- Castellanos (2017) calculated about 8.9 ind/km^2 based on counts of fecal groups and identified visibility and distance to water sources as the main factors influencing abundance. Thus, higher abundances are reported in areas with poor visibility, whereas greater distances to water bodies are associated with lower abundances.

In the Chingaza NNP, where moor and submoor vegetation predominate, Aconcha-Abril (2008) found minor variations in the sex ratio in adults (1:0.6 in Monterredondo and 1:0.9 in La Playa) and juveniles (1:1.12 in Monterredondo and 1:1.7 in La Playa). However, the adult:juvenile ratio showed a higher proportion of adults, namely 2:1 in Monterredondo and 3:1 in La Playa. Based on the definition of 3 age classes, namely fawns, juveniles, and adults, a 2:2:7 ratio was calculated for Monterredondo and 2:2:10 for La Mina (Mateus-Gutiérrez 2014) in this protected area.

Rodríguez-Castellanos (2016), using niche models, proposed that the population inhabiting the Chingaza NNP comprises approximately 4,868 individuals distributed in an area of approximately 237,788 km^2, equivalent to 31% of the total NNP area. This value suggested a population with exponential growth and with a homogeneous distribution in the protected area; this author used the average population density obtained by Mateus-Gutiérrez (2014). To evaluate spatial and temporal variations in white-tailed deer density, the population density and age structure of this species were estimated in the Monterredondo and La Paila sectors of the Chingaza NNP in 2020.

Materials and methods

Study Area. The study area is located in the Chingaza National Natural Park, in the eastern Colombian Andes north of Bogotá and in the departments of Cundinamarca and Meta (Figure 1). It stretches across nearly 76,600 ha, through an altitudinal gradient between 800 m and 4,500 m above sea level, but most of the territory is above 3,300 m a.s.l. The rainfall regime is unimodal, with most rainfall concentrated between May and August and the dry season from December to February (Vargas and Pedraza 2003; Plan de Manejo 2014–2018 2013). Within the protected area, 53 plant communities have been described distributed in seven vegetation types, including *pajonal*, *frailejonal*, scrubs, pastures, *chuscal*, moor forest patches, and shrub forests (Vargas and Pedraza 2003).

For this study, we selected the Monterredondo and La Paila sectors (Figure 1) because they differ in physical and biotic characteristics, as well as in the anthropogenic influence. The Monterredondo sector is characterized by open scrubs, dense scrubs, dense forests, fragmented forest with secondary vegetation, dense pastures with scrubs, dense pastures without trees, and patches of grassland alternating with natural vegetation (Figure 2), where the dominant plant cover in this sector is dense pasture with shrubs (Interpretación Visual de Imagen Satelital Landsat 857 2018).

According to the 2014 to 2018 management plan of the Chingaza National Natural Park (Plan de Manejo 2014–2018 2013), Monterredondo is in a fair state of conservation with low functionality. Additionally, this section shows a greater anthropogenic influence since it includes camping areas for tourists, who sometimes offer food to deer (Plan de Manejo 2014–2018 2013).

On the other hand, the Paila sector is covered by open scrubs, dense scrubs, high dense forests, fragmented forests with pastures and crops, fragmented forests with second-

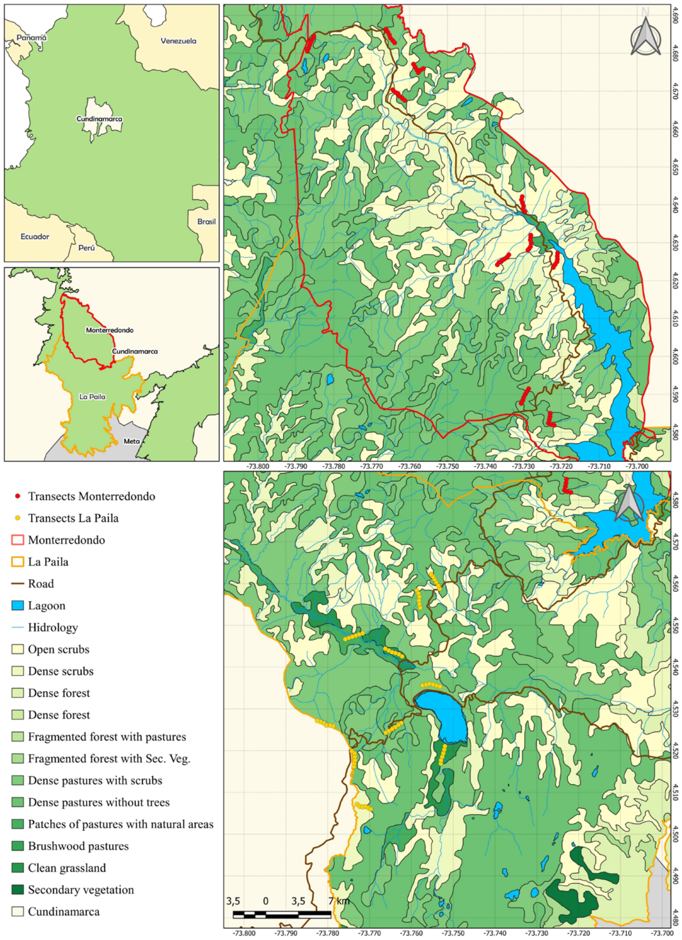

Figure 1. Map of the study area and location of the transects for fecal pellet counting in the Monterredondo (in red, up) and La Paila (in yellow, down) sectors of the Chingaza National.

ary vegetation, dense pastures with scrubs, dense pastures without trees, patches of pastures alternating with natural areas, brushwood pastures, clean grassland, and secondary vegetation (Figure 3), where the high dense forest is the dominant plant cover (Interpretación Visual de Imagen Satelital Landsat 857 2018). This sector harbors submoor species, mainly scrub species of the families Asteraceae (*Pentacalia*, *Diplostephium*, and *Baccharis*), Hypericaceae (*Hypericum*), and Ericaceae (*Macleania, Cavendishia, Gaultheria*, and *Vaccinium*); and moors dominated by frailejonal (*Espeletia grandiflora*, *E. killipii*, *E. uribei*, *E. argentea*, and *Espeletiopsis corymbosa*), pajonal (*Calamagrostis effusa*), and chuscal (*Chusquea tessellata*).

Population Density. Pellet groups were monitored during two field trips. We visited the transects of each sector twice: first during February and March 2020 and subsequently in December 2020. In each sector, we installed 10 transects measuring 500 m long. Each transect included 51 circular plots with a radius of 2 m placed 10 m apart from each other (Figure 4), for a total of 20 transects and 1,020 plots (510 plots per sector).

GIS tools were used to locate the transects at random, considering the type of plant cover of each sector to capture the greatest diversity in terms of units of vegetation cover and land uses for the two sectors evaluated, *i. e.*, Monterredondo (MR) and La Paila (LP), meeting the requirement to be separated at least 800 m in the range as suggested by Mandujano (2014) and Mandujano and Yáñez-Arenas (2016). Additionally, its orientation was refined taking into account elements such as inclination and supplementary information from the Chingaza NNP trail and track network.

In each plot, all fecal pellet groups found were collected, noting the number of pellets, appearance, and texture, considering the report by Mateus-Gutiérrez (2014); one pellet group corresponded to the total number of pellets with similar characteristics grouped in the sampling area (Gallina *et al.* 2014). Additionally, we recorded the date, sector, transect, and plot. When a pellet group was found at the transect boundary, it was recorded if more than 50% of it was within the plot (Mateus-Gutiérrez 2014).

Figure 2. Photographs of some of the types of vegetation and land use in the Monterredondo sector. A) Dense pasture without trees. B) Dense shrubland. C) Deer in the vicinity of the National Natural Park facilities. D) Deer close to visitors and the house. E) Chuza Reservoir. F) Camping area. G) Plant nursery. H) Visitor feeding a deer.

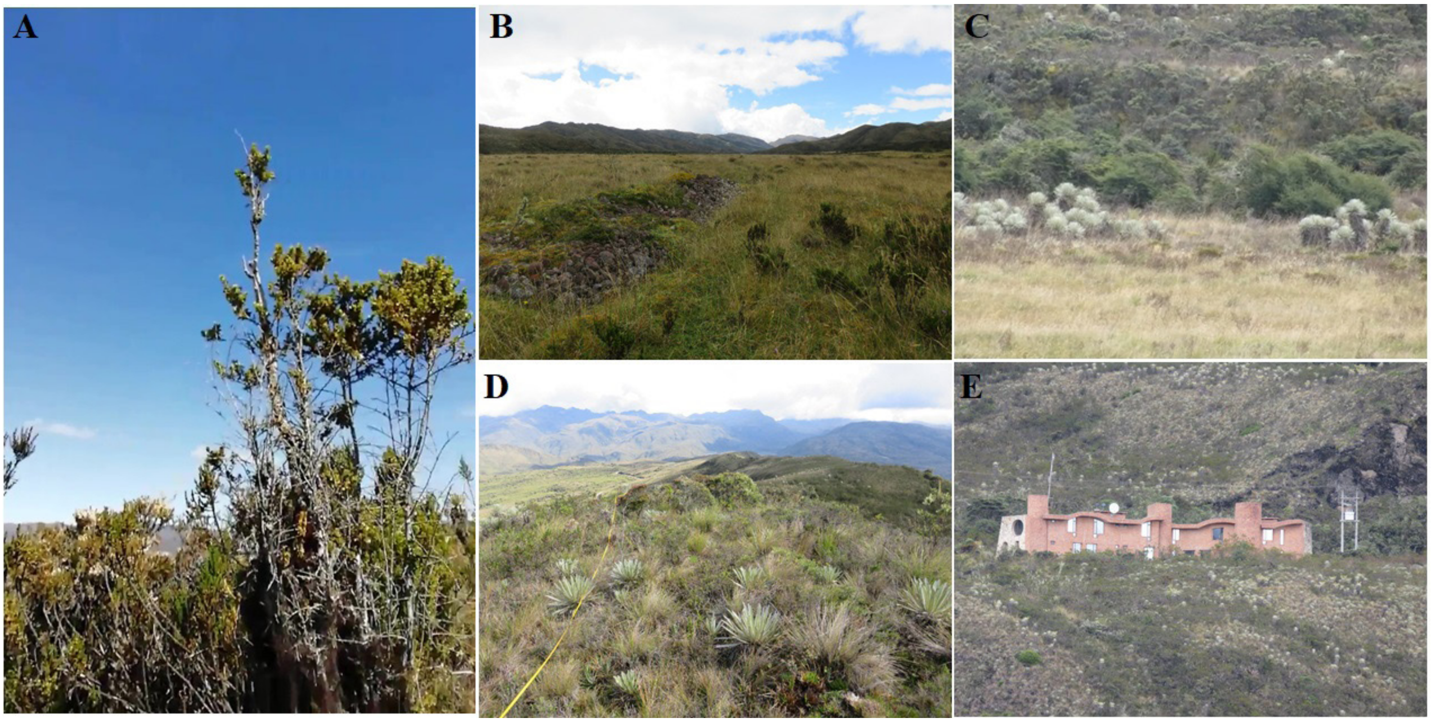

Figure 3. Photographs of some of the types of vegetation and land use in the La Paila sector. A) Dense shrubland. B) Clean grasslands. C) Mosaic of pastures with natural areas. D) Dense pastures without trees. E) Facilities of the National Natural Park.

Population density was estimated using the Eberhardt and Van Etten (1956) model with the following equation, which calculates the number of individuals per square kilometer from the number of fecal pellet groups: D = (NP)(PG)/(TP)(TD). Where *NP* is the number of circular plots or fixed-width transects that fit in 1 km^2. *PG* is the mean number of pellet groups per parcel or transect. *TP* is the decomposition time of pellet groups when using the Fecal Standing Crop (FSC) technique or the deposition rate of pellet groups with the Fecal Accumulation Rate (FAR) technique, and *TD* is the defecation rate.

The White-tailed deer population density was estimated using the FSC and FAR techniques; the FSC technique uses the daily defecation rate and stool persistence to estimate density by analyzing all fecal pellet groups in the plots visited on a sampling trip (Gallina *et al.* 2014). The FAR technique uses the deposition rate of fecal pellet groups and is used when each transect is visited more than once. In this study, transects were sampled on two occasions and the period between the first and second samplings was approximately 300 days for La Paila and 273 for Monterredondo, this due to the closure of the protected area after the COVID-19 pandemic was declared.

A standard defecation rate of 12.7 fecal pellet groups/ind/day obtained from the Eberhardt and Van Etten (1956) model is usually used. However, for this study, we used the values obtained by Mateus-Gutiérrez (2014) in the Chingaza NNP, namely, a defecation rate of 23.26 fecal pellet groups/ind/day and a decomposition time of 277.80 days (Table 1).

Furthermore, density was estimated with the semiautomated PELLET procedure for Excel, developed by Mandujano (2014), in which density is calculated assuming that it depends on the variation of parameters such as defecation rate, time of permanence of the fecal pellet group, and spatial distribution of pellet groups. This seeks to remove the subjectivity by reporting a single value, and incorporates the uncertainty of this type of sampling. The value using PELLET is reported as the mean plus/minus the standard deviation since it is calculated from three defecation rate values, including the one estimated by Mateus-Gutiérrez (2014).

Age Structure and Sex Ratio. To analyze the age structure and sex ratio of white-tailed deer in two sectors of the Chingaza NNP, the longest and shortest lengths were recorded for each pellet; then, the volume of each pellet, the relationship between the two lengths and the means of these variables for each pellet group were calculated.

Fecal pellet groups were first sorted into three age classes based on pellet volume: fawns (0 mm^3 to 290 mm^3), juveniles (291 mm^3 to 605 mm^3), and adults (at least 605 mm^3; Vega *et al.* 2019). Subsequently, fecal pellet groups in the adult class were sorted by sex using clustering analyses; the first was an analysis of k-means establishing two groups, which corresponded to the two sexes (Mateus-Gutiérrez 2014). The second analysis was performed using the Fuzzy clustering tool, selecting two groups corresponding to males and females. Both analyses were carried out using the NCSS program (Sánchez-Rojas *et al.* 2009).

Results

Between February and March 2020, 104 fecal pellet groups were recorded and collected in the Monterredondo sector and 70 pellet groups in La Paila; in December 2020, 85 pellet groups were collected in Monterredondo and 42 in La Paila (Table 1).

Table 1. Values for the calculation of the population density of white-tailed deer in the Monterredondo and La Paila sectors in the Chingaza National Natural Park obtained between February and March (Mar) 2020 and December (Dec) 2020.

	Monterredondo	**La Paila**
No. of transects	10	10
Transect area (m^2)	2,000	2000
Sampled area (m^2)	6,405.6	6405.6
No. of plots	510	510
No. of fecal pellet groups recorded	104 (Mar) – 85 (Dec)	70 (Mar) – 42 (Dec)
Mean number of pellet groups per plot	0.204	0.137
Decomposition time	277.8 days	277.8 days
Defecation rate	23.26 pellet groups/ind/day	23.26 pellet groups/ind/day

The three estimates were obtained; with the first (FSC February), the calculated density for the Monterredondo sector (2.51 ind/km^2) was higher than the density calculated for La Paila (1.69 ind/km^2). Estimates using the semi-automated PELLET procedure for Excel yielded values of 0.7 ± 0.6 ind/km^2 and 0.5 ± 0.8 ind/km^2 for Monterredondo and La Paila, respectively. With the second estimate (FSC December), the above pattern was maintained, showing a higher density in the Monterredondo sector (2.06 ind/km^2) than in La Paila (1.01 ind/km^2). The PELLET procedure calculated 0.28 ± 0.3 ind/km^2 for Monterredondo and 0.09 ± 0.1 ind/km^2 for La Paila (Table 2). With the last estimate using the FAR technique, the deer density was 2.09 ind/km^2 for the Monterredondo sector and 0.94 ind/km^2 for La Paila. Using PELLET for Excel, the population density values were 0.37 ± 0.4 ind/km^2 for Monterredondo and 0.16 ± 0.2 ind/km^2 for La Paila (Table 2).

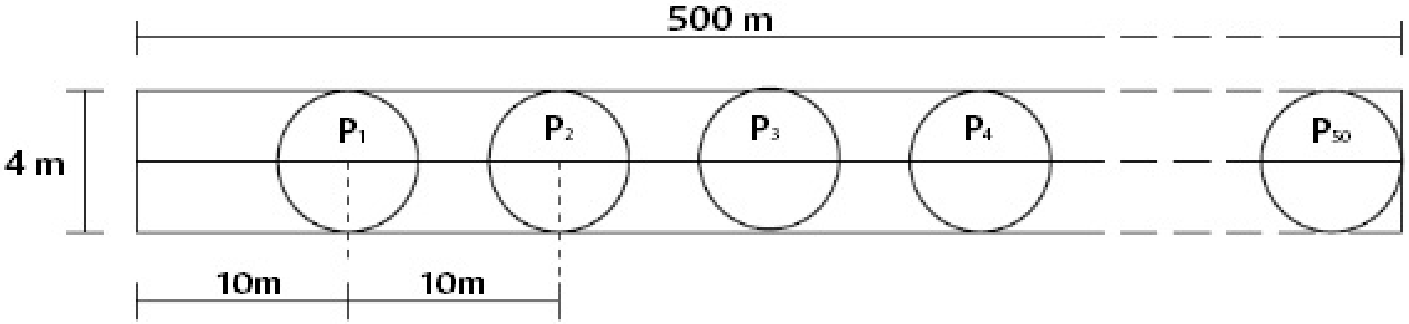

Figure 4. Arrangement of circular plots in a fixed-width transect of 500 m x 4 m (Modified from Mateus-Gutiérrez 2014).

Age Structure and Sex Ratio. When the fecal pellet groups collected throughout the sampling period using the volume ranges proposed by Vega *et al.* (2019), the estimated proportion of age classes (adult, juvenile, and fawn) for the Monterredondo sector was 1:0.29:0, equivalent to 147 adults, 42 juveniles, and no fawns; for La Paila, the proportion was 1:0.57:0.04, corresponding to 69 adults, 39 juveniles and 3 fawns. It is worth noting that La Paila was the only sector where fecal pellet groups corresponding to fawns were found based on their volume.

Once the data were sorted out, the initial analysis of k-means classified the 147 adults of the Monterredondo sector into 57 males and 90 females (Figure 5a); in La Paila, the 69 adults were sorted into 16 males and 53 females (Figure 5b, in blue). It is evident that Monterredondo was the sector that housed most adults and, in general, white-tailed deer individuals.

When adults are sorted by sex using the Fuzzy clustering analysis, the male to female ratio was 1:1.1 for Monterredondo and 1:1.46 for La Paila; these values correspond to 70 males and 77 females in Monterredondo and 28 males and

Table 2. Values for the calculation of the population density of white-tailed deer in the Monterredondo and La Paila sectors in the Chingaza National Natural Park using the FAR (Fecal Accumulation Rate) and FSC (Fecal Standing Crop) techniques.

Methodology		**Monterredondo**	**La Paila**
	FSC February	0.70 ± 0.6 ind/km^2	0.50 ± 0.8 ind/km^2
PELLET	FSC December	0.28 ± 0.3 ind/km^2	0.09 ± 0.1 ind/km^2
	FAR (total)	0.37 ± 0.4 ind/km^2	0.16 ± 0.2 ind/km^2
	FSC February	2.51 ± 0.6 ind/km^2	1.69 ± 0.6 ind/km^2
Eberhardt and Van Etten 1956	FSC December	2.06 ± 0.6 ind/km^2	1.01 ± 0.6 ind/km^2
	FAR (total)	2.09 ± 0.6 ind/km^2	0.94 ± 0.6 ind/km^2

41 females in La Paila. The estimates from the two analyses differ in the number of individuals grouped of each sex.

These analyses were also performed separating the two sampling times, *i. e.*, February- March and December. For the Monterredondo sector, the value with the greatest variation was the number of juveniles because the December sample showed a lower number of juveniles. In La Paila, the number of fecal pellets identified as males was the one with the largest variation, as fewer males were recorded in December (Table 4).

Discussion

The results of this study suggest that the population density of white tailed deer varies temporarily in the two sectors studied, and a decrease in the number of deer per square kilometer has been observed in recent years. Unlike studies carried out in the protected area indicating that the deer population is experiencing exponential growth (Rodríguez-Castellanos 2016), the samples collected in subsequent years, including the present study, suggest that the population density of deers has declined (Figure 6).

When comparing the values estimated by the techniques used (FSC February, FSC December, and FAR) with the methodologies studied (PELLET procedure and Eberhardt and Van Etten 1956), it can be observed that in all cases, the absolute values obtained with the Eberhardt and Van Etten model exceed the upper limit of the intervals obtained with PELLET. Furthermore, the value calculated with FCS February was higher than the two that followed (FSC December and FAR) in all cases; however, no significant differences were observed in these values between sectors or sampling times ($P > 0.05$). The analysis of population density values estimated in previous studies (Table 3) shows variation not only between the sectors within the protected area, with La Paila having the lowest deer density, but also a trend of decreasing population density to the present time.

Thus, the density calculated for the Monterredondo sector in this study ranges between 2.06 ind/km^2 and 2.51 ind/km^2, which is lower than the value calculated by Mateus-Gutiérrez (2014) and Gómez-Castellanos (2017), where density was 17.8 ind/km^2 and 8.9 ind/km^2, respectively. Other estimates of population density in localities near the Monterredondo sector for similar plant covers ranged between 4.6 ind/km^2 and 8 ind/km^2 (Gómez-Castellanos 2017), which are higher than the value obtained in this study. Moreover, when comparing the data with the study carried out by Ramos (1995), the defecation rate was modified by 12.7 pellet groups/ind/day, resulting in a population density of 4.6 ind/km^2 for 2020, higher than that reported by Ramos (1995) of 1 ind/km^2.

Taking into account the above, Rodríguez-Castellanos (2016) reported 4868 white-tailed deer in the Chingaza NNP. However, this value may be overestimated since the modeling was based on the density reported by Mateus-Gutiérrez (2014) in one of the sectors where the presence of the species was most evident; additionally, this estimate does not take into account the spatial variation in population density observed in the present study.

For the La Paila sector, three estimates have been obtained, in which the deer population density was 28.5 ind/km^2, 0.084 ind/km^2, and 0.94 ind/km^2 in 2004, 2019, and 2020, respectively (Rodríguez *et al.* 2004; Caguazango *et al.* 2019; this study). According to the above, although the defecation rate used in these estimates was different, the trend to decrease over time is maintained.

With respect to the findings reported for other moors of Colombia, the values obtained in the present study are higher than the figure reported by Garavito (2004) of 1.1 x 10^{-4} ind/km^2. In contrast, for the Soata moor in Boyacá (Alarcón 2009), deer densities were similar (between 2.44 ind/km^2 and 3.54 ind/km^2), which lie within the range estimated in the present study. In general, in Colombia the most abundant white-tailed deer populations are found towards the eastern plains in flooding savannah ecosystems where they range between 13 ind/km^2 and 43 ind/km^2 based on direct counts (Pérez-Moreno *et al.* 2020). When the population densities estimated for the two Chingaza NNP sectors in the present study are compared with those reported for moor ecosystems in Ecuador (1.6 ind/km^2; Albuja 2007), it is evident that the deer density is higher in the Chingaza moor.

With respect to the densities estimated in studies carried out in other countries, the deer density in Chingaza is similar to those reported by Valenzuela (1994), Ortiz-Martínez *et al.* (2005) and López-Téllez *et al.* (2007) in México, 4.83 ind/

Table 3. Temporal and spatial comparison of population density estimates of white-tailed deer in three sectors of the Chingaza National Natural Park using the Eberhardt and Van Etten (1956) methodology and a defecation rate of 23.26 fecal groups/ind/day in all cases.

Source	Technique	La Mina	Monterredondo	La Paila
Mateus-Gutiérrez (2014)	FSC		17.77 ind/km^2	
Mateus-Gutiérrez (2014)	FSC	23.18 ind/km^2		
Gómez-Castellanos (2017)			8.90 ind/km^2	
Caguazango *et al.* (2019)				0.09 ind/km^2
Este estudio (2020)	FSC Feb		2.51 ind/km^2	1.69 ind/km^2
	FSC Dic		2.06 ind/km^2	1.01 ind/km^2
	FAR		2.09 ind/km^2	0.94 ind/km^2

Table 4. Clustering analysis using K-means and Fuzzy clustering for the sectors in the two samplings.

	Monterredondo				La Paila			
	February - March		December		February - March		December	
	K-means	Fuzzy	K-means	Fuzzy	K-means	Fuzzy	K-means	Fuzzy
Female	45	37	36	36	36	26	17	11
Male	27	35	39	39	15	25	1	7
Juvenile	32	32	10	10	18	18	21	21
Fawn	0	0	0	0	1	1	2	2

km^2, 2.28 ind/km^2, and 1.08 ind/km^2, respectively, and lower than those reported by Mandujano (1992), Gallina (1994), and Camargo-Sanabria (2008) corresponding to 28.1 ind/km^2, 21 ind/km^2, and 5 ind/km^2. On the other hand, the population density obtained in this study lies within the range calculated for Honduras, between 1.35 ind/km^2 and 10 ind/km^2 (Portillo *et al.* 2015).

The white-tailed deer population density is affected by factors including food, water, and shelter availability, the presence of predators and competitors, and hunting and proximity to human settlements (Brokx 1984; Gallina 1994; Gallina *et al.* 1998; Villarreal 1999; Delfín- Alfonso and Gallina 2007; Gallina *et al.* 2010). In the present study, the estimated density for the evaluated sectors may be influenced by hunting, the presence of predators such as puma (*Puma concolor*), of which there are records in the foothills of the protected area (El Espectador 2016), the largest presence of the spectacle bear in the park (Parra-Romero *et al.* 2017), and competition with domestic herbivores (Sánchez-Rojas *et al.* 2009). With respect to the latter, cows were observed during the sampling, mainly in La Paila, which exposes deers to the risk of contagion of zoonotic diseases that may decrease their abundance (Martínez *et al.* 1999; Campbell 2009; Villarreal-Espino *et al.* 2011; Elías and Vásquez 2016).

Additionally, there is evidence of the presence of feral dog herds spotted in various sectors of the park through sequences of photos in camera traps, and accounts of local inhabitants reporting these herds chasing to death white-tailed deers (Reatiga 2015; Rodriguez *et al.* 2019). These represent the factor that probably causes the greatest reduction in the population studied in the protected area (Plan de Manejo 2014–2018 2013). In this sense, better control of feral dogs in the Monterredondo sector associated with increased human activity, park rangers, and visitors, probably contributes to the higher deer density in this sector than in La Paila. Separately, according to Duarte *et al.* (2016), the presence of feral dogs reduces the diversity and abundance of wild animals in natural areas, and white-tailed deer is one of the species most affected by the presence of feral dogs (Bergman *et al.* 2009). Therefore, controlling feral dog herds in the protected area is essential for the conservation of white-tailed deer.

On the other hand, the variation in deer population density estimates may be related to the fact that the places where transects were installed in Monterredondo in previous studies were selected after confirming the presence

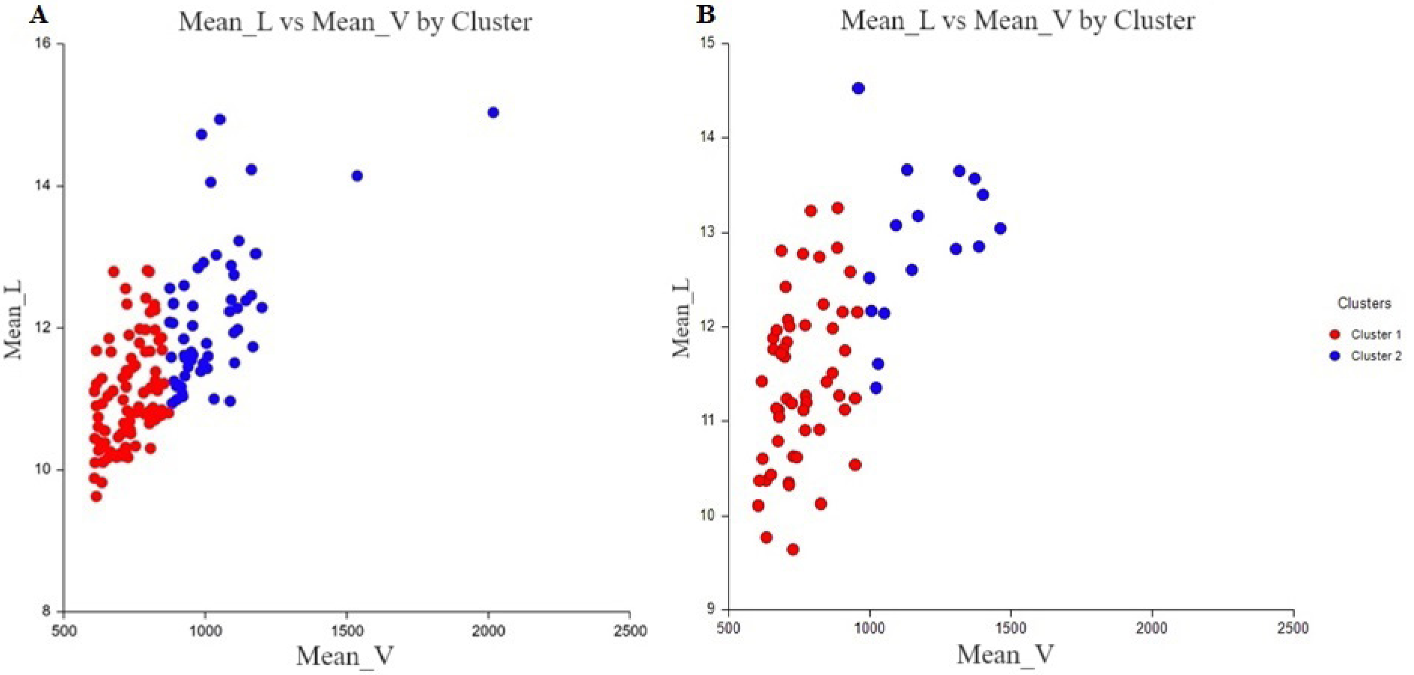

Figure 5. Plot of K-means for the whole sampling in a) Monterredondo and b) La Paila. Cluster 1, in red, corresponds to female pellet groups. Cluster 2, in blue, corresponds to male pellet groups.

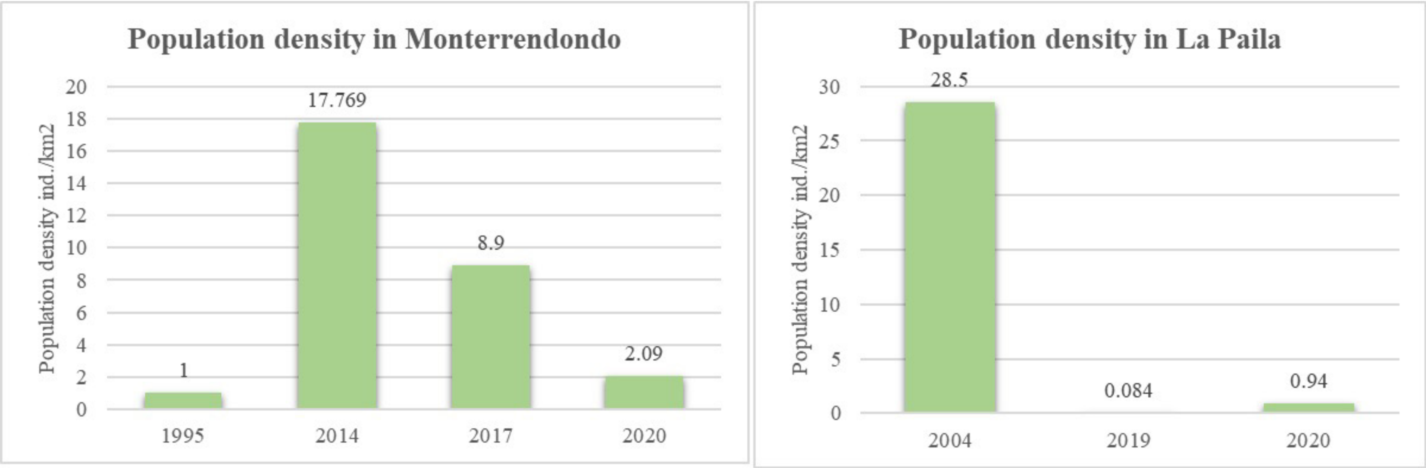

Figure 6. Variation in white-tailed deer population density in two sectors of the Chingaza National Natural Park since 1995 to date (Ramos 1995; Rodriguez *et al.* 2004; Mateus-Gutiérrez 2014; Gómez-Castellanos 2017; Caguazango *et al.* 2019; this study 2020).

of white-tailed deer, while in the 2020 study, they were installed at random and stratified. In addition to the fact that sampling in transects installed with prior knowledge of the areas frequented by deer may lead to overestimating population densities and pose a risk for the species related to its exploitation (Mandujano 2014), random sampling provides better data on population variation (Galindo-Leal and Weber 1998, cited in Pineda 2006). For this reason, Camargo-Sanabria (2004) and Gallina *et al.* (2014) recommend that transects be installed in a stratified manner according to the types of plant cover or habitat quality.

In general, it is estimated that a stable deer population should show an age distribution approximating the 3:2:5 ratio, where the highest proportion is assigned to adults (Teer *et al.* 1965). According to Ojasti (2000), populations with a high proportion of juveniles are expanding, while the predominance of adults is usually related to stationary or declining populations; however, adults are reproductive members of the population that can increase the number of individuals.

In the present study, the estimated population structure (adults:juveniles:fawns) was 1:0.29:0 for Monterredondo and 1:0.57:0.04 for La Paila, evidencing a higher proportion of adults in both sections, consistent with the reports by Mateus-Gutiérrez (2014; 8:2:2 and 10:2:2) and Aconcha-Abril (2008), who found a higher proportion of adults in relation to juveniles (2:1) in Monterredondo, in the Chingaza NNP. These results differ from Valenzuela (1994) and Gallina (1994), who reported a higher proportion of fawns and a higher proportion of juveniles, with 0.23:0.27:0.43 and 0.21:0.51:0.28, respectively. In the case of Gallina (1994), these results may be influenced by poaching and the presence of predators such as puma in the area, which exert greater pressure on adults, leading to their decrease.

Finally, since the management and conservation of deer must be based on population monitoring with reliable estimates of the number of individuals in the areas of interest (Mandujano 2014) — in this case the Chingaza PNN — it is proposed that the deer population density be calculated and studied differentially by park sectors. Also, we recommend that it be estimated with the semi-automated PELLET for Excel procedure developed by Mandujano (2014), which allows calculating a range for population density instead of a single value, thus incorporating the variation of parameters such as defecation rate and pellet decomposition time.

Considering the above, we recommend conducting continuous monitoring of the population using these indirect sampling techniques that offer advantages such as that the observer does not disrupt the study population, and the study is not affected by environmental conditions interfering with the visualization of individuals, among others. In addition, defecation rates and decomposition times already calculated for the area should be used or recalculated during the study following the sampling design recommendations proposed by Mandujano (2014).

Conclusions. The white-tailed deer populations studied in the two sectors of the Chingaza National Natural Park, Monterredondo and La Paila, showed temporal variations evident as a decrease compared to the values reported by previous studies for this same area. According to these studies, the highest abundance of deer was recorded in 2004 for La Paila and in 2014 for Monterredondo; the estimated number of individuals has been decreasing since then.

Furthermore, population density varies spatially, showing a higher population density in Monterredondo compared to La Paila, based on estimates with the two methods and the three techniques used. However, the age structure data suggest that the population is stable, since the largest proportion of individuals corresponds to the adult class, with an evident presence of juveniles and fawns.

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Urgent prioritization of conservation sites for the Jagüilla (*Tayassu pecari*) in the Honduran Moskitia region

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Tayassu pecari (known in Honduras as *jagüilla* and Wari in Miskito), is one of two types of wild pigs (*chanchos de monte*) found in Honduras (Marineros and Martinez 1998). Currently, its conservation status on the IUCN red list is vulnerable (VU) and critically endangered (CR) for Honduras (WCS 2021). According to Portillo and Elvir (2016), the potential area for *jagüilla* distribution is 6,126 km^2 corresponding to 5.5 % of the country territory. The potential area for this species is in three sites, mainly protected area of the Reserva del Hombre and the Biósfera del Río Plátano (RHBRP), with approximately 70 % of the predicted potential distribution (4,288 km^2), 20 % (1,225 km^2) in the indigenous territories of Rus Rus, Mocorón and Warunta, and 10 % (613 km^2) in the Tawahka Asagni Biosphere Reserve. The aim of this note is to contribute to the prioritization of four sites where evidence of small groups of *jagüillas* have been found: 1) Sierra de Agalta National Park. 2) the core zone of the RHBRP. 3) the cultural zone of the RHBRP. 4) the Warunta Mountains. Records of *jagüilla* were obtained from diverse sources (Table 1), mainly from biological monitoring implemented in various locations of the Río Plátano Biosphere (buffer zone, cultural zone, and core zone), Warunta Mountains, riparian forest in Rus Rus River, as well as the Tawahka Biosphere Reserve through the use of camera traps which were carried out between 2016 and 2022. In the RHBRP *jagüilla* were registered in two of the three zones these being the core zone and the cultural zone; no records of the species were obtained in the buffer zone. In these localities, groups of 2 to 45 individuals were documented. For the Warunta region in the Indigenous Federation of Mocoron and Segovia Zone (FINZMOS territory), tracks, and photographic evidence of a large group of 50 to 100 individuals were registered moving in this territory covered mainly by primary broadleaf forest. Hunting by invasive settlers and habitat loss due to deforestation in protected areas, has had an impact on *jagüilla* populations, reducing this species in the Honduran Moskitia region as mentioned by Portillo and Elvir (2016). One of the important aspects of this work is to highlight the findings in NP Sierra de Agalta as a potential site for future research and biological monitoring efforts for the development of conservation processes for the *jagüilla* as a park conservation target (Figure 2) since the last records of this species were documented at La Quebrada del Sol, NP Sierra de Agalta, in 1994 (Marineros and Martínez 1998). It is of utmost importance to establish monitoring and participatory conservation processes with the local communities (Larsen 2019; Martínez *et al*. 2022).

Tayassu pecari, conocido en Honduras como *jagüilla* o como *wari* en miskito y es una de las dos especies de cerdos silvestres (*chanchos de monte*) que se encuentran en Honduras (Marineros y Martínez 1998). Actualmente su estatus de conservación en la lista roja de la UICN es vulnerable (VU) y en peligro crítico (CR) para Honduras (WCS, 2021). De acuerdo con Portillo y Elvir (2016), el área de distribución potencial para la *jagüilla* es de 6,126 km^2 que corresponden al 5.5 % del territorio nacional. El área potencial para esta especie se encuentra ubicada en tres sitios, principalmente: 1) Reserva del Hombre y la Biósfera del Río Plátano (RHBRP) con aproximadamente el 70 % (4,288 km^2) de la distribución potencial predicha. 2) territorios indígenas de Rus Rus, Mocorón y Warunta con un 20 % (1,225 km^2). 3) Reserva de la Biósfera Tawahka Asangni con un 10 % (613 km^2). El objetivo de este trabajo es contribuir con la priorización de cuatro sitios en los cuales se han obtenido evidencias de pequeños grupos de *jagüillas*: 1) el Parque Nacional Sierra de Agalta. 2) la zona núcleo. 3) la zona cultural de la RHBRP. 4) las montañas de Warunta. Los registros de *jagüilla* fueron obtenidos de diversas fuentes (Tabla 1), principalmente de monitoreos biológicos realizados en localidades de la Reserva del Hombre y la Biósfera del Río Plátano (zona de amortiguamiento, zona cultural y la zona núcleo), Montañas de Warunta, bosque ripario en río Rus Rus, así como la Reserva de la Biósfera Tawahka, mediante cámaras trampa entre 2016 y 2022 (Larsen 2019; Martínez *et al*. 2022). En estas localidades dentro de la RHBPR se registraron grupos de entre dos hasta 45 individuos. Uno de los hallazgos relevantes, es el registro de cuatro individuos de *jagüilla*, una hembra y sus tres crías (Figura 2) en el PN Sierra de Agalta, Para la región de Warunta en el territorio de FINZMOS, se registraron huellas y evidencias fotográficas de un grupo entre 50 a 100 individuos aproximadamente. La cacería realizada por colonos invasores y la perdida de hábitat por deforestación, ha tenido un impacto en las poblaciones de la *jagüilla*, reduciendo en la región de la Moskitia hondureña (Portillo y Elvir 2016). Uno de los aspectos relevantes es el hallazgo en el PN Sierra de Agalta, como un sitio potencial para próximos esfuerzos de investigación y monitoreo biológico (Figura 2). Con la información anterior se podría asumir que existen individuos disgregados o aislados en el PN Sierra de Agalta, y que se han adaptado a movilizarse en un gradiente altitudinal de los 1200 msnm a los 2000 msnm, desplazándose entre los ecosistemas de bosque tropical siempreverde submontano, montano y montano inferior.

Keywords: Agalta; core zone; cultural zone; rus rus; río Plátano; Warunta.

Introduction

Tayassu pecari (*jagüilla*), known as Wari in Miskito, is one of the two types of wild peccaries (chanchos de monte) found in Honduras (Marineros and Martínez 1998). They belong to the family Tayassuidae and the order Artiodactyla. Their range extends from northern Argentina to southeastern México, with large populations in the Amazon rainforest (Altrichter *et al.* 2012). Group sizes can range from less than 10 to more than 300 individuals (Sowls 1997; Moreira Ramírez *et al.* 2015; Reyna Hurtado *et al.* 2016). Historically there are reports recording hundreds of peccaries roaming together in the Neotropical understory, however, habitat destruction and hunting have drastically affected group size (Reyna Hurtado *et al.* 2016). In addition, peccaries (*Tayassu pecari*) are a highly valued prey by poachers and subsistence hunters (Reyna Hurtado *et al.* 2016).

Currently its conservation status on the IUCN Red List is Vulnerable (VU) and in Honduras it is Critically Endangered (CR) according to WCS (2021). Forty-eight percent of its current distribution area remains, with reduced abundance and a low to medium probability of long-term survival. Significant range reductions have occurred in Argentina, Paraguay, southern Brazil, Colombia, Venezuela, northeastern Brazil, Guatemala, México, Costa Rica, Honduras, and Panama (Altrichter *et al.* 2012; Keuroghlian *et al.* 2013; Moreno and Meyer 2014; Portillo and Elvir 2016; Meyer *et al.* 2016).

According to an analysis by Altrichter *et al.* (2012) with data from 2005, the range distribution of the peccary (*Tayassu pecari*) had been reduced by 48 % compared to its historical distribution in the previous 100 years, for example, in El Salvador and Uruguay they have been declared extinct. According to Thorton *et al.* (2020), in a study were able to identify 29 populations of white-lipped peccaries scattered among seven countries of Mesoamerica. Twenty of the 29 populations showed a decreasing trend (69 %), four were classified as unknown (14 %) and four were stable (14 %). Only one population was apparently increasing (3 %). Most national populations were estimated as lower than 1,000 animals and in most of the cases current group sizes were estimated at fewer than 50 animals (Altrichter *et al.* 2012; Thorton *et al.* 2020).

For Honduras the records of *jagüilla* have been scarce and sporadic, there has not been a monitoring directed to know its populations in the country. The first data in official lists is presented by Goodwin (1942), however, he mentions it as *Tagassu pecari ringens* (Merriam), describing its type locality, being this: Apazote, near Yohaetum, Campeche, México and with a range of its distribution, from Campeche, Guatemala and mentions that probably Honduras (Goodwin 1942). However, Portillo and Elvir (2016), list records for *jagüilla* in Honduras, between the years 1994 to 2013, with different sources of origin. According to Portillo and Elvir (2016), the potential area for the distribution of *jagüilla* in Honduras is 6,126 km^2 corresponding to 5.5 % of the country's territory. The potential area for this species is located in three sites, mainly: the Reserva del Hombre y La Biósfera del Río Plátano (RHBRP) protected area, with approximately 70 % of the predicted potential distribution (4,288 Km^2), 20 % (1,225 Km^2) in the indigenous territories of Rus Rus, Mocorón and Warunta and 10 % (613 Km^2) in the Tawahka Asangni Biosphere Reserve (Portillo and Elvir 2016). The largest extension of the potential area is found in the department of Gracias a Dios in the broadleaf forest with approximately 95 % of the territory and 5 % between the departments of Colón and Olancho, this based on the 2014 forest cover map (Portillo and Elvir 2016). This species has lost from the 1900s to date, 81.2 % of its habitat represented in the tropical rainforest, which had a historical territorial extension of 26,378 km^2 (Portillo and Elvir 2016). Currently, land use change, habitat fragmentation and hunting are the main causes of its decline (Portillo and Elvir 2016).

The objective of this work is to contribute to the prioritization of four sites that have been identified as evidence of small groups of *jagüilla* in the Sierra de Agalta National Park, the core zone and cultural zone of the RHBRP, and the Warunta Mountains, to protect their populations and habitat from the threats of deforestation, extensive cattle ranching and poaching.

Materials and methods

Area of analysis. The RHBRP (Figure 1) is one of the most important protected areas in the Mesoamerican Biological Corridor and the most important and largest in the Republic of Honduras. It was created in 1980 by Decree No. 977-80 and expanded in 1997 by Decree No. 170-97; it occupies a vast area of approximately 832,335 ha, which represents about 7 % of the national territory. In 1982, UNESCO, through the World Heritage Committee and at the request of our country, granted the reserve the category of World Natural Heritage Site of Humanity, with the identification No. 196, for its diverse composition of terrestrial, marine and cultural ecoregions and for its anthropological richness, incorporating it into the World Network of Biosphere Reserves, it is divided into three zones: the buffer zone (197,421 ha), the cultural zone (424,174 ha) and the core zone (210,734; Larsen 2019).

Sierra de Agalta National Park (NP) is located northeast of the department of Olancho and has an area of 73,924 hectares in a perimeter of 141.57 km. The ecosystems present are the following: Seasonal Tropical Evergreen Aciculifoliated Forest, Submontane, Upper Montane Tropical Evergreen Broadleaf Forest, Lower Montane Tropical Evergreen Broadleaf Forest, Lower Montane Tropical Evergreen Mixed Forest, Tropical Evergreen Mixed Forest, Alti montane and agricultural systems (Mejía and House 2001).

The Warunta Mountains is a mountainous massif situated in the department of Gracias a Dios, located within the territorial council of FINZMOS (Indigenous Federation of the Mocorón and Segovia area), with an approximate land area of 65,369 ha, and with a predominance of tropical evergreen seasonal broadleaf forest ecosystems in lowland undulating karst hills and riparian forest of the Rus

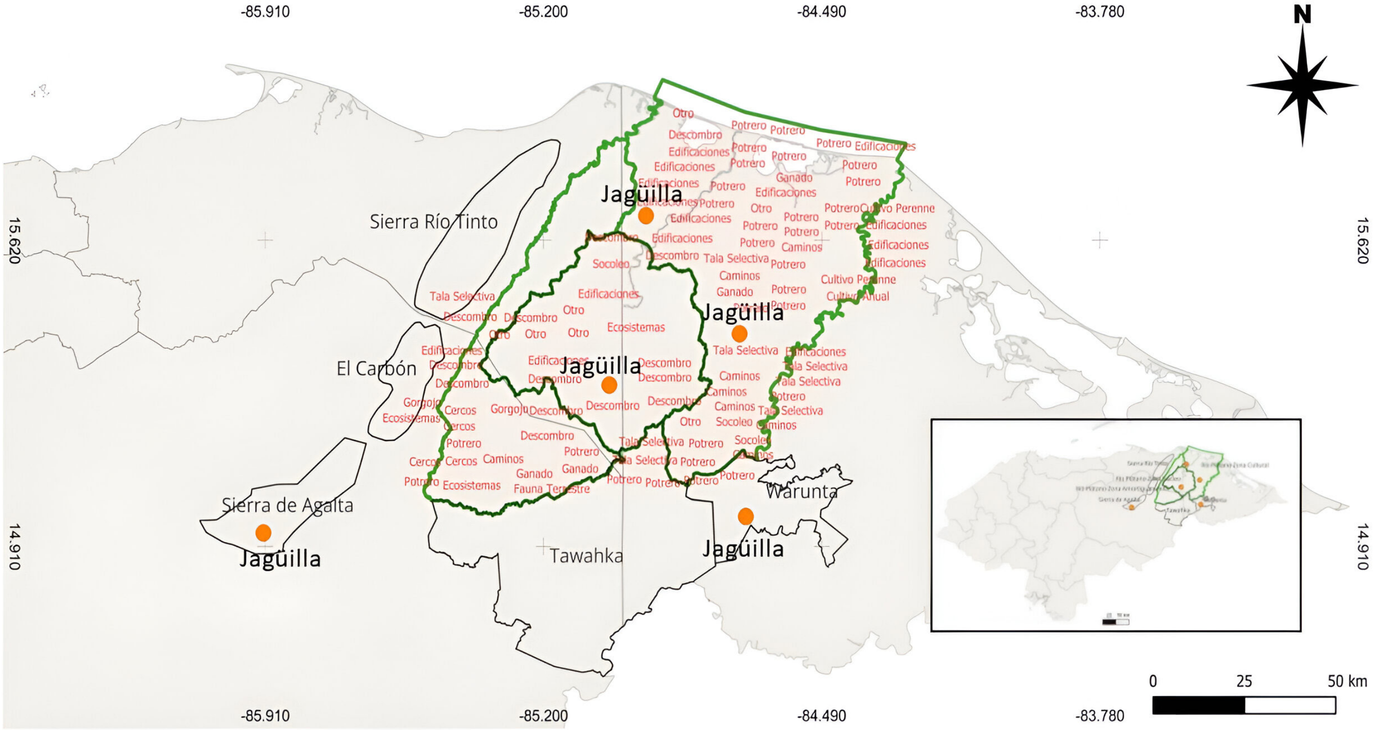

Figure 1. RHBRP, showing the three zones (ZN, ZC, ZA) with anthropogenic activities that are putting pressure on the stability of *jagüilla* populations. These activities include hunting, deforestation for cattle ranching, selective logging of mahogany, road construction, and infrastructure for ranches, among others. Similarly, the protected areas of Sierra de Agalta NP and the region in the Warunta Mountains have recently recorded *jagüillas* (Ssource: WCS 2023).

Rus River (Mejía and House 2001; Portillo and Hernández 2011). This zone is proposed as a protected area under a national park category; however, this designation has not been implemented.

Data collection. To obtain *jagüilla* records we reviewed reports and scientific publications from different sources (Table 1) of biological monitoring that were conducted between the years 2012 to 2022, including only the reports with records of *jagüilla*. Most of the monitoring included the camera trap methodology (with efforts of more than 6,000 camera nights), which were installed in various locations of the Reserva del Hombre y La Biósfera del Río Plátano (buffer zone, cultural zone and the core zone; Larsen 2019; Martínez *et al.* 2022), trails in the Warunta Mountains, camera traps in the riparian forest in Rio Rus Rus, as well as the Tawahka Biosphere Reserve.

Results

In the RHBRP, *jaguillas* were registered in two of the three zones. In the core zone and the cultural zone, but not in the buffer zone. In these localities, thanks to biological monitoring using camera traps, groups of 2 to 45 individuals were recorded (Larsen 2019; Martínez *et al.* 2022).

An important finding is the record of four individuals of *jagüilla* (Figure 2), a female and her three offsprings in Sierra de Agalta NP, municipality of Gualaco, department of Olancho; mentioning the relevance of these records as an opportunity for the conservation of this species.

For the Warunta region in the FINZMOS territory, tracks were observed, and photographic evidence was taken of a large group of approximately 50 to 100 individuals moving in this broadleaf forest territory. In different incursions in the years 2021, 2022, and 2023, local people have recorded the presence of many tracks on roads built by the movement of *jagüilla* troops.

Discussion

According to the potential distribution carried out by Portillo and Elvir (2016), the *jagüilla* distribution range was projected for the Moskitia region, specifically for the RHBRP, RB Tawahka, the Mocorón region, Rus Rus and Warunta. However, the total forest loss in the RHBRP in the last 23 years has been 87,212 ha; in the core zone 1,457 ha, in the buffer zone 31,168 ha and in the cultural zone 20,260 ha. For the Tawahka BR, the loss is 34,327 ha (WCS 2023). Similarly, forest loss in the eastern region (Warunta, Mocorón and Rus Rus) of the Moskitia in the eastern region is approximately 3,000 ha (Portillo and Hernández 2011; Portillo and Elvir 2016). Land use change has had an impact on *jagüilla* populations, as shown by biological monitoring reports for each zone of the RHBRP, Rus Rus Rus indigenous territory, and the Warunta Mountains. Even though specific monitoring has not been developed for the species, the evidence of forest loss and anthropogenic activities monitored in the RHBRP, and replicated in the rest of the Moskitia PAs, leads us to assume the negative impact on *jagüilla*

Table 1. Results of *jagüilla* records in the RBHRP, this being the area of greatest importance for *jagüilla*, as it contains the largest records (Larsen 2019; Martínez *et al.* 2022).

Year	Species	Site	Registration	Source
2012	*Tayassu pecari*	ZA RHBRP	1 ind	report, ICF
2016	*Tayassu pecari*	ZC RHBRP	2 ind	report, ICF
2017	*Tayassu pecari*	ZC RHBRP	2 ind	report, ICF
2019	*Tayassu pecari*	ZN RHBRP	2 ind	report, ICF
2019	*Tayassu pecari*	ZC RHBRP	6 ind	report, ICF
2019	*Tayassu pecari*	ZN RHBRP	16 ind	Larsen, H
2019	*Tayassu pecari*	ZN RHBRP	3 ind	report, ICF
2020	*Tayassu pecari*	ZC RHBRP	6 to 12 ind	report, ICF
2021	*Tayassu pecari*	ZN RHBRP	1 ind	report, ICF
2021	*Tayassu pecari*	ZN RHBRP	45 ind	report, ICF
2021	*Tayassu pecari*	Warunta	50 ind	One Earth Conservation
2022	*Tayassu pecari*	Warunta	100 ind	One Earth Conservation
2022	*Tayassu pecari*	PN Agalta	4 ind	INCEBIO com. pers.

populations throughout this region, considerably reducing spaces for reproduction, feeding and shelter (WCS 2023). The Warunta Mountains is the second site with the largest records of a troop of approximately 100 individuals, so it should be considered as one of the high priority sites for conservation. (Figure 3).

One of the important aspects of this work is to highlight the importance of Sierra de Agalta NP as a potential site for future research efforts, biological monitoring, patrols and operations for the development of conservation processes for the *jagüilla* as a conservation target of the park (Figure 2), since the last records of this species were recorded at the Quebrada del Sol site in Sierra de Agalta NP in 1994 (Marineros and Martínez 1998). Based on the above information, it could be assumed that a population was disaggregated in Sierra de Agalta NP, moving along an altitudinal gradient from 1,200 masl to 2,000 masl, moving between submontane evergreen tropical forest, montane and lower montane ecosystems. There may also be small groups of *jagüilla* within the declared protected area "Pech" Montaña El Carbón Anthropological and Forest Reserve and the proposed protected area Sierra del Río Tinto National Park, because the distances between the core zone of the RHBRP and Sierra del Río Tinto National Park is between 15 to 20 linear km, and the Anthropological and Forestry Reserve 'Pech Montaña El Carbon' and the proposed protected area Sierra del Rio Tinto National Park are part of the same mountainous continuum, but these protected areas do not appear in the modeling of the potential distribution of *Tayassu pecari* (Portillo and Elvir 2016).

Figure 2. Female *Jagüilla* with her three offsprings in the mountains of PN Sierra de Agalta, it is assumed that there is a small population moving in the highlands, between 1,200 and 2,000 masl, in the tropical montane, submontane, and lower montane forest (photographs by Francisco Urbina).

Figure 3. An adult *jagüilla*s recorded in the Warunta Mountains, in the tropical evergreen lowland broadleaf evergreen forest, in the FINZMOS territorial council (photo by Wesly Lacuth).

It is of utmost importance to establish biological monitoring, patrols, and participatory conservation processes with the Miskito communities in the RHBRP, Warunta Mountains and with the local communities of Sierra de Agalta NP in order to know the conservation status of the *jagüilla* groups, to recover and stabilize the populations in these sites. It is a priority to protect and conserve the four sites mentioned in this work, one of them RHBRP, a World Heritage Site, in order to maintain the last registered populations of *Tayassu pecari* for Honduras, a species that is critically endangered in the IUCN red list for Honduras, with a strong perspective to become extinct in the coming years, if the necessary corrective measures for conservation and protection are not taken.

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Persistence of mule deer pellet groups on Chihuahuan Desert

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The persistence of fecal or pellet groups is indispensable when using the pellet group counting technique to estimate population densities and relative abundances of deer, as well as other herbivores. This technique is widely employed worldwide, and in México, the majority of deer abundance estimates have been made using this tool. However, for mule deer (*Odocoileus hemonious*) in México, there is no data on the persistence of pellet groups, and there is only one study on white-tailed deer. The pellet group counting technique has two main methods: a) "Fecal Standing Crop," where the accumulated pellet groups in plots are counted in a single visit, and b) "Fecal Accumulation Rate," which estimates density based on the accumulation of new fecal groups between two sampling periods, initially requiring the removal of all fecal groups from plots and counting again after some time. Both methods require knowing the pellet group disappearance rate during the pellet group accumulation period. This information is fundamental to understanding the ecology and making precise decisions in the management and conservation of mammals, such as mule deer, a species that is declining in some regions of México. Due to the lack of studies on the persistence of pellet group of mule deer in México, the aim of this study was to determine the persistence of mule deer fecal groups and their color changes over time, to establish pellet accumulation periods for estimating population abundances without biases when using this technique in arid habitats. We monitored 102 fecal groups for four years in the Chihuahuan Desert, finding that pellet groups are only lost during the summer rainy season. All pellet groups deposited between October and May were present, and all pellet groups turned white only after the first summer rainy season. The persistence of pellet groups was similar across seasons (fall, winter, spring) and deposition years (2004 to 2006). Some pellet groups persisted for over four years. The data suggest that the only source of degradation of pellet groups is summer rains, and no degradation by biological agents, such as fungi or insects, was observed. In summary, in arid areas, to estimate deer use or density throughout the entire dry season through pellet group counting, it is suggested that only two visits with either of the mentioned techniques are needed. If "Fecal Standing Crop" is used, there is now certainty that all non-white pellets are post the summer rainy season. If the "Fecal Accumulation Rate" technique is used, there is certainty that there will be no loss of pellets groups between the accumulation period of the entire dry season, approximately 7.5 months later. By reducing the number of visits, it allows us to cover more sampling sites, expand the study area, and obtain more precise estimates that will help understand ecological aspects and make management decisions.

La persistencia de excretas o grupos fecales es indispensable al utilizar la técnica de conteo de grupos fecales para estimar densidades poblacionales y abundancias relativas de venados, así como de otros herbívoros. Esta técnica es ampliamente empleada a nivel mundial; y en México la mayoría de estimaciones de abundancias de venados que se han realizado utilizan esta herramienta. Sin embargo, para el venado bura *(Odocoileus hemonious*), en México no existen datos sobre permanencia de grupos fecales y solo hay un estudio en venado cola blanca. La técnica de conteo de grupos fecales tiene dos métodos principales: a) "Fecal standing Crop", dónde se cuentan los grupos de pellets acumulados en parcelas en una sola visita, y b) "Fecal Acumulation Rate", que estima la densidad a partir de la acumulación de grupos fecales nuevos entre dos periodos de muestreo, requiere inicialmente remover todos los grupos fecales de las parcelas y volver a contar después de un tiempo. Ambos métodos requieren saber tasa de desaparición de grupos fecales durante el periodo de acumulación de pellets. Esta información es fundamental para entender la ecología, tomar decisiones precisas en la gestión y conservación, de mamíferos, como el venado bura, especialmente en regiones de México en las cuales están disminuyendo sus poblaciones. Debido a la falta de estudios sobre la tasa de desaparición de grupos fecales de venado bura, el objetivo de este estudio fue determinar el tiempo de permanencia de grupos fecales de venado bura y sus cambios de color a través del tiempo, con el fin de establecer periodos de acumulación de pellets, para estimar las abundancias poblacionales sin sesgos cuando se utiliza esta técnica en hábitats áridos. Se monitorearon 102 grupos fecales durante cuatro años en Desierto Chihuahuense y se encontró que sólo se pierden grupos fecales durante la temporada de lluvias de verano. Todos los grupos fecales depositados entre octubre - mayo estaban presentes y todos los grupos fecales se volvían blancos sólo después de la primera temporada de lluvias de verano. La permanencia de grupos fecales fue similar a lo a largo de las estaciones (otoño, invierno, primavera) y los años de deposición (2004 a 2006). Algunos grupos fecales persistieron hasta después de cuatro años. Los datos sugieren que la única fuente de degradación de los grupos fecales es por las lluvias de verano, y no se observó degradación por agentes biológicos, como hongos o insectos. En resumen, en zonas áridas, para estimar el uso o densidad de venado a lo largo de toda la época seca mediante el conteo de grupos fecales, se sugiere que solo se necesitan dos visitas con cualquiera de las técnicas mencionadas. Si se utiliza "Fecal standing Crop", ahora se tiene la certeza que todos los pellets que no son blancos, son posteriores a la época de lluvias de verano. Si se utiliza la técnica "Fecal Acummulation Rate", está la certeza, que no habrá pérdida de pellets entre el periodo de acumulación de toda la época seca, aproximadamente 7.5 meses después. Al reducir el número de visitas, nos permite abarcar más sitios de muestreo, ampliar el área de estudio y tener estimaciones más precisas que servirán para entender aspectos ecológicos y tomar decisiones de manejo.

Keywords: Mapimí Biosphere Reserve; *Odocoileus hemionus*; pellet group counting; relative abundance.

Introduction

Estimating the abundance of wild mammal populations and evaluating their changes over time or between habitats is essential for understanding species ecology and for effective sustainable management: utilization, conservation, and control (Harestad and Bunnell 1987; Laing *et al.* 2003; Mandujano 2014). To estimate the population density of herbivores, both direct and indirect counting methods have been employed. Direct methods are recommended in areas where deer are abundant and have good visibility in their habitat, and are not easily frightened by humans (Mandujano 2014). However, for many wildlife species, it can be challenging to estimate abundance directly, such as through visual counts, due to factors like low abundance, poor habitat visibility due to bushes, trees, uneven terrain, elusive species, etc., and the potential influence of weather conditions and observer bias (Ezcurra and Gallina 1981; Galindo-Leal and Weber 1998; Hibert *et al.* 2011). Additionally, this method can be costly, and noise from land or air vehicles may disturb the animals, potentially introducing observer bias and fatigue.

When herbivore abundances are low, and the animals are difficult to detect, indirect methods can be a good option. For example, track counts, pellet counts (Harestad and Bunnell 1987; Gallina-Tessaro 1990; Hibert *et al.* 2011; Mandujano 2014). Pellet counting is an attractive option due to its ease of application, non-invasiveness, the potential for adequate sample sizes (Mandujano 2014), minimal training requirements, and cost-effectiveness. This technique provides persistent records of the presence of deer (Ezcurra and Gallina 1981) or other herbivores.

For herbivores, fecal group counting can be used to estimate relative abundances or population density (Lioy *et al.* 2015). To determine population density, the number of individuals in a population, or their distribution, three variables are required: the number of pellet groups or droppings over an area (km^2), the daily deposition rate of feces, and the rate of disappearance of feces or pellet groups for the species under study (Ezcurra and Gallina 1981; Barnes and Barnes 1992; Camargo-Sanabria and Mandujano 2011).

The main techniques used for pellet group counting are: 1) FSC (Fecal Standing Crop), which estimates density by counting all feces or pellet groups accumulated in randomly selected sampling plots. It requires knowledge of the persistence time or disappearance rate of these groups. 2) FAR (Fecal Accumulation Rate). This method estimates density based on the accumulation of new feces between two sampling periods. It initially requires removing all feces from the plots and returning after a fixed time to count how many have accumulated. During this time, there should be no disappearance of feces or pellet groups. Both methods require the daily defecation rate to estimate the population density of the herbivore (Laing *et al.* 2003; Torres *et al.* 2013; Mandujano 2014; Lioy *et al.* 2015).

Additionally, pellet group counting can be employed as an index of abundance, which can be useful for monitoring the same population, detecting changes in populations over time, or comparing populations (Torres *et al.* 2013; Mandujano 2014). Pellet group counts are a good indicator of the relative habitat use (Leopold *et al.* 1984; Loft and Kie 1988; Galindo-Leal and Weber 1998; Sánchez-Rojas and Gallina 2000b; Esparza-Carlos *et al.* 2011; Mandujano 2014). It has been estimated that habitat use measured with different techniques by ungulates and pellet counts is similar in different ecosystems, for example: mule deer, as determined by telemetry and pellet group counts in temperate forest (Loft and Kie 1988); as is the case with Gray Brocket Deer (*Mazama gouazoubira*) the habitat use estimates using GPS and feces did not differ in tropical deciduous forest, savannas and grasslands (Peres *et al.* 2023). It was also similar between habitat use by telemetry and domestic livestock feces (Hernandez *et al.* 1999). Moreover, white-tailed deer abundance estimates have been found to be similar in aerial surveys using thermal cameras and stratified transect pellet group counts (McMahon *et al.* 2021).

The pellet counting technique has been widely extensively employed for herbivores such as cervids, bovids, and leporids in various ecosystems in North America (Harestad and Bunnell 1987; Gallina-Tessaro *et al.* 1991; Hernandez *et al.* 1999; Sánchez-Rojas and Gallina 2000a; Arias-Del Razo *et al.* 2012; Esparza-Carlos *et al.* 2016), as well as in Europe (Gallina-Tessaro 1990; Torres *et al.* 2013, Lioy *et al.* 2015). This method has also been employed in Africa for elephants (Barnes and Barnes 1992) and different ungulate species (Hibert *et. al.* 2011), suggesting that it is a technique applicable for estimate the abundance for any herbivore species.

In México, the technique of pellet group counting to estimate population densities of herbivores began to be used with white-tailed deer (*Odocoileus virginianus*) in Michilía, Durango, in pine-oak forests (Ezcurra and Gallina 1981) and tropical dry forest for (*O. virginianus*; Mandujano y Gallina 1993; Camargo-Sanabria and Mandujano 2011). The technique was also applied to mule deer in pine-oak forests (Gallina *et al.* 1991) and in the Chihuahuan Desert (Sánchez-Rojas and Gallina 2000a, b). Fecal counting has also been used to assess the relative abundance of cattle (Hernandez *et al.* 1999).

To estimate population densities using pellet groups, there are three main methods used: 1) Transects with circular plots, especially in areas with medium to high deer abundances (Ezcurra and Gallina 1981; Galindo-Leal and Weber 1998; Sánchez-Rojas and Gallina 2000b; Mandujano 2014). An assumption of this technique is that these pellet groups persist throughout the measurement period (Harestad and Bunnell 1987). To determine persistence, the plots are cleaned, or existing pellet groups are marked; which can be a time-consuming process and, at times, impractical for large areas (Harestad and Bunnell 1987; Hibert *et al.* 2011). 2) Strip transects, which in are used in areas with medium to low abundances. 3) Line transects in this method, variable-length transects are used, and the perpendicular distance from the pellet group to the transect is measured (Mandujano 2014). 4) Quadrant Transects (Laing *et al.* 2003, Esparza-Carlos *et al.* 2011), which have been employed to estimate relative abundance in arid regions, pellet group censuses for mule deer are carried out within 1 km^2 (Esparza-Carlos *et al.* 2011).

The pellet group counting technique is recommended primarily during the dry season because, during this period, it is unlikely for pellet groups to be lost due to heavy rain wash (Wallmo *et al.* 1962; Hibert *et al.* 2011). Humidity is a key factor in pellet loss due to the development of fungi (Delisle *et al.* 2022) and consumption by insects (Neff 1968; Ezcurra and Gallina 1981; Harestad and Bunnell 1987; Hibert *et al.* 2011); sun and wind also influences in pellet decay in boreal ecosystem (Jung and Kukka 2016). For example, pellet loss is lower in drier sites, such as open areas and coniferous forests, than in deciduous forests, where humidity is higher, and dung beetles and saprophagous invertebrates play a significant role (Torres *et al.* 2013). Other factors related to the loss of pellet groups include concealment by leaf litter (Harestad and Bunnell 1987; Delisle *et al.* 2022), as well as unintentional removal or trampling by domestic or wild mammals. However, in semiarid ecosystem the pellet group decay increases as number or rains increases too (Wallmo *et al.* 1962).

Understanding the persistence or disappearance rates of pellets is crucial for estimating abundances through pellet groups or feces counting (Camargo-Sanabria and Mandujano 2011; Delisle *et al.* 2022). Despite the widespread use of this technique in México and the USA, based on a literature review, we found a lack of pellet group persistence studies for mule deer in México. The existing data in the United States is also outdated. A similar situation exists for white-tailed deer, although we did find one study for México and another for the United States in the last 12 years.

For mule deer, pellet groups have been observed to last from one to two years on steep slopes and bare ground; however, in areas with vegetation cover, leaves, and litter, they can persist for up to five years (Neff *et al.* 1968). In semiarid ecosystems, pellet groups deposited during the rainy season typically decay within two to four months (Wallmo *et al.* 1962). In a savanna ecosystem, during the dry season, the decay percentage of pellets from different ungulate species varies between 2 to 14 %, with insects identified as the primary cause of decomposition, followed by dispersion, scattering, and embrittlement; the trends in the decay and ageing of pellet groups were similar, although the five species differed in size and feeding habits (Hibert *et al.* 2011). In boreal forest elk pellets decay by 69 % after the first growing season, 74 % after the second, and 76 % after the third (Jung and Kukka 2016). In temperate forests, white-tailed deer pellets generally disappear within an average of 70 to 120 days (Delisle *et al.* 2022). In México, where the technique has been widely used, we found only one study estimating the persistence of white-tailed deer pellet groups in deciduous tropical forest, reporting pellets being lost in 123 days (Camargo-Sanabria and Mandujano 2011).

The lack of data on the permanence or decomposition of pellet groups for mule deer or white-tailed deer in various ecosystems or habitats necessitates cleaning study plots at the start of the study. Moreover, it demands regular visits to reduce pellet loss, assuming no pellet groups are lost during this period, incurring significant costs and labor intensity. In the case FSC, white pellets may be considered old, but time deposition remains uncertain. Hence, the objectives of this study is to ascertain the persistence of mule deer pellet groups in the Chihuahuan Desert, document changes in color over time, and record structural characteristics of the pellets. This aims to minimize the bias of abundance estimates for mule deer. Understanding the pellet groups permanence time and identifying pellet groups age based on color will enable us to establish suitable periods for pellet groups deposition without loss; which affect abundance estimates. This is crucial for FSC studies, as it requires knowledge of the persistence time or disappearance rate of these groups. Additionally, for FAR, time periods for counting and recounting plots are established, assuming no pellet groups are lost. Hence understanding pellet group persistence is crucial to estimate mule deer abundances through the pellet group technique. The, mule deer holds significant ecological importance, as one of the great wild herbivores, serving as the main prey of larger carnivores such as the cougar (Gallina-Tessaro *et. al.* 2019). It also pays a vital role as food resource for rural communities and stands as one the most important game species in México (Gallina-Tessaro *et. al.* 2019). Although the mule deer is currently globally classified as a species of least concern in terms of conservation (Sánchez Rojas and Gallina-Tessaro 2016), the specie has disappeared from the southernmost parts of its distribution, and is experiencing a decline in population numbers and reduction in distribution areas, resulting in local extinctions in regions in the northeastern of México (Martínez-Muñoz *et al.* 2003; Gallina *et al.* 2019b). Therefore, understanding the persistence times of pellet groups is crucial for improving abundance estimates of mule deer through pellet group counting, especially in these arid regions where populations are declining. This information is vital for informed management and conservation decisions.

Methods and materials

Study area. The study was conducted in the Mapimí Biosphere Reserve (MBR), located between 26° 41' 17'' to 26° 39' 23'' N and -103° 44' 02'' to -103° 45' 49'' W, at the intersection of the states of Durango, Chihuahua, and Coahuila, México. The MBR is situated in a closed basin characterized by extensive flat areas, small hills, and isolated mountains, with San Ignacio Mountain being the highest and the focus of this study. The climate is arid, with cool winters and warm summers, with mean temperatures of 15 °C and

26 °C, respectively; the annual mean temperature is 21 °C. The average annual precipitation is 287 mm, ranging from 122 mm to 716 mm. Sixty-four percent of this precipitation is concentrated between June and September (summer rains), and 10 % between December and February (winter rains are highly variable annually; data from the weather station, Laboratorio del Desierto Climate Station, Instituto de Ecología A. C. [INECOL]). The terrain where the study was conducted is relatively flat with a uniform slope ranging from 0 to 4°.

The study was conducted in the area known as the "upper bajadas," which is a part of the landscape element of bajadas and hills of igneous and sedimentary origin (37 % of the area). This area is primarily inhabited by mule deer (Sánchez-Rojas and Gallina 2000a, b). The "Upper Bajadas" are characterized by dominant vegetation such as creosote bush (*Larrea tridentata*), ocotillo (*Fouqueria splendens*), prickly pear (*Opuntia rastrera*), yucca (*Yucca rigida*), and agaves (*Agave scabra, A. lechuguilla*; Montaña and Breimer 1988). The diet of mule deer in this area primarily consists of shrubs (43 % of the annual diet), herbs (34 %, mainly in summer), succulents (13 %), and grasses (10 %; Guth 1987). The only agricultural activity in the area is extensive cattle ranching with minimal management. Human population density in the region is 0.12 inhabitants per square kilometer (Esparza-Carlos 2011).

Data collection. After the rainy season, approximately in October of any year, mule deer start to concentrate in the "Bajadas," and pellet groups begin to accumulate. Deer stay there until the next June when the rainy season begins (personal observation), at which time many of them expand their distribution, likely moving to other areas to feed on newly growing vegetation. Specifically, in the "Upper Bajadas" where the study was conducted, most of the terrain features bare soil, spaced-out shrubs, and few patches of grass; herbs only appear during the summer or winter rainy seasons (Personal observation). Therefore, the detection of mule deer pellet groups is easy.

To determine the persistence of pellet groups and relate color to the time of deposition, in one study of mule deer habitat use and predation risk following FSC, a free search for mule deer pellet groups was conducted in one area of 178 ha (Esparza-Carlos *et al.* 2011, 2016). In total, 102 pellet groups were monitored during various climatic seasons and years, excluding the summer rainy season: a) Group 2004, registered on October 12, 2004, with 15 pellet groups recorded. b) Group 2005a, deposited between February 7 and March 11, 2005, with 17 pellet groups. c) Group 2005b, deposited between November 14 and December 3, 2005, with 40 pellet groups. d) Group 2006, deposited between May 14 and May 23, 2006, with 30 pellet groups.

Once the pellet groups were found, their coordinates were recorded using a Garmin 12XL® GPS device. Photographs were taken of each group, and a description of their color and appearance was made. To identify the pellet group during subsequent visits, the area where they were located was marked with three metal rods or green-painted stones. All pellet groups had been deposited for a few hours (except for the Group 2004, which were recent, but the exact day of deposition was not known).

The persistence of the pellet groups, that is, whether it is still considered present, was assessed in two ways: a) Persistence of the pellet group: it was considered that the group was no longer active when there were fewer than 15 pellets left or when the pellets were mixed with others, making it impossible to identify them as a group (n = 1). b) Persistence of the last pellet of the original pellet group. With the aim of describing the aging process, investigating the causes of decay, and determining when pellets turned completely white (as suspected to occur after a year during each visit), we recorded the color and physical characteristics of the pellets. This included factors such as smoothness, the appearance of cracks, pellet rounding, and so forth (Hibert *et al.* 2011). Initially, visits were conducted every 2 to 4 months, but as no pellets were lost, the visit periods were spaced out: a) February 9 to 16, 2005 (Group 2004); b) April 29 to 30, 2005 (Groups 2004 and 2005a); c) December 1 to 3, 2005 (Groups 2004 and 2005a); d) May 10 to 11, 2006 (Group 2005b); e) June 12 to 26, 2006 (start of the rainy season; Groups 2004, 2005a, and 2005b). The remaining visits included all groups: f) April 17 to 20, 2007; g) May 1 to 27, 2008; h) June 2 to 3, 2009. During the study, the feces were exposed to both rainy and dry years: between May 2004 and May 2005, it was a very rainy year. During the summer rainy season, it received 291 mm of rainfall, which is above the annual average. In contrast, 2005 to 2006 was a dry year. During 2006 to 2007, it was rainy again. For 2008 (January-December), we only have the annual precipitation data, which was 277 mm, close to the annual average, and we do not have the precipitation data for 2009 (Table 1).

Analysis. To determine the persistence of mule deer pellet groups, descriptive analyses were conducted with the number and percentage of pellet groups over time. To assess if the persistence rate of pellet groups was similar among the different groups recorded in various seasons and years, a Generalized Linear Model with a binomial distribution type ANCOVA (Analysis of Covariance) was conducted. The independent variable was the proportion of pellet groups present, and the explanatory variables were time, measured in days, and the set of pellet groups classified by year and the date on which they were found. The assumptions of normality and homogeneity of variances were met. Subsequently, a post-hoc test was performed using the "gmodels" package to determine if the slope differed among the categories of mule deer pellet groups. All analyses were conducted using the R programming language (R Core Team 2021).

Results

All pellet groups (n = 102) turned white after the first rainy season, regardless of the month and year they were depos-

Table 1. Precipitation by Season. The rainy season typically begins in late May or early June and ends in September or early October. The dry season spans from October to May. In some years, there might be winter precipitation.

Time period	Precipitation rainy season	Precipitation dry season	Total
June 2004 – May 2005	291		291
June 2005 – May 2006	138	6	144
June 2006 – May 2007	261	132	393
June 2007 – September 2007	147		147
October – December 2007		6.5	
January – December 2008			277

[1] For the year 2008, we only have the total precipitation data, and we do not have the precipitation data for 2009.

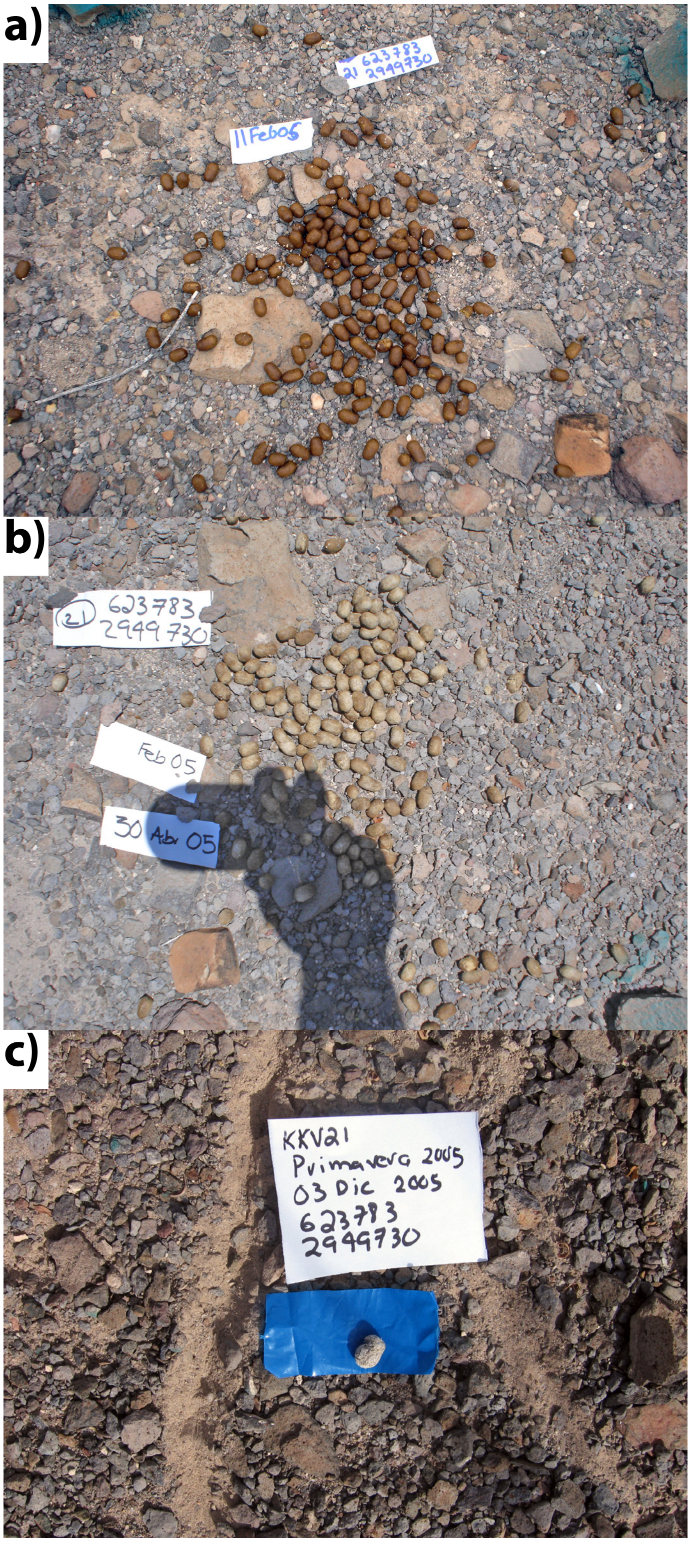

Figure 1. Mule deer pellet group: a) fresh. b) 2 months after being deposited. c) 10 months after the first rainy season, only one white pellet with dark specks like sand remained, with noticeable wear on the edges.

ited by the mule deer (Figures 1 to 3). Freshly excreted pellet groups are olive green in color, with a soft consistency due to moisture, and a smooth, moist outer layer. After a few hours or a day of being deposited, they generally turn a dark brown color, although there can be variations in shades of light brown, brown-yellow, to dark brown or black. However, apart from the tracking described here, we have observed dry pellets of other colors, including pink, white-pink, and yellow-white. As the months pass, some begin to lose color and gradually whiten. Additionally, small white cracks appear in the pellets, which widen and grow as the months go by. The smooth cuticle may peel off in small sections of the outer layer, especially those that have been exposed for more months (Figures 1 to 3).

The color of the pellets starts to fade rapidly with the first summer rains, initially turning from green-white, until becoming a uniform white color after the first summer rainy season. After the first summer rainy season, the outer layers of the pellets become less smooth, and as rainier seasons (years) pass, the outer layers of the pellets lose their smoothness, becoming micro-granular, and the pointed ends (top of the pellet) are lost. The pellets turn a sandy-white color with black spots, and the pellets start to fragment (Figures 1 to 3).

In our study area, all pellet groups remained during the dry season (October to May) for any measured year, even though in 2 years there were rains of 91 and 132 mm during this period (Figure 4, Table 1), which was slightly less than the summer rains during the dry years (138, 147 mm). Pellet groups were only lost after the summer rainy seasons (June-September).

The first set of pellet groups marked in October 2004 was visited in February and April 2005, and no groups were lost. The set of 2005b pellet groups, marked in November 2005, was measured in May, and no losses were detected either (Table 2). However, all sets lost pellet groups during the first rainy season they were exposed to. Even in 2006, at the beginning of the rainy season, several pellet groups from most sets were lost.

During the first rainy season, an average of 47 % of the pellet groups were lost (range 20 to 63 %). For the second rainy season, the cumulative loss of pellet groups was 85 % (range 71 to 93 %). In the third rainy season, the cumulative average was 95 % (range 82 to 100 %), and for the two sets of groups measured at the beginning of the fourth rainy season, 97.1 % were lost (94 % and 100 %; Figures 4 and 5; Table 2).

Regarding the total loss of all pellets and pellet groups, the results were similar, although, obviously, they are lost slightly less than the pellet groups. During the first sum-

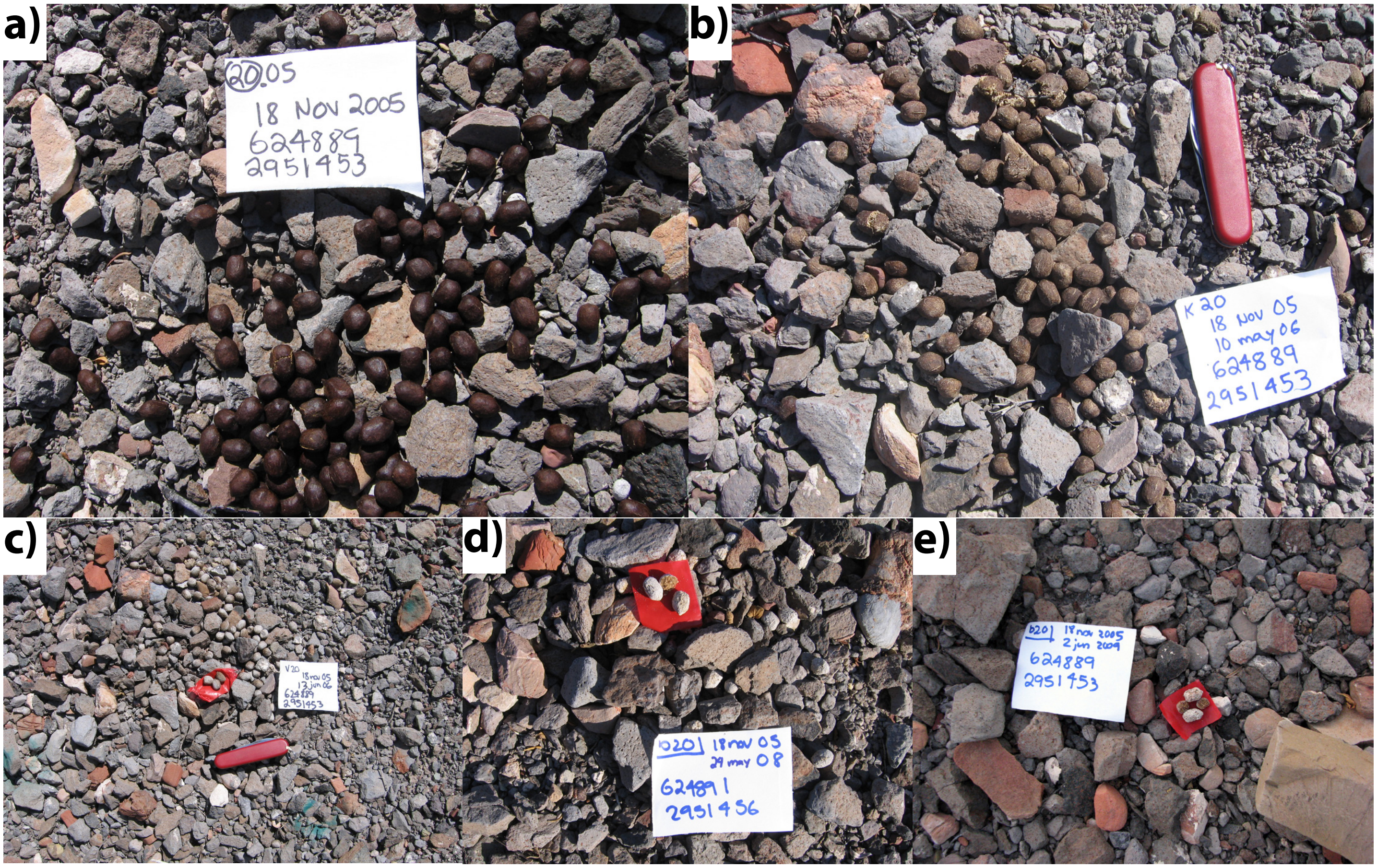

Figure 2. Mule deer pellet group. a) fresh. b) 7 months after being deposited, has lost its color and cracks have appeared. c) 8 months after the first rains. d) 2 years and 7 months later, only a few white pellets with edge wear remain, but they still retain color on the inside. e) some pellets from the original group persisted for at least 3 years and 8 months, which was the last time they were checked.

mer rainy season, an average of 33 % of all pellets were lost (range 20 to 55 %). For the second season, the cumulative loss was 67 % (range 59 to 78 %). In the third summer rainy season, the cumulative loss was 89 % (range 77 to 100 %). Finally, for the two sets of groups measured at the beginning of the fourth rainy season (2004 and 2005a), 97 % were lost (94 % and 100 %; Figures 4 and 5, Table 2).

Although there was no systematic record, we observed that the groups that are lost first are those deposited in micro-channels where water apparently flowed during one or more precipitation events. Those that tend to persist longer are the ones found among gravel, stones, and plants. After the first rainy season, the remaining pellets could be distinguished based on their shape, size, and color. However, after two rainy seasons, it becomes difficult to track the pellets and determine their origin to a specific pellet group. The pellets start to disperse to more than 1 m, and they lose their shape, becoming rounded. All the pellets from various pellet groups turn white with black spots. Identifying their origin becomes challenging, especially after the second rainy season. Some pellet groups, before completely disappearing, leave fewer than 15 pellets (Figures 4 and 5).

The probability of persistence of pellet groups decreases over time, reaching zero or nearly zero around 1000 days (third and the beginning of the fourth rainy seasons) as per the generalized linear model type ANCOVA ($P < 0.001$, $Xi^2_{13} = 30.52$, $df = 13$, explained deviance = 0.92; Table 3 and Figure 5). The *post-hoc* multiple comparison test between pairs of slopes showed that the disappearance rate was similar among all pellet group categories collected in different seasons and years, except for the 2005a category, which was

Table 2. Mule deer pellet group persistence in Chihuahuan Desert. In the Chihuahuan Desert, some sets of mule deer pellet groups persisted for up to 4.1 years. Individual pellets remaining slightly more.

Pellet group categories	Month of deposition	Season of deposition	n	Pellet groups in 2009 (n)	Individual pellets in 2009 (n)	Monitored years (n)
2004	October	Autumn	15	0	0	4.6
2005a	February	Winter	17	1	1	4.3
2005b	November	Autumn	40	1	5	3.5
2006	May	Spring	30	0	3	3.1

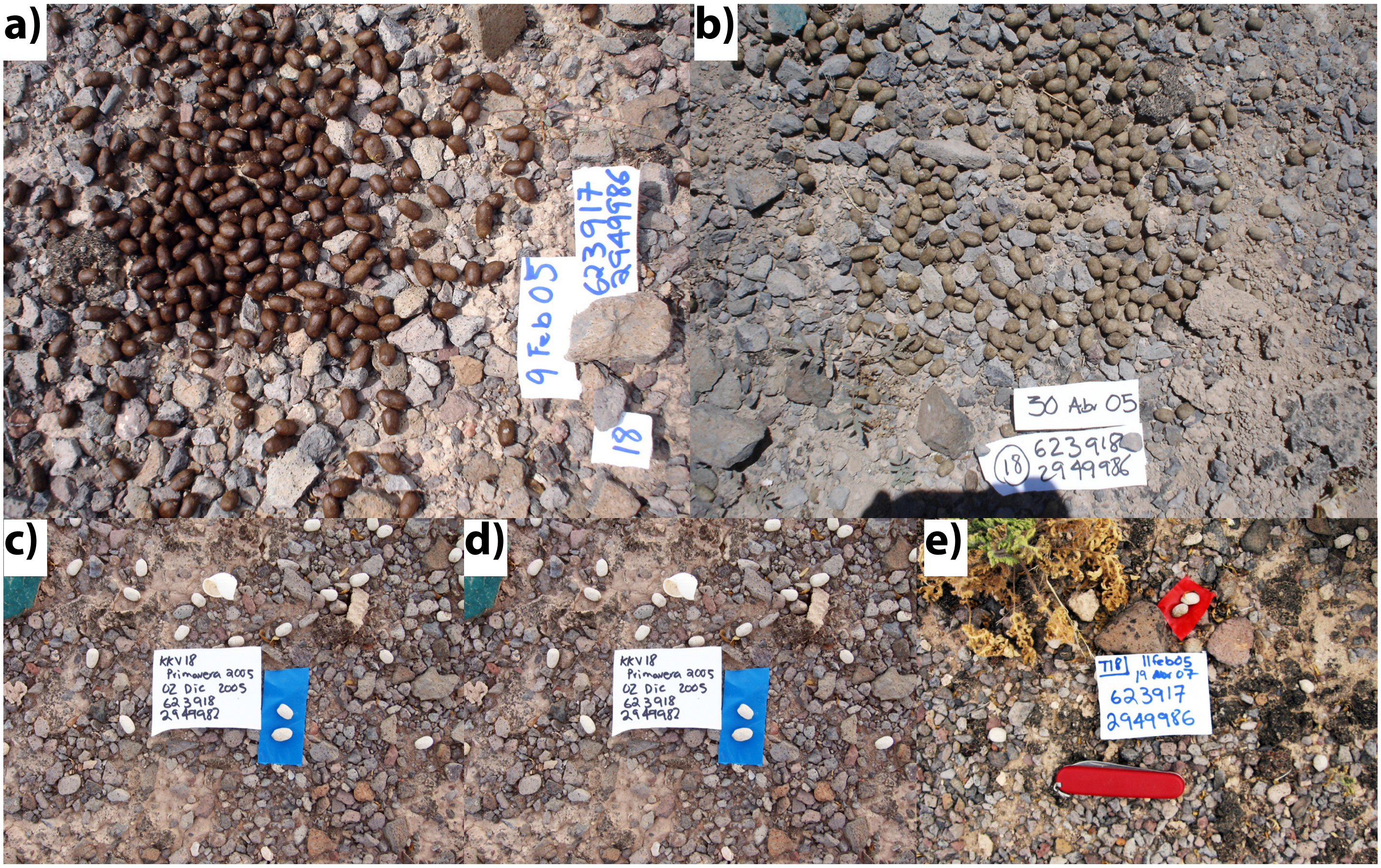

Figure 3. Deer pellet groups a) fresh. b) 2 months after being deposited, they have faded a bit. c) 10 months after the first rains, they are completely white, the pellets have scattered, and the edges have worn out. d) 1 year and 4 months later, at the beginning of the second rainy season, the same pellets remain, only a few white pellets with worn edges, but they still retain their color inside. e) after two rainy seasons, many of the pellets have been lost.

different from the rest (2004, 2005b, 2006), with a slightly higher probability of permanency over time (Table 4; Figure 5). For instance, within categories 2004, 2005b, and 2006, after 713 to 915 days since deposition, 7 to 13% of the pellet groups remained, while for category 2005a, 29 % persisted. After 1114 to 1295 days, the first three categories retained 0 to 3 % of pellet groups, whereas the 2005a category retained 18 %.

Regarding pellet persistence (when the pellet group had < 15 pellets), it decreased over time, according to the generalized linear model type ANCOVA ($P< 0.001$, $Xi^2_{13} = 107.74$, *df* = 19, explained deviance = 0.90; Table 3 and Figure 5). Pellet persistence was slightly higher than that of pellet groups but was similar across all categories. After 1292 days, 13 % of the 2005b category persisted, 6 % of the 2005a category after 1,570 days, and 10 % of the 2006 category after 1,114 days, but 0 % remained after 1,692 days for the 2004 category (Figure 5).

Discussion

The first significant finding of this study is that all pellet groups deposited after summer rainy season, remain until the last of dry season. Furthermore, all pellet groups turn white after being exposed to a summer rainy season in the

Table 3. Results of the generalized linear binomial model type ANCOVA analysis, for the persistence of mule deer pellet groups (top) and pellets (bottom) in the Chihuahuan Desert, Mexico. df = Degrees of freedom.

Category	Deviance change	*df*	Residual Deviance	Deviance Explained (%)	*P*
Groups					
Null		20	361.4		
Pellet groups	2.1	17	359.3	0.6	0.557
Days	318.4	16	40.9	88.1	< 0.001
Pellet groups: days	13.3	13	27.6	3.7	< 0.001
Pellet					
Null		20	294.4		
Days	264.2	19	30.1	89.9	< 0.001

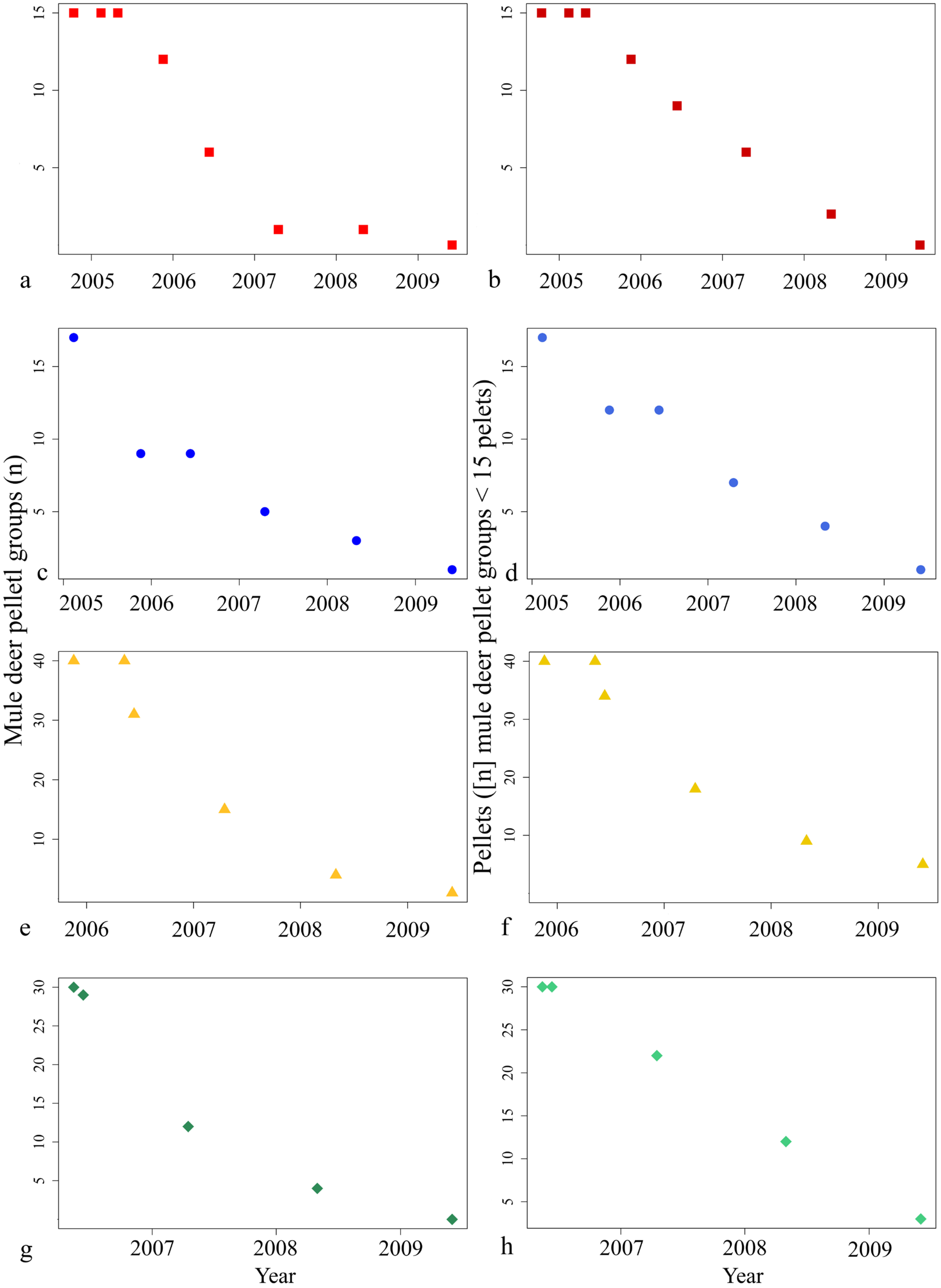

Figure 4. Number of mule deer pellet groups over time. Pellet groups only disappear after the summer rainy seasons. On the left side, mule deer pellet groups (>15 pellets), on the right side, pellets from these (1 - 15) that were no longer considered as pellet groups. Red squares: pellet groups started in October 2004; blue circle: pellet groups started in February 2005; yellow triangle: pellet groups started in November 2005; green rhombus: pellet groups started in May 2006.

Table 4. Post-hoc analysis comparing categories of mule deer pellet groups (top) and pellets (bottom) between different disappearance periods in the Chihuahuan Desert, Mexico. In all cases, degrees of freedom = 1.

Pellet groups categories	**Estimate**	**Standard Error**	**Xi^2 Value**	***P***
2004 - 2005a	- 0.0032	0.00156	4.24	0.040
2004 - 2005b	- 0.0006	0.00163	0.12	0.734
2004 - 2006	0.0011	0.00197	0.30	0.581
2005a - 2005b	0.0027	0.00098	7.35	0.007
2005a - 2006	0.0043	0.00149	8.37	0.004
2005b - 2006	0.0016	0.00155	1.12	0.291

Chihuahuan Desert. This is vital information for using pellet group counting techniques in any approach during the autumn, winter, and spring seasons (excluding the rainy season in summer). For example, if the technique is going to be used as an index of relative abundance or for estimating population density using a single visit Fecal Standing Crop (FSC) in arid areas like the Chihuahuan Desert. This finding relieves us from the need to estimate the pellet disappearance rate over time (Torres *et al.* 2013). This assures us that all colored pellets are subsequent to the summer rainy season and allows us to discard the white-colored ones.

The second important finding is that for the Chihuahuan Desert and possibly other arid areas, the periods of pellet accumulation can be extended according to the study objectives when using the Fecal Accumulation Rate (FAR) technique, which involves two visits. The first visit is to clean all previously deposited pellet groups, and after some time the second to count how many were deposited after some time. With this technique it is suggested that the period between visits to recount pellet groups should be brief to avoid pellet loss (Laing *et al.* 2003). For example, in deciduous tropical forests, white-tailed deer pellet groups disappear after 123 days (Camargo-Sanabria and Mandujano 2011), and in the Chihuahuan Desert, it has been used a period of 90 to 120 month without knowing the pellet disappearance rates (Sánchez-Rojas and Gallina 2000a, b). However, this study demonstrates that in the Chihuahuan Desert, this period can be up to 7.5 months, as no pellet groups was lost between October and May throughout the observation years from 2004 to 2009. For instance, only two visits can be made to determine population density throughout the dry season or habitat use intensity: The first at the end of the summer rainy season, in early October, you can clean the plots and return to count in mid to late May, before the start of the rainy season. This ensures that all pellet groups correspond to the deposition that occurred during this period of time, roughly 7.5 months, have the certainty that no pellet groups will be lost, and none will turn white (this allows us to distinguish them from the dry season of the previous year). Although it had previously been suggested that pellet groups counting should be done during the dry season due to the low likelihood of pellet loss (Wallmo *et al.* 1962; Neff 1968; Ezcurra and Gallina 1981; Mandujano 2014). This work confirms that, at least in the Chihuahuan Desert, no loss of pellet groups occurs during the dry season. In fact, some pellet groups or individual pellets persisted until the end of their monitoring after 3 or 4 years. The percentages of permanence were slightly from elk in boreal forest. After the first growing season the permanence of in this study was 47 compared to 31%; the second growing season was 15 % this study vs 26 %; the third growing season was 5 % vs 24 % (Jung and Kukka 2016). There was no evidence indicating losses due to biological agents such as fungi, insects, or other invertebrates. In savanna ecosystem the principal cause of decay loss was attributed to ants and termites, followed by scattering and embrittlement; however, Bohor reedbuck (*Redunca redunca*) droppings, never were attacked by insects (Hibert *et al.* 2011). The observations consistently point to water runoff during the rainy season (June to September) as the sole cause of pellet group loss. Notably, even when exposed to rain in the supposedly "dry" months of two years with about 50 % of the rainfall of the rainy season,

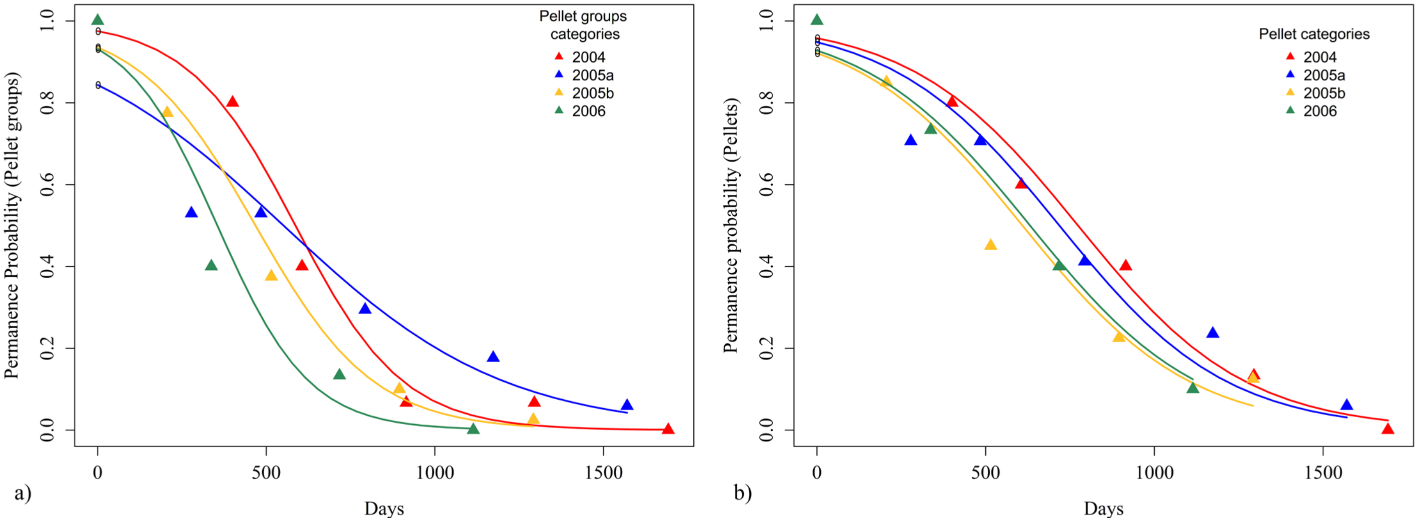

Figure 5. Results of the generalized linear model binomial type ANCOVA on the persistence of: a) pellet groups (left). b) Pellets (Mule deer pellet groups with fewer than 15 pellets) in the Chihuahuan Desert (right) over time. Pellet groups deposited in October 2004 (red), pellet groups deposited in February 2005 (blue), pellet groups deposited in November 2005 (yellow), pellet groups deposited in May 2006 (green).

no pellet groups were lost or turned white. This aligns with findings in other arid areas, where heavy rainfall is identified as the primary cause of mule deer pellet group losses, washing them away (Wallmo *et al.* 1962; Hibert *et al.* 2011). The pellets are dispersed and washed away by run-off or degraded and overed over by seedling vegetation (Hibert *et al.* 2011). This is in agreement with those found in other ecosystems where precipitation and warmer temperatures are the main causes of pellet loss (Delisle *et al.* 2022). It has also been found that in forest ecosystem, pellet groups take longer to disappear in drier habitats, presumably because they dry out faster and become harder compared to more humid habitats (Torres *et al.* 2013); contrary, in boreal forest, Elk (*Cervus Canadensis*) pellets decays more rapidly in drier open habitats, due to exposure to wind and sun (Jung and Kukka 2016). For instance, hare and rabbit pellets start to disappear one month after deposition, while others may take between 4.4 to 9.5 years to vanish, this disappearance is correlated with environmental humidity and precipitation (Flinders and Crawford 1977).

These results have practical implications for estimating deer densities or relative deer abundance using pellet group counting. It is now known with certainty that visiting the study area twice is sufficient when using the Fecal Accumulation Rate method. This can save on costs and time. It also makes it more feasible to cover a larger sampling area since two visits are sufficient, eliminating the need for revisiting the same plots or transects multiple times during the dry season. It is important to note that this applies to the Chihuahuan Desert, and perhaps the Sonoran Desert and some other arid areas. Once in other ecosystems, the rate of pellet loss varies by season (Torres *et al.* 2013). Additionally, in temperate forests or areas with more vegetation, fallen leaves on the forest floor can conceal fecal groups, making them difficult to detect, and in some areas, after a year, only about 10 % of pellet groups are visible for example (Harestad and Bunnell 1987). We assume that in moister areas with more vegetation, such as tropical rainforests, biological decomposition might be significant. Therefore, we suggest conducting studies on the persistence of deer pellet groups in other ecosystems to determine the longevity of pellets. This will help establish the optimal time for revisiting plots without a significant loss of pellet groups or estimating their disappearance rate.

However, there could be potential disturbance factors that might affect the persistence of pellet groups, which were not discussed here but should be considered in other areas. For example, if the study area has a high density of domestic livestock or is frequently used by humans, these factors might lead to pellet loss through mechanical disturbance, such as trampling or bedding areas. In our study area, although there is some livestock use, we believe it is not excessive, especially when compared to areas near water sources.

This result is also significant because it suggests that in certain arid areas, there are very few or no biological agents degrading herbivore feces. In other ecosystems, it has been observed that as humidity increases, more pellet groups are lost because humidity promotes the growth of fungi and the presence of invertebrates that break down feces (Ezcurra and Gallina 1981; Harestad and Bunnell 1987; Torres *et al.* 2013). Throughout all the years of monitoring deer feces groups, there was no evidence of losses due to biological agents. Additionally, during five years of working in the area, conducting deer ecology studies, we never observed any dung beetle or insects in deer pellets (even though we recorded > 20,000 pellet groups (Esparza-Carlos *et al.* 2011, 2016). We also do not recall seeing these in cow dung, which is abundant. This suggests that the abundance of dung beetles is very low or non-existent because dung beetles that consume herbivore dung are polyphagous, and although they have preferences for certain species, they colonize feces from many domestic and wild vertebrates. Furthermore, they prefer feces in open habitats (pastures) over forests (Dormont *et al.* 2007). Therefore, the primary or nearly exclusive means of nutrient reintroduction into the ecosystem in the region, is through the disintegration of pellet pellets, a process facilitated by rain. It is well-documented that white-tailed deer play a significant role in the distribution of nitrogen within ecosystems, such as grasslands, where the nitrogen concentration is higher in deer feces than in Bison feces (*Bison bison*; Pruszenski and Hernández 2020). In our study area, due to the persistence of the pellets, our data suggests that nutrients release may be delayed for several years, and perhaps the distribution of these nutrients is concentrated where water flows, as it appears to be the only or nearly the only source of pellet disintegration. To understand the role of mule deer in nutrients distribution in Chihuahuan Desert, it is recommended to conduct studies on nitrogen and nutrients concentration and release in mule deer pellet groups.

Regarding the color of the pellets, all groups deposited from October to the end of dry season, lose their color gradually, but quickly and become white after the rain season. Therefore, we assume that pellet groups deposited during the rainy season also lose their color after it ends. However, it is uncertain what color feces that were deposited at the end of the rainy season, for example, those exposed to just 1 to 4 rains, would turn to. If we are interested in applying the pellet group counting technique during the summer rainy season, it is recommended to conduct studies of pellet group persistence during this season. Visit the pellet groups every 7 or 15 days and record their persistence and color changes during this period. This approach will allow you to suggest an effective visitation interval for plots with minimal loss of pellet groups during this period. As well as determining if it is a threshold number of rains that causes the pellets to change color or remain the same at the end of the summer rainy season. Furthermore, it would be possible to assess whether, during the rainy season, some pellet groups are lost due to dung beetles or other biological agents, once we were not present for most of the summer rainy season (July to September). Furthermore, for dry season improving color tracking and pellet characteristics could enhance the precision of age assignment to the pellet. Our observations of color and physical changes in pellets offer a broad overview during the dry season. Hence, we propose a more systematic study involving monthly visits. This approach aims to establish age categories based on pellet color and physical changes, documented with photographs and descriptions. The outcome of this systematic study could serve as a guide for estimating pellet age, which may assist in estimating pellet age in a single visit, once appears to be the most useful criterion for dating pellets in five ungulate studied species (Hibert *et al.* 2011). Conducting such studies can provide valuable insights into the dynamics of pellet group persistence and color change during the dry and wet season.

On the other hand, this study further supports the crucial role of mule deer as a significant seed disperser for plant species in the Chihuahuan Desert. Deer groups are recognized as important consumers and dispersers of seeds. For instance, white-tailed deer are known seed dispersers in North America, as they disperse seeds over long distances, and the decay of their pellets facilitates germination for many of plant species (Myers *et al.* 2004; Blyth *et al.* 2013). Previous research in the same area identified mule deer as highly effective dispersers of *Opuntia rastrera* seeds, a common cactus plant in the Chihuahuan Desert (Mandujano *et al.* 1997). Experiments revealed that these seeds require more than a year of dormancy for germination, with mule deer exhibiting the highest germination rates: 0 % for fresh seeds, 58 % after one year, and 85 % after two years, comparable to the control group. The study suggests that being in pellets protects the seeds from predation, and the extensive movements of mule deer contribute to their dispersal over significant distances, enriching the seed bank (Mandujano *et al.* 1997). This study sheds light on this natural process, revealing that pellets decay one to four years after deposition, allowing seeds to be released gradually. This dynamic increases the germination percentage of *O. rastrera* and possibly other species. It underscores the critical role of deer pellets in seed dynamic, acting as potential seed bank in this arid zone where the soil is bare. Therefore, it would be interesting to analyze the germination and disperse role of other seeds species of Chihuahuan Desert.

In summary, mule deer pellet groups exhibit prolonged persistence in the Chihuahuan Desert. Although approximately 40 to 62 % are lost during the initial summer rainy season, some pellets can endure up to 1,700 days (until the beginning of the fourth rainy season). To my knowledge, this is the first published study in México on the persistence of mule deer (*Odocoileus hemionus*). This study also reveals, that All pellet groups deposited during the dry season persist and retain their color until the end. Pellet groups that persist after the rainy season uniformly turn white. This insight enables a reduction in the number of visits for estimating mule deer abundances, when employing mule deer pellet group counting in arid areas, outside of the summer rainy season. This adjustment could help UMAS technicians, CONANP (National Commission of Natural Protected Areas) personnel, and researchers minimize costs associated with the technique by decreasing the required samplings for estimating mule deer abundance. Finally, we recommend conducting persistence studies in diverse ecosystems to determine pellet group disappearance times and establish pellet accumulation periods that enhance optimal pellet group accumulation periods that enhance visit efficiency without losing pellet groups. Such studies may necessitate multiple years of observation due to variations in precipitation and temperature between year.

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Biogeographic analysis of population density of White-tailed deer in Mexico: importance of the protected natural areas and wildlife management units

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The white-tailed deer *Odocoileus virginianus* is the wildlife species with the greatest geographic distribution and economic importance in Mexico. This article presents a biogeographic analysis of the population density of this deer species by federal states, vegetation types, biogeographic provinces, and field methods, based on 200 selected studies. Estimates are highly variable and potentially biased due to the different field designs and statistical analyses. The national average density was estimated at 6.9 deer/km^2 (SD = 5.1); specifically, 75.5 % of the estimates were less than 10 deer/km^2, and only 5.5 % were greater than 15 deer/km^2. The highest densities were obtained in the northern region by applying the strip transect counts; while estimations using the fecal group count method were more variable and were the most used method in temperate and tropical dry forest regions. The states with the highest densities were Coahuila, Tamaulipas, Jalisco, Morelos, Michoacán, and Durango. The highest densities were estimated in the xerophilous scrublands of the northeast, intermediate for temperate, tropical dry, and sub-deciduous forests; and the lowest in the tropical wet forest. The highest densities were reported for the Tamaulipeca province followed by the Altiplano Chihuahuense, Sierra Madre Occidental, Costa Pacífica, and Depresión del Balsas. The results of this analysis could guide management strategies for the conservation and sustainable use of this species in extensive UMAs and ANPs, and also to test ecological hypotheses. However, applying more rigorous field design and statistical analysis is important to obtain confident estimates of population density and other demographic parameters to monitor population dynamics.

El venado cola blanca *Odocoileus virginianus* es una de las especies silvestres de mayor distribución geográfica e importancia económica en México. Este artículo presenta un análisis biogeográfico de las tendencias de densidad de población de venados por estado federativo, tipos de vegetación, provincias biogeográficas y método de campo, basado en 200 estudios. Las estimaciones de la densidad son muy variables y potencialmente sesgadas debido a los diferentes diseños de campo y análisis estadísticos. La densidad promedio nacional se estimó en 6.9 venados/km^2 (DE = 5.1); el 75.5 % de las estimaciones fueron inferiores a 10 venados/km^2, y sólo el 5.5 % fueron superiores a 15 venados/km^2. Las densidades más altas se obtuvieron en la región norte aplicando los conteos en transectos en franja; mientras que las estimaciones fueron más variable con los métodos de conteo de grupos fecales el cual es el más empleado en regiones de bosques templados y tropicales secos. Los estados con mayor densidad fueron Coahuila, Tamaulipas, Jalisco, Morelos, Michoacán y Durango. Las mayores densidades se estimaron en los matorrales xerófilos del noreste, intermedias para bosques templados, tropicales secos y subcaducifolios; y las más bajas en bosques tropicales húmedos. Las mayores densidades se reportaron para la provincia Tamaulipeca seguida del Altiplano Chihuahuense, Sierra Madre Occidental, Costa Pacífica y Depresión del Balsas. Los resultados de este estudio podrían orientar estrategias de manejo para la conservación y uso sustentable de esta especie en UMAs extensivas y Áreas Naturales Protegidas, y también para la inferencia de hipótesis ecológicas. Sin embargo, es importante aplicar un diseño de campo y un análisis estadístico más rigurosos para obtener estimaciones confiables de la densidad de población y otros parámetros demográficos para monitorear la dinámica de las poblaciones.

Keywords: Biogeographic provinces; conservation; federative states; limitations; management; sampling method; vegetation types.

Introduction

The white-tailed deer *Odocoileus virginianus* is a highly ecological and economically-valued species (Ortega-S. *et al.* 2011), and is the most studied deer species in México (Mandujano 2004). Published books on this deer species have been generated in the northeast region dominated by semi-arid scrubs lands (Villarreal-González 1999; Ramírez-Lozano 2004; Fulbright and Ortega-S. 2006), in temperate forests in the Sierra Madre Occidental in Durango (Folliot and Gallina 1981; Galindo-Leal and Weber 1997), the region of central México in the Mixteca Poblana (Villarreal-Espino 2006), and in Oaxaca (Mandujano 2016). Monographs have also been published on the natural history of this species in México and Latin America (Méndez 1984; Gallina *et al.* 2010; Ortega-S. *et al.* 2011; Mandujano *et al.* 2014; Gallina *et al.* 2019). In particular, a significant amount of information has been generated in protected natural areas (ANPs in Spanish), mainly Biosphere Reserves (Gallina *et al.* 2007).

Also, the white-tailed deer is the most important game species in México in the Wildlife Conservation, Management, and Sustainable Utilization Units (UMAs in Spanish; Villarreal-González 1999; Villarreal-Espino 2006). As a consequence, more studies have been generated because the management plans need evaluations of the populations and habitat to define the number of deer to be harvested each year in the UMAs (Gallina 2012), population dynamics, and the minimum viable population for conservation (Mandujano and González-Zamora 2009).

The estimation of white-tailed deer population density is a relatively common practice in México as the result of the ecological research interest in understanding factors affecting the abundance and population dynamics, principally in natural reserves, and also as a result of the need for sustainable management of this species in extensive UMAs. Population density is a key parameter in ecology and conservation, and estimates of density are required for a wide variety of applications in fundamental and applied ecology (Santini *et al.* 2022). Population density is the result of variation in survival, mortality, natality rates, sex proportion, age distribution, and other demographic parameters, and its relationships with habitat and human factors (Santini *et al.* 2022). Thus, density could vary through the years in the same site, and among populations inhabiting different regions, and usually, the density is expressed as the number of individuals per habitat area (DeYoung 2011). Based on the density estimations, inferences can be made about factors such as survival and birth rates that affect density and population dynamics, and whether the populations are within the carrying capacity of the habitat, a fundamental aspect of defining sustainable harvest rates (Mandujano 2007). Therefore, similar to other wildlife species, this parameter is central to the management and conservation of this species (Caughley and Sinclair 1994).

Therefore, a lot of biological and management information has been generated about the white-tailed deer in México, which deserves to be synthesized to describe ecological patterns and the mechanisms involved. The principal objective of this study was to analyze the available information on the population density of white-tailed deer in México. In particular, to know the population density depending on the types of vegetation, biogeographic provinces, federal states, and sampling methods. Additionally, some considerations concerning field method, statistical analysis, and density interpretation, are provided. This analysis could be important to the management and conservation of the white-tailed deer in ANPs and extensive UMAs.

Materials and methods

Sources of information. An intensive search was carried out on the studies reporting data on the population density (usually as ind/km^2) of white-tailed deer in México. The sources considered were published papers in journals, book chapters, theses, divulgation articles, symposiums, and some technical reports from the UMAs, from 1990 to 2016. The following information was recorded for each selected reference: density, federative state, locality, type of vegetation, biogeographic province, site (ANPs, extensive UMAs, communities, ejidos, private ranches), sampling method, field sampling design, total number of counts, and statistical analyses. Considering that the density information was estimated by applying four field methods (direct counts in transects, indirect counts of pellet groups and tracks, and photo trapping), we applied criteria to select the different reports. The criteria are detailed below.

In the case of studies where the fecal or pellet groups counting method was used, the defecation rate used to transform this count into density was noted. The use of different rates is crucial to convert or calibrate the fecal group count index to the number of deer per km^2 (Mandujano 2014a). The lower the defecation rate value, the higher the density estimate, and vice versa. Consequently, for the same number of fecal groups counted in the sampling, the density calculation varies depending on the rate applied. To solve this problem, it would be necessary to: apply the same rate for all studies so that it was a constant, an aspect that could not be done given that the majority of authors do not report their field data, but only the final estimate of the density obtained; or assume a range of defecation rate for the species, which could fluctuate between 9 to 35 fecal groups/deer/day, according to numerous studies in different types of habitats (Mandujano 2014b). We assume that all population density estimates obtained with this method are biased and that the magnitude and direction of this bias are unknown. We also assume that the estimates are within the expected range, given the variation in the species' expected defecation rate. These assumptions allow the use of current estimates in the studies collected.

For the direct counting method, it was defined whether the count was used in strip transects or line transects. In the latter case, the program version used for the analysis was noted, and the algorithm used. This is important because, depending on the algorithm used, a different density calculation will be obtained (Mandujano and Gallina 1995). For the transect line usually used the program DISTANCE considered the dictation probability. While in the strip transect, it is assumed that 100 % of the deer were detected within the previously defined transect width. In the latter case, this restriction may be easily violated in fieldwork since the greater the perpendicular distance, the lower the probability of detection. Consequently, also for these methods, there are biased estimates of local population density.

The track and camera trap methods were the least used. Both convert the index of tracks or photos to the number of deer per area using different algorithms. The tracks count method is based on a series of assumptions about deer movements, which are not necessarily met in all cases (Mandujano 2005). Photo-trapping is based on the assumption of correctly identifying all photographed individuals, an aspect that is not easy given the lack of natural marks of the species (Soria-Díaz and Monroy-Vilchis 2015). Consequently, the estimates obtained with these methods are also biased.

Therefore, based on criteria that considered a lack of specific details in the field design, very few sampling units and observations, insufficient details of the numerical data analysis, the software used, and/or a combination of these factors, from the initial base of 250 references, we selected 200 references for the statistical analysis (Mandujano *et al.* 2016a). The database was incorporated into the National Biodiversity Information System (SNIB) available on the CONABIO website http://www.conabio.gob.mx/institucion/cgi-bin/datos2.cgi?Letras=JM&Numero=16.

Analysis of geographic and statistical data. Biogeographic maps of Floristic Divisions, Biogeographic Provinces, and State Political Divisions in México were taken from Rzedowski and Reina-Trujillo (1990), Arriaga *et al.* (1997), Palacio et al. (2000), and Morrone (2005). All maps were obtained from the databases of INEGI (National Institute of Statistics and Geography, http://mapserver.inegi.org.mx), and CONABIO (National Commission for the Understanding and Use of Biodiversity, http://www.conabio.gob.mx/informacion/gis/). Considering that population density values varied from 0 to positive continuous values, and the density estimates distribution is relatively normal (slightly right skewed, see Figure 2), we used parametric tests. As alternative statistical analyses first standardize the density (mean = 0, SD = 1), or use generalized linear models considering the beta distribution. However, in this study we tested significant differences among categories for each analyzed factor (field method, federative state, vegetation type, and biogeographic province), using a parametric approach. The categories with lower density estimations ($n < 3$ studies) were deleted, and then a one-way ANOVA was applied for each factor. The posterior Honest Significant Difference (HSD) test was applied to identify significant differences among categories for each variable. All analyses were performed in the R package version 4.2.2 (R Development Core Team 2022).

Results

The geographic distribution of the 200 reported white-tailed deer population densities, was not homogeneous in México (Figure 1). The major number of reports were biased to some regions and states, principal in the northeastern, Sierra Madre Occidental, Pacific Coast in Jalisco and Michoacán, in the central region in Puebla and Oaxaca. The statistical distribution of the 200 reports is positively skewed (Figure 2), and the national average density of white-tailed deer was estimated at 6.9 deer/km^2 (median = 6.0, SD = 5.1, range = 0.1 to 25.0). Mainly, 75.5 % of the estimates were

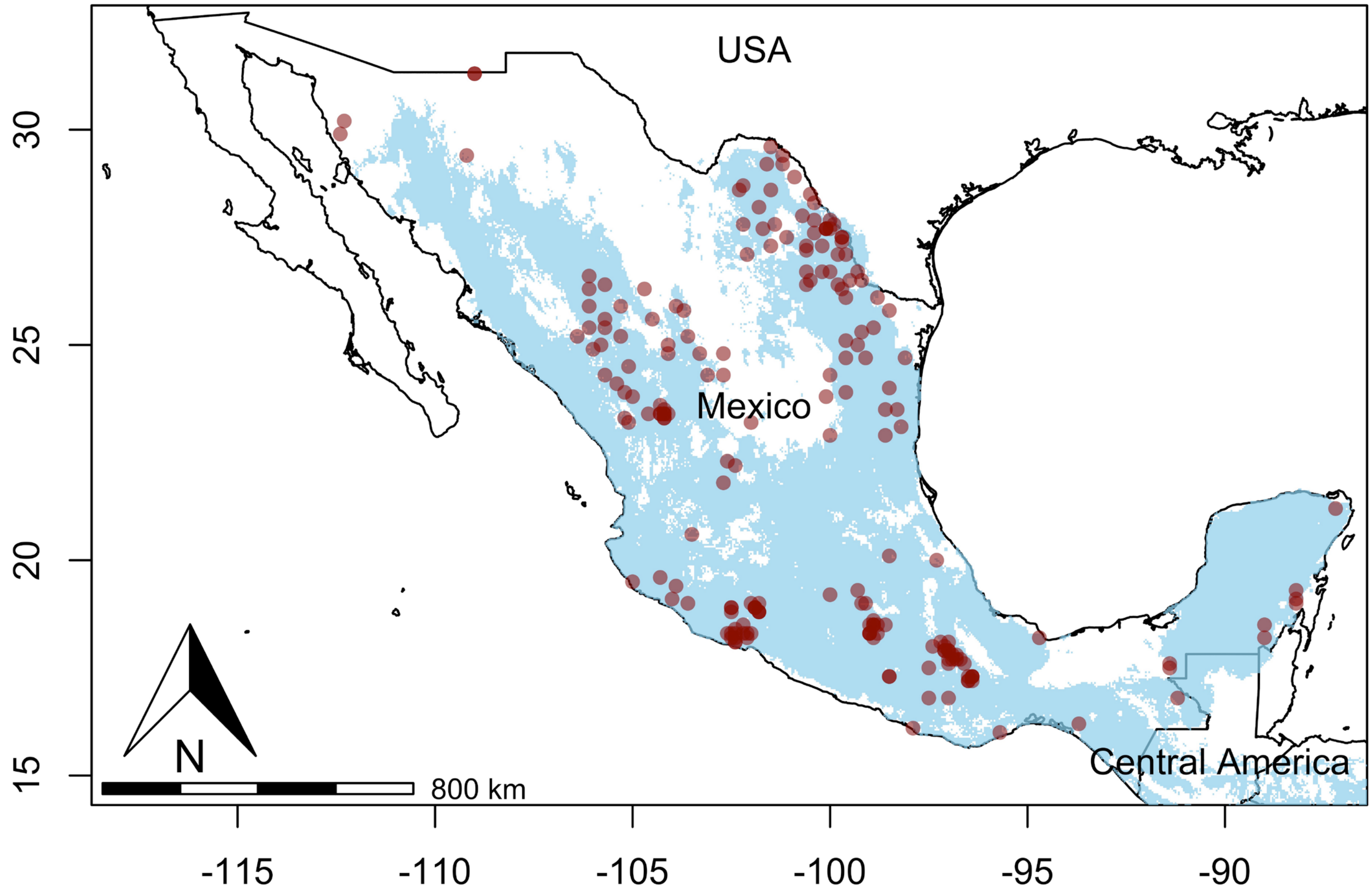

Figure 1. Distribution of locations with density estimates (red circles) in México. Potential geographical distribution of white-tailed deer in México (blue) according to ecological niche modeling (Mandujano *et al.* 2016a).

less than 10 deer/km^2, and only 5.5 % were greater than 15 deer/km^2. From 200 reports, 48.1 %, 38.5 %, and 13.5 % were in ANPs, other (communities, ejidos, private ranches), and extensive UMAs, respectively.

Four field methods were used as the principals to estimate deer density: fecal group counts, direct counts in strip or line transects, track counts, and camera trapping. The strip transects are the standard method in the northern of the country, while the count of fecal groups is used in areas of denser vegetation such as temperate forests and tropical forests. The highest densities were estimated with the direct counts of deer and were statistically significant in comparison to the estimates obtained with the fecal group and track count methods (Figure 3; F = 11.01, *df* = 2, 185, *P* = 0.0001). Even the actual intensive use surprisingly few population density estimations exist using the camera trap method.

The federal states with the highest number of estimates were Coahuila, Nuevo León, Durango, Oaxaca, Michoacán, Tamaulipas, and Puebla. The highest densities were in Coahuila, Tamaulipas, Jalisco, and Morelos; while the lowest was in the States of México, Veracruz, Tabasco, and Chiapas (Figure 4; F = 7.45, *df* = 9, 170, *P* = 0.0001).

The main vegetation types where densities were estimated were xerophilous scrublands, temperate forests, and tropical dry forests. The highest densities were found in the scrublands of the northeast, intermediate for temperate, tropical dry, and sub-deciduous forests, and the lowest in the humid forest and grasslands (Figure 5; F = 7.39, *df* = 3, 188, *P* = 0.0001).

The biogeographic provinces with the most significant number of data were the Tamaulipeca, the Sierra Madre Occidental, and the Depresión del Balsas. The highest densities were reported for the Tamaulipeca province followed by the Chihuahua Altiplano; the most variable for the Sierra Madre Occidental; while the lowest were in the Zacatecano Altiplano, Eje Neovolcánico, Oaxaca, Petén, Sierra Madre Oriental and Soconusco (Figure 6; F = 5.10, *df* = 13, 186, *P* = 0.0001).

Discussion

Biogeographic density trends. The data suggest that the highest densities are found in the northeastern region specifically in the vegetation type dominated by xerophilous scrubs in the Tamaulipeca biogeographic province in the states of Coahuila, Nuevo León, and Tamaulipas. This region is known as one of the principals in México where the white-tailed deer is used in extensive UMAs, principally because the subspecies *O. v .texanus* and *O. v. miquihuanensis* have greater antlers as the principal objective of the sport hunters (Villarreal-González 1999). In this region, deer populations and habitats are managed through different strategies such as control of illegal hunters, animal translocation, repopulation, artificial water supplies, food production in parcels, and salt resources, among the mains. Thus, it is possible that in many UMAs the population densities of this deer have increased as levels highest than carry-

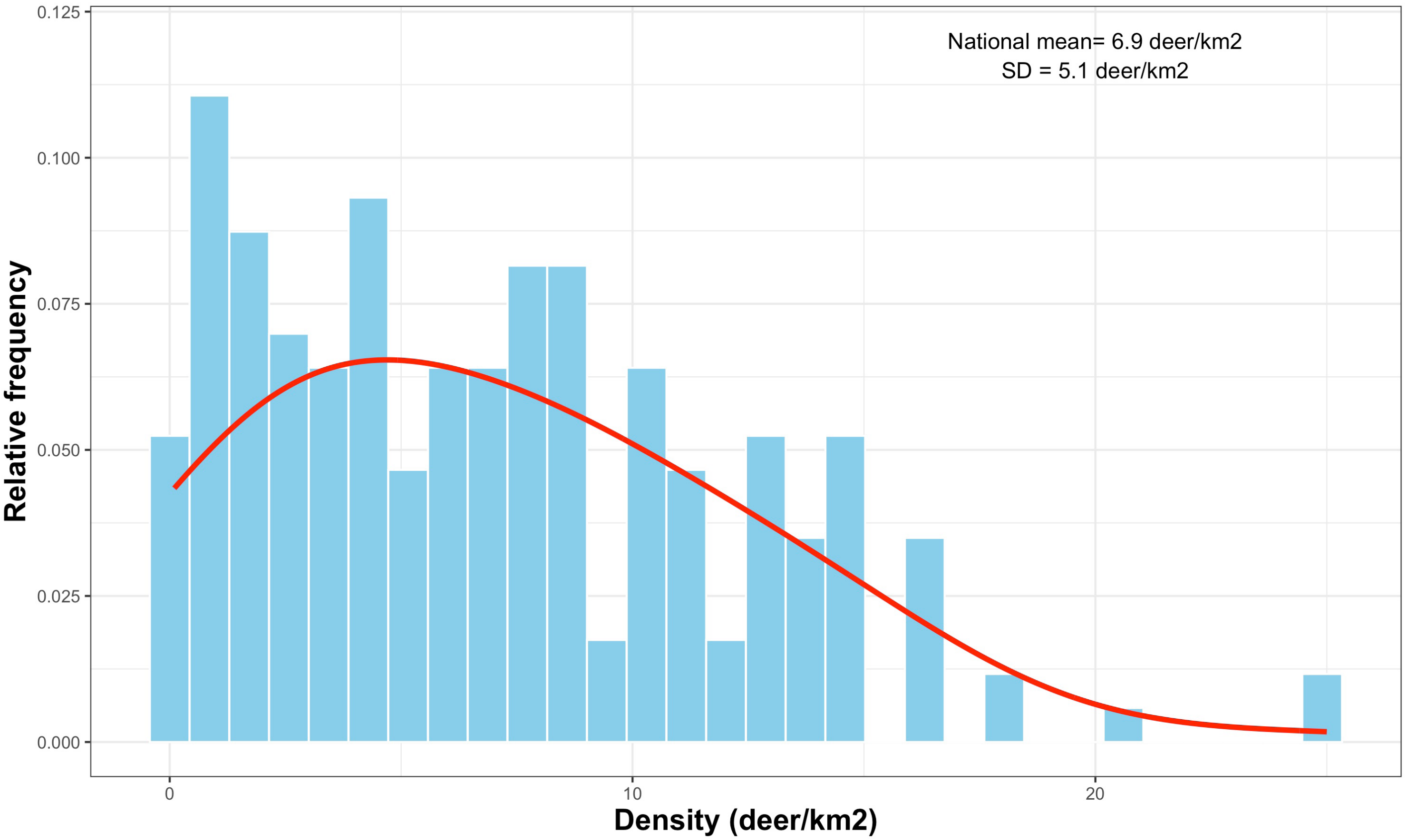

Figure 2. Statistical distribution of the population density estimates (*n* = 200) of the white-tailed deer in México. The red line represents the best fit model to field data.

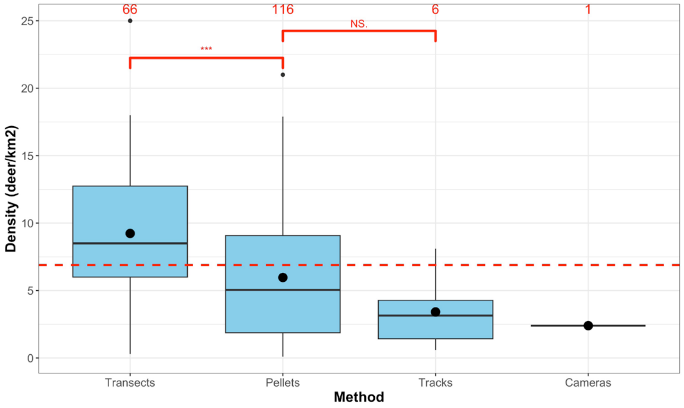

Figure 3. Estimates of the white-tailed deer density by direct observation in transects; fecal groups in plots; tracks on trails and transects; and photos in camera traps. The dotted horizontal red line represents the average density value estimated for the entire country. Symbols: mean (black circle), median (horizontal line), 25 % and 75 % percentile (box), range (vertical line), extreme values (small black dots), and sample size (red color numbers). Continuous horizontal red line grouping categories represent the posterior HSD test with a significant probability $P < 0.01$ (*), $P < 0.0001$ (***), and no differences (NS). Categories with $n < 3$ references, were not considered for statistical inferences.

ing capacity (K) or overpopulation (Martínez *et al.* 1997). In this region is common to apply the field method of counting deer in strip transects. Both strip-transect and distance-transect count methods are used in open habitats around the world. The principal advantage is that direct counts of animals are used for density estimations, and there is no need to correct factors for example the indirect counts of tracks and pellet groups.

The estimations of white-tailed deer densities in the template forest are variable in the different regions. For example, at La Michilía in Durango (Galindo-Leal *et al.* 1993; Gallina 1994), Sierra Gorda in Querétaro (Arroyo-Quiroz *et al.* 2017), La Primavera in Jalisco (Valenzuela 1994), Hidalgo (Sánchez-Rojas *et al.* 2009), Corredor Biológico Chichinautzin in Morelos (Flores-Armillas *et al.* 2011), and Sierra de Juarez in Oaxaca (Briones and García-Cruz 2005; Ortíz-Martínez *et al.* 2005), the application of indirect counts of pellet groups were the common method.

White-tailed deer inhabit the Pacific and Central regions from the scrubland of Sonora (Coronel-Arellano *et al.* 2008; Lara-Díaz *et al.* 2011) to the tropical dry forest of Nayarit, Chamela-Cuixmala in Jalisco (Mandujano and Gallina 1995), Zicuirán-Infiernillo in the Balsas region of Michoacán (Yañez-Arenas *et al.* 2012b; Mandujano *et al.* 2013), La Montañana in Guerrero (Bustamante-González 2018), the coast of Oaxaca (Buenrostro-Silva and García-Grajales 2016), Sierra Huautla in Morelos (Malacara-Velázquez *et al.* 2023), Nanchichitla in Estado de México (Soria-Díaz and Monroy-Vilchis 2015), in the region of the Mixteca in Puebla (Villarreal-Espino 2002), and in Tehuacán-Cuicatlán in the states of Puebla and Oaxaca (Mandujano *et al.* 2016b, 2019). In these tropical regions, the estimations have been obtained principally through indirect methods such as counts of tracks in dirt roads (Mandujano 2005), and the pellet-groups (Camargo and Mandujano 2011) counts and

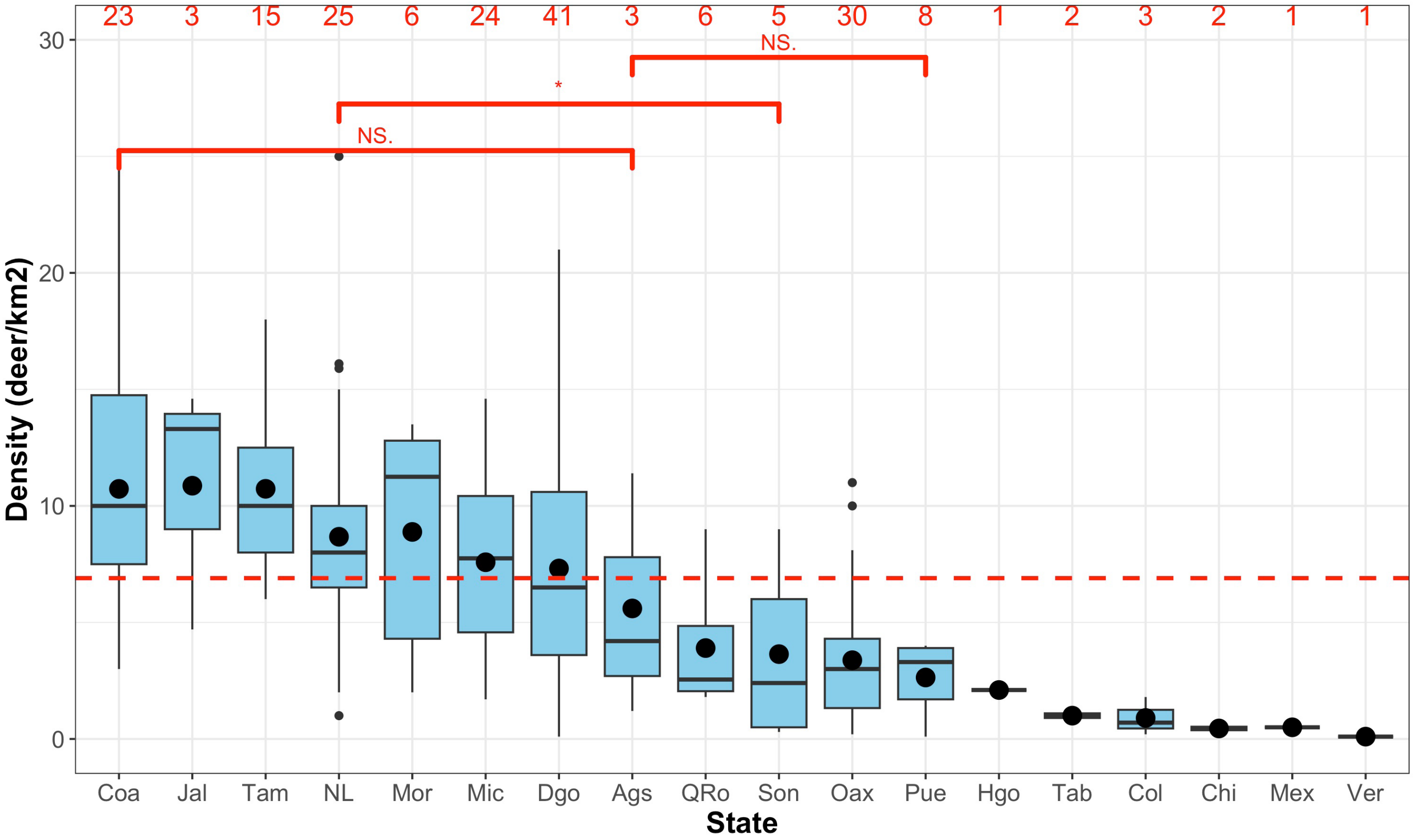

Figure 4. Estimates of the white-tailed deer density obtained in the federal states. Abbreviations: Coahuila (Coa), Jalisco (Jal), Tamaulipas (Tam), Nuevo León (NL), Morelos (Mor), Michoacán (Mic), Durango (Dgo), Aguascalientes (Ags), Quintana Roo (QRo), Sonora (Son), Oaxaca (Oax), Puebla (Pue), Hidalgo (Hgo), Tabasco (Tab), Colima (Col), Chiapas (Chi), Mexico State (Mex), and Veracruz (Ver).

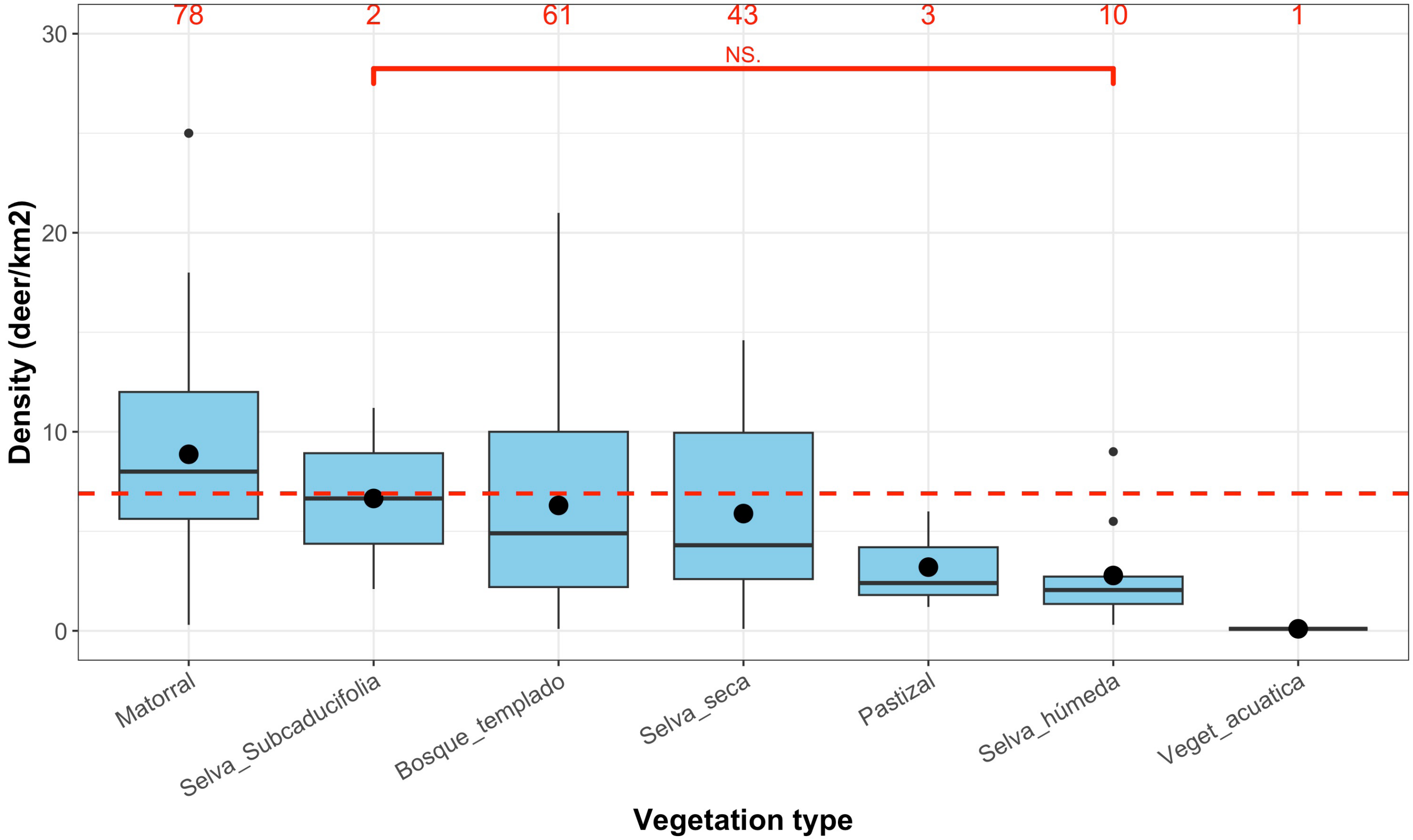

Figure 5. Estimates of the white-tailed deer density obtained in the main types of vegetation. Scrubland ("Matorral"), tropical semi-deciduous forest ("Selva subcaducifolia"), temperate forest ("Bosque templado"), tropical dry forest ("Selva seca"), grassland ("Pastizal"), tropical rain forest ("Selva húmeda), and aquatic vegetation ("Vegetación acuática").

data suggest that this type of habitat has a higher potential for deer production (Mandujano 2007, 2010). Also, in these regions, the white-tailed deer is hunted principally as subsistence and also as a trophy in extensive UMAs (López-Téllez *et al.* 2016).

In comparison with other regions in México, the densities estimations of this species are scarce in the southeastern states of Oaxaca (Yáñez-Arenas *et al.* 2016; González-Pérez and Briones 2000), Tabasco (Contreras-Moreno *et al.* 2015), Chiapas (Chávez-Hernández *et al.* 2011), Campeche (Retana-Guiascón *et al.* 2015) and Yucatán (González-Marín *et al.* 2008). In particular, the utilization of relative index based on track counts along transects has been used in some sites such as Lacandon forest (Naranjo *et al.* 2004a, 2004b), and Calakmul (Reyna-Hurtado and Sánchez-Pinzón 2019). This scarce information contrasts with the enormous interest of this species in subsistence hunting (Montiel-Ortega *et al.* 1999; Segovía *et al.* 2003), and the traditional knowledge of this deer shows the deep relationship between the local people and their landscape (Mandujano and Rico-Gray 1991; Greenberg 1992; Retana-Guiascón and Lorenzo 2016).

The results suggest a mean density of 6.9 ind/km^2 of white-tailed deer in México. Particularly, only 5.5 % of the reports were greater than 15 deer/km^2. In a previous study, Galindo-Leal (1993) reported that 51 % of the estimates analyzed were less than 10 deer/km^2; finding low variation between habitat types. Population density and biomass could vary depending on climatic factors such as the rain pattern and temperature (Mandujano and Naranjo 2010; Yáñez-Arenas *et al.* 2012a), ecological variables such as vegetation type, topographic features, and human factors such as habitat transformation, presence of livestock and illegal hunting (López-Téllez *et al.* 2007; Coronel-Arellano *et al.* 2008; Ramos-Robles *et al.* 2013). The densities of this species are between 5 and 17 deer/km^2 in the United States (Adams and Hamilton 2011). The differences between countries could be the result of different habitat-carrying capacity (K) and management politics which affect the local population dynamics (DeYoung 2011). Therefore, the mean population density in México suggests a possible lower K in comparison to northern regions of the geographical distribution of this species or possible overexploitation that maintains lower densities.

Importance of Natural Protected Areas and extensive UMAs. An important aspect is that many of the population density estimations were generated in studies realized in Biosphere Reserves. For example, La Michilía (Ezcurra and Gallina 1981; Galindo-Leal *et al.* 1993), Sierra de Huautla (Malacara-Velázquez *et al.* 2023), Sierra Gorda (Arroyo-Quiroz *et al.* 2017), Chamela-Cuixmala (Mandujano and Gallina 1995; Mandujano *et al.* 2002), Zicuirán-Infiernillo (Mandujano *et al.* 2013; Yáñez-Arenas *et al.* 2012b), Tehuacán-Cuicatlán (Mandujano *et al.* 2016b, 2019), Montes Azules (Naranjo *et al.* 2004a), Calakmul (Escamilla *et al.* 2000; Reyna-Hurtado and Sanchez-Pinzón 2019), Pantanos de Central (Contreras-Moreno *et al.* 2015), and Los Petenes (Oliva *et al.* 2014). These studies show the importance of the ANPs as sites to study this deer species (Gallina *et al.* 2007).

The analysis of advantages and limitations of the extensive UMA has been discussed extensively (Sisk *et al.* 2007; Gallina *et al.* 2008; Villarreal-Espino *et al.* 2008; Avila-Foucat and Pérez-Campusano 2015; Ortega-Argueta *et al.* 2016; Pineda-Vazquez *et al.* 2019; Romero-de-Diego *et al.* 2020; Gallina *et al.* 2022; Leal-Elizondo *et al.* 2023). In particular, given the ecological, social, and cultural conditions of the central, southeast, and Yucatán peninsula regions of México, the operating criteria of the UMAs have particular considerations (González-Marín *et al.* 2003; Weber *et al.* 2006; García-Marmolejo *et al.* 2008; Álvarez-Peredo *et al.* 2018), and focused on the management of white-tailed deer (López-Tellez *et al.* 2016; Malacara-Velázquez *et al.* 2023). Thus, UMAs emerge as an important model for managing this deer and other wildlife species but they also have important limitations.

An important question is: Is the density the best or adequate parameter to manage deer populations in the extensive UMAs? To answer this crucial question is necessary to define what is population density (D) and its differences but the relational parameter population abundance (N). The key factor to the difference between both D and N is the surface (S) of the habitat for the managed population. N is the total number of individuals in the population, and D is the average number of individuals in the S usually expressed as deer/km^2. The important point is that high density does not imply high abundance, this last would depend on how the population is delimited in the area (S). As a simple first example, if the density is estimated at 10 deer/km^2 (very good density), but the UMA surface is small (*e. g.* 200 ha), the expected abundance is only 20 deer in that population. As a second example, if D = 3 deer/km^2 and S = 10,000 (or 100 km^2), then the expected N = 300 deer. This calculation is based on the supposition of

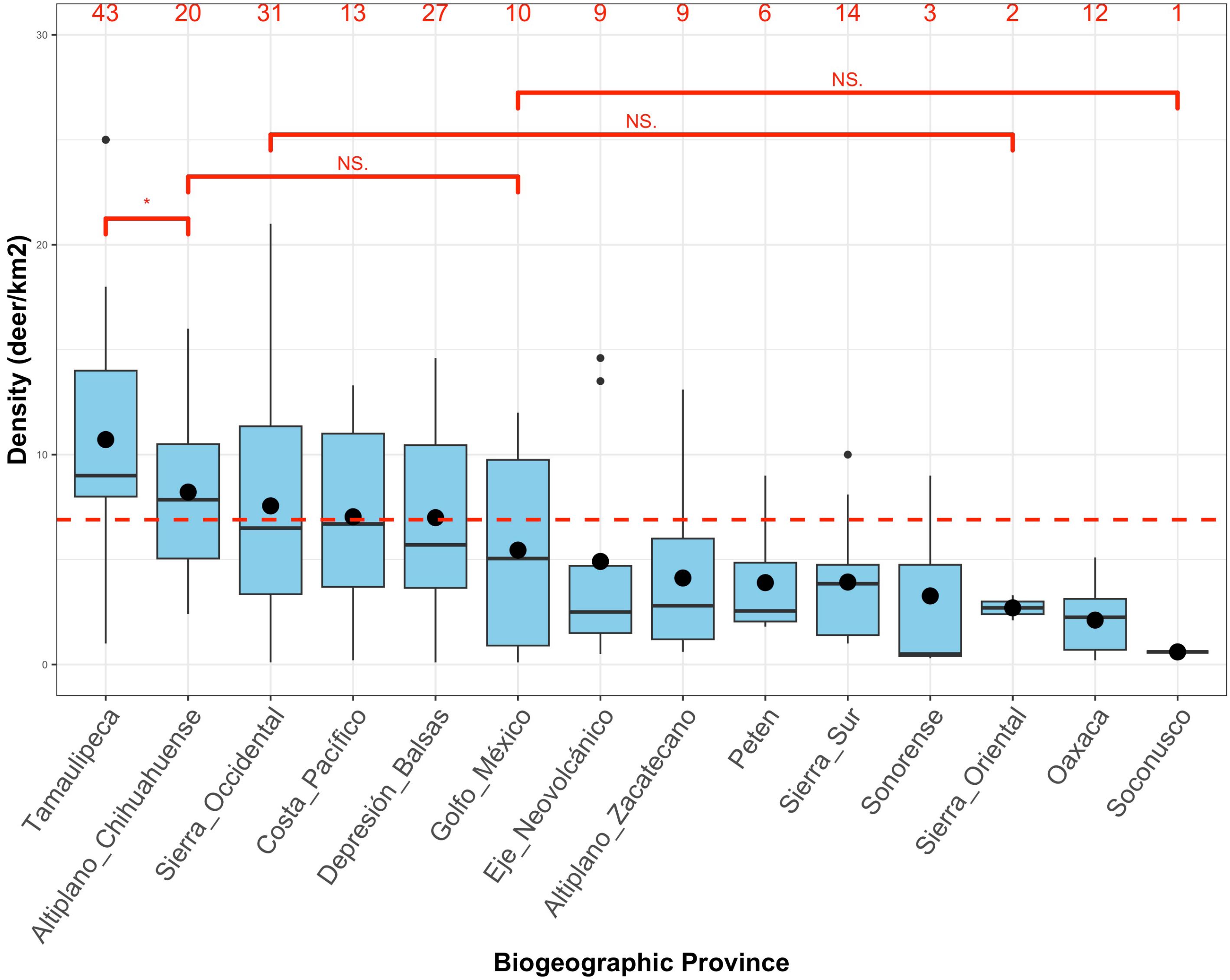

Figure 6. Estimates of the white-tailed deer density obtained in the biogeographic provinces.

homogeneous density distribution in the total area, which is not the natural condition in almost all locations. Therefore, the definition of hunting rates in the UMAs based on population density (usually biased due to the previously commented sampling or an observational error), is a matter that demerits further deep discussion by the authorities that administer the wildlife in México (Ortega-S. *et al.* 2019).

Limitations and suggestions. An important factor that limited obtaining conclusive density trends of this deer species in the different vegetation types, biogeographic provinces, and federative states, was the great variation in the methods and sample designs, the sample size obtained, and the numerical analysis performed. A particular statistical parameter is the variation around the mean, specifically the variance or standard deviation (SD) of the density. However, in many studies, this important statistical parameter is not reported. Thus, it is difficult to know the confidence of density estimations. The estimation of the population density (or any other ecological parameter) is the consequence of the ecological process and the observation or methodological process (Kéry and Royle 2016). These are inherent to counts but the magnitude of each is fundamental to defining the confidence of any estimation (Ahrestani *et al.* 2013). Therefore, understanding the ecological and methodological process is essential because it reflects the variation in climatic year conditions, seasonal habitat features, human intervention, and how this affects the demographic parameters of the deer, and also the detection probability of the animals (Link and Nichols 1994). A possible solution to reduce observation error includes having people with enough experience during the fieldwork, an adequate sample design, applying adequate statistical analysis, and reporting the variation around the density estimations, among others. Some standardized data collection protocols to monitor the white-tailed deer population in different habitats (Rojo-Curiel *et al.* 2007; Gallina *et al. 2014*), and to analyze procedures such as the pellet-groups counts (Mandujano 2014a; 2014b) using different field methods (Camargo-Sanabria and Mandujano 2011), are available. In particular, Villarreal-González (1999) provides a guide to using the strip transect method in the northeastern region.

Another consideration is the actual increase in the use of the camera trap (CT) method as a technique to obtain data on medium and large-size mammal species (Mandujano 2019; Mendoza *et al.* 2022). It is very frequent to calculate the relative abundance index with this technique. However, this index does not estimate the number of deer (or any other species) in a specific location, limiting its usefulness for some ecological and management objectives (Kéry and Royle 2016). Alternatives to estimate the population density of white-tailed deer using CT could be 1) techniques that allow identifying natural or artificial marked individuals and using spatial-explicit capture-recapture models (SCR). 2) the distance method. 3) the random encounter model (REM; Lucas *et al.* 2015; Royle *et al.* 2015; Kéry and Royle 2016). Of the analyzed data in this study, only two studies used CT to estimate white-tailed deer density using classic capture-recapture models (Lara-Díaz *et al.* 2011; Soria-Díaz and Monroy-Vilchis 2015) but in a non-hierarchical framework. Therefore, HMs (Hierarchical Models) open the possibility of estimating deer density for both ecological and management propose (Jimenez *et al.* 2013; Royle *et al.* 2015).

Traditionally, estimation of density usually is obtained at the population level delimited by a specific area (usually called "study area"). However, it is possible to estimate the distribution of the potential abundance in the form of geographic maps using other analytical alternatives. For example, it is known that precipitation could be used to predict ungulate biomass across continental regions (Coe *et al.* 1976; Olff *et al.* 2002; Mandujano and Naranjo 2010). This approach has been applied to a regional level in a Tehuacán-Cuicatlán Biosphere Reserve (Mortero-Montiel 2016). Another approach is through ecological niche modeling, specifically the distance to the centroid of the niche. This has been applied to predict the potential density of this deer at the level of biosphere reserves (Yáñez-Arenas *et al.* 2012a), at the state level in Oaxaca (Yáñez-Arenas *et al.* 2016), and at biogeographic provinces (Mandujano *et al.* 2016a). This approach has been proposed as potentially useful for deer management in UMAs of Campeche (Escalante and Martínez-Meyer 2013). Finally, again considering the actual increase of camera traps to sample this deer and other mammal species, the application of hierarchical models as occupancy, abundance through N-mixture, and Royle-Nichols models, emerge as opportunities for spatial-temporal monitoring of the white-tailed deer (Keever *et al.* 2017; Mandujano *et al.* 2023).

The revision and analysis of studies and reports on the population density of white-tailed deer in this study, bring a general vision of the possible trends of the density in the different federative states, vegetation types, and biogeographic provinces. However, important limitations exist to confidently conclude this trend because of the severe limitations in field designs and statistical data analysis. However, it seems that in México the white-tailed deer population density is generally relatively low (on average 6 to 7 deer/km^2) even in naturally perturbed sites, in comparison to those estimated in the northern region (United States and Canada) of the geographical distribution of this species. An important aspect is that much of the information is the results of specific studies in ANPs, principally Biosphere Reserves, which could be considered ideal sites to study deer populations in relatively better natural conditions. In contrast, the estimation of deer density is very important for the management of this species in extensive UMAs and needs the application of a standardized sampling field and numerical analysis protocols to obtain confident data.

Acknowledgments

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Use of artificial water troughs by deer in the Maya forest, México

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Artificial water troughs have been implemented in the Calakmul region as a measure that contributes to the maintenance of wildlife populations during the drought season. The aim of this study was to estimate the use of artificial water troughs by three species of deer (*Odocoileus virginianus, M. pandora*, and *Mazama temama*) in the Maya Forest of Campeche in southeastern México. The study was carried out in the Calakmul Biosphere Reserve (CBR, in Spanish) in southeastern México. Seventy artificial water troughs were installed, most of them within the core areas of the CBR. Between December 2018 and August 2021, eight digital traps were placed in eight artificial water troughs to monitor the presence of deer. The Photographic Visit Index (PVI) was calculated, and the visit rates of each species were compared by sampling year for each monitoring station. Deer activity patterns were evaluated using circular statistics to assess whether there were differences between visiting times. Watson-Williams tests were performed during the different sampling months. The density of records was analyzed to identify the degree of overlap in the deer activity patterns. With a sampling effort of 4,672 nights/camera, we captured 477 records of *O. virginianus*, 229 of *M. pandora*, and three of *M. temama* using artificial water troughs in the CBR. Due to the scarce records of *M. temama* in water troughs, comparative analyses were performed only with the other two deer species. According to the PVI, in the case of *O. virginianus*, highly significant differences were found between the three sampling years ($H = 12.575$, $df = 2$, $P < 0.001$); similarly, *M. pandora* showed highly significant differences between sampling years ($H = 9.29$, $df = 2$, $P = 0.001$). Regarding activity patterns, *O. virginianus* is mainly diurnal, with peaks of activity in the early hours of the day (8:00 h to 9:00 h). *M. pandora* was also mainly diurnal, showing the highest peaks of activity in the early hours of the day and before dusk. *O. virginianus* and *M. pandora* regularly visit water troughs, and the presence of deer in water troughs responds to their need to drink water for thermoregulation. The activity pattern of deer was mainly diurnal; it is safer for both species to move during the day because predators were recorded constantly in the study area. The degree of overlap recorded between *O. virginianus* and *M. pandora* suggests that both species are active at the same times of the day.

Los bebederos artificiales se han implementados en la región de Calakmul como una medida que contribuye al mantenimiento de las poblaciones de fauna silvestre, durante la época de estiaje. El objetivo de este estudio fue estimar el uso que tres especies de venados (*Odocoileus virginianus, Mazama pandora y Mazama temama*) hacen del agua en bebederos artificiales en la Selva Maya de Campeche en el sureste de México. El estudio se realizó en la Reserva de la Biosfera Calakmul (RBC), en el sureste de México. Se instalaron 70 bebederos artificiales, la mayoría de los cuales se ubican dentro de las zonas núcleo de la RBC. Entre los meses de diciembre de 2018 hasta agosto del 2021, se colocaron ocho cámaras trampas digitales en ocho bebederos artificiales, con el objetivo de verificar la presencia de venados. Se obtuvo el Índice Fotográfico de Visita (IFV), se compararon las tasas de visita de las especies en cada estación de monitoreo, por año de muestreo. Se evaluaron los patrones de actividad de los venados mediante estadística circular para identificar si existían diferencias entre los horarios de visitas. Durante los diferentes meses de muestreo se realizaron pruebas Watson-Williams. Se analizó la densidad de registros para identificar el grado de traslape en los patrones de actividad los venados. Con un esfuerzo de muestreo de 4,672 noches/cámara se obtuvieron 477 registros independientes de *O. virginianus*, 229 de *M. pandora* y tres *M. temama* que utilizan los bebederos artificiales en la CBR. Debido a los escasos registros de *M. temama* en bebederos los análisis comparativos se realizaron con las otras dos especies de venados. De acuerdo con el IFV, para *O. virginianus*, se observaron diferencias altamente significativas al comparar entre los tres años de muestreo ($H=12.575$, $gl=2$, $P<0.001$), de igual forma *M. pandora* mostró diferencias altamente significativas al comparar los registros independientes entre años de muestreo ($H = 9.29$, $gl = 2$, $P = 0.001$). Con respecto a los patrones de actividad. Se encontró que *O. virginianus* es principalmente diurna, con picos de actividad en las primeras horas del día (8:00 a 9:00 h). *M. pandora*, fue principalmente diurna, obteniéndose los mayores picos de actividad en las primeras horas del día y antes del anochecer. Los bebederos son utilizados constantemente por *O. virginianus y M. pandora*. La presencia de venados en los bebederos responde a necesidad de termorregulación, para satisfacer sus necesidades hídricas. El patrón de actividad de los venados fue principalmente diurno, ya que es más seguro para ambas especies moverse durante el día, dado que en el área de estudio se registran de forma constante depredadores. El grado de traslape encontrado entre *O. virginianus* y *M. pandora* sugiere que ambas especies están activas en los mismos horarios.

Keywords: Calakmul; game species; mammals; photo-trapping; ungulate.

Introduction

For large herbivores living in dry environments, water can be a limiting resource that affects their distribution and abundance in periods when water requirements are not met through forage (Villarreal-Espino and Marín 2005; Nagy and Gruchacz 1994; Eliades *et al.* 2022). In these circumstances, many animals depend on access to surface freshwater sources, especially during certain critical periods of the year (Moro-Ríos *et al.* 2008). Water availability is one of the factors that influence the spatial distribution of wildlife to different degrees (Paredes *et al.* 2017); in some cases, it causes changes in the behavior of animals (Pacifici *et al.* 2015). In habitats where water is a limiting resource, animals usually gather around available water sources (Redfern *et al.* 2003).

Worldwide, the implementation of artificial water troughs for wildlife has been reported as a successful strategy to mitigate the consequences of water shortages in drought periods (Epaphras *et al.* 2008). The implementation of these artificial water sources includes various strategies; for example, in some cases, it is sought to concentrate the populations of wild fauna within selected areas, such as protected natural areas (PNA; Sutherland *et al.* 2018), thus preventing the animals from entering inhospitable habitats outside the PNA where they could die. On the other hand, water troughs have been conceived as a strategy that can contribute to the maintenance of wildlife populations in the short term by allowing access to water during the drought season (Mandujano-Rodríguez and Hernández 2019; Borges-Zapata *et al.* 2020).

To counteract the effects of prolonged drought in some areas of México, artificial water sources such as *jagueyes* and water troughs have been used (Villarreal 2006), which have contributed to habitat enrichment and the maintenance of wildlife populations (Bello *et al.* 2004). Particularly, the implementation of water troughs for wildlife in México has been reported to be a successful strategy to mitigate the consequences of water shortages in drought periods, mainly in places where water is a limiting resource (Mandujano-Rodríguez and Hernández 2019; Borges-Zapata *et al.* 2020).

In recent years, increasingly more extreme temperatures have been recorded in the Yucatán Peninsula, with prolonged events of high temperatures (Mardero *et al.* 2020), forcing wildlife to resort to water sources for thermoregulation, as observed in semiarid areas (Bello *et al.* 2004). This trend has affected Calakmul in southeastern México, a region that lacks large rivers or surface water bodies (García-Gil *et al.* 2002). This is important for ungulates inhabiting the Maya Forest (a forest area in the states of Campeche, Chiapas, and Quintana Roo, México), as habitat selection by these mammals has been reported to be strongly influenced by water availability (Pérez-Cortéz *et al.* 2012; Reyna-Hurtado *et al.* 2019). This close relationship could intensify in the coming years, as an imbalance in precipitation patterns has been recorded throughout the region (Mardero *et al.* 2020), reducing the availability of surface water (Reyna-Hurtado *et al.* 2022) and could lead to changes in population dynamics and the behavior of species in the Maya Forest region (Contreras-Moreno and Torres-Ventura 2018).

In the particular case of deer, the water-trough strategy has been used for decades in northern México in Wildlife Management Units (WMU), especially in semiarid and xeric scrub sites (Villarreal 2006; Mandujano-Rodríguez and Hernández 2019). Since 2018, water supply in artificial troughs has been conceived as a strategy that contributes to the maintenance of wildlife populations in the short term by facilitating access to water during the drought season (Borges-Zapata *et al.* 2020; Contreras-Moreno *et al.* 2019b; 2020; Delgado-Martínez *et al.* 2021; Pérez-Flores *et al.* 2021).

Identifying the functionality of artificial water troughs in improving the habitats of deer has become a research priority in México. In this regard, studies in the Maya Forest have recorded that the movements of deer and the size of their home range change during the drought season (Contreras-Moreno *et al.* 2019a, 2021a). Knowing the functionality of water availability for deer in artificial troughs would help improve conservation and management programs for the various deer species (Fulbrigth and Ortega-S. 2007). The objective of this study was to estimate the use of water supplied in artificial troughs by three deer species (*Odocoileus virginianus, Mazama pandora*, and *Mazama temama*) in the Maya Forest region of Campeche, in southeastern México.

Materials and methods

Study Area. The Calakmul Biosphere Reserve (CBR, in Spanish) is located in the Yucatan Peninsula, in southeast Campeche (Figure 1). It is part of the Great Calakmul Region, which includes the Maya Biosphere Reserve in Guatemala and the Rio Bravo Dos Milpas Conservation Area in Belize. It stretches across 728,908 ha (Reyna-Hurtado *et al.* 2022). The CBR has a warm and subhumid climate (Aw) with a mean annual temperature of 24.6 °C; the maximum height above sea level is 390 m on Mount Champerico, and the minimum altitude ranges from 100 to 150 m. The dominant vegetation types are medium semi-evergreen forests, medium subdeciduous forests, and low subdeciduous forests (Martínez and Galindo 2002; Martínez-Ku *et al.* 2008).

Installation of Water Troughs. As part of the efforts of CBR in collaboration with the Global Environmental Facility (GEF) Species at Risk project and the World Wildlife Fund (WWF México), artificial water troughs have been installed in the region since 2018 to counteract the effects of climate change in the region. Approximately 70 water troughs were installed, mainly within the CBR core areas. The artificial water troughs installed in the CBR are black plastic structures (Rotoplast®) with a capacity of 300 liters each. These troughs were distributed along the access road to the CBR, separated by a minimum distance of 2 km between them. At the beginning of the drought season, water was generally supplied twice monthly (every 15 days); however, as the drought season progressed and became dryer, water could be supplied once per week.

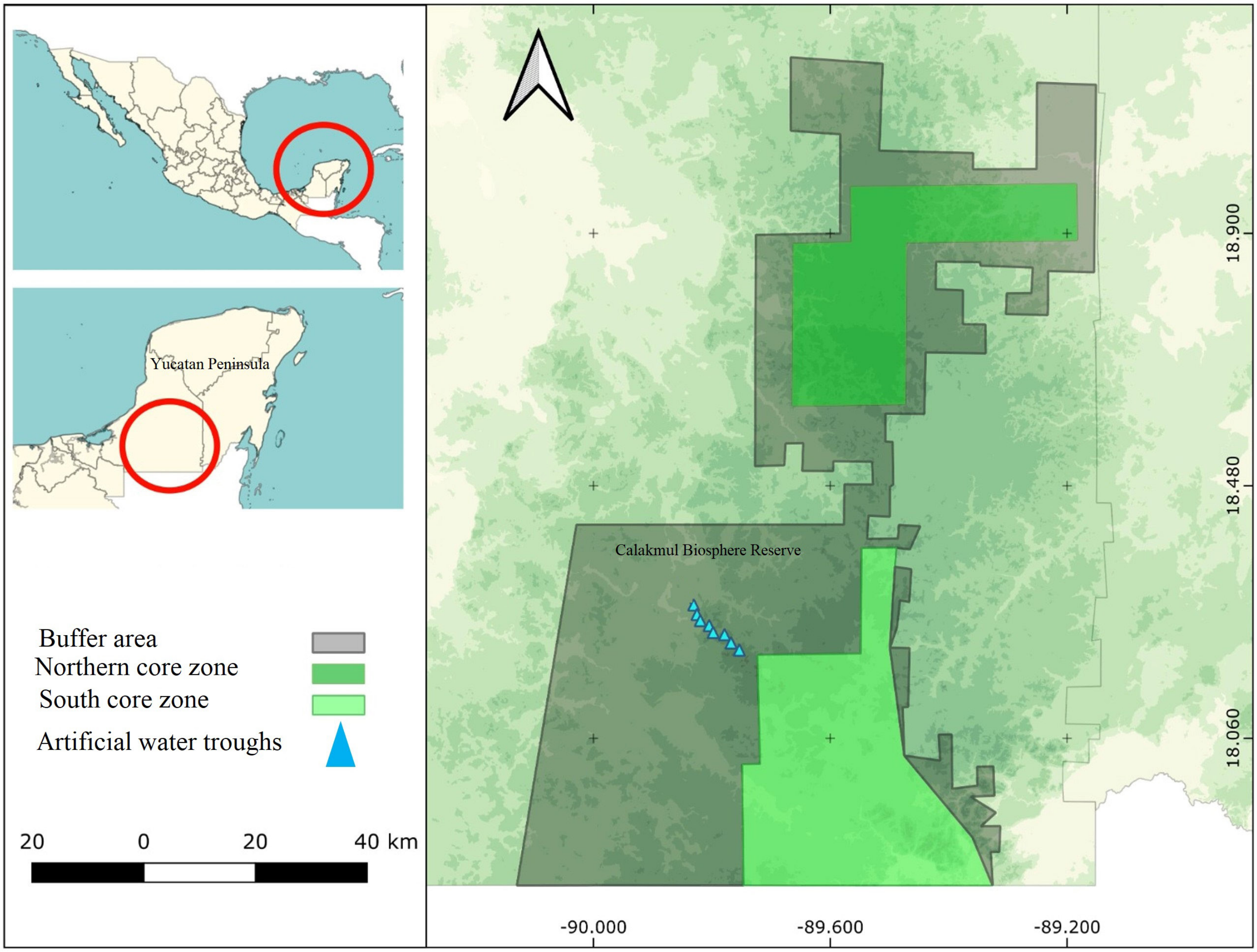

Figure 1. Map showing the location of water troughs monitored in the Calakmul Biosphere Reserve, México, where the study was carried out.

Data Recording with Camera Traps. Photographic recording of mammals with camera traps is a widely used and efficient method in southeastern México (Hidalgo-Mihart *et al.* 2017), particularly in the Calakmul region (Borges-Zapata *et al.* 2020; Contreras-Moreno *et al.* 2019b; 2020, 2021; Delgado-Martínez *et al.* 2021).

Between December 2018 and August 2021, eight Cudddeback camera traps (Non Typical Inc., de Pere, WI, USA) were installed in eight artificial water troughs placed throughout the study area (Figure 1) to record the presence of deer; the data from these eight cameras were used to perform all analyses. The study area comprised areas adjacent to the road leading to the Calakmul archeological zone (from km 20 to 47). The exact location of the water troughs is shown in Figure 1.

The sites where camera traps were placed were the same sites where water troughs were installed (Table 1). One camera trap was placed at each site. The number of days that each trap remained operating varied depending on the characteristics of each device; camera traps were in operation for 143 days minimum. Camera traps were installed 50 cm from the ground in trees adjacent to the water trough; they were set to capture photographs 24 hours a day, with 5-second intervals between captures. A minimum distance of 2 km was maintained between the cameras (same as for water troughs). Operating cameras were reviewed every three weeks. In each review, the photographs were downloaded and assigned a record code number; finally, the proper operation of the cameras was checked, and the batteries were replaced as needed (Hidalgo-Mihart *et al.* 2017). Species were identified manually, entering the following data into a spreadsheet: station, camera-trap name, date, time, species, image name, and number of individuals. After the photographs were captured, a database was built using the *CamtrapR* package in R 3.4.0 (R Core Team 2017; Niedballa *et al.* 2019).

Data Analysis. The Photograph Visit Index (PVI) was captured with the formula $IFV = C/EM*100$ trap-days, where C = number of captures or independent events photographed, EM = sampling effort (number of camera traps per monitoring day) and 100 trap days (standard unit; Hernández-Pérez *et al.* 2020). To avoid overestimating the number of recorded individuals, only independent records were considered for the analyses (Nichols and Karanth 2011).

Independent records were defined as consecutive photographs of individuals of different species and photographs of individuals of the same species captured with a separation of more than 24 hours. If more than one individual was recorded in an independent record, this was noted as one record. In photographs in which several individuals of the same or different species appeared, these cases were also considered single records. Kruskall-Wallis tests were performed to compare the visit rates of a species to each monitoring station and to compare each sampling year, and a Mann-Whitney test (Hernández-Pérez *et al.* 2020) to compare the independent records of the three years between species. These analyses were performed in R 3.4.0 (R Core Team 2017).

Activity patterns. The activity pattern in the study area was evaluated for two deer species (*O. virginianus* and *M. pandora*) with circular statistics to evaluate differences between visiting times. During the different sampling months, a Watson-Williams test was performed with the Oriana 4.0 software (Kovach Computing Service 2011). The degree of overlap in the activity patterns of deer species was assessed using a Kernel density analysis, and the statistical differences between the hours of high activity between species were evaluated with a Wald test supported by the packages *Activity* version 3.5.1 and *overlap* in R 3.4.0 (Ridout and Linkie 2009; Rowcliffe 2016).

Results

With a sampling effort of 4,672 trap/nights, we captured 477 separate records of *O. virginianus*, 229 of *M. pandora*, and 3 of *M. temama* using artificial water troughs in the CBR (Table 1). Due to the scarce records of *M. temama* in water troughs, comparative analyses were performed only with the other two deer species. Regarding the records for *O. virginianus*, highly significant differences were found between the three sampling years (H = 12.575, df = 2, P < 0.001; Figure 2a); similarly, *M. pandora* showed highly significant differences between sampling years (H = 9.29, df = 2, P = 0.001; Figure 2b). When the records for *O virginianus* were compared between sampling stations, no significant statistical differences were observed (H = 4.73, df = 7, P = 0.69); this same result was observed for *M. pandora* (H = 4.22, df = 7, P = 0.75). Similarly, no significant differences were found when comparing independent records of the three monitoring years between both species (W = 229, P = 0.17; Table 1).

Activity patterns. For *O. virginianus*, the records showed a circular mean obtained at 8:15 h. and an angular dispersion ranging from approximately 8:00 h to 9:00 h. It was found that *O. virginianus* is mainly diurnal, with activity peaks in the early hours of the day, contrasting with a lower number of nighttime records (Figure 3a). *M. pandora* was also found to be mainly diurnal, showing activity peaks in the early hours of the day and before dusk (Figure 3). The circular mean of *M. pandora* activity was recorded at 6:00 h, with an angular dispersion ranging from approximately 6:00 h to 18:00 h. (Figure 3b). In 2019, a high degree of overlap was recorded in the use of water troughs by *O. virginianus* and *M. pandora* (*IP* = 0.79, P = 0,023; Figure 4); a similar pattern was observed in 2021 (*IP* = 0.75, P = 0,037; Figure 5).

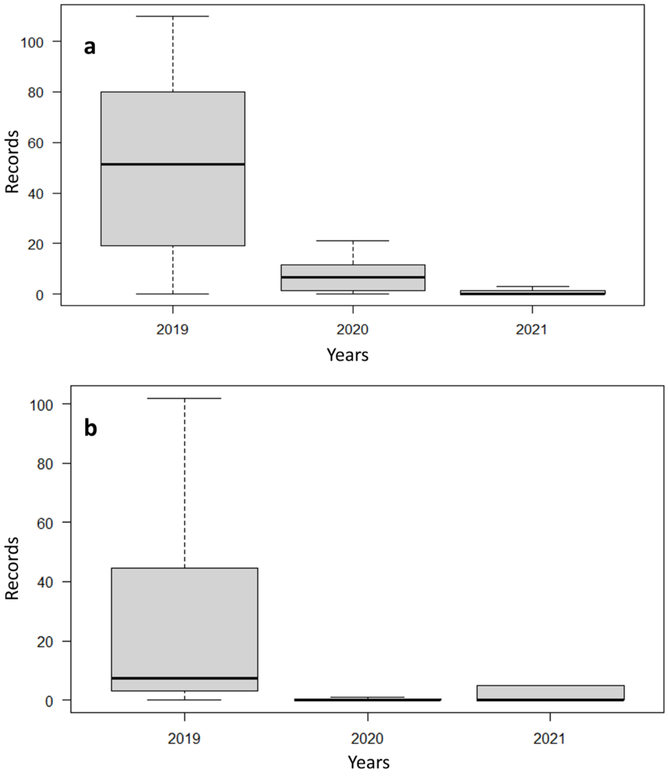

Figure 2. Independent records of *O. virginianus* (2a) and *M. pandora* (2b) during the three sampling years in artificial water troughs in the CBR.

Discussion

Two deer species, *O. virginianus* and *M. pandora*, regularly use water troughs, as shown by the number of records obtained (Table 1). The PVI showed differences between years for *O. virginianus* and *M. pandora*; the number of records in 2019 was significantly higher than in 2020 and 2021 (Table 1). In this regard, some analyses showed a trend of lower precipitation prior to 2019 (Pérez-Flores *et al.* 2021); particularly, 2019 showed drought precipitation conditions in terms of intensity and duration (SMN 2019). The greater presence of deer in water troughs in 2019 responds to their need for thermoregulation through water (Bello *et al.* 2004), so deer visited water troughs more frequently to meet their water needs (Fuller *et al.* 2014). Similarly, 2019 recorded a noticeable increase in the occurrence of tapirs outside the forest (Contreras-Moreno 2020; Pérez-Flores *et al.* 2021).

In arid regions, water is a limiting resource for various vertebrate species (McKee *et al.* 2015). In this study, the average PVI for *O. virginianus* and *M. pandora* for the three years was higher than the values reported in natural water holes (holes in rocky soil produced by erosion and that accumulate rainwater; Delgado-Martínez *et al.* 2018).

Table 1. Independent records of deer and photographic visit index (PVI) for the three sampling years in the Maya Forest, México.

	2019		2020		2021		TOTAL	
	Records	**PVI**	**Records**	**PVI**	**Records**	**PVI**	**Records**	**PVI**
Odocoileus virginianus	411	145.13	60	44.15	6	12.47	477	102.10
Mazama pandora	212	74.86	2	1.47	15	31.19	229	49.02
Mazama temama	0	0	3	2.21	0	0	3	0.64

Similarly, when the findings in the present study are compared with the records of Moreira-Ramírez *et al.* (2019), *O. virginianus* presented higher PVI values here compared to those recorded in Nuevo Becal (11) and the CBR (32.1), while *M. pandora* showed higher values only in two years (2019 and 2021); in contrast, *M. temama* showed lower values in the present study compared to Nuevo Becal. In this study, *O. virginianus* individuals were observed regularly in water troughs, even exceeding the frequency recorded for natural water bodies. This species has been considered a generalist that is able to benefit from disturbed habitats (Gallina-Tessaro *et al.* 2019), and on multiple occasions has displayed a positive behavior toward artificial water supply (Villarreal 2006). *M. pandora* is an ungulate that is considered an opportunist in the Calakmul region because it is able to use the habitat according to its availability. In this regard, an opposite trend was observed in 2020, probably due to the high availability of water in natural water bodies that year (Hernández-Cerda *et al.* 2021). Regarding *M. temama*, the values recorded in the present study (Table 1) were lower than those recorded in Nuevo Becal but were similar for Calakmul, since records were scarce or null in both cases. In this regard, it has been suggested that *M. temama* is more abundant in wet forests within the Maya Forest, such as Nuevo Becal, which contrasts with the characteristics of Calakmul (Moreira-Ramirez *et al.* 2019), where subdeciduous (dry) forests predominate toward the central part of the CBR (Martínez and Galindo 2002).

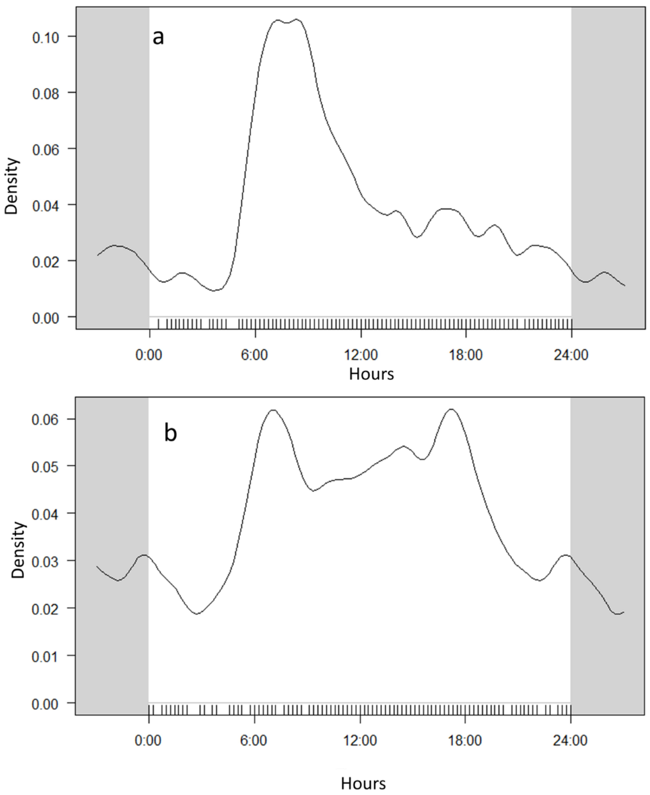

Figure 3. Graphic of the activity patterns of *O. virginianus* (3a) and *M. pandora* (3b) in the CBR.

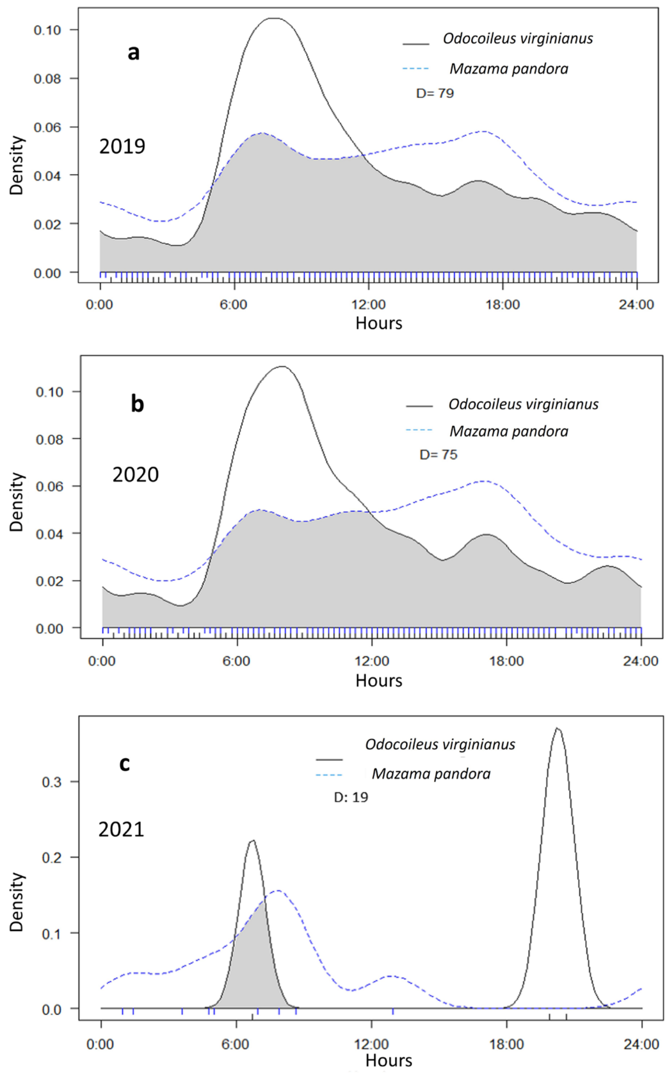

Figure 4. Overlap of the daily activity patterns of *O. virginianus* and *M. pandora* for the three years of records (a: 2019, b: 2020, c: 2021) at the CBR, Campeche, México. The 95 % coefficient of overlap is the area under the curve of both density estimates (marked in gray).

Similarly, the visit rate was higher than that estimated for *O. virginianus* in a WMU in the Tehuacán-Cuicatlán Biosphere Reserve (RBT-C) where the species is utilized (Mandujano-Rodríguez and Hernández 2019). In the present study in the Maya Forest, the visit rate of deer decreased significantly in

2020 and 2021. This result differs from the finding reported by Mandujano-Rodríguez and Hernández (2019), who recorded a larger number of records in the last sampling year (2018). These authors commented that this finding could be a result of the fact that, over time, deer have learned to recognize water troughs as alternative water sources and resort to them once they have located them (Berbert and Fagan 2012). Additionally, these authors considered that 2018 had more adverse climatic conditions (higher temperature and lower precipitation), so deer visited the water troughs more frequently to meet their water needs (Fuller *et al.* 2014).

The lower number of deer records in 2020 and 2021 is likely due to the high water availability in natural reservoirs since 2020 was a relatively rainy year where the first rains occurred in April (Hernández-Cerda *et al.* 2021), followed by tropical storm systems in May (Arthur and Bertha); however, it was Tropical Storm Cristobal (June 1 to 8) that saturated the soils of the region (NOAA 2020), flooding a large area of the Calakmul Biosphere Reserve, so natural water bodies supplied water until the middle of 2021 (Contreras-Moreno pers. comm.).

The use of water troughs has been scarcely analyzed in México. However, mammals have been reported to respond positively (Delgado-Martínez *et al.* 2018; Mandujano-Rodríguez and Hernández 2019; Mandujano-Rodríguez and Hernández-Gómez 2019; Borges-Zapata *et al.* 2020), and are a common practice within wildlife management units (WMU; Gastelum-Mendoza *et al.* 2014).

In the CBR, deer used water troughs regularly during the peak drought season when natural water bodies were dry, confirming that troughs effectively supply water to these herbivores and are a viable option to mitigate the effects of water scarcity in the Calakmul region, as is the case for other mammals in the region (Contreras-Moreno *et al.* 2019; Borges-Zapata *et al.* 2020). No significant differences were observed in the use of water troughs between *O. virginianus* and *M. pandora*, indicating the importance of water troughs for both species. Therefore, the water management and supply carried out likely contribute to the conservation of both species.

A low number of records of *M. temama* in water troughs were captured. This finding has generally been observed within the CBR for this species (Ramírez-Ortiz 2016), since the distribution of this species is associated with wetter areas, such as those adjacent to the reserve (Ramírez-Ortiz 2016). *M. temama* is considered a frugivorous species, at least to a greater extent than white-tailed deer (Weber 2008), which would also explain why *M. temama* visits water bodies, including water troughs, less frequently.

In this regard, climate changes may affect the structure of ecological communities, triggering changes in resource distribution, abundance, and phenology (Kardol *et al.* 2010). This situation becomes adverse in places where water has been identified as a limiting resource since rainfall is a driver of many animal movements (Bello *et al.* 2004). The activity pattern of deer when visiting water troughs was mainly diurnal (Figures 4 and 5), probably because it is much safer for both species to move during the day. Predators and meso predators have been frequently recorded in the study area, which are active mainly during nighttime hours (Sima-Panti *et al.* 2020; Contreras-Moreno *et al.* 2019b, 2020, 2021). Deer often adapt their behavior to manage their time between food search and protection (Schmitz 1991).

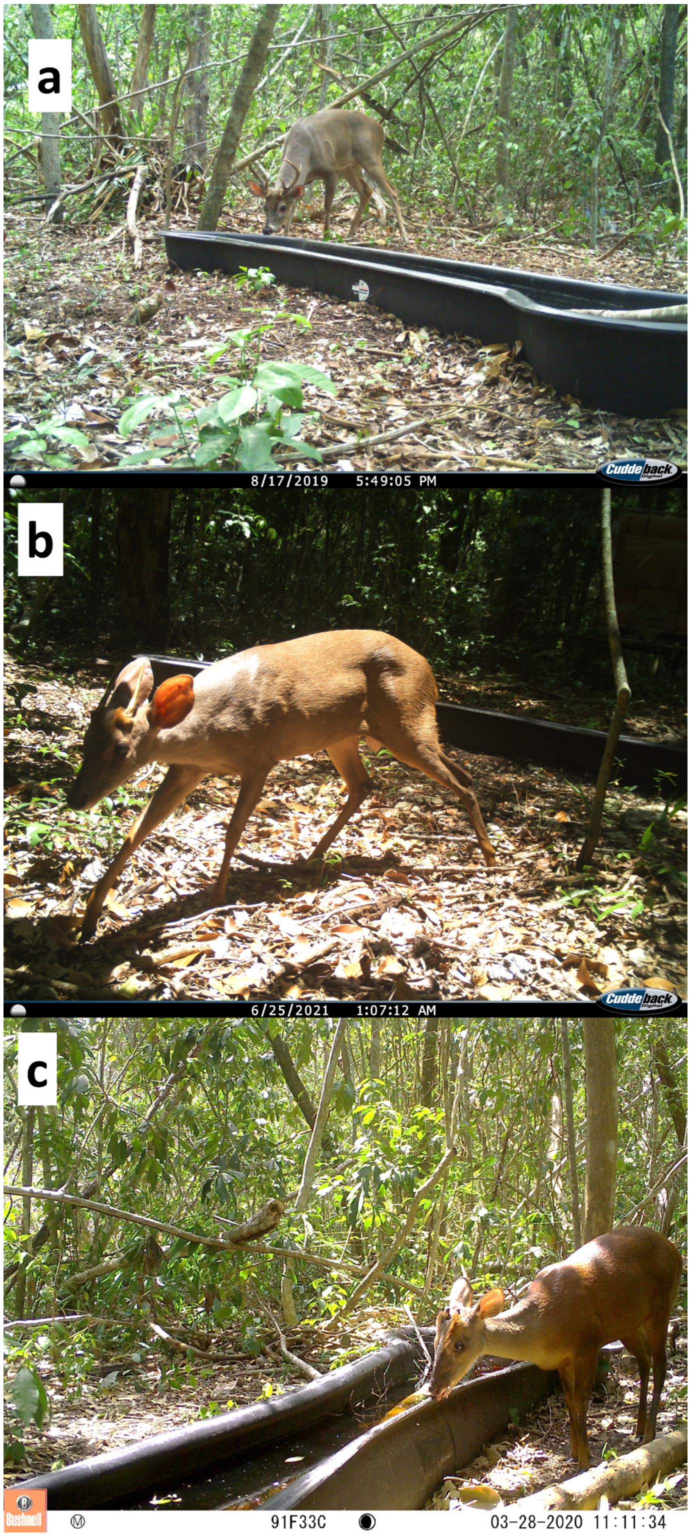

Figure 5. Photographs of the three deer species recorded in artificial water troughs in the present study. 5a: *O. virginianus*, 5b: *M. pandora*, 5c: *M. temama*.

Several studies have documented that prey adapt their behavior to minimize the risk of predation by their natural predators (Mukherjee and Heithaus 2013). In some cases, hunting can force ungulates to modify their visits to water troughs from day to night, but the magnitude of this change may be limited by the risk of predation imposed by large nocturnal carnivores (Crosmary *et al.* 2012).

The activity patterns of *O. virginianus* observed in the present study are similar to those recorded in Laguna de Términos, Campeche (Rodríguez 2015) and Calakmul (Ramírez-Ortiz 2016). It is worth mentioning that in both studies, camera traps were not directed to water troughs, suggesting that deer activity patterns are not affected by artificial water troughs. Similarly, our findings in the present study for *O. virginianus* are similar to those found in the RBT-C (López-Tello *et al.* 2015), which is noteworthy since RBT-C is a semiarid site. However, in some other cases, it has been observed that deer are usually active in twilight hours in the dry season and in daytime hours during the rainy season (Beier and McCullough 1990; Cornicelli et al. 1996; Sánchez-Rojas *et al.* 1997; Galindo-Leal and Weber 1998; Gallina *et al.* 2005). Adjustments of deer to their activity pattern may be related to resource availability (Sánchez-Rojas *et al.* 1997).

In the case of *M. pandora*, the activity pattern recorded in the present study showed activity peaks at dawn and dusk. However, in Calakmul, *M. pandora* recorded daytime activity, with peaks of activity at noon (Ramírez-Ortiz 2016). To note, these species forage throughout the day and probably also during the night to minimize the risk of predation by large felines (Mandujano-Rodríguez and Hernández 2019). The degree of overlap recorded between two species of deer (*O. virginianus* and *M. pandora*) suggests that both species are active at the same hours of the day.

Furthermore, it was observed that in addition to allowing access to fresh water, water troughs facilitate interactions between individuals of different populations. Hence, these could be considered sites that favor socialization and predation, and a specific approach is needed to understand these behaviors. Similarly, additional studies are needed to address both the consumption patterns of deer in all seasons and ways to improve the effectiveness of the current water trough network.

For the Yucatan Peninsula in particular, several models have been generated that suggest a disruption in precipitation patterns (Mardero *et al.* 2020), and it is considered that deer will be directly affected by these alterations derived from climate change (Contreras-Moreno and Torres-Ventura 2018). These models suggest that temperature will rise and precipitation will decrease in the Maya Forest in the near future (O'Farrill *et al.* 2014). It has been proposed that water scarcity could lead to greater intra- and inter-specific negative interactions between fauna and increase metabolic costs (as animals are forced to move further away to find water supplies; Delgado-Martinez *et al.* 2018).

Recently, events have been reported of tapirs going into villages, livestock pastures, hive plots, and roads searching for water, which has raised the level of interaction with people, leading to conflicts where these ungulates can be injured or killed (Pérez-Flores *et al.* 2021). In this sense, there is high pressure to hunt deer in some ejidos of the Maya Forest (Reyna-Hurtado and Tanner 2007), and water shortages may foster the hunting of these ungulates. Artificial water troughs could play a key role in mitigating these adverse effects of drought on deer in the Maya Forest, as they complement the functions of natural water bodies. However, further in-depth research is needed to understand and rule out potential adverse effects on deer populations since it has been suggested that water troughs, being artificial structures arbitrarily introduced into natural systems, may lead to alterations in deer behavior, ecology, and health (*i. e.*, they could be potential foci of zoonoses).

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Microhabitat characterization in the home range of the Mule deer (*Odocoileus hemionus*) in arid zones

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Knowing the home range of a species helps to identify the resources it needs to survive and reproduce and how this behavior is expressed spatially. Within home ranges, core areas are the sites where the main resources are abundant. The microhabitat is a spatial area composed of variables that can affect individual behavior. In this sense, the characterization of this inner part of the home range can contribute significantly to understanding the elements that these areas offer compared to the rest of the habitat of a population. This work characterized the home range and areas outside it, as well as the core areas of female mule deer on a microhabitat scale in the Chihuahuan Desert, México. The structure and composition of the vegetation were characterized according to three habitat use hierarchies: interior of the core areas and zones within and outside the home ranges of seven female mule deer. A Principal Component Analysis (PCA) was performed, and a hierarchical clustering was used to relate the variables. The variation in structure and composition in each hierarchy was evaluated by performing multivariate permutation tests. Twenty-five plant species were recorded in the transects. The PCA showed the most similar use hierarchies are the core and home range inner areas. The core area presents higher density and cover-dominance values, and the zone outside the home range showed high values of distance to the individual closest to the central point and greater variation in this parameter. The MANOVA indicated a significant variation in vegetation structure and composition in relation to use hierarchies. Significant differences in vegetation structure and composition were found at the microhabitat level between the core area of activity and the zones within and outside the home range. The core area has a greater structural complexity of vegetation, with greater plant coverage-abundance and density; this suggests that the core area is located in a more competitive and saturated environment. Outside the home range, the microhabitat has greater spatial heterogeneity of vegetation, with greater distance and variation of plant cover. Future research could address the spatial (micro-macro) and temporal scales to better understand the ecological dynamics of the species in different habitat use hierarchies.

Conocer el ámbito hogareño de una especie ayuda a comprender cuáles son los recursos que necesita para sobrevivir, reproducirse y cómo este comportamiento se expresa de forma espacial. Dentro de estos, las áreas núcleo representan los sitios donde se encuentran disponibles en mayor abundancia los recursos más importantes. El microhábitat es un área espacial compuesta por variables que pueden llegar a afectar el comportamiento individual, en este sentido, la caracterización de este al interior del ámbito hogareño puede contribuir significativamente en entender qué ofrecen estas áreas en comparación con el resto de su hábitat. En este trabajo se caracterizó el ámbito hogareño y las áreas fuera de este, así como las áreas núcleo de hembras de venado bura a una escala de microhábitat al interior del Desierto Chihuahuense, México. Se caracterizó la estructura y composición de la vegetación dentro de tres jerarquías de uso de hábitat: interior de las áreas núcleo, dentro y fuera de los ámbitos hogareños de siete hembras de venado bura. Se realizó un análisis de componentes principales (PCA) y se empleó un agrupamiento jerárquico para relacionar las variables. Para evaluar la variación en la estructura y composición en cada jerarquía se realizaron pruebas de permutación multivariadas. Se registraron 25 especies vegetales en los transectos, el PCA resolvió que las jerarquías de uso más similares son el área núcleo y dentro el ámbito hogareño. El área núcleo presenta valores más altos de densidad y de cobertura-dominancia y fuera del ámbito hogareño se presentaron valores altos de distancia al individuo más cercano al punto central, así como mayor variación en ellas. El análisis de MANOVA indicó una variación significativa en la estructura y composición de la vegetación en relación con las jerarquías de uso. Se encontraron diferencias significativas en la estructura y composición vegetal a nivel microhábitat entre el área núcleo de actividad, y dentro y fuera del ámbito hogareño. El área núcleo tiene una mayor complejidad estructural de la vegetación, con mayor cobertura-abundancia y densidad de las plantas; esto sugiere que el área núcleo se encuentra en un ambiente más competitivo y saturado. Fuera del ámbito hogareño el microhábitat tiene una mayor heterogeneidad espacial de la vegetación, con mayor distancia y variación de la cobertura. Se sugiere que futuras investigaciones puedan abordar la escala espacial (micro-macro) y temporal para obtener una comprensión más completa de las dinámicas ecológicas de la especie en diferentes jerarquías de uso del hábitat.

Keywords: Core area; habitat structure; habitat use; home range; plant composition.

Introduction

The home range is a subject that has been approached from different questions and perspectives to understand the variables that govern it and how, in turn, these relate to the individual, the family group, or other organisms (Spencer 2012). A home range is formed from daily and short-term movements within a given season and area, and this is the area normally used by an individual to feed, reproduce, raise their offspring, rest, and move (Burt 1943; Powell 2000; Mackie *et al.* 2003). Ultimately, the home range of a species involves understanding which resources it needs to survive and reproduce and how this behavior is expressed spatially (Burt 1943; Börger *et al.* 2008).

Within the home range, core areas are the sites where individuals spend most of the time and, in theory, where the most important resources for individuals of a given species are most abundant (Samuel *et al.* 1985; Asensio *et al.* 2012). Knowing and describing these areas significantly contribute to understanding the distribution and abundance patterns of species, so this information is essential for management and conservation strategies (Börger *et al.* 2006).

On the other hand, the conformation of the home range through time and space is part of the habitat use strategy employed by many species to intensely exploit diverse environments, as is the case of the mule deer (*Odocoileus hemionus;* Mackie *et al.* 2003), which is distributed in temperate and arid zones from southern Alaska to northern México. Throughout this distribution range, the species displays a wide variation regarding the size of its home range and the use of resources (Anderson and Wallmo 1984; Geist 1998). Some studies on its habitat have found that the species prefers sites with heterogeneous vegetation and relief, with slopes above 30 % and obstacles (Geist 1981, 1998; Gallina-Tessaro *et al.* 2019b) although, in contrast, some authors have suggested that the slope is not a habitat selection factor (Pérez-Solano *et al.* 2017). These variables facilitate the escape and protection of individuals because the mule deer typically runs upward in a straight line in hills by making large jumps, changing its trajectory instantaneously and unpredictably, unlike the white-tailed deer (*Odocoileus virginianus*), which uses fast gallop to escape their predators (Gallina-Tessaro *et al.* 2019b).

Likewise, it has been suggested that safety, rather than food, has a higher priority for the mule deer in the choice of habitat (Geist 1998; Hernández *et al.* 2005; Esparza-Carlos *et al.* 2011). Plant cover is one of the main drivers for the species, since it chooses sites with medium plant cover that facilitates visibility and provides protection against predators (Esparza-Carlos *et al.* 2011, 2016). These sites are also used to give birth and shelter the offspring and provide them with protection against temperature extremes (Fox and Krausman 1994; Tull *et al.* 2001; Alcalá-Galván y Krausman 2013; Gallina-Tessaro *et al.* 2019b).

In the Chihuahuan Desert in México, mule deer populations live in geographically isolated patches, often surrounded by areas relatively unsuitable for the species due to overgrazing, which negatively influences habitat availability and quality, altering the vegetation structure (Sánchez- Rojas and Gallina 2000a, b; Weber and Galindo-Leal 2005). In this region, the species uses space differentially between seasons and types of plant associations and shows variations between individuals, sexes, age groups, and physiological statuses (Pérez-Solano *et al.* 2016, 2017). Similarly, water is a resource that influences site selection; since individuals do not remain without access to it for long periods, their greatest activity occurs near this resource (Pérez-Solano *et al.* 2017).

Based on the above, it is important to mention that the habitat within the home range of the mule deer in México has not been characterized at the microhabitat level. The available information consists of approximations from assessments at a digital level or without delimiting home ranges (Gallina-Tessaro *et al.* 2019a). According to Morris (1987), the microhabitat is a spatial area composed of variables that can affect individual behavior. In this sense, its characterization within the mule deer home range would contribute to understanding what these areas offer compared to the rest of their habitat and determining the characteristics of core areas, which theoretically offer the best resources. Therefore, the objective of this work was to characterize the home range and the areas outside it, as well as the core areas of female mule deer in a central arid zone of the Chihuahuan Desert.

Materials and methods

Study Area. This study was conducted in the central area of the Mapimí Biosphere Reserve (RBM, in Spanish), located in the Chihuahuan Desert (Figure 1). The local climate is dry and extreme semi-warm, with summer rainfall; the mean annual precipitation is 271 mm. The rainy season runs from July to October, and the dry season from November to June. The mean annual temperature is 20.8 °C, with a mean minimum temperature of 3.9 °C in winter and a maximum of 36.1 °C in summer (Montaña and Breimer 1988; CONANP 2006).

The landscape within the reserve is heterogeneous. Based on the classification by Montaña (1988) and identified by Pérez-Solano *et al.* (2017), there are 11 plant associations named by the most dominant species: 1) *Larrea tridentata* and *Fouquieria splendens*. 2) *Prosopis glandulosa*, *Hilaria mutica*, and *Larrea tridentata*. 3) *Prosopis glandulosa*, *Pleuraphis mutica*, *Larrea tridentata*, and *Opuntia rastrera*. 4) *Hilaria mutica* and *Prosopis glandulosa*. 5) *Larrea tridentata*, *Opuntia rastrera,* and *Fouquieria splendens*. 6) *Opuntia rastrera*, *Agave asperrima,* and *Larrea tridentate*. 7) *Larrea tridentata*, *Opuntia microdasys*, and *Fouquieria splendens*. 8) *Larrea tridentata*, *Agave asperrima*, and *Fouquieria splendens*. 9) *Larrea tridentata* and *Opuntia rastrera*. 10) water-bank vegetation. 11) *Mogote*, *i. e.*, arch-shaped vegetation patches with a main axis perpendicular to the slope, mainly composed by *Prosopis glandulosa*, *Hilaria mutica*, and *Lar-*

rea tridentata. Mogotes are immersed within other plant associations (Montaña 1992).

Habitat Variables. Based on the home ranges and core areas estimated for seven female mule deer living in the RBM (Pérez-Solano *et al.* 2016, 2017), 24 transects were randomly traced assisted with ArcMap 10.0 (ESRI http://www.esri.com), considering a separation of at least 500 m between them. Eight transects were within the core area, eight outside the core area but within the defined home range, and eight outside the home range (Figure 1).

It should be noted that this study only considered female mule deer because only one young male was captured despite a 95-day capture effort over two years; this individual spent half the monitoring time with his mother and then separated (Pérez-Solano *et al.* 2016), so we decided not to include this information to avoid biasing the results.

For the tracing of transects, the home ranges and core areas of each of the seven females were superimposed in such a way that a single polygon could be generated to represent all the home ranges and one for all the core areas because there was an overlap of these areas between the females studied (Pérez-Solano *et al.* 2017). The transects were located at a minimum distance of 500 m from each other and separated at least 1 km between each use hierarchy (*i. e.*, core area, home range, and outside zone); only one transect within the core area (T8CA) was located less than 500 m away from another (T5CA) due to terrain conditions (Figure 1). Transects outside the home range were traced based on logistics and access to the area, seeking to represent the site heterogeneity.

To evaluate the microhabitat of the mule deer, we evaluated the vegetation composition and structure in each 800 m transect using point-centered quarters and the nearest-neighbor method (Mueller-Dombois and Ellenberg 1974) at points marked every 100 m. We recorded the distance (m) of the individual closest to the central point, its height (m), and the largest and smallest diameters of the treetop (m). The species was identified based on a previously created photographic catalog (Grajales-Tam, pers. comm.); only organisms measuring 50 cm in height minimum were considered. Additionally, vertical cover was measured using a 2 m ruler placed perpendicularly at 15 m from the point on the transect. With this rule, visible 20 cm sections were counted between the 0 to 50 cm, 50 to 100 cm, 100 to 150 cm, and 150 to 200 cm ranges to estimate the percentage of visibility. To this end, the rule was divided into 10 sections painted alternately black and white (Griffith and Youtie 1988).

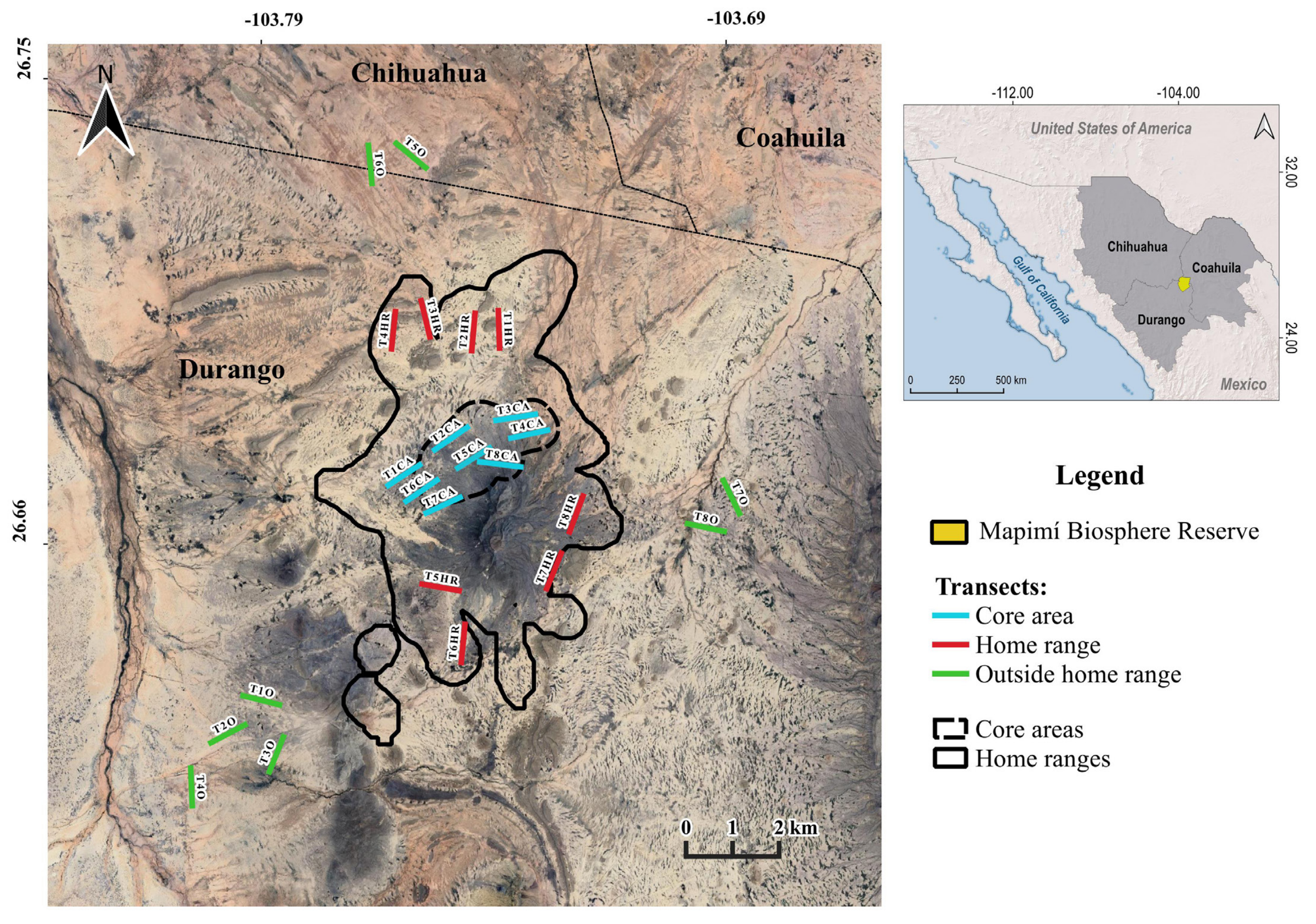

Figure 1. Location of the transects sampled in the core area and the areas within and outside the home range of seven female mule deer in the Mapimi Biosphere Reserve.

Data Analysis. From the variables of vegetation structure, we estimated the following parameters, which were included in the analyses as variables: plant cover (m^2; total value, mean, and standard deviation), which was obtained by estimating the ellipse ($C = \pi \times 0.25 \times major\ diameter \times minor\ diameter$); volume ($m^3$; mean and standard deviation), estimated for each individual depending on its shape, either cylindrical (*e. g.*, *Opuntia rastrera*; $Volcyl = \pi \times r^2 \times h$) or inverted cone (*e. g.*, *Larrea tridentata*; $Volcone = [\pi \times r^2 \times h] / 3$); vegetation absolute density (ind./100 m^2); species richness (number of species per transect), and species dominance by modifying the Braun- Blanquet cover-abundance index (IBB = density x mean cover; Wikum and Shanholtzer 1978).

Similarly, the distance (m) of the individual closest to the central point and the plant height (m) (mean and standard deviation in both cases), as well as the four vertical cover categories (%; mean of each category), were considered variables in the analyses.

Using the 16 variables described above, a Principal Component Analysis (PCA) was performed to represent the set of study units (transects), whose relationships were quantified according to their similarity in structure and composition (Gower 1966; Härdle and Hlávka 2007). The data structure was also visualized with a graphical representation of the groups obtained through the PCA. This approach allowed exploring the clustering of transects at different levels of habitat use hierarchy in the space defined by the first two main components (Wiegleb 1980; Bezuidenhout *et al.* 2012).

We also sought to identify clustering patterns, which provide an understanding of the relationship between habitat use levels (Clarke 1993; Mérigot *et al.* 2010). To this end, we used hierarchical clustering to analyze the characteristics of the microhabitat in the 24 transects, focusing on aspects related to the vegetation structure (height, cover, density, and volume) and composition (species richness and cover-abundance index; McGarigal *et al.* 2000). Euclidean distances between transects were used to calculate similarities, and a dendrogram was created with the UPGMA method using the base package and dendextend in R (Galili 2015; R Core Team 2023).

The variation in microhabitat structure and composition between the different levels of the habitat use hierarchy was evaluated with multivariate permutation tests (999 permutations; MANOVA) using the *vegan* package in R (Oksanen *et al.* 2022). The complexity of the data was assessed through a dimensionality reduction using the first five Principal Components (which explained more than 90 % of data variance). Furthermore, paired comparisons were carried out as a *post hoc* test between specific pairs of levels, allowing us to examine in detail the differences in the composition of use levels using the pairwiseAdonis package in R (Martinez 2020). This analysis, supported by the use of the PCA, provided a deeper perspective on multivariate variation in the structure of biological communities in relation to the use hierarchy.

Results

Sixteen variables of vegetation structure and composition were measured for subsequent evaluation. These included total, mean, and standard deviation values, summarized in Table 1. The core area was the one that had the highest absolute density (4.6 ± 2.2 ind./m^2), and the total plant cover (m^2) was highest in transects outside the home range (102.6 ± 17), followed by the core area (76.6 ± 18.9). The mean vertical cover (%) in the four height categories was higher within and outside the home range (Table 1). Core areas attained higher cover-abundance index (10.3 ± 6.5) and species richness (8.5 ± 1.9; Table 2).

Table 1. Description of the variables used in the PCA. Mean values and standard deviations (±) of the transects for each hierarchy of use in relation to the home range of deer are reported.

Variable	Core area	Home range	Outside of the home range
Total cover (m^2)	76.6 (± 18.9)	61.7 (± 12.3)	102.6 (± 17)
Mean cover	2.1 (± 0.5)	1.7 (± 0.3)	2.9 (± 0.5)
Standard deviation of cover	1.6 (± 0.4)	1.3 (± 0.3)	2.5 (± 1)
Mean volume (m^3)	1.3 (± 0.3)	0.8 (± 0.3)	1.5 (± 0.5)
Standard deviation of volume	1.4 (± 0.4)	0.9 (± 0.4)	1.6 (± 0.9)
Absolute density (ind./m^2)	4.6 (± 2.2)	2.9 (± 2.2)	1.2 (± 0.8)
Species richness	8.5 (± 1.9)	7.0 (± 1.7)	5.1 (± 2.3)
Cover-abundance index	10.3 (± 6.5)	5.3 (± 4.5)	3.8 (± 3.2)
Mean distance (m) of the individual closest to the center point	3.1 (± 1.1)	4.5 (± 1.8)	6.9 (± 3.2)
Standard deviation of the distance of the individual closest to the center point	2.2 (± 1.2)	4.0 (± 2.3)	4.7 (± 3.0)
Mean height (m)	1.0 (± 0.1)	0.9 (± 0.1)	1.1 (± 0.1)
Standard deviation of height	0.4 (± 0.1)	0.4 (± 0.2)	0.3 (± 0.1)
Mean cover, 0 cm–50 cm (%)	16.9 (± 7.8)	28.2 (± 8.1)	32.0 (± 7.8)
Mean cover, 50 cm–100 cm (%)	31.3 (± 7.3)	38.3 (± 5.5)	37.7 (± 7.4)
Mean cover, 100 cm–150 cm (%)	43.1 (± 5.0)	45.5 (± 2.1)	45.5 (± 3.7)
Mean cover, 150 cm–200 cm (%)	46.4 (± 4.1)	48.8 (± 1.2)	48.0 (± 2.7)

We recorded 25 species of plants in the transects, considering all hierarchies together; one species could not be identified (Table 2). The core area showed a species richness of 19 species, where the most dominant were *Larrea tridentata* (6.0 ± 5.2) and *Cordia parvifolia* (1.5 ± 0.8). The species richness in the home range was 17 species, the most dominant again being *L. tridentata* (2.5 ± 3.0) and *Opuntia rastrera* (1.0 ± 1.3). Twelve plant species were recorded outside the home range, with a greater dominance of *L. tridentata* (1.9 ± 2.6) and *Prosopis glandulosa* (1.9 ± 1.6).

The first two principal components accounted for 68.8 % of the explained variance, 38.3 % corresponding to PC1 and 30.4 % to PC2 (Table 3). The three levels of use hierarchy showed a different distribution in the plane defined by PC1 and PC2. The most similar use hierarchies were the core area and the zone within the home range. The core area showed higher density and cover-dominance values, and the zone outside the home range showed high values of distance to the individual closest to the central point and greater variation (Figure 2).

According to the hierarchical clustering, seven transects placed outside the home range (T1O–T6O and T8O) were grouped in one cluster, while the 16 transects in the home range were mixed in two groups (Figure 3). Transect T7O outside the home range and T8CA of the core area were not grouped with the rest of the transects corresponding to the sampled use hierarchy.

The MANOVA analysis indicated a significant variation in vegetation structure and composition in relation to use hierarchies ($F = 5.202$, $P = 0.001$; Table 4). Statistically significant differences were observed between the core area and the zone outside the home range ($F = 5.684$, $p = 0.001$) and between the zones within and outside the home range ($F = 6.217$, $P = 0{,}001$), highlighting the differential influence of these levels on the composition of transects. Likewise, the comparison of the core area vs. the zone within the home range revealed a significant difference ($F = 3.564$, $P = 0.03$), providing greater perspectives on the differences in vegetation composition between habitat use hierarchies.

Discussion

The fauna that inhabits arid ecosystems, including mule deer, has adapted morphologically and physiologically to these sites; these adaptations, together with their behavioral strategies, have allowed them to succeed in habitats with extreme conditions (Ward 2018). One of these behavioral strategies is the movement patterns that define the home range and the core areas of activity within these, which theoretically represent the best combination of habitat variable conditions (Samuel *et al.* 1985). This study

Table 2. Species recorded in the core area, home range, and zone outside the home range. The mean values and standard deviations (±) of the number of individuals (*n*) and the cover- abundance index (IBB) recorded by transect are reported.

Especie	**Core area**		**Home range**		**Outside home range**	
	n	**I_{BB}**	**n**	**I_{BB}**	**n**	**I_{BB}**
Agave asperrima	3.0 (± 1.6)	0.3 (± 0.2)	4.2 (± 2.9)	0.6 (± 0.6)	1.3 (± 0.6)	0.04 (± 0.04)
Atriplex canescens	-	-	-	-	16.5 (± 17.7)	0.8 (± 1.0)
Castela erecta	1.8 (± 1.0)	0.3 (± 0.3)	2.2 (± 2.0)	0.4 (± 0.4)	3.0 (± 2.1)	0.1 (± 0.1)
Cordia parvifolia	2.0 (± 1.4)	1.5 (± 0.8)	4.2 (± 2.9)	0.6 (± 0.6)	-	-
Cylindropuntia imbricata	2	0.1	1	0.1	-	-
Echinocereus enneacanthus	1	0.03	-	-	-	-
Euphorbia antisyphilitica	0.1 (± 0)	0.2 (± 0.2)	7	1.2	-	-
Flourencia cernua	1.6 (± 1.3)	0.4 (± 0.4)	1.6 (± 0.5)	0.1 (± 0.1)	3.0 (± 1.4)	0.4 (± 0.2)
Fouquieria splendens	1.5 (± 0.5)	0.5 (± 0.5)	2.3 (± 1.3)	0.6 (± 0.4)	-	-
Haplopappus sp.	-	-	1.5 (± 0.7)	0.1 (± 0.01)	1	0.2
Jatropha dioica	2.8 (± 1.0)	0.8 (± 0.8)	2.0 (± 0.9)	0.4 (± 0.5)	-	-
Krameria grayi	1	0.1	-	-	3.5 (± 0.7)	0.2 (± 0.1)
Larrea tridentata	16.3 (± 7.8)	6.0 (± 5.2)	17.8 (± 8.6)	2.5 (± 3.0)	11.7 (± 9.5)	1.9 (± 2.6)
Lippia graveolens	0.1 (± 0)	0.2 ± 0.2)	-	-	-	-
Opuntia leptocaulis	0.1 (± 0)	0.2 (± 0.2)	0.1 (± 0)	0.1 (± 0.1)	2.0 (± 0.8)	0.2 (± 0.2)
Opuntia macrocentra	-	-	1	0.02	1.0 (± 0)	0.1 (± 0.1)
Opuntia microdasys	1.5 (± 0.7)	0.9 (± 0.3)	-	-	-	-
Opuntia rastrera	6.5 (± 3.0)	1.2 (± 0.6)	3.6 (± 3.0)	1.0 (± 1.3)	2	0.2
Prosopis glandulosa	3.3 (± 1.5)	1 (± 0.5)	6.0 (± 5.0)	0.9 (± 0.8)	15.8 (± 9.5)	1.9 (± 1.6)
Sarcomphalus obtusifolius	-	-	2.5 (± 2.0)	0.3 (± 0.4)	-	-
Vachellia farnesiana	-	-	4.7 (± 5)	0.3 (± 0.2)	4.5 (± 4.9)	0.5 (± 0.7)
Vachellia vernicosa	1	0.2	-	-	-	-
Parthenium incanum	2.0 (± 1.0)	0.2 (± 0.1)	-	-	-	-
Chrysactinia mexicana	4	0.2	-	-	-	-
Sp1	-	-	3	0.19	-	-

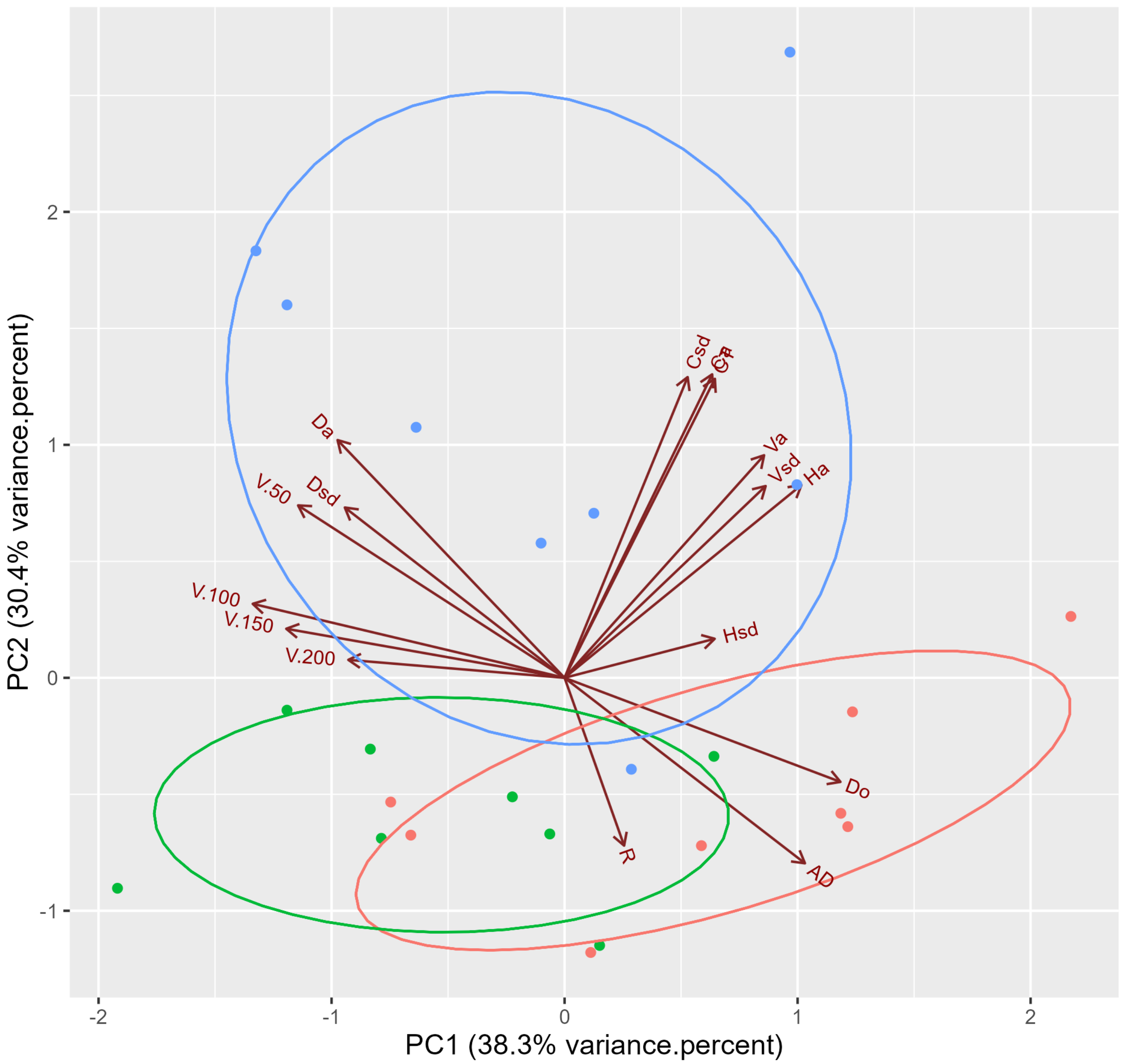

Figure 2. Principal Component Analysis of the vegetation structure and composition variables in the core area and the areas outside and within the home range of seven female mule deer. The red color represents the core area, green represents the home range, and blue represents outside the home range. Total cover (CT), Mean cover (Ca), Standard deviation of cover (Csd), Mean volume (Va), Standard deviation of volume (Vsd), Absolute density (AD), Species richness (R), cover-abundance index (Do), Mean distance (Da), Standard deviation of distance (Dsd), Mean Height (Ha), Standard deviation of height (Hsd), mean vertical cover, 0 to 50 cm (V-50), mean vertical cover, 50 to 100 cm (V-100), mean vertical cover 100 to 150 cm (V-150), mean vertical cover, 150 to 200 cm (V-200).

found statistically significant differences in vegetation structure and composition between the areas of each use hierarchy (core areas, within the home range, and outside the home range), indicating differences in microhabitat within each of them. This finding could explain why female mule deer spend most of their time resting and displaying movement patterns within delimited areas such as home ranges (Pérez-Solano *et al.* 2017, 2019).

The Principal Component Analysis and hierarchical grouping revealed the spatial and structural differences between the deer use hierarchies. The first two principal components showed a clear separation between the core areas, zones within the home range, and zones outside the home range, suggesting the existence of specific factors that determine the plant composition of each area; this approach allowed us to get a deeper insight of the spatial organization of the vegetation. PC1 represents a gradient of vegetation structural complexity, where high values indicated greater cover-abundance, density, height, and mean volume, and low values showed a higher variation coefficient for height at different levels. The core area had high values in PC1, which reveals greater structural complexity of vegetation, with higher plant cover- abundance and density; this suggests that the core area is in a more

Table 3. Microhabitat variables in the first five principal components and percentage of variance explained by each axis.

Variable	PC1	PC2	PC3	PC4	PC5
Eigenvalues	6.14	4.87	1.49	1.14	0.78
Proportion of variance	0.38	0.30	0.09	0.07	0.05
Cumulative proportion	0.38	0.69	0.78	0.85	0.90
Total cover (m^2)	0.17	0.39	0.13	0.13	0.06
Mean cover	0.17	0.39	0.11	0.10	0.03
Standard deviation of cover	0.14	0.39	-0.05	-0.14	-0.16
Mean volume (m^3)	0.23	0.29	0.22	-0.19	-0.16
Standard deviation of volume	0.23	0.25	0.13	-0.42	-0.24
Absolute density (ind./m^2)	0.28	-0.24	0.29	0.05	0.13
Species richness	0.07	-0.22	-0.27	-0.64	-0.23
Cover-abundance index	0.32	-0.14	0.29	0.13	0.24
Mean distance (m) of the individual closest to the center point	-0.26	0.31	-0.07	0.09	-0.06
Standard deviation of the distance of the individual closest to the center point	-0.25	0.22	-0.30	0.04	-0.09
Mean height (m)	0.27	0.25	-0.16	0.04	0.29
Standard deviation of height	0.17	0.05	-0.42	-0.31	0.70
Mean cover, 0 to 50 cm (%)	-0.31	0.22	-0.06	0.08	0.19
Mean cover, 50 to 100 cm (%)	-0.36	0.10	0.07	-0.11	0.17
Mean cover, 100 to 150 cm (%)	-0.32	0.06	0.38	-0.27	0.12
Mean cover, 150 to 200 cm (%)	-0.25	0.02	0.46	-0.34	0.31

competitive and saturated environment, with more interactions between species (Powell and Mitchell 2012; Ward et al. 2018).

On the other hand, PC2 represents a gradient of vegetation spatial heterogeneity, where high values indicate greater plant cover, distance, and standard deviation of plant cover, and low values indicate higher density, species richness, and cover-abundance. Outside the home range, the microhabitat showed a greater spatial heterogeneity of vegetation, with greater distance and variation in plant cover. These findings suggest a more heterogeneous and dispersed environment outside the home range, with fewer resources and competition (Threlfall et al. 2016).

The MANOVA confirmed the significant variation in vegetation structure and composition between use hierarchies, indicating that the use of space by mule deer is a response to the available resources (Gallina-Tessaro et al. 2019b). The variability in the measured variables reflects not only the variation in plant species richness and cover-abundance between areas but also key aspects of vegetation structure, such as density and vertical cover. The formation of different clusters for core areas, zones within the home range, and zones outside the home range suggests the existence of specific dynamics that may be associated with factors such as the intrinsic characteristics of each area or potential disturbances.

The vegetation variables that most influenced core areas are absolute density and the cover-abundance index, which showed high and medium total cover values. These reflect what has previously been reported for the mule deer, *i. e.*, its association with areas that have medium vegetation cover (*e. g.*, between 15 % and 50 % vertical cover), which provides them with shelter against extreme temperatures and suitable spaces to give birth and shelter for fawns (Fox and Krausman 1994; Tull *et al.* 2001; Alcalá-Galván and Krausman 2013) without losing adequate visibility to detect predators (Sánchez-Rojas and Gallina 2000a; Esparza-Carlos *et al.* 2011, 2016). Likewise, the core areas had high values of species richness, which plays a central role in habitat selection by mule deer (Sánchez-Rojas and Gallina 2000a). In contrast, this variable has sometimes not been statistically significant in determining habitat use. This is attributed to the fact that deer constantly move as a strategy of protection against predation and have a varied diet adapted to the habitat, in particular the rosettophyllous scrub with plants such as agaves and prickly-pear cactus associated with steep-slope areas (Geist 1981; Cossio-Bayúgar *et al.* 2015), plant associations, and closeness to water bodies (Pérez-Solano *et al.* 2017).

On the other hand, plant density has been shown to be positively correlated with habitat use by mule deer (Lozano-Cavazos *et al.* 2018). For example, in years with scarce precipitation, the species concentrates its activities in areas with greater forage availability, including candelilla (*Euphorbia antisyphilitica;* Esparza-Carlos *et al.* 2011), which was recorded only in the core area and in the rest of the home range. However, although the distribution of mule deer in the landscape is not uniform, it has been reported to be strongly influenced by water availability, relief heterogeneity (Sánchez-Rojas and Gallina 2000a, b), and precipitation, which is inversely related to population size (Hernández-Silva 2018). This could explain why the time delay in the sampling does not alter the results obtained regarding mule deer presence and habitat use in the RBM.

The cover-abundance of plant species was two-fold within the core area relative to the rest of the home range. *L. tridentata* was the dominant species with the highest cover and abundance in both hierarchies. This result was expected because this species has a broad distribution in the region (Montaña and Breimer 1988) and is present in all plant associations considered (Pérez-Solano *et al.* 2017).

Table 4. Results of the MANOVA that compared the variation in microhabitat structure and composition between the core area, home range, and outside the home range (use hierarchy) of female mule deer.

	DF	Sum of squares	*R2*	*F*	*Pr(>F)*
Use hierarchy	2	109.85	0.3313	5.2022	0.001
Residual	21	221.73	0.6687		
Total	23	331.58	1		

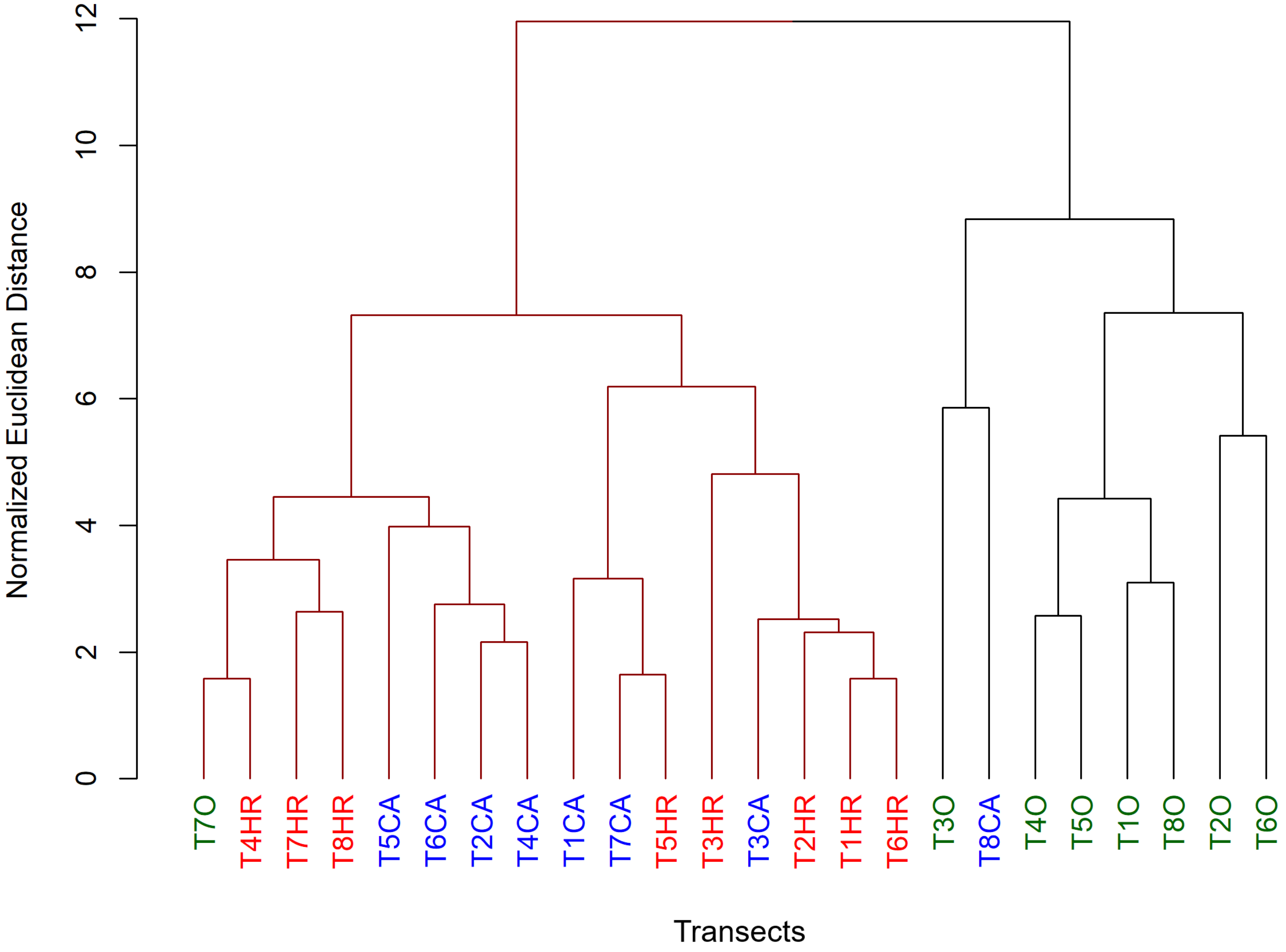

Figure 3. Dendrogram of the vegetation structure and composition variables in the core area and the areas outside and within the home range of seven female mule deer. The black branch marks the clustering of most transects sampled outside the home range. The red branch shows the transects within the home range and core area combined.

Additionally, *L. tridentata* has leaves all year round and can reach a sufficient size to cover a deer, providing them with protection against extreme temperatures and predators.

Finally, this study aimed to offer a detailed view of the structure and composition of the vegetation in different mule deer habitat use hierarchies, specifically the core areas and those within and outside the home range. Despite these revealing findings, this study has some limitations, such as the time scale, since vegetation phenology (Gallina *et al.* 2017) and precipitation patterns have been detected to influence habitat use by mule deer (Hernández-Silva 2018). Future research can address these limitations to better understand the characteristics of vegetation in different habitat use hierarchies. Overall, the results reported here contribute significantly to understanding the ecology of mule deer in arid zones, particularly in México.

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Activity patterns and use of artificial water ponds by White-tailed deer (*Odocoileus virginianus*) in western Campeche

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Artificial Water Ponds (AWP) are widely employed for preserving and managing white-tailed deer (*Odocoileus virginianus*) in arid, and tropical regions of Mexico. However, there is a significant knowledge gap concerning the impact of these AWP on white-tailed deer activity. To determine the effect of AWP on the ecological aspects of white-tailed deer, we assessed the visitation rates and activity patterns of this species in AWP and compared them with areas devoid of water such as Dirt Roads (DR) using camera traps during the dry season within the seasonal wetland region of Nicte Ha, situated in western Campeche, Mexico. The research was conducted in a highly seasonal tropical wetland area at the Nicte-Ha UMA in southwestern Campeche, México. We established set camera trap stations during the dry season of 2019, 2020, and 2021 in seven AWP and 12 DR that operated for at least 80 days and compared the white-tailed deer visitation rate (measured as the Relative Abundance Index, RAI) and activity patterns among both treatments and across the three studied years. We collected a total of 3,640 independent records of white-tailed deer (2,584 in AWP and 1,056 in DR) for three years, with a combined effort of 3,978 camera days (1,306 camera days in AWP and 2,672 in DR). Our analysis revealed that the Relative Abundance Index (RAI) was consistently higher in the AWP than the DR across the three study years. However, we examined RAI variations over the three years and observed differences in the AWP, while the DR exhibited a relatively stable pattern. In the case of the activity patterns, we observed that white-tailed deer were primarily diurnal, with a significant overlap in activity between the two treatment areas. Nonetheless, within the AWP, the species exhibited continuous daytime activity, whereas, in the PR, distinct activity peaks occurred during sunrise and sunset. The results show that the presence of AWP in Nicte Ha has important effects on the presence of white-tailed deer during the dry season since we observed that there is a higher RAI in the sites where there is AWP compared to the PR sites. In the case of activity patterns, the AWP sites maintain constant activity throughout the day compared to DR, where activity peaks associated with sunrise and sunset occur. Our results show the importance that this type of structure has for the management of the species during the dry season of the year in Nicte Ha and the potential benefits of these structures in tropical seasonal areas, especially under a scenario in which drought during the dry season may be more severe in the near future due to the global change.

Los cuerpos de agua construidos artificialmente son una estrategia ampliamente empleada para la conservación y manejo del venado cola blanca (*Odocoileus virginianus*) en regiones áridas y tropicales con estacionalidad marcada en México. Sin embargo, existe una importante laguna de conocimiento sobre el efecto que estos cuerpos de agua artificiales tienen en aspectos las poblaciones de los venados cola blanca. Para determinar la influencia del agua libre disponible en cuerpos de agua artificiales sobre aspectos ecológicos del venado de cola blanca, en la UMA Nicte Ha en Campeche, México, evaluamos las tasas de visita y los patrones de actividad de esta especie en cuerpos de agua artificiales (CAA) y los comparamos con áreas sin agua disponible como Veredas y Caminos (VC) utilizando cámaras trampa. La investigación se realizó en un humedal tropical altamente estacional ubicado en la UMA Nicte-Ha en el suroeste de Campeche, México. Establecimos estaciones de cámaras trampa durante la estación seca de 2019, 2020 y 2021 en siete CAA y 12 VC que operaron durante al menos 80 días. Comparamos la tasa de visita (medido como el Índice de Abundancia Relativa, IAR) del venado cola blanca y los patrones de actividad entre ambos tratamientos y a lo largo de los tres años estudiados. Obtuvimos 3,640 registros independientes de venado cola blanca (2,584 en CAA y 1,056 en VC) en el transcurso de tres años de trabajo, con un esfuerzo combinado de 3,978 días cámara (1,306 días cámara en CAA y 2,672 en VC). Nuestro análisis reveló que el IAR fue consistentemente más alto en el CAA en comparación con el VC durante los tres años de estudio. Sin embargo, cuando examinamos las variaciones del IAR a lo largo de los tres años, observamos diferencias en el CAA, mientras que el VC mostró un patrón relativamente estable. En el caso de los patrones de actividad, observamos que los venados de cola blanca eran principalmente diurnos, con una superposición significativa en la actividad entre las dos áreas de tratamiento. Sin embargo, dentro del CAA, la especie exhibió actividad diurna continua, mientras que en el VC, se presentaron picos de actividad durante el amanecer y el atardecer. Además, si bien el patrón de actividad se mantuvo constante durante los tres años de estudio en el CAA, hubo variaciones anuales en el VC. Los resultados muestran que la presencia de CAA en Nicte Ha tiene efectos importantes sobre la presencia de venado cola blanca durante la época seca ya que observamos que existe un mayor IAR en los sitios donde hay CAA en comparación con los sitios de VC. En el caso de los patrones de actividad, los sitios CAA mantienen una actividad constante durante todo el día en comparación con VC, donde ocurren picos de actividad asociados con el amanecer y el atardecer. Nuestros resultados muestran la importancia que este tipo de estructura tiene para el manejo de la especie durante la estación seca del año en Nicte Ha, y los beneficios potenciales de estas estructuras sobre otras unidades de manejo y vida silvestre en áreas estacionales tropicales, especialmente bajo un escenario en el que la sequía durante la estación seca podría ser más severa en el futuro cercano por efecto del cambio global.

Keywords: Camera trap; drought; Laguna de Terminos; seasonal tropical area; UMA; wetland.

Introduction

In México, white-tailed deer (*Odocoileus virginianus*) is one of the foremost managed species, especially in the north of the country, where it has been demonstrated that it can be a source of economically profitable exploitation, and with ample opportunities in tropical zones from the center and southeast México (Mandujano *et al.* 2019). The importance of this species in México has caused it to be one of the most studied species of ungulates, with extensive information about their reproduction, habitat, foraging patterns, and behavior (Gallina-Tessaro *et al.* 2019).

Free water (*i. e*., water available for drinking) is a fundamental habitat feature for wildlife (Leopold 1987), essential for life processes (Ricklefs 2008) that may influence population dynamics and species distribution (Rosenstock *et al.* 1999; Simpson *et al.* 2011), which has been considered a limiting factor for many species in arid (Rautenstrauch and Krausman 1989; Cain *et al.* 2006) and seasonal environments (Mandujano and Hernández 2019). Free-standing water availability limits large herbivore populations if forage consumption does not meet water requirements, and because it helps with thermoregulation (Mogart *et al.* 2005; Simpson *et al.* 2011). For white-tailed deer, water is an essential nutrient necessary for meeting all their physiological needs, including the water lost from a deer's body through the excretion of wastes and evaporation from the respiratory tract and skin. Also, water is lost when a doe gives birth or is lactating in such a rate that a deer's health may be jeopardized if water is not replaced in less than 48 hours (Hewit 2011). Water bodies also are important for social interactions where evidence shows that white-tailed deer intraspecific contact is more likely in habitats where deer resources such as food and water are concentrated (Palmer *et al.* 2004; Kjær *et al.* 2010).

Water scarcity is a major challenge for wildlife habitats in arid and seasonal environments in North America and México. One way to address this issue is to construct Artificial Water Ponds (AWP), which are an integral component for maintaining and enhancing these habitats (Rosenstock *et al.* 1999). AWP have several purposes. Firstly, they aim to improve the performance of wildlife populations by increasing productivity, reducing mortality, and facilitating management. Secondly, they affect animal movements and distribution, which can have ecological and conservation implications (Bello *et al.* 2001; Destefano *et al.* 2000; O'Brien *et al.* 2006; Simpson *et al.* 2011). Furthermore, AWP can mitigate the loss and degradation of naturally occurring sources of free water, which are increasingly scarce and vulnerable due to climate change and human activity (Rosenstock *et al.* 1999; Simpson *et al.* 2011; Larsen *et al.* 2012).

The importance of water developments for white-tailed deer populations in México has been mostly studied in the north of the country (see Gallina-Tessaro *et al.* 2019 for a review). However, in the south, there is little information about this subject. Most of the water developments in this region are employed in protected areas (Borjes-Zapata *et al.* 2020) and Wildlife Management and Conservation Units (UMA per its Spanish initials; Treviño-Ruiz 2010; Gastelum-Mendoza *et al.* 2014). One of these UMAs is Nicte Ha, located in western Campeche. This UMA covers 2300 ha and has the objective of preserving and practicing legal hunting of white-tailed deer. Nicte Ha is the home of an extensive wetland system that undergoes severe seasonal changes. It has a marked dry season with temperatures above 40 °C (INEGI 2013), which contrasts with an extended flooding season that can last for more than eight months (Rivera-Arriaga and Villalobos-Zapata 2005). These climatic conditions strongly affect the resource availability for the wildlife inhabiting the area (Hidalgo- Mihart *et al.* 2017). To reduce the effect of the dry conditions in the Nicte Ha UMA, AWP were constructed along the property to preserve free water for wildlife. This is the UMA's most important habitat management activity to cope with the extremely harsh conditions during the dry season.

Many studies agree that the conservation of natural, free water sources and the construction of artificial water reservoirs are valuable strategies for wildlife conservation and management, not only in arid climate areas but also in areas with contrasting high seasonality (Martínez-Kú *et al.* 2008; Delgado-Martínez *et al.* 2018; Mandujano and Hernández 2019; Borges-Zapata *et al.* 2020). Previous studies in Nicte Ha reported that the white-tailed deer responds to these contrasting environmental conditions by increasing the daily distances traveled and home range during the harshest portion of the dry season compared to the rainy season (Contreras-Moreno *et al.* 2019a; Contreras-Moreno *et al.* 2021). Additionally, it has been found that fawning synchronizes with the dry months (February- June) of the year, and the area's seasonality is one of its possible causes (Contreras-Moreno *et al.* 2019b).

Previous work in the Nicte Ha area showed that white-tailed deer responded to the AWP, concentrating their home ranges along these free water sources (Contreras-Moreno *et al.* 2021). However, to understand how the white-tailed deer is affected by the presence of AWP in Nicte Ha, it is necessary to determine other aspects, such as the visitation rate and activity patterns in these artificial water sources and in areas where the structures are not present.

White-tailed deer use the available habitats to satisfy basic requirements for food, rumination, movement, social interactions, and rest. The resulting time budget and habitat use pattern may vary with age, sex, time of day, season, weather conditions (Beier and McCullough 1990), predators, and human activities (Kilgo *et al.* 1998). For these reasons, the aim of this research was to describe the activity patterns and visitation rate of white-tailed deer within AWP and dirt Roads using camera traps during the dry season in the seasonal wetland area Nicte Ha, Campeche, México, and how these aspects vary across three studied years (2019, 2020, and 2021). This study will contribute to understanding the behavior of white-tailed deer in the presence of artificial water sources in tropical areas with high seasonality.

White-tailed deer use the available habitats to satisfy basic requirements for food, rumination, movement, social interactions, and rest. However, these requirements may vary depending on several factors, such as age, sex, time of day, season, weather conditions (Beier and McCullough 1990), predators, and human activities (Kilgo *et al.* 1998). For these reasons, the aim of this research was to describe the activity patterns and visitation rate of white-tailed deer within AWP and pathways/trails using camera traps during the dry season in the seasonal wetland area Nicte Ha, Campeche, México and how these aspects vary across three studied years (2019, 2020, and 2021). Our study will contribute to understanding how white-tailed deer adapt to the presence of artificial water sources in tropical areas with high seasonality. This knowledge could help to improve the management and conservation of this species and its habitat.

Materials and methods

Our research was conducted at the Nicte-Ha UMA, located in southwestern Campeche, México (91° 43′ 56″ W, 18° 19′ 56″ N) adjacent to the Laguna de Términos Flora and Fauna Protected Area (Figure 1). The UMA has 2,300 ha of tropical lower coastal plain habitat situated between -1 and 3 m asl. The climate in the region is warm-humid, with a mean temperature of 27 °C and up to 2,000 mm of precipitation per year (INEGI 2013). The vegetation type of the area varies from hydrophilic vegetation, flooded savannas, mangroves, sub-evergreen flooded rain forests, tropical deciduous flooded forests, secondary growth forests, agricultural areas, and induced grasslands for cattle grazing (Ocaña and Lot 1996). In 2010, the owners of Nicte-Ha removed cattle from the ranch, and since then, the area has been exclusively used for sustainable white-tailed deer hunting. Human activity in the UMA is very reduced and consists of sporadic surveillance surveys, yearly road maintenance, and, during hunting season, intermittent hunting parties of no more than two or three persons per month.

Water availability is a key factor for wild ungulates in the Yucatán Peninsula, especially during the dry season (Reyna-Hurtado *et al.* 2010). In Nicte-Ha, a seasonal wetland area, precipitation is concentrated in a single season that usually spans from June to November. This is followed by a dry season that lasts around six months (December-May). The intensity and seasonality of the rains, combined with flat terrain, produce seasonal floods that can reach 0.5 m. The flood lasts for the entire rainy season, but once it is over, water for ungulates remains available but concentrated in numerous puddles within the area that usually dry out by mid-February. After this date, the only sources of water in Nicte Ha are the Rio del Este River and the eight AWPs constructed by the owners. It is important to note that although the Rio del Este is a permanent water body it is hardly accessible for the deer that live far from the river edges. Contreras-Moreno *et al.* (2019a, 2021) observed that in extreme cases when the AWP dry up, the individuals make long excursions of one or two days in which they travel several kilometers to obtain water from the river, returning immediately to their established home ranges inland.

AWPs were excavated with a bulldozer in 2010 and 2011 and initially consisted of a large hole approximately 15 m long, 8 m wide, and 2 m deep in the central part of the pond. The water ponds naturally fill with water during the rainy season and usually maintain water until the end of the dry season. However, in some extreme cases, some water ponds may dry up during the dry season. After the construction, the water ponds have not been excavated again, and because of sedimentation, the ponds have lost depth over the years. Currently, the AWP are surrounded by natural vegetation.

To determine the activity patterns and use of the AWP and Dirt Road (DR) treatments by white-tailed deer during the dry season of 2019, 2020, and 2021, we set camera trap stations at 7 AWP and at 12 sites along DR in Nicte Ha (Figure 1). The camera trap stations consisted of 1 or 2 cameras operated for at least 80 days. However, we could not maintain operating the cameras for this long due to equipment malfunction and theft on several occasions. We intended the separation between camera trap stations to be at least 1 km. However, this was not possible in some cases due to the distance in which some AWPs are distributed on the property. The camera traps were tied to trees at 50 cm above ground and programmed to function 24 hours a day. We obtained the number of white-tailed deer independent photographs at each camera trap station. We considered a record to be independent if the time interval between the photographs was more than 60 minutes (Tobler *et al.* 2008). We obtained the sampling effort per camera station by adding the number of camera days (*i. e.*, a period of 24 h during which the camera station was operating), from the date when the camera was first active to the date of the last photograph, for every year and all the years together. The total sampling effort AWP and DR was obtained by adding the number of camera days each camera operated on each site each studied year. We identified the hour from each white-tailed deer independent record obtained from each one of the per year. We only use independent records for the analysis (Monroy-Vilchis *et al.* 2011).

We estimated the Relative Abundance Index (RAI) for each treatment per year as a measure of visitation rate (O'Brien 2011). RAI was obtained by dividing the total number of independent white-tailed deer records per camera trap per year by the camera trap effort in each station for each site per year. We used the Wilcoxon rank sums test to compare the observed RAI per camera trap station at AWS and DR for each studied year (Siegel and Castellan 1995). We compared the RAI for each camera trap station between years for each treatment using a Kruskal-Wallis test to determine if there were differences in the visit rates derived from the environmental conditions of each year. Dunns pairwise multiple comparisons test was used in case of significant differences were found in the Kruskal-Wallis analysis (Siegel and Castellan 1995). All our analyses were considered significant if $P < 0.05$.

We used a Kernel density estimator (Ridout and Linkie 2009) to generate the activity patterns of the white-tailed deer for each treatment and year. We also pooled all the records from the three studied years to generate a general activity pattern of the species in each treatment. To compare the white-tailed deer activity patterns between the 2 treatments and among each one of the studied years, we compared the treatment pairs per year and with the pooled data (AWP of year 2019 vs. DR of year 2019; AWP of year 2020 vs. DR of year 2020; AWP of year 2021 vs. DR of year 2021; AWP of the three summed years vs. DR of the three summed years) using the R-package overlap (Meredith and Ridout 2014). We calculated the overlap coefficient (Δ) with estimated 95% confidence intervals (CI) using a bootstrap of 1,000 samples. Following Meredith and Ridout (2014), if the smallest sample has less than 50 photographic records, we use the Δ_1 estimator. Otherwise, we used the value of Δ_4 as the overlap output. The estimated overlap coefficient can range from 0 (no overlap) to 1 (complete overlap). Activity was classified as (1) diurnal, 1 h after sunrise to 1 h before sunset; (2) nocturnal, 1 h after sunset to 1 h before sunrise; and (3) crepuscular, 1 h before and after sunrise and sunset (Foster *et al.* 2013).

Results

During the 3 years, we obtained 3,640 independent white-tailed deer records (2,584 in AWP and 1,056 in DR; Table 1) with a total camera trap effort of 3,978 camera days (1,306 camera days in AWP and 2672 in DR). The number of operating cameras in each treatment varied between years due to equipment malfunction or theft (Table 1). We obtained 1,580 records for the year 2019, 1,290 records for 2020, and 770 records for the year 2021 (Table 1)

The RAI was bigger in the AWP than DR among the 3 studied years (Figure 2; 2019: W = 6, N = 18, $P < 0.01$; 2020: W = 0, N = 15; $P < 0.01$; 2021: W = 10, N = 17, $P = 0.013$). We found differences when we compared the observed RAI in the AWP among the studied years (Kruskal-Wallis H = 7.38,

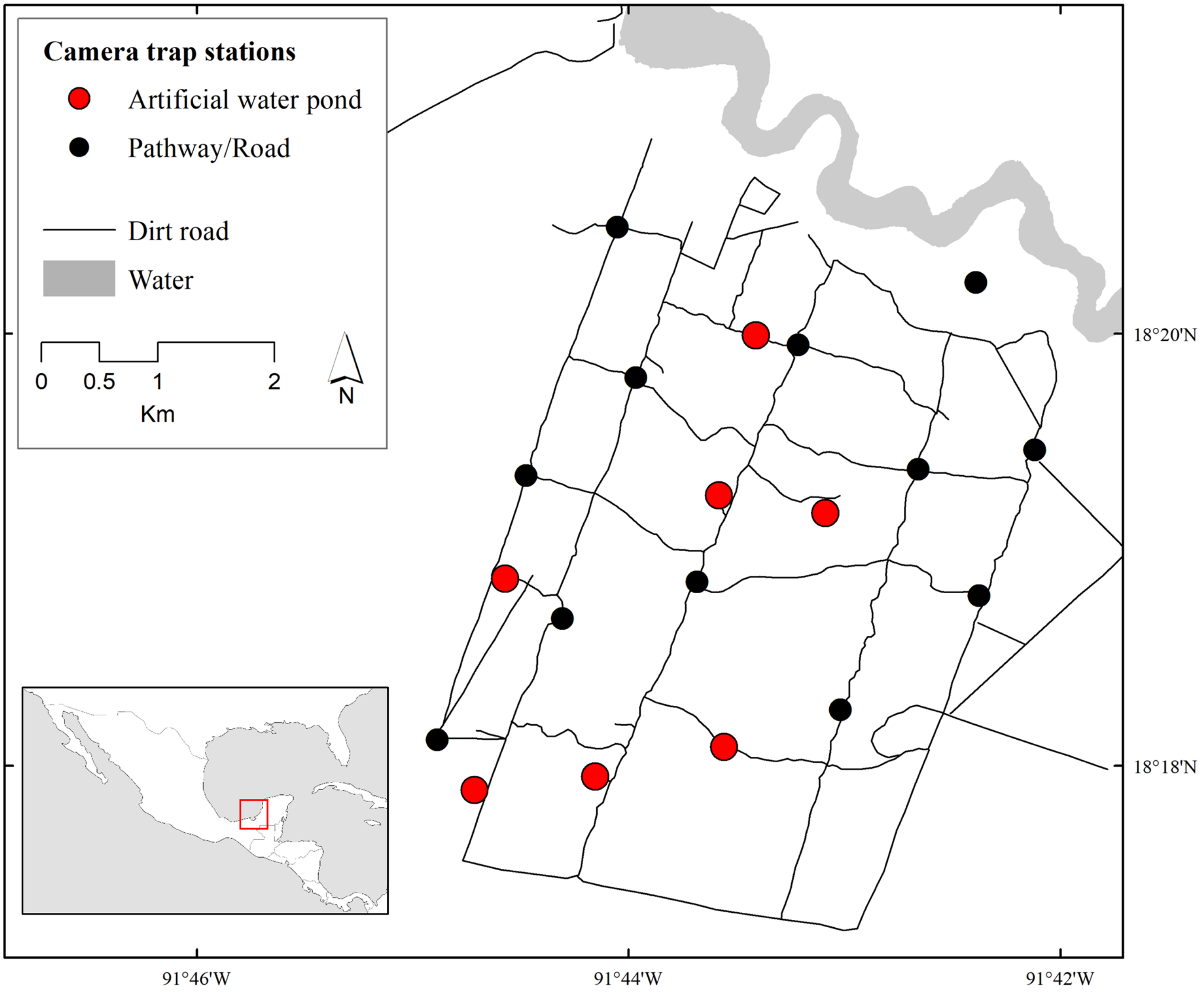

Figure 1. Location of the camera trap stations in the Artificial water ponds and the dirt roads during the dry seasons of 2019, 2020, and 2021 in the UMA Nicte Ha in Campeche, México.

Table 1. Number of white-tailed deer independent records, number of operating camera trap stations and camera trap effort in artificial water ponds and dirt roads located in the seasonal wetland obtained in 2019, 2020, and 2021 in Nicte Ha, Campeche, Mexico.

Year	Treatment	Number of records	Number of operating camera trap stations	Camera trap effort
2019				
	Artificial water pond	1,079	6	435
	Dirt Road	501	12	884
2020				
	Artificial water pond	944	4	308
	Dirt Road	346	11	953
2021				
	Artificial water pond	561	7	563
	Dirt Road	209	11	835
All years combined				
	Artificial water pond	2,584	7	1,306
	Dirt Road	1,056	12	2,672

d. f. = 2, *P* =0.02; Figure 3). Dunn's test results showed differences between the RAI of AWP in 2021 with the RAI in 2019 and 2020 (2019-2021: *P* = 0.042; 2020-2021: *P* = 0.013). However, we did not find differences between 2019 and 2020 RAI (*P* = 0.56). In the case of the RAI, among years in the DR, we found that the RAI was similar among the studied years (Kruskal-Wallis H = 4.17, *d.f.* = 2, *P* = 0.12; Figure 3).

When we pooled the 3 studied years, we found that the mean activity overlaps between both treatments was Δ = 0.885 (Δ CI = 0.853-0.916; Figure 3). In the case of the individual years, we found that the mean activity overlap was Δ = 0.806 in 2019 (Δ CI = 0.762-0.854; Figure 4), Δ = 0.802 in 2020 (Δ CI = 0.745-0.851; Figure 3) and Δ =0.791 in 2021 (Δ CI = 0.726-0.851; Figure 4). Despite the significant overlap between both treatments, we observed in Figure 4 that in the years 2019 and 2020, as well as in the pooled data, in the case of the DR, there is a clear peak of activity at sunset compared to the AWP data, in which the white-tailed deer activity remains very similar throughout the day. Likewise, in these same years, the activity at sunset is lower in DR sites compared to AWP. In 2021, contrary to what was observed in 2019 and 2021, we observed that there is no peak of activity in the DR during sunrise, but it occurs at sunset. In the case of the AWP, it is observed that the activity is maintained mainly during the day and night, but although small peaks are observed at sunrise and sunset, these are not as marked as those that occur in the DR.

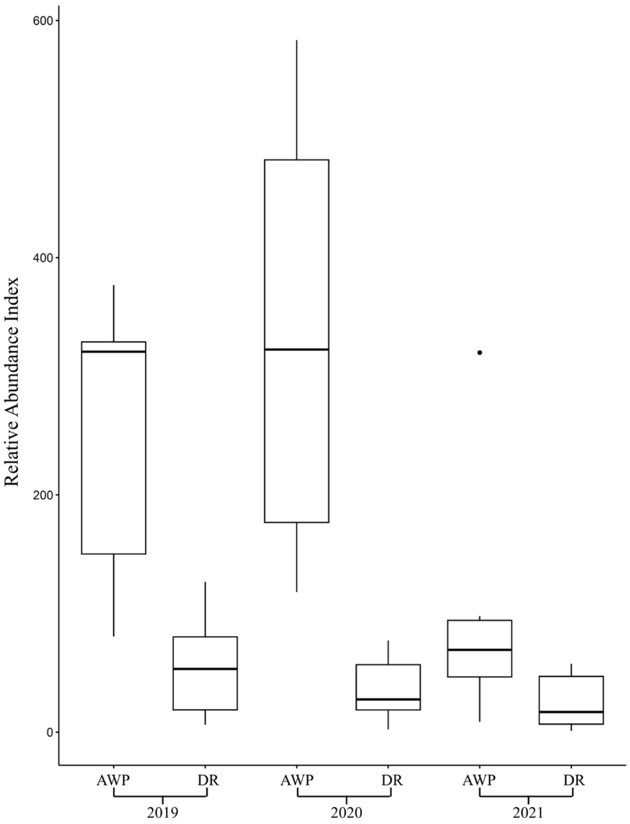

Figure 2. Comparison of the Relative abundance index (RAI) of white-tailed deer obtained in Artificial Water Ponds (AWP) and Dirt Roads (DR) during the dry season 2019, 2020, and 2019 in the UMA Nicte Ha in Campeche, México. The median of the RAI is shown as a line dividing the square, and mustaches represent confidence intervals of 95 %.

Discussion

The results show that the visitation rate of AWP in Nicte Ha has important effects on the presence of white-tailed deer during the dry season because we observed a higher RAI in the sites where there is AWP compared to the DR sites. In the case of activity patterns, white-tailed deer maintain constant activity throughout the day in AWP compared to DR, where activity peaks associated with sunrise and sunset occur.

Montalvo *et al.* (2019), in the tropical dry forest of Santa Rosa, Costa Rica, found that white-tailed deer during the dry season were found equally frequently at waterholes and roads; nevertheless, the species showed some dependency on waterholes. Contrary to this finding, in our study, over the three studied years, white-tailed deer RAI was higher in AWP compared to DR. In Santa Rosa, the lack of selection for waterholes was attributed to a strategy to avoid predation (Montalvo *et al.* 2019). In Nicte Ha, potential white-tailed deer predators such as jaguars are common (Hidalgo-Mihart *et al.* 2019). It is possible that higher temperatures that occur in Nicte Ha (higher than 40°C; INEGI 2013) compared with temperatures occurring in Santa Rosa

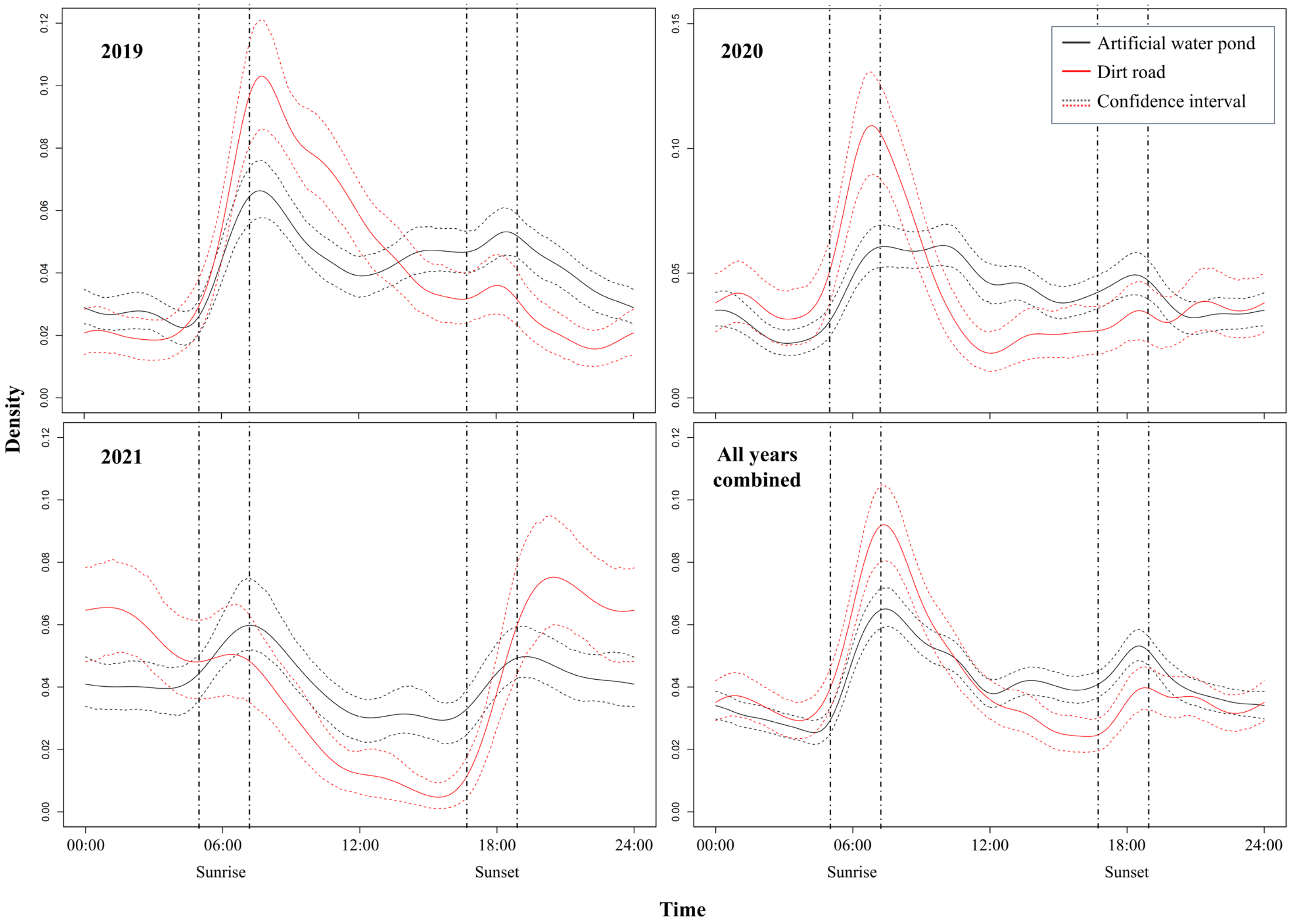

Figure 3. Activity patterns of white-tailed deer recorded in Artificial Water Ponds and Pathways/Roads during the 2019, 2020, and 2021 dry seasons in the UMA Nicte Ha, Campeche, México. Pairwise comparisons of activity overlap and 95 % Confidence Intervals of both treatments (Artificial Water Ponds and Dirt Roads) per year are shown with the identity of each activity pattern for each treatment indicated by color. Vertical dashed lines indicate sunrise (±1 h) and sunset (±1 h).

(37°C: Montalvo *et al.* 2019) could promote dehydration and the need for more water intake (Fuller *et al.* 2014), and therefore more dependency on free water for the white-tailed deer in Nicte Ha.

The white-tailed deer in Nicte Ha were followed as part of a study of home ranges, showing an important association with the AWPs during the dry season. In those cases where the AWPs dried up, they made long exploratory trips to natural water bodies such as the Rio del Este, which usually take one or two days and immediately return to their home ranges (Contreras-Moreno *et al.* 2019a; 2021). This observation would indicate that it is likely that the visitation rate recorded in the AWP areas would be higher than in other sites, as was the case with our results. However, as reported by Contreras-Moreno *et al.* (2021), the capture of the radio-tracked deer was in the AWP, so many of the results reported by them are possible, and the link of the deer to the watering holes could be an effect of the territoriality of the captured organisms and overestimate the importance of AWP on the habitat use by the species. The present study, where we obtain higher RAI in the AWP compared with the DR, supports the idea that white-tailed deer use AWP much more than other areas of the UMA, showing the importance that this type of structure has for the management of the species during the dry season of the year in Nicte Ha.

We observed a significant overlap in the activity pattern between deer in the AWP and DR (between 70 and 85 %, depending on the year). Likewise, we observed that at least in 2019 and 2020, despite the high level of overlap, there was a peak of activity near dawn. It has been observed that, in general, deer in dry and tropical areas of México tend to be more active in the morning than in the afternoon (Mandujano and Hernández 2019; Hernández-SaintMartín *et al.* 2013), derived from the fact that it is at this time that temperatures are lower compared to the temperatures that could appear during the day and particularly during the afternoon. Thus, the deer found in the DRs could be repeating this pattern to reduce the negative impacts of high daytime temperatures, reducing the need for water intake, which must be streamlined since it does not have an available free water source. In the case of the AWP, it is noticeable that there were no clear activity peaks, and the deer could drink water throughout the day regardless of the hour of the day and the thermal conditions. The presence of a free water source probably reduces the stress associated with water loss from high temperatures, reducing the need to adjust their activity patterns to the coolest hours of the day, such as dawn and morning.

We observed that there are differences between years in the daily activity of white-tailed deer throughout periods in which the day was divided (nocturnal, diurnal, and sunset) in the DR, while in the case of the AWP, the percentages of activity were similar throughout the three years studied. This result indicates the importance that the AWP can have since the annual environmental variations of temperature and drought that affect the deer in the DR, modifying their activities, do not affect them like those inhabiting the AWP, owing to more stable conditions. This result is important in understanding how the white-tailed deer could be affected by changes already occurring in the region. The Nicte-Ha area is anticipated to suffer a general decrease in mean precipitation and an increase in drought (Imbach *et al.* 2012; Chiabai 2015). This will probably severely impact the white-tailed deer, as has already been detected in ungulates from the Amazon basin, where extreme drought and flooding are already occurring (Bodmer *et al.* 2014). In this sense, the results of stability during the three studied years in the activity patterns derived from the presence of AWP could reduce the effect of anticipated dry conditions that could affect Nicte Ha in the future.

AWPs are one of the most common strategies made in Campeche to improve wildlife habitat along with reforestation, vigilance, wildlife monitoring, signalization, and opening fire breaks (García-Marmolejo *et al.* 2008). The results of this work are the first evaluation of the ecological effects of AWP in this area of southern México and indicate the significant effects of these structures on aspects such as visitation rate and activity patterns. However, it is essential to evaluate the long-term effects of these structures on white-tailed deer and other species, especially under the controversy surrounding the importance and impact of these AWP in supporting wildlife populations (Simpson *et al.* 2011). Undesirable effects such as the wildlife distribution patterns constriction produced by the availability of free water causing local wildlife population declines due to forage scarcity associated with over-grazing, increased predation on specific species, or reduction in water quality due to excess of organic waste, and the increased risk of disease transmission should be carefully monitored (Marshal *et al.* 2006; Simpson *et al.* 2011; Griffis-Kyle *et al.* 2014).

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