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Additions to the geographical distribution of the critically endangered *Lama guanicoe guanicoe* Müller, 1776 (Camelidae: Artiodactyla) in Paraguay

Adiciones a la distribucion geografica de la especie criticamente amenazada *Lama guanicoe guanicoe* Müller, 1776 (Camelidae: Artiodactyla) en Paraguay

Viviana Rojas-Bonzi[1,2,3,*], Camilo Benítez[1], Nicolás Cantero[1], Hugo Cabral Beconi[1,3,4,5], Belén Achón[1], Marcela Ferreira-Riveros[1,3], Tatiana Galluppi[1] & Jeffrey J. Thompson[1,6]

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[1]Asociación Guyra Paraguay, Asunción, Paraguay.
[2]Wildlife Ecology and Conservation Department, University of Florida, Gainesville, USA.
[3]Instituto de Investigación Biológica del Paraguay, Asunción, Paraguay.
[4]Programa de Pós-Graduação em Biologia Animal, Universidade Estadual Paulista, São José do Rio Preto, SP, Brazil.
[5]Mapinguari – Laboratório de Biogeografía e Sistemática de Anfibios e Répteis, Instituto de Biociências, Universidade Federal de Mato Grosso do Sul, Campo Grande, MS, Brazil.
[6]Instituto Saite, Asunción, Paraguay.
*Correspondance author: vivirojasb@gmail.com.

Abstract.- Our study investigates the presence of *Lama guanicoe guanicoe* (guanacos) in two sites within three protected areas in the Dry Chaco of Paraguay, areas that lie within their recognized geographic range and are of paramount importance for conservation efforts of this species. Using camera traps, with a total effort of 5,350 trap-nights, we documented a total of 87 guanacos records, all in Medanos del Chaco National Park, capturing 1-3 individuals of guanacos per picture. Activity density functions revealed activity peaks during the morning, noon, and early afternoon. Additionally, we documented human and livestock presence in areas where guanacos occur and found moderate activity overlap. The overlap coefficient between human activity and guanacos is $\Delta = 0.54$ and overlap coefficient between guanacos and livestock is $\Delta = 0.49$. Our findings confirm the continued presence of guanacos in Paraguay and highlight the pressing need for collaborative, local-driven and indigenous-led efforts in researching and managing the Medanos region and this relict guanaco population.

Key words: *Dry Chaco, guanaco, Medanos, protected areas.*

Resumen.- Nuestro estudio investiga la presencia de *Lama guanicoe guanicoe* (guanacos) en dos sitios dentro del Chaco Seco de Paraguay, áreas que se encuentran dentro de su rango geográfico reconocido y son de importancia primordial para los esfuerzos de conservación de la especie. Utilizando cámaras trampa, con un esfuerzo total de 5.350 trampas-noche, documentamos un total de 87 registros de guanacos, todos en el Parque Nacional Medanos del Chaco. Documentamos de 1 a 3 individuos de guanacos por imagen. Las funciones de densidad de actividad revelaron picos de actividad durante la mañana, mediodía y primeras horas de la tarde. Además, documentamos la presencia de humanos y ganado en áreas donde se encuentran guanacos y encontramos una moderada superposición de actividad. El coeficiente de superposición entre la actividad humana y los guanacos es $\Delta = 0.54$ y el coeficiente de superposición entre los guanacos y el ganado es $\Delta = 0.49$. Nuestros hallazgos confirman la continua presencia de guanacos en Paraguay y resaltan la urgente necesidad de esfuerzos colaborativos, dirigidos por la comunidad local y liderados por comunidades indígenas en lo que respecta a la investigación y gestión de la región de los Médanos y esta poblacion relictual de guanacos.

Palabras clave: *Áreas protegidas, Chaco Seco, guanaco, Medanos.*

Guanacos, *Lama guanicoe* Müller 1776, are herbivores native to the arid and semiarid regions of South America. They are found from the western side of the Andes in northern Peru to Tierra del Fuego in Argentina, and the Navarino Islands in Chile. To the east, they extend into the Argentinean pampas, southward Bolivia, and northwest of Paraguay, where they are restricted to the

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Dry Chaco region (Cartes *et al*., 2017; Cuellar Soto *et al*., 2017; Franklin, 1982; González *et al*., 2006; Marin *et al*., 2013). The habitat of the guanaco has been reduced to 26% of its original range, with documented population declines across its distribution (Baldi *et al*., 2016). In addition, the negative effects from fencing, road development, and competition with livestock, as well as unregulated hunting, have further contributed to changes in guanaco behavior and local and regional extinctions (Antún & Baldi, 2020; Baldi *et al*., 2016; Cappa *et al*., 2020; Cartes *et al*., 2017). Despite this concerning scenario, guanacos are categorized as "Least concern" at the global level, based upon their wide continental distribution (Baldi *et al*., 2016).

The wide continental distribution of guanacos along different environments such as desert, xeric shrublands, mountain grasslands and temperate forests evidences ecophysiological (e.g., digestive, water-balance, thermo-regulation) and behavioral adaptations (e.g., flexible social behavior) as well as an extensive spectrum of forage types (Franklin, 1982). Guanacos can be classified as an intermediate herbivore or opportunistic (mixed) feeder, foraging on a highly diverse range of food sources, possibly as "forced selectors", among which are some herbs, shrubs, lichens and cacti (Cuellar Soto *et al*., 2017; Puig *et al*., 1997, 2001). Thus, guanacos are an important species in preserving ecosystem function, playing a key role maintaining vegetation composition and structure (Acebes *et al*., 2010; Bradshaw *et al*., 2003; Flores *et al*., 2012).

Historically, four subspecies of guanacos have been recognized (Wheeler, 1995) based on their distribution and phenotype (i.e., body and skull size, and coloration): *Lama guanicoe guanicoe* (Müller, 1776)*, L.g. huanacus* (Molina, 1782)*; L. g. cacsilensis* (Lönnberg, 1913) and *L. g. voglii* (Krumbiegel, 1944). More recently, comprehensive assessments of the molecular diversity of guanacos throughout its distribution have shown evidence of wide range phylogeographic structure, confirming the presence of two subspecies, *L. g. cacsilensis* (northwest guanacos) which encompass populations from Peru to northern Chile and, *L. g. guanicoe* (southeast guanacos) which includes populations from Argentina and the Bolivian Chaco (Marin *et al*., 2008, 2013). The guanaco populations of the Chaco, restricted to southeast Bolivia and northwest of Paraguay, are considered an Evolutionary Significant Units (ESU; Moritz 1994), representing a group of guanacos adapted to dry broadleaf forests, savannahs, temperate grasslands and shrublands (Marin *et al*., 2013). These populations are estimated to be small, fragmented and isolated and thus considered Critically Endangered in Paraguay and Bolivia (Cartes *et al*., 2017; Cuellar Soto & Núñez, 2009).

Despite the growing body of literature on the ecology, behavior and population status of guanacos in the Bolivian Chaco (Cuellar Soto *et al*., 2017; Cuellar Soto & Núñez, 2009), in Paraguay, records of guanacos remain scarce, with only few reports published to the date (Villalba & Bonacic, 2006; Yahnke *et al*., 1998). Up until our research, the largest effort to collect presence and ecological data of guanacos dates to 2004, with a project led by the "Fundación para el Desarrollo Sustentable del Chaco" (DeSdelChaco) and the current Ministry of Environment and Sustainable Development (Villalba, 2004). Considering the few documented, outdated, and sparse records of the species for Paraguay, our main objective was to report presence data of guanacos within its geographical distribution in Paraguay using camera traps.

Materials and methods

Study site

Our research was conducted in the Dry Chaco ecoregion, a mosaic of grasslands, savannahs and xerophytic woodlands forests, covering the territories of Argentina, Bolivia and Paraguay (Olson *et al*., 2001). We focused our sampling

in the Medanos subregion (757,680 ha), within the Paraguayan Dry Chaco (Mereles *et al*., 2013; SEAM, 2013). The mean temperature in Medanos is 25 °C, with maximum temperatures reaching 45 to 48 °C during summer and minimum temperatures reaching -3 to -7°C during winter, with daily thermal variation often spanning 20 degrees, or more (Mereles & Rodas, 2014). Precipitation is the lowest in the country, ranging from 400-500 mm/year (Gill *et al*., 2020; Mereles *et al*., 2013). The landscape is characterized by the presence of sandy dunes of fine grain formed by wind action from sediments of the rivers Grande and Parapeti in Bolivia generating dunes (i.e., "medanos"). The vegetation has a savannah physiognomy with deciduous and semi-deciduous woody shrublands with scattered trees that do not exceed 10 m high (Mereles *et al*., 2013).

We conducted our sampling on two sites (Site 1 and Site 2), located within three major protected areas located in the Medanos ecoregion. Site 1 was within the Medanos del Chaco National Park (605,075 ha; MChNP), managed by the Ministry of Environment and Sustainable Development, and Site 2 comprised stations within the Pykasu Indigenous Reserve (46,300 ha; PK), managed by the indigenous Guarani Ñandeva peoples, and Campo Iris Nature Reserve (3,500 ha; CI), managed by the national NGO Guyra Paraguay (Fig. 1).

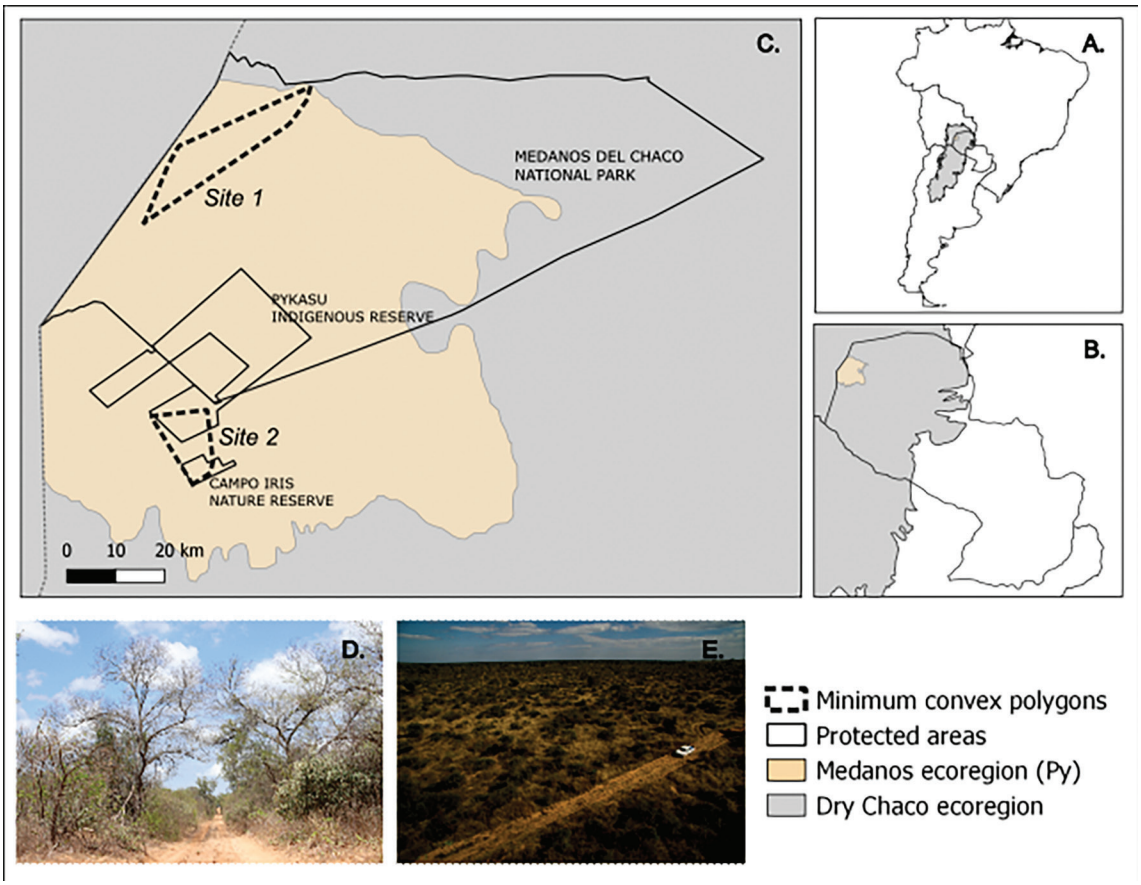

Figure 1: Study site. **A)** The Dry Chaco ecoregion in South America. **B)** The Dry Chaco and Medanos subregion in Paraguay. **C)** Site 1 within the Medanos del Chaco National Park, and Site 2 including the Pykasu Indigenous Reserve and Campo Iris Nature Reserve. **D)** and **E)** views of secondary roads and vegetation of the Medanos subregion.

Table 1. Characteristics of camera trap sites in the Medanos subregion. ***)** Number of active 24-hour cycles completed by independent cameras.

Site	Location	Sampling period	Number of sampling stations	Trap nights*
Site 1	Medanos del Chaco National Park	2018-10-24 to 2019-05-17 and 2019-05-18 to 2019-10-29	28	3,315.5
Site 2	Campo Iris Nature Reserve	2018-07-17 to 2018-10-21	11	1,065
	Pykasu Indigenous Reserve	2018-07-18 to 2018-10-22	11	969.5

Data collection

Field sampling was conducted from July 2018 to November 2019. A total of 50 camera trap stations were deployed, spaced 1–2 km apart. Of these, 48 stations featured paired, opposing camera traps, while two stations used a single camera trap. Browning Strike Force camera traps were mounted on tree trunks or on stakes where trees were unavailable, positioned approximately 35–40 cm above the ground. The traps were unbaited, operated 24 hours a day, and were configured to capture 6–8 images per trigger, with a 5-second interval between triggers.

Site accessibility posed significant challenges due to the sandy dunes that restrict navigable roads and trails, rendering the landscape nearly impenetrable. Consequently, our sampling covered only 4% of the park's total area at Site 1 and 24% at Site 2. Despite these constraints, this study represents the most extensive camera trap effort to date in the region for monitoring guanaco presence. The average minimum convex polygon of our sampling grids was 185.36 km² (Fig. 1).

Data analysis

Images were processed and their contents identified using the digiKam software (available at: https://www.digikam.org/) and managed and analyzed using the camtrapR package (Niedballa *et al*., 2016) in R version 4.1.3 (R Core Team, 2022). We calculated the average number of individuals captured in pictures, activity patterns of guanacos and activity overlap (Δ) with livestock and human activity (e.g., humans by foot or vehicle) throughout the study area using the function *activityOverlap* of the camtrapR package. The estimator used was Δ_1, indicated for small samples ($n < 50$; Ridout & Linkie, 2009). We chose not to implement a time-to-independence filter because it could bias estimates of some species activity patterns (Peral *et al*., 2022).

Results

From 5,350 trap nights (Table 1) there were a total of 87 guanaco records in seven camera trap stations, all from Site 1, Medanos del Chaco National Park (Fig. 2). Guanacos were detected mostly during daylight hours (6 am – 6 pm), with activity density functions revealing daylight activity peaks, during the morning, noon, and early afternoon. We recorded between 1 – 3 individuals of guanacos per picture (Fig. 2).

Within the stations where guanacos were detected, we gathered 28 records of human activity, including people on foot (25%) and in vehicles (75%). The overlap coefficient between human activity and guanacos was $\Delta = 0.54$, with consistent overlap during most of activity hours of guanacos, except for the early morning (Fig. 3). In addition, we documented 9 records of livestock, which included goats (67%) and cattle (33%). The overlap coefficient between guana-

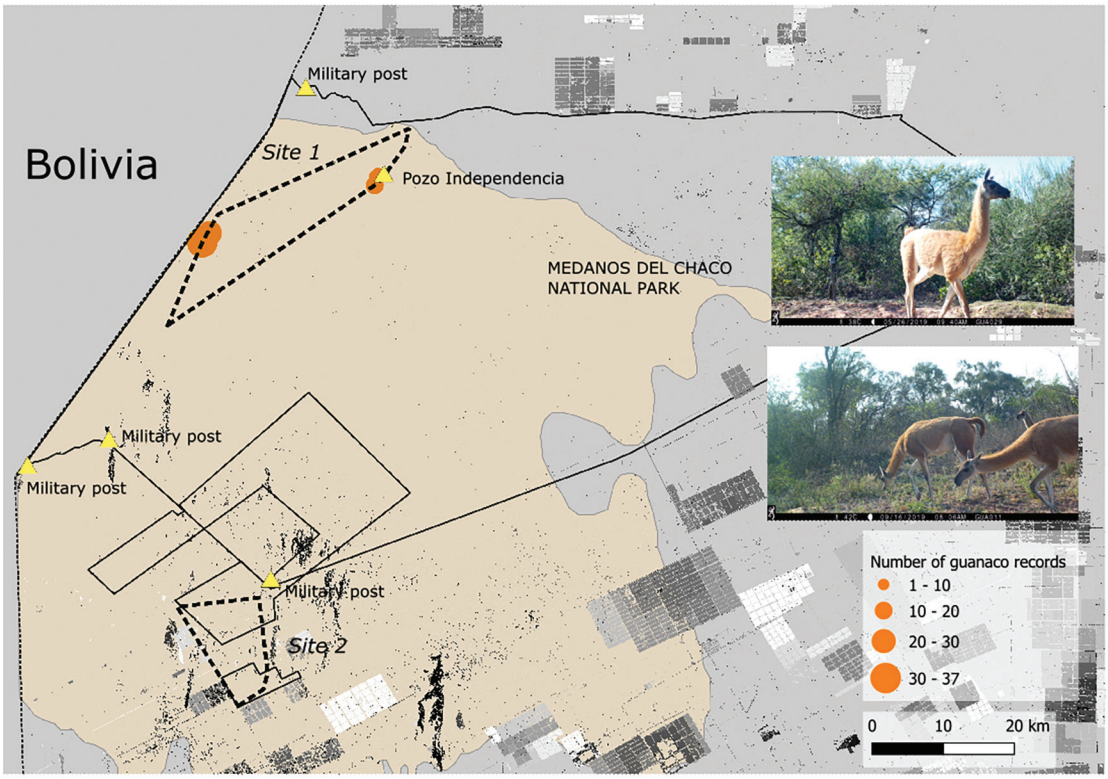

Figure 2: Guanaco records in monitoring stations in Site 1, within Medanos del Chaco National Park. Yellow triangles show military posts surrounding the sites and the location of former hydrocarbon settlement, "Pozo Independencia". Deforestation from 2020 until 2023 shown in grey (Hansen et al., 2013).

cos and livestock was $\Delta = 0.49$, with consistent overlap towards afternoon hours (Fig. 3).

Discussion

Our study confirms the continued presence of guanacos in Paraguay within the Medanos del Chaco National Park and highlights the importance of this protected area for the conservation of the guanacos at the national and regional levels. We recorded solitary individuals as well as groups of 2-3 individuals, with daily activity patterns mainly diurnal, patterns that are congruent with other behavioral studies of guanacos in the Chaco (Cuellar Soto *et al*., 2017). We also documented livestock within the limits of the park and show moderate overlap in activity patterns with guanacos and livestock as well as humans within the Medanos del Chaco National Park.

Most records of human activity and all records of livestock were within the vicinity of the former hydrocarbon settlement "Pozo Independencia", in the northern part of Site 1. The unregulated presence of people inside the park poses a threat to guanacos as hunting has been identified as a main threat to the species (Cartes *et al*., 2017; SEAM & FMB, 2016). Moreover, the presence of livestock could exacerbate the risk to guanacos, as potential resource competition may have adverse effects on this native species (Cappa *et al*., 2020; Traba *et al*., 2017).

Although the presence of guanacos in the Paraguayan Medanos has long been recognized by local indigenous communities, the first documented records of guanacos in the region, almost 20 years ago (Villalba, 2004), prompted a greater emphasis on the guanaco's ecological

and cultural value. This highlighted the need to prioritize research on the ecology of the species and the implementation of conservation strategies to reduce threats. However, the scarce information on the conservation status of the species has limited informed conservation efforts both for the guanaco and the Medanos ecoregion. Furthermore, members of indigenous communities note that the guanaco formerly occupied larger areas of the Medanos (Isabelino Bogado, pers. comm), including Site 2 where the species was not detected in the present study.

The potential reduction in the distribution range of guanacos in Paraguay could be attributed to the previously mentioned threats, compounded by the expanding habitat loss and fragmentation for the Medanos region. A parallel trend has been documented in the Bolivian Chaco, where increased woody plant encroachment, driven by increased cattle ranching and shifts in fire regime (both in severity and frequency), has led to habitat degradation and fragmentation, imperiling the relict and isolated guanaco population due to reduced availability of their preferred habitat (Cuellar-Soto *et al*., 2020).

Hence, there is a pressing need to continue monitoring guanaco populations in the Medanos ecoregion, expanding sampling effort within the Medanos del Chaco National Park and surrounding private cattle ranches which are rapidly developing. We also advocate for locally driven, indigenous-led initiatives to oversee the management of Medanos. This could involve the potential restoration of fire management practices, alongside the imperative for demographic and genetic monitoring of guanacos. Additionally, transboundary conservation strategies with Bolivia should be implemented, considering the cultural significance of the species, local population dynamics, and the preservation of adaptive variation and

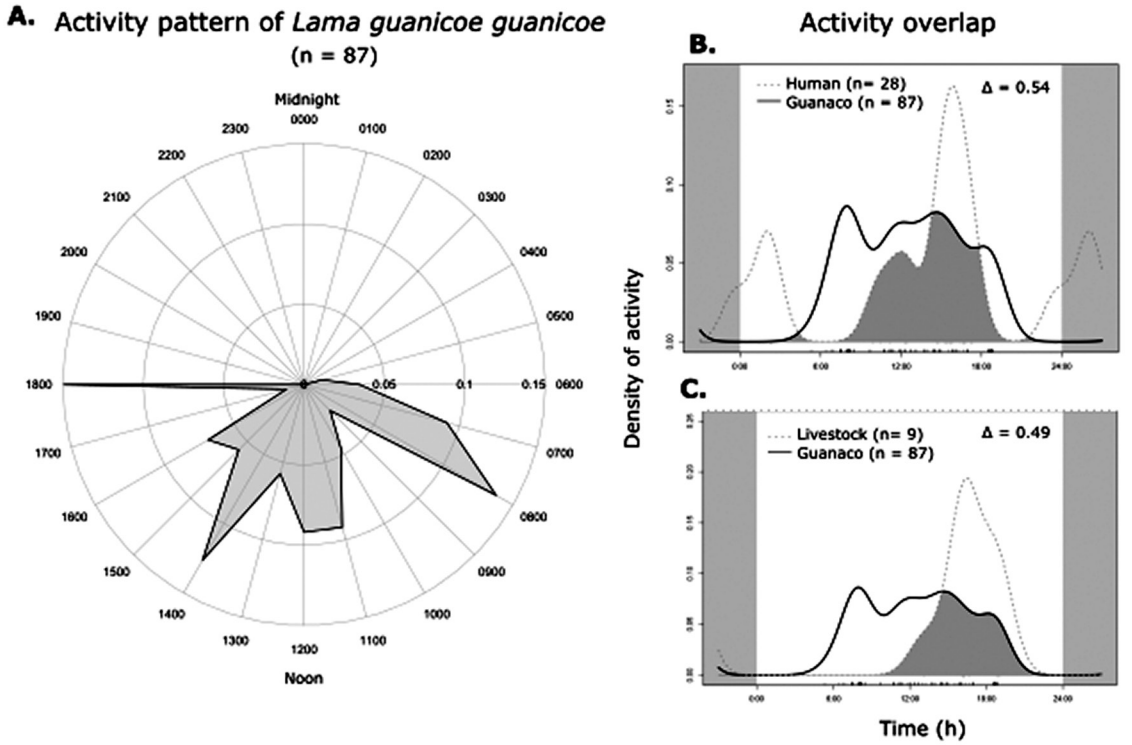

Figure 3: Activity patterns and overlap. **A)** Activity patterns of guanacos. **B)** overlap between human (by foot or car) and guanacos (Δ = 0.54). **C)** Overlap between livestock (goats and cattle) and guanacos (Δ = 0.49).

evolutionary processes, all of which are crucial for safeguarding guanacos in the easternmost extent of their distribution.

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Literature

Acebes, P., Traba, J., Malo, J.E., Ovejero, R. & Borghi, C.E. (2010). Density and habitat use at different spatial scales of a guanaco population (*Lama guanicoe*) in the Monte desert of Argentina. *Mammalia*, 74(1): 57–62. <https://doi.org/10.1515/mamm.2009.071>.

Antún, M. & Baldi, R. (2020). Choosing what is left: The spatial structure of a wild herbivore population within a livestock-dominated landscape. *PeerJ*, 8(e8945): 1–20 . <https://doi.org/10.7717/peerj.8945>.

Baldi, R.B., Acebes, P., Cuellar, E., Funes, M., Hoces, D., Puig, S. & Franklin, W. (2016). *Lama guanicoe. The IUCN Red List of Threatened Species*, 2016(e.T11186A18540211). [Consulted: 2.xii.2024]. <https://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T11186A18540211.en>.

Bradshaw, R.H.W., Hannon, G.E. & Lister, A.M. (2003). A long-term perspective on ungulate–vegetation interactions. *Forest Ecology and Management*, 181(1): 267–280. <https://doi.org/10.1016/S0378-1127(03)00138-5>.

Cappa, F.M., Giannoni, S.M., Ontiveros, Y. & Borghi, C.E. (2020). Direct and indirect effects of roads on activity patterns of the largest South American artiodactyl (*Lama guanicoe*) in a hyper-arid landscape. *Mammalian Biology*, *100*(5): 453–461. <https://doi.org/10.1007/s42991-020-00035-9>.

Cartes, J., Cuellar Soto, E., Neris, N., Saldivar, Thompson, J. & Velilla, M. (2017). Cetartiodactyla y Perissodactyla: animales con pezuñas. Pp. 105–121, *in* S. Saldivar Bellassaii, V. Rojas Bonzi, & D. Gimenez Baez (Eds.). *Libro Rojo de los Mamíferos del Paraguay: Especies amenazadas de extincion* (1st ed.,). Asunción: Asociación Paraguaya de Mastozoología / Secretaría del Ambiente. 139 pp.

Cuellar Soto, E. & Núñez, A. (2009). *Lama guanicoe* (Müller, 1776): Artiodactyla-Camelidae. Pp. 454–456, in Aguirre, L.F., Aguayo, R., Balderrama, J., Cortez, C. & Tarifa, T. (Eds.). *Libro rojo de la fauna silvestre de vertebrados de Bolivia*. La Paz: Ministerio de Medio Ambiente y Agua. x + 776 pp.

Cuellar Soto, E., Segundo, J. & Banegas, J. (2017). El guanaco (*Lama guanicoe* Müller 1776) en el Gran Chaco boliviano: Una revisión. *Ecologia En Bolivia*, 52(1):

38–57.

Cuellar-Soto, E., Johnson, P.J., Macdonald, D.W., Barrett, G.A. & Segundo, J. (2020). Woody plant encroachment drives habitat loss for a relict population of a large mammalian herbivore in South America. *Therya*, 11(3): 484–494.

Flores, C.E., Cingolani, A.M., Müller, A. von, Barri, F.R., Flores, C E., Cingolani, A.M., Müller, A. & Barri, F.R. (2012). Habitat selection by reintroduced guanacos (*Lama guanicoe*) in a heterogeneous mountain rangeland of central Argentina. *The Rangeland Journal*, 34(4): 439–445. <https://doi.org/10.1071/RJ12040>.

Franklin, W.L. (1982). Biology, ecology, and relationship to man of the South American camelids. Pp. 457–489, *in* Mares, M.A. & Genoways, H.H. (Eds.). *Mammalian Biology in South America*. Vol. 6. Linesville: University of Pittsburgh Pittsburgh. xii + 539 pp.

Gill, E., Da Ponte, E., Insfran, K. & Gonzalez, L. (2020). *Atlas del Chaco paraguayo*. Asunción: WWF / DLR. 95 pp.

González, B.A., Palma, R.E., Zapata, B. & Marín, J.C. (2006). Taxonomic and biogeographical status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). *Mammal Review*, 36(2): 157–178. <https://doi.org/10.1111/j.1365-2907.2006.00084.x>.

Hansen, M., Potapov, P., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., Kommareddy, A., Egorov, A., Chini, L., Justice, C. & Townshend, J. (2013). High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342(6160): 850–854. <https://doi.org/10.1126/science.1244693>.

Krumbiegel, I. (1944). Die neuweltlichen Tylopoden. *Zoologischer Anzeiger*, 145: 45–70.

Lönnberg, A. (1913). Notes on guanacos. *Arkiv Für Zoologi*, 8(19): 1–8.

Marin, J.C., González, B.A., Poulin, E., Casey, C.S. & Johnson, W.E. (2013). The influence of the arid Andean high plateau on the phylogeography and population genetics of guanaco (*Lama guanicoe*) in South America. *Molecular Ecology*, 22(2): 463–482. <https://doi.org/10.1111/mec.12111>.

Marin, J.C., Spotorno, A.E., González, B.A., Bonacic, C., Wheeler, J.C., Casey, C.S., Bruford, M.W., Palma, R.E. & Poulin, E. (2008). Mitochondrial DNA Variation and Systematics of the Guanaco (Lama guanicoe, Artiodactyla: Camelidae). *Journal of Mammalogy*, 89(2): 269–281. <https://doi.org/10.1644/06-MAMM-A-385R.1>.

Mereles, F., Cartes, J.L., Clay, R.P., Cacciali, P., Paradeda, C., Rodas, O. & Yanosky, A. (2013). Análisis cualitativo para las definición de las ecorregiones de Paraguay Occidental. *Paraquaria Natural*, 6(2): 12–20.

Mereles, F. & Rodas, O. (2014). Assessment of rates of deforestation classes in the Paraguayan Chaco (Great South American Chaco) with comments on the vulnerability of forests fragments to climate change. *Climatic Change*, 127(1): 55–71. <https://doi.org/10.1007/s10584-014-1256-3>.

Molina, G. (1782). *Saggio Sulla Storia Naturale del Chili*. Bologna: Tomasso d'Aquino. 367 pp.

Müller, P.L.S. (1776). *Des Ritters Carl von Linné vollständiges Naturalsystem*. Supplements und register Band. Núremberg: Gabriel Nicoleus Kaspe. xvi + 536 pp.

Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016). camtrapR : an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7(12): 1457–1462. <https://doi.org/10.1111/2041-210X.12600>.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N.,

Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001). Terrestrial ecoregions of the world: A new map of life on Earth. *BioScience*, 51(11): 933–938. <https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2>.

Peral, C., Landman, M. & Kerley, G.I.H. (2022). The inappropriate use of time-to-independence biases estimates of activity patterns of free-ranging mammals derived from camera traps. *Ecology and Evolution*, 12(10)e9408: 1–10. <https://doi.org/10.1002/ece3.9408>.

Puig, S., Videla, F. & Cona, M.I. (1997). Diet and abundance of the guanaco (Lama guanicoeMüller 1776) in four habitats of northern Patagonia, Argentina. *Journal of Arid Environments*, 36(2): 343–357. <https://doi.org/10.1006/jare.1996.0186>.

Puig, S., Videla, F., Cona, M.I. & Monge, S.A. (2001). Use of food availability by guanacos (Lama guanicoe) and livestock in Northern Patagonia (Mendoza, Argentina). *Journal of Arid Environments*, 47(3): 291–308. <https://doi.org/10.1006/jare.2000.0677>.

R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing. [Consulted: 4.xii.2024]. <https://www.R-project.org>.

Ridout, M.S. & Linkie, M. (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3): 322–337. <https://doi.org/10.1198/jabes.2009.08038>.

SEAM [Secretaría del Ambiente]. (2013). *Resolucion No. 614/13. Por la cual se establecen las ecorregiones para las regiones Oriental y Occidental del Paraguay*. (Resolución ministerial). Asunción: SEAM. 2 pp. + 1 map.

SEAM & FMB [Secretaría del Ambiente & Fundación Moisés Bertoni]. (2016). *Plan de Manejo Parque Nacional Medanos del Chaco 2017-2027*. Asunción: SEAM / PNUD / FMB. 234 pp.

Traba, J., Iranzo, E.C., Carmona, C.P. & Malo, J.E. (2017). Realised niche changes in a native herbivore assemblage associated with the presence of livestock. *Oikos*, 126(10): 1400–1409. <https://doi.org/10.1111/oik.04066>.

Villalba, L. (Ed.). (2004). *Monitoreo de guanacos, Lama guanicoe, en el Chaco Paraguayo*. (Informe técnico). Loma Plata: DeSdelChaco / WCS / USAID / TNC / SEAM. 30 pp.

Villalba, L. & Bonacic, C. (2006). *Rediscovering the Guanaco in the Paraguay Chaco*. The Camelid Quarterly, March 2006: 1–2.

Wheeler, J. (1995). Evolution and present situation of the South American Camelidae. *Biological Journal of the Linnean Society*, 54(3): 271–295. <https://doi.org/10.1111/j.1095-8312.1995.tb01037.x>.

Yahnke, C.J., Gamarra de Fox, I. & Colman, F. (1998). Mammalian species richness in Paraguay: The effectiveness of national parks in preserving biodiversity. *Biological Conservation*, 84(3): 263–268. <https://doi.org/10.1016/S0006-3207(97)00113-4>.

Supplementary material

bmnhnp_v28ae2024012_Sup_01.docx (versión en español del texto / spanish version of the text).